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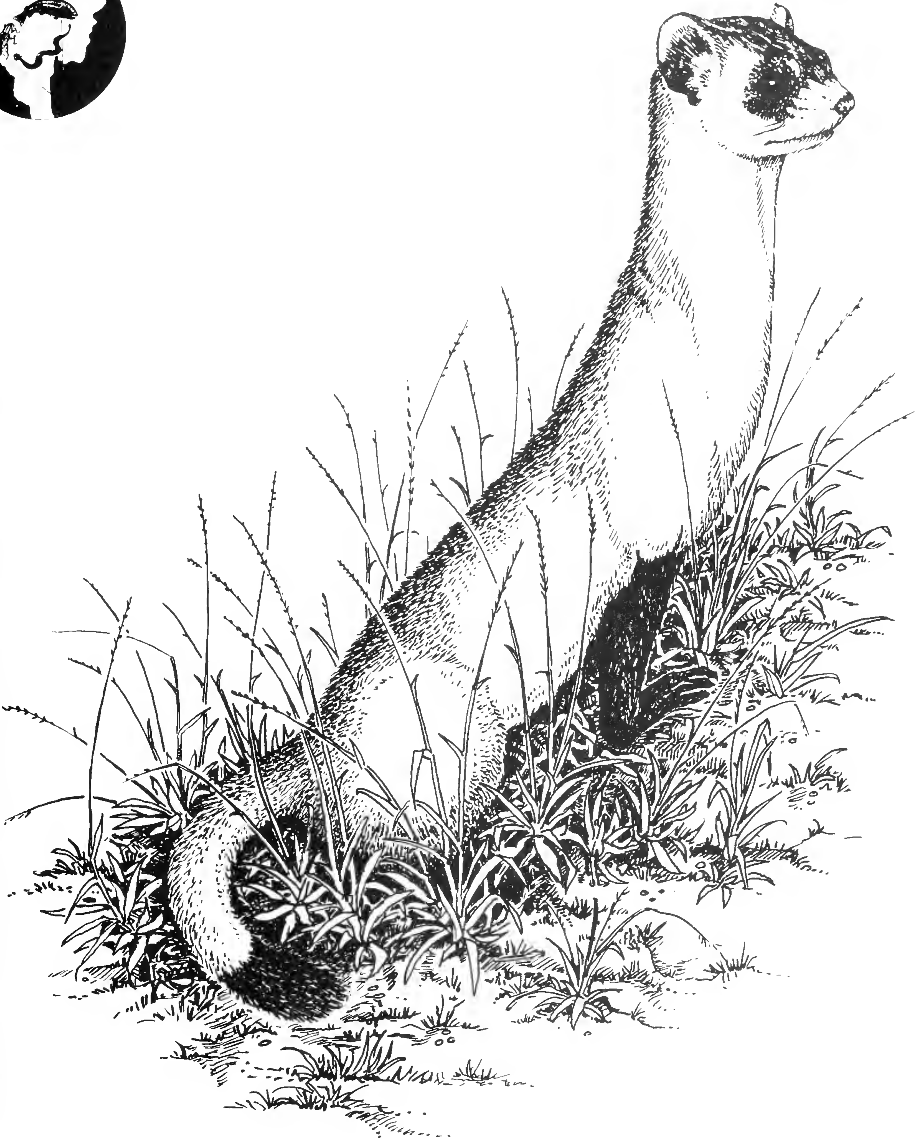

GREAT BASIN NATURALIST

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SPATIAL PATTERNS OF PLANT COMMUNITIES AND DIFFERENTIAL WEATHERING IN NAVAJO NATIONAL MONUMENT, ARIZONA[1]

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Abstract.— Vegetation patterns in Navajo National Monument, Arizona, were studied over a five-year period from 1977 to 1981. Twelve distinct plant community types occur within the boundaries of the park. These communities are characterized and the dominant plant species of each are recorded. The relationships of parent material, soils, and moisture to plant communities are also discussed. It appears that discrete communities occupy soils of different characteristics, particularly with respect to amount of weathering of parent material.

Patterns in vegetative cover across the landscape have been reported in the literature since the time of Darwin and before (Weaver and Clements 1938). Such patterns are generally considered to be the result of a long history of development under the influence of both past and present environmental factors (Walter 1973). Several theories have been proposed to explain these patterns. These include the monoclimax ideas of Clements (1936), the individualistic and continuum approaches of Gleason (1939) and Curtis (1955), the vegetational mosaic and environmental pattern concepts of Billings (1952) and Whittaker (1953), and the functional factorial approach described by Major (1951).

Floristic homogeneity is usually associated with uniformity in climate and soil. Conversely, high habitat diversity often leads to vegetation patterns that are also highly diverse. Such diverse patterns are usually explained on the basis of climatic, orographic, historic, or edaphic differences (Walter 1973). Unfortunately, broad generalizations are usually of little help in studying the vegetation ecology of localized areas, since major differences in climate, soils, and topography are not usually present in small geographic areas. Local differences in vegetation can more likely be explained on the basis of microhabitat and historical differences.

Differential weathering is a potent force in altering conditions at the microhabitat level (Foster 1971, Birkeland 1974). Two important types of weathering are usually recognized. Mechanical weathering, which is largely caused by the action of wind and water on the substrate, breaks up preexisting rock into smaller fragments. Chemical weathering acts on fragments of all sizes to rearrange the mineralogical composition of the original rock. In addition to these, biological weathering, including that which takes place in the presence of living plants, has also been

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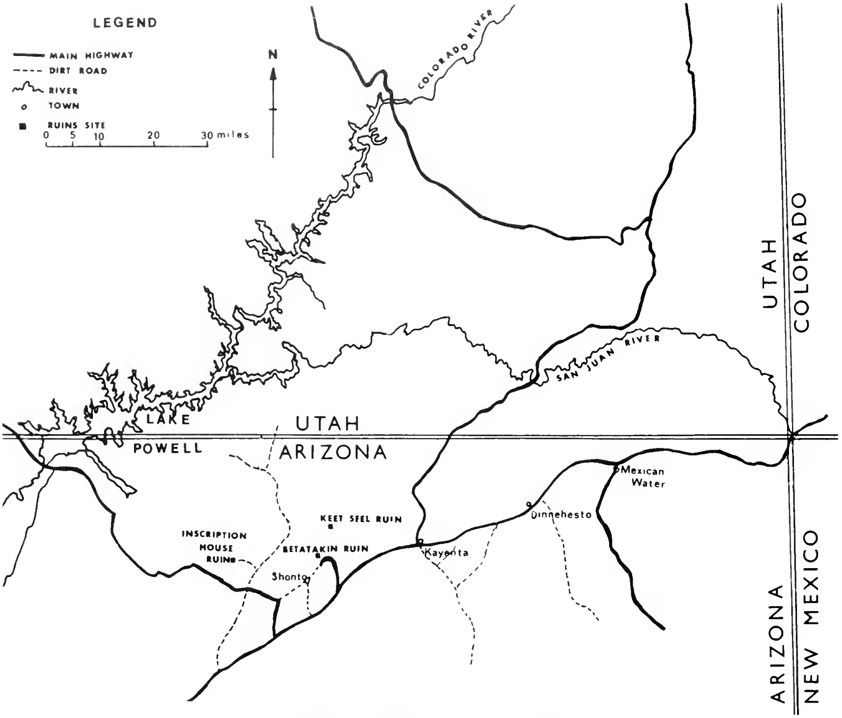


Fig. 1. Map showing the locality of Navajo National Monument in northeastern Arizona.

shown to be important (Foster 1971, Jenney 1958, Wilding and Drees 1969, and Zinke 1962).

The present study was undertaken to describe the plant communities and assess the effects of weathering processes on vegetation in Navajo National Monument. We report below a large diversity of vegetation found within this small geographical area, resulting in 12 major community types whose composition reflects the different substrates produced through differential weathering of the same geological formation.

STUDY SITE

Navajo National Monument is in northeastern Arizona, USA (Fig. 1). The monument headquarters are located on the Shonto Plateau near the head of Betatakin Canyon. The monument is made up of three separate units, each of which contains a large "cliff dwelling" of the Anasazi culture. The three units occur in pinyon-juniper slickrock country with many deep-cut canyons and high-walled sandstone cliffs that often reach heights of 380 m above the streambeds. Each unit occurs in a separate canyon. Betatakin and Keet Seel are two of these canyons and belong to the major Tsegi Canyon complex. Nitzin Canyon (Inscription House) is 32 km west of these and is a branch of Navajo Canyon. A profile diagram of Betatakin Canyon, showing distribution of community types, is illustrated in Figure 2. Figure 3 is a set of vegetation maps of the three segments of the monument.

Climatically the area is in the cold temperature desert region of the Colorado Plateau. The total annual precipitation ranges from a

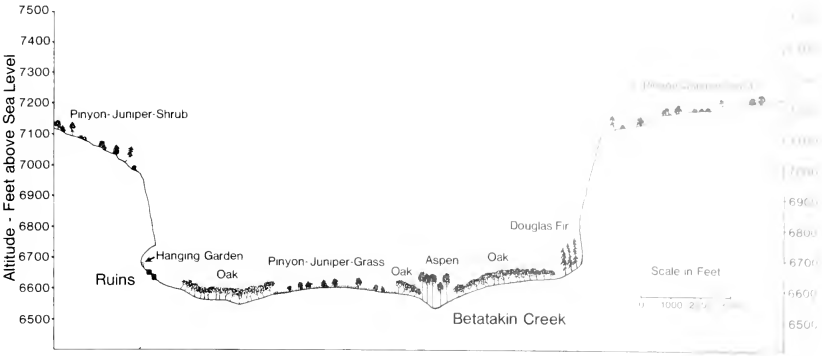


Fig. 2. Profile diagram of Betatakin Canyon. This profile is taken along the line shown in Figure 3.

low of 17 cm to a high of 48 cm, with an average of 29 cm (Brotherson et al. 1978). The period of greatest precipitation is late summer and early fall. Rainfall in the area is often spotty and localized, with cloudbursts occurring more often than general rains. Temperatures fluctuate greatly during the seasons, with lows of –23 C in winter and highs of 39 C in summer. The frost-free season ranges from 107 to 213 days, with an average of 155 days.

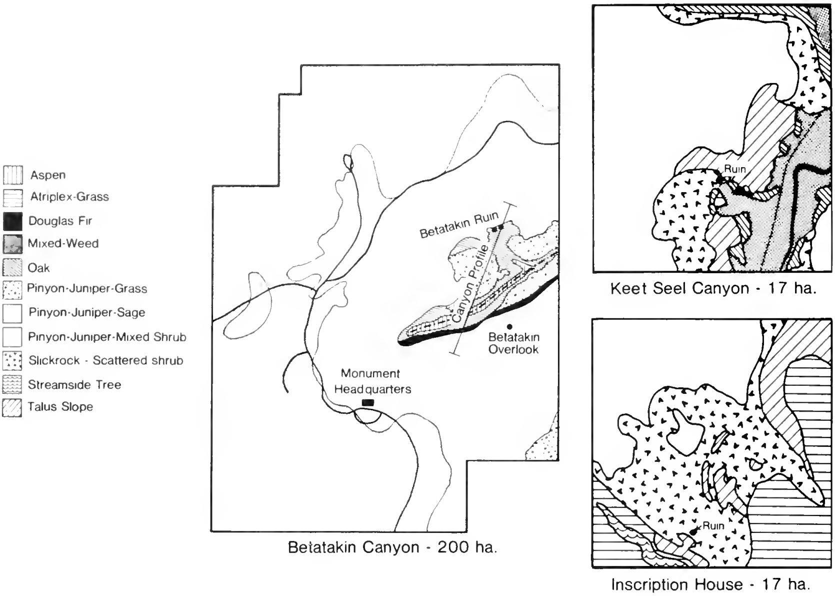
Navajo Sandstone is the major geological formation in all three segments of the monument and is the only exposed rock formation at Keet Seel and Nitzin canyons. At Betatakin Canyon, the Kayenta Formation is periodically exposed in the lower reaches. In all three canyons, Navajo Sandstone cliffs form sheer walls that extend above the creek beds 200 to 250 m. Talus accumulations occur at the base of these cliffs in each canyon. The canyon bottoms are filled with deep deposits of alluvium (Quaternary fill). In Keet Seel and Nitzin canyons these alluvial deposits are deeply eroded. In Betatakin Canyon the alluvial deposits are less extensive and not as thick. Erosion is a predominant feature of the monument and of the surrounding area.

METHODS

One hundred twenty-nine study plots were selected within the 12 plant community types of Navajo National Monument (Brotherson et al. 1978). A minimum of four plots was established in each community type. Each study plot measured 10 x 10 m (0.01 ha) and was randomly located within the community being studied. The plots were subsampled by 20 regularly placed 0.25 m^2 quadrats on a grid in each plot. Observations recorded in each plot included cover of plant species and species groups and physical characteristics, including exposure (aspect), slope, and soil depth.

Cover was estimated using Daubenmire's (1959) cover classes for all species encountered as well as for the five categories: total living cover, cryptogam cover, litter, rock, and bare ground. Plant community composition by life form was obtained by recording species in six life form categories: trees, shrubs, grasses, forbs, annuals, and cryptogams. Percent cover for all categories was subsequently calculated.

Composite soil samples were taken to a depth of 20 cm from the corners and center of each 0.01 ha plot. This depth was considered adequate on the basis of Ludwig's (1969) study of several foothill communities in Utah, which demonstrated that the surface decimeter of soil yielded 80% of the mineral concentration information useful in correlations with plant data. Holmgren and Brewster (1972) also found in a study of desert communities that greater than 60% of the fine roots (those most likely to absorb soil minerals) were concentrated in the upper 20 cm of the soil profile. Soil depth was determined with the use of a 1 m penetrometer.



Betatakin Canyon - 200 ha.

Keet Seel Canyon - 17 ha.

Inscription House - 17 ha.

Fig. 3. Vegetation maps of the three units of Navajo National Monument.

Soil samples were analyzed for texture (Bouyoucos 1951), pH, soluble salts, organic matter, and mineral composition. Soil reaction was measured with a glass electrode pH meter. Total soluble salts were determined with a Beckman electrical conductivity bridge. A 1:1 wt/vol soil-water paste (Russell 1948) was used to determine pH and total soluble salts. Organic matter was determined by weight loss after 24 hours at 450 C in a muffle furnace. Soils were extracted with 1.0 normal ammonium acetate for the analysis of calcium, magnesium, potassium, and sodium (Jones 1973). Zinc, manganese, iron, and copper were extracted from the soils with DTPA (Lindsay and Norvall 1969). Soil phosphorus was extracted with sodium bicarbonate (Olsen et al. 1954). Total nitrogen analysis was carried out using macrokjeldahl procedures (Jackson 1958). Ion concentrations were determined using a Perkin-Elmer Model 403 atomic absorption spectrophotometer (Isaac and Kerber 1971).

Plant nomenclature follows McDougall (1973). Prevalent species of the various plant communities are reported. The prevalent species list includes as many species as the average number of species per 0.01 ha sampling area examined (Warner and Harper 1972). Diversity values were computed using the formula: $B = 1/\Sigma p_i^2$, where B is the diversity index and p_i is a measure of the relative abundance of a species in a given habitat (Levins 1966, MacArthur 1972).

Cluster analysis (Sneath and Sokal 1973) was applied to similarity index values (Ruzicka 1958) using unweighted pair-group clustering (UPGMA). The UPGMA method computes the average similarity of each unit to the cluster using arithmetic averages. It is widely used and has been found to introduce less distortion than other methods (Kaesler and Cairns 1972).

Gradient analysis was used to assess the influence of weathering on soil types within the plant communities. Thirteen soil parameters were selected and treated as gradients. The abiotic properties evaluated were pH, soluble salts, organic matter, calcium, magnesium, potassium, sodium, zinc, iron, copper, manganese, phosphorus, and nitrogen. There were 12 values for each gradient, one for each of the communities. The resulting gradients were divided into five equal segments. Each plant community was assigned to one of the gradient segments according to its mean for that factor and given a rating from one to five corresponding to the gradient segment. The community ratings were summed across all gradients to yield an index of overall position with respect to all 13 gradients.

Linear regression analyses (Cochran and Snedecor 1976) were applied to the biotic and abiotic factors to determine the degree to which these factors were associated. Aspect data were transformed according to Beers et al. (1966) to allow aspect to be used as an independent variable in statistical analysis. Northeast aspects were given a value of 2.0, southwest aspects a value of 0.0, and intermediate aspects varied from 2.0 to 0.0 in both directions.

RESULTS AND DISCUSSION

Plant Communities

Twelve community types were encountered in the monument (Brotherson et al. 1978) (Table 1, Figs. 2 and 3). Two of these, oak and pinyon-juniper-mixed shrub, were found in all segments of the monument. Six of the remaining 10 community types were found in two of the monument areas, and four of the types were restricted to a single monument segment. Betatakin Canyon and its surrounding areas included more variability of vegetation types than the other segments of the monument. This was partially due to the favorable moisture conditions created by the canyon geology and Navajo Sandstone hydrology. Plant communities are described below.

I. Talus slope community. This community was in the monument at the base of large Navajo Sandstone cliffs. Because of differential weathering patterns of the sandstone, it was often found in pockets above canyon bottoms. This community was characterized by having many large and small rocks in its soil. The soil varied in depth from a few inches to several feet. Floristically the community was highly diverse and contained all life forms but was dominated by shrubs and grasses. The species *Atriplex canescens*, *Bouteloua gracilis*, and *Sporobolus cryptandrus* were especially important.

II. Atriplex-grass community. This community was found in two segments of the monument but was most highly developed at Inscription House on deep deposits of alluvial fill in the canyon bottom. Vegetatively this community type was similar to the talus slope type but was less diverse and showed only half as many prevalent species. The two most abundant species were *Atriplex canescens* and *Oryzopsis hymenoides*. Heavy overgrazing has contributed to severe wind and water erosion in this community type.

III. Pinyon-juniper-grass community. This community was found only in the bottom of Betatakin Canyon. It occurred at the base of sandstone cliffs on both northern and southern exposures, in places generally occupied by the talus slope community. It differed from the talus slope type in that the soils

TABLE 1. Vegetative communities of Navajo National Monument and the percentage of land area occupied within each monument segment.

	Monument Segment		
Vegetation type	Betatakin	Keet Seel	Inscription House
Pinyon-juniper-sage	49.9		
Pinyon-juniper-grass	3.1		
Aspen	0.7	Trace°	
Douglas fir	0.4	Trace	
Hanging garden	Trace	Trace	
Oak	2.4	4.8	0.1
Pinyon-juniper-mixed shrub	43.5	59.6	26.0
Mixed weed		13.5	
Talus slope		9.3	11.3
Atriplex-grass		0.2	25.8
Slickrock-scattered shrub		12.6	35.0
Stream side tree			1.8

(Note: Trace means <0.1%.)

were finely textured and lacked a rocky component. It was floristically diverse and had a high degree of cryptogam development. Important species were *Bouteloua gracilis*, *Stipa comata*, *Artemisia tridentata*, *Poa longiligula*, *Juniperus utahensis*, and *Muhlenbergia pungens*.

IV. Slickrock-scattered shrub community. This community was well developed in two of the monument's segments (Table 1). It characteristically exhibited large areas of exposed and unweathered rock. This community type is associated with Navajo Sandstone in much of southern Utah and northern Arizona. Slickrock vegetation grows in pockets in the sandstone created by differential weathering where fine textured materials collect. These pockets vary in size from a meter to a hundred or more meters across and contain a variety of vegetative forms. This community had the highest species diversity of all the monument communities. Important species were *Bouteloua gracilis*, *Oryzopsis hymenoides*, *Ephedra viridis*, *Cercocarpus intricatus*, *Gutierrezia sarothrae*, *Yucca angustissima*, *Vulpia octiflora*, *Opuntia polycantha*, and *Muhlenbergia pungens*. The type showed little or no grazing influence due to the fact that it usually occurred on the tops of rocky rises, bluffs, and cliffs where it was inaccessible to sheep and cattle.

V. Pinyon-juniper-mixed shrub community. This type was found in all segments of the monument and occupied the greatest percent of the land base. Geographically, it occurred between the slickrock and pinyon-juniper-sage communities. The type exhibited large areas of unweathered sandstone, though not to the extent found in slickrock sites. Soil development in the type was also more extensive than in slickrock. A major distinguishing factor in the vegetation of this community was the presence of several major shrub species in the understory that were absent or rare in other pinyon-juniper related communities. The most important species were *Cercocarpus intricatus*, *Pinus edulis*, *Cowania mexicana*, *Fendlera rupicola*, *Juniperus utahensis*, and *Poa longiligula*.

VI. Pinyon-juniper-sage community. This type was represented in the monument only at Betatakin, where it occurred adjacent to the pinyon-juniper-mixed shrub type on the plateau back from the canyon rim. It contained the oldest and largest pinyon and juniper trees. Soils of the area were uniformly distributed with very few rocks and/or slickrock areas. Average living cover was the highest of any of the pinyon-juniper types. Pinyon and juniper contributed exclusively to the overstory canopy, whereas the understory varied but was dominated mainly by *Artemisia tridentata*.

VII. Douglas fir community. This type was found in the Betatakin and Keet Seel segments of the monument. It occurred on northern and northeastern exposures, growing in a narrow band along the base of high sandstone cliffs where water seepage occurred. Floristically it was of intermediate diversity in comparison to other community types in the monument. The overstory and understory were dominated by trees and shrubs, with only 3 of the 14 prevalent species being grasses or forbs. There was a large amount of exposed rock and bare ground in this community, which occurred on steeper slopes than any other community type except hanging gardens. *Pseudotsuga menziesii*, *Poa longiligula*, *Pinus edulis*, *Quercus gambelii*, *Symphoricarpos vaccinoides*, and *Aster arenosus* were the most important vascular species. Moss cover was also significant.

VIII. Oak community. This community was found mainly in the Betatakin and Keet Seel parts of the monument (Table 1). In these areas, it was found in the canyon bottoms below Douglas fir. It occupied the banks of the streams and extended away from them toward the cliff bases, growing mostly on deep deposits of alluvial fill. The canopy was dense and dominated exclusively by *Quercus gambelii*. The understory varied and included *Symphoricarpos vaccinoides*, *Bromus tectorum*, *Mahonia repens*, *Smilacina stellata*, *Thalictrum fendleri*, and *Clematis ligusticifolia*. There was a deep litter layer throughout much of the type that was best developed at Betatakin Canyon, where it often reached a depth of 25 cm.

IX. Aspen community. This community was found at Keet Seel and Betatakin, although it was important only in Betatakin Canyon. The community occupied the central portion of the canyon along the stream and its banks. It was surrounded by the oak community, and together they dominated the riparian canopy of the canyon bottom. The aspen community was of average floristic diversity and was dominated in the understory by shrubs and forbs. The most abundant species were *Betula occidentalis, Cornus stolonifera, Equisetum hyemale, Acer negundo, Symphoricarpos vaccinoides, Clematis ligusticifolia,* and *Smilacina stellata.*

X. *Mixed weed community.* This type was found only in Keet Seel Canyon, where it occupied a considerable portion of the canyon bottom. It consisted of a mixture of introduced and native weeds and was dominated almost exclusively by annuals. The most important species were *Salsola iberica, Bromus tectorum, Sisymbrium altissimum, Cleome serrulata,* and *Epilobium hornemannii.* It occurred on deep deposits of alluvial fill and appeared to be a remnant of past overgrazing.

XI. Hanging gardens. This is an unusual community type occurring in the massive sandstone cliff regions of southwestern North America. This community was present in Betatakin and Keet Seel canyons. The garden at Betatakin was in the cliff dwellings and was associated with two seepage areas where water slowly emerged from the rocks. No runoff water was present. The hanging garden at Keet Seel was more mesic. Here the vascular plants grew attached to a seepage wall at the base of the northern part of the cliff dwellings. At the wettest portion of the garden a small seep emerged to form a puddle at the base of the hanging garden. With the exception of *Rhus toxicodendron*, the gardens were dominated exclusively by forbs, including *Mimulus eastwoodiae, Aquilegia micrantha, Mentezelia albicaulis, Galium aparine, Smilacina racemosa,* and *Habenaria sparsiflora.*

XII. Streamside tree community. This type was found at Inscription House in Nitzin Canyon. It was dominated by *Populus fremontii* and occurred along the stream bank at the cliff base below the ruin. Understory plants were almost nonexistent due to the high activity of domestic sheep and cattle in the area. The animals concentrated in the area along the stream for both feeding and shading. The soil base of the community consisted of deep deposits of alluvial fill. Widespread erosion occured here due largely to extensive overgrazing.

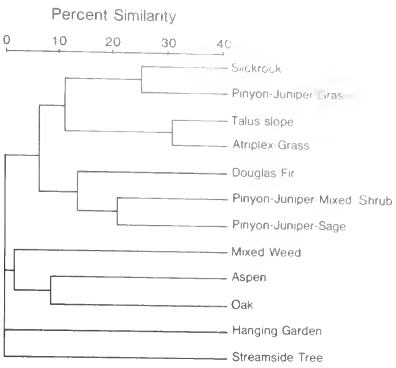


Fig. 4. Cluster dendrogram showing similarities of plant communities in Navajo National Monument.

Ecology

Indices of similarity (Ruzicka 1958) were computed for each community in relation to all other communities on the basis of species cover values. The similarity indices were low, ranging from 0% to 31%, with an average of 4.3%. In 52% of the comparisons the percent similarity was zero, whereas only 13 of a possible 66 comparisons showed similarities exceeding 10%. Such low similarities indicate that the community types were highly distinct. The similarity indices were clustered to produce a graphical representation of relationships between different community types (Fig. 4). Cluster patterns provide insight into community relationships within the monument since those communities most closely related share floristic and environmental elements. However, the most striking aspect of our cluster analysis was the dissimilarity between community types.

Biotic and abiotic environmental data were lumped by community and summarized (Table 2). There was a great deal of variation in these data, both within and between communities. Assuming approximate uniformity in chemical and physical properties of unweathered Navajo Sandstone parent material, differences in the properties of soils between sites should indicate the influence of weathering. To assess this hypothesis, mineral concentrations in the soils of the plant communities were compared to those in the sandstone (Table 3). Some minerals, including

TABLE 2. Means and standard deviations of biotic and abiotic community characteristics of each vegetation type.

	Gradients				
Community type	Talus slope	Atriplex grass	P-J-Grass	Slickrock	P-J-Mixed shrub
BIOTIC FACTORS					
Percent living cover	19.8	12.4	42.1	51.6	15.4
	± 10.8	± 9.9	± 38.1	± 4.0	± 6.2
Percent tree cover	0.0	0.0	5.7	1.3	0.0
	± 0.0	± 0.0	± 6.2	± 2.3	± 0.0
Percent shrub cover	17.4	39.1	19.7	33.3	26.3
	± 3.3	± 25.5	± 17.4	± 10.4	± 16.6
Percent grass cover	41.9	16.9	52.1	33.0	36.5
	± 12.8	± 8.2	± 18.9	± 6.0	± 1.5
Percent forb cover	21.2	4.5	13.8	9.4	13.7
	± 4.9	± 8.8	± 2.7	± 2.5	± 2.2
Percent annual cover	1.7	31.5	0.0	3.1	0.0
	± 2.4	± 28.3	± 0.0	± 2.4	± 0.0
Percent cryptogam cover	0.7	0.1	12.1	5.1	5.5
	± 1.0	± 0.2	± 15.3	± 3.2	± 3.3
Diversity	6.0	3.2	7.0	8.2	2.6
	± 1.5	± 1.4	± 1.9	± 1.5	± 1.2
Mean # of species/stand	14.8	6.5	20.3	19.8	14.9
	± 4.9	± 1.9	± 2.5	± 5.4	± 2.9
GROSS HABITAT FACTORS					
Soil depth (cm)	49.4	51.7	54.2	33.7	20.8
	± 31.0	± 8.3	± 19.3	± 11.5	± 7.2
Aspect	0.7	0.9	0.7	0.2	1.6
	± 0.9	± 0.1	± 1.0	± 0.3	± 0.4
Percent slope	24.2	39.1	20.0	18.3	28.0
	± 10.6	± 8.6	± 22.9	± 11.6	± 14.1
Percent litter cover	6.1	11.4	7.0	4.7	25.9
	± 1.8	± 6.8	± 5.4	± 3.4	± 8.8
Percent rock cover	38.1	16.9	10.1	0.3	15.7
	± 16.9	± 5.2	± 17.5	± 0.5	± 14.9
Percent bare ground	34.1	47.7	33.5	21.0	30.8
	± 14.3	± 10.9	± 12.3	± 6.9	± 15.1
SOIL FACTORS					
Percent sand	85.6	85.3	81.7	89.3	83.0
	± 1.8	± 1.7	± 8.4	± 0.6	± 3.6
Percent silt	7.2	8.9	9.3	4.0	12.1
	± 1.9	± 1.1	± 4.9	± 0.0	± 2.8
Percent clay	7.2	6.2	8.7	7.0	4.9
	± 0.8	± 0.8	± 3.8	± 0.0	± 1.0
Percent fines	14.4	15.1	18.0	11.0	17.0
	± 1.8	± 1.8	± 8.7	± 0.0	± 3.6
pH	7.8	7.9	7.3	7.8	7.4
	± 0.1	± 0.1	± 0.3	± 0.1	± 0.2
Soluble salts	271.4	236.7	205.0	201.0	197.8
	± 33.6	± 68.1	± 129.7	± 13.8	± 52.2
Percent organic matter	3.2	0.7	3.1	1.6	3.9
	± 0.7	± 0.2	± 2.2	± 0.5	± 1.3
Nitrogen (ppm)	0.04	0.03	0.03	0.02	0.05
	± 0.01	± 0.01	± 0.01	± 0.01	± 0.02
Phosphorus (ppm)	12.0	9.5	9.3	9.6	8.2
	± 2.9	± 2.0	± 1.2	± 1.2	± 4.1
Calcium (ppm)	5708.6	3911.0	3331.3	1729.7	2674.9
	± 2668.0	± 832.6	± 3563.5	± 57.6	± 1515.3
Magnesium (ppm)	120.0	412.6	100.0	55.3	526.6
	± 45.5	± 61.3	± 39.9	± 6.4	± 124.4
Potassium (ppm)	170.0	280.1	128.3	63.3	102.1
	± 69.2	± 115.7	± 44.8	± 7.6	± 30.4

TABLE 2. Continued

Gradients						
P-J-Sage	Douglas fir	Oak	Aspen	Mixed weed	Hanging garden	[illegible]
57.4	25.8	26.2	11.7	66.8	[illegible]	0.0
±16.7	±11.9	±24.0	±13.9	±34.6	[illegible]	±0.0
64.3	1.0	0.0	24.9	0.0	[illegible]	0.0
±18.1	±1.9	±0.0	±24.8	±0.0	±4.1	±0.0
22.3	18.8	36.1	25.7	1.0	2.8	[illegible]
±8.3	±17.1	±36.7	±20.6	±1.7	±2.1	[illegible]
13.3	47.8	3.2	1.7	8.5	5.5	0.0
±11.9	±20.8	±4.0	±3.2	±9.3	±4.9	±0.0
1.2	23.5	5.4	34.8	58.2	74.1	0.0
±1.3	±18.1	±6.1	±25.0	±50.7	±9.9	±0.0
0.0	0.1	13.8	0.0	32.3	0.0	6.6
±0.0	±0.2	±29.1	±0.0	±56.0	±0.0	±11.6
6.6	0.5	0.0	0.0	0.0	22.1	0.0
±5.9	±0.7	±0.0	±0.0	±0.0	±13.8	±0.0
2.3	3.8	2.8	3.6	2.5	2.1	1.4
±1.0	±1.3	±0.8	±0.7	±0.6	±1.0	±0.5
8.6	13.3	10.8	11.3	7.7	7.0	3.3
±3.0	±0.7	±4.3	±2.7	±1.5	±2.8	±1.2
32.4	47.9	77.9	37.5	66.6	9.3	33.3
±12.9	±13.6	±21.3	±51.7	±57.7	±5.5	±57.7
1.1	1.0	1.4	1.2	0.7	0.2	1.0
±0.6	±0.5	±0.7	±0.8	±0.7	±0.2	±0.9
7.9	30.6	12.6	10.0	5.3	85.0	23.0
±7.0	±2.7	±4.7	±10.8	±4.6	±7.1	±5.3
36.1	33.6	91.3	70.8	16.4	9.3	34.0
±20.4	±17.6	±9.4	±18.3	±7.6	±11.8	±4.9
0.9	22.0	0.1	0.6	0.0	13.1	0.0
±1.2	±12.6	±0.3	±1.6	±0.0	±0.3	±0.0
43.3	20.2	0.8	3.6	21.3	0.0	64.5
±16.6	±14.7	±1.5	±3.2	±22.1	±0.0	±7.0
83.6	83.5	76.1	83.9	84.7	83.5	85.0
±2.5	±3.8	±3.8	±5.3	±1.5	±0.7	±1.7
11.4	9.9	14.4	10.4	9.0	9.0	6.0
±2.3	±3.0	±2.9	±4.3	±1.7	±0.0	±1.0
5.0	6.6	9.7	5.9	6.3	7.5	9.7
±0.8	±1.1	±2.0	±1.6	±0.6	±0.7	±1.2
16.4	16.5	24.1	16.3	15.3	16.5	15.7
±2.5	±3.8	±4.0	±5.5	±1.5	±0.7	±1.5
7.2	7.4	6.7	7.2	7.5	7.7	8.0
±0.2	±0.3	±0.4	±0.2	±0.1	±0.1	±0.2
136.1	233.9	376.9	286.0	349.7	517.0	568.5
±36.3	±47.5	±75.2	±74.8	±176.1	±281.4	±171.7
2.5	3.4	9.1	5.2	2.9	4.1	2.1
±1.4	±1.6	±3.8	±4.1	±1.1	±1.1	±0.4
0.05	0.05	0.20	0.10	0.06	0.04	0.04
±0.01	±0.02	±0.08	±0.08	±0.01	±0.02	±0.01
5.5	11.6	23.4	12.4	15.9	10.3	[illegible]
±1.1	±3.0	±6.7	±3.5	±2.0	±5.5	[illegible]
1627.5	3027.8	4334.7	3588.0	2336.3	8155.0	[illegible]
±310.3	±1428.2	±1245.4	±1953.8	±615.6	±264.5	[illegible]
645.6	83.3	226.4	108.9	86.7	184.0	[illegible]
±33.5	±36.6	±70.3	±84.1	±6.7	±0.0	[illegible]
88.4	121.9	272.5	181.3	303.3	152.5	[illegible]
±16.7	±44.8	±105.1	±68.9	±75.2	[illegible]	[illegible]

Table 2 continued.

	Gradients				
Community type	Talus slope	Atriplex grass	P-J-Grass	Slickrock	P-J-Mixed shrub
Sodium (ppm)	12.1 ± 3.4	10.8 ± 0.9	10.3 ± 2.8	9.7 ± 1.4	9.8 ± 3.0
Iron (ppm)	1.0 ± 0.3	2.3 ± 0.2	1.8 ± 0.5	0.7 ± 0.1	4.6 ± 2.1
Manganese (ppm)	1.9 ± 0.5	4.4 ± 0.5	1.9 ± 0.2	1.6 ± 0.2	4.3 ± 1.8
Zinc (ppm)	0.4 ± 0.2	1.0 ± 0.2	0.3 ± 0.1	0.2 ± 0.1	1.3 ± 0.4
Copper (ppm)	0.3 ± 0.1	0.4 ± 0.1	0.3 ± 0.1	0.2 ± 0.0	0.4 ± 0.1

Zn, Na, and Ca, were usually lost through weathering due to mobility and leaching. On the other hand, K, Mg, Fe, Cu, Mn, P, and N were apparently concentrated in the upper levels of the soil profile through weathering. This weathering pattern occurred in 9 of the 12 communities.

Our gradient analysis of soil factors resulted in three groups of communities (Table 4, Fig. 5). The first group was composed of the slickrock, pinyon-juniper-grass, and talus slope community types. The soil of the slickrock community appeared the least changed when compared to the parent material. This was as expected, since slickrock sites were associated with large areas of exposed sandstone. The soils of the pinyon-juniper-grass and talus slope communities also tended to show minor changes from parent material. These types were found at the base of sandstone cliffs, where they receive constant input of generally unweathered material from the cliffs above.

A second group included communities with soils of intermediate weathering. Within the group, soils of the streamside tree type appeared to be most weathered, and soils of the mixed weed and Douglas fir types were least weathered.

Soils of the oak community were the most weathered of any occurring in the monument (Fig. 5). These soils were the most acid, lowest in percent sand, and highest in percent fines, organic matter, litter cover, iron, copper, manganese, phosphorus, and nitrogen (Table 2). Oak communities within the monument apparently contribute to the weathering process and enhance soil fertility through the addition of organic matter.

Soil acidity (Fig. 6) in the 12 community types was positively correlated with organic matter ($p<0.001$). This result is consistent with the findings of Zinke (1962) that soils are more acid where influenced by the canopy. Increased acidity from organic matter breakdown likely accelerates the weathering

TABLE 3. Mean concentrations of minerals in Navajo Sandstone parent material together with indicated deviations from these concentrations in soils of the various plant communities.

Mineral	Mean concentration in parent material (ppm)	Number of communities with mean concentration in soils	
		Less than parent material	Greater than parent material
Zn	1.54	12	0
Na	23.0	10	2
Ca	4631.0	9	3
K	111.0	3	9
Mg	53.0	0	12
Fe	.54	0	12
Cu	.14	0	12
Mn	.69	0	12
P	3.6	0	12
N	Trace	0	12

Table 2. Continued

Gradients						
P-J-Sage	Douglas fir	Oak	Aspen	Mixed weed	Hanging garden	[illegible]
9.1	18.0	14.7	12.1	12.0	118.8	48.0
±0.6	±13.1	±4.2	±2.7	±1.3	±107.1	[illegible]
6.7	3.0	10.6	2.8	2.0	0.8	1.2
±1.5	±1.6	±8.7	±2.1	±0.1	±0.4	[illegible]
4.2	2.9	12.9	3.5	3.6	3.8	[illegible]
±1.3	±0.9	±8.4	±1.4	±0.4	±0.1	±0.7
1.2	0.6	0.8	0.7	0.8	0.6	0.5
±0.2	±0.4	±0.5	±0.4	±0.1	±0.1	±0.1
0.5	0.4	0.8	0.4	0.3	0.2	0.3
±0.1	±0.1	±0.3	±0.1	±0.1	±0.0	±0.1

process considerably (Birkeland 1974). In addition, laboratory and field work have demonstrated that chelating agents formed from biological processes in the soil can also bring about significant amounts of weathering when in contact with mineral soil (Schalascha et al. 1967). Indeed, such biotic weathering may exceed that brought about by hydrolysis alone under some circumstances (Birkeland 1974, Schatz 1963, Jackson and Keller 1970).

Physical weathering is important in all community types in the monument. In addition, chemical and biological weathering are important in some communities (particularly those in groups II and III of Fig. 5). Biotic weathering appears to be most important in the oak community type. These weathering processes constitute a potent force in altering conditions of the habitat and creating the variety of environmental conditions suitable to the various plant communities growing there. The plant communities themselves participate in the weathering process as biomass becomes established.

Spatial patterns of plant communities in Navajo National Monument are due to different microhabitats created by weathering processes on Navajo Sandstone as well as availability of water. Water availability influences community distribution in three major ways. First, water has been the primary factor in sculpting canyon morphology, which has, in turn, created a variety of microhabitats. Second, where water is more abundant, physical weathering of parent material is accelerated. Third, soil water differentials have contributed to local variability in vegetation patterns.

These effects are especially well illustrated at Betatakin Canyon (Fig. 2). On the canyon rims, runoff is rapid, little water is retained, soil development is poor, and desertic conditions prevail. Deep in the canyon, water tends to run into the soil rather than on the surface, accumulating in low areas, producing more mesic conditions. Seep lines at the base of steep canyon walls also provide local

Table 4. Relative position of plant community soils along 13 measured gradients. Index (column 14) indicates overall position with respect to parent material. The larger the index, the greater total change from parent material.

Community type	Ca	Mg	P	N	Zn	Mn	Fe	Cu	Na	K	pH	Soluble salts	O.M.	Index
Slickrock	1	1	2	1	1	1	1	1	1	1	1	1	1	14
Pinyon-juniper-grass	2	1	2	1	1	1	1	1	1	1	3	1	2	18
Talus slope	3	1	2	1	2	1	1	1	1	1	1	2	2	19
Mixed weed KS	1	1	3	1	3	1	1	1	1	2	2	3	2	22
Douglas fir	2	1	2	1	2	1	2	2	1	1	3	2	2	23
Atriplex-grass	2	4	2	1	4	2	1	2	1	2	1	2	1	25
Aspen	2	1	2	3	3	1	2	2	1	1	3	2	3	26
Hanging garden	5	2	2	1	2	1	1	1	5	1	2	5	3	27
Pinyon-juniper-mixed shrub	1	5	1	1	5	2	2	2	1	1	2	1	2	28
Pinyon-juniper sage	1	5	1	1	5	2	4	3	1	1	3	1	1	29
Stream side tree	3	2	3	1	2	2	1	1	3	5	1	5	2	30
Oak	2	2	5	5	3	5	5	5	1	2	5	3	5	48

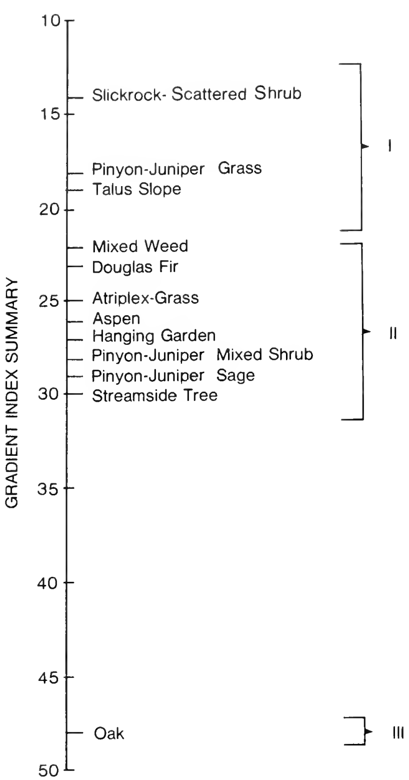


Fig. 5. Community positions on composite gradient of thirteen soil factors.

areas of increased moisture, providing habitats for the unusual Douglas fir and hanging garden communities.

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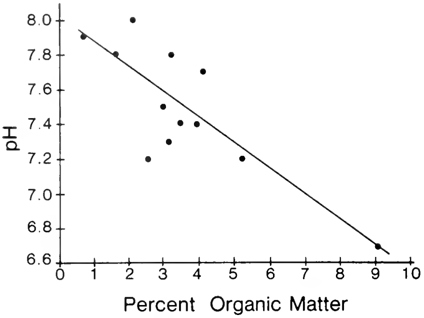

Fig. 6. Relationship between pH and percent organic matter in soils of plant communities in Navajo National Monument.

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CRYPTOGAMIC SOIL CRUSTS: SEASONAL VARIATION IN ALGAL POPULATIONS IN THE TINTIC MOUNTAINS, JUAB COUNTY, UTAH

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ABSTRACT.— The soil algae in the Tintic Mountains, Juab County, Utah, was studied over a one-year period in 1982 and 1983. Fluorescence microscopy was used to measure algal density in samples directly from the field. A total of 30 algal taxa was observed, blue-green algae being most abundant both in terms of density and number of species. Algal density showed peaks in late fall and late spring. Minima were present in September 1982 and July 1983. Several weak correlations between algal density and climatic data existed. In general algae correlated positively with precipitation and negatively with temperature. A combination of low precipitation and hot temperatures was likely responsible for the low density observed in July. The Chrysophyta followed slightly different trends than the other algal groups, having minima in early October 1982 and late August 1983. Field observations indicated that the degree of algal crusting varied noticeably over a period of one year, with highest abundance of hummocking in spring. Heavy summer thunderstorms destroyed algal crusting during July and August of 1983, though absolute density of algae increased during this time in response to the extra moisture.

Soil algae have received considerable study during the last half century (Metting 1981, Starks et al. 1981). Arid land soil algae are an important component of desert ecosystems for several reasons. Algae in association with lichens and mosses form crusts that stabilize the soil surface against wind and water erosion. Improved infiltration of rainwater in crusted soils further reduces erosion by lessening the amount of runoff (Brotherson and Rushforth 1983). Fixation of atmospheric nitrogen by blue-green algae, both free living in the soil and associated with soil lichens, has been well documented. Vascular seedling development tends to be facilitated in areas where crust development is pronounced (St. Clair et al. 1984).

Floristic studies of soil algae have primarily been conducted through the use of enrichment and unialgal cultures (Metting 1981). Recent studies of soil algae in the Great Basin and Colorado Plateau have been performed using distilled water wetting and/or standard culture methods (Anderson and Rushforth 1976, Ashley and Rushforth 1984, Johansen, Rushforth, and Brotherson, 1981, Johansen, Javakul, and Rushforth 1982). Studies of soil algal biomass have been done using several different methods, including chlorophyll *a* content, dilution counts, enrichment counts, plate counts, and direct counts (Metting 1981).

Direct counts of soil algae are difficult to make, since algae are often scarce in uncultured samples and identification of many species without prolonged culture and study of life cycles is often nearly impossible. However, direct counts are more indicative of natural conditions because biomass and diversity estimates are based upon data from communities that have not been modified by culturing. Fluorescence microscopy can greatly aid in examination of soil algae. Although the value of this technique was pointed out more than 30 years ago (Tchan 1952), it has not been widely used. In the present study, direct counts using fluorescence microscopy were used to measure seasonal changes in abundance of arid land soil algae. We recognize that some sacrifice in taxonomic resolution was made in exchange for ecological data based on a less modified algal community.

METHODS

The study site was located in the Tintic Mountains, 7 km west of Tintic Junction, Juab County, Utah, T10S R4W S35. Several well-developed algal crusts were located on a hill crest, 1950-m elevation, in [illegible]*niperus*

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osteosperma-Artemisia tridentata vascular plant community. The soil at the locality was examined and classified using standard references (Soil Conservation Service 1972, Soil Survey Staff 1951, 1975). The soil was classified as Aridic Calcixeroll, fine clayey, mixed, mesic. The surface horizon was a dark greyish brown, sandy clay loam. Other soil characteristics are listed in Table 1.

Samples were collected nine times over a period of one year beginning September 1982 (Table 2). Five samples were collected each time, except 31 October 1982, when 10 samples were collected and processed. One sample collected 15 June 1983 was lost; thus only 4 samples were available for that collection.

All samples were collected from an area approximately 10 m^2 in size. Exact sample localities were subjectively chosen in crusted areas between shrubs. For each collection period, the upper 2 cm of five adjacent algal crust hummocks were collected and returned to the laboratory for immediate analysis. Samples were homogenized with a metal spatula. Six 1-gm subsamples were taken from each of the samples. One subsample was reserved for direct microscopic analysis. The other five were oven dried at (105 C) and weighed again to calculate percent soil moisture (Table 2).

The subsample reserved for microscopic analysis was wetted immediately prior to examination. The soil was placed in a volumetric cylinder, and distilled water was added to a total volume of 10 ml. The sample was then agitated vigorously by hand for 60 seconds. A 1-ml subsample was pipetted from the solution and placed in a dilution tube containing 4 ml of distilled water. This final dilution was used for direct examination under a Zeiss RA microscope with dark field and fluorescence optics. A counting chamber with a depth of 0.18 mm and field length of 10 mm was constructed as suggested by Tchan (1952) and used in all counts. Fluorescing (living) algal cells and colonies were counted under 400X magnification. All algae in 10 transects across the chamber were counted for each sample. Algae were identified to species when possible, or to genus or division when necessary. Some algae were not identifiable and were classified as unknown coccoid algae or unidentifiable algae. Moist plate cultures using Bold's Basal Medium (Bold and Wynne 1978) were started at the initiation of the study to aid in species identification.

Temperature and moisture data were taken from weather records for Eureka, Utah, the nearest weather station (National Oceanic and Atmospheric Administration 1982, 1983). The average daily temperature and precipitation for the two weeks previous to each collection date were calculated (Table 2).

An importance index for all living algal taxa was calculated by multiplying density by percent presence (Ross and Rushforth 1980). This method is often used in studies of terrestrial vascular vegetation (Warner and Harper 1972) and has the value of considering both absolute density data as well as frequency of occurrence. Species with importance values greater than 1.0 were designated prevalent species and were used in subsequent analyses of variance.

Multivariate analysis of variance adapted for a fixed-effect, unbalanced design following the methods of Bryce et al. (1980) was used to analyze differences between treatments (months) and blocks (species). The variance of each taxon was related to the mean. To satisfy the homogeneity of variance

TABLE 1. Soil properties for the Aridic Calcixeroll at the Tintic Mountain site. Soil for tests taken from A1 horizon, 0–28 cm depth, 3 October 1982.

Property	
Sand	55.6%
Silt	20.4%
Clay	24.0%
Gravel	0.9%
Lime content	2.0%
Organic matter	8.4%
Pore space	35.8%
Bulk density	1.7 g/cm^3
Soluble salts	240 ppm
NH_4	100 ppm
P	155 ppm
NO_3	7 ppm
Ca	3.4 meq/liter
Mg	1.2 meq/liter
Na	1.0 meq/liter
HCO_3 and CO_3	3.9 meq/liter
Cl	0.5 meq/liter
K	0.2 meq/liter
pH, saturated paste	7.4

assumption of analysis of variance, a log (x + 1) transformation was used (Bartlett 1947). In each analysis of variance, standardized residuals were plotted against normal scores. In every case the probability plot thus generated was subjectively judged to be normal or close to normal. The Duncan multiple range test was used to determine significance of differences between means when analysis of variance showed significance (Duncan 1955). Unless otherwise stated, the alpha value used for this test was 0.01.

Shannon-Wiener diversity indices were calculated (Shannon and Weaver 1949, Patten 1962) for each subsample for each collection date. Similarity indices for all 49 subsamples collected on the nine collection dates were determined following the methods of Ruzicka (1958). Such indices were also calculated for the nine collection dates using arithmetic averages of subsamples. Similarity indices were then clustered (Sneath and Sokal 1973) to determine the relationships between collection periods. Correlation analysis (Snedecor and Cochran 1980) was performed to determine relationships between algal abundance and precipitation and temperature data.

RESULTS AND DISCUSSION

Description of the Flora

A total of 30 algal taxa was identified during this study (Table 3). Fifteen of these were blue-green algae, 9 were chrysophytes (including diatoms), 3 were green algae, and 3 were placed in the categories flagellates, unknown coccoid algae, and unidentifiable algae. The latter 3 categories were necessary since some of the algae encountered with the fluorescent microscope could not be placed with confidence into known divisions.

TABLE 2. Soil moisture for each collection date and mean high and low temperature and precipitation for two-week period previous to collection date.

Date	Temperature (degrees C)	Precipitation (cm)	Soil moisture (g/kg)
21-IX-1982	8-20	2.4	37.4
3-X-1982	6-16	10.7	205.6
31-X-1982	0-11	1.4	240.9
29-XI-1982	6-4	1.0	275.1
14-I-1983	6-6	0.0	178.0
15-V-1983	1-16	2.4	35.9
15-VI-1983	6-24	1.6	1.2
29-VII-1983	15-28	2.1	19.2
26-VIII-1983	13-26	4.7	25.9

Algal taxa in the Tintic locality with an importance index greater than 1.0 included *Microcoleus vaginatus* (importance value = 351.56), *Nostoc* species (258.92), unidentifiable algae (162.36), unknown coccoids (161.05), *Phormidium minnesotense* (141.97), unknown coccoid Chlorophyta (118.72), unidentified Chrysophyceae (64.27), *Navicula mutica* (58.16), *Hantzschia amphioxys* (56.64), *Anabaena* cf. *variabilis* (33.01), *Synechococcus aeruginosus* (26.37), *Tolypothrix tenuis* (10.15), unknown Chlorosarcinales (5.81), unknown Chroococcaceae (4.25), and *Pinnularia borealis* (2.17).

Multivariate analysis of variance of prevalent species density data showed that significant (p<.001) differences existed between taxa. Duncan's multiple range test showed that *Microcoleus vaginatus* was significantly more abundant than all other species or categories. *Nostoc* species were more abundant than all other less common taxa. Unidentifiable algae, unknown coccoid algae, *Phormidium minnesotense*, and unknown coccoid Chlorophyta formed a group, of which each was more abundant than less common taxa. Chrysophyte cysts, *Navicula mutica*, *Hantzschia amphioxys*, and *Anabaena* cf *variabilis* formed a second group, of which each was more abundant than less prevalent taxa.

The Tintic algal flora is similar in most respects to that we have observed from other localities in the Great Basin and Colorado Plateau (Anderson and Rushforth 1976, Ashley et al. in press, Johansen et al. 1981, 1982, 1984). It is dominated by filamentous blue-green algae, particularly *Microcoleus vaginatus*, *Nostoc* species, and *Phormidium* species. In addition, diatoms are more diverse and often more abundant than green algae. One conspicuous difference between our soil crusts and several others we have examined was the absence of an obvious moss and lichen component. Some lichens were present in our crusts, but they were rare. This is likely due to the fact that the study area is regularly grazed, and grazing is known to cause severe damage to the moss and lichen components of crusts (Anderson et al. 1982, Brotherson et al. 1983).

Diversity and Similarity

Shannon-Wiener diversity indices varied between 2.285 and 3.399 for the individual subsamples. Average Shannon-Wiener diversity for each collecting period ranged between 2.690 and 3.229. These figures are similar to or higher than other Shannon-Wiener values for soil algal studies we have made in other regions of the Great Basin (Johansen and St. Clair in review, Johansen et al. 1982, 1984). The rather low range of diversity for these samples was borne out by species richness figures. Total number of taxa observed per collecting period varied between 14 and 19. Even though variability in diversity was rather low in comparison to other systems we have studied, analysis of variance showed that diversity was significantly different between months. Duncan's multiple range test showed that the diversity in collections from cooler months (especially January and June) was significantly higher than diversity in warmer months (especially August and September).

Stand similarity on the basis of species density data was high, averaging 68% for the winter stands and 50% for the remaining stands. When these data were clustered, only winter stands (31 October, 29 November, 14 January, and 15 May) formed a discrete group. Stand similarity on the basis of species presence or absence was even higher, with an average similarity of 74%. When these data were clustered, the same winter months formed a group, except that the samples from early October and July were included.

TABLE 3. Taxa present at the Tintic Mountain site together with importance values (PFI) and density for each collection date. Unit value for density is 1000 organisms/g dry weight soil.

Taxa	PFI	9/24	10/3	10/31	11/29	1/14	5/15	6/15	7/29	8/26
CYANOPHYTA										
Anabaena cf *variabilis*	33.01		20	15	23	155	7	96	15	52
Chroococcus pallidus	0.08							13		
Chroococcus species	0.02		3							
Gloeocapsa aeruginosa	0.73							57	15	
Gloeocapsa punctata	0.01						1			
Gloeothece linearis var. *composita*	0.56	1	10	3	12	2				
Merismopedia punctata	0.01									3
Microcoleus vaginatus	351.56	240	153	241	275	249	502	514	281	639
Nostoc species	258.92	131	267	234	296	188	235	710	48	305
Oscillatoria geminata	0.18							10		
Phormidium minnesotense	141.97	19	84	138	213	121	266	270	50	98
Synechococcus aeruginosus	26.37	123	30	36	6	22	36	82	20	23
Tolypothrix tenuis	10.15			33	10	16	38	18	12	11
Tolypothrix species	0.33			2						14
Unknown Chroococcaceae	4.25	1	15	47	47	3		7		
CHLOROPHYTA										
Oocystis species	0.02									4
Chlorosarcinales	5.81			3	2			56	36	37
Unknown coccoids	118.72	15	58	124	164	137	124	304	56	99
CHRYSOPHYTA										
Achnanthes species	0.02					3				
Caloneis bacillum	0.01			1						
Hantzschia amphioxys	56.64	81	26	43	87	52	84	46	44	40
Navicula mutica	58.16	71	23	64	87	80	66	75	45	28
Navicula species	0.02							2		1
Pinnularia borealis	2.17	7	6	8	4	6	8	4	3	
Pinnularia species	0.01								1	
Unknown pennate	0.01					2				
Chrysophyceae	64.27	33	48	64	54	69	67	182	36	28
OTHER UNIDENTIFIABLE ALGAE										
Flagellates	0.03	1					[illegible]			
Unknown coccoids	161.05	15	100	32	256	175	231	147	67	201
Unidentifiable algae	162.36	72	153	226	274	173	137	[illegible]	[illegible]	[illegible]

Climatic Factors

Our original hypothesis was that precipitation and total soil algal growth would be positively correlated during all seasons. However, when we ran correlation analyses, we discovered that precipitation and algal growth were almost always negatively correlated, although values were not significant. When we discovered this, we divided total algae into several categories for separate analyses. These categories included Cyanophyta, Chlorophyta, Chrysophyta, and other algae. The negative correlation we noted for total algal growth held for all of these categories whether the period of precipitation prior to collection date used in the analysis was for 3, 7, 14, 21, or 28 days.

In view of these negative correlations, we computed the net increase or decrease in abundance for each algal group for each collection interval. We then correlated these data with climatic data. The results of this correlation of incremental algal growth with precipitation were low, but positive for all algal groups (Table 4).

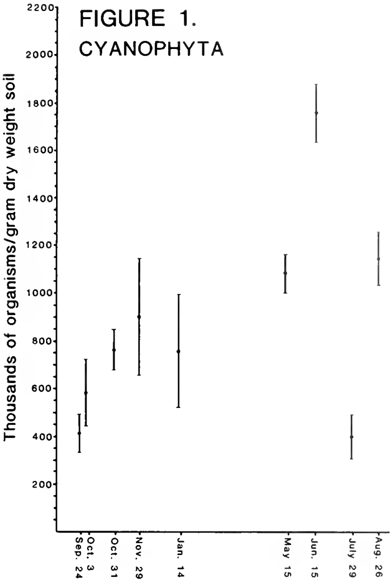
As a whole, our data indicate that algal growth was not related in a linear manner to precipitation. It seems probable that when a minimum amount of moisture is present in the soil, algal growth will not be limited and moisture beyond this threshhold does not enhance growth and may in fact reduce algal density. Stokes (1940) found that soil algae in New Jersey grew best at 40%–60% soil moisture and that growth was strongly curtailed in saturated soil. On the other hand, low moisture is often a limiting factor for algal growth in desert regions (Lynn and Cameron 1973). For instance, Brock (1975) found that the depletion of soil moisture to −7 bars began to deter the growth of *Microcoleus* in desert crusts.

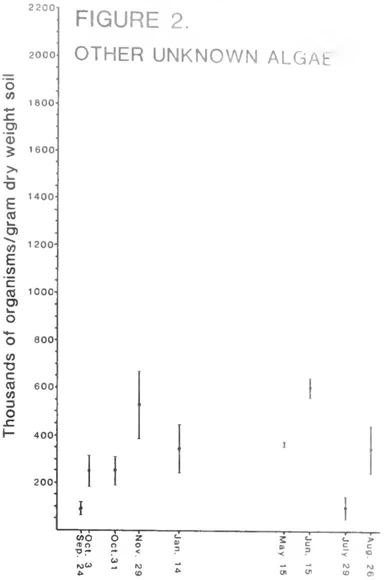
Incremental growth of algal groups was also correlated with air temperature. All correlations were negative, and the largest coefficients were obtained when median temperature rather than maximum temperature data were used (Table 4). Generally, the best correlations occurred when temperature data for the three-day period prior to collection were used rather than data for longer periods. This indicates rapid negative algal response to high air temperatures.

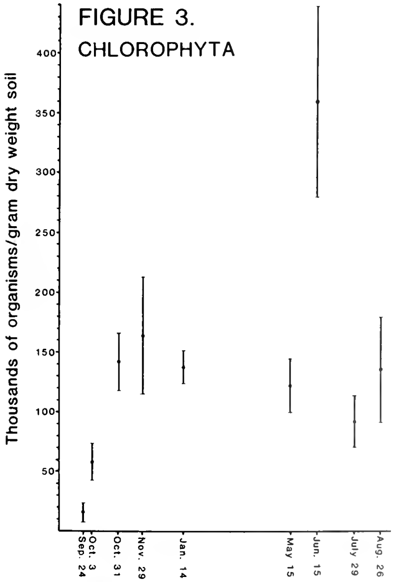
Abundance of blue-green algae was more negatively correlated with temperature than all other groups. This was surprising since many species of blue-green algae are known thermophiles and have been demonstrated to tolerate high temperatures in the laboratory

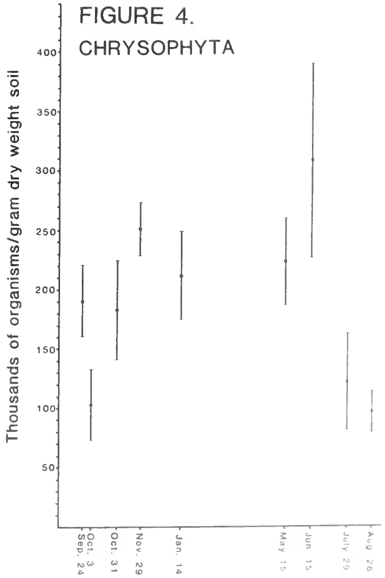
TABLE 4. Correlation coefficients for incremental algal growth versus climatic factors. Climatic factors include mean daily precipitation (PRECIP), mean maximum temperature (MAX-T), and mean midtemperature (MID-T). Means were computed for the 3-, 7-, 14-, 21-, and 28-day periods prior to the collection dates. Significant correlations are asterisked (α < .05°, α < .01°°).

Algal group	Climatic factor	Days 3	7	14	21	28
CYANOPHYTA	PRECIP	.033	−.077	.026	.063	.317°
	MAX-T	−.315°	−.322°	−.342°	−.301°	−.306°
	MID-T	−.429°°	−.382°°	−.386°°	−.321°	−.324°
CHLOROPHYTA	PRECIP	.181	.039	.041	.066	.118
	MAX-T	−.283	−.249	−.236	−.175	−.199
	MID-T	−.375°	−.297°	−.287	−.208	−.234
CHRYSOPHYTA	PRECIP	.312°	−.137	−.189	−.206	−.016
	MAX-T	−.260	−.199	−.240	−.193	−.218
	MID-T	.285	.231	−.275	−.217	−.248
OTHER ALGAE	PRECIP	.000	.113	.236	.251	.331°
	MAX-T	.248	.257	−.199	−.124	−.123
	MID-T	.309°	−.278	−.210	−.116	−.118
TOTAL ALGAE	PRECIP	.129	.060	.169	.212	.332°
	MAX-T	.254	−.234	−.190	−.120	−.130
	MID-T	−.334°	−.266	−.226	−.133	−.147









Figs. 1–4. Mean density and standard deviation of algal groups during collection year: 1, Cyanophyta. 2, Other algae of unknown division. 3, Chlorophyta. 4, Chrysophyta. Note the lows 31 October and 26 August in Chrysophyta although other groups had minima on 24 September and 29 July.

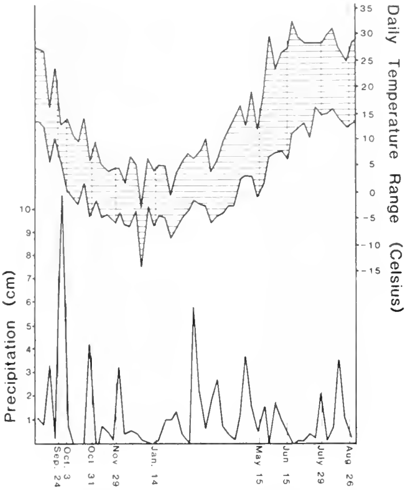


Fig. 5. Precipitation and daily temperature range for the Tintic Mountain site. Vertical lines represent sample times.

(Booth 1946, Castenholz 1969). Chrysophytes demonstrated the smallest correlation values, indicating that they were least affected by high air temperature.

To visualize algal growth throughout the collection period, mean density and standard deviation for each algal group were plotted against time (Figs. 1–4). In general, algal growth of all groups peaked in late fall and again in June. All groups showed a marked decrease in cell density in July and recovery in August. The July decrease was apparently due to high temperatures combined with low precipitation (Fig. 5). Even though a storm occurred immediately prior to the July collecting date, apparently the flora did not have time to respond to the increased moisture. Lynn and Cameron (1973), when studying soil algae of the Curlew Valley, found that algal growth was minimal between mid-July and mid-September. The July and September collections in our study were likewise low in algal density. The recovery in August is perhaps unusual and likely due to the major storms that occurred mid-July to late August (Fig. 5).

Growth curves were remarkably similar for all algal groups (Figs. 1–4). The greatest deviation from the typical pattern was demonstrated by chrysophytes (Fig. 4), which did not show the August recovery. Furthermore, the yearly minimum in Chrysophyta followed a hundred-year storm in late September (Johansen in press). Correlation analyses also demonstrated differences between chrysophytes and the other algal groups (Table 4). It was the only group without any significant negative correlations with temperature, which may indicate that these algae are not as adversely affected by high temperatures.

As a final note, we observed that the degree of hummocking or pinnacling of algal crusts at the study site varied throughout the year. Throughout the fall of 1982 crusts were abundant and well developed. After snowmelt in May 1983 we noted that crusts appeared even more abundant and well developed. At this time, algal hummocks were evident even in jeep roads adjacent to the site. By July crusting in roadways had been destroyed, though crusts elsewhere were still abundant. In late August the crusts at our study site were severely damaged and eroded by powerful rain storms, although algal numbers in the soils remained relatively high. These observations may indicate that the durability and longevity of algal crusts is much less than we had previously thought.

Acknowledgments

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AQUATIC PARAMETERS AND LIFE HISTORY OBSERVATIONS OF THE GREAT BASIN SPADEFOOT TOAD IN UTAH

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Abstract.— The distribution and breeding habitats of the Great Basin spadefoot toad (*Scaphiopus intermontanus*) were investigated in the Bonneville Basin of western Utah. The permanent springs and man-made reservoirs used for breeding were largely found below the 1600 m elevation. The pH's ranged between 7.2 and 10.4 and the total dissolved solids between 170 and 4800 mg/l. The springs were less alkaline than the rain-filled reservoirs. The lack of aquatic vegetation was a common feature of the reservoirs and most of the springs. Observations of breeding without rain are noted as well as the lack of breeding with rain. The snout-vent lengths of adult spadefoots are greater in the Bonneville Basin than in other parts of the Great Basin. Utilization of permanent water sources and stimuli for emergence and breeding, as well as the larger adult size of *S. intermontanus* in the Bonneville Basin, are discussed in relation to the diverse precipitation patterns, the sparseness of the water sources, and the Holocene history of the Great Basin.

Spadefoot toads have been extensively studied in California, Arizona, New Mexico, Texas, and Oklahoma. Very little information is available for the Great Basin spadefoot toad (*Scaphiopus intermontanus*). Tanner (1931) found *S. intermontanus* widely distributed in Utah. Most observations in Utah have been within the Colorado River drainage (Tanner 1931, Hardy 1938, Wood 1935, Wright and Wright 1949). Observations of *S. intermontanus* in the Great Basin ecosystem are less frequent. Tanner (1931) found spadefoots common along the Wasatch Front and reported observations near Gandy and Callao in Utah, near the Nevada border. Synder (1920), Linsdale (1938), and La Rivers (1942) reported the records for Nevada. *Scaphiopus intermontanus* has several unique features that are not found in other spadefoot species: (1) breeding is reported to occur without rainfall for stimulus (Linsdale 1938), (2) a large number of chorusing adults is not essential for breeding (Wood 1935, Blair 1956), and (3) permanent water can be utilized for breeding (Bragg 1961).

This study describes the breeding habitat of *S. intermontanus* in the Bonneville Basin of the Great Basin in western Utah, which is bounded by the ancient shoreline of Lake Bonneville, a lake that desiccated some 11,000 years ago (Currey 1980). Lake Bonneville filled the valleys in western Utah to a height of about 1552 m above sea level, with up to 350 m of water, and covered 5,000,000 hectares. The lake existed at the high level for about 3000 years and filled the valleys at lower levels for 10,000 years. We found that most breeding sites of *S. intermontanus* occurred in areas that were inundated by Lake Bonneville and that many of these sites were associated with permanent springs. This study extends some of the earlier observations that are unique to *S. intermontanus*, describes the breeding habitat, and interprets these observations in terms of the Holocene history of the Bonneville Basin.

Methods and Materials

Chemical analysis was performed by the Uintex Corporation under contract to the Bureau of Land Management and reported in "Water Inventory for Tooele Range Environmental Statement" for the Salt Lake District Bureau of Land Management (March 1981).

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Under this contract conductivity (corrected to 25 C), pH, dissolved oxygen, alkalinity, arsenic, nitrate, phosphate, suspended dissolved solids, total dissolved solids (residues at 185 C), and coliform bacteria analyses were performed. Duplicate field pH measurements included calibration at each site, with standard buffer solutions of pH 4, 7, and 10 at each site. Conductivity was measured by the YSI-33 portable conductivity meter in both the Uintex Corporation contract and in the springs and water sources outside Tooele County. Climatic information was taken from the United States Climatological Records (U.S. Weather Bureau 1979–1981).

Snout-vent (SVL) measurements were made on tadpoles and adults. Tadpoles were caught with a single net sweep. Measurements of SVL of museum specimens were taken from the collections of Utah Museum of Natural History, University of Utah; Museum of Vertebrate Zoology, University of California at Berkeley; and the Monte L. Bean Life Science Museum, Brigham Young University.

Data for the study reported here were largely collected during the years of 1979, 1980, and 1981. The Bureau of Land Management-contracted water inventory in Tooele County occurred in 1980 and consisted of three trips to the water sources between June and September if water was found on the preceding visits. Photographs of the water sources were taken at each visit.

DESCRIPTION OF THE BONNEVILLE BASIN

The Bonneville Basin, contained within the Great Basin of the Intermountain Region, is typical of the basin and range topography common to western Utah and Nevada. The higher mountains vary from 3050 and 3980 m above sea level and, except for the Wasatch Mountains on the eastern margin, generate few perennial streams that reach the basin floor. The basin floors range from 1284 m (historic high level of the Great Salt Lake) to about 1550 m above sea level. Most of the internal mountain ranges do not have permanent streams that reach the valley floors.

Annual average rainfall varies from 12 to 31 cm in the valley floors. In some years the valleys may receive less than 5 cm of rain (Hood and Waddell 1968, 1969, Stephens and Sumsion 1978, Hood, Price, and Waddell 1969, Bolke and Sumsion 1978, Stephens 1977). Evaporation from large bodies of open water is estimated to vary between 107 and 127 cm per year (Hood and Waddell 1968, Hood, Price, and Waddell 1969). During the three study years of 1979, 1980, and 1981, over 50% of the rain from April to October occurred in May, with very little precipitation in June and July (Fig. 1). The Bonneville Basin is characterized as receiving spring rains (Kay 1982).

Air temperatures vary between –24 C and –35 C in January and February to the high values of 39 C and 42 C in summer. Freezing temperatures can be expected from October through April. A large portion of the Bonneville Basin has 120 frost-free days annually. Soil temperatures at Salt Lake City (1290 m above sea level) vary from 0 C to 35 C at a depth of 10 cm and 2 C to 25 C at a depth of 100 cm (U.S. Weather Bureau 1979–1981).

The Bonneville Basin valleys contain four major vegetative types: (1) salt desert, (2) shadscale (*Atriplex confertifolia*), (3) sagebrush (*Artemisia tridentata*)–grass, and (4) pinyon-juniper. Greasewood (*Sarcobatus vermiculatus*) occupies much of the valley floor and areas adjacent to springs and is sometimes considered a wetlands indicator species. Sagebrush-grass occurs in the eastern Bonneville Basin and in Nevada, and is not widely distributed in the Bonneville Basin. Pinyon-juniper lower elevational limits occur between 1600 and 1800 m above sea level (West et al. 1978). *Atriplex* is the most prevalent vegetative type that occupies the desiccated valleys of the Bonneville Basin and is undergoing evolutionary change by chromosome polyploidy and interspecific hybridization (Stutz et al. 1979). The general terrestrial ecology of the Bonneville desert was described by Fautin (1946). Within the Bonneville Basin eight mountain ranges occur that contain boreal associations.

RESULTS

BONNEVILLE BASIN AQUATIC RESOURCES.— In the south central portion of the Bonneville Basin, 169 aquatic sites were investigated (Fig. 2). Most of the sites were observed in

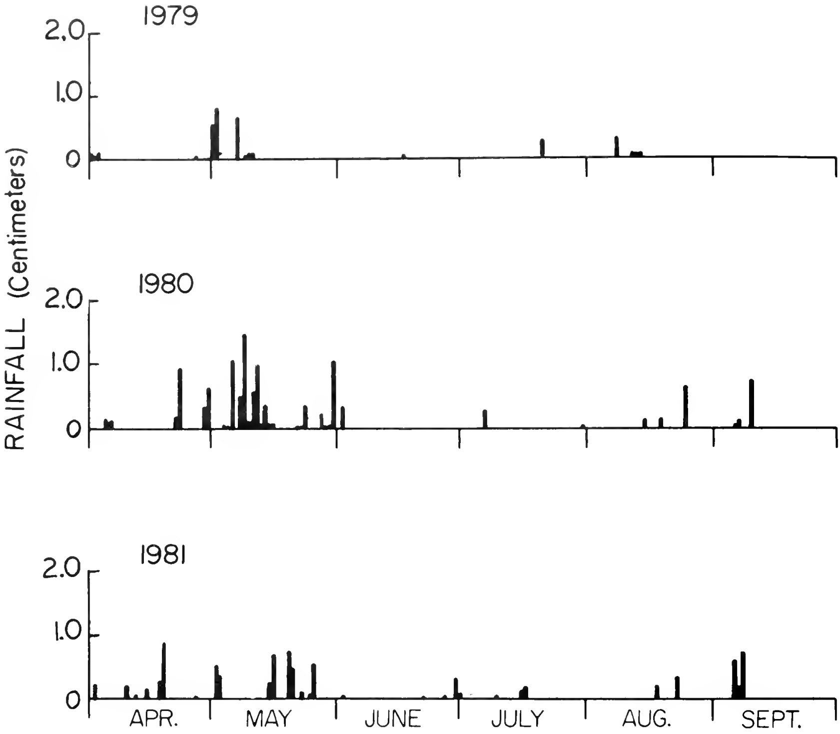

Fig. 1. Precipitation records for Dugway, Utah (40° 11′ North and 112° 56′ West) during the active season of the spadefoot toad (S. *intermontanus*). Data modified from the U.S. Weather Bureau Climatological Records for 1979, 1980, and 1981.

1980, but some sites in Whirlwind and Skull valleys were observed for three years. Of these 169 sites, 51 were used by S. *intermontanus* at least one of the three years. Browns Spring was utilized only one year in five years of observations. The sites varied in size from small seeps (0.08 m^2 by 10 cm deep) to large reservoirs with over 1200 m^3 of water.

The aquatic resources utilized by spadefoots consisted of man-made reservoirs (57%) and springs (43%). The man-made reservoirs formed water sources where none previously existed and can be characterized as having widely fluctuating volumes of water. It is common for a reservoir to be full one year and empty the next year due to the nature of the precipitation patterns. Even when filled during the spring and early summer, water is usually evaporated by autumn. The runoff-filled reservoirs pick up chemicals from the soil and wind-blown particles (including saline dust) over the watershed, or from the bentonite lining of the reservoirs (Stephens and Sumsion 1978).

The springs utilized by the spadefoots were temporary or permanent. The portion of the springs utilized by spadefoots were the associated reservoirs (59%), water troughs (27%), streambeds (5%), and wetlands (42%). The wetlands utilized consisted of the distal end of a natural spring (14%), small seeps (14%), or a spring that was dug out (14%). Often spadefoots bred in the reservoir, water trough, and spring at a given site—thus accounting for more than 100% values. If a series of reservoirs were associated with a spring, the spadefoots bred in the most distal reservoir. Although many of the utilized springs had permanent water, usually the water levels declined by summer to the point a littoral zone could not form. Successful breeding sites were characterized by the absence of aquatic plants in some portion of the aquatic resource.

The elevational distribution of the water sources is shown in Figure 3. Of the total water sources that were utilized by S. *intermontanus*, 74% of the sites were below 1550 m elevation or the height of former Lake Bonneville. Only 27% of the nonutilized sites were below the 1550 m elevation. Less than 14% of the utilized water sources were within the pinyon-juniper region (above 1600 m). The highest elevation spring (2012 m) was utilized by chorusing spadefoots that never bred.

The pH of the water sources utilized by the spadefoots varied from 7.2 to 10.4, with most of the sources having a pH of 8 to 10. Although 84% of the springs contained water with pH of less than 8, the wetlands of these springs often contained water with pH greater than 8. Most of these water sources contained less than 1000 mg/l of total dissolved solids, although Browns Spring contained up to 4800 mg/l.

Under evaporating conditions, phosphate, nitrate, and pH behaved in an unpredictable manner, sometimes increasing and sometimes decreasing in concentration. Alkalinity and total dissolved solids tend to concentrate in a linear manner. No chemical concentrated in direct proportion to the volume—that is, if the volume decreased by a hundredfold, the chemical concentration in many instances did not even increase by tenfold. Often dead tadpoles could be observed in dried-up reservoirs.

ADULT EMERGENCE AND BREEDING.— Although rainfall or the low-frequency sounds of rain falling on the ground are considered stimuli for emergence and breeding for S. *couchi* and possibly for S. *multiplicatus* (Dimmitt and Ruibal 1980b), the stimuli for emergence and breeding of S. *intermontanus* in the Great Basin is unknown. Breeding occurs in April, May, and early June in the Bonneville Basin, where the spring rains can be characterized as generalized and gentle (compared to the localized, torrential rains of late summer). In 1981 five rainfalls were observed from the middle of April (which stimulated the breeding) to the end of May (Fig. 1). At White Rocks seep in Skull Valley, the breeding occurred in the middle of April and

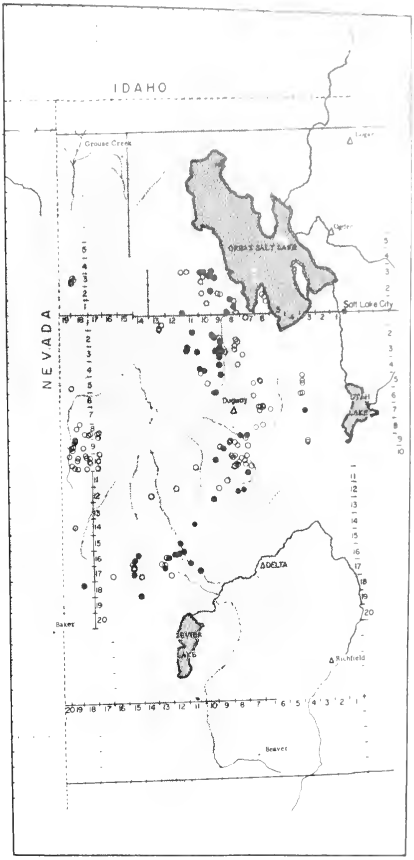

Fig. 2. Breeding sites of the spadefoot toad (S. *intermontanus*) in the Bonneville Basin of the Great Basin. The light shaded area is the extent of former Lake Bonneville according to Synder, et al. (1964). Vertical series of numbers refer to the township number, and the horizontal series of numbers refer to the range. The diameter of each circle represents approximately 5 km. Open circles: water sources not utilized by spadefoots. Closed circles: water sources utilized by breeding spadefoots.

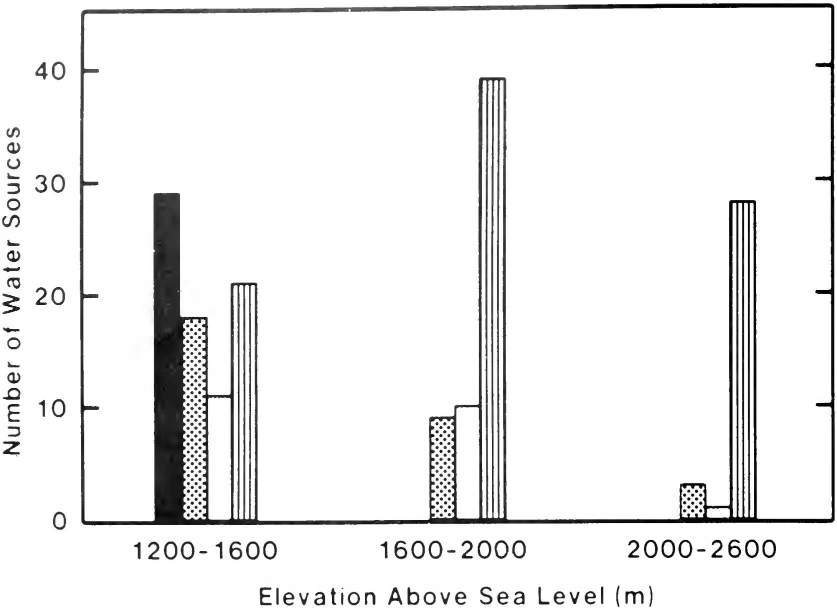

Fig. 3. Distribution of water sources with respect to elevation above sea level. Solid pattern: ephemeral stream-filled reservoirs that were utilized by S. intermontanus. Stippled pattern: ephemeral stream filled reservoirs not utilized by spadefoots. Open pattern: springs utilized by breeding spadefoots. Vertical line pattern: springs not utilized by spadefoots.

again at the end of May after a flash flood scoured the seep. In Tule Valley spadefoots bred in South Tule Spring in April and at the end of May in nearby Painter Spring. It would seem that, if the mid-April rain stimulated the spadefoots to breed, then they would be stimulated to breed four additional times before the end of May.

Conversely, at the end of May one spring contained at least two chorusing spadefoots. No rain had fallen for the previous several days, and the chorusing activity occurred for at least three consecutive evenings without any additional rainfall. Although the general initial breeding seems to be stimulated by rainfall at most sites, exceptions are noted.

TADPOLE OBSERVATIONS.— Tadpole growth rates at six different springs are shown in Figure 4. The initial growth rates varied from 0.53 to 0.66 mm SVL per day at the six springs. If there was abundant water in June, the tadpole growth rate slowed down (see White Rock Spring in Fig. 4). Most metamorphosis occurred by early July. The sizes of the toadlets at metamorphosis varied from 16 to 38 mm SVL.

Tadpoles were found in four springs during August and September. Slower initial growth rates at Henry Spring water trough (Fig. 4) may be responsible for the occurrence of tadpoles in August. Chemical analysis of the springs in Figure 4 varied, with total dissolved solids from 200 mg/l at White Rocks to 2070 mg/l at Eight Mile Spring. Henry Spring was similar to Eight Mile Spring. The population that was observed at Browns Spring in September was probably frozen before metamorphosis could take place. At the time of metamorphosis in August at Henry Spring, numerous dead toadlets were observed near the water.

ADULT SIZE.— At Painter Spring water trough in Tule Valley adult spadefoots were actually observed breeding in 1981. The

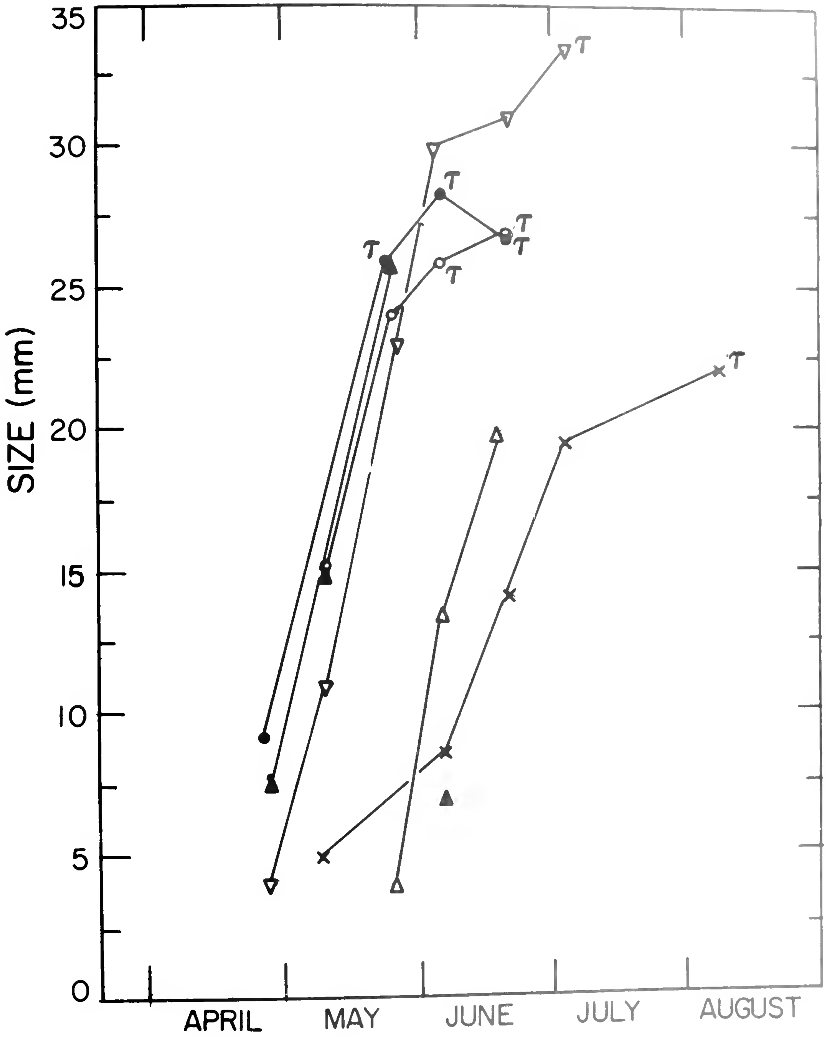

Fig. 4. Tadpole (S. *intermontanus*) growth rates in different springs. The tadpole length (snout-vent length) was measured. ▲, White Rocks seep; x, Henry Spring; ▽, White Rocks Spring; ○, Eight Mile Spring; [illegible], Painter Spring; and ●, South Tule Spring. Metamorphosing tadpoles (with four legs and tail) or toadlets present are indicated by Tau. The tadpoles were caught with a single sweep of the net, measured, and the average size shown in the figure.

average size (SVL) of the nine individuals was 67 mm ± 6.7 (range, 57 to 77 mm). Because of the large size of these spadefoots compared to values in the literature, the collections representing 10 locations in the Bonneville Basin as well as all the other S. *intermontanus* in the Great Basin were measured. Statistical data are shown in Table 1. The specimens from the Bonneville Basin were larger (58 ± 5.3 mm) compared to those specimens from the Colorado River Basin of Utah (52 ± 4.8 mm), Idaho (49 ± 3.9 mm), Nevada (49 ± 4.1 mm), or Washington, Wyoming, Oregon, and Arizona. Both the Bonneville Basin (z = +6.7) and the Humboldt River Basin in Nevada (z = –4.9) have populations of spadefoots whose mean size exceeds the 99% confidence intervals of the total population, indicating that the size difference is real.

Discussion

Scaphiopus intermontanus utilizes every type of water source for breeding in the Bonneville Basin as long as the total dissolved solids are less than 5000 mg/l. Breeding can occur in permanent reservoirs that contain an abundance of vegetative growth, but under these conditions tadpoles may not survive to metamorphosis. The highly successful breedings took place in water sources that either desiccated during the summer or had a large draw-down of water (in which case a littoral zone of vegetative growth was lacking), or breeding occurred in stream beds scoured by flash floods. Only 8% of the water sources were entirely natural. Humans, through range improvements, have created new habitat in the Bonneville Basin for the spadefoots and this new habitat greatly reflects typical breeding habitat of the genus *Scaphiopus.* Some of these new water sources are over 15 km from any existing water sources and, to utilize these sources for breeding, the spadefoots must disperse overland. Although human-made reservoirs are widely utilized, during the 1979 limited rainfall (Fig. 1), permanent springs were utilized in Whirlwind Valley because the reservoirs were without water. Subsequent years (1980, 1981) the reservoirs were utilized and the springs were vacated. The lack of large water sources and the spareness of the water sources in general would not be conducive to large numbers of breeding adults.

The stimulus by which spadefoots emerge and breed has been the low-frequency sounds of rain falling on the ground and not moisture per se (Dimmitt and Ruibal 1980b). Linsdale (1938) was the first to note that spadefoots may breed without the stimulus of rainfall and suggested such several other stimuli as flash flooding and other chorusing spadefoots. Observations in the Bonneville Basin confirm that not all breeding occurs

Table 1. Variations in snout-vent length (SVL) of adult spadefoot toads (*Scaphiopus intermontanus*) in the Great Basin. Z is the measure of confidence interval and equals the deviation from the mean divided by the standard deviation of the subpopulation mean. If Z is between –2.58 and +2.58, then there is a 99% confidence that the normal distribution of the total population contains the subpopulation mean.

Area	Number	Mean size (SVL-mm)	Standard Deviation)	Z
Total	254	51	5.1	
Utah	114	53	5.4	4.1
Bonneville Basin	28	58	5.3	6.6
Colorado River Drainage	77	52	4.8	2.1
Arizona (Coconino County)	8	54	3.2	1.1
Idaho	26	49	3.9	–2.1
Nevada	87	49	4.1	–4.5
Humboldt Drainage	55	48	6.7	–4.9
Western	11	52	5.6	0.7
Southern	21	49	4.7	–1.9
Oregon	12	50	3.3	–0.7
Washington	5	48	3.7	–1.3
Wyoming (+ Daggett County, Utah)	5	52	4.7	0.4

with rainfall, although rainfall may be the main stimulus. Conversely, if rainfall is the main stimulus, not all comparable rainfalls stimulate breeding. Both of these observations may be explained by the postbreeding dispersion of the spadefoots and the scarcity of water sources for breeding. If, for instance, the spadefoot is 5 km from a water source when it hibernates, the first rainfall may cause emergence. The travel time for the spadefoot to reach a water source may be from several days to a month, if a water source is to be reached during the breeding season. Consequently, a delayed response between rainfall and breeding may occur.

Until the historic development of water sources for range management, the water sources in many valleys (west of the Cedar Mountains, Whirlwind Valley, and Puddle Valley) were nonexistent. Furthermore, the rainfall patterns in the Great Basin are diverse, with precipitation peaks in winter (California), spring (central Nevada, Idaho, and Bonneville Basin), and summer (Colorado Plateau) (Kay 1982). These conditions have probably existed in the Great Basin for 4500 years, since the establishment of the present ecosystem (Wells 1983). If spadefoots were to adapt to the cold desert ecosystem in the Great Basin, they would have to have adapted to sparse aquatic breeding habitat, to utilization of flowing spring snowmelt streams, and to spring breeding (tadpoles would not metamorphose in time for July and August breeding).

Upon desiccation of Lake Bonneville, new terrestrial habitat was formed. *Atriplex* evolved with many new polyploid forms and with hybridization (Stutz et al. 1979) and was fully adaptive to this new basin environment. Pinyon-juniper (*Pinus monophylla* and *Juniperus osteosperma* invaded the region from the southern refugium (Wells 1983), and the monotypic subalpine bristlecone pine (*Pinus longaeva*) forest disappeared from the 1660-m elevation level about 10,000 years ago. During the pluvial era, the subalpine forest and the sagebrush approached the lake level (Wells 1983, Currey and James 1982).

During the pluvial era, S. *intermontanus* was isolated on some island ranges or in sand dune regions lake the Escalante Desert in southern Bonneville Basin. Sand dunes were habitat for the relict diploid *Atriplex canescens* (Stutz et al. 1975) and could have furnished the necessary aquatic habitat for spadefoots adjacent to Lake Bonneville. A second possibility is that the spadefoots were in the Mohave refugium along with the pinyon-juniper and migrated north in postpluvial times.

The significance of the larger snout-vent length of the Bonneville Basin spadefoot population could be (1) genetic isolation of small populations during the 3000-year Lake Bonneville period; (2) adaptations for longer periods of hibernation (Jones 1980, Dimmitt and Ruibal 1980a), which would be required during the more xeric conditions that existed in the Bonneville Basin (Currey and James 1982); (3) more food energy going to increase size instead of reproductive potential because spadefoots may not breed every year, apparently because of water scarcity; or (4) reduced adult predation in the Bonneville Basin, which creates older populations.

Scaphiopus intermontanus is not expected to acquire new responses to environmental conditions in the Great Basin in general and the Bonneville Basin in particular in view of the numerous restraints placed on the habitat with respect to precipitation, water sources, and biogeographical changes during the Holocene era. Although S. *intermontanus* gives the appearance of becoming more amphibianlike in its behavior (not responding to precipitation and breeding in permanent water), it certainly has adapted to humanly developed typical *Scaphiopus* habitat in the Bonneville Basin. No other amphibian was found in the 151 water sources inventoried with the exception of the Western Spotted Frog (*Rana pretiosa*), which utilized the permanent portion of the Tule Valley springs.

ACKNOWLEDGMENTS

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NEW SPECIES OF ASTRAGALUS (LEGUMINOSAE) FROM MESA COUNTY, COLORADO

Stanley L. Welsh[1]

Abstract.— Named and described is *Astragalus debequaeus* Welsh from Mesa County, Colorado.

Botanical investigations in central western Colorado during May 1984 yielded several unique taxa, especially endemics from that portion of the Colorado Plateau. The endemic plant taxa are associated with the peculiar habitats available on the raw geological substrates in the region. The Mancos Shale Formation and other fine-textured strata support a phalanx of specially adapted taxa. Thus, it is to be expected that other formations with peculiar physical and chemical properties should support additional rare plants that have been overlooked.

Growing on a varicolored, fine-textured, seleniferous and apparently saline portion (Atwell Gulch Member) of the Wasatch Formation in the De Beque vicinity is an *Astragalus* that is beyond the descriptions of known species in that region (Fig. 1). The plants have white flowers, grow in small to large clumps, and have thinly cartillaginous, inflated pods. Clearly these plants are allied to those taxa in *Astragalus* section Preussiani. The plants key to the couplet dealing with *A. eastwoodae* and *A. preussii* in that section (Barneby 1964). The pods are similar in texture to those of *A. eastwoodae*, but are erect-ascending initially as in *preussii*, although they are ultimately spreading or even descending in pressed material. The white flowers are shared by neither. The pods are proportionately narrower than in those of the allied taxa. The surface of the pods is minutely scabrid-pubescent, becoming almost or quite glabrous in age. This feature occurs sometimes in the allied taxa. Flower number is mostly 7–9 (11) per raceme in the material from De Beque, not 3–7 as in *A. eastwoodae*. In *A. preussii* the flower number varies from few to many. The calyx is conspicuously shorter in the De Beque material than in *A. eastwoodii* (6.3–8 not 10–12.2 mm long).

The De Beque milkvetch lacks the strong scent of selenium characteristic for many species of the section. However, the plant might still be a selenophyte. It grows with the strongly odoriferous selenium indicator, *A. flavus* Nutt., a common inhabitant of the Wasatch Formation in the vicinity.

Astragalus debequaeus **Welsh** sp. nov. Affinis *Astragalo* sectio Preussiano praesertim *A. eastwoodae* in leguminibus et habitu generali sed in floribus plus numerosis et albis calycibus brevioribus legumine ambito et dispositio et caulibus plus numerosis differt.

Plants perennial from a branching caudex, clump-forming, mainly 2–10 dm across, arising from a woody taproot; stems 14–30 cm long, decumbent and curved-ascending; stipules 3–6 mm long, ovate to triangular, free; leaves 2–10 cm long, the leaflets 13–21, elliptic to oblanceolate, obtuse to rounded, glabrous, flat or somewhat folded, the terminal one not confluent with the rachis; peduncles 4.5–8.8 cm long, ascending; racemes 3–5.5 cm long, little elongating in fruit; flowers spreading to ascending in anthesis, 17–21 mm long; bracts 2–2.5 mm long, ovate-acuminate; pedicels 1–3 mm long; bracteoles 1 or 2, reduced or lacking; calyx 2.3–8 mm long, the tube 5–6 mm long, short-cylindric, stramineus to greenish, sparsely black strigose, the teeth 1.3–2 mm long; flowers 17–21 mm long, white, spreading to ascending at anthesis, the banner not strongly arched, but folded along the margins below the apex of the blade; pods ascending, stipitate, the stipe 2–2.5 mm long, the inflated body oblong- to

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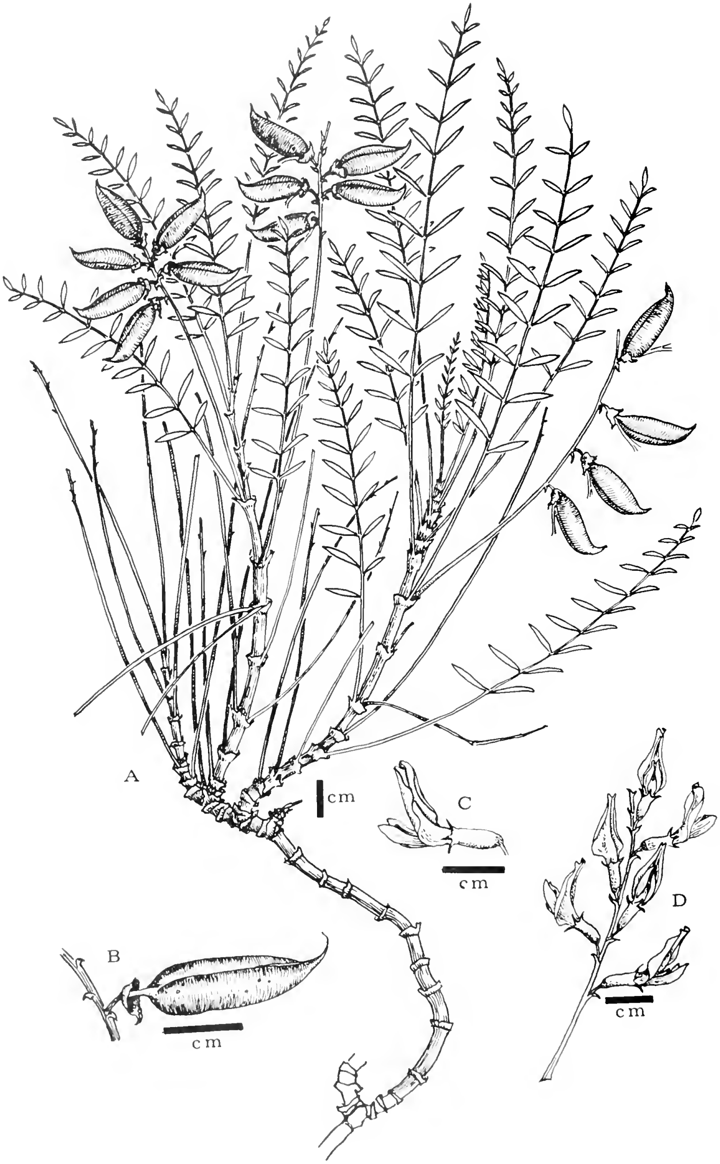

Fig. 1. *Astragalus debequaeus* Welsh: A, Habit of fruiting plant. B, Detail of fruit. C, Flower detail. D Inflorescence.

lance-ellipsoid, 15–23 mm long, 6–11 mm thick, the valves thinly leathery and straw colored, unilocular, scabrid-pubescent, becoming glabrous; ovules 18–24.

TYPE.— USA Colorado. Mesa Co.: Wasatch Formation, T9S, R97W, S26 (SE/SE), ca 12 km S of De Beque, pinyon-juniper and mixed desert shrub, at 1647 m elevation, 16 May 1984, S. Welsh, B. Welsh, & R. Kass 22792 (Holotype: BRY; Isotypes: POM, CAS, UT, UTC, NY, US, MO, COLO, RM, ISC, CS).

ADDITIONAL SPECIMENS.— Colorado. Mesa Co., same provenience and date, S. Welsh, B. Welsh, & R. Kass 22793 and 22802 (BRY). Mesa County., T9S, R97W, [illegible] 5.7 mi S of I-70, 3.2 mi S of pavement end on De Beque Cutoff Road, Atwell Gulch Member of Wasatch Formation, 12 June 1984, J. Anderson 84-15 (BRY).

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A FOURTH SPECIES OF OREOXIS (UMBELLIFERAE)

Stanley L. Welsh[1] and Sherel Goodrich[2]

Abstract.— Described as a new species is *Oreoxis trotteri* Welsh & Goodrich from Utah.

The genus *Oreoxis* is regarded in contemporary treatments (Mathias and Constance 1944, Harrington 1954) as consisting of three species, *O. alpina* (Gray) Coult. & Rose, *O. humilis* Raf., and *O. bakeri* Coult. & Rose. The three species are reported by Harrington (1954) and occurring at elevations of 2898 to 3965 m in Colorado. Goodrich (1984) notes that *O. alpina* grows at 2440 to 3475 m and *O. bakeri* at ca 3660 m in Utah. Thus, we did not expect to find an *Oreoxis* at ca 1464 m on sandstone in the Courthouse Pasture vicinity northwest of Moab in Grand County, Utah. The elevation at the site where the plants grow is almost 1000 m below the lowest reported occurrence of the genus in Utah.

Special attention was given to the plant because of its vertical displacement from other known taxa of the genus. A detailed description was prepared from the collection taken upon discovery. That description was then compared to those of other species in the genus, but especially to *O. alpinus*, with which it is evidently allied. The Courthouse Pasture plants differed in the copious, persistent leaf bases and peduncles, more glandular herbage, fewer leaflet segments, and broader leaflets (Fig. 1). The magnitude of the differences dictates that the plants be recognized at specific rank, as follows:

Oreoxis trotteri Welsh & Goodrich sp. nov. Similis *Oreoxis alpino* sed in foliis basis et pedunculis persistentibus plantis plus glandulosis foliolis segmentis paucioribus et foliis segmentis ultimo latioribus differt.

Plants pulvinate-caespitose, forming clumps to 30 cm wide, 4–8 cm tall, scabrous and more or less glandular, from a branching caudex, this clothed with a thatch of persistent terete leaf bases and peduncles; leaves all basal, bipinnate, with ca 4 opposite pairs of sessile, lateral, primary leaflets, the upper pairs and those of the smaller leaves sometimes once-pinnate and then trifid or pinnatifid; petioles 1–3.5 cm long; blades 1.5–2.3 cm long, oblong in outline, the lowest pair of primary leaflets 3.5–5 mm long, the ultimate segments 1–3.5 mm long, 1–3 mm wide, elliptic to cuneate-ovate; peduncles 4–7.5 cm long; umbel solitary; involucre lacking; rays 5–7, 3–5 mm long, involucels of 4–7 linear-subulate bractlets 2–3.5 mm long, distinct or essentially so; pedicels obsolete or to ca 1 mm long; calyx teeth ca 1 mm long, green or purplish; petals and stamens yellow; styles 1–1.2 mm long; fruit 2.8–4.8 (5) mm long, the ribs with low, corky wings to 0.7 mm wide.

Type.—USA. Utah, Grand County, T24S, R20E, S21, ca 1 km SSE of historic stage station and 20 km NW of Moab, in mixed juniper and desert shrub community, on Navajo Sandstone, at ca 1464 m, 30 April 1984, S. L. Welsh and D. Trotter 22729 (Holotype BRY; 10 isotypes to be distributed). Additional specimens: Utah, Grand County, same locality as above, 30 May 1984, D. Trotter s.n. (BRY, fruit only).

The plants grow in crevices on the joints in Navajo Sandstone, sheltered by pillowlike outcrops in the sandstone. The crevices are more mesic than the surrounding sandstone, which acts like a funnel in concentrating water that flows from its surface into the crevices. The rounded outcrops tend to shade the

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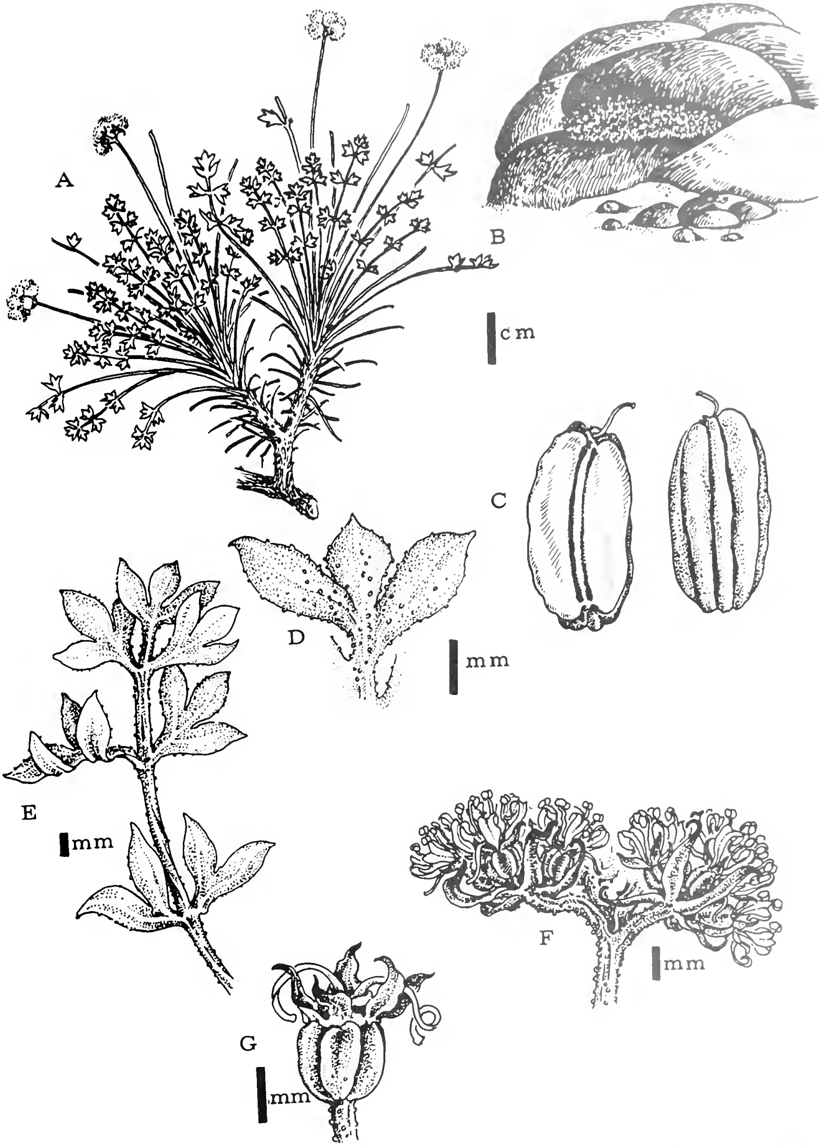

Fig. 1. *Oreoxis trotteri* Welsh & Goodrich. A, Habit. B, Habitat. C, Fruit. D, Foliar detail and glandularity. E, Leaf. F, Inflorescence detail. G, Floral detail.

plants for a portion of the day, decreasing further the stress from drought.

The species is named for Daryl Trotter, of the Bureau of Land Management in Moab, Utah, whose knowledge of the area and willingness to help others with its exploration are hereby acknowledged.

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INSECT COMMUNITIES AND FAUNAS OF A ROCKY MOUNTAIN SUBALPINE SERE

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Abstract.— Insect faunas and communities are characterized for herbaceous and tree canopy layers in meadow, aspen, and spruce/fir stages of a northern Utah sere. A greater percentage of species were in Thysanoptera in both aspen strata, and a greater percentage of individuals were in Lepidoptera in aspen canopy. Our sites were quite similar to a wide variety of other terrestrial sites in their distribution of species or individuals among orders or metamorphosis categories. Insects/m^2 peaked in the aspen stage, but declined in the herbaceous layer with succession. Insects/plant biomass in the herbaceous layer increased with succession. Insects/m^2 and insects/foliar biomass were higher in aspen canopies than in conifer canopies. Insect species/m^2 peaked in the aspen stage. This statistic was comparable in meadow and aspen understory, and lower in conifer understory. Insects/m^2 in the tree canopies were similar to the values in their respective understories. Insect species/plant biomass increased in the herbaceous layer with succession, but decreased in tree canopies with succession. Species evenness in both strata increased with succession. Adult body length was greatest for meadow species, least for conifer species. Adult body length per individual was greatest in aspen. Life cycle complexity was greatest in aspen. Insects on trees were more likely to have complex life cycles than those on herbs.

Studies of insects have been infrequent in the literature of ecological succession (Price 1975). Some have followed through time the insects associated with a discrete nonautotrophic resource (e.g., Park 1931, Savely 1939, Mohr 1943, Coombs and Woodroffe 1963, Payne 1965). Others have considered the insects of vegetation only in certain strata (e.g., Smith 1928, Martin 1966, Schowalter et al. 1981) or temporal subunits (e.g., Murdoch et al. 1972, Hurd and Wolf 1974, Butt et al. 1980, Purvis and Curry 1980, Force 1981, Hawkins and Cross 1982) of the full sere. Some have been restricted to certain insect orders (e.g., Strohecker 1937, Southwood et al. 1979, Boomsma and Van Loon 1982). Studies more inclusive in space, successional time, and taxonomic coverage (e.g., Shelford 1913) have seldom been very quantitative.

Germane to this topic are some studies not ostensibly concerned with succession. These include monitorings of arthropods colonizing vegetation that had been defaunated (Simberloff and Wilson 1969) and the studies of insect communities associated with various kinds of vegetation (e.g., Whittaker 1952, Janzen 1973, Werner 1983).

We report on a study of the insect communities associated with the above-ground portions of three stages of a subalpine forest sere. This work was performed as part of a test of certain of the hypotheses about successional trends in ecosystem properties proposed by Odum (1969). In particular, we address Odum's hypotheses about species variety (richness), species evenness, stratification and spatial heterogeneity, body size, life cycle complexity, and stability. All of these attributes should, if Odum is correct, increase during succession. Our results for vertebrates have been published (Andersen et al. 1980, Smith and MacMahon 1981) for some of these, as well as other hypotheses. We also present findings on other characteristics of these insect assemblages, including their resemblance to those reported for various geographic areas or vegetation categories.

Study Area

Sampling of insects took place on the Utah State University School Forest in the Wasatch Mountains of extreme northern Utah. In the subalpine zone a succession from herbaceous summer–dry meadow through aspen (*Populus tremuloides*) grove to coniferous forest (*Picea engelmannii* and *Abies lasiocarpa*) is common. Forested stages have understories dominated by herbaceous angiosperms, with minimal shrub cover. The nature of this site and sequence is depicted and

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detailed in Schimpf et al. (1980), but the temporal relations of these stages should be discussed here. All three stages are thought to be persistent; the meadows are shrinking from slow centripetal vegetative colonization by aspen, which is followed by conifer establishment. The aspen invasion is thought to be allogenic, permitted by climatic warming since the "Little Ice Age" ended 200 to 300 years ago. Aspen establishment autogenically permits conifer invasion through modification of the environment near the soil surface. Thus the sere may be atypical in the relatively equal ages and long-standing spatial proximity of the three stages. A typical pioneer stage, that is, a short-lived community following disturbance, is absent.

Some sampling took place in 1976, but most of our results are based on samples taken in 1977 and, except for the tree canopies, 1978. The 1977 sampling followed a winter with very low snowfall, whereas the other two years were more typical in this regard (Schimpf et al. 1980).

Methods

Field Sampling—Herbaceous Layer

Sampling of the herbaceous layer of vegetation began 1 June and continued weekly through 20 September 1977. In 1978 weekly sampling began 27 June, ending 15 September. Some late season samples yielded no insects and are not presented in our results. Samples were obtained using a D-Vac suction sampler (Southwood 1978a). The reliability of this method has been documented (Törmälä 1982). Within each seral stage, a net-lined aluminum frame cage was rapidly set over the vegetation. This was done at 20-pace intervals along a randomly chosen compass direction in the meadow and conifer stages. In the spatially more restricted aspen stage, the cage was placed at randomly chosen coordinates. The cage used for the aspen and conifer understories entrapped the insects above 0.25 m^2 of ground. The cage used in the meadows covered 0.50 m^2, the larger size being practical in the absence of coarse woody litter. From 5 to 15 such samples were taken weekly in each stand of a stage; care was used to avoid sampling the same spot more than once. Two stands were sampled in the meadow and conifer stages in 1977 and the meadow and aspen stages in 1978. Three aspen stands were sampled in 1977 and a single conifer stand in 1978.

The vegetation surfaces and net interior were completely vacuumed with a narrow hose D-Vac device through a zippered access in the net. The operator continually manipulated the vegetation during the vacuuming process, which lasted from 1 to 5 min. The insects were drawn into a nylon-organdy collection net and chloroformed within 30 min. Samples were refrigerated until they could be sorted and counted.

Field Sampling—Tree Canopy

Aspen branches of randomly chosen trees were sampled during the same weeks in the same stands in which understory sampling occurred. Muslin bags 79 by 86 cm were thrust over most of the leafy portions of branches while the bag mouth was kept open on a wire hoop on a 3.5 m handle. Immediately after placement, egress was prevented from the terminal 45 cm of the bag by closing its mouth with drawstrings. The branch was clipped next to the bag mouth with an extendible pruning shear. Ladders were used to gain access to branches up to 7 m above ground.

Conifer canopy samples were taken every third week from 7 June to 12 August 1977. Samples were taken in two fir-dominated plots, two spruce-dominated plots, and two plots where spruce and fir co-dominated. In each plot six trees more than 15 cm diameter at breast height were randomly selected for sampling. Each tree was divided into vertical thirds, and one sample was taken from each third every time that individual was sampled. Samples came from a randomly chosen compass sector of the canopy. If no branches occurred within a particular vertical third of the tree, no other trees were substituted.

Sampling sites were reached by use of mountain-climbing equipment and techniques. This included belaying the sampler in a sling and strap to give sufficient mobility. Branches sampled were always located above the sampler's position to reduce mechanical disturbance of the branch and its insects.

Branches were enclosed in muslin bags 1.6 m deep fastened by velcro strips to a 25 x 100 cm wire frame with a 1 m long handle. After drawing the bag over the end of the branch, the bag was quickly closed about 30 cm from the mouth with a drawstring. The branch was sawn off, and the bag removed from the frame and dropped to the ground. The sample bag was put into a heavy plastic bag for 30 min with cotton balls soaked in CCl_4. The sample bag was opened and the branch was vigorously shaken within it before it was removed and cut up for drying. After drying, the cut branch parts were inspected for insects, which were added to those originally collected. Subcortical insects were not sampled.

Laboratory Procedures

Arthropods were sorted from samples under magnification. In contrast to some recent taxonomies (e.g., Daly et al. 1978), we include Collembola within Insecta. Most insects were identified at least to family, then assigned to a binomial species or numbered morphospecies within the family. Some could not be so identified with confidence (e.g., Microlepidoptera). Well-preserved representative adults were incorporated into a synoptic reference collection. Many voucher specimens were verified by the following taxonomists: D. C. Lightfoot (Orthoptera), J. D. Lattin (Hemiptera), P. W. Oman (Homoptera), W. J. Hansen (Diptera), G. E. Bohart, and G. R. Ferguson (Hymenoptera).

The number of individuals in each species was recorded for each sample. Orders were assigned to a metamorphosis type: ametabolous, hemimetabolous, paurometabolous, or holometabolous. Adult body length was estimated for each species by measuring head-anal length of the largest reference specimen to the nearest mm with a rule.

Treatment of Data

Dry mass of leaves was determined for each sample from the tree canopies. Data from individual samples were aggregated by computer to generate data for least-squares linear regressions of insect species number vs. leaf biomass and number of insect individuals vs. leaf biomass for each week. Estimates of leaf biomass/m² (Williams 1977) were entered into the regression models to obtain interpolated estimates of mean number of species/m² and mean number of individuals, in in aspen or conifer canopies during each week.

D-Vac sample data were combined by computer to derive numbers representing 1.0 m² of ground sampled (sample pairs in meadows, quartets in forest understories). Not all possible combinations were created, with the number of pairs or quartets equaling the number of samples. These aggregated data were used to estimate mean number of species/m² and the J′ index of evenness (Pielou 1975). Number of individuals/m² was estimated by doubling or quadrupling the number in a single sample. It is possible that the use of the larger cage in the meadow biased the results by capturing insects more efficiently. This could bias the estimates of abundance or species richness. Species richness estimates could also be biased if the species-area relationship does not have a slope equal to 1.0 over the 0.25 m² to 0.50 m² range. To test for these biases, a set of samples was taken in the same meadows with the smaller cage as well as the normal set with the larger cage on 18 July 1978, a day when insect abundance was reasonably high. The estimates of individuals/m² and species/m² obtained from large samples were statistically compared to those from small samples by means of a t-test.

Total number of species/m² in the aspen and conifer stages was estimated by summing the estimates from the understory and the canopy. We justify this on the basis of observed, but unquantified, limited faunal overlap between the two strata in each forested stage. Because species/m² values in tree canopies do not represent integral numbers of canopy samples, combining of canopy and understory samples for the direct counting of species was not possible.

Spatial homogeneity of the insect community of the herbaceous layer was assessed by the resemblance among samples taken in the same stage on the same day. Absolute percent similarity (Goodall 1973) was computed for each possible pair of samples on the basis of number of individuals in each species. The effect of cage size was first tested by comparing similarity among large vs. small cage samples taken on 18 July 1978 with a t-test after transforming the similarity coefficients to arcsin values.

The seasonal course of the means of the following statistics was plotted as second order least-squares regressions vs. time: number of individuals/m^2, number of species/m^2, J′ evenness, and absolute percent similarity.

Because samples from the canopy were from foliage equivalent to varying amounts of ground surface, analysis of their species evenness by J′ was problematical. Instead, relative evenness was inferred from dominance-diversity plots (see, e.g., Murdoch et al. 1972) for all canopy insects captured during 1977. For similar reasons, it was not appropriate to calculate a composite measure of diversity, i.e., one including both richness and evenness components, for the canopies. This prevented us from calculating a composite diversity measure for the combined strata of our forested stages. To be consistent with our other analyses, we did not compare composite diversities in the herbaceous stratum alone. Even if we could calculate composite diversity measures, they might not provide any more useful information than the measures we present. We agree with Dritschilo and Erwin (1982) that the use of diversity indices is often redundant or misleading, as they found for carabid beetle communities.

A summary of all samples taken in each stage and stratum was used to judge resemblance between the study site and other locations for which insect summaries have been published. Relative percent similarity (Goodall 1973) was calculated between each of our five stages/strata and these other areas. Thiswas calculated on four different bases: faunal ordinal similarity (proportion of all species in each order), community ordinal similarity (proportion of all individuals in each order), faunal metamorphosis similarity (proportion of all species in each metamorphosis category), and community metamorphosis similarity (proportion of all individuals in each metamorphosis category).

RESULTS AND DISCUSSION

Approximately 80,000 insects were obtained by the sampling procedures and used for most of the analyses which follow. This total is composed of about 18,000 from the herbaceous layer in 1977, 13,500 from the canopy in 1977, and 48,500 from the herbaceous layer in 1978. As will be seen below, the greater number in 1978 reflected greater insect abundance, not an increase in sampling effort.

Taxonomic Composition

The distribution of the catch among orders is listed in Table 1, which is based on some

TABLE 1. Ordinal composition of insects caught in each stratum/successional stage from 1976 through 1978. Figures are the percentages contributed by each order to the total number of families, species, or individuals.

	Families						
	Meadow	Aspen understory	Aspen canopy	Conifer understory	Conifer canopy	Meadow	Aspen understory
Coleoptera	15.8	12.2	13.5	7.5	16.0	10.9	3.2
Collembola	2.6	3.1	5.4	3.8	1.2	1.2	1.5
Diptera	27.6	34.7	28.4	40.0	28.4	21.5	26.1
Hemiptera	11.2	4.1	5.4	6.2	6.2	10.1	2.9
Homoptera	8.6	10.2	13.5	8.8	9.9	11.1	7.6
Hymenoptera	23.0	29.6	24.3	23.8	27.2	38.5	42.2
Lepidoptera	5.3	1.0	4.0	2.5	2.5	2.9	0.2
Neuroptera	2.6	1.0	0.0	2.5	4.9	0.8	0.2
Odonata	0.0	0.0	1.4	0.0	0.0	0.0	0.0
Orthoptera	1.3	1.0	1.4	0.0	0.0	0.7	0.5
Psocoptera	0.0	0.0	0.0	1.2	1.2	0.0	0.0
Thysanoptera	2.0	3.0	2.7	3.8	1.2	2.2	15.6
Trichoptera	0.0	0.0	0.0	0.0	1.2	0.0	0.0
TOTAL NUMBER	152	98	74	80	81	585	410

11,000 insects caught in 1976 or 1978 by the same procedures in addition to the 80,000 just mentioned. Inspection shows a lack of any obvious successional trends in faunal composition when orders are weighted by their number of families. At this higher taxonomic level, the various stages and their strata exhibited broad resemblance to one another. The three orders with the greatest numbers of families were always Diptera, Hymenoptera, then Coleoptera. This sequence differed from those in aspen or white spruce (*Picea glauca*) stands in Alaska (Werner 1983). Neither our study nor Werner's sampled subcortical insects, so Coleoptera may be underrepresented.

If orders are weighted by their number of species, a conspicuous rising and falling of Thysanoptera was observed during succession. Hymenoptera always exceeded Diptera, except in the conifer understory, where they were nearly equal. Diptera composed a greater proportion in the understory than in the canopy for both forested stages.

Weighting of orders by number of individuals reveals the great predominance in aspen canopy of Lepidoptera, a group with relatively low abundance elsewhere in the sere. These are mostly leaf-mining Gracilariidae, principally *Phyllocnistis populiella* Chambers. Diptera were a reduced proportion of the aspen canopy community. Again, Diptera exhibited greater representation in forest understories than in the corresponding canopies.

Faunal ordinal similarity of our five insect assemblages, i.e., those of different strata/successional stages, to those from other areas is high in most cases (Table 2). Aspen understory and canopy have the lowest mean similarity values; in most cases this is probably due to the high proportion of Thysanoptera species in these two faunas (Table 1). The mean similarity for all comparisons with other sites (72%) is surprisingly close to the mean similarity among our five stages/strata (80%). Even the similarity of faunas as disparate to a subalpine sere as those of tropical areas, often 70% or more (Table 2), suggests that local relative species richness of insect orders may be little influenced by habitat conditions. At this level of analysis, terrestrial insect assemblages show minimal variation, perhaps due to inherent differences among orders in speciation or extinction rates (Fowler and MacMahon 1982).

Faunal metamorphosis similarity (Table 3) is even higher than ordinal similarity (Table 2), the former having an overall mean of 91% and a mean of 96% among our stages/strata. Variation among sites in species richness of a particular order tends to be compensated for by other orders with the same metamorphosis type. All faunas are dominated by two of the four metamorphosis types, paurometabolous and holometabolous.

Table 1 continued.

Species			Individuals				
Aspen canopy	Conifer understory	Conifer canopy	Meadow	Aspen understory	Aspen canopy	Conifer understory	Conifer canopy
4.6	3.6	14.7	1.3	0.3	0.1	0.2	2.0
1.4	2.7	0.4	8.6	5.5	0.1	3.9	1.0
16.4	33.8	21.9	5.5	26.0	0.9	17.6	7.3
3.6	5.3	7.2	8.6	0.7	0.2	1.8	16.2
11.4	12.9	11.5	42.3	52.9	29.1	45.4	21.4
49.1	32.4	33.0	8.6	13.6	7.2	4.1	31.4
1.8	2.7	7.5	0.3	0.0	40.9	0.4	3.3
0.0	0.9	1.8	0.2	0.0	0.0	0.1	1.3
0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
0.4	0.0	0.0	0.2	0.0	0.0	0.0	0.0
0.0	0.9	1.1	0.0	0.0	0.0	0.0	0.1
11.0	4.9	0.4	24.3	1.0	21.4	26.4	15.9
0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0
281	225	279	55,419	6,508	16,607	6,024	[illegible]

Community ordinal similarity (Table 4) averages 47%, much less than faunal ordinal similarity. Mean similarity of our subalpine communities to one another (59%) is noticeably greater than this. Local habitat conditions evidently affect communities more than they affect faunas. The aspen canopy has especially low similarity to other assemblages, likely due to its very high proportion of Lepidoptera (Table 1). All of the other assemblages are from lower strata (except conifer canopy), but it is unclear whether we should hypothesize that lepidopterous leaf miners are more common in deciduous canopies than in lower strata. This is because these other assemblages resulted from sampling procedures that would not collect immature leaf miners.

Community metamorphosis similarity (Table 5) averages 66%, more than community ordinal similarity and less than faunal metamorphosis similarity. Variation among sites in abundance of a given order tends to be compensated for by other orders with the same type of metamorphosis. As compared with faunas, ametabolous insects are more common and holometabolous ones less common. Metamorphosis similarity among our subalpine communities averages 82%, again quite a bit above the general mean for all comparisons.

Metamorphosis categories are few in number and so similarly distributed in various insect assemblages that they seem to tell little

TABLE 2. Relative percent similarity of insect faunas to those of each stratum and stage of a subalpine sere. Comparisons are based on the proportions of the total number of species in Coleoptera, Diptera, Hemiptera, Homoptera, Lepidoptera, Thysanoptera, and all other orders combined. For sources of data from other areas, see Appendix 1.

Relative percent similarity to				
Meadow	Aspen understory	Aspen canopy	Conifer understory	Conifer canopy
94 Cold desert 1	86 Aspen canopy	86 Aspen understory	87 British trees	91 Cold desert 1
90 Conifer canopy	80 Conifer understory	80 Meadow	84 Tropical 4	90 Meadow
88 Tropical 9	79 Cold desert 1	78 Cold desert 1	83 Tropical 8	89 Tropical 9
86 Deciduous 2	78 Meadow	76 Conifer understory	82 Conifer canopy	89 British trees
86 British trees	75 British trees	73 Conifer canopy	82 Meadow	88 Deciduous 2
82 Temperate field	74 Temperate field	72 British trees	80 Tropical 12	86 Canada
82 Conifer understory	72 Deciduous 2	72 Tropical 11	80 Deciduous 2	85 Tropical 7
81 Tropical 2	71 Conifer canopy	71 Tropical 9	80 Aspen understory	85 Temperate field
81 Tropical 7	70 Tropical 8	71 Tropical 5	79 Tropical 7	85 South African trees
80 Aspen canopy	70 Canada	69 Temperate field	78 Cold desert 1	84 Tropical 5
80 Tropical 5	68 South African trees	68 Deciduous 2	78 Tropical 9	84 Tropical 2
78 Tropical 4	68 Tropical 7	68 Tropical 10	76 Aspen canopy	82 Conifer understory
78 Aspen understory	68 Tropical 4	67 Tropical 8	76 Temperate field	81 Tropical 4
78 South African trees	67 Tropical 9	66 Tropical 7	76 South African trees	81 Tropical 1
78 Tropical 12	66 Tropical 11	66 South African trees	75 Canada	80 Tropical 8
78 Tropical 8	66 Tropical 1	65 Deciduous 1	75 Hot desert	79 Hot desert
76 Canada	65 Hot desert	64 Tropical 4	72 Tropical 2	78 Tropical 3
76 Tropical 11	64 Tropical 12	64 Tropical 1	72 Tropical 13	78 Deciduous 1
76 Deciduous 1	63 Tropical 5	63 Canada	72 Tropical 1	77 Tropical 12
76 Tropical 1	62 Deciduous 1	63 Tropical 3	72 Tropical 5	76 U.S. + Canada
74 Tropical 10	62 Tropical 10	62 Tropical 2	70 Deciduous 1	75 Tropical 13
73 Tropical 3	59 Tropical 2	60 Tropical 12	69 Tropical 3	75 Tropical 11
71 Tropical 6	59 Tropical 3	58 Tropical 6	63 Tropical 11	74 Tropical 10
71 Hot desert	58 Tropical 13	58 Hot desert	62 Tropical 10	74 Tropical 6
69 Tropical 13	53 U.S. + Canada	56 Tropical 13	62 Tropical 6	74 New York State
67 U.S. + Canada	53 New York State	53 U.S. + Canada	61 U.S. + Canada	73 Aspen canopy
64 New York State	51 Tropical 6	50 New York State	60 New York State	71 Aspen understory
52 world 1	36 world 1	40 world 1	44 world 1	61 world 1
77 mean	66 mean	66 mean	73 mean	80 mean

about differences in community structure (sensu MacMahon et al. 1981) or faunal composition. Even feeding categories may show similar patterns on different species of trees in widely separated areas (Moran and Southwood 1982).

Insect Abundance

Herbaceous Layer.— The effect of cage size on estimates of number of insect individuals/m² is summarized in Table 6. In each of the two meadows tested, samples taken with the large cage gave notably greater estimates of insect abundance than did those from the small cage, but the differences were not statistically significant. Inspection of summaries of individual samples revealed that most of the differences in means could be accounted for by high numbers of Aphididae or Thripidae in a few of the samples taken with the large cage. Because these are nonflying or weakly flying organisms, it seems doubtful that they escaped more readily during placement of the small cage. We conclude that most of the difference in means is due to sampling error, but acknowledge that the large cage may be marginally more efficient at trapping strong fliers such as large Diptera or Hymenoptera. The latter groups probably made up a small portion of the total assemblage in the field.

Insect density in the herbaceous layer decreased through most of the summer of 1977

Table 3. Relative percent similarity of insect faunas to those of each stratum and stage of a subalpine sere. Comparisons are based on the proportions of the total number of species in ametabolous, hemimetabolous, paurometabolous, and holometabolous orders. For sources of data from other areas, see Appendix 1.

Relative percent similarity to				
Meadow	Aspen understory	Aspen canopy	Conifer understory	Conifer canopy
99 Deciduous 2	100 Aspen canopy	100 Aspen understory	98 Meadow	99 Cold desert 1
98 Tropical 3	99 Tropical 7	98 Tropical 7	97 Aspen canopy	99 Tropical 4
98 Tropical 8	97 Meadow	97 Meadow	97 Aspen understory	98 Tropical 5
98 Conifer understory	97 Tropical 9	97 Conifer understory	96 Tropical 3	97 South African trees
97 Aspen understory	97 Conifer understory	97 Tropical 9	96 Tropical 8	97 Tropical 1
97 Aspen canopy	96 Deciduous 2	96 Deciduous 2	96 Deciduous 2	97 Tropical 10
97 Tropical 7	96 Tropical 3	96 Tropical 3	96 British trees	96 Tropical 8
97 British trees	95 Tropical 8	95 Tropical 2	96 Tropical 7	96 U.S. + Canada
94 Tropical 9	95 Tropical 2	95 Tropical 12	94 Conifer canopy	96 British trees
94 Conifer canopy	95 Tropical 12	95 Tropical 8	94 Tropical 9	95 Tropical 3
94 Tropical 4	94 British trees	94 British trees	93 South African trees	95 Deciduous 2
94 South African trees	91 Conifer canopy	92 Conifer canopy	93 Tropical 12	95 World 2
94 Cold desert 1	91 Tropical 4	91 South African trees	93 Cold desert 1	95 Tropical 11
93 Tropical 5	91 South African trees	91 Cold desert 1	92 Tropical 2	94 Meadow
93 Tropical 2	91 Tropical 6	91 Tropical 4	92 Tropical 4	94 Conifer understory
93 Tropical 12	91 Cold desert 1	91 Tropical 6	92 Tropical 5	93 New York State
92 Tropical 1	90 Tropical 5	90 Tropical 5	91 Tropical 1	92 Hot desert
91 Tropical 10	89 Tropical 1	89 Tropical 1	90 Tropical 10	92 Tropical 7
90 U.S. + Canada	88 Tropical 10	88 Tropical 10	89 U.S. + Canada	92 Aspen canopy
89 World 2	87 Deciduous 1	87 U.S. + Canada	88 Tropical 11	91 Aspen understory
89 Tropical 11	87 U.S. + Canada	87 Deciduous 1	88 World 2	91 Temperate field
88 Tropical 6	86 Tropical 11	86 Tropical 11	87 Tropical 6	90 Canada
87 New York State	86 World 2	86 World 2	87 New York State	89 Tropical 9
86 Hot desert	84 New York State	85 New York State	86 Hot desert	89 Tropical 12
85 Temperate field	84 Hot desert	84 Hot desert	84 Temperate field	88 Tropical 2
84 Deciduous 1	82 Temperate field	82 Temperate field	84 Canada	83 Tropical 6
84 Canada	82 Canada	82 Canada	83 Deciduous 1	79 Deciduous 1
79 Cold desert 2	81 Cold desert 2	81 Cold desert 2	78 Cold desert 2	73 Cold desert 2
71 Tropical 13	73 Tropical 13	73 Tropical 13	71 Tropical 13	67 Tropical 13
91 mean	90 mean	94 mean	90 mean	91 mean

in the meadows (Fig. 1a), but rose until the third week of July (week 8) under aspen and conifers (Fig. 1b, 1c), declining thereafter. The earlier peaking of the abundance curve in the meadows probably resulted from the earlier melting of snow in this stage as compared with the others; our sampling schedule was most likely too late in this year of early snowmelt to include the period of rising abundance in the meadows. Abundance un-

TABLE 4. Relative percent similarity of insect communities to those of each stratum and stage of the sere. Comparisons are based on the proportions of the total insect catch in Coleoptera, Diptera, Hemiptera, Homoptera, Lepidoptera, Thysanoptera, and all other orders combined. For sources of data from other areas, see Appendix 1.

Relative percent similarity to				
Meadow	Aspen understory	Aspen canopy	Conifer understory	Conifer canopy
82 Conifer understory	85 Tropical 12	59 Meadow	82 Meadow	70 Deciduous 7
72 Tropical 2	83 Deciduous 1	56 Conifer understory	73 Aspen understory	68 Tropical 6
70 Cold desert 2	80 Deciduous 10	49 Conifer canopy	72 Deciduous 1	66 Grass bald
66 Salt marsh 1	79 Deciduous 11	45 Deciduous 13	67 Cold desert 2	66 Pine
65 Deciduous 1	75 Salt marsh 4	43 Deciduous 1	67 Salt marsh 4	64 Meadow
64 Conifer canopy	73 Conifer understory	41 Cold desert 2	67 Tropical 12	63 Tropical 3
64 Aspen understory	72 Salt marsh 5	41 Deciduous 10	64 Salt marsh 2	62 Tropical 1
62 Tropical 12	72 Salt marsh 2	41 Deciduous 11	63 Deciduous 10	62 Pine heath
60 Tropical 13	71 Deciduous 7	40 Tropical 7	63 Deciduous 11	61 Deciduous 7
60 Salt marsh 4	71 Pine heath	39 Deciduous 7	61 Tropical 2	61 Tropical 11
60 Deciduous 11	70 Tropical 2	39 Tropical 2	61 Salt marsh 3	60 Tropical 10
59 Aspen canopy	69 Grass bald	39 Aspen understory	60 Tropical 13	60 Deciduous 10
59 Salt marsh 5	69 Salt marsh 3	38 Tropical 12	56 Aspen canopy	60 Cold desert 2
58 Deciduous 10	68 Deciduous 13	38 Tropical 8	56 Deciduous 7	59 Deciduous 6
57 Deciduous 7	67 Tropical 13	37 Grass bald	55 Tropical 7	59 Deciduous 11
56 Salt marsh 2	66 Tropical 7	37 Tropical 13	55 Salt marsh 1	56 Tropical 9
55 Pine	65 Spruce/fir 1	35 Pine heath	54 Deciduous 13	55 Deciduous 5
53 Pine heath	64 Cold desert 2	34 Pine	54 Salt marsh 5	54 Conifer understory
52 Grass bald	64 Meadow	33 Spruce/fir 1	54 Conifer canopy	54 Tropical 4
52 Tropical 7	62 Pine	30 Hemlock	53 Pine heath	53 Tropical 12
51 Salt marsh 1	62 Salt Marsh 1	30 Deciduous 8	53 Tropical 8	52 Tropical 1
49 Deciduous 13	61 Deciduous 6	30 Salt marsh 1	52 Pine	51 Deciduous 1
48 Tropical 9	61 Tropical 8	30 Salt marsh 2	52 Grass bald	51 Deciduous 13
46 Spruce/fir 1	60 Hemlock	30 Salt marsh 3	49 Spruce/fir 1	51 Salt marsh 5
44 Tropical 3	58 Deciduous 8	30 Salt marsh 4	48 Tropical 9	51 Hemlock
43 Tropical 11	57 Deciduous 4	30 Salt marsh 5	45 Hemlock	50 Alpine dry
42 Hemlock	56 Deciduous 12	30 Tropical 9	44 Deciduous 6	49 Salt marsh 4
42 Deciduous 6	55 Tropical 1	28 Deciduous 6	42 Deciduous 8	49 Spruce/fir 1
42 Tropical 4	53 Deciduous 5	26 Tropical 3	40 Deciduous 12	49 Aspen canopy
42 Tropical 8	52 Tropical 9	25 Tropical 11	40 Tropical 1	48 Heath bald
41 Deciduous 8	49 Tropical 3	24 Deciduous 12	40 Tropical 4	47 Deciduous 9
39 Tropical 10	49 Alpine dry	24 Tropical 4	39 Tropical 3	47 Aspen understory
37 Tropical 6	47 Heath bald	23 Tropical 10	36 Deciduous 5	47 Tropical 7
36 Tropical 1	47 Conifer canopy	23 Deciduous 5	33 Tropical 11	46 Deciduous 12
35 Deciduous 12	46 Deciduous 3	22 Tropical 1	33 Deciduous 3	43 Deciduous 3
32 Deciduous 5	46 Deciduous 9	21 Deciduous 3	32 Alpine dry	41 Spruce/fir 2
31 Alpine dry	45 Spruce/fir 2	20 Deciduous 2	30 Heath bald	40 Deciduous 2
31 Deciduous 3	43 Tropical 11	19 Tropical 6	30 Tropical 10	39 Tropical 5
31 Heath bald	39 Tropical 10	17 Tropical 5	28 Deciduous 9	39 Tropical 13
30 Deciduous 2	39 Aspen canopy	16 Alpine dry	28 Alpine wet	38 Tropical 8
30 Tropical 5	36 Alpine wet	15 Heath bald	26 Spruce/fir 2	36 Salt marsh 2
26 Irish meadow	33 Tropical 6	13 Deciduous 9	25 Tropical 6	35 Salt marsh 3
25 Spruce/fir 2	27 Tropical 5	11 Spruce/fir 2	23 Deciduous 2	31 Salt marsh 1
22 Deciduous 9	21 Deciduous 2	11 Alpine wet	22 Irish meadow	22 Irish meadow
18 Alpine wet	20 Irish meadow	8 Irish meadow	19 Tropical 15	20 Alpine wet
47 mean	58 mean	30 mean	48 mean	51 mean

der aspen was comparable to that in meadows, whereas that under conifers was decidedly lower. Sizable variation among stands occurred within all three stages.

Peak abundance in 1978 was from two to six times the 1977 levels (Fig. 1d, 1e, 1f) and occurred during the first two weeks of August. The later peak dates of this year correspond to the later disappearance of snow as reflected in the much later onset of sampling as compared with 1977. Seasonal changes were more pronounced than in 1977. Abundance

TABLE 5. Relative percent similarity of insect communities to those of each stratum and stage of the sere. Comparisons are based on the proportions of the total insect catch in ametabolous, hemimetabolous, paurometabolous, and holometabolous orders. For sources of data from other areas, see Appendix 1

Relative percent similarity to				
Meadow	Aspen understory	Aspen canopy	Conifer understory	Conifer canopy
94 Conifer understory	97 Deciduous 1	96 Conifer canopy	96 Cold desert	96 Aspen canopy
91 Salt marsh 4	94 Conifer canopy	93 Grass bald	96 Salt marsh 4	94 Aspen understory
91 Tropical 2	91 Aspen canopy	92 Tropical 12	94 Meadow	93 Deciduous 1
91 Salt marsh 2	88 Tropical 12	92 Deciduous 7	90 Tropical 2	90 Tropical 12
90 Cold desert 2	84 Grass bald	92 Deciduous 11	89 Salt marsh 2	89 Grass bald
89 Salt marsh 3	84 Deciduous 11	92 Salt marsh 5	87 Salt marsh 3	89 Deciduous 7
88 Tropical 13	83 Deciduous 7	91 Pine	86 Tropical 13	89 Deciduous 11
83 Salt marsh 1	82 Pine	91 Aspen understory	81 Aspen understory	88 Salt marsh 5
78 Deciduous 1	82 Deciduous 10	89 Deciduous 1	81 Salt marsh 1	87 Pine
76 Aspen understory	82 Salt marsh 5	89 Deciduous 10	79 Deciduous 1	87 Deciduous 10
76 Deciduous 2	82 Tropical 7	86 Pine heath	77 Conifer canopy	83 Pine heath
72 Tropical 9	81 Conifer understory	81 Deciduous 13	74 Tropical 9	79 Cold desert 2
70 Conifer canopy	80 Cold desert 2	80 Tropical 8	73 Aspen canopy	78 Deciduous 13
67 Aspen canopy	80 Tropical 9	77 Tropical 4	71 Deciduous 2	77 Tropical 7
64 Tropical 12	80 Tropical 2	77 Cold desert 2	70 Tropical 12	77 Conifer understory
62 Tropical 7	79 Pine heath	76 Tropical 7	66 Grass bald	77 Tropical 8
60 Grass bald	77 Salt marsh 4	75 Tropical 9	66 Deciduous 11	76 Tropical 9
60 Deciduous 11	76 Meadow	75 Deciduous 8	66 Deciduous 7	76 Salt marsh 4
60 Deciduous 7	76 Tropical 8	74 Tropical 3	65 Salt marsh 5	75 Tropical 2
59 Salt marsh 5	74 Tropical 6	73 Conifer understory	64 Pine	74 Tropical 3
58 Pine	73 Tropical 3	73 Salt marsh 4	64 Deciduous 10	74 Tropical 4
58 Deciduous 10	73 Tropical 4	73 Hemlock	63 Tropical 7	71 Deciduous 8
55 Tropical 8	72 Deciduous 13	72 Spruce/fir 1	61 Pine heath	71 Tropical 6
55 Pine heath	70 Salt marsh 2	71 Deciduous 6	57 Tropical 8	70 Meadow
53 Tropical 6	68 Deciduous 2	71 Tropical 2	55 Tropical 6	70 Hemlock
53 Tropical 3	68 Salt marsh 3	70 Tropical 6	55 Deciduous 13	69 Spruce/fir 1
52 Tropical 4	68 Spruce/fir 1	69 Tropical 1	54 Tropical 3	69 Salt marsh 2
48 Deciduous 13	67 Tropical 11	67 Meadow	54 Tropical 4	68 Deciduous 6
47 Tropical 11	67 Tropical 13	66 Salt marsh 2	49 Tropical 11	67 Salt marsh 3
46 Spruce/fir 1	66 Deciduous 8	65 Deciduous 12	49 Spruce/fir 1	66 Tropical 1
44 Tropical 10	65 Tropical 1	65 Alpine dry	48 Deciduous 8	65 Tropical 13
44 Tropical 1	64 Hemlock	65 Deciduous 5	47 Hemlock	63 Tropical 11
42 Deciduous 8	64 Tropical 10	64 Deciduous 3	46 Tropical 10	63 Deciduous 2
41 Hemlock	63 Deciduous 6	64 Salt marsh 3	46 Deciduous 6	62 Deciduous 12
40 Tropical 5	62 Salt marsh 1	64 Heath bald	46 Tropical 1	61 Deciduous 5
39 Deciduous 6	59 Deciduous 12	62 Tropical 11	41 Deciduous 12	61 Salt marsh 1
35 Deciduous 12	55 Alpine dry	61 Tropical 13	41 Tropical 5	61 Alpine dry
32 Alpine dry	55 Deciduous 5	59 Deciduous 2	38 Alpine dry	60 Deciduous 3
31 Deciduous 5	55 Deciduous 3	59 Tropical 10	38 Deciduous 5	60 Heath bald
31 Deciduous 3	55 Heath bald	58 Salt marsh 1	38 Deciduous 3	60 Tropical 10
31 Heath bald	47 Deciduous 9	56 Deciduous 9	37 Heath bald	52 Deciduous 9
30 Irish meadow	46 Alpine wet	55 Alpine wet	29 Deciduous 9	52 Alpine wet
25 Spruce/fir 2	45 Spruce/fir 2	49 Spruce/fir 2	28 Alpine wet	46 Spruce/fir 2
23 Deciduous 9	43 Tropical 5	37 Tropical 5	26 Spruce/fir 2	38 Tropical 5
22 Alpine wet	27 Irish meadow	22 Irish meadow	26 Irish meadow	23 Irish meadow
59 mean	70 mean	72 mean	60 mean	71 mean

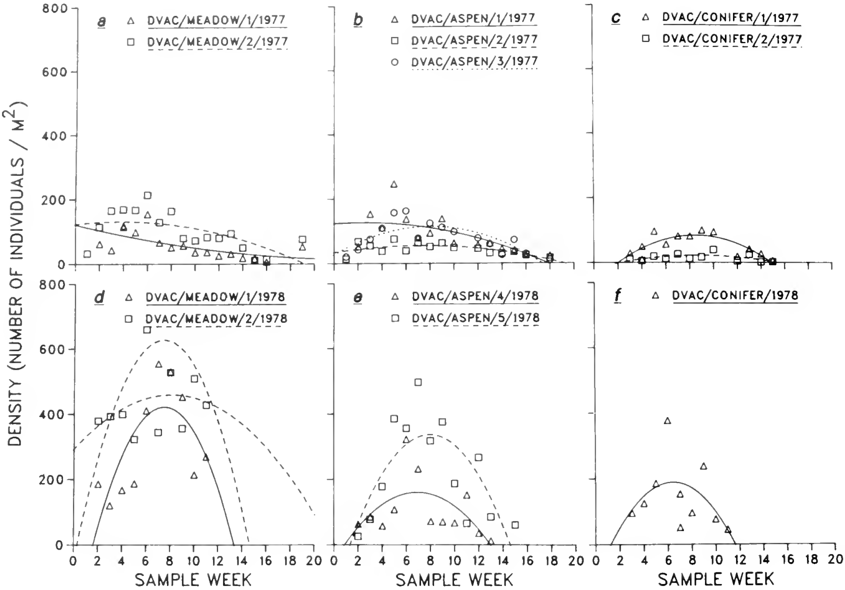

Fig. 1. Mean number of individuals/m² in meadows, aspen understories, and conifer understories as functions of sample week (second order least-squares regressions). Plotted points are weekly means for 1977 (a–c) and 1978 (d–f). Two regression curves are presented for DVAC/MEADOW/2/1978 samples in Fig. 1d. The more steeply peaked of the curves is based on all field data collected, including a mean value of 1372 individuals/m² on sample week 8 (point not shown). This anomalously high value was the result of a concentration of 3477 aphids within one of the eight DVAC samples taken that week. When this value was replaced with 35 aphids, the average value for the other seven DVAC samples taken that week, the mean density was reduced to 527 individuals/m² (point shown on plot), and the less steeply peaked regression curve was obtained.

level differed most between years in the meadows, and least in the two forest understories. This interyear trend was reasonably consistent with that of the herbaceous standing crop, which was 2.3 times as great in the 1978 meadows as during the 1977 drought; the ratios for aspen and conifer understory standing crop are 1.5 and 1.1, respectively (data from Appendix 2). Abundance variation among stands within stages was sizable again in 1978 but did not obscure the seral trend. On the basis of this more typical meteorological year (Schimpf et al. 1980), we conclude that insect abundance/m² in the herbaceous layer declines markedly during succession.

Table 6. Effect of sampling with large (0.50 m²) vs. small (0.25 m²) D-VAC cage on estimates of insect abundance (mean number of individuals/m²), species density (mean number of species/m²), and sample similarity (mean absolute percent similarity). Eight samples were taken with each cage in each meadow 18 July 1978.

Meadow	Cage	Abundance	P*	Species density	P*	Sample similarity	P* †
1	Small	228	.10	38	.10	16.6	.10
	Large	254		40		17.0	
2	Small	331	.10	51	.10	11.8	.05
	Large	480		52		15.3	

*Probability that the mean from the large cage is greater due to chance alone.
†Based on similarity coefficients transformed to arcsin.

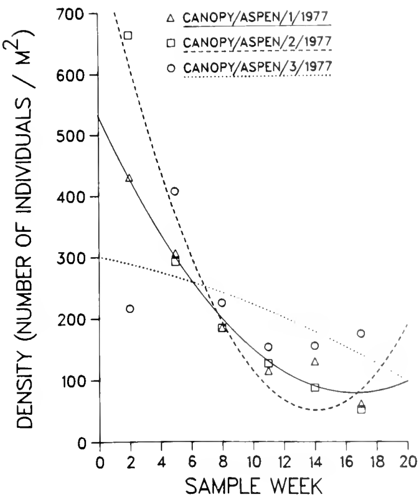

Fig. 2. Mean number of individuals/m² in aspen canopies as functions of sample week, 1977 (second order least-squares regressions). Plotted points are weekly means estimated from abundance vs. biomass regressions.

The trend in 1978 herbaceous standing crop along the sere was the same as that of insect abundance, though the ratios between stages differed. Meadows had 2.9 times the standing crop of aspen understory but only about 2.1 times the peak insect density; the meadow: conifer ratios were 10.0 for plants and 2.8 for insects (plant data from Appendix 2). Thus, insect abundance increases during succession if expressed per unit of aboveground herbaceous biomass rather than per m².

Conifer understories had only about half as many plant species/m² as meadows or aspen understories (Appendix 2). Thus, our abundance trend is consistent with the findings by Pimentel (1961) and Root (1973) of greater concentrations of insects on collards growing in monocultures than on those growing in diverse plant communities. This agreement must be qualified by the fact that the host plant species differ among our three stages. The representation of plant families and life cycle lengths is much the same in all stages (Schimpf et al. 1980), yet the stages could still differ in the physical, chemical, or architectural (sensu Lawton 1983) suitability of their plants for insects. Maiorana (1981) proposed that shade itself promotes a greater abundance of insect herbivores per unit plant biomass, and Schowalter (1981) suggested that shade-induced physiological stress on some plants would lessen their biochemical defenses against herbivory. Greater herbivore abundance would be expected to attract more parasites and predators. Finally, unfavorable weather has greater demographic impact on insects in subalpine meadows than on those in subalpine forests (Ehrlich et al. 1972).

TREE CANOPY LAYER.— Abundance in aspen canopies declined dramatically throughout the 1977 sampling season (Fig. 2), but still remained at a level higher than that of the aspen understory (Fig. 1b). With canopy leaf biomass/m² being about 4.4 times that of understory aboveground biomass/m² (Appendix 2), the number of insects per unit of herbaceous biomass began the season at a higher value in the canopy, with the values in the two strata converging as the season progressed.

The inclusion of leaf-miners in the aspen canopy analysis was responsible for the greater abundance in that stratum than in the understory, where insects within plants were not sampled. However, inspection suggested that leaf-miners were a meager component of the understory community, so the differences were not sampling artifacts.

Abundance in conifer canopies showed the opposite trend, rising substantially during the sampling period (Fig. 3). At all times the number of individuals/m² here was noticeably less than in aspen. Abundance in conifers was well below that in aspen over a wide range of foliar biomass (Table 7). By the second week of August, both conifer strata had similar abundance levels (Figs. 1c, 3). Because tree leaf biomass/m² was some 119 times that of conifer understory herb biomass/m² (Appendix 2), insect concentration on herbaceous tissue was about two orders of magnitude greater in the understory than in the canopy above.

The biological basis for the low numbers of insects in conifer canopies is not known. Our data are consistent with the observation by

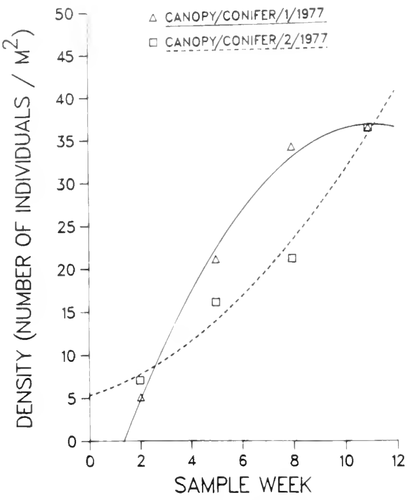

Fig. 3. Mean number of individuals/m² in conifer canopies as functions of sample week, 1977 (second order least-squares regressions). Plotted points are weekly means estimated from abundance vs. biomass regressions.

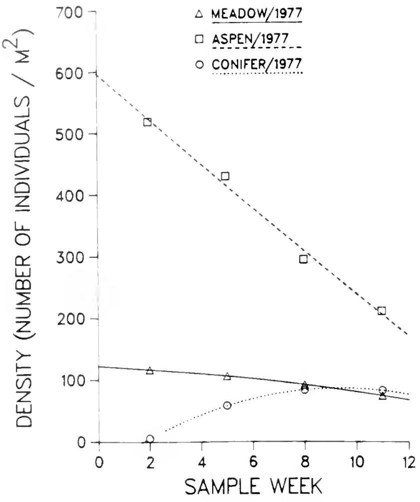

Fig. 4. Mean number of individuals/m² in each stage of the sere as functions of sample week, 1977 (second order least-squares regressions). Plotted points are weekly sums of canopy and understory means.

Moran and Southwood (1982) that narrow-leaved angiosperm trees harbored many fewer insects than broad-leaved species did. Avian predation patterns seem unlikely to influence the seasonal trends in canopy insect abundance. Though insect abundance rose in conifers and fell in aspens during 1977, avian biomass density and consumption rate was greater in the conifers (Smith and MacMahon 1981). Greater avian foraging pressure could contribute to the lower insect abundance in conifers as compared with aspen, but we are unable to estimate the importance of this factor.

TOTAL ABUNDANCE PER STAGE.— Seasonal trends of total abundance per stage of succession are presented in Figure 4. In 1977 densities were highest in the aspen. Likewise, Werner (1983) found greater insect abundance in an Alaskan aspen stand than in a white spruce stand. His numbers/m² considerably exceed ours. If our abundances are expressed per unit herbaceous biomass (understory + tree leaves, Appendix 2), then levels in meadow and aspen were similar to each other and about 20 times that in conifer.

Species Richness

HERBACEOUS LAYER.— The effect of cage size on estimates of number of species/m² is presented in Table 6. As was the case with abundance, sampling with the large cage yielded estimates in both stands that were greater than those from the small cage,

TABLE 7. Comparisons of the individuals—foliar biomass and species—foliar biomass relationships of aspen canopy to those of conifer canopy. Statistical significance of the difference between aspen and conifer in intercept or slope of least-squares linear regressions was determined with a two-tailed t-test. P = probability that the means differ due to chance alone.

Individuals vs. g. foliar biomass						Species vs. g. foliar biomass					
Mean intercept		P	Mean slope		P	Mean intercept		P	Mean slope		P
Aspen	Conifer		Aspen	Conifer		Aspen	Conifer		Aspen	Conifer	
24.12	3.36	.01	1.14	0.0096	.001	5.86	4.71	.05	0.093	0.0025	.001

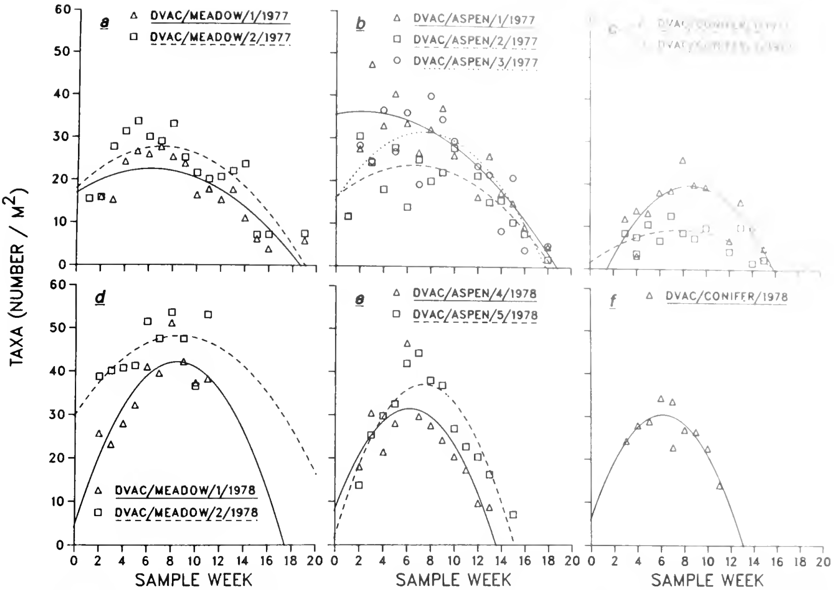

Fig. 5. Mean number of species/m² in meadows, aspen understories, and conifer understories as functions of sample week (second order least-squares regressions). Plotted points are weekly means for 1977 (a–c) and 1978 (d–f).

though not statistically different. The effect of cage size was much less in the case of species richness than in the case of abundance. There seems to be no reason to qualify our comparisons among stages in this regard. However, it must be recognized that the species richness values we obtained may not be those that would have been obtained by sampling a full 1.0 m² plot, depending on vegetation patchiness.

Species/m² in the herbaceous layer peaked between the second and fourth weeks of July 1977 in most of the stands (Fig. 5a, 5b, 5c), declining strongly thereafter in all of them. In 1978, seasonal change was more pronounced, with peaks occurring during August (Fig. 5d, 5e, 5f). Peak richness was about twice as great in 1978 meadow and conifer stands as in 1977, but only slightly greater in aspen. This muted interannual difference in aspen is confounded by the fact that, unlike the other two stages, different aspen stands were sampled in different years. Individual aspen groves were too small to sample for consecutive years without affecting 1978 results. The change in aspen locations in 1978 seems to have had less effect on abundance than on species richness (Fig. 1b, 1e).

Comparison of regression lines shows that in 1977 species/m² rose slightly from meadow to aspen, then declined markedly into the conifer. In 1978 there was a conspicuous decline from meadow to aspen, with little further decline into conifer. Averages of peaks for the two years show meadow and aspen understory with similar species richness. Climax conifer understory species richness was two-thirds that of these earlier stages.

As was the case with abundance, species richness increased with succession if expressed per unit plant biomass instead of per m². The ratio of peak insect species/m² to grams peak herbaceous aboveground standing crop/m² (Appendix 2) was about 0.3 for meadow in both years, 0.8 and 0.6 under aspen, and 1.0 and 1.9 under conifers. Note that the plant and insect peaks were not necessarily simultaneous, a phenomenon also noted by Southwood et al. (1979). This great concentration of insect species on herbage with successional progression is not explained by differences in plant species richness (see

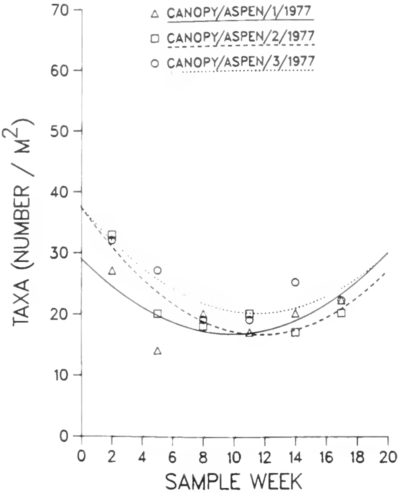

Fig. 6. Mean number of species/m² in aspen canopies as functions of sample week, 1977 (second order least-squares regressions). Plotted points are weekly means estimated from species vs. biomass regressions.

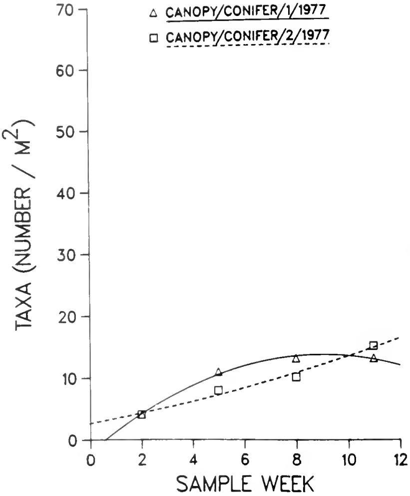

Fig. 7. Mean number of species/m² in conifer canopies as functions of sample week, 1977 (second order least-squares regressions). Plotted points are weekly means estimated from species vs. biomass regressions.

also Usher 1979). The 1977 and 1978 ratios of insect species • plant species^{-1} • m^{-2} were 1.9 and 3.3 in meadow, 2.2 and 2.3 under aspen, and 2.1 and 4.3 under conifer. Although the close agreement of our 1977 ratios supports the general positive correlation between plant and insect species richnesses (Murdoch et al. 1972, Southwood et al. 1979), the different 1978 ratios suggest that other factors contribute to insect species richness. More insect species were present per plant species in 1978, and the ratio differed widely among stages. Increased insect species richness in 1978 cannot be attributed strictly to greater amounts of phytomass, since in the case of the conifer understory phytomass was nearly the same in both years (Appendix 2). Plant growth forms and life cycle categories differ in the richness of their associated insect faunas (Lawton 1982, Lawton and Schroder 1977, Strong 1979, Strong and Levin 1979), but the stages we are comparing in this stratum differ little in form or life cycle length (Schimpf et al. 1980). The greater concentration of insect species on the conifer understory may be due to a more favorable physical environment or a more readily colonizable set of host plant species.

TREE CANOPY LAYER.— Species richness in the aspen canopy was fairly steady through the 1977 sampling period (Fig. 6) despite the precipitous drop in abundance at the same time (Fig. 2). The number of species/m² was roughly comparable to that in the understory (Fig. 1b). Species richness in the conifer canopy (Fig. 7) was about two-thirds as great as that of the aspen canopy and similar to species richness in conifer understory (Fig. 5c).

With the lack of stratification in species richness and much greater plant species richness in the understories vs. the canopies (Appendix 2), insect species • plant species^{-1} • m^{-2} was greater in the canopies than in their understories. It would seem unlikely that all the insect species on 1 m² would occur on each plant species on that plot, and the existence of a smaller number of individuals of many insect species than the number of plant species invalidates this possibility. Therefore, within 1 m² the average herbaceous species harbored fewer insect species than did each tree species. The generality that there is a greater number of insect species per tree species than per herb species for a given amount of geographic range (Strong and Levin 1979) can thus be extended to a smaller spatial scale for one point in time.

The greater number of insect species/m² on tree species vs. herb species may be partly due to the greater standing crop of tree biomass. This can be factored out by dividing insect species • plant species^{-1} • m^{-2} by the terminal standing crop of tree leaves or herb biomass (Appendix 2). Conifer canopy insect species richness is divided by one, not two plant species, since most 1 m² plots are superposed by only one tree species. These ratios are crude approximations, for they assume no faunal overlap among herb species in the same 1 m² plot. Midseason insect species • plant species^{-1} • m^{-2} • 10g^{-1} was 0.4–0.5 in aspen understory, 1.1–1.3 in conifer understory, 1.1 in aspen canopy, and 0.06–0.07 in conifer canopy. On this basis aspen seems no better for the "packing" of insect species than the average conifer understory species, and perhaps worse than understory species of both stages if faunal overlap among plant species is taken into account. Spruce or fir were conspicuously depauperate in comparison to any of the angiosperms. The difference in species richness between aspen and conifer would be even greater on a larger spatial scale (Table 7). This deserves wider investigation, for others (Futuyma and Gould 1979, Neuvonen and Niemalä 1981) have noted low numbers of species of Lepidoptera or Tenthedrinoidea on gymnosperms as compared to angiosperm trees in the same area. Hendrix (1980) proposed that ferns are less hospitable than angiosperms to insect herbivore species; perhaps gymnosperms are also entomologically depauperate. Evergreenness per se may not be important (Faeth et al. 1981). Moran and Southwood (1982) suggested that frequent rubbing of leaves against one another was responsible for depauperate insect assemblages on narrow-leaved species of *Salix*; such an explanation cannot be invoked for the stiff-leaved fir and spruce. Furthermore, aspen leaves strike each other with great frequency, yet that species carried far more insects than the conifers, even if leaf-miners are ignored.

Total Species Richness per Stage.— Seasonal trends of 1977 combined-strata species/m² are shown in Figure 8. Species richness clearly rose, then fell during succession, with the aspen level about twice that of the preceding or following stage. Whether one considers the herbaceous layer, tree canopy, or combined strata, species/m² does not increase throughout succession. This disagrees with the tabulated trend in Odum (1969) but agrees with the preclimax peak in species richness predicted in the text of that paper.

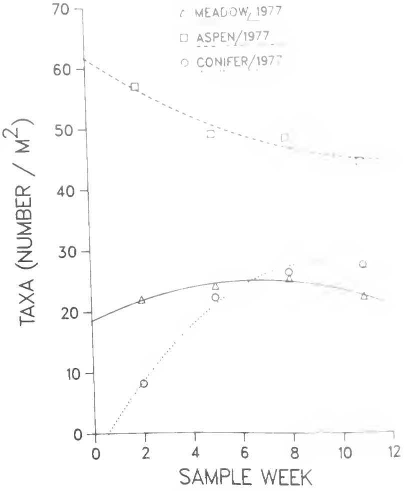

Fig. 8. Mean number of species/m² in each stage of the sere as functions of sample week, 1977 (second order least-squares regressions). Plotted points are weekly sums of canopy and understory means.

Evenness

Herbaceous Layer.— During 1977 evenness peaked in midseason in meadow stands and one aspen stand, but showed midseason minima in the other forested stands (Fig. 9a, 9b, 9c). No successional trends in midseason J′ are evident. Early or late in the sampling period there was a successional increase in evenness. In 1978 evenness was greatest in aspen and conifer (Fig. 9d, 9e, 9f). Values in all stages were generally higher in 1977 than in 1978. This difference may be an artifact of the greater insect abundance in 1978, with consequent more likely inclusion of rare species in samples (Hurlbert 1971), and thus is perhaps not biologically meaningful. The overall pattern is one of increasing insect community evenness during succession, in agreement with the prediction of Odum (1969). This conclusion must be tempered by recognition of the mathematical inadequacies

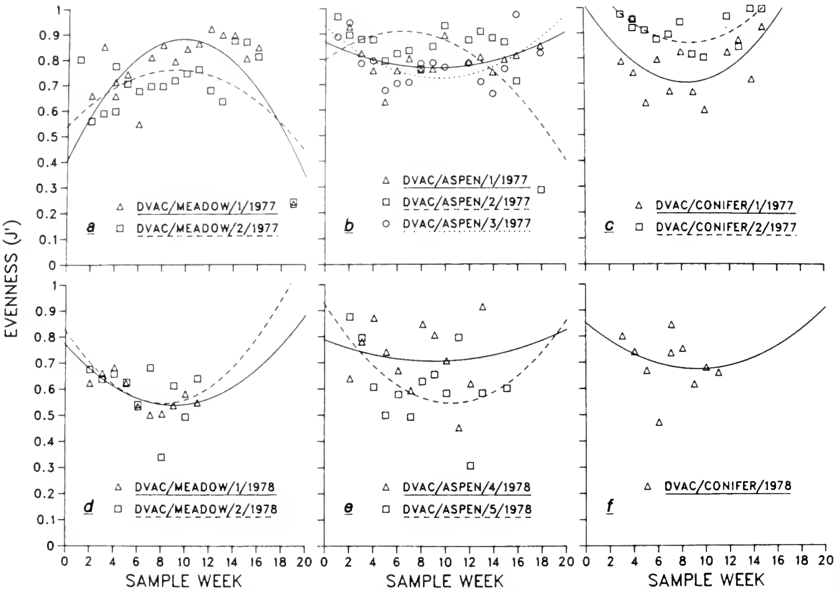

Fig. 9. Mean evenness (J') of sample aggregates totaling 1.0 m² in meadows, aspen understories, and conifer understories as functions of sample week (second order least-squares regressions). Plotted points are weekly means for 1977 (a–c) and 1978 (d–f).

of evenness measures, including J' (Routledge 1983).

Table 8. Variance and coefficient of variation for midseason intrastand sample similarity matrices transformed to arcsin.

Stand	Variance	Coefficient of variation
	1977 week 8	
Meadow 1	41.02	0.35
Meadow 2	30.96	0.27
Aspen 1	92.92	0.73
Aspen 2	74.79	0.90
Aspen 3	93.24	0.52
Conifer 1	35.08	0.25
Conifer 2	90.07	0.60
	1978 week 6	
Meadow 1	45.15	0.27
Meadow 2	26.32	0.23
Aspen 4	51.89	0.41
Aspen 5	40.61	0.26
Conifer	66.36	0.55

Tree Canopy Layer.— In Figure 10, we present dominance-diversity plots. We interpret the trajectories of these to reflect the differences in evenness between conifer and aspen stages. Aspen exhibits greater relative abundance by its most common species than does conifer, with lesser relative abundance of the less common species in aspen. The relative abundance of species in the conifer are less disparate, so we conclude that species evenness in conifer canopies is higher than that in aspen canopies. Note that this approach does not yield a numerical evenness value and is an integration of a full season's samples.

Total Evenness per Stage.— Although the analyses of the understories cannot be numerically combined with those of their respective canopies, the similar trend in both strata allows us to conclude that evenness in-

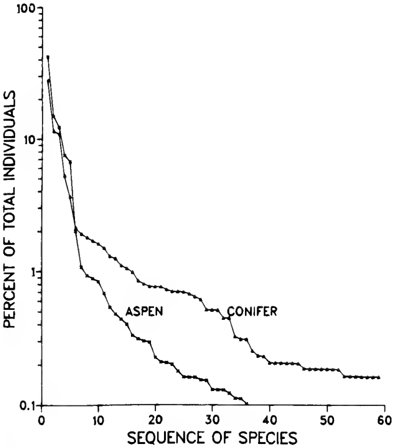

Fig. 10. Dominance-diversity plots for aspen and conifer canopies, 1977. Species are plotted by the percentage of the total season's capture they compose (log scale) in decreasing order of relative abundance.

creases during succession, concordant with the prediction of Odum (1969).

Sample Similarity—Herbaceous Layer

Samples taken with the large cage were slightly more similar than those taken with the small cage (Table 6). Average similarity among samples from the herbaceous layer was low in all stages in 1977 (Fig. 11a, 11b, 11c); no consistent seasonal pattern was observed, and no obvious successional trend was detected. Similarity levels in 1978 were much the same as those in 1977, and seasonal and intrastage spatial variation obscured any successional trends (Fig. 11d, 11e, 11f). If particular insect communities occur in patches, variance in similarity will be higher than in cases where the same mean similarity results from sampling a spatially more homogeneous taxocene. This is because pairs of samples from the same kind of patch will have high similarity and those from different kinds of patches low similarity. Both variances and coefficients of variation indicate that the meadow was the most consistently spatially homogeneous stage in midseason of both years (Table 8).

Although the greater variance under conifers may be an artifact of the lower insect abundance there (Wolda 1981), it is consistent with the greater habitat heterogeneity of the forest floor. As others have documented (Anderson et al. 1969, Knight et al. 1977, Young and Smith 1979), the conifer understory is a mosaic of patches differing greatly in illumination, temperature, date of snowmelt, throughfall precipitation, and plant species composition. Even closely related plant species may support rather different insect assemblages (Seifert 1981). We have evidence that the vegetation of our meadows is more homogeneous, in that the mean number of plant species/m^2 is high (Appendix 2), but the total number of plant species is low (Reese 1981). It should be recognized that horizontal pattern may exist at several spatial scales, and that our results have meaning only with reference to the size and spacing of our samples.

Total Heterogeneity per Stage

Despite lacking information on horizontal heterogeneity in the canopies, we agree with Odum's (1969) hypothesis that pattern diversity increases with succession. We do so on the basis of the weak successional increase in horizontal patchiness in the herbaceous layer's insect communities and the obvious

TABLE 9. Adult body length of all species and all individuals caught in a stratum of a successional stage during one sampling season. $\bar{X}$ = mean, SD = standard deviation.

Stage/stratum	Species unweighted		Species weighted by abundance	
	1977 $\bar{X} \pm$ SD(mm)	1978 $\bar{X} \pm$ SD(mm)	1977 $\bar{X} \pm$ SD(mm)	1978 $\bar{X} \pm$ SD(mm)
Meadow	4.4 ± 4.1	4.1 ± 3.9	3.0 ± 2.4	2.2 ± 1.6
Aspen understory	3.2 ± 2.3	3.2 ± 3.3	3.5 ± 1.6	3.3 ± 1.9
Aspen canopy	3.5 ± 3.3	3.6 ± 2.0	4.6 ± 2.1	5.0 ± 1.6
Conifer understory	2.6 ± 1.7	3.2 ± 3.3	2.0 ± 1.0	2.0 ± 1.9
Conifer canopy	2.4 ± 1.5	—	1.4 ± 0.7	—

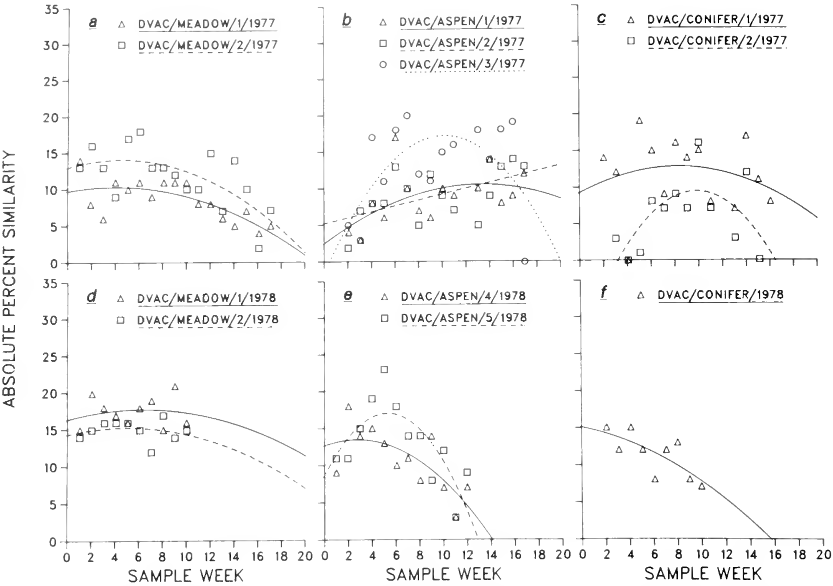

Fig. 11. Mean absolute percent similarity of species composition of samples in meadows, aspen understories, and conifer understories as functions of sample week (second order least-squares regressions). Plotted points are weekly means for 1977 (a–c) and 1978 (d–f).

strong vertical stratification of the forested stages.

Adult Body Length

Mean adult body length declined during succession if species are not weighted by their abundance (Table 9). This accords with the principle that larger organisms, ceteris paribus, will be less influenced by the more pronounced fluctuations of the physical environment of the meadow, due to their lower surface:mass ratios. Ceteris paribus cannot be invoked in this case, since longer insects tend to be proportionately thinner (Rogers et al. 1976, Schoener 1979). Because the relationship between insect length and surface area is unknown, we do not know whether surface:mass declines with increasing length. Species in the aspen canopy were somewhat

Table 10. Distribution among metamorphosis categories of all species and all individuals caught in a stratum of a successional stage during one sampling season.

Stage stratum year		Percent of all species			
		Ametabolous	Hemimetabolous	Paurometabolous	Holometabolous
Meadow	1977	1	0	27	72
Aspen understory	1977	2	0	24	74
Aspen canopy	1977	0	0	27	72
Conifer understory	1977	2	0	31	68
Conifer canopy	1977	1	2	26	72
Meadow	1978	2	0	26	73
Aspen understory	1978	1	0	23	76
Aspen canopy	1978	2	0	29	69
Conifer understory	1978	3	1	25	71

larger than those in aspen understory, whereas the conifer strata showed the reverse relationship. When the species from all stages, strata, and years were averaged (unweighted), a mean of 3.4 mm resulted, remarkably close to the 3.5 mm reported for samples from Massachusetts by Schoener and Janzen (1968).

If species are weighted by abundance, adult body length increased from meadow to aspen, then dropped greatly into the conifer (Table 9). The largest insects were found in the aspen canopy, and the smallest ones in the conifer canopy. The aspen canopy had a large plurality of insects of above-average length (leaf miners), evidenced by the weighted mean's far exceeding of the unweighted mean. The other stages/strata had weighted means similar to or smaller than the unweighted means, suggesting numerical predominance of species of medium or small size. Whether weighted or unweighted, organism size does not increase during succession, thus contradicting Odum's (1969) prediction. The insects of the conifer climax are the smallest, regardless of stratum.

Werner (1983) found heavier insects in white spruce stands than in aspen stands in Alaska. His data are not directly comparable to ours because they represent actual, not necessarily adult, sizes and because he did not sample so as to extract immature leaf miners.

Leaf Cycle Complexity

In Table 10 insect metamorphosis categories are ordered from least (ametabolous) to greatest (holometabolous) complexity of the life cycle. The faunas of all stages, strata, and years are similar when analyzed in this way. When species are weighted by abundance, life cycle complexity increased from meadow to aspen, then dropped in conifer. In both aspen and conifer, the tree canopy had a greater proportion of insects with complex life cycles than did the understory. Life cycle complexity does not increase into the climax as Odum (1969) predicts, but we can partially support his hypothesis in the sense that trees, the successionally later growth form, harbor insects with more complex life cycles than those on herbs. Odum (1969) actually predicted that during succession life cycles would get longer as well as more complex. Although we did not address life cycle length, Brown and Southwood (1983) found that this increased during succession.

Stability

In addition to these planned comparisons, the occurrence of a drought in 1977 permitted us to address another of Odum's (1969) postulates, that concerning stability (resistance to external perturbations). Interestingly, species richness did not differ much between drought and postdrought (1978) years in the herbaceous layer (Fig. 5a–c, vs. 5d–f). Abundance changed most in the meadows and least in the conifer understory (Fig. 1a, 1d vs. 1c, 1f). Effects on evenness were more complex, in that meadows not only changed in time of peak evenness, but also reversed the form of seasonal evenness relationships (Fig. 9a vs. 9d); in aspen understory

Table 10 continued.

Percent of all individuals			
Ametabolous	Hemimetabolous	Paurometabolous	Holometabolous
9	0	67	24
2	0	66	32
0	0	49	51
1	0	74	25
2	0	51	46
9	0	79	12
1	0	86	14
0	0	41	59
4	0	73	22

the form changes are mixed (Fig. 9b vs. 9e), but conifer understory changed little (9c vs. 9f). The nature of the changes observed is the same as those noted by Smith and MacMahon (1981) for the avifauna, and Andersen et al. (1980) for small mammals, on larger plots of the same sere. We concur with Odum (1969) that stability increases with succession, at least in the herbaceous layer.

General Discussion

We have used our analysis of successional trends in the insect component of communities to address "the strategy of ecosystem development" discussed by Odum (1969). The results of this analysis are mixed (Table 11). Similar mixed results were obtained when other taxocenes were analyzed for our sere (Andersen et al. 1980, MacMahon 1980, Smith and MacMahon 1981) as well as for a different one (Witkowski 1979). It is important to remember, when assessing the success of our attempts to test Odum's ideas, that Odum's original postulates apparently described changes for the total ecosystem, not subunits such as the insect assemblages we deal with. There appears to us to be no easy intellectual nor mathematical solution to the problem of equating organisms varying from microbes to trees for purposes of a synthesis of general successional trends. With our piecemeal approach, if trends are the same for every ecosystem subunit studied, the trend should be true for the ecosystem as a whole. In the cases where different subunits of the same sere show different successional

TABLE 11. Comparison of six of Odum's (1969) 24 expected trends in the development of ecosystems to the successional trends in the insect component of a subalpine sere reported herein. Numbers and descriptions of ecosytem attributes and developmental stages are taken from Odum (1969).

Ecosystem attributes	Developmental stages	Mature stages	Accept/Reject	Rationale
		Community structure		
8. Species diversity—variety component	Low	High	Reject	Highest in aspen (Fig. 8)
9. Species diversity—equitability component	Low	High	Accept	J' highest in conifer understory most of time (Fig. 9); dominance-diversity plot flatter in conifer canopy (Fig. 10)
11. Stratification and spatial heterogeneity (pattern diversity)	Poorly organized	Well organized	Accept	Herbaceous horizontal (Table 8) and vertical spatial heterogeneity greater in forests
		Life history		
13. Size of organism	Small	Large	Reject	Smallest in conifers (Table 9)
14. Life cycles	Short, simple	Long, complex	Conditionally accept	Holometabolous greatest in aspen, but greater in trees than their understories (Table 10)
		Overall homeostasis		
22. Stability (resistance to external perturbations)	Poor	Good	Accept	Interyear differences in density (Fig. 1) and evenness (Fig. 9) least in conifer

trends, then it is less easy to make unambiguous statements about trends in ecosystem succession; the information garnered may still have theoretical and applied implications.

Animal communities in a late stage of succession may differ from those of an early stage on the same site for two conceivable major reasons. A greater length of time available to get to the site will allow less vagile animals or those with farther to travel a higher probability of being well represented in the community. Any animal attributes that correlate with time to arrival will then show up as changes in community structure (attribute patterns sensu MacMahon et al. 1981) during succession. The second major reason is that the vegetation changes and, through its autogenic effects, so does the physical and chemical environment. In each vegetation stage, different animal taxa may have the greatest abundances because of these habitat differences, with consequences for community structure if these various taxa have different attributes (MacMahon 1981).

Data from Simberloff and Wilson (1969) indicate that arthropod species richness can return to predefaunation levels in approximately 250 days of colonization time, despite isolation by hundreds of meters of ocean. This suggests that time availability is usually of minor importance in most changes in insect community structure where decades to centuries are involved. The greater vagility and shorter life cycles of insects as compared with those of most plants mean that the rate of change in insect community structure is constrained by the rate of vegetation changes, except perhaps for the first few years after disturbance. In our sere, all three stages are sufficiently long standing (Schimpf et al. 1980) that we can state that the effect of time itself on insect community structural changes is minimal. Therefore the insect community changes we record would seem to be responses to plant succession.

In our relatively simple sere, one can see how the peculiarities of a single plant species may control the successional pattern of insect communities. The dominance of leaf-mining Lepidoptera in the aspen canopy results in that stratum's having the peak values of body size and life cycle complexity in the sere. If we had studied the alternate successional pathway involving lodgepole pine (*Pinus contorta*) instead of aspen as the intermediate stage (Schimpf et al. 1980), we might see different types of community structure and hence successional trends.

Our mixed agreement with the deductive predictions by Odum (1969) suggest that the cybernetic model on which they were based is not entirely adequate. Others (Simberloff 1976, Futuyma and Gould 1979, Lawton and Strong 1981) have assembled substantial evidence that insect communities are loosely organized (cf. Moran and Southwood 1982). We conclude that the successional changes in insect communities on our site are largely the collective results of individualistic responses of various insect taxa to plant succession.

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APPENDIX 1. Key to sources of data used in calculating percent similarity of insect assemblages to those of our strata and stages, as summarized in Tables 2–5.

Abbreviation	Reference	Notes
Alpine dry, wet	Hayward (1952)	dry meadow, wet meadow
British trees	Southwood et al. (1982)	mean of six species
Canada	Danks (1979)	national fauna
Cold desert 1	Shinn et al. (1975)	their Table 45
Cold desert 2	Fautin (1946)	total from four habitats
Deciduous 1,2	Janzen (1973)	his Table 4: (1 = primary, 2 = secondary), understories
Deciduous 3	Kendeigh (1979)	38-year understory summary
Deciduous 5–13	Whittaker (1952)	his Table 4 and 6, understories 5–13 = A,B,C,C',G,L,L',M,N'
Grass bald	Whittaker (1952)	his Tables 4 and 6, stand K
Heath bald	Whittaker (1952)	his Tables 4 and 6, stand D
Hemlock	Whittaker (1952)	his Tables 4 and 6, understory of stand E
Hot desert	Edney (1974)	Table I, p. 313
Irish meadow	Curry and O'Neill (1979)	mean of four stands
New York State	Evans and Murdoch (1968)	statewide fauna
Pine	Whittaker (1952)	his Tables 4 and 6, understory of stand F
Pine heath	Whittaker (1952)	his Tables 4 and 6, understory of stand J
Salt marsh	Davis and Gray (1966)	1 = *S. alterniflora* (all stations) 2 = Bogue Banks 3 = *Juncus* (all stations) 4 = *Distichilis* (all stations) 5 = *S. patens* (all stations)
South African trees	Southwood et al. (1982)	mean of six species
Spruce-fir 1,2	Whittaker (1952)	his Tables 4 and 6, understories of stands H,H'
Temperate field	Evans and Murdoch (1968)	"long list"
Tropical 1–13	Janzen (1973)	1 = mean Tables 4a,b (primary flat) 2 = mean Tables 4a,b (secondary) 3 = Table 4a (primary-hill) 4 = Table 4c (abandoned pasture) 5 = Table 4c (primary riparian) 6 = Table 4c (primary-hill) 7 = Table 4e 8 = Table 4f 9 = Table 4d (corn field) 10 = Table 4d (primary I) 11 = Table 4d (primary II) 12 = Table 4g 13 = mean Tables 4h,i
U.S. + Canada	Evans and Murdoch (1968)	
World 1	Southwood (1978b)	
World 2	Daly et al. (1978)	

APPENDIX 2. Estimated means of plant parameters for stages of the subalpine sere. Data adapted from Williams (1977) and Reese (1981).

Stage	Herbaceous species/m^2	Herbaceous terminal standing crop, g/m^2		Tree leaves, g/m^2
		1977	1978	
Meadow	13.5	74	171	0
Aspen	14.5	39	58	173
Conifer	7.2	15	16	1739

NUTRIENTS IN *CAREX EXSERTA* SOD AND GRAVEL IN SEQUOIA NATIONAL PARK, CALIFORNIA

Raymond D. Ratliff[1]

Abstract.— Nutrients in soil covered by *Carex exserta* sod and in adjacent unvegetated gravel areas were compared at Siberian Outpost, Sequoia National Park, California. The comparisons were part of a study to learn if *Carex exserta* meadow can be reestablished and if herbaceous cover on gravel areas can be increased. Grazing capacity and aesthetic appeal of denuded areas would be improved by better vegetative cover. The sod had higher concentrations of calcium, copper, iron, magnesium, manganese, nitrogen, potassium, and zinc than did the gravel areas. And it had a higher soil pH and percent organic matter. Sod and gravel did not differ in concentrations of phosphorus and sulfur. The differences were as might be expected between climax and badly deteriorated (or early seral) situations, and the results suggest that fertilization may be a useful treatment.

Carex exserta (short-hair sedge) meadows are found throughout the Sierra Nevada of California. Altitudinally, they extend from the subalpine into the alpine zone (Jackson and Bliss 1982). At Siberian Outpost—an unglaciated subalpine valley in Sequoia National Park—stands of *Carex exserta* (Fig. 1) vary in form from sod steps (Klikoff 1965) to nearly continuous sod on gentle slopes. In and around Siberian Outpost are found expansive areas of coarse-grained granitic gravel. Small plants found in the gravel provide little cover.

The sod can withstand considerable use, but continued overuse or trampling will break and eventually destroy it. Sheep are known to have grazed in Sequoia National Park during the late 1800s and early 1900s (Vankat 1970). In parts of Siberian Outpost, pedestaled remnants attest to overgrazing as a cause for destruction of *Carex exserta* sod. More than 15 cm of sod and top soil have been lost in some places, and little recovery is evident. However, the sod appears to be establishing or reestablishing in other places.

Grazing may not be the only reason for the areas of gravel. Sand and gravel may have originated from debris-laden outwash below glacial moraines or may have been deposited in Pleistocene lakes (Benedict and Major 1982). Retreat of glaciers with warmer, dryer summers may have changed the vegetation the areas were capable of supporting. Rapid percolation to deep layers may make precipitation largely unavailable for on-site plant growth. High winds may keep some areas clear of snow. And gravels and sands from weathering of the granite rocks may be deposited over vegetation in some areas about as soon as it becomes established.

Thus, some of the gravel areas in and similar to those of Siberian Outpost may be completely natural—representing early seral stages.

Nevertheless, where the *Carex exserta* sod has obviously been destroyed, an eroded stretch of gravel and sand remains. That and the presence of large tree stumps in gravel and up to 290 m from the present forest border suggest that some areas of gravel, such as found in Siberian Outpost, may once have supported considerably more vegetation than now.

If the present gravel areas were largely a *Carex exserta* meadow at one time, can that vegetation be reestablished, or can cover of vegetation now occupying the gravel areas in Siberian Outpost and elsewhere be increased? Observed differences between sod and gravel areas should reveal how loss of *Carex exserta* sod alters the nutrient status and should suggest nutrients that might be added to gravel areas. On the other hand, if the gravel areas represent natural seral stages, knowledge of how they differ in nutrients will increase understanding of seral and climax communities.

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Fig. [illegible]. Area [illegible] (upper) and pristine *Carex exserta* sod (lower), Siberian Outpost, Sequoia National Park, California.

Information on the soil texture, pH, and organic matter of *Carex exserta* sod is available (Ratliff 1982), but data on its nutrient composition and that of gravel areas are scant. Such information is needed in the selection of programs to revegetate backcountry areas that have been overused, and to rehabilitate trails and campsites.

This paper compares soil organic matter, pH, and nutrients in *Carex exserta* sod with those in gravel in Siberian Outpost, Sequoia National Park.

METHODS

Siberian Outpost at 36°28′N, 118°17′W (U.S. Geological Survey 1956) lies 11.3 km south of Mount Whitney at 3293 m elevation within the "Boreal Plateau erosion surface" (Matthes 1950, 1962), between Rock Creek on the north and Big Whitney Meadow on the south. Siberian Pass Creek drains the area from east to west.

Calamagrostis breweri meadows are found at the bottom areas of Siberian Outpost. The otherwise gravelly slopes have a few species of forbs such as *Oreonana clementis*, *Calyptridium umbellatum*, *Eriogonum incanum*, and *Lupinus culbertsonii*. They have been classified as an *Eriogonum-Oreonana clementis* association (Benedict 1983). *Stipa occidentalis* and *Sitanion hystrix* are occasionally abundant.

A grid with a ground distance of 45 m between intersections (grid points) was superimposed on aerial photographs of Siberian Outpost. Fifty grid points without *Carex exserta* sod (henceforth referred to as *gravel*), and 30 grid points with *Carex exserta* sod (henceforth referred to as *sod*) were randomly selected. Fewer grid points were allocated for the sod because it occupied less area than the gravel. Three soil cores (17 cm long and 4.7 cm in diameter) were extracted at each grid point and combined to make one sample. Material larger than 2 mm was separated and discarded. The fraction less than 2 mm was kept for laboratory analysis. In addition, intact cores were collected at 15 and at 6 arbitrary grid points in the gravel and in the sod, respectively.

Acidity of each soil sample was determined with a saturated paste and an electronic pH meter. Percent soil organic matter was estimated by gravimetry and dry combustion. Bulk density and gravel content were estimated from the intact cores by gravimetry.

Available facilities and funds limited the nutrient analyses that could be made to those common for crop agriculture. Total nitrogen was determined by the ammonia electrode modification of Kjeldahl method (Page et al. 1982). Available phosphorus was determined by the sodium bicarbonate method (Page et al. 1982). Amounts of calcium, copper, iron, magnesium, manganese, potassium, sulfur, and zinc were determined at a commercial laboratory by standard procedures (Reisenauer 1976).

Parametric tests were not appropriate for the data because they either did not conform to the normal distribution, or the variances were not equal, or both. Therefore, the nonparametric rank-sum test with the normal approximation was used (Steel and Torrie 1960). The hypothesis that the sets of values from the sod and gravel belong to a common population was rejected when chance probability of the rank-sum for the sod samples was 5% or less. Presence of a common population was rejected for all the nutrients except phosphorus and sulfur (Table 1).

Because the samples were obtained at arbitrary grid points, bulk density and gravel data were not random sets. Those data, therefore, could not be statistically analyzed but are presented for reader information.

RESULTS AND DISCUSSION

Soil from the sod samples contained more nutrients than did soil from the gravel. The natural openings in the sod were not sampled, and some of the nutrient differences between the sod and gravel may be due to concentration of nutrients in the sod at the expense of the openings within it. Therefore, on an area basis, the differences in nutrients may not be as large as indicatd by the mean values (Table 1). Nevertheless, the gravel samples were relatively low in nutrients for plant growth.

Nitrogen ordinarily ranges from 0.02% to 0.5% of soil. In prairie soils, 0.1% to 0.3% nitrogen is usual (Allison 1957). Nitrogen contents of alpine mine spoils and topsoil were

0.06% and 0.13%, respectively, on the Beartooth Plateau (Brown and Johnston 1976). Soil of the sod at Siberian Outpost, therefore, was relatively high in total nitrogen—about 0.2%. The gravel, on the other hand, had only about 0.04% nitrogen.

With 27 ppm and 24 ppm in the sod and gravel, respectively, available phosphorus (Table 1) at Siberian Outpost should be adequate for herbaceous plant growth. For pasture and range, no response to added phosphorus is likely with more than 10 ppm available phosphorus in the soil (Reisenauer 1976). High soil acidity, however, generally lowers phosphorus availability.

Ammonium acetate extractable potassium was 0.006% in the sod and 0.001% in the gravel (Table 1). Nitric acid extractable potassium in the sod (0.02%) was twice that in the gravel (0.01%). By either extraction process, exchangeable potassium content of the sod bordered on a deficiency (Reisenauer 1976). Potassium content of the gravel appeared clearly deficient and was lower than that reported for mine spoils (Brown and Johnston 1976).

Potassium is more readily released when concentrations of calcium and/or magnesium are high. The concentration of exchangeable calcium in mine spoils (Brown and Johnston 1976) was higher than that in either the gravel (0.7 meq/100 g) or the sod (1.2 meq/100 g) at Siberian Outpost. Also, although higher than in the mine spoils, magnesium concentrations in the sod (0.5 meq/100 g) and in the gravel (0.2 meq/100 g) at Siberian Outpost were lower than in topsoil on the Beartooth Plateau, Montana (Brown and Johnston 1976).

Soils in Siberian Outpost are low in sulfur content. The average concentration of sulfur (1.25 ppm or 0.0001%) in the sod and gravel is equivalent to only 1.4 kg·ha^{-1} to a 10-cm depth. That concentration is 100 times less than the minimum expected.

Amounts of manganese, iron, copper, and zinc in the gravel, though lower than in the sod, appeared adequate for plant growth. However, their amounts were near critical levels for agricultural crops—especially in the gravel. Critical levels suggested for these nutrients (Reisenauer 1976) were 1.0 ppm (manganese), 5.0 ppm (iron), 0.2 ppm (copper), and 0.5 ppm (zinc).

Soil organic matter and soil pH (Table 1) were higher in the sod (6.3% and pH 4.2) than in the gravel (1.7% and pH 4.0)—$P < 0.001$. *Carex exserta* sites studied earlier (Ratliff 1982) had higher values (7.3% organic matter and pH 5.1) for the top 20 cm of soil. Soil bulk density averaged 1.1 g·cm^{-3} in the sod and 1.7 g·cm^{-3} in the gravel. With the difference in organic matter contents, lower bulk density in the sod would be expected. Gravels composed 37% of the soil mass in the gravel and 24% of the soil mass in the sod.

TABLE 1. Soil organic matter, pH, and nutrients in *Carex exserta* sod and gravel in Siberian Outpost, Sequoia National Park, California.

	Sod			Gravel		
Variable	Low	Average	High	Low	Average	High
Organic matter (%)	4.2	6.3	9.8	1.2	1.7[a]	3.8
pH	4.0	4.2	4.5	3.6	4.0[a]	4.5
Nutrients (ppm)						
N	1258.0	2040.07	2951.0	201.0	378.52[a]	1223.0
P	6.7	27.30	56.8	13.0	24.50	37.0
K[b]	31.0	55.77	95.0	8.0	14.58[a]	35.0
K[c]	128.0	191.87	257.0	42.0	94.68[a]	179.0
Ca	160.3	241.60	440.9	40.1	143.49[a]	200.4
Mg	48.6	65.66	97.3	7.3	25.54[a]	48.6
S	0.5	1.37	3.0	0.5	1.13	2.0
Mn	5.4	12.78	26.2	0.5	1.15[a]	3.7
Fe	53.0	102.79	133.0	5.7	12.42[a]	37.0
Cu	0.4	0.74	1.4	0.1	0.31[a]	1.1
Zn	2.9	7.28	17.6	0.5	1.46[a]	6.6

[a] Average value significantly different from short hair sedge sod ($P < 0.001$) by the rank sum test with normal approximation.
[b] Ammonium acetate extractable.
[c] Nitric acid extractable.

The organic matter content of the gravel was only 0.7% lower than in alpine zone topsoil on the Beartooth Plateau (Brown and Johnston 1976) and was greater than that of most Aridisols with a high sand content (Soil Survey Staff 1975). Therefore, the sparse vegetation in the gravel was unlikely to have produced the existing level of organic matter. Denser vegetation at an earlier time could have been responsible for it, however. Loss of the sod by erosion would remove most of the organic matter built up in the soil system and leave the gravel as a pavement. Because organic matter markedly improves the cation-exchange properties of soils, nutrients also would have been removed by erosion.

Conclusions

This study found substantial differences between soils of *Carex exserta* sod and gravel in nutrient and organic matter contents and acidity. The differences were as expected between climax and badly deteriorated soils. If the gravel in Siberian Outpost once supported *Carex exserta* meadow, then loss of sod resulted in removal of 40% of the calcium, 58% of the copper, 88% of the iron, 61% of the magnesium, 91% of the manganese, 81% of the nitrogen, 74% of the potassium, and 80% of the zinc. Losses of those magnitudes can be hypothesized as a consequence of the destruction of *Carex exserta* sod. Alternatively, if the gravel represents a natural seral stage, succession to a *Carex exserta* climax would require nutrient accumulation and conservation as the sod develops.

Brown and Johnston (1979) suggested fertilization with relatively high rates of nitrogen (up to 168 kg·ha^{-1}) for rehabilitating disturbed alpine areas. They also suggested lime applications on alpine disturbances where pH is below 5.5. Given the low pH of Siberian Outpost soils, fertilization with lime may make more phosphorus available.

To increase cover of gravel areas or to rehabilitate disturbed *Carex exserta* sites in Siberian Outpost and similar areas elsewhere (within a present rather than a successional or geological time frame), stimulation by fertilization may be a useful treatment. The differences found between sod and gravel in nutrient contents suggest including nitrogen, potassium, calcium, magnesium, and sulfur in a fertilizer mix.

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MITES (EXCLUDING CHIGGERS) OF MAMMALS OF OREGON[1]

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Abstract.— New information on the ectoparasitic mites of the following species of mammals from Oregon is presented: (1) pika—*Ochotona;* (2) squirrels—*Eutamias, Spermophilus, Tamiasciurus;* (3) grasshopper mouse—*Onychomys;* (4) woodrats—*Neotoma;* (5) muskrat—*Ondatra;* (6) jumping mice—*Zapus;* and (7) weasels—*Mustela, Spilogale.* New records of species for the state and new host records are also given. Finally, a cross-referenced list of all known mites of wild mammals from Oregon is presented.

Over the past several years, we have written a series of papers on the ectoparasites of mammals from Oregon that include data on the mites of mammals from the following genera: *Zapus* (Whitaker 1979), *Arborimus* and *Lagurus* (Whitaker and Maser 1979), *Aplodontia* (Whitaker et al. 1979), *Neurotrichus* and *Scapanus* (Whitaker et al. 1979a), *Sorex* (Whitaker et al. 1980), *Dipodomys* and *Perognathus* (Maser and Whitaker 1980), *Myotis, Antrozous, Eptesicus, Lasionycteris, Lasiurus, Pipistrellus,* and *Plecotus* (Whitaker et al. 1983b), *Microtus* and *Clethrionomys* (Whitaker and Maser 1984), and *Thomomys* (Whitaker et al., in press). Still in preparation are papers on the ectoparasites of the Townsend chipmunk *(Eutamias townsendi)* and of the genus *Peromyscus.*

One purpose of this paper (Part I) is to present new data on the ectoparasitic, phoretic, and other mites regularly associated with mammals for which we have small sample sizes. The second purpose (Part II) is to present a cross-referenced list of all known ectoparasitic and phoretic mites (excluding chiggers) from the wild mammals of Oregon and their host associations.

Part I. Mites of Selected Mammals from Oregon

Mammals for which new data are presented in this paper were from various parts of the state, as given in the species accounts. Mites were preserved in 70% ethanol, cleared and stained in Nesbitt's solution containing acid fuchsin, and mounted in Hoyer's solution. Cover slips were ringed with Euperal. Identifications were verified by specialists as necessary.

Mites that constitute new records from mammals from Oregon are listed below. Numbers in parentheses are the number of hosts with mites and the number of mites found.

Lagomorpha

Pika, Ochotonidae:

Ochotona princeps. Pika (4 from Linn Co.). Mite: *Echinonyssus utahensis* (1/1).

Rodentia

Squirrels, Sciuridae:

Eutamias amoenus. Yellow-pine chipmunk (2 from Union County). Mites: *Androlaelaps fahrenholzi* (2/4), and *Proctolaelaps* sp. (1/4).

Spermophilus beecheyi. Beechey ground squirrel (3 from Curry County). Mites: *Androlaelaps fahrenholzi* (2/2) and *Haemogamasus occidentalis* (1/1).

Spermophilus beldingi. Belding ground squirrel (3 from Malheur County, 1 from Klamath County). Mites: *Androlaelaps fahrenholzi* (4/23), *Dermacarus reticulosus* (3/25), and *Cheyletus linsdalei* (1/1).

Spermophilus lateralis. Mantled ground squirrel (2 from Harney County, 1 from Deschutes County). Mites: *Androlaelaps fahrenholzi* (2/4) and *Dermacarus spermophilus* (1/21). The latter species was described by Fain and Whitaker (1978a).

Spermophilus townsendi. Townsend ground squirrel (10 from Malheur County). Mites: Androlaelaps fahrenholzi (7/40), *Macrocheles* sp. (1/2), *Dermacarus spermophilus* (1/2), and *Euryparasitus* sp. (3/3).

Spermophilus washingtoni. Washington ground squirrel (3 from Morrow County). Mites: *Androlaelaps fahrenholzi* (1/25) and *Macrocheles* sp. (2/2).

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Tamiasciurus douglasi. Chickaree (6 from Benton, Deschutes, Coos, and Linn counties). Mites: *Haemogamasus reidi* (5/16), *Eulaelaps stabularis* (1/1), and *Euryparasitus* sp. (1/1).

Native mice and woodrats, Cricetidae:

Reithrodontomys megalotis. Western harvest mouse (1 from Jefferson County, 1 from Malheur County). Mites: *Androlaelaps fahrenholzi* (3/2), *Eubrachylaelaps debilis* (2/1).

Peromyscus maniculatus. Deer mouse (134 from Lincoln, Lane, Coos, Curry, Linn, Deschutes, Jefferson, Harney, Malheur, and Union counties). Included here is information on ectoparasites of 134 deer mice. Since we have not published this information, we give it here even though the sample size is larger than for most species included in this section. Mites: *Glycyphagus hypudaei* (1/1), *Androlaelaps casalis* (1/1), *A. fahrenholzi* (197/50), *Echinonyssus obsoletus* (10/2), *E.* "*obsoletus*" variant (1/1), *E. utahensis* (11/9), *Eubrachylaelaps circularis* (6/2), *E. debilis* (72/25), *Eulaelaps stabularis* (2/2), *Haemogamasus reidi* (3/3), *Laelaps kochi* (1/1), Anoetidae (1/1), *Cyrtolaelaps* sp. (2/2), *Euryparasitus* sp. (27/11), *Proctolaelaps* sp. (2/2).

Onychomys leucogaster. Northern grasshopper mouse (2 from Malheur County). Mites: *Androlaelaps fahrenholzi* (2/45), *Haemogamasus onychomydis* (2/49), *Ischyropoda armatus* (1/1), *Ornithonyssus bacoti* (1/2), *Radfordia subuliger* (1/1), *Myocoptes musculinus* (1/1), *Glycyphagus hypudaei* (1/1), *Euryparasitus* sp. (2/32), *Proctolaelaps* sp. (2/4), *Bakerdania* sp. (2/79), and *Kleemania* sp. (2/9).

Neotoma cinerea. Bushy-tailed woodrat (11 from Lane, Lincoln, Malheur, and Union counties). Mites: *Androlaelaps fahrenholzi* (2/6), *Haemogamasus reidi* (3/10), *Eulaelaps stabularis* (3/5), *Haemogamasus pontiger* (2/2), *Echinonyssus neotomae* (1/1), *E. utahensis*? (2/2), and *Euryparasitus* sp. (2/2).

Neotoma fuscipes. Dusky-footed woodrat (4 from Curry, Klamath, and Lane counties). Mites: *Androlaelaps fahrenholzi* (1/2) and *Haemogamasus reidi* (2/2).

Neotoma lepida. Desert woodrat (3 from Malheur County). Mites: *Androlaelaps fahrenholzi* (3/6).

Voles, Arvicolidae:

Ondatra zibethicus. Muskrat (12 from Coos and Malheur counties). Mites: *Laelaps multispinosa* (12/317), *Zibethacarus ondatrae* (8/1213), *Listrophorus faini* (5/81), *L. ondatrae* (4/40), *L. americanus* (4/94), *L. validus* (6/46), *L. dozieri* (6/129), and *Radfordia zibethicalis* (1/3).

The muskrat is unique in having several species all in the same genus (*Listrophorus*), often in large numbers on the same individual (see Bauer and Whitaker 1981).

Mites of the genera *Zibethacarus* and *Listrophorus* are tiny and cling to individual hairs. Thus they are often overlooked or taken in relatively small numbers, although they are abundant on nearly every muskrat. Only six of the muskrats in this study were examined thoroughly for these mites.

Jumping mice, Zapodidae:

Zapus trinotatus. Pacific jumping mouse (28 from Lincoln, Lane, Coos, and Linn counties). Mites: *Androlaelaps fahrenholzi* (11/129), *Haemogamasus reidi* (4/6), *H. occidentalis* (1/1), *Dermacarus newyorkensis* (2/11), *Bakerdania* sp. (1/1), and *Euryparasitus* sp. (5/9). Whitaker (1979) reported the following ectoparasites on this host from Oregon: *Androlaelaps fahrenholzi*, *Neotrombicula microti*, *N. harperi*, and *Radfordia ewingi*.

CARNIVORA

Weasels, Mustelidae:

Mustela erminea. Short-tailed weasel (8 from Lane, Coos, and Curry counties). Mites: *Haemogamasus occidentalis* (3/5), *H. reidi* (1/1), *Eulaelaps stabularis* (1/2), *Eubrachylaelaps debilis* (1/1), *Echinonyssus obsoletus* (1/1), *E. utahensis* (1/3), *Glycyphagus hypudaei* (1/12), *Orycteroxenus soricis* (1/1), *Euryparasitus* sp. (1/1), and Anoetidae (1/1).

Mustela frenata. Long-tailed weasel (4 from Coos, Malheur, and Union counties). Mites: *Androlaelaps fahrenholzi* (2/8), *Echinonyssus cynomys* (3/34), *E. longichelae* (3/14), *E. thomomys* (3/9), *E. obsoletus* (1/24), and *Lynxacarus mustelae* (1/16).

Mustela vison. Mink (1 from Lincoln County, 1 from Coos County). Mites: *Lynxacarus nearcticus* (2/875+), *Echinonyssus staffordi* (1/1), *E. obsoletus* (1/1), and *Pseudoparasitus* sp. nymph (1/2).

Spilogale putorius. Spotted skunk (12 from Lincoln, Coos, and Curry counties). Mites: *Androlaelaps fahrenholzi* (1/1), *Eulaelaps stabularis* (3/18), *Haemogamasus reidi* (8/105), *Xenoryctes latiporus* (1/4), *Echinonyssus staffordi* (1/1), *Pygmephorus designatus* (1/1), *Eucheyletia bishoppi* (1/1), and *Euryparasitus* sp. (1/1).

NEW STATE RECORDS FOR MITES:

Laelapidae: *Haemogamasus onychomydis*, *Echinonyssus neotomae*, *E. staffordi*, *E. thomomys*, *Eubrachylaelaps circularis*, *Laelaps multispinosa*. **Glycyphagidae:** *Dermacarus reticulosus*, *D. newyorkensis*, *Xenoryctes latiporus*. **Cheyletidae:** *Cheyletus linsdalei*. **Myobiidae:** *Radfordia subuliger*. **Mycoptidae:** *Myocoptes musculinus*. **Listrophoridae:** *Listrophorus americanus*, *L. dozieri*, *L. faini*, *L. ondatrae*, *L. validus*, *Lynxacarus mustelae*, *L. nearcticus*.

NEW HOST RECORDS FOR PARASITIC MITES:

Ochotona princeps–*Echinonyssus utahensis*.

Eutamias amoenus–*Androlaelaps fahrenholzi*.

Spermophilus beecheyi–*Haemogamasus occidentalis*.

Spermophilus beldingi–*Androlaelaps fahrenholzi*, *Dermacarus reticulosus*, *Cheyletus linsdalei*.

Spermophilus townsendi–*Dermacarus spermophilus*.

Spermophilus washingtoni–*Androlaelaps fahrenholzi*.

Tamiasciurus douglasi–*Eulaelaps stabularis*.

Peromyscus maniculatus–*Echinonyssus obsoletus*, *E. obsoletus* "variant."

Onychomys leucogaster–*Haemogamasus onychomydis*, *Radfordia subuliger*, *Myocoptes musculinus*, *Glycyphagus hypudaei*.

Neotoma cinerea–*Eulaelaps stabularis*, *Haemogamasus pontiger*, *Echinonyssus utahensis*.

Neotoma fuscipes–*Androlaelaps fahrenholzi*.

Zapus trinotatus–*Haemogamasus occidentalis*.

Mustela erminea–*Haemogamasus occidentalis*, *H. reidi*, *Eubrachylaelaps debilis*, *Echinonyssus obsoletus*, *E. utahensis*, *Glycyphagus hypudaei*, *Orycteroxenus soricis*. Most of these parasites are a result of host transfer during predation.

Mustela frenata–*Echinonyssus cynomys*, *E. longichelae*, *E. thomomys*, *E. obsoletus*. *Echinonyssus* spp.

are a result of host transfer during predation; particularly interesting are the first three species, which are indicative of predation on pocket gophers.

Spilogale putorius–Androlaelaps fahrenholzi, Eulaelaps stabularis, Haemogamasus reidi, Xenoryctes latiporus, Pygmephorus designatus, and *Eucheyletia bishoppi.*

Part II: MITES (EXCLUDING CHIGGERS) of Mammals from Oregon

The following list summarizes information on ectoparasitic and phoretic mites currently known from wild mammals of Oregon. Data are presented alphabetically by family, genus, and species. Host taxa identified only to genus are not included. Numbers after the species refer to papers, listed by number, in the literature cited. Those marked with an X are reported for the first time in this paper.

ACARIDAE	
Acotyledon nr *paradoxus* Oudemans, 1903	
RODENTIA	
Glaucomys sabrinus	32
CHEYLETIDAE	
Acaropsellina summersi Smiley & Whitaker, 1981	
RODENTIA	
Glaucomys sabrinus (nest)	29
Caminchelyletus glaucomys Smiley & Whitaker, 1981	
RODENTIA	
Glaucomys sabrinus (nest)	29
Cheyletus linsdalei Baker, 1949	
RODENTIA	
Spermophilus beldingi	X
Eucheyletia bishoppi Baker, 1949	
INSECTIVORA	
Sorex pacificus	38
S. trowbridgei	38
CARNIVORA	
Spilogale putorius	X
Eucheyletia oregonensis Smiley & Whitaker, 1981	
RODENTIA	
Glaucomys sabrinus (nest)	29
CHIRODISCIDAE	
Alabidocarpus calcaratus Lawrence, 1952	
CHIROPTERA	
Myotis californicus	41
M. volans	41
CHORTOGLYPHIDAE	
Aplodontopus latus Fain, 1967	
RODENTIA	
Aplodontia rufa	5, 37
DERMANYSSIDAE	
Dermanyssus gallinoides Moss, 1966	
RODENTIA	
Glaucomys sabrinus	32
GLYCYPHAGIDAE	
Dermacarus hylandi Fain, 1969	
RODENTIA	
Lagurus curtatus	33
Microtus oregoni	34
Dermacarus jonesi Fain & Whitaker, 1976	
RODENTIA	
Eutamias townsendi	39
Dermacarus newyorkensis Fain, 1969	
RODENTIA	
Zapus trinotatus	X
Dermacarus reticulosus Spicka & Gerrits, 1977	
RODENTIA	
Spermophilus beldingi	X
Dermacarus spermophilus Fain & Whitaker, 1978a	
RODENTIA	
Eutamias townsendi	39
Spermophilus lateralis	X, 7
S. townsendi	X
Dermacarus tamiasciuri Rupes, Yunker, & Wilson, 1971	
RODENTIA	
Glaucomys sabrinus (nest)	32
Tamiasciurus douglasi	22
Glycyphagus hypudaei (Koch, 1841)	
INSECTIVORA	
Scapanus townsendi	36
Sorex bendirei	38
S. pacificus	38
S. trowbridgei	38
RODENTIA	
Arborimus albipes	33
A. longicaudus	33
Clethrionomys californicus	34
C. gapperi	34
Eutamias townsendi	39
Lagurus curtatus	33
Microtus montanus	34
M. oregoni	34
M. richardsoni	34
M. townsendi	34
Onychomys leucogaster	X
Peromyscus maniculatus	X
Tamiasciurus douglasi	22
Thomomys mazama	35
CARNIVORA	
Mustela erminea	X
Gohieria sp.	
RODENTIA	
Glaucomys sabrinus	32
Microlabidopus americanus Fain, 1967	
RODENTIA	
Aplodontia rufa	4, 5, 37
Orycteroxenus soricis (Oudemans, 1915)	
INSECTIVORA	
Sorex bendirei	38
S. pacificus	38
S. trowbridgei	38
S. yaquinae	38
CARNIVORA	
Mustela erminea	X

Xenoryctes latiporus Fain & Whitaker, 1973	
CARNIVORA	
Spilogale putorius	X
Zibethacarus ondatrae Rupes & Whitaker, 1968	
RODENTIA	
Microtus oregoni	34
Ondatra zibethicus	X
LAELAPIDAE	
Alphalaelaps aplodontiae Jellison, 1945	
INSECTIVORA	
Sorex trowbridgei	38
S. vagrans	38
RODENTIA	
Aplodontia rufa	18, 23, 37
Eutamias townsendi	39
Androlaelaps casalis (Berlese, 1887)	
INSECTIVORA	
Scapanus orarius	36
Sorex trowbridgei	38
RODENTIA	
Glaucomys sabrinus	32
Microtus montanus	12
Neotoma lepida	12
Onychomys leucogaster	12
Peromyscus maniculatus	X
Androlaelaps fahrenholzi (Berlese, 1911)	
MARSUPIALIA	
Didelphis virginiana	14
INSECTIVORA	
Scapanus orarius	36
S. townsendi	36
Sorex bendirei	38
S. pacificus	38
S. palustris	12
S. preblei	12
S. trowbridgei	38
S. vagrans	12, 38
S. yaquinae	38
RODENTIA	
Arborimus albipes	33
A. longicaudus	33
Clethrionomys californicus	34
C. gapperi	34
Dipodomys ordi	21
Eutamias amoenus	X
E. townsendi	39
Glaucomys sabrinus	32
Lagurus curtatus	12, 33
Microtus longicaudus	12, 34
M. montanus	12, 34
M. oregoni	34
M. richardsoni	34
M. townsendi	34
Neotoma cinerea	X
N. fuscipes	X
N. lepida	X
Onychomys leucogaster	12, X
Perognathus parvus	12, 21
Peromyscus maniculatus	12
Spermophilus beecheyi	X
S. beldingi	X
S. lateralis	X
S. townsendi	X
S. washingtoni	X
Zapus trinotatus	30, X
CARNIVORA	
Mustela frenata	X
Spilogale putorius	X
Androlaelaps geomys (Strandtmann, 1949)	
RODENTIA	
Thomomys bulbivorus	35
T. mazama	35
Echinonyssus affinis (Jameson, 1950b)	
RODENTIA	
Eutamias townsendi	39
Echinonyssus arcuatus (Koch, 1839)	
RODENTIA	
Peromyscus maniculatus (probably a misidentification)	12
Echinonyssus cynomys (Radford, 1941)	
CARNIVORA	
Mustela frenata	X
Echinonyssus nr *cynomys*	
RODENTIA	
Glaucomys sabrinus	32
Echinonyssus femuralis (Allred, 1957)	
RODENTIA	
Thomomys bulbivorus	35
T. talpoides	35
Echinonyssus hilli (Jameson, 1950b)	
RODENTIA	
Dipodomys ordi	21
Perognathus parvus	21
Echinonyssus incomptis (Eads & Hightower, 1952)	
RODENTIA	
Dipodomys ordi	21
Echinonyssus isabellinus (Oudemans, 1913)	
INSECTIVORA	
Sorex vagrans	12
RODENTIA	
Clethrionomys californicus	34
C. gapperi	34
Lagurus curtatus	33
Microtus longicaudus	12, 13
M. montanus	12, 13, 34
M. richardsoni	34
M. townsendi	34
Echinonyssus latiscutatus (de Meillon & Lavoipierre, 1944)	
RODENTIA	
Mus musculus	2
Echinonyssus longichelae (Allred & Beck, 1966)	
RODENTIA	
Glaucomys sabrinus (nest)	32
Thomomys mazama	35
T. talpoides	13, 35
CARNIVORA	
Mustela frenata	X
Echinonyssus longichelae "variant"	
RODENTIA	
Thomomys mazama	35
T. talpoides	35

Echinonyssus neotomae (Eads & Hightower, 1951)	
Rodentia	
Neotoma cinerea	X
Echinonyssus obsoletus (Jameson, 1950b)	
Insectivora	
Scapanus townsendi	13
Sorex trowbridgei	13
Rodentia	
Clethrionomys californicus	34
Microtus townsendi	34
Peromyscus maniculatus	X
Carnivora	
Mustela erminea	X
M. frenata	X
M. vison	X
Echinonyssus obsoletus "variant"	
Insectivora	
Scapanus orarius	36
Sorex bendirei	38
S. pacificus	38
S. trowbridgei	38
S. vagrans	38
S. yaquinae	38
Rodentia	
Peromyscus maniculatus	X
Echinonyssus staffordi (Strandtmann & Hunt, 1951)	
Carnivora	
Mustela frenata	X
Spilogale putorius	X
Echinonyssus thomomys (Allred & Beck, 1966)	
Rodentia	
Thomomys mazama	35
T. talpoides	35
T. townsendi	35
Carnivora	
Mustela frenata	X
Echinonyssus triacanthus (Jameson, 1950b)	
Rodentia	
Dipodomys sp.	16
D. ordi	21
Echinonyssus utahensis (Allred & Beck, 1966)	
Lagomorpha	
Ochotona princeps	X
Rodentia	
Dipodomys ordi	21
Lagurus curtatus	33
Neotoma cinerea	X
Peromyscus maniculatus (originally reported as *E. obsoletus*)	12, 13, X
Thomomys talpoides	35
Carnivora	
Mustela erminea	X
Eubrachylaelaps circularis (Ewing, 1933)	
Rodentia	
Peromyscus crinitus	X
Eubrachylaelaps crowei Jameson, 1947	
Rodentia	
Microtus montanus	12
Onychomys leucogaster	12
Eubrachylaelaps debilis Jameson, 1950a	
Insectivora	
Sorex trowbridgei	38
Rodentia	
Eutamias townsendi	39
Microtus montanus	34
M. townsendi	34
Peromyscus maniculatus	X
Carnivora	
Mustela erminea	X
Eulaelaps stabularis (Koch, 1836)	
Marsupialia	
Didelphis virginiana	14
Insectivora	
Scapanus orarius	36
S. townsendi	36
Sorex trowbridgei	38
S. vagrans	38
Rodentia	
Arborimus albipes	33
Clethrionomys californicus	34
Eutamias townsendi	39
Microtus longicaudus	34
M. montanus	12, 34
M. oregoni	34
M. townsendi	34
Neotoma cinerea	X
Peromyscus maniculatus	12, X
Tamiasciurus douglasi	X
Carnivora	
Mustela erminea	X
Spilogale putorius	X
Haemogamasus ambulans (Thorell, 1872) (recorded from refs. 12, 19, 33, 36, 38, 40; probably all incorrect and should be referred to other species)	
Haemogamasus keegani (Jameson, 1952)	
Insectivora	
Scapanus townsendi	17
Haemogamasus liponyssoides Ewing, 1925	
Rodentia	
Microtus longicaudus	12
M. montanus	12
Haemogamasus mandschuricus Vitzthum, 1930	
Rodentia	
Onychomys leucogaster	12
Haemogamasus nidi Michael, 1892	
Marsupialia	
Didelphis virginiana (probably misidentification)	14
Haemogamasus occidentalis (Keegan, 1951)	
Insectivora	
Neurotrichus gibbsi	19, 37
Scapanus orarius	37
S. townsendi	19, 37
Sorex bendirei	38
S. pacificus	38

S. trowbridgei	38
S. vagrans	38
S. yaquinae	38
Rodentia	
Arborimus albipes	33
Clethrionomys californicus	34
Eutamias townsendi	39
Microtus longicaudus	34
M. montanus	34
M. oregoni	34
M. richardsoni	34
M. townsendi	19, 34
Spermophilus beecheyi	X
Zapus trinotatus	X
Carnivora	
Mustela erminea	X
M. frenata	19
Haemogamasus onychomydis (Ewing, 1933)	
Rodentia	
Dipodomys ordi	21
Onychomys leucogaster	X
Perognathus parvus	21
Thomomys mazama	35
T. talpoides	35
T. townsendi	35
Haemogamasus pontiger (Berlese, 1904)	
Rodentia	
Glaucomys sabrinus	32
Neotoma cinerea	X
N. lepida	12
Haemogamasus reidi Ewing, 1925	
Insectivora	
Scapanus orarius	37
S. townsendi	37
Sorex bendirei	38
S. trowbridgei	38
S. vagrans	38, 40
S. yaquinae	38, 40
Rodentia	
Aplodontia rufa	37
Arborimus albipes	3
Clethrionomys californicus	34
C. gapperi	34
Dipodomys ordi	21
Eutamias townsendi	39
Glaucomys sabrinus	32
Lagurus curtatus	12°, 26, 33
Microtus longicaudus	12°, 26, 34
M. montanus	34
M. richardsoni	34
M. townsendi	34
Neotoma cinerea	X
N. fuscipes	X
Peromyscus maniculatus	X
Tamiasciurus douglasi	X
Thomomys mazama	35
T. talpoides	12°, 35, 36
Zapus princeps	12°, 26
Z. trinotatus	X
Also "Forest Tree Mouse"	
= *Arborimus longicaudus*	26
Carnivora	
Mustela erminea	X
Spilogale putorius	X
(°Originally listed as *ambulans*, reidentified by Redington)	
Haemogamasus thomomysi Williams, Smiley, & Redington 1978	
Rodentia	
Thomomys mazama	35
T. talpoides	35
Haemogamasus sp.	
Rodentia	
Aplodontia rufa	37
Haemogamasus n. sp.	
Rodentia	
Clethrionomys californicus	34
Microtus oregoni	34
M. townsendi	34
Hypoaspis miles (Berlese, 1892)	
Rodentia	
Microtus townsendi	34
Ischyropoda armatus Keegan, 1951	
Rodentia	
Dipodomys ordi	21
Onychomys leucogaster	X
Perognathus parvus	21
Ischyropoda furmani Keegan, 1956	
Rodentia	
Dipodomys ordi	21
Laelaps alaskensis Grant, 1947	
Rodentia	
Lagurus curtatus	12
Microtus montanus	12, 34
M. richardsoni	34
Onychomys leucogaster	12
Thomomys mazama	35
Laelaps kochi Oudemans, 1936	
Insectivora	
Neurotrichus gibbsi	36
Rodentia	
Microtus longicaudus	12°, 34
M. montanus	12°, 34
M. oregoni	34
M. townsendi	34
Peromyscus maniculatus	X
(°*identified as Laelaps pachypus*)	
Laelaps multispinosa (Banks, 1910)	
Rodentia	
Ondatra zibethicus	X
Patrinyssus hubbardi (Jameson, 1949)	
Rodentia	
Aplodontia rufa	37
Listrophoridae	
Aplodontochirus borealis Fain & Hyland, 1972	
Rodentia	
Aplodontia rufa	37
Geomylichus perognathi Fain & Whitaker, 1980	
Rodentia	
Perognathus parvus	9, 21

Geomylichus texensis Fain, Whitaker, Schwan, & Lukoschus, 1981	
RODENTIA	
Dipodomys ordi	21
Leporacarus sylvilagi Fain, Whitaker, & Lukoschus, 1981	
LAGOMORPHA	
Sylvilagus bachmani	11
Listrophorus americanus Radford, 1944	
RODENTIA	
Ondatra zibethicus	X
Listrophorus dozieri Radford, 1944	
RODENTIA	
Ondatra zibethicus	X
Listrophorus faini Dubinina, 1972	
RODENTIA	
Ondatra zibethicus	X
Listrophorus mexicanus Fain, 1970	
INSECTIVORA	
Scapanus townsendi	36
Sorex bendirei	38
RODENTIA	
Clethrionomys californicus	34
Lagurus curtatus	33
Microtus montanus	34
M. oregoni	34
M. richardsoni	34
M. townsendi	34
Listrophorus ondatrae Fain, Kok, & Lukoschus, 1970	
RODENTIA	
Ondatra zibethicus	X
Listrophorus validus Banks, 1910	
RODENTIA	
Ondatra zibethicus	X
Lynxacarus mustelae (Megnin, 1885)	
CARNIVORA	
Mustela frenata	X
Lynxacarus nearcticus Fain & Hyland, 1973	
CARNIVORA	
Mustela vison	X
Quasilistrophorus microticolus Fain, Whitaker, & Lukoschus, 1978	
RODENTIA	
Arborimus albipes	10, 33
A. longicaudus	10, 33
MACRONYSSIDAE	
Cryptonyssus desultorius Radovsky, 1967	
CHIROPTERA	
Eptesicus fuscus	41
Myotis californicus	41
M. lucifugus	41
M. volans	41
Macronyssus crosbyi (Ewing & Stover, 1915)	
CHIROPTERA	
Eptesicus fuscus	41
Myotis californicus	41
M. evotis	41
M. lucifugus	41
M. volans	41
M. yumanensis	41
Macronyssus longisetosus (Furman, 1950)	
CHIROPTERA	
Plecotus townsendi	41
Macronyssus macrodactylus Radovsky & Beck, 1971	
CHIROPTERA	
Lasionycteris noctivagans	41
Ornithonyssus bacoti (Hirst, 1913)	
(host not given)	42
RODENTIA	
Onychomys leucogaster	X
Steatonyssus antrozoi Radovsky & Furman, 1963	
CHIROPTERA	
Antrozous pallidus	41
Steatonyssus emarginatus Radovsky & Furman, 1963	
CHIROPTERA	
Pipistrellus hesperus	41
Steatonyssus furmani Tipton & Boese, 1958	
CHIROPTERA	
Lasiurus cinereus	41
Steatonyssus occidentalis (Ewing, 1933)	
CHIROPTERA	
Eptesicus fuscus	25, 41
macronyssid n. sp.	
CHIROPTERA	
Eptesicus fuscus	41
Lasionycteris noctivagans	41
Myotis californicus	41
M. evotis	41
M. lucifugus	41
M. volans	41
M. yumanensis	41
Plecotus townsendi	41
MYOBIIDAE	
Acanthophthirius caudatus eptesicus Fain & Whitaker, 1978	
CHIROPTERA	
Eptesicus fuscus	41
Acanthophthirius sp. nr *gracilis* Fain & Whitaker, 1978	
CHIROPTERA	
Myotis volans	41
Acanthophthirius oregonensis Fain & Whitaker, 1978	
CHIROPTERA	
Pipistrellus hesperus	8, 41
Amorphacarus hengererorum Jameson, 1948	
INSECTIVORA	
Sorex pacificus	38
S. vagrans	38
S. yaquinae	38
Amorphacarus soricis Fain & Whitaker, 1978	
INSECTIVORA	
Sorex bendirei	8, 38

Eadiea neurotrichus Lukoschus, Klompen, & Whitaker, 1980	
Insectivora	
Neurotrichus gibbsi	20
Eadiea scapanus Fain & Whitaker, 1975	
Insectivora	
Scapanus townsendi	6, 36
Eutalpacarus peltatus Jameson, 1949	
Insectivora	
Neurotrichus gibbsi	36
Protomyobia brevisetosa Jameson, 1948	
Insectivora	
Scapanus townsendi	36
Sorex bendirei	38
S. pacificus	38
S. trowbridgei	38
S. vagrans	38
S. yaquinae	38
Rodentia	
Clethrionomys californicus	34
Pteracarus aculeus Dusbabek & Lukoschus, 1973	
Chiroptera	
Eptesicus fuscus	41
Pteracarus sp. nr *minutus daubentoni* Dusbabek, 1973	
Chiroptera	
Myotis volans	41
Radfordia arborimus Fain & Whitaker, 1975	
Insectivora	
Scapanus townsendi	6, 33
Radfordia ewingi (Fox, 1937)	
Rodentia	
Zapus trinotatus	31
Radfordia hylandi Fain & Lukoschus, 1977	
Rodentia	
Microtus oregoni	34
Radfordia subuliger Ewing, 1938	
Rodentia	
Onychomys leucogaster	X
Radfordia zibethicalis (Radford, 1936)	
Rodentia	
Ondatra zibethicus	X
Myocoptidae	
Myocoptes japonensis Radford, 1955	
Rodentia	
Clethrionomys californicus	34
Microtus richardsoni	34
Myocoptes musculinus (Koch, 1844)	
Rodentia	
Onychomys leucogaster	X
Notoedridae	
Notoedres (*Bakeracarus*) sp.	
Chiroptera	
Eptesicus fuscus	41
Myotis volans	41
M. yumanensis	41
Plecotus townsendi	41
Pygmephoridae	
Pygmephorus designatus Mahunka, 1973	
Insectivora	
Sorex trowbridgei	38
Rodentia	
Clethrionomys californicus	34
Carnivora	
Spilogale putorius	X
Pygmephorus horridus Mahunka, 1973	
Insectivora	
Scapanus orarius	36
Sorex trowbridgei	38
S. yaquinae	28, 38
Pygmephorus johnstoni Smiley & Whitaker, 1979	
Insectivora	
Neurotrichus gibbsi	28
Pygmephorus hutterloughae Smiley & Whitaker, 1979	
Insectivora	
Scapanus townsendi	28
Pygmephorus mahunkai Smiley & Whitaker, 1979	
Insectivora	
Scapanus townsendi	28
Pygmephorus scalopi Mahunka, 1973	
Insectivora	
Scapanus orarius	28
Pygmephorus whitakeri Mahunka, 1973	
Insectivora	
Scapanus orarius	28
Spinturnicidae	
Spinturnix americanus (Banks, 1902)	
Chiroptera	
Antrozous pallidus	41
Eptesicus fuscus	41
Myotis evotis	27, 41
M. lucifugus	12, 41
M. volans	41
M. yumanensis	27, 41
Spinturnix bakeri Rudnick, 1960	
Chiroptera	
Eptesicus fuscus	41
Myotis volans	41
Spinturnix globosus (Rudnick, 1960)	
Chiroptera	
Myotis volans	41
Spinturnix orri Rudnick, 1960	
Chiroptera	
Antrozous pallidus	27, 41

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FOOD OF COUGARS IN THE CASCADE RANGE OF OREGON[1]

Dale E. Toweill[2] and Chris Maser[3]

ABSTRACT.— Animal and nonanimal items were identified in the digestive tracts of 61 cougars (*Felis concolor*) collected between 1978 and 1984 from the western slopes of the Cascade Range in Oregon. Forty-two (69%) of the cougars were taken by hunters in December and January, 18 (30%) were killed at other times of the year because of their proximity to livestock, and one animal was illegally killed in November. Black-tailed deer (*Odocoileus hemionus columbianus*) was the most common prey item, although domestic sheep (*Ovis aries*), porcupines (*Erethizon dorsatum*), and a variety of small mammals were also recorded. Masticated grass was the most common nonanimal item.

The cougar was placed under jurisdiction of the Oregon State Game Commission in 1967 because of a suspected decline in numbers in the 1950s and early 1960s (Oregon State Game Commission 1967). Prior to 1967, the cougar had been subjected to the bounty system established by the Oregon Territorial Government in 1843. The bounty system was repealed by the Oregon Legislature in 1961 (Kebbe 1961), but the cougar was not protected until it was declared a game animal in 1967. It was then protected until 1971, except for individuals that were killing livestock.

The first controlled hunt for cougars in Oregon took place in 1971; 13 were killed. Information on food habits from those 13 animals (3 from the Cascade Range) and from 12 taken in 1972 (none from the Cascade Range) was reported by Toweill and Meslow (1977). The purpose of this paper is to present data on foods of cougars from the Cascade Range of Oregon and to compare these data with other data from Oregon (Maser and Rohweder 1983, Toweill and Meslow 1977) and elsewhere.

METHODS

Most of the animals examined during this study were taken legally by hunters during the annual controlled season in December and January; one cougar illegally killed in November and confiscated by Oregon State Police was also examined. Successful hunters were required to present their cougars to personnel of the Oregon Department of Fish and Wildlife within 48 hours, at which time biological data were collected and ownership of the pelt was validated. Additional cougars, killed to protect livestock (primarily domestic sheep), were obtained throughout the year.

Sex, weight, and physical measurements were recorded for each animal either by personnel of the Oregon Department of Fish and Wildlife or by us. Digestive tracts and reproductive organs were removed, labeled, and frozen for later analysis. Each complete digestive tract was examined as three separate elements: stomach, small intestine, and colon. Because some animals were eviscerated in the field by hunters, many of whom brought in only stomachs, more stomachs than colons were available for analysis. Weight of stomach contents was recorded to the nearest gram. Endoparasites were also preserved.

Complete digestive tracts normally represented at least two meals: one in the stomach and one in the colon, with elements from both often found in the small intestine (Maser and Rohweder 1983). Items from stomachs and from colons were recorded separately. Nonanimal items, particularly fragments of vegetation, were identified to provide insight about the habitats in which meals were ingested.

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[1] This paper is dedicated to the memory of Ronald Rohweder, an employee of the Oregon Department of Fish and Wildlife, who helped initiate the study on cougars of Oregon. Ron was electrocuted 1 July 1984.

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RESULTS AND DISCUSSION

Digestive tracts of 61 cougars containing food items were examined. Information, considered to represent 115 separate meals, was obtained from 61 stomach samples and 54 colon samples.

All cougars examined in this study were collected from the western slopes of the Cascade Range in Oregon between 1978 and 1984, 40 (66%) from Douglas County, 19 (13%) from Lane County, and 1 each from Curry and Hood River counties. Because of hunt unit boundaries and because animals taken to control livestock predation were killed near human habitations, all cougars were taken at elevations below approximately 600 m (2000 ft).

Cougars taken throughout the year were examined, although most were taken during the December–January controlled season. Numbers of animals in this sample by month killed were as follows: January—14, March—6, April—3, May—1, June—1, July—2, September—4, October—1, November—2, and December—27. Data were recorded as legal hunter kills (42) and others (19).

The sex ratio of cougars in our sample was essentially even, 33 males and 28 females. Of these, 20 males and 22 females were taken during the December–January period, and 13 males and 6 females were taken at other times of the year.

Weight of stomach contents ranged from less than 1 g (traces of hair) to 3.97 kg (9 lbs).

Black-tailed deer was the food item most commonly found in cougars in winter. The dominance of deer in the diet seems a constant throughout North America, as is evidenced by studies conducted in Oregon (Maser and Rohweder 1983, Toweill and Meslow 1977), Washington (Schwartz 1943 *in* Young and Goldman 1964), Idaho (Hornocker 1970), California (Dixon 1925), Utah and Nevada (Robinette et al. 1959), Utah (Ackerman et al. 1984), Arizona and New Mexico (Hibben 1937), British Columbia (Spalding and Lesowski 1971), and throughout the western United States (Sperry *in* Young and Goldman 1964). Hippoboscid flies (*Lipoptena depressa pacifica*), a common ectoparasite of black-tailed deer, were recovered from the stomachs of four cougars.

Absence of Roosevelt elk (*Cervus elaphus roosevelti*) in the diet of cougars from the Cascade Range is puzzling. Despite their size, elk are commonly reported in the diet of cougars where ranges of the two species overlap (Ackerman et al. 1984, Hornocker 1970, Maser and Rohweder 1983, Robinette et al. 1959, Toweill and Meslow 1977). Roosevelt elk are relatively common throughout Douglas and Lane counties, although they are most often found at elevations above 600 m (2000 ft) and away from human habitations. We suspect that the lack of elk in the diet of these cougars was a result of the small sample size and low elevations at which the cats were taken.

Depredation of domestic sheep by cougars occurred all year at low frequency but seemed most common during spring. All occurrences of domestic sheep in our sample came from cougars killed because of livestock damage. The high frequency of occurrence of sheep in the diet of these cougars results from the bias introduced by the inclusion of cougars killed as a result of livestock depredations. Our data indicate that these cougars had usually fed on sheep for at least two consecutive meals.

Porcupines were recorded in the cougar diet with some regularity, and many of the cougar carcasses examined showed evidence of contact with porcupines in the form of embedded quills. The importance of porcupines in the cougar diet has been noted by Maser and Rohweder (1983) and Young and Goldman (1964). Deer, porcupines, and grass have been the most commonly reported staples of the cougar diet (Dixon 1982).

The domestic dog (*Canis familiaris*) found in the stomach of one cougar may represent feeding on carrion. Fly larvae, found among clumps of dog hair, indicated that the dog had been dead several hours before it was consumed by the cougar.

Other animals found in the diet of cougars during this study included mountain beaver (*Aplodontia rufa*), muskrat (*Ondatra zibethicus*), beaver (*Castor canadensis*), northern flying squirrel (*Glaucomys sabrinus*), dusky-footed woodrat (*Neotoma fuscipes*), Trowbridge shrew (*Sorex trowbridgei*), and hare (*Lepus* sp.) and may represent opportunistic feeding (Table 1). Such small mammals have also been found in other studies of cougar food habits but usually total less than 10% of the diet by frequency of occurrence and considerably less in terms of relative biomass consumed. Exceptions have been noted, however, in Arizona (Hibben 1937) and southern Utah (Ackerman et al. 1984).

We assumed that fish bones, found in the stomach of one cougar reportedly caught in a leg-hold trap, represented trap bait since only skull bones were found. Further, the bones were associated with litter (Douglas-fir (*Pseudotsuga menziesii*) needles, twigs, pebbles, and soil) typical of ground cover within a closed-forest stand.

Masticated green grass was found in many of the digestive tracts (Table 1), often in large amounts. Although of negligible food value (evidenced by its resistance to digestion), such grass may have served to purge some of the tapeworms commonly found in cougar intestinal tracts. We have observed, in the course of field work, recently passed scats consisting almost entirely of masticated grass with entwined tapeworms.

Vegetation associated with food items suggested that cougars fed most commonly among closed-forest habitats during the winter. Needles of Douglas-fir were found in 62% of the stomachs and 89% of the colons of cougars killed in December and January and were associated with plant remains from ponderosa pine (*Pinus ponderosa*), vine maple (*Acer circinatum*), western redcedar (*Thuja plicata*), Oregon grape (*Berberis nervosa*), and fern (*Polystichum* sp.). Douglas-fir needles were also commonly found in association with food of cougars killed other than during December and January (24% of stomach samples and 63% of colon samples). Several plant species characteristic of dry, open canopy vegetation types, not recorded from cougars taken during winter, were found in cougars collected at other times of the year: oak (*Quercus garryana*), snowbrush ceanothus (*Ceanothus velutinus*), and Pacific poison oak (*Rhus diversiloba*).

Soil, pebbles, and dry wood, evidence of a cougar having cleaned up a kill, were also found.

CONCLUSION

Black-tailed deer, porcupines, and grass are staples of a cougar's diet in the Cascade Range of Oregon, as elsewhere in North America. Cougars prey on domestic sheep when available and may take a number of species of smaller mammals (and perhaps carrion) as available. Data suggest that most feeding by cougars was done in closed-canopy vegetation types during winter and that

Table 1. Items identified from digestive tracts of 61 cougars collected from the western Cascade Range of Oregon. Data presented as number and frequency (in parentheses) of occurrence.

	Stomach[a]		Colon[a]	
Food items	Winter	Other	Winter	Other
Black-tailed deer	27 (64)	3 (16)	23 (61)	4 (25)
Domestic sheep[b]	6 (14)	7 (37)	3 (8)	5 (31)
Domestic dog	0	1 (5)	0	0
Cougar[c]	8 (19)	3 (16)	12 (32)	3 (19)
Porcupine	1 (2)	1 (5)	1 (3)	2 (13)
Mountain beaver	1 (2)	0	1 (3)	1 (6)
Muskrat	1 (2)	0	1 (3)	0
Beaver	1 (2)	0	0	0
Northern flying squirrel	0	0	1 (3)	0
Dusky-footed woodrat	1 (2)	0	0	1 (6)
Trowbridge shrew	1 (2)	0	0	0
Hare	0	0	1 (3)	0
Unidentified mammal	0	0	0	1 (6)
Unidentified fish[d]	1 (2)	0	0	0
Masticated grass	4 (10)	2 (11)	8 (21)	6 (38)
Number examined	42	19	38	16

[a] Winter: taken in December and January.
Other: killed to control livestock predation.
[b] All occurrences in cougars taken to control livestock predation.
[c] Not a food item; hair ingested during grooming.
[d] Assumed to be trap bait.

more open types may be used at other times of the year.

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FACTORS INFLUENCING NESTING SUCCESS OF BURROWING OWLS IN SOUTHEASTERN IDAHO

Richard S. Gleason[1],[2] and Donald R. Johnson[1]

ABSTRACT.— A burrowing owl (*Athene cunicularia*) population nesting on the Idaho National Engineering Laboratory (INEL) in southeastern Idaho utilized burrows excavated by badgers (*Taxidea taxus*) or natural cavities in lava flows as nesting sites. The size of the population was small (N = 13–14 pairs) in relation to the number of available nesting sites, suggesting that factors other than burrow availability limited this population. Rodents and Jerusalem crickets (*Stenopelmatus fuscus*) represented the primary prey utilized during the nesting season. This population demonstrated both a numerical (brood size) and functional (dietary) response to a decrease in the density of three species of rodents on the INEL during a drought in 1977.

Because of the ease with which active nest sites can be discovered and the diet monitored, burrowing owls are suitable subjects for a study of the relationships of nest site and prey availability to nesting success. In this paper we discuss the effects of nest site and prey availability on the reproductive success of a burrowing owl population, basing our conclusions on counts of emerging broods.

METHODS

Field work was conducted on and immediately adjacent to the Idaho National Engineering Laboratory (INEL) from 21 May to 3 August 1976 and from 10 May to 1 October 1977. About 80% of the site is covered by big sagebrush (*Artemisia tridentata*) or Douglas rabbitbrush (*Chrysothamnus viscidiflorus*). The understory vegetation consists of wheatgrasses (*Agropyron* spp.), bottlebrush squirreltail (*Sitanion hystrix*), and Indian ricegrass (*Oryzopsis hymenoides*). Winterfat (*Ceratoides lanata*) and saltbushes (*Atriplex* spp.) occur on moderately saline soils in mixed or relatively pure stands (Harniss and West 1973). Several former sagebrush sites in the southern portion of the reserve have been seeded to crested wheatgrass (*Agropyron cristatum*). These are grazed seasonally by livestock.

All areas accessible by road were searched at least once for nesting pairs. Since this species nests in burrows, attempts to count completed clutches would result in nest failure. Although one could estimate clutch size based on data from egg collections, annual fluctuations in food supply may influence the number of eggs laid by this species (Murray 1976). Henny and Blus (1981) have cautioned against the use of casual counts of broods in calculating productivity because some young have been observed to move to adjacent burrows as early as 10 days following emergence. Our estimates of brood size were not affected by such movements since each was based on at least seven counts during a period of two weeks after the young first emerged.

Castings were recovered from the vicinity of burrow entrances and dissected in the laboratory. Mammalian prey were identified by dental characteristics and the minimum number of individuals estimated from the number of paired mandibles. Invertebrate prey were identified and the minimum number of individuals estimated from counts of heads, mandibles, and elytra.

RESULTS

Only 6 nesting pairs were found on the site annually, a density of 1 pair per 58 km^2. In

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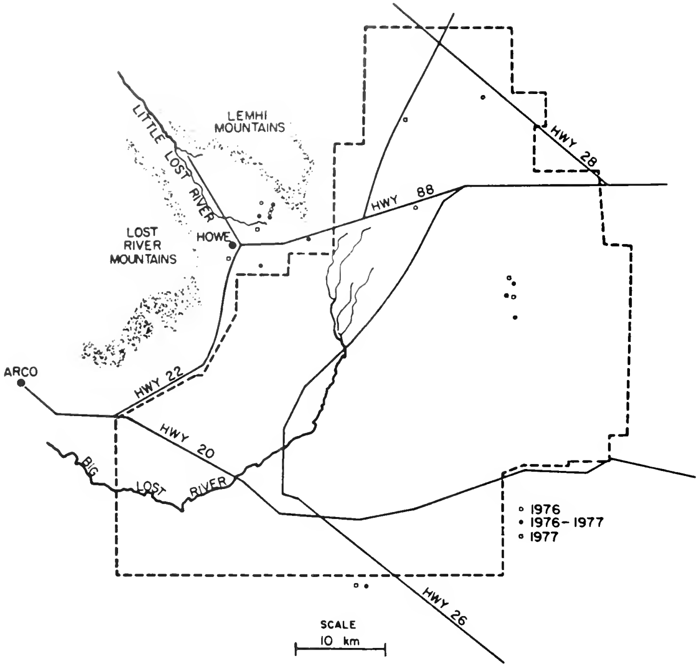

Fig. 1. Distribution of burrowing owl nesting pairs within and adjacent to the INEL, 1976 and 1977.

addition, 7–8 pairs nested adjacent to cultivated land near Howe and 1–2 pairs near Atomic City south of the INEL (Fig. 1). Approximately 75% of the nesting pairs utilized burrows excavated by badgers, and the remainder occupied natural cavities in lava flows.

Productivity was determined for 14 breeding pairs in 1976 and 13 pairs in 1977. The mean brood size of 3.6 per nesting pair (range 1–7) was smaller than that reported for other North American populations (Thomsen 1971, Butts 1971, Martin 1973, Wedgwood 1976). There was no significant difference in brood size between that of 14 pairs nesting near irrigated alfalfa crops at Howe and that of 13 pairs nesting in rangeland elsewhere on the study area ($F = 1.52$, $P > 0.05$). However, there was a significant difference in brood size between 1976, a year with normal precipitation, and 1977, when a drought occurred ($F = 3.77$, $P < 0.05$).

Of the 22 mortalities confirmed (2 nestlings, 15 juveniles, and 5 adults), 6 resulted from collisions with motor vehicles. Most of the others were recovered from the vicinity of nest sites, and the cause of death was not identified. Two nestlings were found dead within a burrow, which was excavated after the nesting pair disappeared. We assume that badgers were the major predator on nestlings prior to emergence. A badger was observed entering one of the nest burrows containing an unknown number of young, only one of which later fledged.

Food availability affected the productivity of the study population. Ord kangaroo rats (*Dipodomys ordii*), deer mice (*Peromyscus maniculatus*), and Great Basin pocket mice (*Perognathus parvus*) composed 40% of the biomass taken by burrowing owls in 1976 and 32% of that taken the following year (Table 1), a reduction in proportion that is highly significant ($Z = 13.3$, $P < 0.001$). This dietary change probably represents a functional response to the decrease in density of these species on the INEL in 1977 (Table 2). Based on analysis of castings recovered from nesting sites, there was a significant positive relationship between the biomass of rodents in the diet of individual nesting pairs and the size of their respective broods in 1976 ($r = 0.56$, $N = 10$, $P < 0.05$) but not in 1977.

DISCUSSION

Most of the burrows on the INEL probably resulted from attempts by badgers to capture Townsend ground squirrels (*Spermophilus townsendii*). However, nesting pairs also utilized badger-excavated burrows of Ord kangaroo rats near Howe, a location where no ground squirrels occurred. Given the wide distribution of prey suitable for badgers, we assume that large portions of the study area lacked burrowing owls because of factors other than the availability of suitable nesting sites.

Although fratricide may have caused some mortality before fledging, we observed no agonistic encounters between siblings. Most mortality occurred after fledging, when the young may be particularly vulnerable to starvation because of their inexperience in capturing prey.

Rodents rather than invertebrates represent a more reliable energy source during periods of food-stress because individual captures provide greater biomass. However, the use of Jerusalem crickets is energetically favorable because of their large size and ease of capture. This insect, which is common throughout the arid portions of the western United States (Essig 1936), is usually active above ground only at night, although some are found at the surface on cool, cloudy days (La Rivers 1948). We have no information on annual changes in the density of Jerusalem

TABLE 1. Diet of burrowing owls on the INEL site based on casting analysis, 1976 and 1977.

	1976			1977		
	N	% N	Percent biomass	N	% N	Percent biomass
Mammals	340	12.6	85.6	160	4.9	61.5
Dipodomys ordii	59	2.2	21.7	44	1.4	23.7
Microtus montanus	89	3.3	22.6	56	1.7	20.8
Perognathus parvus	84	3.1	8.4	39	1.2	5.7
Peromyscus maniculatus	84	3.1	9.6	14	0.4	2.3
Thomomys talpoides	23	0.9	23.1	6	0.2	8.8
Mus musculus	1	<0.1	<0.1	1	<0.1	<0.1
Birds						
Unidentified passerine	1	<0.1	<0.1	1	<0.1	<0.1
Amphibians						
Scaphiopus intermontanus	6	<0.1	0.1	2	<0.1	0.1
Arachnids	520	19.4	4.2	480	14.8	5.8
Scorpionidae	244	9.1	2.4	251	7.8	3.6
Solpugidae	276	10.3	1.8	229	7.1	2.2
Insects	1824	67.8	9.6	2595	80.1	32.3
Gryacrididae	491	18.2	6.6	1451	44.8	28.4
Acrididae	78	2.9	0.3	209	6.5	1.3
Cicadidae	10	0.4	<0.1	—	—	—
Carabidae	69	2.6	<0.1	22	0.7	<0.1
Silphidae	156	5.8	0.3	84	2.6	0.2
Scarabaeidae	267	9.9	0.5	222	6.9	0.6
Tenebrionidae	125	4.6	0.5	15	0.5	0.1
Formicidae	21	0.8	<0.1	33	1.0	<0.1
Unid. Hymenoptera	48	1.8	<0.1	7	0.2	<0.1
Unid. Coleoptera	559	20.8	1.1	552	17.0	1.6
Total	2691			3238		

TABLE 2. Availability (N/100 trap days) and utilization of major prey species on the INEL, 1976 and 1977.

Species	1976		1977		% Biomass in diet	
	Spring	Fall	Spring	Fall	1976	1977
Peromyscus maniculatus	64	87	56	26	3.0	0.3
Perognathus parvus	4	9	6	1	3.7	1.4
Dipodomys ordi	17	33	25	16	1.9	1.6
				Total	8.6	3.3

crickets on the INEL during this period, but their biomass in the diet increased from 6.6% in 1976 to 28.4% in 1977. This food source served to buffer the effects of a reduction in rodent density in 1977. Jerusalem crickets were an important dietary component of this nesting population in an earlier study (Gleason and Craig 1977), as well as that of other nesting populations (Thomsen 1971, Green 1983). We suggest that the density of Jerusalem crickets as well as that of rodents should be monitored in future investigations of numerical and functional responses of burrowing owl populations in the western United States.

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NOTE ON THE DIET OF LONG-BILLED CURLEW CHICKS IN WESTERN IDAHO

Roland L. Redmond[1] and Donald A. Jenni[1]

ABSTRACT.— The diet of Long-billed Curlew chicks is described for the first time. Five insect orders and one arachnid order were identified from nine stomach contents samples. Grasshoppers and carabid beetles were dominant prey items.

Chicks of precocial, nidifugous shorebirds are generally difficult to study because they are very mobile and hard to locate. As part of a larger study of Long-billed Curlew (*Numenius americanus*) behavioral ecology, we collected preliminary data on chick food habits. Owing to the difficulty of obtaining samples without sacrificing any chicks, the data are limited. Nonetheless, they are unique for Long-billed Curlews and rare for any nidifugous species.

The study area was a short-grass rangeland (ca 21,000 ha) lying between the Payette, Boise, and Snake River valleys in western Idaho (Redmond et al. 1981). We collected stomachs from six recently depredated chicks (aged 14–46 days) during June and July 1978. These were stored frozen until the contents could be removed in the lab. In addition, we took samples of stomach contents from three live chicks weighing at least 300 g (aged 34–44 days) during July in 1977 and 1978. As an emetic, we introduced a 1% solution of antimony potassium tartarate directly into the proventriculus (0.4 cc/100 g body mass, modified after Prys-Jones et al. 1974). Chicks were then held in a closed box until they regurgitated a sample (ca 10 min). Prior to release, each chick was fitted with a radio transmitter, and its subsequent movements and growth monitored for a minimum of four days posttreatment. All chicks survived this period with no visible ill effects from the emetic. Stomach contents were placed in 70% ETOH and then sorted according to taxon using a dissecting microscope, reference collections, and appropriate keys.

We identified five insect orders and one arachnid order from the nine stomach contents samples. Orthoptera were found in all nine, Coleoptera in eight, and Hemiptera, Lepidoptera (larvae), and Arachnida were found in just one each. Grasshoppers were the only orthopterans and carabid beetles the only coleopterans that we identified. As such, these two groups appeared to be important prey for Long-billed Curlew chicks.

Grasshopper eruptions on the study area generally began in late May, coincident with the annual peak of Long-billed Curlew hatching, and continued into August. By late June each year, grasshoppers were locally abundant, and they became more conspicuous through July. Given the collection times of our stomach contents samples, the dominance of grasshoppers was expected. A similar prevalence of carabid beetles, however, was surprising. These beetles appeared to be far more abundant earlier in the season (April–May). We suspect that, although grasshoppers might have been more numerous in June and July, their mobility reduced their overall vulnerability to Long-billed Curlew chicks. Conversely, a relatively slow-moving black beetle (Barrs 1979), once encountered, would be easy prey.

Because our ability to identify all material from the stomachs was limited by the nature of the samples (see Custer and Pitelka 1975), our data almost certainly underestimate the diversity of prey types taken by Long-billed Curlew chicks. We conclude that these chicks, like their parents (Sadler and Maher 1976, Bicak pers. comm.), take a wide variety of prey according to what is most available and vulnerable on the rangeland.

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TUNDRA VEGETATION OF THREE CIRQUE BASINS IN THE NORTHERN SAN JUAN MOUNTAINS, COLORADO

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Abstract.— The vegetation of three alpine cirque basins in the northern San Juan Mountains of southwestern Colorado was inventoried and analyzed for the degree of specificity shown by vascular plant communities for certain types of habitats identified as representative of the basins. A total of 197 vascular plant species representing 31 families was inventoried. Growth forms of all species were noted and a growth form spectrum for all of the communities was derived. The caespitose monocot and erect dicot growth forms are the most important growth forms among the community dominants. The most common growth form among all species is the rosette dicot.

Since the early 1900s a number of ecological studies have been undertaken in the alpine tundra of the Front Range of Colorado (Cooper 1908, Holm 1923, Cox 1933, Osburn 1958, Marr 1961, Willard 1963, Komarkova 1976, Flock 1978, May and Webber 1982). However, the alpine tundra of central and southwestern Colorado remains relatively unknown (Langenheim 1962, Johnson 1969). A floristic study was done by Michener (1964) in the subalpine and alpine zones of the Needle Mountains in the southern San Juan Mountains. Another major study in the southern San Juan Mountains, an analysis of snowpack augmentation by Steinhoff and Ives (1976), included the alpine zone as well as the forest ecosystems below. There is no published botanical work on the alpine vegetation of the northern San Juan Mountains. In this study the vegetation of three alpine cirque basins in the northern San Juans was inventoried and analyzed for the degree of specificity shown by individual species and aggregations of species for certain types of habitats.

Study Area

The San Juan Mountains are a discontinuous section of the Southern Rocky Mountains situated along the Continental Divide in southwestern Colorado. They are located between 106 and 108 degrees west longitude and 36 degrees 30 minutes and 38 degrees 15 minutes north latitude (Atwood and Mather 1932). Sharp pinnacles, rounded crests, serrate ridges, and broad upland erosional surfaces characterize the alpine zone of these mountains. The elevation of the San Juans ranges from 1524 m in the southwest corner to 4358 m at the summit of Uncompahgre Peak. They are composed largely of Tertiary volcanic tuffs and lavas that lie unconformably over metamorphic sedimentary and volcanic intrusive rocks of Precambrian age as well as sediments of Paleozoic, Mesozoic, and early Cenozoic age (Casadwall and Ohmoto 1977). Broad regional ice fields and transection glaciers occurred during the Pleistocene, producing cirques, basins, tarns, hanging valleys, and broad U-shaped valleys. Today periglacial features such as active patterned ground, active rock glaciers, and persistent ponds indicate the occurrence of sporadic or discontinuous permafrost (Ives and Fahey 1971, Barsch 1978).

Three alpine cirque basins, representative of the northern San Juan Mountain tundra, were studied. American Basin, Hinsdale County, is characterized by a well-developed moist turf mantle interrupted by areas of bedrock outcrops, talus deposits, and patterned ground features. The vegetation in this basin reflects a more moist climatic regime than in the other two basins, as evidenced by the predominance of moist meadows, absence of dry meadows, and minimal occurrence of fell-fields. The elevational range of this basin is 3536–3962 m.

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Burns Basin, San Juan County, has a northwest–southeast orientation. The convex slopes forming the perimeter of the main basin present an interesting contrast of moisture regimes. The southwest-facing slope is characterized by a dry turf alternating with fell-fields and unvegetated talus. The northwest-facing slope consists of a series of tiers of massive moist and wet ledges with adjacent moist meadows. Midsection of the basin consists of moist and wet meadows. The elevational range of this basin is 3634–3932 m. Both Burns and American basins have rock glacier complexes composed of tongue and lobate units.

Stony Basin, San Juan County, is formed of three broad turf-mantled steps, each separated by a bedrock escarpment. Because of its topographic position, the basin is continually buffeted by strong wind resulting in a more severe climatic regime than is found in the other two basins. Islands of dry meadows and fell-fields interrupt the moist meadow of the upper two steps of the basin. The latter have an abundance of frost-associated features including frost boils, patterned ground, ephemeral ponds, and rock debris islands. The lower step is characterized by a shallow lake and hummocky wet meadow. The elevational range of Stony Basin is 3764–3926 m.

METHODS

Three field seasons, 1981–1983, were involved in the study. One hundred ninety-nine habitats and their associated vascular plant communities were sampled. The abundance of each species was estimated using the standard abundance classes of Daubenmire (1968). As data from multiple samples of a particular habitat type accumulated, the inventoried species and their abundance ratings were analyzed on the basis of constancy of occurrence between samples (Mueller-Dombois and Ellenberg 1974). The terms used in describing the species within a community, dominant, secondary, frequent, occasional, and rare, are defined as follows. A dominant species is very abundant (abundance class) and occurs with a high constancy (80.1%–100%). A frequent species is frequent in abundance and has an intermediate constancy (40.1%– 60%). An occasional species occurs in scattered instances, and its presence or absence is inconsequential to the character of the community in which it may occur. It is occasional in abundance and has a low constancy (20.1%–40%). A rare species is both rare in abundance and rare in constancy (1.0%–20%).

The term *habitat type* in this study refers to all of the area (sum of discrete units) that support one plant community. A habitat type may be considered as the abiotic equivalent of the stand-type in that the habitat type is a synthetic unit whose characteristics are obtained by combining all the samples of a particular habitat. The habitat types defined are: dry ledge, moist-wet ledge, rock crevice, talus slope, patterned ground, fell-field, dry meadow, moist meadow, wet meadow, shrub tundra, and krummholz. Nomenclature follows Kartesz and Kartesz (1980).

RESULTS

In the following description of habitat types and associated communities, only the dominant and secondary or more important species are listed.

Ledge Habitat Type

The rock ledge habitat consists of the bedrock outcrops which, as a result of jointing and weathering, form benches and channels where windborne fines are deposited and organic debris is accumulated to form a substrate for vegetation. The orientation of the bedrock and amount of protection provided by rock overhang are controlling factors in the microenvironment of this habitat type (Younkin 1970). For purposes of vegetation analysis, the ledge habitat is divided along a moisture gradient and includes dry ledges and moist-wet ledges. Two communities are found in the dry ledge habitat and three in the moist-wet ledge habitat.

Geum rossii var. *turbinatum* and *Selaginella densa* are frequent species in one of the dry ledge communities. Other important species include *Aquilegia coerulea, Cystopteris fragilis, Draba crassa, Potentilla subjuga* var. *subjuga, Silene acaulis* var. *subacaulis,* and *Smelowskia calycina*. The other dry ledge community is characterized by *Carex haydeniana, Cerastium earlei, Draba crassa, Festuca brachyphylla, Potentilla nivea, P. rubricaulis, Saxifraga flagellaris* ssp. *platysepala,* and *Trifolium nanum.*

One of the moist-wet ledge communities is dominated by *Geum rossii* var. *turbinatum,* with *Carex albonigra, C. heteroneura* var. *chalciolepis, Erigeron melanocephalus,* and *Saxifraga cespitosa* ssp. *delicatula* as important associates. Another moist-wet ledge community has *Salix reticulata* ssp. *nivalis* as dominant. Associated with this species are *Carex albonigra, Salix arctica, Saxifraga adscendens* ssp. *oregonensis,* and *S. debilis.* Ledges with snowmelt water running through fissures in the rock constitute the third possible moist-wet ledge habitat. These are dominated by *Cardamine cordifolia* at the base of the ledges and *Salix reticulata* ssp. *nivalis* on the benches. *Caltha leptosepala, Carex nova, Primula parryi, Sedum rhodanthum,* and *Sibbaldia procumbens* are present in this community.

Rock Crevice Habitat Type

This is a restrictive habitat type that only includes soil-filled crevices on solitary boulders or contained crevices on rock outcrops or headwalls in the basins. The community concept is loosely applied to the species in these habitats. The only relationship that the singly-occurring species have to one another is their presence on the same boulder or bedrock substrate. Certain species are frequently found in rock crevices: *Androsace septentrionalis, Artemisia scopulorum, Claytonia megarhiza, Draba crassa, D. crassifolia, Festuca brachyphylla,* and *Oreoxis bakeri.*

Talus Slope Habitat Type

Extensive talus slopes occur throughout the basins. White (1981) defines talus as an accumulation of rock debris of various sizes transported from the source areas by gravity, rainwash, snowmelt water, or snow avalanching to a site below. Fine material may be present in the interstices of the rock material; these fines provide a suitable substrate for vegetation. Although dominance within the talus slope community is poorly defined, certain species show a high constancy for this habitat: *Angelica grayi, Aquilegia coerulea, Cerastium earlei, Claytonia megarhiza, Polemonium viscosum, Senecio amplectens* var. *amplectens, S. amplectens* var. *holmii, S. soldanella,* and *S. werneriifolius.*

Patterned Ground Habitat Type

Washburn (1956) defines patterned ground as, "a group term for the more or less symmetrical forms, such as circles, polygons, nets, steps and stripes, that are characteristic of, but not necessarily confined to, a mantle subject to intensive frost action." The forms of patterned ground found in the study basins are nonsorted circles (frost boils and frost hummocks), sorted polygons, and debris islands. The centers of the sorted forms have from little to no vegetation because of the associated frost action that keeps the soil sufficiently disturbed to prevent plant colonization (Johnson and Billings 1962). The communities found in patterned ground habitats vary with the specific type of patterned ground form. Frost boils are another example of a habitat for which the community concept must be loosely applied. Several species are repeatedly found associated with frost boils: *Cerastium earlei, Draba crassifolia, Geum rossii* var. *turbinatum, Oreoxis bakeri,* and *Stellaria umbellata.* Frost hummock areas are traversed by water-filled channels in the wet meadows. The dominant species on the elevated portion of the hummock is *Carex nigricans.* Secondary species are *Carex pseudoscirpoidea* and *Festuca brachyphylla.* Dominant species in the saturated areas at the base of the hummocks are *Carex aquatilis* and *C. vernacula. Caltha leptosepala* and *Carex nova* are secondary species in these areas. Sorted polygons are characterized by lichenized rocks in the borders. The central fines of the polygons support a *Carex nigricans–Sibbaldia procumbens* community. Frequent associates in this community are *Artemisia scopulorum, Erigeron melanocephalus,* and *Juncus drummondii.* Debris islands, a sorted form of patterned ground, occur as repetitive units on talus debris. The vegetation on these islands suggests a successional development from talus slope to meadow. Depending upon the seral stage of development, dominant species may be either *Salix reticulata* ssp. *nivalis* and *Silene acaulis* var. *subacaulis*, or *Senecio amplectens* var. *holmii* and *S. soldanella*.

Fell-field Habitat Type

The fell-field habitat type is characterized by a high proportion of weathered rock material. Soils are coarse textured, with little organic material and only rudimentary profiles. Fell-fields occur on windward sites, with little or no snow cover, thus exposing the plants and soil to severe dessication. The longest growing season in the tundra occurs in this habitat type. The high diversity found in fell-field communities is contributed primarily by the frequent and occasional species. One of the fell-field communities is dominated by *Silene acaulis* var. *subacaulis* and *Geum rossi* var. *turbinatum*, with *Minuartia obtusiloba*, *Potentilla diversifolia*, *Selaginella densa*, and *Trifolium nanum* as secondary species. Another fell-field community has *Carex elynoides* and *Geum rossii* var. *turbinatum* as dominants. Secondary species include *Festuca brachyphylla*, *Minuartia obtusiloba*, *Selaginella densa*, and *Trifolium nanum*. *Carex elynoides* and *Trifolium nanum* are dominants in the fell-field community occurring on slopes and ridge tops. Associated with these species are *Festuca brachyphylla*, *Geum rossii* var. *turbinatum*, and *Silene acaulis* var. *subacaulis*.

Dry Meadow Habitat Type

The dry meadow habitat type occurs on exposed windy slopes high in the basins, where strong winds create snow-free conditions throughout much of the winter. The vegetation in these sites reaches anthesis early in the season, thus completing the growth cycle before vegetation in more protected areas reaches maturity. The most extensive dry meadow community is dominated by *Carex elynoides*. Secondary species include: *Festuca brachyphylla*, *Geum rossi* var. *turbinatum*, *Hymenoxys grandiflora*, *Poa rupicola*, and *Trisetum spicatum*. A minor and highly restricted dry meadow community is dominated by *Kobresia myosuroides*. *Carex ebenea*, *C. heteroneura* var. *chalciolepis*, *C. pseudoscirpoidea*, *Luzula spicata*, and *Trisetum spicatum* are secondary species in this community.

Moist Meadow Habitat Type

This is perhaps the most widespread habitat type in the study basins and is most representative of the tundra in the northern San Juan Mountains. The moist meadows are situated on the lee slopes and in topographical concavities protected from the winter climate by snow accumulation that may remain until mid-July. The moist meadow may be regarded as a complex of several communities, each with a distinct spatial occurrence within the complex. A *Deschampsia caespitosa–Geum rossii* var. *turbinatum* community is found in lower sites on basin slopes and in concavities. Associated with these species are: *Artemisia scopulorum*, *Carex albonigra*, *C. nova*, *Oreoxis bakeri*, *Polygonum bistortoides*, and *Saxifraga rhomboidea*. In flat areas at midslope, a *Carex nigricans–Sibbaldia procumbens* community occurs with *Carex vernacula*, *Erigeron melanocephalus*, *Juncus drummondii*, *Oreoxis bakeri*, *Polygonum viviparum*, and *Ranunculus macauleyi* as secondary species. The third community in the complex, dominated by *Salix reticulata* ssp. *nivalis*, is present on the highest moist meadow sites in the basins. Secondary species include *Artemisia scopulorum*, *Erigeron simplex*, *Salix arctica*, *Sibbaldia procumbens*, and *Silene acaulis* var. *subacaulis*.

Wet Meadow Habitat Type

Wet meadows are situated on relatively flat surfaces below late-lying snowbanks, in catchment areas in the basins, and adjacent to ponds, lakes, and streams. Frequently dissected by rivulets, these areas are often associated with the presence of sporadic permafrost (Johnson and Billings 1962, Ives 1974). As a result of permafrost in the substrate and the runoff, the wet meadows are saturated throughout the growing season. Where shallow, standing water is present, a *Caltha leptosepala–Cardamine cordifolia*-dominated community occurs. The secondary species are *Carex nova*, *Juncus drummondii*, *Pedicularis groenlandica*, *Primula parryi*, *Sedum integrifolium*, and *Trifolium parryi*. A second community, dominated by *Caltha leptosepala* and *Juncus drummondii*, is characteristic of better drained sites. Associated species include: *Carex aquatilis, Festuca brachyphylla, Geum rossii* var. *turbinatum, Primula parryi, Sibbaldia procumbens,* and *Trifolium parryi.*

Shrub Tundra Habitat Type

The shrub tundra habitat type is made up of shrub thickets of *Salix brachycarpa* or *S. planifolia* and associated vegetation. A minor constituent of the basins in this study, this habitat type is limited to moist depressions and drainage areas. The moist areas are dominated by *Salix planifolia.* Secondary species in this community are: *Carex ebenea, C. heteroneura* var. *chalciolepis, C. nova, C. pseudoscirpoidea,* and *Geum rossii* var. *turbinatum.* A *Salix brachycarpa*-dominated community occurs on well-drained slopes. A drier environment is reflected in the associated species: *Phacelia sericea, Polemonium viscosum, Pontentilla diversifolia, Sedum lanceolatum,* and *Trifolium nanum.*

Krummholz Habitat Type

Timberline elevations range from approximately 3535 to 3720 m in the study basins. The ecotonal area characteristically has representative species from both the alpine and subalpine zones. Krummholz conifer species, *Abies lasiocarpa* and *Picea engelmannii,* are dominant and exert a primary influence on the surrounding environment and vegetation. The associated species are highly variable from one krummholz habitat to another; however, a list of the more frequent species serves to illustrate the ecotonal nature of the community: *Aquilegia coerulea, Arnica cordifolia, Dugaldia hoopesii, Minuartia obtusiloba, Polygonum bistortoides, Ribes montigenum, Silene acaulis* var. *subacaulis,* and *Thalictrum fendleri.*

DISCUSSION

A total of 197 vascular plant species representative of 31 families was inventoried in the study basins (Rottman 1984). Basin orientation, variability of moisture regimes, degree of protection from wind, amount and nature of weathering, debris transport, and slope aspect determine the occurrence of specifc habitat types and associated communities in terms of the dominant and secondary species. Minor variations are seen in the occurrence of occasional species. Rare species have a higher occurrence in the rock-predominating habitats, where competition appears to be less than in a closed turf meadow.

A consistent tendency toward dwarfing of species is noted in the *Carex nigricans–Sibbaldia procumbens* and *Salix reticulata* ssp. *nivalis*–dominated moist meadow communities. This appears to correlate with a pattern of late snow release. As noted by Owen (1976), plants of the same species under conditions of higher elevation and later snowmelt mature and flower at a smaller size than plants not under these conditions.

The *Kobresia myosuroides*-dominated dry meadow, which has long been recognized as the climatic climax of the Front Range (Cox 1933, Osburn 1958, Bamberg 1961, Marr 1961, Willard 1963), is highly restricted in its occurrence in the northern San Juan Mountains and is replaced in importance by a *Carex elynoides*-dominated dry meadow community.

Carex Indicators

Some members of the Cyperaceae, *Carex albonigra, C. arapahoensis, C. heteroneura* var. *chalciolepis,* and *C. pseudoscirpoidea,* have rather broad ecological tolerances that enable them to grow in both dry and moist habitats. *Carex nova* and *C. vernacula* occur in moist as well as wet habitats. Other *Carex* species are more specific in their moisture requirements or tolerances and are useful indicators of substrate moisture conditions. Indicators of dry substrates are: *Carex elynoides, C. perglobosa,* and *C. phaeocephala.* Indicators of moist substrates are: *C. nelsonii, C. nigricans, C. norvegica, C. pyrenaica,* and *C. nardina* var. *hepburnii. Carex aquatilis* is an indicator of wet substrates often characterized by standing water.

Species Growth Forms

Each species found in the study basins was assigned to a growth form category. The growth forms of May and Webber (1982) were used. Based primarily on the nature of the shoot habit, these growth forms include: caespitose monocot, single-shooted monocot, erect dicot, rosette dicot, mat dicot, cushion dicot, erect shrub, and dwarf shrub.

The caespitose monocot is a tufted graminoid growth form. Graminoid sods are able to modify the microenvironment to a greater extent than any other growth form or pattern of spatial distribution (Billings 1974). When compared to other growth forms, the percentage of caespitose monocot species is relatively small (9%); however, this growth form contributes the greatest percentage of dominants in the communities analyzed.

The single-shooted monocot growth form is represented primarily by grasses and sedges (25 species, 12% of total). Although this category has more species than the caespitose monocot, it is never dominant within a community.

The highest percentage of species (38%) and the second highest percentage of dominants in the communities are erect dicots. Since both the root and shoot systems of erect dicot plants require less space for lateral spread, this growth form is compatible with extremely rocky habitats where only a minimal amount of soil is available.

The importance of the rosette dicot growth form (26%) is reflected in the fact that approximately 70% of the species with ubiquitous occurrences in the study basins are in this category. This growth form is found in all the habitat types studied and appears to be equally abundant in both meadow and rock habitats.

The mat (6%) and cushion dicot (2%) growth forms are minor in occurrence. Both of these growth forms are considerably more important in tundras to the north, where their greater occurrence is correlated with an increased wind factor. The erect and dwarf shrub growth forms are another minor segment of the growth form spectrum accounting for a combined 7% of the total species.

Community Specificity

The specificity of communities for particular habitat types was evaluated on the basis of community dominants. Although habitat types are physically discrete and recognizable, a one-habitat type/one-community concept is not applicable. A similar finding is reported by Douglas (1972). It was found that virtually all habitat types have more than one potential community with different dominants and that some dominants are repetitive, by themselves or in combination, in different habitat types.

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USE OF BIOMASS PREDICTED BY REGRESSION FROM COVER ESTIMATES TO COMPARE VEGETATIONAL SIMILARITY OF SAGEBRUSH-GRASS SITES

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Abstract.— Regressions between vegetational cover, estimated with a two-tiered, gridded sampling frame, and biomass were used to obtain predicted biomass values from cover values. Comparisons of eight sites based on predicted biomass data and comparisons of the sites based on cover data indicate that predicted biomass data may better identify differences among sites. Also, some suggestions are made regarding the methods of using cover-biomass regressions to obtain predicted biomass values.

Biomass data are generally considered to most precisely represent the relative importance of species in a community (Whittaker 1975). However, biomass sampling is often time consuming, especially when sampling a large number of plots is required. As an alternative, many methods of cover estimation have been used. Methods of weight estimation (Pechanec and Pickford 1937, Wilm et al. 1944, Tadmore et al. 1975) and relative weight estimation (Hutchings and Schmautz 1969) have also been used. However, weight estimation methods are inherently dependent on the skill of the observer and results may vary. Cook et al. (1948) estimated units of cover, determined biomass per unit, and obtained biomass estimates by multiplying mass per unit of cover by number of units of cover for a species. Payne (1974) presented linear regressions between cover and biomass for many herbaceous species. Anderson and Kothmann (1982) presented a method of calculating mass from estimated cover based on linear regression between cover and mass. Such methods can give data that approximate biomass data but require much less time than extensive biomass sampling.

Following methods similar to those of Anderson and Kothmann (1982), I used regressions between biomass and cover to obtain predicted biomass values from cover values for species on eight sagebrush (*Artemisia tridentata*) -grass sites. Cover estimates used in the regressions were obtained by a method that is more consistent and depends less on the skill of the observer than does weight estimation or many other cover estimation methods. The use of a more precise and consistent cover estimation method should result in better cover-biomass regressions. The methods by which regressions were calculated differed most notably from those of Anderson and Kothmann (1982) in that sizes of biomass samples used in my regressions were representative of the range of sizes of cover values commonly encountered in cover sampling. Also, some suggestions are made regarding the methods of using cover-biomass regressions to obtain predicted biomass values. Using the predicted biomass values for these eight sites, I present an assessment of advantages of predicted biomass data over cover in comparing vegetation among sites. I compared vegetational similarity among the eight sites based on predicted biomass values to vegetational similarity among the same sites based on cover values. This comparison indicated that predicted biomass values may often better identify differences among sites than can cover data.

Methods

The results presented here are based on data collected on eight sites in southeastern Idaho for a study of postfire succession in sagebrush-grass areas (Humphrey in press). Each sample site consisted of a 100- x 50-m plot. On each site, ten 50-m lines were established parallel to the 50-m axis of the site.

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These lines were chosen at random from a population of 100 lines that were at 1-m intervals along the 100-m axis. On each 50-m line, there were five sample points at 10-m intervals for a total of 50 sample plots on each site.

A 1.0- x 0.5-m sampling frame consisting of two tiers, superimposed 10 cm apart and gridded off in 1-dm^2 divisions, was used for cover estimation. The superimposed grids made it possible to sight vertically for estimating cover in each 1 dm^2. The frame was placed at each sample plot and leveled by use of adjustable legs and level bulbs on the frame. Cover for each species was estimated to the nearest 1/4 dm^2 (or 1/8 dm^2 in the case of very small plants). This method is more precise and less dependent on skill or bias of the observer than estimation by cover class (e.g., Daubenmire 1959) or other estimation methods that use single-tiered sampling frames because the superimposed grids make it possible to more accurately sight each dm^2. Floyd and Anderson (1982) described the use of a similar frame for cover estimation by point sighting. The point sighting method should also give reliable data and is less time consuming than the cover estimation method used in this study.

On one of every 10 cover plots on each site, the current year's growth of each species was clipped, oven dried, and weighed to determine aboveground biomass. In this way, biomass samples of several sizes representative of the range of sizes of cover samples commonly encountered was obtained. Thus, the regressions could be assumed to be valid for the entire range of cover values encountered. (Alternatively, representative biomass samples for each species could be taken (Anderson and Kothmann 1982), but these samples should encompass the range of sizes of cover samples commonly encountered.) Linear regressions between cover and oven dry biomass were calculated from biomass values and corresponding cover values for the clipped plots, with biomass as the independent variable. (Biomass was chosen as the independent variable because cover was considered to be an estimated value that is dependent on the more precisely determined biomass.) Individual regressions were calculated for single species or for groups of morphologically similar species using pooled data for the eight sites. An equation for inverse prediction from regression equations (Zar 1974) was used to obtain a predicted biomass value from each cover value for each species. If the Y intercept was significantly different from zero, a regression forced through the origin was done (Snedecor and Cochran 1980), and this regression was used to obtain predicted biomass values.

Similarity index values for each site paired with each of the other sites (Bray and Curtis 1957) were calculated with both cover values and predicted biomass values. These similarity index values were used to compare the way these two data sets described differences among the eight sites. The sign test (Snedecor and Cochran 1980) was used to determine if the two sets of similarity index values were significantly different, and the nature of differences between the two sets of similarity index values was examined.

RESULTS AND DISCUSSION

Good cover-biomass regressions were obtained for several individual species and for several groups of two or more species that were judged to be morphologically similar (Table 1). Some of these groups are obviously morphologically similar, such as the group *Chrysothamnus viscidiflorus* (green rabbitbrush), *C. nauseosus* (gray rabbitbrush), and *Gutierreza sarothrae* (broom snakeweed), the group *Artemisia tridentata* (big sagebrush), *A. tripartita* (threetip sagebrush), and the group *Balsamorhiza sagittata* (arrowleaf balsamroot), *B. macrophylla* (bigleaf balsamroot), and *Wyethia amplexicaulis* (mule's ear). Other groups are perhaps less obviously similar, although they are similar enough to provide good cover-biomass regressions. The annual species in group 8 in Table 1 are morphologically similar in that they are all small, slender annuals. *Agropyron dasystachyum* (thickspiked wheatgrass) and *A. spicatum* (blue-bunch wheatgrass) were grouped together because, on these sites, *A. dasystachyum* usually grew in quite dense stands, making its growth habit similar to that of *A. spicatum*. If desired to reduce the number of regressions calculated, or the number of biomass samples taken, it appears that single regressions can often be done for groups of species similar in morphological characteristics such as height, leaf size, and leaf density.

Relationships between cover and biomass for the same species may vary with differences in site characteristics such as productivity, mesicness, and other species present. But a regression should be consistent for the same species on other sites in addition to those sites where biomass samples were obtained, if the data used to calculate the regression cover the range of differences in site characteristics of those other sites, and if the regression explains much of the variance in Y (has a high r^2). Thus, if these conditions are met, the same regressions could be used for different sites and different studies, if the species are in roughly the same seasonal stage of development (for example, peak biomass) and the same cover estimation method is used. In this way, the amount of time-consuming biomass sampling needed to obtain predicted biomass values can be reduced even further. Regressions have been used in a similar manner to obtain biomass estimates for trees (Whittaker 1966, Dabel and Day 1977).

The percent similarity values among sites based on predicted biomass data were significantly different (at the 1% level) from those based on cover data by sign test comparison. Predicted biomass data indicated lower similarity among sites, i.e., greater distinctions among sites over all. The difference between the medians of the two sets of similarity index values was rather small, but the maximum and minimum values of the two sets show that predicted biomass data also indicated greater extremes of high and low sim-

Table 1. Results of cover-biomass regressions for species or groups of morphologically similar species. Cover data was in cm^2; biomass data was in g. For species or species groups where the Y intercept of the regression was significantly different from zero, the results of the regression forced through the origin are presented. Slopes of all regressions listed are significant ($P < 0.05$). Y is cover; X is biomass (independent variable). (Nomenclature of all plants follows Hitchcock and Cronquist 1973.)

Group	Species	Regression	r^2	n
1	*Phlox longifolia*	$Y = 0.30X$ (forced through origin)	0.80	9
2	*Lithospermum ruderale*, *Helianthella uniflora*	$Y = 0.339 + 0.197X$	0.94	14
3	*Crepis acuminata*, *Achillea millefolium*	$Y = -0.158 + 0.632X$	0.91	11
4	*Balsamorhiza sagittata*, *B. macrophylla*, *Wyethia amplexicaulis*	$Y = 0.083 + 0.357X$	0.99	10
5	*Penstemon spp.*	$Y = 0.844 + 0.325X$	0.78	13
6	*Tragopogon dubius*	$Y = 0.184 + 0.517X$	0.84	8
7	*Lupinus spp.*	$Y = 0.272 + 0.286X$	0.92	7
8	*Polygonum douglasii*, *Gayophytum diffusum*, *Collomia linearis*, *Lappula redowskii*	$Y = 1.34X$ (forced through origin)	0.94	14
9	*Cirsium arvense*	$Y = 0.789 + 0.114X$	0.95	8
10	*Bromus tectorum*	$Y = 1.024X$ (forced through origin)	0.86	13
11	*Agropyron dasystachyum*, *A. spicatum*	$Y = 0.114 + 0.488X$	0.80	23
12	*Poa nevadensis*, *P. sandbergii*	$Y = 0.188 + 0.186X$	0.77	14
13	*Poa pratensis*	$Y = 0.597 + 0.439X$	0.95	7
14	*Artemisia tridentata*, *A. tripartita*	$Y = 2.744 + 0.185X$	0.77	17
15	*Chrysothamnus viscidiflorus*, *C. nauseosus*, *Gutierreza sarothrae*	$Y = 0.294 + 0.366X$	0.92	16
16	*Amelanchier alnifolia*, *Symphoricarpos oreophilus*	$Y = 0.968 + 0.235X$	0.80	10
17	*Purshia tridentata*	$Y = 0.275 + 0.235X$	0.99	8

TABLE 2. The median and the maximum and minimum values of the set of similarity index values based on cover and based on predicted biomass.

	Cover	Predicted biomass
Median:	34.1	32.1
Maximum:	56.4	58.8
Minimum:	13.5	10.8

ilarity among sites (Table 2). In other words, similar sites appeared more similar, and dissimilar sites appeared less similar. The difference between each similarity index value based on predicted biomass and the corresponding value based on cover (Fig. 1) illustrates more clearly that predicted biomass data indicated less similarity among sites over all and a greater range of similarities among sites. At low similarities, predicted biomass data indicated lower similarity between sites than did cover; at moderate similarities, it indicated lower similarity than did cover in most cases; while at relatively high similarities it tended to indicate greater similarity between sites than did cover.

This study suggests that predicted biomass data may often describe distinctions among sites better than cover data. For differences to exist between comparisons of sites based on the two types of data, differences in the relationship of biomass to cover must exist among species, and the species with different ratios of biomass to cover must be unevenly distributed among sites. In this study, predicted biomass data tended to indicate greater differences among sites because predicted biomass data emphasized species with higher ratios of biomass to cover, and many species that varied more in abundance among sites had higher ratios of biomass to cover. These were tall herbaceous species (groups 2, 9 in Table 1) and shrubs (groups 14, 16, 17 in Table 1). Similarly, predicted biomass data indicated higher similarity than did cover between some pairs of sites that were both dominated by the same species (of shrubs) that had higher ratios of biomass to cover. Predicted biomass data can provide more accurate information on the relative importance of species in a community than can cover data alone, and it appears that this greater accuracy may often result in greater ability to identify differences among sites.

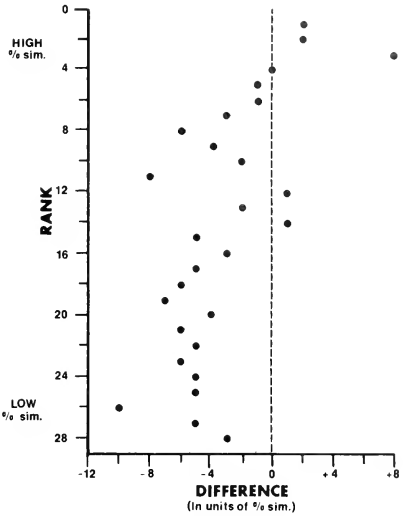

Fig. 1. Differences between similarity index values based on cover and based on predicted biomass. Differences between paired similarity index values (biomass - cover) arranged in order of decreasing percent similarity based on biomass data.

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A NEW COMBINATION AND A NEW VARIETY IN *ARTEMISIA TRIDENTATA*

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Abstract.— The combination *Artemisia tridentata* Nutt. ssp. *spiciformis* (Osterhout) Goodrich & McArthur comb. nov. is made. This high elevation taxon was originally described at the species level and more recently has generally been treated as a form of *A. tridentata* ssp. *vaseyana*. The subspecies designation is supported by its parallel nature to the other *A. tridentata* subspecies and by its relatively widespread and locally abundant populations. Also, a new variety of *A. tridentata* ssp. *vaseyana* is proposed.

Artemisia spiciformis Osterhout was described (Osterhout 1900) from specimens collected at North Park, Jackson County (Larimer County on the label of Osterhout's type specimen, 2011), Colorado. *Artemisia rothrockii* Gray was described (Brewer et al. 1876) from specimens collected at Monache Meadows, Tulare County, California. Plants of these taxa are marked by large heads with about 10–18 flowers, by narrow spicate panicles, and by apically dentate or lobate leaves and often with some entire leaves, especially on the flowering stalks. They are mostly found at subalpine and alpine elevations. Both are members of the endemic North American subgenus *Tridentatae* (McArthur et al. 1981).

Hall and Clements (1923) reduced *A. rothrockii* to a subspecies of *A. tridentata* Nutt., and they reduced *A. spiciformis* to a synonym or a minor variation of *A. tridentata* ssp. *rothrockii*. They listed a distribution for this complex that included Washington to California and east to Wyoming and Colorado. However, they mentioned that the specimens from Colorado including the type specimen of *A. spiciformis* are more gray or white and more densely cinereous, whereas the type specimen of *A. rothrockii* is viscid and less densely cinereous. They listed two specimens from Colorado that had partial features of typical *A. rothrockii*, and further mentioned that most Sierra Nevada plants of the complex were cinereous-canescent and scarcely viscidulous. They maintained that perplexing combinations render impossible the recognition of *A. spiciformis*. We agree that these two taxa are similar, but Ward (1953), Beetle (1960), Shultz (1983), and Welsh (1983) have treated *A. rothrockii* and *A. spiciformis* separately.

Ward (1953) maintained *A. rothrockii* at the species level and included in this taxon only plants of the Sierra Nevada and San Bernardino Mountains of California. He suggested that *A. rothrockii* is composed of three races that possibly have arisen independently and include considerable variation in pubescence, stature, purple pigment in the involucres, reduction in the inflorescence, leaf form, and habitat. He suggested that *A. cana* Pursh, and either or both *A. tridentata* and *A. arbuscula* Nutt. have contributed to the chromosome complement of *A. rothrockii*. This taxon (Sierra Nevada and San Bernardino Mountain *A. rothrockii*) is polyploid ($4x$–$8x$) (Ward 1953, McArthur et al. 1981). Ward (1953) suggested that more work might show *A. spiciformis* as a species or as a form of *A. rothrockii*. With the information available at the time, however, he gave it consideration as a local hybrid that is reasonably fertile due to its presumed tetraploid nature. He suggested *A. cana* and *A. tridentata* as the parents and stated that he had not seen it extend its range beyond the areas in which both putative parents occur. Beetle (1960) maintained *A. rothrockii* at the species level, as did

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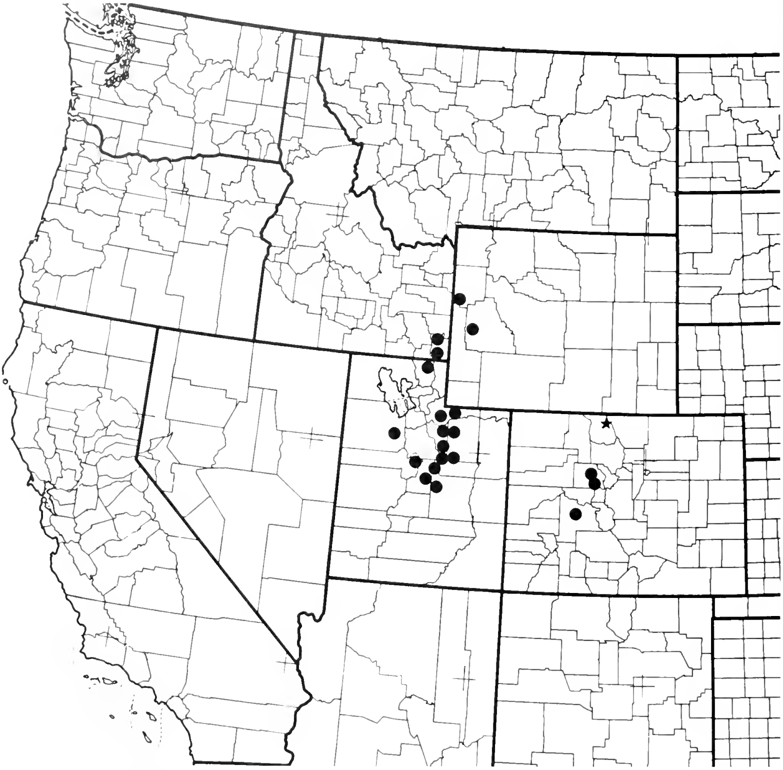

Fig. 1. Distribution of *Artemisia tridentata* ssp. *spiciformis* based on specimens at BRY, OGDF, SSLP, and RM. Type locality indicated by the star.

Ward, but he included in the taxon plants of Colorado, Wyoming, and California. In *A. rothrockii* he included plants with leaves more or less viscid and not densely canescent that give the whole plant a dark green appearance. He pointed out the similarity of large heads in the type of *A. spiciformis* to those of *A. rothrockii*, but he included other plants with much smaller heads in his concept of *A. spiciformis*, and he reduced *A. spiciformis* to *A. tridentata* ssp. *vaseyana* (Rydb.) Beetle f. *spiciformis* (Osterhout) Beetle. He listed the range of f. *spiciformis* as throughout the range of *A. tridentata* ssp. *vaseyana*. He reported frequent confusion with *A. rothrockii*, and he mentioned that leaves of *A. rothrockii* are thicker and often more deeply lobed, and the involucral bracts are dark and often purple. Beetle also suggested that *A. cana* and *A. tridentata* have had a part in the development of *A. spiciformis*.

Shultz (1983a, 1983b) also treated *A. rothrockii* as a species and included in this taxon only plants of California, as did Ward. She described *A. rothrockii* as a root-sprouting shrub with dark green, very resinous leaves, and with up to 20 flowers per head. She commented on frequent confusion in California between *A. rothrockii* and probably hybrids of *A. cana* ssp. *bolanderi* (Gray) Ward and *A. tridentata* ssp. *vaseyana*. However, she maintained unique anatomical features (gelatinous fibers and numerous resin ducts) for *A. rothrockii* as well as noting that the leaves were darker green and viscid. She also treated *A. spiciformis* as a hybrid of *A. cana* and *A. tridentata*, as did Ward.

Based on the work of Ward and Shultz, we accept *A. rothrockii* as a plant of California. That being the case, we feel that *A. spiciformis* warrants recognition as more than a localized hybrid. Plants of *A. spiciformis* are too widespread (Fig.1), and they form homogenous stands that are too large and often too far removed from populations of one or both of the putative parents to be mere local hybrids (McArthur and Goodrich, in press). Welsh (1983) recognized *A. spiciformis* as a taxon with relationships running to both *A. cana* and *A. tridentata*, but he maintained this as a species and not as a hybrid. We do not dispute the probability of a hybrid origin, nor do we dispute the occurrence of intermediate plants where plants of this taxon and plants of either or both *A. cana* and *A. tridentata* come together. We think the large-headed plants of Utah and Wyoming that match Osterhout's type of *A. spiciformis* and other specimens from Colorado are worthy of taxonomic recognition, and we include them as a subspecies of *A. tridentata* to bring them in line with other taxa of the complex. We point out that the addition of ssp. *spiciformis* brings to five the number of subspecies described for *A. tridentata*. Four (ssp. *tridentata*, *wyomingensis* Beetle & Young, *vaseyana*, and *spiciformis*) are widely distributed but separate on the basis of moisture and elevational gradients and on morphological features (Beetle and Young 1965, McArthur 1983, Winward 1983). The other one, ssp. *parishii* (Gray) H. & C., is similar to and perhaps synonymous with ssp. *tridentata*. *Artemisia tridentata* ssp. *spiciformis*, with probably hybrid and polyphylic origins, has similarities with ssp. *wyomingensis*. In the latter case, ssp. *tridentata*, *vaseyana*, and *A. nova* A. Nels. are thought to be involved (Beetle and Young 1965, Winward 1975, McArthur 1983), whereas in the former the putative parents are ssp. *vaseyana* and *A. cana*. Like *A. rothrockii* (sensu Ward and Shultz), ssp. *wyomingensis* is polyploid (4*x*–6*x*; McArthur et al. 1981). However, ssp. *spiciformis* is diploid (2*x*) and tetraploid (4*x*). Utah populations from the Wasatch Plateau and Uinta Mountains are diploid ($n = x = 9$) (McArthur et al. 1981, McArthur and Sanderson, unpublished manuscript). A population in the Wyoming Range of west central Wyoming is tetraploid (McArthur et al. 1981). Because the whole of subgenus *Tridentatae* has a similar genome (replicated various times in polyploids) (McArthur et al. 1981), and hybridization is possible and in places common in the subgenus (Ward 1953, McArthur et al. 1979), ssp. *spiciformis* could and probably did arise independently several times at both the diploid and tetraploid levels. Apparently, genetic composition and selective pressures have led to a stabilized, well-adapted taxon.

For *Artemisia tridentata* ssp. *spiciformis* we accept extreme variability in size, thickness, and lobing of the leaves, and in the pigmentation of the involucres, and some variability in the inflorescence (spiciform to narrow-paniculate). We place the greatest emphasis on number of flowers per head (10–18) and in the size of the heads (5–7 mm long, 4–5 mm wide at maturity). These features seem diagnostic, and they place plants of similar morphology and ecology together. Plants with fewer flowers per head (4–11) and smaller heads that have been referred to as f. *spiciformis* belong to *A. tridentata* ssp. *vaseyana*. We feel that *A. tridentata* ssp. *spiciformis* is closer to *A. rothrockii* in head size, number of flowers, and in the tendency to root-sprout than it is to *A. tridentata* ssp. *vaseyana*, which does not root-sprout.

The variability in features of ssp. *spiciformis* may be a result of several independent origins, as we suggested earlier. This seems reasonable, considering the suggested hybrid origin for the taxon. The plants of California that Shultz reported as possible hybrids are suggested as crosses between *A. cana* ssp. *bolanderi* and *A. tridentata* ssp. *vaseyana*. *Artemisia cana* ssp. *bolanderi* is mostly known from California and Oregon, and *A. cana* ssp. *viscidula* Osterhout is the logical putative parent throughout much of the range of ssp. *spiciformis*. Apparently plants with features of ssp. *spiciformis* have not been found in the range of *A. cana* ssp. *cana*. Perhaps the name ssp. *spiciformis* is best reserved for plants in which *A. cana* ssp. *viscidula* and *A. tridentata* ssp. *vaseyana* are the logical parents, but we do not propose such reservation at this time. The probably hybrid origin raises the question whether ssp. *spiciformis* should be included in *A. cana* or in *A. tridentata*. We have included it with *A. tridentata* because most of the persistent leaves are lobed and because an additional taxon of *A. tridentata* at the upper elevation range for the species makes for a logical and complete elevational and mesic gradient series for the species.

In addition to morphological features, phenology of plants of ssp. *spiciformis* may provide additional evidence that they are unique. Plants of ssp. *spiciformis* from high elevations of the Wasatch Plateau, Utah, and from the Wyoming Range, Wyoming, have been transplanted at low elevations at Provo and Ephraim, Utah. These plants come into full flower as early as the last of May and the first two weeks of June. Plants of *A. tridentata* ssp. *vaseyana* and *A. cana* ssp. *viscidula* have also been transplanted at these locations. They flower at the transplanted sites about the same time or later than they do in their more montane environments. This is about September or October or even into November. In its native habitat, ssp. *spiciformis* flowers from the first of August through September, but its phenology at the transplanted sites indicates a basic difference from either *A. cana* ssp. *viscidula* or *A. tridentata* ssp. *vaseyana*.

Rydberg (1916) described *Artemisia vaseyana* and designated a specimen from Washington (Vasey, 480) as the type. Hall and Clements (1923) examined the type specimen and listed 9–10 flowers per head. They discussed this taxon as a variation of *A. tridentata* ssp. *rothrockii*. Ward (1953) also examined the type specimen and listed 9–11 flowers per head. He discussed this as a form of *A. tridentata* ssp. *tridentata* but explained that it differed by having larger heads, larger leaves, and reduced inflorescences. He attributed the reduced inflorescences to environmental modification but indicated the large head size to be genetically controlled. He also listed several other collections from Washington, Oregon, and Idaho with 7–11 flowers per head. Beetle (1959) included *A. vaseyana* as a ssp. of *A. tridentata*. We agree with this combination.

Ward (1953) pointed out some ecological and cytological variations in this group. He mentioned plants of intermountain areas (areas between mountains) "with rounded shape with the inflorescences mingled with the vegetative shoots and only partly exceeding them." We believe these plants are those Beetle and Young (1965) named as *A. tridentata* ssp. *wyomingensis*, the same tetraploid plants discussed by Ward (1953) that usually grow on poorer, rockier soils, and that are smaller and slower growing than diploid plants. He compared these plants with a form of sagebrush of "timbered or mountainous areas in which the plants are very uniform in size, usually about 2 feet in height, and of a rather spreading, flat-topped habit of growth, with the inflorescence extending upward like plumes above the rest of the bush." He further reported that the two forms retained their different growth rates under uniform conditions in a garden. He discussed these two forms simultaneously but separately from *A. vaseyana*, which he went on to discuss as another form with larger heads. For many years these montane, flat-topped plants with only 4–6 flowers per head have passed for *A. tridentata* ssp. *vaseyana*. We believe they constitute a separate taxon. This small-headed, few-flowered phase is widespread in most of the western states, whereas those matching the type of typical *A. tridentata* ssp. *vaseyana* are most common in the upper elevational sagebrush areas of Washington, Oregon, and Idaho. The morphological differences are striking enough in the extreme, but there is no clear-cut boundary, and we do not dispute that intermediate plants are often encountered. However, each of the phases form large, pure stands, and the geographic ranges are not entirely the same. Hironaka et al. (1983) recognized the two different phases, and designated separate habitat types based on the two phases. The differences will continue to be recognized, and names for both seem to be appropriate.

The following name is proposed for plants with smaller and fewer flowered heads and wider inflorescences:

Artemisia tridentata ssp. *vaseyana* var. *pauciflora* Winward & Goodrich var. nov. Similis *A. tridentata* ssp. *vaseyana* var. *vaseyana* sed in capitulis parvis floribus paucis et inflorescence latis differt.

Type: Utah, Utah County, T7S R4E corner of sections 28, 29, 32, and 33, 9.7 km 85° east of Springville, Uinta N.F., Wasatch Mountains, Left Fork Hobble Cr., 1582 m, sagebrush-grass community in a Gambel oak-bigtooth maple zone. Goodrich, Winward, McArthur, and Lewis 21492. Holotype BRY!, Isotypes ID, MO, NY, RENO, RM, SSLP, UC, UT, and UTC. Paratype: Utah, Utah County T8SR3ES1 SE¼ of NW¼, 5 km 112° east of Springville, 1524 m, sagebrush-grass community. Goodrich, Winward, McArthur, and Lewis 21490. BRY, CS, MONTU, OGDF, OSC, and WTU.

The following key provides a summary for the taxa of *A. tridentata* listed above except for *A. tridentata* ssp. *parishii* (mostly of southern California), which is like *A. tridentata* ssp. *tridentata* except for usually arachnoid and short-villous achenes.

1. Unevenly topped shrubs with the inflorescence and vegetative twigs intermingled, the flower stalks rarely over twice as long as the subtending vegetative twigs; plants of valleys and lower mountains; fluoresces reddish brown in alcohol (Winward and Tisdale 1969) 2

– Evenly topped shrubs; flowering stalks well elevated above the leaves, mostly over twice as long as the subtending vegetative twigs; plants of low to high elevations in mountains; fluoresces bluish cream in alcohol 3

2(1). Plants mostly over 1 m tall, often with a discernible main trunk, diploids; length/width ratio of leaves 4.0 or greater .... *A. tridentata* ssp. *tridentata*

– Plants mostly less than 1 m tall, often quite branched from near the base and then without a readily discernible main trunk, mostly tetraploids; length/width ratio of leaves less than 4.0 .... *A. tridentata* ssp. *wyomingensis*

3(1). Head with 10–18 flowers; plants tending to root-sprout, of subalpine elevations, often in openings in aspen and spruce or fir woods, or where drifting snow accumulates, flowering in August and September in native habitats and in early June when transplanted at low elevations (1370 m), diploids and tetraploids, possibly of hybrid derivation involving *A. tridentata* and *A. cana* .... *A. tridentata* ssp. *spiciformis*

– Heads with 4–11 flowers; plants not root-sprouting, of medium to high elevations in mountains, flowering in September, October, and November when transplanted at low elevations 4

4(3). Heads with 7–11 flowers, over 1.5 mm wide; inflorescence narrow and spiciform with relatively few heads .... *A. tridentata* ssp. *vaseyana* var. *vaseyana*

– Heads with 4–6 flowers, less than 1.5 mm wide; inflorescence paniculate with numerous heads .... *A. tridentata* ssp. *vaseyana* var. *pauciflora*

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UNDERSTORY RESPONSE TO TREE HARVESTING OF SINGLELEAF PINYON AND UTAH JUNIPER

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ABSTRACT— Fifteen widely separated sites within the pinyon-juniper woodlands of the Great Basin were cleared of trees. Understory response was recorded for 2 to 4 years. The array of postharvest plant assemblages were classified into one of four phytosociological groups using discriminant analysis. Pre- and postharvest plant assemblages from the same site appeared in the same phytosociological group, which indicates postharvest response could be predicted from the preharvest plant assemblage. Initial postharvest response appears cyclic in nature, and cycles are controlled by both residual plants and the rapid immigration of shrub species. Perennial plant density generally declined following tree harvest, but the fewer remaining plants produced significantly more cover than in preharvest stands.

Wood harvesting in pinyon-juniper woodlands of the Great Basin has a long and colorful history. In the late 1800s, the harvesting of trees for charcoal used in the smelting of ore and as heating fuel had decimated tree populations for an 80-km radius around many mining camps. An estimated 1600 to 2000 ha of woodland were cleared annually to fuel this burgeoning mining industry (Young and Budy 1979). Concurrently, livestock numbers, including the numerous draft animals used in wood harvesting, were increasing and indiscriminant burning of woodlands was common (Tausch et al. 1981, J. A. Young, pers. comm.). These perturbations left an array of depleted disclimax understory communities (Tueller 1973) upon which the current woodlands would become established. Trees reestablished rapidly in the Great Basin (currently 7.1 million ha, Tueller et al. 1979), and understory cover and productivity was reduced (Tausch et al. 1981, West 1983).

Rising fossil fuel costs have recently increased the demand for cord wood (Meeuwig and Cooper 1981). Thus, widespread tree harvesting is once again a major use of these woodlands. With appropriate management based on a knowledge of probable understory response, wood harvesting could provide a cost effective means of utilizing the wood resource and increasing the forage base.

Understory response to tree harvest is closely linked to the type and number of residual plants (MacMahon 1980, Clary 1974; Dryness 1973, Arnold 1964). Grass and shrub production increases following tree harvesting in the Southwest if these plants are numerous and capable of capturing released resources (Clary 1974, Arnold and Schroeder 1955). But floristically impoverished sites with low site potential for understory production can remain static for several years following tree removal (O'Rourke and Ogden 1969).

Our study tests the hypothesis that postharvest response in fully stocked singleleaf pinyon (*Pinus monophylla*)-Utah juniper (*Juniperus osteosperma*) woodlands of the Great Basin is "site specific cyclic." We hypothesize that a linear replacement series of plant forms does not often occur following tree harvest. If mid-to-late successional understory plants or their immigrating seeds are available to the site, they control the character of postharvest response and negate early successional stages. Rapid reinvasion of trees in the central core of the woodland also truncates midsuccessional shrub dominance. This hypothesis is limited to the midelevation of the woodland and may not be viable at either upper or lower ecotones.

METHODS

In 1977, 1978, and 1979 study sites were established in 15 singleleaf pinyon–Utah juniper stands across the Nevada portion of the Great Basin (Fig. 1). Stands selected for tree

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Fig. 1. Location of study sites in the pinyon-juniper woodlands of the Great Basin. Woodland distribution patterns taken from Tueller et al. (1979).

harvest were fully stocked with trees and had minimal understory. Plots (0.1 ha) were selected for site uniformity in microtopography and understory composition. Trees greater than 1 m in height were hand cut, sectioned, and removed from the plots with minimal distrubance to the soil surface.

A series of five parallel transects 20 m in length were laid out on 5-m intervals parallel to one another across the slope. Tree cover was estimated using line intercept (Canfield 1941) along each transect. A series of frames (50 x 50 cm) were laid down at every meter mark, and plant species cover and density were recorded. Understory response on the harvested sites and on adjacent uncut areas were monitored for 2 to 4 years following tree removal. Predominant preharvest understory species, tree cover (%), elevation, aspect, and year of harvest are given for each site in Table 1.

Discriminant analysis was used to group the array of pre- and postharvest plant assemblages (30 total) based on nine phytosociological parameters. Phytosociological parameters used were areal species richness, "evenness" in cover among plant forms (Brillouin's [H] measure of diversity divided by maximum diversity in distribution of cover possible [J = H/H max] : Poole 1974), aggregation of perennial plants (Morisita's Index of Aggregation : Poole 1974), total plant cover, and proportion of cover by shrub, perennial grass, perennial forb, annual grass, and annual forb. Postharvest data were run using the preharvest groupings to test if postharvest plant assemblages could be predicted from preharvest data.

Pre- and postharvest data sets from the same site are not independent. Thus, data was compared by t-tests of differences. Multivariate matched pair t-tests of differences (Timm 1975) were conducted for closely related parameter pairs, woody and herbaceous cover, annual and perennial cover, total cover and evenness in cover distribution, and perennial plant density and perennial plant aggregation. The test statistic used was Hotteling's t at the 0.05 significance level.

A correlation matrix of the phytosociological variables was used to identify parameters that varied together (P = 0.05) in pre- and postharvest plant assemblages. Proportion of species common to pre- and postharvest plots were included with those variables already mentioned.

Results and Discussion

Lack of climatic effects on plant response to tree harvest.— Precipitation during the final year of postharvest measurement was less than occurred during the year of preharvest measurement. Mean precipitation from six official weather stations closest to the 15 study sites averaged 28.5 cm

Table 1. List of study sites, dominant understory, percent tree cover, elevation, aspect, and harvest year.

Preharvest understory	Study site	Percent cover	Elevation	Aspect	Year
Annual forb dominant					
Phacelia humilis	4	36	2030	N	78
Collinsia parviflora	9	26	2220	E	79
Collinsia parviflora	15	56	2200	E	79
Shrub dominant					
Purshia tridentata	1	60	2300	E	77
Artemisia arbuscula	2	49	2200	N	77
Artemisia arbuscula	8	41	2070	W	79
Ribes velutinum	3	64	2100	E	77
Perennial grass dominant					
Poa sandbergii	5	56	2040	E	78
Poa sandbergii	6	52	2060	N	78
Poa sandbergii	7	58	2190	E	78
Poa sandbergii	11	54	2300	W	79
Poa sandbergii	12	54	2280	S	79
Poa sandbergii	13	43	2200	N	78
Festuca idahoensis	10	28	2340	N	79
Perennial forb dominant					
Penstemon pachyphyllus	14	50	2200	N	79

(September to August) the year of preharvest measurement and 21.1 cm the year of final postharvest measurement. The initial preharvest plant cover (X = 2.71 dm^2/m^2) was not significantly different (P = 0.1) from plant cover on nonharvested plots (X = 2.57 dm^2/m^2) the final year of postharvest measurements. Understory response to tree release was not confounded by precipitation levels following tree harvest.

PLANT RESPONSE TO TREE HARVEST.—Semiarid pinyon-juniper woodlands are characteristically low to moderate in species richness, but this varies with site heterogeneity (Harner and Harper 1976). There was no increase in areal species richness following tree harvest. Preharvest plant assemblages averaged 14 species (± 4 SD), and postharvest plant assemblages averaged 11 species (± 6 SD). On 10 of 15 sites, species numbers were lower after tree harvesting.

The proportion of species common to pre- and postharvest plant assemblages averaged 57% (± 21 SD) among sites. The proportion was lowest on the more depauperate sites (1, 3, and 15) and highest when preharvest cover was more evenly divided among several plant forms (sites 8, 9, 10, 11, and 14).

DISCRIMINANT ANALYSIS OF PLANT RESPONSE.— The array of pre- and postharvest plant assemblages (30 total) were classified by discriminant analysis into (1) annual forb, (2) shrub, (3) perennial grass, and (4) perennial forb phytosociological groups. Pre- and postharvest plant assemblages were intermingled within the groups. The four groups were significantly (P = 0.001) different from each other. Aside from plant form dominance, groups differed significantly (P = 0.001) in areal species richness, perennial plant aggregation, perennial plant density, total cover, and "evenness" in the distribution of cover among plant forms. Figures 2A and B separate pre- and postharvest plant assemblages for ease of interpretation.

The first discriminant function (axis) ordinated plant assemblages along a gradient of increasing perennial grass cover and evenness in distribution of cover among plant forms. The second discriminant function (axis) ordinated plant assemblages along a gradient of increasing species richness, shrub cover, and perennial forb cover. The third discriminant function (axis) emphasized increasing total cover, species richness, and cover of annual forbs. These discriminant functions explained 80% of the variance in the data.

Postharvest response was not unidirectional in phytosociological change. Vectors drawn from pre- and postharvest plant assemblages varied in length and direction (Fig. 1C). Annuals invaded shrub sites, shrubs in-

TABLE 2. Differences between pre- and postharvest phytosociological parameter pairs (multivariate paired t-test of difference).

		Phytosociological Pair 1		Pair 2	
Preharvest group	Site	Total cover (dm^2/m^2)	Evenness in cover (−1 to + 1)	Annuals (dm^2/m^2)	Perennials (dm^2/m^2)
Annual forb	4	−5.66°°	−0.27°°	−42.26°°	13.56°°
Annual forb	9	0.78°°	0.13°°	0.78	3.67
Annual forb	15	2.92°°	0.12	13.94°°	0.70
Shrub	1	3.5°	0.47°°	9.28°°	8.28
Shrub	2	4.9°°	0.33°	9.69	9.75°
Shrub	3	1.83°°	0.05	0	3.35
Shrub	8	1.03°°	0.04	0.16†	4.97†
Perennial grass	5	0.61	0.08†	− 1.67°°	− 1.14
Perennial grass	6	−0.44°°	−0.25°°	− 0.51	1.71
Perennial grass	7	3.39°°	−0.34°°	16.85°°	0.27°°
Perennial grass	10	1.57	0.19	2.62†	5.23†
Perennial grass	11	2.74°°	−0.26	2.22	11.29°°
Perennial grass	12	0.65°°	0	1.26	2.03
Perennial grass	13	1.33°°	0	0.17	6.09°°
Perennial forb	14	3.19°°	0.18°°	1.29	14.66°°

°Significant at 0.1° or 0.05 (°°), Hotteling's t value

†Significant at 0.05, but difference cannot be ascribed to any one parameter.

vaded annual sites, and plant forms already present were differentially favored by tree release, causing intragrouping shifts.

Site membership in postharvest groups was similar to preharvest groups, indicating potential predictability of postharvest response. Discriminant analysis was run again using the postharvest plant assemblages grouped according to the preharvest plant assemblages. We found 80% of the postharvest vegetation transects were placed in the correct preharvest group. Thus opportunities exist for a qualitative prediction of postharvest response from the preharvest plant assemblage.

In only three instances were postharvest assemblages classified in groups different from their associated preharvest plant assemblage (Fig. 2C). In two of these instances the difference could be traced to allogenic factors. Site 4 in the annual forb group was invaded and rapidly dominated by mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*), shifting it to the shrub group. Site 7 in the perennial grass group was subjected to severe grazing pressure, shifting the plant assemblage to the annual forb group. Site 9 was shifted from the annual forb group to the perennial grass group by the rapid response of on-site perennial grasses.

INTERPRETATION OF DISCRIMINANT RESULTS.— Most pre- and postharvest plant assemblages are found in the same phytosociological groups. This supports the hypothesis that early succession was dominated by species on site at the time of disturbance ("initial floristics": Egler 1954). Postharvest response was "site specific cyclic." The complete successional replacement series of plant forms from annuals to grasses to shrubs to trees (Eardman 1970) could not often occur. This was most apparent where (1) mid-to-late understory successional species immediately predominate the postharvest sites, or (2) where invading trees truncate shrub dominant midsuccessional stages. In the first case, shrubs or grasses rapidly became dominant following tree removal and precluded earlier successional stages (sites 1, 2, 3, 4, and 8). In the second case, perennial grasses or forbs were dominant in both pre- and postharvest understory. This demonstrates the incomplete replacement of herbaceous species by shrubs. We speculate the replacement of grasses and forbs by shrubs is truncated by increasing competition between tree and shrub species (sites 5, 6, 9, 10, 11, 12, 13, and 14). Understory response on the annual forb site (site 15) is the anomaly to the "cyclic response" hypothesis. The lack of on-site perennial species provides increased opportunities for establishment of invading species.

TABLE 2. Continued.

pairs			
Pair 3		Pair 4	
Woody	Herbaceous	Perennial plant density (plants/m^2)	Aggregation (Morisita's Index) (I)
(dm^2/m^2)			
13.52°°	-41.74°°	16.6°°	16.9°°
0.92	2.95	0.73	0.1
0	14.61°°	0.4	15.6°°
5.21	8.31	0	-12.0°°
4.93	9.74	- 2.5	- 7.3°°
8.99°	0.16	1.8°°	5.6°°
0.47	0.40°°	0.50°	0.8°°
0.4	- 3.43°°	- 6.4	6.6°°
0	- 2.24	- 5.5	1.2°°
- 0.20	24.8°	- 3.8	2.7°°
- 3.06	20.87°°	- 4.8	0
0.57	14.29°°	- 1.3	0.1
0.66	2.63	- 0.3	0.3
1.03	5.17°°	3.8	0.3
0.33	18.69°°	2.9	0

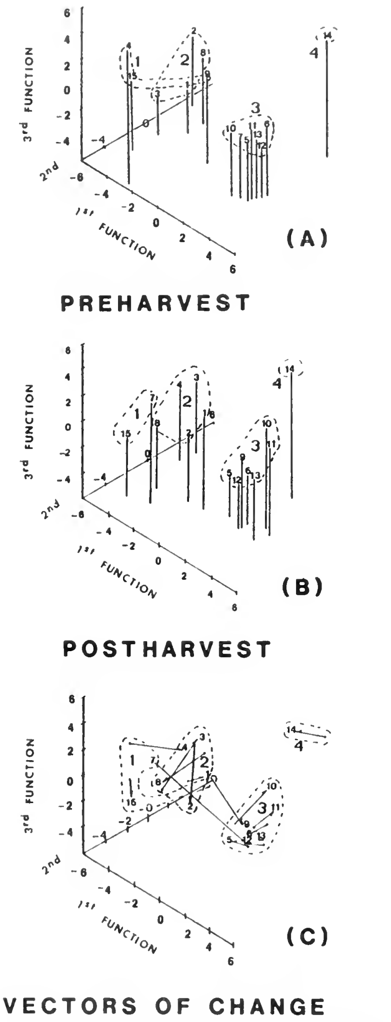

Fig. 2. Discriminant ordination of preharvest (A) and postharvest (B) plant assemblage. Vectors of change (C) within and among groups. From Klecka (1975).

Phytosociological characteristics of plant response.— Total understory cover significantly (P = 0.1 or 0.05) increased following tree harvest on sites not subjected to grazing (sites 5 and 6) or remaining dominated by annual forbs (site 4) (Table 2). The mean increase in cover across sites was 1.48 dm^2/m^2, with a high coefficient of variation (CV = (S/X . 100) = 61%). Mean postharvest understory cover was approximately 200% greater than preharvest understory cover.

Depauperate annual forb sites with few species and unoccupied microsites (loose species packing, Terborgh 1973) were rapidly colonized by herbaceous pioneer species or by shrub seedlings from one of the *Artemisia* taxon. Postharvest response on shrub sites was characterized by increased aggregation of perennial plants, lower species richness, and a less even distribution of cover among the plant forms. Ungrazed grass sites were best characterized by their lack of change in evenness, perennial plant density, and aggregation. Grass sites had high initial species richness, perennial plant density, and evenness in cover distribution among plant forms. Livestock grazing of grass sites altered phytosociological parameters significantly and in one instance caused regression to the annual forb stage.

Evenness in cover distribution among plant forms was low (J max = 1.0), and the overall mean was numerically the same in both pre- and postharvest plant assemblages (X = 0.40 ± 0.26). Changes in the evenness value for a plant assemblage occurred from such a wide array of circumstances that the value itself had little meaning unless the cause was understood.

Perennial plant cover increased on all sites not subjected to severe grazing, but annual cover was more variable. Woody cover increase was dependent upon remnant shrubs, shrub seed sources, and lack of competing grass species. Herbaceous cover increased following tree harvest unless sites were grazed (site 4).

Perennial plants were significantly (P = 0.01) aggregated (I > 1: Morisita's Index) in all pre- and postplant assemblages, with the exception of the regular dispersion of plants (I = 0) on preharvest sites 3, 4, and 15. At least two scales of aggregation were visible on most sites. Understory and tree cover were heterogeneous across the ground surface, causing general patchiness. Within a given patch, understory was generally excluded from the duff areas adjacent the tree, resulting in understory aggregation in the interspace.

Perennial plant density was low in pre-and postharvest plant assemblages: $X = 11.45$ plants/m^2 vs. $X = 11.31$ plants/m^2, respectively. Perennial plants increased on sites initially dominated by annuals (sites 3, 4, and 15) and perennial forbs (site 14), and on a single grass site (site 13), but decreased on all others. Physical damage during tree harvesting, altered microclimate following tree harvest, and postharvest grazing effects (sites 5, 6, and 7) probably contributed to this loss of perennial plants.

CORRELATION MATRIX OF PHYTOSOCIOLOGICAL PARAMETERS.— As perennial grass and forb cover increased, so did species richness, evenness in cover distribution, and perennial plant density (Table 3). High shrub cover was associated with high plant aggregation, low evenness, and low grass cover. The proportion of species common to pre- and postharvest plant assemblages was inversely related to total cover, aggregation, and the shrub-annual forb cover. On sites subject to immigrating shrubs or annual forbs, a sharp change in species composition occurred but species numbers remained less than in grass or forb dominated understory. Diversity of understory increased spatially (aggregation) on shrub sites. Diversity increased floristically (species richness) and structurally (evenness) on grass sites.

CONCLUSIONS

Postharvest response was cyclic and could be predicted from preharvest plant assemblages barring outside perturbations. Postharvest response was best explained by Egler's (1954) "Initial Floristics" model where residual plants and rapidly immigrating species dominate response. Predictability of postharvest response with its high proportion of preharvest species (57%) is consistent with this hypothesis. Predictability of response is increased under this system. Unfortunately, some plant forms may be excluded from the

TABLE 3. Correlation matrix of phytosociological parameters.

Preharvest									
SR[1]	PD	TC	EV	AG	πS	πG	πF	πAG	πAF
1.	*0.66*°[2]	0.0	0.49	-0.11	-0.05	0.37	0.14	0.39	0.36
	1.	-0.07	*0.56*°	-0.18	-0.18	*0.52*°	0.48	0.07	-0.43
		1.	-0.06	-0.13	-0.03	-0.27	-0.18	-0.07	0.36
			1.	-0.28	*-0.53*°	*0.64*°	0.42	0.29	-0.09
				1.	0.52°	-0.21	-0.17	-0.05	-0.33
					1.	*-0.66*°	-0.36	-0.25	-0.49
						1.	0.45	0.28	-0.28
							1.	-0.07	-0.28
								1.	0.015
									1.

Postharvest										
SR	PD	TC	EV	AG	πS	πG	πF	πAG	πAF	πCS
1.	*0.72*	0.14	0.48	-0.49	-0.48	0.48	*0.58*°	-0.23	-0.05	0.26
	1.	0.19	0.32	-0.27	-0.28	*0.57*°	0.43	-0.16	-0.37	0.35
		1.	0.0	-0.07	0.19	-0.44	0.17	-0.48	0.32	-0.52°
			1.	*-0.59*°	-0.41	0.39	0.23	0.34	-0.18	0.26
				1.	0.22	-0.45	-0.29	0.15	0.29	-0.41
					1.	*-0.63*°	-0.27	-0.18	-0.36	-0.30
						1.	0.13	0.09	-0.37	*0.72*°
							1.	-0.15	-0.19	0.18
								1.	-0.20	0.23
									1.	-0.47
										1.

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[1] SR = areal species richness; PD = plant density; TC = total cover; EV = evenness; AG = aggregation; πS, πG, πF, πAG, πAF = proportional cover of shrub, perennial grass, perennial forb, annual grass, and annual forb. πCS = proportion of species common to pre- and postharvest assemblages.

[2] ° denotes significant correlation coefficient ($P < 0.05$).

postharvest plant assemblage. When tree harvesting is done to increase the forage base for livestock or wildlife, the desired species should already be in the understory. Understory species richness was reduced following tree harvest on 10 out of 15 sites as suggested by Loucks (1970) for more mesic forests. Understory diversity increased spatially on shrub sites (aggregation) and increased floristically (species richness) and structurally (evenness) on grass sites.

Total plant cover increased following tree harvest on all sites not subjected to severe livestock grazing. Preharvest understory in the fully stocked stands was severely suppressed. Mean increase in postharvest cover was 1.48 dm^2/m^2 and represented a 200% increase in cover over preharvest conditions.

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AQUATIC BIRDS OF THE WHITE RIVER, UINTAH COUNTY, UTAH

Benjamin B. Steele[1] and Stephen B. Vander Wall[1]

Abstract.— Abundance, seasonal use, and species composition of waterfowl and other aquatic birds are described along a 32.8 km stretch of the White River, Uintah County, Utah, at the site of the proposed White River Dam. Fourteen species of waterfowl and eight other species of aquatic birds were recorded. Waterfowl populations along the river were highest in April, but densities were much lower than on lakes and reservoirs at nearby Ouray National Wildlife Refuge.

Most studies of waterfowl and other aquatic birds are associated with lakes, ponds, marshes, or reservoirs. In arid areas, where standing water is scarce, rivers provide the major habitat for aquatic birds during migration and for nesting. In the Uinta Basin of northeastern Utah, the Green River and its tributaries historically represented the only aquatic habitat. Since the construction of reservoirs for irrigation and hydroelectric power, species composition and use patterns of aquatic birds have changed dramatically (Hayward 1967). Waterfowl and shorebirds, however, still use the Green River and its associated oxbows, sloughs, and backwaters. Smaller numbers of birds use tributaries such as the White River, where standing water and wetlands are not present.

The Utah Division of Water Resources has proposed construction of a dam on the White River (Bureau of Land Management 1980). This earthen dam, 65 km southeast of Vernal, Uintah County, Utah, would create a reservoir 21.8 km long to supply water for oil shale and other energy development. The reservoir would be 774 ha (1860 ac) in area and average 1.1 km wide. Here we report the abundance, seasonal use, and species composition of aquatic birds in a section of the White River extending from 24.1 km above to 8.7 km below the proposed dam site. Potential changes in the aquatic avifauna due to construction of the dam are discussed.

Methods

Aquatic and other birds of riparian habitat were censused along line transects during five months (February, April, June, August, and October) from 1975 through 1981. Transects were located just upstream of the proposed dam site. Each sample consisted of morning censuses on five consecutive days. Transects were approximately parallel to the White River, and thus abundances are reported in individuals/river km. In 1975 and 1976, three ½ km transects were walked. From 1977 to 1980, two 1 km transects were walked and, in 1981, one 1 km transect was walked. All waterfowl, shorebirds, and herons were recorded.

To gain further information on aquatic birds during spring migration, a 32.8 km (20.4 mile) section of the White River (24.1 km above to 8.7 km below the proposed dam site) was floated by canoe for three consecutive days starting 7 April 1982 and again for three days starting 14 April 1983. The number and location of all waterfowl were recorded in river kilometers, beginning at Cowboy Canyon (km 0) and ending at Asphalt Wash (km 32.8).

Study Area

The White River flows westward from its headwaters in the White River Plateau in

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Colorado through semiarid shrub land and pinyon-juniper woodland (mean annual precipitation 20.3 cm) and enters the Green River at Ouray National Wildlife Refuge (Ouray NWR), 45 km south of Vernal, Utah. Flow in the White River varies widely from 130 cubic feet per second (cfs), usually during late summer, to 2800 cfs in May or June (5-year means 1975–1979). The White River is very turbid during spring runoff (800–7000 mg of suspended solids per l) and during local summer thunderstorms (e.g., 61,000 mg/l during a 1979 flash flood) (White River Shale Project 1981).

Within our study area the river meanders through a flood plain approximately 200 m wide. On the flood plain, there is riparian habitat dominated by cottonwood (*Populus fremontii*), salt cedar (*Tamarix pentandra*), and various shrubs.

RESULTS

Waterfowl

Waterfowl along the White River were most abundant during spring migration in April (2.09 ind/river km, Table 1). During winter (February), late summer (August), and fall (October), mean waterfowl abundance was low and relatively constant at 0.31 to 0.36 birds/river km. There was no marked increase in waterfowl along this section of the White River during fall migration. Summer residents (potential breeders) were only slightly more common than winter residents. Coefficients of Variation in abundance over the seven-year period were lowest in April (50.1%), indicating that April had both the highest and most predictable waterfowl populations.

The April canoe censuses in 1982 and 1983 yielded an estimate of waterfowl abundance (3.13 and 2.13 ind/river km, respectively, Table 2) slightly higher than the 1975–1981 line transect mean (2.1 birds/river km). Waterfowl were most abundant upstream of the dam site (3.24 and 2.78 birds/river km). The Canada Goose (*Branta canadensis*), Green-winged Teal (*Anas crecca*), and Mallard (*Anas platyrhynchos*) were the most common species of waterfowl (Table 2). The Northern Pintail (*Anas acuta*) and Bufflehead (*Bucephala albeola*) were present but were not recorded during censuses.

Only the Canada Goose breeds in the study area. We recorded four broods between Cowboy Canyon and Asphalt Wash in June 1981. The Utah Division of Wildlife Resources recorded five pairs of geese with a total of 35 goslings on 9 June 1976 (White River Shale Project 1977).

Other Aquatic Birds

In addition to waterfowl, we recorded seven other species of aquatic birds. They were most commonly recorded in June (0.91 birds/river km) and August (0.60 birds/river km) but were absent in winter (Table 1). Great Blue Herons (*Ardea herodias*) were fairly common transients in spring and summer but are not known to breed in the area.

TABLE 1. Seasonal trends in abundance of waterfowl and other aquatic birds (birds/river km) along the White River from 1975 through 1981. Coefficient of Variation (CV) is standard deviation divided by the mean.

	Year								
Month	1975	1976	1977	1978	1979	1980	1981	Mean	CV
WATERFOWL									
February	0.0	1.6	0.1	0.0	0.0	0.0	0.6	0.33	183.0
April	2.9	2.3	3.0	2.4	2.7	1.1	0.2	2.09	50.1
June	0.3	0.4	1.3	1.6	0.1	0.0	0.2	0.56	113.0
August	0.0	0.0	2.0	0.1	0.0	0.4	0.0	0.31	207.0
October	0.0	0.0	0.0	0.5	0.5	1.5	0.0	0.36	155.8
OTHER AQUATIC BIRDS									
February	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	–
April	0.5	0.5	0.3	0.8	0.0	0.0	0.0	0.30	105.4
June	1.1	1.9	1.3	0.3	0.4	0.4	1.0	0.91	64.2
August	1.7	0.9	0.2	0.3	0.1	0.5	0.5	0.60	91.8
October	0.0	0.0	0.0	0.3	0.0	0.1	0.2	0.09	141.8

Snowy Egrets (*Egretta thula*) were uncommon spring migrants. The Spotted Sandpiper (*Actitis macularia*) was the most common shorebird and the only one known to breed. They were present along the river in all June and August censuses. Killdeers (*Charadrius vociferus*) were fairly common spring migrants and summer residents, but there is no evidence that they breed. Greater Yellowlegs (*Tringa melanoleucus*) and American Avocet (*Recurvirostra americana*) were uncommon spring migrants. Greater Yellowlegs were seen in late April 1976, 1977, and 1979, and seven avocets were recorded 20 April 1978. The Common Snipe (*Gallinago gallinago*) was observed once, on 26 August 1980, near the proposed dam site.

Belted Kingfishers (*Ceryle alcyon*) were occasional spring and fall migrants, but, probably owing to the turbidity of the water, none remained to breed.

Discussion

Aquatic habitat along the White River is apparently important to waterfowl primarily during spring migration, although the Canada Goose nests in moderate numbers. Other aquatic birds use the river during migration, but only the Spotted Sandpiper is known to breed. The river is not heavily used during fall migration.

In terms of total numbers of waterfowl, the White River is not as important as reservoirs and other impoundments near the Green River. Sangster (1977) reported 47,347 (1975) and 27,485 (1976) ducks and geese on Pelican Lake and Ouray NWR near the confluence of the White and Green rivers. If waterfowl densities that we recorded are consistent along the rest of the White River, approximately 360 birds could be expected between Rangely, Colorado, and the Green River (132.0 km). Although the river is not heavily used by waterfowl, it may be one of the few important aquatic habitats within a large area.

Species composition along the White River during April was also different from that at Pelican Lake and Ouray NWR. Canada Goose was the most abundant species on the White River (54% of the total) followed by Green-winged Teal (17%) and Mallard (12%). At Pelican Lake and Ouray NWR, Mallards were most abundant (33%), and the Canada Goose ranked fourth (4.6%). Pelican Lake and the Ouray Refuge were also characterized as having more species (18) than did our study site (14 species), plus a greater percentage of diving ducks (Aythinae and Mergini): 7 of 18 species compared to 4 of 14 species on the White River. This is probably the result of the shallow water and high turbidity, making diving for food an unproductive foraging technique. The only species seen on the White River and not reported by Sangster (1977) was the Red-breasted Merganser.

If the White River Dam is built, changes in the abundance and composition of the aquatic bird fauna of the White River will depend

Table 2. Waterfowl abundance (birds/river km) along the White River from Cowboy Canyon to Asphalt Wash 7–9 April 1982 and 14–16 April 1983.

	Cowboy Canyon to dam site (km 0–24.1)		Dam site to Asphalt Wash (km 24.1–32.8)		Total survey	
Species	1982	1983	1982	1983	1982	1983
Canada Goose	1.88	1.86	1.23	0.34	1.71	1.46
Green-winged Teal	0.52	0.37	0.58	0.35	0.54	0.37
Mallard	0.36	0.25	0.42	0.29	0.38	0.25
Gadwall	0.19	0.19	0.00	0.04	0.14	0.15
American Wigeon	0.10	0.00	0.00	0.00	0.07	0.00
Lesser Scaup	0.08	0.00	0.04	0.00	0.07	0.00
Northern Shoveler	0.00	0.00	0.23	0.00	0.06	0.00
Blue-winged Teal	0.00	0.07	0.19	0.00	0.05	0.05
Red-breasted Merganser	0.07	0.00	0.00	0.00	0.05	0.00
Common Merganser	0.04	0.00	0.00	0.00	0.03	0.00
Ring-necked Duck	0.00	0.04	0.00	0.00	0.00	0.03
Cinnamon Teal	0.00	0.00	0.11	0.00	0.03	0.00
All waterfowl	3.24	2.78	2.80	1.02	3.13	2.31

on three factors: (1) colonization (or introduction) of plants on the margin and bottom of the reservoir, (2) decreased turbidity of the water, and (3) changes in populations of aquatic organisms (e.g., fish, insects, plankton) that are components of the aquatic food web. If marsh vegetation can be established, several species of ducks, herons, and egrets may nest. However, the terrain along the shores of the proposed reservoir will be mostly steep rocky slopes covered with thin soils, allowing establishment of emergent vegetation in only a few locations. The extent of these locations and the success of plantings or natural colonization in them will determine how many birds will breed in the reservoir.

Suspended materials will settle in the reservoir and the water will become less turbid; this should enable the kingfisher to become a breeding species. If cottonwoods are successfully established, they will provide perches for kingfishers and other aquatic birds. Muddy shores in shallow areas may attract more shorebirds.

Decreased turbidity and changes in prey populations, as well as the presence of open water, will be responsible for the major changes in the aquatic avifauna.

Members of Aythinae and Mergini will undoubtedly become more prevalent as will other diving aquatic birds. Coots, gulls, and terns will also probably occur, because they are common at Pelican Lake (Hayward 1967).

If emergent and riparian vegetation are successfully established and water levels remain relatively stable, more aquatic birds will occupy the reservoir than presently use the White River. If, however, revegetation is unsuccessful, the reservoir may be a relatively unproductive avian habitat.

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PATTERNS OF MACROINVERTEBRATE COLONIZATION IN AN INTERMITTENT ROCKY MOUNTAIN STREAM IN UTAH

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Abstract.— Colonization of macroinvertebrates in a headwater mountain stream was monitored using basket and Surber samplers. Taxa showed differences in colonization ability based both on dispersal ability and feeding strategy. Collector-gatherer feeding groups that could actively enter the water, i.e., *Baetis* mayflies, were the first organisms to colonize bare or new substrate. The slowest colonizers were heptageniid mayflies that colonized primarily from upstream migration. All organisms examined increased drifting behavior in response to decreases in discharge.

Intermittent streams provide a unique opportunity to study colonization by macroinvertebrates. Colonization of artificial substrate samplers begins almost immediately after they are placed into permanently flowing streams (Ulfstrand et al. 1974, Townsend and Hildrew 1976, Sheldon 1977, Roby et al. 1978). Similar patterns are seen by disturbing the substrate to remove the existing species and thereby creating open areas for colonization (Waters 1964). However, such a small area of barren substrate, completely surrounded by undisturbed habitat, is atypical of natural streams. The dry sections of intermittent streams are usually more extensive in area and should show the immigration patterns of colonizing species from permanent habitats.

The primary sources of macroinvertebrate colonization in streams are downstream drift, upstream migration, aerial sources (e.g., oviposition), and vertical migration upward from the substrate (Williams and Hynes 1976, Townsend and Hildrew 1976, Williams 1977). Williams (1977) showed that a significant fraction of colonizers in two temporary streams were from the hyporheos, and Hultin et al. (1969), Bishop and Hynes (1969), and Elliott (1971b) documented significant upstream migration of macroinvertebrates. Others (Kennedy 1955, Patrick 1959, Waters 1964) showed the importance of drift in the colonization process. Larimore et al. (1959) suggested aerial sources as being primary in the stream they studied.

We studied an intermittent section of Stewart's Creek, a mountain stream, to determine colonization patterns. We hypothesized that only migrating macroinvertebrates capable of utilizing existing stream conditions would colonize and there would be a succession of organisms. The purpose of this paper is to describe the patterns of colonization seen when water was flowing through the intermittent section of stream.

Methods and Materials

Study Site

Stewart's Creek is a small second-order (Strahler 1957) stream originating from a glacial cirque on the southeast face of Mt. Timpanogos about 33 km northeast of Provo, Utah. Glacial sediments form the substrate through which the stream channel is cut. The dominant substrate particle sizes (Cummins 1962) are cobble and large pebble. Mean annual discharge is 0.25 m^3/sec; mean annual water temperature is 4–5 C. During low water years the receding groundwater level causes a 300 m section of stream to periodically dry up due to the porosity of the sediments and the slope (11%). From October 1976 to May 1978, this section of stream remained dry due to below normal winter snow pack. Following an average snowfall during the winter of 1977–1978, we anticipated that flow in the intermittent reach would resume during spring and summer of 1978. Five sampling stations were established within a 450

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m section. These included both permanent flowing upstream (UP) and downstream (LP) sites and three sites approximately 100 m apart in the temporary stream section: upper temporary (UT), a site 50 m below UP in the temporary channel, middle temporary (MT), 100 m below UT, and lower temporary (LT), which was 100 m below MT and 50 m above LP.

Sampling

On 30 April 1978 ten 30 cm × 30 cm × 15 cm basket samplers were placed in the stream channel at each study site by digging through the snow cover. The samplers were made of steel frame covered with 4 cm^2 mesh hardware cloth on all sides except the top, which was open. Each sampler was filled with cobble from the stream bed. The rocks placed in the samplers were cleaned of all organisms and detritus.

Two baskets randomly chosen were removed weekly from each study site for five weeks beginning the day water entered the temporary sites. The permanent site baskets colonized for 15 d before water entered the intermittent section. Macroinvertebrates were washed from the rocks, preserved in 10% formalin, sorted in the laboratory, identified, and counted.

Since water continued to flow in the channel after all basket samplers had been removed, we continued to sample the macroinvertebrate community using Surber samplers (230 μm mesh). Two Surber samples were collected weekly from each of the temporary (UT, MT, LT) and permanent (UP, LP) sites beginning on week six for nine additional weeks. These samples were processed as described above.

A drift net (250 μm mesh) was placed weekly immediately below UP and above LP. The nets were placed at 1700 h and removed between 1900 and 2000 h. The contents of the nets were processed as described earlier. Discharge was measured at both drift net sites and at MT with a flow meter on each sampling date.

Analysis

Macroinvertebrate data were analyzed with categorical data analysis for cross classified data where categories were site and date. Trends across time and differences between the ratios of the cell frequencies at each site were determined using a log-linear model with orthogonal contrasts (Fienberg 1978). All analyses were performed using RUMMAGE (Scott et al. 1974), a general linear models program. Basket and Surber sample data were analyzed separately. No relationship between these two methods is intended.

RESULTS

The resumption of flow in the intermittent stream section began 15 May 1978. After three days a cold spell stopped snowmelt and the flow was interrupted for three days, after which the stream began to flow again through the intermittent section.

Taxa Richness

The numbers of taxa found at upper and lower permanent sites were not different (basket samplers, $p = .521$ and Surber samplers, $p = .227$) (Table 1). The upper and lower permanent sites had more taxa ($p < .05$) than any of the temporary sites through both the basket and Surber sampling schedules (except the comparison of UT with LP). The UT site had more taxa ($p < .05$) than did

Table 1. Taxa richness and density (number/m^2) for starting basket samplers = SBS, ending basket samplers = EBS, starting Surber samplers = SSS, and ending Surber samplers = ESS for all sampling stations.

	Richness				Density			
Site	SBS	EBS	SSS	ESS	SBS	EBS	SSS	ESS
UP	8	15	16	26	1255	1103	3354	9742
UT	3	11	8	16	112	1589	1222	3345
MT	0	2	5	12	0	835	1089	3311
LT	0	3	6	13	0	440	1232	5534
LP	11	11	15	18	988	2778	1685	6625

MT during the basket colonization but not in the Surber sampling period. The middle temporary site never differed from LT in number of taxa, and both were lower than any other site throughout the study. Both taxa richness and density increased faster at UT than any other temporary site. The number of taxa increased linearly at all sites over time ($p < .01$).

Densities

The upper permanent site (UP) had higher densities ($p < .01$) than any site except LP during the Surber sampling period (Table 1). The densities of organisms were not different ($p > .05$) between middle temporary and lower temporary during the first five weeks (basket sampling) but were higher at LT ($p < .05$) during the following nine weeks (Surber sampling). The permanent sites had higher ($p < .05$) densities than any intermittent site throughout the study.

Community Structure

Horn's (1966) measure of community overlap was calculated for the numbers of species at UP and LP at the start and end of each sampling method (Table 2). The value of overlap, R_o, approaches 1.0 as the amount of overlap increases. The low overlap at the beginning of the experiment ($R_o = .43$) reflects the differences that had developed between the permanent sites while separated during drought conditions for approximately 1.5 to 2.0 years. Following the connection by water after the runoff event, LP and UP showed a linear increase in community overlap as LP became more like UP.

Colonization Patterns of Selected Organisms

The general pattern across taxa was that colonization began later at MT and LT than at UT. Once colonization was initiated, densities rapidly increased until MT and LT were similar to UT. This general pattern was variable between groups of organisms.

Based on their densities throughout the study period and their feeding and dispersal strategies, the following taxa were selected for detailed analyses: *Baetis* spp. (Baetidae: Ephemeroptera), *Neothremma* sp. (Limnephilidae: Trichoptera), and four genera of Ephemeroptera in the family Heptageniidae, *Cinygmula* spp., *Heptagenia* spp., *Epeorus* spp., and *Rhithrogena* spp. *Baetis* and *Neothremma* are both in the collector feeding functional group (Merritt and Cummins 1978), but they exhibit distinct differences in mobility. *Baetis* is an excellent swimmer, actively entering the drift (Corkum et al. 1977, Corkum 1978a,b). *Neothremma*, a sand case-building caddisfly, may be passively distributed (Minshall and Winger 1968). The heptageniids are all in the collector-gatherer feeding functional group. They are all dorsoventrally flattened and adapted for crawling and are not considered good swimmers (Corkum 1978a).

Baetis were the first organisms to colonize the temporary sites (Table 3). The upper permanent site baskets had more *Baetis* than all downstream site baskets ($p < .05$), and UT had more than all sites below it, including LP ($p < .05$). The lower permanent site had the highest density of *Baetis* during the basket sampling ($1333/m^2$), but, over all dates, LP was lower than UP and UT ($p < .05$). By the end of the Surber sampling, UP, MT, and LP had similar numbers of *Baetis* ($p > .05$) and each of these sites had higher numbers of *Baetis* than either UT or LT ($p < .05$).

Neothremma density was greater at UP than at any lower site ($p < .05$) in both the basket and Surber sampling periods (Table 3), although the lower permanent site was colonized before any temporary site. The lower permanent site had more *Neothremma* than all stations above it ($p < .05$) except UP ($p > .05$) by the end of the basket sampling period. At the conclusion of the study a comparison of *Neothremma* density between sites showed UP>UT>MT>LT. Density was higher at LP than LT ($p < .05$), but it was not different from any other site ($p > .05$).

Table 2. Horn's (1966) measure of community overlap (R_o) between Upper Permanent and Lower Permanent sites at the start and end of basket and Surber sampling efforts.

Sampler and period	R_o*
Beginning basket sampling	.43
Ending basket sampling	.57
Beginning Surber sampling	.64
Ending Surber sampling	.74

*1.0 = complete similarity or overlap

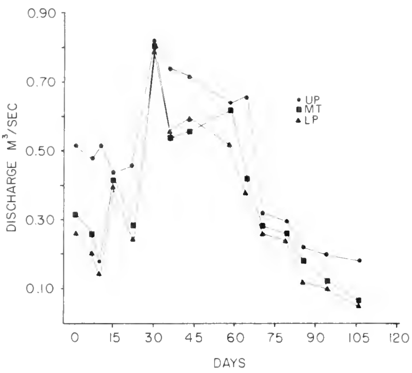

Fig. 1. Spring-summer hydrograph of Upper Permanent (UP), Middle Temporary (MT), and Lower Permanent (LP) sites on Stewart's Creek.

The upper temporary site had the fastest colonization by Heptageniidae (Table 3). During the basket sampling period there were no differences between any site except UT and LT ($p > .05$), where UT was higher. The numbers of heptageniids increased over time at all the temporary sites. Middle temporary had more heptageniids than all sites ($p < .05$) except LP ($p > .05$), which had more than all sites during the Surber sampling.

Drift

Catastrophic drift, caused by high flow conditions, should be reflected in the density of organisms in the drift taken during the ascending limb of the spring hydrograph (Anderson and Lehmkuhl 1968). The patterns for total species, *Neothremma*, *Baetis*, and Heptageniidae are shown in Figure 1. At LP, drift (Fig. 1) was lowest during the ascending portion of the hydrograph (Fig. 2).

The numbers of species increased in the drift over time ($p < .05$) at the lower drift station (Fig. 1). Each group studied; i.e., *Baetis*, *Neothremma*, and Heptageniidae increased in numbers at the lower station between the 9th and 12th sampling weeks. It was during this same interval (9th–12th weeks) that the largest reduction in discharge occurred (Fig. 2).

At the lower site, total species, total organisms, and the density of *Baetis*, *Neothremma*, and heptageniids were positively correlated with discharge during the ascending part of the stream hydrograph (Table 4). These same groups continued to increase when discharge was decreasing ($p < .05$). The upper drift net site had negative but not significant corelation coefficients ($p > .05$) for both the ascending and descending comparisons.

DISCUSSION

The large amount of litter that accumulated in the channel during the dry period was washed out during the ascending limb of the spring hydrograph; however, leaf pack accumulations did remain in the temporary sections. We therefore expected that organisms that feed on detritus and are good dispersers would disperse throughout the intermittent area given sufficient time. *Baetis* are active drifters and good swimmers; they also feed by collecting detritus. *Baetis* were the most similar in their distribution and abundance at all study sites (Table 3) by the end of this study.

If an organism is a passive disperser, then we would expect a pattern of high densities nearer to the source of colonizers, with decreasing densities further from that source. *Neothremma* showed such a pattern. The higher densities at LP could be due to changes in flow conditions, i.e., increased

Table 3. Mean densities (number/m^2) of *Baetis*, *Neothremma*, and Heptageniidae for starting basket samplers = SBS, ending basket samplers = EBS, starting Surber samplers = SSS, and ending Surber samplers = ESS for all sampling stations.

								Sampling
	UP				UT			
Taxa	SBS	EBS	SSS	ESS	SBS	EBS	SSS	ESS
Baetis	256	67	217	244	11	769	89	278
Neothremma	722	356	1835	4667	0	333	445	343
Heptageniid	122	11	456	311	22	233	56	422

settling with reduction in flow, or upstream migration from lower adjacent permanent sections.

The increases in heptageniid density at LP and MT, larger than that of UT and LT, have two possible explanations. First, the heptageniids might have migrated upstream from below LP. Second, heptageniids may have quickly moved through the temporary sites in response to poor food or habitat conditions. A pattern similar to *Neothremma* would be expected if heptageniid drift were passive. If the organisms were moving to better feeding conditions, then they should congregate wherever a food source was found. Being poor swimmers but adapted for crawling, heptageniids may have moved up from LP through LT or down from UP through UT. Since there were no Heptageniidae found in the drift until after the sixth week, we have assumed a crawling migration for Heptageniidae into the temporary sites.

Baetis and Heptageniidae density at MT during July and August was greater than for the other temporary sites. Since MT is an approximate midpoint in the study sites, then the high densities may be a function of the overlap in organisms migrating up from LP and down from UP. The higher densities at middle temporary may also be due to the study terminating before equilibrium densities could be established at UT and LT. *Baetis* drift easily and were shown to be distributed with some equality throughout the study sites. Therefore, an increase in *Baetis* at any one site after sufficient time indicates a selection for a preferred habitat.

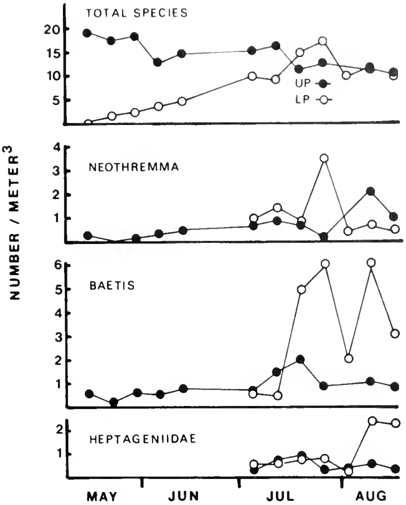

Fig. 2. Changes in the densities (number/m^3) of taxa, *Neothremma*, *Baetis*, and Heptageniidae in drift below the Upper Permanent (UP) and above Lower Permanent (LP) study sites in Stewart's Creek.

Even though there was a significant increase in discharge during the early weeks of the study, drifting organisms did not follow a similar pattern. The numbers of organisms leaving UP increased over time, but did not increase in proportion to the changes in discharge. It was during the period of reduction in flow that drift increased most rapidly. This supports the work of Minshall and Winger (1968). This response may be a function of one or both of the following: (1) There is no net increase in drifting organisms but only a relative increase in density as the discharge decreases and (2) organisms are drifting as a behavioral response to these discharge changes. If No. 1 is correct then, after adjusting the drift densities for discharge and getting numbers/time, the ratio of any pair of data points should be unity. If the numbers of organisms/m^3 are actually increasing because more are actively entering the drift, then the ratios between adjusted pairs should increase

Table 3 continued.

site

MT				LT				LP			
SBS	EBS	SSS	ESS	SBS	EBS	SSS	ESS	SBS	EBS	SSS	ESS
0	922	467	511	0	33	567	200	0	1333	622	100
0	33	144	147	0	0	44	178	256	422	78	500
0	278	367	800	0	244	456	878	11	223	267	822

TABLE 4. Correlation coefficients obtained from analysis of the relationships between either the ascending or descending limb of the hydrograph and total taxa, total numbers, *Baetis*, *Neothremma*, and Heptageniidae.

	Taxa richness		Densities		*Baetis*		*Neothremma*		Heptageniidae	
Site	Ascend	Descend	Ascend	Descend	Ascend	Descend	Ascend	Descend	Ascend	Descend
UP	-.17	-.35	-.58	-.58	-.66	-.17	-.70	-.48	-.50	-.16
LP	.84°	-.59	.91	-.77°	.95°	-.18	-.02	-.81°	.40	-.37

° = p < .05

over time and the slope of the regression of these adjusted numbers against time should not equal zero. The slope of each curve was significantly different from zero (t > critical value, $p < .05$), indicating a behavioral response of the macrobenthos.

The benthic sampling procedures used in this study were not selective for any one colonization vector, i.e., vertical (from hyporheos), aerial (ovipositing), downstream drift, and upstream migration. We felt that the influence of vertical movement and aerial colonization would be uniform throughout the study site, whereas drifting and upstream movement would show a response to distance. This response would depend on the distance from the colonization source and the dispersal ability of the organisms (Waters 1964, McLay 1970, Elliott 1971a). Some researchers have demonstrated significant upstream movement (Hultin et al. 1969, Bishop and Hynes 1969, Elliott 1971b). The distances traveled upstream were up to 600 cm/night (Elliott 1971b). At that rate an organism could hypothetically move upstream the length of the temporary section in 50 d. Although this is possible, the results of the drift measurements show that there are sufficient colonizing organisms in drift to account for the colonization patterns we described for *Baetis* and *Neothremma*.

The established stream communities, UP and LP, were the primary sources of potential colonizers. Active and passive drift organisms leaving UP would first reach UT. Once settling out, an organism may stay or leave depending on the suitability of the habitat, availability of food, space, and flow conditions.

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CHECKLIST OF THE MOSSES OF GRAND TETON NATIONAL PARK AND TETON COUNTY, WYOMING

John R. Spence[1]

ABSTRACT.— A preliminary checklist of the mosses of Grand Teton National Park and Teton County, comprising 106 species, is presented. The following nine species are reported as new to Wyoming: *Sphagnum squarrosum* Crome, *Atrichum undulatum* (Hedw.) P.-Beauv., *Tortella humilis* (Hedw.) Jenn., *Bryum bicolor* Dicks., *Pohlia obtusifolia* (Brid.) L. Koch, *Calliergon sarmentosum* (Wahlenb.) Kindb., *Eurhynchium oreganum* (Sull.) Jaeg., *Plagiothecium piliferum* (Sw. ex C.J. Hartm.) B.S.G., and *Lescuraea stenophylla* (Ren. & Card.) Kindb.

Although the vascular plant flora of Grand Teton National Park and vicinity, in western Wyoming, is well known, basic floristic information on the bryophytes are scarce. Early collections in the state of Wyoming by C.L. Porter led to two papers on the mosses and liverworts, with 54 mosses listed from Grand Teton National Park (Porter 1933, 1935). More recently, Hong (1977) added many new liverwort species to the state flora and Churchill (1979, 1982) added several species of mosses new to Wyoming.

Since the reports by Porter, no additions to the moss flora of the park have been reported. This paper is based on my own collections from the park from 1978 through 1981, as well as collecting trips by Dr. E. Lawton and Mr. F. J. Hermann. Also, literature reports from various monographs have been included.

The physiography of Grand Teton National Park and Teton County is rugged, with extremes of relief greater than 2000 m, providing a wide range of habitats available for bryophytes. The climate of the area has been characterized by Reed (1952), Shaw (1958), and Spence (1981). Major vegetation communities include valley floor coniferous forest and sagebrush steppe, marshes and lakeshore vegetation, riverine gallery forests, subalpine coniferous forest, subalpine meadows, alpine meadows, and alpine fell-fields (Reed 1952, Loope and Gruell 1973, Sabinske and Knight 1978, Spence and Shaw 1981). Bryophyte diversity appears to be highest in moist east-facing canyons in the Teton Range, but most areas of the park have only been slightly collected. This checklist reports 106 species of mosses, representing about one-half the flora of the state. The large numbers of species Porter (1935) reported from Yellowstone National Park to the north of Grand Teton National Park suggests that further collecting will greatly increase the known flora.

The checklist is arranged phylogenetically by family, using Corley et al. (1981), with the following exceptions: the Ditrichaceae are maintained as distinct from the Dicranaceae; the Polytrichaceae follow Smith (1971); the Scouleriaceae are separated from the Grimmiaceae according to Churchill (1981); and *Platydictya jungermannioides* is maintained (=*Amblеystegium jungermannioides* (Brid.) A. J. E. Smith in Corley et al. 1981). For North American endemics synonymy follows Lawton (1971). Collectors (including herbaria collections in which specimens are deposited) are noted as follows: P=Porter (RM); H=Hermann (variously distributed at numerous herbaria); L=Lawton (WTU); S=Spence (UBC); M=Manville (Grand Teton National Park herbarium at Moose, Wyoming). No attempt has been made to verify literature reports. Those species marked with an asterisk (°) are apparently new reports for Wyoming, and were not reported in Porter (1935), Lawton (1971), or any monographs and taxonomic works cited in this paper.

CHECKLIST OF THE SPECIES

Sphagnaceae
  Sphagnum russowii Warnst. P1198.1199; S976.
  °*S. squarrosum* Crome S974.

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Tetraphidaceae

- *Tetraphis pellucida* Hedw. H25571; S973.

Polytrichaceae

- *Atrichum selwynii* Aust. H25548,25765.
- °*A. undulatum* (Hedw.) P.-Beauv. L1736.
- *Polytrichastrum alpinum* (Hedw.) G.L.Smith S291.
- *P. lyallii* (Mitt.) G.L. Smith S352.
- *Polytrichum commune* Hedw. S318.
- *P. juniperinum* Hedw. H25560.
- *P. piliferum* Hedw. H25559; S357.

Buxbaumiaceae

- *Buxbaumia viridis* (DC.) Moug. & Nestl. H25577.

Fissidentaceae

- *Fissidens adiantoides* Hedw. L1730.
- *F. osmundoides* Hedw. P1201; L1730.

Ditrichaceae

- *Ceratodon purpureus* (Hedw.) Brid. S75.
- *Distichium capillaceum* (Hedw.) B.S.G. S334.

Dicranaceae

- *Dicranoweisia cirrata* (Hedw.) Lindb. ex Milde (Porter 1935).
- *D. crispula* (Hedw.) Milde H25554; S333.
- *Dicranum rhabdocarpum* Sull. (Peterson 1979).
- *D. scoparium* Hedw. H25766; S979.

Pottiaceae

- *Bryoerythrophyllum recurvirostrum* (Hedw.) Chen H25575; S995.
- *Desmatodon latifolius* (Hedw.) Brid. S358.
- °*Tortella humilis* (Hedw.) Jenn. H25566.
- *T. tortuosa* (Hedw.) Limpr. P1166,1169.
- *Tortula norvegica* (Web.) Wahlenb. ex Lindb. H25549.
- *T. ruralis* (Hedw.) Gaertn., Meyer & Scherb. S354.

Grimmiaceae

- *Grimmia alpestris* (Web. & Mohr) Schleich. ex Hornsch. H25556,25584; L1728; S986.
- *G. elatior* Bruch ex Bals. & De Not. H25553.
- *G. hartmannii* Schimp. L1738,1759.
- *G. ovalis* (Hedw.) Lindb. (Porter 1935).
- *G. trichophylla* Grev. L1734,1765.
- *Racomitrium canescens* (Hedw.) Brid. L1764.
- *R. fasciculare* (Hedw.) Brid. (Porter 1935).
- *R. sudeticum* (Funck) B. & S. S992a.
- *Schistidium agassizii* Sull. & Lesq. H25543.
- *S. apocarpum* (Hedw.) B. & S. H25544; L1729.
- *S. rivulare* (Brid.) Podp. H25583.

Scouleriaceae

- *Scouleria aquatica* Hook. L1753; H25582.

Bryaceae

- °*Bryum bicolor* Dicks. H25545.
- *B. caespiticium* Hedw. S971.
- *B. capillare* Hedw. S313.
- *B. lisae* De Not. S337.
- *B. pseudotriquetrum* (Hedw.) Gaertn., Meyer & Scherb. H25574,25579; L1756.
- *B. stenotrichum* C. Muell. S359.
- *B. turbinatum* (Hedw.) Turn. L1777,1782.
- *B. uliginosum* (Brid.) B.S.G. M3799.
- *B. weigelii* Spreng. S996b.
- *Leptobryum pyriforme* (Hedw.) Wils. L1733,1751; H25567.
- *Pohlia andalusica* (Höhn.) Broth. Shaw 2704 (Shaw 1981).
- *P. camptotrachela* (Ren. & Card.) Broth. Shaw 2692 (Shaw 1981).
- *P. cruda* (Hedw.) Lindb. L1737; H25568; S343.
- *P. drummondii* (C. Muell.) Andr. Shaw 2695 (Shaw 1981).
- *P. nutans* (Hedw.) Lindb. H25573; S980.
- °*P. obtusifolia* (Brid.) L. Koch S989,993a.
- *P. proligera* (Kindb. ex Limpr.) Lindb. ex Arnell Shaw 2702 (Shaw 1981).
- *P. tundrae* J. Shaw Shaw 2709 (Shaw 1981).
- *P. wahlenbergii* (Web. & Mohr.) Andr. H25564.
- *Roellia roellii* (Broth. ex Roell) Andr. ex Crum S329.

Mniaceae

- *Mnium arizonicum* Amann L1770.
- *M. spinulosum* B.S.G. S980c.
- *M. thomsonii* Schimp. S985a.
- *Plagiomnium cuspidatum* (Hedw.) T. Kop. M3802.
- *Rhizomnium magnifolium* (Horik.) T. Kop. H25562,25580; S970.
- *R. punctatum* (Hedw.) T. Kop. M3788.

Aulacomniaceae

- *Aulacomnium androgynum* (Hedw.) Schwaegr. (Porter 1935).
- *A. palustre* (Hedw.) Schwaegr. S969.

Bartramiaceae

- *Bartramia ithyphylla* Brid. L1761.
- *Philonotis fontana* (Hedw.) Brid. L1766; S999.

Orthotrichaceae

- *Amphidium lapponicum* (Hedw.) Schimp. Cain 4675(UBC).
- *Orthotrichum alpestre* Hornsch. ex B.S.G. L1757.
- *O. cupulatum* Brid. (Porter 1935).
- *O. laevigatum* Zett. H25550,25551; L1731,1760,1768.
- *O. rupestre* Schleich. ex Schwaegr. L1767.

Fontinalaceae

- *Dichelyma falcatum* (Hedw.) Myr. S972.
- *Fontinalis antipyretica* Hedw. S976b.
- *F. hypnoides* C.J. Hartm. M3787.

Climaciaceae

- *Climacium americanum* Brid. L1732.
- *C. dendroides* (Hedw.) Web. & Mohr S314.

Leskeaceae

- *Lescuraea incurvata* (Hedw.) Lawt. L1783.
- *L. radicosa* (Mitt.) Mönk. H25558,25764; L1744-8.
- °*L. stenophylla* (Ren. & Card.) Kindb. Flowers 3833A (UBC).

Ambleystegiaceae

- *Ambleystegium serpens* (Hedw.) B.S.G. (Porter 1935).
- °*Calliergon sarmentosum* (Wahlenb.) Kindb. S996.
- *C. stramineum* (Brid.) Kindb. S981.
- *Cratoneuron commutatum* (Hedw.) Roth L1778.
- *C. filicinum* (Hedw.) Spruce H25563; S978.
- *Drepanocladus aduncus* (Hedw.) Warnst. S978b.
- *D. exannulatus* (B.S.G.) Warnst. S978a.
- *D. uncinatus* (Hedw.) Warnst. H25552; L1726, 1754,1762,1781.
- *Hygrohypnum bestii* (Ren. & Bryhn ex Ren.) Holz. L1769; S998.
- *H. ochraceum* (Turn. ex Wils.) Loeske Cain 4547 (Jamieson 1976).
- *Platydictya jungermannioides* (Brid.) Crum H25572.

Brachytheciaceae

- *Brachythecium albicans* (Hedw.) B.S.G. H25546.
- *B. erythrorrhizon* B.S.G. (Porter 1935).
- *B. fendleri* (Sull.) Jaeg. L1772,1774.
- *B. frigidum* (C. Muell.) Besch. H25578.
- *B. rivulare* B.S.G. (Porter, 1935).
- *B. salebrosum* (Web. & Mohr) B.S.G. H25547.

B. starkei (Brid.) B.S.G. S982.
B. velutinum (Hedw.) B.S.G. L1773.
°*Eurhynchium oreganum* (Sull.) Jaeg. M3797,3792.
Plagiotheciaceae
Isopterygium pulchellum (Hedw.) Jaeg. (Ireland 1969).
Plagiothecium denticulatum (Hedw.) B.S.G. H25565.
°*P. piliferum* (Sw. ex C.J. Hartm.) B.S.G. M3796.
Hypnaceae
Hypnum cupressiforme Hedw. S183.
H. lindbergii Mitt. L1727.
H. revolutum (Mitt.) Lindb. H25557; S335,356.

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ECOLOGICAL INVESTIGATION OF A SUSPECTED SPAWNING SITE OF COLORADO SQUAWFISH ON THE YAMPA RIVER, UTAH

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ABSTRACT.— On 5 July 1981, 13 adult Colorado squawfish were found in spawning condition at river mile 16.5 in the Yampa River, a major tributary to the Green River. An investigation was undertaken to quantitatively describe this section of the river to gain insights on the spawning requirements of this endangered species. The substrate at the suspected spawning site was cobble with large interstitial spaces devoid of organics, silts, or clays. It appeared that larvae of several fish species utilized these cobble areas and the associated voids. Diurnal sampling indicated that larval drift occurred between 0100 and 0125 hours. Substrate size also appeared to be a dominant factor in fish distribution. Feeding intensities of these fish corresponded to macroinvertebrate drift.

Spawning by the endangered Colorado squawfish (*Ptychocheilus lucius*) has not been documented in nature. On 1 July 1981, the Colorado River Fisheries Project [CRFP] of the U.S. Fish and Wildlife Service captured 13 adult Colorado squawfish in spawning condition in one localized area of the Yampa River, known as Cleopatra's Couch, 16.5 miles from the Green River confluence. This gave us the opportunity to intensively sample the immediate area in an effort to locate the site and to document conditions in a natural spawning habitat. This survey was undertaken 24–26 July 1981.

The objectives of this study were:

1. To characterize this river ecosystem at the suspected squawfish spawning site.
2. To document the interactions of the abiotic environment with the biotic community.
3. To document the interactions among and between trophic levels.
4. To compare the structure and function of the ecosystem at this site with that of other similar sites in adjacent tributaries where squawfish were not located.

The above objectives were accomplished by intensively surveying the area where spawning squawfish were observed (mile 16.5) and comparing these data to another similar Yampa River site (mile 18.0) apparently not used for spawning during 1981. Furthermore, these data are compared to a structurally similar area in the White River, a major tributary of the Green River, where successful squawfish spawning has been suspected but not documented. The results of this study are important for recognizing potential squawfish spawning sites and for the future maintenance of the physical and biological integrity of this important Yampa River site in the face of future development within the upper Green River Basin.

MATERIALS AND METHODS

Field

Two field seining sites were established (mile 16.5 and 18.0), and at each of these samples were taken from several different habitat types, e.g. riffles, eddies, and runs. Five seining sample locations were chosen for river mile 16.5 and seven for river mile 18.0. All fish samples were collected with seines (4 x 30 ft, with 1/4-in mesh).

Upon capture, all fish were identified, counted, and measured for total lengths. Fish less than 100 mm were slit abdominally and placed in a 10% formalin solution. The digestive tracts of fish greater than 100 mm were removed and preserved in 10% formalin. A benthic sample (modified Surber sampler) was collected at each seine haul location.

Insects floating in the water column were sampled with drift nets (27.5 cm diameter, 1.0 mm mesh size) at each seine sample location. These nets were anchored to the river bottom and set in the water column approximately 1 m upstream from the area to be seined. Each net was set for approximately 4 hours prior to fish collection and removed

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just prior to seining. Drift material was preserved in 10% formalin.

Physical data at each seining sample location (water temperature, water depth, current velocity, and dominant substrate type) were also determined. A sediment core sample was also collected at each seining sample location using a 4.6-cm-diameter coring device. These interstitial sediment samples were transported to the laboratory and analyzed for size fractions and organic content.

Three cross-river transects at river mile 16.5 and two at river mile 18.0 were established. Water depth, current velocity (0.6 distance from the bottom), and dominant substrate were recorded at transect points every 2 m across the stream. At five equidistant points on each transect, benthic macroinvertebrates and chlorophyll *a* (periphyton) samples were collected. In areas deeper than 1 m, SCUBA was used to sample. All chlorophyll samples were stored on dry ice for transportation.

Laboratory

In the laboratory fish stomachs were removed, and the contents were placed in vials containing 70% ethanol. In fishes with distinct stomachs, such as Ictalurids and some Cyprinids, only the contents of the stomach were taken. In fishes with poorly defined stomachs, such as Catostomids, the anterior portion of the gut from the esophagus to the first bend or distinct constriction of intestine was taken for analysis. Total displaced volumes of stomach contents were measured with a graduated volumetric tube to the nearest 0.01 ml. Contents were then identified, counted, and measured to the nearest millimeter.

Drift net and benthic samples were floated in a sugar-water solution and poured through a 0.25 mm sieve to separate the organic and inorganic portions. Insects and fishes were then manually sorted from all other organic materials. These items were preserved in 70% ethanol, identified, and counted. The remaining debris was dried at 105 C for 24 hours and weighed on a Sartorius balance. All benthic insects were additionally measured to the nearest millimeter.

Interstitial substrate samples collected in the field were dried at 105 C for 24 hours. The sediments were then sieved into five size fractions (see footnote in Table 1), which were each weighed on a Sartorius toploading balance. The 0.25-mm size fraction was redried for 24 hours at 105 C, cooled in a desiccator, and weighed to the nearest 0.01 mg on an analytical balance. These samples were then ashed in a preheated muffle furnace at 550 C for 20 minutes, cooled, and reweighed.

Table 1. Physical and biological data summary for five transects on the Yampa River between river miles 16.5 and 18.0. Figures are an average of river cross-sections with standard deviation.

Transect		Chl a (mg/m^2)	Depth (m)	Velocity (m/sec)	Dominant substrate (cm)	Sediment as a percent	
						A	B
1	mean	12.2	0.9	0.63	9.0	42.6	6.0
	SD	11.9	0.2	0.2	3.4	35.5	7.9
2	mean	31.6	1.4	0.3	0.3	-0-	6.0
	SD	15.1	0.9	0.2	0.4	-0-	14.7
3a	mean	4.6	0.3	2.4	7.5	67.0	20.0
	SD	--	0.1	1.0	-0-	11.3	4.2
3b	mean	30.0	0.4	2.1	5.8	70.0	18.0
	SD	2.3	0.1	0.7	2.9	10.8	5.6
4	mean	7.8	2.3	0.6	6.3	27.2	0.2
	SD	13.1	1.7	0.6	7.9	43.2	0.5
5	mean	8.8	0.3	3.5	9.0	74.2	13.4
	SD	4.6	0.2	1.6	3.4	14.5	9.7

*Sediment size fractions (mm)
A = > 14.7
B = 14.7 – 4.0
C = 4.0 – 0.5
D = 0.5 – 0.25
E = < 0.25

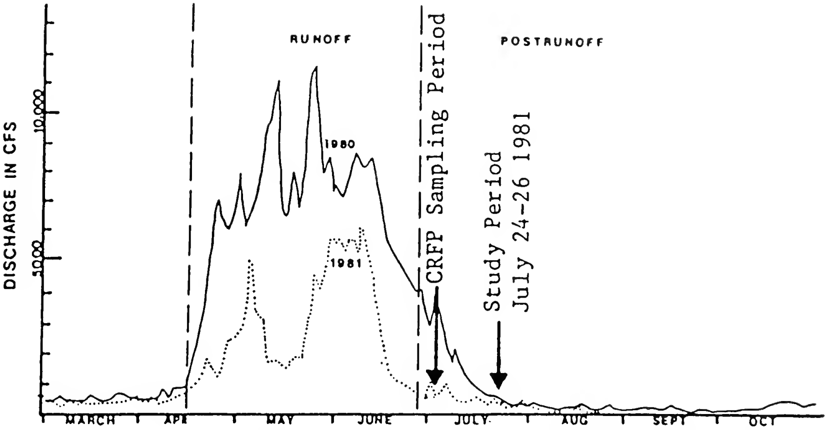

Fig. 1. Discharge levels in the Yampa River during 1980 and 1981. Sample times for the CRFP and this study are given.

The weight loss on ignition was calculated as organic content.

Periphyton biomass was determined by scraping a flat area 4.6 cm in diameter from each rock collected. This scraped material was extracted for chlorophyll in 250 mls of 90% acetone. Core samples containing sand or silt were placed directly into 250 ml of acetone for extraction. Chlorophyll *a* was determined with a Turner Model III fluorometer (American Public Health Association 1980).

RESULTS

Transect Sites

Steep canyon walls always occur on at least one shore of the river between miles 16.5 and 18.0. Cobble-covered islands and

TABLE 1. Continued

size fraction					Macroinvertebrates	
of the total						
C	D	E	Organics	Total detritus (gms/m^2)	Total (#/m^2)	Total biomass (gms/m^2)
6.2	24.8	20.2	.2	9.2	69.2	1.0
4.1	25.0	26.2	.03	16.9	48.1	1.0
15.3	33.7	45.3	0.6	15.6	186.5	1.0
25.6	25.3	28.3	0.8	20.7	203.2	1.3
10.5	2.5	-0-	-0-	1.4	762.0	4.5
6.4	0.7	-0-	-0-	1.6	879.6	9.0
7.7	4.0	0.3	-0-	2.7	233.3	8.1
4.2	2.0	0.6	-0-	3.3	24.7	2.1
10.2	38.6	23.8	0.3	12.2	53.3	1.8
9.1	26.8	30.6	0.3	16.7	28.9	2.6
7.0	1.2	0.8	-0-	1.1	302.9	13.8
4.7	1.3	0.5	-0-	0.9	193.0	7.3

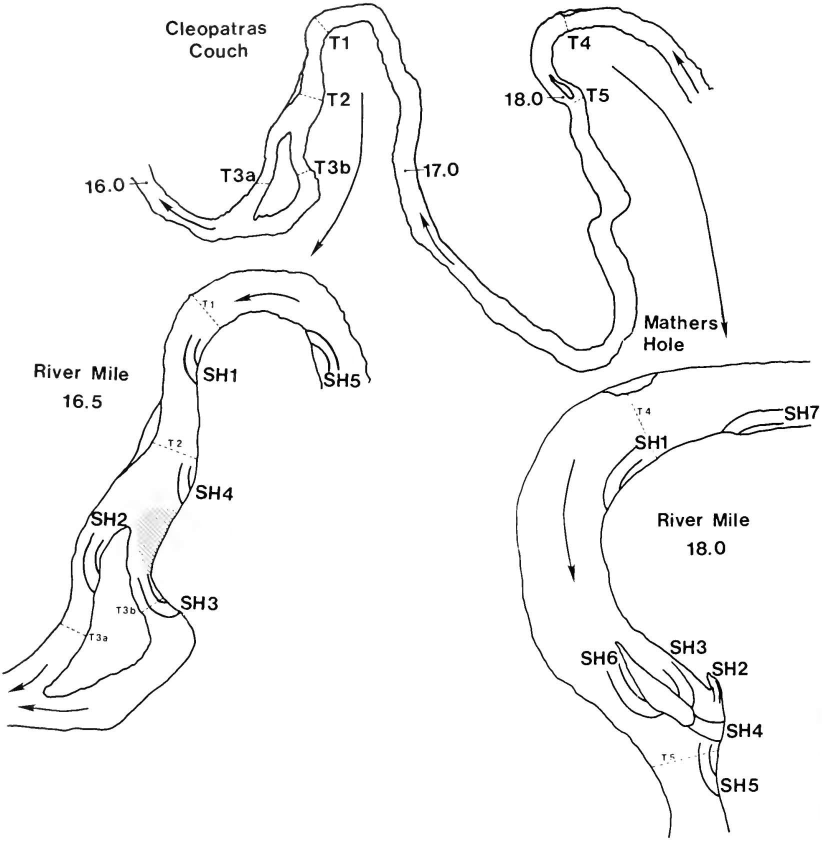

Fig. 2. Locations of study sites at miles 16.5 and 18.0 on the Yampa River. SH represents seine haul locations. T represents transect locations.

shorelines had been recently exposed by reduced flows (Fig. 1). Beaches within zones of deposition were composed of fine sand or organic silt-mud deposits. Backwaters were often marshy with loose organic substrates.

At river mile 16.5 and 18.0, transects and seining sites were established in areas that reflected the maximum number of habitat types found in the river (Table 1). Although a comparison of the water depth, water velocity, and substrate size for these transects indicated that Transects 1, 3, and 5 represented runs or riffles of various sizes and Transects 2 and 4 were indicative of deep runs or pools, it was difficult to rigidly classify the habitats. However, the riffle transects tended to have higher average velocities and were shallower in depth, whereas the run-pool transects were deeper with lower velocities.

A comparison of the biological data indicated the highest average chlorophyll *a* values (31.6 ± 6.7 mg/m^2) were found in Transect 2 and the lowest (7.8 ± 5.9 mg chla/m^2) in Transect 4. Maximum average biomasses ($N = 5$) of macroinvertebrates were found in Transect 3 (10.8 ± 4.07 gms/m^2) and Transect 5 (13.79 ± 3.27 gms/m^2) and corresponded to the highest water velocities.

A comparison between Transect 2 (pool) and Transect 3a-3b (riffle) indicated marked differences in these two habitat types. The major abiotic differences between these two transects were the dominant and interstitial substrate sizes. Transect 2 had sand and silt as the dominant substrate, with interstitial substrates less than 0.5 mm in size. At Transect 3a-3b, the dominant substrate was cobble, with 88% of the interstitial substrates greater than 4 mm. The cobble and absence of silt on this transect provided substantial interstitial voids.

CRFP (1982) observed Colorado squawfish moving from the area of Transect 2 into and out of the cobble area of Transect 3b in apparent spawning behavior (hashed area in Fig. 2). Dominant substrate type and interstitial characteristics at Transect 3a-3b may be critical in the apparent preference of this habitat by spawning Colorado squawfish. At river mile 18.0, a physically similar habitat was found (Transect 5 in Table 1). However, this transect had much higher velocities (>4.5 m/sec) as compared to Transects 3a-3b (2.1-2.4 m/sec), which may have precluded this area from being used for spawning activities during 1981.

Seining Sites

Five locations at river mile 16.5 were sampled intensively for fish, larval fish, macroinvertebrate drift, and benthic macroinvertebrates (Fig. 2). Each of the five seining locations were sampled five times at four-hour intervals. At river mile 18.0, seven locations were sampled twice over an eight-hour period. A comparison of the physical and biological data collected at the seining locations (Table 2) indicates that the ranges of these parameters fall within the ranges observed on the transects (Table 1). Nine species of fish were captured during this survey (Table 3). Three species are endemic, two are native, and the remaining five are nonnative. Among the endemics, the most abundant were roundtail chubs (39% of the total). One fish tentatively identified as a humpback chub was captured. Redside shiners were the most abundant nonnative (15%), followed by red shiners (13%). The ratio of endemics and na-

TABLE 2. Physical and biological data collected at five seining sites from river mile 16.5 on the Yampa River 24–26 July 1981.

Location RM	Location SH	Time (hours)	Area sampled (m^2)	Depth (meters)	Velocity (m/sec)	Dominant substrate (cms)	Substrate organics (gms/m^2)	Macroinvertebrates Density (#'s/m^2)	Macroinvertebrates Biomass (gms/m^2)
16.5	SH$_1$	1620 2030 0000 0910 1435	60	0.44	0.02	2.5	0.26	50	1.252
16.5	SH$_2$	1640 2100 0020 0935 1510	36	0.88	0.23	7.5	1.05	312	18.43
16.5	SH$_3$	1700 2100 0040 0955 1535	30	0.38	1.07	0.75	0.06	777	24.599
16.5	SH$_4$	1715 2125 0100 1010 1605	45	0.78	0.14	0.75	1.55	91	5.952
16.5	SH$_5$	1745 2140 0125 1030 1630	45	0.67	0.30	7.5	0.25	11	0.01

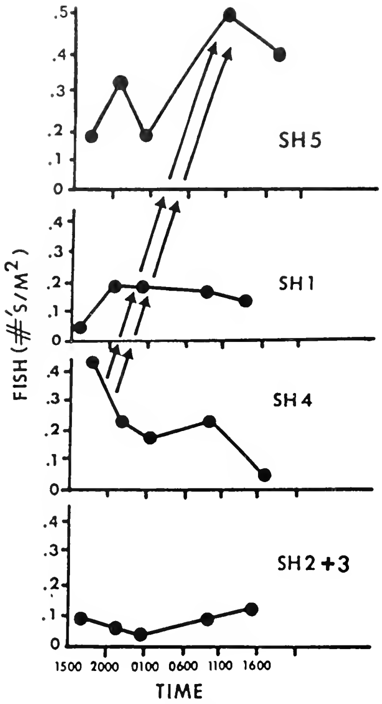

Fig. 3. Distribution of fish captured at five seining sites at river mile 16.5 on the Yampa River over a 24-hour period 24–26 July 1981.

tives to nonnatives was 2:1 by density. The distribution of these fish between seining sites and over time was not constant (Fig. 3). Diurnal movements observed at mile 16.5 were primarily by roundtail chubs.

The temporal distribution of fish captured at the lower end of the cobbled-riffle area (SH2 and SH3) was the lowest observed at any site (Fig. 3). It was apparent that fish were not moving into or out of this fast riffle area. A comparison of all seining sites between 1620 and 1745 hours indicates that maximum density of fish was found at SH4 (0.44 fish/m^2 sampled). Subsequent seine hauls at this site showed continuously reduced densities over the 24 hours sampled. A comparison of the other sites (Fig. 3) indicates the opposite pattern at the upper site (SH5), with no change in the intermediate seining location (SH1). It was believed that the pattern observed resulted from fish moving out of the deep pool (SH4), past the shallow run (SH1), and towards SH5, which was located at the lower stretch of a riffle area.

Macroinvertebrate and larval fish drift samples were taken at each seining site. A comparison of the drift entering (SH4) and leaving (SH2 + SH3) the riffle area, where squawfish were at their highest observed concentrations, indicates that substantial numbers of macroinvertebrates and larval fish originated within this cobble habitat (Fig. 4). For example, the diurnal pattern of drift (macroinvertebrates and larval fish) reached a

TABLE 3. Incidence of food in fishes captured on the Yampa River by seining at river mile 16.5 and 18.0 24–26 July 1981.

Fish species	Species code	Young of the year	
		w/food	w/o food
Bluehead sucker *Catostomus discobolus*	BH	1	0
Flannelmouth sucker *Catostomus latipinnis*	FM	5	1
Fathead minnow *Pimephalus promelas*	FH	0	0
Red shiner *Notropis lutrensis*	RS	0	0
Redside shiner *Richardsonius balteatus*	RD	0	0
Roundtail chub *Gila robusta*	RT	36	4
Sand shiner *Notropis stramineus*	SS	0	0
Speckled dace *Rhinichthys osculus*	SD	2	0
Channel catfish *Ictalurus punctatus*	CC	1	0

maximum between 2125 and 0100 hours. No larval fish and only 500 macroinvertebrates/hour were captured entering the area, whereas over the same time period five larval fish/hour and over 2000 macroinvertebrates/hour were captured leaving this riffle area. Although drift nets were located at each seining location, larval fish were collected only in nets below this cobble area. Five species of larval fish were identified, including: speckled dace, roundtail chub, channel catfish, flannelmouth sucker, and carp. This may indicate that this cobble area habitat may have been used for spawning or as a nursery area by species other than squawfish. In earlier studies, squawfish larvae were collected between river mile 12.1 and 0.1 during 24, 25, and 26 July (Haynes and Muth 1982). These larval fish (9.0–13.0 mm) corresponded closely in age with the dates when adult fish were observed to be spawning at river mile 16.5 (Tyus et al. 1981).

Feeding habits were determined by comparing benthic and drift samples to fish stomachs for the locations and times fish were captured (Strauss 1979). Feeding intensity was determined by using a percentage of stomach volume filled. In Table 4, a comparison is given between the major macroinvertebrate components in the drift or benthos to the major components of each species diet (dominant four fish species only). These data indicate, and it is reflected in Strauss (1979) Electivity Index (Table 5), that the two natives, roundtail chub and speckled dace, have a much richer diet relative to available food when compared to redside and red shiners. The latter two introduced species may be opportunistic and appear to eat food items in the proportion that they are available. Feeding intensity as determined by percentage fullness indicates that red shiners had a significantly greater percentage of stomach contents (62.6 ± 4.5 %) when compared to all other species except sand shiners (49.4 ± 8.9 %). Analysis of variance shows that fullness of all other species did not differ significantly. Comparing all fish species combined with time (Fig. 5) indicated that fish captured between 1950 and 2140 hours were significantly fuller (56.2 ± 3.6 %) compared to those of the other four time periods (41.7 ± 2.4 %). This time period corresponded to maximum invertebrate drift (Fig. 4).

DISCUSSION

An objective of this study was to determine the unique physical and biological features that made Yampa River mile 16.5 attractive to spawning Colorado squawfish. Ideally, the data presented here should have been collected during early July, when spawning fish were observed at the site, but logistical problems prevented this. However, comparative data show similar river conditions between the suspected spawning time of 5 July and this survey period, 24–26 July. During a

TABLE 3. Continued

Subadults/Adults		Total fish captured				
w/food	w/o food	YOY	SA/A	Grand total	% of total	CRFP (1982)
8	0	1	8	9	3%	4%
6	0	6	6	12	4%	5%
1	0	0	1	1	<1%	6%
36	2	0	38	38	13%	16%
40	4	0	44	44	15%	8%
69	5	40	74	114	39%	32%
10	2	0	12	12	4%	3%
50	8	2	58	60	20%	21%
0	0	1	0	1	<1%	2%

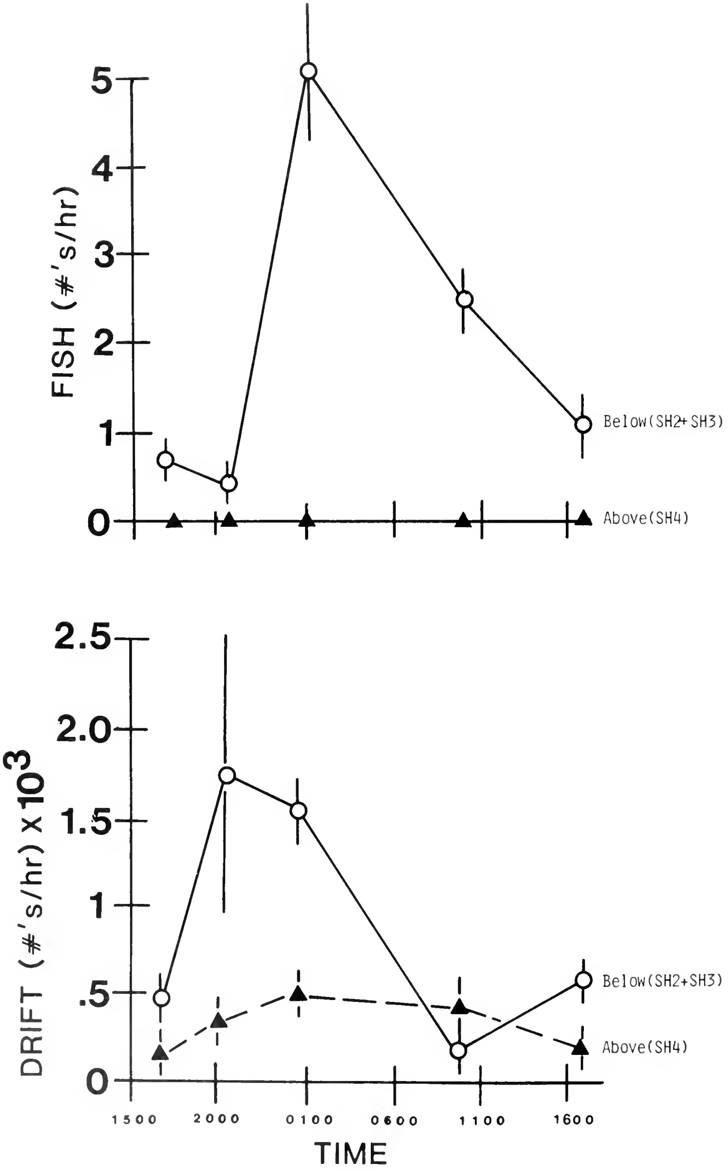

Fig. 4. Densities of drift macroinvertebrates (#'s/hour) and larval fishes (#'s/hour) captured at selected seining sites (SH) at river mile 16.5 on the Yampa River. Data collected 24–26 July 1981.

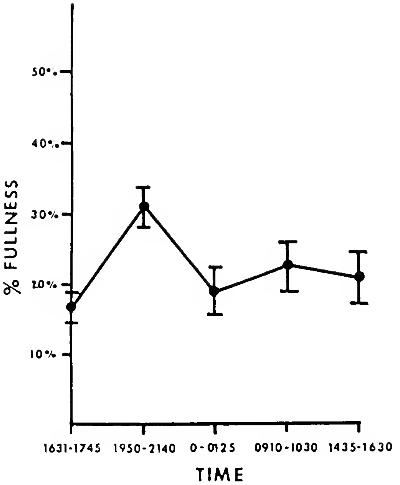

Fig. 5. Feeding intensity (expressed as a percentage of fullness of stomach volume) of all fish compared over time at Yampa River mile 16.5. Fish captured between 1950 and 2140 hours were significantly fuller than fish captured at other times. Data collected 24–26 July 1981.

CRFP (Tyus et al. 1981) survey, at Transect 2, the width of the river was estimated at 70 m compared to 54 m measured for this survey. Both sample periods occurred during postrunoff, with an intervening river stage decrease of approximately 0.6 m and a corresponding flow reduction of 180 cfs (480 cfs to 300 cfs).

The biological community in this study was similar to that documented in previous studies of the Yampa River. The dominant macroinvertebrates (Ephemeroptera: *Rhithrogena*, *Baetis*; Plecoptera: *Isogenus*; Trichoptera: *Hydropsche*, given in order of abundance) were also previously reported by Bailey and Alberti (1952) and more recently by Carlson et al. (1979) and Annear (1980). The density of macroinvertebrates also corresponded to the levels reported by Annear (1980).

The fish species composition of the Yampa River within Dinosaur National Park appears to have changed dramatically in recent years. Carlson et al. (1979) noted that Holden (1973) reported bonytail chub, largemouth bass, bluegill, sunfish, and walleye within this stretch of river. However, in 1979 these spe-

TABLE 4. Percentage composition of macroinvertebrates in the diet of fishes (A) and in benthic or drift samples (B) collected in the Yampa River near river mile 16.5 24–26 July 1981.

	(A) Percentage in each fish species diet				
Orders	Redside shiner	Red shiner	Roundtail chub	Speckled dace	All species
Ephemeroptera	92.7	92.6	78.6	87.5	85.8
Plecoptera	--	--	00.1	--	00.0
Trichoptera	00.1	--	05.1	04.2	03.1
Coleoptera	--	--	--	02.3	00.6
Diptera	05.6	01.5	13.2	05.8	07.8
Hymenoptera	01.3	04.3	02.9	--	02.2
Lepidoptera	--	--	--	00.2	00.1
Hemiptera	00.4	01.6	00.1	00.1	00.4
Hydracrina	--	--	00.1	--	00.0

	(B) Percentage in each sample type	
Orders	Benthic	Drift
Ephemeroptera	94.26	99.58
Plecoptera	00.87	00.09
Trichoptera	04.25	00.22
Coleoptera	00.04	00.01
Diptera	00.12	00.08
Odonata	--	--
Lepidoptera	00.08	--
Hemiptera	00.09	00.00
Homoptera	00.02	00.00
Arachnida	--	00.00
Megaloptera	--	00.00
Oligochaeta	00.19	--

cies were not found, but plains killifish and sand shiners were collected (Seethaler et al. 1979). Data from this study is most similar to that of Carlson et al. (1979). A comparison with the most recent collections (Colorado River Fishery Project 1982) indicates a high degree of similarity except for: (1) the absence of squawfish and the presence of a possible humpback chub in our collections and (2) the higher densities of redside shiners in our collections.

It has been noted by Crosby (1975), Lanigan and Berry (1979), Carlson et al. (1979), and Valdez and Clemmer (1982) that the proportion of nonnative to endemic fishes increases as the major tributary streams approached their confluences with the Green River. Lanigan and Berry (1979) attribute the higher proportion of nonnatives to a decrease in habitat diversity, whereas Valdez and Clemmer (1982) have suggested that riverine habitats occupied by native fishes are often unfavorable to nonnatives. Longitudinal data collected on the White River, a major tributary to the Green River, (Lamarra and Carter 1981) show a high correlation between the presence of endemic fishes and coarse substrates (riffle areas). Conversely, sandy areas with an absence of riffle habitats in the lower stretches of the White River appear to be avoided by the endemic community. Valdez and Clemmer (1982) also report a similar relationship between substrate size and roundtail and humpback chub. Although no longitudinal data were collected in this study, a low proportion of nonnatives to endemics and natives (1:2) was found in the Yampa River site, suggesting a similar correlation. Fish species distribution, food selection, and feeding intensities were determined by means of a diurnal sampling scheme for fish, drift insects, and larval fishes. These data have provided insights into the structure and function of this ecosystem. It is interesting to note

TABLE 5. Calculated linear Electivity Index (Strauss 1979) for the dominant four fish species in the Yampa River near river mile 16.5. Electivity comparisons are made for benthic (A) and drift (B) organisms. Data collected 24–26 July 1981.

(A) Benthic

Orders	Redside shiner	Red shiner	Roundtail chub	Speckled dace	All species
Ephemeroptera	-.016	-.017	-.157	-.068	-.085
Plecoptera	-.009	-.009	-.008	-.009	-.009
Trichoptera	-.042	-.043	.008	-.001	-.012
Coleoptera	.000	.000	.000	.023	.006
Diptera	.055	.014	.131	.057	.077
Hymenoptera	.013	.043	.029	.000	.022
Lepidoptera	-.001	-.001	-.001	.000	.000
Hemiptera	.003	.015	.000	.000	.003
Homoptera	.000	.000	.000	.000	.000
Annelida	-.002	-.002	-.002	-.002	-.002
Hydracrina	.000	.000	.001	.000	.000

(B) Drift

Orders	Redside shiner	Red shiner	Roundtail chub	Speckled dace	All species
Ephemeroptera	-.069	-.070	-.210	-.121	-.138
Plecoptera	-.001	-.001	.000	-.001	-.001
Trichoptera	-.001	-.002	.049	.040	.029
Coleoptera	.000	.000	.000	.023	.006
Diptera	.055	.014	.131	.057	.077
Odonata	.000	.000	.000	.000	.000
Hymenoptera	.013	.043	.029	.000	.022
Lepidoptera	.000	.000	.000	.002	.001
Hemiptera	.003	.015	.000	.000	.003
Homoptera	.000	.000	.000	.000	.000
Arachnida	.000	.000	.000	.000	.000
Megaloptera	.000	.000	.000	.000	.000
Hydracrina	.000	.000	.001	.000	.000

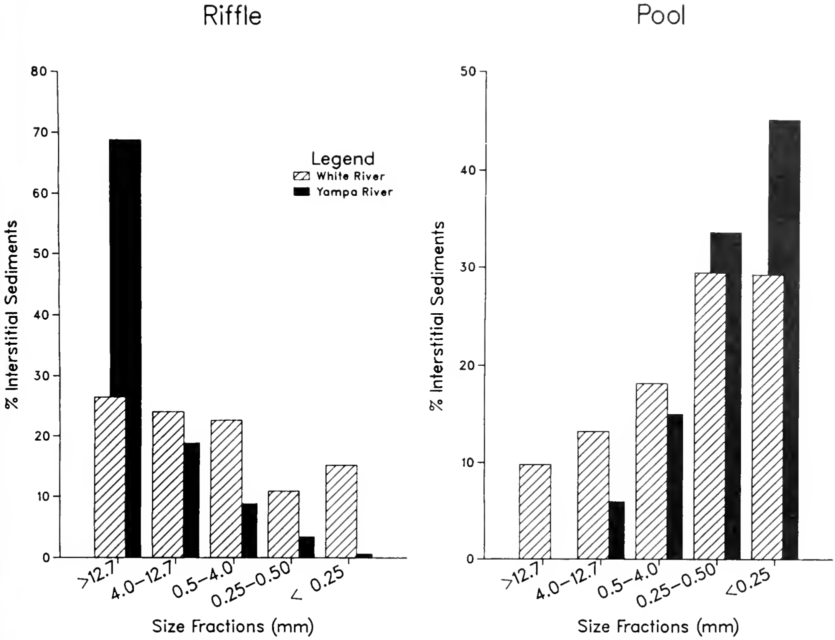

Fig. 6. Distributions of interstitial sediments (percentage of total weight) for representative riffle and pool transects in the White River as compared to representative pool riffle transects in the Yampa River. The smallest two size fractions that are causing armoring in the White River sediments are 25%–30% of the total sediments. These fractions in the Yampa River are only 4% of the total.

that larval fishes were captured only in the vicinity where squawfish were collected and that their movement corresponded to macroinvertebrate drift (2125–0100 hours). Five species of larval fishes emerged from this cobble site. Furthermore, inspection of the data collected at each seining site indicates a potential movement of fish from this same area at approximately the same time (Fig. 4), suggesting that the habitat was utilized by species other than Colorado squawfish.

An important characteristic of this cobble area was the interstitial voids that contained little or no organics. The difference in drift above and below this area strongly suggests that larval fishes utilize these voids. Beamesderfer and Congleton (1982) observed the northern squawfish (*Ptychocheilus oregonensis*) spawning in similar cobble and gravel sites in the St. Joe River, Idaho, where there was an absence of small substrates (sand) with adhering eggs up to 15 cm below the substrate surface. Prewitt et al. (1982) indicated that other similar habitats exist in the White River. However, their analysis of physical habitat and stream flow requirements for spawning squawfish considers only substrate size, not interstitial particles or voids. In the White River, the armored sediments (Fig. 6) prevent interstitial voids from developing, thus making the cobble habitat at Yampa River mile 16.5 unique in comparison to observed sites in other tributaries. It should be noted that Haynes and Muth (1982) did collect larval squawfish at Yampa River mile 17.8 on 14 August 1982. These fish were estimated to be 25 days old, indicating another spawning site above river mile 16.5.

The physical factors that regulate the distribution of organisms in stream environments are varied. Such factors as nutrients (Hynes 1970), turbidity (Mann et al. 1972), temperature (Sprules 1947), light (Westlake 1966), and water velocity (McIntire 1966)

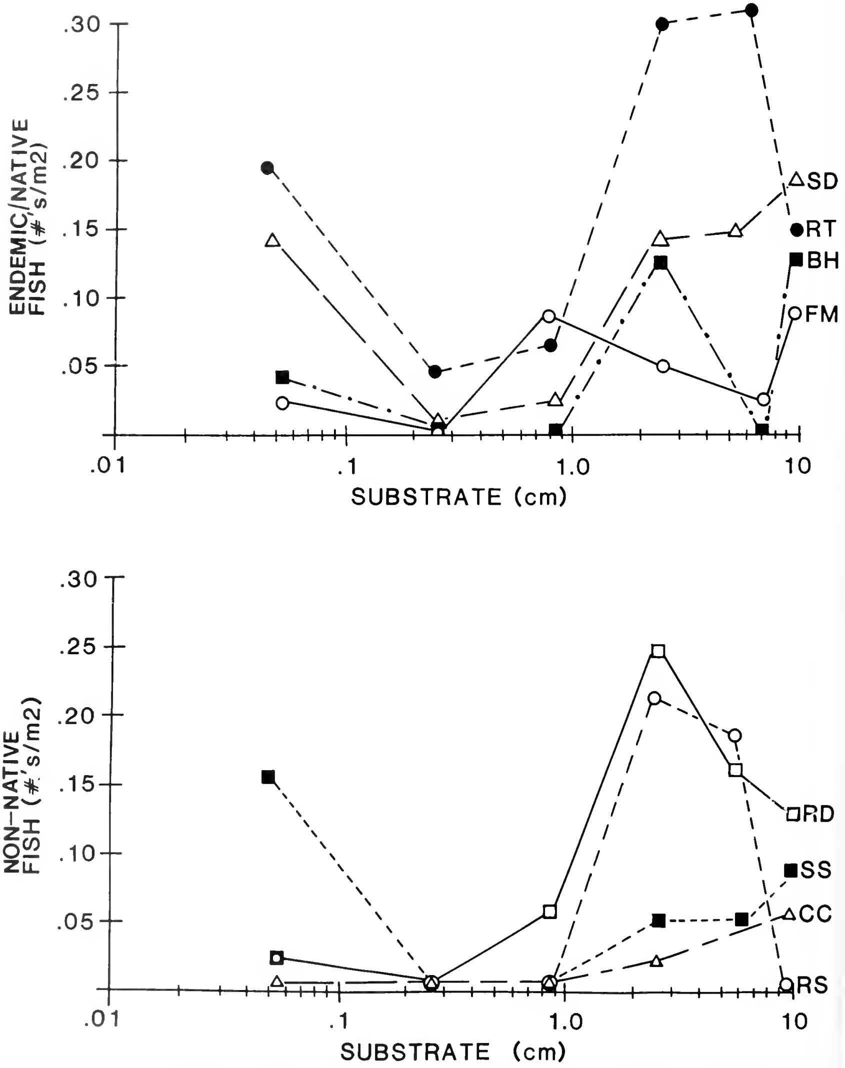

Fig. 7. Distribution of fish by species over substrate types in the Yampa River. Fish were collected between river miles 16.5 and 18.0 24–26 July 1981. See Table 3 for species codes.

have been shown to have profound effects on the river biocenosis. In this study, certain physical factors were also shown to be important in determining the distribution of the aquatic community. A comparison of the major trophic levels (primary producers, detritus levels, macroinvertebrates, and fish) indicates that distribution may be related to substrate size (Fig. 7). The same general pattern appeared for all of the major groups of organisms: avoidance of sand (0.25 cm) and selection for either small substrate (<0 .075 cm) or larger substrate (2.5 to 10 cm). Examination of the interactions between these biotic components and substrate size appears to be consistent with the findings of Cummins and Lauff (1969).

The distribution of fish across the various substrate sizes differed by species. The endemic fish appeared to avoid sand and gravel and select from intermediate to large substrates. Within the nonnative species, sand shiners appeared to prefer environmental conditions associated with the smallest substrate, whereas red and redside shiners favored intermediate (2.5 to 7.5 cm) substrates. All species avoided sand. The mechanisms causing the above observed distributions of endemic and nonnative fishes are unknown; however, the similar distributions of the fish, periphyton, and macroinvertebrates with substrate size indicate important interactions.

As noted previously, the density of the river biocenosis changed markedly over different substrate types; however, as Carlson et al. (1979) have stated, the distribution of organisms may be more influenced by combinations of the effect of physical and biotic characteristics than by physical factors alone. Our data indicate these types of interrelationships are important in the Yampa River. For example, no statistical relationship was found between the biomass of macroinvertebrates and the biomass of periphyton or detritus; however, a significant relationship was found between water velocity and macroinvertebrate biomass ($r^2 = +.45$; $p = .01$). This relationship was believed to be indirect because the dominant benthic macroinvertebrate functional group was found to be fine particulate collectors or filter feeders (98% of the total biomass) that may be responding to areas of high food availability (high flow).

An attempt has been made in this report to quantitatively describe the physical and biological environment at a suspected spawning site for Colorado squawfish. The Yampa River at mile 16.5 was dominated by loose cobble substrate in association with large sandy pools. This site was also found to be free of small interstitial particles and organic material. This area appeared to be heavily used by several species of larval fishes and actively feeding adults. The combination of well-washed coarse substrate (cobble), abundant food (both drift and benthos), and adjacent areas with slow, uniform laminar flow may be critical factors in determining preferred reproductive sites of Colorado squawfish.

CONCLUSIONS

1. A dominant abiotic factor appeared to be substrate type and associated interstitial sediment size fractions.
   a. Yampa River mile 16.5 was dominated by cobble substrate with interstitial voids containing little or no organics.
   b. Associated with these cobble areas were sand-substrate pools.
   c. Periphyton, macroinvertebrates, and fishes were found in lowest densities in or on sandy substrates.
   d. Highest densities of periphyton, macroinvertebrates, and fishes were found over substrates smaller than boulders (except sand).
   e. Roundtail chubs were dominant among the endemic fishes and preferred cobble substrate.
   f. Nonnatives were dominated by redside shiners and red shiners, and both species were most abundant over cobble substrates.
   g. Sand shiners were the only species to demonstrate a preference for silt substrates.
2. Samples showed nocturnal hours to be important periods of biological activity.
   a. Periods of highest macroinvertebrate drift occurred between 1500 and 0200 hours.
   b. Drifting larval fish were collected only after 2000 hours, with the peak occurring at 0100-0125 hours.
   c. Drifting larval fish appear to have originated in a cobble substrate with substantial interstitial voids.
   d. Maximum feeding intensity of fish captured occurred between 1950 and 2140 hours.

e. Fish were found to move from the sandy-pool area into the lower sections of riffles during the same period of time when maximum feeding intensity was observed.

ACKNOWLEDGMENTS

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DIFFERENTIAL EFFECTS OF CATTLE AND SHEEP GRAZING ON HIGH MOUNTAIN MEADOWS IN THE STRAWBERRY VALLEY OF CENTRAL UTAH

J. B. Shupe[1] and Jack D. Brotherson[2]

ABSTRACT.— Species diversity, niche metrics, cover, frequency, and soil relationships were studied on high mountain meadows on adjacent cattle and sheep allotments in Strawberry Valley, Wasatch County, Utah. The cattle allotment vegetation was predominantly Mountain bluebell (*Mertensia ciliata*), and the sheep allotment vegetation was predominantly Smallwing sedge (*Carex microptera*). Other species of importance on both areas included Letterman needlegrass (*Stipa lettermanii*), Mountain bromegrass (*Bromus carinatus*), and Yarrow (*Achillea millefolium*). Tall forbs were most abundant on the cattle allotment, and low forbs, perennial grasses, and sedges were most abundant on the sheep allotment. Vegetation composition on the two allotments was significantly different.

High mountain meadows in Utah have been important to ranchers as forage resources since the pioneers entered the state in 1847. The effects of grazing in Utah have been recorded since 1865 and have shown that vegetation composition and productivity are altered by livestock (Roberts 1930). Recent studies conducted near Elk City, Idaho, show that cattle grazing reduces herbage production, changes species composition, and increases bare ground in dry mountain meadows (Leege et al. 1981). Livestock graze selectively, with sheep being best adapted to browse ranges and cattle showing preference for grass ranges (Stoddart et al. 1975). Depending on levels of grazing, common use by more than one class of livestock can improve the range or accentuate the detrimental effects caused by individual species. Merrill et al. (1968) stated that common use equalized the grazing pressure, and each species benefited from the grazing of the other.

The purpose of this study was to determine the differential effects of 30 years of continuous cattle and sheep grazing upon the vegetative composition of dry mountain meadows. Data from this study are useful for the efficient management of such meadows.

STUDY SITE

The study sites are in the Strawberry Valley west of Strawberry Reservoir approximately 30 km southeast of Heber City, Wasatch County, Utah (Township 3S, Range 12W, Section 8-W¼, Section 17-W½, Section 20-W½, S½, Uintah meridian) (Fig. 1). Elevation of the sites varied from 2789 to 2819 m. The study sites lie at the head of the Mud Creek and Clyde Creek drainages on the lee-

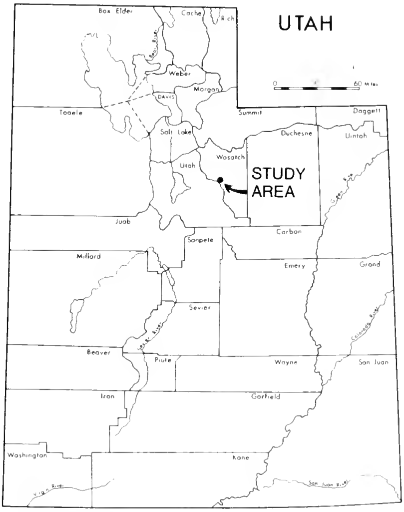

Fig. 1. Map of the study site location in the Strawberry Valley of central Utah.

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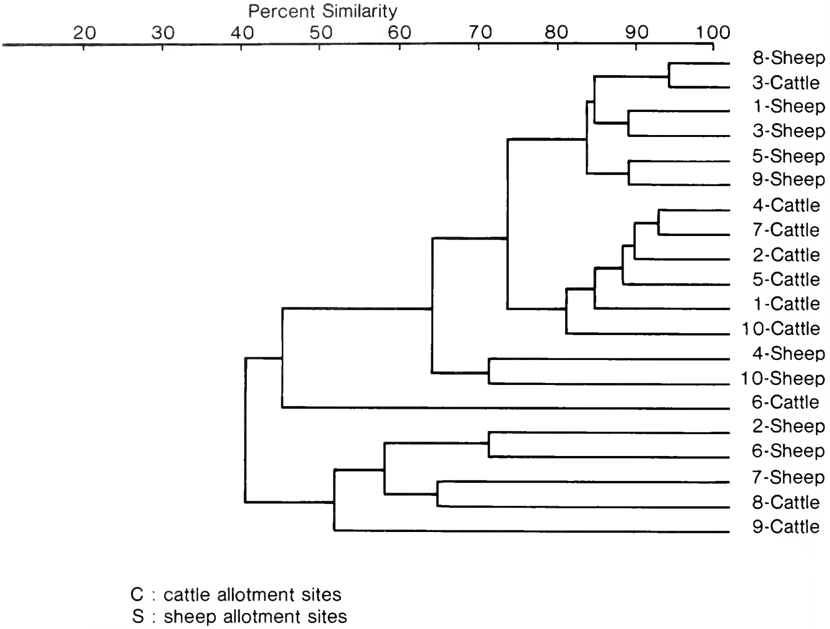

Fig. 2. Cluster diagram of soil factors for the cattle and sheep allotments.

ward side of the ridge top separating Utah and Wasatch counties.

The dry meadows chosen for study occurred in adjacent cattle and sheep allotments located within the aspen-conifer forest. Both allotments have been free of common use grazing since 1952 and are now utilized as summer range by livestock and wildlife. Livestock AUM levels are equivalent on the study sites of both allotments. The area has cool summers and cold winters with heavy snows. Annual precipitation averages 610 mm (24 in), of which 60% falls as winter snow (England 1979). The soils are derived from weathered sandstone and silt-shale. Wind was not measured at the sites but blew continually from the west during the hours we were on the study site.

Methods

Vegetation was sampled by using (0.25m^2) quadrats placed every 3 m along 30 m transects. Twenty transects were randomly selected across the slope, with 10 in the cattle allotment and 10 in the sheep allotment. Monocot plants were identified following Cronquist et al. (1977) and dicots from Welsh and Moore (1973). Cover and frequency of all plant species and plant life form categories were calculated for both cattle and sheep allotments. Cover for each species was estimated as suggested by Daubenmire (1959). Species diversity (Shannon and Weaver 1949, Patton 1962) and prevalent species (Warner and Harper 1972) were determined for the cattle allotment, sheep allotment, and both allotments combined. Vegetative differences between the cattle and sheep allotments were determined by use of cluster analysis (Sneath and Sokal 1973), Spearmans' Rank Correlation (Snedecor and Cochran 1968), and Students t-tests. Niche overlap (based on geographical distribution of individuals) was calculated for each possible pair of species within and between the allotments (Colwell and Futuyma 1971).

Soil samples from the first 20 cm of the soil profile (Ludwig 1969) were taken from each transect and placed in Zip-lock plastic bags to insure water retention. Soil samples were weighed wet, dried in an oven for 20 days at 50 C, and then reweighed. Percentage moisture was determined from the differences in wet and dry weights. Average soil depth was measured with a 1 m penetrometer at the 0-, 15-, and 30-m marks along each transect (Greenwood and Brotherson 1978). Analyses for calcium, copper, iron, magnesium, manganese, nitrogen, phosphorus, potassium, sodium, zinc, organic matter, pH, and texture were conducted by the Soils Analysis Laboratory, Department of Agronomy and Horticulture, Brigham Young University, Provo, Utah. Means, standard deviations, and Students t-tests were used to determine soil differences between cattle and sheep allotments. The study sites were clustered according to the similarity and distribution of soil and vegetation within the allotment meadows (Sneath and Sokal 1973).

RESULTS AND DISCUSSION

Soils in the meadows were loams and sandy loams with a minimum of 1.5 inches of available water-holding capacity. This represents the moisture between wilting point and field capacity (USDA 1975). Although not significantly different, soil moisture values taken in late July had means of 10.5% for the cattle allotment and 13.5% for the sheep allotment. These levels are close to the wilting point for most plants and if drying continues will eventually force the plants to become dormant.

Of the soil factors tested, only iron, bare ground, percent sand, and percent silt showed significant differences between cattle and sheep allotments (Table 2). Percentage bare ground and sand were greater and iron concentrations and percentage silt lower in the cattle allotment.

The cluster of all 20 transects in the cattle and sheep allotments were highly similar (41% or greater), and no definite patterns emerged relative to soil difference between the two allotments (Fig. 2).

The differences in concentrations of iron in the allotment soils do not seem important vegetatively. When large amounts of copper, manganese, and zinc occur in acid soils, iron is usually deficient (USDA 1957, Vose 1982). These chemicals have low concentrations in our soils and therefore should not tie up iron.

Textural differences (Table 1) between the two allotments were significant though the differences were small (8% for sand and 5.6% for silt). To understand if these differences influenced vegetation patterns between the two allotments, soil textures for all transects were superimposed on the cluster (Fig. 6) of vegetative data. No distinguishable patterns emerged. Further, when percentages of sand

TABLE 1. Soil characteristics of cattle and sheep allotment meadows with their means, standard deviations, and coefficients of variation. Significance levels were computed using the Students t-test.

Factor	Cattle			Sheep			Significance level
	$\bar{X}$	S_d	CV	$\bar{X}$	S_d	CV	
Bare ground (%)	31.0	12.86	41.4	21.8	7.61	34.9	.05
Soil depth (cm)	47.1	7.0	14.9	45.5	9.2	20.2	N.S.
Clay (%)	12.1	3.2	26.1	14.5	2.9	20.0	N.S.
Sand (%)	52.6	6.1	11.5	44.6	7.3	16.4	.05
Silt (%)	35.3	4.5	12.6	40.9	5.1	12.4	.05
pH	6.1	0.1	1.6	6.2	0.1	1.6	N.S.
Organic matter (%)	2.5	0.8	32.0	3.0	0.7	23.3	N.S.
Soil moisture (%)	10.5	2.9	27.6	13.4	5.1	38.1	N.S.
Calcium (ppm)	881.3	372.0	42.2	1162.7	388.8	33.4	N.S.
Magnesium (ppm)	80.0	22.5	28.1	92.4	33.8	36.6	N.S.
Sodium (ppm)	18.8	11.6	61.7	18.4	7.9	42.9	N.S.
Potassium (ppm)	183.9	118.9	64.7	186.1	48.6	26.1	N.S.
Iron (ppm)	66.4	19.8	29.8	93.8	24.8	26.4	.05
Copper (ppm)	0.9	0.2	22.2	1.0	0.2	20.0	N.S.
Manganese (ppm)	44.7	11.7	26.2	56.7	19.3	34.0	N.S.
Zinc (ppm)	3.8	1.6	42.1	5.2	1.4	26.9	N.S.
Nitrogen (%)	0.1	0.03	30.0	0.1	0.04	40.0	N.S.
Phosphorus (ppm)	33.6	9.8	29.2	38.2	9.2	24.1	N.S.

and silt from the 20 sites were correlated with the prevalent species, no significant relationships developed.

Bare ground affects the amount of moisture that soaks into the ground or runs off. With greater amounts of bare ground, more moisture runs off and can therefore increase erosion on the sites. However, no differences in erosion patterns on the two allotments were observed. The bare ground on the sites has apparently been accentuated by the differential grazing patterns that have occurred over the past 30 years. Cattle tend to select those plants with greater basal areas, thus leaving greater amounts of exposed ground when they are removed from a site.

Twenty-nine of 38 plants species identified within the study area were located on the cattle allotment and 37 on the sheep allotment (Table 2). Percentage cover and frequency for all species are shown in Table 2 and prevalent species in Table 3. The cattle allotment had 13 prevalent species and the sheep allotment 16. The three most prevalent

TABLE 2. Plant species along with their mean cover and frequency values in the cattle and sheep allotment meadows. The species life form and grazing response are noted.

	Cattle allotment			Sheep allotment		
Species by life form	Cover	Frequency	GR[1]	Cover	Frequency	GR
LOW FORB						
Achillea millifolium	3.7	59	Ic	51	56	Ic
Agoseris glauca	0	0	Ic	0.1	7	Ic
Allium acuminatum	0	0	Ic	0.1	3	Ic
Artemisia ludoviciana	0	0	Ic	0.4	3	Ic
Castilleja sulphurea	1.2	12	Ic	0.5	11	Ic
Collomia linearis	2.5	46	Iv	4.4	51	Iv
Erigeron speciosus	0.9	11	Ic	0.8	23	Ic
Gayophytum ramosissimum	trace	1	Iv	0	0	Iv
Gilia aggregata	0	0	Ic	0.2	1	Ic
Lupinus argenteus	0.1	3	Ic	0.6	12	Ic
Madia glomerata	0	0	Ic	3.4	10	Ic
Orthocarpus tolmei	4.4	67	Iv	1.2	28	Iv
Potentilla gracilis	1.7	20	Iv	2.7	38	Iv
Ranunculus alismaefolius	trace	1	Iv	0.9	11	Iv
Stellaria jamesiana	0.1	5	Ic	0.5	16	Ic
Vicia americana	0.4	4	Ic	0.7	11	Ic
Viola nuttallii	0	5	Ic	1.8	33	Ic
TALL FORB						
Arabis drummondii	0.5	18	Iv	0.2	8	Iv
Artemisia dracunculus	0.9	17	Iv	1.0	8	Iv
Geranium viscosissimum	1.4	11	Ic	2.1	20	Ic
Hackelia floribunda	0.2	2	Iv	0.7	3	Iv
Helenium hoopseii	0.3	5	Ic	0.8	13	Ic
Hieracium scouleri	0.2	6	Iv	2.9	18	Iv
Ligusticum filicinimum	1.2	24	Iv	0.8	11	Iv
Mertensia ciliata	33.1	91	Ic	7.9	37	Ic
Polemonium foliosissimum	0	0	Ic	0.6	8	D
Rudbeckia occidentalis	0	0	Ic	0.8	2	Ic
SHRUB						
Symphoricarpos orbiculatus	0.3	2	Ic	0.2	2	Ic
PERENNIAL SEDGE						
Carex microptera	3.5	16	Ic	23.0	76	Ic
PERENNIAL GRASS						
Agropyron trachycaulum	2.3	56	D	2.0	40	D
Agrostis variabilis	0	0	Ic	0.4	6	Ic
Bromus carinatus	5.4	73	D	4.4	46	Ic
Deschampsia caespitosa	0.1	4	D	0.3	11	D
Festuca elatior	0	0	Ic	1.9	3	Ic
Melica bulbosa	0.1	3	D	0.1	2	D
Poa pratensis	0.1	3	Ic	0.1	3	Ic
Stipa columbiana	0.2	7	Ic	0.6	12	Ic
Stipa lettermani	8.4	71	Ic	9.4	67	Ic

[1] GR = Grazing response. D = Decreaser, Ic = Increaser, Iv = Invader

species on the cattle allotment were Mountain bluebell (*Mertensia ciliata*) (33% cover), Letterman needlegrass (*Stipa lettermanii*) (8% cover), and Mountain brome (*Bromus carinatus*) (5% cover). The three most important on the sheep allotment were Smallwing sedge (*Carex microptera*) (23% cover), Letterman needlegrass (9% cover), and Mountain bluebell (8% cover). All other cattle allotment prevalents provided an additional 23% cover, whereas the remaining sheep allotment prevalents provided an additional 32% cover. This corresponds with the species diversity data, since the cattle allotment sites were less diverse (mean DI = 2.5) than the sheep allotment sites (mean DI = 3.0). The diversity differences were not significant.

The major prevalent species for the cattle and sheep allotments (Mountain bluebell and Smallwing sedge, respectively) appear to be dominant because of the differential grazing patterns of the cattle and sheep. Mountain bluebell, which is a tall forb of the montane zone, occurs primarily on loam or sandy loam soils. It has fair forage value for cattle, but it is considered as very good forage for sheep. Sheep will utilize the entire plant before it becomes dormant. Smallwing sedge grows in dense tufts in loamy soils. It is moderately palatable and fairly good forage for sheep but very good forage for cattle and quite sensitive to grazing pressures. Mountain brome is a perennial bunchgrass that is very palatable to all classes of livestock, with sheep usually preferring the seedheads. It usually inhabits deep, moderately moist soils, but it is also found on drier, harsher sites. Letterman needlegrass is a tufted perennial that often grows in large clumps. It is good forage for both cattle and sheep.

Mountain brome and Letterman needlegrass are prevalent species that occur in about equal amounts on both allotments. There should not be much difference in the the use of Mountain brome and Letterman needlegrass in that their forage ratings are somewhat equal for both cattle and sheep. But, with sheep preferring Mountain bluebell more and Smallwing sedge less than cattle, Mountain bluebell should become more abundant on the cattle allotment and Smallwing sedge more abundant on the sheep allotment as time passes. Of the four major prevalent species, only Mountain brome is considered to be a decreaser and the other three species are considered increasers (Table 2).

Differential grazing pressures on these meadows has caused secondary succession to occur, since the importance of the dominant species has shifted over time. Both allotments were dominated by increaser and invader plant species, with only five decreaser species being present. Of the decreasers on the cattle

Table 3. Prevalent plant species of meadows, along with their cover values for the cattle and sheep allotments combined, the cattle allotment, and the sheep allotment.

Species	Life form	Cattle and sheep	Cattle	Sheep
Mertensia ciliata	TF	18.46	33.13	6.32
Stipa lettermanii	PG	8.88	8.38	9.38
Carex microptera	PGL	8.61	1.38	20.74
Bromus carinatus	PG	4.66	5.43	3.94
Achillea millifolium	LF	4.18	3.70	4.59
Collomia lineatis	LF	2.58	1.75	3.50
Potentilla gracilis	LF	2.30	0.66	4.69
Agropyron trachycaulum	PG	2.05	2.33	1.80
Orthocarpus tolmei	LF	1.97	3.98	0.60
Hieracium scouleri	TF	0.68		1.43
Viola nuttallii	LF	0.48		1.25
Geranium viscossimum	TF	0.52		0.83
Ligusticum filicinimum	TF	0.45	0.61	
Erigeron speciosus	LF	0.43	0.36	0.50
Arabis drummondii	TF	0.38	0.65	
Castilleja sulphurea	LF		0.47	
Helenium hoopseii	TF			0.50
Artemisia dracunculus	TF			0.40
Ranunculus alismaefolius	LF			0.36

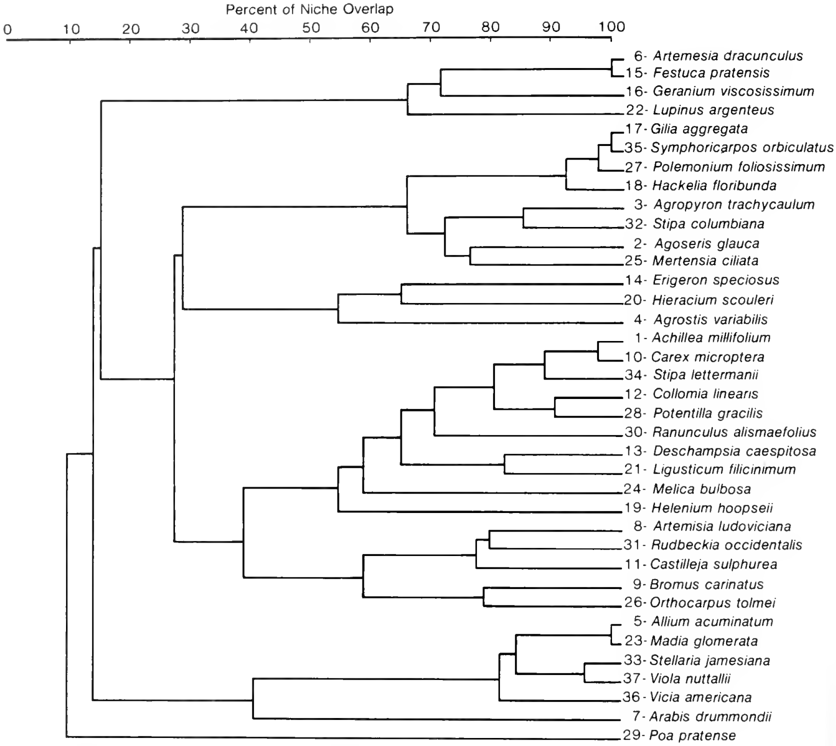

Fig. 3. Cluster diagram of niche overlap, using species of the sheep allotment.

allotment, two were prevalent species and two were not. On the sheep allotment, one was a prevalent species and three were not. All occurred in minimal abundance. This is probably due to the stress of 30 years of grazing pressure. If grazing pressure continues, the plants could decrease in frequency until they disappear from the sites.

Niche overlap values were computed for all species. Our data showed that the distribution patterns of Mountain bluebell and Mountain brome overlapped about 87% and that Mountain bluebell, Mountain brome, and Letterman needlegrass overlapped 57% in general distribution on the cattle allotment. Smallwing sedge and Letterman needlegrass overlapped 89%, and Smallwing sedge, Letterman needlegrass, and Mountain bluebell overlapped 28% on the sheep allotment. When considering all species from both allotments, Smallwing sedge and Letterman needlegrass overlapped 77% and Mountain bluebell and Mountain brome overlapped 77%, yet both pairs overlapped only 37% (Fig. 3–5). This indicates that Smallwing sedge and Mountain bluebell generally had disjunct distribution patterns relative to each other. The disjunct distribution patterns are most likely a result of the differential grazing preferences of cattle and sheep.

Using the cover values of the prevalent species from both the cattle and sheep allotments, Spearmans' rank correlation analysis was used to compare the two allotment meadows as to significant differences in the importance of the dominant species. This analysis showed significant differences in the species rankings on the two allotments

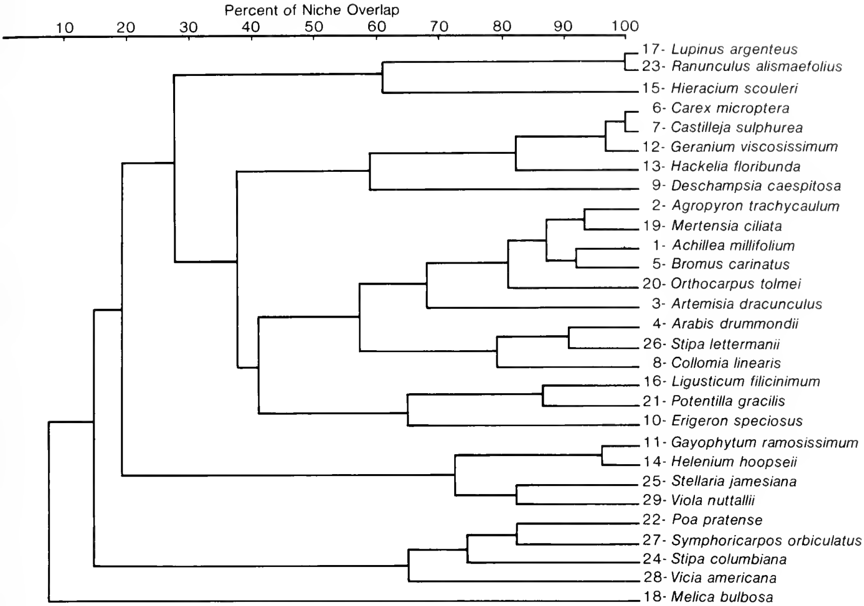

Fig. 4. Cluster diagram of niche overlap, using species of the cattle allotment.

(P<.05), which indicates that, although the two meadows contain many of the same species, the vegetation on the two sites is indeed different. When the 20 transects from the cattle and sheep allotments were clustered on the basis of vegetational characteristics (Fig. 6), all the sheep allotment transects clustered together and 8 of the 10 cattle allotment transects clustered as a unit. The 2 remaining cattle allotment transects clustered with the sheep allotment transects. This also shows the distinct differences in the vegetation of the two allotment meadows.

Since cattle prefer grasses and grasslike plants, and sheep prefer forbs in their diets (Stoddart et al. 1975, Krueger et al. (1974), the plant species were divided into life forms to determine differences existing between allotments (Table 4). The life form classifications used were shrubs, perennial grasses, perennial tall forbs (>12″) and low forbs (<12″). Significant differences (P<.05) appeared relative to low forbs, tall forbs, and perennial sedge life forms. The sheep allotment contained greater amounts of low forbs and perennial sedges, and the cattle allot-

Table 4. Life form types with their average cover and frequency values in the cattle and sheep allotments. Significant differences are based on cover values and Students t-tests.

Plant life form	Cattle allotment Cover	Cattle allotment frequency	Sheep allotment Cover	Sheep allotment frequency	Significance level
Low forbs°	15.0	14	27.4	19	.05
Tall forbs°	37.8	17	17.8	13	.05
Perennial grass	16.6	31	19.2	21	N.S.
Perennial sedge	3.5	16	23.0	76	.05
Shrub	0.3	2	0.2	2	N.S.

°Tall forbs are more than 12 inches tall, and short forbs are 12 inches or less.

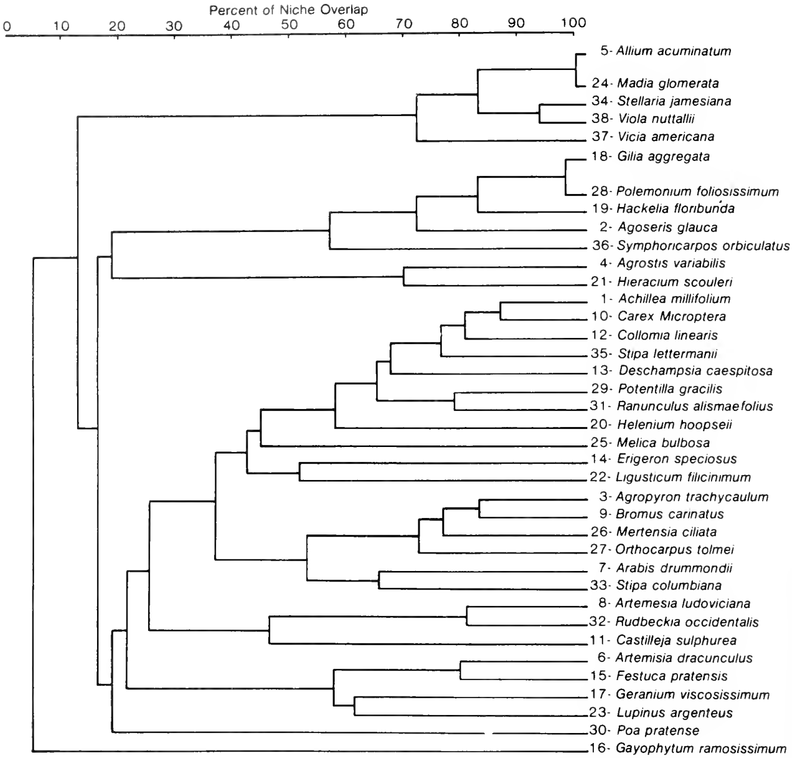

Fig. 5. Cluster diagram of niche overlap, using a combination of the species of the sheep and cattle allotments.

ment had greater amounts of tall forbs. Perennial grasses were more prominent on the sheep allotment, but differences were not significant.

With the soil factors showing little or no differences between allotments, the differences in vegetative composition in the allotment meadows appear to have been caused by grazing pressures. Perennial sedges are preferred by cattle and thus appeared more abundantly on the sheep allotment. Conversely, sheep prefer forbs that were more abundant on the cattle allotment. As grazing pressures increase, preferred vegetative life forms decrease and may disappear from the allotments used by a specific type of livestock.

To more efficiently manage these meadows, plant species and life forms should be grazed evenly. This would reduce the effects of preferential grazing (which tends to favor one species over another), which changes competitive relationships among species. This can be achieved by grazing at the proper time of year and with the proper mix of livestock species and numbers. An appropriate mix or rotation of livestock onto the allotment meadows would allow for a more uniform use of life forms and species to occur without losing any preferred species from the grazing area.

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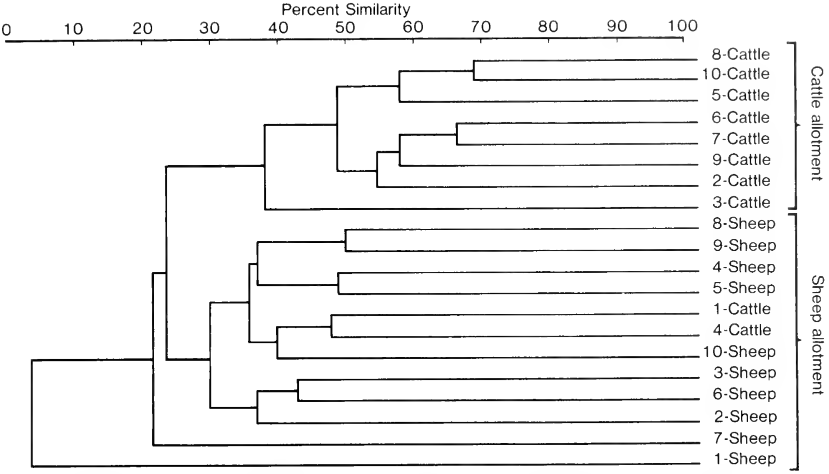

Fig. 6. Cluster diagram of the percentage similarity of vegetation on study sites from both allotments.

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UNUSUAL SOCIAL FEEDING AND SOARING BY THE COMMON RAVEN (*CORVUS CORAX*)[1]

Clayton M. White[2] and Merle Tanner-White[3]

Abstract.— A flock of some 1000 ravens, not associated with night roosts, was seen during the breeding season. Some were feeding on the ground while others soared in the air above them. It is suggested that the large soaring flock acted as information transfers for feeding conditions.

The Common Raven (*Corvus corax*) can be a highly social species. Social aerial soaring, play, and other forms of group interactions are known (Rubey 1933, Lockley 1953, Hewson 1957, Davis 1967, Dorn 1972). There is lack of agreement over the function of such soaring because of its temporal variation (summer vs. winter), as reviewed by Knight and Call (1980). There is likewise little knowledge as to whether participants of such behavior are breeding or nonbreeding individuals (Jollie 1976). The aforementioned social events frequently involve fewer than 200–300 individuals. However, large numbers of over 800 birds are known to gather in autumn and winter at overnight communal roosts (Stiehl 1981). Knight and Call (1980) likewise do not mention literature reference to large feeding aggregations, which may actually take the form of a social aggregation. Ravens may, however, congregate at refuse dumps, but such groups usually occur in the nonbreeding season or in developing areas with exploitable refuse dumps. Unlike the huge winter flocks of the American Crow (*Corvus brachyrhynchos*) that gather at dumps, our experience has been that fewer than 100 or so ravens gather at such feeding sites. The following observations involving more than 1000 ravens, but not at communal roosts, may shed some light on these topics.

On 11 April 1982 at midday, near the junction of US 191 and U-211, about 26 km north of Monticello, Utah, two different groups of ravens were seen about 1 km apart. The first flock contained about 400 birds, (part count, part estimate) feeding on the ground over about a 3-ha area, and more than 380 were counted soaring in a boil above those on the ground. This soaring flock contained individuals from about 50 m to more than 300 m in the air. A second flock of more than 250 was also seen soaring within 1 km northeastward of the former flock. Since none of the birds from the first flock were seen soaring or flying in the direction of the second flock, we are confident that the birds were not double counted.

Those feeding on the ground were in a tansy mustard (*Descurainia*)–native grass–mixed small sagebrush (*Artemisia*) habitat. From what we could determine, they were feeding on an abundant locust hatch. The habitat of the immediate surrounding area consisted of barren rock structures characteristic of the Utah canyonland country and juniper (*Juniperus*) stands. Birds from the first flock that were seen to depart from the main group flew at about 300 m plus in the air in a southwestward direction. We had just seen pairs of ravens still on breeding territories, some with young in the nest, or family groups of recently fledged young (perhaps some year-old groups) about 14–25 km to the west closer to the Canyonlands National Park.

The cumulative data from this observation suggest the following information relative to the initially stated questions. Because of the date, these were not from wintering flocks, unless such flocks remain together long after the start of the breeding season, in which case members of the flock would consist of mainly nonbreeding birds. Because we had earlier seen pairs near nesting territories and

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[1] Data gathered while on Agreement 12354-TSA-1 to Bechtel Group, Inc.

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also postnesting groups, it is likely that the flocks we saw were nonbreeding or certainly postbreeding individuals. The presence of the foraging flock below the soaring birds suggested that soaring not only may have a social or play function, but also an information transfer function. The soaring flock may provide information on food sources as suggested for the idea of "centers of information" in soaring vultures and eagles (Ward and Zahavi 1973, Sherrod et al. 1977). If the latter explanation is reasonable, then some of the birds may be assumed to be members of pairs within commuting distance of the food source. Because of the density of breeding pairs over the distance that such communication could be effective, it seems unlikely that more than 100 of the individuals could have been from breeding territorial birds. Lastly, if these flocks constituted nonbreeding social flocks in the sense of those described by Stiehl (1978), their roosting sites would need to be on cliffs, within the juniper forest, or perhaps on some distant electric power pylon as recently observed by K. Steenhof (pers. comm.).

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THREE ADDITIONAL CASES OF PREDATION BY MAGPIES ON SMALL MAMMALS

Kerry P. Reese[1]

Abstract.— Three acts of predation by Black-billed Magpies (*Pica pica hudsonia*) on small mammals indicate that magpies will not only attack prey opportunistically encountered at close range, as suggested by recent literature, but will also pursue prey detected at long distances.

The brief accounts by predation by the two North American magpies, Black-billed (*Pica pica hudsonia*) and Yellow-billed (*Pica nuttalli*), appear to occur when the birds opportunistically discover mammals at close distances while actively foraging (Blackburn 1968, Goulden 1975, Boxall 1982). Goulden (1975) and Boxall (1982) described interactions between the birds and their mammalian prey (one observed kill each). In this note I describe three observations of Black-billed Magpies attacking and killing small mammals and the defensive movements of the prey.

On 25 February 1979 I was observing magpies at a feeding station baited with meat and located approximately 80 m from my vehicle. The station was at the edge of a small stand of trees adjacent to a large plowed field west of Richmond, Utah. Over 30 cm of snow covered the field.

At 0955 h a vole (Microtus sp.) appeared on the snow approximately 20 m from my vehicle and was highly conspicuous as it moved about. A magpie flew from a tree near the feeding station 80 m away and landed 2 m in front of the vole. The vole ran toward the field's edge while the magpie followed by hopping along and flying 1–2 m at a time. When the magpie was within 6–7 m of the vehicle, the bird noticed me and departed. As it was leaving, a second magpie flew from the direction of the trees and was about to land behind the vole, but saw me and left. The vole ran back across the snow away from the truck and, when it was 15–20 m away from me, a magpie, perhaps the first, landed 0.3 m behind it. The vole turned, stood on its hind legs, and lunged at the bird. The vole charged three times in this manner, and on each charge the bird leapt into the air with wings flapping. After the third charge, the magpie jumped to the vole's side and pecked once at its head and neck. The vole was still and the bird struck 3–4 swift, hard pecks at its head. The magpie picked up the vole, flew back toward the trees, and landed on a fence post. The bird proceeded to peck the vole several times and then carried the carcass into the trees out of sight. The entire incident lasted about two minutes.

At 1045 h the same day, another vole appeared 35–40 m from me in the same field. I had observed the vole on the snow for no more than 15 seconds when a color-banded first-year male magpie, which had been resting in a tree near the feeding station, flew 40 m to the vole and landed directly in front of it. The vole quickly turned and the magpie pecked at its head. When the vole was still, the bird carried it into the trees. No more than 30 seconds elapsed from the time the magpie landed until it departed with the vole.

On 17 March much of the snow had melted, particularly along the edges of the road, where there was a mosaic of snow, tufts of dead, standing grass, and exposed, plowed soil. At 1538 h, a magpie was chased from the feeding station by a more dominant bird and landed on a fence post along the road 30 m in front of the vehicle. At 1541 h, the magpie left the post, flew 15 m across the road, landed and almost simultaneously struck with its beak at a vole exposed on a patch of snow. I had not seen the vole and was unaware of

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how long it had been visible. The vole appeared unhurt and ran into a clump of dead grass. Circling the grass twice, the magpie pecked into it several times, but I was unable to see if the vole was struck. The vole suddenly charged the bird, which jumped into the air as described previously. The vole ran toward an exposed plow furrow 2–3 m away, but was intercepted halfway there by the bird landing in front of it. Pecking the vole's head approximately 15 times, the magpie killed it, picked it up, and dropped it. I left the vehicle to flush the bird away in order to identify the species of vole, but the magpie picked it up again and flew into the trees 70–80 m away.

These observations and those in the literature suggest that Black-billed Magpies respond opportunistically to the presence of small mammals. My observations indicate that magpies will also attempt to kill small mammals when detecting them from up to 80 m away, not just when encountering prey in close proximity. These birds made kills in the immediate vicinity of an ample food source, the feeding station. Perhaps magpies prefer prey over carrion when possible.

All three voles took escape and defensive measures, but to no avail. Voles were highly conspicuous on the snow and, once above the surface, had limited access to refuge from predators. In all three cases the birds (at least two different ones) carried the voles to shelter, presumably to eat them as Boxall (1982) reported. None ate the voles in the open as Goulden (1975) described, even though both days were sunny with no wind.

Boxall (1982) comments on the scarcity of reports of predation by magpies on small mammals in North America. I believe that such events are rare and primarily fortuitous for the birds. The events that I observed may have been due to the presence of voles in a conspicuous and vulnerable setting, not a normal predator-prey situation. In over 500 h of observing magpies over two winters, these were the only acts of predation I witnessed.

These observations were made possible through research supported by the Frank M. Chapman Memorial Fund and the Ecology Center and Department of Fisheries and Wildlife, Utah State University.

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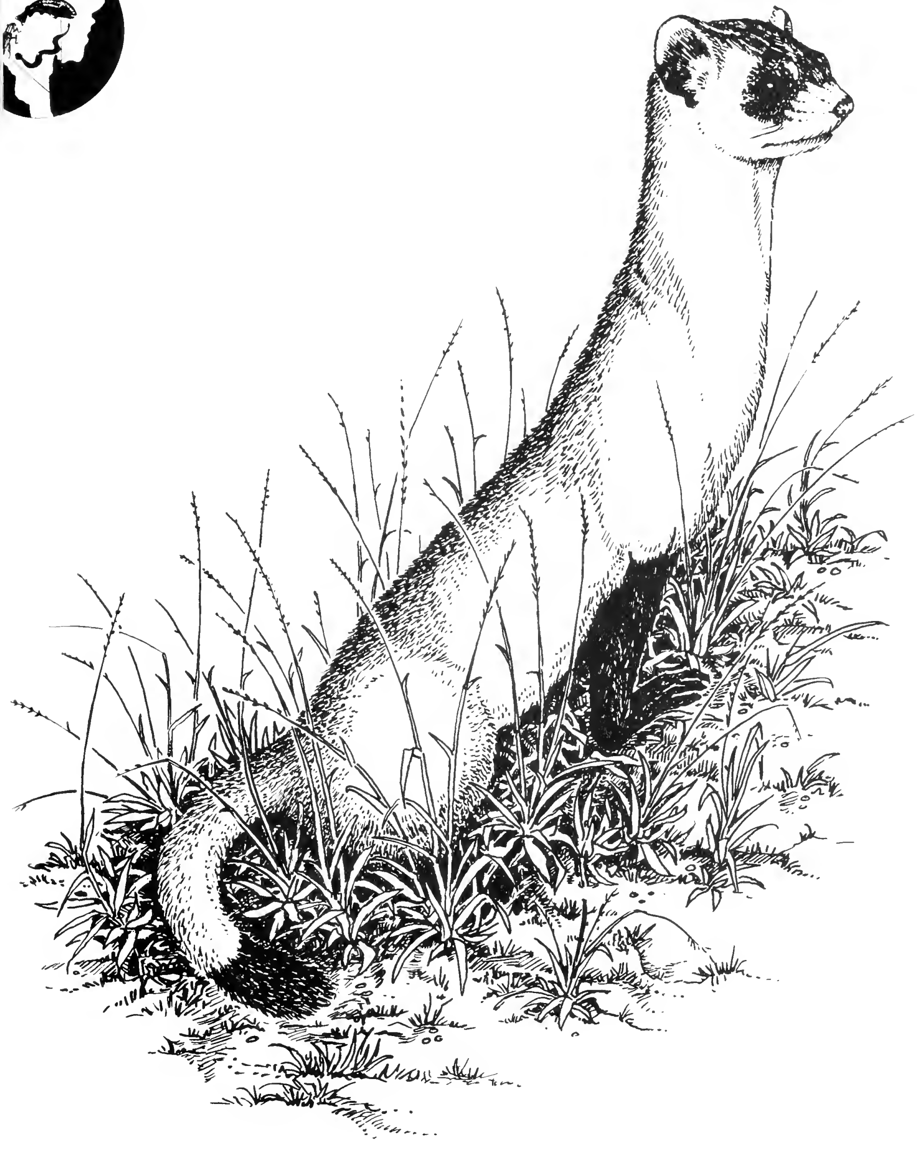

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UTAH FLORA: SAXIFRAGACEAE

Sherel Goodrich[1]

Abstract.— A revision of the Saxifragaceae is presented for the state of Utah. Included are 41 taxa in 12 genera. Keys to genera and species are provided, along with detailed descriptions, distributional data, and comments. *Lithophragma glabra* Nutt. in T. & G. var. *ramulosa* (Suksd.) Goodrich is the only new combination proposed. No new taxa are proposed.

This is another in a series of works leading to a definitive treatment of the flora of Utah. The Saxifragaceae family is of rather small size in the state. Several taxa are cultivated as ornamentals, and some species of *Ribes* are grown for their fruit. For the most part the taxa seem to be well marked, and separation of taxa is rarely compounded by hybridization in the native species of this family. The arabic numerals following the discussion of each taxon indicate the number of Utah specimens examined by me in the preparation of this treatment. The Roman numerals indicate the number of specimens I have collected from Utah.

Acknowledgments

Appreciation is expressed to the curators of the following herbaria in Utah: Brigham Young University, Provo; Forest Service Herbarium, Ogden; Garrett Herbarium, University of Utah, Salt Lake City; Intermountain Herbarium, Utah State University, Logan. I appreciate the loan of specimens from each of these herbaria.

SAXIFRAGACEAE

Saxifrage Family

Perennial herbs or shrubs; leaves basal, alternate, or opposite, with or without stipules; flowers perfect, regular, solitary to many and racemose or cymose; sepals, petals, and stamens borne on a floral cup or hypanthium; hypanthium saucer or cup shaped or tubular, sometimes small or essentially lacking; sepals 4 or 5, often appearing as lobes of the hypanthium, petal-like in *Ribes*; petals 4 or 5, distinct, alternate with the sepals; stamens (4), 5, 8, 10, or more; ovary superior, partly inferior, or inferior; fruit a capsule, follicle, or berry. This is an extremely variable family. As treated herein it includes segregates sometimes regarded as belonging to the Grossulariaceae (*Ribes*) and Parnassiaceae (*Parnassia*). Our woody species with opposite leaves have been included in Hydrangiaceae and in Philadelphaceae.

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1\. Plants shrubs, woody well above ground level 2

— Plants herbaceous, sometimes with woody caudices at or below ground level 7

2(1). Leaves alternate, lobed and toothed; petals shorter than the sepals, not over 4 mm long, often similar in texture and color to the sepals; ovary inferior; fruit a berry .... *Ribes*

— Leaves opposite, entire or toothed; petals longer than the sepals, over 4 mm long (except in *Fendlerella*), of contrasting texture and color from the sepals; ovary not completely inferior; fruit a capsule 3

3(2). Stamens numerous (more than 10); petals 4 (or sometimes more in cultivated plants) .... *Philadelphus*

— Stamens 8 or 10; petals 4 or 5 4

4(3). Leaves toothed, with petioles 2–10 mm long, or rarely sessile; petals 5, 4–13 mm long; stamens 10 5

— Leaves entire, sessile, or the petiole 1–2 mm long; petals 4 and 13–20 mm long, or 5 and only 2–4 mm long; stamens 8 or 10 6

5(4). Flowers rather numerous, paniculate; ovaries and sometimes the petals stellate-pubescent; filaments often petaloid and bifid apically; plants introduced, cultivated .... *Deutzia scabra* Thunb.

— Flowers few, in small cymes; ovaries sericeous-canescent; petals glabrous; filaments hardly petaloid, sometimes dilated basally, not bifid apically; plants indigenous; leaves sericeous-canescent .... *Jamesia*

6(4). Petals 4, 13–20 mm long; stamens 8; styles 4; leaf blades 9–30 mm long, the lower surface without pustulate hairs; shrubs ca 1–2 m tall, of Grand and San Juan counties .... *Fendlera*

— Petals 5, 2–4 mm long; stamens 10; styles 3; leaf blades 4–12 mm long, the lower surface sometimes with pustulate hairs; shrubs to ca 1 m tall, of other distribution .... *Fendlerella*

7(1). Leaves all basal, distinctly and often abruptly petioled, not lobed more than ½ the distance to the midrib; flowers on naked scapes or the scapes with a solitary bract; stamens 5 or 10 8

— Leaves not all basal, or sometimes so in depauperate plants but then the blades not distinctly petioled or else lobed more than ½ the distance to the midrib; flowers often not scapose; stamens 10 12

8(7). Flowers solitary and terminal on long scapes with a solitary bract; petals 6–14 mm long; leaves not toothed, sometimes cordate, otherwise not lobed; fertile stamens 5 .... *Parnassia*

— Flowers not solitary; scapes without bracts; petals 2–4 mm long; leaves either toothed or lobed or both and sometimes cordate as well; fertile stamens various 9

9(8). Leaves peltate, the blades 5–40 cm wide, cupped in the center; petioles and scapes to 10 dm long or more .... *Peltiphyllum*

— Leaves not peltate, the blades to 10 cm wide, not cupped in the center; petioles not over 2.5 dm long; scapes less than 7.5 dm long 10

10(9). Flowers in simple, very narrow, elongate, spikelike, ebracteate racemes; petals parted or divided into filiform segments; leaves toothed and lobed; stamens 5; plants from rhizomes, not clothed at the base with persistent leaf bases .... *Mitella*

– Flowers not in spikelike racemes, or if so then bracteate; petals entire; leaves not both toothed and lobed and stamens 5, or if so then plants from woody caudices and clothed at the base with persistent leaf bases 11

11(10). Leaves crenate-toothed and lobed; stamens 5; stipules fused to and decurrent on the petioles; plants often of dry rocky places .... *Heuchera*

– Leaves subentire, crenate, or very coarsely dentate but not lobed; stamens 10; stipules lacking or free of the petioles; plants mostly of dry meadows or wet places .... *Saxifraga*

12(7). Leaves parted or divided to the midrib the basal ones abruptly constricted into slender petioles 0.5–10 cm long; petals deeply lobed or cleft, with 3–7 lobes; plants from slender bulblet-bearing rhizomes and fibrous roots .. *Lithophragma*

– Leaves entire, toothed, or lobed, but not divided more than ½ the distance to the midrib or if so then sessile or nearly so; petals entire; plants not or rarely from bulblet-bearing rhizomes 13

13(12). Leaf blades of basal and stem leaves crenate-toothed (the teeth more than 10), also shallowly lobed, reniform or orbicular; bracts of inflorescence smaller than the leaves, but similarly toothed; petals pink to deep red; floral cup 4–7 mm long, often reddish or purplish; plants of the Bear River Range .... *Boykinia*

– Leaf blades entire, toothed, or lobed (the teeth or lobes 8 or fewer); upper leaves and bracts entire; petals yellow or white, sometimes with purple markings; floral cup 1–3 mm long, greenish or purplish; plants variously distributed .... *Saxifraga*

Boykinia Nutt. Nom. Cons.

Caulescent, glandular herbs from woody branched caudices and thick scaly rootstocks; leaves petioled, basal, and alternate, with membranous stipules; flowers perfect, regular, borne in compact, few-flowered, bracteate cymes; hypanthium calyxlike; sepals 5; petals 5; stamens 10; ovary ca ½ inferior; styles 2, free or connate below; fruit a capsule; seeds several.

Boykinia jamesii **(Torr.) Engl.** James Saxifrage. [*Saxifraga jamesii* Torr.; *Telesonix jamesii* (Torr.) Raf.; *Therefon heucheriforme* Rydb.; *Boykinia heucheriformis* (Rydb.) Rosend.] Perennial caulescent herbs, 6.5–20 cm tall; caudices clothed with broad marcescent leaf bases; stems hirsute and stipitate-glandular; petioles 1.5–5.5 cm long, glandular; leaf blades 12–60 mm wide and about as long, reniform or orbicular, truncate or cordate at the base, crenate and more or less shallowly lobed; bracts similar to the upper leaves but smaller and less toothed, and the upper ones usually entire; hypanthium 4–7 mm long, campanulate, glandular to pilose-glandular, often reddish or purplish; sepals 3–4.5 mm long, glandular; petals subequal to the sepals or shorter, pinkish or reddish. Crevices, often in limestone at 2680 to 2990 m in the Bear River Range, Cache Co.; Idaho and Montana to Colorado; and southern Nevada (Spring Mts.); 6 (0). Our plants are referable to var. ***heucheriformis*** **(Rydb.) Engl.**

Fendlera Engelm. & Gray

Shrubs with opposite, nearly sessile leaves without stipules, deciduous; flowers perfect, rather showy; hypanthium calyxlike; sepals 4; petals 4; stamens 8, the filaments flattened, lobed at the apex; ovary inferior at the base, 4-loculed; styles 4; stigmas minute; fruit a capsule, over ½ superior, septicidal; seeds few in each locule.

Fendlera rupicola Gray Cliff Fendlerbush. [*F. tomentosa* Thornb.]. Much branched shrubs about 1–2 m tall; bark of twigs longitudinally ridged and grooved, reddish or strawcolored, turning gray; leaves opposite or appearing fasciculate-opposite, 9–30 mm long, 2–7 mm wide, lance-linear, linear, elliptic, or less often ovate, entire, sometimes slightly revolute, sparingly strigose on both sides, the midrib prominent, grooved above, ridged beneath; flowers solitary or 2–3 together at the ends of short branches; hypanthium 2–3 mm long; sepals 3–5 mm long, to 8 mm in fruit, persistent, strigose beneath, tomentose-villous above; petals 13–20 mm long, constricted to a narrow claw, the blade to 11 mm wide, white; stamenal filaments ca 6–8 mm long, to 2 mm wide at the base, 2-lobed at the apex, the lobes 2–3 mm long, the anther shorter or longer than the lobes; styles 4, appearing as 2 at anthesis, glabrous or with multicellular hairs; capsules 8–15 mm long. Blackbrush and pinyon-juniper communities at 1372 to 1707 m in Grand and San Juan counties; west central Colorado and southeastern Utah through Arizona and to Texas; 11 (0).

Fendlerella Heller

Shrubs with opposite, sessile, or nearly sessile leaves, lacking stipules; flowers perfect, in small compound cymes; hypanthium calyxlike; sepals 5; petals 5; stamens 10, the filaments dilated below the narrow apex; ovary about ½ inferior, 3-loculed; styles 3; fruit a capsule, septicidal; seeds 1 in each locule.

***Fendlerella utahensis* (Wats.) Heller** Utah Fendlerella. [*Whipplea utahensis* Wats.]. Sprawling or ascending, much branched shrubs to 1 m tall; bark of twigs strigose, whitish, exfoliating in milky or translucent stripes or flakes; leaves 4–12 mm long, 1–6 mm wide, linear-oblanceolate, linear, elliptic, or less commonly ovate, entire, slightly revolute, strigose, the hairs sometimes pustulate, especially on the lower surface; flowers in small compound cymes; hypanthium inconspicuous at first, finally to 2 mm long in fruit, turbinate-campanulate; sepals 1–1.5 mm long; petals 2–4 mm long, white; staminal filaments dilated and petaloid just below the narrow apex, white; styles ca 1.5–2 mm long; capsules 3–4 mm long. Sagebrush, pinyon, juniper, and mountain brush communities, mostly on sandstone and sandy soil at 1480 to 2135 (2745) m in Garfield, Millard, Uintah, Utah, and Washington counties; northwestern Colorado to Arizona and west to California; 17 (0).

Heuchera L.

Perennial scapose herbs from scaly, somewhat woody branched caudices or rootstocks; leaves basal, stipulate; flowers paniculate or racemose or nearly spicate, bracteate, perfect, regular; hypanthium calyxlike; sepals 5; petals 5, small, entire, usually clawed; stamens 5; ovary partly inferior, 1-loculed; styles 2; fruit a capsule, opening between the 2 more or less divergent stylar beaks; seeds many.

ROSENDAHL, C. O., F. K. BUTTERS, AND O. LAKELA. 1936. A monograph on the genus *Heuchera*. Minnesota Stud. Pl. Sci. 2: 1–180.

1. Stamens shorter than the sepals; petals ca 1–2 mm long; sepals not reddish or pinkish; pedicels 1–2 mm long or nearly obsolete; plants statewide .... *H. parvifolia*
— Stamens exserted 1–4 mm beyond the sepals; petals 3–4 mm long; sepals often pinkish or reddish; pedicels (1) 2–7 mm long; plants of the Great Basin and the southern ⅔ of Utah .... *H. rubescens*

***Heuchera parvifolia* Nutt. in T. & G.** Littleaf Alumroot. [*H. utahensis* Rydb. Type from Salt Lake County.] Scapose glandular herbs, the caudex branches clothed with marcescent leaf bases, 12–71 cm tall; scapes stipitate-glandular; petioles 1–13 cm long, with stipules glandular-puberulent or glabrate; leaf blades (1) 1.5–6.5 cm wide, wider than long, orbicular or reniform, cordate, palmately lobed with 3–7 primary lobes, these crenate and usually again shallowly lobed, commonly with scattered stipitate glands below, glabrate above and sometimes throughout; flowers in open or congested panicles or sometimes racemose or spicate, bracteate, the bracts toothed or fimbriate; inflorescence 2–35 mm long; pedicels obsolete or 1–2 mm long; hypanthium 2.5–3.5 mm long or to 5 mm in fruit; sepals 0.5–1 mm long, sometimes yellowish; petals ca 2 mm long, white; stamens shorter than the sepals; capsules 4–7 mm long. Pinyon, juniper, sagebrush, mountain brush, ponderosa pine, aspen, grass-forb, Douglas-fir, and white fir communities, often in rocky places at 1675 to 3200 m in all counties except Kane, Morgan, and Sevier;

Alberta to New Mexico and west to Idaho and Nevada; 96 (v). Our plants are referable to var. ***utahensis*** **(Rydb.) Garrett.**

Heuchera rubescens **Torr. in Stansb.** Red Alumroot. Scapose perennial herbs, 5–30 (53) cm tall, the stem bases clothed with marcescent leaf bases; scapes glabrous to sparingly glandular-puberulent; petioles 1–6 (8) cm long, glabrate, glandular-puberulent, or hirsute, the stipular bases often fimbriate; leaf blades 0.7–4.3 cm wide, slightly longer than wide to wider than long, orbicular to broadly ovate, cordate or truncate, palmately lobed, the primary lobes sometimes again shallowly lobed, dentate or crenate, hirsute-ciliate; flowers in racemose or spicate panicles, the inflorescence 3–18 (31) cm long; pedicels (1) 2–7 mm long; hypanthium 2–4 mm long, campanulate, pinkish, lavender, or whitish; sepals 1–2.5 mm long, or to 3.5 mm long in fruit, mostly pinkish or lavender; petals 3–4 mm long, white; stamens exserted ca 1–4 mm beyond the sepals; capsules ca 4–6 mm long. There are two varieties in Utah, which more or less show morphological and geographical correlation. However, in the Henry Mountains, Mountain Home Range, and probably elsewhere the morphological differences fail.

1. Petioles hirsute, the spreading hairs to 2 mm long; leaf blades and scapes tending to be glandular-puberulent .... *H. rubescens* var. *versicolor*
– Petioles not hirsute, merely puberulent; leaf blades and scapes less often glandular-puberulent .... *H. rubescens* var. *rubescens*

Var. *rubescens* [*H. versicolor* Greene f. *pumila* Rosend, Butters, & Lakela]. Crevices of rock outcrops and other rocky places, in pinyon, juniper, sagebrush, mountain brush, ponderosa pine, limber pine, bristlecone pine, aspen, fir, and spruce communities at (1525) 1825 to 3355 m in Beaver, Box Elder, Cache, Garfield, Grand, Millard, Piute, Salt Lake, Sanpete, Tooele, Utah, Wayne, and Weber counties; Great Basin, from southeastern Oregon and adjacent Idaho to California, east to northern Arizona, and western Colorado; 59 (viii).

Var. *versicolor* (Greene) M. G. Stewart [*H. versicolor* Greene] Pinyon, juniper, mountain brush, and spruce-fir communities, often on rock outcrops, at 1370 to 2590 m in Garfield, Iron, Kane, San Juan, and Washington counties; Arizona, western New Mexico, and southeastern Nevada; 16 (0). In addition to the hirsute petioles, var. *versicolor* is reported to have filaments not noticeably flattened toward the base and attached at or slightly below the point of attachment of the petals. These features appear to be weakly, if at all, correlated in Utah materials. Our plants might represent intermediates between var. *rubescens* and the more southern var. *versicolor*, or perhaps the distinction is so tenuous as to be of little taxonomic value.

Jamesia T. & G.

Shrubs; leaves opposite, mostly petioled, without stipules; flowers perfect, regular, cymose; hypanthium calyxlike; sepals 5; petals 5, white; stamens 10; filaments narrow; ovary ca ½ inferior, partly 3- to 5-loculed at first, finally 1-loculed; styles 3–5, distinct; fruit a capsule, ca ⅓ inferior, with 3–5 valves, the valves with slender beaks; seeds numerous.

Jamesia americana **T. & G.** Cliff Jamesia [*Edwinia americana* (T. & G.) Heller; *E. macrocalyx* Small]. Shrubs 30–150 cm tall; foliage and young twigs pubescent with multicellular hairs; bark of twigs reddish or whitish, exfoliating in long whitish or translucent strips; petioles 2–10 mm long, canescent or sericeus-tomentose, sometimes lacking; leaf blades 7–40 mm long, (3) 6–32 mm wide, ovate or elliptic, serrate or dentate, rarely nearly entire, green and sparingly strigose on the upper surface, sericeous-canescent below; flowers few in small cymes; hypanthium 1–3 mm long in fruit, sericeous-canescent; sepals 3–4 mm long in flower, 5–6 mm long in fruit; petals 5–11 mm long, white, clawed, somewhat pubescent subapically; filaments gradually dilated basally; capsules 4–5 mm long. Mountain brush and spruce-fir communities, mostly on cliffs and other rocky places at 1220 to 3200 m in Juab, Millard, Salt Lake, Utah, and Washington counties; Wyoming to New Mexico, Nevada, and California; 25 (0).

Lithophragma Nutt.

Small, usually stipitate-glandular herbs from fibrous roots and very slender rhizomes, bearing ricelike bulblets; leaves basal and alternate, variously palmately cleft or divided; flowers in racemes, perfect, regular; hypanthium calyxlike; sepals 5; petals 5, variously palmately lobed or cleft, with a narrow claw and expanded blade; stamens 10; ovary 1-loculed; styles 3; fruit a 3-valved capsule; seeds numerous.

TAYLOR, R. L. 1965. The genus *Lithophragma* (Saxifragaceae). Univ. Cal. Publ. Bot. 37: 1–122.

1. Plants with few to several purple bulblets in the inflorescence and usually in axils of the upper leaves; inflorescence with (1) 2–4 flowers, sometimes branched; lower pedicels 1.5–3 times longer than the hypanthium; lower leaves glabrous or nearly so; stipitate glands dark purple .... *L. glabra*

— Plants without bulblets in inflorescence or in leaf axils; inflorescence mostly with 4 or more flowers; lower pedicels ca 0.5–1.5 times longer than hypanthium; leaves moderately to densely pubescent; stipitate glands whitish or pale purplish 2

2(1). Hypanthium wedge shaped at the base or funnelform, gradually tapering to the pedicel, the hypanthium and sepals 4–6 mm long in flower, to 7 mm long in fruit; petals mainly 3-lobed, 5–9 mm long, excluding the claw, white; ovary inferior or nearly so; plants of north central mountains .... *L. parviflora*

— Hypanthium campanulate, abruptly tapering to the pedicel, the hypanthium and sepals 3–4 mm long in flower and to 5 mm long in fruit; petals 5- to 7-lobed, 3–6 mm long excluding the claw, pinkish or white; ovary ca ½ inferior or less; plants of western and southern Utah .... *L. tenella*

Lithophragma glabra **Nutt. in T. & G.** Fringecup. [*L. bulbifera* Rydb.; *L. glabra* var. *bulbifera* Jepson]. Plants 5–35 cm tall, glandular-pubescent, the gland tips mostly dark purple; petioles of lower leaves 1.2–4.8 cm long; leaf blades 5–24 mm long, 8–48 mm wide, orbicular or reniform in outline, parted or divided and trifoliate or palmate, the main divisions again lobed to parted, reduced above and often with purple bulblets in the axils; inflorescence simple or branched, purple, 1–5 (13) cm long, with (1) 2–4 normal flowers and others reduced to bulblets; pedicels 2–10 mm long; hypanthium 2–5 mm long, campanulate; sepals ca 1 mm long; petals pinkish, white, or pale lavender, the claw 1–2 mm long, the blades 4–7 mm long, 3- to 5-lobed or parted; ovary ca ¼ inferior; seeds muricate. Aspen, oak-maple, sagebrush, pinyon-juniper, mountain brush, riparian, ponderosa pine, spruce, fir, lodgepole pine, and rarely in greasewood communities at 1310 to 3050 m in Beaver, Box Elder, Cache, Carbon, Daggett, Davis, Duchesne, Grand, Juab, Iron, Millard, Morgan, Rich, Salt Lake, San Juan, Sanpete, Sevier, Summit, Tooele, Uintah, Utah, Wasatch, Washington, and Weber counties; British Columbia to California, east to Alberta, the Dakotas, and Colorado; 82 (vi). Our plants are referable to var. *ramulosa* **(Suksd.) Goodrich** comb. nov. [based on *L. tenella* var. *ramulosa* Suksd.].

Lithophragma parviflora **(Hook.) Nutt. in T. & G.** Smallflower Woodlandstar. [*Tellima parviflora* Hook.]. Perennial herbs from fibrous roots and slender rootstocks bearing small bulblets, 9–47 cm tall, pubescent with mostly glandular hairs, rather densely so in the inflorescence; petioles of basal leaves 2–11 cm long; leaf blades 9–35 mm long, 11–50 mm wide, orbicular or reniform in outline, 3-parted or 3-foliolate, with the divisions again lobed, cleft, or parted; stem leaves similar to the basal ones but sometimes reduced upward; racemes congested, 1–2 (3) cm long in flower, to 7.5 cm long in fruit, 4- to 7-flowered, the pedicels 1–5 mm long in flower, to 8 mm long in fruit; hypanthium (3.5) 4–5 mm long in flower, to 6 mm long in fruit, wedge-shaped or funnelform basally, and gradually tapered to the pedicel; sepals 0.7–1.4 mm long; petals white, clawed, the claws 2–3.5 mm long; ovary inferior or nearly so; seeds smooth. Oak-maple, sagebrush, aspen, riparian, meadow, lodgepole pine, spruce, and fir communities at 1450 to 2590 (3050) m in Box Elder, Cache, Carbon, Davis, Emery, Juab, Millard, Morgan, Salt Lake, Sanpete, Summit, Tooele, Uintah, Utah, Wasatch, and Weber counties; British

Columbia to northern California, east to Alberta, South Dakota, and Colorado; 88 (i).

Lithophragma tenella **Nutt. in T. & G.** Slender Woodlandstar. [*L. australis* Rydb.]. Plants 10–43 cm tall, pubescent, the hairs mostly glandular, the gland tips whitish or pale purplish; petioles 0.5–4.5 cm long; leaf blades 4–25 mm long, (5) 9–30 mm wide, orbicular or ovate, parted or 3-foliolate, the main divisions again lobed or parted; racemes ca 1–3 cm long in flower, to 15 cm long in fruit, with 4–13 flowers; pedicels 2–7 mm long; hypanthium campanulate, 2–3 mm long; sepals about 1 mm long; petals pinkish or whitish, the claws 1–2 mm long, the blades 3–6 mm long, with 5–7 lobes; ovary ca ½ inferior; seeds smooth. Pinyon-juniper, sagebrush, mountain brush, ponderosa pine, aspen, riparian, meadow, and spruce communities at (1310) 2075 to 3050 m in Beaver, Box Elder, Cache, Garfield, Grand, Iron, Juab, Kane, Piute, Salt Lake, San Juan, Sevier, Tooele, and Washington counties; western Washington south to Arizona, east to Montana and New Mexico; 50 (ii).

Mitella L.

Scapose glandular-puberulent herbs from rhizomes; leaves basal, palmately lobed, cordate; flowers in racemes, perfect, regular; hypanthium calyxlike; sepals 5; petals 5, pinnately or palmately lobed, small and soon withered; stamens 5; ovary ca ½ inferior, 1-loculed; style 1; fruit a capsule, dehiscent by ventral suture and appearing almost circumscissile; seeds numerous.

1. Racemes secund; pedicels lacking or to 3 mm long; petals with (2) 3 lobes; sepals whitish or purplish; leaf margin often ciliate; scapes often hirtellous or hirsute as well as glandular .... *M. stauropetala*

— Racemes not especially secund; pedicels mainly 2–8 mm long; petals pinnately divided; sepals greenish; leaf margin seldom if ever ciliate; scapes glabrate toward the base .... *M. pentandra*

Mitella pentandra **Hook.** Fivestar Miterwort. Scapose perennial herbs, 10–35 cm tall; petioles 1.8–10 cm long, glabrous or sparingly pilose; leaf blades 1.5–5.7 cm wide, ovate to orbicular, cordate basally, with 5–9 shallow lobes, the lobes dentate, the teeth mucronate, seldom if at all ciliate, glabrous, or more often hirsute to pilose; scapes glandular above; racemes 3–16 cm long, 4- to 20-flowered; pedicels 2–8 mm long, shorter above; hypanthium saucer shaped to campanulate, 1–2.5 mm long; sepals less than 1 mm long; petals 2–3 mm long, greenish, pinnately dissected into 4–10 filiform segments; capsules ca 2 mm long. Meadows, near seeps, springs, streams, lakes, and ponds, often in shaded sites in aspen, conifer, and willow communities at 1740 to 3650 m in Box Elder, Daggett, Davis, Duchesne, Emery, Salt Lake, Sanpete, Summit, Uintah, Utah, and Wasatch counties; Alaska south to northern California, east to Alberta and Colorado; 33 (iii).

Mitella stauropetala **Piper** Smallflower Miterwort. [*M. stenopetala* Piper Type from the Wasatch Mountains.] Perennial scapose herbs 15–50 cm tall or more; petioles 1.2–13 cm long, glandular and sometimes hirsute; leaf blades 1–7.8 cm wide and about as long, orbicular or broadly ovate, cordate, 5- to 9-lobed, the lobes crenate, the margin ciliate, glabrous or minutely glandular and sparingly hirsute; scapes glandular to the base; racemes 4.5–18 (24) cm long, mostly strongly secund, 7- to 24-flowered, mainly with 1 flower per node; pedicels obsolete or to 2 or 3 mm long; hypanthium ca 1–2 mm long, cupshaped; sepals ca 1.5 mm long, oblong, whitish or purplish; petals 2–4 mm long, 3 (2) -lobed or rarely entire, the lobes filiform; capsules ca 2 mm long. Mountain brush, aspen, ponderosa pine, fir, and spruce communities at 1615 to 3050 m in Box Elder, Cache, Carbon, Duchesne, Emery, Juab, Millard, Salt Lake, San Juan, Sanpete, Summit, Tooele, Utah, Wasatch, and Weber counties; eastern Washington and Oregon to Montana, south to Colorado. Our plants are referable to **var. *stenopetala*** **(Piper) Rosend.**; separable from *M. pentandra* by a series of small features, but sometimes confused with that taxon; 65 (ii).

Parnassia L.

Scapose perennial glabrous herbs from short rootstocks; leaves basal, entire; scapes with a solitary, entire bract or bractlike leaf;

flowers solitary and terminal, perfect, regular; hypanthium calyxlike, sometimes nearly obsolete; sepals 5; petals 5, white; stamens 5, alternating with clusters of gland-tipped staminodia; ovary superior or slightly inferior, 1-loculed; styles lacking; stigmas 3 or 4, sessile; fruit a capsule, loculicidal at the apex; seeds numerous.

1. Petals fringed below the middle; petioles (1.5) 3–16 cm long; leaf blades cordate to truncate basally, 12–45 mm wide, broader than long; bract mostly borne above the middle of the scape .... *P. fimbriata*

— Petals entire; petioles 0.7–4 cm long; leaf blades cuneate or obtuse basally (rarely truncate or cordate), 5–20 mm wide, mostly longer than broad; bract borne below the middle of the scape .... *P. palustris*

Parnassia fimbriata **Konig** Fringed Grass-of-Parnassus. Perennial, scapose glabrous herbs, 14–43 cm tall; petioles (1.5) 3–16 cm long; leaf blades 12–45 mm wide, about as long, reniform, orbicular, or broadly ovate, cordate or truncate at the base; bracts of scapes ovate to orbicular, 7–17 mm long, mostly clasping, borne at or above the middle of the scape; flowers solitary and terminal; hypanthium nearly obsolete; sepals 4–7 mm long, 2–4 mm wide, sometimes slightly fimbriate; petals 8–15 mm long, including the narrow clawlike base, strongly fimbriate below the middle; staminodia thickened and scalelike, flared above the middle and usually with a central subterminal larger lobe and 7–9 marginal ones; capsules to 1 cm long. Along springlets, streams, seeps, ponds, and lakes, often in aspen, spruce, fir, and mountain brush communities at 2010 to 2895 (3355) m in Cache, Duchesne, Salt Lake, San Juan, Summit, and Utah counties; Alaska south to California, east to Alberta and New Mexico; 45 (v). Our plants are referable to var. *fimbriata*.

Parnassia palustris **L.** Perennial, scapose glabrous herbs, 8–44 cm tall; petioles 0.7–4 cm long; leaf blades 7–27 mm long, 5–20 mm wide, ovate to nearly orbicular, mostly cuneate or obtuse at the base, rarely truncate; bracts of scapes linear to ovate, (3) 5–25 mm long, sessile and sometimes clasping, borne mostly below the middle of the scape; flowers solitary and terminal; hypanthium ca 2 mm long; sepals 3–10 mm long; petals 6–14 mm long, including the narrow claw, entire, white; staminodia with a thickened scalelike base, flared upward and divided into (5) 7–11 (or many) slender filamentous segments, these terminating in capitate knobs; capsule ovoid 8–10 (12) mm long. Wet meadows, near seeps and springs, and along streams, sometimes in woods at (1375) 1830 to 3415 m in Beaver, Box Elder, Cache, Duchesne, Emery, Garfield, Grand, Iron, Juab, Kane, Piute, Sanpete, Summit, Uintah, Utah, Washington, and Wayne counties; arctic America south to Quebec and British Columbia; Rocky Mountains to Colorado, Nevada (Spring Mts.), and California; Eurasia; 64 (0). Our plants are assignable to var. ***montanensis*** **(Fern. & Rydb.) C.L. Hitchc.** Many of our specimens have been identified previously as *P. parviflora* DC., which is known from well to the north of our area, and which may be only a small-flowered phase of *P. palustris* not worthy of taxonomic recognition.

Peltiphyllum Engl.

Scapose perennial herbs from thick rhizomes; leaves developing after the scapes; petioles long; blades peltate, very large; flowers in bractless, paniculate-corymbose cymes, showy, regular; hypanthium very short, adnate to the ovary; sepals 5; petals 5; stamens 10; carpels 2, free above the hypanthium, tapering to the discoid-capitate stigma; fruit a follicle, fully dehiscent; seeds cellular-rugulose.

Peltiphyllum peltatum **(Torr.) Engel. in Engel. & Prantl** Shieldleaf. Robust perennial herbs; rhizomes fleshy but tough, to 5 cm thick; petioles to 1 m tall or more, hirsute; leaf blades 5–40 cm broad, peltate, depressed at the center above the point of attachment to the petiole, nearly orbicular, 10- to 15-lobed, the divisions again lobed and serrate-dentate; scapes 3–6 dm tall or more, hirsute-glandular, naked, or with a small bract; sepals 2.5–3.5 mm long, reflexed; petals 4.5–7 mm long, white to bright pink; filaments flattened and broad at the base; follicles 6–10 mm long, purplish, fused basally. Known in

Utah from a small colony growing along a cold mountain stream on the east side of Mount Timpanogos, Utah County; coastal southwestern Oregon and northern California; 4 (0). The widely disjunct colony may be from an introduction.

Philadelphus L.

Shrubs; leaves opposite, subsessile or on short petioles; flowers perfect, regular, in few-flowered cymes at the ends of leafy branches; hypanthium calyxlike; sepals 4 (5); petals 4 (5), white or nearly white; stamens many (ca 20–60); ovary at least ⅔ inferior, with 3–5 locules; styles 3–5, distinct or united; fruit a loculicidal capsule, leathery or woody; seeds numerous. **Note:** In addition to the taxa included in the key, *P. verrucosus* Shrad. and x *P. virginalis* Rehd. are occasionally cultivated in Utah. These differ from those treated below in having sepals pubescent on the back, not just on the margins. *P. verrucosus* has single flowers and x *P. virginalis* has double flowers. In addition to these, *P. lewisii* Pursh of the Northwest might also be cultivated in the state.

1. Leaves entire, 4–26 mm long; plants native .... *P. microphyllus*

— Leaves toothed, sometimes larger than above; plants introduced, to 3 m tall, our common cultivated mockorange .... *P. coronarius* L.

Philadelphus microphyllus **Gray** Littleleaf Mockorange. [*P. nitidus* A. Nels.]. Shrubs 8–20 dm tall, with opposite leaves; branchlets appressed pubescent; petioles ca 1 mm long; leaf blades 4–26 mm long, 2–13 mm wide, mostly elliptic or ovate to lanceolate or linear, entire, slightly revolute, sparingly to moderately strigose or glabrate; pedicels to 3 mm long, strigose-sericeous; hypanthium ca 2–3 mm long, pubescent like the pedicels; sepals 2–5 mm long; petals 8–15 mm long, white; stamens about equal to the sepals; capsules 6–8 mm long. Pinyon-juniper, mountain brush, ponderosa pine, aspen, and fir communities, mostly on sandstone at 1220 to 2650 m in Beaver, Carbon, Daggett, Emery, Garfield, Grand, Juab, Millard, Piute, San Juan, Sevier, Tooele, Uintah, Washington, and Wayne counties; Wyoming and Utah to Texas; 80 (iii). Plants from the southern part of the state have leaves that are slightly larger on the average than those from more northern areas, but the difference does not seem to warrant taxonomic recognition.

Ribes L.

Shrubs with or without bristles and spines; leaves alternate, palmately lobed, crenate or dentate; stipules none or adnate to the petiole; flowers perfect, regular, in racemes, or rarely solitary; pedicels subtended by bracts and usually with 2 bractlets about midlength; hypanthium mostly corollalike; sepals 5, mostly petaloid; petals 5 (4), often smaller than the sepals; stamens 5 (4–6); ovary completely inferior, 1-loculed; styles 2, united or distinct; fruit a berry, crowned by the withered flower; seeds several to many. **Note:** The taxa with jointed and disarticulating pedicels, several flowers per raceme, and stipitate-glandular or glabrous berries are referred to as currants. The currants in our area are without spines or bristles except for *R. lacustre* and *R. montigenum*. The taxa with nonjointed and persistent pedicels and with only (1) 2 or 3 flowers per raceme and without stipitate-glandular hairs on the berries are referred to as gooseberries. The gooseberries of Utah all have nodal spines.

Berger, A. 1924. A taxonomic review of currants and gooseberries. N.Y. State Agr. Exp. Sta. Tech. Bull. 109: 1–118.

1. Branchlets armed with nodal spines, sometimes also with internodal bristles (see note at the end of the genus description) 2

— Branchlets unarmed (currants—see note above at the end of the genus description) 8

2(1). Racemes with 3–15 flowers; ovaries and berries with setose-stipitate glands; hypanthium saucer shaped 3

— Racemes with 1–3 flowers; ovaries and berries glabrous or pubescent, but not with setose-stipitate glands; hypanthium tubular or cup shaped 4

3(2). Racemes with 3–8 flowers; berries red; leaves with glandular and nonglandular hairs, the blades cleft ¾ of the way to nearly all the way to the base; plants common and widespread ..... *R. montigenum*

— Racemes with (5) 7–15 flowers; berries black or purple-black; leaves glandular or with a few nonglandular hairs along the veins, the blades lobed ⅔ of the way to the base or less; plants of the Uinta and Wasatch mountains ..... *R. lacustre*

4(2). Leaves 7–20 mm wide; styles connate to near the apex; free hypanthium and sepals pubescent externally; plants of desert ranges of western and southern Utah 5

— At least some of the leaves over 20 mm wide, and/or styles lobed or cleft ¼ to ½ the length; free hypanthium and sepals mostly glabrous externally; plants of various distribution 6

5(4). Free hypanthium 4–5.5 mm long; sepals 4–6 mm long; ovaries and berries mostly glabrous ..... *R. leptanthum*

— Free hypanthium 1–2 mm long; sepals 2–4 mm long; ovaries and berries glabrous to hairy ..... *R. velutinum*

6(4). Hypanthium pubescent within; berries greenish or yellowish (ripening purplish); plants cultivated, persisting, and rarely escaping. English Gooseberry ..... *R. grossularia* L.

— Hypanthium glabrous within, but the styles pubescent; berries reddish or blackish; plants indigenous 7

7(6). Free hypanthium 2–3.5 mm long; stamens usually twice as long as the petals, about equaling the sepals when extended; berries reddish purple; nodal spines 1 (rarely 3) or lacking; branchlets usually glabrous; plants common and widespread ..... *R. inerme*

— Free hypanthium 4–5 mm long; stamens subequal to the petals or rarely to twice their length, not as long as the extended sepals; berries purple-black; nodal spines usually 3; branchlets finely puberulent and sometimes with internodal bristles; plants rather rare, except along the south slope of the Uinta Mountains ..... *R. setosum*

8(1). Flowers bright yellow, often reddish in part in age, glabrous; ovaries and berries glabrous; leaves glabrous, not cordate, with 3 (rarely 5) primary lobes, the primary lobes seldom with more than 3 teeth or lobes ..... *R. aureum*

— Flowers not yellow, often pubescent or glandular; ovaries and berries with sessile or stipitate glands (except in *R. sativum* and *R. inerme*); leaves often pubescent, mostly cordate, with (3) 5–7 primary lobes, these with usually more than 3 teeth or lobes 9

9(8). Leaf blades, flowers, and fruit stipitate-glandular, or if sparingly so then flowers pinkish and berries red; free hypanthium 4–11 mm long, campanulate to cylindric; anthers glandular apically 10

— Leaf blades not stipitate-glandular, glabrous or with hairs mostly on veins, or with sessile glands; flowers rarely pinkish; berries red only in *R. inerme*; free hypanthium mostly less than 4 mm long, variously shaped; anthers eglandular 11

10(9). Flowers (1) 2 or 3 per raceme, pinkish, the hypanthium less than 3 mm wide; berries red; leaf blades 7–30 (44) mm wide, not pilose-hirsute ..... *R. cereum*

– Flowers 4–12 per raceme, greenish white to cream, the hypanthium 3–6 mm wide; berries blackish; leaf blades 30–100 mm wide, at least some, pilose-hirsute and stipitate-glandular .... *R. viscossissimum*

11(9). Ovaries and berries stipitate-glandular or with crystalline, yellowish, sessile glands; lower leaf surface with sessile glands; berries blackish; flowers (5) 8–30 per raceme; styles glabrous 12

– Ovaries and berries glabrous, or if with sessile nonglandular spots then the flower 1–3 per raceme and styles pubescent; berries red or reddish purple 15

12(11). Lower surface of leaves and floral parts with scattered, crystalline yellow glands; racemes many-flowered (to 30); plants strongly aromatic 13

– Leaves and/or floral parts with stipitate glands, or variously glandular, but not with yellow crystalline glands; racemes with (5) 8–16 flowers; plants not strongly aromatic 14

13(12). Sepals longer than the free hypanthium; racemes erect or ascending; plants indigenous .... *R. hudsonianum*

– Sepals shorter than the free hypanthium; racemes spreading to pendulous; plants cultivated. Black or Bedbug Currant .... *R. nigrum* L.

14(12). Bracts of racemes 3–4 mm long, about ½ as long as the pedicels, oblong; flowers whitish or greenish; stipitate hairs of racemes whitish or pale greenish, rarely purplish, often sparse except on ovary and berry; racemes crowded, the upper internodes seldom over 3 mm long; plants of the La Sal Mountains and portions of central Utah .... *R. wolfii*

– Bracts of racemes 1–2 mm long, less than ½ as long as the pedicels, linear to acute; flowers pinkish or purplish; stipitate hairs of racemes mostly with purple tips, usually well developed on rachis and pedicels as well as on ovaries and berries; racemes loose, 1 or more of the upper internodes regularly over 3 mm long, plants of the Deep Creek Mountains .... *R. laxiflorum*

15(11). Flowers 1–3 per raceme, white; sepals longer than wide; free hypanthium ca 2–3.5 mm long; styles pubescent; plants indigenous .... *R. inerme*

– Flowers 8–20 per raceme, greenish; sepals wider than long; hypanthium to 2 mm long; styles glabrous; plants cultivated and escaping. Red Currant .... *R. sativum* Syme

Ribes aureum **Pursh** Golden Currant. Shrubs, 1–3 m tall, unarmed; branchlets glabrous; petioles 0.5–2.5 (3) cm long; leaf blades 0.6–4.7 cm long, 1–6.7 cm wide, orbicular, reniform, obovate, cuneate to truncate basally, strongly 3-lobed, the lobes entire or crenate to lobed, glabrous; racemes with (3) 6–9 flowers; bracts 3–12 mm long, entire; pedicels to 3 mm long; free hypanthium cylindric, yellow, or often reddish in age, corollalike; sepals 4–6 mm long, yellow, spreading; petals ca 2 mm long, yellow, cream, or reddish; stamens subequal to the petals, the anthers longer than the filaments; styles united to near the apex; berries 8–12 mm long, black or translucent-golden, glabrous. Streamsides, washes, ditches, rivers, seeps, and springs in greasewood-shadscale, sagebrush, pinyon-juniper, mountain brush, ponderosa pine, and Douglas-fir communities, also cultivated at 1340 to 2590 m in all Utah counties except Grand and San Juan; Washington to Saskatchewan, south to California and New Mexico; 150 (iii). The golden currant is similar to *R. odoratum* Wendl. of the eastern United States and Canada, which may be cultivated in the state. The berries are the most palatable of any species of *Ribes* in Utah.

Ribes cereum **Dougl.** Wax or Squaw Currant. Shrubs, (0.2) 0.5–1.5 (2) m tall, unarmed; branchlets pilose-villous and stipitate-glandular; petioles 0.4–2.2 (2.9) cm long; leaf blades 0.5–2.5 (3.4) cm long, 0.7–3 (4.4) cm wide, orbicular, reniform, rarely ovate, cordate or truncate basally, with 3–7 shallow lobes, the lobes crenate or dentate, puberulent and stipitate glandular, or glabrous except on margins and along veins beneath; racemes with 2 or 3 flowers, the axis very short; bracts 2–5 mm long ciliate, fringed or lacerate, glandular; free hypanthium 4–11 mm long, pinkish, pilose, sometimes also stipitate-glandular; sepals ca 2 mm long, spreading to deflexed, whitish or pinkish; petals ca 1 mm long, whitish; staminal filaments subequal to the anthers; styles united to near the apex; ovaries stipitate-glandular; berries 6–8 mm long, reddish, sparingly stipitate-glandular, rarely glabrate. Mountain brush, sagebrush, pinyon-juniper, riparian, ponderosa pine, aspen, limber pine, spruce-fir, krummholz, alpine, and less commonly desert shrub communities at 1520 to 3260 m in all Utah counties but Davis; British Columbia to Montana, south to California and New Mexico; 230 (vi). Most of our plants are referable to var. ***inebrians*** **(Lindl.) C.L. Hitchc.,** with bracts of the racemes mostly ovate or obovate, usually pointed, and with margins entire to sharply denticulate or with 2 or 3 shallow lobes. Occasional specimens have fan-shaped bracts that are truncate to broadly rounded and prominently toothed or with as many as 6 lobes. These specimens might be referable to var. *cereum*, but the distinction is tenuous at best. Intergradation of the morphological features is common, and no geographical correlation is apparent in Utah.

Ribes hudsonianum **Richards.** Northern Black Currant. Shrubs, 0.5–1.5 (2) m tall, rather strongly scented, unarmed; herbage bearing crystalline, yellowish glands, usually puberulent; petioles (1) 2.5–8.5 cm long; leaf blades (2.1) 2.7–8.2 cm long, (2) 5–12.2 cm wide, orbicular or ovate in outline, strongly 3-lobed and doubly dentate, the lateral lobes again lobed, cordate basally; racemes ca 20- to 30-flowered, to 12 cm long in fruit; bracts ca 0.5–1.5 mm long, awl-shaped, soon deciduous; free hypanthium to ca 1 mm long, whitish; sepals 2.5–4 mm long, white; petals ca ½ as long as sepals; styles united for more than ½ their length; berries 7–12 mm long, blackish, glabrous except for sessile glands. Streamsides, usually in aspen, lodgepole pine, or spruce-fir communities at 1830 to 2590 m in the Raft River, Wasatch, and Uinta mountains in Box Elder, Duchesne, Salt Lake, Summit, Utah, and Wasatch counties; Alaska to Hudson Bay, south to California, Wyoming, and Minnesota; 11 (i). Our plants are referable to **var.** ***petiolare*** **(Dougl.) Jancz.**

Ribes inerme **Rydb.** Whitestem Gooseberry; Wine Gooseberry. Shrubs 0.75–2 m tall; branchlets often whitish, glabrous, armed at the nodes with 1 (3) spines, or the spines lacking; internodal bristles mostly lacking or few and sparse; petioles (0.3) 0.5–4.5 cm long, sometimes with 1 to few pilose gland-tipped hairs; blades (0.8) 1.5–9 cm long, orbicular or nearly so, cordate to truncate with 3–5 main lobes that are again lobed and crenate-dentate toothed, the major sinuses cut ⅓–⅔ the way to the base, glabrous, glabrate with hairs mostly along the veins or occasionally with moderately dense strigose or short recurved hairs, not glandular, paler beneath than above; racemes 1–4 flowered, the axis to about 12 mm long; bracts 1–2 mm long, greenish, glabrous or glandular ciliolate and puberulent; pedicels 2–5 mm long; free hypanthium 2–3.5 mm long, cylindric to narrowly campanulate, greenish or greenish cream, sometimes purplish tinged, densely pilose to villous-wooly inside; sepals about 3 mm long, colored as the hypanthium; petals about 1–1.5 mm long, obovate to narrowly fan-shaped, white; stamens about (1.5) 2–2.5 times longer than the petals, 2–4 (5) mm long; styles about equal or slightly longer than the stamens, cleft ½–⅔ the way to the base, rather densely pilose on the lower ½ or more; berries 7–10 mm long, reddish or reddish purple, succulent, more or less edible. Pinyon-juniper, mountain brush, aspen, willow, Douglas-fir, spruce-fir, tall forb, and meadow communities, often along streams or in wet places, occasionally among rocks in rather dry places at 1830 to 3100 m, in Cache, Carbon, Daggett, Duchesne, Garfield, Grand, Juab, Piute, San Juan, Salt Lake, Sanpete, Sevier, Summit, Tooele, Uintah, Utah, Wasatch, and Weber counties; British Columbia to California, Montana to New Mexico; 56 (vii). Some Utah specimens have stamens shorter than is traditionally listed for the species. See *R. setosum*.

Ribes lacustre **(Pers.) Poir. in Lam.** Swamp Black Gooseberry. Shrubs, 0.75–1.5 m tall; branchlets armed with internodal prickles and nodal spines, also puberulent but not glandular; petioles 0.3–5 cm long, glabrous or with scattered stipitate-glandular hairs; leaf blades (0.6) 1.5–5.6 cm long, (1) 2–8 cm wide, orbicular in outline, cordate at the base, usually 5-lobed, the lobes again lobed and doubly crenate-dentate, glabrous or sparingly hairy along the veins; racemes rather loosely 5- to 15-flowered, the axis to 4.5 cm long in fruit, stipitate-glandular with reddish or purplish glands, also puberulent; bracts 2–3 mm long, ciliate-glandular; pedicels 3–8 mm long; free hypanthium less than 1 mm long, saucer shaped, yellowish green, pinkish, or reddish; sepals 2.5–3 mm long, yellow-green, pinkish, or reddish; petals shorter than the sepals, pinkish; stamens subequal to the petals; styles parted to the base; berries 6–8 mm long, dark purple, coarsely stipitate-glandular. Along streams and in other moist places often in conifer and aspen woods at 2100 to 3350 m in the Uinta and Wasatch mountains, in Duchesne, Salt Lake, Summit, and Wasatch counties; Alaska to Newfoundland, south to California, Colorado, South Dakota, and Michigan; 20 (iv).

Ribes laxiflorum **Pursh.** Western or Trailing Black Currant. Shrubs to about 0.7 m tall, the stems sprawling or ascending, unarmed; twigs of the season and some older branches puberulent; petioles (0.5) 2–4.5 cm long, puberulent, sometimes short stipitate-glandular near the blade; leaf blades (1) 2–5 cm long, 1.5–6.5 cm wide, orbicular or nearly so, cordate, with 3–5 primary lobes, these again lobed and crenate-dentate, the major sinuses cut about ⅓–½ the way to the base; glabrate or with some puberulent hairs and stipate glandular hairs, especially toward the base on veins beneath, slightly paler beneath with translucent crystalline sessile glands; racemes 5- to 10-flowered, stipitate glandular and puberulent, the axis 2–4 cm long; bracts 1–2 mm long, linear or narrowly triangular, greenish; pedicels 4–10 mm long, jointed just below the ovary, some usually persisting at least until fruit is nearly mature; free hypanthium less than 1 mm long; sepals 2–3 mm long, pinkish or purplish; petals about 1 mm long, 1–1.3 mm wide, broadly fan shaped with concave margins; stamens about equaling the petals; styles cleft ⅓–⅔ their length; berries to ca 1 cm long, blackish, stipitate-glandular, the glands and stalks mostly purplish. Known in Utah from a single small population in the Deep Creek Mountains, Juab County, where abundant in wet shady places among downed timber and boulders, in a spruce-aspen community. Alaska to Washington and along the coast to southwest California, east to Alberta and northern Idaho, widely disjunct in Utah; 2 (i). The closely related *R. coloradense* Cov. of Colorado and New Mexico has been reported for Utah, but I have seen no specimens. It is reported to be separable from *R. laxiflorum* by glandular hairs on the back of sepals (a feature that occasionally shows up in plants as far away as Alaska), by petals nearly twice as broad as long, and by berries without bloom. The separation appears rather tenuous at the species level. A combination has been made [*R. laxiflorum* var. *coloradense* (Cov.) Jancz]. The amazingly disjunct population in Utah seems more closely allied to the coastal and northern plants than to those of Colorado.

Ribes leptanthum **Gray** Trumpet Gooseberry. Shrubs, 0.5–2 m tall; branchlets armed at the nodes with 1–3 spines, usually lacking internodal bristles, puberulent; petioles 0.2–1.2 cm long; leaf blades 0.5–1.6 cm long, 0.7–2 cm wide, orbicular, cordate basally, mostly 5-lobed, the main lobes again shallowly lobed or toothed, glabrous or less commonly puberulent and rarely glandular; racemes 1- to 3-flowered, the axis very short; bracts glabrous except glandular-ciliate or -toothed; pedicels ca 1 mm long; free hypanthium 4–5.5 mm long, whitish, pilose or short-villous; sepals 4–6 mm long, whitish; petals 2.5–3 mm long, whitish; stamens subequal to the petals; anthers shorter than the filaments; styles glabrous, apically notched; berries ca 6–10 mm long, blackish, glabrous. Pinyon-juniper, mountain brush, ponderosa pine, aspen, spruce-fir, and meadow communities at 1830 to 2590 m in Beaver, Emery, Garfield, Grand, Kane, Piute, and San Juan counties; Colorado, Utah, New Mexico, and Arizona; 22 (i).

Ribes montigenum **McClatchie** Gooseberry Currant. [*R. lacustre* var. *lentum* Jones, type from Henry Mts.]. Shrubs, 0.2–0.7 m tall; branchlets armed with 1–5 nodal spines, the internodal bristles lacking or present, puberulent or glabrous; petioles 0.4–4 cm long; leaf blades 0.4–3.7 cm long, 0.6–5 cm wide, orbicular in outline, cordate at the base, usually 5-lobed, the primary lobes again lobed or toothed, the vesture of glandular or nonglandular hairs and sometimes with sessile crystalline glands; racemes 3- to 8-flowered, the axis to 3.5 cm long in fruit; bracts 2–3 mm long, glandular-pubescent; pedicels 1–3 mm long; free hypanthium ca 1 mm long, saucer shaped, lined with a yellowish or pinkish disk, glandular-hairy; sepals ca 3 mm long, pinkish lavendar to whitish; petals ca 1 mm long, pinkish or pink-purple; stamens subequal to the petals; filaments longer than the anthers; style divided to near the base, glabrous; berries mostly 5–10 mm long, red, stipitate-glandular. Spruce-fir, Douglas-fir, lodgepole pine, bristlecone pine, aspen, krummholz, sagebrush-snowberry, and sedge-grass communities, and often in talus and scree slopes at 2135 to 3660 m in all Utah counties except Davis, Millard, Morgan, and Rich; British Columbia to southern California, east to Montana and New Mexico; 151 (v).

Ribes setosum **Lindl.** Missouri Gooseberry. Shrubs 0.75–2 m tall; branchlets sometimes armed with internodal bristles, the nodes with 1–3 spines; petioles 1–4.8 cm long, often puberulent to pubescent, sometimes with a few glandular long setae that are sometimes pilose; blades (1.5) 2–5.7 cm long, orbicular or nearly so, truncate to cordate, with about 5 main lobes that are again lobed and crenate-dentate, the major sinuses cut a little less than ½ to about ⅔ the way to the base of the blade, scattered to moderately pubescent with short curved hairs or rarely glabrate above and beneath, the hairs rarely confined to the nerves, often stipitate glandular and/or with sessile translucent glandular dots beneath and sometimes above, slightly paler beneath than above; racemes 1- to 4-flowered, the axis to about 5 mm long; bracts 1–3 mm long, greenish, minutely glandular ciliate; pedicels about 2–5 mm long; free hypanthium 4–5 mm long, cylindric, greenish white or pinkish tinged, pilose to villous-wooly within; sepals 3–4 mm, the color of the hypanthium; petals about 2 mm long, obovate, white; stamens equaling the petals or slightly excerted, not longer than the mostly erect to ascending sepals; styles about equaling the sepals, cleft ½–⅔ the way to the base, densely pilose on the lower ½ or ⅔; berries 10–12 mm long, blackish or deep purple-black, succulent, more or less edible. With aspen, alder, birch, and willows in riparian or seepy meadow communities or about seeps and springs at 2130 to 2560 (2750) m in (Deep Creek?) Raft River and Uinta mountains in Box Elder, Duchesne, (Juab?), and Uintah counties; Alberta to Utah east to the Dakotas and Michigan; 15 (iii). A few Utah specimens seem intermediate to *R. inerme*.

Ribes velutinum **Greene** Desert Gooseberry. Shrubs, mostly 1–2 m tall, with 1 (2 or 3) nodal spine, lacking internodal bristles; branchlets usually pubescent; petioles 0.3–1.5 cm long; leaf blades 0.5–1.4 cm long, 0.7–2 mm wide, orbicular, 3- to 5-lobed, the main lobes usually again lobed, pubescent or glabrous; racemes 1- to 3-flowered, the axis very short; bracts 2–3 mm long, puberulent; pedicels 1–2 mm long; free hypanthium ca 1–2 mm long, pubescent externally, whitish or pinkish; sepals 2–4 mm long, whitish; stamens subequal to the petals; filaments subequal to the anthers; style entire, subequal to the stamens; styles united to the apex; berries 5–8 mm long, reddish (?), glabrous or hirsute, not very fleshy. Pinyon-juniper, mountain brush, and sagebrush-desert shrub communities at 1340 to 2321 m in Beaver, Kane, Millard, Tooele, and Washington counties; Washington to California, east to Idaho and Arizona; 23 (ii). Our plants are referable to **var. *velutinum*.**

Ribes viscosissimum **Pursh** Sticky Currant. Aromatic shrubs, mostly 1–2 m tall, unarmed; branchlets pilose-hirsute and stipitate-glandular; petioles 0.6–7 cm long; leaf blades 0.9–6.6 cm long, 1.3–10 cm wide, orbicular, rarely ovate, cordate basally, 3- to 7-lobed, the main lobes crenate or dentate and sometimes again lobed, glandular-hairy and often pilose or hirsute; racemes 4- to 12-flowered, the axis 5–30 mm long, glandular; bracts 3–10 mm long, entire to toothed, glandular; pedicels 3–17 mm long; free hypanthium 5–9 mm long, whitish or pale green, stipitate-glandular and pilose-hirsute; sepals 3–5.5 mm long, white or yellow-green, or occasionally pinkish; petals 2–3 mm long, whitish; stamens subequal to the petals; filaments longer than the anthers; styles simple, glabrous or nearly so; berries 10–13 mm long, black, rather dry, stipitate-glandular. Commonly growing in shade of aspen, fir, Douglas-fir, lodgepole pine, and spruce woods, and less commonly in mountain brush, meadows, and openings at 1965 to 2925 m in Box Elder, Cache, Carbon, Daggett, Duchesne, Kane, Millard, Morgan, Salt Lake, Sanpete, Summit, Tooele, Uintah, Utah, Wasatch, and Washington counties; British Columbia, south to California, east to Montana and Arizona. This plant is unique among our species in the dense stipitate-glandular and nonglandular hairs of the herbage and in the rather broad and long hypanthia. Our plants are referable to **var. *viscosissimum***; 42 (ii).

Ribes wolfii **Rothrock** Rothrock Currant. [*R. mogollonicum* Greene]. Shrubs, 0.5–3 m tall, unarmed; branchlets glabrous or puberulent; petioles 0.7–4.5 cm long, glabrous or puberulent; leaf blades 1.2–5.7 cm long, 1.2–8 cm wide, orbicular, cordate basally, 3 (5)-lobed, the main lobes again lobed and variously 1- or 2-crenate or -dentate, glabrous except for sessile, clear crystalline glands; racemes ca 8- to 16-flowered, glandular, the axis ca 1–4 cm long; bracts 3–6 mm long, mostly entire; pedicels 1–5 (7) mm long; free hypanthium ca 0.7–1.5 mm long, green, bowl shaped, glabrous or puberulent; sepals 2–3 mm long, whitish; petals ca 1.5 mm long, white; styles free or united below the middle; berries 6–10 mm long, blackish, not very fleshy, stipitate-glandular. Mountain brush, aspen, Douglas-fir, and spruce-fir communities, usually in shade at 1645 to 3350 m in Carbon, Emery, Grand, Juab, Millard, Salt Lake, San Juan, Sanpete, Sevier, Tooele, and Utah counties; Colorado, Arizona, and New Mexico, and in Washington and Idaho; 80 (iv). Vegetative specimens of *R. wolfii* are sometimes confused with *R. hudsonianum*. Both have sessile, crystalline, glandular dots on the lower surface of the leaves. In *R. wolfii*, these dots are more clear than yellow, smaller, and they are seldom noticeable on the often puberulent petioles and young twigs. In *R. hudsonianum* these dots are yellowish, larger, and more conspicuous, and they often extend down the less puberulent petioles and twigs.

Saxifraga L.

Perennial herbs; leaves alternate or basal; flowers perfect; hypanthium obsolete to well developed; sepals 5, erect to deflexed; petals 5, clawless or clawed, deciduous or persistent; stamens 10, the filaments subulate, linear, or flattened; carpels 2–5, connate only at the base or to near the tip; stigmas capitate; fruit capsular and dehiscent across the top or follicular; seeds numerous.

1\. Leaves all basal, the blades subentire to coarsely toothed but not lobed, commonly over 15 mm long, usually distinctly petioled; flowers mostly more than 10; plants common and widespread 2

– Leaves cauline, at least in part, or if all basal then less than 15 mm long, not distinctly petioled, or if so then the blades lobed but not toothed; flowers 1–5, or rarely more; plants mainly of high mountains 3

2(1). Inflorescence open; leaf blades orbicular or reniform, truncate or cordate; petioles 1.2–23 cm long, usually longer than the blades; plants 16–67 cm tall .... S. *odontoloma*

– Inflorescence congested, occasionally interrupted; leaf blades rhombic, obovate or ovate, cuneate at the base; petioles 0.3–2.5 cm long, usually shorter than the blades; plants 3–20 (30) cm tall .... S. *rhomboidea*

3(1). Petioles evident, 0.5–4.5 cm long, usually longer than the blades; blades orbicular or reniform, palmately lobed or trilobate, cordate or truncate basally, with some usually over 5 mm wide 4

– Petioles not especially evident; blades linear to oblanceolate, entire or 3- to 7-lobed, not cordate or truncate basally, 0.5–5 mm wide 5

4(3). Bulblets present in upper leaf-axils and inflorescence, not at petiole bases of lower leaves; hypanthium ca 1 mm long, not turbinate .... S. *cernua*

— Bulblets not present in upper leaf-axils and inflorescence, often present at petiole bases of lower leaves; hypanthium 2–3 mm long, turbinate .... S. *debilis*

5(3). Leaves toothed (sometimes obscurely so) or lobed; petals white; sepals erect or somewhat spreading, ca ½ as long as the hypanthium; plants glandular 6

— Leaves entire; petals yellow (white in S. *bronchialis*), but fading whitish; sepals spreading to reflexed, mostly more than ½ as long as the hypanthium 7

6(5). Plants depressed caespitose; leaves lobed, those of the stem generally less deeply lobed than the basal ones; petals gradually narrowed to the base, clawless or very shortly clawed; filaments longer than the sepals .... S. *caespitosa*

— Plants not depressed caespitose; leaves usually merely toothed, those of the stems often more prominently toothed than the basal ones; petals abruptly narrowed to a short claw; filaments shorter than the sepals .... S. *adscendens*

7(5). Plants stoloniferous; sepals ascending; hypanthium ca ½ to as long as sepals; herbage stipitate-glandular; leaves ciliate; petals yellow .... S. *flagellaris*

— Plants not stoloniferous; sepals spreading to reflexed or the petals white; hypanthium obsolete or very short; herbage not stipitate-glandular (or only the stem sparingly so); leaves glabrous or if ciliate then the petals white 8

8(7). Petals white; racemes often more than 3-flowered; leaves ciliate; sepals erect to spreading .... S. *bronchialis*

— Petals yellow when fresh; flowers mostly solitary; leaves not ciliate; sepals finally reflexed 9

9(8). Petals 4–5 mm long, short-clawed; sepals 2–3 mm long, glabrous; leaves 4–8 mm long, 0.5–1.5 mm wide; stems with minute stipitate glands, not pilose; plants 2–6 cm tall .... S. *chrysantha*

— Petals 7–10 (15) mm long, not clawed; sepals 4–5 mm long, often pilose; leaves often over 8 mm long and some over 1.5 mm wide; stems often rusty pilose; plants 6–20 cm tall .... S. *hirculus*

Saxifraga adscendens **L.** Wedge-leaf Saxifrage. Plants short-lived perennials, 3–10 cm tall, from a small simple caudex, strongly glandular-pubescent; leaves 5–15 mm long, sessile or gradually narrowed to a petiolelike base, entire, or 3 (5)-toothed or shallowly lobed at the apex, obovate; sepals about 1–2 mm long, usually reddish purple; petals white, about 3–6 mm long, narrowed abruptly to a claw; filaments slender; ovary inferior or nearly so; capsules 3.5–5 mm long. Alpine tundra and rocky slopes in the La Sal and Uinta mountains in Grand, San Juan, and Summit counties; northern Rocky Mountains, Cascades to Colorado, and Europe; 2 (0). Our material is referable to var. ***oregonensis*** **(Raf.) Breit.**

Saxifraga bronchialis L. Spotted Saxifrage. Plants (10) 13–15 cm tall, arising from a caudex with a taproot; caudex branches prostrate to ascending, clothed with densely imbricate persistent leaves; flowering stems glandular-pubescent, with few to several alternate leaves; leaves 3–15 mm long, 1–3 mm broad, sessile, entire, leathery, elliptic to oblong or spatulate, setose-ciliate and spinulose-tipped; flowers showy, yellowish or whitish; sepals greenish, ovate, 2–3 mm long, erect to spreading, glabrous, not ciliate; petals whitish or yellowish, yellow- to red-spotted, 3–6 mm long, indistinctly 3-veined; stamens shorter to longer than the petals, the filaments subulate; ovary only slightly inferior; capsules 4–6 mm long. Open rocky slopes at ca 3050 to 3931 m in the La Sal Mountains in Grand and San Juan counties; Alaska and Yukon, south to Oregon, Idaho, and New Mexico; 9 (0). Our plants are apparently referable to var. *austromontana* (Wieg.) G. N. Jones.

Saxifraga caespitosa **L.** Tufted Saxifrage. [S. *caespitosa* ssp. *exaratoides* var. *purpusii* Engl. & Irmsch., type from the La Sal Mts.].

Plants 1–17 cm tall, arising from a caudex and a taproot; caudex branches prostrate to ascending, clothed with densely imbricate leaves; flowering stems glandular-pubescent, often densely so, with 1-several alternate leaves; basal leaves 3–15 mm long, 2–7 mm wide, with 3–5 (7) apical, triangular to lanceolate or narrowly oblong lobes, cuneate, glandular-ciliate, not spinulose-tipped; cauline leaves often entire; flowers solitary or 2–4, moderately showy; sepals often purplish, nearly linear to ovate, 1–2 mm long, erect, glandular-pubescent and ciliate; petals white, cream, or yellowish, 2–3 mm long, 3-veined; stamens shorter than the petals, longer than the sepals, the filaments subulate; ovary almost completely inferior; capsule 3–4 (7) mm long. Spruce and alpine tundra communities, fell fields, and rocky slopes at 2985 to 3990 m in the La Sal, Tushar, Uinta, and Wasatch mountains, in Beaver, Duchesne, Grand, Piute, Salt Lake, San Juan, Summit, and Utah counties; circumboreal, south to Nevada, Arizona, and New Mexico; 29 (0). Specimens from above 3660 m on Kings Peak have many entire basal leaves and have sometimes been confused with S. *adscendens*. Fresh petals of some plants (Franklin 955 BRY) are yellowish. Our plants seem to be referable to **var. *minima* Blank.**

***Saxifraga cernua* L.** Nodding Saxifrage. Plants 6–15 cm tall, arising from fibrous roots; stems sparsely to densely glandular-villous, with several alternate leaves; basal leaves with petioles 0.5–3 cm long, the blades (3) 5- to 7-lobed, reniform, 4–15 mm long, 6–15 mm wide; cauline leaves becoming smaller, fewer lobed, and shorter petioled upward, at least the upper ones bearing usually purplish bulblets in the axils; flowers showy, solitary (rarely 2) at the apex of the inflorescence, the others replaced by bulblets; sepals green to dark reddish purple, ovate to lanceolate, 2.5–3 mm long, erect, sparsely to densely glandular, somewhat ciliate; petals white, 5–8 (12) mm long, 3- to 5-veined; stamens longer than the sepals, much shorter than the petals; ovary slightly if at all inferior; capsules rarely developing. Rocky places at 3445 to 3960 m in the Uinta and La Sal mountains, in Grand, San Juan, and Summit counties; circumboreal, south to New Mexico; 10 (0).

***Saxifraga chrysantha* Gray** Golden Saxifrage. Plants 2–6 cm tall, arising from slender rhizomes, sometimes mat forming; stems glandular; leaves imbricate at the stem base and scattered upward, 4–8 mm long, 0.5–1.5 mm wide, narrowly spatulate to narrowly oblong, entire, glabrous or occasionally sparsely glandular; flowers solitary; sepals 2–3 mm long, strongly reflexed, glandular externally, green or purplish; petals 4–5 mm long, yellow; stamens longer than the sepals but shorter than the petals; ovaries slightly inferior; capsules 6–8 mm long, ovoid. Alpine tundra, fell fields, and rock stripes at 3415 to 3960 m in the Uinta Mountains in Duchesne and Summit counties; Wyoming south to New Mexico; 6 (0).

***Saxifraga debilis* Engelm.** Pygmy Saxifrage. Plants 2–15 cm tall, arising from fibrous roots; stems usually glandular, rarely pilose; basal leaves sometimes with whitish or purple-tipped bulbils in the axils; petioles 0.5–6 cm long; leaf blades 3–15 (20) mm wide, mostly wider than long, reniform or orbicular, with 3–7 lobes; flowers solitary and terminal or 2 or 3 on naked or bracteate, slender pedicels, 0.5–5 mm long; sepals 1.5–2 mm long; petals 2–5 mm long, white; stamens exceeding the sepals, but shorter than the petals; ovaries only slightly inferior; capsules about 5–8 mm long. Alpine tundra, cirque basins, and Engelmann spruce communities, often near melting snowbanks at 2743 to 3960 m in Beaver, Daggett, Duchesne, Garfield, Grand, Iron, Piute, Salt Lake, San Juan, Summit, Tooele, Uintah, and Utah counties; British Columbia south to California, east to Montana and Arizona; 30 (i). Some plants from Kings Peak are rather densely pilose and have slightly shorter and relatively broader sepals than others from the state. These plants seem more like those from the northern Rocky Mountains and Cascades than others from the state.

***Saxifraga flagellaris* Willd.** Flagellate Saxifrage. Plants 3–10 (12) cm tall, arising from slender rhizomes, and with naked flagellate stolons; stems erect, stipitate-glandular villous, with several cauline leaves; basal leaves 5–17 mm long, 1–5 mm broad, entire, cuneate-oblanceolate to spatulate, setose-ciliate; cauline leaves similar to the basal ones except becoming glandular-ciliate and smaller above; flowers 1 to few, showy; sepals greenish to reddish purple, oblong to lanceolate or ovate, 2.5–4.5 mm long, stipitate-glandular, the glands purplish; petals bright yellow, but faded in dried specimens, 6–12 mm long, 7- to 9-veined; stamens longer than the sepals, the filaments subulate; ovary only slightly to ¼ inferior; capsules 4–5 mm long. Alpine tundra at 3350 to 3962 m in the Uinta and La Sal mountains in Duchesne, Grand, San Juan, and Summit counties; circumboreal, south to Arizona and New Mexico; 7 (0).

Saxifraga hirculus **L.** Yellow Marsh Saxifrage. Plants 6–20 cm tall; flowering stems erect, brownish or yellowish tomentose, at least above, arising from a basal rosette with fibrous roots, with usually several cauline leaves; basal leaves 1.2–3.5 cm long, 1–3 (4) mm wide, entire, linear-oblanceolate to spatulate, glabrous or glabrate; cauline leaves similar to the basal only smaller above; flowers 1–few, showy; sepals greenish to reddish, oblong to lanceolate, 2.5–5.5 mm long, spreading, glandular-villous to glabrate, ciliate; petals bright yellow, 7–12 mm long, 5- to 7-veined; stamens longer than the sepals, the filaments subulate; ovary only slightly inferior; capsules 7–12 mm long. Wet meadows in the Uinta Mountains in Daggett County; circumboreal, south to Colorado; 3 (2).

Saxifraga odontoloma **Piper** Brook Saxifrage. [S. *arguta* D. Don, misapplied]. Plants scapose, 16–78 cm tall, from rootstocks with fibrous roots; leaves all basal, glabrous or nearly so; petioles 1.2–23 cm long; blades 1–9.5 cm wide and about as long, orbicular to reniform, cordate or truncate at the base, coarsely dentate or crenate-dentate; scapes glabrous below, glandular above; inflorescence a spreading cymose panicle, several flowered, stipitate-glandular; sepals 2–3 mm long, strongly reflexed in anthesis, purplish; petals 2.5–4 mm long, white, spreading; stamens equaling or exceeding the petals; capsules 5–9 mm long. Along streams, springlets, and about ponds and lakes, and in other moist sites in montane plant communities at 1830 to 3350 m in all Utah counties except Daggett, Davis, Kane, Millard, Morgan, Rich, Washington, Wayne, and Weber; Alaska to California, east to Alberta and New Mexico; 104 (ii).

Saxifraga rhomboidea **Greene** Diamondleaf Saxifrage. Plants scapose, 3–20 (30) cm tall, from short rootstocks and fibrous roots; leaves all basal; petioles 0.3–2.5 cm long, usually pilose-ciliate or fringed, rather broad and flat, gradually differentiated from the blade; blades 9–35 mm long, 3–20 mm wide, rhombic, obovate, or ovate, dentate or crenate to subentire, not lobed, glabrous or ciliate; inflorescence cymose-paniculate, mostly very congested, globose or headlike, glandular; flowers several to many; sepals 1–2 mm long, more or less triangular, not reflexed; petals 2–4 mm long, white; stamens longer than the sepals, subequal to the petals; capsules 4–6 mm long excluding the stylar beaks. Meadows in alpine tundra and sometimes in ponderosa pine, Douglas-fir, and spruce communities at 2075 to 3965 m in Beaver, Box Elder, Cache, Daggett, Duchesne, Garfield, Grand, Iron, Juab, Millard, Piute, Salt Lake, San Juan, Sevier, Summit, Tooele, Uintah, Utah, Washington, and Wayne counties; British Columbia to Colorado; 111 (iii).

UTAH'S RARE PLANTS REVISITED

Stanley L. Welsh[1] and L. Matthew Chatterley[1]

ABSTRACT.— Presented is a current evaluation of the status and distribution of Utah's rare plant species, including those officially listed as endangered or threatened, those under review for listing, those recommended by the Utah Native Plant Society, and those which recently have been removed from consideration. Taxa are discussed alphabetically. Information on status, distribution, habitat, elevation, and specimens deposited at Brigham Young University are included in the discussion of each species. Maps showing the state distribution of each listed or candidate plant are also provided. New combinations include *Dalea flavescens* (Wats.) Welsh var. *epica* (Welsh) Welsh & Chatterley and *Schoenerambe suffrutescens* (Rollins) Welsh & Chatterley.

As a result of the Endangered Species Act of 1973, a list of proposed endangered and threatened plant species was compiled under the direction of the Smithsonian Institution. The Smithsonian list was published in 1975 (Greenwalt and Gehringer 1975), and since that time information concerning rare plants in the United States has continued to accumulate. Available information concerning the rare plants of Utah has steadily increased. A few months following publication of the Smithsonian list a critical examination of each rare taxon found in Utah was also published (Welsh, Atwood, and Reveal 1975). Data from this more detailed and concentrated survey of rare Utah flora was incorporated into the proposed federal rulemaking published in 1976 by the director of the Fish and Wildlife Service (Greenwalt 1976). Since then two additional publications have attempted to evaluate and summarize the status of rare plants in Utah according to the most up-to-date information. A reevaluation of Utah's endangered and threatened plants was published in the *Great Basin Naturalist* (Welsh 1978), and an illustrated manual was published by the U.S. Fish and Wildlife Service (Welsh and Thorne 1979). Since that time eight species occurring in Utah have been determined as threatened or endangered, and several others are in the final stages of the listing process.

In December 1980 a review of plant taxa considered for listing as endangered or threatened species was published in the Federal Register by the acting director of the U.S. Fish and Wildlife Service (Lamberton 1980). This publication placed species in categories indicating their readiness for listing. Category 1 plants were those species for which the Service had sufficient information to support the appropriateness of their being listed as threatened or endangered. Category 2 plants were those species that required further biological research and field study to determine the appropriateness of their being listed. Category 3 plants were those species no longer being considered for listing as endangered or threatened. There were three subheadings in this category. 3A plants were taxa considered probably extinct. 3B plants were those with unsure taxonomic status. 3C plants were those taxa that had proven to be more widespread than originally believed, or that were no longer subject to any threats. In November 1983 an updated list with current status evaluations was published in the Federal Register by the assistant secretary of Fish and Wildlife and Parks (Arnett 1983).

It is not the purpose of this paper to duplicate the information previously presented in the literature. However, five years have passed since the last publication summarizing or evaluating the status of Utah's rare plants, including those which by statute are considered threatened or endangered. Since that time new taxa have been described from the state, and their status has not been considered. Several major rare plant inventories have also been conducted within the state,

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TABLE 1. County distribution of Utah's rare plants.

Name	Distribution
Arctomecon humilis (L)	Washington
Asclepias cutleri (2)	Grand, San Juan
Asclepias welshii (1)	Kane
Astragalus ampullarius (2)	Kane, Washington
Astragalus barnebyi (2)	Garfield, Wayne
Astragalus cronquistii (1)	San Juan
Astragalus deserticus (2)	Sanpete (?), Utah
Astragalus equisolensis (2)	Uintah
Astragalus hamiltonii (1)	Uintah
Astragalus harrisonii (2)	Wayne
Astragalus iselyi (1)	Grand, San Juan
Astragalus lentiginosus var. *ursinus* (2°)	Iron
Astragalus montii (1)	Sanpete, Sevier
Astragalus perianus (L)	Garfield, Iron, Kane, Piute
Astragalus sabulosus (2)	Grand
Astragalus striatiflorus (2)	Kane, Washington
Astragalus subcinereus var. *basalticus* (2)	Emery, Sevier
Astragalus uncialis (2)	Millard
Castilleja aquariensis (2)	Garfield, Wayne
Castilleja revealii (1)	Garfield, Iron
Cirsium virginensis (2)	Washington
Coryphantha missouriensis var. *marstonii* (2)	Garfield, Kane
Cryptantha barnebyi (1)	Uintah
Cryptantha compacta (1)	Beaver, Millard, Tooele
Cryptantha creutzfeldtii (2)	Carbon, Emery
Cryptantha elata (2)	Grand
Cryptantha jonesiana (2)	Emery
Cryptantha ochroleuca (1)	Garfield
Cuscuta warneri (2°)	Millard
Cycladenia humilis var. *jonesii* (1)	Emery, Garfield, Grand
Cymopterus beckii (2)	Wayne
Cymopterus higginsii (1)	Kane
Cymopterus minimus (2)	Garfield, Iron, Kane
Dalea flavescens var. *epica* (2)	Garfield, San Juan
Draba maguirei var. *burkei* (2)	Box Elder, Weber
Echinocereus engelmannii var. *purpureus* (L)	Washington
Echinocereus triglochidiatus var. *inermis* (L)	San Juan
Epilobium nevadense (2)	Millard, Washington
Erigeron cronquistii (1)	Cache
Erigeron kachinensis (2)	San Juan
Erigeron maguirei var. *maguirei* (1)	Emery
Erigeron maguirei var. *harrisonii* (2)	Wayne
Erigeron mancus (2)	Grand, San Juan
Erigeron proselyticus (1)	Iron, Kane
Erigeron sionis (2)	Kane, Washington
Erigeron untermannii (2)	Duchesne
Eriogonum ammophilum (1)	Millard
Eriogonum arctioides (1)	Garfield
Eriogonum cronquistii (2)	Garfield
Eriogonum humivagans (2)	San Juan
Eriogonum lancifolium (2)	Carbon, Emery
Eriogonum loganum (2)	Cache, Morgan
Eriogonum natum (1)	Millard
Eriogonum smithii (1)	Emery
Eriogonum soredium (2)	Beaver
Festuca dasyclada (2)	Emery, Sanpete, Wasatch
Gaillardia flava (2)	Emery, Grand
Gilia caespitosa (2)	Wayne
Glaucocarpum suffrutescens (1)	Uintah
Hedysarum occidentale var. *canone* (1)	Carbon, Emery
Heterotheca jonesii (2)	Garfield, Kane, Washington
Hymenoxys depressa (2)	Duchesne, Emery, Sevier
Hymenoxys helenioides (2)	Emery, Garfield, Sanpete, Sevier
Lepidium barnebyanum (1)	Duchesne
Lepidium montanum var. *neeseae* (2)	Garfield
Lepidium montanum var. *stellae* (2)	Kane
Lepidium ostleri (1)	Beaver
Lesquerella tumulosa (1)	Kane
Lomatium latilobum (2)	Grand, San Juan
Mentzelia argillosa (2)	Sanpete, Sevier
Najas caespitosus (2°)	Sevier
Oenothera acutissima (2)	Daggett, Uintah
Pediocactus despainii (2)	Emery
Pediocactus winkleri (2)	Wayne
Penstemon atwoodii (2)	Garfield, Kane
Penstemon bracteatus (1)	Garfield
Penstemon compactus (2)	Cache
Penstemon concinnus (2)	Beaver, Iron, Millard
Penstemon goodrichii (2)	Duchesne, Uintah
Penstemon grahamii (1)	Uintah
Penstemon leptanthus (2)	Sanpete
Penstemon nanus (2)	Beaver, Millard
Penstemon parvus (2)	Garfield, Piute
Penstemon scariosus var. *albifluvis* (1)	Uintah
Penstemon tidestromii (2)	Juab, Sanpete
Penstemon wardii (2)	Sanpete, Sevier
Phacelia argillacea (L)	Utah
Phacelia indecora (2)	Emery, San Juan, Wayne
Primula maguirei (1)	Cache
Psoralea epipsila (2)	Kane
Psoralea pariensis (1)	Garfield, Kane
Psorothamnus polyadenius var. *jonesii* (2)	Emery
Ranunculus acriformis var. *aestivalis* (2)	Garfield
Sclerocactus glaucus (L)	Duchesne, Uintah, San Juan
Sclerocactus pubispinus (2)	Beaver, Juab, Millard, Sevier, Tooele
Sclerocactus wrightiae (L)	Emery, Kane, Wayne
Selaginella utahensis (2)	Washington

Table 1 continued.

Name	Distribution
Senecio dimorphophyllus var. *intermedius* (2)	San Juan, Sanpete
Silene petersonii var. *minor* (1)	Garfield, Iron
Silene petersonii var. *petersonii* (2)	Garfield, Sanpete
Sphaeralcea caespitosa (2)	Beaver, Millard
Sphaeralcea psoraloides (2)	Emery, Wayne
Sphaeromeria capitata (2)	Garfield
Sphaeromeria ruthiae (2)	Washington
Swertia gypsicola (2)	Millard
Thelypodiopsis argillacea (1)	Uintah
Thelypodiopsis barnebyi (2)	Emery
Townsendia aprica (1)	Emery, Sevier
Trifolium andersonii var. *friscanum* (1)	Beaver, Millard
Xylorhiza cronquistii (2)	Kane

adding significantly to the knowledge of rare plant distribution of the region. Surveys funded by agencies of the federal government, including studies of M-X related sites in western Utah, oil-shale lands in the Uinta Basin, and inventories in portions of southeastern Utah have added important data. The concerted effort of active individual botanists during the past few years has also been productive. Because of these activities, additional information has been generated that makes desirable further discussion of Utah's potentially threatened or endangered plant species.

No previous discussion has included a summary and update of information concerning those species that have been officially listed from the state. This information is included below. Following the discussion of officially listed taxa, rare plant species being considered for listing are discussed. Taxa that have been considered for listing but were downgraded to category 3 species in the November 1983 Federal Register are discussed at the end of the article.

UTAH'S FEDERALLY LISTED SPECIES

Eight taxa known from Utah are currently included on the federal list of endangered and threatened species. Five of the plants are species of cactus. The other three include a milkvetch, a poppy, and a phacelia. These taxa are some of the state's most rare and endangered plants.

Under the provisions of the Endangered Species Act, protection is provided to any species threatened by (1) the destruction or modification of its habitat, (2) overutilization for commercial or scientific purposes, (3) disease or predation, (4) the inadequacy of existing regulatory mechanisms, and (5) other man-made factors. Two listing classifications are provided. The term *endangered* is given to a species in danger of extinction through all or a significant portion of its range. The term *threatened* is applied to species that are likely to become endangered in the foreseeable future.

To ensure the proper protection of threatened and endangered species, the Endangered Species Act regulates interstate and foreign commerce of protected plants and, perhaps most importantly, provided financial assistance for scientific studies, managerial activities, and land acquisition to ensure the continued existence of rare taxa.

A brief discussion of each officially listed species is given below, including status (threatened or endangered), a discussion of rarity, known distribution, habitat, and elevation. Collections deposited at BRY are listed, including the date of collection, county, township and range, collectors, and collection number. Distribution maps are also included. Figure 1 shows the distribution of officially listed species in the state of Utah by township and range.

Arctomecon humilis Cov.
Map 1

Family: Papaveraceae.
Federal status: endangered.

The dwarf bear poppy is known only from Washington County, Utah. It is perhaps the most endangered of the plants in Utah. Populations occur near St. George in areas where the soil has a high gypsum content. Their proximity to a rapidly expanding city and their existence on lands frequented by off-road vehicles places the continued existence of the species in danger. Recently the U.S. Fish and Wildlife Service has developed a recovery plan for this taxon, and the state of Utah has initiated steps to protect the species. Vegetative types associated with the species are salt desert or warm desert shrub communities. Substrate is clay gypsiferous soils of the Moenkopi Formation. Elevation ranges from 2500 to 2880 feet.

WASHINGTON COUNTY: T43S, R17W, JW Harrison 32-124 (1932); T42S, R15W, WP Cottam 7238 (1937); T43S, R15W, A Terril (1961); T43S, R16W, ND Atwood 1704 (1969); T43S, R15W, SL Welsh & ND Atwood 9695 (1970); T43S, R15W, LC Higgins 4210 (1971); T43S, R16W, D Atwood 6590 (1976); T43S, R16W, D Atwood (1976); T43S, R16W, RK Gierisch 4266 (1978); T43S, R16W, SL Welsh 20388 (1981); T43S, R16W, LC Higgins & BT Welsh 13415 (1983); T43S, R16W, LC Higgins & BT Welsh 13423 (1983); T43S, R15W, E Neese 12896 (1983).

Astragalus perianus Barneby

Map 2

Family: Fabaceae.
Federal status: threatened.

The Rydberg milkvetch was known originally from Piute and Garfield counties. In 1981 Barneby annotated several collections previously designated as *A. serpens* to *A. perianus*, extending the known range of this rare taxon into Iron and Kane counties. The Piute County collections are all from the Tushar Mountains, near Bullion Creek. All the Garfield County collections are from near Mt. Dutton. To ensure protection of the species, the U.S. Forest Service developed a management plan that was signed in 1983. Two monitoring stations were established, one near the type locality and one on Mt. Brigham. A recovery plan is currently in the review stage. This high elevation milkvetch occurs in alpine, aspen, grass-sedge meadow, and mixed conifer woodland community types. Substrates include tertiary igneous gravels, volcanic ash, rocky loam, and clay soils. Elevational range extends from 10,000 to 11,000 feet.

GARFIELD COUNTY: T32S, R3W R & D Foster 5408 (1977); T32S, R3W, JR Murdock s.n. (1975); T32S, R3W, SL Welsh & JR Murdock 12849, 12849b (1975); T32S, R3W, D Atwood 8195 (1981); T32S, R3W, SL Welsh & K Taylor 14454 (1976); T32S, R3W, R & D Foster (1977). IRON COUNTY: T34S, R7W, R & D Foster 4230 (1977); T35S, R7W, R Foster 5586 (1977); T34S, R7W, R & D Foster 4737 (1977). KANE COUNTY: T37S, R2W, R & D Foster 4440 (1977). PIUTE COUNTY: T28S, R5W, SL Welsh & J Henroid 18142 (1978); T28S, R4W, D Atwood 7397 (1979); T27S, R2W, L C Higgins 1155A (1967); T28S, R5W, D Atwood 8045 (1981).

Echinocereus engelmannii (Parry) Rumpler var. *purpureus* L. Benson

Map 3

Family: Cactaceae.
Federal status: endangered.

The purple-spined hedgehog cactus is known from St. George, north to Veyo and east to Leeds and Hurricane in Washington County. Habitat for this variety of the hedgehog cactus includes the blackbrush-ephedra and Mohave Desert vegetation types, where it grows in sandy pockets of the Navajo Sandstone Formation and other substrates. Elevation ranges from 3100 to 3700 feet.

WASHINGTON COUNTY: T42S, R15W, L Benson 13637, POM (1949); T42S, R16W, D Ross 6 (1982); T42S, R15W, D Ross 4 (1982); T41S, R13W, D Ross 2 (1982); T41S, R13W, D Ross 3 (1982); T40S, R16W, D Ross 1 (1982); T42S, R15W, J Anderson (1982); T42S, R15W, J Anderson (1982); T42S, R15W, D Atwood 5096 (1973); T42S, R16W, SL Welsh 20389 (1981); T41S, R13W, D Ross 5 (1982).

Echinocereus triglochidiatus Engelm. var. *inermis* (K. Schum) Rowl.

Map 4

Family: Cactaceae.
Federal status: endangered.

The spineless hedgehog cactus occurs in San Juan County, Utah, but is also known from Colorado. Two collections of the species are deposited at BRY and come from the La Sal Mountains. The cactus grows in pinyon-juniper–galleta grass or pinyon-juniper–*Yucca baccata*–blacksage community types. This plant prefers sites with very shallow, rocky soil, usually less than six inches deep. It is commonly found along edges of sandstone outcrops or exposed sandstone slabs belonging to the Brushy Basin and Salt Wash members of the Morrison Formation. A management plan has been developed for this species, and a monitoring station was established in the La Sals in 1980. Elevation ranges from 5000 to 8000 feet.

SAN JUAN COUNTY: T27S, R24E, SL Welsh, D Atwood 9933 (1970); T27S, R23E, RM Thompson s.n. (1979).

Pediocactus sileri (Engelm.) L. Benson

Map 5

Family: Cactaceae.
Federal status: endangered.

The Siler pincushion cactus is known from near Fredonia in Mohave and Coconino counties, Arizona, and from southeast of St. George in Washington County, Utah. Habitat for the species includes an Atriplex-ephedra-Cowania vegetative community. It grows in clay soils of the Moenkopi Formation.

WASHINGTON COUNTY: T43S, R15W, SL Welsh and AH Barnum 12712 (1975); T43S, R11W, E Neese 12879 (1983); T43S, R14W, E Neese 12902 (1983).

Phacelia argillacea Atwood
Map 6

Family: Hydrophyllaceae.
Federal status: endangered.

The clay phacelia is known only from Utah County. Originally collected by Marcus E. Jones in 1883 and 1894, this phacelia was not recognized at specific level until 1975. There are no known collections of the plant for the period from 1894 until 1971, when Duane Atwood rediscovered the population in Spanish Fork Canyon. Two populations of this rare plant exist. The type locality occurs on the east side of Highway 6. Recently an additional and larger population was discovered on the west side of the highway. Habitat for the clay phacelia is an *Agropyron* community on shale outcrops of the Green River Formation. Elevation is approximately 6600 feet.

UTAH COUNTY: T11S, R8E, ME Jones s.n. (1883); T6S, R12W, ME Jones 5591 (1894); T10S, R6E, ND Atwood et al. 3091, Holotype (1971); T10S, R6E, SL Welsh & K Taylor 15277, 15047, 15047A (1977); T10S, R6E, F Smith, E Neese & J Trent 1722 (1982).

Sclerocactus glaucus (K. Schum) L. Benson
Map 7

Family: Cactaceae.
Federal status: threatened.

The Uinta Basin hookless cactus occurs in Colorado as well as Duchesne, Uintah, and San Juan (?) counties in Utah. Habitat includes salt desert shrub and shrub-grass communities on terrace gravels and commonly on clays of the Uinta Formation. Elevation extends from 4700 to 5800 feet. Classification of cacti has long been difficult, and this genus is no exception. The straight-spined *Sclerocactus glaucus* has been known in Utah primarily from the Uinta Basin. However, a straight-spined plant was recently collected in San Juan County, east of Hite. Current study of Utah's collections (Welsh, in press) questions the appropriateness of species designation for this straight-spined phase of *Sclerocactus*. Possibly straight spines in this genus are not more important taxonomically than spineless phases of other plants scattered through spined taxa elsewhere in the Cactaceae. It may be that *Sclerocactus glaucus*, in Utah, should be placed within a more broadly based concept of another species.

DUCHESNE COUNTY: T4S, R1W, UBM, SL Welsh & E Neese 18303 (1979); T11S, R17E, E Neese & S White 8654 (1980); T4S, R1W UBM, S Welsh & E Neese 18306 (1979); T3S, R6W, UBM, SL Welsh 18512A (1979). UINTAH COUNTY: T7S, R20E, E Neese & BT Welsh 7277 (1979); T11S, R18E, E Neese 4487 (1978); T9S, R19E R Foster 7588 (1979); T8S, R20E, Welsh & Neese 18340 (1979); T9S, R20E, E & J Neese 7584 (1979); T8S, R20E, SL Welsh & E Neese 18324 (1979); T11S, R19E, E Neese & S White 8652 (1980); T11S, R18E E Neese & S White 8655 (1980); T7S, R20E, Neese & B Welsh 7279 (1979); T11S, R17E, E Neese & S White 8653 (1980); T4S, R1W UBM, 7279 (1979); T11S, R17E, E Neese & S White 8653 (1980); T4S, R1W UBM, Welsh & Neese 18307, 18308, 18309, 18309A (1979). SAN JUAN COUNTY: T35S, R15E, SL, BT, ML Welsh 22187 (1983).

Sclerocactus wrightiae L. Benson
Map 8

Family: Cactaceae.
Federal status: endangered.

The Wright fishhook cactus occurs in Emery and Wayne counties. The greatest number of collections come from Wayne County, where populations of the plant occur near Factory Butte and North Caineville Mesa. Habitat includes salt desert shrub, shrub-grass, and juniper communities on Mancos Shale, Dakota, Morrison, Summerville, and Entrada formations. Elevational range extends from 4800 to 6100 feet.

EMERY COUNTY: T24S, R6E, Neese & White 7315 (1979); T24S, R6E, E Neese & K Mutz 11428 (1982); T26S, R11E, Neese & Thorne 7177, 7177A (1979); T23S, R6E, JG Harris 657 (1980). WAYNE COUNTY: T27S, R9E, KD Heil (1978); T27S, R9E, KD Heil (1978); T29S, R11E, KD Heil (1976); T30S, R7E, D Atwood & S Goodrich 8632 (1982); T27S, R9E, KD Heil (1978); T27S, R9E, S, E, & M Welsh 16704, 16723 (1978); T27S, R9E, S Welsh, K Taylor, F Peabody 13094 (1976).

PLANTS CURRENTLY UNDER REVIEW

In December 1981 the Utah Native Plant Society appointed a committee to review information accumulated during the past collecting season. From that review recommendations were made concerning the status of Utah's rare plant species. Taxa were placed in categories based on priorities for listing. Those species considered most threatened were placed in the highest category, and those to which the threat was not as critical were placed in lower categories. In each year since 1981, the Utah Native Plant Society has

Table 2. Utah's rare plants by county.

Beaver
Cryptantha compacta
Eriogonum soredium
Lepidium ostleri
Penstemon concinnus
Sclerocactus pubispinus
Sphaeralcea caespitosa
Trifolium andersonii var. *friscanum*

Box Elder
Draba maguirei var. *burkei*

Cache
Erigeron cronquistii
Eriogonum loganum
Penstemon compactus
Primula maguirei

Carbon
Eriogonum lancifolium
Cryptantha creutzfeldtii
Hedysarum occidentale var. *canone*

Daggett
Oenothera acutissima

Duchesne
Erigeron untermannii
Hymenoxys depressa
Lepidium barnebyanum
Penstemon goodrichii
Schlerocactus glaucus

Emery
Astragalus subcinereus var. *basalticus*
Cryptantha creutzfeldtii
Cryptantha jonesiana
Cycladenia humilis var. *jonesii*
Erigeron maguirei var. *maguirei*
Eriogonum lancifolium
Eriogonum smithii
Festuca dasyclada
Gaillardia flava
Hedysarum occidentale var. *canone*
Hymenoxys depressa
Hymenoxys helenioides
Pediocactus despainii
Phacelia indecora
Psorothamnus polyadenius var. *jonesii*
Sclerocactus wrightiae
Sphaeralcea psoraloides
Thelypodiopsis barnebyi
Townsendia aprica

Garfield
Astragalus barnebyi
Astragalus perianus
Castilleja aquariensis
Castilleja revealii
Coryphantha missouriensis var. *marstonii*
Cryptantha ochroleuca
Cycladenia humilis var. *jonesii*

Table 2 continued.

Cymopterus minimus
Dalea flavescens var. *epica*
Eriogonum aretioides
Eriogonum cronquistii
Heterotheca jonesii
Hymenoxys helenioides
Lepidium montanum var. *neeseae*
Penstemon atwoodii
Penstemon bracteatus
Penstemon parvus
Psoralea pariensis
Ranunculus acriformis var. *aestivalis*
Silene petersonii var. *minor*
Silene petersonii var. *petersonii*
Sphaeromeria capitata

Grand
Asclepias cutleri
Astragalus iselyi
Astragalus sabulosus
Cryptantha elata
Cycladenia humilis var. *jonesii*
Erigeron mancus
Gaillardia flava
Lomatium latilobum

Iron
Astragalus lentiginosus var. *ursinus*
Astragalus perianus
Castilleja revealii
Cymopterus minimus
Erigeron proselyticus
Penstemon concinnus
Silene petersonii var. *minor*

Juab
Penstemon tidestromii
Sclerocactus pubispinus

Kane
Asclepias welshii
Astragalus ampullarius
Astragalus perianus
Astragalus striatiflorus
Coryphantha missouriensis var. *marstonii*
Cymopterus higginsii
Cymopterus minimus
Erigeron proselyticus
Erigeron sionis
Heterotheca jonesii
Lepidium montanum var. *stellae*
Lesquerella tumulosa
Penstemon atwoodii
Psoralea epipsila
Psoralea pariensis
Xylorhiza cronquistii

Millard
Astragalus uncialis
Cryptantha compacta
Cuscuta warneri
Epilobium nevadense

Table 2 continued.

Erigonum ammophilum
Eriogonum natum
Penstemon concinnus
Sclerocactus pubispinus
Sphaeralcea caespitosa
Swertia gypsicola
Trifolium andersonii var. *friscanum*

Morgan
Eriogonum loganum

Piute
Astragalus perianus
Penstemon parvus

Rich
Eriogonum loganum

San Juan
Asclepias cutleri
Astragalus cronquistii
Astragalus iselyi
Dalea flavescens var. *epica*
Echinocereus triglochidiatus var. *inermis*
Erigeron kachinensis
Erigeron mancus
Eriogonum humivagans
Lomatium latilobum
Phacelia indecora
Sclerocactus glaucus
Senecio dimorphophyllus var. *intermedius*

Sanpete
Astragalus desereticus
Astragalus montii
Festuca dasyclada
Hymenoxys helenioides
Mentzelia argillosa
Penstemon leptanthus
Penstemon tidestromii
Penstemon wardii
Senecio dimorphophyllus var. *intermedius*
Silene petersonii var. *petersonii*

Sevier
Astragalus montii
Astragalus subcinereus var. *basalticus*
Hymenoxys depressa
Hymenoxys helenioides
Mentzelia argillosa
Najas caespitosus
Penstemon wardii
Sclerocactus pubispinus
Townsendia aprica

Tooele
Cryptantha compacta
Sclerocactus pubispinus

Uintah
Astragalus equisolensis
Astragalus hamiltonii

Table 2 continued.

Cryptantha barnebyi
Glaucocarpon suffrutescens
Oenothera acutissima
Penstemon goodrichii
Penstemon grahamii
Penstemon scariosus var. *albifluvis*
Sclerocactus glaucus
Thelypodiopsis argillacea

Utah
Astragalus desereticus
Phacelia argillacea

Wasatch
Festuca dasyclada

Washington
Arctomecon humilis
Astragalus striatiflorus
Cirsium virginensis
Echinocereus engelmannii var. *purpureus*
Epilobium nevadense
Erigeron sionis
Heterotheca jonesii
Selaginella utahensis
Sphaeromeria ruthiae

Wayne
Astragalus barnebyi
Astragalus harrisonii
Castilleja aquariensis
Cymopterus beckii
Erigeron maguirei var. *harrisonii*
Gilia caespitosa
Pediocactus winkleri
Phacelia indecora
Sclerocactus wrightiae
Sphaeralcea psoraloides

reviewed and reevaluated the status of rare plants in Utah according to new information accumulated during the previous field season. In 1983 and 1984 the society adopted the same terminology used by the U.S. Fish and Wildlife Service in the Federal Register.

The discussion of each taxon in this paper includes the recommendations made by the Utah Native Plant Society where they differ from the federal recommendations. The November 1983 Federal Register is used for current federal categories, and recommendations from the 1984 meeting of the Utah Native Plant Society are utilized. Current information based on the most recent collection data for each taxon is presented. Taxa that have been named from Utah since 1978 are discussed in more detail than those species included on previous lists. Their original citations are also given. However, some discussion of the following items is attempted for each species: common name, federal and state recommendations, distribution and rarity, habitat, and elevational range. A list of collection data from specimens deposited in the herbarium of Brigham Young University is also given for each species, including year of collection, county, township and range, collector, and collection number. Maps showing the generalized localities and patterns of state distribution for each species are included.

Table 1 lists plant species officially designated threatened or endangered, as well as those currently under review, and gives the counties of occurrence. Table 2 lists Utah counties and the species known to occur in each. The numbers in parentheses indicate whether the plant is considered a category 1 or category 2 species. Figure 2 shows the distribution of candidate threatened or endangered species by township and range.

Asclepias cutleri Woodson
Map 9

Family: Asclepiadaceae.
Federal designation: threatened, category 2.

The Cutler milkweed is known in Utah from four collections at different localities in Grand and San Juan counties. It also occurs in northeastern Arizona. It grows in sandy soil and dunes in warm desert shrub and juniper communities. Associated plants are blackbrush, cliff rose, and Utah juniper. Elevation for the species ranges from 4300 to 5500 feet.

GRAND COUNTY: T26S, R21E, WP Cottam 5799 (1935). SAN JUAN COUNTY: 43S, 15E, BF Harrison 11967 (1952); T40S, R22E, ML Conrad, Morris, Dunn 6656 (1973); T40S, R22E, NH & PK Holmgren, and RC Barneby 8795 (1978).

Asclepias welshii N. & P. Holmgren
Map 10

Family: Asclepiadaceae.
Citation: Brittonia 31:110–114. 1979.
Federal designation: endangered, category 1.

The Welsh milkweed is a recently named species with a severely restricted distribution, known only from Kane County, Utah. There is sufficient information in existence to support the appropriateness of its being officially listed. The Welsh milkweed is a distinctive species with no obvious close relatives. Its habitat is the Coral Pink Sand Dunes, which consist chiefly of active and inactive quartz sand dunes. The elevational range extends from 5800 to 6400 feet. Plants are locally common within the habitat range. All known population locations occur on land administered by the Bureau of Land Management. However, portions of state and privately owned lands adjoin the present habitat areas. The habitat area is utilized for recreational activities, especially by off-road vehicles, and unregulated use could prove a threat to the species.

KANE COUNTY: T43S, R7W, AH Barnum 1323 (1964); T43S, R7W, SL and SL Welsh 9428 (1969); T43S, R7W, SL Welsh et al. 14217 (1976); T43S, R7W, N and P Holmgren 9009, Isotype (1978); T43S, R7W, NH Holmgren 9035 (1978); T43S, R7W, E & JE Neese 9624 (1980).

Astragalus ampullarius Wats.
Map 11

Family: Fabaceae.
Federal designation: threatened, category 2.

The Gumbo milkvetch is known only from southern Utah and adjacent Arizona, where it occurs near the Cockscomb to west of Kanab in Kane County and southeast of Motoqua in Washington County. This species of milkvetch grows on the Chinle and Tropic shale formations in a mixed desert shrub and scattered juniper community type. Elevational range extends from 3200 to 5400 feet.

KANE COUNTY: T43S, R6W, Mrs. Ellen Powell Thompson, s.n. Type (1872); southern Utah, Dr. E Palmer, s.n. (1877); southern Utah, Johnson, s.n. (1871); T43S, R6W, B Olson 19 (1970); T43S, R6W, WW Patton 132 (1970); T43S, R7W, SL Welsh and D Atwood 9709, 9710 (1970); T43S, R6W, SL Welsh and D Atwood 9720 (1970); T43S, R6W, ND Atwood 4599 (1973); T42S, R11/2W, ND Atwood 4602 (1973); T43S, R11/2W, ND Atwood 4664 (1973); T43S, R6W, RK Giersch 4280 (1978); T43S, R2W, NH Holmgren et al. 9141 (1979). WASHINGTON COUNTY: T43S, R15W, Ogden s.n. (1941); T42S, R11W, ND Atwood 5140 (1973); T41S, R17W, D Atwood 6586 (1976); T41S, R17W, LC Higgins & D Atwood 13683 (1983).

Astragalus barnebyi Welsh & Atwood
Map 12

Family: Fabaceae.
Federal recommendation: threatened, category 2.

The Barneby milkvetch is a rare species restricted to Garfield (where it occurs in three locations) and Wayne (where it occurs on

North Cainville Mesa) counties. It grows in a pinyon-juniper and mixed desert shrub community on the Navajo Sandstone and Emery Sandstone Member of the Mancos Shale Formation and on the Carmel Formation. Elevational range of the species extends from 4300 to 6000 feet.

GARFIELD COUNTY: T36S, R12E, BF Harrison 11706 (1951); T36S, R4E, SL Welsh 1697 (1962); T36S, R4E, D Isely et al. 8732 (1964); T35S, R10E, SL Welsh 3994 (1965); T36S, R9E, A Cronquist 10046 (1965); T36S, R4E, ND Atwood 5218 (1973); T37S, R4E, R Foster 3592 (1977); T35S, R3E, E Neese & S White 2999 (1977). WAYNE COUNTY: T28S, R9E, SL Welsh et al. 13096, 13015 (1976); T28S, R9E, SL, E, & M Welsh 16719 (1978).

Astragalus cronquistii Barneby
Map 13

Family: Fabaceae.
Federal designation: endangered, category 1.

The Cronquist milkvetch is known from the Comb Wash area west of Bluff, from near Aneth in San Juan County, and from a recent collection by Barneby in Montezuma County, Colorado. Its habitat is the desert shrub community on low gravelly ridges of red sandstone belonging to the Cutler and Morrison formations. Its elevational range extends from 4000 to 4900 feet. Localities were visited and collections taken from at least three populations during recent field seasons, indicating populations are currently stable.

SAN JUAN COUNTY: T40S, R20E, Welsh 1505 (1961); T40S, R20E, Cronquist 9123 (1961); T40S, R20E, D Atwood 2464 (1970); T40S, R20E, SL Welsh & D Atwood 9967 (1970); T40S, R20E, D Atwood 7187 (1979); T40S, R20E, E Neese et al. 10231 (1981); T40S, R20E, K Mutz 8161 (1981); T41S, R20E, K Mutz & A Hreha 81-63 (1981); T41S, R25E, Goodrich and Atwood 18189 (1983); T40S, R20E, RC Barneby 17897 (1983).

Astragalus desereticus Barneby
Map 14

Family: Fabaceae
Federal designation: threatened, category 2.

Jones first collected the Deseret milkvetch in 1893 and Tidestrom reported it as common in 1909, but the species was not relocated until 1981, when it was discovered by Elizabeth Neese south of Thistle along Highway 89. The plant grows on sandy road cuts and red conglomerate slopes in sagebrush-juniper and mixed mountain brush community types. Elevational range extends from 5000 to 6500 feet. Numerous landslides and subsequent flooding near the town of Thistle during the winter of 1982–83 did not affect populations of the Deseret milkvetch. **Note:** Initial collections by Jones and Tidestrom were cited as "below Indianola" and "Indianola," respectively. Indianola is in Sanpete County, but the plants undoubtedly were taken in Utah County.

UTAH COUNTY: ME Jones, Paratype (1893); Tidestrom 2249, TYPE GH (1909); T10S, R3E, E Neese 10378 (1981); T10S, R3E, E Neese 10391 (1981); T10S, R3E, E Neese 10399 (1981); T10S, R3E, SL Welsh 20629 (1981); T10S, R3E, ME Lewis 7444 (1983).

Astragalus equisolensis Neese & Welsh
Map 15

Family: Fabaceae.
Citation: Rhodora 83: 457. 1981.
Federal designation: endangered, category 2.

Populations of this small perennial milkvetch occur in the vicinity of Horseshoe Bend east of the Green River and south of Vernal in Uintah County. The species grows on river terrace sands and gravels overlying the Duchesne River Formation in a mixed desert shrub community type. Known elevation extends from 4750 to 5200 feet.

UINTAH COUNTY: T7S, R22E, E Neese 4313, Paratype (1978); T6S, R22E, Neese et al. 7251, Paratype (1979); T6S, R21E, Neese et al. 7254, Paratype (1979); T6S, R22E, E Neese and SL Welsh 7380, Holotype (1979); T6S, R22E, E Neese and SL Welsh 8278, Paratype (1979); T7S, R22E, D Atwood 7576 (1980).

Astragalus hamiltonii C. L. Porter
Map 16

Family: Fabaceae.
Federal designation: threatened, category 1.

The Hamilton milkvetch was previously known only from west of the Green River in the northwestern quarter of Uintah County. However, several additional populations were discovered in 1982 near the Colorado border about 10 miles north of Bonanza. Habitat for the species is the pinyon-juniper and mixed desert shrub communities in sandy soil overlying the Duchesne River Formation. Elevational range extends from 5200 to 6350 feet.

UINTAH COUNTY: T5S, R21E, CL Porter 5313, Paratype (1950); T4S, R20E, B Untermann 15a (1955); T5S, R21E, SL Welsh 515 (1956); T5S, R21E, SL Welsh 1782 (1962); T4S, R20E, SL Welsh & G Moore 6755 (1967); T1N, R1E UBM, S Goodrich 5377 (1976); T3S, R21E, S

Goodrich 5681 (1976); T1N, R1E, UBM, S Goodrich 5701 (1976); T4S, R20E, NH Holmgren et al. 8756 (1978); T1N, R1E UBM, E Neese & JS Peterson 5803 (1978); T5S, R20E, E Neese & JS Peterson 5824 (1978); T5S, R21E, Welsh & Neese 18354 (1979); T3S, R21E, E Neese & B Welsh 7523 (1979); T4S, R20E, E Neese & B Welsh 7534 (1979); T5S, R19E, E Neese & B Welsh 7536 (1979); T3S, R21E, SL Welsh 19632 (1980); T8S, R25E, K Thorne & K Snyder 1679 (1982); T5S, R21E, K Thorne & C Fullmer 1756 (1982); T8S, R25E K Thorne & C Fullmer 1757 (1982); T5S, R19E, K Thorne 1863 (1982); T8S, R25E, K Thorne 1879 (1982); T5S, R21E, E Neese & K Snyder 11775 (1982); T8S, R25E, E Neese et al. 11813 (1982); T8S, R25E, F Smith et al. 1693 (1982); T1N, R2E UBM, E Neese and J Sinclear 15053 (1983); T1N, R1E UBM, E Neese 14129a (1983); T1N, R2E UBM, E Neese 14123 (1983).

Astragalus harrisonii Barneby

Map 17

Family: Fabaceae.
Federal designation: endangered, category 2.

The Harrison milkvetch was known historically only from near Fruita in Wayne County and occurs in the pinyon-juniper community on sandy slopes and outcrops of the Navajo formation. It has a known elevational range of 5600 to 6000 feet. This plant occurs near Hickman Bridge in Capitol Reef National Park, where trampling by tourists is a current threat. A large subpopulation was discovered in 1982 along the terrace above Hickman Bridge, away from human activity. Possibly no action is necessary for the protection of this plant, except monitoring. In 1983 a large population was discovered in the Purple Hills region of the Waterpocket Fold.

Wayne County: T29S, R6E, BF Harrison 7393 (1934); T29S, R6E, WP Cottam 9287 (1944); T29S, R6E, Barneby 13131, Isotype (1961); T29S, R6E, SL Welsh 5217, 5217b, Topotype (1966); T29S, R7E, K Harrison 1877 (1975); T29S, R6E, S Goodrich, SL Welsh 15641 (1981); T29S, R6E, SL Welsh 21065 (1982); T29S, R6E, E Neese 11312 (1982); T29S, R6E, D Atwood and S Goodrich 8622 (1982); T29S, R6E, SL and ER Welsh 21180 (1982).

Astragalus iselyi Welsh

Map 18

Family: Fabaceae.
Federal designation: endangered, category 1.

The Isely milkvetch is known from Grand and San Juan counties where it occurs on the La Sal Mountains and a few miles north to Onion Creek. Habitat for the plant is gypsiferous and seleniferous soils overlying the Paradox and Morrison formations in the pinyon-juniper community. Range of elevation for the species is from 5000 to 7600 feet.

Grand County: T26S, R21E, ME Jones (1913); T27S, R23E, J Pederson 23 (1967); T24S, R24E, SL Welsh 11929, 11929a (1973); T27S, R23E, SL Welsh 16389 (1977); T27S, R23E, SL Welsh 16395 (1978); T24S, R24E, D Atwood 7147 (1979). San Juan County: T27S, R23E, CS Schoener 75 (1971); T27S, R23E, S Daines 39 (1971); T27S, R23E, SL Welsh 10970, Holotype, Isotypes (1971); T27S, R23E, SL Welsh 19464 (1980); T27S, R23E, SL Welsh 19464g (1980); T27S, R23E, D Atwood 7470 (1980); T27S, R23E, D Atwood 7472 (1980); T27S, R23E, D Atwood 7473 (1980); T27S, R23E, K Mutz 81-56 (1981); T27S, R23E, SL Welsh 20842 (1981); T27S, R28E, D Atwood and B Thompson 8807 (1982); T26S, R23E, D Atwood et al. 8736 (1982).

Astragalus lentiginosus Dougl. ex Hook. var. *ursinus* (Gray) Barneby

Map 19

Family: Fabaceae.
Federal designation: endangered, category 2, possibly extinct.

The Bear Valley milkvetch was supposedly collected in 1877 by Dr. E. Palmer in Bear Valley, near Paragonah, northeastern Iron County. The type material deposited at NY notes the plant is abundant; however, there has been no collection made of the species since then. As a result of this plant's disappearance, no specific locality, elevation, or habitat information is known.

Iron (?) County: possibly in T33S, R8W, Dr. E. Palmer, Isotype-NY (1877).

Astragalus montii Welsh

Map 20

Family: Fabaceae.
Federal designation: endangered, category 1.

The Heliotrope milkvetch occurs at high elevations on Heliotrope Mountain in Sanpete County, on White Mountain in Sevier County, and on Ferron Mountain, where a large population was discovered by Bob Thompson in 1983. The plant grows on open outcrops of the Flagstaff Limestone formation near the timberline in the spruce-fir association. Elevation ranges from 11,000 to 11,200 feet. This taxon has been treated as a variety of *A. limnocharis* [as var. *montii* (Welsh) Isely]; however, it is distinctive in its larger purple-pink flowers with white wing tips. A proposed rulemaking is still in effect for this plant, and a management plan has been developed by the Forest Service to ensure protection of the species.

Sanpete County: T19S, R4E, SL and J Welsh 15404, Holotype (1977); T19S, R4Ek, ME Lewis 4312 (1976); T19S, R4E, ME Lewis 4775 (1977); T19S, R4E, D Atwood 8000 (1981). Sevier County: T21S, R5E, D Atwood 9132 (1982).

Astragalus sabulosus M.E. Jones

Map 21

Family: Fabaceae.
Federal designation: threatened, category 2.

The Cisco milkvetch is known only from Grand County, where it occurs near the towns of Cisco and Thompson, and in Court House Wash. This showy plant with large yellowish flowers occurs in the salt desert shrub community on hills and knolls of the Mancos Shale and Morrison formations. Elevational range of the species is from 4200 to 5200 feet.

Grand County: banks of Grand River, ME Jones, Isotype (1890); T21S, R20E, OA Beath (1940); T21S, R20E, SL Welsh 3888, 3888a, 3887, 4021 (1965); T21S, R23E, SL Welsh 13337, 13337a (1976); T21S, R23E, SL Welsh & K Taylor 14639, 14746 (1977); T21S, R20E, K Mutz & A Hreha 81-25 (1981); T21S, R23E, SL Welsh 20840 (1981); T24S, R20E, D Atwood and B Thompson 8809 (1982).

Astragalus striatiflorus Jones

Map 22

Family: Fabaceae.
Federal designation: threatened, category 2.

The escarpment milkvetch occurs in dune areas, on sandy terraces, in stream channels, and in sandy depressions on ledges in Kane and Washington counties. Its principal population is in the Coral Pink Sand Dunes. Elevational range for this sand-dwelling milkvetch extends from 4000 to 6300 feet.

Kane County: T42S, R5W, Ripley & Barneby 4815 (1942); T43S, R7 & 8W, ES Castle 108, 113 (1953); T42S, R7W, NH Holmgren et al. 2012 (1965); T43S, R7W, SL Welsh 5302 (1966); T40S, R1W, ND Atwood 3682 (1972); T43S, R1W, LC Higgins 3946 (1972); T43S, R7W, SL Welsh & KH Thorne 14688 (1977); T42S, R6W, R and D Foster 3973 (1977); T43S, R7W, SL Welsh & S Clark 15540, 15552 (1977).

Astragalus subcinereus A. Gray
var. *basalticus* Welsh

Map 23

Family: Fabaceae.
Citation: Great Basin Naturalist 38: 302. 1978.
Federal designation: threatened, category 2.

This variety of the silver milkvetch occurs on volcanic gravels in eastern Sevier and western Emery counties. The plants grow in pinyon-juniper and sparse ponderosa pine woods at an elevation extending from 6000 to 8000 feet. It differs from var. *subcinereus* in its narrower pods, generally larger flowers, and longer stems.

Emery County: T25S, R6E, SL Welsh 14788 (1977). Sevier County: T24S, R5E, SL Welsh et al. 6445, Paratype (1967); T24S, R5E, SL Welsh et al. 6447, Holotype (1967); T24S, R5E, SL Welsh, S Clark 16186 (1977); T24S, R5E, S White, G Moore 89 (1979); T24S, R5E, E Neese et al. 7632 (1979); T23S, R5E, R Foster 8282 (1979).

Astragalus uncialis Barneby

Map 24

Family: Fabaceae.
Federal designation: threatened, category 2.

The Currant milkvetch was previously known only from northeastern Nye County, Nevada, where it occurs along the foothills of the White Pine and Pancake ranges in sandy gullies and on gravelly dry knolls. Recently, however, this tiny milkvetch was discovered in Millard County between 15 to 30 miles southwest of Delta on abandoned beaches of calcareous gravels and silty clay soil. These records were made in 1981, and the plant is now included as one of Utah's rare species. In Utah it is most commonly associated with a shadscale-budsage community type, and its elevational range extends from 4600 to 5300 feet.

Millard County: T18S, R10W, SL Welsh 20312 (1981); T18S, R10W, SL Welsh 20619 (1981); T18S, R10W, E Neese & S Goodrich 10415 (1981); T18S, R10W, E Neese & S Goodrich 10416 (1981); T18S, R11W, E Neese & S Goodrich 10429 (1981); T18S, R11W, E Neese & S Goodrich 10438, 10439 (1981); T19S, R11W, S Goodrich 16527 (1982); T18S, R9W, BT Welsh 1310 (1982); T19S, R11W, R Kass and K Preston 801 (1982).

Castilleja aquariensis N. Holmgren

Map 25

Family: Scrophulariaceae
Federal designation: endangered, category 2.

The aquarius paintbrush is known only from the Boulder Mountain area on the Aquarius Plateau in Garfield County. One collection has been made just north of the county line in Wayne County. The plant occurs at high elevations (from 9600 to 1100 feet) in subalpine grassland and sagebrush meadows. It is eaten by livestock, and one principal population survives in an exclosure.

Garfield County: T32S, R2E, N. & P. Holmgren 4726, Isotype (1970); T31S, R2E, N. & P. Holmgren 8584 (1977); T31S, R2E, E Neese & S White 3584 (1977); T32S, R2E, ME Lewis 5915 (1979); T32S, R2E, D Atwood and B Thompson 7656, 7657 (1980); T32S, R1E, D Atwood & B Thompson 7658 (1980); T32S, R2E, D Atwood 9494, 9495 (1983). Wayne County: T31S, R2E, ME Lewis 6091 (1979).

Castilleja revealii N. Holmgren

Map 26

Family: Scrophulariaceae
Federal designation: endangered, category 1.

When the Reveal paintbrush was named in 1973, known distribution of the plant was restricted to the type locality near Bryce Canyon National Park in Garfield County. During the 1980 field season two additional populations were discovered, one approximately 30 miles north of Bryce Canyon on the Aquarius Plateau, and the other near Cedar Breaks National Monument in Iron County. Habitat for this paintbrush species is the ponderosa pine woodland in the gravelly soil of limestone outcrops. Elevational range extends from 7,500 to 10,000 feet.

Garfield County: T37S, R4W, Weight, Paratype (1931); T37S, R4W, Holmgren and Reveal 2017, Isotype (1965); T37S, R4W, R Graybosch 934 (1980); T32S, R1E, D Atwood & B Thompson (1980); T36S, R4½W, D Atwood 7921 (1981). Iron County: T36S, R9W, D Atwood & B Thompson 7675.

Cirsium virginensis Welsh

Map 27

Family: Asteraceae.
Citation: Welsh, SL. 1982. Great Basin Naturalist 42: 199–202.
Federal designation: threatened, category 2.

The Virgin thistle is a recently described species of this genus. It occurs near St. George in Washington County, and in Mohave County, Arizona. The plant does not appear to be closely allied to other groups of thistles represented in the state, and its relationships are unknown. It occurs in saline seeps and stream terraces in shadscale, creosote bush, mesquite, and hanging garden communities. Elevation ranges from approximately 2800 to 3100 feet.

Washington County: T42S, R15W, DH Galway 8470 (1935); T42S, R15W, DH Galway (1938); T42S, R15W, T Fillmore (1960); T43S, R17W, LC Higgins 836 (1966); T42S, R15W, LC Higgins 10998 (1977); T42S, R15W, SL Welsh and D Atwood 21052 (1982); T42S, R15W, BT Welsh 1383 (1982); T42S, R15W, SL Welsh 21234, Holotype (1982); T42S, R15W, LC Higgins 13155 (1982); T42S, R15W, LC Higgins 13752 (1983).

Coryphantha missouriensis (Sweet) Britt. & Rose var. *marstonii* (Clover) L. Benson

Map 28

Family: Cactaceae.
Federal designation: endangered, category 2.

The range of this species in Utah is thought to extend from northwest of Boulder in Garfield County to the east side of the Buckskin Mountains on the Kaibab Plateau in Kane County. However, the type, which was collected by Clover at Hell's Backbone in 1937, was not preserved. The neotype, from the Buckskin Mountains, Kane County, was collected by Benson in 1953 (Benson, L. 1982. The cacti of the United States and Canada) and is the only other known locality in Utah. No collection of this species has been made since 1953. Known habitat is on hillsides in the ponderosa pine, pinyon-juniper, and mixed shrub-grass communities at 5000 to 7000 feet elevation.

Cryptantha barnebyi Johnst.

Map 29

Family: Boraginaceae.
Federal designation: endangered, category 1.

The Barneby catseye is endemic to the white shale knolls of the Green River Formation in Uintah County between 5000 and 6000 feet elevation. Associated vegetative types include shadscale, greasewood, pinyon-juniper, mixed desert shrub, and sagebrush communities. The known distribution of this plant has been substantially enlarged by field work of recent seasons. Twenty-two collections of the species were made during the 1982 field season alone. Populations occur, however, in the area of Uintah County currently being considered for oil shale development.

Uintah County: T12S, R24E, Ripley & Barneby 8748, Holotype, GH (1947); T13S, R22E, NH Holmgren & JL Reveal 1858 (1965); T13S, R22E, LC Higgins 1584, 1586, 1587 (1968); T13S, R22E, ND Atwood 1562 (1968); T13S, R22E, LC Higgins 1599, 1601 (1968); T13S, R22E, LC Higgins 1884, 1877, 1887 (1969); T12S, R22E, E Neese & JS Peterson 4726 (1978); T11S, R24E, E Neese & JS Peterson 6101, 6104 (1978); T13S, R22E, E Neese & JS Peterson 6110 (1978); T12S, R22E, JS Peterson 1442 (1979); T12S, R23E, JS Peterson 1452 (1979); T13S, R23E, JS Peterson 1465 (1979); T12S, R22E, M Williams & D Atwood 80-138-4 (1980); T12S, R24E, E Neese & F Smith 11390 (1982); T12S, R24E, K Thorne & B Neely 1785 (1982); T11S, R25E, E Neese & C Fullmer 11470

(1982); T12S, R24E, K Thorne & B Neely 1787 (1982); T12S, R24E, K Thorne & B Neely 1790 (1982); T11S, R25E, E Neese & C Fullmer 11477 (1982); T13S, R25E, K Thorne & B Neely 1850 (1982); T12S, R20E, E Neese et al. 11547 (1982); T11S, R25E, E Neese 11925 (1982); T11S, R25E, E Neese & J Trent 11928 (1982); T12S, R25E, Kass and Trent 845 (1982); T11S, R25E, Kass and Trent 825 (1982); T12S, R25E, F Smith 1605 (1982); T12S, R24E, K Thorne 1731 (1982); T12S, R24E, B Neely and K Thorne 817, 824 (1982); T12S, R25E, Kass and Trent 837, 838 (1982); T12S, R25E, F Smith and K Syder 1613 (1982); T12S, R24E, Kass and Trent 847 (1982); T12S, R25E, F Smith and J Trent 1788 (1982); T12S, R25E, E Neese and J Trent 12365 (1982); T13S, R25E, E Neese and J Trent 12369 (1982).

Cryptantha compacta Higgins

Map 30

Family: Boraginaceae.
Federal designation: threatened, category 1.

The compact catseye inhabits gravelly loam slopes, ridges, and outcrops of limestone or Sevy Dolomite in shadscale, matchweed, and mixed shrub communities. Elevation is from 5000 to 6500 feet. Historical populations within or near the Desert Experimental Range in the southwestern portion of Millard county have been recently documented as viable. Recent field work has also extended the distributional range of the plant in Millard County to near Notch Peak and near Oak City; and in 1983 populations of the plant were located in Beaver and Tooele counties as well.

Beaver County: T26S, R19W, S Goodrich 18525, 18541 (1983). Millard County: Whitesage Valley, BF Harrison 6371 (1935); T25S, R18W, B Wood 102 (1964); T25S, R18W, RC Holmgren 501 (1966); T24S, R17W, RC Holmgren 521 (1966); T24S, R18W, LC Higgins 1462, 1613 (1968); T25S, R17W, SL Welsh 13313 (1976); T25S, R17W, K Ostler & D Anderson 1040, 1060 (1978); T24S, R17W, K Ostler & D Anderson 1124 (1978); T25S, R18W, K Ostler & D Anderson 1230 (1978); T25S, R18W, SL Welsh & M Chatterley 19574 (1980); T19S, R14W, C Fullmer 11 (1980); T16S, R4W, S Goodrich 14364 (1980); T16S, R4W, S Goodrich 15607 (1981); T18S, R4W, S Goodrich 15554 (1981); T19S, R14W, R Kass and S White 468 (1981); T24S, R17W, S Goodrich 16551 (1982); T25S, R17W, S Goodrich 16628 (1982); T23S, R16W, K Heil 1650 (1982); T24S, R17W, S Goodrich 16955 (1982); T25S, R17W, S Goodrich 16635 (1982); T25S, R17W, S Goodrich 16632, 16930 (1982); T19S, R14W, R Kass 296 (1982); T25S, R15W, S Goodrich 18729 (1983); T25S, R15W, S Goodrich 18727 (1983); T24S, R18W, S Goodrich 18688 (1983); T25S, R18W, K Heil 1650 (1983). Tooele County: T10S, R6W, S Goodrich 18884, 18894, 19067 (1983).

Cryptantha creutzfeldtii Welsh

Map 31

Family: Boraginaceae.
Citation: Welsh, SL. 1982. Great Basin Naturalist 42: 203–204.
Federal designation: none.
UNPS recommendation: threatened, category 2.

The Creutzfeldt catseye is a recently described species known from Carbon and Emery counties. It occurs on the Blue Gate Member of the Mancos Shale Formation below the coal measures of the Mesa Verde Group. Associated vegetative types include shadscale, pinyon-juniper, sagebrush, and saltbush communities. Elevational range extends from 6000 to 6700 feet.

Carbon County: T14S, R10E, L Arnold s.n. (1981). Emery County: T21S, R6E, SL Welsh 20470 Holotype (1981); T18S, R7E, J Allan 762 (1976); T21S, R6E, E Neese & S White 7362 (1979); T20S, R6E, D Atwood 7518 (1980); T22S, R6E, S White 15 (1979); T18S, R7E, J Allan 947 (1979); T21S, R6E, S White & G Moore 77 (1979); T20S, R6E, M Lewis 7411 (1982).

Cryptantha elata (Eastw.) Payson

Map 32

Family: Boraginaceae.
Federal designation: threatened, category 2.

The tall catseye is restricted to Grand County in Utah but also occurs in Mesa County, Colorado. It grows on the heavy clay soil of the Mancos Shale Formation in a mixed desert shrub community type. Elevational range extends from 4600 to 5500 feet.

Grand County: T22S, R24E, SL Welsh 6952 (1968); T22S, R24E, LC Higgins 1479, 1479a (1968).

Cryptantha jonesiana (Payson) Payson

Map 33

Family: Boraginaceae.
Federal designation: threatened, category 2.
UNPS recommendation: category 3C.

Distribution of the Jones catseye is limited to the San Rafael Swell in Emery County, where it occurs on clay soil barrens of the Moenkopi Formation. Habitat includes pinyon-juniper and mixed desert shrub communities. Elevational range of the species extends from 5200 to 6800 feet.

Emery County: San Rafael Swell, ME Jones (1914); T19S, R13E, ND Atwood 1301 (1968); T20S, R11E, LC Higgins & JL Reveal 1265 (1968); T21S, R12E, LC Higgins & JL Reveal 1275, 1299 (1968); T19S, R11E, LC Higgins 1308 (1968); T21S, R12E, LC Higgins 1322 (1968); T19S, R13E, ND Atwood 2418 (1970); T22S

R12E, S Daines 22 (1971); T22S, R12E, KD Kaneko 1 (1971); T22S, R12E, SL Welsh 10953 (1971); T20S, R11E, SL Welsh 10959, 10960 (1971); T22S, R12E, M Wright 57 (1971); T20S, R11E, S Daines 24 (1971); T20S, R11E, KD Kaneko 21 (1971); T20S, R11E, NH & PK Holmgren & RC Barneby 8779 (1978); T19S, R13E, Thorne & Neese 494 (1979); T19S, R14E, JG Harris 69 (1979); T24S, R10E, S Goodrich & D Atwood 16580 (1982); T22S, R12E, LC Higgins 13176 (1983).

Cryptantha ochroleuca Higgins
Map 34

Family: Boraginaceae.
Federal designation: endangered, category 1.
UNPS recommendation: category 2.

The yellow-white catseye is known only from Garfield County and is found growing on the pink limestone member of the Wasatch Formation in Red Canyon in the ponderosa and bristlecone pine zone. Its elevational range is from 6500 to 8000 feet. Collections from the area within the past two years indicate the populations are still viable.

Garfield County: T35S, R4½W, Higgins 1788 Holotype (1968); T35S, R4½W, JL & CG Reveal 1031 (1968); T35S, R4½W, ND Atwood 1879 (1969); T35S, R4½W, ND Atwood 1890 (1969); T35S, R4½W, ND Atwood 1891 (1969); T35S, R4½W, D Atwood 7627, 7631 (1980); T36S, R4½W, ND Atwood 7925 (1981).

Cuscuta warneri Yuncker
Map 35

Family: Cuscutaceae.
Federal designation: endangered, category 2, possibly extinct.

The Warner dodder is known only from the type collection, taken in the vicinity of Flowell, Millard County. The plant is parasitic on Phyla cuneifolia, a species uncommon in the Great Basin, but locally abundant near a temporary lake known as "The Sink," near Flowell. Mr. Lloyd Warner conducted a search of the type locality in 1984 with Kaye Thorne but was unable to locate the cuscuta, even though the *phyla* was common.

Millard County: ca T21S, R5W, L Warner, Isotype (1957).

Cycladenia humilis Benth. var. *jonesii* (Eastw.) Welsh & Atwood
Map 36

Family: Apocynaceae.
Federal designation: endangered, category 1.

There are five known populations of the Jones cycladenia. The type collection was discovered by ME Jones in 1914 and occurs in Emery County. It was rediscovered in 1979 and now an additional population on the San Rafael Desert in Emery County is also known. Two populations occur in Grand County, one in Castle Valley and the other near Onion Creek, northeast of Moab. In 1983 a fifth, disjunct population was discovered west of Waterpocket Fold in Garfield County. This beautiful and distinctive taxon grows on the Cutler, Summerville, and Chinle formations in salt desert shrub, ephedra-buckwheat, blackbrush, and scattered juniper communities. Elevational range extends from 4400 to 5970 feet.

Emery County: Jones, Isotype (1914); T22S, R13E, JG Harris 606 (1979); T22S, R13E, J Harris, S Welsh, E Neese 633 (1979); T22S, R13E, JG Harris 654 (1980); T22S, R13E, BT Welsh 350 (1980); T22S, TR13E, D Atwood 7449 (1980); T22S, R13E, JG Harris 694 (1980); T22S, R14E, E Neese 8700 (1980); T22S, R14E, E Neese 8713 (1980); T22S, R14E, E Neese 8714 (1980); T22S, R14E, JG Harris 807 (1980). Garfield County: T36S, R8E, BT Welsh, M Chatterley 1442, 1443 (1983). Grand County: T25S, R23E, SL Welsh 7013 (1968); T25S, R23E, SL Welsh, G Moore 7168 (1968); T25S, R23E, SL Welsh et al. 14754 (1977); T24S, R24E, D Atwood 7159 (1979); T24S, R24E, E Neese, SL Welsh 8767, 8768 (1980).

Cymopterus beckii Welsh & Goodrich
Map 37

Family: Apiaceae.
Federal designation: threatened, category 2.

Known distribution of the Beck cymopterus is restricted entirely to the Capitol Reef region of Wayne County. However, its full range is yet to be determined. The plant grows in sandy crevices along cliff bases of Navajo Sandstone at elevations extending from 5500 to 7000 feet.

Wayne County: T29S, R6E, BF Harrison 7392, Paratype (1934); T29S, R6E, DE Beck, Holotype (1938); T29S, R6E, S Goodrich & D Atwood 16564 (1982); T29S, R6E, SL & ER Welsh 21175d (1982); T29S, R6E, SL Welsh 21261 (1982); T29S, R6E, D Atwood, S Goodrich 8623 (1982).

Cymopterus higginsii Welsh
Map 38

Family: Apiaceae.
Federal designation: threatened, category 1.

The Higgins biscuitroot is pink flowered and is known only from Kane County from northwest of to several miles east of Glen Canyon City. It occurs on saline soils of the

Tropic Shale Formation in either desert or salt desert shrub communities. Elevation extends from 4200 to 4800 feet.

Kane County: T42S, R4E, D Atwood 3439, Paratype (1972); T42S, R2E, Atwood et al. 3493, Paratype (1972); T42S, R6E, Atwood 4549, Paratype (1973); T42S, R4E, SL Welsh 12740, Holotype (1975).

Cymopterus minimus (Mathias) Mathias
Map 39

Family: Apiaceae.
Federal designation: endangered, category 2.

This species of biscuitroot is known from Iron (near Cedar Breaks National Monument), Garfield, and Kane counties, where it occurs on the pink and white limestone of the Wasatch or Claron formations. It is associated with ponderosa pine, bristlecone pine, spruce-fir, and perhaps pinyon-juniper communities. The plant is similar to *Cymopterus purpureus* var. *rosei* and var. *purpureus*. It may only be a part of the *purpureus* complex, but it is currently recognized at the specific level. Elevational range of the plant is from 10,000 to 10,500 feet.

Garfield County: T35S, R4½W, JL & CG Reveal 1030 (1968); T36S, R6W, D Atwood, B Wood 5329 (1973); T36S, R4W, NH & PK Holmgren 8449 (1977); T35S, R1W, E Neese, S White 3848 (1977); T37S, R4W, R & D Foster 4798 (1977); T37S, R4W, D Atwood (1980); T35S, R4½W, D Atwood 7628 (1980); T36S, R4½W, D Atwood 7931 (1981); T34S, R1W, D Atwood 8165 (1981); T34S, R1W, S Goodrich 15664 (1981); T34S, R1W, ES Nixon 11584 (1982). Iron County: T36S, R9W, Mathias 723, Type-MO (no date); T36S, R9W, B Maguire 19027, non-BRY (1940); T36S, R9W, D Atwood & B Thompson 7673 (1980); T36S, R9W, J Anderson (1981); T35S, R9W, SL Welsh 21295 (1982). Kane County: T38S, R8W, D Atwood 7436 (1979); T38S, R9W, D Atwood, B Thompson 7693 (1980); T41S, R4½W, J Grimes 2034 (1981); T39S, R5W, D Atwood 7941 (1981).

Dalea flavescens (Wats.) Welsh var. *epica* (Welsh) Welsh & Chatterley comb. nov. [based on: *Dalea epica* Welsh Great Basin Nat. 31:90, 1971]
Map 40

Family: Fabaceae.
Federal designation: threatened, category 2.

Until recently there was only one known population of the Hole-in-the-rock prairie clover. It was located along the Hall's Crossing road southwest of Lake Powell in San Juan County. However, in 1983 the plant was also found growing in the dry wash sands of Ticaboo Canyon on the Garfield County side of Lake Powell and close to Hall's Crossing in San Juan County. This taxon is now combined in recognition of its relationship to *Dalea flavescens* (Wats.) Welsh, a Navajo Basin endemic, within whose range it occurs. The variety grows in sand dunes and on bedrock of the Navajo Sandstone Formation and is associated with a blackbrush-sagebrush community type. Elevation is from 3750 to 4800 feet.

Garfield County: T35½S, R13E, SL Welsh et al. 22034 (1983). San Juan County: T38S, R12E, SL Welsh 5205, Holotype (1966); T39S, R13E, SL Welsh 9816; T39S, R13E, SL Welsh & D Atwood 9990,9994 (1970); T38S, R11E, LC Higgins, BT Welsh 13179 (1983).

Draba maguirei C.L. Hitchc. var. *Burkei* C.L. Hitchc.
Map 41

Family: Brassicaceae.
Federal designation: threatened, category 2.

This variety of the Maguire whitlowgrass was named in 1932 and was known only from the type locality in Box Elder County east of Honeyville until 1972 when two additional populations were discovered in Weber County on the slopes of Mt. Ogden and Mt. Ben Lomond. It occurs at elevations ranging from 8500 to 9600 feet on rocky and talus slopes in the subalpine conifer zone.

Box Elder County: T10N, R3W, M Burke 2968,2969,2970, Type-UTS (1932). Weber County: T5N, R1E, SL Clark 2214 (1972); T7N, R1W, SL Clark 2332 (1972).

Epilobium nevadense Munz
Map 42

Family: Onagraceae.
Federal designation: threatened, category 2.

The Nevada willowherb was previously known only from Clark County, Nevada, and Washington County, Utah. During the 1980 field season it was also located in the Canyon Mountains in Millard County. Habitat for this species is rocky limestone outcrops and talus slopes in pine duff of the ponderosa pine—aspen community. Elevation extends from 7500 to 9200 feet.

Millard County: T17S, R3W, S Goodrich 14918 (1980); T17S, R3W, S Goodrich 15144 (1980). Washington County: T42S, R18W, Higgins 778 (1966); T38S, R19W, D Atwood 6822 (1976); T42S, R18W, J Anderson (no date).

Erigeron cronquistii Maguire
Map 43

Family: Asteraceae.
Federal designation: threatened, category 1.

The Cronquist daisy is restricted to northeastern Cache County. It occurs in rock crevices on cliffs in fir and spruce communities at elevations extending from 5800 to 8200 feet.

Cache County: T14N, R2E, Maguire & Maguire 14063 (1936); T14N, R3E, Maguire & Maguire 14122 (1936); T14N, R2E, Maguire & Maguire 14173 (1936); T13N, R3E, B Maguire et al. 13923 (1936); T12N, R3E, Maguire 16681, Type-NY (1939); T13N, R3E, K & JP Thorne 2143 (1982).

Erigeron kachinensis Welsh & Moore
Map 44

Family: Asteraceae.
Federal designation: endangered, category 2.

The kachina daisy is known from three populations, one in San Juan County in the area of Natural Bridges National Monument, another in Dark Canyon, and a third in Colorado. Habitat for this narrow endemic is moist sandstone outcrops in hanging garden communities. Elevation of the Natural Bridges locality is approximately 5920 feet. This population is passed by a major tourist trail.

San Juan County: T37S, R17E, Welsh and Moore 2398, Holotype (1963); T37S, R17E, SL Welsh & G Moore 7160 (1968); T34S, R16E, LM and JS Shultz 2016 (1976); T36S, R17E, LC Higgins et al. 14257 (1983).

Erigeron maguirei Cronq. var. *maguirei*
Map 45

Family: Asteraceae.
Federal designation: endangered, category 1.

The typical variety of the Maguire daisy is known only from a restricted area in Emery County. A collection of the daisy on the San Rafael Swell in 1980 and one in 1982 are BRY's only records of the species since the type collection in 1940. Elevational range is from 5400 to 5500 feet, and the habitat is a desert shrub community on the Navajo Sandstone Formation. A collection from near Fruita in 1982 and two collections from Wayne County (1934, 1938), previously considered as *E. maguirei*, have been found to vary slightly from the type materials and are now designated *var. harrisonii* Welsh.

Emery County: T20S, R11E, Maguire 18459, Type (1940); T20S, R11E, JG Harris 956 (1980); T20S, R11E, J Anderson 373 (1982).

Erigeron maguirei Cronq. var. *harrisonii* Welsh
Map 46

Family: Asteraceae.
Original citation: Welsh, S.L. 1983. Great Basin Naturalist 43: 367.
Federal designation: none.
UNPS recommendation: threatened, category 2

This variety is distinguished only technically from var. *maguirei*, which has fewer heads per stem, wider ray corollas, and longer disk corollas. The taxa are separated geographically, with var. *harrisonii* occurring near Fruita in Wayne County. The morphological differences may be the result of ecological responses, but the plant is currently recognized as a separate taxon. It grows in Navajo Sandstone, in dry sandy washes, within a juniper community type. Elevation is approximately 5700 feet.

Wayne County: T29S, R6E, BF Harrison 7385 (1934); T29S, R6E, DE Beck s.n. (1938); T29S, R6E, SL and ER Welsh 21178 (1982); T29S, R6E, SL Welsh 21262 (1982).

Erigeron mancus Rydb.
Map 47

Family: Asteraceae.
Federal designation: threatened, category 2.

The depauperate daisy has, since its first observation, remained obscure. It is known only from the La Sal Mountains, where it occurs in both Grand and San Juan counties. Habitat for the species is rocky igneous ridges in a spruce-fir community type. Elevational range extends from 10,000 to 12,000 feet. The type specimen was collected by Rydberg and Garrett in 1911. Only two specimens from the state are deposited at BRY.

UTAH: La Sal Mtns., Rydberg & Garrett 8671, Type-NY (1911). Grand County: T26S, R24E, ME Lewis 6330 (1979). San Juan County: T27S, R24E, ND Atwood 7103 (1978).

Erigeron proselyticus Neson
Map 48

Family: Asteraceae.
Federal designation: endangered, category 1.

Until recently the cliff daisy was known only from near Cedar Breaks National Monument in Iron County. However, in 1979 an additional population was discovered some miles to the south of Cedar Breaks in Kane County near Navajo Lake. Known distribution is currently restricted to these two localities, until 1984, when materials were taken in the Kolob area of Washington County in a ponderosa pine community. The spruce-fir or bristlecone pine communities and talus slopes of the Wasatch Formation are characteristic of appropriate habitat for the plant. Elevational range extends from 8,500 to 10,000 feet.

Iron County: T37S, R9W, Maguire 14947, Holotype-NY (1934); T36S, R9W, WP Cottam (1948); T37S, R9W, R and D Foster 4587 (1977); T36S, R9W, D Atwood & B Thompson 7667 (1980); T36S, R9W, D Atwood & B Thompson 7680 (1980); T37S, R10W, J Anderson (1980); T37S, R9W, R Kass 1097 (1982); T37S, R10W, SL Welsh & E Neese 21351 (1982). Kane County: T38S, R8, D Atwood 7431 (1979); T38S, R9W, D Atwood & B Thompson 7691 (1980).

Erigeron sionis Cronq.

Map 49

Family: Asteraceae.
Federal designation: endangered, category 2.

Until recently the Zion fleabane was known only from the type collection obtained by Pilsbry in 1925 from Zion National Park in Washington County. The species was not relocated for more than 50 years. In 1979 a population of the plant was located in a side canyon of Parunaweap Canyon just outside the park boundary in Kane County. In the fall of 1982, a collection was made along the west rim trail of the park. A specimen from 1925, collected by A. M. Woodbury and originally determined to be *E. trifidus*, was annotated to *E. sionis* by Welsh in 1981. This collection also came from the west rim trail. Though the known distribution of this rare endemic has not been greatly enlarged, current populations of it are now known, whereas previously it was obscure. Habitat for the species is rock crevices of the Navajo Sandstone Formation in the ponderosa pine community. Elevation is from 4400 to 7500 feet.

Washington County: Zion National Park, Pilsbry s.n., Type (1925); T40S, R10W, AM Woodbury (1925); T42S, R9W, J Anderson, Cedar City BLM (1979); T40S, R10W, R Kass et al. 1095 (1982); T40S, R10W, E Neese, R Kass 12613 (1982); T41S, R10W, SL Welsh 21377 (1982).

Erigeron untermannii Welsh & Goodrich

Map 50

Family: Asteraceae.
Original citation: SL Welsh. 1983. Great Basin Naturalist 43: 367.
Federal designation: none.
UNPS recommendation: category 2.

The Untermann daisy is a recently described taxon occurring in Duchesne and Uintah counties. It is endemic to the calcareous shales and sandstones of the Uinta and Green River formations and occurs in the pinyon-juniper community at elevations ranging from 7000 to 7800 feet. It is probably allied to *E. compactus* Blake but also has similarities with *E. nematophyllus* Rydb.

Duchesne County: T5S, R6W UBM, ND Atwood 7554 Holotype (1980); T5S, R6W UBM, S Goodrich 5317 (1976); T5S, R6W UBM, S Goodrich 12402 (1979). Uintah County: Red Pine Canyon, S Goodrich 5652 (1976).

Eriogonum ammophilum Reveal

Map 51

Family: Polygonaceae.
Federal designation: endangered, category 1.

The sand-loving buckwheat was previously known only from near Ibex Warm Point in Millard County. However, recent collections have extended the known range westward into the Ferguson Desert. Deep sandy alluvium in desert shrub and juniper community types are habitats of this buckwheat. This elevational range of the plant extends from 5200 to 6000 feet. This plant was reduced to varietal rank within *E. nummulare* by Welsh (1984).

Millard County: T22S, R14W, RC Holmgren 479 (1965); T22S, R14W, Holmgren & Holmgren Type-US (1970); T23S, R14W, P Beels (1979); T20S, R17W, SL Welsh & M Chatterley 19503 (1980); T22S R15W, SL Welsh & M Chatterley 19506, 19684, 20125 (1980); T22S, R14W, SL Welsh 20614 (1981); T22S, R14W, SL Welsh 20617 (1981); T21S, R14W, R Kass 997 (1982); T20S, R17W, D Atwood 8904 (1982).

Eriogonum aretioides Barneby

Map 52

Family: Polygonaceae.
Federal designation: endangered, category 1.

The Widtsoe buckwheat is known from only two locations within Garfield County, one near the town of Widtsoe and the other on the low ridges of Red Canyon. Habitat for the species is dry ridge tops and rocky outcrops of the pink limestone member of the Wasatch formation in a scattered pinyon-juniper and western bristlecone pine community. Elevational range extends from 7500 to 8000 feet.

Garfield County: T34S, R2W, Ripley & Barneby 8570, Type-NY (1947); T34S, R2W, Holmgren et al. 2254 (1965); T35S, R4W, Rose & Reveal (1969); T35S, R4W, JL & CG Reveal 4470 (1976); T35S, R4W, D Atwood 7923 (1981).

Eriogonum cronquistii Reveal

Map 53

Family: Polygonaceae.
Federal designation: endangered, category 2.

Only one population of the Cronquist buckwheat is known to exist, and it occurs on the west slope of Bull Mountain in Garfield County. Habitat for the species is the gravelly soil of granitic talus slopes in the mountain shrub community type at 8300 to 9250 feet elevation. This plant was reduced to varietal rank within *E. corymbosum* by Welsh (1984).

GARFIELD COUNTY: T31S, R11E, Cronquist & Holmgren, Paratype (1961); T31S, R11E, Holmgren & Reveal 3010, Isotype (1967); T31S, R11E, K Mutz 81-357 (1981); T31S, R11E, K Mutz 81-361 (1981).

Eriogonum humivagans Reveal

Map 54

Family: Polygonaceae.
Federal designation: endangered, category 2.

The spreading buckwheat is known only from east of Monticello in San Juan County, where it occurs along the roadside of Utah Highway 666. Only one population of this species exists in an area occupied by dry farms. Habitat for the spreading buckwheat consists of sandy soil and alluvium clay hills in the desert shrub community. Elevation is approximately 6800 feet. This species was relocated in 1981, but no new populations have been discovered. This plant was reduced to varietal rank within *E. corymbosum* by Welsh (1984).

SAN JUAN COUNTY: T34S, R26E, Holmgren & Reveal 3001, Isotype (1966); T34S, R26E, Reveal 2546 (1971); T34S, R26E, Holmgren, Shultz, and Shultz 16316 (1976); T34S, R26E, K Mutz 81-370 (1981).

Eriogonum lancifolium Reveal & Brotherson

Map 55

Family: Polygonaceae.
Federal designation: endangered, category 2.

The lance leaf buckwheat is known primarily from Carbon County, where it occurs in a small area east of Wellington. However, an additional population was recently discovered in Emery County south of the junction of US I-70 and Utah Highway 10. The grayish clay soil of the Mancos Shale Formation and the salt desert shrub community are representative of the habitat for this species. Elevational range extends from 4900 to 5700 feet. This name was reduced to synonymy within *E. corymbosum* by Welsh (1984).

CARBON COUNTY: T15S, R11E, Welsh & Moore 1836 (1962); T15S, R11E, JL & CG Reveal 727 (1966); T15S, R11E, G Moore 661 (1966); T15S, R11E, Reveal & Davidse 955, Paratype (1967); T15S, R11E, Reveal and Davidse 957, ISOTYPE (1967); T15S, R11E, Reveal 2923 (1972); T16S, R11E, Reveal and Reveal 2925 (1972); T16S, R12E, JL Reveal 4002 (1975); T15S, R11E, Welsh 16270 (1977); T15S, R11E, E Neese 8552 (1979). EMERY COUNTY: T24S, R6E, E Neese & D Williams 8530 (1979).

Eriogonum loganum A. Nelson

Map 56

Family: Polygonaceae.
Federal designation: endangered, category 2.

Populations of the Logan buckwheat occur at two localities in Cache County, one locality in Morgan County, and two localities in Rich County. The species grows in a mountain shrub–grassland community type on white shale, clay, and gravelly alluvial substrates. Elevational range of the plant is from 4800 to 7000 feet. Recognition of this taxon at species level is questionable. Future taxonomic interpretation may consider it a variety of another species in the complex. This plant was reduced to varietal rank within *E. corymbosum* by Welsh (1984).

CACHE COUNTY: T12N, R1E, Smith 1704, Type-RM (1909); T12N, R1W, Holmgren and Reveal 2756 (1966); T12N, R1E, Holmgren & Reveal 2757 (1966); T12N, R1E, K Mutz 80-108 (1980); T12N, R2W, K Mutz 80-111 (1980); T12N, R1E, K Thorne 2196 (1982); T12N, R1E, K Mutz 80-108 (1980). MORGAN COUNTY: T5N, R4E, K Thorne et al. 2755 (1983). RICH COUNTY: T9N, R6E, K Thorne 1474 (1981); T12N, R6E, K Snyder 631 (1983).

Eriogonum natum Reveal

Map 57

Family: Polygonaceae.
Federal designation: threatened, category 1.

Occurrences of the terrace buckwheat are restricted entirely to Millard County. Most known localities exist along Highway 50-6 west of Delta. However, the plant has also been collected on the foothills of the Cricket Mountains between Delta and Milford. This rare buckwheat occurs on saline playa remnants in the salt desert shrub community type at 4800 to 5800 feet elevations. This plant was reduced to varietal rank within *E. corymbosum* by Welsh (1984).

MILLARD COUNTY: T20S, R12W, Reveal & Reveal 3924, 3999, 4000 (1975); T22S, R9W, JL Reveal 4612 (1976); T24S, R13W, JL Reveal 4613 (1976); T19S, R11W, SL & SL Welsh 18200 (1978); T20S, R12W, SL & SL Welsh 18202 (1978); T20S, R12W, BF Harrison & KH Thorne 13196 (1979); T23S, R9W, C Fullmer 19 (1981).

Eriogonum smithii Reveal
Map 58

Family: Polygonaceae.
Federal designation: endangered, category 1.

Numerous collections of the Smith buckwheat have been made since the plant was first discovered in 1965, but they have all been from a restricted area near Little and Big Flat Top on the San Rafael desert. The species grows in stabilized red blow sand from the Entrada formation in a desert shrub community type. Elevational range of the plant extends from 4500 to 5500 feet. This plant was treated at varietal rank within *E. corymbosum* by Welsh (1984).

Emery County: T26S, R13E, Smith s.n. (1965); T26S, R13E, NH Holmgren & JL Reveal 3012, Isotype (1966); T26S, R13E, JL Reveal & G Davidse 950, 951 (1967); T26S, R13E, SL Welsh et al. 10891 (1970); T26S, R13E, JL Reveal 2921 (1972); T26S, R13E, SL Welsh et al. (1976); T26S, R13E, Welsh & Clark 16226 (1977); T26S, R13E, K Mutz 81-340,343,346,348 (1981); T26S, R13E, J Tuhy 578 (1982).

Eriogonum soredium Reveal
Map 59

Family: Polygonaceae.
Citation: Great Basin Naturalist 41: 229–231. 1981.
Federal designation: endangered, category 2.

This newly described buckwheat species has been collected in Beaver County near the old mining town of Frisco on privately owned mining claims. It is a low mat-forming species that is rare in occurrence. The plant grows on calcium carbonate deposits in the sagebrush and juniper community type and has a known elevational range of 6600 to 7300 feet.

Beaver County: T27S, R13W, K Ostler & D Anderson 1261 (1978); T26S, R13W, K Ostler & D Anderson 1350 (1978); T27S, R13W, SL Welsh & M Chatterley 19653, Paratype (1980); T27S, R13W, SL Welsh et al. 20192, ISOTYPE (1980).

Festuca dasyclada Hackel.
Map 60

Family: Poaceae.
Federal designation: endangered, category 2.

The sedge fescue was first collected from the state in 1875. Collection data indicates the specimen was taken from somewhere in Emery County, but that population has never been relocated. In 1913 the species was collected on the Manti National Forest in Sanpete County. The plant was not located again in Utah until 1981 and 1982, when a new population was discovered south of Strawberry Reservoir on the Tavaputs Plateau in Wasatch County. Habitat for this population is barrens of the Green River Shale Formation in the sagebrush community. Elevational range extends from 8300 to 9300 feet.

Emery County: Joes Valley, Parry s.n., Isotype-US (1875). Sanpete County: Wagon Road Ridge, JA Willey s.n., Topotype (1913). Wasatch County: T5S, R11W, UBM, S Smith & C Lopez s.n. (1981); T5S, R11W, E Neese 12043 (1982); T5S, R11W UBM, S Goodrich 17303 (1982); T5S, R11W, SL Welsh & E Neese (1982); T5S, R11W UBM, S Goodrich 17795 (1982); T5S, R11W, S Goodrich 17799, 17811 (1982); T5S, R11W UBM, D Atwood 9112 (1982).

Gaillardia flava Rydberg
Map 61

Family: Asteraceae.
Federal designation: threatened, category 2.

The yellow blanket flower occurs on the sandy gravel of alluvial fans and river and stream terraces derived from the Mancos Shale Formation and is associated with *Salix* and *Populus*. Distribution of the species is in western Emery and eastern Grand counties. Elevational range extends from 4200 to 5400 feet.

Emery County: Price River, ME Jones 6412, Isotype (1898); T21S, R16E, Cottam & Hutchings 2176 (1927); T17S, R16E, SL Welsh 14931, 14941 (1977). Grand County: T19S, R16E, Welsh et al. 14735 (1977); T19S, R16E, SL Welsh et al. 14837 (1977); T19S, R16E, SL Welsh 16292 (1977).

Gilia caespitosa Gray
Map 62

Family: Polemoniaceae.
Federal designation: endangered, category 2.

The Rabbit Valley gilia has a distribution restricted to Wayne County. It occurs in the pinyon-juniper community on Navajo Sandstone or on white talus slopes of the Carmel Limestone Formation. Elevational range extends from 5700 to 8500 feet. A collection of the species was made during the 1982 season near Fruita.

Wayne County: Rabbit Valley, Ward s.n., Isotype (1875); T29S, R4E, SL Clark 4 (1964); T29S, R4E, NH Holmgren et al. 2138 (1965); T29S, R7E, K Harrison 1827 (1975); T29S, R4E, SL Welsh & SL Clark 16211 (1977); T29S, R4E, D Atwood 6923 (1978); T29S, R6E, SL & ER Welsh 21176 (1982).

Glaucocarpon suffrutescens (Rollins) Rollins

Map 63

Family: Brassiacaceae.
Federal designation: endangered, category 1.

Known populations of the Rollins thelypody are restricted to Uintah County in the area south of Ouray. Its habitat is a mixed desert shrub community amid scattered pinyon and juniper on the Green River Shale Formation. Elevational range extends from 5400 to 6500 feet. This species is herein regarded as *Schoencrambe suffrutescens* (Rollins) Welsh & Chatterley comb. nov. [based on: *Thelypodium suffrutescens* Rollins in Graham Ann. Carnegie Mus. 26:224. 1937].

Uintah County: T12S, R20E, Graham 895A, Type-GH (1935); T12S, R20E, R Rollins 1700 GH (1937); T12S, R20E, L England 374 (1976); T12S, R20E, SL Welsh et al. 14396 (1976); T11S, R19E, SL Welsh et al. 14399 (1976); T12S, R19E, SL Welsh et al. 14415 (1976); T12S, R20E, SL Welsh 14853 (1977); T11S, R19E, E Neese & JS Peterson 4681 (1978); T12S, R20E, E Neese & JS Peterson 4696 (1978); T12S, R20E, E Neese 4977 (1978); T13S, R20E, L England 1790 (1979); T12S, R20E, RC & KW Rollins 79130 (1979); T12S, R20E, E Neese et al. 11551 (1982); T12S, R20E, R Kass 871 (1982).

Hedysarum occidentale Greene var. *canone* Welsh

Map 64

Family: Fabaceae.
Federal designation: threatened, category 1.

This variety of the western sweetvetch occurs in Carbon and Emery counties. Variance in leaflet features from the main body of the species (which occurs in Washington, Montana, Idaho, Wyoming, Utah, Colorado, and British Columbia) makes the occurrences in Carbon and Emery counties taxonomically significant. The plant occurs in mountain brush, pinyon-juniper, sagebrush, and streamside communities at an elevation extending from 7400 to 8300 feet. The Forest Service has developed a management plan to ensure protection of this variety.

Carbon County: T13S, R12E, Welsh & Christiansen 6614, 6598 (1967); T14S, R14E, Welsh & Murdock 9146 (1969); T14S, R14E; Welsh & Taylor 15075 (1977); T13S, R12E, SL Welsh & K Taylor 15256, Holotype (1977); T13S, R9E, R Foster 8149 (1979); T14S, R14E, S Jennings s.n. (1981). Emery County: T17S, R15E, SL Welsh 14923 (1977); T19S, R6E, ME Lewis 4719 (1977); T16S, R6E, ME Lewis 6607 (1980).

Heterotheca jonesii (Blake) Welsh & Atwood

Map 65

Family: Asteraceae.
Federal designation: endangered, category 2.

The Jones golden aster is known from Springdale near Zion National Park in Washington County and from Hell's Backbone on the Aquarius Plateau in Garfield County. According to the specimens at BRY, no collection of the species has been made from Springdale since the type specimen was taken by Jones in 1894. However, the plant was seen in eastern Washington County by Welsh in 1982. The Garfield County populations, however, have been collected periodically since their discovery in 1942. In 1980 a new population of the species was found at the southern end of Bryce Canyon National Park in Kane County. The species occurs in sandy or gravelly subtrates from limestone outcrops in a ponderosa pine–manzanita community type. Elevation extends from 4000 feet (Jones's type collection) to 9000 feet at Hell's Backbone.

Garfield County: T33S, R3E, WP Cottam 9101 (1942); T33S, R3E, BF Harrison 12343 (1954); T33S, R3E, E Neese & S White 3942 (1977); T33S, R3E, ME Lewis 6124 (1979); T33S, R3E, SL Welsh 19333, 19336 (1979). Kane County: T37S, R3W, R Graybosch 924 (1980). Washington County: T41S, R10W, ME Jones 5249, Type-POM (1894).

Hymenoxys depressa (T. & G.) Welsh & Reveal

Map 66

Family: Asteraceae.
Federal designation: threatened, category 2.

The type of this species was taken by Fremont on his second expedition in the Rocky Mountains, possibly from the Uinta Basin. However, it was not until recently that any collection was reported from there. Most known populations are scattered throughout Emery County, and Fremont could have collected the species when he traversed that area. The literature indicates the plant's distribution extends into Garfield County, but no specimens at BRY corroborate this. During the 1982 field season the species was also discovered south of Duchesne in Duchesne County. Habitat for the species is the pinyon-juniper or mixed desert shrub communities on barren exposures and, often, the rimrock of cliffs. Elevation extends from 4400 to 8400 feet.

Duchesne County: T6S, R4W, UBM, Goodrich & Atwood 16806 (1982). Emery County: San Rafael Swell, WD Stanton s.n. (no year); T22S, R13E, BF Harrison 5591 (1931); T19S, R11E, BF Harrison 8128 (1936); T19S, R11E, SL Welsh & ND Atwood 9907 (1970); T19S, R12E, K Despain 240 (1977); T19S, R7E, ME Lewis 4729 (1977); T19S, R7E, S Welsh & S Clark 15417 (1977); T18S, R12E, S Welsh & S Clark 16140, 16165 (1977); T21S, R14E, K Despain 306 (1978); T19S, R12E, K Despain 355 (1978); T19S, R12E, J Harris 126 (1979); T24S, R6E, S White & G Moore 64 (1979); T20S, R10E, K Despain 530, 542 (1979); T21S, R14E, J Harris 409 (1979); T18S, R11E, J Harris 542 (1979); T22S, R6E, BT Welsh 336 (1980); T22S, R6E, BT Welsh 344, 349 (1980); T22S, R13E, JG Harris 712 (1980); T20S, R10E, K Despain 608 (1980); T24S, R13E, J Harris 786 (1980); T26S, R9E, JG Harris 822 (1980); T26S, R9E, J Harris 842 (1980); T26S, R9E, J Harris 864 (1980); T19S, R11E, JG Harris 891 (1980); T26S, R9E, J Harris 920 (1980); T25S, R9E, J Harris 922 (1980); T20S, R11E, J Harris 961 (1980); T22S, R13E, M Williams & D Atwood 80-123-2 (1980); T26S, R8E, JG Harris 979 (1980); T21S, R14E, J & M Harris 1084 (1981); T26S, R9E, Atwood and Goodrich 8652 (1982); T25S, R9E, Atwood and Goodrich 8654 (1982); T22S, R14E, E Neese 13331 (1983). Sevier County: T24S, R5E, San Rafael Swell, J Harris 579 (1979).

Hymenoxys helenioides (Rydb.) Cockerell

Map 67

Family: Asteraceae.
Federal designation: threatened, category 2.

Range of distribution for this taxon in Utah includes Emery, Garfield, Sanpete, and Sevier counties. Its habitat is mountain brush, sagebrush, and aspen communities, often in meadows, at 8000 to 10,700 feet elevation. This plant has remained obscure in Utah, partially due, no doubt, to its resemblance to *Helenium hoopesii*, with which it occurs in the aspen communities of central and southern Utah.

Emery County: T16S, R7E, RM Thompson s.n. (1980); T16S, R7E, RM Thompson s.n. (1980); T14S, R7E, ME Lewis 6606 (1980). Garfield County: T31S, R5E, Beck & Tanner s.n. (1936); T31S, R5E, K Harrison 1273 (1973); T32S, R5E, E Neese & S White 3635 (1977). Sanpete County: T18S, R4E, SL Welsh et al. 16130 (1977); T20S, R4E, D Atwood 8049 (1981); T20S, R4E, D Atwood 8050 (1981). Sevier County: T21S, R4E, B Albee 4687 (1979); T21S, R4E, E Neese & S White 9287 (1980).

Lepidium barnebyanum Reveal

Map 68

Family: Brassicaceae.
Federal designation: endangered, category 1.

The Barneby peppergrass occurs on the Uinta and Green River Shale formations and is known only from near Duchesne in Duchesne County. Its habitat is mixed desert shrub and pinyon-juniper community and has an elevational range from 6200 to 6500 feet. Several collections of the species from the 1980 season are deposited at BRY, indicating a slight extension beyond the previously known populations.

Duchesne County: T4S, R5W UBM, Ripley & Barneby 8699, Type-WTU (1947); T4S, R5W UBM, NH Holmgren et al. 1759 (1965); T4S, R5W UBM, JL & CG Reveal 848 (1967); T4S, R5W UBM, E Neese and SL Welsh 8909, 8910, 8924, 8926 (1980); T4S, R5W UBM, E Neese & SL Welsh 8962, 8964 (1980); T4S, R5W UBM, D Atwood 7637 (1980).

Lepidium montanum Nutt. in T. & G. var. *neeseae* Welsh & Reveal

Map 69

Family: Brassicaceae.
Federal designation: threatened, category 2.

This tiny variety of *L. montanum* is known from high elevations (9000 feet) only and occurs on Navajo sandstone in the vicinity of Hell's Backbone, north of Escalante in Garfield County. Habitat consists of a ponderosa pine–manzanita community type.

Garfield County: T32S, R3E, E Neese & S White 3332, Holotype (1977); T33S, R3E, E Neese & S White 3944 (1977); T32S, R3E, D Atwood 7616 (1980).

Lepidium montanum Nutt. in T. & G. var. *stellae* Welsh & Reveal

Map 70

Family: Brassicaceae.
Federal designation: endangered, category 2.

This species is known only from one location southeast of Cannonville in Kane County. It occurs on white bare shale knolls among scattered juniper in a blue-grama grassland.

Kane County: T38S, R2W, JL Reveal et al. 789, Holotype (1967); T38S, R2W, SL & SL Welsh 12841, Holotype (1975); T38S, R2W, D Atwood 7201 (1979).

Lepidium ostleri Welsh & Goodrich

Map 71

Family: Brassicaceae.
Original citation: Great Basin Naturalist 40: 80. 1980.
Federal designation: endangered, category 1.

The Ostler lepidium is a rare and endemic Utah plant known only from the San Francisco Mountains, near Frisco, in Beaver

County, where it occurs in a severely restricted distribution on private mining claims. Known elevational range of the species is from 5800 to 6900 feet. The plant grows on gravelly limestone slopes. It has been collected, at its lowest elevation, within a shadscale community type, but its largest population occurs in a pinyon-juniper community.

Beaver County: T27S, R13W, K Ostler & D Anderson 1210 (1978); T27S, R13W, K Ostler & D Anderson 1258, Holotype (1978); T27S, R13W, K Ostler 1415, Paratype (1978); T27S, R13W, K Ostler 1588, Paratype (1978); T27S, R13W, J Anderson s.n. (1980); T27S, R13W, SL Welsh & M Chatterley 19654, 19655 (1980).

Lesquerella tumulosa (Barneby) Reveal

Map 72

Family: Brassicaceae.
Federal designation: endangered, category 1.

The Kodachrome twinpod has a known distribution restricted to Kane County, just south of Cannonville. Its habitat is white shale outcrops derived from the Winsor Member of the Carmel Formation, among scattered junipers. Elevational range extends from 5500 to 5870 feet.

Kane County: T38S, R2W, Barneby 14424, Type-NY (1966); T38S, R2W, JL Reveal et al. 788 (1967); T38S, R2W, SL Welsh 12765, 12840 (1975); T38S, R2W, JL & CG Reveal 4452 (1976); T38S, R2W, R Foster 3740 (1977); T38S, R2W, D Atwood 7203 (1979); T38S, R2W, K Mutz & A Hreha 81-93 and 81-94 (1981).

Lomatium latilobum (Rydb.) Mathias

Map 73

Family: Apiaceae.
Federal designation: threatened, category 2.

The broad-leaved biscuitroot occurs in Arches National Monument in Grand County and a few miles south of Moab in San Juan County. Recent reports of the species from Colorado indicate a broader range. It grows in crevices and sandy soil of the Entrada sandstone formation among scattered pinyon-juniper and desert shrubs. Elevational range extends from 4800 to 5000 feet.

Grand County: T26S, R23E, Rydberg & Garrett 8371, Type-NY (no date), T24S, R22E, BF Harrison 11133 (1947); T24S, R21E, BF Harrison 11137 (1947); T23S, R21E, BF Harrison 11142 (1949); T23S, R21E, Holmgren et al. (1955); T23S, R21E, Barnett, Pitts, and Pyrah 51 (1963); T23S, R21E, Allan 10, 69, 350 (1972); T23S, R21E, Allan 494 (1974), T26S, R23E, D Atwood, B Thompson 8785 (1982). San Juan County: T27S, R22E, SL Welsh 20841 (1981).

Mentzelia argillosa Darlington

Map 74

Family: Loasaceae.
Federal designation: none.
UNPS recommendation: threatened, category 2.

This species is known only from Sanpete and Sevier counties in Utah. However, it has also been reported from Garfield County, Colorado. It is endemic to the Arapien shale formation and grows in shadscale, ephedra, juniper, buckwheat, greasewood, and desert shrub communities at 5600 to 6200 feet elevation. More information needs to be accumulated concerning the plant's distribution in Utah.

Sanpete County: T19S, R2E, SL Welsh, G Moore 3381 (1964); T19S, R2E, S Goodrich, ME Lewis 17439 (1982). Sevier County: T22S, R1W, DW Lindsay s.n. (1962); T22S, R1W, SL Welsh, ND Atwood 11724 (1972); T22S, R1W, D Williamson 40 (1976); T23S, R1W, L Greenwood s.n. (1979); T23S, R1W, L Greenwood s.n. (1979); T23S, R1W, L Greenwood s.n. (1979).

Najas caespitosus (Maguire) Reveal

Map 75

Family: Najadaceae.
Federal designation: threatened, category 2, possibly extinct.

The Fish Lake naiad is known only from near Pelican Point at Fish Lake in Sevier County. This rare species is known only from the type locality where it was collected in 1940 by Bassett Maguire. It occurs in an aquatic habitat in shallow water to one foot deep with a sand-gravel bottom. Elevational range is approximately 8600 feet.

Sevier County: T26S, R2E, B Maguire 19888, Isotype (1940).

Oenothera acutissima Wagner

Map 76

Family: Onagraceae.
Citation: Syst. Bot. 6(2): 153–155. 1980.
Federal designation: threatened, category 2.

This recently named and rare species of yellow-flowered evening-primrose occurs in Uintah and Daggett counties in Utah and in Moffat County, Colorado. It was first collected in Moffat County in 1966. The first Utah population was discovered in 1978 (see below). *O. acutissima* is related to *O. flava* but is distinguished by its long, slender, branching taproot and its linear, irregularly dentate leaves. It grows in moist, sandy soils and occasionally on rock outcrops in meadow, sagebrush, ponderosa pine, and streambed communities. Elevation ranges from 7000 to 7800 feet. The plant occurs in several small and scattered populations.

Daggett County: T2N, R22E, JS Peterson 1293, Paratype (1978); T2N, R22E, E Neese, JS Peterson 5428, Isotype (1978); T2N, R22E, JS Peterson, G Kruzel 1566 (1980); T2N, R22E, E Neese 12016 (1982). Uintah County: T1S, R24E, E Neese 5715 (1978); T1S, R24E, E Neese 5697 (1978); T4S, R25E, E Neese, K Snyder 11767 (1982); T4S, R25E, E Neese, K Snyder 11912 (1982); T4S, R25E, F Smith et al. 1702 (1982).

Pediocactus despainii Welsh & Goodrich

Map 77

Family: Cactaceae.
Original citation: Great Basin Naturalist 40: 83. 1980.
Federal designation: endangered, category 2.

Known distribution of the Despain pediocactus is restricted to a small portion of the San Rafael Swell in Emery County. Habitat for this diminutive cactus species is open areas of pinyon-juniper on the exposed Carmel Limestone Formation. Elevational range extends from 6000 to 6200 feet. The population is subject to threat from off-road vehicles, primarily, as well as from trampling by grazing animals.

Emery County: T20S, R10E, K Despain 266 (1978); T19S, R10E, K Despain 266a, Holotype (1978); desert, K Heil 1002, NCC-S (1979); T19S, R10E, E Neese & K Thorne 504 (1979); T19S, R10E, K Despain 445, Paratype (1979); T19S, R10E, JG Harris 670 (1980).

Pediocactus winkleri Heil

Map 78

Family: Cactaceae.
Original Citation: Cact. & Succ. J. (U.S.) 51: 28. 1979.
Federal designation: endangered, category 2.

The Winkler pediocactus is known only from near Notom in Wayne County, where it was first discovered in 1978. Common vegetation associated with the habitat area is of the salt desert shrub community. Mat-atriplex is a particular dominant. Soil is high in clay content. Elevational range extends from 4800 to 5400 feet. Additional habitat for this species exists, but the plant has not been extensively searched for. Further field work is necessary to more accurately determine its range.

Wayne County: T30S, R7E, K Heil (1978); T30S, R7E, K Heil 989, NCC-S (1979); T29S, R8E, Neese et al. 7195 (1979); T29S, R8E, E Neese 8732 (1980); T29S, R7E, E Neese & K Mutz 11425 (1982).

Penstemon atwoodii Welsh

Map 79

Family: Scrophulariaceae.
Federal designation: threatened, category 2.

The Atwood beardtongue is known from southern Garfield County and north central Kane County. Habitat for the species is ponderosa pine and pinyon-juniper woodlands, where it grows in grayish sand and clay loam of the Kaiparowits, Wahweap, and Straight Cliffs formations. Elevational range extends from 6200 to 8000 feet.

Garfield County: T35S, R2E, Cottam 4418 (1929); T37S, R1E, Atwood 5177, Paratype (1973); T37S, R1E, Welsh & Murdock 12867, Paratype (1975); T37S, R3E, NH & PK Holmgren 8446 (1977). Kane County: T38S, R3E, Atwood s.n., Paratype (1969); T38S, R1W, ND Atwood 5165 (1973); T39S, R4E, ND Atwood 5207 (1973); T39S, R4E, Welsh & Murdock 12793, 12793a, Paratype (1975); T38S, R2W, Welsh & Welsh 12800, Holotype (1975); T38S, R2E, R & D Foster 4107 (1977).

Penstemon bracteatus Keck

Map 80

Family: Scrophulariaceae.
Federal designation: threatened, category 1.

The Red Canyon beardtongue occurs on the limestone slides and gravelly soils of Red Canyon in the Bryce Canyon area of Garfield County. The Pink Limestone Member of the Wasatch Formation supports this, as well as other, rare and indigenous Utah plants. A mixed ponderosa pine and pinyon pine community type is associated with the species. Elevational range extends from 6900 to 8300 feet.

Garfield County: T37S, R3W, Weight B-32, UT (1932); T35S, R4½W, Pennell & Schaeffer, UC,UT,UTC (1938); T35S, R4½W, B Maguire 19080 (1940); T37S, R4W, NH Holmgren et al. 2018 (1965); T35S, R4½W, JL & CG Reveal 4468 (1976); T36S, R4W, NH & PK Holmgren 8452 (1977); T37S, R4W, R & D Foster 4389 (1977); T37S, R4W, R Graybosch 791b (1980); T37S, R4W, D Atwood 7620 (1980); T35S, R4½W, D Atwood 7626 (1980); T36S, R4½W, D Atwood 7922 (1981).

Penstemon compactus (Keck) Crosswhite

Map 81

Family: Scrophulariaceae.
Federal designation: threatened, category 2.

Distribution for the Cache beardtongue is limited to Cache County. The majority of collections have come from near Tony Grove Lake and Mt. Naomi. However, other populations have been found in Logan Canyon, Franklin Basin, and near Mt. Magog and Wellsville Peak. Habitat for the plant is rocky outcrops in spruce-fir and aspen community types. Elevational range extends from 6700 to 9500 feet.

CACHE COUNTY: T11N, R2W, S Flowers 219, UT (1924); T14N, R3E, S Flowers 703, UT (1928); T14N, R3E, Maguire & Hobson s.n., UTC (1936); T14N, R3E, Maguire & Hobson 14054 (1936); T13N, R3E, Maguire 16134, UTC (1938); T14N, R2E, Maguire 16148, Type-UTC (1938); T13N, R2E, Holmgren 3591 (1944); T13N, R2E, Tillett & Crockett 206, UTC (1953); T13N, R2E, Clark 320 (1965); T14N, R3E, AC Hull s.n., UTC (1970); T13N, R3E, NH & PK Holmgren 8501 (1977); T13N, R3E, KH & JP Thorne 2153 (1982); T13N, R2E, B Neely 389 (1981); T14N, R3E, B Neely 468 (1981).

Penstemon concinnus Keck

Map 82

Family: Scrophulariaceae.
Federal designation: threatened, category 2.

All collections of this taxon are from Beaver County, Utah, except for one specimen from Pine Valley in Iron County, the type from Tunnel Springs in Millard County, and two specimens from the Mountain Home Range, also in Millard County. This unique beardtongue grows from 6240 to 7500 feet elevation in pinyon-juniper, sagebrush, rabbitbrush, blue-grama grass, and mountain mahogany associations. Substrate ecology includes gravelly bluffs, alluvial outwash, limestone outcrops, dolomite, and ryholite. Several populations of this species exist, but they occur within a restricted range.

BEAVER COUNTY: T26S, R19W, SL Welsh, G Moore 3199 (1964); T30S, R19W, SL Welsh et al. 13276 (1976); T30S, R19W, K Ostler, D Anderson 1181, 1200 (1978); T27S, R18W, K Ostler, D Anderson 1247 (1978); T29S, R15W, K Ostler, D Anderson 1303 (1978); T28S, R19W, K Ostler, D Anderson 1315 (1978); T28S, R19W, K Ostler, D Anderson 1314 (1978); T28S, R18W, K Ostler, D Anderson 1352 (1978); T26S, R19W, K Ostler 1438 (1978); T26S, R19W, K Ostler 1440 (1978); T30S, R16W, K Ostler 1461 (1978); T30S, R15W, K Ostler 1472 (1978); T29S, R19W, SL Welsh, M Chatterley 19556 (1980); T29S, R19W, SL Welsh, M Chatterley 19688 (1980); T29S, R15W, K Thorne, B Welsh 1529 (1981); T29S, R15W, K Thorne, B Welsh 1535 (1981); T30S, R15W, B Welsh, K Thorne 1294 (1981); T30S, R15W, B Welsh, K Thorne 1296 (1981). IRON COUNTY: T31S, R17W, K Ostler, D Anderson 1398 (1978). MILLARD COUNTY: T24S, R17W, Cottam 5635 Type-DS (1938); T26S, R19W, SL Welsh, M Chatterley 19734 (1980); T25S, R19W, SL Welsh, M Chatterley 19742 (1980).

Penstemon goodrichii N. Holmgren

Map 83

Family: Scrophulariaceae.
Federal designation: threatened, category 2.

The Goodrich beardtongue is known only from the Uinta Basin, primarily in Uintah County. One collection of the plant comes from Duchesne County. Habitat of the species includes clay soils of the Duchesne River Formation in pinyon-juniper, sagebrush, shadscale and fourwing saltbush communities. Elevation ranges from 5600 to 6200 feet.

DUCHESNE COUNTY: T1N, R2W UBM, E Neese 7710 (1979). UINTAH COUNTY: T4S, R20E, S Goodrich 5917 (1976); T1N, R1E UBM, S Goodrich 5896 (1976); T1N, R1E UBM, S Goodrich 5364 (1976); T1N, R1E UBM, S Goodrich 5392 (1976); T5S, R19E, NH & PK Holmgren, RC Barneby 8760, Type (1978); T1N, R1E UBM, E Neese, JS Peterson 5802 (1978); T5S, R20E, E Neese, JS Peterson 5822 (1978); T1N, R1E UBM, S Goodrich 11712 (1978); T1N, R1E UBM, E Neese 7694 (1979); T1N, R1E UBM, D Atwood 7561 (1980); T1N, R1E, S Goodrich 16773 (1982); T1N, R1E UBM, E Neese 14128 (1983).

Penstemon grahamii Keck

Map 84

Family: Scrophulariaceae.
Federal designation: threatened, category 1.

The Graham beardtongue is known only from Uintah County and from one location in Carbon County south of Sand Wash near the Uintah County line. During the 1982 field season, several new populations of this species were discovered in the southeastern portion of Uintah County. Prior known localities were restricted to the southwestern part of the county. Habitat for the species is white outcrops of Green River Shale in the pinyon-juniper and mixed desert shrub communities. Elevational range extends from 5700 to 6500 feet.

UINTAH COUNTY: T12S, R18E, Graham 7883, Type-CM (1933); T13S, R22E, Holmgren et al. 1845 (1965); T11S, R17E, E Neese 4496 (1978); T12S, R21E, E Neese & S Peterson 4734 (1978); T12S, R18E, E Neese 5249 (1978); T13S, R20E, L England 1780 (1979); T12S, R23E, K Thorne & B Neely 1761 (1982); T12S, R24E, K Thorne & B Neely 1796 (1982); T11S, R25E, E Neese & C Fullmer 11483 (1982); T12S, R24E, F Smith & K Snyder 1611 (1982); T12S, R24E, F Smith & K Snyder 1615 (1982); T12S, R25E, K Thorne, B Neely, C Fullmer 1826 (1982); T12S, R25E, Kass & Trent 839 (1982); T12S, R25E, Kass & Trent 844 (1982); T11S, R25E, E Neese & C Fullmer 11478 (1982); T11S, R25E, E Neese & C Fullmer 11488, 11500 (1982); T12S, R25E, K Thorne 1894

(1982); T11S, R25E, E Neese & C Fullmer 11682 (1982); T10S, R25E, E Neese, C Fullmer 11673 (1982); T10S, R25Ed, E Neese, C Fullmer, W Rogers 12056 (1982); T10S, R25E, E Neese & F Smith 12055 (1982); T12S, R25E, E Neese & J Trent 12363 (1982).

Penstemon leptanthus Pennell
Map 85

Family: Scrophulariaceae.
Federal designation: endangered, category 2.

The only BRY record of this beardtongue from the state was collected by Mont Lewis in 1978. That population is in lower Dry Canyon of the Manti-La Sal National Forest in Sanpete County. Pennell states that the type (deposited US) was collected in central Utah by L. F. Ward in 1875 and that it was probably part of Ward's no. 280, collected at Twelve Mile Creek Canyon near Mayfield, although it bears the label of Ward 546 from The Button, Aquarius Plateau. It was originally distributed by Ward as *P. acuminatus*. Elevation of the species is approximately 6200 feet. It occurs in the pinyon-juniper community.

Sanpete County: T16S, R2E, ME Lewis 5439.

Penstemon nanus Keck
Map 86

Family: Scrophulariaceae.
Federal designation: threatened, category 2.

The low beardtongue is known primarily from Millard County, where it occurs in appropriate habitat areas of Pine Valley and the Cricket Mountains. It is also known from Beaver County, where it occurs in Pine Valley and on the Wah Wah Mountains. Habitat for this small beardtongue is calcareous gravel of the Sevy Dolomite Formation in a pinyon and mixed desert shrub community type. Elevation extends from 5400 to 6400 feet.

Beaver County: T26S, R15W, ND Atwood 1510 (1968); T26S, R15W, SL Welsh et al. 13325 (1976); T26S, R15W, K Ostler & D Anderson 1176 (1978); T28S, R16W, K Ostler & D Anderson 1135 (1978); T28S, R16W, K Ostler & D Anderson 1254 (1978); T26S, R15W, K Ostler & D Anderson 1255 (1978); T27S, R16W, K Ostler & D Anderson 1266 (1978); T27S, R15W, K Ostler & D Anderson 1320 (1978); T28S, R17W, K Ostler & D Anderson 1353 (1978); T26S, R15W, SL Welsh & M Chatterley 19527 (1980); T28S, R16W, SL Welsh & M Chatterley 19541 (1980); T28S, R16W, SL Welsh & M Chatterley 19535 (1980); T26S, R15W, SL Welsh & M Chatterley 19569 (1980); T26S, R15W, SL Welsh & M Chatterley 19711 (1980); T27S, R16W, SL Welsh & M Chatterley 19733 (1980); T26S, R18W, S Goodrich 18654 (1983). Millard County: T24S, R17W, MG Barlow 50 (1964); T24S, R17W, MG Barlow 52-a (1964); T24S, R17W, NH Holmgren et al. 2576 (1966); T24S, R17W, SL Welsh et al. 13303 (1976); T25S, R18W, K Ostler & D Anderson 1228 (1978); T21S, R9W, SL Welsh & E Neese 18762 (1979); T25S, R17W, SL Welsh & M Chatterley 19498 (1980); T23S, R15W, SL Welsh & M Chatterley 19508 (1980); T24S, R15W, SL Welsh & M Chatterley 19517 (1980); T25S, R18W, SL Welsh & M Chatterley 19572 (1980); T22S, R16W, C Fullmer 10 (1980); T23S, R14W, SL Welsh & M Chatterley 19663 (1980); T23S, R14W, SL Welsh 20538 (1981); T25S, R18W, S Goodrich 18395 (1983).

Penstemon parvus Pennell
Map 87

Family: Scrophulariaceae.
Federal designation: none.
UNPS recommendation: category 2.

This species of beardtongue is known only from the Aquarius Plateau in Garfield County and from Parker Mountain in Piute County. It grows at an elevation of 8500 to 9800 feet in clay soil and sandy gravels of the sagebrush-grass community. More information needs to be gathered to establish an accurate picture of the distribution and ecological needs of this plant.

Garfield County: T33S, R2E, DE Beck 8900 (1938); T33S, R2E, DE Beck s.n. (1938); T31S, R2E, NH Holmgren et al. 2257 (1965); T31S, R2E, E Neese, S White 3287 (1977); T31S, R2E, NH & PK Holmgren 8583 (1977); T31S, R2E, E Neese, S White 3582 (1977); T32S, R2E, D Atwood, B Thompson 7655 (1980). Piute County: T29S, R1W, SL Welsh et al. 14173 (1976).

Penstemon scariosus Pennell var. *albifluvis* (England) N. Holmgren
Map 88

Family: Scrophulariaceae.
Federal designation: threatened, category 1.

This new combination, based on *Penstemon albifluvis* England, recognizes the taxon as a variety of *P. scariosus*. It is distinguished from varieties *scariosus* and *garrettii* by its slightly larger anther-cells, lavendar to pale blue flower color, and geographical distribution. It occurs in west central Uintah County and adjacent Rio Blanco County, Colorado. The plant grows on shale slopes of the Evacuation Creek and Parachute Creek members of the Green River Shale Formation in pinyon juniper, mountain mahogany, and mixed desert shrub communities. Elevation ranges from 4975 to 6800 feet. It is questionable as to whether this variety should be considered a candidate for listing.

Uintah County: T11S, R24E, LC Higgins 1579, 1604 (1968); T10S, R25E, A Cronquist 11462 (1976); T10S, R24E, JL England 2046 (1980); T10S, R25E, E Neese, C Fullmer 11456 (1982); T10S, R24E, SL Welsh 19607 (1980); T10S, R24E, K Thorne, B Neely 1833 (1982); T9S, R25E, E Neese, J Trent 12353 (1982); T10S, R25E, F Smith, K Snyder 2097 (1982); T9S, R25E, F Smith, E Neese 1646 (1982); T11S, R25E, F Smith, K Snyder 1851 (1982); T10S, R25E, B Neely, K Thorne 839 (1982); T12S, R25E, F Smith, K Snyder 1610 (1982); T11S, R25E, E Neese, C Fullmer 11471 (1982); T12S, R22E, E Neese 11539 (1982); T12S, R22E, K Thorne 1855 (1982); T12S, R22E, F Smith, K Snyder 1631 (1982); T12S, R23E, K Thorne, B Neely 1801 (1982); T11S, R25E, E Neese, C Fullmer 11486 (1982); T11S, R25E, E Neese, et al. 11660 (1982); T11S, R25E, E Neese 11667 (1982); T13S, R23E, K Thorne, B Neely 1913 (1982); T11S, R25E, R Kass, J Trent 904 (1982); T11S, R25E, E Neese 11664 (1982); T11S, R25E, F Smith, J Trent 1786 (1982); T11S, R25E, F Smith, J Trent 1791, 1792 (1982); T11S, R25E, E Neese, J Trent 12047 (1982); T11S, R25E, F Smith, J Trent 1796 (1982); T11S, R25E, F Smith, K Snyder 2089 (1982); T11S, R25E, E Neese 12378 (1982); T11S, R25E, F Smith, K Snyder 2109 (1982); T11S, R25E, E Neese, J Trent 12358 (1982).

Penstemon tidestromii Pennell

Map 89

Family: Scrophulariaceae.
Federal designation: threatened, category 2.

The Tidestrom beardtongue is known only from the San Pitch Mountains in Sanpete County and from one location south of Levan in southeastern Juab County. The plant occurs in desert shrub, sagebrush, snowberry, and juniper community types and on a variety of substrates. Elevational range extends from 5600 to 8200 feet.

Juab County: T15S, R1E, SL Welsh et al. 14817 (1977). Sanpete County: T17S, R1E, Tidestrom 1296 (1908); T17S, R1E, L Greenwood s.n. (1978); T17S, R2E, L Greenwood s.n. (1978); T17S, R1E, L Greenwood s.n. (1979); T17S, R1E, L Greenwood s.n. (1979); T19S, R2E, L Greenwood 4950 (1980); T18S, R2E, ME Lewis 6981 (1982).

Penstemon wardii Gray

Map 90

Family: Scrophulariaceae.
Federal designation: threatened, category 2.

The Ward beardtongue is known from Sanpete County south of Manti and west of Centerfield and from a wider range within Sevier County. Habitat for the species is clay shale hills of the Arapien, Bald Knoll, and Colton formations in pinyon-juniper and greasewood communities. Elevational range is from 5250 to 6800 feet.

Sanpete County: T18S, R2E, D Atwood 1521 (1968); T19S, R1W, L Greenwood s.n. (1978). Sevier County: T23S, R1½W, Ward 162, Type-US (1875); T22S, R1E, NH Holmgren et al. 1968 (1965); T23S, R1W, SL Welsh & D Atwood 11720 (1972); T23S, R1W, SL Welsh 12801 (1975); T23S, R3W, D Williamson 36 (1976); T22S, R1W, D Williamson 38 (1976); T21S, R2W, SL Welsh et al. 16931 (1978); T25S, R4W, Greenwood (1979); T21S, R1E, L Greenwood (1979); T25S, R4W, L Greenwood (1979); T23S, R3W, L Greenwood (1979); T23S, R3W, L Greenwood (1979).

Phacelia indecora J.T. Howell

Map 91

Family: Hydrophyllaceae.
Federal designation: endangered, category 2.

The drab scorpion plant is known from three geographically separate localities, one from near Bluff in San Juan County, one from an area west of Hanksville in Wayne County, and the other from Castle Valley in Emery County. The plant occurs in salt desert shrub and blackbrush communities on clay and basalt hills. Elevational range of the species extends from 4400 to 5500 feet.

Emery County: T19S, R9E, JG Harris 269 (1979). San Juan County: T40S, R21E, ME Jones, Type-CAS (1919). Wayne County: T28S, R9E, ND Atwood 1363 (1968).

Primula maguirei L.O. Williams

Map 92

Family: Primulaceae.
Federal designation: threatened, category 1.

Populations of the Maguire primrose are restricted to Logan Canyon in upper Cache County. This primrose is a remarkably beautiful species growing on damp overhanging rocks and in crevices. It occurs in the montane shrub, mixed aspen, and conifer communities. Elevational range extends from 4800 to 5500 feet.

Cache County: T12N, R1E, Aldous & Owen s.n., UTC (1911); T12N, R2E, Maguire & Maguire 3650, Type-MO (1932); T12N, R1E, Berber 3650a, UTC (1932); T12N, R1E, Burke 3651, UTC (1932); T12N, R2E, Muencher & Maguire 2399, UTC (1933); T12N, R2E, Williams 2149, MO (1935); T12N, R1E, A Cronquist 433-37 (1937); T12N, R1E, L & J Shultz 2436 (1978).

Psoralea epipsila Barneby

Map 93

Family: Fabaceae.
Federal designation: endangered, category 2.

The Kane breadroot is known only from southern Kane County a few miles east of Kanab and just across the Arizona border in Mohave County. It occurs in clay soil of the Chinle and Moenkopi formations in either mixed desert shrub, sagebrush, or juniper communities. Elevational range of the plant extends from 4000 to 5200 feet.

Kane County: T43S, R3W, Ripley & Barneby 4832, Type-CAS (1943); T43S, R4W, ND Atwood 2668 (1971); T43S, R4W, RK Giersch 4380 (1978).

Psoralea pariensis Welsh & Atwood

Map 94

Family: Fabaceae.

Federal designation: threatened, category 1.

The Paria breadroot is known only from Bryce Canyon National Park in Garfield County and from No Man's Mesa and Cottonwood Wash in central Kane County. Habitat for the species is a ponderosa pine woodland community, with substrate of alluvial materials derived from the Wasatch Limestone Formation. Elevation extends from 5600 to 8000 feet.

Garfield County: T37S, R4W, H Buchanan 1494 Paratype (1970); T37S, R4W, Welsh & Welsh 12810, Paratype (1975); T37S, R4W, Murdock (1975); T37S, R4W, Welsh & Murdock 12859, Holotype (1975); T37S, R4W, JR Murdock s.n. (1975). Kane County: T40S, R1W, Atwood 3684 (1972); T40S, R3W, D Atwood 6782 (1976).

Psorothamnus polyadenius (Torr.) Rydb. var. *jonesii* Barneby

Map 95

Family: Fabaceae.

Original citation: Mem. New York Bot. Gard. 27: 52. 1977.

Federal designation: endangered, category 2.

The Jones indigo bush is known from only two localities in Emery County, one at the south base of Mexican Mountain and the other near the airport west of Greenriver. It occurs in a salt desert shrub community dominated by ephedra and shadscale on clay hills covered with a pedimental gravel. Elevation is approximately 4700 feet.

Emery County: T22S, R15E, D Atwood & B Thompson 7579 (1980); T21S, R13E, JG Harris 976 (1980); T21S, R15E, B Welsh & M Chatterley 738 (1981).

Ranunculus acriformis Gray var. *aestivalis* L. Benson

Map 96

Family: Ranunculaceae.

Federal designation: endangered, category 2.

The type locality of the autumn buttercup is a few miles north of Panguitch in Garfield County, where Lyman Benson collected the plant in 1948. That population has been relocated only recently by Kathy Mutz. However, the plant, belonging to *R. acriformis*, but not the var. *aestivalis*, was collected near Muddy Creek in Sanpete County during the 1982 season, and var. *aestivalis* was found by Kathy Mutz in the Sevier River Valley in Garfield County in 1982 and 1983. It occurs in a meadow community. Elevation of the type and Garfield County populations was approximately 6400 feet. The Muddy Creek population occurs at an elevation of approximately 9700 feet.

Garfield County: T34S, R5W, L Benson 13420, Isotype (1948); T33S, R5W, K Mutz 1025 (1982); T33S, R5W, K Mutz 7 (1983). Sanpete County: T20S, R5E, ME Lewis 7369 (1982).

Sclerocactus pubispinus (Engelm.) L. Benson

Map 97

Family: Cactaceae.

Federal designation: category 3C.

UNPS recommendation: category 2.

The Great Basin fishhook cactus is a pretty barrel cactus that is widespread in Utah and Nevada. It is known from Beaver, Juab, Millard, Sevier, and Tooele counties in Utah, and Elko and White Pine counties in Nevada. However, the species is never abundant at any one location, and it is evident that it is affected by even minor fluctuations of the ecosystem. Habitat for the species is rocky hillsides and ancient shoreline terraces of calcareous or dolomitic gravels and a mixed desert shrub community. Elevation ranges from 5000 to 6440 feet.

Beaver County: T27S, R13W, K Ostler & D Anderson 1265 (1978); T27S, R18W, SL Welsh & M Chatterley 19550 (1980); T27S, R16W, SL Welsh & M Chatterley 19533 (1980); T26S, R20W, SL Welsh & M Chatterley 19562 (1980); T26S, R15W, SL Welsh, M Chatterley (1980); T26S, R15W, SL Welsh & M Chatterley 19713 (1980); T27S, R16W, SL Welsh & M Chatterley 19729 (1980); T28S, R11W, B Welsh & K Thorne 1301 (1981). Juab County: T13S, R19W, SL Welsh et al. 16807 (1978). Millard County: T26S, R20W, K Ostler & D Anderson 1304 (1978); T22S, R15W, SL Welsh & M Chatterley 19504 (1980); T24S, R16W, SL Welsh & M Chatterley 19516 (1980); T24S, R14W, SL Welsh & M Chatterley (1980); T21S, R16W, C Fullmer 8 (1980); T25S, R18W, SL Welsh & M Chatterley 19576 (1980); T24S, R14W, SL Welsh & M Chatterley 19641 (1980); T22S, R15W, SL Welsh & M Chatterley 19686 (1980); T25S, R19W, SL Welsh & M Chatterley 19740 (1980);

T15S, R12W, R Kass & J Herrick 349 (1981); T23S, R17W, S Goodrich 18711 (1983). SEVIER COUNTY: T25S, R3W, S Welsh 16485 (1978); T25S, R4W, S Welsh 16526 (1978); T25S, R4W, E Neese & D Williams 7148 (1979). TOOELE COUNTY: T8S, R18W, S Welsh et al. 16854 (1978).

Selaginella utahensis Flowers
Map 98

Family: Selaginellaceae.
Federal designation: threatened, category 2.

The type of this species was collected by Cottam in Zion National Park in 1931. A second collection was made by him approximately 16 miles north of St. George in 1941. Since that time no observations of the plant have been reported in Utah until 1982, when the taxon was collected again in Zion National Park. Habitats of the 1931 and 1941 collections include wash bottoms and shady slopes, respectively. The 1982 collections are from populations growing on the Navajo sandstone formation in the ponderosa pine community type. Elevation ranges from 4000 to 7500 feet. Intermountain Flora reports that this species also occurs on the Charleston Mountains in southern Nevada.

WASHINGTON COUNTY: T41S, R10W, Cottam 5644, Type (1931); ca T40S, R15W, Cottam 8817 (1941); T41S, R10W, R Kass et al. 1093 (1982); T41S, R10W, SL Welsh 21385 (1982).

Senecio dimorphophyllus Greene var. *intermedius* T.M. Barkley
Map 99

Family: Asteraceae.
Federal designation: threatened, category 2.

Until recently the intermediate groundsel was only known from the La Sal Mountains in San Juan County, where it occurred in swampy areas of high alpine or subalpine meadows. However, in 1982 the plant was collected by Sherel Goodrich and Mont Lewis near the town of Ferron in Sanpete County. Additional fieldwork needs to be conducted to understand the ecological needs affecting range and distribution of this taxon. Elevational range of the species extends from 9,200 to 10,500 feet.

SAN JUAN COUNTY: T27S, R24E, Payson & Payson 4097, Type-MO (no date); T27S, R24E, B Thompson 18 (1976); T27S, R24E, ND Atwood 7079 (1978). SANPETE COUNTY: T20S, R4E, S Goodrich, ME Lewis 17428 (1982).

Silene petersonii Maguire var. *minor* Hitchc. & Maguire
Map 100

Family: Caryophyllaceae.
Federal designation: threatened, category 1.

The Red Canyon catchfly occurs only on the pink limestone member of the Wasatch formation. Populations exist on this formation in Red Canyon in Garfield County and near Cedar Breaks National Monument in Iron County. Mixed ponderosa pine, fir, and western bristlecone pine community types are associated with the occurrence of this species. Elevational range of the plant extends from 7,000 to 10,400 feet.

GARFIELD COUNTY: T35S, R4½W, Maguire 19550, Type-UTC (1940); T35S, R6W, R & D Foster 4758 (1978); T35S, R4W, LC Higgins 10829 (1977). IRON COUNTY: T36S, R9W, BF Harrison & A Carter 9860 (1940); T36S, R9W, LC Higgins 11217 (1977); T36S, R9W, D Atwood & B Thompson 7672 (1980); T36S, R9W, R Graybosch 933 (1980).

Silene petersonii Maguire var. *petersonii*
Map 101

Family: Caryophyllaceae.
Federal designation: threatened, category 2.

Most historical reports of the plateau catchfly have been from southeastern Sanpete County, near Skyline Drive on the Manti-La Sal National Forest. However, during the 1981 field season, occurrences of the plant were also observed on the Escalante Mountains, east of Widtsoe, in Garfield County. Rabbitbrush, scattered spruce, subalpine meadows, or conifer community types are all possible habitat for the species. However, substrate usually consists of white limestone gravel and talus slopes belonging to the Flagstaff Formation. Elevational range extends from 9,700 to 11,200 feet.

GARFIELD COUNTY: T34S, R1W, D Atwood 8162 (1981); T34S, R1W, D Atwood 8173 (1981). SANPETE COUNTY: T19S, R4E, Maguire 20000, Type-UTC (1940); T19S, R4E, NH Holmgren & JL Reveal 1497 (1964); T19S, R4E, ME Lewis & R Thompson 4241 (1976); T19S, R4E, ME Lewis 4306 (1976); T19S, R4E, S Welsh & S Clark 15382 (1977); T19S, R4E, SL & BJ Welsh 15396 (1977); T18S, R4E, E Neese & S White 3707 (1977); T19S, R4E, E Neese & S White 3714 (1977); T19S, R4E, S Clark 2880 (1977); T17S, R5E, S Clark 3192 (1977); T19S, R4E, D Atwood 7990 (1981); T19S, R4E, D Atwood 7999 (1981); T20S, R4E, D Atwood 8133 (1981); T19S, R4E, D Atwood 8142 (1981).

Sphaeralcea caespitosa Jones

Map 102

Family: Malvaceae.
Federal designation: threatened, category 2.

The Jones globemallow is a low, showy species restricted to limestone and dolomite outcrops and is known only from western Millard and Beaver counties. Habitat includes mixed shrub, pinyon-juniper, and grass community types. Elevational range of the plant extends from 5000 to 6500 feet. Recent fieldwork has indicated that the species is somewhat widespread, but never common.

Beaver County: T26S, R15W, ME Jones s.n., Type-POM (1906); T27S, R16W, K. Ostler & D Anderson 1267, 1270 (1978); T26S, R16W, K Ostler & D Anderson 1321 (1978); T27S, R16W, SL Welsh & M Chatterley 19530 (1980); T26S, R16W, SL Welsh & M Chatterley 19716 (1980); T27S, R16W, SL Welsh & M Chatterley 19732 (1980). Millard County: West Desert, WP Cottam 5628 (no date); Whitesage Valley, BF Harrison 6366 (1935); T20S, R8W, BF Harrison 10161 (1941); T24S, R17W, WP Cottam 8510 (1941); T25S, R18W, B Maguire 20876 (1941); T25S, R18W, BF Harrison 11631 (1950); T25S, R18W, RC Holmgren 265 (1963); T24S, R17W, MG Barlow 49 (1964); T25S, R18W, ND Atwood 1502 (196_); T24S, R17W, J Jefferies 161 (1972); T25S, R17W, SL Welsh et al. 13298, 13304 (1976); T25S, R18W, 14492 (1976); T25S, R18W, L Hart, s.n. (1977); T24S, R17W, K Ostler & D Anderson 1033 (1978); T25S, R18W, K Ostler & D Atwood 1229 (1978); T25S, R17W, SL Welsh & M Chatterley 19496 (1980); T25S, R18W, SL Welsh & M Chatterley 19573 (1980).

Sphaeralcea psoraloides Welsh

Map 103

Family: Malvaceae.
Original citation: Great Basin Naturalist 40: 36. 1980.
Federal designation: endangered, category 2.

The type population of this recently described globemallow is located several miles west of Hanksville in Wayne County. Other populations were discovered on the San Rafael Swell several miles north of the type locality in Emery County. A Grayia-Ephedra community is habitat for the species. It is associated geologically with clay barrens of the Carmel Formation. Elevational range extends from 4600 to 6000 feet.

Emery County: T26S, R10E, JG Harris 857 (1980); T26S, R9E, JG Harris 860 (1980); T25S, R7E, JG Harris 986 (1980); T26S, R8E, JG Harris 1009 (1980). Wayne County: T27S, R8E, SL Welsh 13345, 13348, Holotypes (1976).

Sphaeromeria capitata Nutt.

Map 104

Family: Asteraceae.
Federal designation: none.
UNPS recommendation: category 2.

This rare species is known from only one location in Utah, along the east fork of the Sevier River in Garfield County. However, the species also occurs in Montana and Wyoming. The plant grows with western bristlecone pine on ridges of Cedar Breaks limestone at an elevation of approximately 7800 feet.

Garfield County: T35S, R4W, JL & CG Reveal 1023 (1968).

Sphaeromeria ruthiae Holmgren, Shultz, & Lowrey

Map 105

Family: Asteraceae.
Federal designation: threatened, category 2.

The Zion tansy is known only from Zion National Park in Washington County. Habitat for the plant is the crevices and canyon walls of the Navajo Sandstone Formation. Range of elevation is about 4800 feet.

Washington County: T41S, R10W, Nelson 10098, Paratype-NY-UTC (1972); T41S, R10W, Holmgren, Shultz, & Lowery 16003, Isotype (1974); east of Parunuweap Canyon, park boundary, J Anderson (1979); T40S, R10W, Neese and Kass 12609 (1982).

Swertia gypsicola Barneby

Map 106

Family: Gentianaceae.
Federal designation: endangered, category 1.

The green gentian has previously been known only from Nevada, where it occurs in Nye County. In 1983 Cronquist collected the taxon north of Garrison in Millard County, Utah. The plant grows on exposed calcareous slopes in a salt desert shrub community, where it is associated with other mound-forming plants and sagebrush. Elevation ranges from 5150 to 5600 feet.

Millard County: T20S, R19W, A Cronquist 11838 (1983).

Thelypodiopsis argillacea Welsh & Atwood

Map 107

Family: Brassicaceae.
Federal designation: endangered, category 1.

Several populations of this species are known, but they are restricted in location to near the east slope of Big Pack Mountain in Uintah County. Habitat for the species is a desert shrubland and scattered pinyon-juniper community on the Green River Shale

Formation. Elevation is approximately 5000 feet. This species was transferred to Schoencrombe by Rollins (1982).

Uintah County: T11S, R20E, D Atwood 6627, Holotype (1976); T11S, R20E, Neese & England 4284 (1978); T11S, R20E, E Neese & JS Peterson 4620 (1978); T11S, R20E, E Neese 4962, 4972 (1978); T11S, R20E, KM Mutz, non-BRY (1979); T10S, R18E KM Mutz, non-BRY (1979); T10S, R19E, KM Mutz, non-BRY (1979); T11S, R19E KM Mutz, non-BRY (1979).

Thelypodiopsis barnebyi Welsh & Atwood in Welsh

Map 108

Family: Brassicaceae.
Citation: Brittonia 33: 300. 1981.
Federal designation: threatened, category 2.

The Barneby thelypody is known only from the type locality near Sy's Butte on the San Rafael Reef in Emery County. It occurs in a salt desert shrub community dominated by *Ephedra* and shrubby *Eriogonums* on rocky outcrops and in sandy soil. Elevational range of the population extends from 5400 to 5750 feet. This species was transferred to Schoencrombe by Rollins (1982).

Emery County: T26S, R9E, JG Harris 840, Holotype (1980); T26S, R9E, JG Harris 1007, 1008, Paratypes (1980); T26S, R9E, SL Welsh 20345, Holotype (1981); T26S, R9E, D Atwood, S Goodrich 8646, 8644 (1982).

Townsendia aprica Welsh & Reveal

Map 109

Family: Asteraceae.
Federal designation: endangered, category 1.

The last-chance townsendia occurs in two Utah counties, Emery and Sevier. The plant grows on tuffaceous strata of the Mancos Shale Formation in a mixed pinyon-juniper and grassland community. Elevational range extends from 6000 to 7400 feet.

Emery County: T24S, R6E, M Wright 51 (1971), T24S, R6E, Neese & White 7321, 7330 (1979); T24S, R6E, S White & G Moore 62, 65, 91 (1979); T24S R6E, JG Harris 647 (1980). Sevier County: T24S, R5E, Reveal & Welsh 721, Holotype (1966), T24S, R5E, SL Welsh et al. 8972 (1969); T24S R5E, E Neese & S White 3017 (1977).

Trifolium andersonii Gray var. *friscanum* Welsh

Map 110

Family: Fabaceae.
Original citation: Great Basin Naturalist 38: 355. 1978.
Federal designation: endangered, category 1.

This newly described variety was known to occur only on the rocky ridges and limestone gravels of the San Francisco Mountains, near Frisco in Beaver County. However, it was discovered in 1982 in similar habitat areas on the Tunnel Spring Mountains in the Desert Experimental Range in Millard County. It has been regarded as endangered, but that designation should probably be tentative until additional information can be gathered. Elevational range of the plant is from 6700 to 8000 feet.

Beaver County: T27S, R13W, F Peabody et al. 406, Holotype (1976); T27S, R13W, K Ostler & D Anderson 1206, 1260 (1978); T26S, R13W, K Ostler & D Anderson 1349 (1978); T27S, R13W, SL Welsh & M Chatterley 19526 (1980); T27S, R13W, SL Welsh & M Chatterley 19658 (1980). Millard County: T24S, R17W, S Goodrich 16953 (1982); T24S, R17W, S Goodrich 16972 (1982).

Xylorhiza cronquistii Welsh & Atwood

Map 111

Family: Asteraceae.
Original citation: Brittonia 33: 302. 1981.
Federal designation: threatened, category 2.

Only a single large and uniform population of the Cronquist xylorhiza is known, and this occurs near Horse Mountain in north central Kane County. The plant is confined to the badlands topography of the Kaiparowits Formation and is associated with a broad-leaved phase of *Grayia brandegei*. Elevation of the species is approximately 6600 feet.

Kane County: T38S, R2E, SL & SL Welsh 12819, Holotype (1975).

PLANTS NO LONGER UNDER REVIEW

Plants that have previously been considered in categories 1 or 2 but which were downgraded to category 3 in the November 1983 *Federal Register* are dicussed below. No distribution maps are included for these species. All but one of the taxa are category 3C plants, meaning that the distribution of the plant is wider than previously supposed or that there are no current threats to the taxa. However, if additional threats to these species are discovered, the plants could once again become candidates for listing.

Angelica wheeleri Wats.

Family: Apiaceae.
Federal designation: category 3C.

The Wheeler angelica is a rare plant, apparently restricted to the northern and central parts of Utah. It is fairly widespread, one population having been located in each of five separate counties. However, the populations are extremely disjunct, and the reason for this distribution pattern is not known. Though the plant is no longer under review for listing, as additional information about the species is accumulated its status may change. *Angelica wheeleri* is a streamside or wet meadow species and grows at elevations ranging from lower foothills to approximately 10,000 feet.

Cache County: T12N, R2E, LC Higgins 10371 (1977). Juab County: T12S, R2E, S Goodrich 15862 (1981). Piute County: T27S, R1W, LC Higgins 4721 (1971). Sevier County: T26S, R2E, LC Higgins (1977). Utah County: T5S, R3E, Cottam 3845 (1928).

Astragalus chamaemeniscus Barneby

Family: Fabaceae.
Federal designation: category 3C.

The ground-crescent milkvetch was, until recently, considered restricted to east central Nevada, where it grows in Lincoln, White Pine, and Nye counties. However, during the 1981 field season it was collected on the Escalante Desert in Iron County, Utah. It occurs on hillsides and valley floors in deep sands derived from limestone formations, generally in a sagebrush community type. Elevation extends from 4900 to 6500 feet. Only one population is known from Utah, and so the plant is considered rare in this state even though its total distribution does not warrant current consideration for listing. Seven collections from Nevada are deposited at BRY.

Iron County: T33S, R17W, F Smith & S Jensen, s.n. (1981).

Astragalus consobrinus (Barneby) Welsh

Family: Fabaceae.
Federal designation: category 3C.

The Bicknell milkvetch is based on *A. castaneiformis* var. *consobrinus*. Collections of the species at BRY are from three counties. However, Barneby's discussion of the basionym includes two additional counties as part of the distribution. This milkvetch grows in alluvial soils of varied compositions, usually on open gravelly knolls and hillsides in sagebrush-grasslands and pinyon-juniper communities. Elevational range extends from 6000 to 8000 feet.

Emery County: T23S, R6E, Neese & White 7355 (1979); T20S, R6E, R Foster 8262 (1979); T19S, R11E, D Atwood and B Thompson (1983). Sevier County: T26S, R4E, D Atwood and B Thompson 7597 (1980). Wayne County: T28S, R4E, Ripley & Barneby 8605 NY (1947); T29S, R5E, NH Holmgren et al. 2092 (1965); T28S, R3E, SL Welsh et al. 13088 (1976); T28S, R3E, SL Welsh, et al. 13090 (1976); T30S, R6E, SL Welsh 13356 (1976); T28S, R4E, SL Welsh & G Moore 13837 (1976); T27S, R4E, SL Welsh 14973 (1977); T27S, R5E, SL and ER Welsh 21214 (1982).

Astragalus henrimontanensis Welsh

Family: Fabaceae.
Federal designation: category 3C.

Distribution of the Dana milkvetch is restricted to Garfield County where all but one population occurs on the Henry Mountains. The other is from the Aquarius Plateau. This species grows in quaternary alluvium and colluvium over various geologic strata in a mixed ponderosa pine, pinyon, juniper, and sagebrush community. Elevational range extends from 7400 to 9200 feet.

Garfield County: T31S, R10E, A Cronquist and N Holmgren 9296 (1961); T33S, R3E, NH Holmgren et al. 2106 (1965); T32S, R10E, SL Welsh 9817 (1970); T31S, R10E, B Wood s.n. (1972); T31S, R10E, E Neese 1697 (1976); T31S, R10E, E Neese 1738a (1976); T31S, R10E, E Neese & S White 3087 (1977); T31S, R10E, E Neese, S White 3415 (1977); T32S, R10E, E Neese and S White 3459 (1977); T33S, R11E, E Neese & S White 4096 (1977); T31S, R10E, E Neese 5061 (1978); T33S, R10E, E Neese 5128 (1978); T34S, R11E, E Neese & A Tye 9948 (1980).

Astragalus lentiginosus Dougl. ex Hook. var. *pohlii* Welsh & Barneby

Family: Fabaceae.
Citation: Iselya 2: 1–2. 1981.
Federal designation: category 3C.

The Pohl milkvetch is known from three localities in Tooele County, one from south of Benmore, another from north of Vernon, and the third from Skull Valley. This unique member of the lentiginosus complex grows in silty gravels of a greasewood-sagebrush community type at an elevation ranging from 4350 to 5500 feet.

Tooele County: T9S, R4W, JD Walker s.n., Paratype (1962); T7S, R5W, SL Welsh 16498, 16501, Paratype (1978); T8S, R5W, SL Welsh et al. 16743, Holotype (1978); T4S, R8W, A Taye 1332 (1981).

Astragalus lutosus Jones

Family: Fabaceae.
Federal designation: category 3C.

Populations of the Dragon milkvetch are centered in Utah near the junction of the White River and the Colorado-Utah border in eastern Uintah County. However, the plant is abundant over a wide area and also occurs in Colorado. The species is confined to white shale outcrops of the Green River Shale Formation. Habitat for the taxon is a mixed desert shrub community, and elevational range extends from 5200 to 6950 feet. During the 1982 field season one dozen new collections of the species were made, twice as many as had been previously collected. Two of the recent collections come from Wasatch County, which extends the distribution of this species in Utah.

UINTAH COUNTY: White River, ME Jones, Isotype (1908); T12S, R25E, ME Jones, Paratype (1908); T12S, R24E, E Neese & JS Peterson 6103 (1978); T12S, R24E, L England 1772 (1979); T12S, R24E, L England 1775 (1979); T11S, R24E, SL Welsh 19617 (1980); T12S, R24E, E Neese & F Smith 11387, 11391 (1982); T11S, R24E, E Neese & C Fullmer 11468 (1982); T11S, R25E, E Neese & C Fullmer 11469, 11476 (1982); T12S, R24E, K Thorne & B Neely 1791 (1982); T12S, R25E, K Thorne et al. 1827 (1982); T11S, R25E, E Neese & C Fullmer 11487 (1982); T10S, R25E, K Thorne & C Fullmer 1937 (1982); T10S, R25E, E Neese & C Fullmer 11677 (1982); T10S, R25E, E Neese & F Smith 12054 (1982). WASATCH COUNTY: T5S, R11W UBM, S Goodrich, 11790, 11793 (1982); T5S, R11W UBM, S Goodrich et al. 19733 (1983).

Astragalus monumentalis Barneby

Family: Fabaceae.
Federal designation: category 3C.

The monument milkvetch occurs in San Juan County from Canyonlands National Park to west of Natural Bridges National Monument and in Garfield County west of the Colorado River, near Hite. The plant grows on exposed rim rock and slick rock of the Cedar Mesa Sandstone Formation in pinyon-juniper and warm desert shrub communities. Elevational range extends from 4000 to 6200 feet.

GARFIELD COUNTY: T33S, R14E, SL Welsh 5214 (1966); T33S, R14E, SL Welsh & G Moore 7122 (1968); T32S, R12E, KD Kaneko 24 (1971); T33S, R14E, SL Welsh 11027 (1971); T32½S, R15E, A Cronquist 11382 (1976); T33S, R14E, E Neese & S White 2816 (1977); T33S, R14E, SL Welsh 20352 (1981); T33S, R14E, KD Heil 1622 (1983); T33S, R14E, SL and BT Welsh, M Chatterley 21953 (1983); T32S, R14E, SL Welsh 21784 (1983). SAN JUAN COUNTY: T36S, R16E, BF Harrison 11595 (1950); T30S, R19E, SL Welsh et al. 2888 (1964); T31S, R19E, SL Welsh et al. 2901 (1964); T30S, R19E, SL Welsh et al. 2954 (1964); T30S, R19E, G Moore 307 (1965); T30S, R19E, G Moore 348a (1965); T34S, R15E, SL Welsh 5191 (1966); T35S, R5E, SL Welsh 5211 (1966); T34S, R15E, SL Welsh 5212 (1966); T30S, R19E, SL Welsh 7030 (1968); T30S, R19E, SL Welsh et al. 8900 (1969); T33S, R14E, CS Schoener 24 (1971); T36S, R15E, D Atwood 7503 (1980); T30S, R19E, SL Welsh et al. 21113 (1982); T32S, R18E, SL Welsh 21144 (1982); T33S, R14E, BT, SL & ML Welsh 1428 (1983).

Cryptantha johnstonii Higgins

Family: Boraginaceae.
Federal designation: category 3C.

Occurrences of the Johnston catseye are known only from an area in the middle of Emery County where the plant grows on low rolling hills and sandy clay soil of the Carmel Formation. Associated vegetative types include mixed desert shrub and scattered pinyon and juniper communities. Elevational range of the species extends from 5200 to 5800 feet.

EMERY COUNTY: San Rafael, Harrison 5628 (1931); T19S, R11E, Higgins 1310, Holotype, Isotype (1968); T20S, R13E, LC Higgins 3520 (1970); T20S, R13E, LC Higgins 3522 (1970); T22S, R8E, A Cronquist 11417 (1976); T20S, R9E, NH Holmgren et al. 9111 (1979); T23S, R9E, D Atwood 7211 (1979); T22S, R8E, SL Welsh 20457 (1981); T19S, R12E, D Atwood 9236 (1983).

Eriogonum clavellatum Small

Family: Polygonaceae.
Federal designation: threatened, category 2.

The Comb Wash buckwheat is restricted in distribution to a small area west of Bluff in San Juan County near Comb Wash. It occurs on the clay or sandy clay slopes of the Moenkopi Formation in the desert shrub community. Elevation extends from 3300 to 4500 feet. The species has also been discovered in Montezuma County, Colorado.

SAN JUAN COUNTY: Barton Range, Eastwood 132, Type-NY (1895); T42S, R21E, Maguire 5853 (1933); T40S, R20E, Reveal et al. 840 (1967); T40S, R20E, Atwood 2472 (1970); T40S, R20E, Welsh & Atwood 9977 (1970); T40S, R20E, D Atwood 7183 (1979); T41S, R19E, D Atwood 7872 (1981).

Eriogonum corymbosum Benth.
var. *matthewsae* Reveal

Family: Polygonaceae.
Federal designation: category 3C.

The Matthews buckwheat is known from near Zions Canyon in Washington County. Taxonomic problems exist with this variety. It is probable that it should be considered as a morphological subunit of another species in the genus. The taxon occurs on the purplish siltstone and sandy loam soil of the Chinle formation at 3800 to 4000 feet elevation.

Washington County: T42S, R10W, Welsh et al. 9509, Isotype (1969); T41S, R10W, R Foster 5663 (1977); T42S, R10W, JD Brotherson 3124 (1982); T41S, R10W, J Anderson (1982).

Eriogonum nanum Reveal

Family: Polygonaceae.
Federal designation: category 3B.

High elevation talus slopes and limestone outcrops in the subalpine conifer zone are habitat for this species. Elevation ranges from 8,500 to 10,050 feet. Until recently, occurrences of the dwarf buckwheat were considered restricted to Weber and Box Elder counties. However, in 1977 the plant was collected on Mt. Bartles, in Carbon County. Current taxonomic studies suggest that the variation attributed to this taxon may stem from ecological responses and that the plant may not be worthy of specific designation.

Box Elder County: T8N, R1W, JL & CG Reveal 4608, 4609 (1976). Carbon County: T13S, R14E, S Welsh & S Clark 15905 (1977). Weber County: T8N, R1, Reveal & Holmgren 665, Type (1964); T5N, R1E, SL Clark 2224 (1972); T8N, R1W, SL Clark 2327 (1972).

Eriogonum tumulosum (Barneby) Reveal

Family: Polygonaceae.
Federal designation: category 3C.

This small mat-forming buckwheat occurs primarily in central Duchesne County. However, several populations exist in Emery County, one population has been reported from Uintah County, and one population has been discovered in Juab County. The plant grows in clay soils and sandstone ledges and is associated with a mixed desert shrub, pinyon-juniper community type. Elevational range extends from 5700 to 6600 feet.

Duchesne County: T3S, R6W UBM, NH Holmgren et al. 1941 (1965); T4S, R5W UBM, JL & CG Reveal 849 (1967); T2S, R5W UBM, JL Reveal 964 (1968); T3S, R5W UBM, E Neese 4414 (1978); T3S, R5W, Welsh 18516 (1979); T1S, R7W UBM, R Foster 7846 (1979); T4S, R6W UBM, E Neese & SL Welsh 8897 (1980); T3S, R6W UBM, B Albee 5015 (1981); T4S, R5W UBM, K Thorne & C Fullmer 1624, 1739 (1982); T3S, R6W UBM, S Goodrich 16749 (1982); T4S, R5W UBM, K Thorne, C Fullmer 1739 (1982). Emery County: San Rafael Swell, WP Cottam 5233 (1932); T19S, R13E, LC Higgins & JL Reveal 1297 (1968); T24S, R11E, ND Atwood 1849 (1969); T24S, R9E, JG Harris 969 (1980). Juab County: T17S, R2W, S Goodrich 18137 (1983). Uintah County: T3S, R21E, S Goodrich 5686 (1976).

Gutierrezia sarothrae (Pursh) Britt. & Rusby var. *pomariensis* Welsh

Family: Asteraceae.
Federal designation: category 3C.

This Uinta Basin endemic is known from Duchesne and Uintah counties but occurs primarily near Vernal. It grows in clay, silt, or sandy clay substrates, on semibarren sites, in desert shrub and scattered juniper community types. This is a unique but somewhat common phase of *G. sarothrae*, and much possible habitat occurs within its relatively limited distributional range. Elevations extend from 4900 to 7000 feet.

Duchesne County: T1S, R4W UBM, E Neese & SL Welsh 8274 (1979). Uintah County: T4S, R24E, J Brotherson 800, 803 (1965); T4S, R23E, J Brotherson 831 (1965); T4S, R20E, SL Welsh & G Moore 6754 (1967); T6S, R24E, ND Atwood & LC Higgins 5853 (1973); T6S, R23E, E Neese & JS Peterson 6083 (1978); T5S, R21E, E Neese 6325 (1978); T5S, R22E, E Neese & L England 6686, 6689 (1978); T7S, R21E, BT Welsh & G Moore 249 (1979); T1S, R4W UBM, E Neese, SL Welsh 8274 (1979); T1N, R1E UBM, S Goodrich 13688 (1979); T4S, R24E, E Neese & M Chatterley 9887 (1980); T5S, R19E, Neese et al. 11017 (1981); T5S, R25E, E Neese & J Trent 12294 (1982); T6S, R25E, E Neese & J Trent 12315 (1982); T5S, R25E, E Neese & J Trent 12334 (1982).

Lomatium junceum Barneby & Holmgren

Family: Apiaceae.
Original Citation: Brittonia 31: 96. 1979.
Federal designation: category 3C.

This clump-forming lomatium was originally known only from the San Rafael Swell in Emery County, but has since been located on Fishlake National Forest lands in the southeastern corner of Sevier County, and along the Waterpocket Fold in both Wayne and Garfield counties. Habitat for the plant is barren clay draws and shaley hills of the Moenkopi formation in desert shrub and pinyon-juniper communities. Elevational range of the species extends from 5300 to 7700 feet.

Emery County: T20S, R11E, LC Higgins & JL Reveal 1268 (1968); T20S, R11E, SL Welsh 10963 (1971); T20S, R11E, S Daines 26 (1971); T20S, R11E, CS Schoener 59 (1971); T22S, R12E, M Wright 68 (1971); T20S, R11E, B Albee 2594 (1975); T22S, R11E, Welsh et al. 14767

(1977); T20S, R11E, SL Welsh 14770 (1977); T21S, R6E, SL Welsh 14783 (1977); T25S, R6E, SL Welsh 14794 (1977); T20S, R6E, S Clark & K Taylor 2463 (1977); T21S, R6E, ME Lewis 5366 (1978); T22S, R6E, S White 16, 95 (1979); T22S, R10E, JG Harris 680 (1980); T20S, R6E, D Atwood 7523 (1980); T25S, R10E, S Goodrich & D Atwood 16597 (1982). Garfield County: T34S, R7E, S Goodrich & SL Welsh 15648 (1981). Sevier County: T26S, R4E, D Atwood 7601 (1980). Wayne County: T32S, R7E, E Neese 11319 (1982); T32S, R7E, S Goodrich & D Atwood 16567 (1982).

Lygodesmia entrada Welsh & Goodrich

Family: Asteraceae.
Original citation: Great Basin Naturalist 40: 83. 1980.
Federal designation: category 3C.

This white-flowered skeleton plant with a characteristic bird's nest appearance is only known from west-northwest of Moab in Grand County and from southwest of Greenriver in Emery County. It is found growing on the Entrada Sandstone Formation in a juniper community type at an elevation of 4800 feet. It is related to the more common *L. arizonica*; however, its features are strikingly different from other plants of *Lygodesmia* in Utah.

Grand County: T24S, R21E, JS Allan 132 (1972); T24S, R19E, SL & SL Welsh 16725, Holotype (1978). Emery County: T22S, R14E, K Despain 401 (1978).

Parrya rydbergii Botsch.

Family: Brassicaceae.
Federal designation: category 3C.

The Rydberg parrya is known from near Bald Mountain in Summit County, Leidy Peak on the border of Uintah and Daggett counties, and Dead Horse Pass and the King's Peak area in Duchesne County. The plant is restricted to a habitat of rocky talus slopes and a spruce or alpine tundra community type. It is a high elevation species usually occurring between 10,500 and 12,200 feet.

Daggett County: Yellowstone Pass, C Lambert and CL Woods, USFS-INT (1926); T2N, R17E, AH Holmgren 7135 (1947). Duchesne County: T4N, R4W UBM, Murdock 54 (1950); T4N, R4W UBM, SL Welsh, E Neese, D Atwood 18933 (1979); T5N, R4W UBM, SL Welsh, E Neese, D Atwood 19010 (1979); T4N, R2W, SL Welsh, E Neese, D Atwood 19042 (1979). Summit County: Uinta Mtns, S Watson 54, Type-NY (1869); Uinta Mtns, ME Jones s.n. (1890); T1S, R11E, Weins 4959 (1974); T2N, R11E, Ostler 677 (1977); T1S, R9E, Ostler & McKnight 1628 (1978). Uintah County: T4N, R1E UBM, Waite 252, 297 (1971); T1S, R19E, D Atwood et al. 7955 (1981).

Sphaeralcea leptophylla (Gray) Rydb. var. *janeae* Welsh

Family: Malvaceae.
Original citation: Great Basin Naturalist 40: 36. 1980.
Federal designation: category 3C.

This variety of globemallow has been observed only in the area of the type collections at Canyonlands National Park, but threats seem to be minimal to the plant. It occurs on sandy slopes in a blackbrush community type along the White Rim road.

San Juan County: T29S, R18E, SL Welsh 7064, Paratype (1968); T29S, R18E, SL Welsh 7085, Holotype (1968).

Yucca toftiae Welsh

Family: Agavaceae.
Federal designation: category 3C.

Known populations of the Toft yucca occur along or near Lake Powell in southeastern Utah. Two populations occur in hanging gardens on the east side of the lake in San Juan County. The other known localities occur on ridges or along tributaries adjacent to the western edge of Lake Powell in Kane County. Habitat for the plant is sandy alluvium and sandstone outcrops. Approximate elevation is 4300 feet.

Kane County: T42S, R7E, SL Welsh & G Moore 11779, Paratype (1972); T41S, R8E, ES Nixon et al. 11073 (1982). San Juan County: T41S, R9E, ND Atwood 4112, Paratype (1972); T41S, R9E, SL Welsh 11935a, Holotype (1973).

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Welsh, S. L., and K. H. Thorne. 1978. Illustrated manual of proposed endangered and threatened plants of Utah. U.S. Fish and Wildlife Service publication. 318 pp.

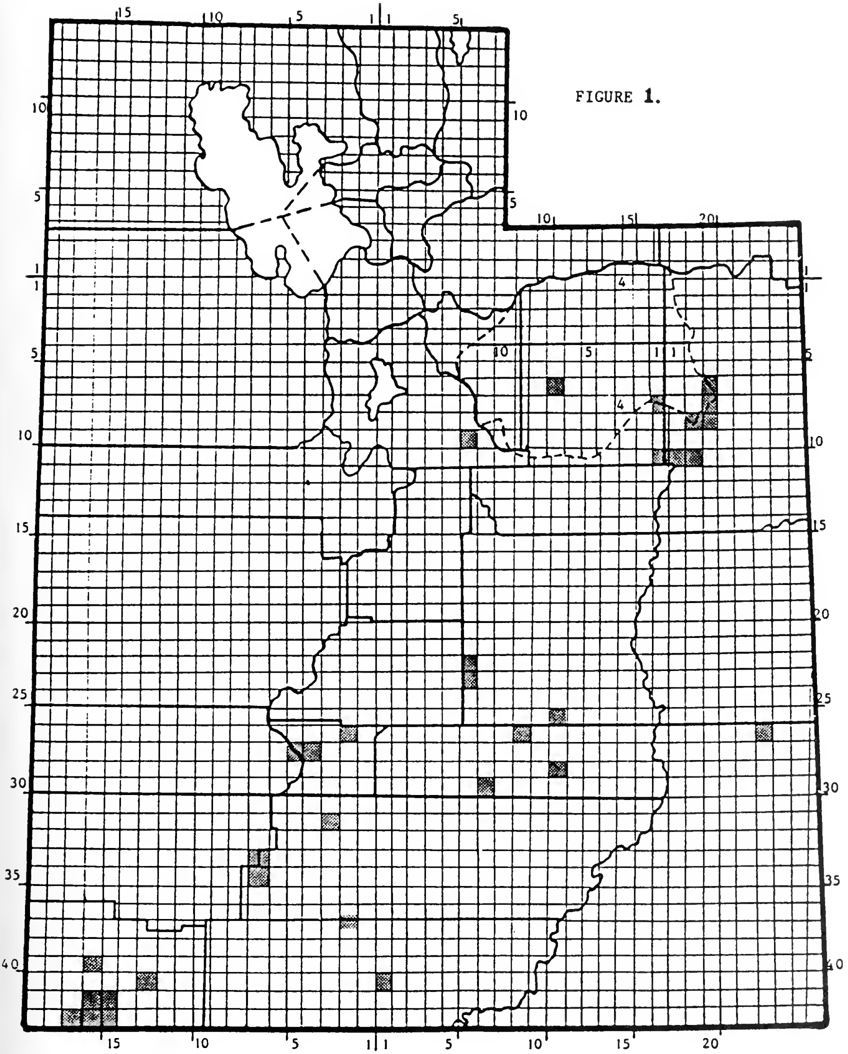


Fig. 1. Distribution by township and range of Utah's federally listed species.

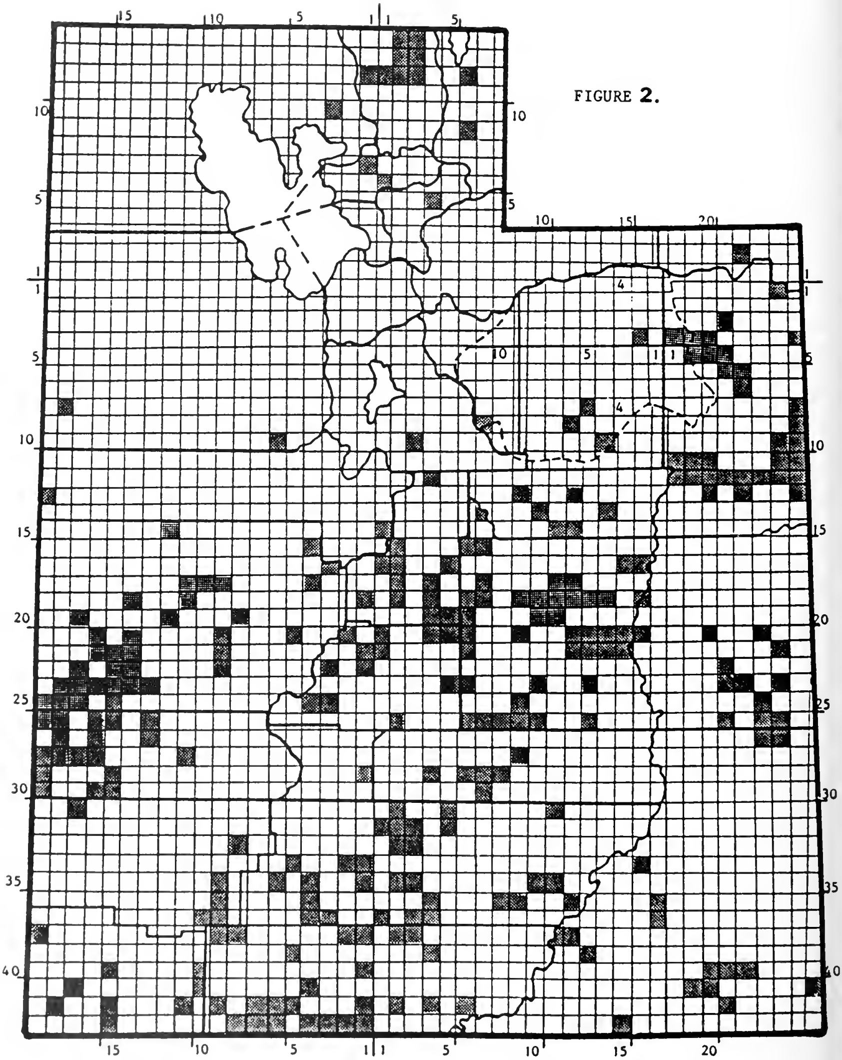
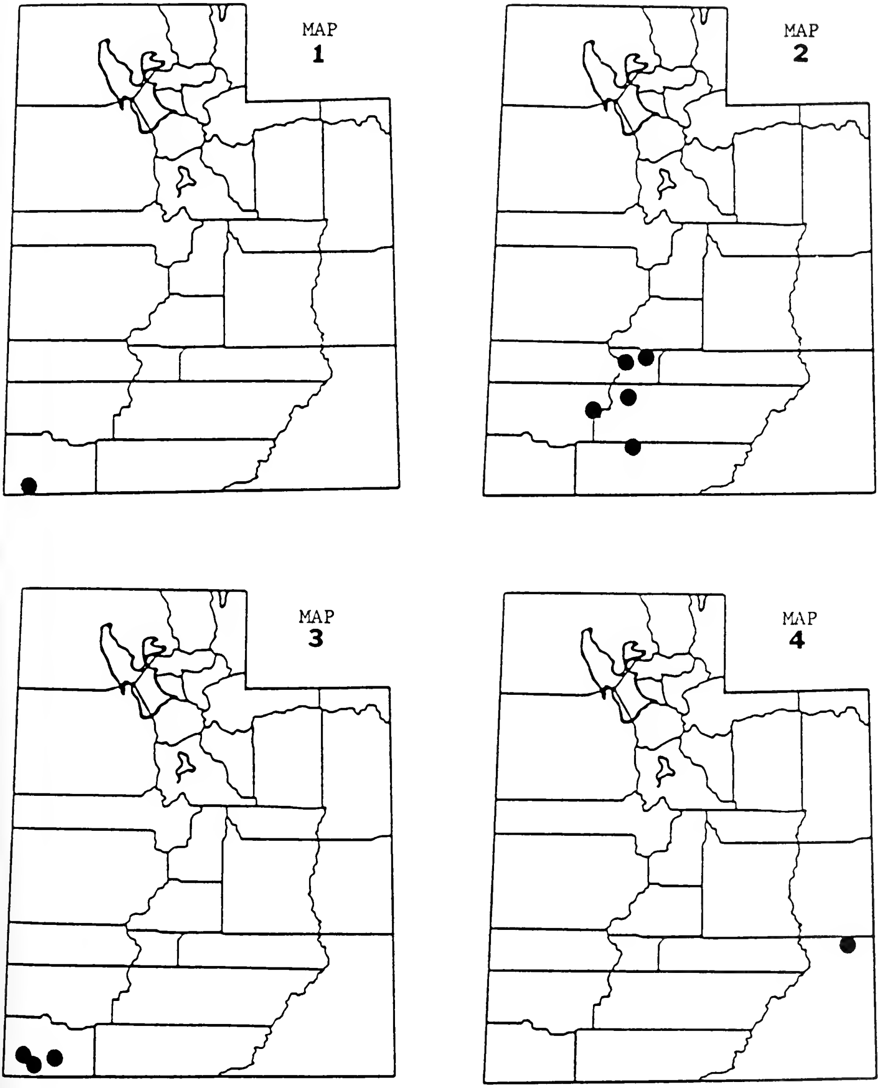
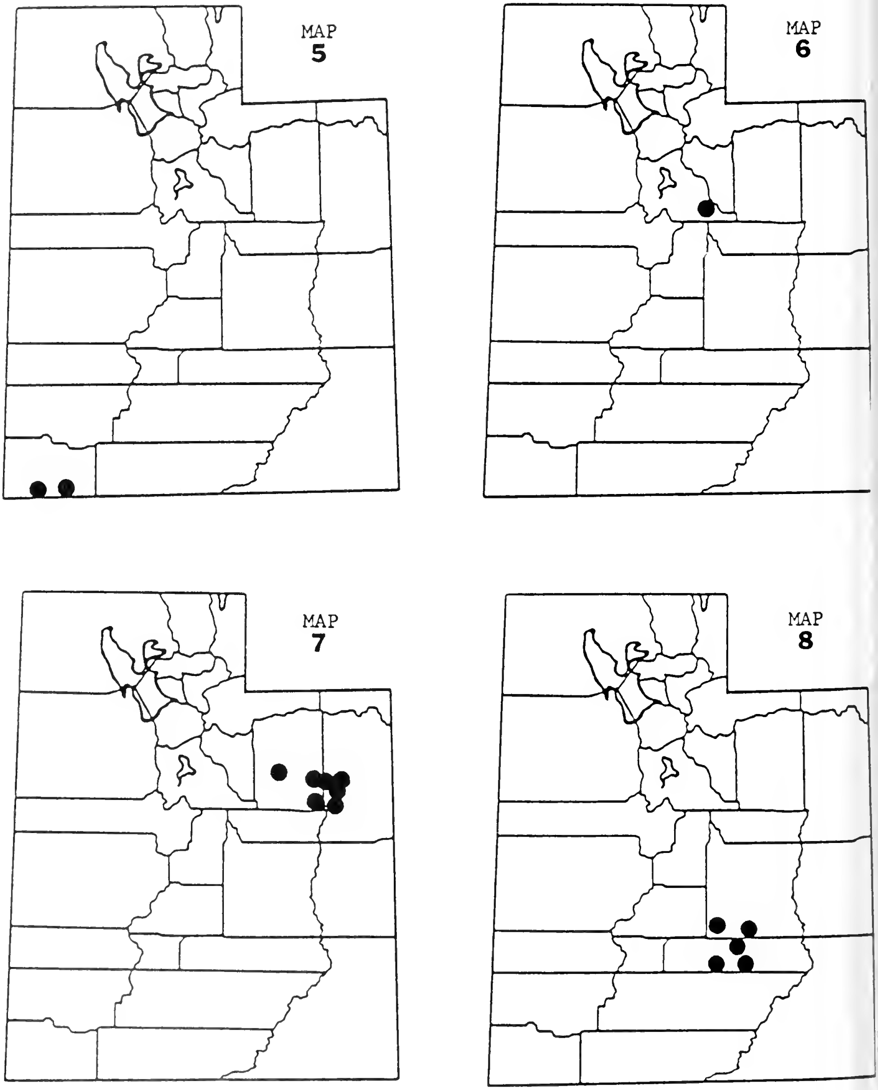


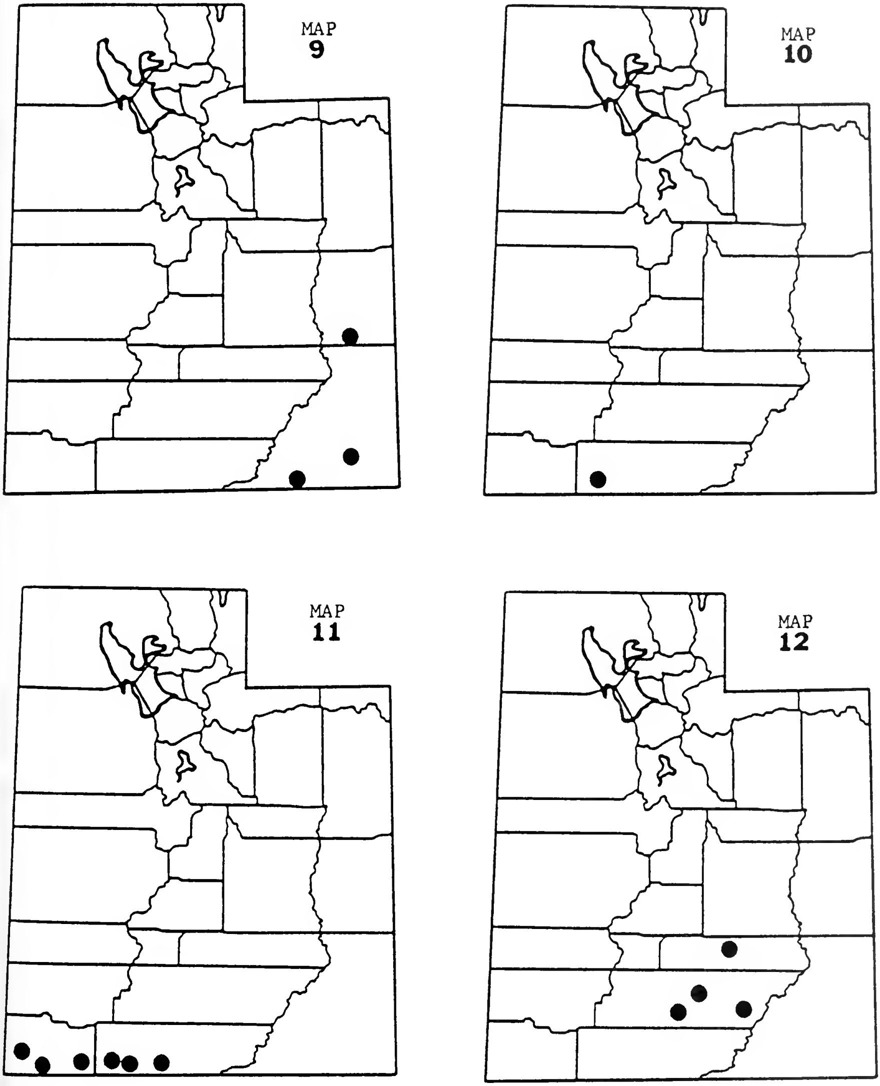
Fig. 2. Distribution by township and range of Utah's rare plant taxa under review for listing.



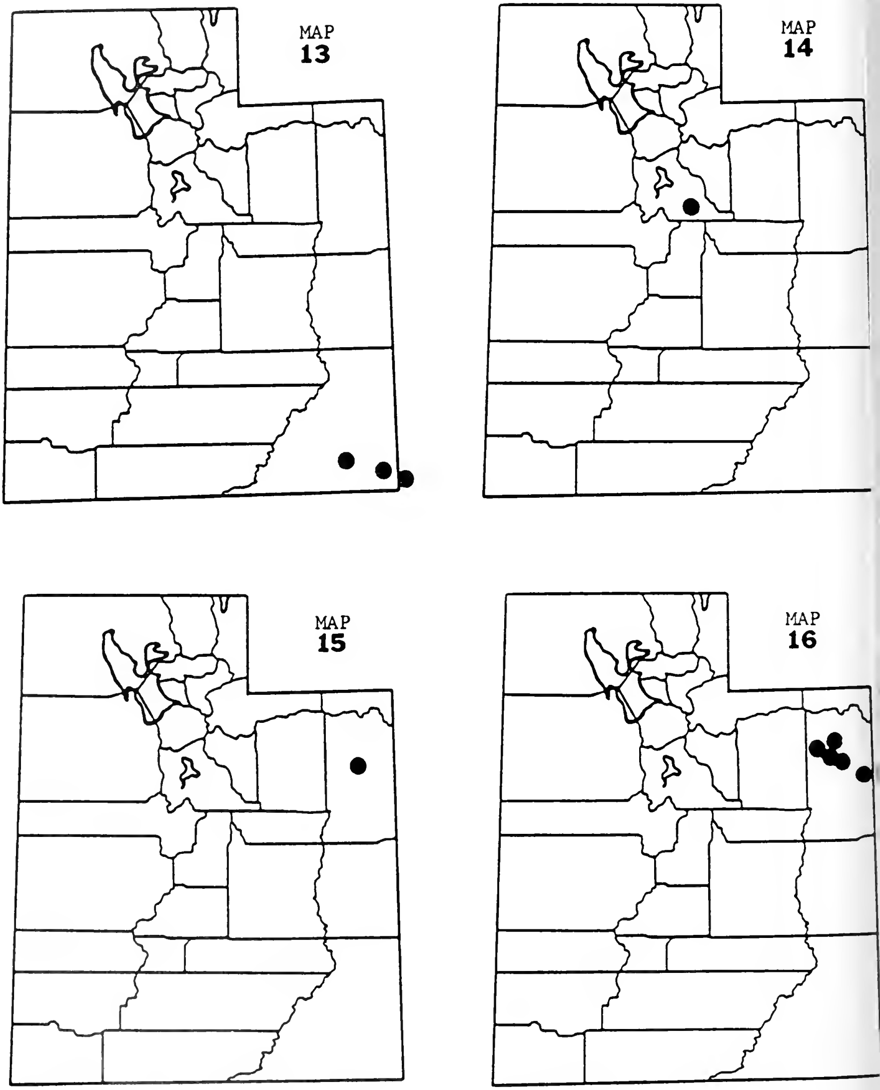
Maps 1–4. Distribution of (1) *Arctomecon humilis*, (2) *Astragalus perianus*, (3) *Echinocereus engelmannii* var. *purpureus*, and (4) *E. triglochidiatus* var. *inermis*.



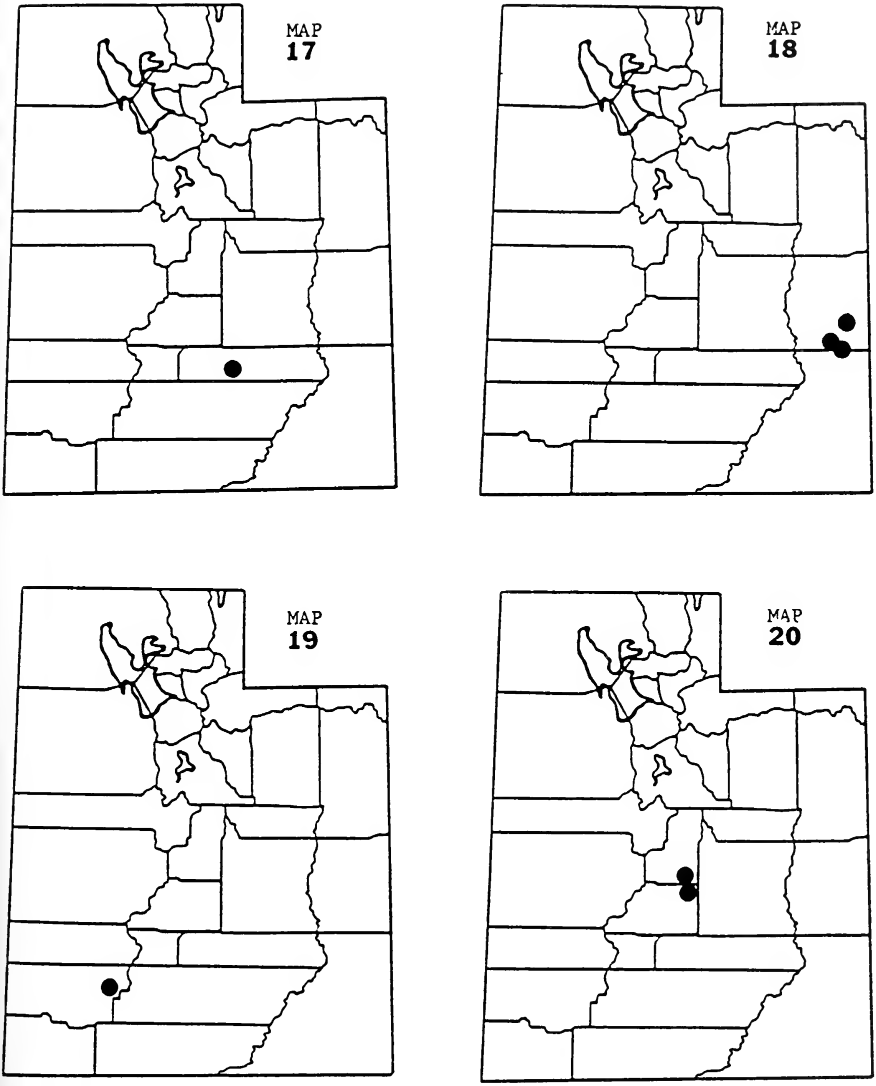
Maps 5–8. Distribution of (5) *Pediocactus sileri*, (6) *Phacelia argillacea*, (7) *Sclerocactus glaucus*, and (8) *S. wrightiae*.



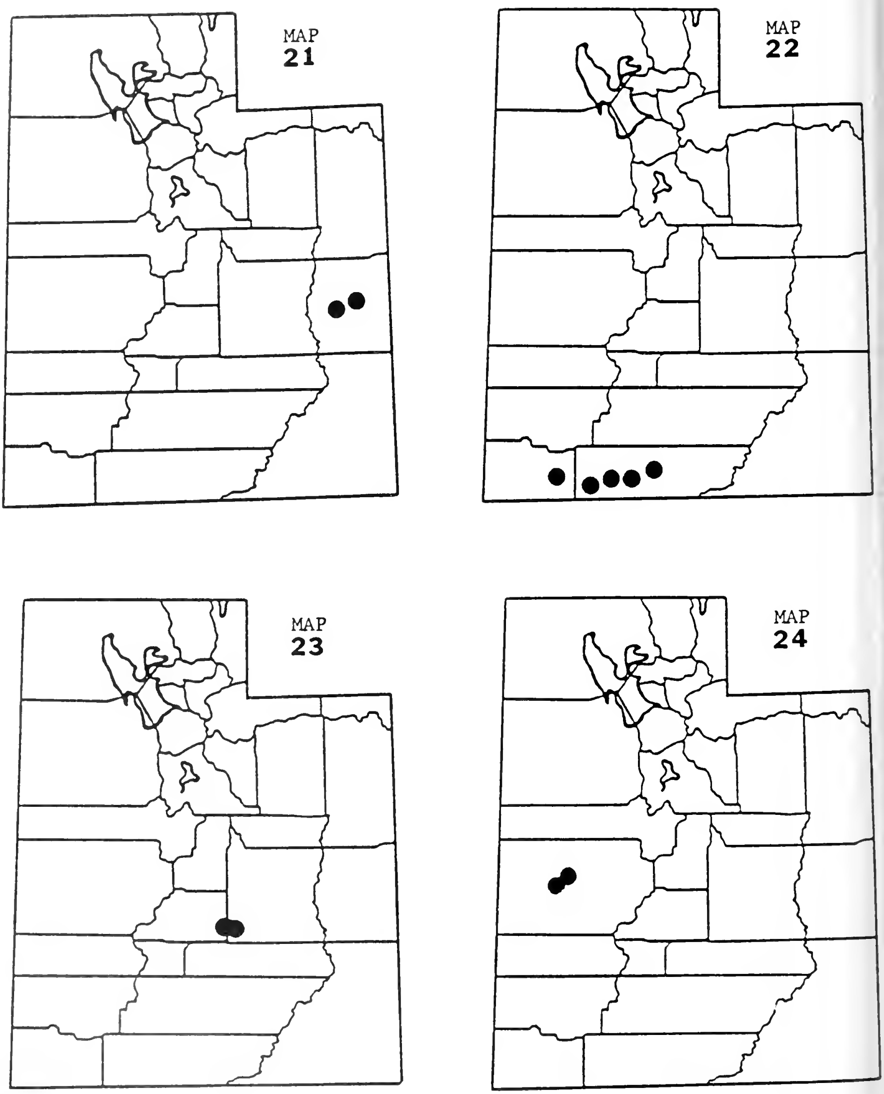
Maps 9–12. Distribution of (9) *Asclepias cutleri*, (10) *A. welshii*, (11) *Astragalus ampullarius*, and (12) *A. barnebyi*.



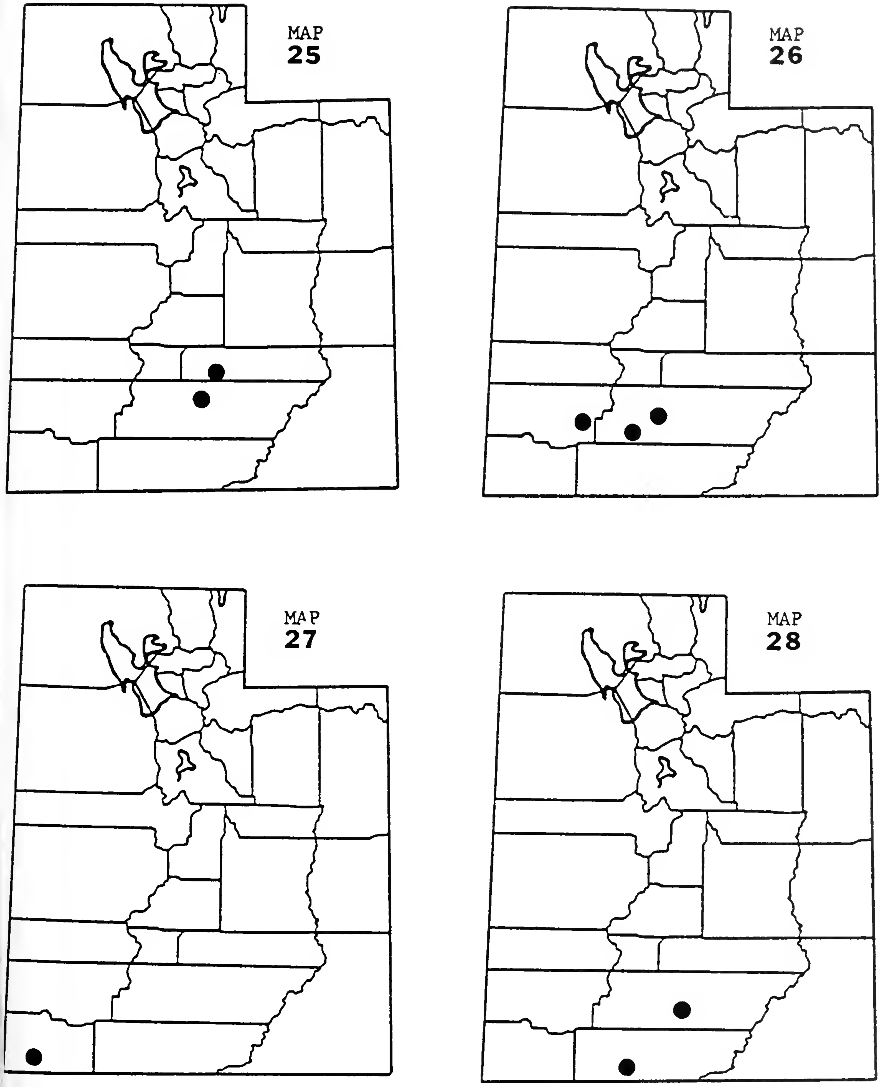
Maps 13–16. Distribution of (13) *Astragalus cronquistii*, (14) *A. desereticus*, (15) *A. equisolensis*, and (16) *A. hamiltonii*.



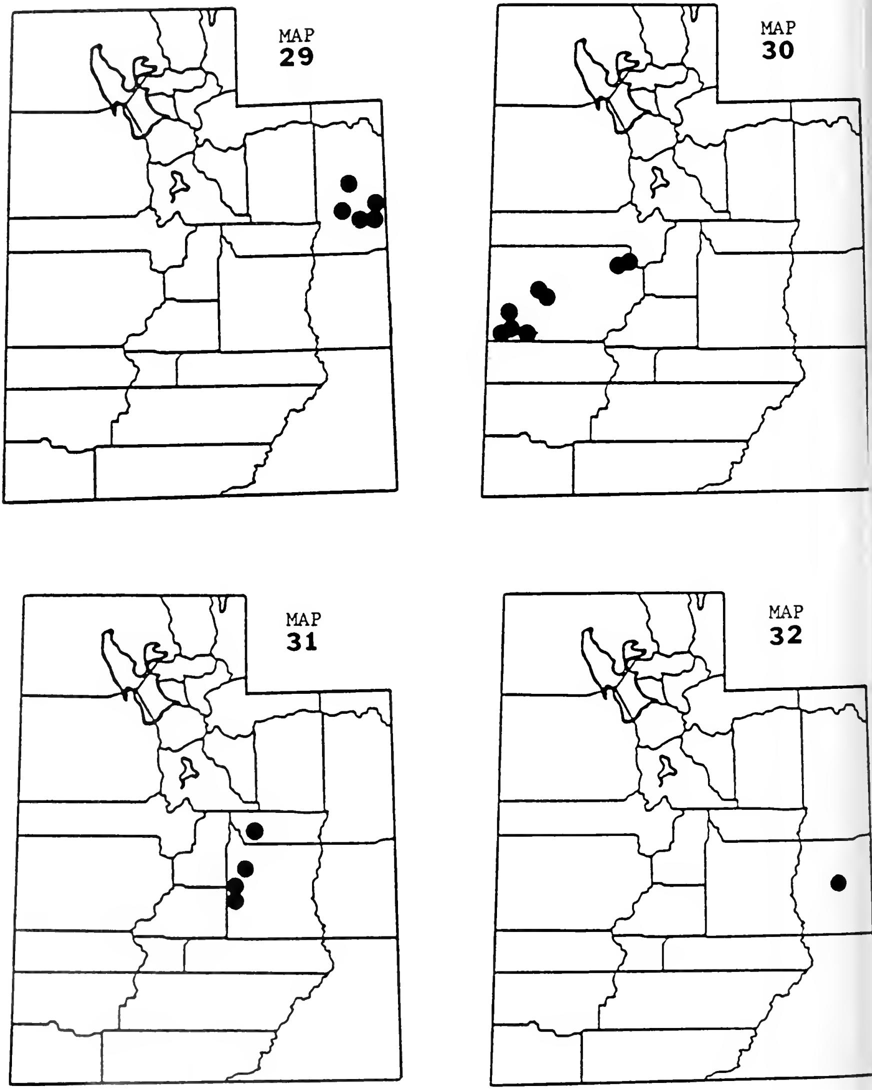
Maps 17–20. Distribution of (17) *Astragalus harrisonii*, (18) *A. iselyi*, (19) *A. lentiginosus* var. *ursinus*, and (20) *A. montii*.



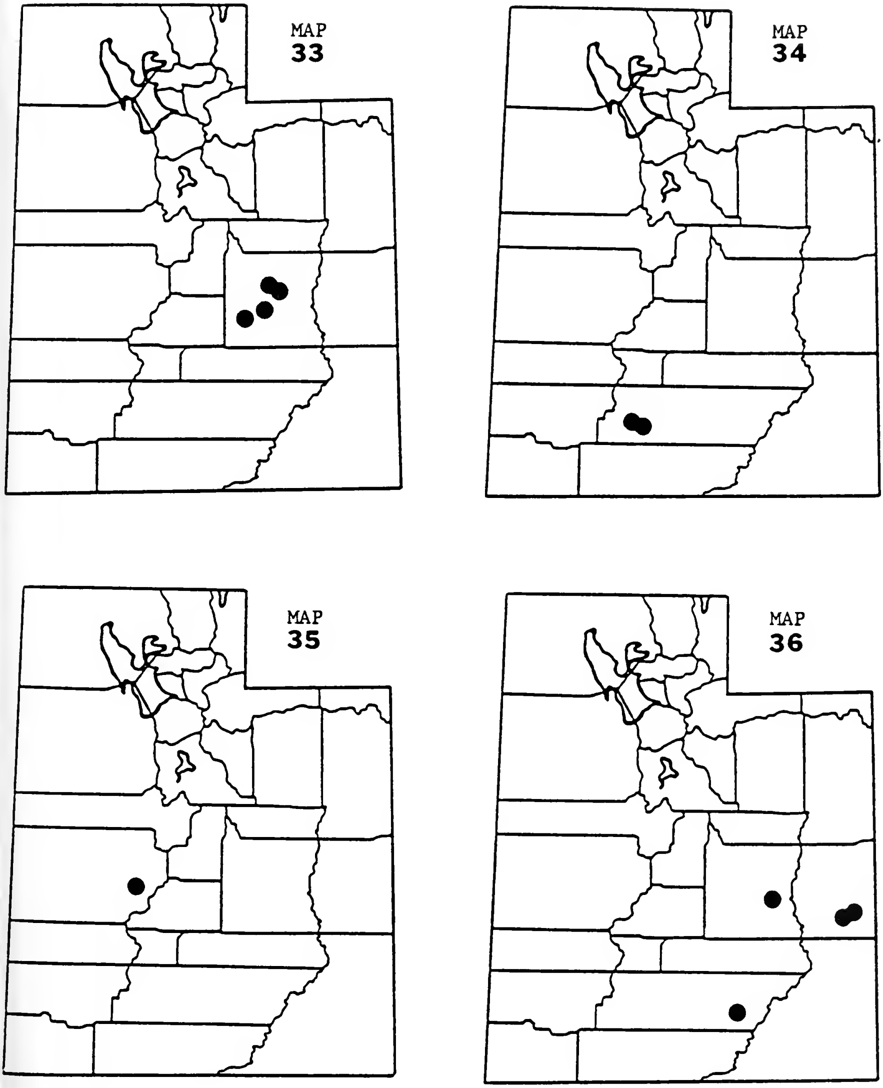
Maps 21–24. Distribution of (21) *Astragalus sabulosus*, (22) *A. striatiflorus*, (23) *A. subcinereus* var. *basalticus*, and (24) *A. uncialis*.



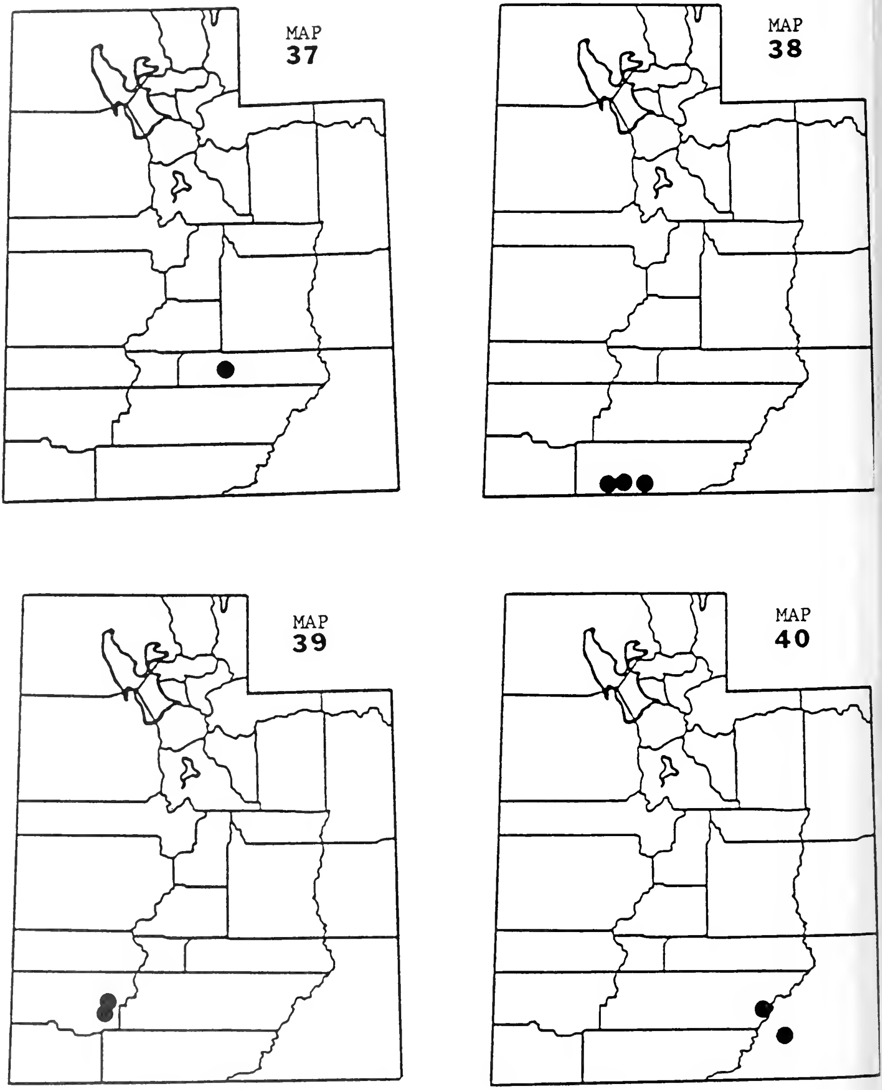
Maps 25–28. Distribution of (25) *Castilleja aquariensis*, (26) *C. revealii*, (27) *Cirsium virginensis*, and (28) *Coryphantha missouriensis* var. *marstonii*.



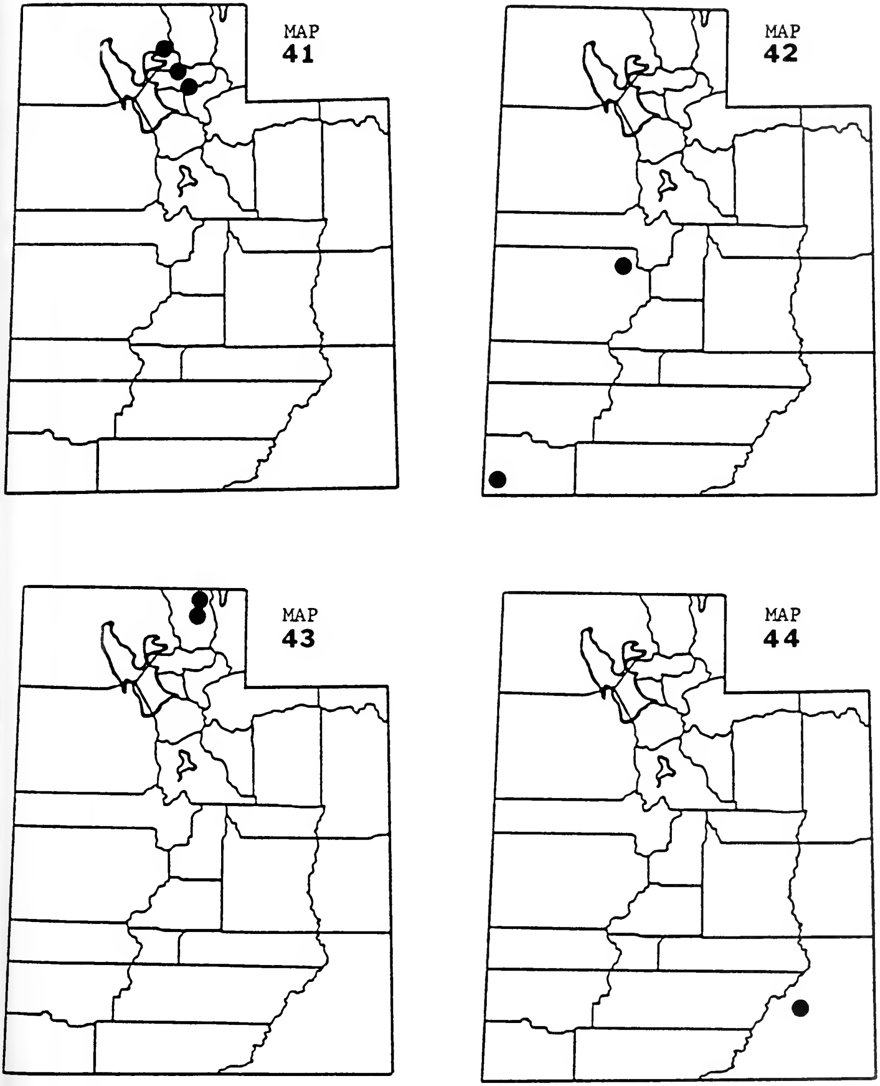
Maps 29–32. Distribution of (29) *Cryptantha barnebyi*, (30) *C. compacta*, (31) *C. creutzfeldtii*, and (32) *C. elata*.



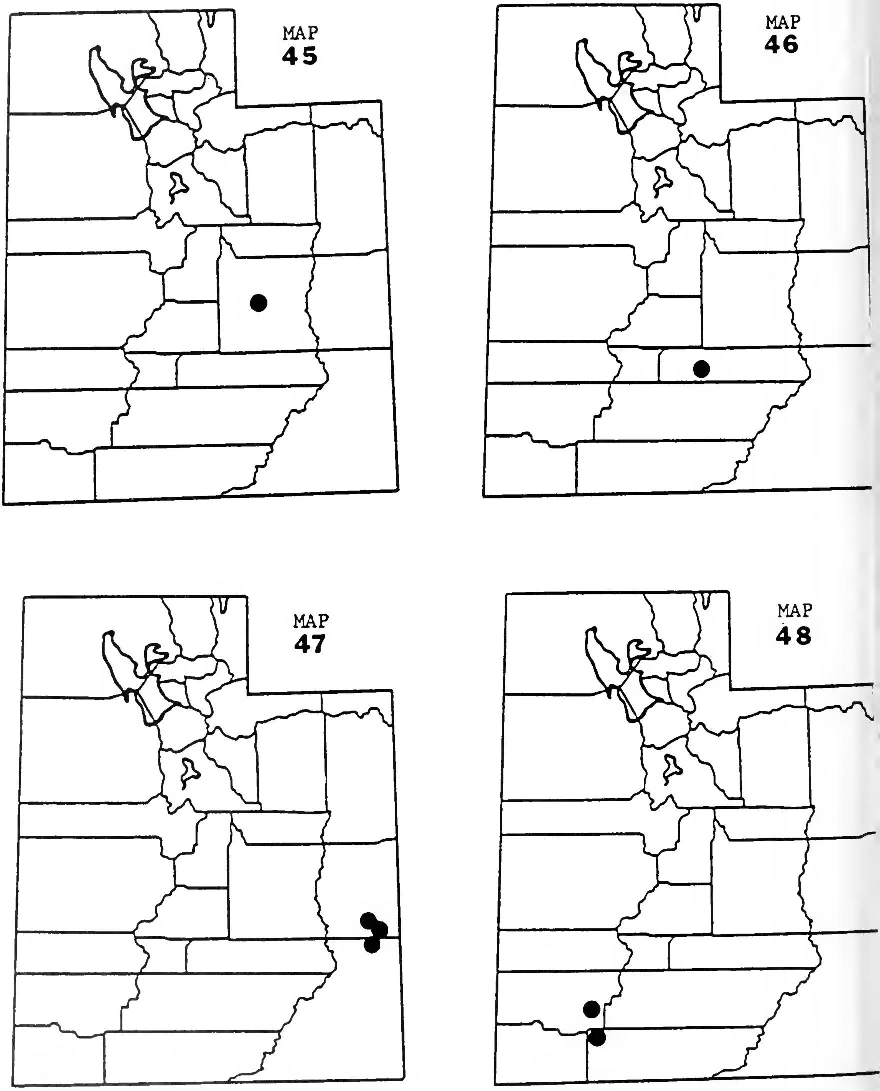
Maps 33–36. Distribution of (33) *Cryptantha jonesiana*, (34) *C. ochroleuca*, (35) *Cuscuta warneri*, and (36) *Cycladenia humilis* var. *jonesii*.



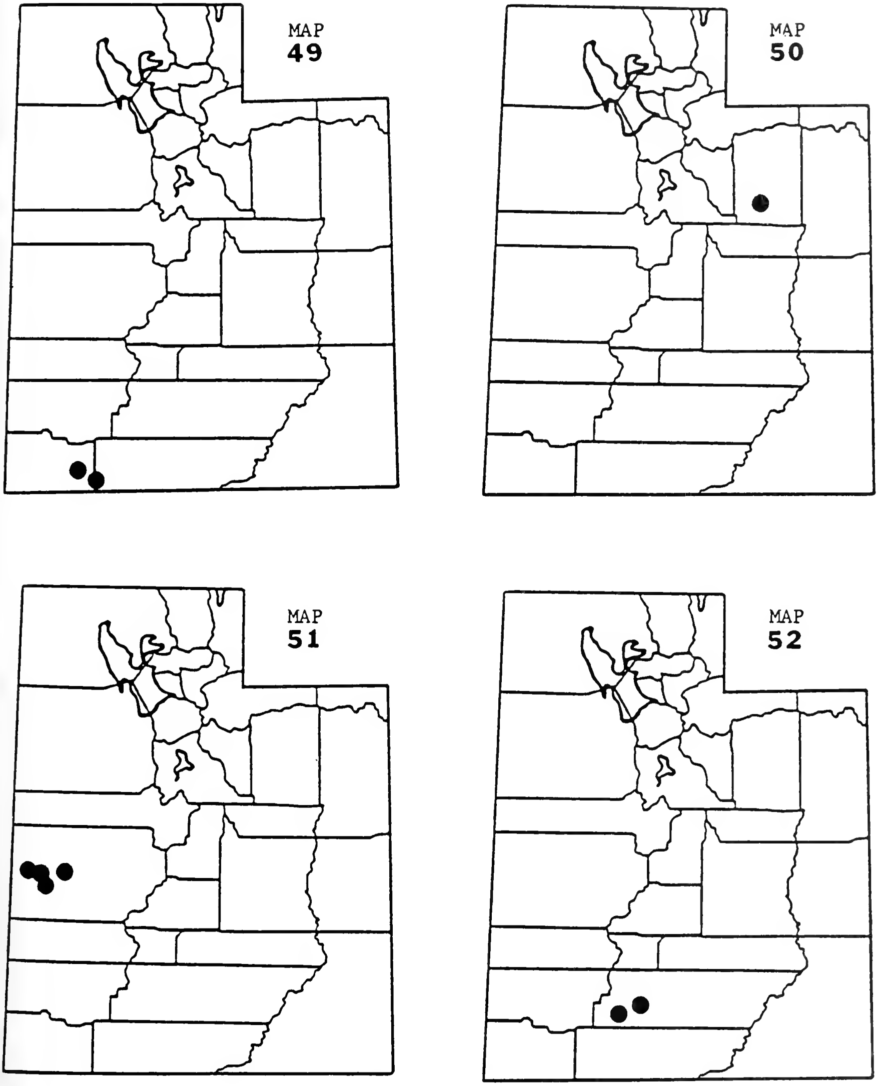
Maps 37–40. Distribution of (37) *Cymopterus beckii*, (38) *C. higginsii*, (39) *C. minimus*, and (40) *Dalea flavescens* var. *epica*.



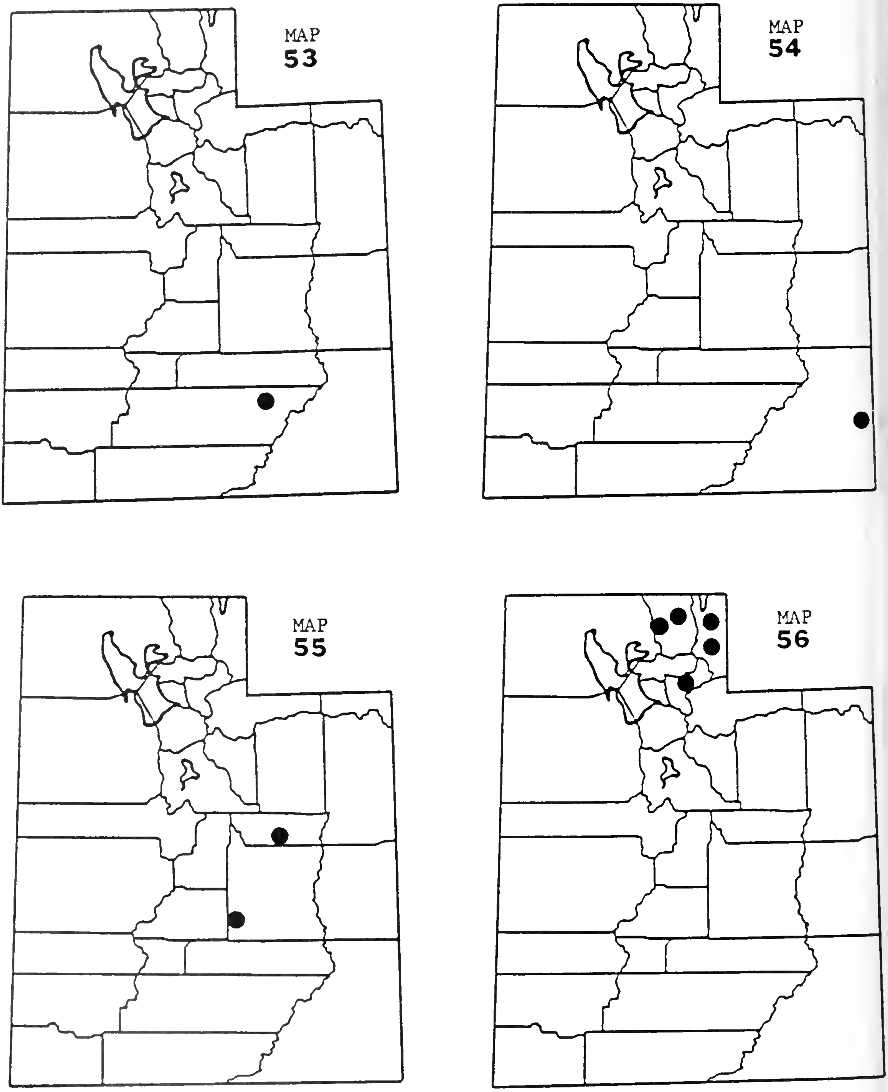
Maps 41–44. Distribution of (41) *Draba maguirei* var. *burkei*, (42) *Epilobium nevadense*, (43) *Erigeron cronquistii*, and (44) *E. kachinensis*.



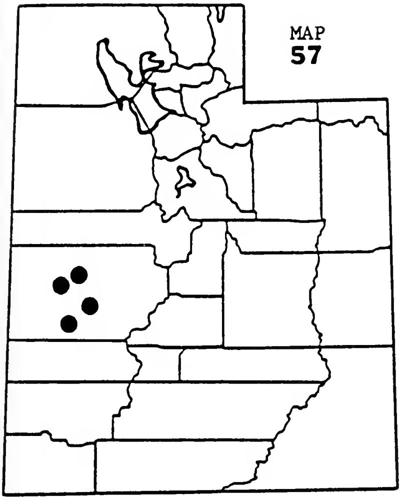
Maps 45–48. Distribution of (45) *Erigeron maguirei* var. *maguirei*, (46) *E. maguirei* var. *harrisonii*, (47) *E. mancus*, and (48) *E. proselyticus*.

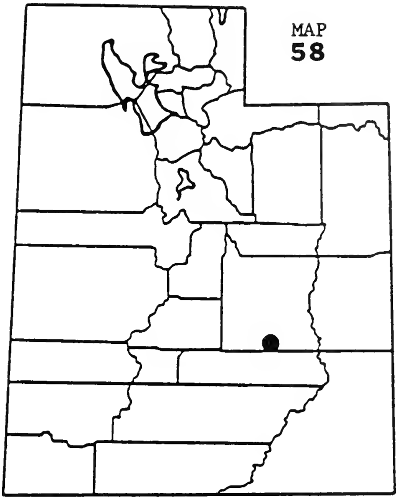


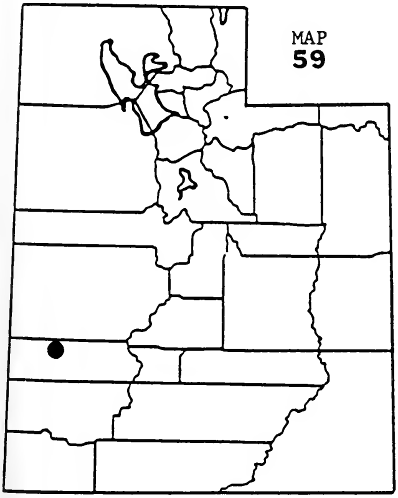
Maps 49–52. Distribution of (49) *Erigeron sionis*, (50) *E. untermannii*, (51) *Eriogonum ammophilum*, and (52) *E. aretioides*.

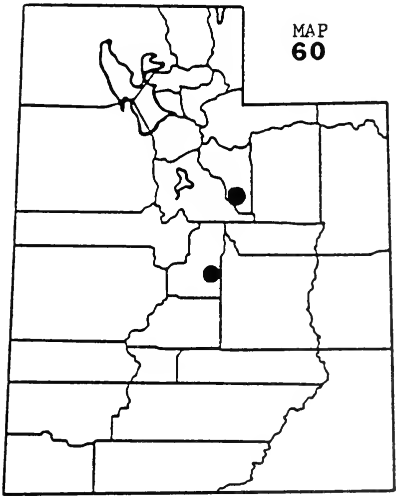


Maps 53–56. Distribution of (53) *Eriogonum cronquistii*, (54) *E. humivagans*, (55) *E. lancifolium*, and (56) *E. loganum*.

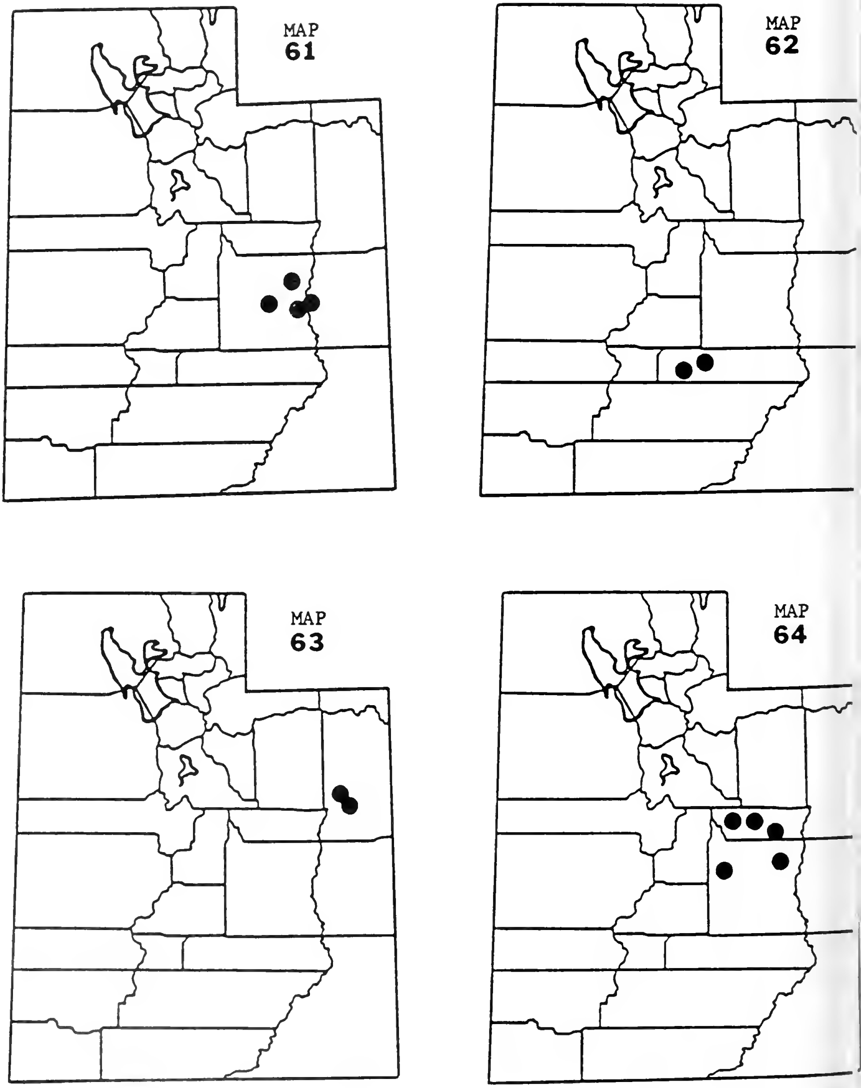




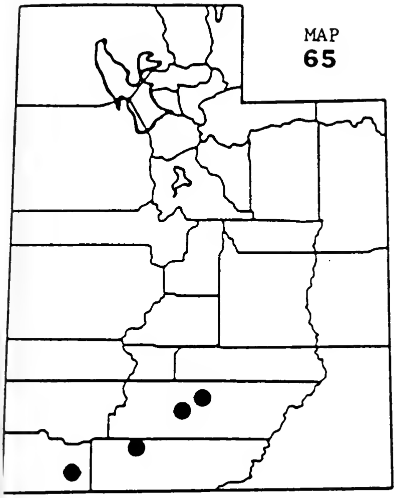


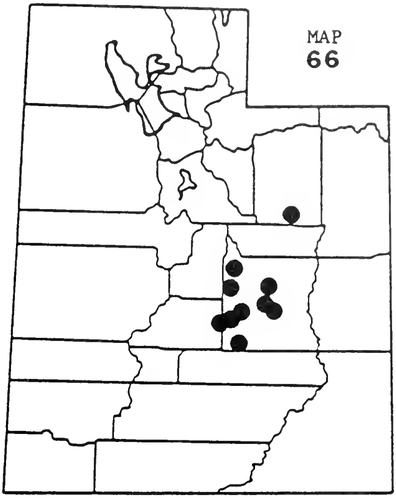


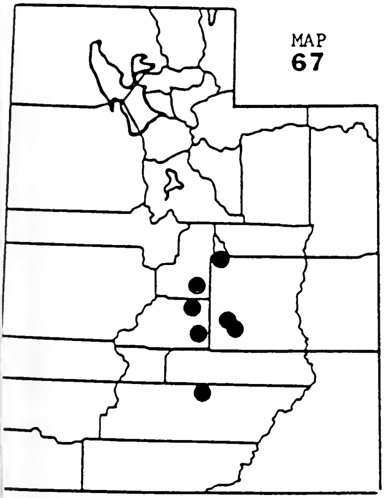
Maps 57–60. Distribution of (57) *Eriogonum natum*, (58) *E. smithii*, (59) *E. soredium*, and (60) *Festuca dasyclada*.

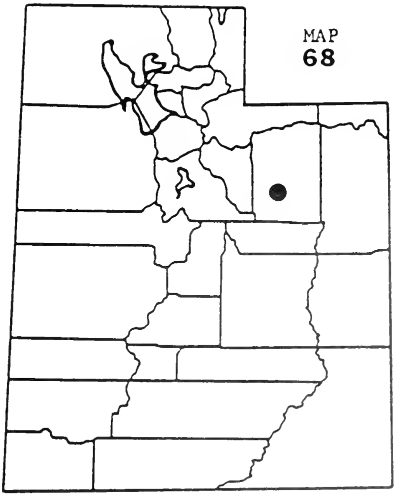


Maps 61–64. Distribution of (61) *Gaillardia flava*, (62) *Gilia caespitosa*, (63) *Glaucocarpon suffrutescens*, and (6 *Hedysarum occidentale* var. *canone*.

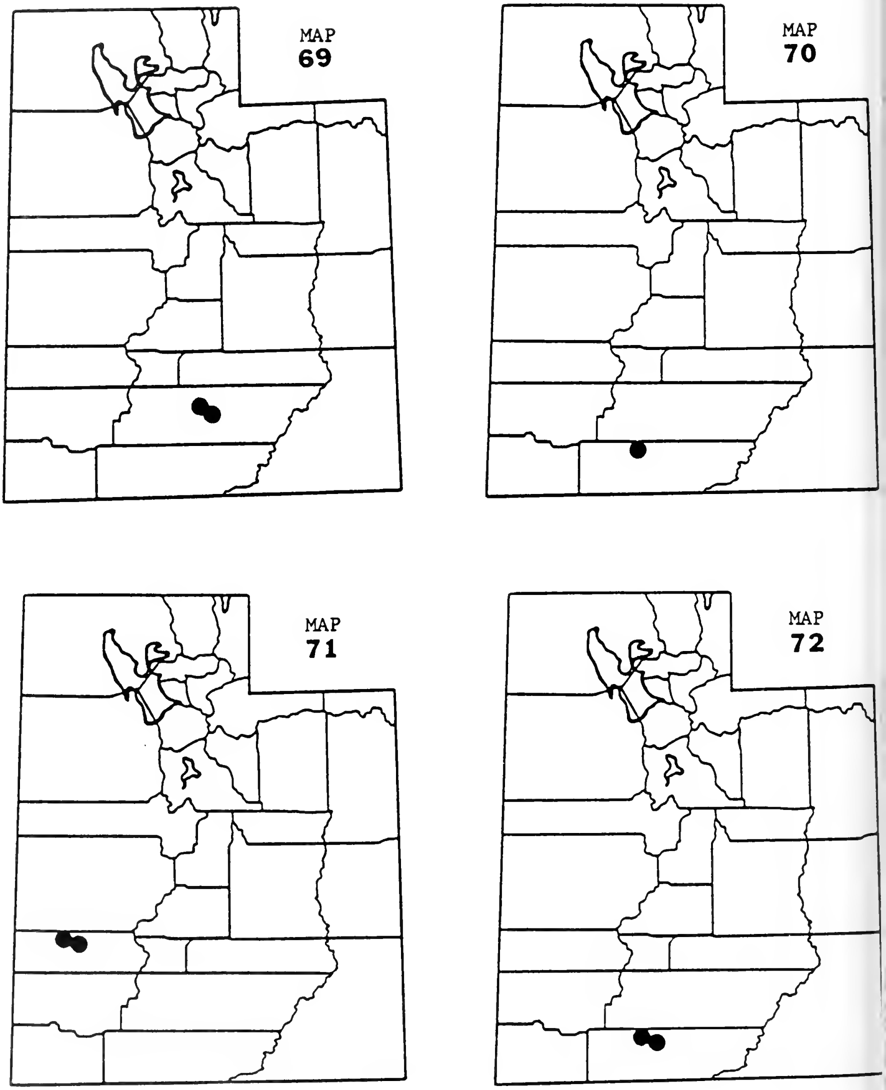




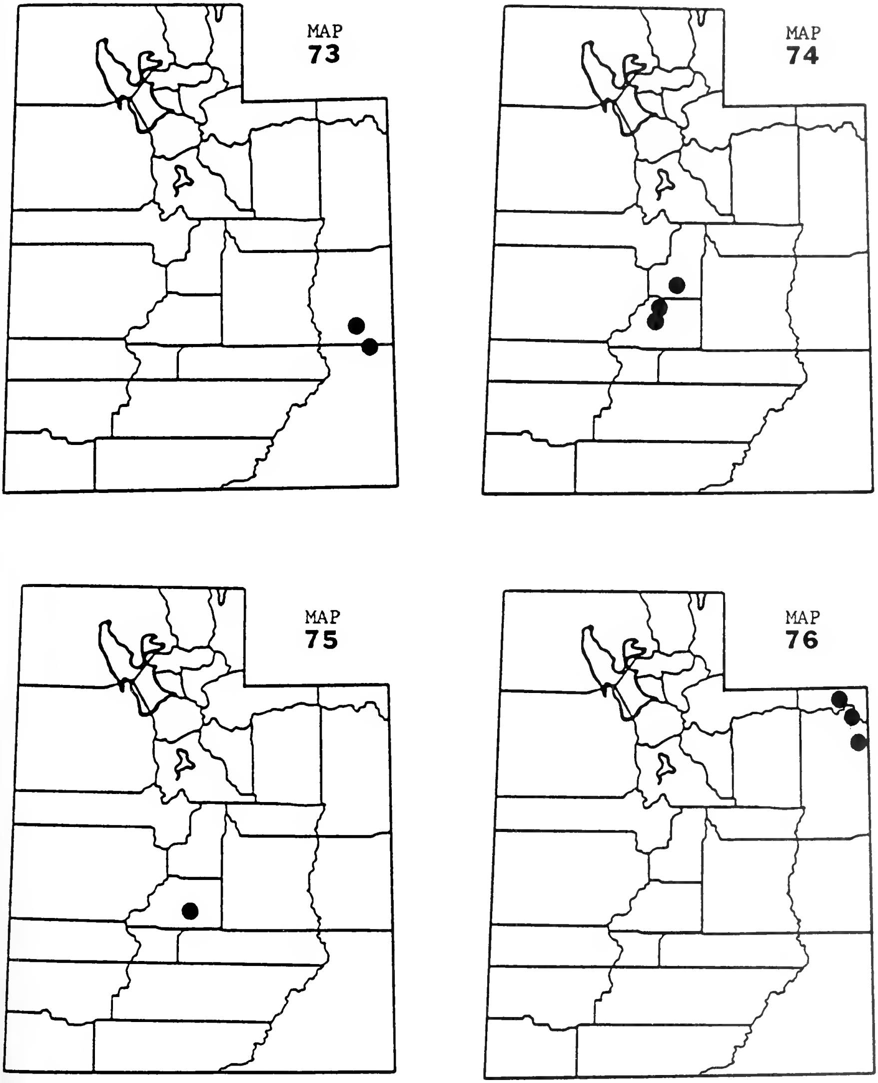




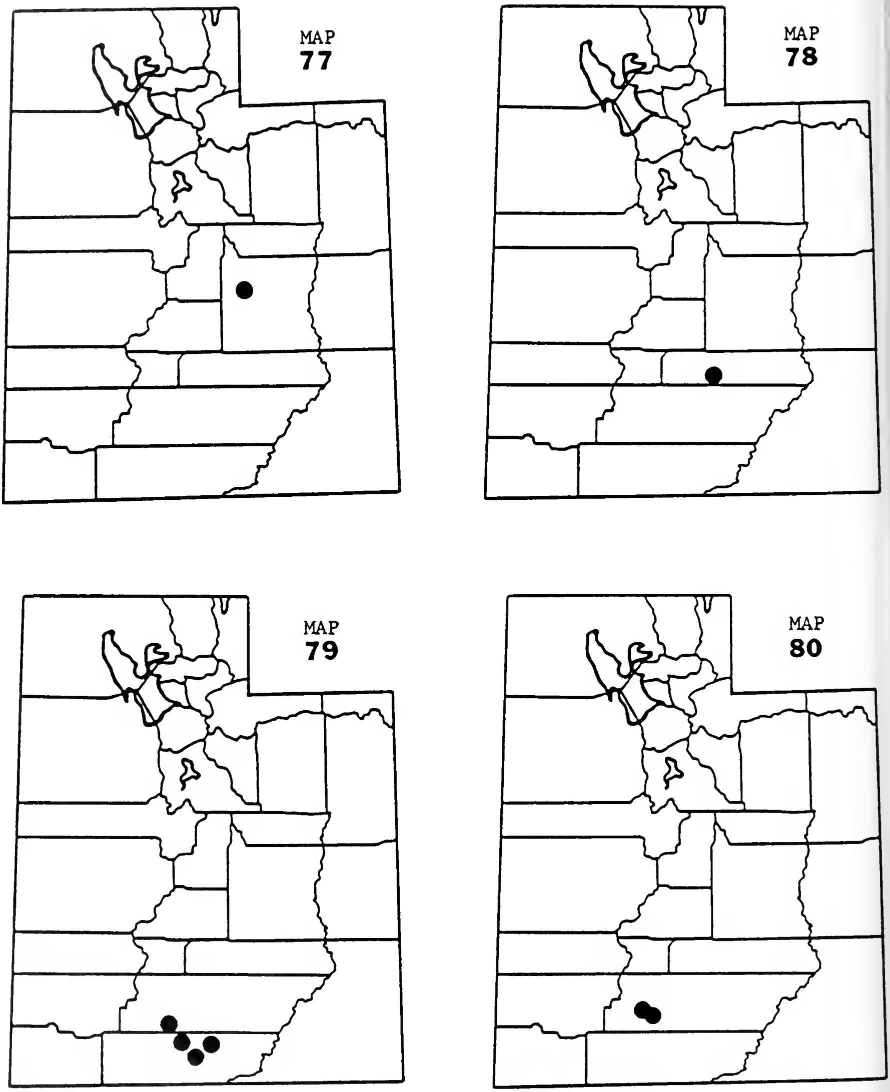
Maps 65–68. Distribution of (65) *Heterotheca jonesii*, (66) *Hymenoxys depressa*, (67) *H. helenioides*, and (68) *epidium barnebyanum*.



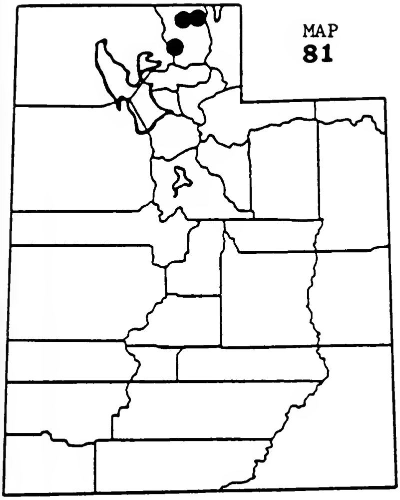
Maps 69–72. Distribution of (69) *Lepidium montanum* var. *neeseae*, (70) *L. montanum* var. *stellae*, (71) *L. ostleri*, and (72) *Lesquerella tumulosa*.

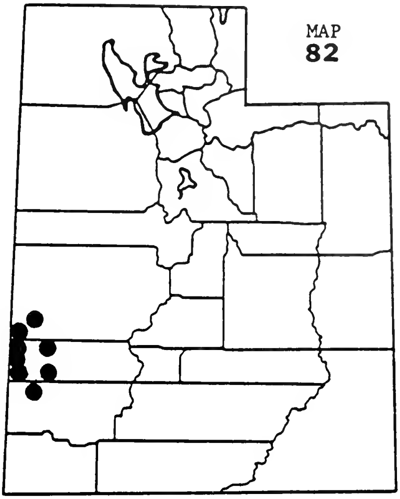


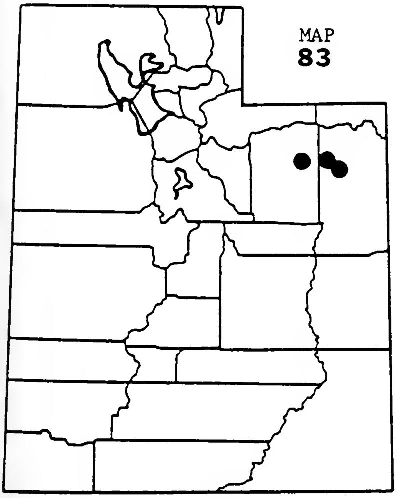
Maps 73–76. Distribution of (73) *Lomatium latilobum*, (74) *Mentzelia argillosa*, (75) *Najas caespitosus*, and (76) *Oenothera acutissima*.

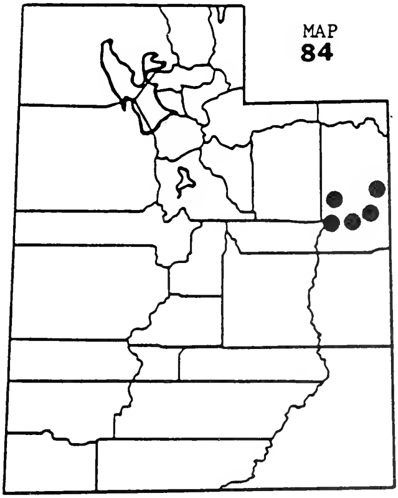


Maps 77–80. Distribution of (77) *Pediocactus despainii*, (78) *P. winkleri*, (79) *Penstemon atwoodii*, and (80) *P. bracteatus*.

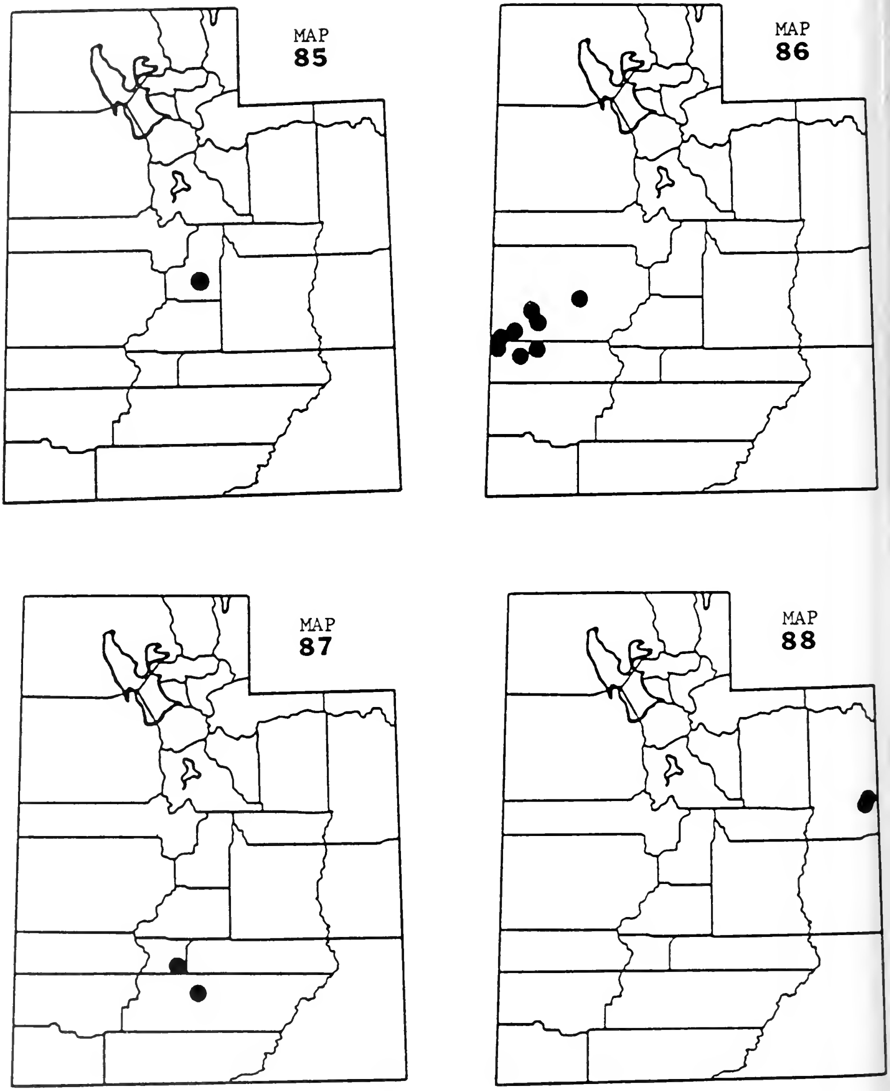




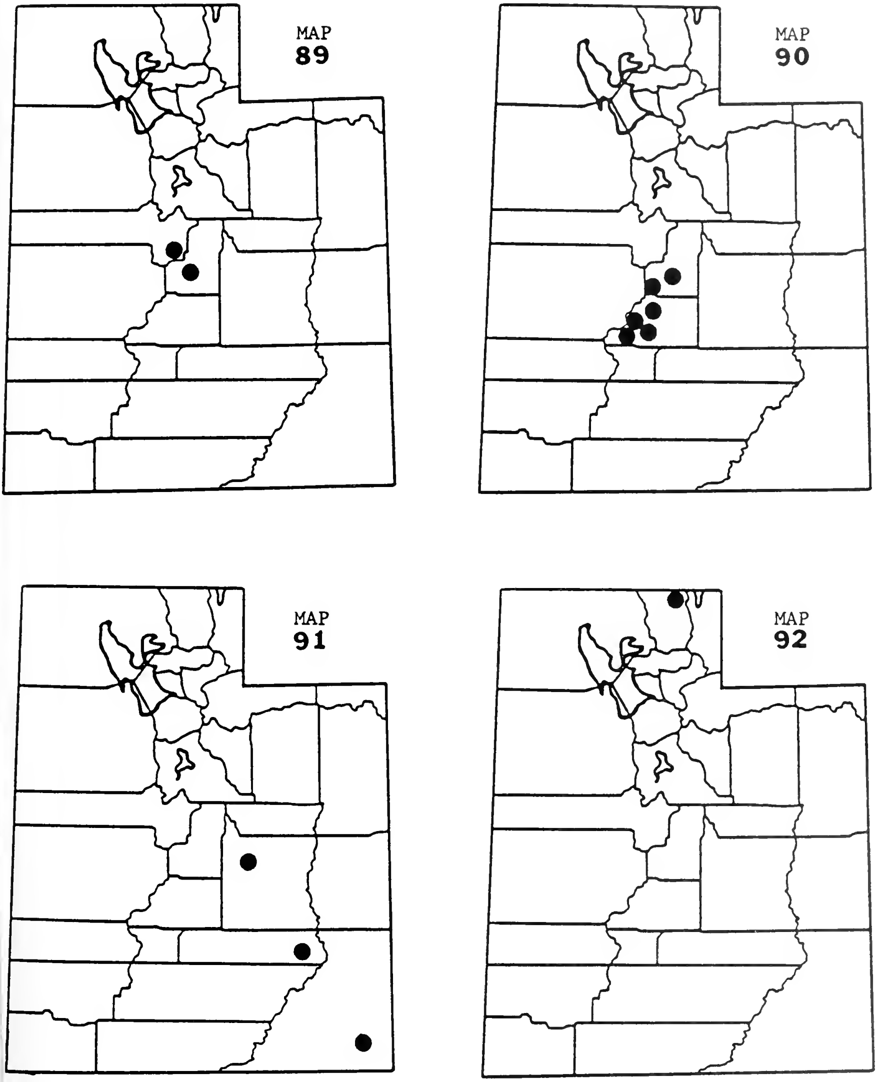




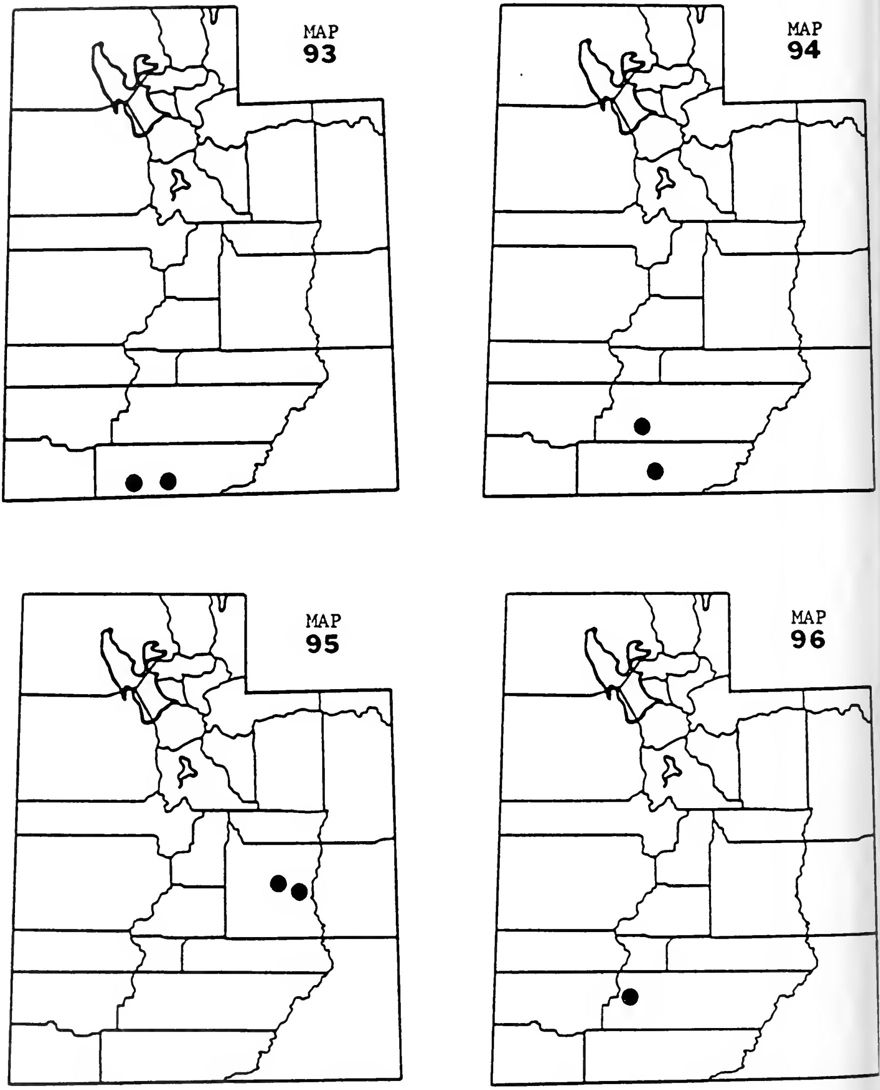
Maps 81–84. Distribution of (81) *Penstemon compactus*, (82) *P. concinnus*, (83) *P. goodrichii*, and (84) *P. grahamii*.



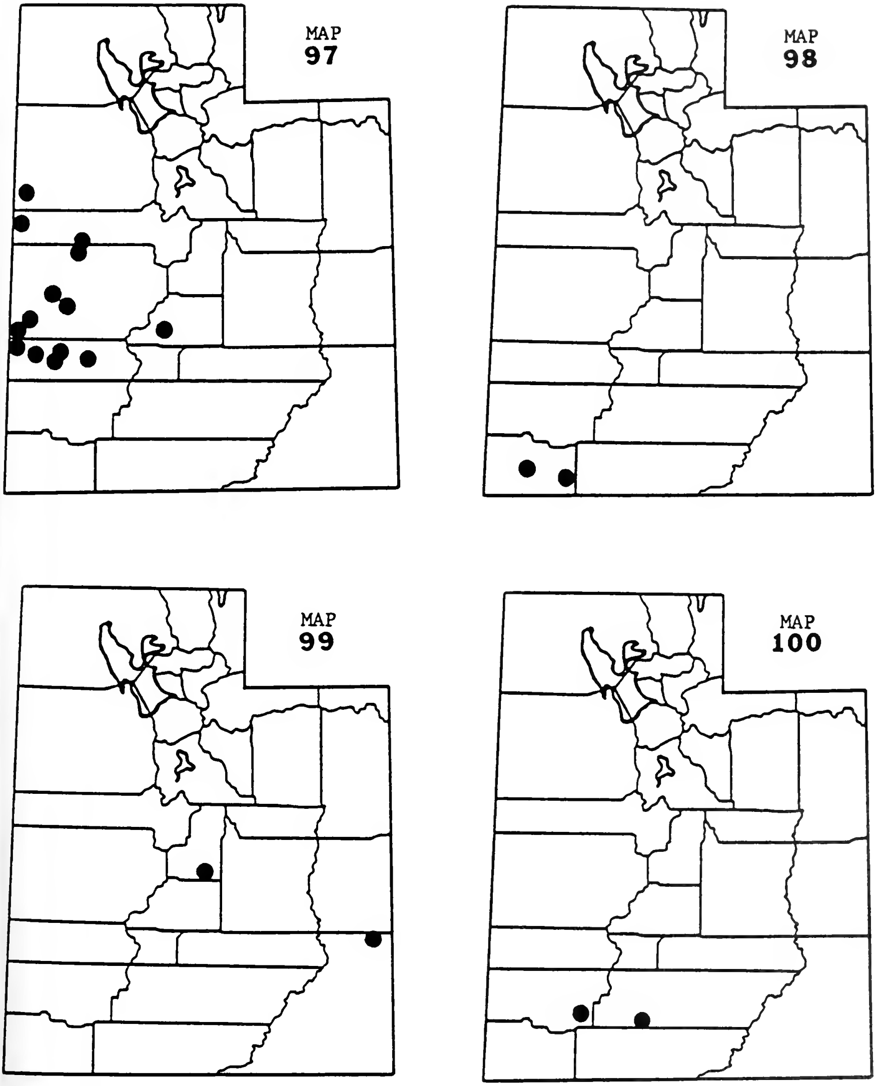
Maps 85–88. Distribution of (85) *Penstemon leptanthus*, (86) *P. nanus*, (87) *P. parvus*, and (88) *P. scariosus* var. *albifluvis*.



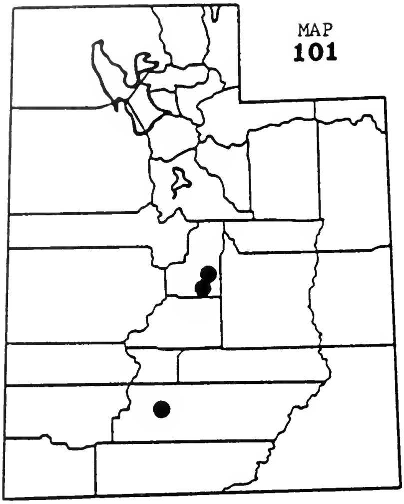
Maps 89–92. Distribution of (89) *Penstemon tidestromii*, (90) *P. wardii*, (91) *Phacelia indecora*, and (92) *Primula maguirei*.

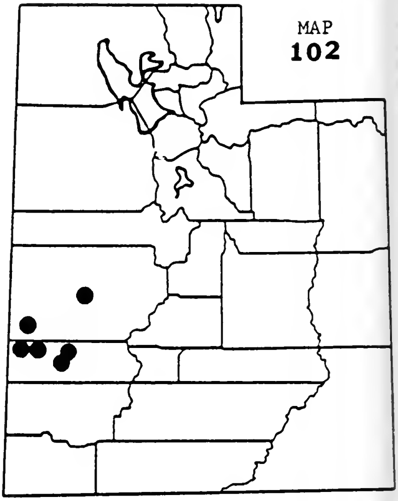


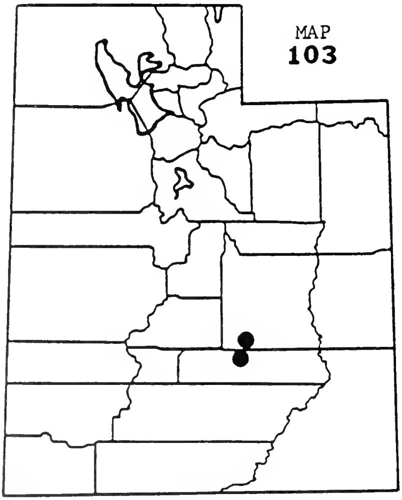
Maps 93–96. Distribution of (93) *Psoralea epipsila*, (94) *P. pariensis*, (95) *Psorothamnus polyadenius* var. *jonesii*, and (96) *Ranunculus acriformis* var. *aestivalis*.

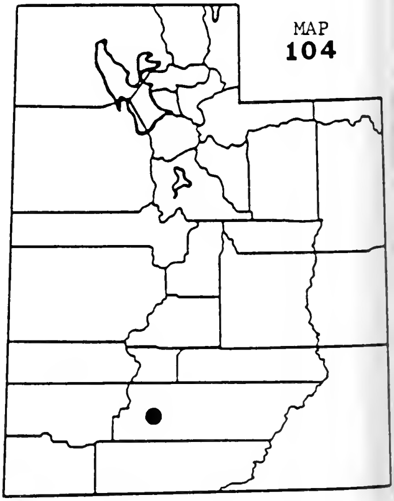


Maps 97–100. Distribution of (97) *Sclerocactus pubispinus*, (98) *Selaginella utahensis*, (99) *Senecio dimorphophyllus* var. *intermedius*, and (100) *Silene petersonii* var. *minor*.

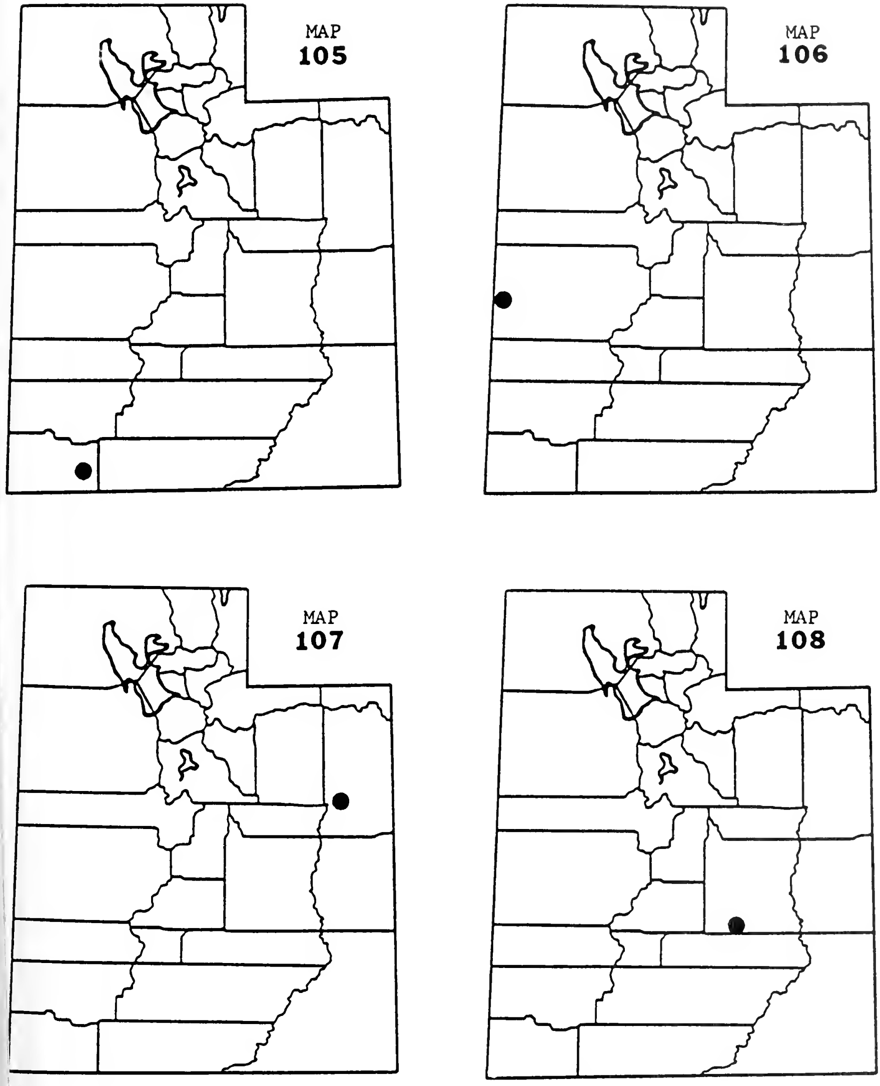




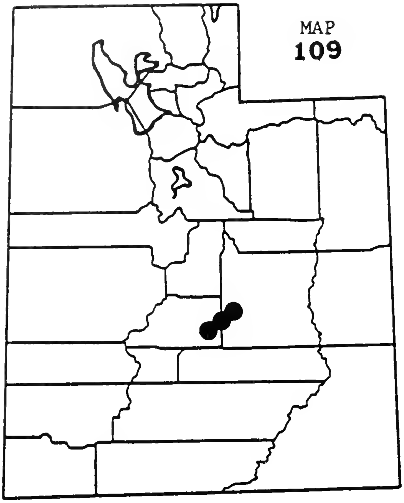


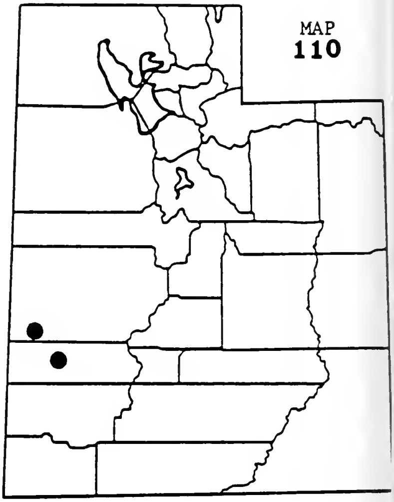


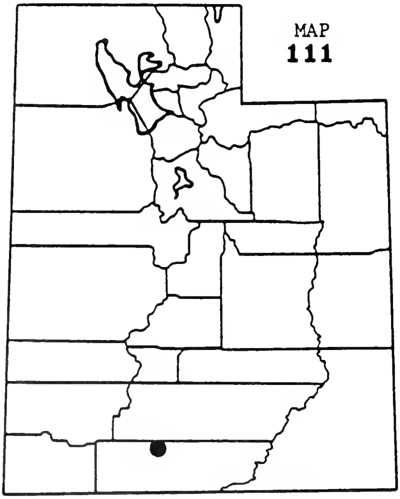
Maps 101–104. Distribution of (101) *Silene petersonii* var. *petersonii*, (102) *Sphaeralcea caespitosa*, (103) *S. psoraloides*, and (104) *Sphaeromeria capitata*.

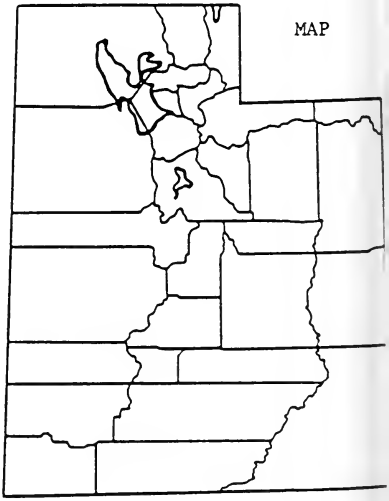


Maps 105–108. Distribution of (105) *Sphaeromeria ruthiae*, (106) *Swertia gypsicola*, (107) *Thelypodiopsis argillacea*, and (108) *T. barnebyi*.









Maps 109–111. Distribution of (109) *Townsendia aprica*, (110) *Trifolium andersonii* var. *friscanum*, and (111) *Xylorhiza cronquistii*.

NEW RECORDS AND COMPREHENSIVE LIST OF THE ALGAL TAXA OF UTAH LAKE, UTAH, USA

Samuel R. Rushforth[1] and Lorin E. Squires[1]

ABSTRACT.— Utah Lake is a slightly saline ecosystem containing more than 700 algal taxa. During the past decade a total of 106 algal taxa has been found that has not previously been reported in this water. These new records are reported herein, together with a comprehensive listing of all algal taxa reported from Utah Lake to date.

Utah Lake is a shallow, slightly saline hypereutrophic lake located in the central part of Utah at the eastern edge of the Great Basin geologic province. It is one of the largest freshwater lakes in western North America. The Lake is composed of three major subsystems, Goshen Bay, Provo Bay, and the main body of the lake. Goshen Bay has the highest salinity in the lake, ranging up to 2300 mg/1 TDS during summer months. Provo Bay is significantly less saline, with TDS generally less than 600 mg/1. The main body of the lake is intermediate in salinity, ranging between 790 and 930 mg/1 TDS (Grimes and Rushforth 1983). Littoral areas in the lake are diverse and include rocky, sandy, and marshy shorelines as well as extensive clay ooze. Emergent vegetation of several vascular species is common in these littoral regions. This wide diversity of major habitat types with disparate salinities coupled with a broad array of microhabitats contributes to an unusually large number of algal taxa found in the lake.

The algal flora of Utah Lake has been of interest for some time. The first reports were published more than 50 years ago by Tanner (1930, 1931) and Snow (1932). After a 40-year hiatus, Utah Lake algae were again examined and reported in two brief communications by Harding (1970, 1971).

The first extensive examination of Utah Lake diatoms was undertaken by Bolland (1974), who studied a 5-m core collected offshore from Geneva. Two additional cores from the main lake and one core from Provo Bay were analyzed by Javakul et al. (1983). Diatoms from the surface sediments of the lake have also been reported in two papers by Grimes and Rushforth (1982, 1983).

Phytoplankton of Utah Lake was sampled in the mid 1970s by workers of the U.S. Environmental Protection Agency (1977). Their report included a short list of genera present in the lake, together with accessory water chemical data. More extensive phytoplankton sampling was reported by Whiting et al. (1978) in a paper on the environmental requirements of selected Utah Lake algal taxa. This paper included a discussion of several of the dominant species in the lake, together with their environmental preferences. The following year, Squires et al. (1979) discussed the environmental requirements of the dominant phytoplankters that occupy the lake during some summers. These authors demonstrated competitive displacement of the dinoflagellate *Ceratium hirundinella* by the blue-green alga *Aphanizomenon flos-aquae.*

A summary of research on the algae in the water column of the lake performed from 1974 through 1978 (Rushforth et al. 1981) included a comprehensive species list of the phytoplankters and ecological and distribution information on other major taxa.

Grimes et al. (1980) published the only paper to date dealing with the epiphytic algae of the lake. Their paper dealt exclusively with the diatom assemblages on living and dead stems of the grass *Phragmites australis,* which grows in many littoral areas of the lake.

The present paper provides a list of all algal species reported in the literature from all

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habitats of Utah Lake during the years 1930–1978. It also presents the species we have taken in our studies of the lake during 1978–1982, including a significant number of new records from the lake.

METHODS

More than 1000 algal samples were collected from Utah Lake during the period 1978–1982. These samples were collected from all major habitat types and the majority of microhabitats in the lake as part of a long-term cooperative analysis of the lake ecosystem. Collections included qualitative plankton tows, quantitative total plankton samples, qualitative epiphyton samples, and quantitative bottom sediment samples, as well as various qualitative grab samples for strictly taxonomic study.

Samples were returned to our laboratory at Brigham Young University and studied as soon as possible for living nondiatom taxa. Following such study, permanent diatom slides were prepared using standard acid oxidation procedures. All samples were examined on Zeiss RA microscopes using Nomarski and bright field microscopy. Diatom slides have been deposited in the Brigham Young University diatom collection.

All published papers dealing with the algal flora of Utah Lake were studied, and the species names were categorized according to division, class, and order. In examining these papers, we accepted only species that were reported as occurring in the lake or in the marshes at the edge of the lake. This was especially important for Snow's (1932) paper, since she studied a number of waters around the lake that represent separate habitat types.

RESULTS

A total of 686 citations of algal names has been reported in the literature for Utah Lake. In addition, we present herein 106 new records to bring the total number of reported taxa to 792 (Table 1). It should be mentioned that this figure is somewhat misleading since 81 of the citations in the literature are generic names only without specific epithets, and some of these would undoubtedly be duplicates of names used by other authors. In addition, some of the names used by various authors are synonyms of those used by others. We have noted a few of these, but a complete determination of conspecificity is beyond the scope of this paper. We hope to work on selected genera in the future to help resolve this problem.

The largest group of algae in the lake is the diatoms, which are represented by 532 taxonomic names in 51 genera. The Chlorophyta is represented in the lake by a total of 150 taxa in 56 genera. Blue-green algae are also common in the lake, with a total of 69 taxa being reported in 24 genera. The Chrysophyceae is represented by 3 genera containing 9 taxa and the Xanthophyceae by 5 genera containing 13 taxa. In addition, 5 genera including 13 species of Euglenophyta, 2 genera including 4 species of Pyrrhophyta, and 2 genera of Cryptophyta are found in the algal flora of Utah Lake.

The new records for the algal flora of Utah Lake reported herein (Table 1) include 63 species and one genus of diatoms, 14 species and one genus of Chlorophyceae, one species of Xanthophyceae, 25 species and three genera of Cyanophyceae, and three species of Euglenophyta.

TABLE 1. Algal taxa collected from Utah Lake from 1930 to the present. The reference number refers to the literature citation provided at the end of the table.

	Reference													
Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14
DIVISION CYANOPHYTA														
CLASS CYANOPHYCEAE														
Order Chroococcales														
Anacystis rupestris (Lyngb.) Drouet & Dail.										10				14
Aphanocapsa grevillei (Hass.) Rabh.			3											
Aphanocapsa virescens (Hass.) Rabh.			3											

Table 1 continued.

Species	Reference 1	2	3	4	5	6	7	8	9	10	11	12	13	14
Aphanothece gelatinosa (Henn.) Lemm.														14°
Chroococcus minutus (Kuetz.) Naeg.										10				14
Chroococcus turgidus (Kuetz.) Naeg.														14°
Gloeocapsa punctata Naeg.										10				14
Gomphospheria aponina Kuetz.										10				14
Gomphospheria lacustris Chod.										10				14
Holopedium irregulare Lager.										10				14
Marsonniella elegans Lemm.										10				14
Merismopedia elegans A. Braun.	1													
Merismopedia glauca (Ehr.) Naeg.										10				14
Merismopedia tenuissima Lemm.														14°
Microcystis aeruginosa Kuetz. em. Elenk.				4						10				14
Microcystis incerta Lemm.										10				14
Microcystis protocystis Crow								8		10				14
Order Chamaesiphonales														
Chamaesiphon incrustans Grun.			3											14
Xenococcus species			3											
Order Oscillatoriales														
Anabaena azollae Stras.			3											
Anabaena cylindrica Lemm.			3											
Anabaena flos-aquae (Lyngb.) Breb.								8		10				14
Anabaena oscillarioides Bory														14°
Anabaena spiroides Kleb.								8						
Anabaena spiroides var. *crassa* Lemm.				4						10				14
Anabaena torulosa (Carm.) Lager.														14°
Anabaena variabilis Kuetz.														14°
Anabaena species	1													
Anabaena species							7							
Aphanizomenon flos-aquae (Lemm.) Ralfs		2		4				8		10				14
Lyngbya aerugineo-caerulea (Kuetz.) Gom.														14°
Lyngbya aestuarii (Mert.) Liebm.														14°
Lyngbya epiphytica Hier. ex Eng. & Prant.														14°
Lyngbya major Meneg.			3											
Lyngbya majusculla (Dill.) Harv.			3							10				
Lyngbya martensiana Meneg.										10				
Lyngbya species			3											
Microcoleus paludosus Kuetz.) Gom.														14°
Nodularia harveyana (Thwaites) Thuret														14°
Nodularia spumigena Mert.			3											
Nostoc caeruleum Lyngb.										10				14
Nostoc species	1													
Oscillatoria agardhii Gom.														14°
Oscillatoria amoena (Kuetz.) Gom.														14°
Oscillatoria amphibia Ag.														14°
Oscillatoria angusta Koppe														14°
Oscillatoria angustissima West & West										10				14
Oscillatoria articulata Gard.										10				
Oscillatoria limosa (Roth) Ag.														14°
Oscillatoria nigro-viridis Thwaites			3											
Oscillatoria sancta (Kuetz.) Gom.														14°
Oscillatoria subbrevis Schmidle										10				
Oscillatoria subtillissima Kuetz.														14°
Oscillatoria tenuis Ag.										10				14
Oscillatoria species	1													
Oscillatoria species							7							
Phormidium ambiguum Gom.														14°
Phormidium autumnale (Ag.) Gom.			3											

Table 1 continued.

Species	Reference 1	2	3	4	5	6	7	8	9	10	11	12	13	14
Phormidium incrustatum (Naeg.) Gom.														14°
Phormidium inundatum Kuetz.														14°
Phormidium tenue (Meneg.) Gom.														14°
Phormidium species	1													
Plectonema boryanum Gom.														14°
Rivularia species	1													
Schizothrix lacustris A. Braun ex Kuetz.										10				
Spirulina laxa G.M.Sm.														14°
Spirulina major Kuetz.														14°
Tolypothrix species		2												
Tolypothrix species			3											
CHLOROPHYTA														
CLASS CHLOROPHYCEAE														
Order Volvocales														
Carteria cordiformis (Cart.) Dill.										10				14
Carteria klebsii (Dang.) France em. Troitz.										10				14
Carteria stellifera Nyg.										10				14
Chlamydomonas altera Skuja										10				14
Chlamydomonas globosa Snow										10				14
Chlamydomonas polypyrenoideum Pres.										10				14
Eudorina elegans Ehr.				4										
Pandorina morum (Muell.) Bory			3	4						10				14
Pandorina species	1													
Pleodorina illinoisensis Kofoid										10				
Pteromonas cordiformis Lemm. em Fott														14°
Pteromonas cruciata Playf.														14°
Pteromonas species							7							
Sphaerellopsis aulata (Pasch.) Gerl.										10				14
Wislouchiella planktonica Skv.										10				14
Order Tetrasporales														
Gloeocystis ampla (Kuetz.) Lager.					5									
Sphaerocystis schroeteri Chod.										10				14
Tetraspora lubrica (Roth) Ag.			3											
Order Ulotrichales														
Cylindrocapsa geminella Wolle			3											
Geminella scalariformis G.West			3											
Microspora crassior (Hansg.) Hazen			3											
Microspora floccosa (Vauch.) Thur.					5									
Microspora loefgrenii (Nordst.) Lager.			3											
Microspora stagnorum (Kuetz.) Lager.			3											
Microspora tumidula Hazen			3											
Microspora species		2												
Ulothrix aequalis Kuetz.			3											14
Ulothrix cylindricum Pres.														14°
Ulothrix scalariformis G.West			3											
Ulothrix tenerrima Kuetz.			3											
Ulothrix tenuissima Kuetz.			3											
Ulothrix variabilis Kuetz.			3											
Ulothrix zonata (Web. & Mohr.) Kuetz.			3	4										14
Ulothrix species	1													
Order Chaetophorales														
Aphanochaete repens A.Braun			3											
Chaetophora elegans (Roth) Ag.			3											

Table 1 continued.

Species	Reference 1	2	3	4	5	6	7	8	9	10	11	12	13	14
Gongrosira species			3											
Myxonema (= *Stigeoclonium*) species		2												
Stigeoclonium aestivale Hazen														14°
Stigeoclonium attenuatum (Hazen) Coll.														14°
Stigeoclonium stagnatile (Hazen) Coll.										10				14
Stigeoclonium subsecundum Kuetz.			3											
Stigeoclonium tenue (Ag.) Kuetz.			3											14
Order Oedogoniales														
Oedogonium capilliforme Kuetz.			3											
Oedogonium capilliforme var. *debaryanum* (Chm.) Hirn.			3											
Oedogonium species	1													
Order Ulvales														
Enteromorpha crinita (Roth) Ag.			3											14
Enteromorpha intestinalis (L.) Grev.			3											
Enteromorpha prolifera (Dan.) Ag.			3											
Enteromorpha species ? (recorded as *Enteromorcha*)	1													
Enteromorpha species		2												
Order Cladophorales														
Cladophora callicoma Kuetz.			3											
Cladophora crispita (Roth) Kuetz.			3											
Cladophora fracta (Dill.) Kuetz.			3											
Cladophora glomerata (Lemm.) Kuetz.			3	4						10				14
Cladophora insignis (Ag.) Kuetz.			3											
Cladophora species	1													
Rhizoclonium hieroglyphicum (Ag.) Kuetz.			3											14
Order Chlorococcales														
Actinastrum gracilimum G.M.Sm.					5									14
Actinastrum hantzschii Lager.					5					10				14
Actinastrum hantzschii var. *elongatum* G.M.Sm.														14°
Actinastrum hantzschii var. *fluviatile* Schr.										10				14
Ankistrodesmus convolutus Corda										10				14
Ankistrodesmus falcatus (Corda) Ralfs					5			8		10				14
Ankistrodesmus falcatus var. *mirabilis* (West & West) G.S.West										10				14
Ankistrodesmus falcatus var. *stipitatus* (Chod.) Lemm.										10				14
Ankyra judayi (G.M.Sm.) Fott.								8		10				14
Botryococcus braunii Kuetz.				4										
Botryococcus sudeticus Lemm.														14°
Characium species		2												
Chlorococcum infusionum (Schr.) Meneg.				4										
Closteriopsis longissima var. *tropica* West & West				4						10				14
Coelastrum microporum Naeg.										10				14
Crucigenia quadrata Morr.										10				14
Crucigenia tetrapedia (Kirch.) West & West										10				14
Dictyosphaerium ehrenbergianum Naeg.				4				8		10				14
Franceia droescheri (Lemm.) G.M.Sm.														14°
Kirchneriella lunaris (Kirch.) Moeb.										10				14
Lagerheimia longiseta var. *major* G.M.Sm.										10				14
Lagerheimia wratislawiensis Schr.										10				14
Micractinium pusillum Fres.					5					10				14
Oocystis borgei Snow										10				14
Oocystis elliptica W.West										10				
Oocystis gigas Arch.										10				14
Oocystis gloeocystiformis Borge										10				14
Oocystis lacustris Chod.										10				14

Table 1 continued.

	Reference													
Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Oocystis novae-semliae Willie										10				
Oocystis parva West & West										10				14
Oocystis pusilla Hans.										10				14
Oocystis submarina Lager.										10				14
Pediastrum boryanum (Turp.) Meneg.			3		5					10				14
Pediastrum duplex Meyen								8		10				14
Pediastrum duplex var. *brachylobum* A.Braun										10				
Pediastrum duplex var. *clathratum* (A.Braun.) Lager.				4						10				14
Pediastrum duplex var. *gracilimum* West & West										10				14
Pediastrum simplex (Meyen) Lemm.										10				
Pediastrum simplex var. *duodenarium* (Bail.) Rabh.										10				
Pediastrum tetras (Ehr.) Ralfs.										10				14
Pediastrum tetras var. *tetraodon* (Chorda) Rabh.										10				14
Pediastrum species	1													
Planktosphaeria gelatinosa G.M.Sm.					5									14
Quadrigula closteriodes (Bohlin) Printz														14°
Quadrigula lacustria (Chod.) G.M.Sm.										10				14
Scenedesmus abundans var. *brevicauda* G.M.Sm.					5					10				14
Scenedesmus acuminatus (Lager.) Chod.										10				14
Scenedesmus arcuatus var. *platydisca* G.M.Sm.					5									
Scenedesmus bijuga (Turp.) Lager														14°
Scenedesmus bijuga var. *alterans* (Rein.) Hansg.										10				14
Scenedesmus bijuga var. *flexuosus* Lemm.										10				14
Scenedesmus dimorphus (Turp.) Kuetz.				4						10				14
Scenedesmus longus var. *naegelii* (Breb.) G.M.Sm.										10				14
Scenedesmus opoliensis P.Richter										10				14
Scenedesmus perforatus Lemm.				4						10				14
Scenedesmus quadricauda (Turp.) Breb.				4						10				14
Scenedesmus quadricauda var. *longispina* (Chod.) G.M.Sm.										10				14
Scenedesmus quadricauda var. *parvus* G.M.Sm.					5									
Scenedesmus quadricauda var. *maximus* West & West													13	
Scenedesmus quadricauda var. *quadrispina* (Chodat) G.M.Sm.														14°
Scenedesmus quadricauda var. *westii* G.M.Sm.													13	
Scenedesmus species	1													
Scenedesmus species							7							
Schroederia setigera (Schr.) Lemm.								8		10				14
Schroederia species							7							
Selenastrum bibraianum Reinsch										10				14
Selenastrum gracile Reinsch				4						10				14
Selenastrum westii G.M.Sm.										10				14
Treubaria triappendiculata Bern.								8		10				14
Order Zygnematales														
Closterium moniliferum (Bory) Ehr.														14°
Closterium venus Kuetz.					5									
Closterium species	1													
Closterium species										10				
Cosmarium margaritiferum Meneg.			3											
Cosmarium oculiferum Lagh.			3											
Cosmarium ralfsii Breb.			3											
Cosmarium tetraophthalmum (Kuetz.) Breb.			3											
Cosmarium species	1													
Desmidium species	1													
Docidium species		2												
Genicularia species		2												
Mougeotia species		2												
Mougeotia species			3											

Table 1 continued.

	Reference													
Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Spirogyra decimina (Muell.) Kuetz.			3											
Spirogyra formosa (Trans.) Czur.														14°
Spirogyra porticalis (Muell.) Cl.														14°
Spirogyra species	1													
Staurastrum natator West					5									
Staurastrum paradoxum Meyen					5					10				14
Staurastrum tetracerum Ralfs										10				14
Zygnema species	1													
Class Charophyceae														
Chara species			3											
Division Chrysophyta														
Class Chrysophyceae														
Order Chromulinales														
Hydrurus foetidus (Vill.) Trev.				4										
Order Ochromonadales														
Dinobryon bavaricum Imhof		2												
Dinobryon divergens Imhof										10				
Dinobryon sociale var. *americanum* (Brunn.) Bach.										10				
Dinobryon sertularia Ehr.				4										
Mallomonas acaroides Perty										10				
Mallomonas caudata Iwan.										10				14
Mallomonas pseodocoronata Pres.										10				14
Mallomonas tonsurata Teil.										10				14
Class Xanthophyceae														
Order Mischococcales														
Characiopsis cylindrica (Lamb.) Lemm.					5									
Chlorobotrys regularis (W.West) Bohl.					5									
Ophiocytium cochleare (Eich.) A.Braun.			3											
Ophiocytium cuspidatum (Bail.) Rabh.			3											
Ophiocytium majus Naeg.			3											
Ophiocytium parvulum (Perty) A.Braun.			3											
Order Tribonematales														
Tribonema bombycinum (Ag.) Derb. & Sol.			3	4						10				14
Tribonema minus Hazen			3	4										14
Tribonema utriculosum Hazen			3											
Tribonema species	1													
Order Vaucheriales														
Vaucheria borealis Hirn														14°
Vaucheria geminata (Vauch.) DeCand.			3											
Vaucheria sessilis var. *clavata* (Vauch.) DeCand.			3											
Class Bacillariophyceae°°														
Achnanthes affinis Grun.											11			14
Achnanthes chilensis var. *subaequalis* Reim.													13	
Achnanthes clevei Grun.						6				10			13	14
Achnanthes clevei var. *rostrata* Hust.											11		13	14

Table 1 continued.

	Reference													
Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Achnanthes deflexa Reim.										10				14
Achnanthes exigua Grun.										10	11		13	14
Achnanthes gibberula Grun.														14°
Achnanthes hauckiana Grun.									9	10	11		13	14
Amphora species									9					
Anomoeoneis costata (Kuetz.) Hust.						6								14
Anomoeoneis serians var. *brachysira* (Breb. ex Kuetz.) Hust.														14°
Anomoeoneis sphaerophora (Ehr.) Pfitz.						6			9	10	11		13	14
Anomoeoneis sphaerophora var. *guentheri* O.Muell.						6								
Anomoeoneis vitrea (Grun.) Ross											11		13	14
Anomoeoneis species											11			
Asterionella formosa Hassall				4		6			9	10	11		13	14
Bacillaria paradoxa Gmelin										10	11			14
Bacillaria paxillifer (Muell.) Hend. (= *B. paradoxa*)													13	
Biddulphia laevis Ehr.										10	11			14
Caloneis amphisbaena (Bory) Cl.										10	11		13	14
Caloneis bacillaris var. *thermalis* (Grun.) Cl.											11			14
Caloneis bacillum (Grun.) Cl.						6				10	11		13	14
Caloneis fenzlii (Grun.) Patr.						6								
Caloneis fenzlioides Cl.-Eul.									9	10	11		13	14
Caloneis lamella Zakr.											11			
Caloneis lewisii Patr.													13	
Caloneis limosa (Kuetz.) Patr.						6							13	14
Caloneis oregonica (Ehr.) Patr.											11			14
Caloneis permagna (Bail.) Cl.													13	14
Caloneis schumanniana (Grun.) Cl.										10				
Caloneis schumanniana var. *fasciata* Hust.											11		13	14
Caloneis schumanniana var. *linearis* Hust.											11			
Caloneis silicula (Ehr.) Cl.											11		13	14
Caloneis silicula var. *limosa* (Kuetz.) VanLand.											11		13	
Caloneis ventricosa (Ehr.) Meist.						6					11			14
Caloneis ventricosa var. *subundulata* (Grun.) Patr.														14°
Caloneis ventricosa var. *truncatula* (Grun.) Meist.													13	14
Campylodiscus clypeus Ehr.											11			14
Campylodiscus hibernicus Ehr.										10				
Campylodiscus noricus var. *hibernicus* (Ehr.) Grun. (= *Campylodiscus hibernicus*)											11		13	
Chaetoceros elmorei Boyer		2												14
Cocconema (= *Cymbella*) species		2												
Cocconeis diminuta Pant.						6				10	11		13	14
Cocconeis disculus (Schum.) Cl.						6					11		13	14
Cocconeis fluviatilis Wall.						6								
Cocconeis pediculus Ehr.						6				10	11		13	14
Cocconeis placentula Ehr.						6								14
Cocconeis placentula var. *euglypta* (Ehr.) Cl.						6			9	10	11			14
Cocconeis placentula var. *lineata* (Ehr.) V.H.						6			9	10	11	12	13	14
Coscinodiscus lacustris Grun.										10				14
Coscinodiscus species									9					
Cyclotella antiqua W.Sm.										10				14
Cyclotella bodanica Eulen.										10				14
Cyclotella comta (Ehr.) Kuetz.											11			
Cyclotella kuetzingiana Thwaites						6			9	10	11			14
Cyclotella kuetzingiana var. *planetophora* Fricke											11		13	14
Cyclotella meneghiniana Kuetz.						6			9	10	11	12	13	14
Cyclotella meneghiniana var. *pumila* (Grun. ex V.H.) Hust.											11			14
Cyclotella ocellata Pant.						6				10	11		13	14

Table 1 continued.

	Reference													
Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Cyclotella stelligera (Cl.) Grun.										10				14
Cyclotella striata (Kuetz.) Grun.														14°
Cyclotella striata var. *ambigua* Grun.														14°
Cyclotella species 1											11			
Cyclotella species 2											11			
Cylindrotheca gracilis (Breb.) Grun.										10				14
Cymatopleura angulata Grev.														14°
Cymatopleura elliptica (Breb.) W.Sm.										10	11		13	14
Cymatopleura elliptica var. *constricta* Grun.						6								14
Cymatopleura solea (Breb.) W.Sm.						6				10	11		13	14
Cymatopleura solea var. *palffyi* (Pant.) Cl.-Eul.														14°
Cymatopleura solea var. *regula* (Ehr.) Grun.						6								
Cymbella affinis Kuetz.									9	10	11		13	14
Cymbella amphicephala Naeg. ex Kuetz.											11			14
Cymbella cistula (Ehr.) Kirch.						6				10	11		13	14
Cymbella cymbiformis Ag.										10	11		13	14
Cymbella ehrenbergii Kuetz.						6								
Cymbella inaequalis (Ehr.) Rabh.											11		13	14
Cymbella mexicana (Ehr.) Cl.						6				10	11		13	14
Cymbella microcephala Grun.										10				14
Cymbella minuta Hilse ex Rabh.									9					14
Cymbella minuta f. *latens* (Krasske) Reim.														14°
Cymbella minuta var. *pseudogracilis* (Cholu.) Reim.											11			14
Cymbella minuta var. *silesiaca* (Bleisch ex Rabh.) Reim.										10	11		13	14
Cymbella muelleri Hust.									9	10	11	12	13	14
Cymbella muelleri f. *ventricosa* (Temp. et Perag.) Reim.											11		13	14
Cymbella prostrata (Berk.) Cl.									9	10	11			14
Cymbella prostrata var. *aeurswaldii* (Rabh.) Reim.											11		13	14
Cymbella protracta Ost.														14°
Cymbella pusilla Grun.											11			14
Cymbella sinuata Greg.										10	11			14
Cymbella subturgida Hust.						6								
Cymbella tumida (Breb. ex Kuetz.) V.H.										10	11		13	14
Cymbella tumidula Grun. ex A.Schmidt										10				14
Cymbella turgida Greg.						6								
Cymbella species		2												
Cymbella species									9					
Cymbella species 1										10				
Cymbella species 2										10				
Denticula elegans Kuetz.										10	11		13	14
Denticula elegans var. *kittoniana* (Grun.) DeT.											11			
Denticula elegans f. *valida* Pedic.										10				14
Denticula subtilis Grun.														14°
Denticula tenuis Kuetz.														14°
Denticula tenuis var. *crassula* (Naeg.) West & West											11			14
Diatoma anceps (Ehr.) Kirchn.						6								14
Diatoma hiemale (Roth) Hieb.											11			14
Diatoma hiemale var. *mesodon* (Ehr.) Grun.											11			14
Diatoma tenue Ag.										10	11		13	14
Diatoma tenue var. *elongatum* Lyngb.									9	10	11	12		14
Diatoma vulgare Bory										10	11		13	14
Diatoma vulgare var. *breve* Grun.											11			14
Diatoma vulgare var. *grande* (W.Sm.) Grun.										10				
Diatoma species	1	2												
Diatomella balfouriana Grev.											11			14
Diploneis elliptica (Kuetz.) Cl.											11		13	14
Diploneis marginestriata Hust.											11		13	14
Diploneis oblongella (Naeg. ex Kuetz.) Ross									9	10	11		13	14
Diploneis oculata (Breb.) Cl.													13	

Table 1 continued.

Species	Reference													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Diploneis pseudovalis Hust.						6				10	11		13	14
Diploneis puella (Schum.) Cl.													13	14
Diploneis smithii (Breb. ex W.Sm.) Cl.						6								
Diploneis smithii var. *dilatata* (M.Perag.) Boyer										10	11		13	14
Diploneis smithii var. *pumila* (Grun.) Hust.										10				
Diploneis species 1											11			
Diploneis species 2											11			
Diploneis species													13	
Encyonema (= *Cymbella*) species	1													
Entomoneis alata (Ehr.) Ehr.										10				14
Entomoneis paludosa (W.Sm.) Reim.						6					11		13	14
Epithemia adnata (Kuetz.) Breb.						6			9	10				
Epithemia adnata var. *minor* (Perag. et Herib.) Patr.											11		13	14
Epithemia adnata var. *porcellus* (Kuetz.) Patr.									9		11			
Epithemia adnata var. *proboscidea* (Kuetz.) Patr.									9		11			
Epithemia argus (Ehr.) Kuetz.						6					11		13	14
Epithemia argus var. *alpestris* Grun.											11			
Epithemia argus var. *longicornus* (Ehr.) Grun.													13	
Epithemia argus var. *protracta* A.Mayer											11		13	14
Epithemia hyndmanii W.Sm.											11			14
Epithemia intermedia Fricke						6					11		13	14
Epithemia ocellata (Ehr.) Kuetz.													13	14
Epithemia sorex Kuetz.						6				10	11			14
Epithemia turgida (Ehr.) Kuetz.						6				10	11		13	14
Epithemia turgida var. *granulata* (Ehr.) Brun.						6				10	11			14
Epithemia turgida var. *westermannii* (Ehr.) Grun.														14°
Epithemia zebra (Ehr.) Kuetz.						6								
Epithemia zebra var. *saxonica* (Kuetz.) Grun.						6								
Epithemia species	1													
Eunotia arcus var. *bidens* Grun.										10	11			14
Eunotia curvata (Kuetz.) Lagerst.											11			14
Eunotia diodon Ehr.						6								
Eunotia incisa W.Sm. ex Greg.											11			14
Eunotia pectinalis (O.F.Muell.) Rabh.											11		13	14
Eunotia pectinalis var. *minor* (Kuetz.) Rabh.											11			14
Eunotia tenella (Grun.) Cl.														14°
Eunotia species		2												
Fragilaria bicapitata A.Mayer						6								
Fragilaria brevistriata Grun.						6			9	10	11			14
Fragilaria brevistriata var. *capitata* Herib.						6				10				14
Fragilaria brevistriata var. *inflata* (Pant.) Hust.						6			9	10	11	12	13	14
Fragilaria capucina var. *mesolepta* Rabh.						6					11			14
Fragilaria construens (Ehr.) Grun.						6			9	10	11	12	13	14
Fragilaria construens var. *binodis* (Ehr.) Grun.						6			9	10	11		13	14
Fragilaria construens var. *pumila* Grun.						6				10	11		13	14
Fragilaria construens var. *venter* (Ehr.) Grun.						6			9	10	11	12	13	14
Fragilaria crotonensis Kitton									9	10			13	14
Fragilaria lapponica Grun.						6			9		11		13	14
Fragilaria leptostauron (Ehr.) Hust.						6				10	11		13	14
Fragilaria leptostauron var. *dubia* (Grun.) Hust.						6					11		13	14
Fragilaria pinnata Ehr.						6			9		11	13		14
Fragilaria pinnata var. *intercedens* (Grun.) Hust.											11			14
Fragilaria pinnata var. *lancettula* (Schum.) Hust.						6			9					14
Fragilaria similis Krasske									9		11		13	14
Fragilaria vaucheriae (Kuetz.) Peters.						6			9	10	11	12	13	14
Fragilaria vaucheriae var. *capitellata* (Grun.) Patr.														14°
Fragilaria virescens Ralfs						6			9		11		13	14
Frustulia rhomboides (Ehr.) DeT.						6								14

Table 1 continued.

	Reference													
Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Frustulia vulgaris (Thwaites) DeT.											11			14
Gomphoneis herculeana (Ehr.) Cl.						6								
Gomphonema acuminatum Ehr.											11			14
Gomphonema affine Kuetz.									9					14
Gomphonema affine var. *insigne* (Greg.) Andrews											11			
Gomphonema angustatum (Kuetz.) Rabh.						6				10	11		13	14
Gomphonema angustatum var. *intermedia* Grun.														14°
Gomphonema clevei Fricke										10	11			14
Gomphonema dichotomum Kuetz.											11		13	14
Gomphonema gracile Ehr. em. V.H.						6			9		11			14
Gomphonema intricatum Kuetz.						6			9	10	11		13	14
Gomphonema intricatum var. *vibrio* (Ehr.) Cl.														14°
Gomphonema lanceolatum Ag.														14°
Gomphonema olivaceum (Lyngb.) Kuetz.						6			9	10	11		13	14
Gomphonema olivaceum var. *calcarea* (Cl.) Cl.											11		13	14
Gomphonema parvulum Kuetz.									9	10	11		13	14
Gomphonema septum Mogh.														14°
Gomphonema sphaerophorum Ehr.										10				
Gomphonema subclavatum (Grun.) Grun.											11			14
Gomphonema subclavatum var. *commutatum* (Grun.) A.Mayer									9		11			14
Gomphonema subclavatum var. *mexicanum* (Grun.) Patr.											11			14
Gomphonema tenellum Kuetz.									9					14
Gomphonema truncatum Ehr.										10				14
Gomphonema truncatum var. *capitatum* (Ehr.) Patr.											11		13	
Gomphonema truncatum var. *turgidum* (Ehr.) Patr.											11			
Gomphonema ventricosum Greg.						6			9	10	11		13	14
Gomphonema species	1													
Gomphonema species									9					
Gyrosigma acuminatum (Kuetz.) Rabh.						6				10	11	12	13	14
Gyrosigma attenuatum (Kuetz.) Rabh.						6								
Gyrosigma macrum (W.Sm.) Griff. & Henfr.						6					11			14
Gyrosigma spencerii (Quek.) Griff. & Henfr.											11		13	14
Gyrosigma spencerii var. *curvula* (Grun.) Reim.						6								
Gyrosigma strigilis (W.Sm.) Cl.											11		13	14
Hannaea arcus (Ehr.) Patr.						6				10				14
Hantzschia amphioxys (Ehr.) Grun.										10	11		13	14
Hantzschia amphioxys f. *capitata* O.Muell.										10				14
Hantzschia virgata (Roper) Grun.											11			14
Mastogloia elliptica var. *dansei* (Thwaites) Cl.						6				10	11		13	14
Mastogloia pumila (Grun.) Cl.														14°
Mastogloia smithii Thwaites ex W.Sm.						6							13	14
Mastogloia smithii var. *lacustris* Grun.						6					11		13	14
Melosira distans (Ehr.) Kuetz.											11			14
Melosira granulata (Ehr.) Ralfs						6		8	9	10	11	12	13	14
Melosira granulata var. *angustissima* O.Muell.						6			9	10	11	12	13	14
Melosira islandica O.Muell.											11		13	
Melosira italica (Ehr.) Kuetz.									9	10	11	12	13	14
Melosira roseana Rabh.											11			14
Melosira varians Ag.										10	11		13	14
Melosira species							7							
Meridion circulare (Grev.) Ag.						6								14
Meridion circulare var. *constrictum* (Ralfs) V.H.											11			
Meridion species	1													
Navicula abiskoensis Hust.											11		13	14
Navicula accepta Hust.											11			
Navicula accomoda Hust.													13	14

Table 1 continued.

	Reference													
Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Navicula amphibola Cl.										10	11			14
Navicula anglica Ralfs											11		13	14
Navicula angusta Grun.											11			
Navicula arenaria Donk.									9					14
Navicula arvensis Hust.									9	10			13	14
Navicula atomus (Kuetz.) Grun.											11			14
Navicula auriculata Hust.														14°
Navicula aurora Sov.						6			9	10	11			14
Navicula bacillum Ehr.						6					11		13	
Navicula bicephala Hust.						6								
Navicula capitata Ehr.						6				10	11			14
Navicula capitata var. *hungarica* (Grun.) Ross						6			9	10	11	12	13	14
Navicula capitata var. *luneburgensis* (Grun.) Patr.											11		13	14
Navicula cincta (Ehr.) Ralfs									9		11		13	14
Navicula circumtexta Meist. ex Hust.									9	10	11		13	14
Navicula clementis Grun.											11			14
Navicula crucicula (W.Sm.) Donk.										10				
Navicula cryptocephala Kuetz.						6			9	10	11		13	14
Navicula cryptocephala var. *veneta* (Kuetz.) Rabh.									9	10	11	12	13	14
Navicula cuspidata (Kuetz.) Kuetz.										10	11	12	13	14
Navicula cuspidata var. *heribaudi* Perag.											11		13	14
Navicula cuspidata var. *major* Meist.											11		13	14
Navicula difficillimoides Hust.						6					11			14
Navicula dulcis Patr.														14°
Navicula elginensis (Greg.) Ralfs														14°
Navicula elginensis var. *rostrata* (A.Mayer) Patr.														14°
Navicula exigua Greg. ex Grun.									9	10			13	14
Navicula exigua var. *capitata* Patr.										10				14
Navicula festiva Krasske													13	
Navicula gastrum (Ehr.) Kuetz.													13	14
Navicula gottlandica Grun.													13	
Navicula graciloides A.Mayer									9	10	11		13	14
Navicula gregaria Donk.						6					11			14
Navicula grimmei Krasske														14°
Navicula halophila (Grun.) Cl.											11		13	14
Navicula halophila f. *tenuirostris* Hust.														14°
Navicula heufleri Grun.													13	14
Navicula heufleri var. *leptocephala* (Breb. ex Grun.) Perag.									9				13	14
Navicula inflexa (Greg.) Ralfs.													13	
Navicula insociabilis var. *dissipatoides* Hust.											11			
Navicula integra (W.Sm.) Ralfs						6								
Navicula lacustris						6								
Navicula laevissima Kuetz.														14°
Navicula lanceolata (Ag.) Kuetz.						6			9	10	11		13	14
Navicula lapidosa Krasske						6								
Navicula menisculus var. *upsaliensis* (Grun.) Grun.										10	11		13	14
Navicula minima Grun.						6			9	10	11		13	
Navicula minuscula Grun.										10	11			14
Navicula molestiformis Hust.											11			
Navicula muralis Grun.						6								
Navicula mutica Kuetz.						6					11		13	14
Navicula mutica var. *cohnii* (Hilse) Grun.											11		13	14
Navicula mutica var. *nivalis* (Ehr.) Hust. (= *Navicula nivalis*)													13	14

Table 1 continued.

	Reference													
Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Navicula mutica var. *undulata* (Hilse) Grun.						6								14
Navicula nivalis Ehr.											11			14
Navicula oblonga (Kuetz.) Kuetz.						6			9	10	11		13	14
Navicula odiosa Wall.											11			14
Navicula omissa Hust.											11			
Navicula pelliculosa (Breb. ex Kuetz.) Hilse										10	11		13	14
Navicula peregrina (Ehr.) Kuetz.									9	10	11		13	14
Navicula placentula (Ehr.) Kuetz.						6					11		13	14
Navicula placentula f. rostrata A.Mayer														14°
Navicula protracta Grun.											11		13	14
Navicula protracta f. *subcapitata* (Wisl. et Por.) Hust.											11			
Navicula pseudotuscula Hust.											11			
Navicula pupula Kuetz.						6				10	11		13	14
Navicula pupula var. *capitata* (Skv.) Meyer														14°
Navicula pupula var. *elliptica* Hust.														14°
Navicula pupula var. *mutata* (Krasske) Hust.											11			14
Navicula pupula var. *rectangularis* (Greg.) Grun.						6				10	11		13	14
Navicula pygmaea Kuetz.						6				10	11			14
Navicula radiosa Kuetz.						6				10	11		13	14
Navicula radiosa var. *parva* Wall.													13	
Navicula radiosa var. *tenella* (Breb. ex Kuetz.) Grun.									9		11		13	14
Navicula reinhardtii (Grun.) Grun.						6					11		13	14
Navicula reinhardtii var. *elliptica* Herib.										10	11		13	14
Navicula rhyncocephala Kuetz.									9	10	11		13	14
Navicula rhyncocephala var. *amphiceros* (Kuetz.) Grun.											11	12	13	14
Navicula rhyncocephala var. *germainii* (Wall.) Patr.														14°
Navicula salinarum Grun.									9	10			13	14
Navicula salinarum var. *intermedia* (Grun.) Cl.									9	10	11			14
Navicula schroeteri var. *escambia* Patr.									9		11			14
Navicula scutelloides W.Sm. ex Greg.						6				10	11		13	14
Navicula secreta var. *apiculata* Patr.										10	11		13	14
Navicula secura Patr.											11		13	14
Navicula seminulum Grun.														14°
Navicula seminuloides Hust.											11	12		
Navicula septata Hust.						6								
Navicula strenzkei Hust.											11			
Navicula subbacillum Hust.														14°
Navicula subhamulata Grun.						6					11		13	14
Navicula symmetrica Patr.											11			14
Navicula tenelloides Hust.									9	10	11		13	14
Navicula tenera Hust.														14°
Navicula tripunctata (O.F.Muell.) Bory									9	10	11		13	14
Navicula tripunctata var. *schizonemoides* (V.H.) Patr.									9		11		13	14
Navicula tuscula Ehr.										10	11		13	
Navicula viridula (Kuetz.) Kuetz. em V.H.										10			13	14
Navicula viridula var. *avenacea* (Breb. ex Grun.) V.H.											11			14
Navicula viridula var. *rostellata* (Kuetz.) Cl.											11			14
Navicula wardii Patr.													13	
Navicula wittrockii (Lagerst.) Temp. et Perag.											11			
Navicula species	1	2												
Navicula species									9					
Navicula species											11			
Navicula species										10				
Neidium affine (Ehr.) Pfitz.						6					11			

Table 1 continued.

	Reference													
Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Neidium affine var. *amphirhynchus* (Ehr.) Cl.											11			
Neidium bisulcatum var. *baicalense* (Skv. & Meyer) Reim.														14°
Neidium dubium (Ehr.) Cl.											11		13	
Neidium iridis (Ehr.) Cl.						6				10	11	12	13	14
Nitzschia acicularis W.Sm.						6			9	10			13	14
Nitzschia acicularoides Hust.											11			
Nitzschia acuta Hantz.						6								14
Nitzschia amphibia Grun.									9	10	11		13	14
Nitzschia angustata (W.Sm.) Grun.						6					11		13	14
Nitzschia angustata var. *acuta* Grun.											11		13	
Nitzschia apiculata (Greg.) Grun.						6			9		11	12		14
Nitzschia capitellata Hust.														14°
Nitzschia clausii Hantz.						6								
Nitzschia communis Rabh.										10				14
Nitzschia denticula Grun.											11			14
Nitzschia dissipata (Kuetz.) Grun.						6			9	10	11	12		14
Nitzschia dubia W.Sm.											11			
Nitzschia epithemioides Grun.														14°
Nitzschia filiformis (W.Sm.) Hust.						6			9	10	11			14
Nitzschia fonticola Grun.										10				14
Nitzschia frustulum (Kuetz.) Grun.						6			9	10	11		13	14
Nitzschia gracilis Hantz.						6			9		11		13	14
Nitzschia granulata Grun.											11		13	14
Nitzschia hantzschiana Rabh.						6			9	10	11		13	14
Nitzschia holsatica Hust.									9					
Nitzschia hungarica Grun.						6				10	11	12	13	14
Nitzschia inconspicua Grun.									9		11		13	14
Nitzschia intermedia Hantz. ex Cl. & Grun.											11		13	14
Nitzschia lacunarum Hust.						6								
Nitzschia linearis (Ag.) W.Sm.						6			9	10	11		13	14
Nitzschia longissima var. *closterium* (W.Sm.) V.H.									9	10	11			14
Nitzschia microcephala Grun.														14°
Nitzschia minuta Bleisch											11			
Nitzschia obtusa W.Sm.						6								14
Nitzschia ovalis Arnott									9	10	11			14
Nitzschia palea (Kuetz.) W.Sm.						6			9	10	11	12	13	14
Nitzschia paleacea Grun.									9	10	11			14
Nitzschia perminuta Grun.										10				
Nitzschia punctata (W.Sm.) Grun.						6			9	10	11		13	14
Nitzschia pusilla (Kuetz.) Grun. em. Lange-Bert.														14°
Nitzschia recta Hantz.											11			
Nitzschia romana Grun.						6					11		13	14
Nitzschia sigma (Kuetz.) W.Sm.											11		13	14
Nitzschia sigmoidea (Ehr.) W.Sm.									9	10	11		13	14
Nitzschia spectabilis (Ehr.) Ralfs											11			14
Nitzschia stagnorum Rabh.									9		11			14
Nitzschia subacicularis Hust.														14°
Nitzschia subtilis (Kuetz.) Grun.											11		13	14
Nitzschia thermalis Kuetz.											11			14
Nitzschia thermalis var. *minor* Hilse						6								
Nitzschia tryblionella Hantz.										10	11		13	14
Nitzschia tryblionella var. *debilis* (Arnott) A.Mayer						6				10	11		13	14
Nitzschia tryblionella var. *genuina* Grun. (= *Nitzschia tryblionella* var. *tryblionella*)										10				
Nitzschia tryblionella var. *levidensis* (W.Sm.) Grun.										10	11		13	14
Nitzschia tryblionella var. *victoriae* Grun.						6				10	11		13	14
Nitzschia valdestriata Aleem et Hust.														14°

Table 1 continued.

Species	Reference													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Nitzschia species 1									9					
Nitzschia species 2									9					
Nitzschia species 1											11			
Nitzschia species 2											11			
Nitzschia species 3											11			
Opephora martyi Herib.									9	10	11		13	14
Pinnularia abaujensis var. *linearis* (Hust.) Patr.														14°
Pinnularia abaujensis var. *subundulata* (A.Mayer ex Hust.) Patr.											11			
Pinnularia acrosphaeria W.Sm.														14°
Pinnularia appendiculata (Ag.) Cl.											11			14
Pinnularia biceps Greg.											11			
Pinnularia borealis Ehr.						6					11		13	14
Pinnularia borealis var. *rectangularis* Carlson										10				
Pinnularia brebissonii (Kuetz.) Rabh.										10	11			14
Pinnularia burkii Patr.													13	
Pinnularia maior (Kuetz.) Rabh.											11		13	14
Pinnularia microstauron (Ehr.) Cl.						6				10	11		13	14
Pinnularia molaris (Grun.) Cl.						6								
Pinnularia nobilis (hr.) Ehr.														14°
Pinnularia obscura Krasske													13	14
Pinnularia ruttneri Hust.											11			
Pinnularia viridis (Nitz.) Ehr.						6				10	11		13	14
Pinnularia viridis var. *minor* Cl.											11		13	14
Plagiotropis arizonica Czar. & Blinn.											11			14
Plagiotropis vitrea (W.Sm.) Grun.										10				14
Plagiotropis vitrea var. *scaligera* (Grun. ex Cl. & Grun.) Perag.														14°
Pleurosigma australe Grun.										10				14
Pleurosigma delicatulum W.Sm.						6				10	11	12	13	14
Rhizosolenia minima Levan.														14°
Rhoicosphenia curvata (Kuetz.) Grun. ex Rabh.				4		6			9	10	11		13	14
Rhopalodia gibba (Ehr.) O.Muell.						6			9	10	11		13	14
Rhopalodia gibba var. *ventricosa* (Kuetz.) H. et M.Perag.										10	11		13	14
Rhopalodia gibberula (Ehr.) Muell.														14°
Rhopalodia gibberula var. *protracta* Grun.										10				14
Rhopalodia gibberula var. *vanheurckii* O.Muell.									9		11		13	14
Rhopalodia musculus (Kuetz.) O.Muell.										10	11		13	14
Scoliopleura peisonis Grun.						6				10	11	12	13	14
Stauroneis anceps Ehr.														14°
Stauroneis anceps var. *siberica* Grun. ex Cl.						6								
Stauroneis kriegeri Patr.														14°
Stauroneis muriella f. linearis Lund						6								
Stauroneis phoenicenteron (Nitz.) Ehr.						6				10	11		13	14
Stauroneis phoenicenteron var. *brunii* (M.Perag & Herib.) Voigt						6								
Stauroneis phoenicenteron f. *gracilis* (Ehr.) Hust.						6								
Stauroneis smithii Grun.											11			14
Stauroneis wislouchii Poretz. & Anis.											11			
Stauroneis species													13	
Stephanodiscus astraea (Ehr.) Grun.						6			9	10				14
Stephanodiscus astraea var. *minutula* (Kuetz.) Grun.									9	10		12		14
Stephanodiscus carconensis var. *pusilla* Grun.											11			
Stephanodiscus dubius (Fricke) Hust.											11	12	13	
Stephanodiscus hantzschii Grun.											11	12		
Stephanodiscus invisitatus Hohn & Heller.											11	12	13	14
Stephanodiscus minutus Cl. & Moell.											11	12		

Table 1 continued.

Species	Reference													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Stephanodiscus niagarae Ehr.				4		6			9	10	11		13	14
Stephanodiscus subtilis V.Goor											11	12	13	
Stephanodiscus species												12		
Stephanodiscus species 1													13	
Stephanodiscus species 2													13	
Surirella angusta Kuetz.						6			9	10	11		13	14
Surirella biseriata Breb.											11		13	14
Surirella linearis W.Sm.						6					11		13	14
Surirella linearis var. *constricta* Grun.						6								
Surirella ovalis Breb.						6				10	11	12	13	14
Surirella ovalis var. *brightwellii* (W.Sm.) Cl.-Eul.									9	10	11		13	
Surirella ovata Kuetz.									9	10	11	12	13	14
Surirella ovata var. *pinnata* W.Sm.						6								14
Surirella patella Ehr.											11			14
Surirella pseudovalis Hust.											11			
Surirella robusta Ehr.											11			14
Surirella robusta var. *splendida* (Ehr.) V.H.											11		13	
Surirella spiralis Kuetz.						6					11			
Surirella striatula Turp.										10	11		13	14
Surirella species		2												
Synedra acus Kuetz.						6			9		11		13	14
Synedra amphicephala var. *austriaca* (Grun.) Hust.													13	
Synedra capitata Ehr.						6				10	11		13	14
Synedra cyclopum Bruts.														14°
Synedra delicatissima var. *angustissima* Grun.									9	10	11	12	13	14
Synedra famelica Kuetz.														14°
Synedra fasiculata (Ag.) Kuetz.														14°
Synedra fasiculata var. *truncata* (Grev.) Patr.									9	10	11			14
Synedra filiformis var. *exilis* Cl.-Eul.						6								
Synedra mazamensis Sov.									9	10	11			14
Synedra minuscula Grun.											11			14
Synedra parasitica (W.Sm.) Hust.													13	
Synedra parasitica var. *subconstricta* (Grun.) Hust.														14°
Synedra pulchella Kuetz.														14°
Synedra radians Kuetz.														14°
Synedra rumpens Kuetz.														14°
Synedra rumpens var. *familiaris* (Kuetz.) Grun.						6				10				14
Synedra rumpens var. *fragilarioides* Grun.										10	11			14
Synedra rumpens var. *meneghiniana* Grun.											11		13	
Synedra rumpens var. *scotica* Grun.										10	11			14
Synedra socia Wall.									9					14
Synedra tenera W.Sm.										10	11			14
Synedra ulna (Nitz.) Ehr.						6			9	10	11	12	13	14
Synedra ulna var. *contracta* Oestr.									9	10	11			14
Synedra ulna var. *danica* (Kuetz.) Grun.														14°
Synedra ulna var. *longissima* (W.Sm.) Brun.						6								
Synedra ulna var. *oxyrhynchus* (Kuetz.) V.H.														14°
Synedra ulna var. *oxyrhynchus* f. *mediocontracta* (Forti) Hust.													13	
Synedra ulna var. *spathulifera* (Grun.) V.H.						6								
Synedra ulna var. *subaequalis* (Grun.) V.H.											11			
Synedra species	1	2												
Tabellaria flocculosa (Roth) Kuetz.				4										
Tabellaria species		2												
Tetracyclus lacustris Ralfs						6								
Thalassiosira fluviatilis Hust.											11			14
Thalassiosira species										10				
Thalassiosira species											11			
Thalassiosira species												12		

Table 1 continued.

	Reference													
Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14
DIVISION EUGLENOPHYTA														
CLASS EUGLENOPHYCEAE														
Order Euglenales														
Euglena ehrenbergii Klebs										10				14
Euglena gracilis Klebs										10				14
Euglena oxyuris Schmar.										10				14
Euglena proxima Dang.										10				14
Euglena tripteris (Duj.) Klebs														14°
Euglena viridis Ehr.														14°
Euglena species							7							
Lepocinclis salina Fritsch										10				14
Phacus chloroplastes Pres.										10				14
Phacus spiralis All. et Jahn														14°
Phacus tortus (Lemm.) Skv.										10				
Strombomonas fluviatilis (Lemm.) Defl.										10				14
Trachelomonas crebea (Kill.) Defl.										10				14
DIVISION PYRRHOPHYTA														
CLASS DINOPHYCEAE														
Order Peridiniales														
Ceratium hirundinella (Muell.) Dujard.		2		4				8		10				14
Order Glenodiniales														
Glenodinium dinobryonis (Wol.) Lind.										10				14
Glenodinium penardiforme (Lind.) Schill.										10				14
Glenodinium species							7							
CRYPTOPHYTA														
CLASS CRYPTOPHYCEAE														
Order Cryptomonadales														
Chroomonas species							7							
Cryptomonas species							7							

Column numbers refer to the following papers:

1. Tanner (1930)
2. Tanner (1931)
3. Snow (1932)
4. Harding (1970)
5. Harding (1971)
6. Bolland (1974)
7. EPA (1977)
8. Whiting (1978)
9. Grimes et al. (1980)
10. Rushforth et al. (1981)
11. Grimes and Rushforth (1982)
12. Grimes and Rushforth (1983)
13. Javakul and Rushforth (1983)
14. Present report

°Algal species previously unreported from Utah Lake.
°°Diatoms are listed in alphabetical order.

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HOST-PARASITE STUDIES OF *TRICHOPHRYA* INFESTING CUTTHROAT TROUT (*SALMO CLARKI*) AND LONGNOSE SUCKERS (*CATOSTOMUS CATOSTOMUS*) FROM YELLOWSTONE LAKE, WYOMING

R. A. Heckmann[1] and T. Carroll[2]

ABSTRACT.— *Trichophrya* sp. (Protozoa) on the gills of cutthroat trout (*Salmo clarki*) and longnose suckers (*Catostomus catostomus*) was studied using light and electron microscopy and tracer techniques. All cutthroat trout, 14 cm in total length and above, from Yellowstone Lake, Yellowstone National Park, Wyoming, were infested with the suctorian. No trichophryans were found on fry or fingerling cutthroat trout. Sixty percent of the examined longnose suckers from the same location were infested. Light microscopy disclosed extensive pathology of gill epithelium in longnose suckers infested with *Trichophrya* that was not observed for infested cutthroat trout. Electron micrographs show damage to immediate host gill cells by both parasites, depicted by a reduction and lack of mitochondria. Both parasites form attachment helices (0.52×0.04 μm), which may originate in the protozoan cell membrane and function for maintenance of parasite position on the host cell. There was no uptake of ^{14}C, injected into host fish, via the attachment helices by the parasite that further substantiated the mechanical function for the spiral structure. Protozoan feeding on host tissue may be accomplished by use of necrotic gill tissue and mucus.

Trichophrya clarki (Heckmann 1970, 1971) was found on the gills of all adult cutthroat trout (*Salmo clarki*) examined from Yellowstone Lake, Yellowstone National Park, Wyoming, during the summers of 1968 and 1969. *Trichophyra catostomi* (Heckmann 1970, 1971) was present on the gills of 60% of the adult longnose suckers (*Catostomus catostomus*) examined from the same region.

Butschli (1889) reported *Trichophrya* in perch (*Perca*) and pike (*Esox*) from Europe and assigned the species name *T. piscium.* Davis (1937, 1942) was the first to report *Trichophrya* in the Northern Hemisphere. He assigned the name *T. micropteri* and *T. ictaluri* for the gill parasites of smallmouth black bass (*Micropterus dolomieui*) and channel catfish (*Ictalurus punctatus*), respectively. No name was given for *Trichophrya* in brook trout (*Salvelinus fontinalis*). He also was the first to suggest that it may have a pathogenic effect. Chen Chih-leu (1955) and Prost (1952) added to Chinese and European records by assigning *T. sinensis* to infested white and black Amur fishes and *T. intermedia* to infested salmon-fry (*Salmo salar*). Lom (1960) added to the host record for *T. intermedia* by including brown trout (*Salmo trutta*) and three other fishes in Czechoslovakia. Culbertson and Hull (1962) summarized all host records of *Trichophrya* and suggested *T. piscium* be used for all species found in fishes. This suggestion was followed by Sandeman and Pippy (1967), who reported on four salmonids of Newfoundland infested with *Trichophrya.* Hoffman (1967) stressed the need for further taxonomic study of trichophryan species and their symbiotic effects. Heckmann (1970), used the same criteria outlined by Culbertson and Hull (1962) and transmission electron microscopy of the protozoan, described two new species, one in cutthroat

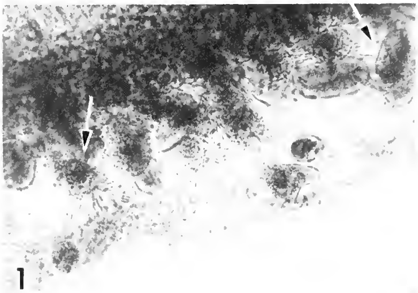

Fig. 1. A gill macerate from an infested cutthroat trout from Yellowstone Lake showing numerous suctorian ciliates, *Trichophrya clarki*, next to gill filaments. (1000X)

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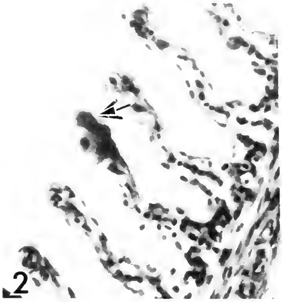

Fig. 2. A gill section from a cutthroat trout showing a Trichophryan attached closely to the epithelial cells at the tip of the filament (arrow). (400X)

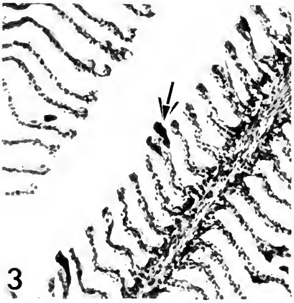

Fig. 3. Another section of cutthroat trout gill tissue showing numerous suctorian ciliates attached to the tip of gill filaments (arrow). (100X).

trout (*T. clarki*) and one in longnose suckers (*T. catostomi*).

The objective of this study was to examine the host-parasite relationship of *Trichophrya* on cutthroat trout and longnose suckers. Three methods were used for study of this problem: light microscopy, electron microscopy (transmission TEM and scanning SEM), and radioactive tracers. To date there has been no ultrastructural description of the host-parasite relationship or the interface between the ectoparasite and host cells. Meyer (1966) questioned the parasitic nature of *T. ictaluri* and stated the main effect may be mechanical interference with respiration. Davis (1967) reported heavy loss among fingerling and adult smallmouth bass, raised in hatcheries, due to *T. micropteri*. These were attached to the gills by a broad base, closely applied to the epithelium, causing hyperplasia and necrosis of host tissue.

Materials and Methods

Light Microscopy

Fishes ranging in size from 3.5 to 45.7 cm total length, were obtained from several sites in Yellowstone Lake and Yellowstone River. Intact gills, infested with *Trichophrya*, were scraped and the macerate was examined (Fig. 1). Infested gills were also fixed with 10% formalin and prepared by standard methods for histological examination (Davenport 1960). Sections were stained with the following: Harris' hematoxylin and eosin, periodic acid Schiff (McManus 1956), mercuric bromphenol blue (Mazia et al. 1953), five-dye stain (Greenstein 1961), and Schiff's reagent (Davenport 1960).

Electron Microscopy

Infested gill macerate and gill filaments were placed in small plastic vials containing 2.5% gluteraldehyde buffered with potassium phosphate (0.1M, pH 7.3). Post fixation was accomplished with 1% osmium tetroxide in the same buffer. Standard methods were used in preparing the tissue for sectioning (Dawes 1971). The dehydrated material was embedded in Araldite epoxy plastic and sectioned, then poststained with uranyl acetate and Reynold's lead citrate. In an attempt to determine possible differences in the cytochemical nature of magnified structures, the staining procedure was varied in the following manner: no poststain, uranyl acetate only, and lead citrate only. Fixed gill macerate and filaments were sent to Florida State University for examination by scanning electron microscopy.

Tracer Study

A tracer experiment was conducted with four infested cutthroat trout of approximately equal size from Yellowstone River. Each fish was anesthetized with MS 222 and injected intracardially with 5 microcuries of ^{14}C-D-Glucose (U). Previous to the injection blood samples were qualitatively checked for

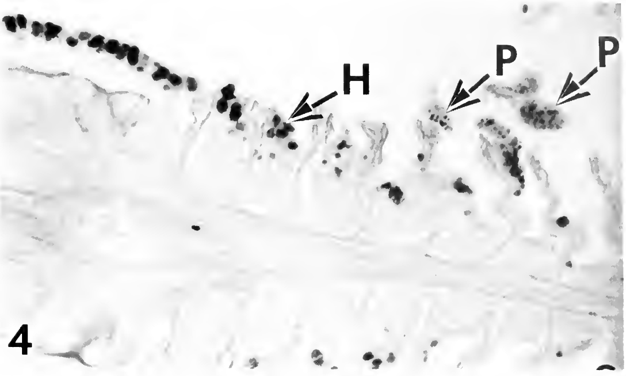

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Fig. 4. This is a section of cutthroat trout gill tissue stained with periodic acid Schiff to emphasize mucopolysaccharides. Note the dark staining granules in the host (H) epithelial cells and similar granules in the cytoplasm of the suctorian ciliate (P). The protozoan could be using mucus as a source of food (400X)

glucose, using chromatography. The fish were sacrificed 1, 2, 4, and 8 hours after injection. The gills were removed and washed in physiological saline and fixed in 10% formalin. Samples of 25 *Trichophrya* and 0.4 grams of gill filament were analyzed from each fish using liquid scintillation counting (Arnoff 1960, Chase and Rabinowitz, 1962). The suctorians and gill filaments were placed in liquid scintillation vials containing 0.5 and 1.0 ml, respectively, of hydroxide of Hyamine (Rohm and Haas) for 12 hours to disrupt the cell membranes. Scintillation fluid was added and each sample was counted for a period of 20 minutes. The trichophryans were fixed with 10% formalin and washed three times with changes of formalin.

The wet film method for autoradiography (Pelc 1947, MacDonald et al. 1948) was used to corroborate the data from liquid scintillation counting. Gills from the injected fish were prepared histologically (Davenport 1960) and sectioned at 20 μm. Duplicate thin sections from each fish were spread on glass slides that were immersed in water along with unexposed film (Fuji plate film; ET2F-9327). A strip of film was then removed from the plate and placed over the tissue sections. The tissue-film preparation was subsequently removed from the water, air dried, and stored in light-tight film boxes. The preparation was developed and stained with Mayer's hematoxylin after 2, 4, 6, and 8 weeks' exposure (Shigematsu 1969a, 1969b). It was then observed with a compound microscope.

RESULTS

Light Microscopy

HISTOLOGY.— The suctorian parasites on cutthroat trout are usually concentrated on the lamellar tips of the gill filament where they are closely attached to the epithelial cells (Figs. 2 and 3). Cutthroat trout samples, with the largest number of trichophryans, had 7.1% of the gill surface covered by the parasite. In one 36 cm trout, there was an average of 31 suctorians per gill filament totaling about 42,000 organisms. The macro- and micronucleus of *T. clarki* were Feulgen positive (Schiff's reagent) and the mercuric bromphenol stain showed an intense blue area between the parasite and the epithelial host cell. Periodic acid Schiff staining revealed similar particles in both protozoans and the adjacent surface of the gill epithelium (Fig. 4).

HISTOPATHOLOGY.— Sections of gills from cutthroat trout infested with *T. clarki* had no apparent cytological damage (Figs. 2 and 3), whereas longnose suckers inhabited by *T. catostomi* were definitely affected by the parasite (Figs. 5 and 6). There was definite damage to the gill lamellae, characterized by hyperplasia and hemorrhaging of the adja-

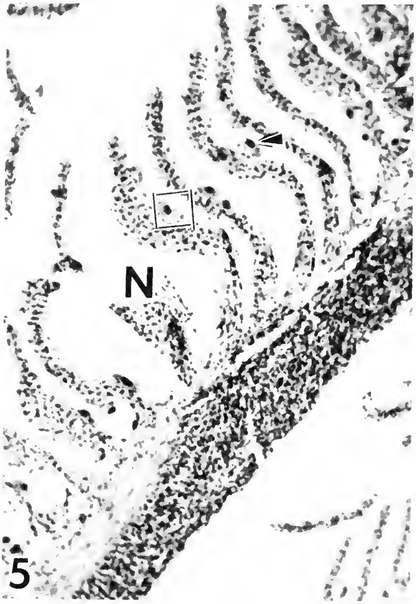

Fig. 5. This is a section of longnose sucker gill tissue. The suctorian ciliates are causing pathological damage to the host (arrow and box) tissue that includes hemorrhaging and hyperplasia of the gill lamellae. Necrosis (N) also occurs in the infested tissue with subsequent clubbing of filaments. (400X)

Fig. 6. In infested longnose sucker gills, the Trichophryans are not attached to the tips of the gill filaments but locate at the base (arrow) of the structure. (600X)

cent host tissue with subsequent necrosis (Fig. 5, 6).

Transmission Electron Microscopy

The ultrastructural characteristics of *T. clarki* and the gill epithelial cells have been described (Heckmann 1970).

Sections of the interface between the host epithelial cell and parasite were prepared. A helical structure in the interface attaches the parasite to the gill epithelium (Fig. 7). This structure (referred to as attachment helix) has the following measurements: length, 0.52 μm (range 0.20 to 0.82 μm) and width 0.04 μm (range 0.03 to 0.06 μm). The filament making up the helix appeared circular in transverse section (Fig. 8) and revealed an electron transparent center bound by an opaque ring. Lom, 1970, described a similar structure for suctorian infested fish concurrent with this initial description (Heckmann 1970). The attachment helix is found only on the side of the protozoan next to the host cell (Fig. 7). It appears to originate as a cleft in the outer wall of the protozoan. The protozoan membrane, in the cleft, moves into the space between the host cell and parasite and expands into a long filament (Figs. 9 and 10). The filament then contracts to form the helix. Cytochemical evidence from ultrathin sections along with histochemical analyses of specimens suggest that the origin of the helix is the outer wall of the protozoan. The helix was osmophilic when unstained thin sections of oxmium-fixed protozoa were viewed. It was mercuric bromphenol blue positive. Lipo-protein material, found in biological membranes, have an affinity for osmium whereas protein stains blue with bromphenol blue.

A series of electron micrographs shows organelle changes to the epithelial cells of cutthroat trout due to *T. clarki*. In gill epithelial cells not infested with *T. clarki*, there are numerous mitochondria with well-defined

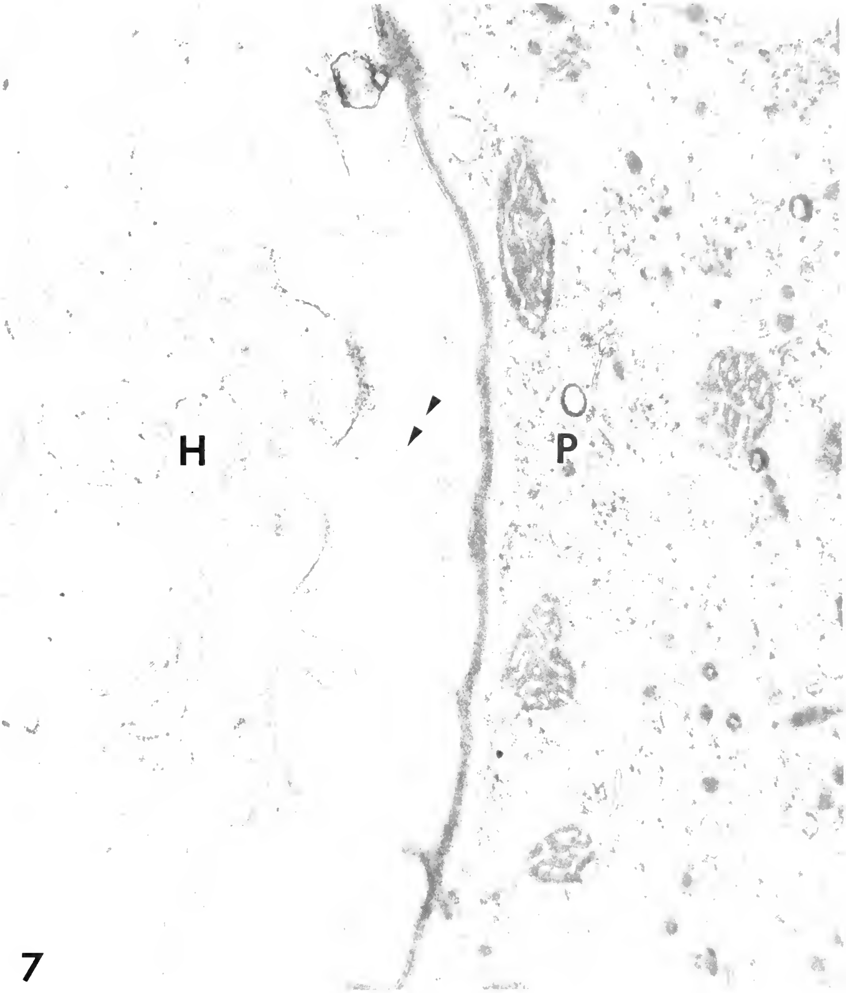

Fig. 7. At the electron microscopic level of magnification, attachment helices (arrows) are visible between fish host cells (H) and the protozoan (P). These structures aid in holding the suctorian ciliate next to the host epithelial cell. (12,000X)

cristae (Fig. 11). Infested cells show, in comparison to normal cells, swollen mitochondria that have fewer cristae and lack the outer enveloping membrane (Fig. 12). Thus damage is detected as the number of host cell mitochondria decrease and disappear. Similar damage was observed for *T. catostomi* in longnose suckers.

Scanning Electron Microscopy

Scanning electron microscopy shows *T. clarki* to be saucer-shaped, with the convex

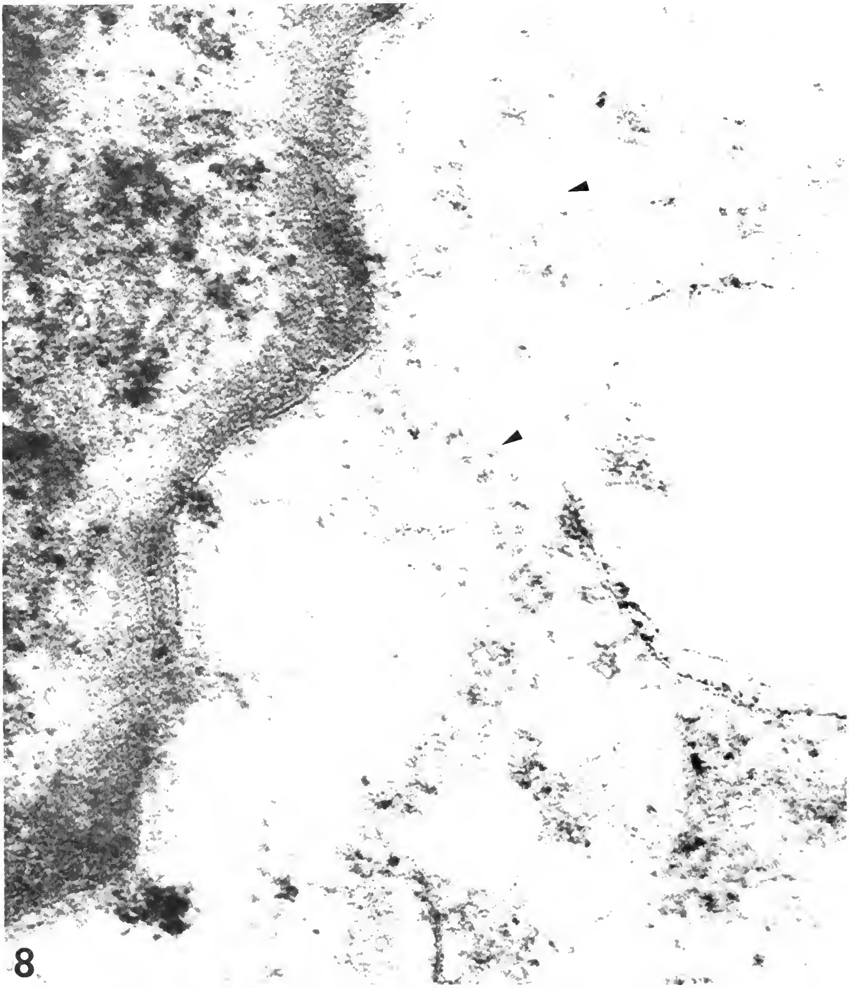

Fig. 8. This electron photomicrograph shows the interface between the fish epithelial cell and the protozoan. Note the spiral, hollow nature of the attachment helices (arrows). (125,000X)

surface attached to the gill epithelium. There are fine filaments between the suctorian and the host cells that are probably aggregations of attachment helices (Fig. 13).

Tracer Study

Liquid scintillation counts and autoradiography indicate there is no uptake of ^{14}C by *T. clarki* from the fish host during eight hours following injection. The isotope was still present in the gill epithelium after two hours and was presumably available to parasites using sustenance directly from the host. Silver grains in the autoradiographic film developed in all four gill samples after four weeks exposure. Samples from fish sacrificed at one- and two-hour intervals after ^{14}C injection had

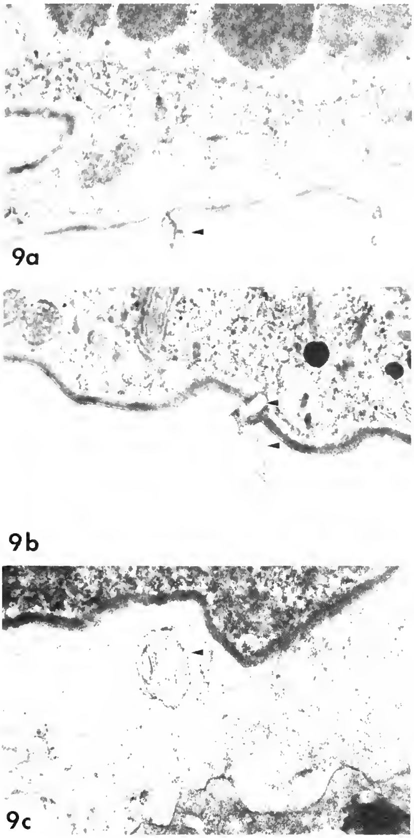

Fig. 9. A possible origin for the attachment helix is from the cell membranes of the Trichophryan. Figure 9a shows a "wedge" of membrane breaking away from the protozoan and starting to lengthen (9b) followed by a spiral-like development (9c). (10,500X)

exposed silver grains only over the lumen of blood vessels and capillaries of the gills. The four-hour sample demonstrated radioactivity in these same regions and also in the epithelial cells of the gill filament. Distribution of radioactivity in the eight-hour sample was similar to that in the four-hour sample but of less intensity (approximately 50% fewer grains visible).

Discussion

Host-Parasite Relationship

There is no uptake of ^{14}C by *T. clarki*, but TEM disclosed definite changes in the mitochondria of host epithelial cells. The mitochondria decrease in number and apparently disappear, which is probably due to the masking effect the parasite has on respiratory activity (Davis 1942, Meyers 1966). Strobel (1965) observed a reciprocal response by mitochondria for hydrating spores of *Puccinia striiformis* that was also related to respiration. The pathological signs in longnose suckers infested with *T. catostomi* are more extensive. Infested gill tissue shows areas of hyperplasia and necrosis, which is visible with light microscopy, in addition to the previously described fine structure.

The exclusive use of free-living protozoa as food for fish suctoria has been questioned (Davis 1942). The tentacles of other suctoria are used in obtaining food, immobilizing prey, and transporting cytoplasm to the central body (Hull 1961a, 1961b). Phialocysts (Batisse 1967a, 1967b) or haptocysts (Bardele and Grell 1967) at the tip of the tentacles are used to hold and impale prey. Rudzinska (1954, 1965, 1966) described *Tokophrya infusionum* feeding on live ciliates using its tentacles as described. No other protozoa were observed in the fish gills or on the trichophryan tentacles in infested fishes (*T. intermedia*) of Czechoslovakia (Lom 1960). Prost (1953) suggested that *T. intermedia* feed on host necrotic tissue. In this study no free-living protozoa were found impaled on the tentacles of the two suctorian species, and it was observed that *T. catostomi* may feed on the necrotic gill tissue of longnose suckers. The mucus layer on the surface of gill epithelium may also be a source of food. Periodic acid Schiff preparations show particles (complex polysaccharides) of similar stain intensity both in *T. clarki* and on the surface of host epithelium.

The attachment helix is an organelle that functions in holding the parasite next to the epithelial host cell. This structure may hold the parasite in position when water flows across the gill surface. Other structures in the interface of the parasite and host have been

Fig. 10. This figure shows a sequence in the development of the attachment helix. The cell membrane strands lengthen out (a) in the cell interface (b) and start to form a spiral (c, d), with the helix being the final product (e). (10,500X). The protozoan is on the left-hand side of the figure, and the epithelial cell of a fish gill is on the right-hand side.

described. Uspenskaja (1966) found small cytoplasmic extensions ("rootlets") from *Myxidium* into the urinary bladder epithelium of *Esox lucius*. He considered these to function primarily as absorption organelles rather than for attachment. Scholtyseck and Hammond (1966a, 1966b) noted ribbonlike extensions (15 mm by 2 μm) from *Eimeria* macrogmetocytes into host cells and postulated that their function was ingestion of nutrients.

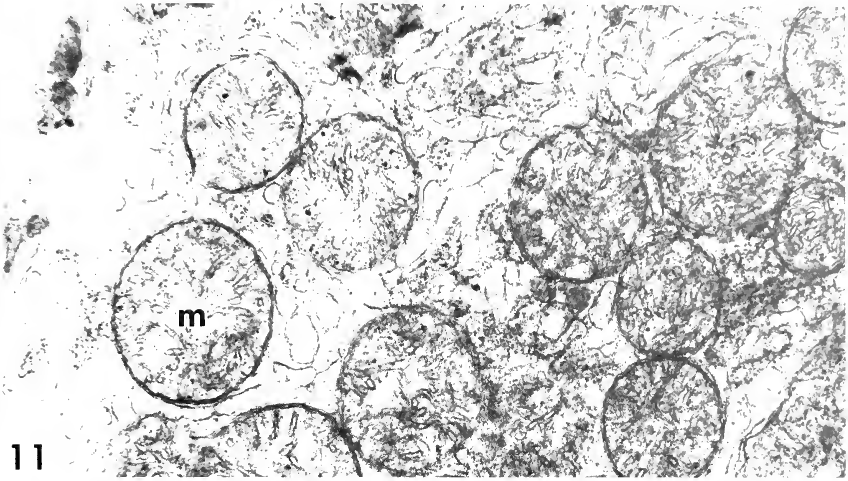

Fig. 11. This is a fish gill epithelial cell containing characteristic mitochondria (m). (10,500x)

ACKNOWLEDGMENTS

Dr. C. J. D. Brown directed the study; Dr. Gary Strobel and Dr. Akiyo Shigematsu offered technical assistance. Cooperation was received from the National Park Service and U.S. Sport Fisheries and Wildlife. Financial support was given by Montana Cooperative Fisheries Unit, Montana State University Agricultural Experiment Station, Project 410, Paper 157, Journal Series.

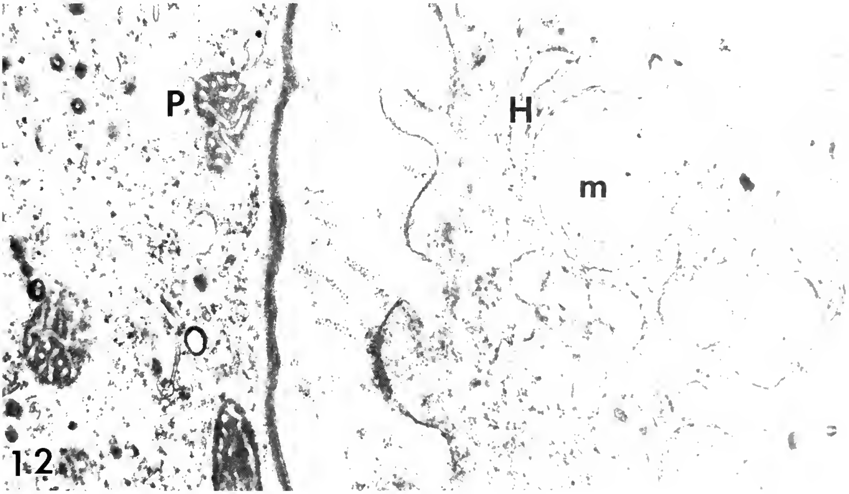

Fig. 12. When the Trichophryan attaches to the gill filament, the immediate epithelial cells show mitochondrial (m) and organelle degeneration, probably due to the masking effect of the protozoan. (10,500X)

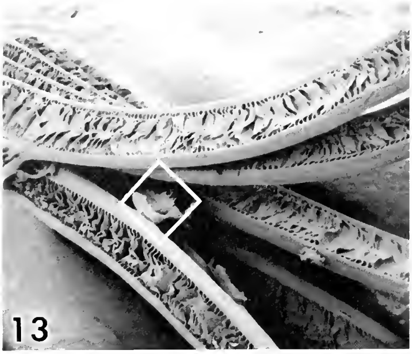

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Fig. 13. This is a scanning electron microscopy of a cutthroat trout gill. The Trichophryan is attached to the gill lamellae (box) and appears to be saucer-shaped. (1000X)

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NEW SYNONYMY AND NEW SPECIES OF BARK BEETLES (COLEOPTERA: SCOLYTIDAE)

Stephen L. Wood[1]

ABSTRACT.— New synonymy in Scolytidae is proposed as follows: *Camptocerus opacicollis* (Eggers) (= *Camptocerus aquilus* Wood), *Cladoctonus corumbensis* (Eggers) (= *Hoplitophthorus bolivianus* Wood), *Cladoctonus interruptus* (Eggers) (= *Hoplitophthorus sentus* Wood), *Cnemonyx errans* (Blandford) (= *Ceratolepis barbatus* Schedl), *Cnemonyx flavicornis* (Chapuis) (= *Cnemonyx vianai* Schedl), *Cnesinus dividuus* Schedl (= *Cnesinus dryographus* Schedl, *Cnesinus laevicollis* Schedl), *Cryptocurus spinipennis* Schedl (= *Hyloperus caudatus* Browne, *Hyloperus bicornis* Browne), *Dendrosinus ater* Eggers (= *Dendrosinus hirsutus* Schedl), *Hylesinus aculeatus* Say (= *Hylesinus imperialis* Eichhoff), *Hylesinus cordipennis* Lea (= *Hylesinus papuanus* Eggers), *Hylesinus macmahoni* (Stebbing) (= *Hylesinus alternans* Schedl, *Leperisinus fraxinoides* Beeson, *Leperisinus fraxinoides* Schedl), *Hylesinus niligrinus* Eggers (= *Trogloditica robusta* Schedl), *Phloeosinopsoides triseriatus* (Schedl) (= *Xylechinus papuanus* Schedl), *Phloeotribus scarabaeoides* (Bernard) (= *Phloeotribus americanus* Dejean), *Scolytogenes darwini* Eichhoff (= *Nigritus similis* Eggers, *Nigritus major* Eggers, *Scolytogenes cryptolepis* Schedl), *Scolytodes notatus* Eggers (= *Hexacolus pseudobicolor* Eggers, *Hexacolus subparalleus* Eggers, *Hexacolus pelicerinus* Schedl), *Scolytopsis puncticollis* Blandford (= *Scolytopsis argentinensis* Schedl, *Scolytus bruchi* Schedl, *Scolytopsis toba* Wichmann), *Tomicus piniperda* (Linnaeus) (= *Blastophagus khasianus* Murayama), *Xylechinus spathifer* Schedl (= *Pteleobius lomatiae* Schedl). Species new to science are described as *Acanthotomicus ipsimorphus* (Costa Rica), *Acrantus opimus* (Indonesian New Guinea), *Bothrosternus hirsutus* (Venezuela), *Cnesinus discretus* (Venezuela) *Cnesinus minor* (Costa Rica), *Corthylus trunacatus* (Peru), *Hylurgus indicus* (India), *Pachycotes minor* (Australia), *Phloeosinopsoides pumilus* (Papua New Guinea), *Xylechinosomus pilosus* (Brazil).

During the past several years, a world revision of the genera of Scolytidae has been in preparation. While conducting that study, I have had the opportunity to visit several museums for the purpose of studying type material. This led to the discovery of a number of synonyms and to the detection of several species new to science. The above abstract summarizes 29 cases of synonymy from all parts of the world and lists the names and country of origin for 10 previously unnamed species. The new species represent 9 different genera and come from Australia (1), Brazil (1), Costa Rica (2), India (1), New Guinea (2), Peru (1), and Venezuela (2).

Of special interst to American students is conclusive placement in synonymy of *Hylesinus imperialis* Eichhoff and of the nomen nudum, *Phloeotribus americanus* Dejean.

NEW SYNONYMY

Camptocerus opacicollis (Eggers)

Loganius opacicollis Eggers, 1929, Wiener Ent. Zeit. 46:61 (Holotype, male; Ostbolivia; Eggers Coll., apparently on loan to Wien Nat. Mus.)

Camptocerus aquilus Wood, 1972, Bull. Ent. Res. 62:244 (Holotype, male; 12° 49′ S 51° W, Brazil; British Mus. Nat. Hist.). *New synonymy*

The male holotype of *Loganius opacicollis* Eggers was deposited in the Eggers Collection, but it never reached the U.S. National Museum with the Eggers Collection. It was found in Schedl material at the Wien Museum and was compared to a male paratype of *Camptocerus aquilus* Wood. Only one species is represented by this material. For this reason, the junior name is placed in synonymy as indicated above.

Cladoctonus corumbensis (Eggers)

Hoplites corumbensis Eggers, 1950, Ent. Blätt. 45–46:149. (Holotype: Corumba, Matto Grosso, Brazil; Eggers Collection, apparently on loan to Wien Nat. Mus.)

Hoplitophthorus bolivianus Wood, 1961, Great Basin Nat. 21:106 (Holotype, female; Route between Boyuilbe and Charagua via Cueva, Ingri, etc. Bolivia; U.S. Nat. Mus.). *New synonymy*

Because the holotype of *Hoplites corumbensis* Eggers was missing from the Eggers Collection at the U.S. National Museum, it could not be compared to species sub-

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sequently named in this genus. When it was found in Schedl material at Wien, it was compared to paratypes of *Hoplitophthorus boliviae* Wood and found to be identical. For this reason, the name *bolivianus* must be placed in synonymy as indicated above.

Cladoctonus interruptus (Eggers)

Hoplites interruptus Eggers, 1940, Arb. morph. taxon. Ent. 7:126 (Holotype; Guadeloupe; Fleutiaux Coll.)

Hoplitophthorus sentus Wood, 1961, Great Basin Nat. 21:3 (Holotype, female; La Cuchilla, Sevilla, Colombia; Wood Coll.). *New synonymy*

A male cotype of *Hoplites interruptus* Eggers was found among the Schedl material at Wien and was compared directly to a male paratype of *Hoplitophthorus sentus* Wood. The two specimens represent the same species. For this reason the name *sentus* is placed in synonymy as indicated above.

Cnemonyx errans (Blandford)

Ceratolepis errans Blandford, 1896, Biol. Centr. Amer., Coleopt. 4(6):127 (Lecotype, male; in "Mexican" tobacco refuse; British Mus. Nat. Hist., designated by Wood, 1972, Great Basin Nat. 32:19)

Ceratolepis barbatus Schedl, 1954, Dusenia 5:24 (Holotype, male; Nova Teutonia, Brazil; Wien Nat. Mus.). *New synonymy*

The holotype of *Ceratolepis barbatus* Schedl was examined and compared directly to my homotypes *C. errans* Blandford. Because only one species is represented by this material, Schedl's name is placed in synonymy as indicated above.

Cnemonyx flavicornis (Chapuis)

Loganius flavicornis Chapuis, 1869, Synopsis des Scolytides, p. 53 (Two syntypes; Cumana; Brussels Mus.)

Cnemonyx vianai Schedl, 1950, Acta Zool. Lilloana 9:289 (Holotype; Valle Hermoso, Dep. Punilla, Cordoba, Argentina; Wien Nat. Mus.). *New synonymy*

The type and two paratypes of *Cnemonyx vianai* Schedl in the Schedl material at Wien were placed by Schedl as a synonym of *Loganius flavicornis* Chapuis, but this was apparently never published. Because I have examined both syntypes of *flavicornis* and the Schedl holotype, I concur with his decision and place Schedl's name in synonymy as indicated above.

Cnesinus dividuus Schedl

Cnesinus dividuus Schedl, 1938, Rev. Soc. Ent. Argentina 10:22 (Lectotype, female; Tigre, Buenos Aires, Argentina; Wien Nat. Mus., present designation)

Cnesinus dryographus Schedl, 1951, Dusenia 2:78 (Lectotype, female; Nova Teutonia, Brasil; Wien Nat. Mus., present designation). *New synonymy*

Cnesinus laevicollis Schedl, 1951, Dusenia 2:79 (Lectotype, female; Nova Teutonia, Santa Catarina, Brasil; Wien Nat. Mus., present designation). *New synonymy*

The "holotypes" cited by Schedl (1979) for his species *Cnesinus dividuus*, *C. dryographus*, and *laevicollis* are all of the same sex and all are syntypes. As indicated above, I here designate those "holotypes" as lectotypes of *dividuus*, *dryographus*, and *laevicollis* respectively. They were compared directly to one another and to my series from Nova Teutonia and were found to represent the same species. The two junior names must, therefore, be placed in synonymy as indicated above. It was a common practice of Schedl to designate male and female "holotypes," one of each for his collection and one of each for the collection of institutions submitting the specimens for identification. Hence, the confusion of "holotypes.".

Cryptocurus spinipennis Schedl

Cryptocurus spinipennis Schedl, 1957, Ann. Mag. Nat. Hist. (12) 10:870 (Holotype, male; Moshi district, Tanganyika; British Mus. Nat. Hist.)

Hyloperus caudatus Browne, 1970, J. Nat. Hist. 4:547 (Holotype, male; Gyel Nyaki, Mambilla Plateau, Nigeria; British Mus. Nat. Hist.). *New synonymy*

Hyloperus bicornis Browne, 1970, J. Nat. Hist. 4:546 (Holotype, female; Gyel Nyaki, Mambilla Plateau, Nigeria, British Mus. Nat. Hist.). *New synonymy*

The male holotypes of *Cryptocurus spinipennis* Schedl and *Hyloperus caudatus* Browne were compared directly to one another and obviously are the same species. The female paratypes of *spinipennis* in the Schedl collection were compared directly to female paratypes of *H. bicornis* Browne and my paratypes to the holotype of *bicornis*. The females are identical. Schedl's series was taken from the host, apparently from the same tunnels, and appears to indicate an accurate association of the sexes. If this is correct, both of Browne's species are junior synonyms of Schedl's name and are placed in synonymy as indicated above.

Dendrosinus ater Eggers

Dendrosinus ater Eggers, 1930, Ent. Blätt. 26:167 (Holotype, male; Ostbolivia; U.S. Nat. Mus.

Dendrosinus hirsutus Schedl, 1958, Acta Zool. Lilloana 16:38 (Lectotype, female; Santa Fe, Dep. Garay Maclas, Argentina; Wien Nat. Mus., present designation). *New synonymy*

The description of *Dendrosinus hirsutus* Schedl is composite. Because of this the "holotype" cited by Schedl (1979:117) is here designated as the lectotype of this species. This lectotype is a specimen of *D. ater* Eggers in which the elytral setae are not fully colored and appear pale. For this reason, Schedl's name must be placed in synonymy as indicated above.

Hylesinus aculeatus Say

Hylesinus aculeatus Say, 1824, J. Acad. Nat. Sci. Philadelphia 3:322 (Syntypes; Missouri; apparently lost).

Hylesinus imperialis Eichhoff, 1868, Berliner Ent. Zeitschr. 12:149 (Syntypes; Wisconsin, Georgia; 1 male labeled Amer. Bor., Ulke Coll. is probably a cotype, labeled "holotype" by Schedl; Wien Nat. Mus.). *New synonymy*

The male of *Hylesinus imperialis* Eichhoff in the Schedl collection and labeled by him as the holotype appears to be an Eichhoff specimen obtained by Schedl during World War II from the Stettin Museum. Since other Stettin Museum specimens of Eichhoff now in the Schedl collection appear to be authentic, I see no reason to doubt the authenticity of this specimen. However. it should be cited as a lectotype, not as a holotype. This specimen now makes it possible to remove all doubt from its placement as a synonym of *aculeatus* as indicated above.

Hylesinus cordipennis Lea

Hylesinus cordipennis Lea, 1910, Proc. Roy. Soc. Victoria, n.s., 22:144 (Syntypes; Cairns, Queensland, Australia; one syntype Wien Nat. Mus.)

Hylesinus papuanus Eggers, 1923, Zool. Meded. 7:133 (Lectotype, male; Insel Yule bei Neu Guinea; Wien Nat. Mus.). *New synonymy*

A female syntype of *Hylesinus cordipennis* Lea in the Wien Museum and the male lectotype of *H. papuanus* Eggers were compared directly to my series from Bulolo, New Guinea. These specimens all represent the same species. If the Schedl syntype actually does represent Lea's species, then the name *papuanus* must be placed in synonymy as indicated above.

Hylesinus macmahoni (Stebbing)

Sphaerotrypes macmahoni Stebbing, 1909, Indian For. Mem., Zool. Ser. 1(2):16 (Two syntypes; Sangar Scallon, near Takt-i-Suliman Mountain, 7,000 ft., Baluchistan, Pakistan; Forest Research Institute, Dehra Dun)

Hylesinus alternans Schedl, 1959, Indian For. Rec., n.s., Entomology 9(8):172 (Holotype, male; Rawalpindi, Punjab, India; Wien Nat. Mus.). *New synonymy*

Leperisinus fraxinoides Beeson, 1941, Ecology and Control of the Forest Insects of India, p. 287. *Nomen nudum*

Leperisinus fraxinoides Schedl, 1959, Indian For. Rec., Entomology 10(2):39 (Paratype, female; Lolab, Putshai, Kashmir, India; Wien Nat. Mus.). *New synonymy*

Two cotypes of *Sphaerotrypes macmahoni* Stebbing, the male holotype of *Hylesinus alterans* Schedl, a female paratype of *Leperisinus fraxinoides* Schedl, and 25 other specimens from the Indian states of Jammu, Kashmir, and Punjab were examined. It is quite clear that only one species is represented, although the sexual dimorphism is more conspicuous than in most members of this genus. None of the Indian specimens reported by Schedl to have been returned to the Forest Research Institute ever reached their destination. In fact, the available evidence indicates that they were never mailed and still reside in the Schedl Collection at Wien. Consequently, the "missing" holotype of *fraxinoides* probably never existed and is represented only by the paratype cited above. Whatever that situation might be, it is clear that both of Schedl's names must be placed in synonymy as indicated above.

Hylesinus niligrinus Eggers

Hylesinus niligrinis Eggers, 1923, Zool. Meded. 7:133 (Holotype; Nilgiri Hills, Ostindien; lost with Hamburg Mus.)

Trogloditica robusta Schedl, 1975, Rev. Swisse Zool. 82:453 (Holotype; Nilgiri, Madras, India; Mus. Hist. Nat. Geneve). *New synonymy*

Paratypes of *Trogloditica robusta* Schedl in the Schedl Collection (Wien Nat. Mus.) are identical to 12 specimens from southern India and more than 100 from Sri Lanka that I recognize as *Hylesinus niligrinus* Eggers (= *persimilis* Eggers 1927). This species fits the

Eggers description in every detail, and it is the only known Indian species that is even remotely similar to it. Schedl's name, therefore, must be placed in synonymy as indicated above.

Phloeosinopsoides triseriatus (Schedl)

Phloeosinopsis triseriatus Schedl, 1964, Tijdschr. Ent. 107:297 (Holotype, female; Sumba-Insel; Schedl Coll.)

Xylechinus papuanus Schedl, 1970, Proc. Linn. Soc. New South Wales 94(2):128 (Holotype, male; Long Island, L.A. Bulolo, Morobe district; CSIRO Coll., Canberra). *New synonymy*

The female holotype of *Phloeosinopsis triseriatus* Schedl was compared directly to the male paratype of *Xylechinus papuanus* Schedl in the Schedl material at Wien and to a pair of this species from Bulolo, New Guinea, in my collection. All represent the same species.

Phloeotribus scarabaeoides (Bernard)

Scolytus scarabaeoides Bernard, 1788, Mem. Hist. Nat. Provence 6:271 (Syntypes?; France; lost. Neotype, female; Galliae meridionalis in *Olea*; Kiel part of Copenhagen Fabricius Coll., designated by Wood, 1975, Bull. Zool Nomencl. 32:122)

Phloeotribus americanus Dejean, 1837, Cat. Coleopt., ed. 3, p. 331 (Amer. bor; nomen nudum)

Although the name *Phloeotribus americanus* Dejean, nomen nudum, has been cited in the literature on several occasions, efforts to locate the specimen on which Dejean's name was based were fruitless until I found it in the Wien Museum (original collection, not part of the Schedl material). It is labeled "Amer. bor., *Phloeotribus americanus* Dej." It is an incorrectly labeled specimen of *P. scarabaeoides* apparently from southern Europe and is not part of the American fauna.

Scolytogenes darwini Eichhoff

Scolytogenes darwini Eichhoff, 1878, Mem. Soc. Roy. Sci. Liege (2) 8:497 Stettiner Ent. Zeit. 39:387 (Holotype; Hindostan, "Birma" on type; Wien Nat. Mus.)

Nigritus similis Eggers, 1923, Zool. Meded. 7:142 (Lectotype; Java; U.S. Nat. Mus., designated by Anderson and Anderson, 1971, Smithsonian Contrib. Zool. 94:30). New synonymy

Nigritus major Eggers, 1927, Philippine J. Sci. 33:69 (Lectotype; Surigao, Mindanao, Philippines; U.S. Nat. Mus.) *New synonymy*

Scolytogenes cryptolepis Schedl, 1951, Tijdschr. Ent. 93:55 (Holotype; Nakronda, Dehra Dun, Uttar Pradesh, India; Wien Nat. Mus.). *New synonymy*

The holotypes of *Scolytogenes darwini* Eichhoff and *S. cryptolepis* Schedl and cotypes of *Nigritus similus* Eggers were compared directly to one another and to my specimens. My specimens were also compared directly to the lectotypes of *N. major* Eggers and *N. similis*. All represent the same, common, widely distributed species. It occurs in vines from India and Sri Lanka to the Philippines and northern Australia.

Scolytodes notatus (Eggers)

Hexacolus notatus Eggers, 1940, Arb. Morph. Taxon. Ent. Berlin-Dahlem 7:133 (Holotype, male; Trois Rivieres, Guadeloupe; "Eggers Coll.")

Hexacolus pseudobicolor Eggers, 1940, Arb. Morph. Taxon. Ent. Berlin-Dahlem 7:132 (Holotype, male; Trois Rivieres, Guadeloupe; U.S. Nat. Mus.). *New synonymy*

Hexacolus subparallelus Eggers, 1940, Arb. Morph. Taxon. Ent. Berlin-Dahlem 7:134 (Holotype, Trois Rivieres, guadeloupe; Fleutiaux Collection). *New synonymy*

Hexacolus pelicerinus Schedl, 1952, Dusenia 3:358 (Holotype, male; Mexico?; Wien Nat. Mus.). *New synonymy*

Paratypes (or cotypes) of *Hexacolus notatus* Eggers, *H. pseudobicolor* Eggers, and *H. subparallelus* Eggers, and the holotype of *H. pelicerinus* Schedl in the Schedl Collection (Wien Nat. Mus.) were examined and compared directly to one another All represent the same common Carribean species.

Scolytopsis puncticollis Blandford

Scolytopsis puncticollis Blandford, 1896, Biol. Centr. Amer., Coleopt. 4(6):123 (Syntypes; Guatemala; Bristish Mus. Nat. Hist.)

Scolyptosis argentinensis Schedl, 1937, Rev. de Ent. 7:84 (Lectotype, female; Prov. Tucuman. Argentina; Wien Nat. Mus., designated by Schedl, 1979, Kat. wiss. Samml. Nat. Mus. Wien. Ent. 2:25). *New synonymy*

Scolytus bruchi Schedl, 1939, Not. Mus. La Plata 4:170 (Lectotype, male; Misiones orillas del Ignazu, Argentina; Wien Nat. Mus., designated by Schedl 1979:48). *New synonymy*

Scolytopsis toba Wichmann, 1914, Ent. Blätt. 10:136 (Holotype; Santa Sofia, Paraguay; Nat. Mus. Wien). *New synonymy*

The holotype of *Scolytopsis toba* Wichmann and the lectotypes of *S. argentinensis* Schedl and *S. bruchi* Schedl, and a pair of my homotypes of S. *puncticollis* Blandford were all compared directly to one another. Because only one species is represented by this material, the Schedl and Wichmann names are placed in synonymy as indicated above.

Tomicus piniperda (Linnaeus)

Dermestes piniperda Linnaeus, 1758, Systema Naturae, ed. 10, p. 355 (Syntypes; Europae; presumably at Uppsala).

Blastophagus khasianus Murayama, 1959, Bull. Brooklyn Ent. Soc. 54:75 (Holotype, Shillong, Assam, India; U.S. Nat. Mus.). *New synonymy*

Murayama named *Blastophagus khasianus* from a specimen in poor condition that came from a long series taken by C. F. C. Beeson. After examining the Murayama type, the entire series of Beeson at the Forest Research Institute, and long series from other parts of Asia and from Europe, it is apparent that *khasianus* represents a very minor variation that does not warrant either specific or subspecific status.

Xylechinus spathifer Schedl

Xylechinus spathifer Schedl, 1955, Rev. Chil. Ent. 4:256 (Lectotype; Laguna de Malleco, Pemehne, Chile; Wien Nat. Mus., present designation)

Pteleobius lomatiae Schedl, 1975, Stud. Neotrop. Fauna 10:2 (Holotype, male; Nahuel Huapi National Park, Argentina; Wien Nat. Mus.). *New synonymy*

The description of *Xylechinus spathifer* Schedl is composite. The specimen cited by Schedl (1979:233) as the "holotype" and labeled holotype in the Schedl collection is here designated as the lectotype of this species. This lectotype and the holotype of *Ptelobuis lomatiae* Schedl were compared directly to one another and were found to represent the same species. The junior name is placed in synonymy as indicated above.

NEW TAXA

Acanthotomicus ipsiformus, n. sp.

This species is distinguished from *mimicus* (Schedl) by the slightly larger, stouter body form, by the sculpture of the frons as described below, by the coarser, closer elytral punctures, and by the deeper, coarser, more *Ips*-like elytral declivity.

MALE.— Length 2.2 mm (paratypes 2.2–2.3 mm), 2.8 times as long as wide; color reddish brown.

Frons resembling *mimicus* except lower half of frons much more strongly, transversely impressed, upper half less strongly convex; surface more nearly rugose, with rather numerous, coarse, isolated granules. Vestiture similar but coarser.

Pronotum 1.1 times as long as wide; similar to *mimicus* except asperities slightly smaller, punctures on posterior half slightly smaller, not as deep.

Elytra 1.4 times as long as wide; similar to *mimicus* except strial and interstrial punctures slightly smaller, deeper, much closer, usually somewhat confused near base particularly near suture. Declivity not quite as steep, more deeply impressed, as in 4-spined *Ips;* punctures on striae 1 and 2 mostly in rows, others confused; margin armed by four denticles positioned exactly as in *mimicus* but considerably larger, 4 pointed, and about twice as large as 3; lower margin from denticle 4 to suture acutely, moderately explanate, with crest undulating to form three indefinite cusps somewhat resembling those of some *Orthotomicus*. Vestiture as *mimicus* except slightly finer.

Antennal sutures procurved as in *mimicus* and many other *Acanthotomicus* and rather similar to Ips *concinnus* (Mannerheim) and *mexicanus* (Hopkins) of North America.

TYPE LOCALITY.—Santa Rosa National Park, Guanacaste, Costa Rica.

TYPE MATERIAL.—The male holotype and two male paratypes were taken at the type locality in 1982, by George Stevens. The host was not recorded but could have been *Spondias mombin*. A male and a female from Bahia, Brazil could be this species but are excluded from the type series.

The holotype and paratype are in my collection.

This species, supported by *mimicus*, is remarkable in that it represents the closest structural approach to the *Ips-Orthotomicus* group yet found and greatly increases the probability of a neotropical origin of this segment of the Ipini.

Acrantus opimus, n. sp.

Recent literature treating the genus *Acrantus* is chaotic. Representatives of an assemblage of species from three or more genera have been thrown together with little or no thought given to basic characters, and a majority of the species that actually belong here currently reside in still other, unrelated genera. Among material at hand, the species described here appears allied to *mundulus* Brown, although the relationship is not close. It is distinguished from *mundulus* by the larger size and by numerous other characters cited below.

Male.— Length 2.9 mm, 2.2 times as long as wide; color very dark brown, vestiture pale.

Frons shallowly, broadly concave on about central third, gradually transcending to flattened or feebly convex on surrounding areas; surface mostly smooth, brightly shining, becoming subreticulate toward vertex, punctures moderately abundant, rather small, shallow but distinct, much smaller in concave area. Vestiture absent, apparently abraded (a few short, erect, scalelike setae on one side.)

Pronotum 0.84 times as long as wide; outline about as in *mundulus* except transverse impression on anterior fourth stronger; surface shining, punctures shallow, of moderate size, dense, running into one another, margins of a few in lateral areas subcrenulate. Vestiture mostly abraded, of erect, short, stout, almost scalelike setae.

Elytra 1.4 times as long as wide; sides almost straight on basal two-thirds, broadly rounded behind; crenulations on bases small, narrow, distinct, about 13 on each elytron; striae narrowly, distinctly impressed, punctures deep, close; interstriae about twice as wide as striae, convex, covered by resin but apparently shining, almost smooth, with minute, confused punctures, each with numerous confused, narrow, sharp crenulations (each equal to one-fourth width of an interstriae), these transcend into uniseriate tubercles at base of declivity. Declivity steep, convex; interstriae narrower than on disc, with fine, uniseriate rows of tubercles at base, these reduced and almost obsolete toward apex. Vestiture of abundant, erect, small scales in ground cover; each interstriae with a row of longer erect scales, each four times as long as ground scales, about six times as long as wide.

Type locality.— Pak Pak on south coast of Bombarai, Vogelkop, Dutch New Guinea.

Type material.— The male holotype was taken at the type locality on 4-VI-1959, between 100 and 700 m.

The holotype is in my collection.

Bothrosternus hirsutus, n. sp.

This species is distinguished from *truncatus* Eichhoff by the finer, much longer elytral setae, and by differences in the pronotal and elytral sculpture cited below.

Male.— Length 2.3 mm (paratypes 2.2–2.5 mm), 2.1 times as long as wide; color dark brown to almost black.

Frons about as in *truncatus* except upper area less strongly convex, glabrous on a small area less than one-fourth as extensive; most of surface granulate-reticulate.

Pronotum very similar to *truncatus* except more finely, closely aciculate, grooves much longer, not as deep; rather dull. Vestiture finer, more abundant.

Elytra similar in outline to *truncatus;* striae more abruptly impressed, punctures almost obsolete, strongly reticulate; interstriae three times as wide as striae, strongly reticulate, shallow, obscure punctures mostly on margins. Declivity rather steep, broadly convex, about as in *truncatus*. Vestiture of fine, strial and interstrial hair, moderately abundant, longest setae near base of declivity equal in length to twice width of an interstriae; somewhat shorter on lower half of declivity. Proepisternal pubescent area large, setae white (in both sexes).

Female.— Similar to male except epistoma bearing a transverse, subcarinate elevation as in *truncatus;* glabrous area on upper frons about half as large as in *truncatus* and less strongly convex.

Type locality.— Rancho Grande, Aragua, Venezuela.

Type material.— The male holotype, female allotype, and 10 paratypes were taken at the type locality 9-IV-1970, 1100 m. No. 429, *Serjania*, by me. Eleven paratypes bear the same data labels except for collection No. 420, taken from *Tabebuia* twigs.

The holotype, allotype, and paratype are in my collection.

Cnesinus discretus, n. sp.

This species (male) is distinguished from *nitidus* Eggers (male homotype) by the stronger epistomal impression, with the upper, convex area of the frons more coarsely sculptured, by the more strongly impressed and more closely punctured discal striae, and by other characters.

MALE.— Length 2.2 mm, 3.1 times as long as wide; color very dark brown, elytra reddish brown.

Frons as in *nitidus* except lower third of frontal area more strongly, transversely impressed; surface rather coarsely granulate, some granules at summit of convexity forming an obscure, indefinite, irregular carina.

Pronotum as in *nitidus*, punctures slightly closer and a bit more longitudinally strigose.

Elytra as in *nitidus* except discal striae very slightly more strongly impressed, many punctures confluent (never confluent in *nitidus*); declivital interstriae 2 less strongly reduced in width, tubercles on its upper half much smaller.

TYPE LOCALITY.— Rancho Grande, Aragua, Venezuela.

TYPE MATERIAL.— The male holotype was taken at the type locality on 9-IV-1970, 1100 m, from the broken twig of an unidentified tree, by me.

The holotype is in my collection.

Cnesinus minor, n. sp.

This species is distinguished from *electinus* Wood by the much smaller size, by the different sculpture of the female frons as described below, and by other differences cited below.

FEMALE.— Length 1.6 mm, 2.5 times as long as wide; color dark reddish brown.

Frons as in *electinus* except epistomal callus shorter (on longitudinal body axis), ornamental setae uniformly distributed on summit of callus (without a median glabrous area as occurs in *electinus*); setae on lateral margins reduced in number and in length.

Pronotum 1.1 times as long as wide; about as in *electinus* except punctures not quite as elongate.

Elytra 1.6 times as long as wide; similar to *electinus* except strial punctures larger, interstriae only slightly wider than striae; declivity steeper, less strongly impressed; interstrial setae at base of declivity slightly flattened on their distal halves (not at all flattened in *electinus*).

TYPE LOCALITY.— Grecia, Costa Rica.

TYPE MATERIAL.— The female holotype was taken on 27-XI-1955, by B. Malkin.

The holotype is in my collection.

The type series of *electinus* (from Jalisco, Mexico) is entirely distinct from this species. However, other series from Nayarit and Guerrero are intermediate in size and show some indications of intergradation. If additional specimens are found in Central America that show additional intergradation, the population represented by this species may have to be reduced to subspecific rank.

Corthylus truncatus, n. sp.

This unique species is unmatched in this remarkable genus. It is distinguished from all other species in the genus by the very stout body form, by the elytra being equal in length to the ponotum, by the truncate, margined, elytral declivity, and by other characters described below.

FEMALE.— Length 4.0 mm, 1.8 times as long as wide; color yellowish brown (mature color?).

Frons deeply, broadly excavated from eye to eye, from epistoma to vertex; surface almost smooth, minutely irregular; lateral margins below eye subacute; epistomal margin rather strongly emarginate. Vestiture largely restricted to upper half of concavity, moderately abundant, longer toward upper margin; lateral margins below eye to epistomal emargination ornamented by a dense, confused row of rather long hair. Antennal club minutely pubescent, very large, rather strongly asymmetrical; sutures aseptate except possibly 1 at extreme anterior margin, showing as shallow grooves, 1 slightly oblique, 2 straight; cirrus very slender, consisting of about six setae, exceedingly long, left cirrus extending over back ending near right margin of pronotum.

Pronotum 0.81 times as long as wide; outline almost semicircular; transversely very broadly convex, longitudinally almost straight except feebly declivous on anterior third; asperities, weak, few in number, restricted to median third of declivous area; surface smooth, apparently slightly shagreened, punctures minute, sparse, inconspicuous. Glabrous.

Elytra 0.98; sides almost straight and parallel to declivital margin; posterior margin almost straight, weakly curved; disc smooth, shining, punctures sparse, minute, apparently confused. Declivity abrupt, subvertical, weakly convex, margin marked by an elevated circumdeclivital costa, its crest acute, continuous from suture at base to suture at apex without undulations or denticles; surface smooth, finely reticulate, punctures minute, confused, not close, a sparse row of fine granules in position of interstriae 3. Vestiture of short hair, sparse on disc, a bit more conspicuous on declivity; of variable length.

Type locality.— Jungle near Leonpampa, Hwanuco Department, Peru.

Type material.— The female holotype was taken at the type locality on 6-XII-1937, 800 m, No. 3811, by F. Woytkowski.

The holotype is in my collection.

Hylurgus indicus, n. sp.

Although several species have been assigned to this genus in past history, this appears to be only the third that actually belongs here. It is distinguished from *micklitzi* Watchl by the smaller size, by the absence of a frontal tubercle, by the vestiture, and by other characters cited below.

Female.— Length 3.2 mm (paratypes 3.0–3.3 mm), 3.0 times as long as wide; rather dark reddish brown.

Frons resembling *micklitzi* except much more strongly convex, without a transverse impression just below middle, more coarsely tuberculate; median carina on epistoma of uniform height, without tubercle or tooth at dorsal end; vestiture apparently longer, more abundant.

Pronotum 1.1 times as long as wide; resembling *micklitzi* except more quadrate, sides more nearly parallel, almost straight; punctures apparently deeper, closer; vestiture shorter, more abundant.

Elytra 1.9 times as long as wide; resembling *micklitzi* except strial punctures more distinct, slightly larger; vestiture with much fewer setae in ground cover, erect setae mostly in rows on both disc and declivity (abundant and strongly confused in *micklitzi*).

Male.— Apparently not represented in material at hand.

Type locality.— Kumaon (region), W. Almora, U.P., India.

Type material.— The female holotype, and three female paratypes were taken at the type locality by H. G. Champion. Other paratypes include two labeled Ranikhet, Kumaon, U.P. India, 6-VIII-1916, *Pinus longifolia* logs, H. G. Champion, and 1 from U. Gumti Val., W. Almora, U.P., India, from the same host and collector. The current name of the host is *Pinus roxburghii.*

The holotype and four paratypes are in the Forest Research Institute Collection, Dehra Dun, U.P., India. Two paratypes are in my collection.

Pachycotes minor, n. sp.

This species is distinguished from *villosus* Schedl by the smaller size, by the much less abundant vestiture, by the much smaller strial punctures, by the smaller, more widely spaced declivital interstrial tubercles, and by other characters cited below.

Male.— Length 2.3 mm (paratypes 2.3–2.6 mm), about 2.1 times as long as wide; color very dark brown.

Frons impressed (almost flat but not concave) on median half from slightly above eyes to below level of antennal insertion; lower half of impressed area shining, coarsely reticulate, dull, finely subreticulate and deeply, rather coarsely, somewhat closely punctured in remaining areas; epistomal margin slightly produced on median third; epistomal processes distinct and almost subtuberculate near median line. Glabrous on shining, coarsely reticulate area; rather coarse, moderately long, hairlike setae in lateral areas, shorter above. Antenna about as in *araucariae* Schedl, except scape very slightly longer.

Pronotum 0.9 times as long as wide; widest on basal fourth, sides convergently arcuate. Surface finely reticulate, rather dull; punctures moderately small, distinct but not deep, irregularly spaced by one to four diameters of a puncture. Vestiture short, sparse, most setae about equal in length to diameter of punctures from which they arise.

Elytra about 1.3 times as long as wide (spread slightly); sides almost straight and parallel on more than basal two-thirds, broadly rounded behind; basal margins with individual crenulations recognizable (not costate as in some species); striae weakly impressed, punctures small, their centers reticulate-granulate, spaced in a row by about three diameters of a puncture; interstriae feebly convex, subreticulate, dull, each with a central row of low, poorly formed crenulations, crenulations decrease from half width of interstriae at base to subtubercles at base of declivity. Declivity steep, convex; striae more strongly impressed, punctures closer; interstriae more distinctly convex, each bearing a row of 7 to 9 moderately coarse, rounded tubercles to near apex, tubercles spaced by distances about equal to width of an interstriae. Vestiture sparse, consisting on posterior half of small, moderately abundant, amber scales, and rows of erect, rather short, moderately stout hairs; a few hairlike setae may extend to basal half.

FEMALE.— Similar to male except frons uniformly convex, without a glabrous, reticulate-granulate area on lower half; strial punctures less distinct.

TYPE LOCALITY.— Palen Creek, about 96 km (60 miles) south of Brisbane, Queensland, Australia.

TYPE MATERIAL.— The male holotype, female allotype, and 1 male and 5 female paratypes were reared 14 August 1972 from a piece of *Araucaria cunninghamii* taken by R. A. Yule that came from the type locality. These specimens emerged with an enormous series *Pachycotes clavatus* Schedl and were found by me among that material.

The holotype and allotype are in the Australian National Collection, Canberra; the paratypes are in my collection.

Phloeosinopsoides pumilus, n. sp.

This species is distinguished from *triseriatus* Schedl by the much smaller size, by the deeply, extensively excavated male frons, by the much larger, deeper, strial punctures, and by other characters cited below.

MALE.— Length 1.5 mm (paratypes 1.4–1.5 mm), 2.4 times as long as wide; color reddish brown, vestiture pale.

Frons broadly, deeply, subcircularly excavated from eye to eye, from epistoma to well above eyes; surface reticulate-subgranulate, punctures small, obscure; vestiture of sparse, coarse, long setae uniformly distributed.

Pronotum 0.94 times as long as wide; widest slightly behind middle, sides moderately arcuate, rather broadly rounded in front; surface smooth, dull, punctures small, close, their anterior margins elevated into very fine crenulations from base to apex; vestiture of rather numerous, short, pale, recumbent scales.

Elytra 1.5 times as long as wide; outline about as in *triseriatus;* striae slightly impressed, punctures very coarse, deep, close; interstriae half as wide as striae, punctures small, uniseriate, their anterior margins elevated, thereby causing interstriae to appear subserrate. Declivity steep, convex; details as on disc. Vestiture consisting of uniseriate interstrial rows of recumbent (anteriorly) to semirecumbent (declivity) short scales; each scale widest near its apex, about twice as long as wide.

FEMALE.— Similar to male except frons convex, surface reticulate-granulate, with very small, shining granules; pronotal crenulations distinctly larger.

TYPE LOCALITY.— Near Bulolo, Morobe District, New Guinea.

TYPE MATERIAL.— The male holotype, female allotype, and six paratypes were taken 6-VIII-1972, No. 91, from an unidentified vine by me.

The holotype, allotype, and paratypes are in my collection.

Xylechinosomus pilosus, n. sp.

This species is distinguished from *hirsutus* Schedl (2.9 mm) by the smaller size, by the presence of some scalelike setae in the elytral ground cover, and by the absence of a small, rounded granule beside each puncture on the pronotum.

MALE.— Length 2.3 mm (allotype 2.4 mm), 2.2 times as long as wide; color brown.

Frons moderately concave from slightly below upper level of eyes to level of antennal insertion; surface shining, obscurely reticulate, punctures small and very obscure above, larger and more distinct below. Vestiture of fine, short, inconspicuous hair of uniform distribution.

Pronotum 0.82 times as long as wide; somewhat like *contractus* (Chapuis) except punctures much closer, each with its floor (interior) strongly reticulate; spaces between punctures smooth. Vestiture of rather abundant, fine, moderately long hair.

Elytra 1.5 times as long as wide; about as in *hirsutus;* striae slightly impressed, punctures rather small, deep; interstriae about twice as wide as striae, shining, each with rather numerous, small, confused crenulations, smaller, rounded, and more numerous at base, reduced to pointed uniseriate tubercles at base of declivity. Declivity convex, moderately steep; interstriae each with a row of small, pointed tubercles. Vestiture of rather abundant, fine, long hair; some setae on declivity of slender, pointed scales.

FEMALE.— Similar to male except frons irregularly convex, punctures more distinct; interstrial crenulations and tubercles much smaller; vestiture on pronotum and elytra distinctly shorter.

TYPE LOCALITY.— Curitiba, Parana, Brazil.

TYPE MATERIAL.— The male holotype and female allotype were taken at the type locality on 13-I-1969 in *Araucaria angustifolia* bark by C. W. and L. O'Brien.

The holotype and allotype are in my collection.

NEW NEVADA ENTITIES AND COMBINATIONS IN *ERIOGONUM* (POLYGONACEAE)

James L. Reveal[1]

Abstract.— New species and varieties of the plant genus *Eriogonum* (Polygonaceae) that occur in Nevada are proposed. *Eriogonum tiehmii* and *E. ochrocephalum* var. *alexanderae* are endemic to Nevada, and *E. lewisii* is restricted to extreme northeastern Nevada and adjacent Utah. These entities belong to the subgenus Eucycla. Two varieties of *E. umbellatum* (of the subgenus Oligogonum) are proposed. The first, var. *juniporinum*, is found in eastern Nevada and in the desert ranges of southeastern California. The second is var. *furcosum*, which is restricted to the Sierra Nevada. One new combination is also proposed: *E. nudum* var. *gramineum*.

The following new entities are validated for a treatment of *Eriogonum* in a companion article (Reveal 1985).

Eriogonum ochrocephalum S. Wats. var. *alexanderae* Reveal, var. nov.

A var. *ochrocephalo* caulibus pubescentibus differ.

Low, rounded to spreading cespitose perennial herbs forming open to compact mats 1–8 dm across and up to 2 dm high, with a much branched, woody caudex arising from a stout, gnarled, woody taproot; *leaves* erect to spreading, numerous, the leaf-blades lanceolate to narrowly ovate, 1–2 cm long, 0.5–1.5 cm wide, white-tomentose on both surfaces, the petiole 2–5 cm long, tomentose; *stems* erect, 3–10 cm long, tomentose; *involucres* turbinate, (3.5) 4–5 mm long, 2–2.5 mm wide, rigid and tubular, tomentose without, the 5–6 lobes 0.3–0.5 mm long and erect; *flowers* yellow with yellowish green midribs, 2–3 mm long, the tepals oblong, united about ⅓ to ½ their length; *stamens* exserted, the filaments 3–4 mm long, pilose basally, the anthers yellow, 0.4–0.5 mm long, oblong; *achenes* light brown, 3–3.5 mm long, the narrow base tapering to a long, 3-angled beak.

Type.— NEVADA, Lyon Co.: Along Nevada Highway 3 in Wilson Canyon between Smith and Mason, 12.8 mi NE of Smith and 2.5 mi SE of the junction of Nevada Highway 3 and Norydike Cutoff, on volcanic tuff hills S of the West Fork of the Walker River, associated with *Atriplex*, at about 1460 m (4800 ft) elevation, 21 Jun 1978, *Reveal et al. 4737*. Holotype, US! Isotypes BRY! CAS! DUKE! F! GH! MARY! MEXU! MO! NY! OKL! RENO! RSA! TEX! UC! UTC! and elsewhere.

Additional specimens examined.— NEVADA. Lyon Co.: SW slope of Wassuk Range, 13 Jun 1947, *Alexander & Kellogg 5314* (OKL, UC); 0.5 mi NW on Nevada Highway 22 from rd E along the East Walker River, 6 Jun 1981, *Tiehm 6527* (MARY); Aldrich Grade along Nevada Highway 3C N of Fletcher Springs, 6 Jun 1981, *Tiehm 6558* (MARY). Pershing Co.: 2.8 air mi N of Trinity Peak, Trinity Range, 28 Jun 1980, *Tiehm 6133* (MARY); W of Cooper Valley, SE end of Sahwave Mts., 29 May 1983, *Tiehm & Tucker 7758* (MARY). Washoe Co.: NE side of Hungry Valley near Hungry Spring, 31 May 1980, *Tiehm et al. 5769* (MARY); W of site of Leadville, Granite Range, 30 Jun 1983, *Tiehm 8017* (MARY); 1.5 air mi NE of Grass Valley Range, NW end of Granite Range, 6 Jul 1983, *Tiehm 8075* (MARY).

The var. *alexanderae* is named for Annie M. Alexander (1867–1950) who discovered this plant during her last botanical expedition to Nevada with Louise Kellogg in 1947. Miss Alexander was then 80 years old. It is a pleasure to remember this fine Nevada collector by naming this variant in her honor.

The var. *alexanderae* is generally found on the eastern edge of the distribution of var.

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ochrocephalum. The latter may have glabrous or glandular stems, but those of var. *alexanderae* are always tomentose. To date, the two variants have not been found growing sympatrically.

Eriogonum lewisii Reveal, sp. nov.

A *E. desertoro* (Maguire) R. J. Davis foliis brevioribus et angustioribus cum caulibus floccosis nec tomentosis, involucris floccosis apice.

Low, rounded perennial herbs forming a compact to slightly spreading mat 1–4 dm across and up to 1 dm high, with a much branched, woody caudex arising from a stout, gnarled, woody taproot; *leaves* erect to spreading, numerous, the leaf-blades elliptic to ovate, 1–1.5 cm long, 4–6 (7) mm wide, grayish tomentose on both surfaces, becoming less so and greenish beneath the tomentum with age on the upper surface, the petiole 0.8–1.8 (2) cm long, tomentose; *stems* erect, 4–8 (10) cm long, floccose; *involucres* turbinate-campanulate, 2.5–3 mm long, 2–2.5 mm wide, rigid, floccose without with the hairs restricted (by late anthesis) to the 5 spreading, 1–1.5 mm long, lobes; *flowers* yellow with reddish yellow midribs, (2) 2.5–3 mm long, the tepals oblong, united about ¼ of their length; *stamens* exserted, the filaments 3–4 mm long, pilose basally, the anthers yellow, 0.4–0.5 mm long, oblong; *achenes* light brown, 3–3.5 mm long, the narrow base tapering to a long, 3-angled, minutely bristled beak.

TYPE.— NEVADA, Elko Co.: White Elephant Butte, S of Elk Mtn, on a steep, open, gravelly slope, associated with *Cercocarpus* and *Senecio*, sec. 4, T46N, R61E, at 2530 m (8300 ft) elevation, 30 Jul 1976, *Reveal & Reveal 4596*. Holotype, US! Isotypes, BRY! CAS! F! GH! MARY! MEXU! MICH! MO! NY! OKL! RENO! RSA! TEX! UC! UTC!

ADDITIONAL COLLECTIONS EXAMINED.— NEVADA. Elko Co.: Independence Mts., 12 Aug 1980, *Tiehm & Birdsey 5193* (RENO). UTAH. Box Elder Co.: Copper Mtn, 13 Jun 1928, *Cottam 3089* (BRY, F).

This new species of *Eriogonum* is named in honor of Mont E. Lewis, long a major collector of intermountain plants for the United States Forest Service and an authority on the genus *Carex*. It was on the basis of a collection he made that I searched the White Elephant Butte area for this unusual buckwheat. It, like *E. ochrocephalum* var. *alexanderae* proposed above, belongs to the subgenus Eucycla (Nutt.) Kuntze.

In Nevada, Lewis's buckwheat may be distinguished by its floccose stems and involucres, small leaves, and high elevation habitat. It differs from the lower elevation and more southern *Eriogonum desertorum* by these features and others, notably the well-defined yet somewhat papery involucral tube that retains its rigid characteristics. In Utah and Idaho the capitate forms of *Eriogonum brevicaule* var. *laxifolium* (Torr. & Gray) Reveal most closely resemble *E. lewisii*. The variety tends to be restricted to the Wasatch Ranges of Idaho and Utah, ranging eastward to southwestern Wyoming. Like *E. desertorum*, the var. *laxifolium* has a well-defined and densely tomentose involucre. In addition, the leaves of this more eastern expression are decidedly longer and narrower than those of *E. lewisii*.

Eriogonum tiehmii Reveal, sp. nov.

A *E. anemophilo* Greene involucris longioribus et floribus sparse glandulosis differt.

Low, spreading perennial herbs forming a dense compact mat up to 3 dm across and to 1.6 dm high, with a much branched woody caudex arising from a stout, gnarled taproot; *leaves* erect to spreading, numerous, persistent, with a bluish gray hue, the leaf-blades elliptic to oblong, (0.8) 1–2 (2.5) cm long, 5–8 (10) mm wide, entire, grayish to whitish tomentose on both surfaces, often slightly greenish under the tomentum with age on the upper surface, the petiole 0.5–1.6 (2) cm long, tomentose without, glabrous within, with an expanded petiole base 3–5 mm long and 1–2 mm wide; *stems* erect, (0.6) 1–1.3 (1.5) dm long, floccose, greenish or reddish under the hairs; *involucres* turbinate-campanulate, 4–5 mm long, 3–4 mm wide, rigid, floccose and reddish without, glabrous within except for a few hairs at the very tip in some, with 5–6 erect to slightly spreading, 1.5–2 mm long, narrowly triangular lobes, the bractlets linear, 2–4 mm long, minutely grandular and toothed, the pedicels exserted, 4–7 mm long, glandular throughout and especially so near the apex; *flowers* yellowish white or whitish to cream with reddish midribs and apices or merely reddish to reddish green midribs, often with a greenish yellow base, 2.5–3.5 mm long at anthesis, up to 4 mm long in early fruit, the tepals oblong, the outer slightly broader than inner, both with out-rolled margins, the apices truncate with a slightly emarginate apex in the outer series of tepals, stipitate glandular along the midrib and base without, sparsely glandular within, united 1/5 to 1/4 of the length; *stamens* exserted, the filaments 3–4 (4.5) mm long, pilose basally, the anthers pale yellow, 0.4–0.5 mm long, oval to oblong; *achenes* light brown, 3–4 mm long, the subglobose base tapering to a long, 3-angled beak about ⅓ the length of the fruit, the stigma 1–1.2 mm long.

TYPE.— NEVADA, Esmeralda Co.: Silver Peak Range just N of the road from Silverpeak to Fish Lake Valley, 1.2 air mi NNW of Cave Springs, sec. 27, T1S, R37E, 1830 m (6000 ft) elevation, 31 May 1984, *Tiehm, Reveal, Williams and Reveal 8534.* Holotype, US! Isotypes, BRY! CAS! MARY! NY! RENO! RSA! UTC! and elsewhere.

ADDITIONAL SPECIMENS EXAMINED.— NEVADA: Esmeralda Co.: Silver Peak Range, 1.2 air mi NNW of Cave Springs, 18 May 1983, *Tiehm 7707* (BRY, CAS, MARY, NY, RSA, UTC).

This remarkable species, named for Arnold ("Jerry") Tiehm, may be immediately recognized by its large, distinctly lobed involucres, cream-colored flowers, and stipitate-glandular tepals. In this latter feature, *Eriogonum tiehmii* is unique. Minute glands are common on the inner surface of tepals in many species of cespitose buckwheats belonging to the subgenus Eucycla. Tiehm's buckwheat is the only species with well-defined stipitate glands on the outer surface. In Nevada, *E. tiehmii* is morphologically most similar to *E. anemophilum* Greene and the cream-colored phase of *E. beatleyae* Reveal. The scapes of the latter are glandular, not floccose as in *E. tiehmii*, and the involucre of both established species does not approach the size of *E. tiehmii*.

Eriogonum nudum Benth. var. *gramineum* (S. Stokes) Reveal, comb. nov.

Based on *E. gramineum* S. Stokes, Gen. Eriog. 60. 1936. Type. California, Inyo Co.: Argus Mts., 1897, *Purpus 5676.* Holotype, UC! Isotypes, GH! K! MIN! P! US!

The concept of *Eriogonum nudum* var. *pubiflorum* Benth. in DC. has become increasingly restricted in its definition so that now the plant is defined as a northern element ranging from the central Sierra Nevada of California northward to south central Oregon. In Nevada, var. *pubiflorum* is found only in the extreme northwestern portion of the state, and then it is infrequent. In southern California, the long recognized var. *pauciflorum* S. Wats. of the Transverse ranges (and southward to northern Baja California Norte) has not been confused with var. *pubiflorum*, but in the southern portion of the Sierra Nevada the distinction is not always readily apparent. Howell (1976) proposed var. *westonii* (S. Stokes) J. T. Howell for the plants of the Tehachapi region and the western slope of the Sierra Nevada. The definition of that variety, as noted by Howell, cannot be expanded to include the plants of the desert range and eastern slope of Sierra Nevada common to Inyo and Mono counties, California. Thus, the var. *gramineum* is proposed. At present, var. *gramineum*, characterized by its yellow pubescent flowers and inflated stems, is not known from Nevada. It is to be sought in the Death Valley region of the state.

Eriogonum umbellatum Torr. var. *furcosum* Reveal, var. nov.

A var. *elliptico* foliis subglabris vel glabris supra.

Low, rounded subshrubs up to 4.5 dm high and 8 dm across, infrequently forming a spreading mat to 5 dm across at higher elevations; *leaves* in loose rosettes, the leaf-blade elliptic to oblong, (0.7) 1–2.5 (3.5) cm long, 3–8 (13) mm wide, densely white tomentose below, thinly floccose or more commonly glabrous and bright green above, the petiole 3–10 (12) mm long; *flowering stems* erect, slender, 0.5–2 dm long, thinly floccose; *inflorescences* compoundly umbellate, 0.5–1.5

dm long, the branches floccose; *involucres* with tubes 2–3 (4.5) mm long, the usually reflexed lobes shorter to as long as the tube, floccose without; *flowers* bright yellow, (5) 6–8 mm long including the stipe.

Type.— CALIFORNIA, El Dorado Co.: Along California Highway 89, 2.2 mi S of U.S. Highway 50, on sandy granitic soil, associated with *Arctostaphylos*, *Artemisia*, and juniper-pinyon, 23 Aug 1975, *Reveal 3971*. Holotype, US! Isotypes, ARIZ! BRY! CAS! DUKE! F! GH! K! MARY! MEXU! MICH! MO! NY! OKL! RENO! RM! RSA! TEX! UC! UTC! and elsewhere.

Representative specimens.— CALIFORNIA. Alpine Co.: Silver Lake, 2 Sep 1933, *Mason 7255* (IA, UC). Amador Co.: Bear River, 30 Jul 1896, *Hansen 1966* (B, MIN). Calavaras Co.: Dorrington, 7 Aug 1923, *Jepson 10058* (JEPS). El Dorado Co.: 5.5 mi S of Meyers, 9 Aug 1941, *Wheeler 402* (JEPS). Fresno Co.: Mono Creek Dam, 16 Jul 1935, *Everett & Johnson 7313* (DS, IDS, LA, MO, OKL, RSA, TAES, UC, UT). Kern Co.: ridge SE of Pine Flat, 28 Jul 1965, *Twisselmann 11330* (CAS, UTC). Madera Co.: The Niche, East Fork of Granite Cr., 17 Aug 1958, *J.T. Howell 34552* (CAS). Mariposa Co.: above Nevada Falls, Yosemite N.P., 10 Jul 1889, *Chestnut & Drew s.n.* (KANU, UC). Nevada Co.: Puddingstone Ridge, 5 mi E of North Columbia, 24 Jul 1971, *True 6903* (CAS). Placer Co.: Cisco, 14 Sep 1938, *Rose 38257* (RM). Sierra Co.: Sierra Valley, Sep 1872, *Lemmon s.n.* (ISC). Tulare Co.: Burnt Ridge, 18 Sep 1962, *Twisselmann 7780* (CAS). Tuolumne Co.: 0.8 mi E of Dardanelle, 28 Jul 1972, *Reveal & Reveal 2813* (BRY, CAS, DUKE, F, MICH, MO, NY, OKL, RSA, TEX, UTC). NEVADA. Washoe Co.: nr Verdi, 19 Jun 1903, *Stokes s.n.* (RSA).

The var. *furcosum* has been included under the name of the Pacific Northwest expression, var. *stellatum* (Benth. in DC.) M. E. Jones, or, as this must now be called due to a recent change in the *International Code of Botanical Nomenclature*, var. *ellipticum* (Nutt.) Reveal (Reveal 1983), in recent treatments of the genus in California (Reveal & Munz 1968). This expression is primarily found in the Sierra Nevada, and then mainly along the more gentle western slope. As the elevation of this range decreases to the north, the variety crosses the crest of the Sierra Nevada and enters into the Lake Tahoe Basin of California and onto the eastern foothills in extreme western Nevada.

In southern California, the var. *furcosum* gives way to var. *munzii* Reveal in the Transverse Ranges and to var. *subaridum* S. Stokes on the arid eastern slopes of the Sierra Nevada. The var. *chlorothamnus* Reveal in Munz is found along the eastern foothills of the Sierra Nevada bordering the Intermountain Region; this variant is isolated from var. *furcosum* by the Sierran crest. To the north, the new variety is replaced by another compoundly umbellate expression of *Eriogonum umbellatum*. This northern expression, which extends into the Siskiyou-Trinity region of California and adjacent southern Oregon, is as yet unnamed. Along the Coast Ranges of California is the distinctive var. *bahiiforme* (Torr. & Gray) Jeps. This expression is not found in the Sierra Nevada.

Eriogonum umbellatum Torr. var. *juniporinum* Reveal, var. nov.

A var. *subaridio* S. Stokes floribus cremeis differ.

Plants forming low shrubs or subshrubs up to 8 dm high and 10 dm across; *leaves* in loose rosettes, the leaf-blade elliptic, (0.7) 1–2 cm long, (3) 5–10 (12) mm wide, greenish or whitish floccose to glabrous on both surfaces, becoming greenish floccose above with maturity; *flowering stems* slender, erect, 1–2.5 dm long, green and floccose to nearly glabrous; *inflorescences* compound umbellate, 0.5–1.5 (2) dm long, floccose; *peduncles* slender, 0.5–5 (6) cm long, floccose; *involucres* with tubes (2.5) 3–3.5 mm long, the reflexed lobes 1–2.5 mm long, thinly floccose; *flowers* cream colored or whitish, (4) 5–6 mm long.

Type.— NEVADA, White Pine Co.: Along U.S. Highway 50-6 at Sacramento Pass, on the northern end of the Snake Range, about 11 mi northwest of Baker, on sandy soil associated with juniper-pinyon and *Artemisia*, at about 2180 m (7150 ft) elevation, 13 Aug 1975, *Reveal & Reveal 3925*. Holotype, US! Isotypes, BRY, CAS, MARY, NY, OKL, TEX.

Representative specimens.— CALIFORNIA. San Bernardino Co.: Upper Cottonwood Canyon, Mid Hills, 30 Aug 1973, *Henrickson 12727* (RSA); 2 mi from Kingstone

Peak, S slope of Kingstone Mts., 23 Oct 1977, *Henrickson & Prigge 16298* (RSA); above Keystone Spring, New York Mts., 13 Oct 1935, *Munz 13854* (CI, DS, POM, UC, UTC); Mitchells Caverns State Park, Providence Mts., 20 Jun 1973, *Thorne & Tilforth 44033* (RSA, in bud); NW of Pachalka Springs, Clark Mts., 6 Oct 1935, *Wolf 7605* (LA, OKL, RSA). NEVADA. Lincoln Co.: Horse Spring Basin, Mormon Range, 28 Jun 1954, *Gullion 566* (OKL, UC); Silver Canyon, Mt. Irish, 19 Jun 1938, *Jaeger s.n.* (POM, not in flower). White Pine Co.: Pole Canyon, Snake Range, 15 Aug 1964, *Holmgren & Reveal 1664* (BRY, CAS, DS, MO, NY, RENO, RM, RSA, UC, UTC); Ward Mtn., S of Ely, 4 Aug 1969, *McClintock s.n.* (CAS); 1.3 mi E of Robinson Summit, 15 mi NW of Ely, 13 Aug 1975, *Reveal & Reveal 3927* (MICH).

The var. *juniporinum* is closely related to var. *subaridum* S. Stokes in terms of its habit and habitat but more like var. *dichrocephalum* Gand. and var. *versicolor* S. Stokes as to flower color. The latter two variants are spreading, matted perennials and not at all shrubby, and in general the leaves are tomentose, at least on the lower surface in these expressions. The disjunct distribution of var. *juniporinum* is intriguing not only because the variant occurs in both the Great Basin cold desert habitat in southeastern Nevada and in the warm desert habitat of the Mojave Desert in southeastern California, but also because there is a delay in flowering between the two areas. In Nevada the variety comes into flower in late June and continues to flower into early September. In California, plants begin to flower in July and continue to flower well into late October. It is likely this difference in flowering time is due to the seasonality of rainfall. The var. *juniporinum* is generally a plant of the desert foothills and low passes in Nevada, reaching its upward limits about 2250 m elevation. The var. *dichrocephalum* and var. *versicolor* are found in the mountain ranges across southern Nevada between the two disjunct populations of var. *juniporinum*. These variants generally occur at higher elevations, or at least at points higher on mountain slopes than var. *juniporinum*. In California the new variety is found on the higher slopes, but it may be found as low as 1350 m elevation in the Providence Mountains and on the Kingstone Range.

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GROWTH AND REPRODUCTION OF THE FLANNELMOUTH SUCKER, *CATOSTOMUS LATIPINNIS*, IN THE UPPER COLORADO RIVER BASIN, 1975–76[1]

Charles W. McAda[2,3] and Richard S. Wydoski[2,4]

Abstract.— Growth rates estimated using the scale annuli of flannelmouth sucker, *Catostomus latipinnis*, did not differ between fish collected from the Gunnison and Colorado rivers, and the Green and Yampa rivers. However, body condition and fecundity were significantly greater in the former population. Age of first maturity for male and female fish from all rivers was IV; and most fish were mature by age VII. The smallest mature female collected was 405 mm, and the smallest mature male was 391 mm total length. Fecundity ranged from 4,000 ova in fish 450 mm long to 40,000 ova in a 500-mm fish: mean ovum diameter was 2.39 mm. Ripe male flannelmouth suckers were collected from early April through June; ripe females were collected from both study areas during May and early June.

The flannelmouth sucker, *Catostomus latipinnis*, is one of the most abundant and widely distributed native fishes in the warm water tributaries and mainstream rivers of the Upper Colorado River Basin (Tyus et al. 1982). However, its distribution in the Lower Colorado River Basin has been substantially reduced by habitat alteration resulting from channelization and water development (Minckley 1973). Despite its importance as a native species endemic to the Colorado River system, little is known of the biology of the flannelmouth sucker (McDonald and Dotson 1960, Wiltzius 1976, Carlson et al. 1979). In this report we describe the growth, maturity, and fecundity of the flannelmouth sucker in the major rivers of the Upper Colorado River Basin.

Methods

Flannelmouth suckers were collected from the confluence of the Yampa and Green rivers in Dinosaur National Monument and from reaches of the Colorado and Gunnison rivers near their confluence in western Colorado (Fig. 1). Descriptions of sampling sites were provided by McAda and Wydoski (1980), whereas an account of the general physical and ecological features of the large rivers of the Upper Colorado River Basin was provided by Bishop and Porcella (1980).

Fish were sampled between April and November 1975 and 1976 by using trammel nets (26–90 m long, 2.5 cm-mesh inner wall, 25 cm-mesh outerwall) and seines (30 m long, 2.5 cm mesh; and 5 m long, 3 mm mesh) and by electrofishing. Collected fish were weighed (g) and measured in total length (mm). Scales from midway between the lateral line and the anterior insertion of the dorsal fin were used for age determination. An age determination for an individual fish was considered to be accurate when agreement on the number of scale annuli occurred between the first and second examinations. A fish was excluded from analyses that involved fish age when no agreement on the number of scale annuli could be reached after a third examination of the scales.

Total body length (TL, mm) at time of annulus formation was estimated using the equation $TL = b_0 + b_1SR + b_2SR^2 + b_3SR^3$ (Carlander 1956), where SR is the radius to that particular annulus × 80 and $b_0 - b_3$ are

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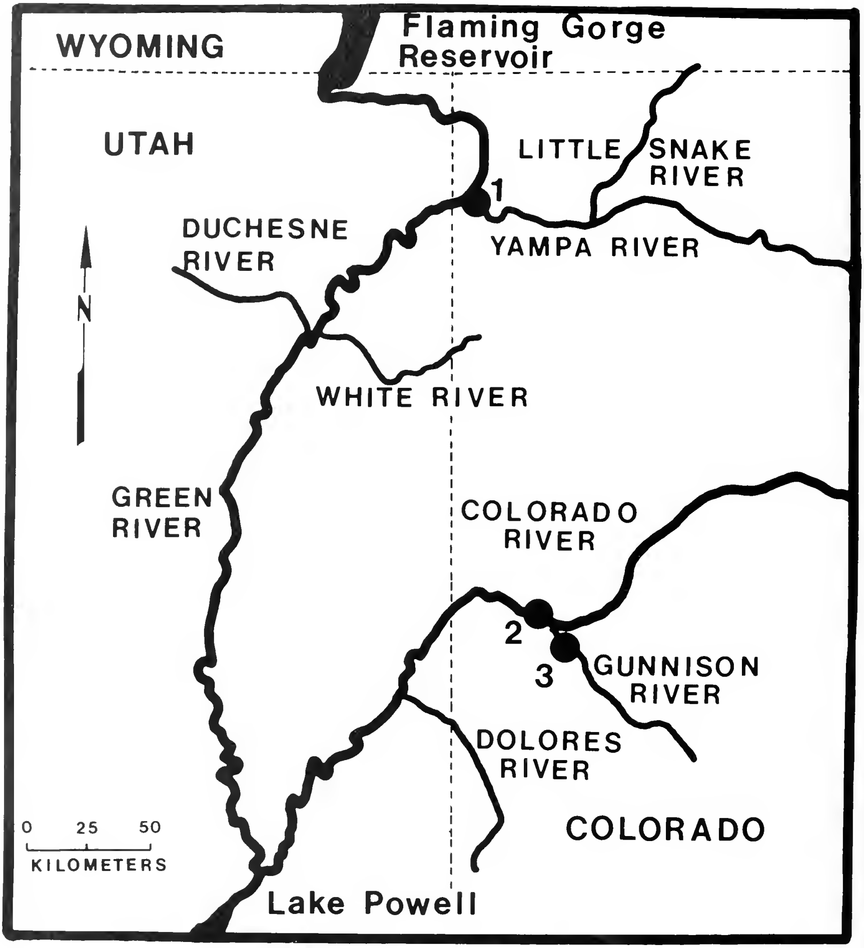

Fig. 1. Locations of sampling points in the Upper Colorado River Basin. (1) Confluence of the Yampa and Green rivers; (2) Colorado River below the mouth of the Gunnison River; and (3) lower Gunnison River.

empirical constants derived using multiple regression analysis. Length-weight relationships were estimated using the equation Log $W = b_1$ Log $TL - b_0$ (Tesch 1971), where W is body weight (g) and b_0 and b_1 are empirical constants derived using least-squares analysis.

Fish were dissected to determine sex and stage of sexual maturity. Females were considered mature when ovaries contained large, opaque, yellow ova; males were considered mature when the testes were enlarged and white. Fish were considered ripe when sex products were expressed with light pressure on the abdomen. Ovaries from mature females collected between April and June 1975 and 1976 were used to estimate fecundity. Fecundity was estimated gravimetrically in the laboratory, where about 10% of each ovary was weighed to the nearest 0.1 g and the individual mature ova from this subsample

TABLE 1. Length-weight, body-scale and length-fecundity relationships for flannelmouth suckers from the Gunnison, Colorado, Green, and Yampa rivers, 1975–1976.

LENGTH-WEIGHT

Yampa/Green: $\text{Log } W = 3.13 \text{ Log } TL - 5.37$ ($n = 297$, $R^2 = 0.9$)
Colorado/Gunnison: $\text{Log } W = 3.09 \text{ Log } TL - 5.21$ ($n = 292$, $R^2 = 0.9$)

BODY-SCALE

Yampa/Green Rivers

Male: $TL = -18.6342 + 4.8894\ SR - 0.0054\ SR^2 - 0.0004\ SR^3$ ($n = 139$, $R^2 = 0.9$)
Female: $TL = -8.7835 + 3.5187\ \text{SR} + 0.0131\ SR^2 - 0.0001\ SR^3$ ($n = 137$, $R^2 = 0.8$)

Colorado/Gunnison Rivers

Male: $TL = -8.7835 + 2.9904\ SR + 0.0156\ SR^2 - 0.0001\ SR^3$ ($n = 158$, $R^2 = 0.8$)
Female: $TL = 46.385 + 0.2820\ SR + 0.0443\ SR^2 - 0.0002\ SR^3$ ($n = 137$, $R^2 = 0.8$)

LENGTH-FECUNDITY

Yampa/Green: $\text{Log } F = 4.03 \text{ Log } TL - 6.70$ ($n = 58$, $R^2 = 0.6$)
Colorado: $\text{Log } F = 3.00 \text{ Log } TL - 3.76$ ($n = 45$, $R^2 = 0.7$)
Gunnison: $\text{Log } F = 3.48 \text{ Log } TL - 5.14$ ($n = 15$, $R^2 = 0.6$)

were counted. The fecundity of that fish was then estimated by proportion using total ovary weight. Total counts of ova from two fish demonstrated that estimated fecundity differed from actual fecundity by less than 5%. The mean diameter of mature ova from individual fish was derived from measurements of 30 ova made with an ocular micrometer. The total length-fecundity relationships were determined using the equation $\text{Log } F = b_1 \text{ Log } TL - b_0$ (Bagenal 1967), where F is fecundity and b_0 and b_1 are empirical constants derived using least-squares analysis.

Statistical comparisons between length-weight, body-scale, and length-fecundity regression equations were made using analysis of covariance (Snedecor and Cochran 1967).

RESULTS

Age and Growth

About 80% of the flannelmouth suckers used in our analyses were collected between April and July. The collection from the Gunnison River was made in April 1976. Body-scale relationships differed significantly between male and female fish among the study areas ($P<0.05$: Table 1). However, mean length at annulus formation was similar for the study groups and they were averaged for this report (Fig. 2). Average growth increments of all fish were greatest at the formation of the third annulus and declined steadily thereafter.

Data for the two sexes were combined because there was no significant difference between the length-weight relationships for male and female flannelmouth suckers ($P>0.05$). No statistical difference was detected between length-weight regressions from data on fish from the Gunnison and Colorado rivers ($P>0.05$). Flannelmouth suckers from the Colorado and Gunnison rivers were significantly heavier than fish of equal length from the Yampa and Green rivers ($P<0.001$: Table 1).

Reproduction

In the Colorado and Gunnison River collections, the smallest mature female was 421 mm long, and all females longer than 490 mm were mature. The smallest mature male was 391 mm long, and all males 470 mm or longer from the Colorado and Gunnison rivers were mature. In the Yampa and Green River collections, the smallest mature male was 393 mm long, and all males were mature at 460 mm: the smallest mature female was 405 mm long and all females were mature at 470 mm (Table 2). Thus, fish began to mature at age IV and most were mature by age VI.

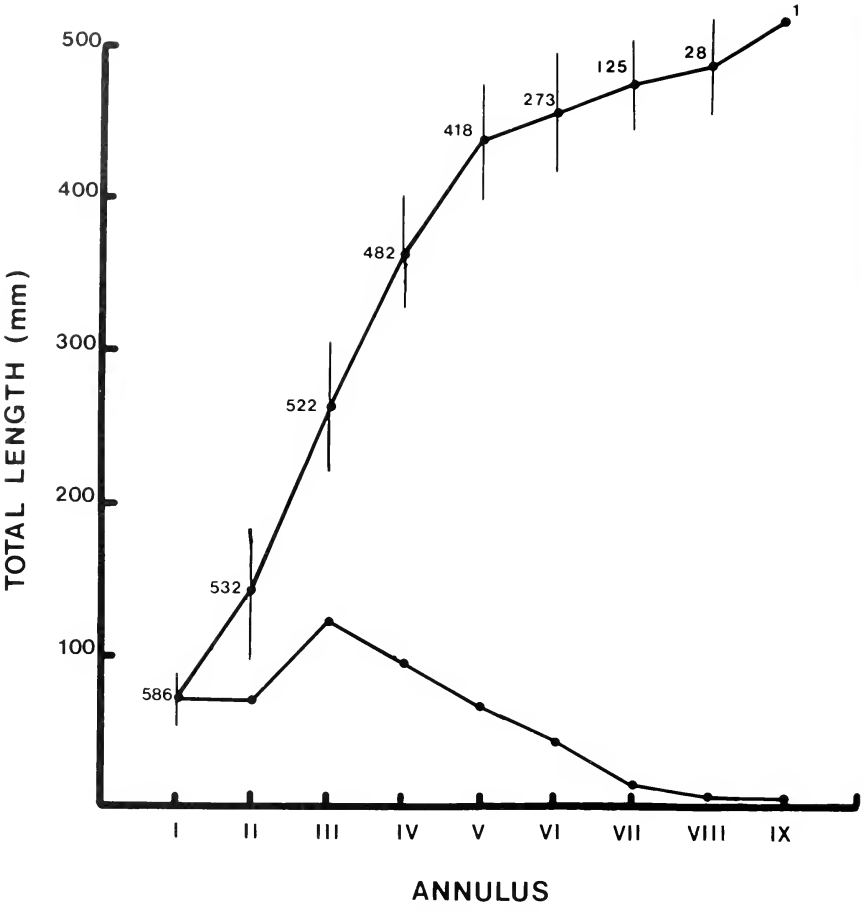

Fig. 2. Mean total length and growth increments at annulus formation for male and female flannelmouth suckers from the Gunnison, Colorado, Green, and Yampa rivers, 1975–1976. Numbers indicate sample size. Bars indicate one standard deviation.

The diameters of preserved, mature ova ranged from 1.99 to 3.15 mm (mean = 2.39 mm; n = 49). The relationship between ova diameter and fish length was not significant ($P > 0.05$).

Fish from the Yampa and Green rivers produced significantly fewer mature ova than did fish from the Gunnison or Colorado rivers ($P < 0.001$: Table 1). Flannelmouth suckers from the Gunnison River also produced significantly fewer ova than did those from the Colorado River. Based upon the regression equations, a fish 450 mm long from the Yampa River produced about 9,800 ova, whereas fish of this length from the Gunnison and Colorado rivers produced about 12,700 and 15,900 ova, respectively.

Ripe male flannelmouth suckers were collected from both study areas when sampling began in early April and on through June.

Table 2. Relation of total length to sexual maturity in flannelmouth suckers from the Yampa, Green, Colorado, and Gunnison rivers, 1975–1976.

Total length (mm)	Colorado and Gunnison Rivers				Yampa and Green Rivers			
	Female		Male		Female		Male	
	Number of fish	Percent mature	Number of fish	Percent mature	Number of fish	Percent mature	Number of fish	Percent mature
381–390	3	0	4	0	1	0	3	0
391–400	3	0	6	17	1	0	1	100
401–410	1	0	6	33	5	20	3	100
411–420	2	60	7	71	2	0	5	80
421–430	5	0	6	67	7	43	7	100
431–440	2	60	6	100	3	67	19	100
441–450	9	75	11	91	5	40	18	94
451–460	4	80	14	93	6	67	12	92
461–470	5	100	16	100	14	93	11	100
471–480	7	92	14	100	9	100	11	100
481–490	14	100	12	100	5	100	9	100
491–500	15	100	6	100	9	100	1	100
501–510	8	100	5	100	13	100	4	100
511–520	9	100	2	100	10	100		
521–530	13	100	1	100	3	100		
531–540	7	100			5	100		
541–550	5	100			3	100		
551–560	7	100			—	—		
561–570	1	100			2	100		
571–580	—	—			1	100		

Ripe females were collected in May and early June, but none were collected after this period.

In the Yampa and Colorado rivers, ripe male and female flannelmouth suckers were collected at the upstream points of cobble bars in water about 1 m deep, with a water velocity of about 1 m/sec. Although spawning activity was not observed, the presence of ripe females (collected only over the cobble bars) suggested that spawning probably occurred nearby. Flannelmouth suckers reproduced successfully in both 1975 and 1976 as evidenced by the abundant young of the year (30–40 mm TL), which we readily captured at all study areas by midsummer.

Discussion

The back-calculated length of flannelmouth suckers at the time of annulus formation for annuli I and II were similar to those estimated by McDonald and Dotson (1960) for flannelmouth suckers from the upper Green River and by Carlson et al. (1979) for fish from the upper Yampa River; however, our estimates of total body length at the formation of annuli III and greater were longer than their estimates. They also observed a decline in annual growth increments at age IV, similar to this study, which probably reflects the diversion of energy from growth to reproduction at the onset of reproductive maturity.

Although annual growth increments did not differ significantly between rivers, the significant difference in the length-weight relationships reflects heavier body weight for a given length of fish from the Colorado and Gunnison rivers. This observation probably reflects a difference in the nutritional status of the fish examined in this study. However, the similarity between back-calculated length at annulus formation during previous years suggests that these differences may not always occur. Similar differences in weight of razorback sucker, *Xyrauchen texanus*, and fecundity of bluehead sucker, *C. discobolus*, from these study sites were observed by McAda and Wydoski (1980, 1983 [respectively]) during the same period. Although this observation probably reflects a difference in the nutritional status of the fish examined in this study, we cannot speculate whether this phenomenon represents consistent differences between the two study areas or merely reflects differences that occurred during the study period. However, the similarity between back-calculated lengths at annulus formation during previous years suggests that these differences may not always exist.

Vanicek and Kramer (1969) documented a decline in the growth rate of Colorado squawfish, *Ptychocheilus lucius*, and roundtail chub, *Gila robusta*, in the Green River after the closure of Flaming Gorge Dam, which they attributed to the resultant decrease in water temperature. Although probably a contributing factor, the lower water temperature in the Green River cannot be completely responsible for the observed differences in fecundity and body weight because flannelmouth suckers in this study were primarily collected in the mixing zone of the Green River with the Yampa River, which maintains its historic temperature regime.

ACKNOWLEDGMENTS

We thank Karl Seethaler, George Kidd, Dennis Cox, John Henderson, Larry Maclain, and Craig Reger, who assisted in the field; and Jay King, Calvin Larson, Kevin Priest, Kurt Rudd, and Joy Wydoski, who assisted in the laboratory. Lynn Kaeding, P. W. Eschmeyer, and Ross Bulkley provided valuable comments to early versions of this manuscript.

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BURROWING OWL FOODS IN CONATA BASIN, SOUTH DAKOTA

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ABSTRACT.— Burrowing Owls (*Athene cunicularia*) were studied in a prairie dog town of southwestern South Dakota. Pellets regurgitated by Burrowing Owls contained a wide variety of prey remains. Insects, spiders, small mammals, and vegetation were the most frequent items identified in the pellets. Mammals were consumed most frequently during spring and early summer. Insects were consumed in large numbers during the entire period of this study, but they became more frequent in owl pellets during late summer and fall in association with a decline of mammal remains. Some prey items observed around owl nest sites were not found in the pellets examined. Possible secondary poisoning of some prey of Burrowing Owls has not produced any change in owl food habits, based on other studies reported in the literature.

Published information on Burrowing Owls (*Athene cunicularia*) pertains mostly to food habits (Robertson 1929, Hamilton 1940, Sperry 1941, Bond 1942, Marti 1974, Gleason and Craig 1979). However, Thomsen (1971), Coulombe (1971), and Martin (1973) also examined Burrowing Owl behavior and ecology. Little is known about ecology of Burrowing Owls in South Dakota except that they are summer residents in all but the Black Hills area (Whitney et al. 1978).

Burrowing Owls are frequently associated with prairie dogs (*Cynomys ludovicianus*) in southwestern South Dakota, where they use prairie dog burrows as nest sites and escape cover. Aufforth (1981) stated that Burrowing Owl numbers are declining in the Northern Great Plains. The information available on Burrowing Owl population trends in South Dakota suggests, however, that they are stable (N. R. Whitney, pers. comm.). Recent prairie dog poisoning programs may have resulted in the direct or secondary poisoning of Burrowing Owl prey when Compound 1080 and strychnine were in use. Poisoning of Burrowing Owl prey could have altered the food resources of the study area and owl food habits.

The purpose of this study was to examine Burrowing Owl food habits throughout the owl's annual period of residency on the study area.

STUDY AREA AND METHODS

The study was conducted in Conata Basin, which is on the Buffalo Gap National Grasslands in southwestern South Dakota. Conata Basin is a lowland area surrounded by buttes and mesas and is bordered on its northern, eastern, and western edges by Badlands National Park. The basin supports short-grass prairie dominated by blue grama (*Bouteloua gracilis*), buffalo grass (*Buchloe dactyloides*), western wheatgrass (*Agropyron smithii*), carices (*Carex* spp.), red three-awn (*Aristida longiseta*), scarlet globemallow (*Sphaeralcea coccinea*), wooly Indian wheat (*Plantago spinulosa*), and plains prickly pear (*Opuntia polyacantha*).

The study area has been grazed by cattle since 1900, and forage utilization is often in excess of 60% (Uresk et al. 1982). Prairie dogs historically and currently occupy the entire Conata Basin area ($\simeq$ 700 km^2) despite poisoning programs (Merriam 1902). The last major prairie dog poisoning effort occurred in 1979. Follow-up poisoning at a maintenance level may be conducted to control prairie dog reinvasion.

Prey remains identified from regurgitated pellets were used to estimate Burrowing Owl food habits from April to October 1981. Fresh pellets were collected every two weeks or whenever visits were made to the study

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area. The accumulation of prey remains at nest sites also provided additional information on foods that did not show up in the pellets (Thomsen 1971).

All owl pellets were oven dried at 60 C for 48 hours, then weighed. Pellets were then placed in fine mesh nylon bags and agitated in warm water in a clothes washer until the pellets fell apart and all soluble material was cleared. The bags were then tumbled dry in a clothes dryer. This procedure was developed by Johnson and Hansen (1979) for the analysis of coyote (*Canis latrans*) feces.

Mammal remains were identified by hair characteristics (Moore et al. 1974) and/or comparison of teeth with reference materials. Feathers were identified to order using characteristics described by Day (1966). Reference materials were used to identify birds beyond order when possible. Arthropod remains were identified to family by comparison with insects and spiders collected from the area.

Owl food habits were quantified as percent frequency for each two-week collection, based on the number of items in the pellets, not the number of pellets examined. A two-way analysis of variance was used to test for differences among prey categories (mammals, birds, reptiles, and arthropods) and months. Tukey's method was used to determine which factors accounted for any differences.

RESULTS

Data on Burrowing Owl foods was obtained from 145 pellets. The mean dry weight of a pellet was 1.1 ± 0.4 grams. Arthropods accounted for the majority of items in owl pellets during each month of study, whereas mammals were the next most abundant prey item. Reptile remains were infrequent in the pellets, but vegetation was abundant. Vegetation in owl pellets was usually represented by small plant fragments, presumably originating from the stomachs of prey. However, large pieces of grass were also recovered (Table 1).

Mammal remains were most frequent in owl pellets in May, June, and July; then they decreased substantially ($P < 0.05$) in August and September. Arthropod remains became more frequent ($P < 0.05$) in the pellets in conjunction with the decrease in mammals. No other significant differences were detected in Burrowing Owl food habits.

Prey remains that were found at nest burrows but did not show up in the pellets were Lark Bunting (*Calamospiza melanocorys*), great plains toad (*Bufo cognatus*), chorus frog (*Psuedacris triseriata*), unidentified fish, and tiger salamander (*Ambystoma tigrinum*).

DISCUSSION

Burrowing Owls in southwestern South Dakota consume a wide variety of animals and some vegetation. Most other studies have reported similar results (Robertson 1929, Hamilton 1940, Bond 1942, Thomsen 1971, Marti 1974, Gleason and Craig 1981). Although Burrowing Owls are reported to be primarily insectivorous (Earhardt and Johnson 1970), Gleason and Craig (1979) pointed out that, on a biomass basis, mammals may be more important. Thomsen (1971) found mammals to be more frequent than insects in Burrowing Owl pellets in California.

The shift in frequency of mammals and insects in owl pellets between the May-June-July and August-September periods was the biggest difference in owl food habits in this study. Diet diversity (H′, Shannon-Weiner index, Pielou 1975) did not differ by much between these two periods, 2.6 and 2.4, respectively, but diet breadth (Levins 1968) did, 4.7 and 2.1, respectively. Thus, owls consume a wider variety of prey during spring and early summer than during late summer and fall. Marti (1974) also reported a decrease in mammal consumption by Burrowing Owls in August and September. Errington and Bennet (1935) noted an increase in insect consumption in late summer and suggested that it was related to the fledging of young owls.

Burrowing Owl feathers were frequently found in the pellets examined. Earhardt and Johnson (1977) cited studies that have reported Burrowing Owls to be cannibalistic. In this study only one or two owl feathers were encountered in a pellet, and they were usually breast feathers, suggesting that the feathers were ingested while preening.

Although plant parts were found in almost every pellet examined, they were primarily small plant fragments from prey stomachs. In

TABLE 1. Mean percent frequency of occurrence[1] of foods found in pellets regurgitated by Burrowing Owls in Conata Basin, South Dakota.

Food item	Month				
	May	June	July	August	September
MAMMALS	12.5	9.9	12.2	1.2	5.5
Peromyscus spp.	7.8	3.1	5.8		2.5
Sylvilagus floridanus	2.7	0.4	1.2		
Microtus ochrogaster	0.5	0.4	0.6		0.5
Spermophilus tridecemlineatus	0.5	5.2	2.1		
Perognathus spp.	0.5				
Geomys bursarius	0.5	0.4			2.0
Myotis sp.			0.6		
Cynomys ludovicianus		0.4			
Mus musculus					0.5
Unidentifiable			1.9	1.2	
BIRDS	5.1	4.9	2.2	3.8	7.2
Athene cunicularia[2]	3.6	1.9	1.0	3.8	6.7
Eremophila alpestris	0.5				
Passerine	0.5	2.6	1.2		
Unidentifiable	0.5	0.4			0.5
REPTILES		1.5		1.2	0.5
Lizard				1.2	
Snake		1.5			0.5
ARTHROPODS	54.0	50.2	53.9	70.9	63.6
Coleoptera					
Carabidae	16.6	7.4	9.5	12.7	11.1
Chrysomelidae			3.8		
Cincindelidae	0.5		0.6	10.0	
Coccinellidae	0.5				
Curculionidae	0.5		0.6	2.6	1.0
Histeridae	12.1	10.5	12.4	3.7	9.6
Scarabidae	6.2	0.4	2.5	1.4	
Silphidae	0.5	1.5	0.6	2.7	0.5
Tenebrionidae	2.1	11.2	7.9	16.9	12.0
Larvae					0.5
Diptera					
Larvae		0.4			
Hemiptera					
Unidentifiable		0.8			
Hymenoptera					
Formicidae	0.5	1.9	5.4	2.6	12.9
Ichneumonidae		2.3	2.3		
Proctotrupidae	0.5				
Sphecidae				1.4	
Unidentifiable		0.8			
Lepidoptera					
Larvae					1.0
Orthoptera					
Acrididae	10.9	2.7	1.8	16.9	12.5
Araneida					
Lycosidae	3.1	10.4	6.5		2.5
VEGETATION	16.3	18.9	18.5	19.2	15.5
Grass	0.5		3.1	1.2	
Plant fragments	15.8	18.9	14.8	18.0	15.5
Wood			0.6		
Optuntia polyacantha seed			0.6		
MISCELLANEOUS	12.1	14.6	12.6	3.7	7.7
Bone	12.1	14.2	12.6	3.7	7.7
Egg shell		0.4			

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[1] Based on number of items recovered from pellets.

[2] Based on the occurrence of feathers in owl pellets. See Discussion.

some pellets we did find large pieces of grass and woody material that had been ingested directly by an owl. They could have been ingested during efforts to capture and kill prey. Thomsen (1971) also frequently found vegetation in Burrowing Owl pellets.

Because some items consumed by Burrowing Owls do not show up in the pellets, prey remains at nest sites must also be examined. Thomsen (1971) reported five prey items at nest sites that were not present in Burrowing Owl pellets. This absence could have at least two explanations: (1) it is not possible to find every pellet an owl produces, and (2) some foods or parts thereof may be completely digested. For example, we found that when Burrowing Owls ate great plains toads they typically placed the toad on its back and consumed the viscera and muscles of the legs, leaving the skeleton and other less digestible portions.

The similarity of Burrowing Owl food habits among this study and others reported in the literature indicates that possible poisoning of owl prey did not effect owl food habits.

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ADDENDUM TO THE DISTRIBUTION OF TWO HERPTILES IN IDAHO

Timothy D. Reynolds[1] and William F. Laurance[2]

Abstract.— Due to an error in printing quality of an earlier article, the distribution maps for the night snake (*Hypsiglena torquata*) and the tiger salamander (*Ambystoma tigrinum*) in Idaho are reprinted.

Recently we presented county by county distributions of the night snake (*Hypsiglena torquata*) and the tiger salamander (*Ambystoma tigrinum*) in Idaho (Laurance and Reynolds 1984). Our objective in that article was to confirm the presence of these species within the Idaho ranges indicated by Stebbins (1966, map 5 and 175), and document any range extensions or gaps in distribution. The information was collected from the scientific literature, accounts of historical expeditions into Idaho, and interviews with various university, state agency, and qualified lay persons. The results were presented in two figures and two tables. The figures were intended to graphically illustrate and com-

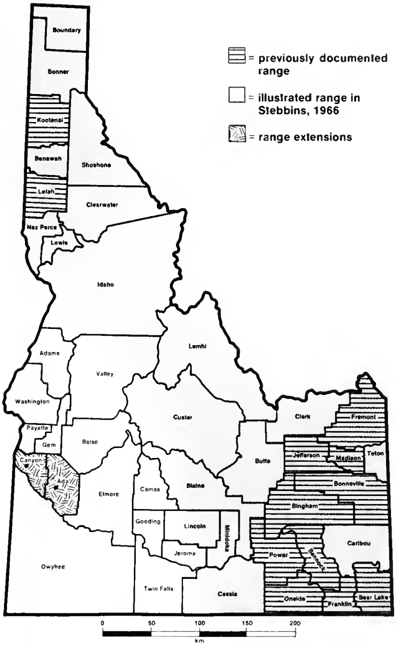

Fig. 1. Range extension and previously documented range for *Ambystoma tigrinum* in Idaho compared with the range illustrated in Stebbins (1966).

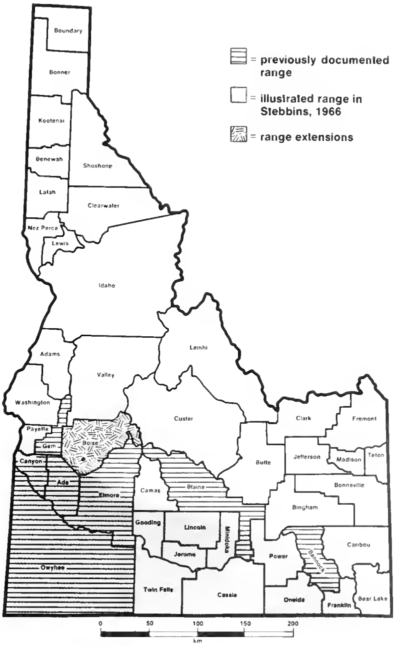

Fig. 2. Range extension and previously documented range for *Hypsiglena torquata* in Idaho compared with the range illustrated in Stebbins (1966).

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pare (1) Stebbins' (1966) ranges for both the night snake and tiger salamander in Idaho, (2) previously documented accounts of these species in Idaho, and (3) new records of each for the state.

Unfortunately, because of a printing error, the figures presenting Stebbins' (1966) ranges were reproduced so poorly in our paper (Laurance and Reynolds 1984) that the fundamental objectives of that effort were compromised. Here we again present Stebbins' (1966) ranges, the previously documented accounts, and new records for the tiger salamander (Fig. 1) and night snake (Fig. 2) in Idaho.

Our conclusions remain the same. First, the tiger salamanders observed and collected from Canyon and Ada counties in SW Idaho represent a significant westward range extension for that species. Second, county by county documentation of both species within the ranges indicated by Stebbins (1966) is lacking. Last, the lack of records for the tiger salamander in several north central counties and for the night snake in the south central counties suggests either a true discontinuity in each population or the absence of diligent attempts to census herptiles in those counties. Additional efforts are needed to fully elucidate the distribution of these and other herptiles in Idaho.

We thank the editor of the Great Basin Naturalist for appreciating the fundamental importance of the printing error to our previous article and consequently encouraging us to submit this addendum.

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NESTING AND PREDATORY BEHAVIOR OF SOME *TACHYSPHEX* FROM THE WESTERN UNITED STATES (HYMENOPTERA: SPHECIDAE)

Nancy B. Elliott[1] and Frank E. Kurczewski[2]

ABSTRACT.— The first published observations on the nesting and predatory behavior of *Tachysphex antennatus* Fox, *T. occidentalis* Pulawski, *T. williamsi* Bohart, *T. yolo* Pulawski, *T. alpestris* Rohwer, *T. clarconis* Viereck, *T. apricus* Pulawski, and *T. cockerellae* Rohwer are presented herein. Also included are host and behavioral data on *T. tarsatus* (Say), *T. apicalis fusus* Fox, *T. similis* Rohwer, *T. ashmeadii* Fox, and *T. mundus exsectus* Fox.

The genus *Tachysphex* Kohl contains many rather small ground nesting species that utilize orthopterous prey. Nesting specifics are important in elucidating phylogenetic relationships in this large genus (Kurczewski and Elliott 1978). Some of the common eastern species have been studied extensively, but many western *Tachysphex* have never been observed. Biological data heretofore have been published for only 9 of the 46 western species (Krombein et al. 1979, Pulawski 1982). Thus, studies on western *Tachysphex* are needed to fill gaps in our understanding of the phylogeny and evolution of this large genus.

In this paper we bring together information accumulated on the behavior patterns of *Tachysphex* species from the western United States, along with prey records for several species based on museum specimens. Included are the first published notes on *T. antennatus* Fox, *T. occidentalis* Pulawski, *T. williamsi* Bohart, *T. yolo* Pulawski, *T. alpestris* Rohwer, *T. clarconis* Viereck, *T. apricus* Pulawski, and *T. cockerellae* Rohwer. In preparing the paper we have followed the nomenclature used by Krombein et al. (1979) and Pulawski (1982). The species are listed alphabetically by species group as in Krombein et al. (1979).

POMPILIFORMIS SPECIES GROUP

Tachysphex antennatus Fox

E. J. Kurczewski collected two females with prey at Erie, Pennsylvania, in 1981. Each made low, short flights. Both acridids were determined as nymphal *Melanoplus* sp.

Tachysphex apricus Pulawski

A paratype of this species, collected at Tucson, Arizona (W. Benedict), is pinned with a specimen of the phasmid *Parabacillus hesperus* Hebard, more than four times its length. We report this record, although Pulawski (pers. comm.) questions its authenticity.

Tachysphex occidentalis Pulawski

A paratype of this species, collected at 5500 ft at Antelope Spring, California, by M. E. Irwin, is pinned with a nymph of the acridid *Schistocerca shoshone* (Thomas).

Tachysphex tarsatus (Say)

Previus authors (Williams 1914, Evans 1970, Alcock and Gamboa 1975) reported females making single-celled nests and storing one, rarely two, large acridid nymphs (*Melanoplus* spp., *Trimerotropis* spp.). The first of two females collected at St. Anthony, Idaho, carried prey on the ground; the other carried prey in a series of short flights. We report the following prey records: *Dissosteira carolina* (L.) (Walworth, Wisconsin; 17 July 1913); *Melanoplus complanatipes* Scudder (1 mi SW Tom's Place, Mono Co., California; 13 August 1963; C. A. Toschi); 2 *Melanoplus* sp. nymphs (Erie, Pennsylvania; 13 July, 25

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August 1980; E. J. Kurczewski); *Pseudopomala brachyptera* (Scudder) nymph (Bath, Mason Co., Illinois; 3 July 1968; G. C. Gaumer); *Orphulella pelidna* (Burmeister), male (Closter, New Jersey; 16 July 1963; M. Statham). The last record is of the first adult prey reported for this species.

Tachysphex williamsi Bohart

A female collected at San Francisco, California, in May 1960 by J. A. Powell is pinned with a nymph of *Trimerotropis occidentalis* (Bruner) no larger than she. Another wasp from Cornish, Utah (27 July 1973; G. Eickwort and G. Bohart), identified as either this species or *T. tarsatus*, is pinned with a nymphal *Melanoplus sanguinipes* (Fabr.)

Tachysphex yolo Pulawski

One paratype was collected with a small nymph of *Melanoplus foedus* Scudder (St. Anthony, Idaho; 15 July 1977). The prey was being carried on the ground.

TERMINATUS SPECIES GROUP

Tachysphex alpestris Rohwer

A specimen from Morro Bay, California (J. A. Powell), is pinned with a nymphal acridid, *Oedaleonotus* sp.

Tachysphex apicalis fusus Fox

This species usually nests in sand cliffs (Kurczewski and Snyder 1968, Williams 1914), but Rau and Rau (1918) reported a female attempting to nest in the mortar of a building foundation and another starting a nest from an antlion burrow. One of us (F. E. K.) has observed this species searching in the openings between the siding shingles of a cottage. A female was observed at St. Anthony, Idaho (23 June 1979), digging in the soft sand of a previous excavation. When first seen, she was throwing sand out of the entrance. Upon completing it, she left the entrance open, oriented in a hovering flight, and flew away. Twice she returned without prey, hovered near the entrance, and flew off. When returning to the nest with prey, she landed nearby, although sometimes up to 1.5 m away, before resuming flight and carrying the prey directly into the open entrance. This wasp averaged 5.5 minutes between eight successive provisioning trips and 2 minutes within the nest between such trips.

The unfinished nest contained a single cell at the end of a burrow 7.5 cm long. This cell contained seven nymphal acridids; the female had been carrying an eighth when collected. Prey were placed head inward, venter upward or head inward, on the side. The prey were identified as *Melanoplus sanguinipes* (Fabr.).

Williams (1914) reported that one female of this species was unable to fly with a large grasshopper. He excavated a single-celled nest with two prey, but Kurczewski and Snyder (1968) reported that *T. a. apicalis* constructs multicelled nests, and stores several prey per cell.

Tachysphex clarconis Viereck

Four females were observed at St. Anthony, Idaho, during June 1979. One made 40 digging entries into the nest. The time spent inside increased as her digging progressed toward completion ($\bar{x}$ = 22.1 sec, first 10 entries; $\bar{x}$ = 31.3 sec, last 10), as did the time spent outside leveling sand ($\bar{x}$ = 12.2 sec, first 10; $\bar{x}$ = 29.0 sec, last 10). The female interrupted digging to chase away a satellite fly.

After removing and distributing the sand, this female walked around the entrance and threw sand back toward it. Periodically she took flight and hovered or perched on plants. After 3.5 min she reentered the nest and remained inside for 7.25 min. Then she temporarily closed the entrance, hovered 7.5 cm above the nest for a few seconds, flew in a circle, and landed before flying away. Total observation time was 44 minutes.

Prey were usually carried in flight directly to the nest area. A female would deposit her prey near the entrance, open and enter the nest, reappear headfirst, and pull in the grasshopper by its antennae. One female deposited her prey for about 10 minutes while searching for her nest. Then she located and opened the nest and took in the prey as described. The same female was later seen carrying a rather large grasshopper in a series of short flights. During carriage the acridid's head protruded anteriorly beyond the wasp's. Three wasps stored from three to six grasshoppers per cell, as indicated by successive provisioning trips. Three acridids were recovered from one of the cells. Prey included *Melanoplus foedus* Scudder, nymph (1), and *M. sanguinipes* (8).

The only parasite observed, besides the miltogrammine fly, was a chrysidid, probably *Hedychridium* sp., seen digging into one of the nests while the wasp was away.

Tachysphex similis Rohwer

Two nests were excavated at Wamego, Kansas, in July 1968. One had a single cell with three prey; the other, four cells containing 3, 3, 5, and 3 prey. Prey used by *T. similis* at this locality included nymphs of *Melanoplus* sp. (8), *Mermiria* sp. (1), *Oplia obscurus* (Thomas) (2), and *Pseudopomala brachyptera* (Scudder) (8).

UNDATUS SPECIES GROUP

Tachysphex ashmeadii Fox

This species was studied at Lakin, Kansas, in August 1964 and at St. Anthony, Idaho, in July 1977. We also include several new prey records from other collections. Our observations and previously published data indicate a greater range of variability in this species than is characteristic of many other *Tachysphex*.

Females started digging nests either from the sand surface or from preexisting depressions such as animal tracks. Digging wasps entered the burrow headfirst and threw sand backward with the forelegs while backing out of the nest to distances of 1.6 to 3.2 ($\bar{x}$ = 2.3) cm. One female made 21 entries from inception to completion of her nest; another, 25. The two wasps averaged 56 (4–159) seconds inside the burrow and 16 (6–40) seconds outside during digging and sand removal, respectively. There were no changes in duration of times as digging progressed. One female, digging in extremely hot sand, frequently left the nest and flew to nearby vegetation. She flew backward out of the nest, throwing the sand behind her, and averaged only about half as long on the sand surface as had other females.

Wasps left their entrances open while hunting. They also left intact the ovoidal-elongate tumuli that accumulated during digging. One such tumulus was 5 cm long, 3 cm wide, and 0.5 cm high. Following completion of the burrow, females walked around their entrances and sometimes reentered. They then made low flights above the site and flew to nearby vegetation to hunt. Females made the most rapid hunting movements of all *Tachysphex* we have observed. Periodically they returned without prey and reentered their burrows. One such female returned four times: 5, 29, 33, and 105 minutes after she first left to hunt. Some females dug within the entrances during these returns.

Previous records (Williams 1914, Evans, pers. comm.) and many of our own observations indicate that females of *T. ashmeadii* usually prey on large acridids in the late nymphal or adult stage and transport them to the nest on the ground. However, we have seen females carrying smaller prey (up to 2.2 times the wasp's weight) directly into the nest in flight, while holding the prey's antennal bases with the mandibles. Times between provisions ranged from 22 to 178 ($\bar{x}$ = 106; n = 5) minutes. Females using more than one prey per cell spent an average of 2.5 minutes inside their nests before leaving to hunt again.

Nest dimensions for three burrows at Lakin, Kansas, were as follows: burrow length: $\bar{x}$ = 9.6 (8.9–10.4) cm; cell depth: $\bar{x}$ = 5.3 (5.0–5.9) cm. These nests were single celled, and each contained a single grasshopper (weights: 59, 200, and 232 mg). Williams (1914) and Alcock and Gamboa (1975) also reported a single prey per cell, but two single-celled nests in Idaho each contained two prey. In one the egg was on the larger grasshopper, which was taken into the nest last. H. E. Evans (pers. comm.) excavated a nest of this species at Rodeo, New Mexico, and found a single prey bearing an egg in the distal burrow rather than in the cell.

TABLE 1. Prey of *Tachysphex ashmeadii*.

Species	State of collection	Source or collector
Ageneotettix deorum (Scudder)	KS, WY	Williams 1914, Lavigne and Pfadt 1966
Arphia sp.	ID	NBE
Bruneria sordida (McNeill), nymph	ID	NBE
Cordillacris crenulata (Bruner), adult	KS	Williams 1914, Krombein et al. 1979
Cordillacris occipitalis (Thomas)	WY	Lavigne and Pfadt 1966
Melanoplus bivittatus (Say) ?	KS	FEK
Melanoplus lakinus Scudder, nymph	AZ	P. Rauch
Melanoplus sanguinipes (Fab.)	ID	NBE
Melanoplus sp., nymph	CO, AZ	G. C. Gaumer, G. and K. Eickwort
Metator sp., nymph	—	Krombein and Burks 1967
Opeia sp., nymph	—	Krombein and Burks 1967
Orphulella sp., adult	TX	R. E. Acciavatti
Phlibostroma sp., adult	—	Krombein and Burks 1967
Trachyrhachys kiowa (Thomas), male	KS, WY	Williams 1914, Lavigne and Pfadt 1966
Trimerotropis sp., nymph	KS	FEK
Trimerotropis bilobata Rehn & Hebard, male and nymph	ID	NBE
Trimerotropis pallidipennis (Burm.), adult and nymph	TX	J. E. Gillaspy

Prey collected in Kansas were invariably placed venter upward, head inward, but Alcock and Gamboa (1975) reported lateral placement from a nest in Arizona. Eggs were laid on either side, transversely between the prey's pro- and mesothoracic legs.

Acridids from 11 genera have been preyed upon by this species (Table 1).

BRULLII SPECIES GROUP

Tachysphex mundus exsectus Fox

One female was collected with a nymph of a tettigoniid, *Conocephalus* sp., at Wamego, Kansas, in July 1968 (G. C. Gaumer). Kurczewski (1979) has described the nesting behavior of this species, which also occasionally preys on gryllids.

JULLIANI SPECIES GROUP

Tachysphex cockerellae Rohwer

A specimen from Napa Co., California (D. & W. Dunenmacher), is pinned with a nymph of the mantid, *Litaneutria minor* (Scudder).

DISCUSSION

Krombein et al. (1979) divided the North American species of *Tachysphex* into five species groups, based on morphological criteria. Our studies, especially those on members of the Terminatus species group, show that behavioral traits may also characterize these groups.

Members of the Terminatus group usually nest in flat sand, except for *T. a. apicalis* and *T. apicalis fusus*, which nest in sand cliffs (Kurczewski and Snyder 1968). All species construct multicelled nests which are provisioned with small, nymphal acridids. Since the prey are small, they are usually carried to the nest in flight, and several are used to stock each cell. Species in this group close the nest while hunting, after elaborately leveling the tumulus, except for the subspecies of *T. apicalis*, whose vertical nesting sites preclude this behavior (Kurczewski and Snyder 1968). Nesting behavior of *T. clarconis*, reported here for the first time, supports its placement in the Terminatus group because it shares this set of nesting components.

All previously studied members of the Brullii group prey upon orthopterans other than acridids. *Tachysphex alayoi* Pulawski preys upon blattids (Pulawski 1974, Elliott et al. 1979), and *T. belfragei* and *T. mundus* prey mostly upon tettigoniids (Krombein et al. 1979, Kurczewski 1979). *Tachysphex coquilletti* Rohwer, the only previously studied North American species of the Julliani group, preys upon mantids (Alcock and Gamboa 1975). Our report of mantids as prey of

T. cockerellae substantiates its placement in this group.

The large Pompiliformis group now contains 44 North American species (Krombein et al. 1979, Pulawski 1982). Many species in this group also share a suite of similar behavioral traits, including the making of single-celled nests, utilizing one or a few large prey per cell, carrying prey on the ground, leaving the nest open while hunting, and not leveling the tumulus (Kurczewski 1964, Williams 1914). Although Krombein et al. (1979) placed *T. ashmeadii* in the Undatus group, components of its nesting behavior match very closely those described above. This suggests that *T. ashmeadii* has close affinities with the species in the Pompiliformis group.

Studies on certain species in the Pompiliformis group, however, indicate considerable variation in behavior. *Tachysphex pechumani* Krombein demonstrates many of the group's characteristics but makes a rudimentary temporary closure. Based on its morphology and behavior (Kurczewski et al. 1970, Kurczewski and Elliott 1978), we have suggested that this species occupies a unique phylogenetic position intermediate between the Terminatus and Pompiliformis species groups. *Tachysphex krombeini* Kurczewski makes single-celled nests but stores several small acridids and tettigoniids, mixed, and carries them to the nest in flight (Kurczewski 1971). *Tachysphex krombeini* is the only Nearctic species in the group that preys on families other than Acrididae. Should the record of *T. apricus* preying on phasmids be substantiated, this would further increase the range of prey families reported for this group. We also report that females of *T. yolo* and *T. williamsi* use rather small prey in comparison with many previously studied members of the group. It is probable that further studies of species in this group will identify affinities in behavior that separate the large group into several smaller ones. Pulawski (1982) noted that, morphologically, the group is less distinct than other species groups of *Tachysphex* and has suggested the grouping may be artificial.

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W. J. Pulawski, California Academy of Sciences, determined the *Tachysphex* species. Prey were determined by A. B. Gurney, USDA, Systematic Entomology Laboratory; M. A. Brusven, University of Idaho; D. C. Rentz, CSIRO, Canberra, Australia; and I. J. Cantrall, Museum of Zoology, University of Michigan.

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POLLINATORS OF *ASTRAGALUS MONOENSIS* BARNEBY (FABACEAE): NEW HOST RECORDS; POTENTIAL IMPACT OF SHEEP GRAZING

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ABSTRACT.— Important bee species inhabiting the study area are listed, including those observed and collected foraging on *Astragalus monoensis*, a California rare plant. The significance of each species as a potential pollinator is assessed, based on frequency of occurrence in collecting, observed and published host plant records, and morphology. Three pollinator categories are proposed: observed and/or collected on the plant, probable visitors, and possible visitors. New host plant records for these species are listed.

Current sheep grazing practices in the *A. monoensis* habitat endanger pollinators in four ways: (1) destruction of potential nest sites, (2) destruction of existing nests and contents, (3) direct trampling of adult bees, and (4) removal of food resources. Exposure of the major bee species to each of these factors is assessed utilizing experimental data and published information.

Astragalus monoensis Barneby, "Mono Rattleweed" or "Mono Milkvetch," is a perennial legume endemic to the California portion of the Great Basin (Barneby 1964, Munz and Keck 1959). It is listed as endangered by the Federal Government (Ayensu and DeFilipps 1978) and rare and endangered by the California Native Plant Society (Smith et al. 1980). It occurs in the region east of the Mono Craters between 7500 and 8000 feet (2286¼438 m) elevation (Smith et al. 1980, K. Teare, pers. comm., unpubl. data). The number of individual plants in each population varies from several thousand to less than 100.

A detailed description of *A. monoensis* appears in Munz and Keck (1959). It is a papilionaceous bee flower, as characterized by Percival (1965), and produces considerable nectar, as evidenced by the regularity of visits to its flowers by bumble bees. Males of the anthidiine ("carder" or "mason") bees *Anthidium clypeodentatum* and the relatively large *Callanthidium formosum* (Megachilidae) also frequent the flower. Pollen from *A. monoensis* is also collected by these and other species. It is an obligate outcrosser, requiring insect transferal of pollen between flowers of different plants to set seed (Sugden 1984, R. Barneby, pers. comm.). Plant associates are relatively few, dominated by the nectarless *Lupinus duranii* Eastw. (Fabaceae). Also prominent are *Hulsea vestita* Gray and *Chrysothamnus parryi vulcanicus* (Greene) Hall & Clem. (Asteraceae), the primary local nectar sources for early and late parts of the summer, respectively (unpubl. data). Other associates are *Eriophyllum lanatum* var. *monoense* (Rydb.) Jeps. (Asteraceae), *Phacelia frigida* Greene (Hydrophyllaceae), *Calyptridium umbellatum* var. *caudiciferum* (Gray) Jeps. (Portulacaceae), and *Mimulus coccineus* Congd. (Scrophulariaceae). *Eriogonum umbellatum* Torr. (Polygonaceae), a widely insect-utilized nectar source, occurs at several sites.

A majority of the known *A. monoensis* populations occur with the above plant associates in isolated sand flats, the soil of which is composed of coarse gravel and sand of volcanic pumice origin. The flats are typically surrounded by a second-growth forest of *Pinus contorta* Doug. ex Loud. (Lodgepole Pine) and *Pinus jeffreyi* Grev. & Balf. in A. Murr. (Jeffrey Pine). The forest floor is essentially sterile with respect to pollen and nectar. Hence, the wildflower patches of the sand flats exist as resource "islands" for pollinators. Beetle burrows in many trees and logs provide abundant nest cavities that are utilized by solitary bees. *Thomomys talpoides*, the Northern Pocket Gopher, inhabits the sand flats, and its many abandoned burrows are probably utilized by bumble bees as

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nest cavities. *Bombus huntii* queens have been observed entering such burrows, apparently nest-searching (pers. obs.).

The largest populations of *Astragalus monoensis*, which occur on federal land, are subjected annually to the influence of sheep grazing. This usually occurs in midseason, when the plants are in flower and before most seed is set. In the sand flat region, 12,000 sheep in herds of up to 2,000 individuals may be stationed at springs or watering tanks near the known *A. monoensis* populations (C. Chamberlain, pers. inquiry of sheepherders). In the sand flats per se, the ground is often completely denuded of vegetation where the sheep forage. Over the course of several days the grazed area may extend in a continuous swath, 100 m or more in width, to cover an entire flat (pers. obs.). The loose soil of the habitat is subject to extreme disturbance by the spadelike action of sheep hooves, which may uproot or expose the crowns of mature plants and destroy seedlings (pers. obs.). Typical effects of grazing on the habitat are shown in Figure 1.

Although the toxicology of *A. monoensis* is unknown, foliage and flowers of the plant are often grazed (C. Chamberlain, K. Teare, pers. comm.). Sheep merely passing over a site, i.e. not feeding, do less damage than those allowed to forage (C. Chamberlain, pers. comm.).

This paper examines the hypothesis that, in addition to direct disturbance, the plant may suffer reproductive setback due to the negative impact of intensive sheep grazing on its pollinators. These are various bee species, several of which nest in or near the ground where sheep are herded and all of which are part of the sand flat community. Postulated below are four types of impact:

(1) *Destruction of potential nest sites.* Bumblebees often construct their nests in abandoned rodent burrows, including those of *Thomomys* spp. (Thorp et al. 1983). Such burrows are abundant in and near the *A. monoensis* habitat. Sheep collapse the entrances of these burrows and hence remove many potential nest sites from discovery by bumblebee queens in the spring. The frequency of burrow encounter by sheep is indicated by the fact that rodent holes are the major cause of livestock loss (through broken legs) in the region (pers. inquiry of sheepherder). Solitary ground-nesting bee species require specific substrate conditions to establish nests (Linsley 1958). Disturbance of the soil by sheep hooves probably alters the acceptability of many potential nest sites. Pithy stems may be broken and trampled by sheep if near the ground, removing potential cavities for species that utilize stick nests.

(2) *Destruction of existing nests and contents.* Ground nesting bees construct delicate burrows and chambers in the soil. Depending on the species, the brood chambers may be either close to the surface, sometimes within three to four inches (Thorp 1969), or several feet below (Malyshev 1936). Soil disturbance may destroy all or part of such nests, damage existing brood and provisions, and/or displace nest-entrance landmarks, which female bees utilize in orientation to the exact location of their burrows. Many bees construct nests in preexisting cavities above the ground, often in hollow sticks. Such nests may be shattered or disoriented by trampling and exposed to rainfall. Many of the bees concerned here are solitary, nonaggressive species and have no means of nest defense against sheep.

(3) *Removal of food resources.* Sheep grazing greatly reduces the density of many herbaceous plants. Among these are the nectar and pollen sources on which local bee populations subsist. For many species, these resources may be important to the completion of an entire life cycle. (Due to its limited distribution and population size, it is unlikely that *A. monoensis* provides all the annual nutritional requirements for individuals of any single bee species. Its nectar and pollen-yielding plant associates are important in this respect and are heavily impacted by sheep grazing as reported here.)

(4) *Direct trampling.* Male bees of several species are known to "sleep" singly or in aggregations on vegetation close to the nest sites of females (Linsley 1962, Rust et al. 1974) or in shallow, temporary burrows or emergence holes (Linsley 1958). Early in the season, before nests are constructed, female bees may also rest in similar positions. In this situation, particularly during the cool hours of night or morning, when bees are torpid and unable to escape, they may be in danger of being trampled by sheep.

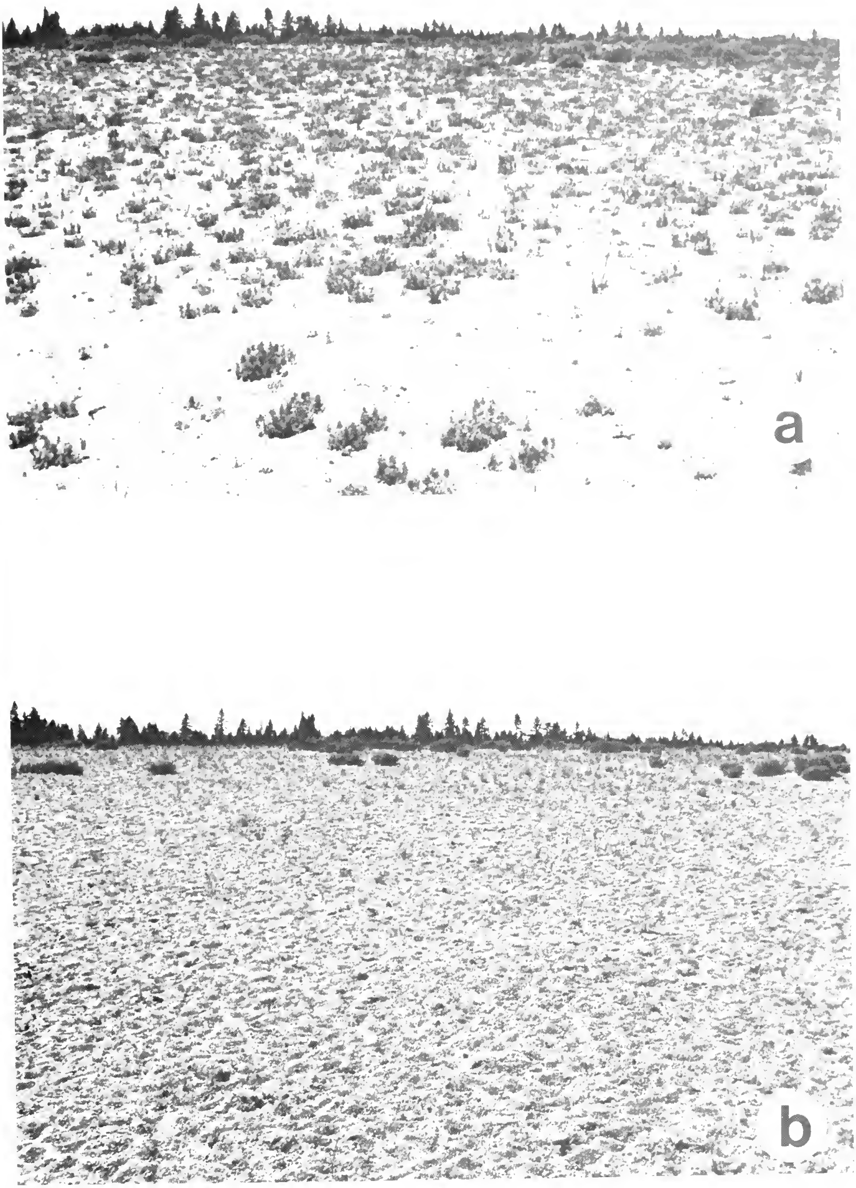

Fig. 1. (a) Typical aspect of *Astragalus monoensis* habitat prior to grazing. Big Sand Flat, June 1980. Plants in foreground are primarily *Lupinus duranii*. (b) Same view following grazing by domestic sheep.

METHODS

Bee species listed are those which appeared two or more times in occasional collecting during 1979–1982. All specimens were collected with a standard insect net and are currently deposited in the R. M. Bohart Museum, Department of Entomology, University of California, Davis.

For this study, insect "abundance" is defined as the relative number of individuals appearing in occasional collections from the *Astragalus monoensis* habitat.

In recording host plant data from the literature, a conservative approach was maintained. A host record designated only to genus was counted as a species record only if no other species records from that genus were given in the sources consulted. For congeneric listings of more than one species, genus records without species designations were not counted.

Floras and references consulted for plant names and identifications are Munz and Keck (1959), Taylor (1981), and Willis (1973).

Plant distributions were obtained by mapping the study sites into a grid of one square hectare units and sampling randomly near the center of each unit with a one square meter quadrat sampler.

Insect densities were obtained from direct observation of insects on flowers. Two identical walking transects covering 2.2 km and between 36 and 52 minutes in duration were made daily at approximately 11:00 and 14:00 hours. Densities are given as counts per kilometer per hour to make comparisons with a second study site utilized in another project, where transects were of a different length, and as a partial correction factor for variable duration of transects.

Average ambient temperature at 1 m above the ground is expressed as an average of three readings per transect. Previous minimum temperature is the previous night's low ambient temperature at one meter. All readings were taken on a Taylor maximum-minimum mercury thermometer calibrated in salted ice water to 0 C.

RESULTS

Table 1 lists bee species collected in the sand flat region during 1979–1982. These are divided into three groups based on inferred probability of importance as pollinators of *Astragalus monoensis*. Group I consists of those species collected or observed foraging on the plant. For these data and number of individuals collected and/or observed are indicated, with sex and caste, where appropriate, for those collected. Relative abundance is given as the number of discrete collection events (date × locality) resulting in an extant voucher specimen. Group II consists of four species which, although neither collected nor observed foraging on *A. monoensis*, are pollinator candidates by virtue of their locally great abundance, widely polylectic habits, and published or observed host records, including other *Astragalus* spp., *Lupinus duranii*, the dominant flowering plant in the community, and/or other papilionaceous legumes. These bees are robust, moderate to large in size, and morphologically capable of pollinating the *A. monoensis* flower. Group III species have a low or intermediate abundance. Some have been reported to forage on other *Astragalus* spp., and all of them have published papilionaceous legume host records.

Species from Table 1 are listed in Table 2 with host plant information. To these data new information has been added from personal observation (Appendix I). For each bee species the total number of published host plant families, genera, species, and species of *Astragalus* are given. Papilionaceous legume hosts are given as proportions of the total number of host plant genera and species. All bee species appearing in Table 2 whose host specificity is known have been categorized as "polylectic" (many flower hosts), with the exception of *Andrena cleodora* ssp. *cleodora*. It is listed as an "oligolege of ceanothus" (restricted to a single species or group of closely related species of host plants) (Krombein et al. 1979).

From Table 1, it can be seen that a wide diversity of bees is associated with *A. monoensis*. Observed visitors alone represent 3 families, 5 genera, and at least 7 species. Probable and possible visitors comprise 5 families, 4 genera, and 14 species. The predominance of megachilids in this assemblage, particularly in the genera *Osmia* and *Anthidium*, is a reflection of the general composition of the bee fauna in the dry, high altitude

TABLE 1. Bee associates of *Astragalus monoensis* Barneby. Relative abundance refers to number of collection events in which species appear. w = worker, q = queen, m = male. S = extant specimens, O = field observation, R.A. = relative abundance.

Species	Date	Number, sex, caste	S or O	R.A.
GROUP I—Observed or collected on *Astragalus monoensis*				
APIDAE				
Bombus (*Pyrobombus*) *huntii* Greene	8.VII.'79	7w,2q	S	5
	14.VII.'79	3w	S	
B. (*Bombias*) *nevadensis nevadensis* Cresson	8.VII.'79	4w,1q	S	1
B. (*Pyrobombus*) *vosnesenskii* Radoszkowski	7.VII.'79	1w	S	5
MEGACHILIDAE				
Anthidium (*Anthidium*) *clypeodentatum* Swenk	14.VII.'79	2m,2f	S	1
Anthidium sp.	17.VII.'79	1	O	—
Callanthidium formosum (Cresson)	8.VII.'79	1f,2m	S	6
	14.VII.'79	2f,1m	S	
Osmia (*Monilosmia*) *cara* Cockerell	14.VII.'79	1f	S	1
O. (*Nothosmia*) *grindeliae* Cockerell	7.VII.'79	1f	S	3
	14.VII.'79	1f	O	—
O. spp.	14.VII.'79	1	O	—
	16.VII.'79	4	O	—
	17.VII.'79	4	O	—
GROUP II—Probable visitors				
ANTHOPHORIDAE				
Anthophora (*Anthophora*) *urbana urbana* Cresson			S	10
APIDAE				
Apis mellifera L.			S	10
Bombus (*Separatobombus*) *morrisoni* Cresson			S	9
MEGACHILIDAE				
Hoplitis (*Monumetha*) *albifrons argentifrons* (Cresson)			S	10
GROUP III—Possible visitors				
ANDRENIDAE				
Andrena (*Trachandrena*) *cleodora cleodora* (Viereck)			S	2
A. (*Plastrandrena*) *prunorum prunorum* Cockerell			S	2
COLLETIDAE				
Colletes consors consors Cresson			S	2
MEGACHILIDAE				
Anthidium (*Anthidium*) *banningense* Cockerell			S	4
A. (*A.*) *mormonum* Cresson			S	3
A. (*A.*) *tenuiflorae* Cockerell			S	4
Hoplitis (*Monumetha*) *fulgida platyura* (Cockerell)			S	6
Osmia (*Chenosmia*) *calla* Cockerell			S	3
O. (*Monilosmia*) *densa densa* Cresson			S	3
O. (*Acanthosmia*) *integra* Cresson			S	2

TABLE 2. Unweighted host plant data for bee associates of *Astragalus monoensis* Barneby. Bee species listed alphabetically by group (see Table 1). Data for *Apis mellifera* omitted. Sources: Krombein et al. (1979), Moldenke and Neff (1974), Thorp et al. (1983), personal observations reported in Appendix 1 of this paper.

Bee species	No. families	No. genera	No. species	No. *Astragalus* species	Papilionaceous legume hosts as proportion of total: Genera	Species
GROUP I						
Anthidium clypeodentatum	4	6	11	2	.50	.67
Bombus huntii	18	39	39	1	.21	.21
B. nevadensis nevadensis	9	16	16	1	.38	.38
B. vosnesenskii	38	117	142	1	.09	.15
Callanthidium formosum	6	9	9	1	.44	.44
Osmia cara	7	11	18	1	.27	.39
O. grindeliae	3	3	3	1	.33	.33
GROUP II						
Anthophora urbana	3	103	174	1	.10	.11
B. morrisoni	16	35	35	1	.20	.20
Hoplitis albifrons argentifrons	15	29	34	1	.07	.06
GROUP III						
Andrena cleodora cleodora	10	12	15	0	.08	.07
A. prunorum prunorum	32	89	101	0	.03	.03
Anthidium banningense	6	11	16	0	.45	.33
A. mormonum	8	14	26	1	.29	.38
A. tenuiflorae	9	15	19	1	.27	.37
Colletes consors consors	4	5	6	0	.20	.17
Hoplitis fulgida platyura	17	34	49	1	.12	.12
Osmia calla	12	22	33	1	.18	.30
O. densa densa	21	29	43	0	.17	.26
O. integra	3	4	4	1	.50	.50

sand flat region. Three species of *Megachile* and *Dianthidium parvum* ssp. *parvum* occur regularly on the flower heads of *Hulsea vestita* but are not observed to forage on other plants. The latter is considered an oligolege of composites (Krombein et al. 1979).

Group I

It is not surprising that bumblebees visit *Astragalus monoensis.* Although populations fluctuate in the *A. monoensis* habitat, as has been found elsewhere (Bohart and Knowlton 1952), their long-lived colonies, large body size, and caste polyethism make them vigorous foragers and important pollinators of many plant species. *Bombus huntii* and *B. vosnesenskii* were present every year of the study. *Bombus nevadensis* has been collected only once and only on *A. monoensis.* This species is at most an intermittant member of the sand flat fauna, perhaps due to population fluctuation. All three bumblebee species are widely polylectic and readily visit papilionaceous legumes. *Bombus huntii* was the most commonly collected bee on *A. monoensis* and has been regularly observed to forage on *Lupinus duranii.* Its overall abundance is matched by *B. vosnesenskii.*

Close in size to early season bumblebee workers are individuals of *Callanthidium formosum.* This species is relatively common in the study area. It apparently exhibits an affinity for *A. monoensis* and other legume species, based on its minimal host records. Two individuals of *Anthidium clypeodentatum* were collected on *A. monoensis* in 1979. Although its abundance is low, its papilionaceous legume preference is apparently at least as high as that of *C. formosum,* and it has been recorded on at least one other *Astragalus* species. It has not been collected on *L. duranii.*

Osmia is the most speciose bee genus of the sand flats, represented by at least 13 sympatric species (unpubl. data). *Osmia grindeliae* may have some affinity for *A. monoensis,* although its host records are too sparse to be useful as indicators of general papilionaceous legume preference. Its abundance is moderate. *Osmia cara* is rare in the area. Neither of these two species have been collected on *L. duranii.*

Group II

Honeybees, *Apis mellifera*, are present in the sand flats at relatively low density, despite their apparently great abundance in comparison to wild bees of the study area (pers. obs.). It is likely that this relatively resource-depauperate region supports only a few small feral colonies. Honeybees avidly collect pollen from *L. duranii* (pers. obs.). Pollen tentatively identified as that of *A. monoensis* has been observed in pollen trap samples from experimental honeybee hives at Little Sand Flat (unpubl. data). *Bombus morrisoni* is a common bumblebee in the study area. It readily visits *L. duranii* and has been recorded on other *Astragalus* species. Although its general preference for papilionaceous legumes seems somewhat lower than that of other bumblebees, it remains a good candidate for pollination of *A. monoensis.*

Anthophora urbana is a widely occurring species that forages on virtually every major pollen or nectar source plant in the sand flats. It is capable of visiting *A. monoensis* and probably does so, although its papilionaceous legume host record appears moderate because of the large diversity of records.

Hoplitis albifrons ssp. *argentifrons* is the most common species associated with *Hulsea vestita*. Its foraging habits are so flexible that it frequently visits plants from two widely disparate taxa on a single foraging flight, e.g., *L. duranii* and *Mimulus coccineus* or *Hulsea vestita* and *Chrysothamnus parryi* var. *vulcanicus* (pers. obs.). An intense survey would probably show that *H. albifrons* visits and pollinates *A. monoensis.*

Group III

Bees in this group are variable in their pollination potential for *A. monoensis.* The smaller species, *Anthidium mormonum, A. tenuiflorae, Osmia calla,* and *Hoplitis fulgida* ssp. *platyura* have each been recorded on *Astragalus*; *A. tenuiflorae* and *O. calla* have been collected on *L. duranii.* The three remaining megachilids are relatively large, robust species that would be expected to be good pollinators of papilionaceous legumes. Only *O. integra* has not been recorded on *L. duranii. Andrena prunorum* ssp. *prunorum* and *A. cleodora* ssp. *cleodora* are the least likely pollinator candidates, but they have both been recorded on papilionaceous legumes. It appears possible that these species contribute to pollination of *A. monoensis.*

Table 3 lists Group I, II, and III bee species with known or probable nest type and respective susceptibility to the three types of grazing-associated damage described above. Ground-nesting bumblebees are particularly vulnerable in this regard. *Bombus nevadensis* may be less vulnerable, because it is known to nest in aboveground cavities on occasion. *Anthophora urbana, Colletes consors consors,* and *Andrena* spp. represent species whose nests are in jeopardy. The anthidiines, including *Anthidium* spp. and *Callanthidium formosum*, are apparently flexible in their nest location. They may be exposed to nest or nest site damage, depending on their local nest-building habits. Many cavity nesters, principally *Osmia* spp., are presumably exempt from this hazard because their nests are mostly in beetle holes in logs or standing trees (pers. obs.). Possible exceptions are species in the *Acanthosmioides* subgenus, many of which nest in open, sandy sites in ground burrows. Burrows of *Acanthosmioides* species were not found at the study sites but likely occur there. An existing population of *O. (A.) integra* at Panum Crater, several kilometers west of the nearest known *A. monoensis* population, nests at the base of *Lupinus duranii* plants (pers. obs.). This species is also found in ground nests associated with sparse vegetation on sand dunes in northwestern California (D. Gordon, pers. comm.). Nests of *O. (A.) nigrobarbata* also occur at the base of plants (Rozen and Favreau 1967). Grazing hazards are significant for these ground-nesting bees and others that may nest in hollow or pithy stems of herbaceous plants, which includes many of the species from Table 3.

Small solitary bees are limited in their flight range (Kapyla 1978) and are therefore more dependent on local floral resources. Since a large proportion of nectar and pollen plants may be decimated by sheep grazing in the *A. monoensis* habitat, solitary bees dependent on such resources may be subject to

TABLE 3. Nesting habits and type of exposure to intensive sheep grazing for bee associates of *Astragalus monoensis* Barneby. Nest type of a congenor may be listed where information on an *A. monoensis* associate is unavailable or supplementary. N = potential nest substrate disturbance, C = damage to nests and contents, R = depletion of trophic resources, T = direct trampling, ( ) = questionable.

Species	Exposure	Nest
GROUP I		
Bombus huntii	N C (R)(T)	Abandoned rat nest in building (Medler 1959); underground, surface, and aboveground domiciles (Hobbs 1967, Richards 1978); abandoned rodent burrows (pers. obs.).
B. nevadensis	N C (R)(T)	Aboveground domicile (Richards 1978); surface and aboveground hives (Hobbs 1965, Hobbs et al. 1962); rafters of building (pers. obs.).
B. vosnesenskii	N C (R)(T)	Abandoned rodent burrows (Thomomys spp.) (Thorp et al. 1983).
Anthidium clypeodentatum	(N)(C) R (T)	*A. maculosum*: wooden trap nests (Horning 1971); probably beetle burrows in trees or other insect ground burrows in study area.
Callanthidium formosum	(N)(C) R (T)	Wooden trap nests (Parker and Bohart 1966); *C. illustre*: floral scape of *Yucca* sp. and oak stumps (Krombein et al. 1979).
Osmia cara	R (T)	Driftwood (Graenicher 1935); probably beetle burrows in study area.
O. grindeliae	R (T)	*O. pumila*: wooden trap nests (Krombein 1967, Medler 1967).
GROUP II		
Apis mellifera	R	Aboveground cavities, hollow trees or logs (Seely and Morse 1976).
B. morrisoni	N C (R)(T)	Abandoned rodent burrows?
Anthophora urbana	N C R (T)	Horizontal and vertical soil banks (Mayer and Johansen 1976).
Hoplitis albifrons	R (T)	*Hoplitis* spp.: elderberry stems (Clement and Rust 1976); probably beetle burrows in study area.
GROUP III		
Andrena cleodora	N C R (T)	Ground burrows (Krombein et al. 1979).
A. prunorum	N C R (T)	Ground burrows (Krombein et al. 1979).
Colletes consors	N C R (T)	*C. stepheni*: ground burrows (Hurd and Powell 1958).
Anthidium banningense	(N)(C) R (T)	Paper and wooden trap nests (Jaycox 1967); ground burrows (Krombein et al. 1979).
A. mormonum	(N)(C) R (T)	Beetle burrows, oak stumps, ground burrows (Hicks 1929).
A. tenuiflorae	(N)(C) R (T)	Rock crevices (Krombein et al. 1979).
Hoplitis fulgida	R (T)	Elderberry stems (Clement and Rust 1976); probably beetle burrows in study area.
O. calla	R (T)	*O. atriventris* and *O. clarescens*: wooden trap nests (Fye 1965; Krombein et al. 1979).
O. densa	(N)(C)(R)(T)	unknown.
O. integra	N C R (T)	Ground burrows (pers. obs.); *O. longula*: under stones (Parker 1975); *O. nigrifrons*: trap nests (Rust et al. 1974); *O. nigrobarbata*: ground burrows (Rozen and Favreau 1967).

artificial resource depletion, which could constrain or curtail their brood-rearing activities. Catastrophic lowering of nectar availability may stress individual adult bees and induce or increase competition for this resource. Partial pollen depletion might negatively influence brood development. In support of these assertions, data have been collected on temporary changes in foraging bee density on *Hulsea vestita* and *Lupinus*

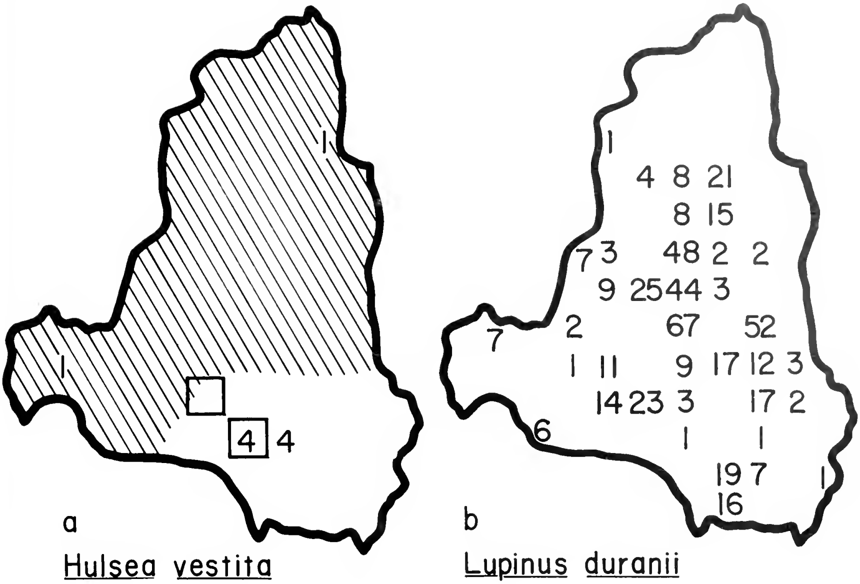

Fig. 2. Distributions of (a) *Hulsea vestita* and (b) *Lupinus duranii* as mapped in June and July 1980. Both species are perennial. Figure 2a shows the location of the two, one square hectare study plots utilized for insect density transects and the approximate area that was grazed 2 August 1982 (hatched).

duranii in response to grazing of adjacent areas.

In 1982 the density of flower-foraging insects was recorded on two study plots at Little Sand Flat before and after sheep were introduced to the area. The distributions of the dominant plant species at the study site appear in Figure 2. On the afternoon of 2 August, approximately 75% of the flat was grazed by a herd of 2000 sheep (Fig. 2a). Essentially all the aboveground vegetation was removed in the grazed area (cf Fig. 1).

Results for the most often observed bee/plant combinations are shown in Figure 3. Note that densities of bees increase dramatically after sheep grazing. Transects from before and after grazing were compared utilizing the Mann-Whitney two sample rank test. Differences were not significant for native bees on *Hulsea vestita* ($p = 0.1071$), although this analysis does not take into account the progressive decline in bee densities prior to grazing. This was probably due to a drop in ambient temperature (Fig. 3) and a decline in nectar availability, accentuated by a severe freeze on the evening of 1 August. Extrapolation from this trend would predict a density close to zero 3 August. Densities for honeybees on *Lupinus duranii* differed significantly between pre- and postgrazing transects ($p = 0.0413$), displaying an increase of several fold 3 August, despite relatively low ambient temperature. Note that the relative proportion of *L. duranii* removed by grazing was greater than that of *H. vestita* (Fig. 2a,b).

Species occurrences on *L. duranii* also changed markedly (Table 4). Prior to grazing, no more than 3 bee species per day were observed (average 1.4), compared to 6 species 3 August. In addition, 5 of the 6 species observed 3 August had not been observed during the previous 5 days, and, of the 3 species observed prior to grazing, only *Apis mellifera* was recorded 3 August. Species occurrences on *Hulsea vestita* remained unchanged from pre- to postgrazing transects, with the exception of the appearance of a previously unrecorded *Osmia* sp. and the conspicuous absence of *Apis mellifera* 3 August. Pre- and postgrazing densities of less frequently occur-

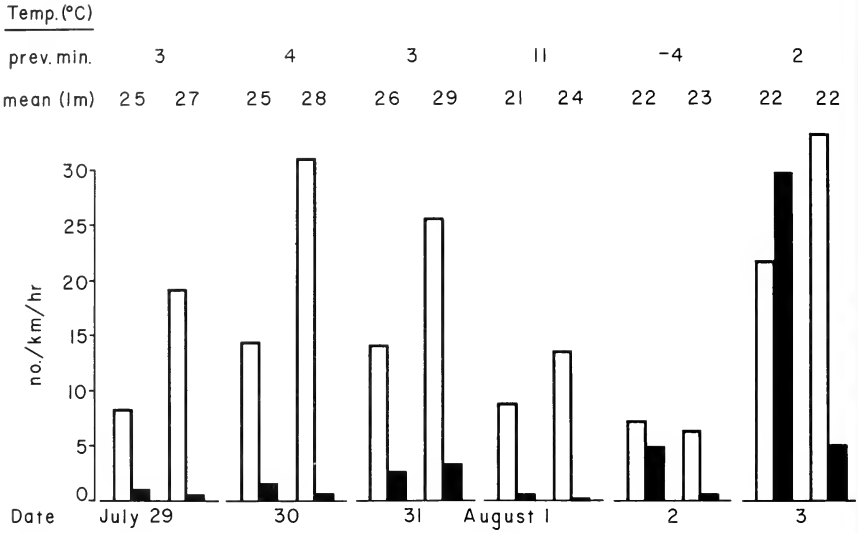

Fig. 3. Insect densities on flowers before and after nearby sheep grazing. Open bars: native bees on *Hulsea vestita*. Shaded bars: Honeybees on *Lupinus duranii*. Each pair of bars represents one of two daily transects taken at 1030 and 1300 hrs. Appearing above are average ambient temperature at one meter for each transect and the previous night's low temperature. Native bees in decreasing order of abundance: *Hoplitis albifrons*, *Osmia montana*, *Megachile* spp., *Anthidium* spp., *Anthophora urbana*, *Xeromelecta californica*, *Hoplitis fulgida*, *Osmia* spp., *Bombus morrisoni*, Misc.

ring insect/plant combinations were recorded and tested as above for those cases where data permitted analysis. None were significantly different between treatments.

The remainder of the flat was grazed on the evening of 3 August, and insect densities dropped effectively to zero on the following day.

Apis mellifera and *Bombus* spp. may forage many kilometers from the colony (Gary 1979, Heinrich 1979, respectively) and therefore might be less affected by the outcome of local flower grazing as mentioned above. If, however, grazing is extensive, bumblebees and honeybees nesting in this area may be forced to fly longer distances to forage, incurring a greater energy cost through local foraging. If such costs are significant, colony survival may be reduced. Potential effects of resource depletion may be intensified by natural spatiotemporal variation in floral resources, as demonstrated for similar habitats (Tepedino and Stanton 1980).

The danger of direct trampling is the least known and therefore most speculative of the three hazard types. Sleeping behavior is known for many bee and wasp species in which adults gather, often in large aggregations, on vegetation or in shallow ground shelters (Linsley 1958, Evans and Linsley 1960). Bumblebee queens are active and nestless in the early season, April through June, after emerging from winter hibernation. They often spend the evenings in temporary shelters near the ground and thus exposed to physical crushing by passing sheep. Males are produced in the late summer. Currently, sheep are herded in the sand flat region between these times, i.e., late June through August. Trampling hazard may be variably important for different bumblebee species depending on yearly weather patterns, timing of the colony cycle, and arrival of sheep in the area. Most solitary species have begun nesting by the time sheep grazing commences. For these, trampling exposure may interfere with nest orientation by females due to the disruption of local landmarks. Sleeping aggregations of males might also be disrupted.

TABLE 4. Bee species on *Lupinus duranii* at Little Sand Flat before and after nearby sheep grazing.

	Pregrazing					Post grazing
	July			August		
Species	29	30	31	1	2	3
Anthophora urbana						X
Apis mellifera	X	X	X	X	X	X
Bombus huntii						X
B. morrisoni	X					
B. vosnesenskii						X
Callanthidium formosum						X
Osmia montana			X			
unidentified species						X

CONCLUSION

In this study, field observations and literature survey have contributed to an analysis of the most important pollination relationships of *Astragalus monoensis*, a rare, bee-pollinated plant. Pollinators of maximum importance are bees that forage from its flowers and other species that would be expected to do so based on local abundance, host plant records, morphology, and behavior.

The evidence presented herein supports the hypothesis that pollinating bees, including those found in association with *Astragalus monoensis*, may be adversely affected by the regular movement of large numbers of domestic sheep through the sand flats. An investigation on the local nesting biology of these bees would require a specialized and intensive effort. However, the existing literature suggests that the nests of many of these species are made within the range of substrate disturbance by passing sheep. The data presented here demonstrate that bees respond to localized resource depletion by sheep grazing. The resultant long-term effects on the population size and structure of *A. monoensis* remain to be investigated. If pollination becomes limiting for the plant, seed set may decline.

Other factors are obviously important to the system as it is perturbed. For example, a certain degree of soil disturbance, as would be caused by movement of sheep through the habitat, may create favorable conditions for seed germination, such as increased scarification, which has been shown to be important to many desert plant species (B. Kay, pers. comm.). *Astragalus monoensis* usually occurs in low density compared to its most abundant insect-visited plant associates. For this reason, it could be under competition for insect pollination. Heavy grazing might alter such a relationship by increasing the pollinator/flower ratio in favor of *A. monoensis* if its flowers were relatively less grazed and if bee populations did not proportionately decline.

Further research into the floral ecology, autecology, and population genetics of *Astragalus monoensis* is necessary for the establishment of criteria necessary for its protection, as suggested for other endangered plant species (Järvinen 1982). The importance of such research is emphasized by a recent increase in grazing allotments for the Mono Basin and adjacent areas (BLM 1982).

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APPENDIX I. New host records for bees associated with *Astragalus monoensis* Barneby. Location for all records: Mono Craters region, Mono County, California. *Astragalus monoensis* records included in text, Table 1. f = female, q = queen, m = male. Host plant abbreviations: C.p.v. = *Chrysothamnus parryi vulcanicus* (Greene) Hall & Clem. (Asteraceae), H.v. = *Hulsea vestita* Gray (Asteraceae), L.d. = *Lupinus duranii* Eastw. (Fabaceae), P.f. = *Phacelia frigida* Greene (Hydrophyllaceae), E.u. = *Eriogonum umbellatum* Torr. (Polygonaceae), C.u. = *Calyptridium umbellatum* (Torr.) Greene (Portulacaceae), M.c. = *Mimulus coccineus* Congd. (Scrophulariaceae).

Species	Host plant	Date	Number, sex, or caste
ANDRENIDAE			
Andrena (*Trachandrena*) *cleodora cleodora* Viereck	E.u.	28.VI.'81	2f
	E.u.	1.VII.'81	4f
A. (*Plastandrena*) *prunorum prunorum* Cockerell	E.u.	28.VI.'81	2f
ANTHOPHORIDAE			
Anthophora urbana urbana Cresson	H.v.	26.VI.'79	1f
	L.d.	7.VII.'79	1f
	C.p.v.	8.VIII.'79	1f
APIDAE			
Bombus (*Pyrobombus*) *huntii* Greene	H.v.	8.VII.'79	1w
	P.f.	24.VII.'79	2w,1q
	C.p.v.	8.VIII.'79	1w
	L.d.	21.VIII.'81	1w
B. (*Separatobombus*) *morrisoni* Cresson	P.f.	13.VII.'79	3w,1q
	P.f.	14.VII.'79	3w,1q
	P.f.	24.VII.'79	1w
	P.f.	8.VIII.'79	2w
	L.d.	24.VII.'79	4w
	L.d.	8.VIII.'79	1w
	L.d.	21.VIII.'81	4w
	C.p.v.	8.VIII.'79	3w
	C.p.v.	21.VIII.'81	1w
B. (*Pyrobombus*) *vosnesenskii* Radoszkowski	P.f.	14.VII.'79	1w
	P.f.	24.VII.'79	1w
	L.d.	8.VIII.'79	1w
	C.p.v.	21.VIII.'81	1w
COLLETIDAE			
Colletes consors consors Cresson	P.f.	13.VII.'79	3f
	P.f.	14.VII.'79	3f
MEGACHILIDAE			
Anthidium (*Anthidium*) *banningense* Cockerell	P.f.	14.VII.'79	1f
	L.d.	4.VII.'80	1m
A. (*A.*) *mormonum* Cresson	P.f.	4.VII.'80	1f
A. (*A.*) *tenuiflorae* Cockerell	H.v.	8.VII.'79	1f
	H.v.	14.VII.'79	1f
	L.d.	14.VII.'79	1f

Appendix 1 continued.

Species	Host plant	Date	Number, sex, or caste
Callanthidium formosum (Cresson)	L.d.	24.VII.'79	1f
	C.p.v.	21.VIII.'81	1m
Hoplitis (*Monumetha*) *albifrons argentifrons* (Cresson)	M.c.	15.VII.'80	1f
Osmia (*Chenosmia*) *calla* Cockerell	L.d.	8.VI.'79	5f
O. (*Monilosmia*) *densa densa* Cresson	P.t.	24.VII.'79	1f
	L.d.	13.VII.'79	1f
O. (*Nothosmia*) *grindeliae* Cockerell	M.c.	9.VI.'80	1f
O. (*Acanthosmia*) *integra* Cresson	M.c.	9.VI.'80	1f

VEGETATIONAL AND GEOMORPHIC CHANGE ON SNOW AVALANCHE PATHS, GLACIER NATIONAL PARK, MONTANA, USA

David R. Butler[1]

ABSTRACT.— Six subalpine snow avalanche paths studied in 1975 were revisited in the summer of 1983, with the purpose of examining geomorphic and vegetational change that may have occurred during this eight-year period. Repeat photography and field reconnaissance were used to assess vegetational and geomorphic change. Vegetational responses to avalanches were apparent on several of the avalanche paths, generally by an increase in brush cover. Geomorphic changes were not apparent, suggesting that avalanches need not be geomorphically effective to initiate substantial vegetative disruption.

Long-term records of geomorphic and vegetational change in subalpine and alpine environments of North America are scarce, because of the limited period of historical settlement and problems of inaccessibility. Recent studies have reported geomorphic change on alpine debris slopes based on periods of observation ranging from 7 to 15 years (Gardner 1979, 1982, 1983a, Luckman 1981). Subalpine slopes, however, have been relatively ignored in long-term studies.

In 1975, Butler examined the general vegetative conditions and geomorphic processes active on 12 subalpine avalanche paths in Glacier National Park, Montana, USA (Butler 1979). The intent of the study presented here is to describe the geomorphic and vegetational changes that took place on six of these snow avalanche paths during the eight-year interval from 1975 to 1983. The occurrence and synchroneity of large-scale destructive avalanches were of particular interest.

Sites MV3, MV4, SN5, SN6, SN7, and SN8 were revisited in 1983 (Fig. 1). MV3 and MV4 had also been revisited briefly in 1981. These paths all impinge on either a highway (MV3 and MV4 in the McDonald Creek Valley), a heavily used foot trail (SN6, SN7, and SN8 in the Snyder Creek Valley), or a popular backcountry campsite (SN5 in the Snyder Creek Valley), and thus major avalanche events are noted by National Park personnel. These six avalanche paths were selected for further study because: (1) some had tree-ring and/or highway and trail crew maintenance records of avalanche frequency and magnitude (MV3, MV4, SN5, and SN7); (2) some were encountered enroute to the above paths and had similar characteristics of vegetation and site conditions (SN6 and SN8); and (3) time limitations restricted revisitation to the most easily accessible paths. Detailed site descriptions of the six revisited paths may be found in Butler (1979).

Tree species present on the drier avalanche paths of the Snyder Creek Valley include *Abies lasiocarpa* and a few *Pseudotsuga menziesii*, whereas the paths of the McDonald Valley support *Betula papyrifera* and *Picea engelmannii*. Flexible-stemmed shrubs and small trees, able to withstand avalanche impact pressures of up to about 10 t m^{-2}, include *Acer glabrum*, *Alnus* spp., *Sorbus scopulina*, and *Crataegus douglassii*. *Acer* and *Alnus* are most common (Butler 1979). Smaller, flexible berry bushes (e.g., *Vaccinium*) are also common.

METHODS

Repeat Photography

Repeat photography allows qualitative assessment of geomorphic and vegetational changes that may occur over a given interval. Photographs taken during field work in 1975 were repeated in 1981 for MV3 and MV4 and on all six sample paths in 1983. Photographs were taken looking up-path from the farthest down-path point (in the case of SN5,

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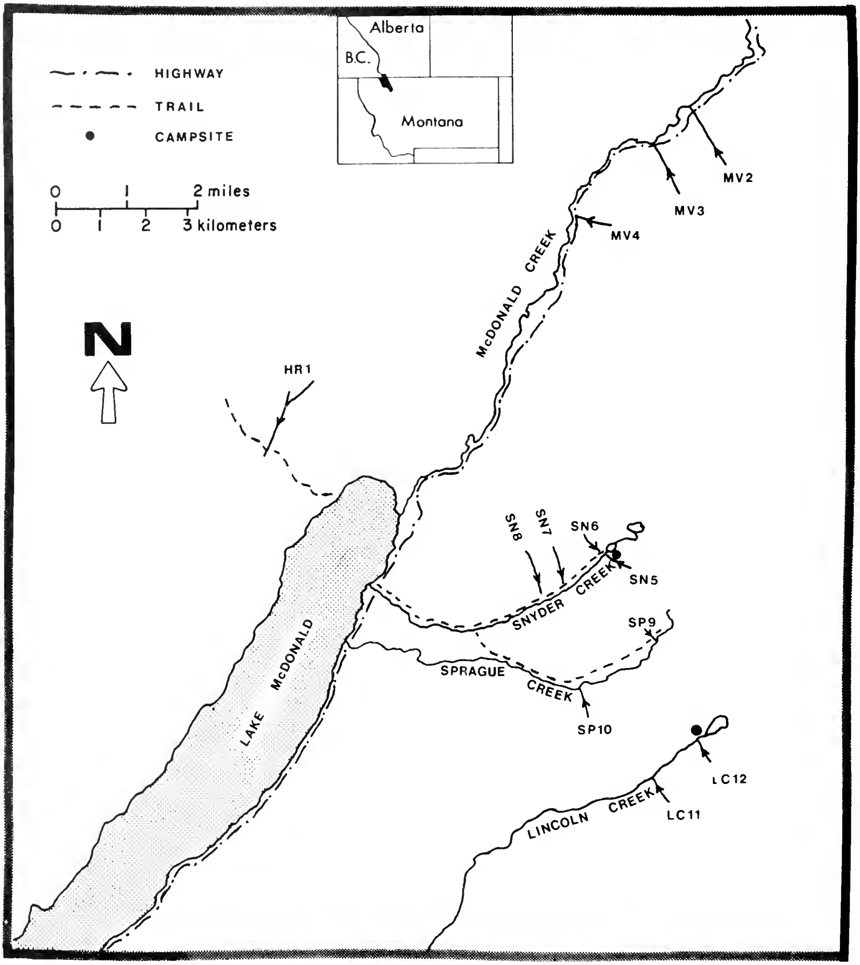

Fig. 1. Map of the study area in the central portion of Glacier National Park, Montana, showing the location of the avalanche paths mentioned in the text. The inset map shows the location of Glacier National Park in relation to Montana and the Canadian–USA border.

heavy brush cover dictated that photographs be taken about 100 m from the path, on the opposite valley side). Figure 2 illustrates a typical subalpine avalanche path (SN8) as it appeared in 1983.

Dendrogeomorphology

Butler (1979) tagged 30 trees in the runout zone of path SN7 in 1975. Relocation of these trees and assessment of their condition would indicate whether a large-scale destructive avalanche had occurred during the interval between visits. Additional tree-ring dating of high magnitude avalanche events had been planned for paths SN5, SN6, and SN8. Access to Snyder Creek drainage was closed, however, on 24 June 1983, because of the presence of two families of grizzly bears (*Ursus arctos horribilis*). The drainage was

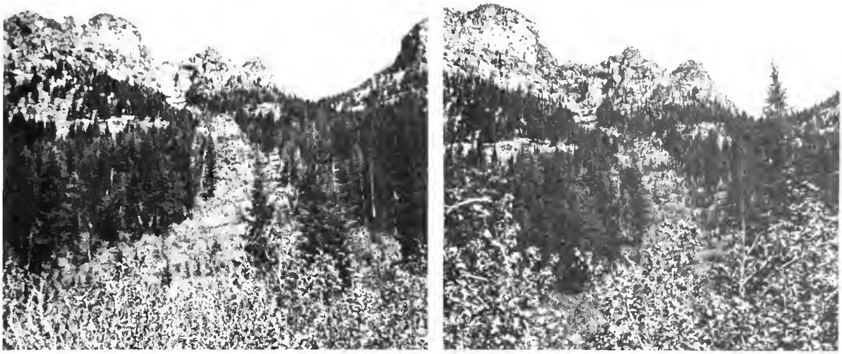

Fig. 2. Left, View up-path on path SN8 in 1975. Right, View up-path on path SN8 in 1983. Notice the increase in alder in the runout zone and growth of subalpine fir and Engelmann spruce in the upper reaches of the path.

not opened again during the field season. Prior to the closing of the valley five cross-cut samples from avalanche-damaged trees at the base of path SN8 were collected for dendrogeomorphic analysis.

Historical and Observational Records

The *Hungry Horse News*, a weekly newspaper published in Columbia Falls, Montana, regularly records information on avalanches that close highways in the Glacier National Park area. Reports and photographs from the newspaper were used to assess large-scale avalanche frequency on paths MV3 and MV4. Trail crew and highway personnel provided additional observations of avalanche events, from both direct observation and observation of avalanche debris in backcountry areas.

RESULTS

The data on avalanche occurrences provided the context in which to assess any geomorphic and vegetational changes as revealed by site examination and repeat photography. The following section presents specific results from each of the six avalanche paths; this is followed by a discussion of the geomorphic and vegetative implications of the study.

Path MV3 continues to annually experience snow avalanches that descend to Going-to-the-Sun Highway, as revealed through conversations with park personnel. Photographs taken in 1975, 1981, and 1983 revealed snow cover in the avalanche path but essentially no vegetational or geomorphic change. Individual trees along the sides of, and within, the path are identifiable in photographs from each year, illustrating that no new high magnitude avalanches have occurred since 1975. On other avalanche paths in the park, post-1975 avalanches have extended both the longitudinal and transverse trimlines along path margins (Butler and Malanson 1985, in press). No major geomorphic change is detectable on path MV3; the stream channel within the path has remained stationary, no deposits of fresh rock debris were detected in the runout zone in 1981 or 1983, and no new erosional scouring has been identified.

Path MV4 has experienced avalanches that reached the lower portions of the runout zone in all but two years since 1975. Vegetational characteristics have remained remarkably similar during the years between 1975 and 1983, with *Acer glabrum* and *Alnus* spp. continuing to dominate the path. Trees seen along the margins of the path in 1975 were again identifiable in 1981 and 1983, indicative of no major high magnitude event during the intervals between visits. Individual boulders photographed in the runout zone in 1975 were reidentified in the same positions in 1981 and 1983, and no noticeable addition of clasts has occurred.

In contrast to conditions in the McDonald Creek Valley, three of four paths reexamined in the Snyder Creek drainage have undergone extensive vegetational change since

1975. Only path SN7 appears little changed. The tagged trees at the base of the runout zone of path SN7 were successfully relocated. No new avalanche damage was discernible, and the very presence of the same trees indicates an absence of high-magnitude avalanche events. Small subalpine firs (*Abies lasiocarpa*) within the runout zone and lower track were also relocated by repeat photography. Shrubs (primarily *Acer glabrum*) experienced no increase in number and grew very little. Geomorphic changes were not apparent anywhere on the path.

Path SN5 has experienced at least one large avalanche since 1975. Trail crew personnel encountered vegetative destruction and deposition at the Snyder Lake backcountry campsite (Fig. 1) in the early summer of 1979 (J. Oelfke, pers. comm., February 1983). The destruction of trees was attributed to a large avalanche event during the 1978–1979 avalanche season. Vegetation encountered in 1983 was very dense, with a large increase in *Alnus* spp. over what had been present in 1975. The increase in deciduous shrubs suggests that 1978–1979 was not the only avalanche winter since 1975, because such flexible shrubs are themselves indicators of a continued avalanche frequency of every one to three years (Schaerer 1972, Butler 1979); coniferous succession on disturbed areas in the park occurs if the disturbance ceases (Parker 1982). Grizzly bears are known to prefer the shrub and berry habitat of avalanche paths (Martinka 1972), and the increase in shrubs (and berry bushes) may be partially responsible for the presence of grizzlies in 1983. This dense shrub cover that developed between 1975 and 1983 effectively precluded useful repeat photography. Gross morphology of the track and runout zone remained unaltered from their 1975 appearance.

Conditions on path SN6 were very similar to that described for SN5, with a dramatic increase in size of *Acer glabrum* and *Alnus* spp. masking any geomorphic change that may have occurred. No data were available on avalanche frequency because of the drainage closure on 24 June 1983. The level of brushiness suggests, however, that avalanches have been frequent.

Path SN8 experienced a great deal of vegetational change during the eight years between visits; yet it apparently remained geomorphologically static. No fresh clasts were located in a reconnaissance of the runout zone, the small stream channel in the path had not shifted position, nor were other changes apparent in repeat photography comparisons. Repeat photography was difficult, however, because of the profusion of alder (*Alnus* spp.) that had grown since 1975, obscuring the view up-path (Fig. 2). Cross-sections from avalanche-damaged Engelmann spruce (*Picea engelmannii*) and subalpine fir located in the runout zone all recorded evidence of trauma (reaction-wood growth, corrasion scars, and severely suppressed rings) from the avalanche seasons of 1978–1979, and 1981–1982. The only firm dendrochronologic data suggesting avalanche-induced trauma prior to 1975 were for 1965–1966. These data suggest that avalanches have reached the runout zone in the last eight years more frequently than in the previous 25 years, probably accounting for the increase in alder, as well as *Vaccinium* bushes. The path has become, because of increased avalanche frequency, prime grizzly habitat; recently clawed trees and fresh scat attested to the presence of grizzlies in the path in June 1983.

Discussion

Dendrochronologic data indicate that a major avalanche event occurred on path SN8 during the 1978–1979 avalanche season. This date is correlative with the destructive campsite event on path SN5, as well as with other major avalanches in the park that occurred in February 1979 (Panebaker 1982, Butler and Malanson 1985, in press). Previous work (Butler 1979) that suggested that no path-to-path synchroneity of avalanche events occurred in the central portion of Glacier National Park may be partially in error; work is continuing on this topic.

Observations of geomorphic change based on field examinations and repeat photography indicate that no differences developed in gross path morphology between 1975 and 1983. On a small scale, individual clasts identifiable in photographs taken in 1975 remained in the same locations in 1981 and 1983, again indicative of an absence of geomorphic change. Snow avalanches that occur on the same paths apparently do not come into effective erosional contact with the ground surface. This conclusion was suggested in previous work, which stated that snow-on-snow avalanches prevented damage to lower portions of trees on avalanche paths (Butler 1979:26). Recently, Gardner (1983b) has shown that even avalanches that move over snow-free and thawed surfaces may have no erosional impact, a result of a protective layer of snow deposited by a moving avalanche. In spite of the geomorphically ineffective avalanches that occurred during the study period, vegetative damage was sustained on several paths, and shrub density increased. Snow avalanches need not be in effective geomorphic contact with the ground surface to produce vegetative responses. Research will continue in Glacier National Park to further examine the question of the geomorphic effectiveness of subalpine snow avalanches.

ACKNOWLEDGMENTS

Thanks are extended to Susan Panciera and K. Billington for their help in the field in 1983; to personnel of Glacier National Park for arranging necessary permits and access to field sites; and to George P. Malanson, Oklahoma State University, and Paul E. Carrara, U.S. Geological Survey, for their constructive comments on earlier drafts of this manuscript.

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EFFECTIVENESS OF THE SEED WING OF *PINUS FLEXILIS* IN WIND DISPERSAL

Ronald M. Lanner[1]

Abstract.— Limber pine (*Pinus flexilis* James) seeds are usually wingless but occasionally have short, stubby wings. To determine the effectiveness of these wings in slowing seed descent, rates of fall were determined before and after wing removal. A similar experiment was conducted with seeds of Himalayan blue pine (*P. griffithii* McClelland), a white pine with typically long seed wings. The short wings of limber pine seeds were found to influence rate of seed fall far less than the wings of Himalayan blue pine. This is consistent with evidence suggesting that limber pine seeds are not effectively dispersed by wind but are dependent for dispersal on Clark's Nutcracker (*Nucifraga columbiana*).

The seeds of limber pine (*Pinus flexilis* James) are usually described as lacking the membraneous wing typical of most Pinaceae or as having only rudimentary wings (Sargent 1891–1902, Harlow et al. 1979, Dallimore & Jackson 1961, Lanner 1984). During the course of recent research, numerous limber pine seeds from throughout Utah, Wyoming, and Montana have been examined in this laboratory. Winged seeds were occasionally found in cones collected in all three of these states, though they are scarce. The outer cone-scale tissue from which seed wings are formed is maternal in origin, and therefore of uniform genotype. Thus, all the seeds of a tree bearing winged seeds are winged, and all the seeds from a tree bearing wingless seeds are wingless.

Limber pine and some other western American wingless-seeded pines (*P. edulis* Engelm., *P. monophylla* Torr. & Frém., *P. albicaulis* Engelm.) have recently been found to be at least partially dependent on corvids, principally Clark's Nutcracker (*Nucifraga columbiana*) and the Piñon Jay (*Gymnorhinus cyanocephalus*), for dispersal of their seeds and establishment of their seedlings (Vander Wall and Balda 1977, Lanner 1980, Lanner and Vander Wall 1980, Hutchins and Lanner 1982). In brief, the corvids harvest conifer seeds from cones and bury them in the soil as food stores which, if not retrieved, often germinate. There is strong evidence that whitebark pine (*P. albicaulis*) is systematically dispersed and established only by Clark's Nutcracker, all other potential disperser-establishers being ineffective (Hutchins and Lanner 1982). Limber pine has not received thorough enough study to determine whether this is also true of its regeneration, but the similarity of its potential dispersing fauna to that of whitebark pine suggests this may be so. However, the occasional presence of seed wings in limber pine raises the possibility that a limited amount of wind dispersal also occurs. If so, the hypothesis of dependence on corvids, or other animals that may subsequently be found effective, would fail. The purpose of the experiment reported here was to determine whether the rudimentary wings of limber pine seeds are aerodynamically capable of effecting seed dissemination by the wind.

Methods

Limber pine cones from the Beartooth Mountains, Montana, were allowed to open naturally in the laboratory. Cones from several trees (trees 1, 2, and 3) bore seeds with wings at least as long as any hitherto encountered and were selected for study. These wedge-shaped wings were up to 5 mm long. Seeds were individually dropped 9 m down a stairwell in still air. Descent time was determined with a stopwatch. Seeds were retrieved and dropped again after removing the wing. A "slowdown factor" was com-

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TABLE 1. Rates of fall (meters sec^{-1}) of winged and de-winged *Pinus flexilis* seeds from three trees from the Beartooth Mountains, Montana, during a 9-m descent.

	Tree 1		Tree 2		Tree 3	
	Winged	De-winged	Winged	De-winged	Winged	De-Winged
			Rate of fall, meters sec^{-1}			
Mean	4.21	4.67	4.12	4.61	4.20	1.56
S.D.	0.40	3.7	0.50	0.54	0.16	0.84
n	7	6	7	7	10	10

puted by dividing the rate of fall of de-winged seeds in meters per second by the rate of fall of winged seeds. A similar experiment was performed with seeds of Himalayan blue pine, *P. griffithii* McClelland, but these long-winged seeds tended to drift easily and thus were dropped to the floor of a laboratory from a height of 2.9 m.

RESULTS

Limber pine seed descent was linear, with little tendency to autorotate, whether wings were present or absent. The mean rate of descent of limber pine seeds before wing removal was 4.18 meters sec^{-1}; and after removal of wings the rate was 4.61 meters sec^{-1} (Table 1). The slowdown factor for individual trees' seeds ranged from 1.09 to 1.12, with a mean of 1.10. Therefore, winged seeds required 1.1 times as long to fall one meter as did de-winged seeds.

Himalayan blue pine seeds immediately began to autorotate when released and drifted in response to even very slight air movements. Winged seeds fell at an average rate of 1.12 meters sec^{-1} (filled) and de-winged seeds fell 4.06 meters sec^{-1} (Table 2). The slowdown factor for filled seeds was therefore 3.63, meaning that the long membraneous wings of these seeds delayed their fall by a time factor of 3.63. Empty seeds fell somewhat more slowly, both with and without wings, and had a slowdown factor of 3.94.

DISCUSSION AND CONCLUSIONS

The winged seeds of Himalayan blue pine are typical of the white pines. According to USDA Forest Service (1974), they weigh about 9100 per pound, or roughly .05 gm each. Limber pine seeds weigh about .09 gm each, according to the same source. The wings of samaras, which these seeds are in functional terms, initiate autorotation, thus slowing descent and allowing wind currents to exert lateral force on seed flight; so it can be assumed that a wing that is highly effective in slowing the rate of descent is adaptive in the context of wind dispersal. It is apparent that if the slowdown factor of Himalayan blue pine seed wings is taken as typical for the white pine group, of which limber pine is also a member (Critchfield and Little 1966), then the rudimentary wing of limber pine seeds is a comparatively ineffective braking mechanism. It therefore appears that wind dispersal of limber pine seeds is unlikely to be effective beyond the crown projection of the individual seed tree and that dispersal by corvids, especially Clark's Nutcracker, is of far greater ecological significance.

ACKNOWLEDGMENTS

Harry E. Hutchins assisted in some of the measurements of seed fall velocity. Seeds of limber pine were provided by personnel of the Custer National Forest, Montana, and seeds of Himalayan blue pine by the Institute of Forest Genetics, U.S. Forest Service, Placerville, California. This study was supported by National Science Foundation Grant DEB 78-02808 and the McIntire-Stennis program and is published as Utah Agricultural Experiment Station Journal Paper 3035.

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TABLE 2. Rates of fall (meters sec^{-1}) of filled and empty *Pinus griffithii* seeds before and after wing removal, during a 2.9-m descent.

	Filled seeds		Empty seeds	
	Winged	De-winged	Winged	De-winged
	Rate of fall, meters sec^{-1}			
Mean	1.01	4.06	.98	3.86
S.D.	.21	.49	.06	.43
n	9	9	11	11

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HABITAT RELATIONSHIPS OF THE BLACKBRUSH COMMUNITY (*COLEOGYNE RAMOSISSIMA*) OF SOUTHWESTERN UTAH

James Callison and Jack D. Brotherson[1]

ABSTRACT.— Eight general study sites in the blackbrush (*Coleogyne ramosissima*) zone of southwestern Utah were examined. Soils data were gathered and plant cover was estimated. Shrubs were found to be positively correlated with shallow, sandy soil. Nonwoody plants were found to be positively correlated with deeper, silty soils. Cryptogamic soil crusts were positively correlated with silt and nitrogen in the soil and therefore may play a role in elevating soil fertility. Shrubs and grasses were negatively correlated. Management implications are discussed.

The community formed by blackbrush (*Coleogyne ramosissima*) and associated species is an important vegetation type in southern Utah. Kuchler (1964) estimated that the blackbrush community covers 2.5 million acres in Utah alone. It also occupies large acreages in Arizona, California, and Nevada. However, little has been written about blackbrush either as a species or a community type. Bowns (1973) studied the autecology of blackbrush in southern Utah. Other investigations deal with specialized aspects of the ecology of the blackbrush community (Beatley 1966; Loope 1978). Several government reports refer to the blackbrush community in an oblique manner (Little 1978; USDI BLM 1979). Most of these studies included field observations and contain valuable comments on relationships in the blackbrush community but offer little quantitative information about the blackbrush community of Utah. The purpose of our study was threefold. We have provided a quantitative analysis of the blackbrush community, compared our analysis to previously observed relationships, and postulated new relationships.

SITE DESCRIPTION

Our study sites were located in the Dixie Corridor between the Beaver Dam Wash and the Beaver Dam Mountains in southwestern Utah. This area is a transition zone between the hot desert of the Mojave and the cold desert of the Great Basin. The soils are shallow, well drained, and have from 2% to 7% slopes. One site was on a sandstone bench overlooking Manganese Wash. The other sites were on the alluvial plain west of the Beaver Dam Mountains, with the furthest site being 20 miles from Manganese Wash. All sites had been grazed in the past, though some were not being grazed at the time of the study. There was no evidence of burning on any of the sites. Parent materials are mixed alluvium formed from limestone, gneiss, schist, sandstone, and basalt (Bowns 1973). Altitude at the study plots ranged from 1070 m (3511 ft) to 1400 m (4593 ft). The average annual precipitation, recorded over a 30-year period at the nearby Gunlock powerhouse was 296 mm (11.65 in). The average annual temperature, from the same location, was 16.1 C (61 F) (Hodges and Reichelderfer 1962). Eubank and Brough (1979) list extremes of temperature from 46.7 C (116 F) to -23.9 C (-11 F) at St. George, which is on the edge of the blackbrush range.

METHODS

Eight general study sites were selected. Five 10 × 10 m sampling plots were randomly placed at each site. All plots were placed on sites of uniform topography, with ravines and rock outcroppings being avoided. Each plot was subsampled with fifteen 1 m^2 quadrats. The quadrats were distributed uniformly in three rows of five quadrats each within the study plots. Vascular plant cover was estimated for each species (Daubenmire 1959) at each quadrat. In addition, cover

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Table 1. Prevalent species in the blackbrush zone. The number of prevalent species is equal to the average number of species on the 10 × 10 m study plots.

Species	Mean cover	Standard deviation	Mean frequency	Standard deviation
Coleogyne ramosissima	37.8	8.3	96.7	5.4
Bromus rubens	3.4	3.1	66.3	30.0
Bromus tectorum	2.8	2.7	63.2	39.7
Ephedra nevadensis	1.2	1.9	7.3	8.3
Thamnosma montana	0.8	2.3	6.2	12.3
Prunus fasciculata	.5	1.1	3.2	5.0
Xanthocephalum microcephela	.4	1.2	2.1	5.6
Yucca brevifolia	.4	1.1	2.4	4.9
Yucca baccata	.4	0.9	4.1	5.4

contributed by rock, litter, and cryptogamic crusts was estimated. Soil depth was measured with a penetrometer (Greenwood and Brotherson 1978) at each corner and center of each plot (the five readings were averaged to give a single estimate for each plot). Percent slope and exposure were obtained for each plot using an Abney level and compass, respectively. Elevation at each plot was taken from USGS 1:24,000 topographic maps.

Three samples of the surface 20 cm of soil were taken in each plot (from opposite corners and the center). Subsamples were later pooled for laboratory analyses. Dependence on surface samples alone seemed justified, since Ludwig (1969) has shown that the surface decimeter of soil from Utah foothill communities provided over 80% of the information useful in correlation analyses relating soil mineral content with plant parameters. Holmgren and Brewster (1972) also showed that over 50% of the fine roots (those most likely to absorb soil minerals) were found concentrated in the upper 15 cm of soil profile of Utah cold desert shrub communities. With respect to grasslands, Christie (1979) likewise found that the top layer of soil supplies most of the minerals taken up by plant roots.

Soil samples were analyzed for texture (Bouyoucos 1951), pH, mineral composition, and organic matter. Soil reaction was taken with a glass electrode pH meter on a 1:1 soil-water paste (Russell 1948). Soils were extracted with 1.0 normal neutral ammonium acetate for exchangeable calcium, magnesium, potassium, and sodium (Jackson 1958, Hesse 1971, Jones 1973). Zinc and copper were extracted from the soils by use of DPTA (diethylenetriamine-penta-acetic acid) extracting agent (Lindsay and Norvell 1969). Individual ion concentrations were determined by using a Perkin-Elmer Model 403 atomic absorption spectrophotometer (Isaac and Kerber 1971). Soil phosphorus was extracted using sodium bicarbonate (Olsen et al. 1954). Total nitrogen was determined by macro-Kjeldahl procedures (Jackson 1958). Organic matter was determined by loss on ignition of 10 grams of soil at 950 C in a LECO medium temperature resistance furnace (Allison 1965).

Prevalent species (those most frequently encountered during sampling) were selected using the procedure of Warner and Harper (1972). Prevalent species were selected on the basis of both cover and frequency values. Niche overlap values (Colwell and Futuyma 1971) were calculated. Although niche overlap values can measure various aspects of interspecific association, in this study we used them to measure the degree to which various species pairs coexist in specific geographical compartments. A dendrogram of interspecific association (Sneath and Sokal 1973) was developed from the niche overlap values. The degree to which pairs of environmental variables were positively correlated in the 40 study plots was analyzed with correlation coefficients. Clustering procedures followed the weighted-pair group method (Sneath and Sokal 1973). Means and standard deviations are reported for biotic and abiotic variables across the 40 sampling plots.

Results and Discussion

Table 1 lists the prevalent species, their average cover and frequency. The most

Table 2. Environmental factors in the blackbrush zone.

Environmental factor	Mean	Standard deviation
Biotic factors		
Total living cover (%)	55.5	9.0
Percent composition		
Shrubs	42.7 (76.9)[*]	7.5
Forbs	1.2 (2.2)	1.8
Grass	6.3 (11.4)	4.3
Cryptogams	5.3 (9.5)	5.2
Spp./stand	7.7	2.3
General site factors		
Elevation (m)	1271.3	94.5
Slope (%)	9.6	9.7
Litter (%)	7.9	3.8
Rock (%)	38.7	10.3
General soil factors		
Clay (%)	12.9	3.7
Silt (%)	26.2	6.9
Sand (%)	60.9	9.2
OM (%)	.5	.5
Soil depth (dm)	1.3	.7
pH	8.5	.2
EC (mmhos/cm)	.6	.2
Soil mineral nutrients		
Nitrogen %	.05	.02
Phosphorus (ppm)	15	5
Calcium (ppm)	9639	5335
Magnesium (ppm)	800	400
Sodium (ppm)	2709	149
Potassium (ppm)	211	78
Zinc (ppm)	1	1
Copper (ppm)	1	1

[*] Numbers in parenthesis indicate relative cover values.

abundant species is blackbrush, which contributes 75% of all vascular plant cover. Annual grasses (*Bromus rubens* and *Bromus tectorum*) account for 12% of the total cover. The remaining species on the prevalent species list are shrubs. Combined, they make up 7% of the total vascular plant cover. Although no forbs appear as prevalent species, 28 forbs were encountered in the study. However, all were uncommon and together they contributed only 2% of the total vascular plant cover.

Soils at most sites were strongly skeletal and often had shallow $CaCO_3$ pans. As a result, penetrometer readings were also shallow, averaging only 1.3 dm (5.1 in.) in depth (Table 2). Shallowness of soil is an important characteristic of the blackbrush community and may partially determine the abundance and/or distribution of blackbrush. Thatcher (1975) and Doughty et al. (1976) concluded that edaphic factors were highly influential in the distribution of blackbrush. In addition to being shallow, soils that support blackbrush have abundant exposed rock (38.7%) and a high sand content (60.9%). The soils had an average pH of 8.5. Such high pH values are undoubtedly related to elevated levels of calcium (9639 ppm) and sodium (2710 ppm) in the soils. Soils analyzed by Bowns (1973) in the same vegetation zone showed patterns similar to those reported here.

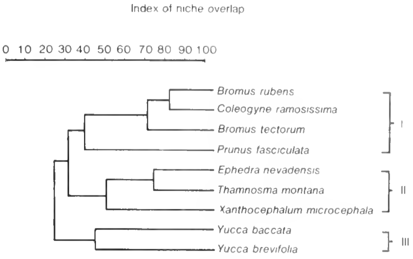

Fig. 1. Cluster diagram based on niche overlap values for the prevalent species in the blackbrush community.

Relative cover of shrubs, grasses, and forbs is in about the same proportions as the representation of those life form groups on the prevalent species list. Nearly 10% of the total plant cover was contributed by cryptogamic crusts. Although the role of cryptogamic crusts is not completely understood, their abundance indicates that they should not be ignored in the ecology of the blackbrush community.

Figure 1 depicts a cluster of species based on niche overlap values. For purposes of discussion, the nine species have been divided into three groups. In group I, blackbrush, red brome (*Bromus rubens*), and cheatgrass (*Bromus tectorum*) are closely associated. This occurs because red brome and cheatgrass often take advantage of the microhabitat provided by blackbrush individuals by living directly underneath the canopy of the blackbrush. Even though red brome and cheatgrass have a high niche overlap value with blackbrush, there is a negative correlation between grasses and shrubs. This is because niche overlap and correlation analyses measure different aspects of plant distribution. Desert almond (*Prunus fasciculata*)

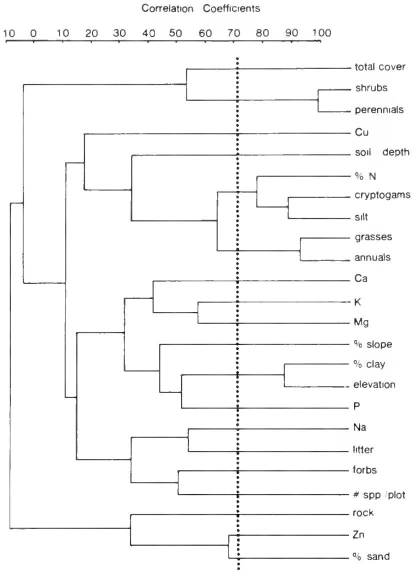

Fig. 2. Cluster diagram based on correlation coefficients for pairs of variables on all plots in the blackbrush community. Associations to the right of the dotted line are significant at the 0.01 level. Associations to the left of the dotted line are not significant.

occurs somewhat randomly on our study sites but tends to be more closely associated with blackbrush than other species. The species in group II are all hardy and relatively unpalatable shrubs that predominate on southern exposures where soils are shallow and conditions less favorable than surrounding areas. The distribution of the two *Yucca* species in group III is enigmatic. *Yucca baccata* and *Yucca brevifolia* occur intermixed in stands only occasionally and on the fringes of their respective ranges. Because neither *Yucca* species is in its preferred habitat in the blackbrush zone, their association may only be coincidental.

Figure 2 is a cluster of biotic and abiotic variables based on correlation coefficients. Associations to the right of the dotted line are significant at the 0.01 level. Associations to the left of the dotted line are considered insignificant. The 0.01 level of significance was used because the large number of correlations used to construct the dendrogram might allow too many correlations at the 0.05 level. Several relationships are distinguishable. Cryptogamic crusts, silt, percent soil-nitrogen, grass, and annuals are closely associated. Also positively associated, but less closely, are soil depth, copper, calcium, potassium, magnesium, phosphorus, sodium, clay, litter, and number of species per plot. These patterns suggest that grasses, cryptogamic crusts, and forbs are more common on deeper soils where clay, silt, and mineral nutrients are more abundant. Shrubs, on the other hand, are more common on more shallow, sandy soils. Correlation data for pairs of variables (Table 3) confirm these observations. Shrubs are positively correlated with sand and negatively correlated with clay, silt, and soil depth. Grasses are positively correlated with clay, silt, and soil depth but are negatively correlated with sand. We conclude from these patterns that the relative proportions of shrubs, grasses, forbs, and cryptogamic crusts are controlled by edaphic factors in the blackbrush community. This conclusion corroborates that of Doughty et al. (1976) and Thatcher (1975), who found that presence of blackbrush was related to the presence of certain soil types. Although nonwoody plants often take advantage of the microhabitat provided by the shrubs, they also increase in abundance where soils are deeper, have finer particles, and are more fertile. Deep, silty soils store more soil moisture for nonwoody plants than shallow, sandy soils. Shrubs fill a somewhat different niche by being more abundant on sandy, shallow soils. Shrubs are better able to extract water from shallow, sandy soils than are nonwoody plants. Sandy, shallow soils are more common than deep, silty soils in the study area. Thus, shrubs are the regional dominant in our study.

The relationships between soil nitrogen, silt, and cryptogamic crusts bear comment. The relationship among silt and cryptogamic crusts have been observed earlier by several authors (Loope and Gifford 1972, Kleiner and Harper 1977, Anderson et al. 1982, Brotherson and Rushforth 1983). Kleiner and Harper (1977) argued that, once established, the crusts tend to trap silt at the soil surface. Components of the cryptogamic crusts (i.e., bluegreen algae) have been shown to be nitrogen fixers (MacGregor and Johnson 1971,

TABLE 3. Correlation coefficients for environmental factors.

Environmental factor	Environmental factor Clay	Sand	Silt	Soil depth	Shrubs
Sand	−.755				
Silt	.474	−.935 b			
Soil depth	.152	−.279	.292		
Shrubs	−.504	.907 b	−.946 b	−.229	
Grasses	.681	−.879 b	.813 a	.550	.870 a

[a] Significant at the .01 level
[b] Significant at the .001 level

Reddy and Gibbons 1975). Anderson and Rushforth (1976), while working on the floristics of the cryptogamic crusts in southwestern Utah, described 11 species of blue-green algae as components of the crusts. The presence of blue-green algae in crusts of the blackbrush community may well explain the significant ($P < .01$) positive correlation between percent nitrogen in the soil and the presence of cryptogamic crusts. This may also indicate the value of cryptogamic crusts in elevating the fertility of associated soils.

Although no data were gathered on blackbrush reproduction, blackbrush seedlings were observed on only one of the eight general study areas. Those seedlings were all approximately 16 years old, but it is difficult to age blackbrush precisely because of stem splitting (Bowns 1973). The scarcity of blackbrush seedlings indicates that blackbrush reproduction occurs infrequently.

The information discussed in this paper does have bearing on current management practices in the blackbrush community of southwestern Utah. Since our data suggest that the sites on which blackbrush occur are predisposed toward dominance by shrubs, the current widespread practice of burning blackbrush sites to convert them to grasslands may be fighting against the natural trends of the sites. Bowns (1973) states that burning of blackbrush stands may give unpredictable or undesirable results. We concur with his statement and suggest that other alternatives to the burning of blackbrush sites be investigated.

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SIZE SELECTION OF FOOD BY CUTTHROAT TROUT, *SALMO CLARKI*, IN AN IDAHO STREAM

William D. Skinner[1]

Abstract.— The mean size of food and amount of food consumed by cutthroat trout from Palisades Creek in southeastern Idaho increased with trout length. Number of organisms of terrestrial origin, number of aquatic larvae, number of ants, and number of berries from redstem dogwood were related to trout length. The size range and number of taxa consumed increased with trout size, indicating that as trout get larger, they broaden their feeding menu. The minimum size of food consumed was relatively constant for all trout, but larger trout appeared to feed more from the stream bottom. Trout may have a minimum length of food, below which items cannot be detected as food. Other possible factors affecting the feeding of cutthroat trout are mentioned.

Ecologists have been investigating the factors governing the feeding of stream trout for several years (Allan 1983). Trout have been assumed to be generalists or opportunists, feeding on invertebrates in relation to their abundance in the drift (Elliott 1973). One alternate hypothesis that has gained prominence is that of food selection by prey size. Prey size may work through reaction distance (Ware 1972, 1973), or merely through baseline availability, because a minimum length may exist below which trout cannot detect prey (Bisson 1978). The size hypothesis has been identified to play at least a partial role in the feeding of brown trout, *Salmo trutta* (Thomas 1964, Elliott 1967, Ringler 1979), eastern brook trout, *Salvelinus fontinalis* (Allan 1981), and rainbow trout, *Salmo gairdneri* (Bisson 1978). The objectives of the present study were to determine if food size selection by cutthroat trout occurs in a mountain stream in Idaho and if a linear relationship exists between the number of various food items in cutthroat trout stomachs and length of the trout. The hypotheses were that the mean length of food and abundance of food items in the stomach of a cutthroat trout will increase with trout length. The food habits of this species have not been extensively studied (Fleener 1952, McMasters 1970, Griffith 1974) even though this trout has a widespread distribution in the Intermountain West (Scott and Crossman 1973).

Study Area

Palisades Creek is a third order stream, draining the Palisades range of southeastern Idaho, and flowing into the South Fork of the Snake River. For late summer, maximum stream velocities of 100+ cm/sec, maximum depths of 1.5 m, and stream widths of 15 m are common. Riparian vegetation includes willows (*Salix* sp.), cottonwoods (*Populus* sp.), birch (*Betula* sp.), Douglas fir (*Pseudotseuga menziesii*), and lodgepole pine (*Pinus contorta*). In many areas of the stream, canyon walls extend to the stream margin, providing nearly continuous shading throughout the day, whereas other stretches flow through small meadows. Few typical pools exist, because riffle-runs, bank-runs and debris dams predominate.

Methods

Forty-eight cutthroat trout, ranging in length (head to tail fork) from 12.5 to 46 cm were collected by angling between 23 and 25 August 1983. Angling has been used by other researchers (Reed and Bear 1966, Hunt and Jones 1972, Tippets and Moyle 1978) and may be particularly well suited for high-gradient, fast-moving streams where collection by electroshocking is impaired. Trout length was measured at streamside, and stomachs were preserved in 70% ethyl alcohol for

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TABLE 1. Correlation analysis for the selected variables and fish length.

Variable	r	r^2	P	% occurrence
Total number prey	0.489	0.239	< 0.001	100
Number terrestrial	0.142	–	> 0.02	83
Number aquatic adults	0.377	0.142	< 0.005	73
Number aquatic larvae	0.027	–	> 0.50	100
Number C. stolonifera	0.241	–	> 0.05	50
Number E. doddsi	0.489	0.239	< 0.001	92
Number Formicidae	0.172	–	> 0.20	73
Mean length all food	0.381	0.145	< 0.005	–
Mean length aquatic larvae	0.472	0.223	< 0.001	–
Number taxa	0.342	0.117	< 0.01	–
Range of length	0.286	0.082	< 0.02	–

later analysis. All items in the stomachs were measured under a dissecting microscope and identified to the lowest taxonomic level practical (terrestrial animals other than Formicidae were lumped together, but most aquatic forms were taken to genus or species). To enable the use of correlation analysis, data were transformed to logarithmic scale prior to statistical analysis (Zar 1974).

RESULTS

Over 30 taxa, ranging in length from 2 to 70 mm, were recovered from stomachs of the 48 trout (see Appendix). The strong correlation for total number of prey and trout length (Table 1) suggests that overall food consumption is dependent on trout size. This is also true for consumption of *Ephemerella doddsi* larvae, the most frequently occurring aquatic insect larvae found in the stomachs of the cutthroat trout sampled. However, consumption of total number of organisms of terrestrial origin, number of berries from redstem dogwood (*Cornus stolonifera*), number of ants (Formicidae), and number of aquatic insect larvae were not related to trout size. Some of the berries from redstem dogwood did appear partially digested, indicating that trout may be gaining some nutritional value from them.

It is possible that correlation analysis was redundant for the number of ants and number of organisms of terrestrial origin and for the number of *E. doddsi* and number of aquatic insect larvae. Although no hidden relationship was detected for the ant component, the relationship between trout length and *E. doddsi* would have been missed had one relied solely on the aquatic larvae variable.

Mean length and the range of length (longest minus shortest) of aquatic insect larvae ingested by cutthroat trout were also related to trout length. As cutthroat trout from Palisades Creek grow, it appears that they rely on larger food, but still take smaller food items (Fig. 1). Cutthroat trout from Palisades Creek did not consume prey shorter than 2 mm, whereas almost 94% had a minimum prey length of at least 3 mm. With increasing trout length, the number of different food items increased. Apparently, as they grow, cutthroat trout in Palisades Creek do not shift entirely to larger prey or to a narrower range of taxa.

Since certain variables (e.g., number of aquatic larvae and number of organisms of terrestrial origin) were shown to be unrelated to trout length, one cannot automatically assume the positive relationships found for other variables and trout length are allometric, with the possible exception of total food item number. Since large prey were found in the stomachs of small trout, although infrequently, it is not possible to assume that the relationship between mean prey length and trout length is strictly a function of trout (mouth) size.

These observations are based on a small sample of trout, taken from only one season; consequently, it is difficult to extrapolate these findings to the same population during seasons having different benthic invertebrate abundances and diversities. More research into these variables appears warranted.

DISCUSSION

Prey size as a factor affecting the feeding of fish has been suggested for salmonids (Ware 1972) and strongly indicated in the

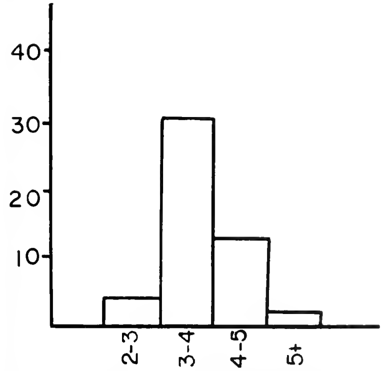

Fig. 1. Histogram of minimum lengths of food consumed and their frequency of occurrence in the 48 cutthroat trout stomachs sampled.

ecology of other fishes (e.g., *Lepomis* sp. in Werner and Hall 1974). Ware (1972), in laboratory experiments, has shown reaction distances by rainbow trout of lake origin to increase with increasing prey size. Ware (1973) included prey size in a model formed for predicting prey vulnerability to predation by rainbow trout, and he found the intensity of predation should closely parallel the change in prey size.

As shown, the mean length of food taken by cutthroat trout from Palisades Creek during the summer increased with trout length. Because small trout did have the ability to consume comparatively large prey, the question of why they don't take more of them arises. Smaller trout may spend too much energy in capturing, handling, and ingesting large food. If so, this would preclude them from taking great numbers of large prey, yet not entirely prevent an occasional large invertebrate from being taken. It may also be that trout are intimidated by large prey and avoid them. Large bodies may be representative of predators, and this may explain why there is a linear relationship between food size and trout size. A third possible cause could be social interaction within the trout population. Large trout may be dominant over smaller trout, enabling first choice of valuable food items (e.g., large prey) to be given to large individuals.

Ringler (1979) found brown trout in an artificial stream to consume small prey, even when larger prey were available. Increasing the size of prey and the assortment of prey types without reducing the range in prey length, as observed for cutthroat trout in the present study, may improve the energy gain for an individual fish. Overall energy expense should increase with body size; hence, large trout, especially drift feeders, would be at a disadvantage if they restricted their intake. Bisson (1978) postulates that smaller prey should at least repay the energy spent in their consumption by trout.

Prey lengths of about 2 mm have been suggested as minimum detection levels for rainbow trout, below which prey cannot be distinguished from other drifting material (Bisson 1978). The results of this study on cutthroat trout support this postulate. However, since lengths of members of the prey populations in Palisades Creek were not taken during the present study, it is difficult to speculate on the lowest possible lengths of invertebrates available. Benthic samples taken approximately two weeks earlier revealed large abundances of invertebrates of 1 to 3 mm sizes, indicating that smaller prey may have been present. This minimum length of detection hypothesis suggests that only prey larger than about 2 mm be used in estimating the available cutthroat trout food in a stream.

The strong correlation between the number of *E. doddsi* larvae and trout length is most interesting. This species is not a notable drifter in Palisades Creek (unpublished observations by author), and it may be possible that the majority of *E. doddsi* were taken from the stream bottom. If so, then as cutthroat trout get larger, they tend to feed more from the stream bottom than the drift. Tippets and Moyle (1979) observed a similar trend in the feeding of rainbow trout from the McCloud River, because larger trout contained food items more common to the benthos than the drift.

Simpson and Wallace (1978) suggest that terrestrial organisms form a major portion of the diets of cutthroat trout in Idaho. McMasters (1970) sampled cutthroat trout during July from a similar size stream in southeastern Idaho and found 33% to have fed upon terrestrial organisms. Of the trout sampled in the present study, 83% fed upon terrestrial organisms (Table 1). It is also interesting that so many trout (73%) had taken ants. Jenkins (1969) made use of marked ants in an experimental manipulation of drifting food and the feeding activities of rainbow and brown trout. The use of a prey organism in such manipulative studies should be predicated upon its natural occurrence in the diet of the fish being studied. Results from the present study indicate that ants are a common item in cutthroat trout diets; hence, adaptation of Jenkins's (1969) study to cutthroat trout should be feasible.

The occurrence of berries from redstem dogwood (*Cornus stolonifera*) in the cutthroat trout stomachs indicates an omnivorous trait of this species. Since half the trout sampled contained this food item, it seems easy to conclude that a generalist attitude exists toward feeding by cutthroat trout. However, optimal foraging theory (Krebs 1978) indicates that it may be more advantageous for trout to consume the vegetable than the invertebrate portion of their diet, depending upon caloric or nutrient value of the respective items and the energy spent in obtaining them. Since the number of berries from redstem dogwood apparently was not related to trout size, it is not reasonable to say that larger fish may benefit more than smaller fish by feeding on this item.

The data from the present study indicates that food size selection is occurring in a population of stream cutthroat trout. Size selection may be an important mechanism in the feeding of this species; however, it must be noted that, although the r values were significant—in some cases $p < 0.001$—the r^2 values were relatively low (0.145 for mean length of all prey and 0.222 for mean length of aquatic larvae). This suggests that other factors, possibly of equal importance, are operating on this interaction. For instance, Otto and Sjorstrom (1984) suggest morphology of stonefly larvae and the role of cerci and antennae in modifying their predator-prey relationship with first-year brown trout. Irvine and Northcotte (1984) observed rainbow trout fry in artificial stream channels to feed significantly more from groups of live *Simulium* sp. larvae than dead *Simulium* sp. larvae, a situation attributed to some invertebrate behavior that could not be exhibited by dead *Simulium* sp.. An interaction may also exist among prey size, morphology, and behavior.

ACKNOWLEDGMENTS

Field assistance was generously provided by Dennis E. and Rhoda T. Skinner, and laboratory work was aided by Rhoda T. and Kimberely A. Skinner. Dr. James D. McIver identified the Formicidae and Dr. Karl E. Holte identified the *Cornus stolonifera*; both are faculty at Idaho State University. Constructive criticism of the manuscript was provided by Drs. G. Wayne Minshall of Idaho State University and James R. Barnes of Brigham Young University.

APPENDIX

Assortment of food items found in the stomachs of 48 cutthroat trout taken from Palisades Creek, Bonneville County, Idaho.

- Ephemeroptera
  - Baetidae
    - *Baetis* sp.
      - larvae and adult
  - Siphlonuridae
    - *Ameletus* sp.
  - Heptageniidae
    - *Epeorus* sp.
    - *Cinygmula* sp.
  - Ephemerellidae
    - *Ephemerella coloradensis*
    - *E. doddsi*
      - larvae and emerging adults
    - *E. inermis*
- Plecoptera
  - Perlidae
    - *Acroneuria* sp.
  - Perlodidae
    - *Megarcys* sp.
    - *Skwala* sp.
      - larvae and adult
  - Nemouridae
    - *Zapada* sp.
  - Chloroperlidae
- Trichoptera
  - Limnephilidae
    - *Neothremma* sp.
  - Glossossomatidae
    - *Glossossoma* sp.
  - Ryacophilidae
    - *Ryacophila* sp.
  - Hydropsychidae
    - *Arctopsyche* sp.

Odonata
  Gomphidae

Diptera
  Tipulidae
    Antocha sp.
    Tipula sp.
    Dicranota sp.

  Simulidae
    larvae and pupae

  Chironomidae

Coleoptera
  Elmidae
    larvae and adult

  Dytiscidae

Terrestrial
  Formicidae
  Hymenoptera
  Diptera
  others

Terrestrial vegetation
  Cornus stolonifera

Fishes
  Cottidae
    Cottus bairdi

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ASPECTS OF THE BIOLOGY OF THE FLATHEAD CHUB (*HYBOPSIS GRACILIS*) IN MONTANA

William Gould[1]

ABSTRACT.— Mature flathead chubs (*Hybopsis gracilis*) were present in mid-July and mid-August collections from the Musselshell River, Montana. The estimated numbers of mature eggs present in eight females were 360–753 per female. The smallest mature female and male collected were 113 and 123 mm in total length, respectively. The male to female sex ratio in collections was about 1:1. Only small differences were detected among the length-weight relationships of males and females and samples taken from various seasons and localities in Montana. Observations on size groups, fish associates, and habitat characteristics of flathead chubs are presented.

The life histories of several species of *Hybopsis* are poorly known (Lee et al. 1980). One of these is the flathead chub, *Hybopsis gracilis* (Cross 1967, McPhail and Lindsey 1970, Brown 1971, Scott and Crossman 1973, Pflieger 1975 and Lee et al. 1980). Most of the published information on the natural history of this species in the United States is contained in a systematic study by Olund and Cross (1961) and a bionomics study by Martyn and Schmulbach (1978). This report presents additional biological information on the flathead chub.

DESCRIPTION OF THE STUDY SITE

The collection site was on the Musselshell River (T8N R25E S22) in central Montana. At this location the river is a plains stream having an elevation of about 971 m and a substrate of sand- and silt-covered pebbles.

Records taken at the collection site over a four-year period (USGS 1979, 1980, 1981, 1982), showed the pH range was 7.7–8.5, with 90% of the measurements being 8.0 or greater. Average monthly values were 100–1700 mg/l for suspended solids, 240–830 mg/l (as $CaCO_3$) for alkalinities, and 4–31 m^3/s for flows. Flows were usually highest in May or June and lowest in August or September. Water temperatures ranged from 0.0 to 23.0 C, with lows occurring from December through February and annual highs from June through August. Flathead chub typically inhabit fluctuating streams with alkaline, turbid waters (Olund and Cross 1961, Brown 1971).

METHODS AND MATERIALS

Specimens were collected with an 11.0 × 3.7 m seine having an 8-mm-square mesh and preserved in 10% formalin. In addition, collections in the Vertebrate Museum of Montana State University (MSU) were examined. The total length (TL) of each specimen was measured to the nearest 1 mm; standard length (SL) was derived from TL in the linear regression SL = 0.2665 + 0.7863 TL, which was obtained from measurements of 65 specimens 70–134 mm TL. The weight of each blot-dried specimen was determined to the nearest 0.01 g on a Mettler Model H16 balance. The sex of each fish was determined by examination of the gonads under a dissecting microscope. Egg size was measured with an ocular scale calibrated with a stage micrometer. The total number of mature eggs in a fish was estimated by using:

$$M_T = \frac{W_T M_S}{W_S}$$

where M_T = the total number of mature eggs in the fish's ovaries, W_T = the total weight of the fish's ovaries, M_S = the number of mature eggs in the sample of the ovary, and W_S = the weight of the sample of

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TABLE 1. The average diameter (mm) of 10 of the largest eggs in 58 specimens of *Hybopsis gracilis* collected from the Musselshell River, Montana.

Collection date	Total length of fish (mm)	Average egg diameter in mm (numbers of specimens)
31 Mar 81	71–123	0.2(12), 0.3(2) 0.5(1), 0.7(7) 0.8(2)
19 Jul 83	113–155	0.2(4), 0.3(1) 0.4(2), 0.5(3) 0.6(2), 0.8(1) 1.0(1), 1.1(3) 1.2(1), 1.3(1) 1.4(1)
15 Aug 83	117–160	0.2(1), 0.3(1) 0.4(3), 0.5(1) 0.6(3), 1.3(1)
11 Nov 82	114–134	0.2(1), 0.6(2) 0.7(1)

the ovary. Two estimates were made of the M_T in each fish. The length-weight relationships in specimens were determined by using $\log_{10} w = \log a + b (\log_{10} L)$, where w = blot-dried weight in grams, L = total length in millimeters, and a and b were constants derived from the data.

RESULTS

Reproductive Condition of Females

Fifty-eight females were collected prior to, during, and after the presumptive spawning season for an evaluation of their reproductive condition (Table 1). Females with the largest eggs (1.0–1.4 mm in diameter) were found in July and August 1983 collections. These specimens were considered mature because of the large size and orange color of the eggs. Examination of 23 females from eight collections at MSU showed that females with eggs of a comparable size were present only in July samples; none were present in August and September collections. The average daily maximum and minimum water temperatures associated with the collection of mature females in this study were 23 and 18 C in July and 25 and 21 C during the first 15 days in August (unpublished data, Montana Department of Fish, Wildlife, and Parks).

The estimated average number of mature eggs (1.0 mm or greater in diameter) in the eight mature specimens collected during this study was about 491 (Table 2). There was no trend for larger females to have more eggs than smaller ones within the size range treated (r = 0.15). The smallest mature female collected (Table 2) was 113 mm TL (89 mm SL). The smallest mature female found in nine museum collections of MSU was 112 mm TL (88 mm SL).

The ovaries of the eight mature fish in Table 2 weighed 0.59–0.99 g and were 2.3–5.9% of total body weights. In the 22 immature females collected concurrently with the mature fish in this study, ovary weights were 0.10–0.71 g and 0.5–1.8% of total body weights.

Reproductive Condition of Males

Milt was stripped from 13 males taken in July and August 1983 (Table 3). The smallest ripe male was 123 mm TL (97 mm SL). However, some males larger than this were not ripe in August.

TABLE 2. Estimated numbers of mature eggs in eight *Hybopsis gracilis* collected from the Musselshell River, Montana.

Collection date	Total length of fish (mm)	Total weight of fish (g)	Estimated total numbers of mature eggs from two samples	Average diameter of 10 mature eggs (mm)
19 Jul 83	113	12.99	442/293	1.0
	120	16.72	453/521	1.1
	122	17.55	508/524	1.1
	124	18.50	539/446	1.3
	130	20.04	483/441	1.2
	136	22.95	638/633	1.1
	155	36.02	753/360	1.4
15 Aug 83	160	37.72	453/372	1.3

Table 3. The reproductive condition of 18 male *Hybopsis gracilis* collected from the Musselshell River, Montana. Numbers of specimens in parentheses.

Collection date	Total length of males in mm	
	Ripe	Not ripe
19 Jul 83	123, 128, 129 132, 133, 143	–
15 Aug 83	127, 132, 135 (2), 136 (2), 146	122, 124, 127 132, 140

Sex Ratio

The male to female sex ratios of specimens examined were not significantly different from 1:1 (Table 4). This ratio did not change significantly with increases in the size of specimens examined.

Length-Weight Relationships

The length-weight relationships of a sample of males and females taken 31 March 1981 were calculated separately (Table 5). An F test of the slope and intercept showed the two regressions were not statistically different ($P=0.66$), so length-weight data from all fish were combined.

The length-weight relationships of flathead chubs collected during different seasons and from different localities in Montana were similar (Table 5). The relationship was also similar among different size groups.

Fish Associates

Fish captured with *H. gracilis* in the Musselshell River were *Couesius plumbeus*, *Cyprinus carpio*, *Hybognathus argyritis*, *H. placitus*, *Carpiodes carpio*, *Catostomus commersoni*, *C. platyrhynchus*, *Moxostoma macrolepidotum*, *Micropterus dolomieui*, and *Noturus flavus*. *Hybognathus placitus* and *C. commersoni* were reported previously by Olund and Cross (1961) as associates of flathead chubs.

Age and Growth

The length-frequency analysis of 305 specimens 29–127 mm TL collected from the Musselshell River 31 March 1981 indicated three size groups were present. The approximate average total length of specimens in each size group was 43 ($N=116$), 81 ($N=149$), and 116 ($N=40$) mm. Attempts to verify these size groups as age groups by examination of scales, opercula, and vertebrae proved unsuccessful.

DISCUSSION

Most of the characteristics studied in flathead chubs from Montana were similar to those reported for the species in the midwestern U.S. The July and August spawning season for flathead chubs in Montana was the same as has been reported for this species in Kansas (Cross 1967) and Iowa (Martyn and Schmulbach 1978), but it is more extended than the July season suggested by Brown (1971) and reported by Bishop (1975) for Montana and Peace River, Canada specimens. The water temperatures recorded during the spawning season of the flathead chub in Montana were virtually the same as those

Table 4. The numbers of males and females in samples of *Hybopsis gracilis* from Montana.

Sources of specimens	Total length (mm)	Sample size	Number of males	Number of females	Calculate X^2
Musselshell River, this study	71–171	75	38	37	0.007
Collections in MSU museum	79–154	53	25	28	0.085
Composite of above sources	71–171	128	63	65	0.016

Tabular X^2 = 3.84 at P = 0.05 with one degree of freedom.

TABLE 5. The length-weight relationships in collections of *Hybopsis gracilis* from Montana.

Collection locations and dates	Sample size	Total length (mm)	Intercept	Slope	Correlation coefficient (r)
Musselshell River,					
3 Mar 81	27 (males)	77–127	-5.299	3.082	0.98
3 Mar 81	23 (females)	71–123	-5.472	3.203	0.99
3 Mar 81	80°	30–127	-5.275	3.105	0.99
11 Mar 82	33	54–159	-4.991	2.936	0.99
19 Jul 83	24	62–155	-4.924	2.958	0.99
Five other locations,					
25 Jul 48 6 Jul 57 15 Jul 57 22 Jul 65 23 Jul 66	36	56–187	-5.395	3.151	0.99

°Includes the 50 specimens listed above

taken periodically during their breeding season in Iowa (Martyn and Schmulbach 1978). Other chubs also spawn when water temperatures reach about 25 C (Lee et al. 1980).

The minimum lengths of sexually mature flathead chubs found during this study were similar to those reported from Montana (Brown 1971), Kansas (Olund and Cross 1961), and Iowa (Martyn and Schmulbach 1978). The length-weight relationships of flathead chubs in Montana and Iowa (Martyn and Schmulbach 1978) also were alike.

The length groups of Montana flathead chub found during this study approximated the length at ages reported by Brown (1971) for an undetermined number of Montana conspecifics. If the length groups in this study represent age groups, it means Montana flathead chub grew more slowly than Iowa specimens (Martyn and Schmulbach 1978) during the first 3 years of life, respectively. This would also signify that Montana fish generally become sexually mature at age 3, but those in Iowa (Martyn and Schmulbach 1978) and Canada (Bishop 1975) mature at ages 2 and 4, respectively.

Olund and Cross (1961) and Cross (1976) reported the presence of minute tubercles on male flathead chubs and associated this with spawning activity. However, small tubercles were found on males and females as small as 78 (62 mm SL) and 85 mm TL (67 mm SL) during this study and were visible on representatives of both sexes as early as March and as late as November. Therefore, tubercles were also present on immature fish, and their existance was not limited to the known spawning season.

The maximum ovary weights as percents of total body weights of mature Montana flathead chubs were only about 60% of those found in Iowa flathead chubs (Martyn and Schmulbach 1978). This may mean Montana fish have fewer or smaller eggs.

The basic information available on the food habits, age and growth, and fecundity of the flathead chubs is fragmentary and inadequate. Information on the seasonal movements and habitat usage, spawning behavior, embryology, and interactions with other fish species appears to be nonexistent. Virtually all the limited biological information available on this species has been obtained from work on populations near the center of its range. Studies undertaken from near the extremes of the range of this species, the mouth of the Mississippi River (Douglas 1974) and the delta of the Mackenzie River (Scott and Crossman 1973), should show the maximum variations in the life history parameters of the flathead chub.

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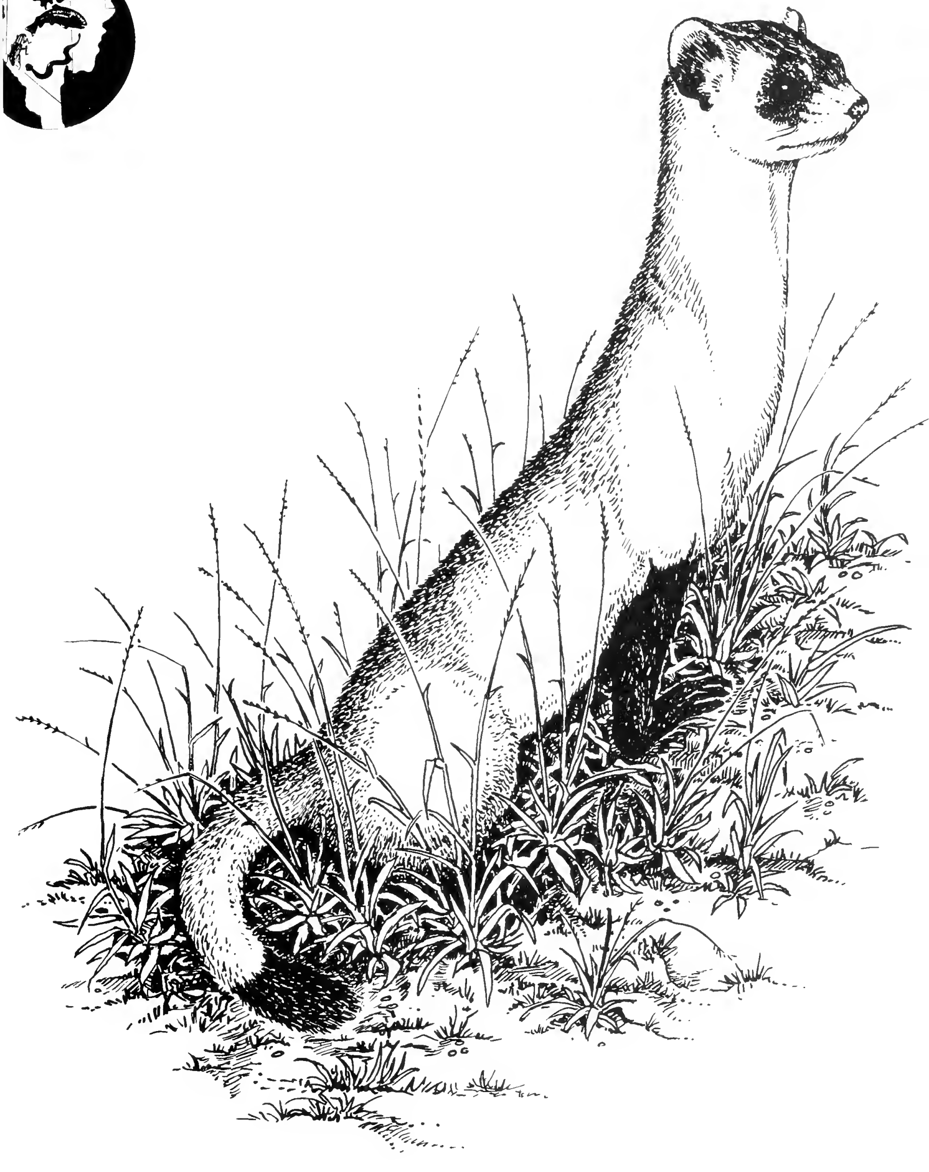

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QUATERNARY PALEONTOLOGY AND PALEOECOLOGY OF CRYSTAL BALL CAVE, MILLARD COUNTY, UTAH: WITH EMPHASIS ON MAMMALS AND DESCRIPTION OF A NEW SPECIES OF FOSSIL SKUNK

Timothy H. Heaton[1]

ABSTRACT.— Crystal Ball Cave is located in a small outlier of the Snake Range in Snake Valley 1.7 km (1 mile) west of Lake Bonneville at its highest level. Original vertebrate skeletal material (mostly mammalian) has been found in shallow dry dust 61 m (200 feet) inside the cave. Radiocarbon dates show that fossils have been accumulating since at least 23,000 Y.B.P. It appears that wood rats and possibly small carnivores transported the fossils into the cave because only the smallest elements of large mammals are represented.

The fossil assemblage represents a much more boreal community than the present local fauna. Fish, *Ondatra zibethicus*, and *Mustela* cf. *vison*, which require perennial water, were recovered, as were *Ochotona princeps*, *Lepus* cf. *americana*, *Microtus* cf. *pennsylvanicus*, *Vulpes vulpes*, and *Martes americana*, which have also been extirpated from the Snake Range. *Marmota flaviventris*, *Neotoma cinerea*, cf. *Cervus elaphus*, and *Ovis canadensis* were recovered but now occur only at higher elevations in the range. Extinct taxa recovered are *Smilodon* cf. *fatalis*, *Equus* species, *Camelops* cf. *hesternus*, *Hemiauchenia* cf. *macrocephala*, cf. *Symbos cavifrons*, and a new species of *Brachyprotoma*, herein named *B. brevimala*. This is the first recovery of *Brachyprotoma* from the western United States.

Crystal Ball Cave is 4.8 km (3 miles) northwest of the town of Gandy, Utah, and 0.9 km (0.6 miles) east of the Utah-Nevada border (Sec. 30, T. 15 S, R. 19 W, Salt Lake Base Line and Meridian) in the northeast side of Gandy Mountain, a small outlier on the northeastern edge of the Snake Range (Figs. 1 and 2). The cave is at an elevation of 1760 m (5775 feet), 195 m (644 feet) above Lake Bonneville at its highest level (see Currey 1982, Gilbert 1890) and has about 150 m (500 feet) of passage and a floor area of about 1860 square m (20,000 square feet). Calcite crystals and speleothems cover most of the cave walls and floors, but some shallow sediments are present that contain locally abundant unaltered vertebrate fossils.

It is uncertain if native Americans knew of Crystal Ball Cave, for no ancient human artifacts were found in this study. The cave was discovered by the late George Sims of Gandy in February 1956. He found the original 1-m (3-foot) diameter entrance that leads into a large chamber (Fig. 3). The original east entrance was enlarged, the north entrance was blasted out through a soil-filled passage at the other end of the cave (Fig. 3), and other improvements were made by Cecil R. and Jerald C. Bates of Gandy, Utah, and Thomas E. Sims of Elko, Nevada (J. C. Bates 1983, pers. comm.).

Herbert H. Gerisch and Robert Patterson collected bones from site 1 (Fig. 3) in 1956 that they donated to the Los Angeles County Mu-

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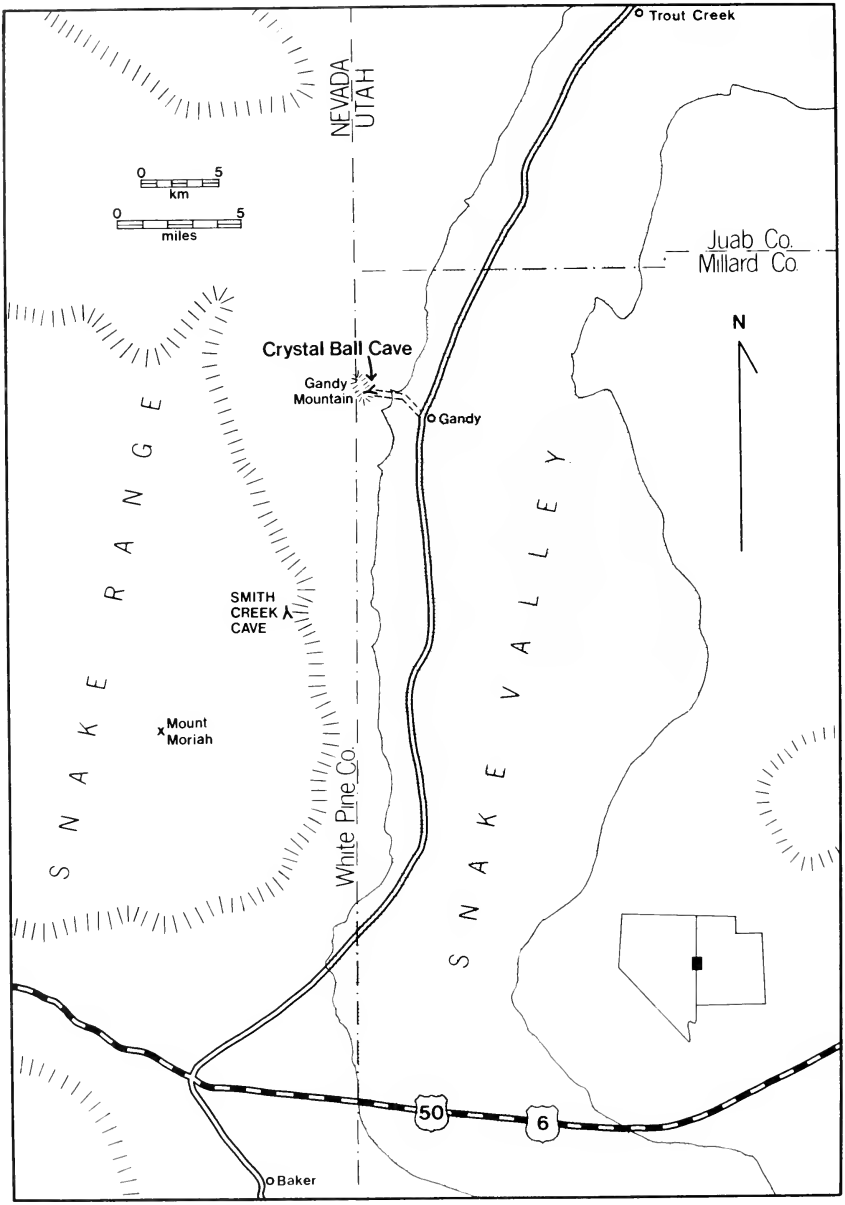

Fig. 1. Index map showing the location of Crystal Ball Cave and other features of the Snake Range and Snake Valley. The stippled area represents the extent of Lake Bonneville at the Bonneville Level.

Fig. 2. Looking west at Gandy Mountain. The arrow marks the location of Crystal Ball Cave.

seum (H. H. Gerisch 1983, pers. comm.). Later Michael Stokes of the Los Angeles County Museum collected additional specimens from site 1. These early collections consisted of float only and included bones of extinct horses and camels. On at least one of these early expeditions, some specimens were also collected from Gandy Mountain Cave, a smaller cave that lies about 0.4 km ($\frac{1}{4}$ mile) south of and 30 m (100 feet) higher than Crystal Ball Cave. Specimens from these two caves are indistinguishable in the Los Angeles County Museum collection because the cave in which each specimen was recovered was not recorded. I dug several test pits in Gandy Mountain Cave in 1981 and found preservation to be poor and specimens to be few and probably all Recent. So, although some specimens were collected from Gandy Mountain Cave, they are not considered in this study, except some which may be among the Los Angeles County Museum collection.

The first extensive collecting in Crystal Ball Cave was done in 1977 by Wade E. Miller and his students from Brigham Young University, who used fine screens to obtain thousands of specimens (all from site 1). Miller (1982) described this investigation and listed the genera identified in a report on vertebrate fossils from Lake Bonneville deposits. Miller and I operated similar collecting projects in 1981 and 1982 (sites 1, 2, and 3), and I wrote a preliminary report on this study (Heaton 1984). Crystal Ball Cave is Los Angeles County Museum locality 4534 and Brigham Young University vertebrate paleontology locality 772; the specimens from the cave are catalogued as LACM 123655-123711 and BYUVP 5300-8888, 8911-8933. Taxa recovered are listed in Table 1.

The Crystal Ball Cave assemblage is the first Late Wisconsinan age fauna to be described from the state of Utah. Although Utah has extensive Pleistocene deposits from Lake Bonneville, surprisingly few vertebrate fossils have been recovered from them (Miller 1982). The only other Pleistocene assemblage that has been described from Utah is the Silver Creek fauna of north central Utah, 22 km (14 miles) east of and 360 m (1200 feet) above Lake

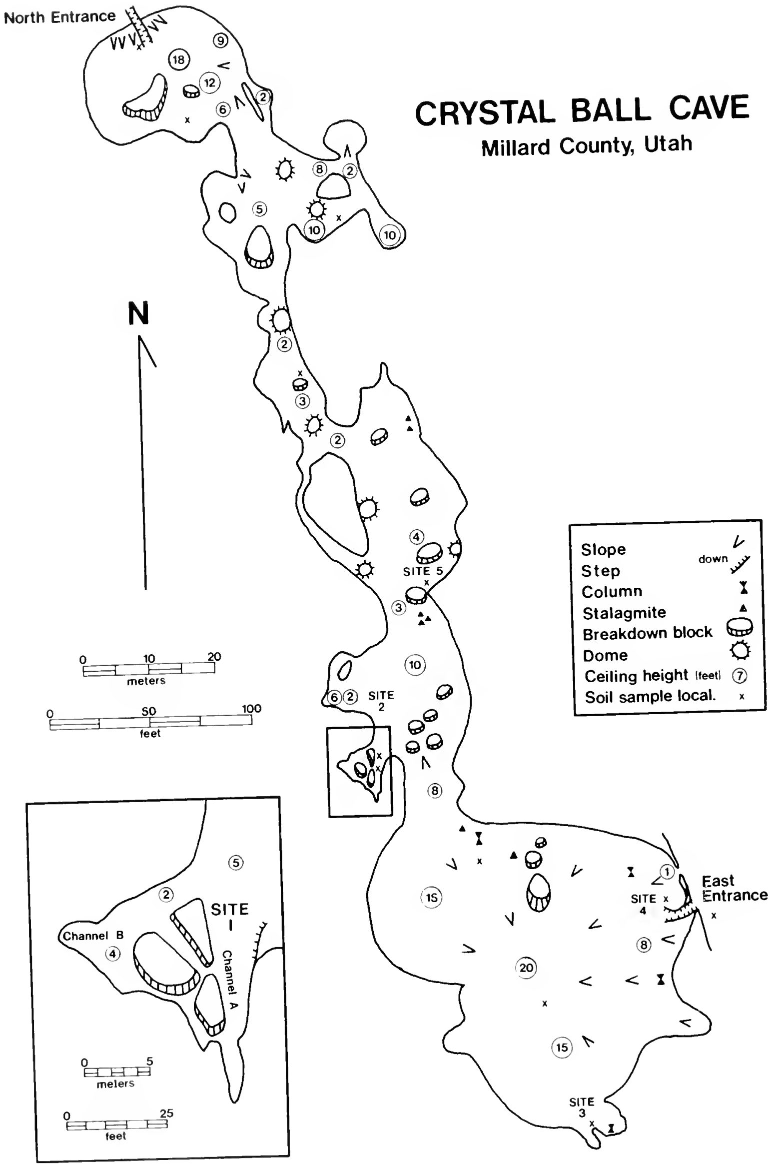

Fig. 3. Planimetric map of Crystal Ball Cave (modified from Halliday 1957) showing the location of fossil sites.

TABLE 1. List of taxa recovered from Crystal Ball Cave.

Taxa recovered	Common name	Minimum number of individuals, including referred material	Current range and status		
Kingdom Plantae					
Division Tracheophyta					
Class Gymnospermae					
Subclass Gneteae					
Family Ephedraceae					
Ephedra cf. *viridis*	Mormon tea	1	*		3
Class Angiospermae					
Subclass Dicotyledoneae					
Family Asteraceae					
Chrysothamnus sp.	rabbitbrush	1	*		3
Haplopappus nanus	goldenweed	1	*		3
Perityle stansburii	rockdaisy	1	*		3
Family Brassicaceae	mustard	1	*		3
Family Cactaceae					
Opuntia sp.	cactus	1	*		3
Family Caprifoliaceae					
Symphoricarpos cf. *longiflorus*	snowberry	1	*		3
Family Poaceae					
cf. *Elymus*	wildrye	1	*		3
cf. *Panicum*	panicgrass	1	*		3
Kingdom Animalia					
Phylum Mollusca					
Class Gastropoda					
Order Pulmonata					
Family Helicidae					
Oreohelix strigosa	land snail	9	*		1
Phylum Arthropoda					
Class Crustacea					
Order Isopoda					
Family ? Armadillidae	pill bug	1	*		3
Class Insecta					
Order Coleoptera					
Family Scarabaeidae					
Aphodius distinctus	dung beetle	1	i		3
Phylum Chordata					
Class Osteichthyes					
Infraclass Teleosti	fish	3	*	×	3
Class Reptilia					
Order Squamata	lizards and snakes	67	*	×	3
Class Aves	birds	15	*	×	3
Class Mammalia					
Order Insectivora					
Family Soricidae					
Sorex sp.	shrew	14	*		3
Order Chiroptera					
Family Vespertilionidae					
Myotis sp.	mouse-eared bat	3	*		2
? *Plecotus townsendii*	Townsend's big-eared bat	0	*	+	3
Antrozous pallidus	pallid bat (large bat)	2	*		2

Key to symbols:
* Taxon has been reported living in the Snake Range in Recent times by Durrant (1952) and/or Hall (1981).
i Taxon lives in the Snake Range but was introduced by man in Recent times.
e Taxon has been extirpated from the Snake Range.
† Taxon is extinct.
\+ Taxon has been captured live in Crystal Ball Cave by author.
× Taxon has been reported in Snake Valley near Gandy by J. C. Bates (1983, pers. comm., 1984, pers. comm.).
0 Taxon does not presently live in the Snake Range or Snake Valley.
1 Taxon lives in the Snake Range but rarely if ever comes as low as Snake Valley.
2 Taxon lives in the Snake Range and occasionally comes into Snake Valley.
3 Taxon presently lives in Snake Valley around Gandy.

TABLE 1 continued.

Taxa recovered	Common name	Minimum number of individuals, including referred material	Current range and status		
Order Lagomorpha					
Family Ochotonidae					
Ochotona princeps	pika	15	e		0
Family Leporidae					
Sylvilagus idahoensis	pigmy rabbit	3	*		3
Sylvilagus nuttallii	Nuttall's cottontail	4	*	×	3
Lepus cf. *americanus*	snowshoe rabbit	1	e		0
Lepus townsendii	white-tailed jackrabbit	10	*		1
Lepus californicus	black-tailed jackrabbit	1	*	×	3
Order Rodentia					
Family Sciuridae					
Marmota flaviventris	yellow-bellied marmot	41	*		1
Spermophilus townsendii	Townsend's ground squirrel	288	*	×	3
Ammospermophilus cf. *leucurus*	white-tailed antelope squirrel	2	*		3
Eutamius minimus	least chipmunk	4	*	×	3
Eutamius dorsalis	cliff chipmunk	4	*	×	3
Family Geomyidae					
Thomomys umbrinus	southern pocket gopher	9	*		3
Family Heteromyidae					
Perognathus cf. *formosus*	long-tailed pocket mouse	2	*		3
Microdipodops megacephalus	dark kangaroo mouse	7	*		3
Dipodomys microps	chisel-toothed kangaroo rat	5	*		3
Family Cricetidae					
Peromyscus maniculatus	deer mouse	2	*	+	3
Peromyscus cf. *crinitus*	canyon mouse	2	*		3
Peromyscus cf. *truei*	pinion mouse	1	*		3
Neotoma lepida	desert wood rat	3	*	+	3
Neotoma cinerea	bushy-tailed wood rat	57	*		1
Ondatra zibethicus	muskrat	2	e		0
Microtus cf. *longicaudus*	long-tailed vole	15	*		3
Microtus cf. *montanus*	montane vole	2	*		2
Microtus cf. *pennsylvanicus*	meadow vole	1	e		0
Lagurus curtatus	sagebrush vole	28	*		3
Order Carnivora					
Family Canidae					
Canis cf. *latrans*	coyote	1	*	×	3
Canis cf. *lupus*	gray wolf	1	*		3
Vulpes vulpes	red fox	3	e		0
Vulpes velox	kit fox	2	*	×	3
Family Mustelidae					
Mustela cf. *frenata*	long-tailed weasel	3	*	×	3
Mustela cf. *vison*	mink	1	e		0
Martes americana	marten	2	e		0
Brachyprotoma brevimala, sp. nov.	western short-faced skunk	1	†		0
Family Felidae					
Smilodon cf. *fatalis*	saber-tooth cat	1	†		0
Felis concolor	mountain lion	1	*	×	2
Lynx cf. *rufus*	bobcat	1	*	×	3

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TABLE 1 continued.

Taxa recovered	Common name	Minimum number of individuals, including referred material	Current range and status
Order Perissodactyla			
Family Equidae			
Equus cf. *scotti*	large horse	2	† 0
Equus ? *conversidens*	small horse	4	† 0
Order Artiodactyla			
Family Camelidae			
Camelops cf. *hesternus*	camel	2	† 0
Hemiauchenia cf. *macrocephala*	llama	1	† 0
Family Cervidae			
cf. *Cervus elaphus*	wapiti	1	* 1
Odocoileus hemionus	mule deer	11	* × 3
Family Bovidae			
Antilocapra americana	pronghorn	1	* × 3
Ovis canadensis	bighorn sheep	1	* × 2
Ovis cf. *aries*	domestic sheep	1	i × 3
cf. *Symbos cavifrons*	musk ox	1	† 0

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Bonneville's highest level and of Late Sangamon to Early Wisconsinan age (Miller 1976).

The nearest described Pleistocene vertebrate localities are four shelters located in Smith Creek Canyon, White Pine County, Nevada, 14 km (9 miles) south of Crystal Ball Cave. New species of mountain goat (Stock 1936), eagle (Howard 1935), and gigantic vulture (Howard 1952) were described from Smith Creek Cave, the primary site. Literature on the Smith Creek Canyon sites includes a description of the avifauna by Howard (1952), the micromammalian fauna by Goodrich (1965), the herpetofauna by Brattstrom (1976), the whole fossil assemblage by Miller (1979) and Mead et al. (1982), and the archaeology by Bryan (1979), Harrington (1934), and others. Although the Crystal Ball Cave fauna is chronologically and geographically close to that of Smith Creek Canyon, it differs in having its fossils deep in the cave, and this has resulted in significant differences between these assemblages. Crystal Ball Cave, for example, has more abundant mammal fossils but less abundant bird fossils than the Smith Creek Canyon sites.

The Crystal Ball Cave assemblage contains only small bones with a maximum length of about 10 cm and maximum weight of about 50 grams. Since only the smallest elements of the large species, which have rarely been considered in other studies, are represented, some problems exist in identifying them. The assemblage, however, is very large and is important because few assemblages of Late Pleistocene age have been reported from the region. The size of this assemblage and the time restraints upon the project have limited the depth to which each taxon could be studied. For taxa with large numbers of specimens, only the best specimens were considered. Additional work could turn up more species, and statistical studies on the more abundant taxa could yield much additional information.

GEOLOGY OF THE CAVE

The Snake Range is a north-south-trending Basin and Range horst composed of Early Paleozoic rocks. Gandy Mountain is an outlier of this range (Gilbert 1890, Nelson 1966). The cave lies in unnamed Middle Cambrian limestone on the upper plate of the Snake Range Thrust Fault, which is exposed at the north and south ends of Gandy Mountain (Nelson 1966). The massive beds around the cave strike N35W and dip 20NE (Halliday 1957), following the local trend throughout Gandy Mountain (Nelson 1966). The limestone is cavernous and contains many small solution cavities, in addition to Crystal Ball and Gandy Mountain caves.

I have recognized four distinct stages of the cave's history: (1) a period of dissolution of limestone to form the cave; (2) a period of precipitation forming a layer of large calcite crystals ("nail head" spar) up to 0.3 m (1 foot) thick on the cave walls, ceiling, and floor; (3) a period of partial dissolution of these crystals in the upper portions of the cave, the appearance of joints that cut the large calcite crystals, and the dislodging of breakdown from the ceiling of the large entrance room; and (4) the formation of vadose calcite speleothems and influx of sediment and fossils from outside the cave.

The beginning of stage 1, the dissolution of the cave, is of uncertain date. Davis (1930) demonstrated that limestone dissolution to form caves occurs predominantly in a thin zone just below the water table, which is rich in carbon dioxide from groundwater percolating down from the surface. Once it reaches the water table, this groundwater dissolves the rock as it moves very slowly down the water table slope (Davies 1960). This appears to be the case in Crystal Ball Cave, since no scalloped or stream-cut passages are present to suggest the presence of fast-moving water expected in an above-water table origin (Malott 1938, Myers 1969). The cave tends to parallel the strike of the beds and is relatively horizontal, as would be expected if the cave were formed at the water table. Green (1961) cited evidence that some caves in western Utah predate the tilting associated with the Basin and Range uplift. The fact that Crystal Ball Cave is roughly horizontal and parallel to the strike of the beds suggests that it postdates this tilting. But, since the cave is high in a small, isolated hill, considerable uplift and/or erosion must have taken place since the cave was at the water table. The cave does not parallel the present land surface as the water table tends to do (Myers 1969), and this further suggests that much overburden has been removed since the original dissolution of the cave.

Stage 2, the precipitation of large calcite crystals, represents a different groundwater environment than the preceding dissolutional stage. It is generally agreed that such "nail head" spar forms in still, calcite-saturated water where nucleation centers are free to grow into large euhedral crystals (Hill 1976). This shift from dissolution to precipitation does not necessarily represent a significant change in the level of the water table, but it does represent the drastic reduction in the carbon dioxide content of the groundwater necessary for calcite precipitation (Moore and Nicholas 1964). Several vertical cavities (domes) extend upward into the cave ceiling, and these predate the calcite precipitation because they are partly filled by it. Moore and Nicholas (1964) cited evidence that such domes form late in cave dissolution and provide more direct water and air connections to the surface. Myers (1969) stated that they are of vadose (above water table) origin and caused by vertical seepage. Perhaps the formation of these domes allowed gas exchange between the groundwater in the cave and the surface, permitting carbon dioxide to escape and calcite to be precipitated.

Stage 3 includes several events that are not chronologically separable. Some of the calcite crystals in the roof of the cave are completely dissolved, and locally some of the limestone bedrock underneath it is also. This is especially evident in the aforementioned domes. Joints and breakdown, both of which cut the previously formed calcite crystals, probably represent one or several earthquakes. If any uplift postdates the cave's origin, it probably occurred during this stage. These cracks and breakdown blocks were later filled and covered by the speleothems of stage 4, showing their chronologic relationship.

Stage 4 postdates the loss of voluminous standing water in the cave and the opening of entrances large enough to allow considerable gas exchange and sediment into the cave. Vadose speleothems such as the stalactites, columns, and rimstone pools found in Crystal Ball Cave form subaerially in caves having enough gas exchange with the surface to allow carbon dioxide to escape from the dripping groundwater (Moore and Nicholas 1964). Near the east entrance of the cave some small columns have formed upon and been partly covered by sediment coming in from the entrance, showing the concurrence of these events. The vertebrate material under study entered the cave during stage 4, when cave openings were sufficiently large to allow their entry and dry conditions allowed their preservation; therefore cave stages 1 through 3 predate the oldest fossils.

Twelve sediment samples were collected at sites throughout the cave and screened to determine the degree of sorting. All samples are poorly sorted, but samples farthest from known entrances tend to have a higher percentage of fine particles. Particles under 0.061 mm (0.0024 inch) in diameter make up over half the weight percent of three such samples. Samples were placed in hydrochloric acid to remove all calcite. Sediment from site 1 (Fig. 3) is composed of about 80% calcite and 20% very fine but poorly sorted clastic grains, namely quartz, mica, and an unidentified ferromagnesian mineral. Larger clastic grains were found in samples closer to each entrance and comprised greater portions of the sediment.

The calcite portion of the sediment is composed of both crystal fragments, probably derived from broken "nail-head" spar, and cryptocrystalline calichelike crust associated with clastic fragments, almost certainly precipitated in the cave. The clastic fragments could have been washed in, blown in, brought in by animals, released from the cave walls as impurities in the limestone, or a combination of these factors. The sediments at site 1 show no sign of ever having been wet except in some areas where they have been cemented with calcite. But water does run in through the east entrance during storms, filling the large entrance chamber with mud. Wind gusts can be quite strong through the cave during storms, but only because the north entrance was artificially opened. The importance of these factors is difficult to determine, but the fact that the bulk of the sediment far inside the cave is calcite suggests that the sediments are mostly derived from within the cave by weathering of the limestone and calcite crystals rather than from outside sources.

METHODS

The dry, dusty sediments of sites 1 and 2 are composed of nearly 10% vertebrate bones by volume. These fossiliferous sediments are unstratified and never more than 0.5 m (1.5 feet) thick, so no meaningful relative dating is feasible. Collecting was done mainly at sites 1 and 2, but a few specimens were taken from sites 3 and 4 (Fig. 3). No significant differences were found between fossils from the various sites, so the site at which each specimen was collected is not reported here but can be found in the Brigham Young University Vertebrate Paleontology Laboratory catalogs.

On early collecting trips most of the field time was spent digging through the sediments and collecting specimens by hand. Sediment was also taken to the lab in bags and screened to recover smaller bones and teeth. After using this method for several trips, the collection had overwhelming numbers of rodent and lagomorph fossils, but bones of larger mammals were few. So, on the last collecting trip, large volumes of cave sediment were screened inside the cave with a coarse screen, and the number of larger bones in the collection was thereby more than doubled.

Little laboratory preparation was necessary with the larger Crystal Ball Cave fossils. A few required removal of hardened dirt or calcite. All were washed to remove dust. Considerable time was spent manually separating small bones and teeth from cave sediments. This was done in the laboratory with forceps after the sediments had been washed through a fine screen and allowed to dry. Approximately 1 cubic meter (35 cubic feet) of cave sediment was prepared in this manner, and virtually all the bone was removed.

Because of the great abundance of small mammal fossils recovered, only the skulls and jaws were studied. All identifiable material was used for larger mammals because they were not as well represented and because few dental elements were recovered. Identification was made by comparison to Recent specimens housed at the Brigham Young University Monte L. Bean Museum, fossil and Recent specimens housed at the Brigham Young University Vertebrate Paleontology Laboratory, and by extensive use of the literature.

TABLE 2. Radiometric dates of bone samples from Crystal Ball Cave provided by Geochron Laboratories, Cambridge, Massachusetts in July 1984.

Cat. Number	Taxon	Description	Age
Uncataloged	large mammal	Limb bone fragment	12,980 +2680 −2000 years B.P.
Uncataloged	large mammal	Middle limb bone	18,600 +2000 −1600 years B.P.
BYUVP 7687	*Equus* (small)	Thoracic vertebra	18,820 +1510 −1270 years B.P.
BYUVP 7568	*Equus* (small)	Distal metapodial	More than 23,000 years B.P.

Small living mammals were captured inside Crystal Ball Cave and around Gandy Spring at the base of Gandy Mountain. This trapping was not extensive, but it did indicate what species are abundant in and around the cave. The species trapped are recorded in Table 1. Jerald C. and Marlene Bates of Gandy (1983, pers. comm., 1984, pers. comm.) were interviewed for additional information about the modern local fauna and recent history of the cave, including its modification by man.

ANTIQUITY OF THE ASSEMBLAGE

One problem with the Crystal Ball Cave assemblage is that it is impossible to separate fossil bones from Recent bones using superposition, because the sediments in which they are found are shallow and unstratified. Some of the best specimens of extinct species were found on the surface by early expeditions. The cave seems to have been accumulating fossils continuously from some date in the past, when an entrance was formed, until the present. The purpose of radiometric dating was to establish when fossils were first deposited and if the rate of fossil deposition has been uniform since then.

Four bone samples were sent to Geochron Laboratories, Cambridge, Massachusetts, for carbon-14 dating. Because of the small size of bones in the assemblage, these samples (which included some of the largest recovered) were just over 25 grams, the minimum weight suggested for dating. Two were of small extinct horses: a thoracic vertebra (BYUVP 7687) and a distal metapodial epiphysis (BYUVP 7568); and two were fragments of unidentified limb bones of large mammals. Geochron Laboratories cleaned and washed the four samples in acetic acid to remove adhering materials, then crushed them and soaked them in agitated acetic acid for 24 hours to remove normal carbonates. The samples were then hydrolized under vacuum with hydrochloric acid to dissolve bone apatite and evolve its carbon dioxide for collection. The carbon dioxide samples were converted to methane and counted in a low-background beta counter (with C-13 correction), and dates were based on the Libby half-life (5570 years). The ages reported are listed in Table 2. The oldest date of "over 23,000 Y.B.P." was given because no C-14 was detected in that sample.

The oldest date of 23,000+ Y.B.P. gives a minimum age for the time fossils first entered the cave. The youngest horse bone date of about 19,000 Y.B.P. gives a maximum age for the loss of that species from the area, although other studies have shown that small horses lived beyond 10,370 Y.B.P. in Idaho and until about 8,000 Y.B.P. in Arizona and Alberta, Canada (Kurten and Anderson 1972, 1980, Martin 1967). Otherwise the four dates give only a general age for the assemblage and provide no information about the antiquity of individual taxa. The fact that all four dates are over 12,000 Y.B.P. suggests that bones, at least of large mammals, may have been deposited more frequently during the Late Pleistocene than during the Recent. If so, this could be due to a greater abundance of the animals themselves, a change in what animals (or other processes) deposited the fossils, or the former presence of larger or additional entrances.

Thirty radiometric dates have been reported from the Smith Creek Canyon sites (Thompson 1979, Thompson and Mead 1982, Valastro et al. 1977), and they demonstrate that accumulation of fossils there was concurrent with fossil deposition at Crystal Ball Cave. The two oldest Smith Creek dates are 28,650 Y.B.P. (Smith Creek Cave) and 27,280 Y.B.P. (Ladder Cave), which correlate well with the date of "over 23,000 Y.B.P." from Crystal Ball Cave. The other 28 Smith Creek Canyon dates are younger than 18,000 Y.B.P., with the majority being from 10,000 to 13,000 Y.B.P. The mean age of the four dated Crystal Ball Cave specimens is considerably older than the mean age of dated specimens from any of the Smith Creek Canyon sites, suggesting that its major period of fossil deposition was earlier; but a sample size of four dates is not statistically significant enough to demonstrate this.

Paleoecological Setting

The Pleistocene-Recent boundary was a period of intense climatic and faunal change in North America. The changes at this fossil site were particularly drastic due to its close proximity to Lake Bonneville, which dried up during the period that fossils were being deposited. According to Currey (1982), the Bonneville Level terraces at Gandy are at an elevation of 1565 m (5165 feet), showing that the lake rose to 195 m (644 feet) below and 1.7 km (1 mile) east of Crystal Ball Cave and filled Snake Valley as far as 60 km (36 miles) south of the cave (Fig. 1). My previous statement that Gandy Mountain was once an island in Lake Bonneville (Heaton 1984) was based on data from an earlier study and is unconfirmed. Lake Bonneville started its last cycle of filling prior to 26,000 Y.B.P. and reached its highest level (Bonneville Level) about 16,000 Y.B.P. (Currey 1982, Scott et al. 1983). The lake remained at the Bonneville Level until 14,000 or 15,000 Y.B.P. when the flood at Red Rock Pass, Idaho, dropped the lake to the Provo level, where it remained until about 13,000 Y.B.P. (Currey 1982, Scott et al. 1983). At the Provo level the lake had only a shallow arm extending southward into Snake Valley to a point 8 km (5 miles) east of Crystal Ball Cave (Currey 1982). Further lowering of the lake after 13,000 Y.B.P. caused its quick retreat northward out of Snake Valley to a point 65 km (40 miles) northeast of the cave by 10,300 Y.B.P. (Currey 1982). Based on these dates Lake Bonneville was very close to Crystal Ball Cave for at least half the time that fossils were being deposited and within Snake Valley for about two-thirds of that time or longer. Then, within a few thousand years, the fossil site changed from being near the shore of a large continental lake to being in a dry desert, as it is today.

In addition to Lake Bonneville, many pluvial lakes filled the valleys of Nevada, including one just west of the Snake Range, 30 km (18 miles) west of Crystal Ball Cave (Mifflin and Wheat 1979). Based on studies of temperature and precipitation correlation, Mifflin and Wheat (1979) estimated that development of pluvial lakes in the area involved a temperature decrease of 3 C (5 F). Lower temperatures and higher annual precipitation caused floral boundaries to move lower in elevation and latitude during the Wisconsinan glacial (Thompson and Mead 1982, Wells 1983). This shift had a dramatic effect on small boreal mammals in the Great Basin because it allowed them to disperse between ranges, whereas now the intermontane basins act as absolute barriers (Brown 1971, 1978, Harper et al. 1978). Brown (1971, 1978) demonstrated that distribution of small boreal mammals is relectual from the Wisconsinan glacial and not a case of colonization-extinction equilibrium. The Crystal Ball Cave fauna shows what taxa have been extirpated from the Snake Range since the Wisconsinan glacial, and it documents northward shifts in the ranges of several species at the close of the Pleistocene.

Another striking feature of the Late Pleistocene is the well-documented megafaunal extinction. At the end of the Wisconsinan glacial, 41 species of large mammals went extinct—3 times more than at the end of any of the other Pleistocene glacials (Kurten and Anderson 1980). Different workers have attributed this to a rapid postglacial climatic shift (Martin and Neuner 1978, Webb 1969) and to overkill by early man (Martin 1967, Mosimann and Martin 1975). The Crystal Ball Cave assemblage contains several of these extinct taxa, but the fact that it lacks human association and stratigraphic control makes it unable to provide any substantial data to resolve this controversy.

Consideration needs to be given to the role Crystal Ball Cave played as a shelter and the means by which fossils got into the cave. When the cave was discovered in 1956, the east entrace was a 1-m (3-foot) diameter opening in solid rock, half filled with soft soil, which sloped downward into the large entrance chamber (Fig. 3). Several 0.3-m (1-foot) diameter entrances (which are often filled with woodrat nesting material) also exist just north of the east entrance. The north entrance was completely filled with debris, which if removed could make it 2.5 m (8 feet) high and 6 m (20 feet) wide. It could have been a large important entrance when the earlier bones were being deposited, but several factors preclude this. First, there are very few fossils in the deep dry sediments of the north half of the cave; the rich bone deposits are in the south half. Second, the fossil assemblage provides no evidence that there ever was a large entrance since large mammals are represented only by their smallest elements. If the north entrance ever was large, it was probably prior to deposition of the fossils under study.

Neotoma lepida, *Peromyscus maniculatus*, and *Plecotus townsendii* were captured alive inside the cave, so their presence in the assemblage is easy to explain. Other small mammals could also have lived in the cave or used it as a shelter. Small carnivores and scavengers could have brought their prey into the cave to eat. The presence of only the smallest isolated elements of large mammals suggests that these bones were brought into the cave individually after the carcasses deteriorated. Small carnivores could have contributed to this, but it is my opinion that these bones were taken into the cave primarily by wood rats since these animals are known to take materials into the cave now, many bones have rodent gnaw marks, and all the bones in the assemblage are small enough for a wood rat to transport. Because the cave has small entrances and because the bones are found far within the cave, it is very unlikely that birds transported prey inside. There is also no evidence that prehistoric humans brought material into Crystal Ball Cave. This suggests that the species found in the assemblage lived and died in or near the cave and were not transported long distances, as could have occurred at Smith Creek Cave (Bryan 1979, Harrington 1934).

It is unusual for caves to have their richest bone deposits far inside the cave rather than near an entrance. The east entrance of Crystal Ball Cave takes in water during storms, and other areas are damp from seepage. Sites 1 and 2, which contain the richest bone deposits, are in one of the dryest areas of the cave and are just outside the zone of total darkness when the sun shines through the east entrance. North of sites 1 and 2 the passage constricts and enters total darkness but remains dry. Wood rat nests are particularly common at sites 1 and 2, which helps explain why rich bone deposits are present if wood rats play an important role in getting them there. The extremely dry conditions at sites 1 and 2 and their proximity to the east entrance, which I consider the primary entrance, are probably the reason why these sites have been so productive. Rarity of fossils nearer the east entrance is probably due to poorer preservational conditions and poorer sites for wood rat dwellings. Lack of rich bone deposits in the northern half of the cave is probably due to constricted passages and greater distance from a Late Pleistocene entrance.

The following taxa were recovered from Crystal Ball Cave.

KINGDOM PLANTAE
Division Tracheophyta
Class Gymnospermae
Family Ephedraceae
Ephedra cf. *viridis*

MATERIAL.— Two stem fragments.

Class Angiospermae
Family Asteraceae
Chrysothamnus sp.

MATERIAL.— One branching stem fragment.

Haplopappus nanus

MATERIAL.— One group of involucres, 4 single involucres.

Perityle stansburii

MATERIAL.— Four involucres on stem fragments.

Family Brassicaceae
Genus and species indet.

MATERIAL.— Two stem fragments, 2 stem fragments with empty seed capsules, 4 empty seed capsules.

Family Cactaceae
Opuntia sp.

MATERIAL.— Twelve spines.

Family Caprifoliaceae
Symphoricarpos cf. *longiflorus*

MATERIAL.— One branching stem fragment, 4 straight stem fragments, 56 leaves and partial leaves.

Family Poaceae
cf. *Elymus*

MATERIAL.— Two fruits.

cf. *Panicum*

MATERIAL.— Three connected fruits, 3 rachis fragments.

DISCUSSION.— About 250 small plant fragments were recovered from the Crystal Ball Cave sediments by the same process that small bones and teeth were recovered. From among them Howard C. Stutz (1984, pers. comm.), a botanist at Brigham Young University, identified the above taxa. All the taxa identified still live in the immediate area of Crystal Ball Cave (partly because a sample of plants from immediately around the cave comprised most of the comparative material), so they do not document any floral changes since the Pleistocene. Further research could turn up additional taxa since not all the plant fragments were identified.

The great abundance of *Symphoricarpos* compared to the other plant taxa recovered is noteworthy. Stutz (1984, pers. comm.) found a thicket of *Symphoricarpos* at the bottom of a cliff in the nearby House Range that was full of rodent nests and burrows. This suggests that this plant is a favorite nest-building material for rodents, and wood rats may have brought pieces of it into Crystal Ball Cave for that purpose.

No pollen analysis has been done at Crystal Ball Cave, and no pollen was noticed in the cave sediments studied. A more extensive search could turn up pollen, however, and, since plant fragments are rare in the sediments, it could help identify what plants inhabited the area during the Pleistocene.

KINGDOM ANIMALIA
Phylum Mollusca
Class Gastropoda
Order Pulmonata
Family Helicidae
Oreohelix strigosa

MATERIAL.— Nine complete shells ranging from 3 to 10 mm in diameter.

DISCUSSION.— These land snails, which still inhabit the Snake Range, live in moister conditions than those at Crystal Ball Cave today (Chamberland and Jones 1929), so they are probably late Pleistocene or early Recent in age. Since there are only nine specimens, they were probably never abundant near the cave, but lack of abrasion on the shells suggests that they were not transported far.

Phylum Arthropoda
Class Crustacea
Order Isopoda
Family ? Armadillidae
Genus and species indet.

MATERIAL.— Partial dried shell.

DISCUSSION.— Pill bugs are native to North America (S. L. Wood 1984, pers. comm.), and little work has been done on them. Representatives of several families, including family Armadillidae, presently live in Utah, but the partial specimen did not allow further identification. These terrestrial crustaceans inhabit moist recesses throughout Utah and Nevada today, so the presence of this specimen is not surprising, although little can be said about its age.

Class Insecta
Order Coleoptera
Family Scarabaeidae
Aphodius distinctus

MATERIAL.— Complete dried specimen.

DISCUSSION.— This small beetle lives in cattle dung and was introduced from Europe in Recent times (S. L. Wood 1984, pers. comm.). It is therefore Recent in age and has little significance to the assemblage.

Phylum Chordata
Class Osteichthyes
Infraclass Teleosti

MATERIAL.— Thirty-seven amphicoelous vertebrae ranging from 1 to 5 mm in diameter and length (BYUVP 7939–7973).

DISCUSSION.— Presently, the closest water body to Crystal Ball Cave is Gandy Spring on the south side of Gandy Mountain. This spring emits voluminous warm water (27 C, 81 F) that is high in calcium (J. C. Bates 1983, pers. comm.). Small minnows are the only native fish found living in the stream that exits Gandy Spring, but bass and blue gill were introduced in the 1960s and still survive; carp are also found in reservoirs in the area (J. C. Bates 1984, pers. comm.). Mead et al. (1982) reported *Salmo* and *Gila* from nearby Smith Creek Cave, which is higher in elevation and farther from a perennial water source than Crystal Ball Cave, and Smith (1978) and Smith et al. (1968) reported Pleistocene fish from Lake Bonneville deposits.

A dichotomy in the size of the fish vertebrae from Crystal Ball Cave suggests that at least two species are represented, but no attempt at generic identification has been made. The possibility that these vertebrae are Recent cannot be eliminated, but they probably represent fish that lived in Lake Bonneville when it was at or near the Bonneville level, or in perennial Pleistocene streams in the area. In any case, they had to be transported up Gandy Mountain to the cave site. Carnivores or scavengers could have done this, and wood rats could have taken them inside the cave.

Class Reptilia
Order Squamata

MATERIAL.— Two hundred sixty-five lizard and snake jaws (BYUVP 8004–8217). Postcranial material is also represented but has not been separated from that of mammals.

DISCUSSION.— The reptile specimens have not yet been studied but will be reported in a future paper by Jim I. Mead and Timothy H. Heaton. The reptiles recovered from the deeper levels of Smith Creek Cave demonstrate that their present distribution in the Great Basin is more ancient than previously believed (Brattstrom 1976, Mead et al. 1982). The large number of reptile jaws from Crystal Ball Cave will help establish what species have been extirpated from the area, but, unless dated individually, they will not help establish the antiquity of their ranges.

Class Aves

MATERIAL.— Six hundred eleven specimens representing all skeletal elements of small passerines and skull and vertebrae fragments of larger forms (BYUVP 6606, 8301–8888, 8911–8933, LACM 123655).

DISCUSSION.— The bird specimens have not yet been studied but will be reported in a future paper by Steven D. Emslie and Timothy H. Heaton. Miller (1982) reported ? *Aquilla* from Crystal Ball Cave from among this same material.

Class Mammalia
Order Insectivora
Family Soricidae
Sorex sp.

MATERIAL.— One maxilla pair with all teeth (BYUVP 5321). Another 5 partial maxillae and 27 partial dentaries (some with teeth, BYUVP 5300–5320, 5322–5332) were recovered that cannot be generically identified but compare favorably with *Sorex*.

DISCUSSION.— Identification was based on the presence of five unicusp teeth behind the upper incisor, the first four of which taper slightly in size posteriorly and are visible laterally, and the last of which is tiny, peglike, unpigmented, and not visible labially. *Microsorex* and *Blarina* also have five unicusp teeth in each maxilla, but *Microsorex* has only the first three visible laterally and *Blarina* has the third and fourth of subequal and smaller size than in *Sorex*. *Notiosorex* and *Criptotis*, the other two North American genera, have only three and four unicusp teeth in each maxilla, respectively (Hall 1981). All the other soricid specimens are either lower jaws and teeth, which I was unable to distinguish at the generic level, or are maxillae without the diagnostic unicusp teeth. All these soricid specimens compare well with *S. vagrans* and *S. palustris*, which presently live in the region of the cave (Hall 1981), but no dental character could be found to distinguish them.

Order Chiroptera
Family Vespertilionidae
Myotis sp.

MATERIAL.— Two palates without teeth (BYUVP 5340, 5357), anterior portion of right maxilla with P4/, M1/ (BYUVP 5338). Twelve right dentaries (BYUVP 5336, 5341–5346, 5352, 5353, 5358–5360) and 12 left dentaries

(BYUVP 5339, 5347–5349, 5354–5356, 5361–5364, 5366) were recovered that are *Myotis* or *Plecotus*.

Discussion.— *Myotis* maxillae have the diagnostic presence of two small unicusp premolars following the incisor, as opposed to one or none in all other vespertilionids. Dentaries of *Myotis* and *Plecotus* are virtually identical, both having the dental formula of I/3, C/1, P/3, P/3 and similar size and proportions, and no character could be found to separate them. Dentaries of *Lasionycteris* and *Pizonyx* also share this tooth formula but are considerably larger. *Myotis* has not been reported living in Crystal Ball Cave, but *M. lucifugus*, *M. evotis*, *M. thysanodes*, *M. volans*, and *M. subulatus* are all found in the region (Hall 1981). Little work has been done to separate species of *Myotis* dentally, and I was unable to find any species variation that was greater than individual variation.

? *Plecotus townsendii*

Material.— Twenty-four dentaries were recovered of *Myotis* and/or *Plecotus* (as listed and discussed above).

Discussion.— *Plecotus townsendii* is the only bat reported living in the cave. Specimens were captured by Halliday (1957) and by myself in 1982 and 1983. Halliday (1957) and other workers have referred to this bat as *Corynorhinus rafinesquii*, but Handley (1959), in his synthesis of the big-eared bats, considered both *Corynorhinus* and *Idionycteris* as only subgenera of the European genus *Plecotus*. He also regarded *P. rafinesquii* (presently in southeastern U.S.) and *P. townsendii* (presently in western U.S.) as two distinct species. *Plecotus mexicanus*, the third living species of the subgenus *Corynorhinus*, and *P. hyllotis*, the only member of the subgenus *Idionycteris*, both inhabit Mexico and north into the southern tip of Arizona. Two extinct Pleistocene species of the subgenus *Corynorhinus* are also recognized: *P. alleganiensis* from Cumberland Cave in Maryland and *P. tetralophodon* from San Josecito Cave in Mexico (Handley 1959). Handley (1959) listed no characters to distinguish the dentaries of different species of *Plecotus*, but the bats living in the cave are clearly *P. townsendii*.

Lack of positive evidence for this species in the Crystal Ball Cave assemblage could represent lack of chance preservation or a recent change in the species that inhabit the cave. Since the assemblage contains indistinguishable Pleistocene and Recent specimens, even if the lower jaws could be identified as *Plecotus*, unless dated individually they would not reveal how long this species has inhabited the cave. Humphrey and Kunz (1976) postulated that mild winters during the Late Pleistocene allowed *P. townsendii* to roost in trees rather than caves and to avoid the present habit of long winter hibernation, whereas this bat now uses caves as refugia to survive the intolerably cold post-Pleistocene winters. Humphrey and Kunz (1976) cited evidence that this bat is very sedentary and now survives only in isolated areas where suitable winter hibernacles are available. Handley (1959) stated that very few specimens of *Plecotus townsendii* have been reported considering its large geographic range. Durrant et al. (1955) said this species was thought to only inhabit the southern half of Utah until a few isolated citings were made in northern Utah caves, one of which (in Logan Canyon) contained the bat in large numbers. It is, therefore, very possible that *P. townsendii* has not inhabited Crystal Ball Cave, at least to the large degree that it does now, until Recent times.

Antrozous pallidus

Material.— Anterior portion of left maxilla with C1/, P4/ (BYUVP 5365), anterior portion of fused dentary pair with left P/4, M/1 (BYUVP 5351), posterior portion of right dentary with M/2 (BYUVP 5333), posterior portion of left dentary with M/1 (BYUVP 5334). A posterior fragment of a left dentary (BYUVP 5350) and a right M/2 (BYUVP 5335) probably also belong to this taxon based on their large size and chiropteran affinities.

Discussion.— This is the largest species of bat found in the assemblage and is easily distinguishable from other vespertilionids by its unique tooth formula of I1/2, C1/1, P1/2, M3/3, the configuration of the incisors and fenestra in the anterior palate, and the high coronoid process on the dentary. *Antrozous pallidus* has not been reported living in the cave, but it presently occurs from the region of the cave southward into Mexico and along the west coast of the United States and southern British Columbia. *Antrozous bunkeri* is now considered a subspecies of *A. pallidus* (Hall 1981). *Antrozous dubiaquercus* occurs in Mexico and Central America and is distinguished from *A. pallidus* by normally having 3 lower incisors instead of 2. *Antrozous koopmani* occurs only in Cuba. All the material listed above matches perfectly with modern *A. pallidus*, which lives in the region of Crystal Ball Cave.

Order Lagomorpha
Family Ochotonidae
Ochotona princeps

MATERIAL.— Anterior portion of skull with all teeth (BYUVP 5387), right maxilla with M1/,2/ (BYUVP 5407), right maxilla with M2/ (BYUVP 5406), right maxilla without teeth (BYU 5385), anterior portion of right maxilla with M1/ (BYUVP 5404), 2 anterior portions of right maxillae without teeth (BYUVP 5386, 5405), 4 partial right maxillae without teeth (BYUVP 5368, 5409, 5410, 5412), 6 left maxillae without teeth (BYUVP 5381, 5383, 5384, 5396, 5397, 5417), 3 anterior portions of left maxillae without teeth (BYUVP 5374–5376), 5 partial left maxillae without teeth (BYUVP 5369, 5382, 5408, 5415, 5416), right dentary with P/4, M/2,/3 (BYUVP 5399), right dentary with M/2,/3 (BYUVP 5393), right dentary with M/2 (BYUVP 5395), 5 right dentaries without teeth (BYUVP 5390–5392, 5401, 5419), partial right dentary with P/4 (BYUVP 5370), 4 partial right dentaries without teeth (BYUVP 5367, 5411, 5413, 5414), 2 anterior portions of right dentaries without teeth (BYUVP 5371, 5372), left dentary with P/4, M/1,/2 (BYUVP 5402), left dentary with M/1,/2 (BYUVP 5398), 3 left dentaries without teeth (BYUVP 5394, 5403, 5418), anterior portion of left dentary with P/4, M/1,/2,/3 (BYUVP 5388), posterior portion of left dentary with M/1,/2,/3 (BYUVP 5389), 2 posterior portions of left dentaries without teeth (BYUVP 5377, 5400), partial left dentary with M/1,/2 (BYUVP 5378), 3 partial left dentaries without teeth (BYUVP 5373, 5379, 5380).

DISCUSSION.— Ochotonids are easily distinguished from leporids by the lingual curve in the maxilla behind the cheek teeth, the presence of 5 upper cheek teeth rather than 6, and M/3 and its socket being anteroposteriorly short instead of triangular. *Ochotona princeps* presently inhabits high elevations within 190 km (120 miles) of Crystal Ball Cave, both to the east and west (Hall 1981). The only other extant species, *O. collaris*, occurs exclusively in northwestern Canada and Alaska (Hall 1981) and has been found in fossil deposits only in that region (Kurten and Anderson 1980). The only extinct Quaternary North American species of *Ochotona* is *O. whartoni*, which is known from the Early Pleistocene and is distinctly larger than the extant species (Kurten and Anderson 1980). All the specimens listed above are indistinguishable from Recent *O. princeps*.

Why *O. princeps* has been extirpated from the Snake Range is uncertain, but fossils have been recovered from Smith Creek Cave (Miller 1979) and many other Great Basin localities where this species does not live today. For example, Grayson (1977) recovered *O. princeps* dated at 7,000 to 12,000 Y.B.P. from the Fort Rock Basin of south central Oregon. That area is now dominated by sagebrush, grasses, and sparse junipers, but modern pikas in the region only live where there is more succulent vegetation. Grayson (1977) attributed the disappearance of *Ochotona* to either a shift to more xeric habitat or to an eruption of Mt. Mazama 7,000 Y.B.P. A similar extirpation in the Snake Range 500 km (315 miles) to the southeast supports the former of Grayson's hypotheses.

Family Leporidae
Sylvilagus idahoensis

MATERIAL.— Right dentary with P/4, M/1,/2 (BYUVP 5534), right dentary without teeth (BYUVP 5444), right dentary fragment with P/3 (BYUVP 5584), left dentary with P/3,/4, M/1 (BYUVP 5536), left dentary fragment without teeth (BYUVP 5434).

DISCUSSION.— *Sylvilagus idahoensis* is distinguished from all other leporids by its small size (Fig. 4) and from *Ochotona* by the characters listed above. The P/3 of *S. idahoensis* does not widen posteriorly, as in other species of *Sylvilagus*, and the second reentrant angle is not crenulated as it is in many leporids. BYUVP 5536 is larger than any of the 31 Re-

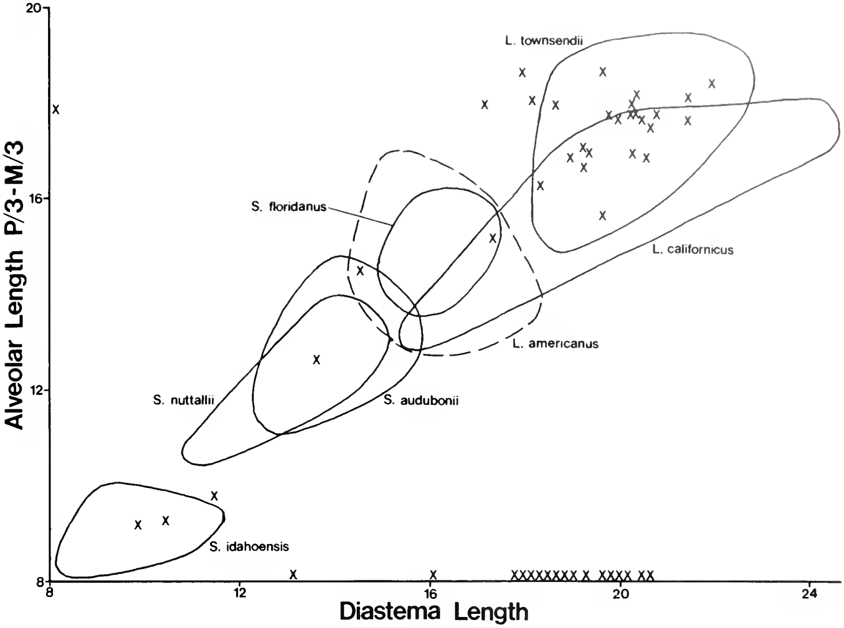

Fig. 4. Plot of *Sylvilagus* and *Lepus* dentaries from Crystal Ball Cave (X's) and ranges of variation for all species of leporids presently living in and near Utah and Nevada (circumscribed). Some of the measurements of Recent specimens were made by the author from the Brigham Young University Monte L. Bean Museum mammal collection, and some were provided by J. A. White (1984, pers. comm.). The number of Recent specimens measured were 31 of *S. idahoensis*, 22 of *S. nuttallii*, 33 of *S. audubonii*, 12 of *S. floridanus*, 40 of *L. americanus*, 36 of *L. californicus*, and 29 of *L. townsendii*. Symbols on the plot margins represent Crystal Ball Cave specimens on which only one of the two plotted measurements could be made. Measurements are in millimeters.

cent *S. idahoensis* specimens to which it was compared (but smaller and distinct from other species of leporids), and the other Crystal Ball Cave specimens are also comparatively large, suggesting that this species may have decreased in size at the end of the Pleistocene. This species presently lives in the region of the cave and to the north and west (Hall 1951, 1981).

Sylvilagus nuttallii

MATERIAL.— Anterior portion of right dentary without teeth (BYUVP 5493), left dentary with M/1 (LACM 123658), anterior portion of left dentary with I/1, P/3,/4, M/1 (BYUVP 5578), 4 right P/3's (BYUVP 5717, 5731, 5769, 5794), 4 left P/3's (BYUVP 5773, 5782, 5795, 5810).

DISCUSSION.— *Sylvilagus* is commonly distinguished from *Lepus* by its smaller size, although there is some overlap (namely, *S. aquaticus* and *S. cunicularius* are larger than *Lepus americanus*; J. A. White 1984, pers. comm.). The species of these genera presently living in the region are usually discernible by size, but the species within each genus are usually not (Fig. 4).

Of the two species of *Sylvilagus* presently living in the Snake Range, *S. audubonii* has a larger mean size and tends to have much more crenulation in the second reentrant angle of P/3 than *S. nuttallii* (although there is overlap in both characters). *Sylvilagus floridanus*, which occurs just south of Utah and Nevada, has an even larger mean size than *S. audubonii* but has little crenulation in the P/3 like *S. nuttallii*. BYUVP 5493 and LACM 123658 compare well in size with *S. nuttallii* and *S. audubonii* (Fig. 4), but none of the nine P/3's of *Sylvilagus'* size from Crystal Ball Cave have much crenulation in the second reentrant angle of P/3, suggesting that they belong to *S. nuttallii* rather than *S. audubonii*. Although other species could be represented, the evidence suggests that at least the majority of the specimens listed above are of *S. nuttallii*.

Sylvilagus nuttallii presently inhabits the region of the cave and northward, whereas *S. audubonii* inhabits the region of the cave and southward. *Sylvilagus nuttallii* also tends to occur at higher elevations and in more wooded or bushy areas than *S. audubonii*, which lives in plains or open country (Hall 1951). Since Gandy Mountain is presently covered with only sparse bushes and is surrounded by open plains, the presence of *S. nuttallii* and absence of *S. audubonii* in the assemblage suggests a replacement of woodland-alpine vegetation by the present desert conditions since the Pleistocene.

Lepus cf. *americanus*

MATERIAL.— Right dentary with /I, P/3,/4, M/1,/2 (BYUVP 5519), anterior portion of left dentary with P/4, M/1 (BYUVP 5543). A left dentary with /I (BYUVP 5430) falls within the size range of *L. americanus* and *L. californicus*.

DISCUSSION.— The jaw dimensions and P/3 widths of these specimens are intermediate in size between the *Sylvilagus* specimens (described above) and the majority of the *Lepus* specimens (described below). They fall in and near the range of variation of the smallest *L. californicus* and largest *S. audubonii* specimens (Fig. 4), but most of the P/3's of these two species have a highly crenulated second reentrant angle, whereas the P/3 of BYUVP 5519 does not. These specimens are also indistinguishable from *S. floridanus*, but this species has never been reported living or as a fossil from Utah or Nevada.

Lepus americanus does not presently occur in the Snake Range but does occur 160 km (100 miles) to the north and east, mainly at high elevations (Durrant 1952, Hall 1951). Since the assemblage generally contains more species that presently range north of the cave than south of the cave, it is not at all unreasonable that *L. americanus* could have inhabited the region of the cave in the recent geologic past. Kurten and Anderson (1980) listed a number of Pleistocene fossil sites where *L. americanus* has been found south of its present range.

Lepus townsendii

MATERIAL.— Fused dentary pair with right P/3,/4, M/1,/2,/3, left /I, P/3,/4, M/1,/2 (BYUVP 5488), right dentary with M/1,/2 (BYUVP 5467), right dentary with /I (BYUVP 5533), left dentary with all teeth (BYUVP 5442), left dentary with /1, P/3,/4, M/1,/2 (BYUVP 5484), 5 left dentaries without teeth (BYUVP 5424, 5429, 5474, 5532, LACM 123657), anterior portion of left dentary without teeth (BYUVP 5439), 7 isolated right P/3's (BYUVP 5733, 5770–5772, 5793, 5796, 5802), 7 isolated left P/3's (BYUVP 5735, 5736, 5780, 5783, 5790, 5791, 5804). A partial left dentary with P/3 (BYUVP 5485), 28 dentaries lacking P/3 (BYUVP 5422, 5427, 5436, 5438, 5448, 5450, 5454, 5456, 5458, 5462, 5473, 5475, 5478, 5483, 5487, 5489, 5493, 5495, 5500–5502, 5524, 5527, 5530, 5531, 5540–5542), 7 isolated right P/3's (BYUVP 5617, 5732, 5745, 5768, 5774, 5778, 5792), and 5 isolated left P/3's (BYUVP 5716, 5775, 5776, 5801, 5809) show characteristics common to both *L. townsendii* and *L. californicus*.

DISCUSSION.— *Lepus townsendii* and *L. californicus* are distinguished from *Sylvilagus* and *L. americanus* by their large size. They are distinguished from each other by *L. townsendii* having a larger mean size (Fig. 4) and having less crenulation in the second reentrant angle of P/3 than *L. californicus* (Hibbard 1952). Miller (1976) observed *L. californicus* to have a highly crenulated P/3 in most, but not all, cases, and Hibbard (1944, 1963) noted that individual variation is very great. My observations and those of J. A. White (1984, pers. comm.) show that many individuals of these species cannot be distinguished by either size or the amount of crenulation in P/3; but statistical analysis can be used to estimate their relative abundance (Grayson 1977). Hibbard (1952) stated that the anterior part of P/3 is narrower in *L. townsendii* than in *L. californicus*, but, although I noticed variation in the narrowness and roundedness of the anterior P/3's, it did not correlate with the amount of crenulation in the second reentrant angle of that tooth. BYUVP 5424, 5467, and 5474 have greater alveolar length (P/3–M/3) to diastema length ratios than any Recent leporid specimens measured (Fig. 4), but they fall closest in size, especially based on their large tooth row length, to *L. townsendii*.

Since 11 of the 43 measurable *Lepus* dentaries are larger than any modern *L. californicus* specimens measured (Fig. 4), and over half of the large *Lepus* P/3's from the assemblage show no crenulation (a very rare condition in *L. californicus*), it is clear that *L. townsendii* is well represented. Most of the 29 jaws that could be either *L. townsendii* or *L. californicus* are closer to the mean size of *L. townsendii*, and the isolated 13 P/3's of *L. townsendii* or *L. californicus* have slight crenulation in the second reentrant angle, yet are considerably less crenulated than the vast majority of *L. californicus* specimens. Since only two highly crenulated P/3's clearly belonging to *L. californicus* (listed below) were found, most of these 13 P/3's with intermediate crenulation probably belong to *L. townsendii*. Based on this information I estimate that the ratio of *L. townsendii* to *L. californicus* specimens from the Crystal Ball Cave assemblage is about 10 to 1.

Grayson (1977) stated that *L. townsendii* is a more northern species and inhabits higher elevations and more grassy habitats than *L. californicus*, which prefers dryer shrubby areas. With *Sylvilagus*, the more northern species is represented in the assemblage, and the more southern species is not. This is also the trend with *Lepus*. Hall (1981) reported *L. townsendii* in the area of Crystal Ball Cave but Durrant (1952), in a more detailed map, did not. Both reported *L. californicus* throughout the Bonneville Basin area. I have seen numerous *L. californicus* around Gandy but never a *L. townsendii*, and J. C. Bates (1984, pers. comm.) reported never noticing any *L. townsendii* but seeing numerous *L. californicus*. This difference between the fossil and living species at Gandy suggests that climatic boundaries have shifted northward in latitude and upward in elevation since the Pleistocene. Grayson (1977), using both fossil and Recent data, demonstrated that *L. californicus* increased in number at the expense of *L. townsendii* during the Recent and that it became the more dominant species in the Great Basin 5,000 to 7,000 Y.B.P. Although the ecological and adaptational differences between these two species are not fully understood, Grayson (1977) attributed this change to a post-Pleistocene warming trend. The species shift indicated by the Crystal Ball Cave assemblage reiterates the data presented by Grayson (1977).

Lepus californicus

MATERIAL.— Right P/3 (BYUVP 5781), left P/3 (BYUVP 5734). Twenty-nine dentaries and 13 other P/3's (listed under *L. townsendii*) show characters found in both *L. townsendii* and *L. californicus*. A left dentary with /I (BYUVP 5430) falls within the size range of *L. americanus* and *L. californicus*.

DISCUSSION.— *Lepus californicus* differs from *L. townsendii* in having a smaller mean size (Fig. 4) and a more crenulated second reentrant angle in P/3 as discussed above. The two P/3 specimens listed above have more crenulation than was seen in eight Recent *L. townsendii* specimens but are typical of *L. californicus*. The 13 P/3s of either *L. townsendii* or *L. californicus* (listed and discussed above) show less crenulation than the vast majority of *L. californicus* specimens studied, but some of them could represent *L. californicus* since crenulation in the P/3 is not always present (Miller 1976). *Lepus californicus* is presently the most common lagomorph around Crystal Ball Cave (J. C. Bates 1983, pers. comm.), so its poor representation in the fossil assemblage suggests that it has only recently become abundant there.

Order Rodentia

Family Sciuridae

Marmota flaviventris

MATERIAL.— Anterior portion of skull with right M1/,2/,3/, left M1/,3/ (BYUVP 6528), anterior portion of skull without teeth (LACM 123663), dentary pair with right M/1,/3 (BYUVP 6536), right dentary with P/4, M/1,/3 (LACM 123665), right dentary with M/1,/2,/3 (BYUVP 6543), right dentary with M/2,/3 (BYUVP 6621), right dentary with M/3

(BYUVP 6620), left dentary with /1, M/1,/2,/3 (BYUVP 6477), left dentary with M/1,/2,/3 (LACM 123669). Another 70 partial maxillae (some with teeth), 70 partial dentaries (some with teeth), and approximately 300 isolated cheek teeth (BYUVP 6476, 6478–6518, 6520–6527, 6529–6535, 6537–6542, 6544–6605, 6607–6619, 6622–6648, LACM 123664, 123666–123668, 123670) are of *Marmota* and compare favorably with *M. flaviventris*.

DISCUSSION.— *Marmota* is distinctly larger than other living sciurids (Hall 1981) but distinctly smaller than the extinct *Paenemarmota* (Repenning 1962). *Marmota flaviventris* is distinguished from *M. monax* by its anteriorly divergent upper tooth rows and from *M. caligata*, *M. olympus*, and *M. vancouverensis* by its smaller size (Hall 1981). *Marmota flaviventris* is also distinguished from these other species by its less massive dentition, M3/ being longer than it is wide, and M/3 having a triangular rather than a quadrangular outline (Logan 1983). Hay (1921) named *M. arizonae* based on a partial skull from northern Arizona and said it was similar to *M. flaviventris*. Since this specimen is probably Late Pliocene in age and the validity of the species is uncertain (Kurten and Anderson 1980), it is not considered a candidate for the Crystal Ball Cave specimens, all of which are indistinguishable from Recent *M. flaviventris*.

The presence of *M. flaviventris* in the Crystal Ball Cave assemblage represents a shift in the climate and vegetation of the area because this species now inhabits only much higher elevations in the Snake Range (Hall 1981, Mead et al. 1982) and does not live on or around Gandy Mountain (J. C. Bates 1983, pers. comm.). Hall (1946) reported fossil *M. flaviventris* from several caves far south of the present range of this species. Zimina and Gerasimov (1969) proposed that the marmot greatly expanded its distribution and numbers under Late Pleistocene periglacial conditions for which it was well adapted, but it has since diminished its range significantly. *Marmota flaviventris* is not a cave-dwelling species, so its great abundance in the Crystal Ball Cave assemblage suggests that it once lived on Gandy Mountain in large numbers, strongly supporting the hypothesis of Zimina and Gerasimov (1969).

Spermophilus townsendii

MATERIAL.— Anterior portion of skull with both I/'s (BYUVP 6060), partial skull with right P4/, M1/,2/ (BYUVP 6255), partial skull without teeth (BYUVP 6462), 7 right dentaries with all teeth (BYUVP 6107, 6109, 6141, 6282, 6284, 6326, 7256), and 2 left dentaries with all teeth (BYUVP 6421, 6433). Another 439 partial maxillae (some with teeth), 562 partial dentaries (some with teeth), and approximately 4,000 isolated cheek teeth compare favorably with *S. townsendii*.

DISCUSSION.— *Spermophilus townsendii* has the smallest mean size of any North American species of *Spermophilus* and is also slightly smaller than *Ammospermophilus leucurus* (Hall 1981). *Spermophilus* also differs from *Ammospermophilus* by having distinctly larger masseteric tubercles just anterior to the upper tooth rows (Hall 1981). The three partial skulls listed above and many of the partial maxillae without teeth have large masseteric tubercles that distinguish them from *Ammospermophilus*. All the specimens listed above compare best in size with *S. townsendii*, but some of those only referred to this species are probably *Ammospermophilus*. Kurten and Anderson (1980) listed 13 extinct species of *Spermophilus*, but the only one close enough in size and age of deposits to the Crystal Ball Cave specimens to be considered is *S. taylori*, named by Hay (1921) and based on a single specimen from Texas. Kurten and Anderson (1980) considered this a doubtful species and most likely a synonym of *S. townsendii*. It is therefore not considered here.

The presence of a single species of *Spermophilus* at Crystal Ball Cave is a striking contrast to the five possible species recovered from Smith Creek Cave in subequal numbers (Mead et al. 1982). These include *S.* cf. *townsendii*, *S. variegatus*, and *S.* cf. *lateralis*, which still inhabit the Snake Range, and *S.* cf. *richardsonii* and *S.* cf. *beldingi*, which have been extirpated but still inhabit Utah and/or Nevada (Hall 1981). The reason for this difference may be that Smith Creek Cave is at the base of 3,673 m (12,050 foot) Mount Moriah and at the edge of the flat open Snake Valley, an area of diverse niches in contact with several diverse environments even now, and certainly an area across which climatic boundaries crossed many times during the Pleistocene. Gandy Mountain, on the other hand, is only a small hill far out in Snake Valley, the area most favorable to *S. townsendii* (Hall 1946), and is isolated from the main Snake Range by 10 km (6 miles) of flat valley.

The abundance of *Spermophilus townsendii* fossils at Crystal Ball Cave suggests that this squirrel lived around Gandy Mountain in large numbers for a long time, probably since fossils started accumulating in the cave. Durrant (1952) said this species is well suited to the western Utah desert and is particularly abundant around springs. Hall (1946) told how *S. townsendii* was a traditional food for native American Indians. *Spermophilus townsendii* is not a cave-dwelling animal as is *Neotoma*, and yet it is over twice as abundant as *Neotoma* in the assemblage (contrary to my earlier statement that *Neotoma* was the best represented genus, Heaton 1984). *Neotoma* has a much more restricted niche than *Spermophilus* and is never found in large numbers. Since squirrels are very unlikely to venture deep into caves, all the specimens must have been brought in by wood rats and/or small carnivores. It is interesting that fossil deposition occurred so rapidly, even deep in this isolated cave, that an outside species is better represented than the primary cave-dwelling species. J. C. Bates (1984, pers. comm.) reported seeing no squirrels on Gandy Mountain and only a few in the surrounding valley in the many years he has lived in Gandy. This, in contrast to its abundance as a fossil, suggests that *S. townsendii* reduced its numbers at the close of the Pleistocene in Snake Valley.

Ammospermophilus cf. *leucurus*

MATERIAL.— Right maxilla without teeth (BYUVP 8295), 2 left maxillae without teeth (BYUVP 8296, 8297). Some of the 439 maxillae, 562 dentaries, and approximately 4,000 isolated cheek teeth listed under *Spermophilus townsendii* probably also belong to this taxon.

DISCUSSION.— *Ammospermophilus* is distinguished from *Spermophilus* by its smaller masseteric tubercles and its less robust lower cheek teeth (Hall 1981). *Ammospermophilus leucurus* now lives around Gandy Mountain, but *A. harrisii*, *A. interpres*, *A. insularis*, and *A. nelsoni*, the other four extant species, occur only south of Utah (Hall 1981), so the Crystal Ball Cave specimens are referred to *A. leucurus* although no character could be found to rule the others out.

According to Durrant (1952) *A. leucurus* commonly occurs with *S. townsendii* but has a more restricted habitat, preferring rocky terrains. *Ammospermophilus* is best adapted for high temperatures (Vaughan 1972), and its low abundance in the assemblage compared to *Spermophilus townsendii* suggests that it has not inhabited the area as long, at least not in its present abundance. With summers becoming hotter and drier at the close of the Pleistocene, *Ammospermophilus* may have increased its numbers at the expense of *Spermophilus* in Recent times.

Eutamius minimus

MATERIAL.— Right dentary with P/4, M/1,/2 (BYUVP 6812), 3 right dentaries with P/4, M/1 (BYUVP 6171, 6210, 6755), left dentary with all teeth (BYUVP 6190).

DISCUSSION.— *Eutamius* has two premolars in each maxilla, whereas *Tamius* has only one. *Eutamius minimus* is the smallest species of *Eutamius* and has a narrower and squarer P/4 than *E. dorsalis* or *E. umbrinus*. All the specimens listed above match *E. minimus* with respect to the P/4 and are smaller than the other species. *Eutamius minimus* and *E. dorsalis* live in the region of Crystal Ball Cave, and *E. umbrinus* lives higher in the Snake Range and westward into Nevada (Hall 1981). *Eutamius minimus* was also recovered from Smith Creek Cave (Mead et al. 1982). *Eutamius minimus* inhabits diverse habitats from deserts to forests, so its presence in the assemblage is not surprising.

Eutamius dorsalis

MATERIAL.— Right dentary with P/4, M/1,/2,/3 (BYUVP 6233), right dentary with P/4, M/1 (BYUVP 6257), 2 right dentaries with M/1 (BYUVP 5974, 6304), 2 left dentaries with M/1 (BYUVP 6129, 6134). Three partial right maxillae with M1/ (BYUVP 6064, 6288, 6295) and a partial left maxilla with M1/ (BYUVP 6000) also compare favorably with this species.

DISCUSSION.— *Eutamius dorsalis* is distinctly larger than *E. minimus* and slightly larger than *E. umbrinus* (Mead et al. 1982). It has a distinct isolated mesoconid on M/1 that is lacking in *E. umbrinus* and is part of an ectolophid in *E. minimus* (Miller 1976). The M/1's of the six dentaries listed above match *E. dorsalis* in this character, and the four maxillae listed above match best in size with *E. dorsalis* but cannot be positively distinguished from *E. umbrinus*. Of the larger chipmunks, only *E.* cf. *umbrinus* was reported from Smith Creek Cave (Mead et al. 1982), and I have found only *E. dorsalis* in Crystal Ball Cave. Their present ranges help explain this difference since *E. umbrinus* only inhabits the Snake Range west of Crystal Ball Cave and *E. dorsalis* inhabits the entire range (Hall 1981). Their ranges show that *E. umbrinus* is more isolated in areas of high elevation and more commonly absent from the areas once covered by Lake Bonneville.

Family Geomyidae

Thomomys umbrinus

MATERIAL.— Anterior portion of skull with both I/'s (BYUVP 6656), anterior portion of skull with left I/ (LACM 123672), right dentary with /I, P/4, M/1 (BYUVP 6657), left dentary with P/4 (BYUVP 8283). Four palates without teeth (BYUVP 6653, 6654, 6664, 6665), 4 right dentaries without cheek teeth (BYUVP 6660, 6663, 6666, 8281), and 8 left dentaries without cheek teeth (BYUVP 6655, 6658, 6659, 6662, 6681, 7009, 7010, 8282) also compare favorably with this species.

DISCUSSION.— *Thomomys* is distinguished from other North American geomyids by the absence of a superficial groove on the anterior face of the upper incisors (illustrations in Hall 1981), and none of the I/'s listed above have this groove. *Thomomys umbrinus* differs from *T. talpoides* and *T. monticola*, the only other species of *Thomomys* living in Nevada, Utah, or surrounding areas, by having a sphenoidal fissure, by not having the palatine foramina fully anterior to the anterior openings of the infraorbital canals (Durrant 1952), and by the absence of a lingual indentation in the anterior lobe of P/4 (Hall 1946). The two *Thomomys* skulls from Crystal Ball Cave have the sphenoidal fissure, and their palatine foramina are fully anterior to the infraorbital canals. The two P/4's also lack the lingual indentation as in *T. umbrinus*. My observations and also those of Hall (1946, Fig. 308–321) indicate that *T. umbrinus* has a larger mean size than the other two species mentioned (contrary to Bergman's rule), and all the Crystal Ball Cave specimens compare best in size with the larger *T. umbrinus*.

Thomomys umbrinus is the only geomyid currently inhabiting the Snake Range, and it is a southern species, ranging from Nevada and Utah southward into Mexico (Hall 1981). *Thomomys bottae* and *T. townsendii* are now considered as subspecies of *T. umbrinus* (Hall 1981). *Thomomys talpoides*, which inhabits mountain ranges to the east and west of the Snake Range, has Nevada and Utah as almost its southern boundary and extends northward into Canada. *Thomomys talpoides* tends to inhabit higher elevations than *T. umbrinus* as well as higher latitudes. *Thomomys* cf., *talpoides* was the only geomyid reported from Smith Creek Cave (Goodrich 1965).

Hall (1946) pointed out that, although *T. umbrinus* is usually a lower-elevation species than *T. talpoides*, *T. umbrinus* is the only geomyid in the Snake Range and occurs at all elevations (but is less abundant at higher elevations than is *T. talpoides* at similar elevations in other ranges). Hall (1946) attributed this to antiquity of occupancy and proposed that *T. umbrinus*, having no competitors in the Snake Range, developed populations adapted to higher elevations. Since *T. umbrinus* was the species best adapted to the valleys surrounding the Snake Range, no species better adapted to higher elevations could pass through to their favorable habitat. This could explain why the Crystal Ball Cave assemblage suggests no northward range shift for species of *Thomomys* as it does for other groups such as lagomorphs. If Hall (1946) is right, the tentative assignment of the Smith Creek Cave specimen to *T. talpoides* (Goodrich 1965) must be in error. Another possibility is that predatory birds transported the specimen to the cave, but this seems unlikely since *T. talpoides* occurs only as close as 75 km (45 miles) to the northwest and 180 km (108 miles) to the east of Smith Creek Cave. Hall (1946) also pointed out that geomyids, as individuals, are extremely sedentary, and this could be the cause of their slow invasion and northward retreat compared to other mammals.

Family Heteromyidae

Perognathus cf. *formosus*

MATERIAL.— Partial right maxilla with P4/ (BYUVP 6682), 2 right dentaries with P/4 (BYUVP 6859, 6879), 2 right dentaries with M/2 (BYUVP 6711, 6856), left dentary with all teeth (BYUVP 6697), left dentary with P/4, M/1 (BYUVP 6786), left dentary with P/4, M/2 (BYUVP 6115).

DISCUSSION.— *Perognathus longimembris*, *P. parvus*, and *P. formosus* now inhabit the Crystal Ball Cave area, and the closest other species range more than 250 km (150 miles) to the east and south (Hall 1981). Of the three local species, *P. longimembris* can be ruled out because its M/3 is distinctly smaller than its P/4 (Hall 1981), and the BYUVP 6697 has the opposite condition. *Perognathus parvus* and *P. formosus* are very similar dentally, and the Crystal Ball Cave specimens match well with both of them. *Perognathus formosus* has a larger mean size than *P. parvus*, and the Crystal Ball Cave specimens compare best in size with *P. formosus*, although *P. parvus* and several other western species cannot be ruled out. Miller (1979) referred all the *Perognathus* specimens found at Smith Creek Cave to *P.* cf. *parvus*, but, since the identification was tentative at both caves, it does not seem wise to speculate about a possible difference between the two assemblages with respect to this genus.

Microdipodops megacephalus

MATERIAL.— Right maxilla with P4/, M1/,2/ (BYUVP 6695), right maxilla with P4/, M2/ (BYUVP 6781), right maxilla with M1/ (BYUVP 6709). Three partial right maxillae with P4/ (BYUVP 6669, 6674, 6797), a partial right maxilla with a partial M1/ (BYUVP 6759), a right dentary with /I, P/4, M/1 (BYUVP 6693), 2 right dentaries with P/4 (BYUVP 6795, 6860), and a left dentary with P/4 (BYUVP 6708) are of *Microdipodops* and compare favorably with *M. megacephalus*.

DISCUSSION.— *Microdipodops* is similar to *Perognathus* but can be distinguished dentally by the molars having a single enamel loop as opposed to the biloph nature of *Perognathus* molars. The P/4's are also distinct in being more hypsodont and having a straight posteriolabial border as opposed to the round and symmetrical nature of the *Perognathus* P/4's. *Microdipodops megacephalus* ranges throughout most of Nevada and into neighboring states including Utah, and it is currently found around Crystal Ball Cave (Hall 1981). *Microdipodops pallidus*, the only other species, occurs along the southern Nevada-California border more than 320 km (200 miles) southwest of Crystal Ball Cave (Hall 1981). *Microdipodops megacephalus* can be distinguished from *M. pallidus* by the latter's possessing a small notch in the labial side of M1/, and all the Crystal Ball Cave specimens possessing the M1/ are clearly *M. megacephalus*. *Microdipodops* cf. *megacephalus* was reported at Smith Creek Cave (Miller 1979), and all heteromyid taxa recovered were low in abundance as at Crystal Ball Cave. This low abundance is probably due to a low density in life, since even now they are rarely seen in the area.

Dipodomys microps

MATERIAL.— Two right dentaries with /I (BYUVP 6672, 8284), left dentary fragment with P/4 (BYUVP 6676). Nine maxillae without teeth (BYUVP 5593, 6667, 6668, 6670, 6675, 6677–6680) and 2 right dentaries without teeth (BYUVP 6673, 6683) also compare favorably with this taxon.

DISCUSSION.— *Dipodomys* is distinctly larger than other heteromyid genera. *Dipodomys microps* is distinguished from other species of *Dipodomys* by having chisel-shaped lower incisors (anterior face flat) rather than awl-shaped lower incisors (anterior face round), and the incisors of BYUVP 6672 and 8284 are chisel-shaped. The P/4 of *D. microps* is also distinct in having a larger and more isolated anterior loph than that of *D. ordii* or *D. merriami* but not a complete separation of lophs as in *D. deserti*, and the P/4 of BYUVP 6676 clearly matches *D. microps*. The referred specimens also match perfectly with Recent *D. microps* but lack the diagnostic teeth. Of the four species of *Dipodomys* presently living in Utah and Nevada, *D. microps* and *D. ordii* are found in the Snake

Range and *D. merriami* and *D. deserti* occur more than 200 km (125 miles) to the south and west (Hall 1981). *Dipodomys microps* has a much smaller range than *D. ordii*, occurring only in Nevada and parts of surrounding states (Hall 1981). The *Dipodomys* specimens recovered from Smith Creek Cave (Miller 1979) were referred to *D. ordii* because they had awl-shaped lower incisors. This difference between the two assemblages is difficult to explain because the range differences between these species do not suggest distinct differences in habitat preference.

Family Cricetidae

Peromyscus maniculatus

Material.— Right maxilla fragment with M1/,2/ (BYUVP 6703), left maxilla with M1/,2/,3/ (BYUVP 6782), left maxilla fragment with M1/,2/ (BYUVP 6771). Thirty-nine *Peromyscus* dentaries containing one or more molars compare favorably with *P. maniculatus* and *P. crinitus*.

Discussion.— Of the six species of *Peromyscus* that inhabit Utah and Nevada, only *P. maniculatus*, *P. truei*, and *P. crinitus* currently live around Crystal Ball Cave (Hall 1981). *Peromyscus maniculatus* was captured live inside the cave by the author in 1982 and 1983. *Peromyscus* fossils from Smith Creek Cave were not identified to the species level (Goodrich 1965, Mead et al. 1982, Miller 1979). Dental characters that distinguish species of *Peromyscus* are few and not always reliable. *Peromyscus maniculatus* and *P. truei* belong to the subgenus *Peromyscus*, which has accessory tubercles or enamel loops on the labial side of M1/ and M2/; *P. crinitus* belongs to the subgenus *Haplomyomys*, which lacks these features (Hall 1981). I found this character to be quite reliable, and the specimens listed above all have prominent cusps on M1/ and M2/. In further refinement of this character, Miller (1971, 1976) was able to separate *P. maniculatus* from all other western species of *Peromyscus* by the presence of an anteroconule on M1/ with direct attachment to the anterocone rather than being joined to it by a distinct loph as in *P. truei*. Specimens listed above fit *P. maniculatus* in this respect. Species of the subgenus *Haplomyomys* usually lack the anteroconule entirely (Hall 1981, Miller 1971, 1976). Unfortunately, excessive wear on the teeth erases this character.

Of the 40 *Peromyscus* dentaries containing one or more molars, 39 compare best in size with the smaller *P. maniculatus* and *P. crinitus*, but no character could be found to separate these species based on dentaries. Miller (1976) found the P/3's of *P. maniculatus*, *P. crinitus*, and *P. eremicus* to be relatively more reduced than *P. boylii* and *P. truei*. The 8 Crystal Ball Cave *Peromyscus* dentaries containing M/3 tend to have M/3 relatively reduced as in *P. maniculatus*, *P. crinitus*, and *P. eremicus*, and in size all the 39 dentaries listed above compare best in size with the smaller *P. maniculatus* and *P. crinitus*.

Peromyscus cf. *crinitus*

Material.— Right maxilla with M1/,2/ (BYUVP 6780), left maxilla with M1/,2/ (BYUVP 6769), left maxilla with M1/ (BYUVP 6715). Thirty-nine *Peromyscus* dentaries containing one or more molars compare favorably with *P. maniculatus* and *P. crinitus*.

Discussion.— These specimens lack accessory tubercles and enamel loops on the two principal outer angles of M1/ and M2/, so they probably belong to the subgenus *Haplomyomys* (Hall 1981). Of the two species of *Haplomyomys* found in Utah, *P. crinitus* and *P. eremicus*, the Crystal Ball Cave specimens compare better in size with the smaller *P. crinitus* (although there is considerable overlap). Some of the 39 dentaries discussed under *P. maniculatus* (above) could also belong to this species since no character was found to distinguish them based on dentaries. *Peromyscus crinitus* is presently found around the cave, but *P. eremicus* ranges only as close as 225 km (135 miles) to the south (Hall 1981), further suggesting that these specimens are *P. crinitus*.

Peromyscus cf. *truei*

Material.— Left dentary with M/1 (BYUVP 6718).

Discussion.— *Peromyscus truei* is the largest species of *Peromyscus* living in Utah and Nevada (Durrant 1952, Hall 1981), and the M/1 listed above compares well in size with this species and is larger than the mean size of *P. eremicus* and *P. boylii* and distinctly larger than any *P. maniculatus* or *P. crinitus* M/1's examined. Identification is based only on size since no other character could be found to distinguish M/1's of *Peromyscus*. This species is found throughout the Great Basin, so its presence in the assemblage is not surprising.

Neotoma lepida

MATERIAL.— Partial skull without teeth (LACM 123671), 2 partial right maxillae with M1/ (BYUVP 7045, 7065), left maxilla with M1/ (BYUVP 7154), partial left maxilla with M1/ (BYUVP 7246).

DISCUSSION.— *Neotoma lepida* and *N. cinerea* are the only species of *Neotoma* that presently inhabit the Snake Range (Hall 1946, 1981). Of three wood rats that I trapped in Crystal Ball Cave and two elsewhere on Gandy Mountain in 1982 and 1983, all were *N. lepida*. I did trap a *N. cinerea* in another cave in the Snake Range 35 km (22 miles) south of Crystal Ball Cave, so they are known to inhabit caves in the area. Miller (1979) reported both *N. lepida* and *N. cinerea* from Smith Creek Cave but did not comment on their relative abundance. Of these two species, *N. cinerea* is much more boreal than *N. lepida*, having a more northern range and being found at higher elevations (Finley 1958, Hall 1946, 1981). Durrant (1952) and Hall (1981) also reported *N. albigula*, *N. mexicana*, and *N. stephensi* living in Utah but far to the south and east of Crystal Ball Cave.

Neotoma cinerea is usually distinguishable from *N. lepida* by its larger size and deeper anterolabial reentrant angle on M1/ (Finley 1958). According to Hall (1946), the maxillary alveolar length is always 8.8 mm or less in *N. lepida* and 9.1 mm or more in *N. cinerea* for the Nevada subspecies, and Finley (1958) reported only a slight overlap for the Colorado subspecies. The three other Utah species of *Neotoma* are intermediate in size between *N. lepida* and *N. cinerea*, and *N. albigula* has the M1/ pattern of *N. lepida* whereas *N. mexicana* and *N. stephensi* have the M1/ pattern of *N. cinerea* (Finley 1958). Because these are the most diagnostic characters, only maxillae with M1/ and/or a measurable alveolar length were considered.

The Crystal Ball Cave specimens listed above compare best in size with *N. lepida*, the only species of *Neotoma* known to presently inhabit the cave. Maxillary alveolar lengths of *Neotoma* specimens from the cave show a strongly bimodal distribution, suggesting that *N. albigula*, *N. mexicana*, and *N. stephensi* are not represented since they are intermediate in size between *N. lepida* and *N. cinerea*. The shallow anterolabial reentrant angle of the M1/'s also compares favorably with *N. lepida*. The scarcity of *N. lepida* specimens in the assemblage suggests that this species probably has not always inhabited the cave as it does now.

Neotoma cinerea

MATERIAL.— Anterior portion of skull with both I/, M1/,2/ (BYUVP 7384), maxilla pair with all teeth except left I/ (BYUVP 7281), maxilla pair with right M1/,2/,3/, left M1/,2/ (BYUVP 7282), maxilla pair with both M1/,2/ (BYUVP 7067), maxilla pair with right M1/,2/ (BYUVP 7015), maxilla pair with left M1/ (BYUVP 7213), 9 right maxillae with M1/,2/,3/ (BYUVP 7136, 7149, 7158, 7167, 7214, 7248, 7254, 7314, 7320), 3 right maxillae with M1/ (BYUVP 7273, 7316, 7330), 25 partial right maxillae with M1/ (BYUVP 7014, 7018, 7024, 7038, 7046, 7104, 7114, 7125, 7134, 7138, 7147, 7170, 7177, 7180, 7182, 7197, 7204, 7216, 7242, 7247, 7249, 7276, 7344, 7348, 7349), ·10 right maxillae without teeth (BYUVP 7255, 7343, 7353, 7367, 7377, 8286–8290), 7 left maxillae with M1/,2/,3/ (BYUVP 7095, 7212, ,7250, 7257, 7274, 7376, 7379), 4 partial left maxillae with M1/,2/ (BYUVP 7101, 7174, 7179, 7324), partial left maxilla with M1/,2/ (BYUVP 7017), 34 partial left maxillae with M1/ (BYUVP 7021, 7061, 7062, 7072, 7073, 7087, 7099, 7106, 7133, 7140, 7142, 7144, 7145, 7151, 7162–7164, 7172, 7175, 7183, 7189, 7200, 7205, 7217, 7220, 7225, 7267, 7300, 7317, 7318, 7322, 7351, 7362, 7371), 6 left maxillae without teeth (BYUVP 7171, 7346, 8291–8294). Another approximately 200 maxillae, 200 dentaries, and 2000 isolated molars compare best with this species.

DISCUSSION.— *Neotoma cinerea* is recognized by its large size and deep anterolabial reentrant angle on M1/ as discussed above.

Neotoma cinerea has the largest mean size of any species of *Neotoma*, and all the specimens listed above match Recent *N. cinerea* in size and have the deep anterolabial reentrant angle on M1/ when this tooth is present. This makes *N. cinerea* the second best represented species in the Crystal Ball Cave assemblage after *Spermophilus townsendii*. The fact that *N. cinerea* is abundant in the assemblage but not found in the cave now, whereas *N. lepida* is rare in the assemblage but now the only wood rat living in the cave, suggests that a replacement of *N. cinerea* by *N. lepida* has recently taken place in the area. The great abundance of *N. cinerea* remains at sites 1 and 2 of Crystal Ball Cave also helps substantiate my hypothesis that wood rats were the primary means of transporting fossils, especially of large mammals, into the cave. The dominance of *N. cinerea* over *N. lepida* in the assemblage suggests that *N. cinerea* was the primary species involved in this transport.

The ecological differences between *N. cinerea* and *N. lepida* have significance both to the replacement of the former species by the latter and to the accumulation of fossils in the cave. Finley (1958), in his detailed study of Colorado wood rats, found den sites to be the most limited resource for all species. Since all wood rats prefer the same basic types of den sites, namely rocky crags and caves, multiple species are rarely found coexisting (Finley 1958). This suggests that, when conditions at Crystal Ball Cave reached a threshold where they favored *N. lepida* over *N. cinerea*, the replacement took place quickly. *Neotoma cinerea* prefers higher elevations and latitudes than *N. lepida*, and hot summers in arid regions seem to be a limiting factor for this species (Finley 1958, Hall 1981). The changing conditions that led to the replacement of *N. cinerea* by *N. lepida* may have been the increase in temperature and decrease in moisture at the close of the Pleistocene, the shift in vegetation caused by it, or both. Regarding food, Finley (1958) stated that *N. cinerea* prefers soft-leaved shrubs, forbs, and montane conifers, whereas *N. lepida* prefers xerophytic shrubs, forbs, cacti, and shrubby trees.

Species of *Neotoma* differ somewhat in den preferences and collecting habits. Finley (1958) stated: "Dens of *N. cinerea* are usually in high vertical crevices in cliffs or caves, whereas those of . . . *N. lepida* are usually in low horizontal crevices or under boulders or large fallen blocks. Dens of [*N.*] *cinerea* usually contain larger accumulations of sticks and bones." That *N. cinerea* collects more material, especially bone, is very significant since I consider wood rats as the primary mechanism of fossil deposition at Crystal Ball Cave. This suggests that the rate of bone deposition decreased when *N. lepida* replaced *N. cinerea*, and it helps explain why many elements of the present local fauna are so poorly represented in the assemblage and why all the dated fossils are Late Pleistocene rather than Recent in age.

A replacement of *N. cinerea* by *N. lepida* parallels the replacement of *Sylvilagus nuttallii* by *S. audubonii* and *Lepus townsendii* by *L. californicus* (discussed above) and helps confirm that a warming trend took place in the recent past. Although *N. cinerea* still lives in the area, it seems to have been driven to higher elevations in the Snake Range.

Ondatra zibethicus

MATERIAL.— Palate without teeth (BYUVP 7383), partial right dentary with anterior $\frac{2}{3}$ of M/1 (BYUVP 7391).

DISCUSSION.— *Ondatra* is easily distinguished from other microtine rodents by its large size combined with rootless molars. *Ondatra zibethicus* is now considered the only extant species of *Ondatra* (Hall 1981), and the Crystal Ball Cave specimens are indistinguishable from this species. A number of fossil species have been named, but there is considerable confusion about their status (Miller 1976). All the extinct species considered valid by Semken (1966) and Nelson and Semken (1970) are smaller than *O. zibethicus*. The Crystal Ball Cave dentary is almost as large as the largest *O. zibethicus* to which it was compared. The M/1 is 7.9 mm long and 2.5 mm wide which best matches measurements taken from Wisconsinan-age *O. zibethicus* specimens (Nelson and Semken 1970). The palate is slightly smaller than the mean of *O. zibethicus* but well within its range of variation.

Ondatra zibethicus has not been reported living near Gandy but occurs as close as 56 km (35 miles) to the northeast and 160 km (100 miles) to the south (Hall 1981). Since *Ondatra* is a reliable indicator of permanent water (Nelson and Semken 1970), the retreat of Lake Bonneville and loss of perennial streams in the area probably lead to its extirpation from the Snake Range.

Microtus cf. *longicaudus*

Material.— Two left M3/'s (BYUVP 6940, 6981), 7 right M/3's (BYUVP 8220–8226), 15 left M/3's (BYUVP 7002, 8227–8241). Numerous other partial jaws and isolated molars cannot be distinguished from *Lagurus* but lack characters that would assign them to other species of *Microtus*, some of which are likely *Microtus* since over a third of the microtine M/3's belong to *Microtus*. Among these are a partial skull with both M1/,2/ and the posterior incisive foramina (BYUVP 8285) and a right maxilla with M1/,2/ (BYUVP 6943).

Discussion.— *Microtus* differs from *Lagurus*, the only other microtine of its size with rootless molars, in having 3 transverse loops on M/3 rather than 4 prisms, some of which are closed triangles, and in having a large semicircular posterior loop on M3/ rather than a simple elongate loop (Hall 1981). The 2 M3/'s and 22 M/3's from Crystal Ball Cave listed above clearly match *Microtus* in this respect. There are many species of *Microtus*, some of which have distinct dental characteristics and some of which do not.

The only two species of *Microtus* now inhabiting the Snake Range are *M. longicaudus* and *M. montanus*, and no character could be found to distinguish them dentally. The incisive foramina of *M. longicaudus* are not constricted posteriorly as are those of *M. montanus*, but they differ from those of *Lagurus* only in having slightly curved rather than straight external margins. Since only the posterior end of the incisive foramina are found on skulls that could be *Microtus* from Crystal Ball Cave, skulls of *M. longicaudus* in the collection are indistinguishable from *Lagurus*. Of 13 skulls containing incisive foramina that may be *Microtus*, 2 have constricted incisive foramina as in *M. montanus* (listed below), and 11 compare well with *M. longicaudus* and *Lagurus*.

Three other species of *Microtus* presently occur in Utah but not in the Snake Range: *M. pennsylvanicus* and *M. richardsoni* in the central mountain ranges and *M. mexicanus* in the southwestern corner of the state. *Microtus pennsylvanicus* has a posterior loop on M2/ not found in other species, and this character was only found on one specimen (listed below). *Microtus richardsoni* is distinctly larger than the other species described here, and none of the microtine specimens from Crystal Ball Cave are large enough to compare with it. *Microtus mexicanus* is dentally indistinguishable from *M. montanus* and *M. longicaudus*, and its incisive foramina are identical to *Lagurus* and similar to *M. longicaudus*.

The specimens listed above are identical to Recent specimens of *M. longicaudus*, *M. mexicanus*, and more distant ranging species. But since *M. longicaudus* presently occurs at Crystal Ball Cave whereas *M. mexicanus* occurs more than 400 km (250 miles) to the southeast (Hall 1981), and because the general trend in the region is for range boundaries to be migrating northward, the Crystal Ball Cave specimens (except the few discussed below) are referred to *M. longicaudus*.

Microtus cf. *montanus*

Material.— Two partial palates without teeth, which include the posterior end of the incisive foramina (BYUVP 8218, 8219).

Discussion.— *Microtus montanus* is the only microtine of its size presently occurring in Utah or Nevada with incisive foramina that abruptly constrict posteriorly and are narrower posteriorly than anteriorly. The posterior ends of the incisive foramina in these two specimens are too narrow to be *M. longicaudus*, *M. pennsylvanicus*, *M. mexicanus*, or *Lagurus curtatus*. *Microtus townsendii* and *M. oregoni* also have incisive foramina like *M. montanus*, but they both occur only along the Pacific Coast from northern California to southern British Columbia. Since *M. montanus* presently occurs in the Snake Range (Hall 1981), the Crystal Ball Cave specimens are referred to it. *Microtus montanus* tends to occur at higher elevations than other species of *Microtus* in Utah (Durrant 1952), so its presence in the assemblage suggests that conditions at the cave during the Late Pleistocene may have been like those of higher elevations in the Snake Range now.

Microtus cf. *pennsylvanicus*

MATERIAL.— Partial skull with right M1/,2/ (BYUVP 6973).

DISCUSSION.— *Microtus pennsylvanicus* is unique in having a rounded posterior loop behind the 4 closed angular sections of M2/. This single specimen from the assemblage has this posterior loop, but the loop is not completely closed off from the preceding triangle as in the Recent specimens to which it was compared. Since the distinguishing character is not fully developed, the specimen is only referred to *M. pennsylvanicus*. This species is not presently found in the Snake Range, but it occurs 190 km (114 miles) east of Crystal Ball Cave in the mountains of central Utah and is a northern species (Hall 1981). Considering the climatic shifts since the recession of Lake Bonneville, it is not unlikely that it could have inhabited the Snake Range during the Late Pleistocene.

Lagurus curtatus

MATERIAL.— Skull with right I/, M2/,3/, left I/, M1/,2/ (BYUVP 6899), left dentary with M/1,/2,/3 (BYUVP 6977), left dentary with M/2,/3 (BYUVP 6986), 28 right M/3's (BYUVP 8242–8270), 9 left M/3's (BYUVP 8271–8280). Numerous partial jaws and isolated molars may be *L. curtatus* but cannot be distinguished from *Microtus longicaudus* (as discussed above).

DISCUSSION.— The differences between *Lagurus* and *Microtus* are discussed above. *Lagurus curtatus*, the only North American species of *Lagurus*, is distinguished from Old World representatives by having four instead of five closed triangles on M/3 and cement present in the reentrant angles of the molars (Hall 1981). This species presently occurs in the Snake Range and northward into Canada (Hall 1981). *Lagurus* specimens are nearly twice as abundant as those of *Microtus* in the assemblage, but, since no information on their Recent relative abundance or habitat differences could be found, it is difficult to understand the reason for this.

Order Carnivora

Family Canidae

Canis cf. *latrans*

MATERIAL.— Lower incisor (BYUVP 7459), right C/1 (LACM 123675), partial left M/1 (BYUVP 7460). The frontal region of a skull (LACM 123676) and an anterior fragment of a left dentary without teeth (BYUVP 7458) also compare favorably with this species.

DISCUSSION.— These specimens are indistinguishable from specimens of Recent *C. latrans*, generally recognized as the only species of coyote in the Pleistocene or Recent (Giles 1960). Dentally, *C. latrans* falls within the wide range of variation of the domestic dog, *C. familiaris* (Anderson 1968), so the possibility that the Crystal Ball Cave specimens are *C. familiaris* cannot be totally eliminated. Nevertheless, *C. latrans* is presently very abundant around the cave (J. C. Bates 1983, pers. comm., Hall 1981) and has been recognized from nearby Pleistocene assemblages that have better stratigraphic control (Kurten and Anderson 1972, Miller 1979), so there is no reason to believe it would not be found in the assemblage. Also, domestic dogs tend to have many more tooth malformations than coyotes (Anderson 1968), and none are seen in the Crystal Ball Cave specimens. Lack of human fossils and artifacts at Crystal Ball Cave makes domestic dogs less likely to be present than at sites that contain such remnants of human occupation. Although residents of Gandy have domestic dogs that sometimes roam on Gandy Mountain, the lack of any canid specimens in the assemblage that cannot be referred to native species also supports the conclusion that the Crystal Ball Cave specimens are *C. latrans*.

Canis cf. *lupus*

MATERIAL.— Partial right M1/ (BYUVP 7455), left P/1 (BYUVP 7457), posterior end of right M/1 (BYUVP 7456), left M/1 (LACM 123674), axis (LACM 123710).

DISCUSSION.— Identification of these canid fossils is based on their size, being substantially larger than *C. latrans* but considerably less robust than *C. dirus*. They do, however, fit within the large size range of *C. familiaris*, so the identification must be tentative. Goodrich (1965) reported *C. lupus* from Smith Creek Cave but did not describe the material. *Canis lupus* has been reported living in the Snake Range in Recent times (Hall 1981), although man has now reduced its range and numbers considerably.

Vulpes vulpes

Material.— Skull with right P1/,2/,4/, left P4/, M2/ (BYUVP 8299), posterior portion of right maxilla with M1/,2/ (BYUVP 7466), partial left maxilla with M1/,2/ (BYUVP 7467), 2 right C1/'s (BYUVP 7468, 7470), left C1/ (BYUVP 7469), right P4/ (BYUVP 7474), left P4/ (BYUVP 7471), right dentary with M/2 (BYUVP 7461), posterior portion of right dentary with P/4, M/1,/2 (BYUVP 7463), left dentary with M/1,/2 (BYUVP 7464), anterior portion of left dentary with M/1,/2 (BYUVP 7462), right P/4 (BYUVP 7475), left P/4 (BYUVP 7472). An anterior fragment of a right dentary without teeth (BYUVP 7465) and an anterior fragment of a left dentary without teeth (BYUVP 7476) also compare favorably with this species.

Discussion.— *Vulpes* is distinguished from *Urocyon* by the configuration of the crest on the top of the skull and the lack of a prominent "step" on the posteroventral margin of the dentary. The ventral margin of the dentary of *Vulpes* curves upward posteriorly beginning at the posterior end of the tooth row, but in *Urocyon* it remains uncurved well behind the tooth row all the way to the "step." *Urocyon*, which now ranges from the cave site southward and throughout North America, is intermediate in size between *V. vulpes* and *V. velox*. Four of the Crystal Ball Cave specimens include the posterior dentary and lack the "step" characteristics of *Urocyon*, and all the Crystal Ball Cave specimens are larger than the largest *Urocyon* specimen examined but compare well in size and shape to *V. vulpes*.

Vulpes vulpes does not presently occur around Crystal Ball Cave but *V. velox* and *U. cinereoargenteus* do (J. C. Bates 1983, pers. comm., Hall 1981). The presence of the more northern *V. vulpes* but not the more southern *U. cinereoargenteus* in the cave assemblage represents a northward shift of the boundary between these two species. The ranges of *V. vulpes* and *U. cinereoargenteus* do overlap to a degree now, but in the western United States the overlap is not great, and where it does occur *V. vulpes* favors the higher elevations and *U. cinereoargenteus* the lower elevations (Hall 1981). Based on range maps in Hall (1981), the range of *V. vulpes* in the western United States is quite scattered, suggesting that it is relectual and that this species is diminishing in numbers there. *Urocyon cinereoargenteus* has a distinct northern boundary across Utah and Nevada with no remnant populations, suggesting that this species has been making a northward invasion. The Crystal Ball Cave assemblage confirms that *U. cinereoargenteus* has been expanding its range at the expense of *V. vulpes*.

Vulpes velox

Material.— Left dentary with P/3 and partial M/1 (BYUVP 7477), posterior portion of left M/1 (BYUVP 7479). A partial left dentary with M/2 (BYUVP 7478) also compares favorably with this species.

Discussion.— *Vulpes velox* and *V. macrotis* are now considered conspecific (Hall 1981). The dentary (BYUVP 7477) lacks the "step" of *Urocyon*, and the M/1 lacks a small cuspule found on the posterolabial margin of the main cusp of all the *Urocyon* specimens but none of the *Vulpes* specimens examined. The Crystal Ball Cave specimens listed above are smaller than *U. cinereoargenteus* but may be similar in size to the smaller *U. littoralis*, which is known only from islands along the coast of southern California (Miller 1971).

Since *V. velox* still lives around Crystal Ball Cave (J. C. Bates 1983, pers. comm.), its presence in the assemblage is not surprising. Its low frequency compared to the now extirpated *V. vulpes* suggests that it may not have always inhabited the area, may have inhabited it in much smaller numbers, or may have had a different microhabitat causing it to frequent the cave area less than *V. vulpes*. The ranges of *V. vulpes* and *V. velox* presently overlap to a degree, especially in the midwest, but in the western United States this overlap is small (Hall 1981). Although *V. velox* occurs in the Snake Range now, it is a more southern species than *V. vulpes*, so its northern range extentions may be of Recent age.

Family Mustelidae

Mustela cf. *frenata*

Material.— Left M1/ (BYUVP 7487), right dentary with P/2,/3, M/1,/2 (BYUVP 7483), partial right dentary without teeth (BYUVP

7484), left dentary with M/1,/2 (BYUVP 7488), left dentary with M/1 (BYUVP 7485), partial left dentary with M/1,/2 (BYUVP 7486).

DISCUSSION.— All these *Mustela* specimens compare best in size with *M. frenata*, which presently lives around Crystal Ball Cave. The size range of *M. frenata* is overlapped by the smaller but more variable *M. erminea* (Kurten and Anderson 1980), which also ranges in the cave area (Hall 1981). The specimens could belong to *M. erminea* since this species is dentally similar to *M. frenata*. *Mustela rixosa* is always smaller and *M. nigripes* and *M. vison* are always considerably larger than the Crystal Ball Cave specimens. *Mustela frenata* was the most abundant mustelid at Smith Creek Cave, but *M. erminea* was also present (Miller 1979). Since all the Crystal Ball Cave specimens fall in the narrow size range of *M. frenata*, they are referred to this species.

Mustela cf. *vison*

MATERIAL.— Left M1/ (BYUVP 7482). A juvenile left dentary without teeth (BYUVP 7491) also compares well with this species.

DISCUSSION.— This isolated tooth was compared to a variety of Recent mustelids and other small carnivores and found most similar to *M. vison*. This is North America's largest extant species of *Mustela* (although the extinct sea mink, *M. macrodon*, was larger) and is distinctly larger than, but similar in shape to, *M. frenata* (described above). *Mustela vison* was recovered from Smith Creek Cave (Miller 1979) and presently occurs 160 km (100 miles) north and east of Crystal Ball Cave (Hall 1981), but it does not currently live in the Snake Range. This species requires lakes or streams to survive (Hall 1946), so its extirpated nature in the Snake Range may have been due to the recession of Lake Bonneville and/or loss of perennial streams in the area at the end of the Pleistocene.

Mustela vison is sometimes confused with *M. nigripes* since both are of similar size (Kurten and Anderson 1980), and no distinction in isolated molars could be found in the literature. *Mustela nigripes* is currently endangered, and no comparative material was available. It has never been reported from western Utah or Nevada, so the Crystal Ball Cave specimens are referred to *M. vison*, which is known to have lived in the area.

Martes americana

MATERIAL.— Left dentary with M/1 (BYUVP 7480), left M/1 (BYUVP 7481). The anterior portion of a right dentary without teeth (BYUVP 7489) and the posterior portion of a right dentary without teeth (BYUVP 7523) probably also belong to this taxon.

DISCUSSION.— Anderson (1970), in her systematic review of the genus *Martes*, considered *M. nobilis* (found in four caves in Wyoming, Idaho, and northern California) to be a distinct species from *M. americana*. Of the two, *M. nobilis* is larger, and its lower carnasial has a relatively shorter trigonid. The lower canines of *M. nobilis* sometimes have faint grooves on the external surface not found in *M. americana* (Anderson 1970). The only other species of *Martes* presently living in Utah is *M. pennanti*, the fisher. It is considerably larger than *M. americana*, *M. nobilis*, and the Crystal Ball Cave specimens. Neither *M. americana* nor *M. pennanti* currently live in the Snake Range, but both occur in the mountains of central Utah and northward.

BYUVP 7480 is as large as the largest *M. americana* specimen to which it was compared, and, judging from the incisor socket, its incisor was slightly larger. The other specimens are the same size as most Recent *M. americana* specimens. Both lower carnasials match perfectly in shape with *M. americana* and do not show a relatively shorter trigonid, so they are assigned to *M. americana*. A right M1/ of *M. nobilis* was recovered from Smith Creek Cave (Miller 1979), but *M. americana* has never been reported. The ecological and chronological separation of these two species in the Snake Range is, therefore, problematic. Brown (1971) listed *M. americana* as one of eight species of boreal mammals that presently range in the Sierra Nevada and the Rocky Mountains but on none of the isolated Great Basin ranges in between. This citing demonstrates that *M. americana* did range at least as far east in the Great Basin as the Snake Range before becoming extirpated.

Brachyprotoma brevimala, sp. nov.

TYPE.— Anterior portion of skull including a complete palate except the most posterior

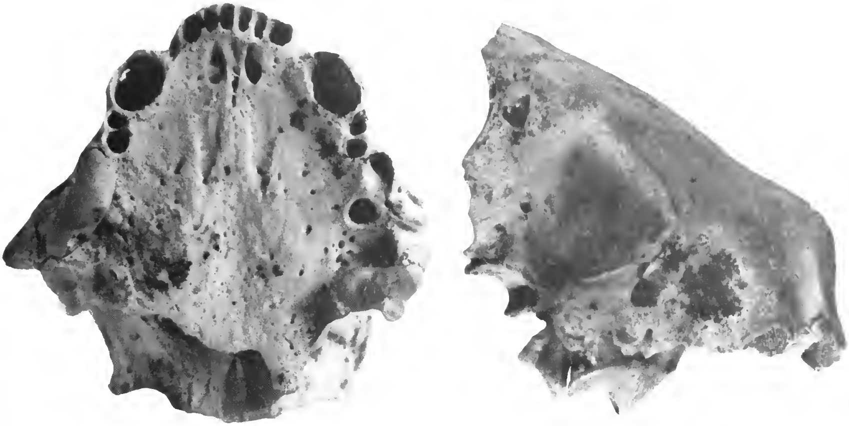

Fig. 5. Photographs of the type specimen of *Brachyprotoma brevimala* (BYUVP 7490) in palatal and right side view (3X).

(smallest) socket of each M1/ and extending posteriorly to include the entire anterior wall of the braincase (BYUVP 7490, Fig. 5). Only the right P4/ was found *in situ*, but a right and left M1/ (previously cataloged as BYUVP 7492 and 8298, respectively) fit perfectly into the sockets of the type specimen, where they have been permanently mounted. The type specimen is of a young adult based on complete fusion of the premaxillae, maxillae, nasals, and frontals and on lack of significant tooth wear. Both the skull and isolated M1/'s were recovered from site 1, channel A, Crystal Ball Cave, Millard County, Utah (Figs. 1 and 3) by Wade E. Miller and party 19 March 1977. The type specimen is housed at the Brigham Young University Vertebrate Paleontology Laboratory.

DIAGNOSIS.— *Brachyprotoma brevimala* has a short face and a maxillary tooth formula of I3/-3/, C1/-1/, P2/-2/, M1/-1/ as in *B. obtusata*. Face and maxillary dental measurements average 15% smaller than those of *B. obtusata*. *Brachyprotoma brevimala* is distinguished from *B. obtusata* by P4/ being transversely narrower and having a more posteriorly directed lingual cusp and by M1/ being more reduced and distinctly shorter anteroposteriorly. In other known characters *B. brevimala* is equivalent to *B. obtusata*. *Brachyprotoma brevimala* has the most reduced P4/ and M1/ and the shortest maxilla of any known skunk, and it is for this latter character that the species is named.

DESCRIPTION.— The maxillary dental formula of I3/-3/, C1/-1/, P2/-2/, M1/-1/ is known among the mustelids only in two genera of skunks, *Conepatus* and *Brachyprotoma* (although I found one abnormal Recent *Spilogale putorius* specimen with this formula). The Crystal Ball Cave specimen is clearly a skunk (subfamily Mephitinae) based on the presence of only two pairs of upper premolars (mephitines have two or three, all other mustelids have three or four), the small size (only the subfamilies Mustelinae and Mephitinae have such small adult individuals), the lingual cusp of P4/ extending from the middle of the tooth (as opposed to the more anterior extention in the mustelines), M1/ being anteroposteriorly shorter labially than lingually (mustelines have the opposite condition), and the internal nares extending almost as far anteriorly as the posterior end of the tooth row (they are much more posterior in mustelines).

Compared to extant mephitines, the Crystal Ball Cave specimen represents an individual of similar size to *Spilogale* but much smaller than *Conepatus* and *Mephitis*. The palate is shorter and wider than that of *Spilogale putorius*, but the interorbital breadth shows that the type specimen represents a larger individual than the average *S. putorius*. The P4/ is similar to *Spilogale*, differing only in having the lingual cusp slightly more posterior, but it is proportionally much narrower than the P4/ of *Mephitis* and *Conepatus*. The M1/'s are proximo-distally shorter than any of the living mephitines (especially *Conepatus* and *Mephitis* that have large square M1/'s) and are closest to *Spilogale* in shape and cusp pattern. The rostrum of the type specimen is shorter than that of *Spilogale*, matching that of *Conepatus* in proportions. The external nare is steep as in *Conepatus*, but it is relatively small and round as in *Spilogale*. Both infraorbital canals are single rather than double or triple, a species-diagnostic character in *Conepatus* (Hall 1981) but variable in *Mephitis* and *Spilogale*.

In addition to the three extant genera, three Pleistocene skunk genera have been named: *Buisnictis*, *Brachyprotoma*, and *Osmotherium* (Kurten and Anderson 1980). *Osmotherium* can be ruled out since it is large and very similar to *Mephitis* (Kurten and Anderson 1980), the living skunk genus that is most distinct from the Crystal Ball Cave specimen. Both *Buisnictis* and *Brachyprotoma* are small and have proportionally short jaws like the Crystal Ball Cave specimen. *Buisnictis* has been recovered from Late Pliocene deposits of southwestern Idaho (Bjork 1970) and Middle Pliocene to Early Pleistocene deposits of Kansas and Oklahoma (Hibbard 1941, 1950, 1954), but it has no record in the Late Pleistocene or Recent. *Buisnictis* has a short jaw with crowded premolars, but it differs from the Crystal Ball Cave specimen in having three pairs of upper premolars instead of two (Kurten and Anderson 1980). Based on an illustration by Hibbard (1954), the P4/ of *Buisnictis* has its lingual cusp extending from the anterior part of the tooth as in the mustelines, and the M1/ is distinctly longer than that of the Crystal Ball Cave specimen. These morphologic and age differences show that the Crystal Ball Cave specimen is distinct from *Buisnictis*.

The Crystal Ball Cave specimen matches the genus *Brachyprotoma* in having short jaws, only two pairs of upper premolars, P4/ and M1/ similar in shape and cusp pattern to *Spilogale*, and in the age of deposits in which they have been recovered. Until recently *Brachyprotoma* was only known from a few Early Pleistocene to Early Recent age cave deposits in the eastern United States. But during the period of this study, P. M. Youngman (1984, pers. comm.) recovered several *Brachyprotoma* specimens from two fossil sites in the Yukon Territory of Canada. Although no previous *Brachyprotoma* specimens have been reported closer than 1880 km (1130 miles) from Crystal Ball Cave, morphology clearly allies the Crystal Ball Cave specimen with this genus. But there are specific differences between the Crystal Ball Cave specimen and other skulls that have been assigned to the genus *Brachyprotoma*. To test the amount of variation to be expected within a species of skunk, 73 specimens of Recent *Spilogale putorius* were measured, 60 from the Harvard University Museum of Comparative Zoology and 13 from the Brigham Young University Monte L. Bean Museum. *Spilogale putorius* makes a good standard for the expected individual variation in species of *Brachyprotoma*, both because *Spilogale* is probably the most closely related extant genus to *Brachyprotoma* and because *S. putorius* borders on being divisible into multiple species (although most workers presently consider it a single species). Based on the great amount of variation seen between the Crystal Ball Cave specimen and other skulls assigned to the genus *Brachyprotoma* compared with the amount of variation seen among individuals of *S. putorius*, I believe the Crystal Ball Cave specimen warrants the status of a new species.

The *B. brevimala* type is smaller than specimens of *B. obtusata* in most measured characters, averaging about 15% smaller (Table 3). The greatest differences occur in P4/ and M1/, which are the most varied maxillary teeth between skunk taxa. The mean length of P4/ in *B. obtusata* is only 7% greater than in *B. brevimala*, although the mean width is 22% greater. The lingual cusp of P4/ in *B. brevimala* also points more posteriorly than in *B. obtusata*, being nearer M1/ at its lingual tip rather than closer at its base or parallel as in *B. obtusata*. The M1/ of *B. obtusata* is 16% transversely wider on the average, but the labial anteroposterior length is 30% greater and the lingual anteroposterior length is 59% greater than in the *B. brevimala* type on the average.

TABLE 3. Skull measurements of *Brachyprotoma* specimens and mean skull measurements of *Brachyprotoma obtusata* and *Spilogale putorius*. Brigham Young University Vertebrate Paleontology (BYUVP) 7490 is from Crystal Ball Cave, Utah. American Museum of Natural History (AMNH) 12426 and 11772 are from Connard Fissure, Arkansas (Brown1908, Hall 1936). U.S. National Museum (USNM) 8155 is from Cumberland Cave, Maryland (Gidley and Gazin 1938, Hall 1936). Carnegie Museum (CM) 11057A and 20233 are from Frankstown Cave, Pennsylvania (Hall 1936, Peterson 1926, P. M. Youngman 1984, pers. comm.). A skull misidentified as Carnegie Museum (CM) 308 (here listed as Cra. Pit) is from Crankshaft Pit, Missouri (Oesch 1967, Parmalee et al. 1969). Starred measurements are based on photos only. Measurements are in millimeters. The coefficients of variability (C.V.) have been multiplied by 100.

Location of measurement	BYUVP 7490	AMNH 12426	AMNH 11772	USNM 8155	CM 11057A	CM 20233	Cra. Pit	*B. obtusata* Mean	*B. obtusata* C.V.	*S. putorius* Mean	*S. putorius* C.V.
Width between orbits	17.1	18.0	—	18.2	—	17.0	—	17.7	3.63	17.0	7.52
Width between outer molars	19.8	20.5	—	20.1	—	19.6	—	20.1	2.25	19.3	6.62
Length of rostrum to internal nare	18.6	17.0*	18.0*	—	—	17.4	—	17.5	2.88	20.3	8.49
Length of cheek teeth series	11.2	11.0*	12.1	12.2	—	11.7	14.2*	12.2	9.75	14.2	6.80
P4/ anteroposterior length	5.7	5.9	6.2	6.2	6.4*	5.7	6.3*	6.1	4.32	6.0	8.80
P4/ greatest transverse width	3.3	3.8	3.9	3.9	4.0*	3.5	4.5*	3.9	8.30	3.7	9.97
M1/ labial anteroposterior length	3.0	3.8	4.1	4.0	3.8*	3.9	3.9*	3.9	2.98	4.8	7.96
M1/ lingual anteroposterior length	2.2	3.0	3.3	3.8	3.5*	3.5	3.6*	3.5	7.94	4.0	9.16
M1/ greatest transverse width	5.0	5.7	6.0	6.3	5.8*	5.3	5.7*	5.8	5.77	5.7	6.97

Since there is only minor variation in these characters among *B. obtusata* skulls (Table 3) but distinct difference between them and the Crystal Ball Cave specimen, and because the differences between the *B. brevimala* type and specimens of *B. obtusata* are far greater than would be expected within a species (based on the variation found among 73 individuals of *Spilogale putorius*, the most closely related extant species), erection of a new species for the Crystal Ball Cave specimen is clearly justified.

DISCUSSION.— *Brachyprotoma* specimens have been previously recovered from the following deposits of Early Pleistocene to Early Recent age: Port Kennedy Cave and Frankstown Cave, Pennsylvania (Cope 1899, Peterson 1926), Cumberland Cave, Maryland (Gidley and Gazin 1938), Crankshaft Cave and Brynjulfson Cave, Missouri (Oesch 1967, Parmalee and Oesch 1972, Parmalee et al. 1969), Connard Fissure, Arkansas (Brown 1908), and two sites in northern Yukon Territory, Canada (P. M. Youngman 1984, personal communication). Most of these specimens are lower jaws, and the only seven skulls (or skull fragments) that have been previously reported are Carnegie Museum 11057A and 20233, American Museum of Natural History 11772 and 12426, U.S. National Museum 8155 and 11960, and a specimen identified as Carnegie Museum 308 by Oesch (1967) but which does not correspond to that number in the Carnegie Museum catalogs (M. R. Dawson 1984, pers. comm.). Parmalee et al. (1969) illustrated this latter specimen but did not identify it by catalog number.

Cope (1899) named *Mephitis* (*Spilogale*) *obtusatus* for a single small dentary from Port Kennedy Cave, but E. D. Cope died before the completion of this paper, and a footnote stated that "none of the specimens labelled by Prof. Cope bear this name." Brown (1908) named the genus *Brachyprotoma*, and he considered *M. obtusatus* to belong to this genus as well as *M. fossidens* and *M. leptops*, two species named by Cope previous to the naming of *M. obtusatus*. From Connard Fissure Brown (1908) reported *B. fossidens*, *B. leptops*, and *B. obtusata* based on dentaries, and he named *B. pristina* based on two partial skulls and three dentaries (the skull cataloged as American Museum of Natural History 12426 is the type for the type species of this genus) and *B. spelaea* based on one dentary. The dentaries Brown (1908) identified as *B. fossidens* and *B. leptops* are far too large to belong to the same genus as the small specimens he identified as *B. obtusata*, *B. pristina*, and *B. spelaea*, and no one since has considered these two species as belonging to the genus *Brachyprotoma*. Later Hay (1923) named *B. putoria* from Frankstown Cave.

The naming of multiple species of *Brachyprotoma* in the early publications listed above has been widely criticized by later workers because the amount of variation among specimens is less than that seen within living species. Hall (1936) and Kurten and Anderson (1980) considered the genus *Brachyprotoma* to be clearly monotypic, with the only valid species being *B. obtusata*, the earliest named species that can be applied to the genus. The *Brachyprotoma* skull from Crystal Ball Cave is the first specimen of *Brachyprotoma* distinct enough from *B. obtusata* to warrant the erection of an additional species of this genus.

Concerning the paleoecology of *Brachyprotoma*, Kurten and Anderson (1980) stated that this genus has always been associated with boreal faunas, although other skunk genera were also recognized at each site. This matches the "more boreal than present" nature of the Crystal Ball Cave assemblage and suggests that the post-Pleistocene climatic shift may have lead, directly or indirectly, to the extinction of *Brachyprotoma*. Since fossils of *Brachyprotoma* are only found in a few deposits and even then are few in number, this genus probably never had a high density of individuals in life.

The *Brachyprotoma brevimala* type was first misidentified as *Spilogale* (Heaton 1984), the most similar living genus. Miller (1982) reported cf. *Spilogale* from Crystal Ball Cave, possibly based on this same specimen. *Mephitis* was also mentioned in my preliminary report (Heaton 1984), but further examination proved that the anterior right dentary (BYUVP 7489) upon which the identification was based was equally referable to *Martes americana*, which is represented by additional material. Although both *Mephitis mephitis* and *Spilogale putorius* (*gracilis*) now inhabit the Snake Range (Hall 1981), and *Spilogale* has been recovered from deposits over 12,000 years old in Smith Creek Cave (Mead et al. 1982), their presence is unconfirmed in the Crystal Ball Cave assemblage.

Since *Brachyprotoma* seems to have lived contemporaneously with other skunk genera, it is interesting to speculate about how their niches varied. All living skunks tend to be nocturnal and omnivorous, so they are rarely tied to specific foods or habitats. Minor niche differences do occur between living North American genera: *Spilogale* is the most carnivorous, *Mephitis* the most herbivorous, and *Conepatus* the most insectivorous. *Spilogale* has narrow sharp teeth, *Conepatus* at the other extreme has very broad teeth, and *Mephitis* is intermediate but has the longest tooth rows. *Brachyprotoma* (especially *B. brevimala*) has pushed the narrowing of the teeth seen in *Spilogale* to an extreme, converging on the carnivorous genus *Mustela*. This suggests that *Brachyprotoma* was more carnivorous than any of the living skunks.

Why *Brachyprotoma* lost P2/ and shortened its tooth rows, paralleling the genus *Conepatus*, is a mystery. Members of the genus *Mustela* have longer tooth rows than skunks, so in that respect *Brachyprotoma* diverged from *Mustela*. *Brachyprotoma* was trending in a direction that is difficult to explain. *Brachyprotoma* also did not survive the post-Pleistocene changes as did the aforementioned genera (although some species were lost and ranges altered). I propose that these two facts are correlated. *Brachyprotoma* was probably adapting to a specialized niche that existed during the Pleistocene but disappeared during the Recent. I also propose that this specialization was a feeding habit and/or preference for a particular prey item since the specializations discussed are all dental. No postcranial material has been reported to document additional specializations, and the most diagnostic skunk characters, scent glands and color patterns, are in the soft anatomy, which is obviously unavailable. With such limited data (about 27 specimens from nine sites), further speculation would be unwarranted. All that can be concluded is that *Brachyprotoma* was restricted to boreal conditions, was widespread in North America, was probably low in density, and did not survive the post-Pleistocene changes.

The evolution of the genus *Brachyprotoma* has been discussed by Kurten and Anderson (1980). They stated that it seems most closely related to *Spilogale*, but both were probably derived from the Mio-Pliocene genus

Promephitis. No intermediate forms are available to show the exact phylogeny, however. Some speculation can be made about the relationship of *B. brevimala* to *B. obtusata*. *Brachyprotoma brevimala* has gone to a greater extreme in the characters that differentiate *Brachyprotoma* from other skunks (shorter face and narrower teeth) and is therefore more specialized. Since specialists almost always evolve from generalists, *B. brevimala* probably evolved from *B. obtusata*. The fact that *B. obtusata* has been found in deposits from Early Pleistocene to Early Recent age (Kurten and Anderson 1980) and *B. brevimala* is known only from a Late Pleistocene to Recent deposit also supports this conclusion.

Family Felidae

Smilodon cf. *fatalis*

MATERIAL.— Partial left ectocuneiform (BYUVP 7530), claw (BYUVP 7497). Miller (1982) reported cf. *Smilodon* from Crystal Ball Cave based on a single vertebra (W. E. Miller 1983, pers. comm.), but this specimen is apparently lost (possibly due to an explosion that affected the collection).

DISCUSSION.— The ectocuneiform is dense, worn, and coated with a calcite crust. The claw is missing the outer plates but is otherwise in good condition. The specimens were compared with *Smilodon* and *Felis atrox*, the only two Late Pleistocene cats large enough to be considered, and both compare best with *Smilodon* (W. E. Miller 1984, pers. comm.). The ectocuneiform was previously referred to *Panthera atrox* (Heaton 1984), but comparison with actual specimens rather than casts shows that it is clearly *Smilodon*. The only previous citing of *Smilodon* in Utah is from the Silver Creek fauna of north central Utah (Miller 1976), but it has been found in Pleistocene assemblages throughout North America.

Kurten and Anderson (1980) considered *S. fatalis* to be the only valid species of Late Pleistocene *Smilodon* in North America, but it has been known by many other names. Based on this synonymy, the Crystal Ball Cave specimens are referred to *S. fatalis* although they are doubtfully identifiable to the species level.

Felis concolor

MATERIAL.— First right metacarpal (BYUVP 7502), 4 claws (BYUVP 7498–7501).

DISCUSSION.— *Felis concolor* is the only cat of its size presently living in North America, but similar-sized species of *Acinonyx* and *Homotherium* existed during the Pleistocene. *Lynx* and other species of *Felis* (disregarding those often placed in the genus *Panthera*) are distinctly smaller than *F. concolor*, and *Smilodon*, *Panthera atrox*, and *P. onca* are distinctly larger. The Crystal Ball Cave specimens were compared with material of *Felis* species, *Acinonyx*, and *Homotherium* at the Los Angeles County Museum and found to match perfectly in size and shape with specimens of *F. concolor*; but they clearly differ from the other felids mentioned. *Felis concolor* presently lives throughout the Snake Range (Hall 1981), and J. C. Bates (1983, pers. comm.) reported a citing in the Snake Valley near Gandy as well as many higher in the mountains.

Lynx cf. *rufus*

MATERIAL.— Right C1/ (BYUVP 7494), right P/4 (BYUVP 7496). The anterior portion of a right maxilla without teeth (BYUVP 7495) is probably also referable to *Lynx*.

DISCUSSION.— *Lynx rufus* currently inhabits the area of Crystal Ball Cave (J. C. Bates 1983, pers. comm.), but *L. canadensis* ranges only as close as central Utah and northward and prefers colder climates (Hall 1981). *Lynx canadensis* is slightly larger than *L. rufus* and has considerably larger feet (Ingles 1965). The specimens recovered fall in the size range of both *L. rufus* and *L. canadensis*, but they tend to be closer in size to *L. rufus*. None of the claws recovered could be referred to this genus, so the difference in foot size was not helpful. Since *L. rufus* presently lives around the cave, the specimens are referred to it.

Order Perissodactyla

Family Equidae

Equus cf. *scotti*

MATERIAL.— Left cuneiform (BYUVP 7542), right lunar (BYUVP 7544), 2 right scaphoids (BYUVP 7549, 7550), right magnum (BYUVP 7561), second phalanx (LACM

TABLE 4. Measurements of *Equus* first phalanges from Crystal Ball Cave. All measurements are in millimeters and parallel to the main bone axes.

Catalog number	Maximum proximo-distal length	Maximum proximal width		Minimum medial width		Maximum distal width	
		Transverse	Antero-posterior	Transverse	Antero-posterior	Transverse	Antero-posterior
BYUVP 7580	76.8	38.1	28.6	27.0	17.7	35.8	20.8
BYUVP 7581	72.0	38.3	30.6	24.2	16.8	33.2	20.0
BYUVP 7582	—	—	—	—	16.4	—	16.1
BYUVP 7583	75.8	38.6	30.3	24.8	17.4	33.9	19.5
LACM 123681	74.9	39.7	31.5	27.0	18.0	37.5	21.7
LACM 123682	74.1	—	31.8	25.4	17.6	34.4	20.4

TABLE 5. Measurements of *Equus* second phalanges from Crystal Ball Cave. All measurements are in millimeters and parallel to the main bone axes.

Catalog number	Maximum proximo-distal length	Maximum proximal width		Minimum medial width		Maximum distal width	
		Transverse	Antero-posterior	Transverse	Antero-posterior	Transverse	Antero-posterior
BYUVP 7587	—	—	27.7	—	—	—	—
BYUVP 7588	47.5	48.7	31.7	42.3	21.7	46.5	25.6
BYUVP 7589	44.2	41.5	28.1	33.2	19.4	35.5+	23.9
BYUVP 7590	—	—	25.4	—	—	—	—
BYUVP 7591	39.3+	—	27.0+	—	21.2+	—	25.5
BYUVP 7593	37.0	39.1	22.8	30.4	—	31.1+	17.1
BYUVP 7594	36.5	31.9	24.0	28.2	15.6	30.4	19.2
LACM 123683	51.8	62.0	35.2	52.7	24.1	57.1	28.8
LACM 123684	45.2	44.0+	30.8	37.2	21.2	37.1	24.5
LACM 123685	40.6	42.1	26.7	36.7	19.5	39.1	25.0

TABLE 6. Measurements of *Equus* third phalanges from Crystal Ball Cave. All measurements are in millimeters and parallel to the main bone axes.

Catalog number	Anterior height	Maximum transverse width	Maximum antero-posterior width	Articulation surface	
				Transverse	Antero-posterior
BYUVP 7595	40.6	61.7	44.2	49.2	22.4
BYUVP 7596	39.4+	—	—	—	—
BYUVP 7597	32.7	39.6	38.0+	36.0	13.8
BYUVP 7600	47.0+	48.7	49.1+	37.8	14.8
BYUVP 7601	34.0	37.1	34.6+	34.0	16.6
BYUVP 7602	—	—	—	34.4	14.0
BYUVP 7603	—	—	—	41.0	13.6
BYUVP 7605	35.2	41.1	38.0	37.3	13.6
BYUVP 7606	37.7	—	—	33.7	14.1
BYUVP 7607	40.8	—	—	29.2	15.3
BYUVP 7608	39.0	—	—	40.7	13.8
BYUVP 7610	—	33.2	27.8+	—	—

123683), third phalanx (BYUVP 7595). A juvenile left P/2 (BYUVP 7623), a partial juvenile first phalanx (BYUVP 7586), a second phalanx (BYUVP 7588), 3 partial third phalanges (BYUVP 7596, 7607, 7608), and a distal sesamoid (BYUVP 7622) probably belong to this species also. Phalanx measurements are listed in Tables 4, 5, and 6.

DISCUSSION.— Several species of large horses have been recognized from the Late Pleistocene of western North America. The Rancho La Brea asphalt deposits have yielded a single species of large horse (Savage 1951) usually referred to *E. occidentalis* (Merriam 1913, Stock 1963, Willoughby 1974), although the validity of this name has been questioned (Miller 1971). Based on comparative material and measurements made by Willoughby (1974), the large Crystal Ball Cave horse is distinct from the Rancho La Brea horse in

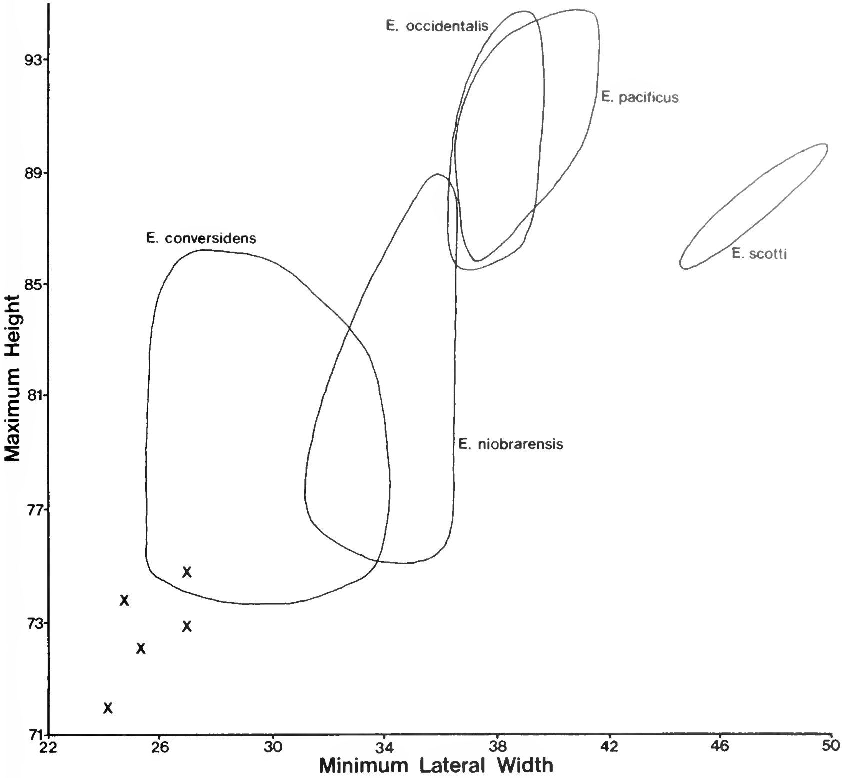

Fig. 6. Plot of *Equus* first phalanges from Crystal Ball Cave (X's) and ranges of variation for some Late Pleistocene North American species (circumscribed). The number of specimens plotted to show the range of variation were 46 of *E. conversidens*, 9 of *E. niobrarensis*, 6 of *E. occidentalis*, 6 of *E. pacificus*, and 2 of *E. scotti*. These measurements were taken from Dalquest and Hughes (1965), Gazin (1936), A. H. Harris (1984, pers. comm.), and Harris and Porter (1980). Measurements are in millimeters.

having more transversely broad phalanges (Figs. 6, 7, and 8) and carpals with relatively larger articulation surfaces. The Crystal Ball Cave specimens are distinctly larger than *E. niobrarensis* based on measurements given me by A. H. Harris (1983, pers. comm.) and in Harris and Porter (1980). Harris (1983, pers. comm.) also provided me with measurements of *E. pacificus* (although the validity of this species has been questioned by Savage 1951) from Fossil Lake, Oregon, and phalanges of this species match well in size with the large Crystal Ball Cave horse but are not as transversely broad.

Gazin (1936) listed measurements of the type specimen of *E. scotti*, and, of all specimens and data seen, only it has phalanges that are as transversely broad as the Crystal Ball Cave specimens. The second phalanx (LACM 123683) is slightly larger than the *E. scotti* type but has identical proportions (Fig. 7), and the third phalanx (BYUVP 7595), although smaller because it is of a subadult, has the same proportions as the anterior third phalanges of the *E. scotti* type (Fig. 8). Dalquest (1964) stated that *E. scotti* was very heavily built, and this would suggest that the foot and toe bones are broad compared with

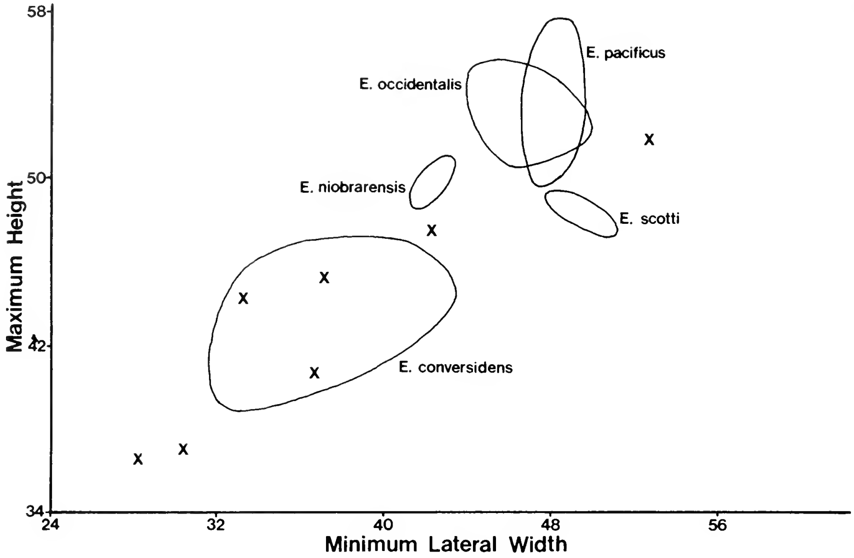

Fig. 7. Plot of *Equus* second phalanges from Crystal Ball Cave (X's) and ranges of variation for some Late Pleistocene North American species (circumscribed). The number of specimens plotted to show the range of variation were 26 of *E. conversidens*, 3 of *E. niobrarensis*, 8 of *E. occidentalis*, 4 of *E. pacificus*, and 2 of *E. scotti*. These measurements were taken from Dalquest and Hughes (1965), Gazin (1936), A. H. Harris (1984, pers. comm.), and Harris and Porter (1980). Measurements are in millimeters.

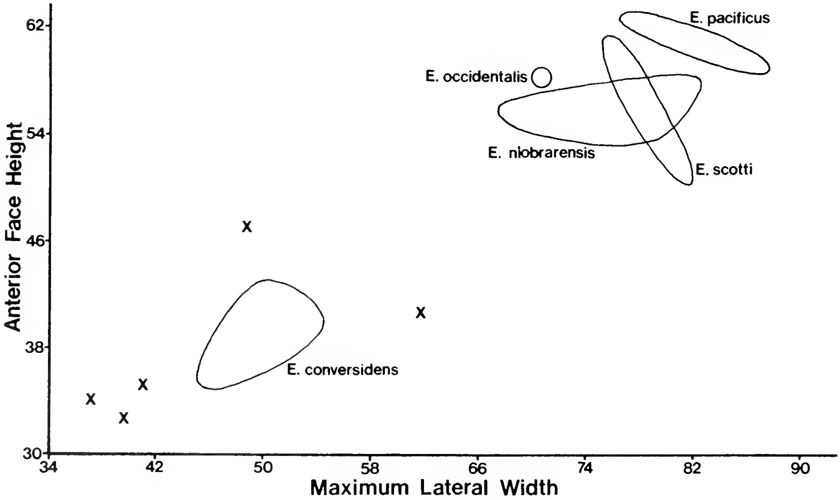

Fig. 8. Plot of *Equus* third phalanges from Crystal Ball Cave (X's) and ranges of variation for some Late Pleistocene North American species (circumscribed). The number of specimens plotted to show the range of variation were 6 of *E. conversidens*, 5 of *E. niobrarensis*, 1 of *E. occidentalis*, 2 of *E. pacificus*, and 2 of *E. scotti*. These measurements were taken from Dalquest and Hughes (1965), Gazin (1936), A. H. Harris (1984, pers. comm.), and Harris and Porter (1980). Measurements are in millimeters.

other species of *Equus*. The large carpals from Crystal Ball Cave mentioned above, especially the cuneiform and magnum, are broad and have much larger articulation surfaces than the Rancho La Brea horse. Based on this limited information in the literature, the largest carpals listed above compare most favorably with *E. scotti* also.

Equus scotti was originally named and described from Texas by Gidley (1900), and most specimens have been found in that state (Dalquest 1964, Gidley 1903, Johnston 1937). Hopkins et al. (1969) recovered a left metatarsal from the Late Pleistocene American Falls Lake Beds of southeastern Idaho that they referred to *E. scotti*. It is therefore not unlikely that *E. scotti* lived in Utah. A large horse was represented at Smith Creek Cave by a single vestigial metapodial (Miller 1979), but no attempt was made to identify it to species.

BYUVP 7588 is not as laterally broad as LACM 123683 but is too large to belong with the smaller species. The epiphysis is not fully fused, showing that it represents a subadult. It is the only bone from Crystal Ball Cave that matches well with the Rancho La Brea horse, although it is slightly smaller. But, since it may differ by only individual, foot, or age variation from the better represented *E.* cf. *scotti*, it is tentatively referred to that species.

Equus ? *conversidens*

MATERIAL.— Right M3/ (LACM 123677), thoracic vertebra (BYUVP 7687), 3 right pisiforms (BYUVP 7536–7538), left pisiform (BYUVP 7539), 2 right cuneiforms (BYUVP 7540, 7541), 4 right lunars (BYUVP 7543, 7545–7547), partial left lunar (BYUVP 7548), 4 right scaphoids (BYUVP 7551–7554), 4 partial left scaphoids (BYUVP 7555–7558), 2 right trapezium-trapezoids (BYUVP 7559, 7560), 2 right magnums (BYUVP 7562, 7563), partial right magnum (BYUVP 7564), left magnum (LACM 123678), 2 partial right unciforms (BYUVP 7565, 7566), proximal tibia epiphysis (BYUVP 7570), distal epiphysis of right tibia (BYUVP 7571), partial distal epiphysis of left tibia (BYUVP 7572), right calcaneum (LACM 123679), left calcaneum (BYUVP 7573), right astragulus (BYUVP 7575), right juvenile astragulus (BYUVP 7574), left astragulus (LACM 123680), right navicular (BYUVP 7576), left navicular (BYUVP 7577), left cuboid (BYUVP 7579), right meso-ento (BYUVP 7578), proximal portion of left metatarsal (BYUVP 7567), 2 distal metapodial epiphyses (BYUVP 7568, 7569), 6 first phalanges (BYUVP 7580, 7581, 7583, LACM 123684, 123685), 3 partial first phalanges (BYUVP 7582, 7584, 7585), 5 second phalanges (BYUVP 7589, 7593, 7594, LACM 123684, 123685), 4 partial second phalanges (BYUVP 7587, 7590–7592), 5 third phalanges (BYUVP 7597, 7600, 7601, 7605, 7606), 2 partial third phalanges (BYUVP 7602, 7603), juvenile third phalanx (BYUVP 7610), 11 proximal sesamoids (BYUVP 7611–7621). Phalanx measurements are listed in Tables 4, 5, and 6.

DISCUSSION.— In addition to the fossils of large horses from Crystal Ball Cave (referred to *E.* cf. *scotti*) are numerous bones of smaller horses. Some of these compare well with *E. conversidens*, the species to which most small Pleistocene North American horse fossils have been assigned, but others do not. Considerable time has been spent evaluating the size and morphologic variation among these bones and comparing the results with descriptions and measurements in the literature. But both complexities within this collection and disagreements regarding valid species in the literature have prevented positive species identification of these small horse bones.

Equus conversidens (Owen 1869) has been considered by some workers to be the only valid species of small Pleistocene horse in North America (Harris and Porter 1980, Miller 1971), and most other named species of small Pleistocene horses have at some time been synonymized with this species (Dalquest and Hughes 1965, Hibbard 1955, Hibbard and Taylor 1960). However, most workers presently recognize at least two species. Owen (1869) named *E. tau* at the same time he named *E. conversidens*. Poor illustrations of the type specimens have caused some workers to consider *E. conversidens* and *E. tau* synonymous (Hibbard 1955). But Dalquest (1979) and Mooser and Dalquest (1975), after researching the early descriptions (the type specimen of *E. tau* is lost), considered these two species distinct. The teeth that Mooser and Dalquest (1975) assigned to *E. tau* are smaller than those of *E.*

conversidens, and the metapodials are longer and more slender. Skinner (1942) assigned a first phalanx from Papago Springs Cave, Arizona, to *E. tau* because it was much narrower than those of *E. conversidens* from the same assemblage. But, based on his measurements, this phalanx is narrower transversely than anteroposteriorly, making it doubtful of being horse at all.

Hay (1915) named *E. francisci*, which was synonymized with *E. conversidens* by Hibbard and Taylor (1960). But Lundelius and Stevens (1970) reprepared the metatarsal of the type specimen and found it to be distinctly longer and narrower than that of *E. conversidens.* Lundelius and Stevens (1970) therefore considered *E. francisci* a valid species, and they synonymized *E. quinni* (based on the similar long metatarsal) and *Onager zoyatalis* (based on dental similarities) to it. Dalquest (1979) considered *E. francisci*, as well as *E. littoralis*, *E. achates*, and *E. quinni*, to be synonymous with *E. tau*, and he considered *E. conversidens* and *E. tau* the only two valid species of small Pleistocene North American horses.

Based on an illustration in Lundelius and Stephens (1970), the M3/ of *E. francisci* is distinctly wider transversely than that of *E. conversidens*, although they are of similar anteroposterior length. LACM 123677, although quite worn, has the same width and length as the *E. franscisci* type and has an enamel pattern most similar to it also. Dalquest (1979) synonymized *E. francisci* with *E. tau*, but the M3/ of the lectotype of *E. tau* illustrated by Mooser and Dalquest (1975) is not transversely broad like the *E. francisci* type and Crystal Ball Cave M3/. Unfortunately the only phalanx measurements given in the literature are for *E. conversidens*, except the questionable first phalanx assigned to *E. tau* by Skinner (1942).

The only phalanges from Crystal Ball Cave that compare well with measurements of *E. conversidens* phalanges in the literature are three of the five second phalanges (Fig. 7). The other two second phalanges (BYUVP 7593, 7594) are distinctly smaller than any assigned to *E. conversidens* yet have complete epiphyseal fusion. All nine first phalanges are from individuals intermediate in size between those represented by the two sets of second phalanges, and all are small compared with the first phalanges assigned to *E. conversidens* in the literature (Fig. 6). Six of the eleven third phalanges articulate well with the three larger second phalanges yet are smaller than the third phalanges assigned to *E. conversidens* in the literature (Fig. 8). The other third phalanx (BYUVP 7600) is larger than any assigned to *E. conversidens* and too large to articulate with any of the second phalanges under discussion.

It is important to consider sexual dimorphism, individual variation, and variation among different feet of the same individual to see how much variation is expected within a species. Willoughby (1974), in a table of bone measurements from 25 species and races of *Equus*, listed mean dimensions for both sexes with respect to two characters: metacarpal midwidth and metacarpal midwidth divided by length. Metacarpals of males had a midwidth of 3.1% to 7.3% greater than females and a midwidth divided by length of 2.3% to 6.9% greater than females. Species with more sexual dimorphism in metacarpal width tended to also have more dimorphism in width relative to length, so male metacarpals tend to be more robust and just slightly longer than female metacarpals. These measurements show that sexual dimorphism is not great in *Equus* and certainly not sufficient to have caused the variability seen among the small Crystal Ball Cave equids.

Howe (1970), in a study of *Equus* (*Plesippus*) *simplicidens*, showed that individual variation in bone size can be greater than previously thought. Because the large number of specimens at Nebraska's Broadwater Quarry fell into a single size curve with no gaps, he concluded that they all represent a single species, and he synonymized a number of species that had previously been named based on limited material at other sites. Table 5 of Howe (1970) shows that the largest metacarpal and metatarsal lengths and widths average 32% larger than the smallest corresponding measurements, and none are more than 36% larger. Even with a sample size of 97 to 190, the metapodials measured by Howe (1970) show less variation than do the few second and third phalanges from Crystal Ball Cave.

TABLE 7. Measurements of first phalanges of *Camelops* cf. *hesternus* (*C*) and *Hemiauchenia* cf. *macrocephala* (*H*) from Crystal Ball Cave. All measurements are in millimeters and parallel to the main bone axes.

		Maximum proximo-distal	Maximum proximal width		Minimum medial width		Maximum distal width	
Catalog number	ID	length	Transverse	Antero-posterior	Transverse	Antero-posterior	Transverse	Antero-posterior
BYUVP 7627	*C*	117	39+	35+	20	18	33+	28
LACM 123689	*C*	114	43	35	22	19	35	29
LACM 123691	*C*	—	32	32	17	18	—	—
BYUVP 7640	*H*	—	23	19	—	—	—	—
LACM 123690	*H*	100	28	32	15	14	22	18

Isolated front and rear phalanges are usually indistinguishable and therefore have an additional degree of variation. Front and rear phalanx measurements were taken from recent *E. caballus* and *E. burchelli* specimens, and the larger measurements for each species averaged 4.2% larger than the smallest corresponding measurements with a maximum of 9.4% larger. But even this much variability, in addition to sexual and individual variation, does not adequately account for the great size range among the small Crystal Ball Cave equids.

Six measurements of the 5 second phalanges from Crystal Ball Cave (excluding those referred to *E. scotti*) show that the largest measurements are 24% to 43% larger than the smallest corresponding measurements with an average of 31.5% larger. Eleven measurements of the 9 third phalanges from Crystal Ball Cave show that the largest measurements are 7% to 122% larger than the smallest corresponding measurements with an average of 50.7% larger. Considering the second and third phalanges separately, each has enough variation to make it marginal whether they could all be assigned to the same species considering sexual, individual, and foot variation. The variation seems even more extreme when one considers that the smallest second phalanges (BYUVP 7593, 7594) are from much smaller individuals than the smallest third phalanx, and the largest third phalanx (BYUVP 7600) is from a larger individual than the largest second phalanx. This is far more variation than can be accounted for by the sexual, individual, and foot variation for a single species as discussed above, and it suggests that multiple species of horse smaller than *E.* cf. *scotti* are represented at Crystal Ball Cave.

Finding a dividing line between two species in this material is nearly impossible, however. Most of the material could be assigned to a species of horse 15% smaller than the smallest material assigned to *E. conversidens*, but the two smallest second phalanges (BYUVP 7593, 7594) and the largest third phalanx (BYUVP 7600) seem too far from the mean to belong to this supposed species. Until more phalanx measurements are available for small Pleistocene horses other than *E. conversidens*, it is difficult to determine how many species are represented by the smaller *Equus* fossils from Crystal Ball Cave and whether most of the material represents an unusually small variety of *E. conversidens*, a species distinct from *E. conversidens* such as *E. tau* and/or *E. francisci*, or both.

Order Artiodactyla
Family Camelidae
Camelops cf. *hesternus*

MATERIAL.— Right scaphoid (LACM 123686), left scaphoid (LACM 123687), left lunar (BYUVP 7624), left magnum (BYUVP 7625), right unciform (BYUVP 7626), distal fragment of metapodial (BYUVP 7629), 2 first phalanges (BYUVP 7627, LACM 123689), proximal portion of first phalanx without epiphysis (LACM 123691), partial proximal epiphysis of first phalanx (BYUVP 7638), 3 second phalanges (LACM 123692, BYUVP 7630, 7632), 3 proximal portions of second phalanges (BYUVP 7633, 7634, 7637), 3 partial proximal portions of second phalanges (BYUVP 7628, 7635, 7636), 3 third phalanges (BYUVP 7639, 7641, 7642). Six sesamoids (BYUVP 7644–7649) are probably of *Camelops* but may represent *Bison*. Phalanx measurements are listed in Tables 7, 8, and 9.

Table 8. Measurements of second phalanges of *Camelops* cf. *hesternus* (*C*) and *Hemiauchenia* cf. *macrocephala* (*H*) from Crystal Ball Cave. All measurements are in millimeters and parallel to the main bone axes.

Catalog number	ID	Maximum proximo-distal length	Maximum proximal width		Minimum medial width		Maximum distal width	
			Transverse	Antero-posterior	Transverse	Antero-posterior	Transverse	Antero-posterior
BYUVP 7630	*C*	70+	35	29	24	17	30+	22
BYUVP 7632	*C*	67+	37	31	29	19	—	—
BYUVP 7633	*C*	—	31+	31	27	20	—	—
BYUVP 7634	*C*	—	34+	28+	—	—	—	—
BYUVP 7635	*C*	—	—	31	—	—	—	—
BYUVP 7636	*C*	—	—	26+	—	—	—	—
BYUVP 7637	*C*	—	34+	30	—	19	—	—
LACM 123692	*C*	69	37	31	26	19	35	23
BYUVP 7631	*H*	52	28	23	20	14	23	20

Table 9. Measurements of third phalanges of *Camelops* cf. *hesternus* from Crystal Ball Cave. All measurements are in millimeters and parallel to the main bone axes.

Catalog number	Maximum proximo-distal length	Maximum proximal width	
		Transverse	Antero-posterior
BYUVP 7639	23+	22	21
BYUVP 7641	29+	23	22
BYUVP 7642	33+	25	23

Discussion.— Webb (1965, 1974) recognized only four valid genera of Late Pleistocene North American camels: *Titanotylopus*, *Camelops*, *Hemiauchenia* (=*Tanupolama*), and *Paleolama* (in order of decreasing size). *Titanotylopus* is somewhat common and *Camelops* is very common in Late Pleistocene assemblages of western North America, but neither has been found in the east (Webb 1974). *Hemiauchenia* is found in Late Pleistocene deposits throughout the Americas (Webb 1974) and is commonly associated with *Camelops* (Miller 1979). *Paleolama* has only been found in Florida, Texas, and southern California in Pleistocene deposits of North America (Miller 1976). Miller (1982) identified *Camelops* and *Hemiauchenia* from Crystal Ball Cave.

The specimens listed above fall within the range of variation of *Camelops hesternus* measurements from Rancho La Brea, southern California (Webb 1965) and Selby and Dutton, eastern Colorado (Graham 1981). T. E. Downs (1984 pers. comm.) provided me with 8 first phalanx measurements of *Titanotylopus* sp., 21 of *Camelops hesternus*, and 21 of *Hemiauchenia* sp. from southern California deposits. Those of *Titanotylopus* range from 105 to 138 mm in length with an average of 121 mm, those of *Camelops hesternus* range from 105 to 125 mm in length with an average of 116 mm, and those of *Hemiauchenia* range from 91 to 110 mm in length with an average of 94 mm. The two complete first phalanges from Crystal Ball Cave, both of which are of adults based on epiphyseal fusion and bone density, measure 114 and 117 mm in length (Table 7). Although there is some overlap in first phalanx length between these genera, the Crystal Ball Cave specimens clearly match best with *Camelops*.

Savage (1951) recognized four valid species of *Camelops*: *C. hesternus* and *C. huerfanensis*, which are larger, and *C. sulcatus* and *C. minidokae*, which are smaller; and Webb (1965), in his detailed description of *Camelops*, supported this system. Based on limb bone measurements given by Savage (1951), *C. minidokae* was about 14% smaller than *C. hesternus*. *Camelops huerfanensis* can only be distinguished from *C. hesternus* and *C. sulcatus* can only be distinguished from *C. minidokae* based on dental characters (Graham 1981, Savage 1951). Both *C. minidokae* and *C. sulcatus* are too small to match the Crystal Ball Cave specimens, and both are known only from pre-Wisconsinan deposits (Kurten and Anderson 1980).

Camelops hesternus and *C. huerfanensis* are very similar and may be conspecific (Hopkins 1955, Savage 1951). Both are known from the Late Pleistocene, and both are known from Idaho (Gazin 1935, Hopkins 1955, Hopkins et al. 1969) and Colorado (Cragin 1892, Graham 1981). *Camelops hesternus* is the only species of *Camelops* reported from Utah. A *Camelops hesternus* skull was recovered from a lava tube 140 km (87 miles) east-southeast of Crystal Ball Cave (Romer 1928, 1929) and dated at 11,075 ± 225 Y.B.P. (Nelson and Madsen 1979). *Camelops* cf. *hesternus* was reported from the Silver Creek fauna in north central Utah (Miller 1976). *Camelops* sp. was reported from Smith Creek Cave (Harrington 1934, Stock 1936, Miller 1979), but the only material mentioned is a right navicular (Miller 1979), and no attempt was made to identify it to species.

Since the Crystal Ball Cave specimens match measurements of *C. hesternus* by T. E. Downs (1984, pers. comm.), Graham (1981), and Webb (1965), and since *C. hesternus* is the only species reported from the state of Utah, the Crystal Ball Cave specimens are referred to this species. But, since the only diagnostic character to distinguish *C. hesternus* from *C. huerfanensis* is a dental feature not applicable to the Crystal Ball Cave specimens (Hopkins 1955, Savage 1951), *C. huerfanensis* cannot be positively eliminated on the basis of these foot elements.

Hemiauchenia cf. *macrocephala*

MATERIAL.— Distal right portion of metapodial (LACM 123688), first phalanx (LACM 123690), partial proximal portion of first phalanx (BYUVP 7640), second phalanx (BYUVP 7631). Phalanx measurements are listed in Tables 7, 8, and 9.

DISCUSSION.— Two genera of small camels are recognized from the Pleistocene of North America: *Hemiauchenia* and *Paleolama* (Webb 1974). Based on illustrations of *Hemiauchenia* (=*Tanupolama*) *macrocephala* (=*stevensi*) by Stock (1928), and *Paleolama mirifica* by Webb (1974), the metapodials of *H. macrocephala* are 63% longer but 3% transversely narrower at the distal end than those of *P. mirifica*. The Crystal Ball Cave metapodial fragment is 12% transversely narrower than the *H. macrocephala* specimens illustrated by Stock (1928) and measurements from the Vallecito Creek site in southern California and Ringold site in Washington State provided by T. E. Downs (1984, pers. comm.). The first phalanges from Crystal Ball Cave fall well within the range of *Hemiauchenia* specimens reported by T. E. Downs (1984, pers. comm.), McGuire (1980), and Schultz (1937). Nothing was available to compare the second phalanx with, but it is from the same size of camel as the other elements. The Crystal Ball Cave specimens clearly match the more narrow-legged *Hemiauchenia* rather than the more broad-legged *Paleolama*.

Webb (1974) synonymized the North American genus *Tanupolama* with the South American genus *Hemiauchenia* and recognized six valid species. Of these, only *H. macrocephala* is found in the late Pleistocene of North America. *Hemiauchenia macrocephala* represents the synonymy of a number of previously named North American species (Webb 1974), and it is the best-known Pleistocene llama (Kurten and Anderson 1980). Since only this species matches the age and locality of the Crystal Ball Cave assemblage, and since the Crystal Ball Cave specimens match specimens from other sites assigned to this species, the four Crystal Ball Cave specimens are referred to *H. macrocephala*. Characters separating this species from others of *Hemiauchenia* are almost entirely dental (Webb 1974), however, and are therefore not applicable to the Crystal Ball Cave material.

Miller (1982) reported *Hemiauchenia* from Crystal Ball Cave based on the same material reported here. Miller (1979) reported ? *Hemiauchenia* sp. from Smith Creek Cave based on a left cuboid, the proximal portion of a scapula, and a juvenile metapodial. *Hemiauchenia* is better represented than *Camelops* at Smith Creek Cave by a ratio of 3 to 1, but *Camelops* is better represented than *Hemiauchenia* at Crystal Ball Cave by a ratio of 7 to 1. This difference seems even more dramatic in light of the selection for smaller bones at Crystal Ball Cave but not at Smith Creek Cave. Although this difference could be explained by slight age differences in these faunas, human intervention, or chance preservation, I feel it is more likely due to habitat differences between these two genera of camels.

Kurten and Anderson (1980) stated that ". . . *Hemiauchenia* had a long stride and was highly cursorial. It was a plains-dweller and probably fed primarily on grass." About *Camelops* they stated: "Although primarily a grazer, *Camelops*, with its long neck and legs, was probably an occasional browser." Although these two camels are thought to have been plains-dwelling grazers, it is interesting to speculate about their habitat differences. Webb (1974) presented strong evidence that *Hemiauchenia* gave rise to the mountain-dwelling South American llamas. *Camelops*, on the other hand, probably resembled the living dromedary camel (Kurten and Anderson 1980), which prefers flat plains habitats. The fact that *Camelops* is by far the better represented camel at Crystal Ball Cave, located in a small outlier surrounded by a flat valley, and *Hemiauchenia* is better represented at nearby Smith Creek Cave, located in a canyon at the base of a high mountain, suggests that *Hemiauchenia* preferred higher elevations and/or more rugged terrain than *Camelops*.

Family Cervidae

cf. *Cervus elaphus*

MATERIAL.— First phalanx (BYUVP 7811).

DISCUSSION.— Several cervid phalanges from Crystal Ball Cave are intermediate in size between *Cervus* and *Odocoileus*. BYUVP 7811 (60.2 mm long) is the largest of these and is much closer in size to *Cervus*. In comparison with the others it is distinctly larger and more robust, yet high bone porosity suggests that it is of a subadult. *Navahoceros fricki* is another Late Pleistocene cervid found as close to Utah as Arizona and Wyoming, and its size is intermediate between *Odocoileus* and *Cervus* (Kurten and Anderson 1980). No character has been described to differentiate phalanges of *Navahoceros* and *Cervus*, and no comparative material of *Navahoceros* was available to the author. *Cervus elaphus* was recovered from Smith Creek Cave (Miller 1979) and has been reported living in the Snake Range in Recent times (Hall 1981), so the phalanx is referred to this species.

Odocoileus hemionus

MATERIAL.— Partial right dentary with P/3,/4, M/1 (BYUVP 7651) and anterior left dentary with P/3,/4, M/1,/2 (BYUVP 7650, probably from the same individual), partial right dentary with P/3 (BYUVP 7652), left patella (BYUVP 7934). Of 21 first and 51 second phalanges of noncamelid artiodactyls, most compare best in size and proportions with *Odocoileus*.

DISCUSSION.— BYUVP 7650 and 7651 are of a juvenile and compare best in size and degree of hypsodonty with juvenile individuals of *O. hemionus*. The P/4's in these dentaries have three lobes rather than two, a condition seen in juveniles of *Odocoileus* but not *Antilocapra*. The P/3 of BYUVP 7652 is identical to adult *O. hemionus* and distinctly larger and less hypsodont than *A. americana*. The first and second phalanges from Crystal Ball Cave that compare best with *Odocoileus* have a slightly larger mean size than those of Recent *O. hemionus* living in Utah. This demonstrates that the Crystal Ball Cave specimens are of *O. hemionus* rather than the smaller *O. virginiana* (Hall 1981), and it suggests that deer decreased in size at the end of the Pleistocene much as did *Ovis canadensis* (Harris and Mundel 1974).

Based on numbers of phalanges, *Odocoileus* is the best represented artiodactyl in the Crystal Ball Cave assemblage; but *Antilocapra americana* is now the dominant artiodactyl of the local fauna. *Odocoileus* sp. was reported at Smith Creek Cave by Goodrich (1965), but no material was found by Miller (1979). Mule deer now live in Smith Creek Canyon (Miller 1979) and sometimes come down to Gandy at night to feed in cultivated fields (J. C. Bates 1984, pers. comm.). The replacement of *Odocoileus* by *Antilocapra*, suggested by comparison of the Crystal Ball Cave assemblage with the living community, shows that plant communities preferred by deer apparently moved upward in altitude from Snake Valley to higher elevations in the Snake Range at the close of the Pleistocene.

Family Bovidae

Antilocapra americana

MATERIAL.— Partial left maxilla with M1/, 2/,3/ (BYUVP 7656).

DISCUSSION.— The M3/ was distinguished from *Odocoileus* by being very hypsodont, transversely narrower, and having a more pointed posterior end as in *Antilocapra*. It is identical in size and proportions to the largest male specimen of *A. americana* available for comparison and distinctly larger than the extinct Pleistocene antilocaprids.

Since *A. americana* presently lives around Gandy Mountain in small herds, it is not surprising to find it in the assemblage. But it is not well represented as a fossil, suggesting that Snake Valley has not always been the treeless desert that it is now. Since *Odocoileus hemionus* is the dominant artiodactyl in the fossil assemblage and *Antilocapra americana* is the dominant living artiodactyl in the area, *Antilocapra americana* must have become abundant in the area in Recent times and replaced *Odocoileus hemionus*, probably due to changes in the vegetation.

Ovis canadensis

MATERIAL.— Posterior portion of right dentary with M/1,/2,/3 (LACM 123695) and posterior portion of left dentary with M/3 (LACM 123696, probably from the same individual), left magnum (BYUVP 7780).

DISCUSSION.— The molars of LACM 123695 and 123696 are distinctly larger and more robust than living *Ovis aries* and are even slightly larger than Recent *O. canadensis*. This suggests that the jaws are Pleistocene rather than Recent in age because Harris and Mundel (1974) demonstrated that *O. canadensis* became reduced in size at the end of the Pleistocene.

Bighorn sheep are commonly found in Pleistocene assemblages in the Great Basin (Hibbard and Wright 1956, Stokes and Condie 1961). Even in historic times they have been reported natively in the Snake Range (Durrant 1952, Hall 1946, 1981). *Ovis canadensis* was temporarily lost from the Snake Range but was reintroduced in the middle 1900s and presently thrives in the higher elevations (Mead et al. 1982). Shortly after this reintroduction, one young ram lived on Gandy Mountain for several months (J. C. Bates, 1983, pers. comm.), but this is the only citing known to me for such a low elevation in the area.

Ovis canadensis is the best represented ungulate in the Smith Creek Cave assemblage, and *Oreamnos harringtoni* is also well represented (Miller 1979). No *Oreamnos* material has been identified from Crystal Ball Cave, and *Ovis* is less represented than horse, camel, and deer. This difference between the two assemblages is probably because wild goats and sheep are mountainous animals and would rarely venture into Snake Valley. It may also represent the fact that Smith Creek Cave was a shelter for humans since many *Ovis* fossils found there appear butchered (Miller 1979).

Ovis cf. *aries*

MATERIAL.— Right metacarpal and 2 first phalanges found associated (BYUVP 8300).

DISCUSSION.— These associated bones were found as float near the east entrance of Crystal Ball Cave, and their greasy appearance suggests that they are Recent. The length and shape of the metapodial demonstrates that it is of the genus *Ovis*, and it is slightly longer than the *O. aries* specimens to which it was compared but distinctly smaller than living *O. canadensis*. *Ovis aries* is now a common domestic animal in the area, and many roam on Gandy Mountain each winter (J. C. Bates 1984, pers. comm.).

Since this species is a Recent introduction from Europe, its presence has little significance to this study. It does show, however, that the smaller bones of large mammals are still being deposited in Crystal Ball Cave, probably by woodrats since gates on the cave entrances would keep out all but the smallest carnivores. These specimens were found just north of the east entrance, an area where woodrats and their nests are often found.

cf. *Symbos cavifrons*

MATERIAL.— Second phalanx (BYUVP 7923), distal portion of second phalanx (BYUVP 7924), 2 partial second phalanges (BYUVP 7925, 7926), 2 distal portions of second phalanges (BYUVP 7921, 7922).

DISCUSSION.— These short, broad second phalanges compare best among living species to *Ovibos moschatus* but are slightly longer and narrower. BYUVP 7923 is the most complete specimen, missing only one side of the distal extention. It has a length of 42 mm, a proximal transverse width of 27 mm, and a proximal anteroposterior width of 26 mm. BYUVP 7924 has the same proximal measurements as BYUVP 7923, and BYUVP 7925 has a proximal anteroposterior width of at least 26 mm. The distal ends taper in such a way that they are hard to measure. The general shape of these second phalanges shows that they are from an animal more closely related to *Ovibos* than any other living bovid. Few phalanx measurements of Pleistocene oxen are available, but Nelson and Madsen (1980) and Stokes and Hansen (1937) reported abundant isolated *Symbos cavifrons* and *Bootherium bombifrons* crania from Lake Bonneville deposits, and McGuire (1980) reported *Euceratherium* from a Late Pleistocene deposit in central Nevada.

Kurten and Anderson (1980) described *Symbos cavifrons* as being taller and more slender than *Ovibos moschatus*, and this description matches the difference between the Crystal Ball Cave specimens and *Ovibos moschatus* perfectly. *Bootherium* is smaller than *Symbos* and is thought by many to represent females or juveniles of that genus (Kurten and Anderson 1980, Nelson and Madsen 1980). *Euceratherium* was larger and more heavily built than *Ovibos* (Kurten and Anderson 1980), and a first phalanx illustrated by McGuire (1980) is far too big at the distal end to match the second phalanges from Crystal Ball Cave. So, although no comparative material was available, both the description and known range of *Symbos cavifrons* make the Crystal Ball Cave specimens most referable to that species.

CONCLUSIONS

The Crystal Ball Cave assemblage is the first Late Wisconsinan fauna reported from the state of Utah and represents the closest known terrestrial fossil deposit to Lake Bonneville. The assemblage differs from most other cave faunas by its fossils being far inside the cave where man and birds probably had no influence on what was deposited. As a result, the assemblage is better than average in representing the proportions of animals that lived in the area, but there are some obvious biases. *Neotoma*, always an animal of low density, was the second most abundant genus in the assemblage simply because it is one of the few animals that lives in the cave. But, other than cave-dwelling species, the assemblage probably gives a fairly good record of the abundance of most groups, at least those that lived in the immediate vicinity of the cave. The assemblage, for example, contains a ratio of small mammals to large mammals and carnivores to herbivores that might be expected in a living community. One very strong bias is the size of bones in the assemblage that I have attributed to the limit of bone size that a wood rat can carry. Bones of large mammals were brought in after the carcasses deteriorated, as evidenced by the presence of only small isolated elements. This bias tends to make large species less represented in the assemblage than in the living community and very large species unrepresented. Proboscidian fossils have been found in Lake Bonneville deposits (Nelson and Madsen 1980) but not in Crystal Ball Cave, probably because there was no means to transport such large bones inside.

It is difficult to say if any other animals besides wood rats contributed to transporting fossils into the cave. No other rodents are known to transport bones as wood rats do. Small carnivores could have done so, but the low abundance of carnivore fossils in the assemblage suggests that none habitually used the cave as a home. The small size of the original cave entrance would have prevented the entry of any large mammals. Both the distance of the fossils inside the cave and the low abundance of birds compared to mammals suggests that birds did not transport any fossils in, and this is one of the main differences between Crystal Ball Cave and Smith Creek Cave (and most other cave deposits). Clearly no inorganic processes such as wind, water, or gravity could have been responsible for the fossil deposits since they are in fine dust in an isolated part of the cave where none of these forces have a magnitude capable of transporting bones.

Crystal Ball Cave has been accumulating fossils from at least 23,000 years ago to the present. Although some of the fossils are Recent, the assemblage as a whole shows dramatic differences from the present-day local fauna. The poor representation of many mammals that currently live in the area may be due to the shift from *Neotoma cinerea* to *N. lepida* as the wood rat that inhabited the cave, and it also suggests that the shift to the present climate occurred very recently in the history of the assemblage. *Brachyprotoma*, *Smilodon*, several species of *Equus*, *Camelops*, *Hemiauchenia*, and *Symbos* (or a closely related genus) are represented in the assemblage, all of which are now extinct. As mentioned earlier, there was a widespread extinction of large mammals at the close of the Pleistocene, the cause of which is under debate. This assemblage does not resolve that problem, but it does demonstrate that a marked climatic shift did take place contemporaneously with the extinctions, and this suggests to me that the extinctions were also a result of this climatic shift.

Equally as significant as the extinctions are the shifts in species ranges that the Crystal Ball Cave assemblage documents. The presence of *Ondatra zibethicus* and *Mustela* cf. *vison*, both of which require perennial water and are extirpated from the area, represent the drying of Lake Bonneville and perennial streams around Gandy Mountain. *Ochotona princeps* and *Martes americana* were extirpated from the Snake Range without replacement but still live at high elevations in nearby ranges. *Marmota flaviventris*, *Cervus elaphus*, and *Ovis canadensis* are represented in the assemblage but now inhabit only higher elevations in the Snake Range.

In other cases, species now abundant at Gandy Mountain are unrepresented or poorly represented in the assemblage, and their more boreal counterparts, now extirpated or rare in the area, are well represented as fossils. Among jackrabbits, *Lepus californicus* is presently the dominant species, but *L. townsendii*, its more boreal counterpart, is by far the better represented species in the fossil assemblage. Among cottontails, *Sylvilagus audubonii* and *S. nuttallii* make up the present local fauna, but only *S. nuttallii*, the more northern species, is found in the assemblage. *Lepus americanus*, a functional cottontail (J. A. White 1984, pers. comm.) and a very boreal animal, is probably represented but is now extirpated from the Snake Range. *Neotoma lepida*, the only wood rat seen living in Crystal Ball Cave, is rare in the assemblage, but *N. cinerea*, its more boreal counterpart, is one of the two most abundant fossil species. *Vulpes vulpes* is well represented in the cave assemblage but extirpated from the area, and *Urocyon cinereoargenteus*, a more southern fox of similar size, now inhabits the area but is not found as a fossil.

Although the Crystal Ball Cave assemblage differs dramatically from the present-day local fauna, it is not atypical of Late Pleistocene assemblages in the region. Figure 9 shows the location of and Table 10 compares the mammalian taxa recovered from 10 Late Pleistocene-Recent cave assemblages within 400 km (240 miles) of Crystal Ball Cave. The most unique feature of the Crystal Ball Cave assemblage is the presence of *Brachyprotoma* since it represents the first citing of the genus from the western United States and the first recovery of the new species herein named *B. brevimala*. *Ondatra zibethicus* was found in Crystal Ball Cave but not at the other localities, probably because of this cave's close proximity to Lake Bonneville. *Symbos cavifrons* may be present at Crystal Ball Cave but absent from the other assemblages for the same reason since it is most common in Lake Bonneville deposits.

Some interesting paleoecological information can be inferred from the differences between the Smith Creek Cave and Crystal Ball Cave assemblages in particular since they are close geographically but located in somewhat different habitats. Several species of *Spermophilus* have been recovered from Smith Creek Cave, but large numbers of a single species have been recovered from Crystal Ball Cave. This can probably be attributed to the greater habitat diversity at Smith Creek Cave, which is at the base of a high mountain. Among camels, *Hemiauchenia* is better represented at Smith Creek Cave, but *Camelops* is better represented at Crystal Ball Cave. Although based on a small sample size, this suggests that *Hemiauchenia* favored higher and/or more rugged terrain than *Camelops* because Smith Creek Cave is located in the main Snake Range and Crystal Ball Cave is located in an outlier in Snake Valley. Of the non-camelid artiodactyls, *Odocoileus hemionus* is the best represented in the Crystal Ball Cave assemblage and *Ovis canadensis* is the best represented in the Smith Creek Cave assemblage. *Oreamnos harringtoni* fossils have been found in Smith Creek Cave but not in Crystal Ball Cave. Now *Antilocapra ameri-*

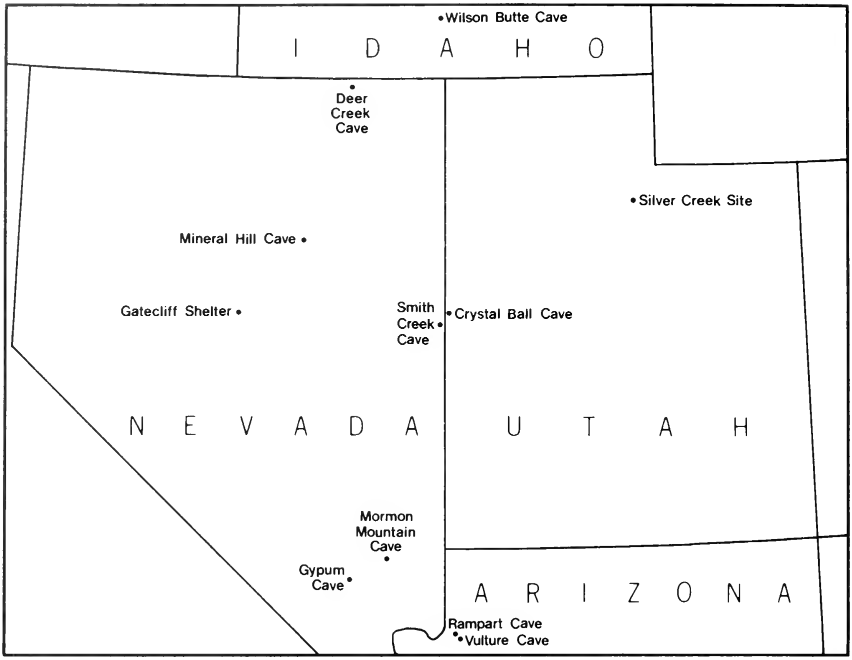

Fig. 9. Map showing the location of 10 Late Pleistocene cave faunas (see Table 10 for a list of the mammalian taxa recovered) and the Silver Creek fossil site described by Miller (1976).

Table 10. Comparison of the Crystal Ball Cave fauna with nine other Late Pleistocene/Early Holocene mammalian cave faunas located within 400 km (240 miles) of Crystal Ball Cave. The locations of these caves are shown in Figure 9.

1 Crystal Ball Cave, Utah (Heaton this report).
2 Wilson Butte Cave, Idaho (Gruhn 1961, Lundelius et al. 1983).
3 Deer Creek Cave, Nevada (Ziegler 1963).
4 Mineral Hill Cave, Nevada (McGuire 1980).
5 Gatecliff Shelter, Nevada (Grayson 1983, Thomas 1983).
6 Smith Creek Canyon caves, Nevada (Miller 1979, Mead et al. 1982).
7 Mormon Mountain Cave, Nevada (Jefferson 1982).
8 Gypsum Cave, Nevada (Mehringer 1967, Lundelius et al. 1983).
9 Rampart Cave, Arizona (Harington 1972, Lundelius et al. 1983).
10 Vulture Cave, Arizona (Mead and Phillips 1981).

Species/Localities	1	2	3	4	5	6	7	8	9	10
Sorex sp.	X				X	?				
S. vagrans					X					
Notiosorex sp.							X			X
N. crawfordi							X			X
Myotis sp.	X						X			
Eptesicus fuscus							X			
Plecotus townsendii	?						X			
Antrozous pallidus	X					cf.	X			
Nothrotherium								X	X	
N. shastensis								X	X	
Ochotona princeps	X	X	X	X	X	X	X			
Sylvilagus sp.	X	X	X	X	X	X	X	X	X	
S. idahoensis	X	X	X		X	X				

TABLE 10 continued.

Species/Localities	1	2	3	4	5	6	7	8	9	10
S. nuttallii	X	X			X		X			
Lepus sp.	X	X	X	X	X	X		X	X	
L. americanus	cf.									
L. townsendii	X				cf.					
L. californicus	X	X			cf.	cf.			cf.	
Marmota sp.	X	X	X	X	X	X	X		X	X
M. flaviventris	X	X	X	X	X	X	X		X	cf.
Spermophilus sp.	X	X	X	X	X	X	X		X	X
S. armatus		X								
S. townsendii	X	X			X	cf.				
S. richardsonii		X				cf.				
S. beldingi		X			X	cf.				
S. variegatus						X	X			X
S. lateralis					X	cf.	X			
Ammospermophilus leucurus	cf.				X					cf.
Eutamias sp.	X	X		X	X	X	X			
E. minimus	X	X			X	X				
E. umbrinus					X	cf.				
E. dorsalis	X				X		cf.			
E. amoenus							X			
Thomomys sp.	X	X	X	X	X	X				
T. talpoides		X				cf.				
T. umbrinus	X				X					
Perognathus sp.	X				X	X	X			
P. parvus					X	cf.	X			
P. formosus	cf.									
P. intermedius										cf.
Microdipodops sp.	X				X	X				
M. megacephalus	X				X	cf.				
Dipodomys sp.	X				X	X				X
D. ordii						cf.				
D. microps	X									
Castor canadensis			X							
Reithrionomys sp.							X			
R. megalotus							X			
Peromyscus sp.	X	X		X	X	X	X			X
P. maniculatus	X	X					X			
P. crinitus	cf.				X					
P. truei	cf.						X			
Onychomys sp.					X					
Neotoma sp.	X	X	X	X	X	X			X	X
N. lepida	X				X	X				
N. cinerea	X	X	X		X	X				
Ondatra sp.	X									
O. zibethecus	X									
Cleithryonomys sp.		X								
C. gapperi		X								
Phenacomys sp.		X			X	X				
P. intermedius		X			cf.	cf.				
Microtus sp.	X	X		X	X	X	X		X	X
M. californicus									X	
M. longicaudus	cf.	X			cf.	cf.	cf.			
M. montanus	cf.	X			cf.	cf.				
M. pennsylvanicus	cf.									
Lagurus curtatus	X	X								
Zapus princeps					cf.					
Erethizon dorsatum			X		X	X				X
Canis sp.	X		X		X	X		X		
C. familiaris			X							
C. latrans	cf.			X	X	cf.				
C. lupus	cf.		X			cf.				
Vulpes sp.	X	X		X	X	X		X		

TABLE 10 conintued.

Species/Localities	1	2	3	4	5	6	7	8	9	10
V. vulpes	X				X	X				
V. velox	X					X		X		
Urocyon sp.				X						
Ursus sp.			X			X				
U. horribilis			X							
Bassariscus sp.						X			X	X
B. astutus						X				X
Mustela sp.	X	X		X		X		X		
M. erminea		X				X				
M. frenata	cf.	X				X				
M. vison	cf.					X				
Martes sp.	X	X	X			X				
M. americana	X	X	X							
M. nobilis						X				
Taxidea taxus				X		X				
Spilogale sp.		X		X	X	X				
S. putorius		X			X					
Mephitis mephitis					X					
Brachyprotoma sp.	X									
B. brevimala	X									
Smilodon fatalis	cf.									
Panthera atrox						?				
P. onca						X				
Felis concolor	X					X	X		X	
Lynx sp.	X		X	X	X	X			X	
L. rufus	cf.		X		X	X		X	X	
Equus sp.	X	X		X		X		X	X	
E. sp. (large)	X					X				
E. scotti	cf.									
E. occidentalis								X		
E. sp. (small)	X					X				
E. conversidens	?									
Camelops sp.	X	X				X		X		
C. hesternus	cf.					X				cf.
Hemiauchenia sp.	X	X		X		?		X		
H. macrocephala	cf.									
Cervus sp.	cf.		?		X	X				
C. elaphus	cf.				X	X				
Odocoileus sp.	X		X			X		X		X
O. hemionus	X							X		
Antilocapra sp.	X		X	X	X	X				X
A. americana	X		X		X	X				X
Capromeryx minor						?				
Oreamnos sp.						X			X	
O. harringtoni						X			X	
O. americanus						cf.				
Ovis sp.	X		X	X	X	X	X	X	X	X
O. canadensis	X		X	X	X	X	X	X	X	X
O. aries	cf.					cf.				
Bison sp.		X	?		X	?				
B. bison					X					
Eucerotherium sp.				X						
Symbos cavifrons	cf.									

cana is the best represented artiodactyl in Snake Valley, *Odocoileus hemionus* is the best represented artiodactyl in the Snake Range, *Ovis canadensis* is found only at high elevations in the Snake Range, and *Oreamnos harringtoni* is extinct. This suggests that these four artiodactyls can be placed in the following order of elevation preference starting at the highest: *Oreamnos harringtoni*, *Ovis canadensis*, *Odocoileus hemionus*, and *Antilocapra americana*. At the end of the Pleistocene, in rough terms, each of these species moved upward in elevation to fill the habitat of the next higher species. The one at the top went extinct; the one at the bottom became abundant. Differences of lesser magnitude between the Crystal Ball Cave and Smith Creek Cave assemblages must be dealt with more carefully because they may represent slight differences in the age of the deposits, biases in the mode of deposition, human intervention, or chance preservation. Identification of more material, especially at Smith Creek Cave, could make comparison of these two assemblages a very valuable paleoecological study.

The Crystal Ball Cave fauna, like many previously studied faunas, shows that a dramatic climatic shift occurred at the end of the Pleistocene and caused many species to move northward in latitude and upward in elevation and to become extinct. This shift is particularly well expressed in the Crystal Ball Cave assemblage because its close proximity to Lake Bonneville made the drying trend very severe in the area. The Crystal Ball Cave fauna documents the previous ranges and abundances of many taxa that help in reconstruction of details of the last Pleistocene ice age.

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FIRST RECORD OF *CLIMACIA CALIFORNICA* (NEUROPTERA: SISYRIDAE) AND ITS HOST SPONGE, *EPHYDATIA MULLERI* (PORIFERA: SPONGILLIDAE), FROM IDAHO WITH WATER QUALITY RELATIONSHIPS

William H. Clark[1]

Abstract.— The spongillafly, *Climacia californica* Chandler, and its sponge host, *Ephydatia mulleri* (Lieberkuhn) are reported from the state of Idaho for the first time. *Climacia californica* has not previously been reported from *E. mulleri*. Collections were made in the Burley–Twin Falls area, and detailed water quality data are provided for the first time for spongillafly larvae. The water quality data also expand the known tolerance limits of *E. mulleri* for water temperature, conductivity, pH, hardness, silica, and residue.

On 16 July 1980, six larvae of *Climacia californica* Chandler were collected in the Snake River (near River Mile 653.7) at Heyburn, Minidoka County, Idaho, at an elevation of 1265 m (Fig. 1). The Snake River at this point is part of Milner Lake, due to Milner Dam, which is located approximately 21 km downstream to the west.

The spongillaflies were collected on the surfaces of the crustose sponge, *Ephydatia mulleri* (Lieberkuhn) (Fig. 2). The sponges were found near shore growing on the under-

Fig. 1. Snake River at Heyburn, Idaho. Habitat of *Climacia californica* and *Ephydatia mulleri*.

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Fig. 2. The sponge *Ephydatia mulleri* from the Snake River near Heyburn. Scale: Pen is 13 cm in length.

side of rocks, bricks, and pieces of concrete and asphalt in approximately 0.25–0.5 m of water (Fig. 1).

MATERIALS AND METHODS

Specimens were hand collected by pulling up rocks and debris and preserved in 70% alcohol. Voucher specimens of *C. californica* are deposited in the Orma J. Smith Museum of Natural History, College of Idaho, Caldwell (CIDA); the Entomology Collection, University of Idaho, Moscow (UI); the Department of Biology, Boise State University, Boise, Idaho (BSU); and in the private collections of A. D. Allen and R. C. Biggam. Specimens of *E. mulleri* are deposited in the collections of the O. J. Smith Museum of Natural History, College of Idaho, Caldwell (CIDA) and the Department of Biology, University of New Orleans, New Orleans, Louisiana.

Water quality and quantity data were collected and analyzed by the U.S. Geological Survey in accordance with their standard procedures, as well as with "Standard Methods" (American Public Health Association 1971).

RESULTS AND DISCUSSION

The aquatic neuropterous family Sisyridae has not previously been reported from Idaho. *Climacia californica* was originally described from California (Chandler 1953) and was previously known from only California and Oregon (Chandler 1963). The species determination of the Idaho specimens is based on comparisons of the larvae with the illustrations of Brown (1952) and Chandler (1953) and on a collection of adults taken by sweeping shoreline vegetation at Echo Lake near the Snake River at Twin Falls, Twin Falls County, by Albert D. Allen 13 July 1976. Additional specimens were collected at this locality by R. C. Biggam 22 July 1976 and by R. C. Biggam and L. R. Schoenike 19 August 1982. Twin Falls is approximately 42 river km downstream from the Heyburn locality.

The sponge, *E. mulleri*, is listed as widely distributed in the Northern Hemisphere by a variety of workers (Gurney and Purfin 1959, Pennak 1953, Penney 1960, and Penney and Racek 1968, to list a few) but has apparently not been reported from Idaho.

TABLE 1. Water quality parameters for the Snake River near Burley, Idaho 1974–1981.[1]

Parameter	Units	(N)	Mean	Standard Deviation	Maximum	Minimum
Water temperature	CENT	70	10.20	7.10	23.00	0.00
Flow	CFS	69	6519.30	4590.01	21300.00	390.00
Turbidity	JTU	44	6.30	4.32	22.00	1.00
Conductivity	Micromho	70	447.0	71.08	842.00	351.00
Dissolved oxygen	MG/L	67	10.60	1.96	14.50	6.80
DO saturation	Percent	61	107.00	16.52	163.00	59.00
COD low level	MG/L	33	12.70	13.28	77.00	0.00
COD high level	MG/L	31	12.80	8.36	38.00	0.00
pH	SU	68	8.20	0.49	8.90	6.30
Carbon dioxide	MG/L	42	1.90	1.46	7.20	0.50
Total alkalinity as $CACO_3$	MG/L	47	160.00	20.55	202.00	124.00
HCO_3 ion HCO_3	MG/L	41	189.00	23.92	230.00	150.00
CO_3 ion CO_3	MG/L	40	4.00	5.56	22.00	0.00
Total nitrogen as N	MG/L	70	0.95	1.10	8.40	0.20
Organic nitrogen as N	MG/L	70	0.60	0.93	7.80	0.02
Ammonia total-NH_4	MG/L	22	0.06	0.07	0.27	0.00
$NH_3 + NH_4 - N$ total	MG/L	70	0.05	0.05	0.25	0.00
Total Kjeldahl nitrogen	MG/L	70	0.63	0.94	7.90	0.05
NO_2 and NO_3 N total	MG/L	70	0.32	0.46	3.10	0.00
Total PO_4 PO_4	MG/L	4	0.08	0.05	0.15	0.03
Phosphorus total	MG/L	70	0.06	0.03	0.14	0.01
Total organic carbon	MG/L	49	2.96	1.32	7.00	1.40
Total hardness as $CaCO_3$	MG/L	12	165.83	53.17	190.00	0.00
Calcium dissolved	MG/L	11	47.00	3.44	51.00	42.00
Magnesium dissolved	MG/L	11	15.60	1.12	17.00	14.00
Sodium dissolved	MG/L	11	19.30	2.80	23.00	15.00
Potassium dissolved	MG/L	11	3.40	0.34	4.00	2.90
Chloride total	MG/L	11	18.54	3.93	23.00	13.00
Sulfate total	MG/L	11	41.80	8.27	58.00	27.00
Silica dissolved	MG/L	49	14.80	5.65	25.00	3.00
Arsenic total	µG/L	53	3.40	1.08	7.00	1.00
Cadmium total	µG/L	53	5.40	4.74	12.00	0.00
Chromium total	µG/L	52	2.70	4.36	10.00	0.00
Copper total	µG/L	53	36.50	48.62	170.00	2.00
Iron total	µG/L	53	259.00	186.27	1100.00	10.00
Lead total	µG/L	53	55.70	44.08	100.00	0.00
Zinc total	µG/L	53	45.30	65.19	420.00	0.00
Mercury total	µG/L	53	0.10	0.18	1.10	0.00
Selenium total	µG/L	50	0.30	0.51	2.00	0.00
Fecal coliform bacteria	/100 ML	53	30.00	25.56	86.99	0.00
Suspended solids at 150 C	MG/L	26	14.90	17.07	87.00	2.00
Residue suspended at 180 C	MG/L	14	17.90	16.59	59.00	3.00
Residue dissolved at 180 C	MG/L	50	264.00	34.06	338.00	201.00

[1] Data from U.S. Geological Survey (1975–1982).

Little has been reported concerning the water quality requirements of spongillaflies. Roback (1974) describes the larvae of Sisyridae as not especially tolerant of extremes of water chemistry. He goes on to state that "*Climacia areolaris* was found at alkalinity greater than 210 ppm, total hardness greater than 300 ppm, and sulfate greater than 400 ppm." The mean alkalinity at the Burley Snake River station was 160 mg/l (mg/l = ppm) with a range of 124–202 mg/l; mean total hardness was 165.83 mg/l (range 0–190 mg/l); and the mean sulfate concentration was 41.8 mg/l (range 27–58 mg/l) (Table 1). In addition, Table 1 provides, for the first time, detailed water quality information pertaining to this insect.

Harrison (1974) summarized the available water quality data for the sponge, *E. mulleri*. He listed the following ranges of parameters for which I have comparable data; conductivity 31–100 micromhos/cm; total hardness 60–160 mg/l; pH 6.1–8.5; residue 42–75 mg/l; $S:O_2$ 0.7–11.6 mg/l; and temperatures of

16–24 C. Data for the above parameters from the Snake River, Burley station, are as follows: conductivity, $\bar{X}$ = 447 micromhos/cm (range 351–842); total hardness, $\bar{X}$ = 165.83 mg/l (range 0–190); pH, $\bar{X}$ = 8.2 (range 6.3–8.9); silica, $\bar{X}$ = 14.8 mg/l (range 3–25); and temperature, $\bar{X}$ = 10.2 C (range 0–23). The term *residue* listed in Harrison (1974) could refer to several forms (Table 1). Suspended solids is one of the most commonly used measurements of residue and for the Snake River station had a range of 2–87 mg/l ($\bar{X}$ = 14.9). The Snake River data thus expands the known water quality tolerances of *E. mulleri* for temperature, conductivity, pH, hardness, silica, and residue.

Table 1 lists 33 additional water quality parameters that have not been previously reported for either *C. californica* or *E. mulleri*.

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POA L. IN NEW MEXICO, WITH A KEY TO MIDDLE AND SOUTHERN ROCKY MOUNTAIN SPECIES (POACEAE)

Robert J. Soreng[1]

ABSTRACT.— The 23 species and subspecies of *Poa* that occur in New Mexico are described in detail. Collection locations of these species in New Mexico are given in dot distribution maps. A descriptive key to the species of *Poa* that occur in Arizona, Colorado, Utah, Wyoming, and New Mexico, including general distribution for species not in New Mexico, is provided. Three new nomenclatural combinations are proposed: *Poa arctica* subsp. *aperta*; *P. fendleriana* subsp. *longiligula*; *P. f.* subsp. *albescens*. Subgeneric affinities of species of the southern Rocky Mountain region are indicated. Of the 25 species that occur within the region, the geographic affinities are: circumpolar (*P. alpina*, *P. arctica*, *P. glauca*, *P. interior*, and *P. leptocoma*), Beringian (*P. lettermanii*, and *P. pattersonii*), Eurasian weeds (*P. annua*, *P. bulbosa*, *P. compressa*, *P. palustris*, *P. pratensis* (also circumpolar), and *P. trivialis*), Pacific Northwest (*P. bolanderi*, *P. cusickii*, *P. nervosa*, and *P. stenantha*), northern Great Plains (*P. arida*), southern Great Plains and South American Pampas (*P. arachnifera*), Great Basin–Californian (*P. fendleriana* and *P. secunda*), and Middle and Southern Rocky Mountain (*P. bigelovii*, *P. curta*, *P. occidentalis*, *P. reflexa*, and *P. tracyi*). The only native diploid *Poa* species known in the Southern Rocky Mountains, the contiguous United States, and southern Canada are *P. lettermanii* and *P. occidentalis*.

POA L. (Bluegrass)

Low or moderately tall annuals or perennials, tufted, rhizomatous, or stoloniferous. *Blades* flat, folded, or rolled, tips usually curved and prowlike, glabrous on back, glabrous, scabrous, or pubescent above. *Sheaths* glabrous to pubescent, margins fused at least at base. *Ligules* membranous, sometimes hairy on back, smooth or minutely fringed terminally. *Inflorescence* an open or contracted panicle. *Spikelets* with 2–several (rarely 1) florets, disarticulating above glumes and between florets. *Glumes* narrow to broad, sharply acute to rounded, usually keeled on back, 1- to 3-nerved, shorter equaling or rarely longer than first lemma. *Lemmas* awnless, acute to rounded at apex, typically firm with scarious hyaline margin and tip, usually 5-nerved (3–11), prominently keeled on back or rounded (Secundae), glabrous scabrous or pubescent, with hairs confined to nerves or throughout, frequently with tuft of long cobwebby hairs from callus (pubescence characters are best seen on lower lemmas of spikelet). *Paleas* with chlorophyll (unlike *Koeleria*), two keels glabrous, scabrous, ciliate, or villous. *Flowers* perfect or unisexual (dioecious, gynodioecious, gynomonecious). *Stamens* 3, anthers 0.2–4 mm long, or vestigial (early aborted). *Pistil* glabrous. *Caryopses* ellipsoidal and usually somewhat compressed ventrally, hilum oval, less than 2/5 the caryopses in length. *Lodicules* membranous, broadly lanceolate, usually lobed, 0.3–1.2 mm long. *Basic chromosome number* X = 7. (Reported 2n chromosome numbers are recorded in species descriptions, modal numbers are in italics, and frequent numbers are boldfaced.)

About 250 species in temperate and colder regions worldwide, extending into the subtropics and tropics as montane species and as cool-season grasses at low altitudes. Identification of *Poa* species is difficult because of the large number of species and because the limited variety of characters distinguishing them mostly overlap. In addition, our traditional species criteria fail in certain groups (i.e., Poa, Stenopoa, and Secundae) wherein the high frequency of asexual reproduction by seed (agamospermy), high polyploidy, and hybridization combine to make the variation more or less continuous among many of the taxa.

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New Mexico county abbreviations: B = Bernalillo, DA = Dona Ana, CB = Cibola, CT = Catron, CV = Chaves, CF = Colfax, E = Eddy, GU = Guadalupe, GR = Grant, HD = Hidalgo, HR = Harding, LA = Las Alamos, LN = Lincoln, LU = Luna, MK = McKinley, MR = Mora, OT = Otero, RA = Rio Arriba, SD = Sandoval, SF = Santa Fe, SJ = San Juan, SM = San Miguel, SC = Soccoro, SR = Sierra, V = Valencia, TO = Taos, TR = Torrence, U = Union.

Distribution records for all the species were checked at GH, NMC, NMCR, NY, UNM, US, UTP. Much of these data come from fieldwork, vouchers for which are housed at NMC.

Subgeneric classification of the species of *Poa* occurring in the Southern Rocky Mountains is as follows:

SUBGENUS	SECTION	SPECIES TREATED HERE
Poa	Poa	*P. pratensis*, *P. arctica*
	Bolbophorum A. & G.	*P. bulbosa*, *P. alpina*
	Ochlopoa (A. & G.) Jiras	*P. annua*
	Coenopoa Hylander	*P. trivialis*
	Diversipoa Chrtek & Jirasek	*P. bigelovii*
	"unclassified"	*P. occidentalis*, *P. bolanderi*, *P. reflexa*, *P. tracyi*, *P. curta* (*sensu auct*)
	Oreinos A. & G.	*P. leptocoma*
	Abbreviatae Nannf. ex Tzvel.	*P. lettermanii*, *P. pattersonii*
	Stenopoa Dumort.	*P. palustris*, *P. glauca*, *P. interior*, *P. nemoralis*.
	Tricopoa A. & G.	*P. compressa*
	"unclassified"	*P. arida*
	"Secundae"	*P. secunda sensu lato.*
	"unclassified"	*P. stenantha*.
Dioicopoa E. Desv. ex C. Gay		*P. arachnifera* [*P. fendleriana*, *P. cusickii*, *P. nervosa*?]

KEY TO SOUTHERN ROCKY MOUNTAIN SPECIES OF *POA*

This key includes all the species of *Poa* found in Arizona, Colorado, Utah, Wyoming, and New Mexico. Species definitely known from New Mexico are typed in bold face. Those species not known from New Mexico are preceeded by their general geographic distribution and followed by an author citation.

1. Anthers, most of them, over 1 mm long, or aborted (vestigial); flowers perfect, unisexual, or forming bulblets; perennial 10

— Anthers consistently 1 mm or less in length; flowers mostly perfect; annual or perennial 2

2(1). Callus of lemmas long webbed; lemmas glabrous to minutely scabrid on the keel; plants annual, of midmontane habitats, rare in n UT, ID, NV, and WA, mostly in CA, OR. . . . . *P. bolanderi* Vasey

— Callus of lemmas webbed or not; lemmas glabrous to pubescent, if webbed, then prominently pubescent at least on nerves; plants annual or perennial, of various habitats. 3

3(2). Callus glabrous; lemmas glabrous or with a few minute hairs on keel, 2.5–3 mm long, relatively broad, blunt at apex; spikelets 3–4 mm long, anthers averaging 0.6 mm long; alpine plants 2–10 cm tall; sw CAN, w US, to COL . . . . *P. lettermanii* Vasey

— Callus webbed or, if glabrous, lemmas prominently villous at least on keel; other characters various 4

4(3). Plant perennial, sometimes flowering first year, sometimes alpine; if flowering first year, then callus webbed and panicle branches eventually widely spreading or reflexed; palea keels various 6

5(4). Callus glabrous; panicles more or less open . . . . **P. annua**

— Callus webbed; panicles long and contracted . . . . **P. bigelovii**

— Plants annual, rarely biennial, rarely alpine; callus glabrous and lemmas villous on all 5 nerves, or callus webbed and panicle narrowly contracted; palea more or less villous on keels 5

6(4). Plants 3–15 cm tall, tufted from narrow base; panicles narrow, short branched, little-exerted above basal leaves; callus sometimes webbed; lemmas pale green to purple, not bronze colored at tip, puberulous all over or pubescent only on nerves, rarely nearly glabrous; basal sheaths persistent, papery, upper ones closed $\frac{1}{4}$ the length or less; leaves green, soft, flat, lax; plants high alpine, on cold exposures, uncommon, sw CAN to UT and CO . . . . ***P. pattersonii*** Vasey

— Plants mostly over 15 cm tall, loosely tufted; panicle relatively broad, long branched, well exerted above basal tuft of leaves; callus webbed; other characters variable; plants of midelevations to low alpine 7

7(6). Sheaths closed $\frac{1}{5}$ or less the length; ligules mostly fringed on margins; first glume mostly 3-nerved (short anthered plants of *P. nemoralis* and *P. palustris*) 19

— Sheaths closed $\frac{1}{4}$–$\frac{2}{3}$ the length; ligules entire or jagged, smooth on margins; first glume mostly 1-nerved 8

8(7). Sheaths rarely glabrous, more or less densely retrorse-scabrous; panicle (8) 13–40 cm long, internodes (3) 4+ cm long; palea nerves glabrous or sparsely scabrous; lemmas mostly sparsely puberulent between 5 nerves, mostly pale green, margins and tips white-hyaline or sometimes purple tinged; plants of midmontane forested habitats . . . . ***P. occidentalis***

— Sheaths glabrous, roughened, or sparsely retrorse-scabrous; panicle mostly less than 12 cm long, internodes shorter than 3.5 cm; palea nerves mostly villous or ciliate-scabrous; lemmas rarely pubescent between the nerves, pale green to strongly purplish, tips bronze tinged or white-hyaline; plants usually of more moist subalpine and alpine habitats 9

9(8). Palea keels glabrous, scabrous, or with relatively regularly spaced, antrorsely curved, ciliate hairs, internerves with long cells only; glumes and lemmas narrowly lanceolate, unequal, first very narrow; lemmas sharply acute, intermediate nerves usually obscure, never villous; plants of wet habitats . . . ***P. leptocoma***

— Palea keels rarely glabrous, mostly villous-pilose, internerves with both short and long cells; glumes and lemmas broadly lanceolate, glumes subequal; lemmas bluntly acute, intermediate nerves frequently distinct, frequently somewhat villous; plants of wet or dryish habitats . . . . ***P. reflexa***

10(1). Florets normally forming leafy bulblets; plants tufted, culms somewhat bulbous at base . . . . ***P. bulbosa***

— Florets not normally forming bulblets; habits various, but culms not bulbous at base 11

11(10). Callus glabrous (infrequently with hairs similar to and continuous with those of lemma-keel), or (in *P. stenantha* and less often in *P. secunda*) with short, relatively straight hairs generally distributed around top of callus, these not restricted to dorsal side 22

— Callus webbed with tuft of short-kinky or long-sinuate hairs on dorsal surface, these isolated from those of lemma-keel 12

12(11). Plants dioecious, rhizomatous; panicle oblong, compact, terminal branches densely flowered from near base and, at least in female plants, densely scabrous; plants of se Great Plains, rare and doubtfully native in our area . . . . ***P. arachnifera***

— Plants perfect flowered (rarely pistillate); if pistillate, panicles more open, branches sparsely flowered in distal $\frac{1}{2}$ 13

13(12). Sheaths closed $\frac{1}{2}$–$\frac{9}{10}$ length; flowers perfect with anthers averaging 2.2 mm long, and/or pistillate with vestiges of anthers; panicles mostly 13–29 cm long, lower internodes mostly over 3.5 cm long, branches widely spreading to sharply reflexed; tall subrhizomatous plants . . . . ***P. tracyi***

— Sheaths closed ca $\frac{1}{2}$ or less the length; flowers normally all perfect; panicles mostly less than 13 cm long, internodes rarely over 3.5 cm long (if panicles and internodes longer, then lemmas glabrous between nerves and anthers less than 1.9 mm long); habits various. 14

14(13). Culms and nodes strongly flattened; plants strongly rhizomatous; sheaths closed $\frac{1}{4}$ or less the length; panicle short, compact to loose, with short branches; spikelets compact; ligule ciliate margined; lemma with a weak web . . . . ***P. compressa***

— Culms and nodes not decidedly flattened; other characters variable 15

15(14). Plants densely tufted (or in damp habitats with only a few culms in a bunch and then decumbent at base and rooting at nodes, but not definitely rhizomatous); sheaths closed near base to ca $\frac{1}{5}$ ($\frac{1}{4}$) the length (to ca $\frac{1}{2}$ in *P. trivialis*); panicle branches distinctly scabrous, mostly angled. 18

— Plants with strong rhizomes present; sheaths closed ca $\frac{1}{3}$–$\frac{1}{2}$ the length; panicle branches glabrous to sparsely scabrous, terete. 16

16(15). Glumes distinctly keeled, scabrous on nerves, second evidently shorter than first lemma; lemmas villous on keel and marginal nerves, glabrous between them (intermediate nerves rarely distinct, rarely sparsely pubescent); callus strongly webbed; ligules truncate, fringe margined; panicle often with 4 or more branches at lowest node; plants mostly lower than alpine . . . . ***P. pratensis***

— Glumes weakly keeled, nearly glabrous, second subequal to or longer than first lemma; lemmas villous on keel and marginal nerves and frequently on intermediate nerves, often puberulent between nerves; callus hairs variable; ligules truncate to long-acute, entire; panicle usually with fewer than 4 branches at lowest node; plants subalpine and alpine 17

17(16). Callus web scant and short to long and copious; panicles loose, branches flexuous; culms not wiry, mostly single, with several sterile shoots; ligules truncate to acute. . . . . ***P. arctica* subsp. *grayana*** (*sensu lato*)

— Callus web scant, short; panicles narrow or wide open, branches strict; culms wiry, mostly closely tufted, with relatively few sterile shoots; ligules acute to acuminate. . . . . ***P. arctica* subsp. *aperta***

18(15). Lemmas pubescent on keel below, glabrous or rarely very sparsely puberulent on marginal nerves, glabrous between nerves; ligules 3–10 mm long, entire or lacerate; first glume very narrow, 1-nerved, curved inward. . . . . ***P. trivialis***

— Lemmas pubescent on keel and marginal nerves and often between nerves; ligules less than 4 mm long, often minutely ciliate fringed on margins; first glume very narrow or quite broad, 3-nerved, not strongly arched inward; (long-anthered individuals of *P. pattersonii* may key out here, see lead 6) 19

19(7,18). Culms somewhat scabrous near nodes, stout, leafy to well above middle, frequently decumbant and rooting at nodes, sometimes branching above base, mostly 25–120 cm tall; ligules (1) 2–6 mm; panicles mostly 10–30 cm long, branches with abundant tertiary branching, many flowered; lemmas glabrous between keel and marginal nerves, abruptly incurved near tip; callus-web well developed; rachilla glabrous or scabrous. . . . . ***P. palustris***

— Culms mostly glabrous near nodes, either, "lax, slender, leafy to above middle," or, "wiry, strict, with few leaves, these mostly in lower $\frac{1}{3}$," never decumbent and rooting at nodes, never branching above base, height variable; ligules 0.2–3 mm long; panicles mostly shorter (except in *P. nemoralis*), main panicle-branches unbranched or with some secondary branches, mostly fewer flowered; lemmas glabrous or pubescent between keel and marginal nerves, not abruptly incurved near tip; callus-web from a minute tuft to well developed; rachilla glabrous, scabrous, or puberulent 20

20(19). Glumes very narrow (subulate), margins nearly straight; anthers 0.8–1.2 mm long; ligules nearly absent to 0.2 (1) mm long, truncate, pubescent on back, fringe margined; panicles many flowered, 5–25 cm long, branches widely spreading; foliage green; introduced, rare in w US, not known from our region . . . . *P. nemoralis* L.

— Glumes broader, margins of second frequently angled outward; anthers (1) 1.2–2 mm long; ligules various; panicles mostly fewer flowered, mostly less than 12 cm long, branches ascending; foliage green or glaucous; native species 21

21(20). Lemmas glabrous between nerves, rarely sparsely villous on intermediate nerves; callus web short or infrequently absent; plant green; culms erect, lax to slender-wiry, often geniculate at lower nodes, uppermost node in middle $\frac{1}{3}$; ligules ca 0.3–1.5 (2) mm long, scabrous on back, truncate, fringe margined; glumes sharply keeled, sharply acute and frequently curved in or out at tip; panicles 2–15 cm long, somewhat lax (or strict in small alpine forms), branches slender . . . . **P. interior**

— Lemmas mostly pubescent between nerves or pubescent on intermediate nerves; callus web well developed to frequently absent; plant green or glaucous; culms erect or spreading, stout to wiry, strict, uppermost node in near base; ligules 1–3+ mm long, similar to *P. interior* or, more often, rounded to obtuse and lacerate and then less scabrous on back and not or weakly fringe margined; glumes similar to *P. interior*, or less sharply keeled, more obtuse at tip and tips not divergent; panicles mostly less than 6 cm long, strict, branches more stout . . . . **P. glauca** (*sensu lato*)

22(11). Sheaths closed $\frac{2}{3}$–$\frac{9}{10}$ the length, glabrous; panicles 10–20 cm long, open and diffusely flowered, lowest axial internodes mostly 2.5–6 cm long, branches mostly reflexed; plants loosely tufted, short-rhizomatous, perfect-flowered or anthers of some or most flowers vestigial; lemmas strongly keeled, glabrous to sparsely hirtelous or puberulent on keel base and between nerves near base; plants of midmontane habitats, uncommon, ne UT, w ID, w WY, possibly to sw CAN . . . . *Poa curta* (*sensu. auct* non Rydb.)

— Sheaths closed $\frac{9}{10}$ to only near base, if closed over $\frac{2}{3}$ length and plant rhizomatous, then panicles mostly less than 13 cm long, axial internodes less than 2.5 cm long, branches mostly ascending, and at least lower sheaths puberulous; panicles various, mostly more condensed, or axial internodes mostly less than 2 cm long, branches mostly ascending; plants rhizomatous or not, variously flowered, lemmas various; plants of various habitats, mostly more widespread. 23

23(22). Flowers predominently perfect, stamens and stigmas more or less synchronously developed (remnants of a few anther sacs usually remain on even the most mature plants, filaments persistent); lemmas keeled or not; sheaths frequently closed $\frac{1}{4}$ the length or less (unless rhizomatous) 30

— Flowers pistillate (anthers vestigial or partially developed but nonfunctional) or staminate (ovaries and stigmas very reduced or undeveloped) or infrequently perfect in part; lemmas keeled on the back; sheaths closed $\frac{1}{3}$–$\frac{9}{10}$ the length. 24

24. Plants strongly rhizomatous; culms few, loosely tufted; upper culm blade well developed; basal tuft of leaves weakly developed; ligules of lower culm leaves obtuse to truncate, finely scabrous to puberulent on back; spikelets green; lemmas villous to scabrous on keel and marginal nerves and mostly scabrous between; sheaths (at least lower ones) finely puberulent (rarely nearly glabrous); midmontane forest openings and thickets, to lower alpine, widespread . . . . **P. nervosa** var. **wheeleri**

— Plants tufted, culms several to many or, if stolonous or rhizomatous, then the upper culm blade mostly very reduced; basal tuft of leaves well developed (except in *P. epilis*); ligules various; spikelets green or pale green and shining; lemmas and sheaths various; plants of various habitats 25

25(24). Lemmas sparsely to prominently pubescent on keel and marginal nerves, sometimes pubescent on intermediate nerves, and infrequently between nerves 28

— Lemmas scabrous to glabrous, less commonly finely and very sparsely puberulous on the lower keel and marginal nerves 26

26(25). Plants tufted, short-rhizomatous; culm blades strongly reduced upward, uppermost blade reduced or absent on most culms; basal blades relatively broad (1–3.5 mm wide) and firm; sheaths mostly smooth to sparsely scabrous, collar margins spiculate; ligules 0.25–1 (2) mm long, truncate to rounded, very scabrous on back, fringed on upper margin; lemmas mostly very smooth, sparsely scabrous to very sparsely puberulent on keel and marginal nerves, glabrous between nerves; plants of Sierra Madre Occidental . . . . **P. fendleriana subsp. *albescens***

— Plants densely tufted, never rhizomatous; culm blades not regularly and strongly reduced upward, uppermost blade mostly over 1 cm long; basal blades mostly 1 mm broad or less; ligules various; lemmas glabrous, or scabrous on nerves and frequently between them, infrequently very sparsely puberulous on keel; plants not known from south of s UT-CO state line in interior United States. 27

27(26). Panicle axis and branches moderately to densely scabrous; blades mostly basal, mostly filiform, involute, culm blades few, occasionally broader above and to 1.5 mm wide; culm sheaths more or less scabrous, mostly covering nodes, upper sheath often rather loose; lemmas scabrous on nerves, and usually between them, never glabrous all over; spikelets pale green, shining; plants either pistilate or staminate; n Great Plains grasslands, high sagebrush communities to alpine grasslands, widespread nw US, sw CAN, infrequent in n UT and CO (*P. subaristata* Rydb. form in Rocky Mts.) . . . . *P. cusickii* Vasey subsp. *cusickii*

— Panicle axis and branches smooth to infrequently moderately scabrous; blades about equally basal and cauline, basal ones usually filiform, involute, culm blades generally broader and flatter and mostly over 1.5 mm wide; culm sheaths mostly glabrous, mostly exposing culm nodes; lemmas glabrous or scabrous on and between nerves, rarely very sparsely puberulous on keel; spikelets green, often purple tinged; flowers pistilate; subalpine to alpine, common w US, sw CAN, to s UT and CO . . . . *P. cusickii* subsp. *epilis* (Scribn.) W. A. Weber

28(25). Lemmas more or less evenly pubescent over basal portion; plants densely tufted, lacking any rhizomes; blades very narrow, basal ones less than 1 mm wide, uppermost blade usually filiform and over 5 mm long; flowers rarely with well developed anthers; dry hills, w ID, w MT, w WY, ne UT, nw CO, and across northern plains of CAN, in ALB, SKW, MAN. (Although the type of this is like *P. cusickii*, many of the plants that key-out here are more like *P. fendleriana* in having firm, broader, folded blades, with the upper ones very reduced. This taxon appears to have evolved from hybridization between the two species) . . . . *P. cusickii* subsp. *pubens* Keck

— Lemmas strongly villous on keel and marginal nerves, infrequently pubescent between nerves; plant more loosely tufted, mostly with short, lateral, rhizomatous shoots; blades over 1.5 mm wide, uppermost blade, when present, firm, mostly very reduced; flowers pistilate or staminate, (staminate plants found occasionally in CO and more frequently to south and west); widespread 29

29(28). Ligules from merely a spiculate ridge to 1 (2) mm long, truncate to rounded and minutely fringed terminally, mostly quite scabrous on back; sheaths mostly scabrous (especially so on margins about collar) or finely puberulous; lemmas infrequently villous on intermediate nerves, glabrous between nerves. . . . . *P. fendleriana* subsp. *fendleriana*

— Ligules 1.8–11 mm long, obtuse, acute, or acuminate, mostly sparsely scabrous to glabrous on back, entire; sheaths glabrous to scabrous or minutely puberulous, but not distinctly so on margins near collar; lemmas occasionally villous on intermediate nerves, glabrous or occasionally sparsely puberulent between nerves. . . . . *P. fendleriana* subsp. ***longiligula***

30(23). Anthers not more than 1.2 mm long; lemmas distinctly keeled; foliage bright green; panicles not much exerted above basal tuft of leaves; blades less than 2 mm broad, soft, lax; plants narrowly-tufted, 2–15 cm tall; plants of high alpine situations, with both vegetative and fertile shoots; uncommon. . . . . (see *P. pattersonii*, couplet 6)

— Anthers usually more than 1.2 mm long; lemmas keeled or not; foliage green or glaucous; panicles well exerted above basal tuft of leaves; blades various; plants, if less than 15 cm, tall and alpine, then tufts dense, (in *P. glauca*, most shoots fertile, leaves relatively firm and strict). 31

31. Lemmas prominently pubescent; sheaths closed $\frac{1}{3}$–$\frac{1}{2}$ the length, or, open most of length 34

— Lemmas glabrous or scabrous, rarely very sparsely puberulent on keel; sheaths open most of length. 32

32(31). Ligules 2.5–6 mm long, acute or acuminate, glabrous or sparsely scabrous on back . . . . *P. secunda* (***P. nevadensis*** form)

— Ligules 0.25–4 mm long, truncate to obtuse, sparsely to densely scabrous on back; culms in large loose tufts (plants rarely rhizomatous). 33

33. Foliage somewhat coarse; blades involute, mostly less than 1.5 mm wide; plants mostly of low mountains and desert plains in poorly drained soils, Great Basin, WA to MT, south to UT and CO . . . . *P. secunda* (*P. juncifolia* form)

— Foliage more lax; blades flatish, mostly 1.5–3 mm wide; plants of high sagebrush slopes and higher, mostly of well-drained, rich soils . . . . . *P. secunda* (***P. ampla*** form)

34(31). Plants densely tufted; lemma pubescence variable 36

— Plants rhizomatous; lemma pubescence definitely stronger on nerves than between them, or glabrous between them 35

35(34). Sheaths closed ($\frac{1}{4}$) $\frac{1}{3}$–$\frac{1}{2}$ the length; glumes weakly keeled; lemma tips acute; callus glabrous or with an inconspicuous web; panicle branches strict or flexuous; plants subalpine to alpine . . . . . . ***P. arctica*** subsp. ***grayana*** s. str. (see also couplet 17)

— Sheaths closed $\frac{1}{5}$ the length or less; glumes strongly keeled; lemma tips often blunt; callus glabrous or with a few hairs continuous with and like those of the lemma keel; panicles and branches strict; plants of arid, alkaline plains and piedmont valleys, e (rare w) of continental divide . . . . ***P. arida***

36(34). Upper sheaths closed more than $\frac{1}{4}$ the length; culm bases enclosed in persistent, thickened, closely overlapping sheaths; foliage green; spikelets broadly rounded, almost cordate at base; panicle branches glabrous to sparsely scabrous, terete, strongly divergent, intricately rebranched, and closely flowered; plants of moist alpine situations, circumboreal, to s UT and CO . . . . *P. alpina*

— Upper sheaths closed less than $\frac{1}{4}$ the length; culm bases not enclosed in persistent, thickened, closely overlapping sheaths; foliage green or glaucous; spikelets broadly rounded or more elongate, not at all cordate at base; panicle branches moderately to strongly scabrous, distinctly angled to terete, but the branches not strongly divergent, intricately rebranched, and closely flowered; plants of various situations 37

37(36). Lemmas distinctly keeled, 4–6 mm long, pubescence longer and stronger on nerves than between them, or glabrous between them; rachilla internodes mostly over 0.8 mm long; spikelets mostly over 7 mm long; panicles open, somewhat lax, mostly 7–17 cm long, lower panicle branches mostly more than 3.5 cm long, variously divergent, moderately scabrous on weak angels; plants 2.5–6 cm tall, with few flowering shoots and many vegetative shoots; blades mostly well over 3 cm long, soft, lax, bright green; ligules 2–4 mm long, obtuse to acute, entire to lacerate on margins; callus often with hairs across top around base of lemma (different from those of surface of lemma); plants of mountain slopes, AK, sw CAN, to n UT, and central CO, where rare [including *P. macroclada* Rydb.] . . . . *P. stenantha* Trin.

— Lemmas keeled or not; if keeled, lemmas to 4 mm long, rachilla internodes mostly less than 0.8 mm long, spikelets less than 5 mm long, panicles less than 7 cm long with branches less than 4 cm long, plants less than 3 dm tall 38

38(37). Lemmas keeled on back, pubescence mostly longer and stronger on keel and marginal nerves than between them, occasionally glabrous between them; plants mostly less than 30 cm tall, with few vegetative and many flowering shoots; callus glabrous; rachillas to 0.8 mm long; panicles strict, branches strictly ascending, strongly scabrous on prominent angles; leaf blades less than 3 cm long, strict, not thin and soft; foliage green or glaucous; ligules 1–2 mm long, truncate to obtuse, often minutely fringe margined; plants of high mountains on dry slopes and ridges . . . . **P. glauca** subsp. **rupicola** (see also couplet 19)

— Lemmas more or less rounded across back, crisp-puberulent all across base, pubescence usually not or little longer and stronger on nerves (except in *P. gracillema* form), infrequently nearly glabrous between nerves; callus glabrous or with a few hairs no longer than and not separated from those of lemma keel, or with hairs across top around base of lemma (different from those of surface of lemma); plants of various heights, with many vegetative shoots and few flowering shoots; rachilla (0.6) 0.8–1.9 mm long; panicles various, branches moderately scabrous, weakly angled; leaf blades of various lengths, lax, very thin, soft; foliage green or infrequently glaucous; ligule 2–7 mm long, acute to acuminate, margins entire or lacerate; plants of various habitats . . . . (forms of ***P. secunda***, continue to couplet 39)

39(38). Plants mostly less than 4 dm tall; basal tuft of leaves fine, mostly less than 3 cm long and panicles contracted except in anthesis; plants of dry open ground at moderate elevations, flowering in early spring, sw CAN, to UT, and n CO . . . . *P. sandbergii* form

— Plants mostly over 4 dm tall; basal tuft of leaves mostly over 4 cm long, or panicles persistently open; plants of more mesic situations or higher elevations, flowering late spring to late summer 40

40. Panicles persistently open, lemmas evenly puberulent over base, or frequently with stronger pubescence on nerves than between them; plants of high mountains to alpine, sw CAN, south to n UT and CO . . . . *P. gracillema* form

— Panicles open only in anthesis, lemma pubescence fairly evenly developed over base; plants of various situations, widespread . . . . ***P. canbyi*** form

TAXA OF *POA* IN NEW MEXICO

Poa annua L.

Poa annua L., Sp. Pl. 68. 1753. Annual Bluegrass.

Annual, slender, tufted. Culms erect or ascending, often geniculate at the nodes, 0.1–3+ dm tall. Leaves light green, soft, glabrous. Sheaths closed about $\frac{1}{2}$ the length. Ligules glabrous, entire, about as long as blade is wide. Blades mostly flat, soon withering, mostly 1–2 (4) mm wide, 1–8 cm long. Panicles 1–5 cm long, open, ovate or broader, branches smooth, strict, divergent, densely flowered in distal $\frac{1}{2}$. Spikelets 2–6-flowered, 2.5–6 mm long. Glumes narrow, unequal, the first often curved inward and $\frac{1}{2}$–$\frac{2}{3}$ as long as adjacent lemma, second glume about $\frac{2}{3}$–$\frac{3}{4}$ as long as adjacent lemma. Lemmas broadly lanceolate, smooth, prominently 5-nerved, villous on nerves (rarely nearly glabrous) and glabrous between. Callus glabrous, rachilla internodes glabrous and short. Paleas mostly villous on nerves, glabrous between. Flowers of lower florets perfect, terminal one reduced to nob on rachilla, or developed and then pistillate (gynomonecious). Anthers 0.3–1 mm long. Chromosome numbers: 24–26, 28, 52.

HABITAT: A common lawn weed, potential in every habitat in New Mexico so long as there is shade, winter moisture, and disturbance. Flowering continually in irrigated areas, otherwise primarily late winter–early spring.

DISTRIBUTION: Introduced from Europe. New Mexico: B, DA, OT, LN, RA, SD, and SF, but probably in every county.

COMMENT: This species is perhaps one of the world's most widespread weeds. It was present in Sitka, Alaska, by at least 1829, where collected and mixed with the type of *Poa leptocoma* Trin. Probably the first collection in New Mexico was made by S. M. Tracy in 1887 near Santa Fe.

Poa arachnifera Torr.

Poa arachnifera Torr., in Marcy, Expl. Red Riv. 301. 1853. Lectotype (A. Hitchc.): Marcy "crop timbers, Arkansas," in 1852 (NY). Texas Bluegrass.

Perennial from long, slender rhizomes. Culms tufted, erect, 2.5–8.5 dm tall. Leaves green, firm. Sheaths closed $\frac{1}{3}$–$\frac{1}{2}$ the length, keeled. Ligules 1–4 mm long, acute. Blades flat or folded, often inrolled on margins, 1.5–4.5 mm wide, elongate. Panicles oblong, contracted, somewhat lobed, 3–15 cm long, branches slender, strongly scabrous (female) to nearly glabrous (male), terminal ones densey flowered. Spikelets slightly dimorphic, compact, compressed; male 2–10-flowered, 4–8 mm long; female 2–5-flowered, 4–9 mm long. Glumes 1–5-nerved, smooth to scabrous, narrow, subequal. Lemmas 5–7-nerved, smooth to sparsely papillose-roughened; male 3.5–5 mm long, acute, sparsely villous to scabrous on keel, callus with several slender, long, villous hairs; female 4.2–6.4 mm long, with long hyaline, acute tips, densely villous on keel and marginal nerves, sometimes sparsely so on intermediate nerves, glabrous between nerves, callus with a copious tuft of long, plicate hairs. Paleas glabrous to sparsely long-ciliate (male) to villous (female). Rachillas glabrous, internodes less than 1 mm long. Flowers unisexual (dioecious, hermaphroditic flowers developed infrequently and then resembling the female ones). Anthers 1.6–2.7 mm long. Chromosome numbers: 42, ca 54, 56, ca 63, 84.

HABITAT: One record in New Mexico from Bosque del Apache (V), in salty flood plain, ca 1520 m, in 1957. Flowering May. Doubtfully native in New Mexico. One collection, *C. Wright 2042* in 1851–1852 labeled as "New Mexico," belongs to this species, but where it was actually collected it is not known.

DISTRIBUTION: Apparently native to the south central Great Plains in Kansas, Oklahoma, Texas, Arkansas, but possibly introduced from South America in historical times. Introduced in all the southeastern states, but rare to the west. Seeded as a pasture and lawn grass in some areas.

COMMENT: *Poa arachnifera* is more similar to such South American dioecious species as *P. denudata* Steud., *P. bonarensis* (Lam.) Kunth., and *P. montevidensis* Arech. than to any other North American species.

Poa arctica R. Br.

Poa arctica R. Br., in suppl. App. Parry's Voy. 288 ("188"). 1823. TYPE: Parry Mellville Island, Arctic America.

Poa arctica subsp. *aperta* (Scribn. & Merr.), *comb. nov.*

Poa arctica subsp. *aperta* (Scribn. & Merr.) *comb. nov.*; *Poa aperta* Scribn. & Merr., USDA, Div. Agrost. Circ. 35:4. 1901. TYPE: *Shear & Shear 98*, open mountainside, 2896 m elev., Telluride, Colo., 1 Sept. 1900 (US 28611600!, NY).

Perennial with rhizomatous. Culms wiry, decumbent, often densely tufted, smooth, 2–6 dm tall. Leaves greenish to glaucesent. Sheaths $\frac{1}{4}$–$\frac{1}{2}$ open, rounded. Ligules 3–7 mm long, acute to attenuate, smooth. Blades ascending, strict, flat or folded, to 2.5 mm wide. Panicles erect, narrow to ovate, 4–15 cm long, few-flowered, branches strict and steeply ascending (or sharply divergent in anthesis). Axis internodes mostly 1–2 cm long, rarely over 3 cm long. Spikelets ovate, 2–3 (4) flowered, proportionally more green and less purple than typical *P. arctica*. Glumes large, lanceolate, the second broadly so, with broad-hyaline-margins, smooth, weak keel glabrous or very sparsely scabrous near tip, second glume subequaling first lemma in length. Lemmas 3.5–6 mm long, lanceolate, acute, obscurely 5-nerved, densely villous on keel and marginal nerves, abundantly short villose between nerves, this occasionally nearly restricted to intermediate nerves, pubescence occasionally uniformly and abundantly short villose over nerves and whole base of lemma. Callus glabrous to sparsely webbed. Paleas glabrous, sparsely scabrous, or abundantly villous on keels, glabrous to puberulent between them. Rachilla internodes glabrous, usually visible from side. Flowers perfect but anthers occasionally abortive. Anthers 1.4–2.5 mm long, yellow to purplish (aborted ones remaining yellow). Chromosome number: 99.

HABITAT: Spruce-fir forest to alpine meadows and grasslands, mostly 2440–3800 m. Flowering July–August. Occurring from deep, rich soils to rocky places, in somewhat drier and warmer situations than the other subspecies.

DISTRIBUTION: Southern Rocky Mountains in s Utah, s and c Colorado. New Mexico B, RA, SD, SM, TO.

COMMENT: This subspecies is a most distinctive race of *Poa arctica* s. lat. It is markedly different on first sight in its more tufted and stricter habit, with fewer sterile shoots and proportionally more flowering shoots, more pale or glaucus foliage, and more southerly and often subalpine habitat. It may introgress with *Poa secunda*, but it shows strong affinity to *P. arctica* and grades into that species.

Poa arctica subsp. *grayana* (Vasey) Love, Love & Kapoor

Poa arctica subsp. *grayana* (Vasey) Love, Love & Kapoor, Arctic & Alpine Res. 3:143. 1971; *Poa grayana* Vasey, Contr. U.S. Nat. Herb. 1:272, 1893. TYPE: *Patterson 14*, Grays Peak, Colorado, (US!). *Poa alpicola* Nash in Rydb., Mem. N.Y. Bot. Gard. 1:272, 1893. *Poa phoenicea* Rydb., Bull. Torr. Bot. Club 32:605, 1905. *Poa chionogenes* Gandog., Bull. Soc. Bot. France 66:302, 1920. *Poa longipila* Nash in Rydb., Mem. N.Y. Bot. Gard. 1:46, 1900. *Poa callichroa* Rydb., Bull. Torr. Bot. Club. 32:603, 1905. *Poa tricolepis* Rydb., ibid., 606, 1905. Arctic Bluegrass.

Perennial, with well developed rhizomes. Culms usually decumbent, loosely tufted, smooth, 1–6 dm tall. Leaves green, firm. Sheaths closed $\frac{1}{4}$ to $\frac{1}{2}$ the length. Ligules 2–3 (4) mm long, truncate to acute, mostly entire. Blades flat or folded, 1–3 mm wide, those of culms less than 8 cm long, often curved upward. Panicles erect to nodding, ovate, 3.5–15 cm long. Branches 2–3 (5) per node, slender, often drooping or contorted, smooth to sparsely scabrous, bearing few spikelets toward tip. Axis internodes mostly 1–2 cm long, rarely over 3 cm long. Spikelets ovate, loosely, 2–6-flowered, 4–8 mm long, strongly purplish. Glumes large, lanceolate, second broadly so, with broad, purplish, hyaline margins, smooth, weak keel glabrous or very sparsely scabrous near tip, second glume subequaling first lemma in length. Lemmas (3) 4–6 mm long, 5-nerved, compressed-keeled, densely villous on keel and marginal nerves, mostly villous on intermediate nerves, mostly sparsely puberulent between nerves at base, mostly strongly purplish, bronze colored near tip. Callus glabrous or scantly webbed [subsp. *grayana* (s. str.)] to densely long-villous [*P. longipila* form]. Paleas glabrous, sparsely scabrous, or abundantly villous on keels, glabrous to puberulent between them. Rachilla internodes glabrous or villous. Flowers perfect but anthers occasionally abortive. Anthers 1.4–2.5 mm long, yellow to purplish (aborted ones remaining yellow). Chromosome numbers 36–106, most frequently reported being 56 and 70.

HABITAT: Alpine. Occurring most frequently in cold, mesic sites, usually in peaty soils, 3100–3800 m in New Mexico. Flowering July–August.

DISTRIBUTION: The typical subspecies: Circumboreal, high arctic. Subspecies *grayana*: Cascade Mountains, and Canadian Rocky Mountains south to n New Mexico. CF, MR, RA, TO. *Poa longipila* is the most common form of subsp. *grayana* in the n Rocky Mountains and is known in the U.S. from as far south as s Colorado, where it is less common than the subspecies *grayana* in the strict sense.

COMMENT: Rocky Mountain phases of *Poa arctica*, based on the supposed larger stature of the plants, are often referred to *P. grayana*. However, population studies in Alaska and the Rocky Mountains do not support this distinction. Subspecies *grayana*, as originally proposed, is a heterogenous group and included all U.S. material of the species. However, many plants and populations from the Rocky Mountains match or lie between the more northern complex of the species. The complex requires a comprehensive study of population and herbarium material from its full geographic range.

Poa arida Vasey

Poa arida Vasey, Contr. U.S. Natl. Herb. 1:270. 1893. TYPE: *Vasey*, Socorro, New Mexico, in 1881 (US, GH!). *Poa planifolia* Scribn. & Will. in Scribn. USDA Div. Agrostol. Circ. 9:3. 1899, not Kuntze, 1898; *Poa glaucifolia* Scribn. & Will., ibid. 10:6. 1899. TYPE: *Williams 2814*, moist banks, Spring Creek, Big Horn Basin, Washakie Co., Wyo., 4 Aug. 1897 (US). Plains Bluegrass.

Perennial with strong rhizomes. Culms round, 1.5–8 dm tall, not crowded, glabrous to scabrous, conspicuously striate. Leaves pale green, often glaucous, quite firm. Sheaths closed about $\frac{1}{6}$ the length, mostly glabrous. Ligules 1–4 mm long, acute, entire or lacerate. Blades 1–5 (mostly 2) mm broad, flat to folded, uppermost leaf usually 1–6 cm long. Panicles 4–12 (18) cm long, narrow and compact or infrequently open, branches more or less scabrous on sharp angles. Axis internodes 1–2 rarely over 3 cm long. Spikelets (2) 3–7-flowered, 4–7 mm long, compact, ovate or longer. Glumes glabrous or more often sparsely scabrous on upper portion of keel, $\frac{2}{3}$–$\frac{3}{4}$ as long as subtended lemmas. Lemmas 2.5–4 mm long, obtuse to acute, prominently 5-nerved, often weakly keeled, densely pubescent on keel and marginal nerves and usually also on intermediate nerves, densely short-villous between nerves to glabrous. Callus glabrous. Rachilla usually pubescent. Paleas villous to long scabrous on keels. Flowers perfect. Anthers 1.3–1.7 (2+) mm long. Chromosome numbers: 63, 64, 76, 84, 90, 103, (*P. glaucifolia* form: 50, 56, 70, 81, 84, 86, ca 100).

HABITAT: In New Mexico, *P. arida* is the only native perennial bluegrass on the open plains and alkaline or saline flood plains, 1070–1980 m. Flowering May–July.

DISTRIBUTION: Western Great Plains Canada south to New Mexico; B, CV, G, MR, SC, SM, U, V. The several Utah records of this species I have seen are all alpine and are referable to *Poa arctica* subsp. *aperta*. The Arizona records of this species have been based on rhizomatous specimens of *Poa fendleriana*.

COMMENT: *Poa glaucifolia* appears to be a shade or mesic form having more lush foliage, smaller, more numerous, less pubescent spikelets, and larger, more open panicles. *Poa arida* shows some affinity to the *P. secunda* complex and appears to hybridize with it where ranges overlap. This species may have evolved from Pleistocene hybridization between species of section *Poa* and the "Secundae" group.

Poa bigelovii Vasey & Scribn.

Poa bigelovii Vasey & Scribn., in Grasses U.S. Descr. Cat. 81. 1885, *nomen nudum*; Vasey & Scribn. in Vasey, Contr. U.S. Natl. Herb. 1:270. 1893. TYPE: *Fendler 931*, New Mexico [probably along Santa Fe Cr. above Santa Fe], in 1847. *Poa annua* var. *stricta* Vasey, Bull. Torrey Bot. Club 10:31. 1883. Bigelow Bluegrass.

Erect, loosely tufted annuals (rarely biennial). Culms sometimes geniculate at base, leafy, 1–6 dm tall. Leaves bright green, mostly cauline. Sheaths sharply keeled, closed ca $\frac{1}{4}$–$\frac{1}{2}$ the length. Ligules 1–6 mm long, acute, entire, glabrous to scabrous on back. Blades 1.5–5 mm broad, flat or folded, prominently keeled and prow tipped. Panicles very narrow, elongate, internodes frequently over 4 cm long. Branches appressed, often flowered from base, scabrous. Spikelets crowded on branches, compact, 4–7 mm long, ovate, strongly compressed. Glumes narrow, tending to curve inward, first subequal to second, scabrous on 1–3 nerves, with narrow hyaline margins. Lemmas broadly lanceolate, acute to blunt, with whitish hyaline margins, 3–5 mm long, 5-nerved, intermediate usually distinct, villous on keel and marginal nerves and sometimes on midnerves, finely papillose-roughened glabrous or puberulent between nerves on lower $\frac{1}{2}$. Callus with tuft of long hairs. Paleas mostly sparsely short villous on keels (at least near middle) and scabrous above, papillose between nerves. Rachilla internodes glabrous, slender, short, and hidden from side view. Flowers perfect, mostly cleistogamous. Anthers 0.2–1 mm long. Chromosome numbers: 28, 28+1.

HABITAT: Frequent to locally abundant in warm deserts to ponderosa pine zone, sporadic northward and upward. In shade of rocks and shrubs and in arroyo bottoms 1070–2900 m in New Mexico. Flowering March–May.

DISTRIBUTION: Southwestern U.S., Oklahoma, s Colorado, s Utah, s Nevada, to California, Arizona, south to Texas, Baja California, and c Mexico. New Mexico: CB, DA, ED, CT, HD, LU, LN, MK, MR, OT, RA, SC, SD, SF, SM, TO, TR.

COMMENT: Although considered by most authors to be close to *Poa annua*, *P. bigelovii* is more closely related to *P. occidentalis*.

Poa bulbosa L.

Poa bulbosa L., Sp. Pl. 70, 1753. Bulbous Bluegrass.

Perennial, densely tufted. Culms 0.5–6 dm tall, somewhat bulbous at base. Leaves green. Sheaths round, usually smooth, closed only at base, lower ones often reddish, basal ones fibrous. Ligules 2–3.5 mm long, glabrous, obtuse, entire or lacerate. Blades near base of plant soft and filiform, those of culm 1–2 mm wide. Panicles lax, broadly lanceolate, up to 10 cm long. Spikelets usually with few "normal" florets beneath terminal, mostly bulbiferous ("viviparous") florets, compressed. Glumes mostly normal, sparsely scabrous on keel. Lemmas of normal florets strongly keeled, glabrous to sparsely villous on keel and marginal nerves, minutely papillose-roughened between nerves, with or without a sparse web on callus. Paleas sparsely scabrous on keels. Flowers at base of spikelet usually perfect but often incompletely developed, the upper producing bulbous vegetative offsets. Anthers 1.2–1.5 mm long, questionably functional. Chromosome numbers: *14*, 21, 28, 39, 40, **42**, 45, 56, 58.

HABITAT: The few collections to date (1936 and 1938) from New Mexico have been from grassland communities. It is likely to have spread into ponderosa pine zone of northern New Mexico as well, 1830–1980 m. Flowering April–September.

DISTRIBUTION: Introduced from Europe, widespread in w North America. New Mexico: MK, RA, SJ.

Poa compressa L.

Poa compressa L., Sp. Pl. 69. 1753. Canada Bluegrass.

Perennial, strongly rhizomatous, frequently sod forming (reportedly cespitose in one strain, but this not known from New Mexico). Culms slender to very stout, flattened, often geniculate at the nodes, nodes strongly flattened, 20–60 cm tall, lower internodes usually shorter than sheaths. Leaves green, firm. Sheaths flattened, closed from only near base up to $\frac{1}{4}$ the length. Ligules 1–3 mm long, mostly obtuse, jagged, ciliate fringed on margin, mostly glabrous on back. Blades of culm mostly regularly divergent, 1.5–4 mm broad, 2–10 cm long flat or folded, upper-one fixed well above middle of culm. Panicles mostly erect, contracted, 2–10 (15) cm long. Branches short, mostly less than 3.5 cm long, mostly steeply ascending (to widely spreading in anthesis), strongly scabrous on prominent angles. Axis internodes mostly less than 3 cm long. Spikelets strongly compressed, 2.5–8 mm long. Glumes mostly $\frac{1}{2}$–$\frac{2}{3}$ as long as adjacent lemmas, mostly 3-nerved, scabrous on keel in upper part. Lemmas broadly-acute to blunt, hyaline-tipped, strongly 5-nerved, villous on keel and marginal nerve, glabrous between nerves and distinctly finely papillose-roughened. Callus mostly with short web, sometimes glabrous. Paleas scabrous on keels, glabrous between. Rachillas short, glabrous. Flowers perfect. Anthers 1.3–1.8 mm long. Chromosome numbers: *14*, 35, 39, ***42***, 45, 49–50, *56*, 84.

HABITAT: Open ground, roadsides, disturbed meadows, often in riparian areas, in forested habitats, 1520–3050 m in New Mexico. Flowering June–August.

DISTRIBUTION: Introduced from Europe, widespread in North America. New Mexico CF, CT, HR, LN, MK, OT, RA, SD, SF, SM, TO, TR.

COMMENT: Frequently confused with *Poa pratensis*, but the latter has more closed, weakly keeled sheaths and terete culms.

Poa fendleriana (Steud.) Vasey

Poa fendleriana subsp. *fendleriana*

Poa fendleriana (Steud.) Vasey subsp. *fendleriana*, USDA Div. Bot. Bull. 13(2):pl. 74. 1893; *Eragrostis fendleriana* Steud., Syn. Pl. Glum. 1:278. 1854. LECTOTYPE (Marsh): *Fendler* 932 "Mexico" [New Mexico, probably in Santa Fe Canyon above Santa Fe.], in 1847 (NY!, plant no. 1 of that sheet); ISOTYPES: NY!, GH!, GH!. Fendler Muttongrass.

Perennial, tufted, usually producing short rhizomes (these infrequently collected). Culms mostly slender to stout, (15) 25–45 (60) cm tall (male), (15) 30–60 (80) cm tall (female). Leaves green, infrequently bluish, quite firm, mostly basal, basal tuft 2–40 cm tall. Sheaths closed ca $\frac{1}{3}$ the length, strongly striate, more or less coarsely spiculate about collar near sheath margins, mostly puberulent or finely scaberulous (if glabrous or sparsely scabrous, then lemmas quite villous on keel nerve). Ligules from merely spiculate ridge to 1 (2) mm long, truncate to rounded, spiculate fringed on upper margin and abundantly scabrous on back. Blades (0.5) 0.8–2 (3) mm wide, thick, firm, mostly scabrous to puberulent ventrally, flat or folded, occasionally with margins inrolled, within a plant upper blade of at least some culms 0–3 mm long, others occasionally exceeding 1 (4.5) cm in length. Panicles narrowly oblong, compact (more open in flower), branches scabrous, often flowered from base, spikelets loosely arranged on short pedicels, sexually dimorphic, 2–6 (9) cm long in males, (3) 4–8 (12) cm long in females. Axis internodes mostly less than 2.2 (3) cm long. Spikelets ovate, somewhat plump, 3–10 mm long, 2–7-flowered, mostly shiny, and pale green, sometimes turning purplish, ca 15–60 per panicle. Glumes lanceolate to broadly so, 1–3-nerved, mostly glabrous and shining. Lemmas 3–6 mm long, smooth to papillose-roughened, 5-nerved, intermediate nerve often obscure, prominently long-villous on keel and marginal nerves and glabrous between them (1% of New Mexico specimens sparsely villous on intermediate nerves as well). Callus glabrous or with hairs no longer than those on rachilla internodes. Paleas roughened, scabrous to villous on keels and between them. Rachillas less than 1.3 mm long, glabrous to scabrous, infrequently pubescent. Flowers unisexual, (dioecious). Anthers 1.5–3 mm long. Chromosome number: ***56***.

HABITAT: Rocky slopes and meadows, upper desert-grasslands, interior chaparral to subalpine grasslands, frequent in ponderosa pine–gambel oak associations, 1220–3350 m. Flowering February–June (October). One of most abundant early spring flowering species in New Mexico.

DISTRIBUTION: Southern Montana south to n Mexico, w Utah, Arizona, Wyoming, South Dakota, Colorado, Oklahoma, Texas, Coahuila, Chihuahua, New Mexico DA, B, CB, CF, CT, GR, HD, LA, LN, LU, MK, MR, OT, RA, SC, SD, SF, SM, SR, TO, TR, U.

COMMENT: This subspecies appears to be restricted to areas under the influence of summer monsoons. As averaged over the range, approximately 15% of the specimens are male plants, these originating predominently from New Mexico, Arizona, and Texas. Intermediate sexual populations between this and subsp. *longiligula* occur where the sexual races of each subspecies are geographically in contact. Many of the plants from outside the sexual zones exhibit intermediate characteristics as well, but most tend strongly toward one or the other sexual race in morphology and ecology.

Poa fendleriana subsp. *albescens* (Hitchc), comb. nov.

Poa fendleriana subsp. *albescens* (Hitchc.), comb. nov.; *Poa albescens* Hitchc., Contr. U.S. Nat. Herb. 17(3):375. 1913. HOLOTYPE: *Rose 11648*, Mexico, Chihuahua, Minaca, 1 Apr 1908, (US 454361!). *Poa griffithsii* Hitchc., Contr. U.S. Nat. Herb. 17(3):375. 1913. HOLOTYPE: *Griffiths 4865*, Mexico, Sonora, Cananea, 7–8 Jul 1907, (US 691228! (an aberrant specimen, tending to be bulbiferous)). Mexican Muttongrass.

Similar to *Poa fendleriana* subsp. *fendleriana*. Culms slender to stout, 20–60 cm tall. Leaves mostly basal, green. Sheaths glabrous to rarely strongly scabrous, collars spiculate near leaf margins. Ligules from nearly absent to 1.8 mm long, truncate to rounded, spiculate-fringed on margin, scabrous on back. Blades flat or folded, sometimes inrolled on margins. 1–2.5 (3.5) mm wide, uppermost blade 0–6 (12) mm long. Panicles (3) 4–12 (20) cm long, branches scabrous. Axis internodes 1–3 cm long. Lemmas glabrous to sparsely puberulous on keel, sometimes sparsely scabrous on upper keel, marginal nerves usually obscurely and regularly short ciliate, glabrous between nerves. Paleas glabrous between keels. Rachillas glabrous. Flowers unisexual (dioecious; primarily sexual but asexual populations known). Anthers 1.5–3 mm long. Chromosome number: 28+1.

HABITAT: Pine-oak to spruce forests and subalpine grasslands, in rocky, organic soils and steep meadows, 1680–3350 m.

DISTRIBUTION: Sierra Madre Occidental Mexico in w and Chihuahua, ne Sonora, in the U.S. in the mountains of se Arizona and sw New Mexico: HD.

COMMENT: *Poa albescens* and *P. griffithsii*, each described from single specimens, differ only in minor ways. Since their publication, an array of specimens have been collected that are intermediate and serve to bridge the main differences between them. The lemmas of plants of *P. f.* subsp. *albescens* are mostly glabrous or very sparsely pubescent, and the sheaths are mostly glabrous. Other than in the characters mentioned above, subspecies *albescens* stands only slightly morphologically removed from the typical subspecies, yet it is cytologically distinct. The proposed subspecies is restricted to the Sierra Madre Occidental. This taxon intergrades to subsp. *fendleriana* where the two occur together, but very few intermediate staminate specimens have been discovered.

Poa fendleriana subsp. *longiligula* (Scribn. & Will.), comb. nov.

Poa fendleriana subsp. *longiligula* (Scribn. & Will.), comb. nov.; *Poa longiligula* Scribn. & Will., USDA Div. Agrost. Circ. 9:3, 1899. HOLOTYPE: *Jones 5149*, Silver Reef, Washington Co., Utah, 3 May 1894 (US 28539100!. ISOTYPES: MO!, OSC!); *Poa fendleriana* var. *longiligula* (Scribn. & Will.) Gould, Madrono 10:94, 1949. Longtongue Muttongrass.

Perennial, tufted, sometimes stooling, but less evidently rhizomatous, and generally more robust than typical subspecies. Leaves firmer, pale green to somewhat bluish. Sheaths glabrous to scabrous or infrequently puberulent, but hairs not noticeably coarser and congested around collar margins. Ligules obtuse to acuminate, entire or only very faintly scabrous on margin, glabrous to sparsely scabrous on back, (1.5) 2–18 mm long. Blades somewhat broader than in typical subsp., (0.8) 1.5–2.2 (4) mm wide, flat or folded, rarely inrolled on margins, glabrous, scabrous, or puberulent ventrally, upper culm blade of some culms reduced to 4 mm long or less, longest ones to 2 (7.8) cm long. Panicles slightly dimorphic, (2) 3–8 (10) cm (males), (2) 5–12 (30) cm long (females). Axis internodes to over 4 cm long. Spikelets 2–13-flowered, 4–12 mm long, pale green, shiny. Lemmas 5-nerved, intermediate nerves obscure to prominent, prominently long villous on keel and marginal nerves, glabrous or sparsely villous on intermediate nerves, glabrous or occasionally puberulent between nerves. Rachillas hirtellous to puberulous. Flowers unisexual, (dioecious, infrequently perfect in part). Anthers 1.5–3.8 mm long. Chromosome numbers: 56.

HABITAT: From interior chaparral and pinyon-juniper to subalpine meadows, often in somewhat dryer situations than typical subsp., 1830–2440 m in New Mexico, 910–3510 m elsewhere. Flowering March–July.

DISTRIBUTION: Mexico in Baja California, California, Oregon, Idaho, Nevada, Oregon (almost exclusive of subsp. *fendleriana*), sw Canada in British Columbia, Arizona, Colorado, Montana, South Dakota, Utah, Wyoming (where occasionally intermediate to subsp. *fendleriana*). Northwest New Mexico: B, CB, MK, SC, SD, SJ, TO.

COMMENT: This subspecies is predominately distributed west of the summer monsoon region. Agamospermy is the predominant mode of reproduction in this subspecies, but staminate plants are frequent in Arizona, Utah, and s California and Nevada. Only one staminate plant has been collected in New Mexico. In contrast to subsp. *fendleriana*, about half the plants of subsp. *longiligula* exhibit pubescent lemma intermediate nerves. None of the New Mexico material of the species has pubescence between the lemma nerves, but to the north and west some plants of subsp. *longiligula* are hairy in this region.

Poa glauca Vahl.
Poa glauca subsp. *glauca*

Poa glauca Vahl subsp. *glauca*, Fl. Dan. fasc. 17:3. Pl. 964. 1790. TYPE: Norway. Glaucous Bluegrass (Timberline Bluegrass).

Perennial, cespitose, most shoots flowering. Culms mostly 1–3+ dm tall, strict, stout, wiry, mostly ascending, glabrous or rarely sparsely scabrous about the nodes. Leaves glaucous, few on culm. Sheaths rounded or slightly keeled, closed from near base up to $\frac{1}{4}$ the length. Ligules 0.5–3+ mm long, short-truncate to obtuse, upper edge entire to erose, often minutely fringed, sparsely to strongly scabrous on back. Blades 1–2.5 mm broad, firm, upper one located below middle of culm, 1–5 (6) cm long. Panicles 1.5–7 (12), open or closed, ovate to lanceolate, branches strict and steeply ascending, to 3+ cm long, mostly strongly scabrous on angles, and with a few flowers near tips. Axis internodes rarely over 2 cm long (in Rocky Mountains). Spikelets compressed, ovate, glaucous, often somewhat purplish, 2–3 (5)-flowered, 2–5 (7) mm long. Glumes mostly 3-nerved, subequal, mostly sparsely scabrous on nerves and frequently between them, the second mostly with margin distinctly angled or rounded near middle, $\frac{3}{4}$–$\frac{7}{8}$ as long as first lemma. Lemmas 2–4 mm long, distinctly 5-nerved, papillose-roughened to nearly smooth, glabrous to sparsely puberulent between nerves, villous on keel and marginal nerves and frequently also on intermediate ones, hyaline margin narrow, obtuse, and frequently blunt at tip. Callus with distinct tuft of hairs up to $\frac{1}{2}$ as long as lemma. Paleas scabrous or infrequently glabrous on keels, papillose, scabrous, or puberulent between keels, usually short spiculate between keels. Rachillas glabrous, scabrous, or puberulent. Flowers all perfect but frequently anthers infertile. Anthers 1.4–2 mm long. Chromosome numbers: 42, 44, 56–58, 62–63, 70–72, 75, 78.

HABITAT: Subalpine to alpine, meadows, rocks, exposed ridges, wind balds, from open ground to among densely thatched cushion plants, 3350–3960 m in New Mexico. Flowering July–August.

DISTRIBUTION: Circumpolar boreal. *Poa glauca* subsp. *glauca* is found in most of tiaga-tundra, subalpine, and alpine regions of Canada but is infrequent southward in U.S. Rocky Mountains, occurring south to south central New Mexico: LN, OT, RA, SF, TO.

COMMENT: *Poa glauca* subsp. *glauca* is less frequent than subsp. *rupicola* in the U.S. Rocky Mountains. The latter may be distinguished by its smaller, more slender, and erect culms, greener foliage, and the presence of pubescence between the lemma nerves, and callus with a minute web or glabrous. The transition between the forms is highly complex. In population samples of "*P. rupicola*" from the Rocky Mountains, it is common to find the extremes of *P. glauca* and *P. interior*, and all intermediate combinations of habit, coloration, and spikelet pubescence. However, subsp. *rupicola* occasionally forms monomorphic populations, and in some regions of the west, such as in the Sierra Nevada, this is the only form present. In transplant studies with Rocky Mountain alpine material, identified in the field as "*P. rupicola*," glaucousness or greenness, spikelet pubescence, shape of spikelet parts, and general leafiness were stable characters. Stature and panicle dimensions tended to be more plastic.

Western U.S. *Poa glauca* (*s. lat.*) is part of an extremely variable agamic complex. It often occurs with, and shows forms intermediate to, *P. secunda*, but in most cases may be distinguished as keyed.

Poa glauca subsp. *rupicola* (Nash) W. A. Weber

Poa glauca subsp. *rupicola* (Nash) W. A. Weber, Phytologia 51:375. 1982; *Poa rupicola* Nash, Bull. Torrey Bot. Club 14:94. 1887. LECTOTYPE (A. Hitchc.): *Wolf 341*, South Park, Colorado, in 1873 (NY!); *Poa rupestris* Vasey, not Roth 1817, not Bieb 1831, not With. 1796; *Poa glauca* var. *rupicola* B. Boivin, Naturaliste Canad. 94:527. 1967. Timberline Bluegrass.

Similar to subspecies *glauca*, but varying as follows: Culms more slender and erect, mostly 0.5–1.5 (2.5) dm tall. Leaves green to somewhat glaucous, few on culm. Blades 1–2 mm wide, firm, upper-one usually located below middle of culm and 1–3 (4) cm long. Panicles 1.5–5 cm long, open or closed, ovate to lanceolate, branches more slender. Axis internodes to 2 cm long. Spikelets more compact, usually somewhat glaucous, often reddish or purplish, 2–3 (4) flowered, 2–5 mm long. Glumes mostly sparsely scabrous on nerves and frequently between them, both broad, mostly 3-nerved, subequal, the second mostly with margin distinctly angled or rounded near middle. Lemmas 2–3.5 mm long, distinctly papillose-roughened, villous on keel and marginal nerves and often on intermediate nerves, usually puberulent between nerves, acute to obtuse and sharp or blunt at tip. Callus with tiny tuft of crinkled hairs or glabrous. Anthers 1.1–1.6 mm long. Chromosome numbers: 48–50, 54–56.

HABITAT: Subalpine to alpine, meadows, rocks, exposed ridges, wind balds, from open ground to among densely thatched cushion-plants, 3350–3960 m in New Mexico. Flowering July–August.

DISTRIBUTION: Alpine regions of Western North America. Generally replacing typical subspecies throughout western U.S. Canada in Alberta and British Columbia, south to alpine of California, northern Arizona, and south central New Mexico: LN, OT, RA, SF, TO.

COMMENT: This race occurs to the exclusion of subsp. *glauca* and *P. interior* in the Pacific cordillera. However, see comments under those taxa.

Poa interior Rydb.

Poa interior Rydb., Bull. Torrey Bot. Club 32:604. 1905. TYPE: *Tweedy 3706*, Headwaters of Clear Cr. and the Crazy Woman Rv. Wyoming, in 1900 (NY!); *Poa nemoralis* var. *interior* (Rydb.) Butt. & Abbe; *Poa nemoralis* subsp. *interior* (Rydb.) W. A. Weber, Phytologia 51:375. 1982. Inland Bluegrass.

Perennial, cespitose, most shoots fertile. Culms 0.5–5 dm tall, densely tufted at base, slender, wiry, frequently geniculate at lower nodes, more or less glabrous about nodes. Leaves green, sometimes reddish, usually several on the culm. Sheaths as in *P. glauca*. Ligules truncate to rounded, to 2 mm long, mostly scabrous on back, upper margin frequently jagged, mostly minutely fringed. Blades 1–2.5 mm wide, strictly ascending to divergent at about 60°, sometimes lax, upper one (3) 6–15 cm long. Panicles strict or somewhat lax, 2–15 cm long, the 1–3 (4) branches prominently scabrous on distinct angles, slender, ascending, to 6 cm long. Axis internodes to 4 cm long. Spikelets 2–3-flowered, 2.5–5 mm long, compressed, ovate, mostly bright green, sometimes purplish. Glumes narrow to broad, mostly 3-nerved, scabrous on keel, tips sharply acute, usually abruptly curved in or outward at apex, second glume mostly with distinct to rounded angle near middle of margin. Lemmas 5-nerved (intermediate nerves frequently obscure), prominently villous on keel (to near tip) and marginal nerves, only occasionally villous on intermediate nerves (then sparsely so), glabrous and papillos-roughened between nerves. Callus web minute, or to about $\frac{1}{2}$ lemma in length. Paleas scabrous to occasionally glabrous on keels. Rachillas as in *P. glauca*. Flowers perfect. Anthers 1.1–1.8 mm long. Chromosome numbers: 28, 42, 43, 56.

HABITAT: In Douglas-fir and spruce-fir forests in moist meadows, on mossy ledges, to alpine meadows and wind balds, 2740–3660 m in New Mexico. Flowering July–August.

DISTRIBUTION: Interior w North America extending to the Great Lakes region, north to Alaska, south to Arizona (reported from, but doubtfully in, Texas) and New Mexico: B, CB, CF, RA, SD, SM, TO.

COMMENT: Frequently intergradient with and difficult to distinguish in forest and meadow habitats from *Poa palustris*, to thoroughly intergradient with populations of *Poa glauca* Vahl at higher elevations. A close relationship to the introduced *P. nemoralis* L. is evident, but the forms of *P. interior* in the western United States more closely approach *P. glauca*. A thorough, worldwide study of population samples from this facultatively agamospermous complex is sorely needed.

Poa leptocoma Trin.

Poa leptocoma Trin., Mem. Acad. St. Petersb. VI, 1:374. 1830. HOLOTYPE: *D. Mertens* Sitka, Alaska (LE!). Bog Bluegrass.

Perennial, loosely tufted or somewhat rhizomatous in mossy habitats. Culms 2–10 dm tall, smooth or scabrous. Leaves bright green. Sheaths closed $\frac{1}{4}$–$\frac{1}{2}$ the length, smooth or scabrous. Ligules 1.5–4 mm long, truncate to obtuse, entire to jagged, glabrous on back. Blades flat or folded, mostly lax, 1–4 mm wide, upper (5) mostly 8–15 cm long (in U.S. Rocky Mountains). Panicles nodding, lax, open, the 1–3 (mostly 2) branches per node capillary, scabrous, spreading to occasionally strongly reflexed, few- to many-flowered in distal $\frac{1}{3}$. Axis internodes mostly less than 4 cm long. Spikelets green to strongly purplish, strongly compressed, narrowly ovate to oblong, loosely 2–5-flowered, 4–8 mm long. Glumes sharply acute, mostly scabrous on nerves, unequal, the first shortest, very narrow, 1-nerved, the second lanceolate, 1–3-nerved. Lemmas 5-nerved, intermediate nerves mostly obscure, very smooth and glabrous between nerves, densely to sparsely villous on lower $\frac{2}{3}$ of keel and marginal nerves (to nearly glabrous), hyaline margin prominently bronze colored near tip (unlike *P. occidentalis*). Callus with a sparse, long web. Paleas keels with regularly spaced, slender, antrorsely curved scabers, or nearly glabrous, with only long cells between the nerves. Rachillas elongate, usually visible from sideview at maturity. Flowers perfect, mostly cleistogamous. Anthers 0.25–1 (1.1) mm long. Chromosome numbers: ***42***.

HABITAT: Subalpine and alpine, in wet meadows, along stream banks, springs, and bogs, 2200–3350 m in New Mexico. Flowering June–August, generally slightly later than the very similar, and frequently sympatric, *P. reflexa*.

DISTRIBUTION: Northeast Asia, boreal w North America to the Canadian Rocky Mountains (*P. paucispicula* Scribn. & Merr.), se Alaska south and east through high montane and alpine regions of w North America to s New Mexico (*P. leptocoma*). New Mexico: CB, CF, LN, OT, SF, TO.

COMMENT: This species and *Poa reflexa* often occur together in mixed stands, and the species are sometimes considered as varieties. However, the species have different chromosome numbers, and intermediate plants are rare. The morphological distinctions, once recognized, make them easy to distinguish and indicate that they may be only distantly related (see subgeneric placement above).

Poa nervosa (Hook.) Vasey

Poa nervosa (Hook.) Vasey. Bull. U.S. Depr. Agr. Div. Bot. 132:pl. 81. 1893; Festuca nervosa Hook. Fl. Bor. Am. 2:251, pl. 232. 1840. TYPE: *Scouler*, Nootka Sound, Vancouver Isl., British Columbia (NY!, GH!, US!).

Poa nervosa var. *wheeleri* (Vasey) C. L. Hitchc.

Poa nervosa var. *wheeleri* (Vasey) C. L. Hitchc. Vascl. Pl. Pac. Northwest. 1:671. 1969; *Poa wheeleri* Vasey in Rothr. Cat. Pl. Surv. W. 100th Merid. 55. 1874. TYPE: *Wolf 1131*, South Park, Colorado (US!). *Poa curta* Rydb. (*non auct.*) Bull. Torr. Bot. Club 36:534. 1901. TYPE: *Tweedy 13*, Spread Creek, Teton Co., Wyoming (NY!).

Perennial, loosely tufted, with prominent short rhizomes. Culms erect, often decumbent at base, terete, 20–85 cm tall. Leaves light green. Sheaths prominently striate, round to weakly keeled, closed ($\frac{1}{3}$) $\frac{1}{2}$ to nearly entire length, at least those of lower culm usually finely retrorsely scabrous-puberulent, infrequently glabrous throughout. Ligules 1–3 (4) mm long, truncate to acute (above), usually densely spiculate on back (especially below). Blades flat to folded, weakly keeled, soft, steeply ascending, glabrous to sparsely spiculate above, glabrous below, those of culm 1.5–3 mm broad, and to 10 cm long, upper culm one 1–6 cm long, those of innovations to 30 cm long. Panicles erect, nodding at tip, (3.5) 5–13 (18) cm long, narrowly ovoid, sparsely flowered, long-peduncled. Branches spreading to ascending, scabrous on angles, (1) 2–4 per node, with (1) 3–8 (11) spikelets in distal $\frac{1}{2}$. Axial internodes mostly 1–3.5 cm long. Spikelets compressed, 5–11 mm long, 2–8-flowered, light green to somewhat purplish. Glumes about $\frac{2}{3}$ the length of subtended lemma, acute, keels distinct, sparsely scabrous above. Lemmas, keeled, 4–6 mm long, broadly acute, papillose-roughened to sparsely spiculate between nerves, frequently scabrous above, 5-nerved, often scabrous on nerves, occasionally puberulent on keel and marginal nerves. Callus glabrous. Paleas moderately to sparsely scabrous along keels, sparsely spiculate between keels. Rachilla internodes usually spiculate. Flowers pistillate or infrequently appearing hermaphroditic (in var. *wheeleri*), (dioecious or gynodioecious and sexually reproducing in the typical variety, reproduction by agamospermy in var. *wheeleri*). Anthers to 3 mm long, usually vestigial in var. *wheeleri*. Chromosome numbers: 28, 29, *56*, 61–64, 70, 74, 91.

HABITAT: Open mountain slopes from upper sagebrush and lower pine belts to lower alpine (New Mexico subalpine), in rich soils and duff. The one New Mexico collection from 3500 m. Flowering (May) June–August.

DISTRIBUTION: Southwestern Canada, Pacific Northwest, south to California, and Nevada. In Rocky Mountains south to north central New Mexico: TO.

COMMENT: *Poa nervosa* (sensu stricto), applies to the sexually reproducing race found west of the Cascade Mountains in the Pacific Northwest. It is distinguished by the presence of long hairs on the collar margins. Variety *wheeleri* is one of the most common native *Poas* of the northern Rocky Mountains and, although highly variable in form, is distinguishable by its puberulent lower sheaths and ligules, relatively uniformly developed upper culm leaves, and pistillate florets. However, the one New Mexico collection (Gold Hill) has glabrous sheaths, only sparsely puberulent ligules, and pubescent lemmas. The complex needs further evaluation.

Poa occidentalis Vasey

Poa occidentalis Vasey, Contr. U.S. Natl. Herb. 1:274. 1893. HOLOTYPE: *Vasey*, Las Vegas, New Mexico, in 1881 (US 28537500!); *Poa platyphylla* Rydb. New Mexico Bluegrass.

Perennial, loosely tufted, probably short-lived. Culms stout, erect or decumbent, reddish at base, erect, 2–11 dm tall. Leaves mostly cauline, commonly blue-green. Sheaths longer than internodes, closed $\frac{1}{4}$–$\frac{1}{2}$ the length, strongly keeled, glabrous or mostly abundantly retrorsely scabrous, lower ones often reddish. Ligules acute to acuminate, entire, scabrous on back, those of upper culm leaves to 12 mm long, mostly longer than leaf is wide. Blades strongly keeled, tip distinctly prow shaped, upper 4–18 cm long, 1.2–5.5 (10) mm wide. Panicles open, pyramidal, elongate, (6) 12–40 cm long, with loosely ascending branches when young, erect and with widely spreading branches at maturity, tips drooping. Branches 5–23 cm long, densely flowered in distal $\frac{1}{2}$, moderately to sparsely scabrous. Axis internodes mostly over 4 cm long. Spikelets oblong, strongly compressed, 3–8 mm long, usually longer than pedicel, 2–7-flowered. Glumes subequal, sharply acute, the first narrowly lanceolate, 1-nerved, the second broader, 1–3-nerved, nearly equaling first lemma in length. Lemmas usually green with whitish hyline margin and tip, sometimes purplish but rarely bronze colored at tip (unlike *P. leptocoma*), 2.6–4.2 mm long, usually distinctly 5-nerved, keel scarcely incurved at tip, villous on lower $\frac{1}{2}$ of keel and lower $\frac{1}{3}$ of marginal nerves, glabrous to sparsely puberulent between them. Callus with sparse long web. Paleas glabrous to finely scabrous on keels, with long and short cells between keels. Rachilla internodes glabrous, usually hidden from side view. Flowers perfect, mostly cleistogamous. Anthers 0.3–1.0 mm long. Chromosome numbers: *14*, ca 28.

HABITAT: Montane. Usually in mesic situations, on cool exposures, in sparsely vegetated, disturbed, and natural forest openings, 2300–3500 m. Flowering mid-July–September.

DISTRIBUTION: Southwestern Colorado, White Mountains of e Arizona, to the Guadalupe Mountains of Texas. New Mexico: B, CB, CF, GR, LN, OT, RA, SD, SF, SM, SR, TO. Past, more northerly reports of this species (including Utah and Wyoming) have been in error. *Poa occidentalis*, *sensu* Harrington, 1954, is mostly *P. tracyi*.

Poa palustris L.

Poa palustris L., Syst. Nat. 10th ed. 2:874. 1759. Fowl Bluegrass.

Perennial, most shoots fertile. Culms loosely tufted, often decumbent at base and rooting at nodes, stoloniferous, stout, more or less scabrous below nodes, loosely tufted, 2–12 dm tall, often branching above base. Leaves green, often turning reddish, mostly cauline and numerous. Sheaths keeled, usually closed less than $\frac{1}{4}$ the length, mostly glabrous. Ligules 2–6 mm long, rounded to acute, mostly fringed on margin, entire or jagged, often scabrous on back. Blades 1–4 mm wide, flat or folded, those of culm steeply ascending, longer ones drooping, uppermost one fixed well above middle of culm, 5–20 cm long. Panicles open, (narrow and congested when young), elongate, broad, densely flowered, mostly 10–30+ cm long. Branches mostly 4 or more per node, usually 2 or 3 times rebranched, capillary, and spreading, scabrous on the angles. Axis internodes mostly over 3 cm, to 6 cm long. Spikelets compressed, smallish, 1–6 (mostly 2–4) flowered, 2–4 mm long. Glumes subequal, about $\frac{7}{8}$ as long as the subtended lemma, narrow, broadest near middle, scabrous on keel, second glume margin mostly gradually rounded. Lemmas 2–2.7 mm long, 5-nerved (intermediate nerves mostly obscure) villous on keel and marginal nerves, glabrous and finely papillose-roughened between nerves, tip distinctly incurved, broadly acute, obtuse, or blunt, prominently bronze colored, hyaline margin very narrow. Callus with sparse but prominent web. Paleas scabrous to minutely ciliate on keels. Rachillas glabrous or scabrous. Flowers perfect. Anthers 0.8–1.4 mm long. Chromosome numbers: 28, 30, 32, 42.

HABITAT: Montane. Mixed-conifer forests from riparian, where often in shallow water, to moist meadows and open ground, ca 2440–3050 m in New Mexico. Flowering June–August.

DISTRIBUTION: Introduced from Europe, common to the north. New Mexico CF, GR, RA, SM, TO.

COMMENT: *Poa palustris* appears to intergrade in form and habitat with *P. interior*, and frequently entire populations cannot be satisfactorily assigned to one or the other taxon.

Poa pratensis L.

Poa pratensis L., Sp. Pl. 67. 1753. *Poa agassizenssis* Boivin & D. Love, Bernard, Svensk Bot. Tidsker, 53:371. 1959, *nomen nudum*; *Poa agassizenssis* Boivin & D. Love, Naturaliste Canad. 87:176. fig. 1. 1960. Kentucky Bluegrass.

Perennial with extensive creeping rhizomes, often forming dense sods. Culms 0.5–80 cm tall, only slightly compressed. Leaves green to glaucescent. Sheaths prominently nerved, closed $\frac{1}{4}$–$\frac{1}{2}$ their length, glabrous or occasionally sparsely long villous. Ligules 0.5–3 mm long, mostly truncate, ciliate on upper margin, glabrous to minutely scabrous on back. Blades flat or folded, soft or occasionally rather firm, strict, 1.5–2.5 (5) mm broad, prominently keeled and prow tipped, those of upper culm 1–10 cm long and only slightly divergent. Panicles (1.5) 5–10 (16) cm long, pyramidal to elliptic, mostly erect with (2) 4 or more branches at lower nodes, branches sparsely scabrous. Axial internodes mostly 1–2 cm long, rarely over 3 cm long. Spikelets compact-ovate, crowded on branches, strongly compressed, green or purplish, 2–7 mm long, 2–7 flowered. Glumes 1–3-nerved, strongly keeled, more or less scabrous on upper $\frac{1}{2}$ of keel, the first narrow, often somewhat curved inward, both sharply acute and about $\frac{2}{3}$–$\frac{3}{4}$ the length of subtended lemma. Lemmas 2–4 mm long, 5-nerved, intermediate nerves usually faint, glabrous and minutely papillose-roughened between nerves, keel and marginal nerves densely villous, rarely with few hairs on intermediate nerves. Callus with copious tuft of kinky hairs from $\frac{1}{2}$ to as long as lemma. Paleas glabrous, or closely and finely scabrous on keels, glabrous between keels. Rachilla internodes glabrous, short. Flowers perfect. Anthers 1.2–2 mm long. Chromosome numbers: 25–127 (with nearly every intervening number recorded).

HABITAT: An aggressive and variable weedy species composed of numerous apomictic races worldwide, but which are poorly understood in our region. Widespread from ponderosa pine zone to subalpine, where it often forms a turf along water courses. Occasional in lower habitats along perennial water courses, in greasewood communities, and on northeastern plains of New Mexico. Commonly planted in lawns and pasture mixes. Important as a soil-stabilizer and as a forage. Naturalized from ca 1700–3500 m. Flowering May–September.

DISTRIBUTION: Holarctic, now occurring worldwide except for low elevations in the tropics. Introduced or possibly native in temperate latitudes of North America. First collected in New Mexico in 1887 by S. M. Tracy, near Santa Fe. New Mexico: B, CB, CT, DA, LA, LN, MK, OT, RA, SD, SF, SJ, SM, TO, TR, and undoubtedly all others.

COMMENT: Successful synthetic hybrids have been formed between *Poa pratensis* and members of most other sections of *Poa*. It appears that such hybridization is a continuing process in nature. Specimens and partial populations identifiable as *P. pratensis* infrequently display intermediate characteristics between it and some sympatric native species. A peculiar, possibly native form, which has prominent long spiculae on ventral blade surfaces and is sparsely hairy between lemma nerves, has been collected in MR and LN counties.

Poa reflexa Vasey & Scribn.

Poa reflexa Vasey & Scribn., Contr. U.S. Natl. Herb. 1:276. 1893. Holotype: *Letterman* Kelso Mt. near Torrey Pk. in 1885 (US 28544900!). Nodding Bluegrass.

Short-lived perennial. Culms slender, loosely tufted, 1–6 dm tall. Leaves bright green, mostly cauline. Sheaths closed $\frac{1}{3}$–$\frac{2}{3}$ the length, keeled, smooth. Ligules 1.5–3.5 mm long, truncate to obtuse, entire to jagged, glabrous. Blades of the culm flat or folded, 1.5–4 mm broad, upper 2–10 cm long, prominently keeled and prow tipped (broad and short relative to *P. leptocoma*). Panicles nodding, open, pyramidal, 4–15 cm long, branches capillary, glabrous, mostly 1–3 per node, widely divergent to steeply reflexed, with spikelets crowded in distal $\frac{1}{3}$. Axis internodes mostly shorter than 4 cm. Spikelets green to purplish, strongly compressed, mostly 3–4-flowered, ovate, compact, rachilla rarely visible in side view. Glumes acute, smooth or sparsely scabrous on keel near tip, subequal, the first lanceolate, 1-nerved, the second broadly lanceolate, 1–3-nerved. Lemmas broadly lanceolate, acute, 5-nerved, densely villous-pilose on keel (to near the tip) on marginal nerves and often on intermediate nerves, mostly glabrous between nerves to sparsely pubescent between them on upper florets, hyaline margin narrow. Callus long webbed. Paleas villous (sometimes obscurely so) on keels, with long and short cells between keels. Flowers perfect, frequently cleistogamous. Anthers 0.25–1 mm long. Chromosome numbers: 28.

Habitat: Subalpine, alpine, from dry open ground to meadows, streams, and bogs, 3050–3660 m in New Mexico. Flowering July to August.

Distribution: Middle and Southern Rocky Mountains (very sporadic westward), occurring from s Montana to n Arizona and n New Mexico: CF, SF, TO.

Comment: See comment under *Poa leptocoma*, and subgeneric placement above. *Poa reflexa* appears to be closely related to *P. occidentalis*.

Poa secunda Presl

Poa secunda Presl, Rel. Haenk. 1:271. 1830. Type: *Haenke*, "Cordillera Chilensibus," in 1790 (PR, MO, GH). (It has been remarked by Marsh and Keck, among other workers, that the type may have come from s California rather than Chile, but, according to historian S. D. McKelvey (1955), if the 1790 date is correct, this could not be because Haenke had not reached North America until 1791.) *Poa sandbergii* Vasey, Contr. U.S. Natl. Herb. 1:276. 1893. *Poa incurva* Scribn. & Will. *Poa scabrella* (Thurb.) Benth. ex Vasey. *Poa canbyi* (Scribn.) Beal. *Poa gracillema* Vasey. [The following two taxa are considered to be conspecific with *P. secunda* (*s. lat.*). However, they are considered to be distinctive ecotypes and are described separately: *Poa ampla* Merr., Rhodora 4:145. 1902. Type: *Vasey 3009* Steptoe, Washington (US 28610400). *Poa nevadensis* Vasey ex Scribn., Bull. Torrey Bot. Club 10:66. 1883. Type: *Jones* Austin, Nevada (US 28858200).] Sandberg Bluegrass. (Pine Bluegrass, Canby Bluegrass).

Perennial, cespitose, Culms densely tufted, erect or divergent, wiry, 1.5–12 dm tall, frequently becoming reddish. Leaves mostly basal, green or occasionally glaucescent. Sheaths nearly open or closed to $\frac{1}{4}$ the length, glabrous to scabrous, weakly keeled. Ligules 1.5–5 (7) mm long, acute to acuminate, entire to lacerate, glabrous to scabrous on back. Blades firm or mostly soft, mostly 1–5 cm long on culm, steeply ascending or sometimes laxly so, 1–3 mm wide, flat or weakly folded, basal leaves often filiform. Panicles mostly narrowly contracted, 2–27 cm long, branches (2) 3–4 (8) per node, mostly scabrous. Spikelets 3.5–9 (12) mm long, generally more than 3 times as long as wide (closed), 2–6-flowered, more or less terete in cross-section. Glumes lanceolate, 1–3-nerved, with broad hyaline margins, broadest about middle, mostly gradually rounded on margins, mostly smooth below and sparsely scabrous toward tip on keel and less scabrous on lateral nerves. Lemmas relatively long and narrow, tapered to tip from well above middle, acute, obtuse, rounded, or retuse at tip, 5-nerved, intermediate nerves often obscure, weakly keeled or keel obscure, papillose-roughened to scabrous over surface, basal portion glabrous or usually uniformly puberulent, this infrequently confined to nerves (rarely much denser or longer on nerves). Callus glabrous (sometimes with few short hairs). Paleas mostly scabrous on keels to puberulent on lower half, puberulent between keels below and scabrous in upper portion. Rachillas glabrous, scabrous, or puberulent, usually elongate and visible from side view. Flowers perfect, anthers occasionally abortive. Anthers 1–3.8 mm long, yellow or purple or both. Chromosome numbes 44, 56, 61–66, 68, 70–72, 78, 81–106.

HABITAT: Upper pinyon-juniper, ponderosa pine, subalpine, and alpine, 2130–2440 m and 3350–3810 m in New Mexico. Flowering June–August.

DISTRIBUTION: South America in Chile and Argentina. North America, se Alaska across s Canada (sporadic east of Rocky Mountains), all w United States and n plains states to Great Lakes region, and Gaspé Peninsula. Infrequent in n Arizona. New Mexico: SJ (*canbyi* form), SF & TO (alpine forms usually referred to *P. canbyi*).

COMMENT: *Poa secunda* (*s. lat.*) is a large, polymorphic, facultatively agamospermous species composed of many ecotypes. Of 40 different taxa that have been proposed, modern taxonomic treatments of this group recognize as few as one to as many as 13 species and subspecies. Although I have not studied this group in depth, I am familiar with the variation patterns in other agamous complexes in *Poa* and am inclined to follow the monographers who recognize only one species here. Beyond this, it would be useful from an ecological perspective to recognize the more distinctive races at a subspecific level. However, appropriate name combinations are not available, and, until the most recent revision of the complex is published, I refrain from proposing any new ones. New Mexico is at the southern boundary of the complex where several of the more customarily recognized races are apparent and allopatric. The above description applies to Rocky Mountain forms included as species of the "scabrellae" group by A. S. Hitchcock. The following descriptions apply to two forms he included as species in the "nevadenses" group. It must be kept in mind, though, that these are intergradient over their greater ranges.

The highly variable alpine forms of this complex occurring in the Rocky Mountains are usually referred to *P. canbyi*, but frequently they are exceedingly difficult to differentiate from *Poa glauca*, and occasionally from *P. arctica*. This taxon can generally be distinguished from the latter alpine species by the presence of more lax foliage, generally reddish culm bases, long acute ligules, short, uniform lengthed puberulence of the lemmas, and elongate spikelets. However, it appears that there are continuous intergrades between these facultatively agamous species.

Poa ampla phase of *Poa secunda*
Big Bluegrass

Robust perennials, infrequently rhizomatous. Culms several in large tufts, 6–18 dm tall. Leaves green to very glaucous. Ligules 0.25–4 mm long, sparsely to densely scabrous on back, obtuse to truncate, entire to jagged. Blades 2–5.5 mm wide, those of culm 9–20 cm long, flat to weakly folded, mostly rather firm. Panicles mostly 12–25 cm long, rather narrow. Glumes 3-nerved, scabrous on keel. Lemmas 4–6 mm long, glabrous and papillose-roughened all over to very sparsely puberulent on lower keel and marginal nerve, scabrous or glabrous on upper keel. Callus glabrous. Paleas scabrous on keels. Rachillas glabrous. Flowers perfect. Anthers 1.5–3.5 mm long. Chromosome numbers: 62–65, 68, 70–71, 91, ca 100.

HABITAT: The only records of *Poa ampla* in New Mexico have been from ponderosa pine zone, in open ground, 2130–2440 m. Flowering May–August.

DISTRIBUTION: Alaska, Alberta, British Columbia, North Dakota, South Dakota, Nebraska, Montana, Wyoming, Idaho, Washington, Oregon, Nevada, California, and nw $\frac{1}{3}$ Colorado. Introduced into New Mexico along roads and in campgrounds in CB, GR (SM?, not seen); all three collections made since 1980.

Poa nevadensis phase of *Poa secunda*
Nevada Bluegrass

Similar to *P. secunda* 5–10 dm tall, very leafy throughout, sheaths and blades often scabrous, flat or folded, bright to pale green, 1–3.5 mm wide, upper ligules 3–6 mm long, acute to acuminate. Panicles narrow, elongate, to 25 cm long, somewhat loose. Spikelets 2–5-flowered, 4–8 mm long. Glumes more strongly keeled than typical of species. Lemmas 3.5–5 mm long, scabrous apically or throughout, usually somewhat obtuse. Chromosome numbers: 62, *63–66*, 70.

HABITAT: In New Mexico: Moist ground around springs and moist meadows, ponderosa pine zone, 2350–2450 m. Flowering June–July.

DISTRIBUTION: California, Oregon, Montana, Idaho, Wyoming, Colorado, Utah, Arizona, and New Mexico. Not collected in New Mexico since 1906, CF (Bell), CT (Fitzgerald Cienaga, n of Reserve). A collection of Dr. Bigelow's *1853–4 #3* (NY) made somewhere between Fort Smith, Arkansas, and the Rio Grande, also appears to represent this form.

Poa tracyi Vasey

Poa tracyi Vasey, Bull. Torrey Bot. Club 15:49. 1888. LECTOTYPE: *Tracy*, New Mexico, mesa sides near Raton, in 1887 (US 556764!). *Poa flexuosa* var. *robusta*. *Poa f.* var. *occidentalis*; *Poa occidentalis* (Vasey) Rydb. (not *P. occidentalis* Vasey). Tracy Bluegrass.

Perennial, frequently subrhizomatous. Culms erect or decumbent at base, 25–125 cm tall, mostly glabrous. Leaves blue-green, mostly cauline. Sheaths mostly shorter than internodes, closed $\frac{1}{2}$–$\frac{9}{10}$ the length, strongly keeled, retrorsely puberulent, or scabrous, mostly glabrous. Ligules obtuse to acute, glabrous to abundantly hairy on back, those of the upper leaves to 4.5 cm long, mostly shorter than leaf is wide. Blades strongly keeled, flat, prominently prow shaped at tip, upper ones 6–18 cm long, 2–5.5 mm wide. Panicles narrowly to broadly pyramidal, (8) 13–29 cm long. Branches 1–5 per node, 2.5–18 cm long, sparsely flowered in distal $\frac{1}{2}$, widely spreading to reflexed at maturity, sparsely scabrous. Axis internodes mostly over 4 cm long. Spikelets strongly compressed, oblong, 3–8 mm long, mostly shorter than pedicels, 2–8-flowered. Glumes narrowly lanceolate, acute, the first usually less than $\frac{1}{2}$ the length of first lemma, 1-nerved, the second slightly shorter than first lemma, 1–3-nerved. Lemmas 2.6–5 mm long, lanceolate, keel scarcely incurved at tip, pale green with white hyaline margins, 5-nerved, intermediate nerves often obscure, villous on lower $\frac{1}{2}$–$\frac{3}{4}$ of keel, less so on marginal nerves, usually sparsely puberulent between nerves at base. Callus with long cobwebby hairs abundant (rarely nearly absent). Paleas mostly minutely scabrous on keels, sometimes also minutely puberulent near base, with long and short cells between keels. Rachillas usually visible from side view, glabrous. Flowers perfect or pistillate, two types usually mixed within panicle, sometimes all one or the other (partially gynodioecious). Anthers vestigial (aborted) or 1.25–3 mm long. Chromosome numbers: 28, 28+1 fragment.

HABITAT: Montane. In gambel oak thickets, mixed-conifer and spruce-fir forest openings, and subalpine meadows, mesic sites, in humus-rich soils, 2000–3500 m. Flowering May–mid-July and in south central New Mexico in August.

DISTRIBUTION: Southern rocky Mountains of Colorado and New Mexico; B, CF, LN, OT, RA, SM, U. All of the Wyoming records of *P. tracyi* that I have seen represent other species, especially *P. leptocoma*.

COMMENT: Mature material of *Poa tracyi* is easily distinguished (by longer, or vestigial anthers) from *P. occidentalis*, *P. leptocoma*, and *P. reflexa*. *Poa tracyi* is morphologically very similar to the more western *P. curta* (s. *auct*), and both species are partially gynodioecious. However, they are geographically isolated from one another, and the morphological distinctions between them are not bridged.

Poa trivialis L.

Poa trivialis L., Sp. Pl. 67. 1753. Meadow or Roughstem Bluegrass.

Short-lived perennial, frequently stoloniferous. Culms loosely tufted, erect, or decumbent and rooting at lower nodes, 4–11 dm tall, smooth to densely scabrous. Leaves bright green, mostly cauline. Sheaths closed for $\frac{1}{4}$–$\frac{1}{3}$ the length, often keeled and prominently striate. Ligules (1.5) 3–10 mm long, acute, entire or lacerate, glabrous or sparsely scabrous on back. Blades of culm flat, 2–8 mm wide, 10–25 cm long, lax, tips scarcely prow shaped. Panicles (4) 6–22 cm long, open, pyramidal to oblong, slender branches spreading-ascending in flower and fruit, many flowered from near base, lower branches often in 5s. Axis internodes 2–5.2 cm long. Spikelets small, 3–5 mm long, strongly compressed, 2–4-flowered, ovate to elliptic. Glumes unequal, the first narrowly lanceolate, more or less incurved and with narrow white hyline margin, the second somewhat broader and less curved, the 1–3 nerves prominent, pale, and mostly scabrous. Lemmas 2.5–4 mm long, prominently 5-nerved, smooth or faintly, finely papillose-roughened, sparsely villous on lower keel, otherwise glabrous. Callus with web of villous hairs $\frac{1}{2}$ as long to longer than lemma. Paleas very finely and closely scaberulous to papilose-roughened on keels. Rachilla internodes short, slender, and glabrous. Flowers perfect. Anthers 1.4–2 mm long. Chromosome numbers: ***14***, 15, 28.

HABITAT: Expected to spread in montane New Mexico in shady, cool, wet to mesic soils, in disturbed sites, from 1980–3050 m. Flowering May–July.

DISTRIBUTION: Introduced from Europe, common in nw and ne U.S. but infrequent in interior West. The one New Mexico record of this species (*Soreng & Ward 1609*, Eagle Cr., in 1982) was growing in wet soil, at water's edge, at about 8000 ft: LN.

COMMENT: This species is superficially very similar to *P. occidentalis*, but has branches flowered from near the base; has longer anthers and is partially self-incompatable; has a frequently stolonous habit, tuberculate nobs on the palea keels, no pubescence between the lemma nerves or on the marginal nerves and narrow, scarcely prow-tipped blades.

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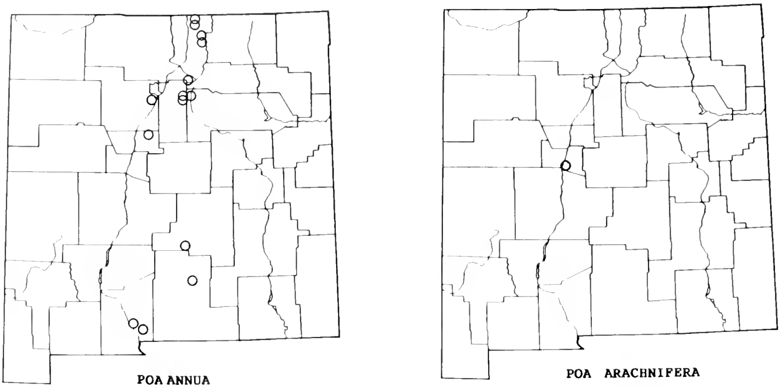
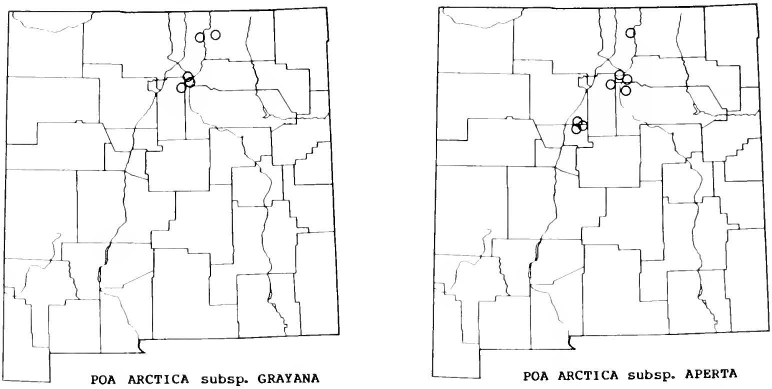


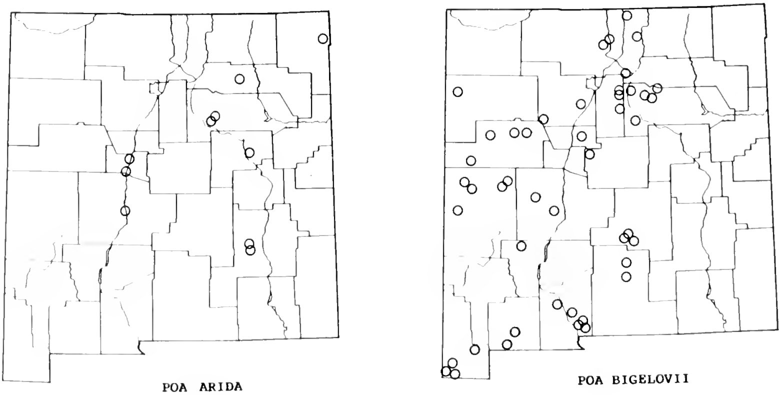
POA ANNUA

POA ARACHNIFERA



POA ARCTICA subsp. GRAYANA

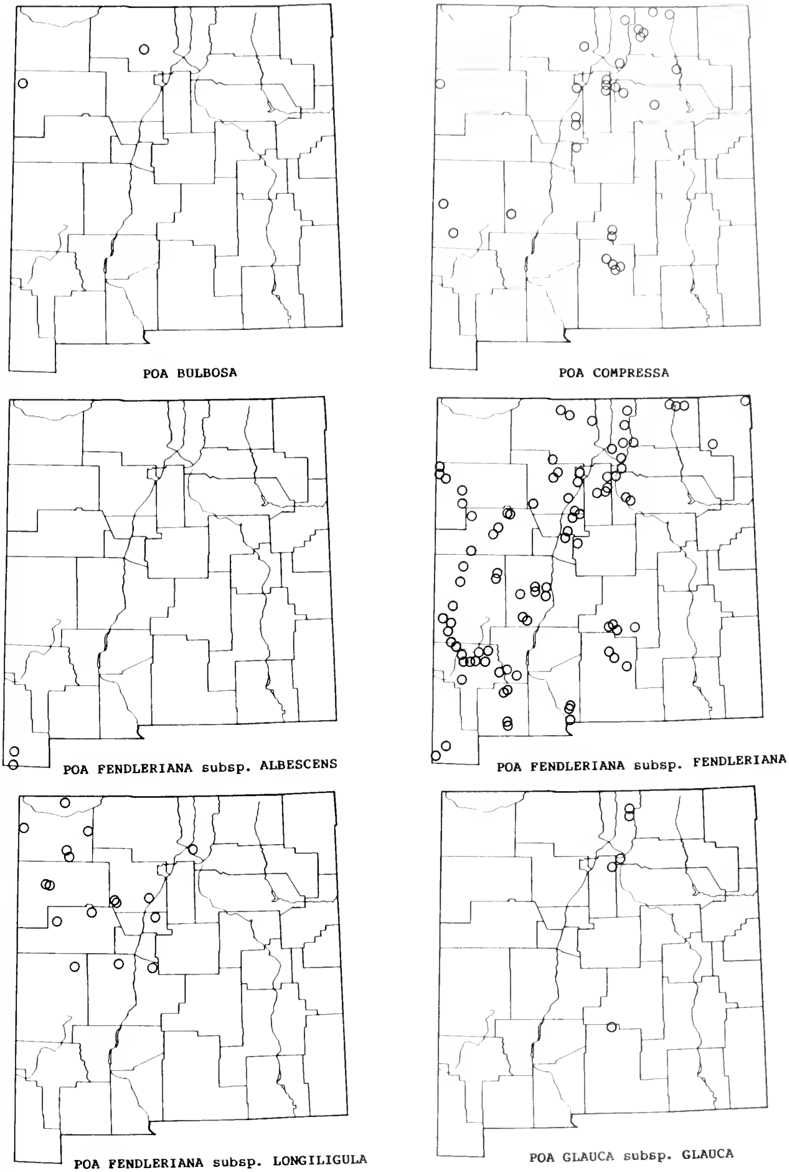
POA ARCTICA subsp. APERTA



POA ARIDA

POA BIGELOVII

Fig. 1. New Mexico distributions for *Poa* spp., as labeled.



POA BULBOSA

POA COMPRESSA

POA FENDLERIANA subsp. ALBESCENS

POA FENDLERIANA subsp. FENDLERIANA

POA FENDLERIANA subsp. LONGILIGULA

POA GLAUCA subsp. GLAUCA

Fig. 2. New Mexico distributions for *Poa* spp., as labeled.

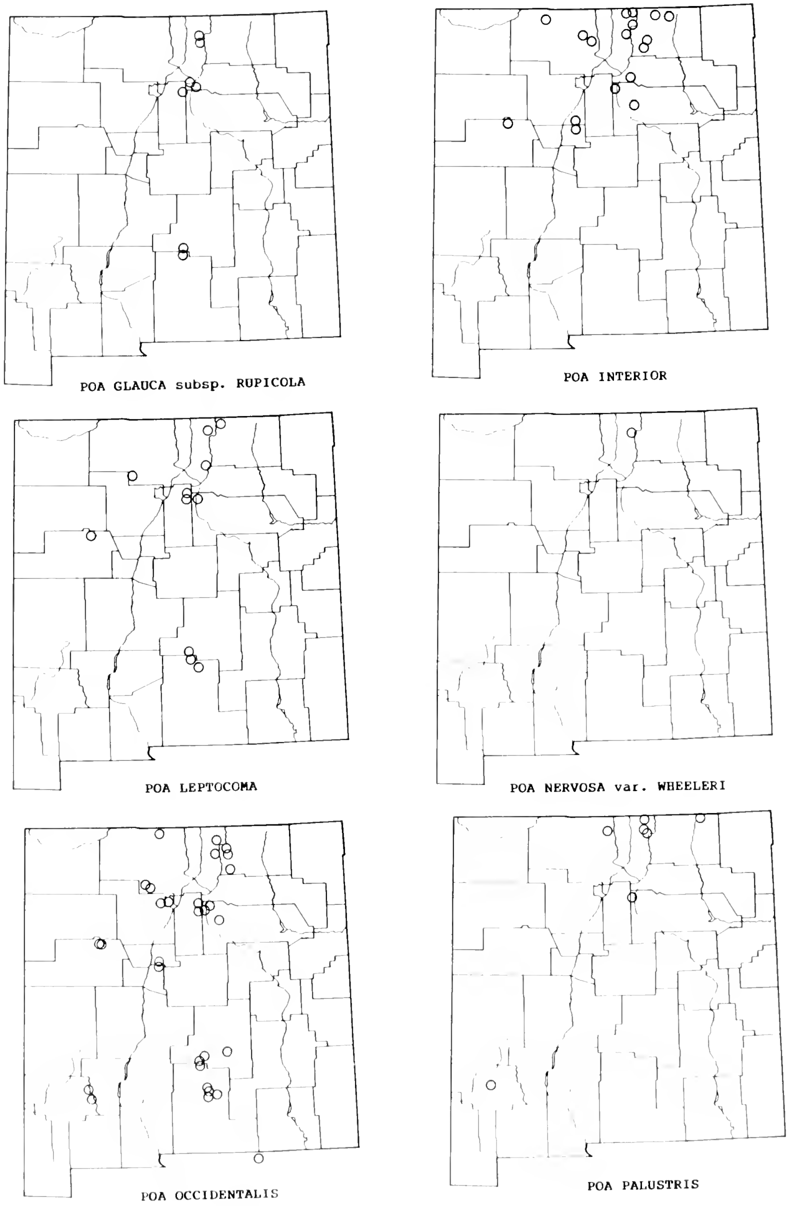


Fig. 3. New Mexico distributions for *Poa* spp., as labeled.

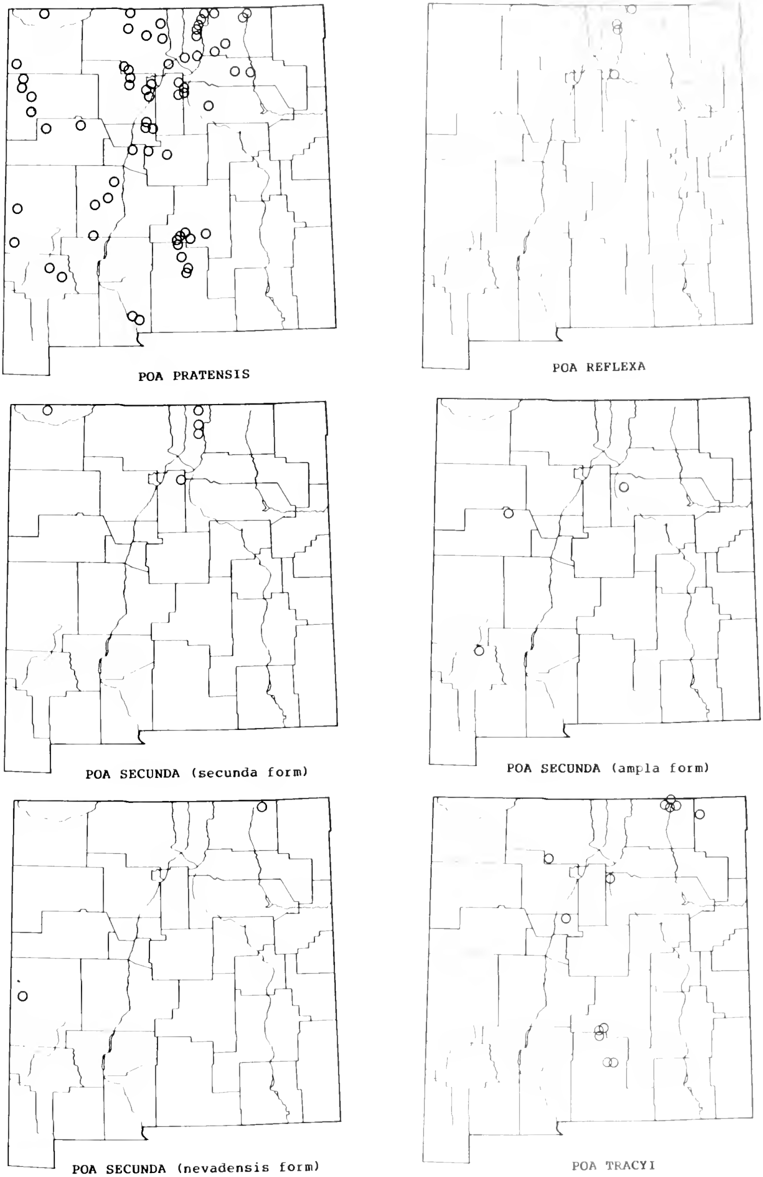


Fig. 4. New Mexico distributions for *Poa* spp., as labeled.

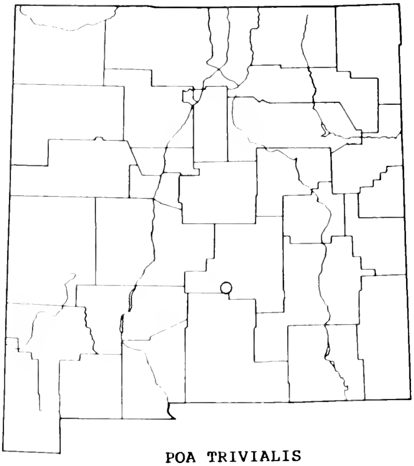


Fig. 5. New Mexico distribution for *Poa trivialis*.

DWARF MISTLETOE–PANDORA MOTH INTERACTION AND ITS CONTRIBUTION TO PONDEROSA PINE MORTALITY IN ARIZONA

Michael R. Wagner[1] and Robert L. Mathiasen[1]

ABSTRACT.— The interaction between Southwestern dwarf mistletoe, *Arceuthobium vaginatum* subspecies *cryptopodum*, infestation and defoliation by the pandora moth, *Coloradia pandora pandora*, on the Kaibab Plateau in Arizona was evaluated. Heavy defoliation of ponderosa pine, *Pinus ponderosa*, in 1979 and 1981 resulted in mortality of individual trees in areas of heavy dwarf mistletoe infestation. Postmortem evaluation of ponderosa pines indicated that dead trees had a significantly higher dwarf mistletoe rating than did nearby paired live trees. Of 25 tree pairs evaluated, only two live trees had higher dwarf mistletoe ratings than the paired dead tree. Mean dwarf mistletoe ratings were: live trees 2.9, dead trees 4.6 (6 class dwarf mistletoe rating system). Implications for management of the pandora moth are discussed.

An outbreak of the pandora moth, *Coloradia pandora pandora* Blake (Lepidoptera: Saturniidae), began in 1979 on the Kaibab Plateau in northern Arizona. Defoliation of ponderosa pine, *Pinus ponderosa* Dougl. ex Laws., occurred over 5,000 acres in 1979 and 19,000 acres in 1981 (Bennett and Ragenovich 1982). Pandora moth defoliation resulted in radial growth loss between 17% (Miller 1983) and 25% (Bennett and Andrews 1983). Tree mortality was not significantly greater in defoliated plots than nondefoliated control plots (Bennett and Andrews 1983). Though there was no significant effect of defoliation on mortality on a stand basis, there were clearly small pockets of mortality (Wagner pers. obs.). Field observations by the authors indicated that many of the trees that died were infected with Southwestern dwarf mistletoe, *Arceuthobium vaginatum* subsp. *cryptopodum* (Engelm.) Hawksw. & Wiens. Bennett and Andrews (1983) found that radial growth loss in trees with mistletoe and pandora moth was greater than for those with only pandora moth in this area.

Many insects and diseases do not cause direct serious impact on their host but rather function to predispose trees to other damaging agents. Numerous authors have reported that pandora moth defoliation increased the incidence of bark beetle mortality (Carolin and Knopf 1968, Keen 1952, Massey 1940, Patterson 1929, Wygant 1941). Dwarf mistletoes, which are serious damaging agents in western forests (Hawksworth 1961, Hawksworth and Wiens 1972), are a common agent predisposing trees to other agents. The numerous interactions between dwarf mistletoes and forest insects have been reviewed by Stevens and Hawksworth (1984). We report in this paper that ponderosa pine mortality, following the pandora moth outbreak in northern Arizona, occurred primarily on trees heavily infected with dwarf mistletoe.

MATERIALS AND METHODS

The study site was approximately two miles north of Jacob Lake, Arizona, in an area heavily defoliated in 1979 and 1981 by the pandora moth. The sample area was approximately 100 acres in size and constituted the largest pocket of mortality that had occurred following defoliation (Wagner pers. obs.). The study site was outside the area sprayed with Acephate® in 1981 (based on maps in Bennett and Ragenovich 1982).

A systematic sample with a random start was used to survey the area of mortality. Sample plots were two chains apart and one chain in radius. The nearest dead tree to the plot center was selected, and the nearest live tree of similar diameter (maximum acceptable difference four inches dbh) identified (Fig. 1). The diameter breast height (dbh) and 6-class dwarf mistletoe rating (DMR) (Hawksworth

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Fig. 1. Typical paired sample of a living and dead ponderosa pine. Note the heavier dwarf mistletoe infection on the dead tree.

TABLE 1. Mean diameters and dwarf mistletoe ratings of paired live and dead ponderosa pines.

	Live trees		Dead trees	
	dbh	DMR	dbh	DMR
Mean ($\bar{X}$)	16.4	2.84	16.5	4.64
SD	8.1	1.75	8.1	1.35
Range	5.9–35.9	0–6	5.6–34.2	1–6

1977) were determined for each tree in the pair. If a suitable pair of trees could not be located within a plot, the plot was rejected. A total of 38 plots were examined, of which 25 met the criteria of having a suitable pair of trees.

Data were analyzed using a nonparametric sign test (Conover 1980) ($\alpha = 0.05$). The sign test indicates whether one random variable in a pair tends to be larger than the other random variable in the pair. The null hypothesis was that there was no difference in the dwarf mistletoe ratings between dead and live trees in the stand.

RESULTS

The mean diameters and mean DMR's of the paired trees are given in Table 1. There was no statistically significant difference in mean dbh between live and dead trees, as should be expected because of the pairs chosen. However, there was a highly significant difference in the mean DMR of live and dead trees. Dead trees sampled generally had signs of heavy dwarf mistletoe infection (DMR 5 or 6). Dead trees had a higher mean DMR rating than their paired live trees in all but two sampled pairs, where the live tree had a higher DMR than the dead tree. We observed that the mortality occurred over a considerable range of tree diameters. None of the dead trees we examined were free of dwarf mistletoe.

DISCUSSION

Our data indicate ponderosa pine mortality tended to occur on trees that were heavily infected with dwarf mistletoe. We can conclude that the probability of mortality as a result of pandora moth defoliation is greater in stands heavily infested with dwarf mistletoe. Our experimental design does not permit the establishment of a cause-effect relationship, but it appears reasonable that dwarf mistletoe is predisposing trees to mortality following defoliation. We do not feel there is evidence to suggest that the pandora moth prefers dwarf-mistletoe-infested trees, since defoliation is often uniform over large areas. Rather, we feel trees weakened by dwarf mistletoe infection probably are less tolerant of defoliation than are healthier trees. We did not attempt to systematically determine the cause of mortality of each sampled tree in the study area. However, the few trees we did examine did not appear to be killed by bark beetles or other secondary agents.

These findings have important implications for management of the pandora moth. Since growth loss is moderate and probably does not occur for more than one or two years, control attempts directed at reducing growth loss are not justified. Mortality is a more serious impact and would justify control measures if expected to occur over large areas. We would recommend controlling the agent predisposing trees to mortality (dwarf mistletoe) as the preferred option. Silvicultural control strategies for dwarf mistletoes are well established (Scharpf and Parmeter 1978). We would specifically recommend selectively removing trees with a DMR of 3.0 or greater in stands likely to be heavily defoliated by the pandora moth. Because the importance dwarf mistletoes play in reducing growth is well known (Hawksworth and Wiens 1972), the added effect of expected defoliation would certainly justify control efforts in managed forest stands.

In forest areas not under intensive forest management, defoliation by the pandora moth may actually have a beneficial effect. Since mortality preferentially occurs on the more heavily dwarf-mistletoe-infected trees, pandora moth defoliation may have the affect of reducing stand mistletoe infestation levels. This may increase the desirability of these areas for future use as managed stands. Certainly the mortality of some trees would provide considerable wildlife habitat for a variety of cavity-nesting birds.

ACKNOWLEDGMENT

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OCCURRENCE OF ANISAKID LARVAE (NEMATODA: ASCARDIDIA) IN FISHES FROM ALASKA AND IDAHO

Richard Heckmann[1] and Terry Otto[1]

ABSTRACT.— All 25 sablefish (*Anoplopoma fimbria*) examined from two bays near Sitka, Alaska, were infected with anisakid larvae. There were 1 to 11 larvae per infected fish, with worms encysted in the musculature of the body wall of 5 fish and in the liver of 4 fish. For the other hosts the viscera was the site of infection. Chinook salmon (*Onchorhynchus tshawytscha*) from Barrow, Alaska, and Obsidian, Idaho, were also infected with anisakid larvae. These data extend the known northern distribution of the anisakids along the Pacific Coast for sablefish and chinook salmon. The pathogenesis of the migratory pathway of anisakid larvae is described, and comments on human health implications are presented.

Anisakine nematodes have been a major problem in the fishing industry for years because their presence reduces the commercial value of fish (Meyers 1979, Wootten and Waddell 1977, Wootten 1978). During the past 10 years it has been observed that two genera, *Anisakis* sp. and *Phocanema* sp., are dangerous to humans in South America and North America who consume raw or poorly cooked infected fish (Jackson 1975, Meyers 1975, Cattan 1976, Kates 1973, Morbidity and Mortality Weekly Report 1975). The primary species observed for this study was *Anisakis simplex*. The disease, anisakiasis, has been recognized in Europe and the Far East for several decades (Oshima 1972, Shiraki 1974, Smith and Wootten 1978). The survival of anisakid larvae in various fish-processing methods has been demonstrated by Hauch (1977). Precautions are necessary in preparing fish for human consumption.

During the last two decades there has been renewed interest in the importance of the anisakine nematodes (Myers 1979, Hadidjaja et al. 1978). Surveys have been conducted throughout the world to determine the occurrence and distribution of the anisakids in fish, especially those hosts of commercial value. The larval worms have recently been reported in a bowhead whale (*Balaena mysticetus*) harvested at Barrow, Alaska, (Migaki et al. 1982) and in fish from Chile (Carvafal 1981, Torres et al. 1983). It appears that these larvae have a worldwide distribution in fish. One study of fish hosts demonstrated the presence of anisakid larvae in 138 species in marine fish and one species of squid (Ono 1975).

One objective of this study was to extend the northern geographical distribution of anisakias and to determine pathogenesis for host tissue. Because of the availability of the main host species, sablefish (*Anoplopoma fimbria*) were studied in Sitka, Alaska, to determine the geographical range of anisakine larvae. A limited number of chinook salmon were obtained from two other sites for study.

The proposed life cycle of *Anisakis* begins with the release of eggs from the adult worm that usually is found in the large intestine of marine mammals (cetaceans and pinnipeds: Myers 1970, Vik 1964, Smith and Wootten 1978). The eggs develop into stage I and II larvae, which are preyed upon by krill and other crustaceans such as *Thysanoessa* sp. (Smith 1971). The larvae penetrate the intestinal tract and develop into stage III larvae in the crustacean host. Fish prey upon the infected crustaceans and become paratenic hosts for marine mammals that are the definitive hosts. In marine mammals the anisakids develop into adult worms and release eggs (Smith and Wootten 1978).

Anisakid larvae found in fish are usually tightly coiled on the mesenteries, liver, and gonads and in the musculature of the body wall. Prusevich (1964) demonstrated that the capsule surrounding the larvae is of host origin and that the inflammatory reaction to the presence of the parasite in the liver of the shorthorn sculpin began during the first few

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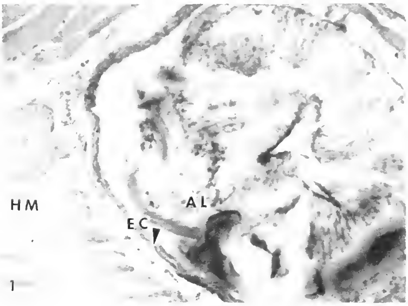

Fig. 1. Anisakid larva (AL) encapsulated (EC) in host muscle (HM). (400 ×)

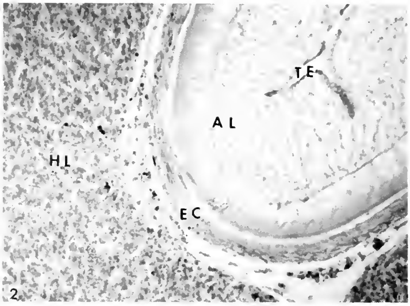

Fig. 2. Anisakid larva (AL) found encapsulated (EC) in host liver (HL). Note the characteristic tripartite esophagus (TE) of the worm. (400 ×)

hours of the invasion. The musculature of herring was a common sight of infection for the host taken from British marine waters (Davey 1972). The infection in herring was independent of host age or length.

Freshwater fish such as *Hemibarbus barbus* (Ono 1975) and trout (Wootten and Smith 1975) have also been reported as hosts for anisakid larvae.

MATERIALS AND METHODS

During the summer months of 1978, 25 sablefish (*Anoplopoma fimbria*) were taken by line from Starrigavan Bay and Thompson Harbor, Sitka, Alaska. Sixteen fish were harvested from Starrigavan Bay and nine from Thompson Harbor. Each fish was examined immediately upon death or 24 hours later. The later fish were stored under refrigeration until examined. Infected muscle and liver tissue were fixed in 10% buffered formalin followed by histological preparation by standard methods (Humason 1972). The tissue sections were stained with haemotoxylin and eosin (H + E) and Mallory's Triple, a trichrome stain. During 1982 and 1983 a total of 10 chinook salmon, from the spawning traps near Obsidian, Idaho, were examined for parasites including *Anisakis*. Samples of infected chinook salmon were sent to the senior author from Barrow, Alaska.

The occurrence of anisakid larvae was tabulated. Sections from the sablefish infected with anisakine larvae were studied in the laboratory using light microscopy.

RESULTS AND DISCUSSION

All of the 25 sablefish from Alaska were infected with anisakid larvae. The number of larvae found in each fish ranged from 1 to 11. Five fish had infections in the liver, four infections in musculature of the body wall, and the other larvae were found in the other viscera. The musculature infections could be due to worm migration following death of the host. These data correlate with Meyers (1979) with the exception of more worms per host in Alaska. No gross lesions were evident at the infection site except for one case where the anisakid larvae occupied an area near the epidermis of the skin. Prepared histological slides displayed a chronic inflammatory response for infected liver and muscle (Figs. 1 and 2). The host response consisted of organ compression, collagenous tissue encapsulation (Fig. 3), and cellular exudate forms, including free macrophages, lymphocytes, heterophils, fibroblasts, and occasional eosinophils in the area. These cells characterize an inflammatory response by the host. Migratory pathways were also observed for anisakid infected fish tissue. Observations for our infected fish tissue correlated with studies done elsewhere (Wootten 1978).

Host cell necrosis was associated with anisakid larvae in both the liver and muscle (Figs. 1 and 2). Hepatocytes had pyknotic nuclei, reduced cell size, and cytoplasmic eosinophilia. Organ compression was evident adjacent to the collagenous tissue capsule (Fig. 3).

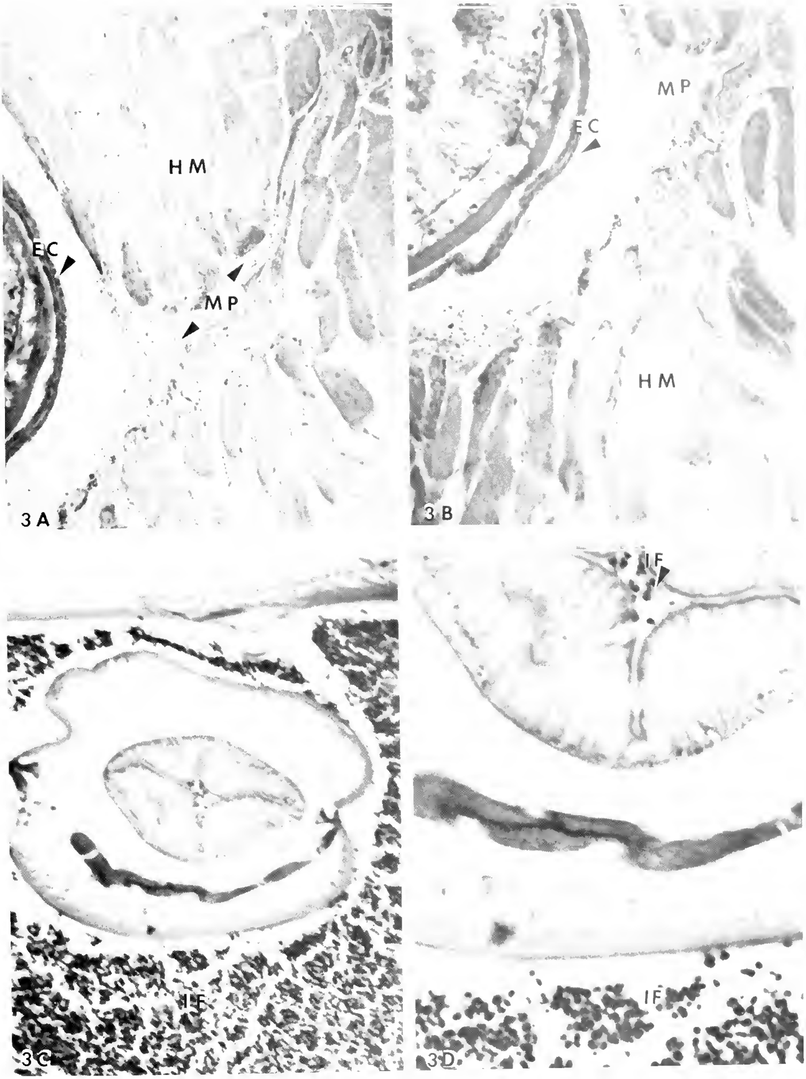

Fig. 3. These four pictures depict the inflammatory response and migratory pathway of an anisakid nematode larva. Micrograph 3A shows the route followed by the migrating anisakid (MP) through the host musculature (HM) followed by the formation of a prominent capsule (EC) depicted by figure 3B. The inflammatory response (IF) caused by the larval anisakid is shown by 3C and 3D. Note the dark-staining nature of the cells characteristic of lymphocytes, macrophages, and granular white blood cells. Note for 3D that host inflammatory cells (IF) are in the digestive tract in the anisakid worm (3C; 400×) (3D; 100×).

Small anisakid larvae were observed in a dermal papilla measuring 1 cm in diameter near the anal orifice of one fish. The papilla was raised 1–2 mm and was pale in color. Microscopic examination of the papilla showed numerous encapsulated larvae with associated inflammatory response from host tissue.

Many surveys have been conducted to determine the incidence of anisakid larvae in fish. Due to the human potential of anisakiasis, it is recommended that fish reported to be hosts for anisakids be properly cooked and prepared for consumption.

These data extend the known northern geographical distribution of anisakid larvae in sablefish to Alaska. During 1980 the first author received a specimen of chinook salmon from Barrow, Alaska, that contained an anisakid larvae (Heckmann 1980). Four of the 10 salmon examined in Idaho were infected with the roundworm. The spawning fish had carried their roundworm parasites several hundred miles inland from the Pacific ocean.

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SOIL ALGAE OF CRYPTOGAMIC CRUSTS FROM THE UINTAH BASIN, UTAH, U.S.A.

John Ashley[1], Samuel R. Rushforth[2], and Jeffrey R. Johansen[3]

Abstract.— The algal flora of selected soils in the Uintah Basin, Uintah County, Utah, was studied. A total of 45 species was identified from the top soils of three different vascular plant habitats. The soil algal flora was dominated in biomass by filamentous Cyanophyta, including *Microcoleus vaginatus*, *Phormidium minnesotense*, and three species of *Nostoc*. These algae formed the algal matrix of the soil within which other Cyanophyta as well as Chlorophyta, Bacillariophyta, and Euglenophyta occurred.

Cryptogamic crusts composed primarily of algae, lichens, mosses, and fungi are common in soils of much of western North America (Anderson and Rushforth 1976). Such crusts are one of the most important factors in stabilizing arid soils of this region (Rushforth and Brotherson 1982).

Algal components of cryptogamic crusts are found in the top few millimeters of soil (Hunt and Durrell 1966). Filamentous algae particularly have been shown to be important in binding surface soil particles (Anantani and Marathe 1974, Durrell and Shields 1961). Durrell and Shields (1961) showed that the thick gelatinous sheaths surrounding filaments of some algal species act as organic binding agents in soils even if the algae are dead. Such sheaths hold water (Bailey et al. 1973, Brotherson and Rushforth 1983) and retard desiccation of soils following storms. Kleiner and Harper (1972, 1977) found that crusts stabilize erodible soils and thus add to the long-term stability of desert grasslands.

Soil fertility appears to be increased by cryptogamic crusts (Fletcher and Martin 1948, Shields and Durrell 1964). Nitrogen fixation by cryptogamic crusts on soil surfaces constitutes an important input to many arid land ecosystems (Mayland et al. 1966, Rychert and Skujins 1974, Shields et al. 1957). Algal components also provide the organic resources required for heterotrophic nitrogen fixers as their thalli decompose (Klubek and Skujins 1980).

Cryptogamic soil communities have been observed to be important in the establishment of higher plant seedlings (Breazeale 1929, Fletcher and Martin 1948). This facilitates vascular plant colonization or regeneration on new or disturbed ecosystems (Nebeker and St. Clair 1980, St. Clair et al. 1984).

All these characteristics of cryptogamic crust communities make them extremely valuable to the soils of arid regions. Because of this, the possible use of soil algae in reclaiming poor soils has been suggested by several researchers. For instance, Lewin (1977) presented the results of several experiments that demonstrated that soil algae increased binding of the soil, elevated water retention, and increased levels of soil nitrogen. In view of these results, Lewin discussed the possibility of using algae as commercial soil reclamation agents. Likewise, other researchers have suggested the use of soil algae in land reclamation (Ali and Sandu 1972, MacKenzie and Pearson 1979, Singh 1950). Starks and Shubert (1978, 1982, Shubert and Starks 1979, 1980) studied soils of strip-mined lands and showed that significant stabilization of such land could be attributed to algae.

A knowledge of the component organisms of cryptogam crusts and their usefulness in soil stabilization, enhanced fertility, and reclamation is particularly important in western North America. Serious reclamation problems in fragile arid ecosystems will occur following ecosystem and soil disturbance due to proposed oil shale mining and processing. This paper is companion to another that discussed the establishment and growth of soil algae on processed oil shale (Ashley and Rush-

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forth 1984). The purpose of the present paper is to identify all algal species found in cryptogam crusts of selected undisturbed sites of the Uintah Basin, Utah.

SITE DESCRIPTION

The Uintah Basin is a topographic depression ranging between 1500 and 1800 m in elevation located in northeastern Utah and northwestern Colorado. During Tertiary times the basin was the site of several large freshwater lakes, within which were deposited extensive lacustrine sediments, including the oil-shale-bearing Green River Formation. Much of the central portion of the Uintah Basin is desertic, with annual precipitation less than 24 cm. Summer rains make up about half of the total precipitation and occur mostly as thunderstorms that are generally short lived but of high intensity. Snow averages about 75 cm per year and melts quite slowly, allowing water to saturate the soils. Soil erosion in the study area, mostly due to violent summer storms, has been classified as critical (Wilson et al. 1975).

METHODS

Cryptogam crusts were sampled from soils at six localities in the three dominant vascular plant communities (pinyon-juniper, shadscale, and greasewood) of the regions in the Uintah Basin to be impacted directly by oil shale development. Samples were placed in sterilized plastic bags and returned to our laboratory for analysis.

A portion of each crust sample was placed in a sterilized petri dish with 15 ml of distilled water for culturing to allow identification of algal species. Most crust subsamples showed algal growth after two days. Even so, we did not begin identification until after two weeks of growth under continuous light to insure encountering the maximum number of species.

Nondiatom algae were identified by direct microscopical examination of wet mounts. Permanent diatom slides were made by boiling diatoms in concentrated nitric acid following standard procedures (St. Clair and Rushforth 1976). All organisms were studied and photographed using Zeiss RA microscopes with Nomarski, bright field, and phase contrast optics.

RESULTS AND DISCUSSION

Soil algal floras tend to show high similarity throughout wide geographic regions. For instance, all the soil floras we have examined in western North America contain a common suite of species, are dominated by blue-green algae, show a paucity of green algae, and have relatively diverse diatom floras. The Uintah Basin flora is no exception. Of the 45 alga taxa identified from our crust samples, 16 were blue-green algae (Cyanophyta), 4 were green algae (Chlorophyta), 24 were diatoms (Bacillariophyta), and 1 was *Euglena gracilis*. The most abundant species in our samples were all filamentous Cyanophyta, especially *Microcoleus vaginatus*, *Phormidium minnesotense*, and *Nostoc commune*. *Microcoleus vaginatus* was most important in binding the soil and producing the initial crust. The importance of *Microcoleus* has been observed in many localities in arid soils of western North America (Anderson and Rushforth 1976).

Even though the Uintah Basin algal flora shows strong similarities to other floras of western North America, it contains several new distribution records. The following taxa have not previously been reported from Utah soils: *Achnanthes exigua*, *Calothrix parietina*, *Chroococcus hansgiri*, *Gomphonema parvulum*, *Navicula asellus*, *Navicula cryptocephaloides*, *Navicula minima*, *Navicula paramutica*, *Navicula tenelloides*, *Nitzschia communis*, *Nitzschia hantzschiana*, *Nitzschia inconspicua*, *Palmella miniata*, *Scytonema hofmanni*, and *Stigonema hormoides*. Two of these, *Chroococcus hansgiri* and *Navicula asellus*, also represent new records for the state of Utah.

The algal species identified in our samples are described briefly in the following section. In addition, each is illustrated in the drawings and/or photographs composing the accompanying plates.

DIVISION CYANOPHYTA

Anabaena cf. *variabilis* Kuetz. (Fig. 10). Plants filamentous; cells 2–4 μm long, 4–6 µm wide, irregular barrel shaped; heterocysts and akinetes not observed. Since we did not observe akinetes or heterocysts, the placement of our specimens into this taxon remains tentative. However, we have seen this species in nearly all of the soil samples we have previously examined from the Great Basin and Colorado Plateau.

Calothrix parietina (Naeg.) Thuret (Fig. 11). Plants filamentous, brown to almost black; trichomes 5–9 µm wide, tapering, sometimes to a hair; cells granular, subquadrate to quadrate, 3–6 µm long by 5–8 µm wide; heterocyst basal, hemispherical, 6–10 µm wide; sheaths hyaline, not lamellate. *Calothrix* species are occasionally reported from moist soils, and we have often collected them from wet walls in western North America. However, this is the first time we have found *Calothrix* in the soils of our area.

Calothrix species (Fig. 12). Plants filamentous, yellowish to brown; filaments 3.5–5 µm wide; short and stubby, but similar to *Calothrix parietina*; cells 1–4 µm long.

Chroococcus hansgiri Schmidle (Fig. 1). Plants unicellular or in small clusters, often aggregated into irregular masses; cells reddish, 8.5–10.5 µm in diameter. This is the first report of this taxon from Utah soils.

Chrococcus turgidus (Kuetz.) Naegeli (Fig. 2). Plants unicellular or spherical colonies; colonies 9–25 µm in diameter, containing 2–3 cells, occasionally more; colonial sheaths hyaline, slightly lamellate, 1 µm thick; cells ovoid if single, usually hemispherical if colonial, 4–10 µm in diameter. Our specimens of *C. turgidus* were somewhat smaller than those collected from aquatic habitats. However, we have observed this commonly with this taxon (Anderson and Rushforth 1976, Johansen et al. 1981).

Lyngbya limnetica Lemm. (Fig. 6). Plants filamentous; trichomes 2–2.5 µm wide, straight, not constricted at cross walls, not tapering; cells 6–11 µm long, pale grey-green, not granular; sheaths firm, colorless, thin. This species is commonly observed in the soils of the Great Basin.

Microcoleus vaginatus (Vauch.) Gom. (Figs. 7–8). Plant filamentous with evident sheath, one to many trichomes within sheath; cells 2.5–6 µm wide, quadrate or longer than broad, crosswalls not constricted; terminal cell attenuated, rounded or capitate, with or without calyptra. *M. vaginatus* was the most abundant species in our samples. This taxon usually dominates the soil algal floras in the Intermountain West. It is often the primary constituent of algal mats and cryptogam crusts and has been reported as being important in stabilizing desert soils (Anderson and Rushforth 1976, Rushforth and Brotherson 1983).

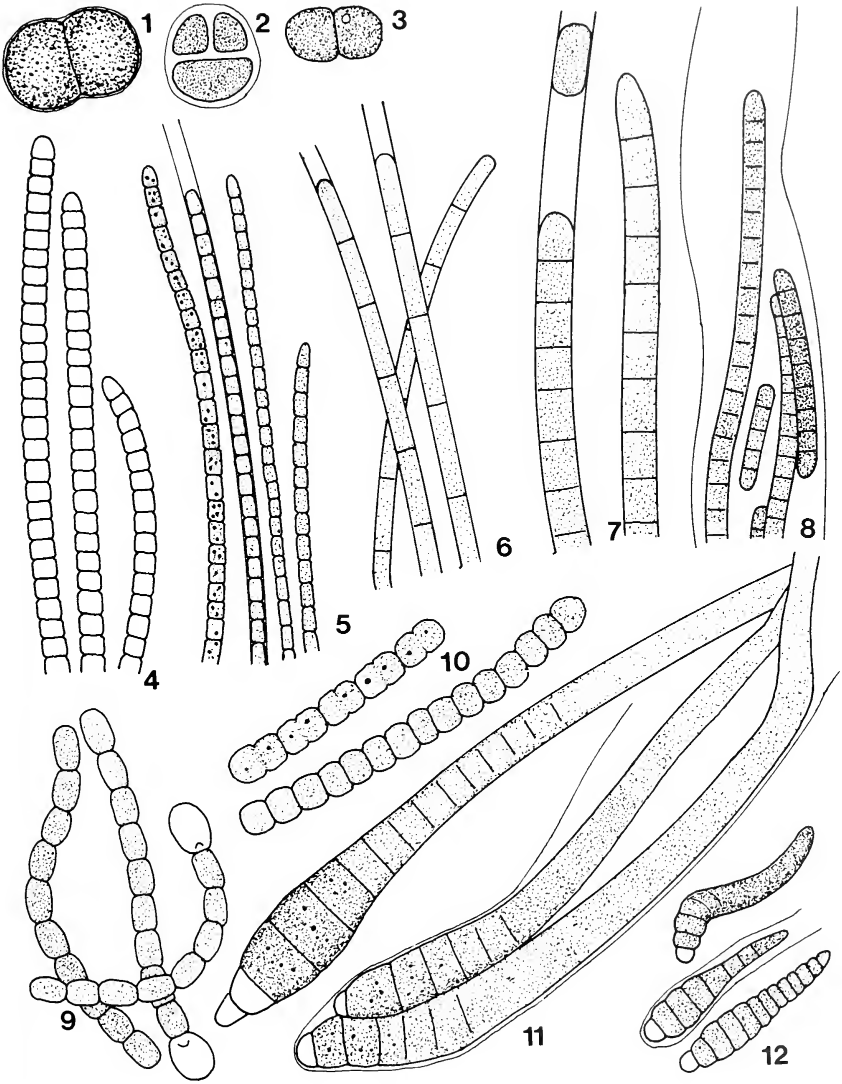
Nostoc commune Vaucher (Fig. 9). Plants cream colored to olive green, globular, firm, with age becoming lobed and clathrate; trichomes closely entangled and intertwined; cells subglobose or barrel shaped, 4–6 µm long by 3.5–4 µm wide; heterocysts frequently spherical, 5–6 µm in diameter. Several species of *Nostoc* are important in the soil algal floras of the Great Basin and Colorado Plateau. *Nostoc* is often very important in soil biology because of nitrogen fixation and soil binding.

Nostoc muscorum Agardh (Figs. 13–14). Plants yellow to brown, individual trichomes ensheathed; cells globose to elliptical, 3–4 µm in diameter by 4.5–6 µm long; heterocysts globose, singular, 4.5 µm in diameter by 5–7 µm long. This taxon is very similar to *N. commune*, differing primarily in having smaller cell size and oblong heterocysts.

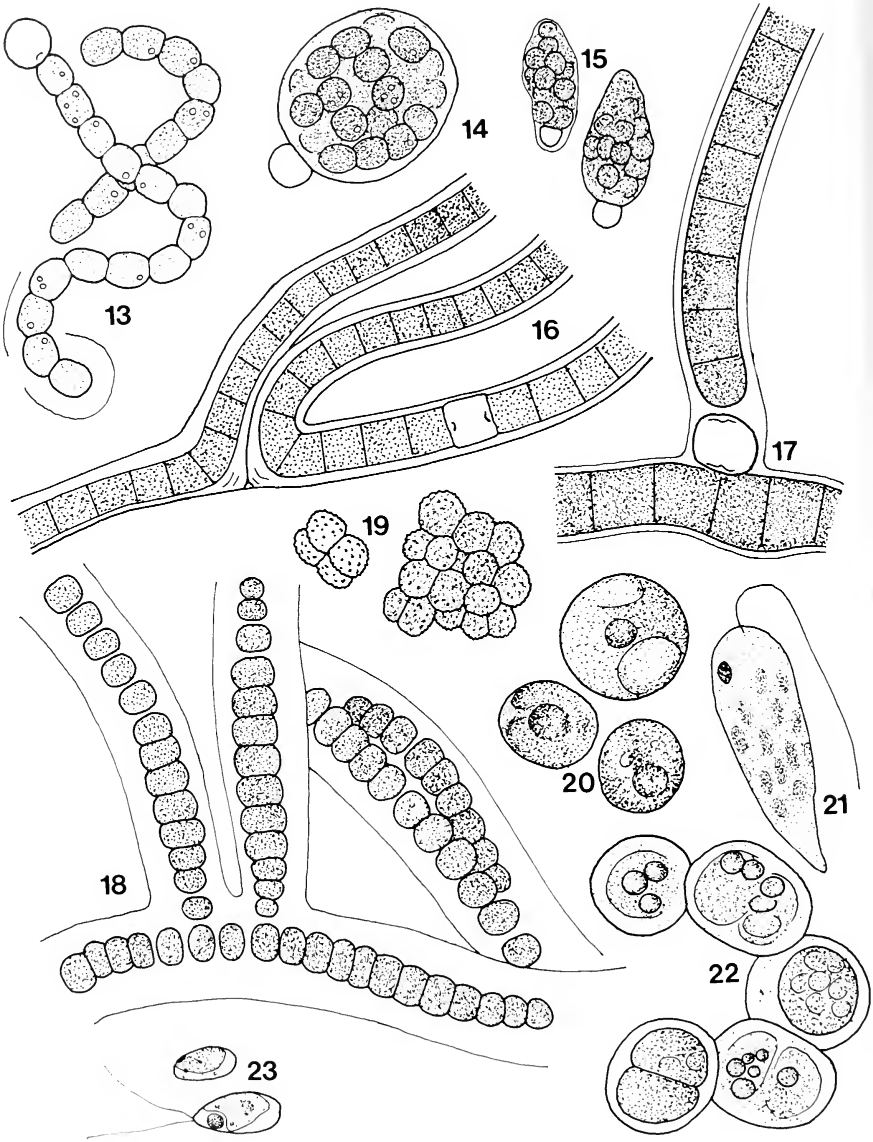
Nostoc punctiforme (Kuetz.) Hariot (Fig. 15). Plants small, blue-green colonies with firm sheath and indistinct trichomes; cells globose, 2–4 µm in diameter; heterocysts apical, spherical, often flattened at point of attachment, 2.5–3.5 µm in diameter. This *Nostoc* has smaller cells than either *N. commune* or *N. muscorum*. Our specimens were similar to those described by Desikachary (1959).

Oscillatoria tenuis Agardh (Fig. 4). Plant filamentous; sheaths absent; trichomes 2–3 µm wide, straight or slightly flexuous in apical portion, not tapering, constricted at crosswalls; apical cells convex, smooth, not capitate; cells 2–3 µm wide, slightly broader than long; cell contents granular. This *Oscillatoria* is commonly seen in the soils of our area. It is generally present in small numbers.

Phormidium minnesotense (Tilden) Drouet (Fig. 5). Plant filamentous; trichomes 2–3 µm wide, slightly curved, constricted at crosswalls, not tapering; cells 2–3 µm long by 1.5–2 µm wide; apical cell rotund; cell contents homogenous, gas vacuoles often present. This



Figs. 1–12: 1, *Chroococcus hansgiri*; 2, *Chroococcus turgidus*; 3, *Synechococcus aeruginosus*; 4, *Oscillatoria tenuis*; 5, *Phormidium minnesotense*; 6, *Lyngbya limnetica*; 7–8, *Microcoleus vaginatus*; 9, *Nostoc commune*; 10, *Anabaena* cf. *variabilis*; 11, *Calothrix parietina*; 12, *Calothrix* species. All figures are X1000.



Figs. 13–23: 13–14, *Nostoc muscorum*; 15, *Nostoc punctiforme*; 16, *Scytonema hofmanni*; 17, *Tolypothrix tenuis*; 18, *Stigonema hormoides*; 19, *Chlorosarcina* cf. *brevispinosa*; 20, *Chlorococcum* cf. *humicola*; 21, *Euglena gracilis*; 22, *Palmella miniata*; 23, *Chlamydomonas* species. All figures are X1000.

Phormidium is important in crust formation in many of the arid soils of our region.

Scytonema hofmanni Agardh (Fig. 16). Plant mass caespitose to floccose, dark blue-green to blackish; trichomes 7–8 μm wide forming upright fascicles; false branches rare, single or in pairs; sheaths firm, thin to thick; cells 2–5 μm long, 4–7 μm wide; heterocysts cylindrical, rounded at the ends; cell contents homogeneous. *Scytonema* is occasionally observed on the soil. However, we have not collected this species previously.

Stigonema hormoides (Kuetz.) Born. and Flah. (Fig. 18). Basal filaments long, decumbent, uniseriate, rarely biseriate in places, densely matted, forming a thin, felty, brownish plant mass; filaments 10–20 μm wide, sparsely and irregularly branched, side branches about as broad as main filaments; sheaths thick, colorless; cells spherical to compressed ovoid, 2.5–5 μm wide. This *Stigonema* was important in forming crusts in our samples. It was characterized by dark-colored cells and superficially resembled *Calothrix* species. It differed from *Calothrix* in the presence of true branched filaments.

Synechococcus aeruginosus Naegeli (Fig. 3). Plant unicellular or bicellular, occasionally with 4 cells; cells ovoid to cylindrical, 6–16 μm long by 6–8 μm wide; cellular contents granular, greyish. This organism is generally aquatic, but we have observed it from soils in the Uintah Basin and Tintic Mountains of Utah.

Tolypothrix tenuis Kuetz. (Fig. 17). Plant mass caespitose to floccose, blue-green to brownish; filaments 5–12 μm wide; false branches single, uncommon; sheaths membranaceous, thin, colorless or yellowish, somewhat inflated at the bases; trichomes 5–8 μm wide, slightly or not constricted at cross walls; cells equal to or longer than broad; cell contents blue-green to olive; heterocysts single or double, rounded, colorless. This taxon has been observed in other Utah soils. It is characterized by its yellowish color and rare false branching.

DIVISION CHLOROPHYTA

Chlamydomonas sp. (Fig. 23). Cells 7–10 μm long by 3–5 μm wide, biflagellate; pyrenoids one to several. This species was very rare in our samples.

Chloroccum cf. *humicola* (Naeg.) Rabh. (Fig. 20). Cells spherical or rarely ellipsoidal, solitary or in small aggregates, granular, bright green, 9–16 μm in diameter; chloroplast covering most of the cell wall. Chlorophyta were not common in our Uintah Basin soils. This is not surprising since it has been reported that alkaline soils are poor in green algae (Metting 1981). Due to the paucity of specimens, it was not possible for us to confirm species assignment. *Chlorococcum* spp. are separated from *Chlorosarcina* spp. by the absence of cell packets. We did not observe sexual phases in any of our coccoid green algae.

Chlorosarcina cf. *brevispinosa* Chant. and Bold (Fig. 19). cells spherical to ovoid, in colonies of 2–4, often forming dense irregular families; enclosed by wide, lamellate sheath; cells 2.5–5 μm in diameter.

Palmella miniata Leiblein (Fig. 22). Plants unicellular or aggregated into loose groups of 2–7 cells; cells spherical to ovoid, 10–14 μm long by 9–17 μm wide, imbedded in copious mucilage; starch grains abundant. This alga occasionally formed reddish colored patches on our soils after several weeks of culturing. We have collected this taxon from other subaerial habitats, but it appears to be more abundant on wet walls than in soils.

DIVISION EUGLENOPHYTA

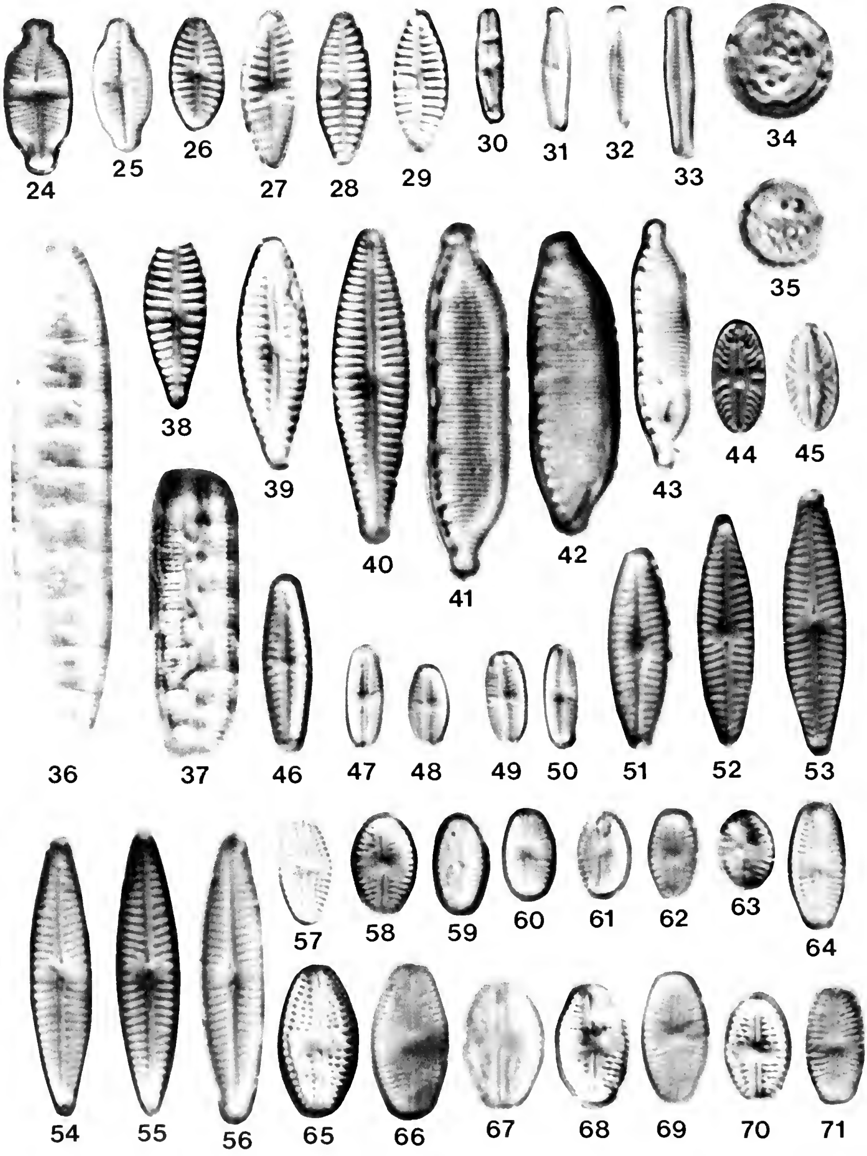
Euglena gracilis Klebs (Fig. 21). Cells active, elliptical, rounded anteriorly, tapering posteriorly, 30 μm long by 10 μm wide. We saw only a few specimens of this Euglena after culturing.

DIVISION BACILLARIOPHYTA

Achnanthes exigua Grun. (Figs. 24–25). Valves 11–13 μm long by 5–6 μm wide; striae on both valves 20–23 in 10 μm, finer towards ends. *Achnanthes exigua* has not previously been reported from the soils of our area.

Achnanthes lanceolata (Breb.) Grunow (Figs. 26–29). Valves 7–14 μm by 4.5–6 μm wide; striae slightly radiate, 11–15 in 10 μm on both valves. This taxon is rare in Utah soils.

Achnanthes linearis (W. Smith) Grunow (Figs. 30–33). Valves 9–13 μm long by 2–3 μm wide; striae on both valves 24 in 10 μm in the



Figs. 24–71: 24–25, *Achnanthes exigua*; 26–29, *Achnanthes lanceolata*; 30–33, *Achnanthes linearis*; 34–35, *Cyclotella kuetzingiana* var. *planetophora*; 36–37, *Denticula elegans* f. *valida*; 38–40, *Gomphonema parvulum*; 41–43, *Hantzschia amphioxys*; 44–45, *Navicula asellus*; 46, *Navicula tenelloides*; 47–50, *Navicula minima*; 51–56, *Navicula cryptocephaloides*; 57–71, *Navicula mutica* var. *cohnii*. All figures are X2000.

center becoming about 30 near the ends. *A. linearis* is the most common *Achnanthes* in soils of cold deserts of western North America.

Cyclotella kutzingiana var. *planetophora* Fricke (Figs. 34–35). Valves 8–17 μm in diameter; striae marginal, 20–22 in 10 μm. This species has been observed in several localities in Utah. Most of our specimens are eroded, and we have never observed living cells. This taxon, *Cyclotella bodanica* and *Stephanodiscus carconensis* are the only centric diatoms to regularly occur in soils of our region.

Denticula elegans f. *valida* Pedic. (Figs. 36–37). Valves 20–44 μm long by 5–8 μm wide; costae 3–4 in 10 μm; alveoli rows 19–21 in 10 μm. This taxon appears to be a thermophile in the Great Basin and Colorado Plateau. We have often collected it in thermal springs, drip walls with high insolation, and soils.

Diploneis sp. Valves 73 μm long by 20 μm wide; costae 9–10 in 10 μm. Only fragments of this *Diploneis* were observed. Our specimens may belong to *Diploneis smithii* that has been observed in southern Utah soils (Anderson and Rushforth 1976).

Epithemia turgida Kuetz. Valves 67–92 μm long by 12–14 μm wide; costae 2–4 in 10 μm; alveoli rows 10 in 10 μm; 2–4 alveoli rows between costae. This *Epithemia* occurs in small numbers but consistently in the soils of Utah we have studied. It is generally observed as broken valves.

Gomphonema parvulum Kuetz. (Figs. 38–40). Valves 16–26 μm long by 5–6.5 μm wide; striae 12–15 in 10 μm. *Gomphonema* species are rare in the soils of our region. The only specimens we have observed have been associated with well-developed cryptogamic crusts.

Hantzschia amphioxys (Ehr.) Grunow (Figs. 41–43). Valves 20–32 μm long by 5–7.5 μm wide; fibulae 4–9 in 10 μm; striae 19–26 in 10 μm. This species is the most abundant diatom in soils of our area and perhaps of the world.

Navicula asellus Krasske (Figs. 44–45). Valves 9–10 μm long by 4–5 μm wide; striae 16–18 in 10 μm. This is the first record of this taxon in western soils. It is also the first record of occurrence of this species in Utah. It is similar to *N. excelsa*, which has been observed in soils of central Utah.

Navicula crytocephaloides Hust. (Figs. 51–56). Valves 16.5–25 μm long by 4.5–5.5 μm wide; striae 13–14 in 10 μm at midvalve, becoming 16–18 in 10 μm at ends. Our specimens were very closely related to *N. cryptocephala* var. *lancettula*, differing primarily in the characteristics of the central area.

Navicula minima Grunow (Figs. 47–50). Valves 7–9 μm long by 3–4 μm wide; striae 28 in 10 μm at midvalve becoming 30–34 in 10 μm near ends. This species was common in soils of the Uintah Basin. It has not been observed in our other soil studies.

Navicula mutica Kuetz. (Figs. 72–85). Valves 12–28 μm long by 5–8 μm wide; striae 18–20 in 10 μm. This is a very common soil diatom, occurring in all soils of our area. Several varieties of this taxon occur in soils. The nominate and *N. mutica* var. *cohnii* are most common. *N. mutica* var. *nivalis*, a common species in Utah soils, was conspicuously absent from our samples from the Uintah Basin.

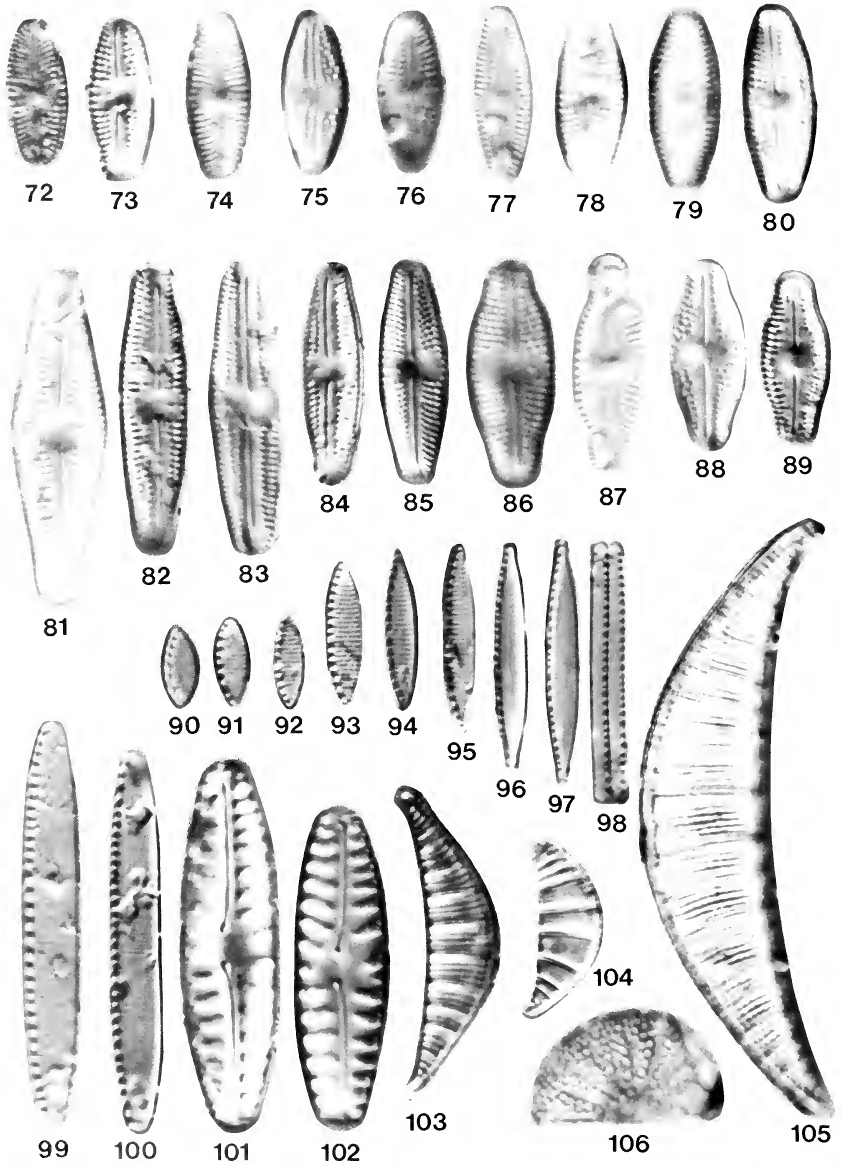
Navicula mutica var. *cohnii* (Hilse) Grunow (Figs. 57–71). Valves 6.5–13 μm long by 4.5–6.5 μm wide; striae 16–22 in 10 μm. Several of our specimens were quite close to *N. imbricata* (Figs. 57–63). However, we placed them into *N. mutica* var. *cohnii* because of the presence of transitional forms between the two and because the majority of our specimens fit the latter very well (Figs. 64–71).

Navicula paramutica Bock (Figs. 86–89). Valves 14–19 μm long by 6–7.5 μm wide; striae 18–20 in 10 μm. This species is similar to *N. mutica*, differing by the presence of attenuated ends.

Navicula tenelloides Hust. (Fig. 46). Valves 15 μm long by 4 μm wide; striae 15 in 10 μm at midvalve, becoming 18 in 10 μm near ends. This taxon is common in the aquatic systems of our area but has not been previously reported from Utah soils.

Nitzschia communis Rabh. (Figs. 99–100). Valves 31–34 μm long by 4.5–5 μm wide; fibulae 9–12 in 10 μm; striae 32–36 in 10 μm. This is the first report of this taxon from Utah soils.

Nitzschia hantzschiana Rabh. (Figs. 93–95). Valves 12–16 μm long by 2.5–3 μm wide; fibulae 12–14 in 10 μm; striae 26–27 in



Figs. 72–106: 72–85, *Navicula mutica*; 86–89, *Navicula paramutica*, 90–92, *Navicula inconspicua*; 93–95, *Nitzschia hantzschiana*; 96–98, *Nitzschia palea*, 99–100, *Nitzschia communis*; 101–102, *Pinnularia borealis*; 103–105, *Rhopalodia gibberula* var. *vanheurckii*, 106, *Stephanodiscus carconensis*. All figures are X2000.

10 μm. This species was rare in our samples and has not been observed previously in the soils of our area.

Nitzschia inconspicua Grunow (Figs. 90–92). Valves 7–8 μm long by 2.7–3.5 μm wide; fibulae 12–14 in 10 μm; striae 28–30 in 10 μm. This taxon has not been reported previously from soils of the Great Basin and Colorado Plateau.

Nitzschia palea (Kuetz.) W. Smith (Figs. 96–98). Valves 17–22 μm long by 2.5–3 μm wide; fibulae 12–16 in 10 μm; striae unresolved. This taxon has occasionally been found in soils throughout the West. It was rare in samples from the Uintah Basin.

Pinnularia borealis Ehr. (Figs. 101–102). Valves 26–31 μm long by 7–8.5 μm wide; striae 5–6 in 10 μm. This taxon is a common constituent of soils worldwide. It was one of the most common diatoms observed in this study, ranking third in importance behind *Hantzschia amphioxys* and the *Navicula mutica* complex. Many of our valves have the rectangular outline typical of *P. borealis* var. *rectangularis* but did not have the coarser striae characteristic of that variety.

Rhopalodia gibba (Ehr.) O. Mueller. Valve 55 μm long by 16 μm wide; costae 8 in 10 μm; alveoli rows 14 in 10 μm. Only a single specimen of this taxon was observed in our samples.

Rhopalodia gibberula var. *vanheurckii* O. Mueller (Figs. 103–105). Valves 15–49 μm long by 5.5–11 μm wide; costae 4–7 in 10 μm; alveoli rows 16–20 in 10 μm. We have observed this taxon in other soils of Utah where it is as rare a species as it is here. The samples from the Uintah Basin contained some very small specimens that were well below the minimum size recorded by other authors. The larger specimens (Fig. 105) are transitional between *R. gibberula* var. *vanheurckii* and the nominate variety.

Stephanodiscus carconensis (Eulens.) Grunow (Fig. 106). Valve 16 μm in diameter; costae 3 in 10 μm; aerolae forming 4 rows between costae, 12 in 10 μm. This species is widely distributed in the soils of Utah and Arizona, though it is always present in low numbers (Johansen et al. 1981, 1984). It has occasionally been reported as *S. astraea* var. *minutula* (Anderson and Rushforth 1976).

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IN MEMORIAM: WILLIAM WALLACE NEWBY (1902–1977)

William H. Behle[1]

Abstract.— W. W. Newby, professor of biology at the University of Utah from 1927 to 1971, was reknowned as a great teacher and a clear and forceful writer and for his meticulous research in invertebrate embryology. Ancillary skills were counseling (especially of premedical students), illustrating, wood crafting, and paper preserving. Some of his writings pertained to the history of research in the biological sciences at the University of Utah. His specialty areas in teaching were embryology and genetics, and he served as chairman of the Department of Genetics and Cytology from the year of its creation in 1948 until 1962. The most outstanding example of his research pertained to the early embryology of the echiuroid worm *Urechis caupo*.

Among his colleagues at the University of Utah he had the reputation of being one of the finest teachers that the university ever had. This appraisal of his teaching ability was shared by thousands of students whom he came in contact with during a teaching career that spanned 44 years (1927–1971).

He was particularly appreciated by premedical students, since one of the many courses he taught was embryology, part of a sequence of required courses in biology in his time for this group. Early in his professional life he did pioneer research in the specialized field of developmental embryology. In later years he eschewed research in favor of committee work and premedical counseling, in which activities he again made significant and prolonged contributions. He served as head of a newly created Department of Genetics and Cytology from 1948 to 1962.

He liked to work with his hands and make things. One of his attributes was a remarkable skill in drawing and preparing illustrations for his own research reports and numerous laboratory manuals. He was also an expert wood craftsman.

Upon his retirement in 1971, at which time he received a distinguished teaching award and the honorary rank of professor emeritus of biology, President James C. Fletcher characterized Dr. Newby as one who was "always willing to go the extra mile not only for students but for colleagues as well." Upon retirement he continued to work at the university as a volunteer in the library, serving as a specialist in paper preservation and restoration.

The following resumé of Dr. Newby's life and work not only elucidates his career and pays tribute to the man, but also touches on the history of the University of Utah, with which he was affiliated for 50 years. He was one of the outstanding scholars who helped make it the great institution that it is.

Fig. 1. William Wallace Newby.

William Wallace Newby was born in Dayton, Ohio, on 17 September 1902, the son of William Wallace and Emelia Vornholt Newby. His father was a photoengraver and moved several times through the midwest fol-

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lowing this trade. The family lived for several years in Norwood, Ohio, near Cincinnati, where young W. W. Newby received his early education in the elementary schools. (He received a certificate for good penmanship while in the third grade.) He recalled seeing the last passenger pigeon in the Cincinnati Zoo and was greatly impressed that a thousand dollars had been offered for a mate in the hope that if one were found the pair would propagate and save the species, but the effort came too late.

The family next moved to Kansas City, Missouri, where Newby attended Westport High School from 1917 to 1920. He had a natural aptitude for working with his hands, so as a freshman (his ninth year) he took a course in carpentry shop and made a book shelf, table, and couch. This was prophetic of his working up to bigger and better things. The next year he took a course in pattern making that involved the preparation of sand castings of iron and brass. His good work in these classes led to a job in the summer of 1918 making wooden propellers for airplanes used in World War I. His third year he took machine shop, which gave him experience in forging and shaping metal, but he preferred woodworking over metalworking. The fourth year of high school he repeated carpentry shop just to have a place to work so he could continue to make various items of furniture for the family home.

High school was followed by two years (1920–1922) attending Kansas City Junior College. During his last two years of high school and the two years in junior college, he held several jobs after school and on Saturdays in various shops, big and little, in Kansas City. He worked one summer on a surveying crew mapping a portion of the Missouri River. He was active in the Boy Scouts, and during the summer after junior college, as an assistant Scout executive, he helped run a Scout camp at Noel, Missouri, in the Ozark Mountains. The next summer he assisted at a camp at Pleasant Hill, Missouri, for underprivileged boys from Kansas City. His supervisors urged him to continue in counseling work with them, but he was offered a position at the Haskell Institute, which was one of the federal boarding and training schools for Indian children. The buildings for the education complex were situated on the campus of the University of Kansas at Lawrence. He had charge of the smaller children and received board and room plus a salary of $25 per month. Occasionally he would bring a carload of children to Kansas City to see the sights and attend a movie. The group slept on the floor of his mother's living room. In return, the children painted tribal symbols on a tanned deer skin which they presented to him.

During the academic years 1924–1926, he was a student at the University of Kansas at Lawrence. During this time he became interested in fencing and developed proficiency in the sport, winning a medal at one special event and being elected vice-president of the Fencing Club. He joined the DeMolay organization, which led to his joining the Masons. He was active while at Kansas and for his first year in Utah, but, as responsibilities of academic life increased, he gradually became inactive.

At the University of Kansas he initially planned to go into engineering but instead switched to zoology, probably being influenced by Dr. H. H. Lane, who was the head of that department. Newby served during his senior year as president of the Zoology Club. He focused on mammals, especially rodents, doing some collecting and preparation in the field with follow-up museum curatorial work. He obtained the A.B. in 1926. By this time he had decided he wanted to teach for his livelihood and thinking that a master's degree would enhance his chances of obtaining a university position, he next went to Iowa State College (later Iowa State University) at Ames, Iowa, where he had been offered a teaching assistantship. His major professor there was George O. Hendrickson and his thesis problem pertained to rodents. He completed the required course work and did his research during the regular 1926–1927 academic year and wrote his thesis during the following summer. The M.A. degree was awarded him in 1927.

During the spring of 1927, being reasonably sure that he could finish his work at Ames by the end of the summer term, he commenced looking for a teaching position and received offers from three institutions: Lawrence College in Appleton, Wisconsin; Christian College, a girl's school in Columbia, Missouri; and the University of Utah. He chose the latter. For one thing, it was a university rather than a college. It was also the farthest west of the three institutions and hence closest to the Pacific Ocean. Apparently he harbored a latent interest in marine life and a desire to work sometime in a marine laboratory. Furthermore, Utah was situated in the intermountain region, and he had never experienced mountains. Here his ever present curiosity about nature was manifest, but there was also a fortuitous element involved. The head of the Department of Zoology at the time was Harold R. Hagan, who was a friend of Dr. Hendrickson at Iowa State. Dr. Hendrickson had taught in Utah at one time. In a letter to him Dr. Hagan appended a note saying "We have an opening. Do you have anybody?" The opening was occasioned by the resignation of David T. Jones. Newby was told of the position and immediately wrote to Dr. Hagan. Before anything was finalized, Hagan became seriously ill and was replaced as department head by Dr. Ralph V. Chamberlin. It happened that Dr. Chamberlin was a friend of Dr. Lane at Kansas, whom Newby had suggested as a reference. Also Chamberlin was searching for a mammalogist, which Newby was at the time. So Newby was selected for the position. He arrived on the University of Utah campus about a week before the autumn term started for the 1927–1928 academic year. He rented a room from Professor and Mrs. F. F. Hintze near the campus but went elsewhere for his meals. Dr. Hintze was in the Geology Department, which was then housed along with biology in the Museum Building.

Newby's teaching assignment that first year was strenuous, especially for a person with little experience and virtually no time for prior preparation. It consisted of three classes per quarter, and they were large-sized classes. The first term he had two sections of genetics and one of invertebrate zoology. The genetics sections continued through the next two quarters, but the zoology changed. Winter quarter he taught comparative anatomy of vertebrates. This was followed spring quarter with a class in ecology. The second year the pressure eased a little, because the schedule was the same. The writer was a member of Dr. Newby's second winter quarter comparative anatomy class in 1928. I was impressed with his youthful appearance, friendly personality, enthusiasm for the subject matter, and his teaching effectiveness. A year or so later I took an advanced genetics class from him.

When Dr. Newby arrived on the University of Utah campus, the Biology Department occupied the second floor of the building on the lower campus then known as the Museum Building. Later it became the Biology Building, then the North Biology Building (when a "South" Biology Building was built), and finally the James E. Talmage Building of today. The Geology Department was on the ground floor, and the top floor was mostly a large, open, high-ceilinged hall that served as an auditorium for assemblies, lectures, and plays. There was a stage at the east end, and folding chairs were used. Some classrooms at the west end were used mostly by the Psychology Department.

As the biology area was growing rapidly under Dr. Chamberlin's leadership, he anticipated that before long more space would be needed. Soon after Newby's arrival, Dr. Chamberlin, knowing of Newby's manual dexterity and shop work experience, asked him one day if he knew how to make blueprints. When Newby replied yes, he was given the assignment of drawing up plans for the division of the open space on the top floor into classrooms, laboratories, and offices. Dr. Chamberlin wanted something tangible to show to President Thomas so as to "sell" the administration on expanding quarters for biology. This approach was successful and the remodeling was subsequently done according to the plans that Newby drew up, even to the extent of using his blueprints without the further aid of an architect.

Biology got all the space on the top floor except that previously assigned to psychology. Eventually, biology crowded out both psychology and geology and took over the entire building, which then became known as the Biology Building. Every time after that, when alterations were made on the structure, Newby was consulted since he knew where the bearing walls and other architectural features such as lowered ceilings were located. Ironically, the top floor was partly opened up again in Newby's later years when certain partitions were torn out and the two large rooms at both the east and west ends were converted into large classrooms for teaching by television.

Another project he did soon after his arrival was to make wooden models to illustrate all the changes in chromosomes during the stages of mitosis or cell division. Indeed he made duplicate sets, since there were often several sections of the genetics course. Later he prepared large drawings showing the differences between regular cell division and the reduction division that occurred in the production of gametes. The comparable stages were arranged side by side to show the contrast. He also prepared charts comparing spermatogenesis with oogenesis. These aids were tremendously effective and came at a time when such items could not be easily purchased from biological supply houses.

Newby's father died on 6 November 1927, not long after Newby had arrived in Utah. His mother and brother decided to join him out West. He rented an apartment for them, and they made the move just before Christmas.

One of the people in the Biology Department when Newby arrived was Elizabeth Johnson, a student at the university whose home was in Midway, near Heber City. She was working at the time for board and room at the home of Professor and Mrs. Joseph Merrill of the Engineering Department. Dr. Dolly Lutjeharms, who was then assistant professor of botany, also lived with the Merrills. Through this connection Beth gained employment in the Biology Department doing some secretarial work but mostly serving as a reader for examination papers for Dr. Chamberlin's courses in zoology and evolution. (She must have graded some of the examinations of the writer, for I took all of Dr. Chamberlin's courses).

Newby's almost daily contact with her led to a romance. She had been addressing him formally as Mr. Newby. One day he suggested that she call him by his middle name, Wallace—apparently he didn't care for his first name, William, or the nickname Bill. It seems she had an aversion to the name Wallace, however, so she started calling him Kim, which name stuck. They were married on 7 June 1928 at her home in Midway. They had one daughter, Navee, who specialized in nutrition at the University of Utah, later married, and moved east. She is employed as a nutritionist with a government food supplier.

Kim retained his youthful appearance all through the years. People who knew him for a long time often remarked how little he changed. This and his always being impeccably dressed made him seem eternally youthful. He especially liked to wear bow ties, and he had a penchant for many styles of shoes.

Kim came from a deeply religious Baptist family; his great grandfather had built a handsome Baptist church in Seymour, Indiana. So Kim affiliated with the First Baptist Church in Salt Lake City. An incidental point, going back to his University of Kansas days, is that in his early years on the University of Utah campus he and Professor Joseph Smith used to fence together. They were the only two on the faculty who knew this sport. Later Kim fenced with a medical student Marcell Marquis, an experienced fencer and organizer of fencing clubs. Kim eventually gave up fencing, again because of his teaching responsibilities.

Having arrived at the University of Utah with a master's degree, Newby next set a goal to obtain the doctor of philosophy degree. In keeping with his long-standing desire to see the ocean and study marine life, he decided to attend Stanford University's marine station at Pacific Grove near Monterey, California. In the meantime, Stephen D. Durrant had moved into the field of mammalogy, and Dr. Chamberlin wanted Newby to specialize in experimental biology.

The Newbys first went to the marine station in the summer of 1930. Kim bought a Model A Ford and, with Beth and Navee, who was then only about 10 months old, journeyed across western Utah and Nevada on graveled roads, taking three days to reach Pacific Grove. He took three marine invertebrate courses that summer.

His destiny turned from the planned experimental biology specialization to developmental morphology when he elected to study the early development of a marine worm *Urechis caupo*, an unpretentious denizen of the mud flats of the intertidal zone. His interest in *Urechis* was initially aroused by contact with Professor G. E. MacGinitie, who was one of the describers of the species, but it was Dr. Harold Heath who pointed out the need for studies on the embryology of invertebrates in general and the suitability of the eggs and larval stages of *Urechis* in particular for such studies. Newby started his research under Professor Heath. His first publication (1932) dealt with the early embryology of this worm. When Heath retired in 1933, Newby continued his work under Professors Douglas M. Whitaker and Tage Skogsberg. Whitaker became chairman of Kim's graduate committee. After three summers at Pacific Grove, Kim spent a full academic year, 1933–1934, on the main Stanford campus at Palo Alto continuing his research, taking further course work, passing the qualifying examinations, and starting the writing of his dissertation. He obtained the Ph.D. in 1939.

Dr. Whitaker was greatly impressed with Newby's meticulous morphological work and cell lineage studies and envisioned that his research would accentuate the relatively new specialty area in experimental embryology whereby particular cells could be marked at critical stages and the results of many generations of cell divisions subsequently traced with great precision. He stopped off in Salt Lake City one time on his way east to urge Kim to expand his research. Kim did so, even though it delayed completion of the dissertation. Later Dr. Whitaker arranged for the results to be published in the memoirs of the prestigious American Philosophical Society (1940). The book was illustrated by 85 of Newby's superb original drawings. With publication of the book, many co-workers in embryology wrote to Dr. Newby complimenting him on his fine, meticulous contribution. Among those who did so were such illustrious people as E. G. Conklin, J. Frank Daniels, and E. D. Goldsmith. Dr. Skogsberg was especially lavish in his praise of Kim's work being an original contribution. Kim was mentioned in the *Encyclopedia Britanica* in conection with his work on *Urechis.*

Dr. Newby's embryological study contributed to taxonomy in that it helped establish the echiuroid group of worms as a separate phylum according to some authorities. A sequel paper (1941) was concerned with the development and structure of the slime-net glands of *Urechis.* Several years later (1946) Dr. Newby made a similar study of the slime glands and thread cells of the hagfish *Polistrotrema stouti,* one of the Cyclostome or jawless fishes. The material was furnished by Rolf Bolin, an associate at Hopkins Marine Station and a former Utahn, whose father taught physical education at the University of Utah. (Incidentally, Newby's colleague Seville Flowers bought the Bolin residence near the campus).

A carryover from the Stanford period was that Newby established in one of the laboratories in the Biology Building at the University of Utah an aquarium for marine invertebrates for teaching purposes. He brewed up salt water with the same constituents as the ocean and obtained sea anemones, starfish, and other marine organisms from Dr. Bolin, who collected them along the Pacific Coast. This effort was not long sustained because of the difficulties of continuously providing the proper environment for species whose habitat was the intertidal zone, especially during the long summers when no classes in invertebrate zoology were given.

The momentum and stimulus of his research for the doctorate motivated Newby for several more years. For the 1941–1942 academic year he took a sabbatical leave to become research associate professor at the University of Texas. He worked with Dr. J. T. Patterson and his team studying development in the fruit fly *Drosophila.* The approach was to first study the development of normal *Drosophila* larvae as a basis for comparison with larvae of strains possessing structural or biochemical abnormalities. One paper by Newby (1942) soon appeared dealing with intersexes produced by a dominant mutation in *Drosophila viridis.* Some years later a second paper (1949) dealt with abnormal growths on the head of *Drosophila melanogaster.*

About the time the Newbys arrived in Texas, war clouds were gathering, and the United States soon became actively engaged in World War II. At Texas, Kim was approached by U.S. Army recruiters about taking part in a new high-altitude aviation physiology program of research and instruction of pilot trainees. It was hinted that if he signed up his initial rank would be that of captain. Being a patriotic and compulsive individual, Kim enlisted but strangely didn't discuss the matter with his wife. After only one full quarter of resumed teaching at the University of Utah, autumn quarter 1942, Beth was shocked to receive a telephone message coming to the house that Second Lieutenant Newby was to report for duty on a certain date in February 1943, and that his assignment was in the Aviation Corps of the U.S. Army.

He obtained a military leave from the University and spent the next three years or thereabouts in a new phase of his career in the Army. He had short initial assignments at Randolph Field in Texas and at an air base near Philadelphia, followed by about two years at Santa Ana Army Air Base in California. The last year he was stationed at Nellis Air Base at Las Vegas, Nevada, where he was attached to the hospital unit and taught night vision. Also he was an instructor in high-altitude physiology in the basic training program, utilizing chambers specially designed for that purpose. He received commendation for the high calibre of his work, his effectiveness as an instructor, and for his many other contributions to the success of the ground training program—and he was promoted to the rank of first lieutenant. While Newby was in the army, the writer taught one of his courses at the University of Utah, namely, vertebrate embryology, which was taken mostly by premedical students in the Army Specialized Training Program.

Upon Newby's release from the army in September 1945, he once again resumed his teaching duties at the University of Utah. While on military leave he had been advanced to full professor rank. Promotions and salary raises came slowly during the time that Dr. Chamberlin was head of the Biology Department. In Newby's case he was an instructor from 1927 to 1934 and assistant professor from 1934 to 1939. Having obtained the doctorate in 1939, he was promoted to associate professor that year, which rank he held until 1945 when he became a full professor. It is not clear whether Dr. Chamberlin offered the promotion to get Kim to return to Utah or whether Dr. Newby made that a condition of his return. In any event, Dr. Chamberlin visited Kim while he was stationed in Las Vegas.

Unfortunately for the science of developmental embryology, the long period of military service interrupted Newby's research and seemingly lessened his desire to do more of it. Furthermore, when he returned to Utah, classes in the postwar period were very large, and numerous sections were held to accommodate the great influx of postwar students. Hence teaching loads for instructors in the department increased. I recall one quarter when Kim had three laboratory sections for his embryology course going at the same time. Although he had teaching assistants for each, he was continuously rotating between them up and down stairs many times an afternoon.

Still another factor was that he was now one of an intermediate group of professors on whom committee work rested heavily. Among the more important of his committee assignments was the involvement of serving many years on the Scholarship Standards Committee, including two years as chairman; being on the Committee on Academic Freedom and Tenure; and serving on the Faculty Council. In addition, he served many years on the Academic Board of the U.S. Navy unit on campus.

All were time-consuming and tension-producing assignments carried in addition to a full teaching load plus administrative duties. All this reduced time for research. Being a conscientious individual, he would not shirk other duties to do research so the latter had to suffer. He remarked once that some staff members could teach, serve casually on committees, and still do taxonomic research, but that with his type of research he couldn't and wouldn't. He felt that it was a decision forced upon him that he had to give up research. During the summer of 1949, Dr. Newby taught a course in embryology at Stanford University.

Several years after the strenuous postwar interval, another responsibility was thrust upon him in connection with a new advanced placement program designed to identify gifted students in high school and allow them to enter universities even before their graduation from high school. This was a coordinated statewide movement, and Dr. Newby was selected to serve as director of advanced placement at the University of Utah. Working with Dean Sydney W. Angleman and the general education board, he was responsible for developing a curriculum, counseling students, some as young as 15 years of age, and synchronizing the university's program with that of other institutions in the state. He served in this capacity from 1965 to 1969.

Another development in which he was vitally involved was a reorganization of the Biology Department. Although the catalog indicated for many years that there were two departments in the biology area, botany and zoology, in reality there was but one large Biology Department, with Ralph V. Chamberlin as head. Most members of the professorial staff retired in those days at age 65, but Dr. Chamberlin evidently had an understanding that he could continue to 68. As his retirement approached, there was considerable discussion concerning a departmental reorganization.

Dr. Newby led one faction, urging retention of a single integrated biology department with a new chairman being brought in from outside the university. Supporting this position were the writer, Walter P. Cottam, Elden J. Gardner, and several others.

Taking a different position were doctors Chamberlin, Rees, Woodbury, and their supporters. Their rationale was that the creation of several departments would lead to greater representation on the Faculty Council and to greater funding from the administration.

The end result was that the Chamberlin group prevailed, and five departments were formed within a Division of Biology. The departments and their chairmen were as follows: Botany, Walter P. Cottam; Invertebrate Zoology, Don M. Rees; Vertebrate Zoology, Angus M. Woodbury; Genetics and Cytology, W. W. Newby; General Biology, William H. Behle.

To establish harmony Dr. Horace Davenport, chairman in the Department of Physiology in the Medical School, was persuaded to serve for a time as chairman of the division. The writer, in addition to heading the general biology, was selected to act as executive secretary of the division and be the liaison person with Dr. Davenport, and I moved into the former office of Dr. Chamberlin, which was centrally located.

The division, with its multiple departments, was an artificial arrangement that seemed to the writer to have been motivated largely to reward several full professors, but it worked for several years because we all wanted it to work and pulled together. In the many long meetings Kim Newby's sound thinking and composure constituted a steadying influence. After three years, Dr. Davenport stepped out, and Dr. Rees became chairman of the division in addition to being department head of Invertebrate Zoology. The writer could see no need for the position of executive secretary any longer, with everything now centralized, so that job was abandoned and Dr. Rees moved into Dr. Chamberlin's old office.

Without going into all the details, eventually a consolidation took place piecemeal over the years, and we were back to one big Biology Department, the situation that Dr. Newby et al. had argued for in the first place. Dr. Newby served as chairman of the Genetics and Cytology Department for 14 years, until 1962. Dr. Vickery then served as chairman of the Department of Genetics for three years, 1962–1965, before another reorganization led to a merger of the Department of Genetics with the Department of Experimental Biology, which had been established in the meantime.

Another phase of Dr. Newby's career to note was his serving as premedical counselor, succeeding the writer in that position. One of his innovations was the preparation of a "Guide for Premedical Students" (1954a). This he personally published, but it had to be sold through the bookstore in accordance with university regulations. Many years later it was revised and reissued, this time in pamphlet form published by the university (1967). A second such aid was called "Becoming a Doctor." It too started as a mimeographed product circa 1956 and was later published as a pamphlet by the university (1965a). It covered a broader scope than just the premedical curriculum at the university, and the realistic advice contained therein was helpful to parents as well as students. For both of these aids he adopted a question and answer format, first posing the question in boldface type, which was then followed by the answer or explanation. Dr. Newby enthusiastically carried on this premedical counseling for 18 years until his retirement. As premedical counselor and instructor in the premedical embryology course, Dr. Newby had the burden, as did Durrant, of writing hundreds of letters of recommendation, no small task. His appraisals of applicants were highly regarded by medical admissions committees throughout the country as well as at the University of Utah.

Although Dr. Newby had largely forsaken research for these various new assignments, he continued his affiliation with several professional societies. He was a member of the American Association for the Advancement of Science, the American Institute of Biological Sciences, the Genetics Society of America, Sigma Xi, Phi Sigma, Phi Kappa Phi, and the Utah Academy of Sciences, Arts, and Letters. He didn't go to many meetings but did attend the Genetics Congress held in Montreal in 1958. Through the years he had one graduate student who obtained the Ph.D. under him and more than 10 others who received the M.S. or M.A. degrees.

Even though research was essentially behind him and he was overburdened through the years with a heavy teaching load, committee work, and special assignments, Dr. Newby continued to write and be creative. In his teaching, in addition to his carefully prepared lectures, he always stressed laboratory work as a practical learning experience. In the laboratory sections of his embryology course in the early years, he used a bulky carbon arc projector to show images on a screen of structures appearing in prepared slides, mostly cross sections of embryos. His routine in the laboratory was to have an initial orientation session using this instrument, followed by the students studying slides with individual microscopes and making drawings of the structures seen.

Newby enhanced his teaching by preparing teaching aids such as charts and models and especially laboratory manuals, which had elaborate drawings to depict the structures, organs, and organ systems. Not only did he prepare and publish laboratory manuals for his own classes, but the effort carried over to the general education classes as well. Since there were multiple sections of general biology being taught by many different instructors, the use of his manuals helped the writer coordinate the coverage by all instructors of certain proscribed subject matter.

The mechanism of reduction division as opposed to normal cell division was particularly difficult for students to visualize. Troublesome, too, were certain phenomena of heredity such as crossing over. Dr. Newby, with the collaboration of a colleague in his department, Dr. George Lefevre, Jr., prepared "An Illustrated Introduction to Heredity and Development" (1954b). Portions of this were extracted and published for use in the general biology course.

The laboratory manuals that Newby prepared underwent various revisions over a period of many years under various titles (see 1956a, 1956b, 1964, 1965b). One deserves additional comment, namely, his "Guide to the Study of Development" (1960). Although this was designed for his course in embryology, it was actually a textbook in his specialized field. Seemingly, an earlier informal mimeographed version of this had appeared as early as 1953.

There are some tag ends concerning his writing and bibliography to note in passing. An early paper with student Perry Plummer, who later became a prominent field biologist with the U.S. Forest Service, described a technique for preparing microscopic sections of stems and roots. This was when Newby was teaching a course in microtechnique. A second item is an abstract (1950) of a paper he gave before the Utah Academy of Sciences discussing the recapitulation theory of development. Another was a joint paper (1965c) on the embryonic development of the California Gull. Dr. Newby's publications, listed chronologically at the end of this memorial, fall into four categories, namely, reports on his research, his laboratory manuals and supplements, the guides for premedical students, and articles dealing with historical aspects of the university, especially pertaining to research in the field of biology. Regarding those in the first two categories, his exquisite detailed drawings are especially noteworthy.

There are some miscellaneous items worthy of comment in connection with Dr. Newby's long and distinguished career. He was invited by George Lefevre to teach embryology and genetics at Harvard University as a visiting professor during the summer of 1963, and he continued to do so during the summers of 1964 and 1965. Bob Vickery had preceded Kim in the summer of 1961, teaching genetics there.

Kim was once asked how students at Harvard compared with those at Utah. He didn't think they were more highly endowed intellectually, but they were "better read" and hence more knowledgeable. He attributed this to a cultural factor wherein reading was more traditional for eastern students, correlated with their having more free time to do so. In contrast, many students at Utah had to work while attending the university. Nevertheless, he thought that Utah students were better trained in mathematics and biology.

Kim was impressed with the Harvard custom of everyone being introduced as Mr. or Mrs. rather than by their academic title of Dr. or Professor. Another surprise was the standing ovation given him at the end of the course in appreciation for his instruction.

Newby influenced many students to become biologists—and not through proselyting. Rather, their decisions were the subtle result of students desiring to emulate him. The best example is Stephen D. Durrant, who turned from studying languages to zoology and went on to become a reknowned mammalogist.

Another Newby quality was his gregariousness. A round table in a corner of the Panorama Room Restaurant in the student union was reserved for faculty. A certain group of professors that included Newby regularly met there for lunch. Many of these same people joined others for morning coffee in the faculty lounge, so Kim became conversant with university and faculty affairs. He was prominent in the affairs of the Aztec Club, an intellectual and social group that met monthly on campus. Membership consisted mostly of university people, but there were a few from downtown. Kim was vice-president in 1965–1966 and president in 1966–1967.

As a result of all these contacts, he became well known both on and off campus and was called upon many times by the administration for special assignments. For example, to celebrate the fifteenth anniversary of the founding of the graduate school, a special series of public lectures by distinguished scholars was arranged, and on 20 February 1961 a symposium on "Graduate Education: The Basis of Our Technical Society" was held. Newby gave one of the papers for this (1961a). It was titled "The Spirit of Research at the University." To commemorate the same occasion, a booklet was published called "The Advancement of Learning: Fifteen Years of Graduate Instruction, Research, and Service at the University of Utah 1946–1961." For this Dr. Newby (1961a) prepared the chapter on the biological sciences.

When the old Biology Building on the lower campus was rechristened the James E. Talmage Building, after one of the early presidents of the institution, Dr. Newby was asked to tell the history of the building. Indeed, he had earlier been involved in selecting names among the university's presidents for all the buildings on the lower campus in the area that came to be known as the President's Circle.

All through the years Dr. Newby was closely associated with Sydney W. Angleman in the general education program, one feature of which was an orientation course for freshmen entering the university. A syllabus for this course was originally prepared by a committee under the editorship of Dr. Virginia P. Frobes. The third edition of the syllabus was edited by Dr. Newby, assisted by an advisory committee. This entailed an extensive rewriting. The first five chapters were written by Dr. Newby with subsequent modifications by others. The remainder of the syllabus was taken from earlier editions with minor changes.

Dr. Newby was a charter member of University of Utah chapters for two professional societies. The first was the Alpha Lambda Chapter of Phi Sigma Biological Society. The writer as a senior student happened to be president of the predecessor society when it "went national" and recalls how helpful Kim Newby was at the time of the installation ceremonies. Indeed, he and Beth were staunch supporters through all the years of the chapter's existence. The second was the Society of the Sigma Xi. Kim was one of the group of researchers who petitioned that a chapter be established at the University of Utah. He served on numerous committees through the years and one term as president of the local chapter for the 1963–1964 academic year.

Two high honors were bestowed on Dr. Newby by the university. In 1966 he was made an honorary alumnus of the College of Medicine in recognition of his many years of teaching premedical students and serving as premedical counselor. Steve Durrant was similarly honored at the same time. In 1971, the last year of Newby's teaching, he was one of four professors selected by senior students to receive the prestigious Distinguished Teaching Award, as mentioned earlier. Two of many favorable comments made by these students on nomination forms were that he "makes difficult material clear" and "he is out to teach, not to outguess students." The award was presented to him at the annual commencement exercises, at which time the rank of professor emeritus in biology was conferred upon him.

That same year, shortly after his retirement, the older group among the members of the staff of the biology department solicited letters of appreciation from his colleagues, the administration, and as many of his former students as could be contacted. The person largely responsible for this was Bob Vickery. The letters received were then bound and presented to Dr. Newby. It became one of his treasured possessions. A significant sidelight in this connection is that one of the last things that Sid Angleman did on campus was to personally deliver to Bob Vickery his letter of appreciation for the book of letters. The next day Dean Angleman died following heart surgery. His death coming just prior to Kim's retirement affected Kim greatly. Subsequently, Kim instigated a movement to place a rock bearing a bronze memorial plaque along the south side of the east-west mall on the upper campus near the education building.

One of the inherent characteristics of Dr. Newby, as previously noted, was his ability to work with his hands. He shared this skill with his brother Gordon, who taught manual training and art at Highland High School in Salt Lake City for many years and on the side made many artifacts of wood such as cabinets, fireplace fronts, and carved statues. (Incidentally, Kim and Gordon looked remarkably alike.) Kim made about 20 small ornamental mahogany tables, 15 of which he gave to friends. Each was carved with a special design appropriate to the scholar. Later he made canes with wooden handles fitted specially to the grip of each recipient.

As sort of a sequel to this, during his six years after retirement, he volunteered many hours to the Marriott Library working on the preservation and restoration of early manuscripts, published books, maps, and prints in the Special Collections Division of the Library. According to Dr. Everett Cooley, curator of this collection and university archivist, Dr. Newby contributed his own time to learn paper preservation. Indeed, Kim went to Harvard University one summer to learn the techniques at a special workshop. His subsequent work at Utah was invaluable in that he de-acidified and sealed in mylar envelopes hundreds of early maps and about 750 extremely valuable lithographs of American Indians from the Edward Curtis collection that had been purchased by the university. This made it possible for material to be handled by researchers that before had been too fragile to touch.

Kim's work on the preservation of rare and valuable items in the Marriott Library led to his being chosen in 1973 to serve on the board of directors of the Friends of the Library, an organization created to increase university and public awareness of the needs and achievements of the library. He served on the board two terms, during which time he played an important role in developing a significant Friends program. For his service to the library and Beth's volunteer work in cataloging manuscripts, they were both made Honorary Friends of the University of Utah Library.

Kim was also active in the Professors Emeriti Club and served one term as president during the 1973–1974 academic year. Beth also worked for many years as a volunteer in the Salt Lake City Public Library.

Dr. Newby was not a robust individual, but he had no physical problems either. Yet the subtle effects of many years of stress had taken its toll. In the spring of 1968 the premedical honor society Alpha Epsilon Delta was invited to hold its 17th annual national meeting at the University of Utah. Dr. Newby and the officers of the local chapter had the responsibility of making local arrangements and planning the program. Just prior to the meeting in the first week of April, Kim suffered a heart attack while at his home. The first action of the convention after it convened was to pass unanimously a resolution thanking Dr. Newby for the excellent arrangements he had made and wishing him a speedy recovery. After a stay in the hospital he was brought home on the very day that his colleague Bill Flowers died from a heart attack. To recuperate, Kim determinedly followed a regimen involving walking at least three miles a day. This was often done at the university. He figured out how many times around the landing on the outside of the main floor of the new South Biology building (where he had his office) it took to constitute a mile, and then at noon around and around he would go until the three miles were covered. He also took up golf and played several times a week. Perhaps as a result of this regimen, he lived for nearly ten more years. The end came suddenly on the evening of 24 March 1977 at the Hotel Utah while he was the guest of Everett Cooley at a dinner meeting of the Timpanogos Club, another intellectual society of essentially prominent people downtown. After the lecture, during the discussion period, he suddenly slumped forward on the table without a sound. Although there were several doctors in the group, including some who had taken his classes as premedical students, he couldn't be revived. Thus ended his 74-year life span, his 50-year association with the University of Utah, his 44 years of teaching and research, and a long, productive, varied career. Memorial services were held at noon on 28 March 1977, with interment in the City Cemetery in Heber.

Dr. Newby was one of a triumvirate of scholars in diverse fields who were recruited by the University of Utah from institutions in other states all about the same time in the late 1920s. The others were Sydney W. Angleman, who initially taught English literature, and Jacob Geerlings, whose specialty area was Greek and Roman history. The three became fast friends, and their combined influence and academic leadership at the university for roughly four decades is incalculable. Dr. Angleman became dean of the lower division and thus built up and guided the general education program for many years, assisted by Newby and others. Dr. Geerlings served as the first dean of the faculty. Dr. Newby became head of the Department of Genetics and Cytology and eventually the elder statesman of the biology area.

In retrospect, William Wallace Newby was a model of perfection as a teacher. He made highly important contributions in his research in developmental embryology. He was a superb illustrator. He was an effective administrator. As a premedical counselor, he gave advice that was timely and realistic. Although not an alumnus of the University of Utah, no one could have been more loyal to or supportive of the institution. The university and his adopted state suffered a great loss with his passing.

I am greatly indebted to Beth Johnson Newby, Everett Cooley, and Robert K. Vickery for their help in furnishing information for this memorial. They, along with Gordon L. Newby, reviewed the manuscript. Their suggestions are greatly appreciated.

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SYMBOS CAVIFRONS (ARTIODACTYLA: BOVIDAE) FROM DELTA COUNTY, COLORADO

Jerry N. McDonald[1]

ABSTRACT.— A partial cranium belonging to the extinct woodland musk-ox, *Symbos cavifrons*, is reported from the headwaters of Oak Creek, Delta County, Colorado. This is the first cranium of the genus *Symbos* to be described from the Colorado Plateau, and it helps to define the southwest boundary of the known range of the genus.

The extinct musk-ox genus *Symbos* was distributed widely across much of North America during the late Quaternary, ranging from Alaska to Louisiana and from California to the Atlantic continental shelf off New Jersey and Virginia (Kurtén and Anderson 1980, J. N. McDonald, unpubl. data, C. E. Ray, unpubl. data). Records of *Symbos* from the Basin and Range Province, however, are rare except from the pluvial Lake Bonneville region of Utah and its discharge area in southeastern Idaho. Indeed, all 16 cranial specimens from the Basin and Range identified as *Symbos* in the literature are from this area (Gazin 1935, Nelson and Madsen 1978). At least 10 other cranial specimens are known from Basin and Range localities, including: Minidoka County (4) and one unknown location (1) in Idaho; Modoc County (1), California; Delta (1) and Montezuma (1) counties, Colorado; Wasco County (1), Oregon, and Whitman County (1), Washington (S. W. Neusius, written comm., 12 January 1984; J. A. White, oral comm., 9 May 1984; J. N. McDonald, unpubl. data; C. E. Ray, unpubl. data). In addition to specimens positively identified as *Symbos*, several other ovibovine specimens are also known from the Basin and Range, including cranial records assigned to the low-horned genera *Boötherium* and *Gidleya* as well as numerous postcranial, facial, mandibular, and dental remains that cannot yet be identified with confidence to the genus level (Gidley 1906, Cossmann 1907, Allen 1913, Gazin 1935, Nelson and Madsen 1978, Kurtén and Anderson 1980, J. N. McDonald, unpubl. data, C. E. Ray, unpubl. data).

A partial skull treated here as *Symbos cavifrons*, from Delta County, Colorado, is of special interest because (1) it represents the first record of *Symbos* from the Colorado Plateau, and (2) it falls upon, and thus helps to define, the southwestern limits of the documented range of the genus (Fig. 1). This specimen was donated to the Field Museum of Natural History, Chicago, Illinois, in August 1946 by Alfred A. Look of Grand Junction, Colorado. The following notes made by Bryan Patterson upon receipt of the specimen at the museum provide some relevant historical details:

> In July, 1946, Mr. Alfred A. Look of Grand Junction, Colorado, to whom Paleontology is indebted for the discovery or preservation of a number of interesting fossil vertebrates, sent in for determination an incomplete cranium of an extinct musk-ox. This specimen had been turned over to him by the members of a fishing party who had found it on the south side of Grand Mesa, near the rim, at an elevation of some 9000 feet. Mr. Look later visited the spot, which he informs me is about 200 yards downstream on Oak Creek from the dam face of Davey Reservoir. This places it approximately in Section 17, Twp 13 S, R 96 W, Delta Co. The fossil was evidently derived from a pit south of the dam out of which sand and clay had been taken for construction purposes. He was unsuccessful in finding any additional remains. Thanks to the original finders and to Mr. Look, the specimen has been presented to this Museum and now bears number PM ____.
>
> The deposits from which the fossil appears to have come is almost surely post-Wisconsin. Henderson (1923) has described glacial tills on the top of Grand Mesa that he attributed to the Wisconsin stage. (See also Flint et al., 1945); it is likely that the sediments observed by Mr. Look in the pit just mentioned were derived from this source. (Notes attached to letter: B. Patterson to C. E. Ray, Nov. 4, 1968).

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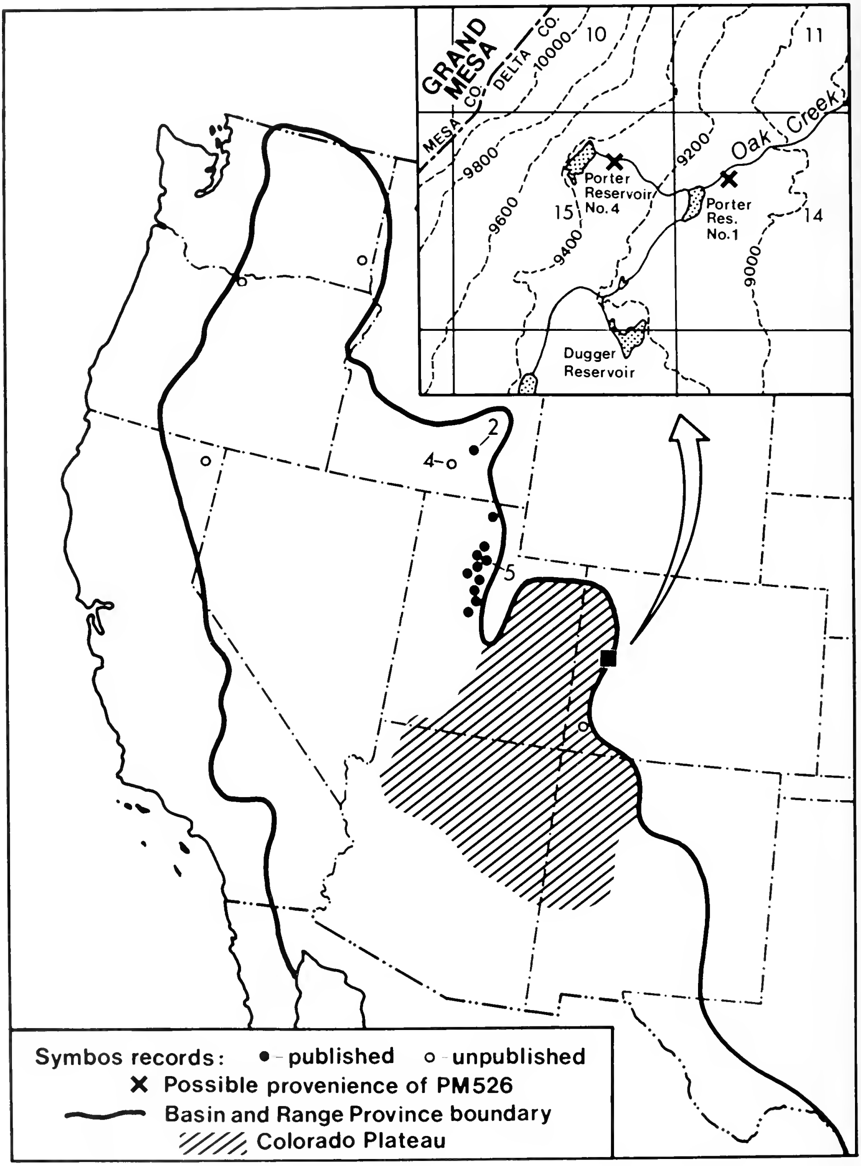

Fig. 1. Records of *Symbos* from the Basin and Range Province of the western United States, and the provenience of PM 526 near Grand Mesa, Colorado. The insert is from the Hells Kitchen, Colorado, Quadrangle, USGS 7.5′ series, 1965 edition.

Later, Patterson wrote in a foreword to Look's book on the Colorado Plateau that Look "has followed leads that have taken him hunting a fossil musk-ox in the pines and spruces at ten thousand feet on Grand Mesa" (Look, 1955: ix).

The specimen is cataloged as PM 526. The museum records that put the place of discovery in Section 17, T 13 S, R 96 W are, however, incorrect. Section 17 lies about 10,000 ft atop Grand Mesa, > $1\frac{1}{2}$ miles west of the "Davey" (actually Davies, now Porter) reservoirs, outside the Oak Creek watershed (Grand Mesa National Forest, Colorado, Map, USFS, 1959 ed.; Indian Point, Colorado, Quadrangle, USGS 7.5′ series, 1965 ed.; L. Brooks, oral comm., 9 May 1984). Porter Reservoir 4 (formerly Little Davies Reservoir) is located in Section 15, just below 9400 ft elevation, at the base of the southeast-facing scarpment of Grand Mesa (Fig. 1). Porter Reservoir 1 (formerly Davies Reservoir) lies at about 9100 ft elevation in Section 14. The segment of Oak Creek below Porter 4 flows southeasterly through forest, whereas the first half-mile of Oak Creek below Porter 1 flows northeasterly through a treeless region. Porter 1 is nearer the elevation of discovery as recorded in Patterson's notes. Available information does not permit an unequivocal determination of the provenience of this specimen, yet Patterson's notes and the battered condition of the specimen indicate that it came from below, not on, Grand Mesa. The provenience should be given, therefore, as along or near Oak Creek, Section 14 or 15, T 13 S, R 96 W, Hells Kitchen, Colorado, Quadrangle, USGS 7.5′ series (Fig. 1). The geographic coordinates of this area are approximately 38°55′30″ N, 108°6′ W; it lies within the 1-km square formed by UTM coordinates 750,500 E, 4,312,000 N, 12, N.

Symbos cavifrons is considered to have been extant from the late Irvingtonian to the Wisconsin-Holocene boundary (i.e., from ca. > 500,000 y.a.–10,000 y.a.) (Kurtén and Anderson 1980).

Description of the Specimen

This specimen consists of most of the cranium caudal to the orbits; it is badly abraded and weathered and is stained by iron. Most of the horn cores are missing, as are most of the left and part of the right occipital condyles, the jugular processes, the lateral part of the right half of the basioccipital, the rostral part of the presphenoid, the zygomatic processes, and the external occipital process, the nuchal line, and the temporal crest. The pattern of bone loss found in this specimen suggests that it has been battered by heavy objects and "rounded," such as would probably occur to skulls subjected to stream transport (Harington 1968, 1975, Shipman 1981).

The dorsal surface of the parietals and remaining frontals is concave transversely. The depression occupying the intercornual region is oval, with the greatest breadth being near the caudal edge of the horn cores. Although the intercornual surface shows abrasive damage, it appears to have been completely covered with exostoses associated with the spread of the keratinous bases of the horn sheaths into the intercornual region. There is no evidence that a longitudinal crest and trough of exostoses existed on the median plane. Some of the frontal sinuses are exposed, probably a result of abrasion of the dorsal surface (Fig. 2).

The bases and proximal parts of both horn cores remain. The dorsal surface of the horn core bases are relatively flat (i.e., they are not concave) rostrocaudally, but this flatness could have been exaggerated by abrasion. The horn core bases are convex on the ventral surface where—especially on the right core—prominent longitudinal grooves are evident (Fig. 3). The transverse breadth of the cranium at the level of the frontal sinuses is greater than the breadth at the temporal fossae (Fig. 4). The frontoparietotemporal suture is roughly parallel to the dorsal surface of the cranium (Fig. 3).

The caudal surface of the cranium is abraded and so badly weathered that most of the natural bone surface is missing (Fig. 5). Part of the natural surface of the right half of the occipital remains, and the deeper reaches of the right insertion for *M. semispinalis capitis* is evident. The breadth of the caudal end of the basioccipital, if complete, would be approximately one-half that of the complete occipital condyles. The lateral edges of the basioccipital trend gradually, then abruptly, toward the median line, producing a V or shield shape with the apex directed rostrad. A

Fig. 2. Dorsal surface, PM 526. Rostral direction toward top. Line represents 10 cm.

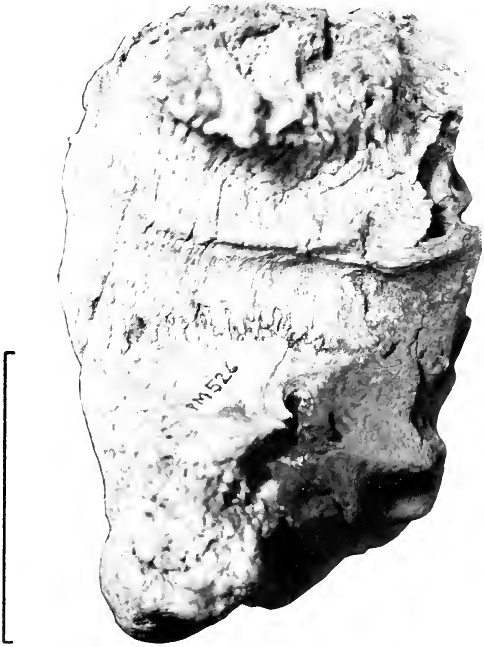

Fig. 3. Lateral surface, right side, PM 526. Rostral direction toward right. Line represents 10 cm.

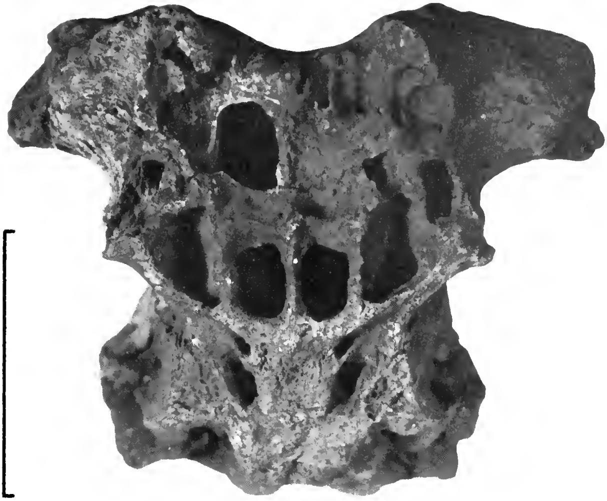

Fig. 4. Rostral view, PM 526. Line represents 10 cm.

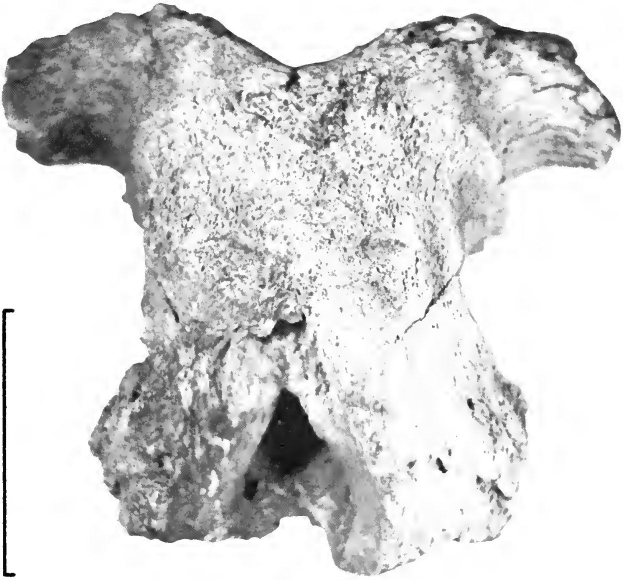

Fig. 5. Caudal surface, PM 526. Line represents 10 cm.

Fig. 6. Ventral surface, PM 526. Rostral direction toward top. Line represents 10 cm.

median groove divides the caudal half of the basioccipital into right and left halves (Fig. 6). Measurements of selected characters are given in Table 1.

Identity of the Specimen

PM 526 is referred to *Symbos* (Osgood 1905a, 1905b) on the basis of the concave, exostosis-covered dorsal surface of the parietals and the remaining frontals, the deep frontal sinuses, and the morphology of the ventral surface of the basioccipital, including (a) the presence of a median groove, (b) the V or shield shape resulting from the convergence of its lateral edges rostrally toward the median plane, and (c) the relatively great transverse breadth of the caudal part, being approximately one-half the transverse breadth of the occipital condyles (Leidy 1852, Osgood 1905a, Harington 1968, 1975, J. N. McDonald, unpubl. notes).

TABLE 1. Cranial measurements (mm).

Greatest breadth, occipital condyles		137.2
Greatest breadth, occipital condyles with auxiliary articular surface		(156.3)[a]
Greatest breadth of basioccipital		(76.2)[a]
Least breadth of parietals		132.4
Least breadth, dorsal surface of frontals		156.0
Least breadth of frontals at the ventral base of horn cores		160.9
Greatest (rostrocaudal) length, horn core base	R - 111.9	L - 105.4
Greatest dorsoventral diameter, horn core base	R - ——	L - 66.2
Greatest circumference of horn core	R - ——	L - 268.0

[a] Values in parentheses are estimates.

Symbos is considered informally to be a monospecific genus containing only *Symbos cavifrons* (Kurtén and Anderson 1980), to which species this specimen is referred on the basis of its horn core, dorsal cranial, and basioccipital morphology and frontoparietotemporal suture pattern. The difference in size between the type specimen of *Symbos cavifrons* (Leidy 1852, Osgood 1905a) and PM 526 is slight. The characters of PM 526 differ from those of the type specimen of *Symbos cavifrons* (Leidy 1852, Osgood 1905a) and other referred specimens only in minor details, none of which seem to be greater than should be expected of individual variation within a representative population sample.

ACKNOWLEDGMENTS

I thank William Turnbull (Field Museum of Natural History) for permission to study PM 526 and Len Brooks (U.S. Forest Service), Clayton E. Ray (National Museum of Natural History), and John A. White (Idaho Museum of Natural History) for providing unpublished information for use in this paper. I also thank Susan L. Woodward for preparing Figure 1.

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COMPARISONS OF PRESCRIBED BURNING AND CUTTING OF UTAH MARSH PLANTS

Loren M. Smith[1,2] and John A. Kadlec[1]

ABSTRACT.— The efficacy of cutting (haying) versus burning was compared for control of marsh vegetation in Utah. Cutting reduced production of hardstem bulrush (*Scirpus lacustris*), alkali bulrush (*S. maritimus*), and cattail (*Typha* spp.) compared to levels found on burned plots, but differences were significant ($P < 0.05$) only within the alkali bulrush vegetation type. Clipping saltgrass (*Distichlis spicata*) plots greatly reduced production upon reflooding, which produced results similar to prescribed burning and reflooding. Heat penetration into the sediments during the fire was not sufficient to cause substantial belowground mortality. Without belowground mortality, prescribed burning alone did not change aboveground production or species composition. Flooding after fire did eliminate saltgrass, but a single prescribed burning or cutting was not an effective management tool for reducing production of cattail, hardstem bulrush, and alkali bulrush.

Dense emergent marsh plants often restrict nesting and loafing by waterfowl. Wetland managers attempt to reduce the density of emergent marsh plants with prescribed burning or cutting (haying) (Nelson and Dietz 1966, Linde 1969). Smith and Kadlec (1985a) detailed the effects of fire on cattail (*Typha* spp.), saltgrass (*Distichlis spicata*), hardstem bulrush (*Scirpus lacustris*), and alkali bulrush (*S. maritimus*). In this study the objective was to compare the effects of cutting relative to fire on primary production of these four vegetation types and to assess the impact of heat penetration into the soil on aboveground plant response. Although some data exist for cattail (Nelson and Dietz 1966), little has been published regarding heat penetration and the cutting of the other vegetation types.

STUDY AREA

The study was conducted at Ogden Bay Waterfowl Management Area, Weber County, Utah. The area was established in the 1930s and 1940s when dikes were constructed along the shore of the Great Salt Lake that entrapped freshwater from the Weber River (Nelson 1954). Four species dominated the emergent vegetation: saltgrass, alkali bulrush, hardstem bulrush, and cattail (Smith and Kadlec 1983). Botanical nomenclature follows Cronquist et al. (1977) and Scoggan (1978).

Unit 1 of Ogden Bay (see Nelson 1954 for detailed description) was drained in April 1981. Portions of the area were burned 2 September 1981. The fire removed all aboveground plant material. There was a wind speed of 16.6 km with a mean dew point of 5 C and a maximum temperature of 28.5 C on the day of the fire (Smith et al. 1984).

METHODS

Annual production was determined in burned and unburned sites for cattail, alkali bulrush, hardstem bulrush, and saltgrass communities. Five quadrats in each vegetation type within the unburned area were clipped at the substrate level and raked when the other plots were burned. Quadrat size was 1.0 × 0.5 m in cattail, alkali bulrush, and hardstem bulrush sites and only 0.25 × 0.25 m within saltgrass sites due to its smaller size and high shoot density (see below). Five quadrats in each vegetation type were also established within the burned area.

Standing crops were estimated six times (May–August) during 1982 using length-mass regressions on tagged shoots (Smith and Kadlec 1985b) of alkali bulrush, hardstem bulrush, and cattail. Because water depths influence plant recovery, depths were also recorded throughout the season in burned and mowed plots. Total annual production

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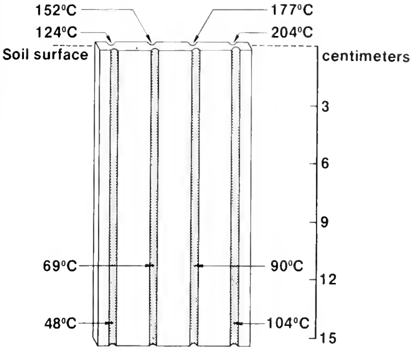

Fig. 1. Schematic of asbestos board illustrating spacing of depressions that contained waxes with a specific melting point. Boards were used to indicate temperature gradient within the soil during prescribed burning at Ogden Bay Waterfowl Management Area, Utah, 1981.

and mowed plots. Total annual production was calculated by incorporating mortality of tagged shoots. Because of the dense nature of saltgrass (2000 shoots/m^2), seasonal estimates of biomass were not made and total production was estimated using clipped plots at peak standing biomass. Biomass was also estimated for the proposed burned and unburned areas for all species prior to treatment. If pretreatment estimates of biomass were different among proposed treatment sites, pretreatment biomass was used as a covariate in subsequent analyses of variance (Steel and Torrie 1980). Data were square root transformed according to Zar (1974) to conform with normal variate assumptions.

Heat penetration into the soil during the prescribed burn was estimated by using 7 asbestos strips (Fig. 1) within each vegetation type. Each strip had waxes with 8 different melting points. Tops of the strips were placed flush with the soil surface prior to the fire (Shearer 1975). Temperature profile in the soil during the fire was reconstructed by linearly measuring the depth to which the various waxes had melted. Mortality of roots and rhizomes was estimated by taking 20 randomly located soil cores (5.0 × 15.2 cm) within each vegetation type immediately prior to and after the prescribed burn. The number of living roots and rhizomes was

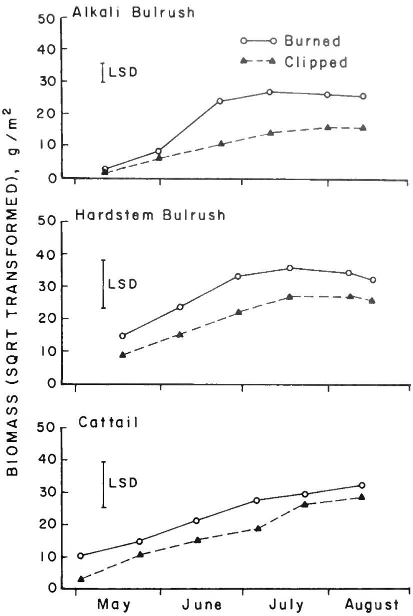

Fig. 2. Comparisons of standing crops among burning and clipping treatments within cattail, hardstem bulrush, and alkali bulrush vegetation types ($P = 0.05$; LSD = 14.2, 15.1, 6.0, respectively) at Ogden Bay Waterfowl Management Area, Utah.

number of living roots and rhizomes was counted at 4 depths: 0–3.8, 3.8–7.6, 7.6–11.4, and 11.4–15.2 cm. A solution of orthotolidine $(C_6H_3\text{-}4NH_2\text{-}3\text{-}CH_3)_2$ in 95% methanol and a 3% hydrogen peroxide (H_2O_2) solution (Hare 1965, Shearer 1975) were sprayed on the surface of the flattened core. Living material reacted by producing a blue color, but dead material did not change in color.

RESULTS

Smith and Kadlec (1985a) demonstrated that burning did not affect the subsequent annual production of hardstem bulrush, alkali bulrush, or cattail, but saltgrass was virtually eliminated as a result of flooding following fire. In this study, standing crop biomass on clipped plots was consistently less than on burned plots (Fig. 2), but the difference was significant ($P < 0.05$) only within the alkali bulrush vegetation type. Total annual production results also indicated a significant ($P < 0.05$) reduction in clipped versus burned plots (Table 1) only within the alkali bulrush sites. Within saltgrass sites cutting was similar ($P > 0.05$) to prescribed burning in that little vegetative biomass was produced following clipping and reflooding. Water depths following the prescribed burn were not different ($P > 0.15$) among burned and clipped plots, respectively, for saltgrass (8.0, 10.2 cm), cattail (22.2, 16.8 cm), hardstem bulrush (14.2, 15.0 cm), and alkali bulrush (16.8, 16.4 cm). Therefore, water levels in the two areas were not a factor in production differences.

Heat penetration into the soil (Table 2) sufficient to kill (Shearer 1975) plant tissue (60 C) was minimal but greatest within saltgrass and alkali bulrush vegetation types. Temperatures within the 48–69 C range were never deeper than 3.8 cm.

In cattail, the number of living roots and rhizomes decreased after the prescribed burn at all 4 depths (Table 3; $P < 0.05$). There was no decrease ($P > 0.20$) in the upper 3.8 cm of sediment in hardstem bulrush sites; however, differences were evident ($P < 0.05$) in the three deepest zones. Within alkali bulrush sites differences existed ($P < 0.05$) in the number of living roots and rhizomes for the three most shallow categories but not ($P > 0.10$) in the 11.4–15.2 cm range. Saltgrass sites also did not show a difference ($P > 0.20$) in the number of roots and rhizomes in the upper 3.8 cm, but differences were evident ($P < 0.05$) in the three deepest categories.

TABLE 1. Mean annual production ($g \cdot m^{-2} \cdot yr^{-1}$) of 4 vegetation types under clipping and burning treatments at Ogden Bay Waterfowl Management Area, Utah.

Vegetation type	Burned	Clipped
Distichlis spicata[a,b]	89(122)[c]	268(179)
Scirpus lacustris	1559(811)	920(612)
Scirpus maritimus	849(229)	319(129)
Typha spp.[b]	1173(1161)	979(616)

[a] Peak standing biomass
[b] Not adjusted for covariate
[c] Standard deviation in parentheses

DISCUSSION

Data on rhizome mortality and heat penetration provided insight into the effects of prescribed burning on aboveground vegetative-reproduction. Cattail and alkali bulrush sites were the only vegetation types where differences in the number of living roots and rhizomes occurred in the upper 3.8 cm of soil (Table 3). This zone is where temperature during the fire was greatest (Table 2) and suggests that the prescribed burn may have caused belowground plant mortality in these two cases. However, most vegetation types

TABLE 2. Mean heat penetration (cm) into the soil, within 4 vegetation types, during a prescribed burn at Ogden Bay Waterfowl Management Area, Utah, 1981.

	Temperature (C)							
Vegetation type	48	69	90	104	124	154	177	204
Distichlis spicata	2.21 (0.63)[a]	1.56 (0.51)	1.01 (0.24)	0.77 (0.37)	0.60 (0.45)	0.29 (0.23)	0.13 (0.11)	0.07 (0.10)
Scirpus lacustris	1.91 (0.83)	1.33 (0.72)	0.89 (0.66)	0.63 (0.57)	0.49 (0.55)	0.29 (0.36)	0.13 (0.19)	0.03 (0.08)
Scirpus maritimus	2.34 (0.70)	1.84 (0.61)	0.93 (0.30)	0.69 (0.29)	0.37 (0.21)	0.13 (0.11)	0.06 (0.05)	0.03 (0.05)
Typha spp.	1.50 (0.85)	1.01 (0.65)	0.64 (0.52)	0.43 (0.46)	0.28 (0.29)	0.13 (0.18)	0.08 (0.12)	0.04 (0.07)

[a] Standard deviation in parentheses

TABLE 3. Mean number of living roots and rhizomes at four depths in four vegetation types prior to and after a prescribed burn at Ogden Bay Waterfowl Management Area, Utah, 1981.

	Depth range (cm)							
	Prefire				Postfire			
Vegetation type	0.0–3.8	3.8–7.6	7.6–11.4	11.4–15.2	0.0–3.8	3.8–7.6	7.6–11.4	11.4–15.2
Distichlis spicata	2.8 (1.4)[a]	2.9 (1.4)	3.0 (1.6)	2.2 (1.6)	2.3 (1.3)	2.0 (1.1)	1.7 (1.1)	1.1 (1.0)
Scirpus lacustris	0.8 (0.6)	1.3 (0.9)	1.7 (0.9)	1.4 (0.7)	0.6 (0.9)	0.7 (0.7)	0.7 (0.7)	0.5 (0.8)
Scirpus maritimus	2.4 (1.1)	2.0 (0.7)	1.3 (0.8)	0.6 (0.8)	1.0 (0.9)	1.4 (1.0)	0.8 (0.8)	0.2 (0.5)
Typha spp.	1.5 (1.0)	1.6 (0.7)	1.3 (0.9)	1.1 (0.8)	0.8 (0.7)	0.8 (0.6)	0.9 (0.5)	0.4 (0.5)

[a] Standard deviation in parentheses

had decreases in the number of living roots and rhizomes in the three deepest sediment categories, where lethal heat penetration into the soil was not common. Mortality that occurred at these depths therefore should be regarded as non-fire-induced, and perhaps that was also true in more shallow layers.

Therefore, decreases in the number of roots and rhizomes in the three deepest categories (3.8–15.2 cm) were natural or resulted from the drawdown preceding the fire, which caused decreased soil moistures and increased salinities. (Smith and Kadlec 1983). Valiela et al. (1976) noted that biomass of cordgrass (*Spartina* spp.) roots peaked in midsummer and declined through autumn. At Farmington Bay Waterfowl Management Area, Utah, Anderson (1977) found that, under the stress of increased salinity, the growth of a fungus (*Chaetophoma confluens*) was encouraged on the surface of cattail rhizomes. Anderson noted the fungus was consistently associated with rhizomes of declining plants. Because the aboveground production of cattail and alkali bulrush was not reduced following fire (Smith and Kadlec 1985a), belowground decreases were apparently unimportant in terms of potential control of these vegetation types. In contrast, the decrease of saltgrass biomass was not due to fire per se because there was no decrease in living roots and rhizomes. Saltgrass decreases therefore were likely due to fire and reflooding acting together.

Faulkner and de la Cruz (1982) found that both increased soil temperature and slight increases in sediment nutrients (from fire residue) may have aided vegetation recovery and resulted in increased nutrient levels found in plant tissues after fire. At Ogden Bay, biomass of clipped plots were consistently lower than burned plots (Fig.2), suggesting that nutrients released by the fire may have speeded vegetation recovery. De la Cruz and Hackney (1980) compared clipped and burned plots within a cordgrass marsh and stated, "Presumably, nutrients left by the ash enhanced the growth of plants in the burned area." Nitrogen levels of the postburn vegetation increased in some species at Ogden Bay (Smith et al. 1984), which suggests a possible nutrient effect. An alternative hypothesis is that fire caused enough rhizome mortality to reduce intraspecific competition and allow increased vigor in individual shoots, such as cattail at Ogden Bay (Smith and Kadlec 1985a), which resulted in vegetative recovery.

CONCLUSIONS

Controlled burning has been used with limited success to control dense and undesirable plants such as cattail, *Phragmites*, and cordgrass (Lay 1945, Nelson and Dietz 1966, Ward 1968). Reasons cited for poor control include lack of proper water levels and little belowground mortality. Nelson and Dietz (1966) reported that cattail could be controlled if the area was flooded to greater than 45 cm immediately after fire. Water levels of that depth are often difficult to attain. In this study sediments were dry (Smith and Kadlec 1983) and heat penetration into the sediments was slight, resulting in little belowground plant mortality. Sediments of higher organic content might allow greater belowground mortality and better overall control. Control of saltgrass through burning or cutting and subsequent reflooding was effective. However, saltgrass is usually considered as good nesting cover for waterfowl and seldom is control warranted.

Mowing (haying) may be more effective, albeit probably temporary, than a single fire for control of emergent macrophytes, which may be due to the availability of ash (nutrients) on burn plots. Clipped plots did not receive this pulse of nutrients.

Also, rather than using vegetative removal methods to reduce cattail, salinity manipulations may promote more desirable species. Dropping water levels may lead to increased salinity (Smith and Kadlec 1983) favoring alkali bulrush. Nelson and Dietz (1966) found that cattail plots dried for two years (thereby increasing salinity) and mowed often showed increases in alkali bulrush.

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NEW SPECIES AND RECORDS OF NORTH AMERICAN *PITYOPHTHORUS* (COLEOPTERA: SCOLYTIDAE), PART IV: THE SCRIPTOR GROUP

D. E. Bright[1]

Abstract.— Six new species of *Pityophthorus* from Mexico are described. The new species, all in the Scriptor group, are: *atkinsoni*, *diminutivus*, *equihuai*, *thamnus*, *trunculus* and *zexmenivora*. An additional locality record for *P. coronarius* Blackman is included. A new key to the 22 species included in the Scriptor group is presented.

Recently, Dr. T. H. Atkinson (Colegio de Postgraduados, Centro de Entomologia Y Acarologia, Chapingo, Mexico) sent a large collection of *Pityophthorus* collected by himself and his students to me for identification. A number of samples were collected from plants not previously known to harbor scolytids and are thus a rich source of previously unknown and unsuspected host relationships. A preliminary count indicated that almost 23 undescribed species were included in the collection.

Rather than simply describe and name the new species, I have segregated them into species groups as used in my recent monograph of the genus (Bright, 1981, Mem. Ent. Soc. Canada 118). The species in each group will be described separately, and a new key will be presented where appropriate. The present contribution is the first and includes those species in the Scriptor group. Consult my recent monograph for group diagnoses, for keys to species groups, and for other information.

I thank Dr. T. H. Atkinson for sending the specimens and my colleagues Dr. Y. Bousquet and Dr. J. R. Vockeroth for reading the initial draft of this manuscript.

Pityophthorus atkinsoni, n. sp.

Length 1.9–2.2 mm, 3.0 times longer than wide.

Female.— Frons flattened on a semicircular area extending from epistoma to well above upper level of eyes, flattened area occupying about 66% of distance between eyes, surface of flattened area densely and finely punctured with dense yellowish setae, these longer and incurved on periphery and along epistoma, surface above and lateral to flattened area shining with large, sparse punctures. Antennal club 1.25 times longer than wide, widest through segment 2; first two sutures straight; first two segments occupy almost $\frac{2}{3}$ of total club length. Pronotum 1.2 times longer than wide, widest at level of summit; sides evenly, moderately arcuate; asperities on anterior slope arranged into two to four evenly concentric rows, if two then two additional rows irregularly arcuate, usually one or two additional broken rows at summit; summit distinctly elevated; posterior area of disc with deep, moderate punctures, these separated by distance equal to or less than their diameters, decreasing in size and more widely separated laterally; surface between punctures shining, with numerous fine impressed points; median line evident, flat, impunctate, with fine impressed points. Elytra 1.9 times longer than wide; apex slightly acuminate; discal striae punctured in even rows, punctures definitely larger than those on posterior portion of pronotal disc, deeply impressed, close, decreasing slightly in size posteriorly, each puncture bearing a very short seta; discal interstriae narrower than striae, surface shining, minutely sculptured with impressed points and lines or reticulate and glabrous. Declivity steep, weakly bisulcate; interstriae 1 moderately elevated, very slightly higher than interstriae 3, with a me-

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dian row of four or five small rounded granules; interstriae 2 very slightly impressed, surface moderately shining, minutely reticulate, slightly wider than interstriae 1 or 3; interstriae 3 weakly elevated, lower than 1, with a median row of five or six small rounded granules; punctures in striae 1 weakly visible, those in striae 2 obsolete.

MALE.— Frons deeply, transversely impressed from epistoma to upper eye level, margins of impressed area sharply defined, especially medianly, surface of impressed area with large, close punctures, a very weakly elevated, longitudinal, impunctate line may be visible, surface above and lateral to impressed area deeply and closely punctured. Pronotum and elytra essentially as in female. Declivity as in female except granules may be slightly larger and punctures in striae 2 may be weakly visible.

TYPE MATERIAL.— The holotype (♀) bears the labels: "Cardonal (cerca Ixmiquilpan), Edo. Hgo. 27.III.81, 2250 msnm, S-209, col. T. H. Atkinson"/"Hosp.: Compositae"/ "HOLOTYPE Pityophthorus atkinsoni D. E. Bright, 1985." The allotype and four paratypes bear the same labels plus appropriate type labels. Twenty-eight paratypes bear the same labels plus the host label "Hosp. *Flourencia resinosa.*"

The holotype, allotype, and 10 paratypes are in the Canadian National Collection of Insects, Ottawa (CNC No. 18402). Twenty paratypes were returned to Dr. Atkinson, and 2 paratypes were sent to S. L. Wood, Brigham Young University, Provo, Utah.

COMMENTS.— This species does not appear to be related or similar to any species presently placed in the Scriptor group. Adults differ from those of all other species in the group by the combination of the slightly acuminate elytral apex, by the deeply, transversely impressed male frons, by the weakly bisulcate elytral declivity, by the large strial punctures, and by the characters of the female frons.

This species is named after its collector, Dr. T. H. Atkinson, who has collected many new species of Scolytidae in Mexico.

Pityophthorus diminutivus, n. sp.

Length 0.9–1.0 mm, 3.0 times longer than wide.

FEMALE.— Frons deeply concave from epistoma to well above upper level of eyes, concavity more strongly impressed just above epistoma; surface of concave area brightly shining, with very fine points, or less shining, with fine microreticulation, periphery of concavity with closely placed, long, yellowish setae, those on vertex of concavity reaching about midway to epistoma. Antennal club oval, about 1.3–1.4 times longer than wide, widest near middle; only one suture visible, straight, located just below middle; anterior face glabrous, shining. Pronotum about 1.2 times longer than wide, widest at middle; side straight, parallel; asperities on anterior slope arranged into three definite concentric rows, a vague fourth row detectable at summit; posterior area of disc shining and densely, minutely reticulate, punctures widely separated, very obscure, shallow, barely apparent; median line very vague, faint, impunctate, shallowly impressed. Elytra 2.0 times longer than wide; apex distinctly acuminate; striae punctured in regular rows, punctures large, close, each with an extremely short seta; interstriae about half as wide as striae, impunctate. Declivity steep, generally flattened, bisulcate; interstriae 1 distinctly elevated above 2, impressed on upper portions slightly below level of interstriae 3, bearing a median row of very small acute granules; interstriae 2 impressed, widened toward apex, surface glabrous, shining, smooth; interstriae 3 slightly elevated, about as high as 1 on lower half, armed with median row of distinct but small acute granules, these larger than those on interstriae 1; punctures in striae 1 and 2 generally distinct, only slightly smaller than those on disc; vestiture of very fine, hairlike setae.

MALE.— Frons very slightly flattened or shallowly, transversely impressed from epistoma to upper level of eyes, upper margin marked by a weak transverse carina; surface with scattered fine setae. Pronotum as in female except asperities in more even, clearly defined concentric rows. Elytra as in female except vestiture on base and face of declivity distinctly broader and scalelike. Declivity essentially as in female except interstriae 1 slightly more deeply impressed below interstriae 3, granules slightly larger; granules on interstriae 3 distinctly larger, arranged near middle of declivital face; apical and lateral margins more definitely acute, subtuberculate, extending from interstriae 3 around apex to opposite interstriae 3; punctures in striae 1 and 2 obscure.

TYPE MATERIAL.— The holotype (♀) is labeled "Estacion de Biologia, Chamela, Edo. Jalisco, 19-VIII-82, S-761, 110 msnm, Col. Armando Equihua"/"Host.: Leguminosae"/ "HOLOTYPE Pityophthorus diminutivus D. E. Bright, 1985." The allotype and nine paratypes bear the same labels plus the appropriate type labels.

The holotype, allotype, and four paratypes are in the Canadian National Collection of Insects, Ottawa (CNC No. 18403). Five paratypes were returned to Dr. Atkinson.

COMMENTS.— This very small species seems to be most closely related to *P. hylocuroides* and related species but differs by the less deeply impressed declivital interstriae 1, by the very different female frons, and by the much smaller size.

Pityophthorus equihuai, n. sp.

Length 1.4–1.8 mm, 2.6 times longer than wide.

FEMALE.— Frons broadly flattened from epistoma to well above upper level of eyes and laterally nearly from eye to eye; surface shining and densely pubescent over entire area, setae on periphery much longer, very densely placed, setae arising on upper margin reaching to or beyond epistoma. Antennal club narrowly oval, 1.3 times longer than wide, widest through segment 2; sutures 1 and 2 straight, transverse; first two segments occupy more than half of total club length. Pronotum about 1.2–1.3 times longer than wide, widest at level of summit; asperities on anterior slope arranged into four somewhat irregular concentric rows, these more even and regular on lateral areas, with one or two irregular rows around summit; summit weakly elevated; posterior area of disc with shallow, small, ill-defined punctures, these widely separated by a distance greater than their diameter; surface between punctures weakly shining, very finely reticulate; median line distinct, narrow, shallowly impressed, impunctate. Elytra 1.6 times longer than wide; apex distinctly acuminate; discal striae punctured in uneven regular rows, punctures larger and deeper than those on posterior portion of pronotum, very close, more irregularly placed on base, each with a very short seta; discal interstriae narrower than striae, surface more brightly shining than surface of pronotum, smooth, with scattered minute points, glabrous. Declivity moderately deeply bisulcate; interstriae 1 distinctly elevated, slightly lower than interstriae 3 on upper portions, with a distinct row of five to seven small rounded granules; interstriae 2 distinctly, moderately impressed, slightly widened on apical half, surface smooth, shining, or moderately dull, with numerous very fine points or very fine reticulate; interstriae 3 convex, moderately elevated, slightly higher than interstriae 1 on upper portions, bearing a median row of three to five distinct rounded granules, these slightly larger than those on interstriae 1; several very small granules present lateral to interstriae 3 on apex of interstriae 4–8; punctures in striae 1 and 2 small, weakly impressed but readily visible, especially in striae 2.

MALE.— Frons shallowly, transversely impressed from epistoma to well above upper level of eyes, surface of impressed area shining, densely, finely punctured with numerous, erect, short setae, surface above and lateral to impressed area more deeply, sparsely punctured, glabrous, shining. Pronotum as in female except asperities on anterior slope larger, in more even concentric rows. Elytra as in female except strial punctures larger, more deeply impressed, declivity more deeply bisulcate, interstriae 1 distinctly lower than interstriae 3 and granules on interstriae 1 and 3 much larger, acute.

TYPE MATERIAL.— The holotype (♀) is labeled: "Est. de Biologia Chamela, Edo. de Jalisco, S-832, 12-XI-82, 100 m, col. Armando Equihua M"/"HOLOTYPE Pityophthorus equihuai D. E. Bright, 1985." The allotype and 18 paratypes bear the same label plus an appropriate type label.

The holotype, allotype, and eight paratypes are in the Canadian National Collection of Insects, Ottawa (CNC No. 18404). Eight paratypes were returned to Dr. Atkinson and two paratypes were sent to S. L. Wood, Brigham Young University, Provo, Utah.

COMMENTS.— Adults of this species are similar to those of *P. mexicanus*, *coronarius*, and *vesculus* but differ in a number of significant characteristics as mentioned in the key.

This species is named after its collector, Armando Equihua, who has collected many undescribed species of Scolytidae in recent years.

Pityophthorus thamnus, n. sp.

Length 1.9–2.1 mm, 3.0 times longer than wide.

FEMALE.— Frons flattened on large area extending from epistomal margin to upper level of eyes, laterally occupying about 86% of distance between eyes; surface densely, finely punctate, bearing dense, short, erect setae, all of about equal length. Antennal club oval, 1.3 times longer than wide, widest at middle through segment 2; sutures 1 and 2 transverse; segments 1 and 2 together occupy more than half of total club length. Pronotum very slightly longer than wide, widest at middle; sides weakly arcuate, very weakly constricted before anterior margin; asperities on anterior slope arranged into four concentric rows, with one or two small, vague additional rows at summit; summit weakly elevated; posterior portion of disc with moderate size punctures, these widely separated by a distance greater than their diameter; surface between punctures moderately shining, densely, finely, minutely reticulate-punctate; median line weakly elevated behind summit, broad, impunctate toward base. Elytra 2.0 times longer than wide; apex moderately acuminate; discal striae punctured in regular rows, punctures very slightly larger than those on posterior portion of pronotal disc, moderately impressed; discal interstriae about as wide as striae, smooth, moderately shining, minutely reticulate. Declivity sloping, moderately deeply bisulcate; interstriae 1 distinctly elevated, impressed below level of 3 on upper portion, with a few fine granules on basal area and toward apex, central portion devoid of granules; interstriae 2 moderately deeply impressed, widened toward apex, surface smooth, minutely reticulate; interstriae 3 distinctly, moderately elevated, higher than 1 on upper portions, bearing a median row of fine large granules, each bearing an erect seta; puncture in striae 1 and 2 obsolete; if visible, then much smaller, shallower than those on disc.

MALE.— Frons flattened on an area equal to female, weakly, transversely impressed above epistoma; surface with coarse rather large punctures, lower median area just above epistoma weakly, longitudinally elevated, impunctate; vestiture sparse. Pronotum and elytra essentially as in female except punctures, asperities etc. coarser. Declivity as in female except interstriae 3 more strongly elevated above interstriae 1, granules larger; interstriae 1 more deeply impressed and strial punctures slightly larger.

TYPE MATERIAL.— The holotype (♀) is labeled: "Pachuca Edo. de Hidalgo, S-462, 21.V.82, 2400 m., col. A. Equihua M."/ "Zaluzania angusta (Lag.) Sch. Bip. (Compositae)"/"HOLOTYPE Pityophthorus thamnus D. E. Bright, 1985." The allotype and two paratypes bear the same data and appropriate type labels.

The holotype, allotype, and two paratypes are in the Canadian National Collection of Insects, Ottawa (CNC No. 18405). Four paratypes were returned to Dr. Atkinson.

COMMENTS.— Adults of this species are similar to those of *P. coronarius* and related species but differ by the more gradually sloping elytral declivity, by the smaller granules on declivital interstriae 3, by the less strongly acuminate elytral apex, and by the female frons that bears setae all equal in length.

Pityophthorus trunculus, n. sp.

Length 1.0 mm, 3.0 times longer than wide.

FEMALE.— Frons broadly flattened on a semicircular area extending from epistoma to slightly above upper eye level and laterally occupying about 65% of distance between eyes; surface of flattened area densely, finely punctured, a minute tubercule evident just above epistomal margin in some specimens; vestiture short, moderately abundant, generally of equal length, slightly longer on periphery. Antennal club oval, about 1.2 times longer than wide, widest through segment 2; first two sutures straight, first two segments occupy slightly more than half of total club length. Pronotum less than 1.1 times longer than wide, widest on posterior half; sides moderately arcuate; asperities on anterior slope arranged into three concentric rows, a vague fourth row detectable at summit; posterior area of disc distinctly to weakly shining, punctures entirely obscure, only very weakly indicated; median line not obvious. Elytra 2.0 times longer than wide; apex distinctly acuminate; discal surface completely, minutely reticulate, strial punctures not visible, or at most very weakly indicated. Declivity convex, sloping; interstriae 1 weakly elevated, devoid of granules; interstriae 2 weakly impressed, not sulcate; interstriae 3 not elevated or only weakly so, equal or very slightly higher than 1, with a median row of extremely fine granules; punctures in striae 1 and 2 obsolete. Vestiture sparse, consisting of fine, hairlike setae on declivital interstriae 1, 3, 5, etc., those on interstriae 1 much shorter.

MALE.— Frons weakly transversely impressed from epistoma to above upper level of eyes, upper margin of impression slightly more evidently elevated into a short, transverse carina; surface finely, densely punctured. Pronotum and elytra as on female except granules on declivital interstriae 3 very slightly larger.

TYPE MATERIAL.— The holotype (♀) bears the labels: "Est. de Biologia Chamela, Edo. de Jalisco, S-831, 12-XI-81, 100 m, col. Armando Equihua M."/"HOLOTYPE Pityophthorus trunculus D. E. Bright, 1985." The allotype and seven paratypes bear the same data plus appropriate type labels.

The holotype, allotype, and two paratypes are in the Canadian National Collection of Insects, Ottawa (CNC No. 18406). Five paratypes were returned to Dr. Atkinson.

COMMENTS.— This species will key to *P. dimidiatus* Blackman or to *P. minutalis* in my 1982 key. Adults of *P. trunculus* differ from those of both species by the entirely impunctate, reticulate elytra (faint strial punctures visible in some specimens), by the nearly impunctate posterior area of the pronotum, and by the smaller size.

Pityophthorus zexmenivora, n. sp.

Length 1.8 mm, 2.7 times longer than wide.

MALE.— Frons broadly flattened from epistoma to slightly above upper eye level, very weakly transversely impressed above epistoma; surface with coarse, dense, moderate-size punctures, these distinctly impressed, each bearing a short, yellowish, semirecumbent seta. Antennal club oval, about 1.6 times longer than wide, widest through segment 2; sutures 1 and 2 transverse; segments 1 and 2 occupy more than half of total club length. Pronotum as long as wide, widest on posterior half; sides subparallel on basal half, weakly but distinctly constricted before anterior margin; asperities on anterior slope arranged into four concentric rows with one or two indistinct rows at summit; summit very weakly elevated; posterior area of disc with coarse moderate size, distinctly impressed punctures, these separated by a distance equal to their diameter; surface between punctures moderately shining, with minute lines and points. Elytra 1.8 times longer than wide; apex strongly acuminate; discal striae punctured in regular rows, punctures equal to or slightly larger than those on posterior portion of pronotum, moderately deep; discal interstriae about as wide or slightly wider than striae, surface smooth, moderately shining, very finely reticulate, impunctate, except near declivity. Declivity sloping, strongly sulcate; interstriae 1 slightly elevated, bearing a few acute granules on base and 1 or 2 large granules at apex; interstriae 2 deeply impressed, broadened toward apex, surface smooth, very minutely reticulate; interstriae 3 strongly elevated, much higher than 1 on upper two-thirds, bearing a median row of large acute granules and long, hairlike setae; punctures of striae 1 and 2 obsolete.

TYPE MATERIAL.— The holotype (♂) is labeled "Pachuca, Edo. de Hidalgo, S-461, 21.VI.82, 2400 m, Armando Equihua"/"Zexmenia sp. (Compositae)"/"HOLOTYPE Pityophthorus zexmenivora D. E. Bright, 1985." One paratype bears the same data with an appropriate type label.

The holotype is in the Canadian National Collection of Insects, Ottawa (CNC No. 18407). The paratype was returned to Dr. Atkinson.

COMMENTS.— Adults of *P. zexmenivora* are similar to those of *P. mexicanus* but differ by the lack of a fine, elevated median line on the posterior portion of the pronotum, by the finer, shallower punctures on the pronotum, and by the impunctate elytral interstriae. Adults also key out near *P. equihuai* but differ by the size, by the characters of the declivity, and by other characters given in the key.

Pityophthorus coronarius Blackman

Pityophthorus coronarius Blackman, 1942, Proc. U.S. Nat. Mus. 92: 220; Bright, 1981, Mem. Ent. Soc. Canada 118: 33; Wood, 1982, Great Basin Nat. Mem. 6:1115.

This species was previously known from Jalisco, Mexico, from *Sambucus* sp. A series of eight specimens are labeled: "Rancho Tetela, Cuernavaca, Mor.[elos], Compositae, 10 Enero 1982, 1750 m, Col. BUSA-SACE-MAFE."

Key to species in Scriptor group
(Modified from Bright 1981)

1. Interstriae 1 moderately to strongly impressed below level of interstriae 3 on upper declivity (especially in males); granules on declivital interstriae 3 usually large and prominent 2

— Interstriae 1 not impressed on declivity or only weakly impressed, equal in height to interstriae 3, or at most very slightly lower; granules on interstriae 3 usually very small 15

2(1). Declivital sulcus very wide, flattened to interstriae 5, interstriae 1 only slightly lower than 3 on upper half; male frons strongly, transversely impressed from epistoma to upper level of eyes; posterior portion of pronotum obscurely punctured, reticulate; body slender, about 3.1 times longer than wide; Guatemala . . . . *elegans* Schedl

— Declivital sulcus more convex, more deeply bisulcate; male frons variable; posterior portion of pronotum distinctly punctured 3

3(2). On conifers in SW United States; declivital interstriae 2 very broad, moderately sulcate; pronotal asperities arranged in even or irregular rows; female frons pubescent over entire surface, setae on periphery longer and incurved . . . . *arcanus* Bright

— On shrubs in SE and W United States or in deciduous trees or shrubs in Central America; declivital interstriae 2 not broadly sulcate; pronotal asperities scattered or in even concentric rows; female frons variable but not as above 4

4(3). Pronotal asperities numerous, confused, in no apparent order; declivital striae 1 and 2 with distinct punctures, these almost equal in size to those on disc; declivital setae of male narrowly spatulate; Panama . . . . *vesculus* Wood

— Pronotal asperities arranged in even concentric rows; punctures in declivital striae obscure; declivital setae hairlike in males 5

5(4). Larger species; male frons convex, without a carina; declivity more gradual, apex strongly acuminate, interstriae 3 armed by median row of distinct granules, forming lateral margin of declivity 6

— Small species; male frons transversely impressed, with a distinct, transverse carina at upper level of eyes; declivity steeper, apex moderately to weakly acuminate; interstriae 3 granulate to middle of declivital face, not forming lateral margins of declivity 11

6(5). Declivity sloping, beginning on posterior one-fourth of elytra, moderately impressed, granules on interstriae 3 small; elytral apex moderately acuminate; female frons with short setae, all equal in length; Mexico . . . . *thamnus* Bright

— Declivity steep, beginning on posterior third of elytra, usually strongly impressed, granules on interstriae 3 large; elytral apex moderately to strongly acuminate; female frons with long setae, especially on periphery 7

7(6). Posterior portion of pronotum bearing rounded, elevated granules on lateral or posterior edges of punctures; surface between punctures on posterior portion of pronotum strongly and densely reticulate; female frons densely pubescent, with longer, downward-pointing setae on upper and lateral margin 8

— Posterior portion of pronotum not bearing rounded, elevated granules on edges of punctures; surface between punctures on posterior portion of pronotum not strongly reticulate, or punctures obsolete; females frons variable 9

8(7). Body slender, about 2.9–3.0 times longer than wide; female frons broadly flattened, densely pubescent with long setae on upper and lateral margins; male frons flattened; interstriae 1 on declivity with small granules along entire length, granules on interstriae 3 slightly larger; Mexico. . . . . *coronarius* Blackman

— Body stouter, 2.7–2.8 times longer than wide; female frons broadly concave, with long setae on complete periphery; male frons moderately, transversely impressed; interstriae 1 on declivity devoid of granules except at base and at apex, granules on interstriae 3 acute, prominent; Mexico. . . . . *concinnus* Wood

9(7). Median line on posterior portion of pronotum sharply, narrowly elevated; punctures on posterior portion of pronotum large, deep, almost touching; discal interstriae 1, 3, 5, 7 usually with a median row of sparse setae extending nearly to base; Mexico . . . . *mexicanus* Blackman

— Median line on pronotum not elevated; punctures on posterior portion of pronotum finer, shallower, and more widely separated; discal interstriae usually impunctate. 10

10(9). Body length 1.8 mm; declivity deeply sulcate, interstriae 3 strongly elevated, inner slope abrupt; median portion declivital interstriae 1 devoid of granules; Mexico . . . . *zexmenivora* Bright

— Body length 1.4–1.8 mm; declivity weakly sulcate, interstriae 3 only slightly higher than 1, granules on interstriae 1 and 3 very large; setae on female frons very long, extending from vertex to epistoma; Mexico . . . . *equihuai* Bright

11(5). Length 0.9–1.0 mm; female frons concavely impressed, shining, glabrous in center, periphery with long, yellowish setae; punctures on posterior portion of pronotum obsolete, surface between punctures reticulate; Mexico. . . . . *diminutivus* Bright

— Length greater than 1.2 mm; female frons flattened, densely pubescent over entire surface; punctures on posterior portion of pronotum distinct, surface between punctures smooth 12

12(11). Declivity deeply sulcate in male, moderately sulcate in female, interstriae 3 much higher than 1 on declivital base, with large coarse granules; interstriae 2 distinctly broadened toward apex in male, punctures in striae 2 obscure in male, distinct in female. 13

— Declivity shallowly sulcate, interstriae 3 moderately or only slightly higher than 1, with moderately large or small granules; interstriae 2 variable, but not broadened toward apex in male, punctures in striae 2 distinct in both sexes 14

13(12). Declivity of male very steep, flattened, with an acute, tuberculate margin extending from top of interstriae 3 around apex to opposite interstriae 3, granules on interstriae 1 and 3 large, acute; declivity of female convex, less deeply sulcate, with prominent granules on interstriae 1 and 3; central Mexico. . . *hylocuroides* Wood

— Declivity of male less steep, obscurely flattened on lower half, lateral margin lateral to interstriae 3 rounded, granules on interstriae 1 small to absent, on interstriae 3 slightly larger, acute; declivity of female more convex, less deeply sulcate, with small granules on interstriae 1 and 3; Idaho to northern Mexico and west Texas . . . . *virilis* Blackman

14(12). Granules on declivital interstriae 1 and 3 small; female frons evenly pubescent on a large semicircular area, setae slightly longer on periphery; male frons moderately deeply, transversely impressed; southeastern USA . . *scriptor* Blackman

— Granules on declivital interstriae 1 and 3 moderately large; female frons densely pubescent, the setae on the periphery very closely placed and very long, extending downward almost to epistoma and masking surface of frons; male frons shallowly, transversely impressed; Honduras . . . . *hermosus* Wood

15(1). Declivity distinctly flattened, very weakly sulcate, interstriae 1 and 3 very weakly elevated with fine granules; male frons distinctly, transversely impressed, impression deeply punctured; female frons densely, evenly pubescent; Mexico . . . . *atkinsoni* Bright

— Declivity variable but distinctly convex and bisulcate; male frons flattened or weakly, transversely impressed; female frons variable 16

16(15). Basal half of pronotum dull, minutely reticulate, punctures barely visible, if at all; Mexico . . . . *dimidiatus* Blackman

— Basal half of pronotum dull to shining, smooth, punctures usually distinctly visible 17

17(16). Punctures in declivital striae 2 obscure, difficult if not impossible to see 18

— Punctures in declivital striae 2 distinct, obvious 23

18(17). Declivital interstriae 1 and 3 devoid of granules or granules extremely minute 19

— Declivital interstriae 1 and 3 with generally distinct granules 20

19(18). Elytral strial punctures obsolete, entire surface minutely reticulate; punctures on posterior surface of pronotum obsolete; female frons flattened, with abundant setae of equal length over surface; length 1.0 mm; Mexico . . . . *trunculus* Bright

— Elytral strial punctures distinct, in even rows, entire surface smooth; punctures on posterior surface of pronotum distinct; female frons flattened, pubescence long on periphery, somewhat sparser on a median longitudinal space; length 1.0–1.2 mm; Mexico . . . . *minutalis* Wood

20(18). Male frons convex, with a weak longitudinal carina; female frons concave, uniformly covered with dense pubescence, setae on periphery longer and incurved; southwestern USA. . . . . *torridus* Wood

— Male frons very weakly, transversely impressed, with an extremely fine, longitudinal carina or a narrow, longitudinal, smooth space; female frons flattened, with either three tufts of extremely long, fine setae extending downward to apex of mandibles or with flattened area uniformly pubescent 21

21(20). Female frons with three tufts of extremely long, downward-pointing setae that extend almost to tips of mandibles; male frons generally convex, narrowly, transversely impressed above epistoma, with a weak longitudinal carina; Guatemala . . . . *nugalis* Wood

— Female frons uniformly pubescent on a subcircular area occupying 70%–75% of distance between eyes, setae short, usually all of equal length; male frons weakly, transversely impressed from epistoma to upper level of eye, usually with a longitudinal smooth space; Mexico 22

22(21). Size smaller, 0.8–1.2 mm; declivital interstriae 2 very weakly impressed, interstriae 3 weakly elevated, granules on 1 and 3 minute, obscure . . . *atomus* Wood

— Size larger, 1.2–1.5 mm; declivital interstriae 2 more deeply impressed, interstriae 3 distinctly elevated, granules on 1 and 3 distinct . . . *attenuatus* Blackman

23(17). On *Pinus* spp.; surface between punctures on posterior portion of pronotum smooth, with only a few minute points and/or lines 24

— On vines; surface between punctures on posterior portion of pronotum densely micropunctate; Costa Rica . . . . *sobrinus* Wood

24(23). Elytral apex distinctly, strongly acuminate, apices projecting downward on female; southern Mexico and Guatemala (see Confertus group). . . . *subsimilis* Schedl

— Elytral apex moderately acuminate, apices not projecting downward on female; southern Mexico (see Confertus group) . . . . *subimpressus* Bright

NEW SPECIES AND NEW RECORDS OF NORTH AMERICAN *PITYOPHTHORUS* (COLEOPTERA: SCOLYTIDAE), PART V: THE JUGLANDIS GROUP

Donald E. Bright[1]

ABSTRACT.— Five new species of Mexican *Pityophthorus* in the Juglandis group are described: *P. ablusus* (Hidalgo), *P. costifera* (Guerrero), *P. cracentis* (Morelos), *P. desultorius* (Puebla), and *P. insuetus* (Morelos). New locality or host records are given for *P. costabilis* Wood, *P. costatulus* Wood, and *P. diligens* Wood. Previously published keys are modified to accommodate these species.

This is the second contribution describing the unnamed species of *Pityophthorus* collected by Dr. T. H. Atkinson and his colleagues (Centro de Entomologia y Acarologia, Colegio de Postgraduados, Chapingo, Mexico). As in the previous paper (Great Basin Nat. 45:467–475), all the species in a species group are described together, and the key in my 1981 monograph (Mem. Ent. Soc. Canada 118:72) is modified to accommodate the newly named taxa.

I wish to thank Dr. T. H. Atkinson for sending the specimens to me and also thank him and his students for their diligence in searching for Scolytidae in previously unrecognized host plants. I also thank my colleagues Dr. Y. Bousquet and Dr. J. M. Campbell for reviewing the manuscript of this paper.

Pityophthorus ablusus, n. sp.

Length 1.4–1.7 mm, 3.2 times longer than wide.

FEMALE.— Frons convex, slightly to almost indeterminably flattened in median area extending to or above upper eye level; surface moderately shining with numerous, shallow, indefinite punctures and short, fine, scattered setae; epistoma with a very weak, blunt, median callus, this sometimes extended into a weakly elevated, longitudinal carina extending across flattened area. Antennal club oval, 1.5 times longer than wide, widest through segment 2; sutures 1 and 2 transverse, 1 heavily septate for almost entire length, 2 septate at lateral margins only; segments 1 and 2 together occupy two-thirds of total club length. Pronotum 1.1 times longer than wide, widest at middle; sides parallel behind middle, slightly constricted and broadly rounded before middle; asperities on anterior slope arranged into three distinct concentric rows and 1 additional short, slightly irregular row around summit, asperities in each row distinct; summit distinctly elevated; posterior area weakly impressed behind summit, with large, distinct, moderately deep punctures, these separated by a distance nearly equal to diameter of puncture; surface between punctures moderately shining, marked with numerous fine lines and surface irregularities; median line not evident. Elytra almost 2.0 times longer than wide; apex narrowly rounded; discal striae punctured in regular rows, punctures large, moderately impressed, about equal in size and depth to those on posterior portion of pronotum; interstriae about 2.0 times wider than striae, surface impunctate, smooth, shining. Declivity sloping, weakly bisulcate; interstriae 1 moderately elevated, equal in height or slightly lower than 3, devoid of granules, with a few very fine punctures and setae; interstriae 2 weakly impressed, flat, broader than discal width, surface moderately shining with numerous fine lines and points; interstriae 3 weakly elevated, devoid of granules; punctures in striae 1 distinct but only very weakly impressed, those in 2 almost obsolete, much smaller than those on disc; interstriae 3, 5, 7 with a median row of several short setae.

MALE.— Frons moderately deeply, transversely concave on each side of median line; surface with slightly larger and deeper punc-

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tures than on female, setae sparser. Pronotum as in female except punctures on posterior portion more distinct. Elytra and declivity similar to that of female.

TYPE MATERIAL.— The holotype (♀) is labeled: "Pachuca, Edo. Hgo., 21-V-82, S-461, 2400 m, Col. T. H. Atkinson"/"Zexmenia sp."/ "HOLOTYPE Pityophthorus ablusus Bright, CNC No. 18434." The allotype and 14 paratypes bear the same labels plus appropriate type labels; 7 additional paratypes bear the same data except that the collector is A. Equihua M.

The holotype, allotype, and 6 paratypes are in the Canadian National Collection, Ottawa (CNC), 2 paratypes were sent to S. L. Wood, Brigham Young University, Provo, Utah, and the remaining paratypes were returned to T. H. Atkinson.

COMMENTS.— Adults of this species are distinguished from those of *P. franseriae* Wood by the absence of granules in declivital interstriae 1 and 3, by the very weakly flattened female frons, by the male frons, which is concave on each side of a weakly elevated median line, and by the distributions.

Pityophthorus costifera, n. sp.

Length 1.2–1.4 mm, 2.4 times longer than wide.

FEMALE.— Frons evenly, weakly convex; surface smooth, with small, shallow, evenly spaced punctures, these separated by distances equal to their diameters; pubescence sparse, nearly absent. Antennal club about 1.2 times longer than wide, widest through segment 2; sutures 1 and 2 transverse, straight, 1 distinctly septate, 2 septate only at lateral margins; segments 1 and 2 together occupy more than half of total club length. Pronotum as long as wide, widest at level of summit; anterior margin broadly rounded with a subserrate elevated costa; anterior slope bearing four elevated, evenly concentric, subserrate costae, these not divided into individual asperities, with one or two indistinct costae around summit; summit weakly elevated, distinct; posterior portion of disc distinctly, evenly punctured, punctures shallow, of moderate size, separated by distances about equal to their diameters; surface between punctures moderately shining, with numerous minute points; median line broad, impunctate, not elevated. Elytra 1.5 times longer than wide; apex broadly rounded; discal striae punctured in regular rows, punctures small, shallowly impressed; discal interstriae about 2.0 times wider than striae, surface moderately shining, densely micropunctate. Declivity very weakly impressed; interstriae 1 narrowly, weakly elevated, weakly impressed below elytral surface, with a median row of about four extremely small granules, each with a short, fine, erect seta at base; interstriae 2 very weakly flattened, essentially as on disc; interstriae 3 very weakly elevated, devoid of granules, with median row of short, fine erect setae; punctures in striae 1 and 2 obsolete, striae 1 narrowly impressed.

MALE.— Very similar to female except frons less strongly convex, very weakly impressed above epistoma, with a low subtuberculate elevation at midpoint on epistoma, declivital setae very slightly stouter, declivital interstriae 3 with a median row of very fine granules, and striae 1 and 2 more conspicuously punctured on declivity.

TYPE MATERIAL.— The holotype (♀) is labeled: "Taxco, Guerrero, 22.II.82, S326, 1900 msnm, col. Atkinson y Equihua"/ "Apocynaceae"/ ♀ /"HOLOTYPE Pityophthorus costifera, D. E. Bright, 1985, CNC No. 18420." The allotype and six paratypes bear the same data plus appropriate type labels. One specimen, thought to be this species but not designated as a paratype, is labeled: "Chilapa, Guerrero, 23.II.83, S-344, 1640 msnm, col. Atkinson y Equihua." Eight additional paratypes are labeled: "Cuautla, Morelos, 1 Oct-82, 1230 m, SM-119, E. Saucedo—A. Burgos"/"(Apocynaceae) *Thevetia peruviana*" and a paratype label.

The holotype, allotype, and 6 paratypes are in the CNC, 6 paratypes were returned to T. H. Atkinson, and 2 paratypes were sent to S. L. Wood.

COMMENTS.— This species is closely related to *P. costatulus* Wood but differs by its larger size, by the very different female frons as indicated below, and by the very weakly impressed elytral declivity.

Pityophthorus cracentis, n. sp.

Length 1.1–1.2 mm, 3.3 times longer than wide.

FEMALE.— Frons flattened on a small area extending from epistomal margin to well above eyes, flattened area laterally occupying about 60% of distance between eyes; surface of flattened area densely, minutely punctured, with moderately long, erect, yellowish setae, these longer on upper portion, becoming progressively shorter toward epistoma; surface above and lateral to flattened area smooth, shining, glabrous, with a few widely separated, small punctures. Antennal club small, about 1.2 times longer than wide, widest through segment 2; sutures 1 and 2 transverse, lightly septate at lateral margins, 1 more strongly septate than 2; segments 1 and 2 together occupy about two-thirds of total club length. Pronotum less than 1.1 times longer than wide, widest at middle; sides very slightly converging behind middle, broadly rounded before middle; asperities on anterior slope arranged into four definite, regular, concentric rows, fourth row small, placed around summit, asperities in each row distinct; summit weakly elevated; posterior area with widely separated, small, very shallow punctures; surface between punctures smooth, shining to very finely reticulate; median line evident as a narrow, weakly elevated line extending from summit to posterior margin. Elytra about 1.5 times longer than wide; apex broadly rounded; discal striae punctured in regular rows, punctures large, distinctly but shallowly impressed, these much larger, deeper than those on posterior portion of pronotum, each puncture with an extremely short seta equal to or slightly longer than diameter of puncture; discal interstriae shining, about 1.5 times wider than striae, surface impunctate, marked with extremely fine lines. Declivity steep, weakly bisulcate; interstriae 1 weakly elevated, slightly impressed below level of 3 on upper half, each interstriae with 1 small, acute granule near apex; interstriae 2 weakly bisulcate, shining, glabrous; interstriae 3 slightly elevated above 1, with a median row of 3 small but distinct, acute granules, middle granule larger than other two; remaining interstriae unmodified with a few, long, erect setae.

TYPE MATERIAL.— The holotype (♀) is labeled: "Carr. Xochicalco—Cuentepec, Km. 6, Temixco, Mor., 14-Julio-84, 1220 m, SM-347, E. Saucedo—E. Martinez"/"Compositae"/"HOLOTYPE Pityophthorus cracentis D. E. Bright, 1985, CNC No. 18430." Four female paratypes bear the same labels plus appropriate paratype labels.

The holotype and 1 paratype are in the CNC, the remaining 3 paratypes have been returned to T. H. Atkinson.

COMMENTS.— This species seems to be unique among the *Pityophthorus* known to me. Adults differ from the other species in the Juglandis group by the distinctly but slightly impressed elytral declivity. It cannot be placed in the Scriptor group since the elytral apex is not acuminate, and it doesn't fit at all in the other species groups with concentric rows of pronotal asperities. However, to avoid creating monotypic species groups unless absolutely necessary, I have broadened the concept of the Juglandis group to include this species.

Pityophthorus desultorius, n. sp.

Length 1.2–1.4 mm, 2.8 times longer than wide.

FEMALE.— Frons flattened on a small area extending from epistomal margin to upper level of eyes, with a weakly elevated, impunctate, longitudinal carina extending from epistoma to upper margin of flattened area, flattened area laterally occupying about 60% of the distance between eyes; surface on each side of carina shining, with distinct small, shallowly impressed punctures and with short, scattered, inconspicuous setae. Antennal club circular, as long as wide, widest through segment 2; sutures 1 and 2 transverse, straight, septate at lateral margins; segments 1 and 2 together occupy about two-thirds of total club length. Pronotum 1.1 times longer than wide, widest at level between summit and posterior margin; asperities arranged into three or four irregular rows, these especially irregular on median portion, rows more regular on lateral areas; summit weakly elevated; posterior portion of disc moderately shining, with large, deep punctures, these separated by distances much less than their own diameters; surface between punctures with extremely fine lines and points; median line flat, broad, impunctate. Elytra 1.2 times longer than wide; apex broadly rounded; discal striae punctured in distinct, regular rows, punctures about same size and depth as those on posterior portion of pronotum, each puncture bearing a very short seta equal to or slightly longer than diameter of puncture; discal interstriae moderately shining, equal in width or slightly narrower than striae, surface impunctate, moderately shining with very fine points and lines. Declivity steep, almost evenly convex, very weakly bisulcate; interstriae 1 weakly elevated, devoid of granules; interstriae 2 very weakly impressed, moderately shining; interstriae 3 convex, not elevated, equal in height to 1, devoid of granules; punctures in striae 1 and 2 not visible; interstriae 1, 3, 5, 7, each with a median row of narrowly spatulate setae.

Male.— Almost identical to female, differs by frons more distinctly convex, setae shorter and sparser.

Type material.— The holotype (♀) is labeled: "Oriental, Pue., 4.V.81, 2370 m, col. T. H. Atkinson, A. Equihua, S-213"/"Hosp.: Compositae"/"HOLOTYPE Pityophthorus desultorius, D. E. Bright, 1985, CNC No. 18421." The allotype and 10 paratypes bear the same labels plus appropriate type labels.

The holotype, allotype, and 4 paratypes are in the CNC, four paratypes were returned to T. H. Atkinson, and 2 paratypes were sent to S. L. Wood.

Comments.— Adults of this species are similar to those of *P. insuetus* (described below) but differ by the larger, deeper punctures on the posterior portion of the pronotum, by the steeper, more convex elytral declivity, and by the slightly smaller size.

Pityophthorus insuetus, n. sp.

Length 1.5–1.8 mm, 3.1 times longer than wide.

Female.— Frons convex, very weakly flattened, with a distinct, weakly elevated longitudinal carina extending from epistoma to above upper level of eyes; surface on each side of carina shining, with densely placed, weakly impressed punctures; pubescence sparse, erect, consisting of short, scattered, erect setae, these longer along epistomal margin. Antennal club oval, about 1.5 times longer than wide, widest through segments 1 and 2; sutures 1 and 2 transverse, 1 more distinctly septate; segments 1 and 2 together occupy more than half of total club length. Pronotum about 1.1 times longer than wide, widest slightly behind level of summit; asperities arranged into four irregular concentric rows, these especially irregular in median portion of first two rows, these first two rows more even laterally, rows around summit more even, regular; summit weakly elevated; posterior portion of disc shining, punctures moderate, deep, very close, these separated by less than diameter of puncture; surface between punctures with very finely impressed, minute points; median line weakly elevated, smooth, impunctate. Elytra 2.0 times longer than wide; apex narrowly rounded; discal striae punctured in distinct regular rows, punctures distinctly, moderately impressed, each with a seta slightly longer than diameter of puncture, punctures slightly smaller than those on posterior portion of pronotum; discal interstriae smooth, equal in width or slightly narrower than striae, impunctate. Declivity convex, weakly bisulcate; interstriae 1 weakly elevated, weakly impressed below level of interstriae 3, devoid of granules; interstriae 2 very weakly impressed, flattened, shining, equal in width to discal width; interstriae 3 very weakly elevated above interstriae 1 and 2, devoid of granules; punctures in striae 1 and 2 moderately distinct, much smaller than those on disc, striae 1 narrowly impressed; interstriae 1, 3, 5, 7 each with median row of sparse, erect setae.

Male.— Very similar to female except frons more deeply, densely punctured, median carina slightly more strongly elevated, declivity slightly more deeply bisulcate, setae on posterior portion of elytral interstriae narrowly flattened or narrowly spatulate.

Type material.— The holotype (♀) bears the labels: "Huitzilac, MOR., 25-IX-81, 2700 m, S252, Col. Atkinson—Equihua"/"Hosp.: Compositae"/"HOLOTYPE Pityophthorus insuetus D. E. Bright 1985, CNC No. 18422." The allotype and 15 paratypes bear the same data plus appropriate type labels.

The holotype, allotype, and 6 paratypes are in the CNC. 7 paratypes were returned to T. H. Atkinson, and 2 paratypes were sent to S. L. Wood.

Comments.— This species does not appear to be very closely related to any species in the

Juglandis group but is similar to *P. desultorius*. It will key out in my 1981 key to *P. detentus* Wood but differs by the sparsely pubescent female frons (densely pubescent in *P. detentus*), by the more deeply impressed elytral declivity, by the more distinct strial punctures in striae 1 and 2 on the declivity, and by the irregular concentric rows of asperities on the pronotum (very evenly concentric in *P. detentus*). Adults differ from those of *P. desultorius* by the characters mentioned below.

REVISED KEY TO SPECIES IN THE JUGLANDIS GROUP

1\. Anterior slope of pronotum bearing 4 or more concentric, continuous costae, the summit of each costa subserrate, individual asperities not detectable; female frons flattened to weakly concave, pubescence short; male frons convex, distinctly punctured, devoid of carina; posterior portion of pronotum with numerous impressed points on surface between punctures 2

— Anterior slope of pronotum with asperities arranged in several concentric rows, each row strongly serrate, divided to or near their bases, individual asperities usually detectable; female and male frons variable but not as above; surface between punctures on posterior portion of pronotum smooth and shining or reticulate 4

2(1). Sutures of antennal club straight to moderately procurved; declivital striae 1 and 2 finely punctured in both sexes; interstriae 2 weakly impressed on declivity in female; male frons subglabrous 3

— Sutures of antennal club strongly procurved; declivital striae 1 and 2 rather coarsely punctured in female, interstriae 2 more strongly impressed on declivity in female; male frons pubescent near epistoma; body length 1.6–1.8 mm; Jalisco, Guerrero . . . . *costabilis* Wood

3(2). Female frons flattened with moderately abundant, long, erect, equal length setae evenly scattered over surface; declivity not impressed, declivital interstriae 1 and 3 with median row of fine granules in both sexes; body length 0.9–1.2 mm; Jalisco, Oaxaca . . . . *costatulus* Wood

— Female frons convex, setae absent or very sparse, inconspicuous; declivity very weakly impressed, declivital interstriae 3 devoid of granules in female, granules distinct but very small in declivital interstriae 1 and 3 in male; body length 1.2–1.4 mm; Guerrero, Morelos . . . . *costifera* Bright

4(1). All declivital interstriae (except 2 and rarely 6) with a median row of short setae 5

— Declivital interstriae 1, 3, 5, 7 with a median row of short setae 8

5(4). Pronotum evenly arched from base to anterior margin, pronotal summit not elevated and transverse impression not present; pronotal asperities arranged in up to 8 broken concentric rows; interstriae 1 on declivity impressed below level of interstriae 3; Guatemala . . . . *tenax* Wood

— Pronotum with a definitely elevated (sometimes weak) pronotal summit and with a transverse impression behind summit; pronotal asperities arranged in 3–5 even, concentric rows; declivity variable 6

6(5). Declivital interstriae 3 with small but distinct granules; declivital setae scalelike in male, hairlike in female; Costa Rica . . . . *galerius* Wood

— Declivital interstriae 3 devoid of granules; if present, granules extremely minute; declivital setae hairlike in both sexes 7

7(6). Antennal club elongate-oval, more than 1.4 times longer than wide; female frons flattened on a very large semicircular area extending far above upper level of eyes, pubescence dense and long on periphery, sparser in central area, male frons flattened on a smaller area, pubescent but pubescence much less dense than on female; Mexico. . . . . *bursera*e Wood

— Antennal club oval, 1.4 times or less longer than wide; female frons convex, pubescence short, male frons weakly, transversely impressed, punctured, Costa Rica. . . . . *strictus* Wood

8(4). Declivital interstriae 3 higher than 1. 9

— Declivital interstriae 3 equal in height to 1 or lower 11

9(8). Interstriae 1 on elytral declivity distinctly impressed below level of interstriae 3, with one, small, acute granule near apex; interstriae 3 distinctly elevated, with three larger, acute granules; female frons flattened, pubescent on small median area; body very slender, about 3.3 times longer than wide; Morelos. *cracentis* Bright

— Interstriae 1 on elytral declivity only very slightly impressed below level of interstriae 3, with or without a median row of numerous small granules; interstriae 3 weakly elevated, with or without a median row of numerous small granules; body stouter, 3.0 or less times longer than wide 10

10(9). Pronotal asperities arranged into three concentric rows (vague 4th row infrequently seen); declivital interstriae 3 devoid of granules in both sexes or granules extremely fine; female frons pubescent over entire surface, setae short, of equal length; declivity steep, interstriae 3 only slightly higher than 1; Mexico. . . . . *diligens* Wood

— Pronotal asperities arranged in four or more definite concentric rows; declivital interstriae 3 of male with distinct granules, female devoid of granules; female frons densely pubescent only on lower portion below upper level of eyes, setae long, dense, extending at least to midpoint of mandibles; declivity sloping, interstriae 3 slightly but definitely higher than 1; Mexico. . . . . *nanus* Wood

11(8). Antennal club with only one suture septate; declivity evenly convex; male frons strongly convex, surface dull, minutely reticulate, impunctate; Mexico . . . . *indigens* Wood

— Antennal club with two sutures septate; declivity evenly convex to weakly impressed; male frons weakly convex, transversely impressed or broadly flattened, surface punctured 12

12(11). Declivital interstriae 2 weakly impressed, below level of 3. 13

— Declivital interstriae 2 not impressed, equal in height to 3. 14

13(12). Declivital interstriae 1 and 3 devoid of granules; declivity sloping; female frons very weakly flattened, male frons concave on each side of weakly elevated median line; Hidalgo. . . . . *ablusus* Bright

— Declivital interstriae 1 and 3 with a median row of fine granules; declivity more steeply convex; female frons distinctly flattened, male frons transversely impressed, with transverse carina at upper level of eyes; New Mexico . . . . *franseriae* Wood

14(12). Elytral declivity strongly, evenly convex, punctures in striae 1 and 2 distinct; serrations on anterior margin of pronotum located in median area only; pronotal asperities in broken concentric rows; female frons flattened to well above eyes, setae on upper margin very long, masking surface; Mexico . . . . *pudicus* Blackman

— Elytral declivity less strongly convex to flattened, punctures in striae 1 and 2 indistinct to obsolete; serrations on anterior margin of pronotum more generally located, extending to lateral margin; pronotal asperities in even to slightly broken concentric rows; female frons variable but not as above 15

15(14). Body length 1.7–2.0 mm; declivital interstriae 1 and 3 each with a row of small granules in male; concentric rows of pronotal asperities usually somewhat irregular; southwestern United States . . . . *juglandis* Blackman

— Body length 1.2–1.8 mm; declivital interstriae 1 and 3 devoid of granules in both sexes; pronotal asperities arranged in regular to irregular concentric rows; Mexico 16

16(15). Pronotal asperities in regular, even rows; punctures in striae 1 and 2 obsolete on declivity; declivity evenly convex; female frons flattened, with long setae . . . . *detentus* Wood

— Pronotal asperities irregular in median portion, more even laterally; punctures in striae 1 and 2 visible, smaller than those on disc; declivity weakly bisulcate to almost evenly convex; female frons convex, with short, sparse setae 17

17(16). Declivity sloping, weakly bisulcate, more deeply impressed in male; punctures on posterior portion of pronotal disc moderate in size, deeply impressed; body length 1.5–1.8 mm . . . . *insuetus* Bright

— Declivity steeper, almost evenly convex in both sexes; punctures on posterior portion of pronotal disc larger, more deeply impressed; body length 1.2–1.4 mm . . . . *desultorius* Bright

NEW RECORDS

Pityophthorus costabilis Wood

Pityophthorus costabilis Wood, 1976, Great Basin Nat. 36:352; Bright, 1981. Mem. Ent. Soc. Canada 188, p. 74; Wood, 1982, Great Basin Nat. Mem. 6:1121.

This species was previously known from eight specimens from Jalisco. A series of 19 specimens that are probably this species were seen with the labels: "Chilapa, Guerrero, 23.II.82, S-344, 1640 msnm, Col. Atkinson y Equihua."

When this species was named, the frons of the females was undescribed because it was largely concealed on the available specimens. The discovery of additional specimens enable the following comments to be made.

The female frons is broadly flattened, weakly plano-concave on a large area extending well above eyes, with very dense, minute punctures and dense, erect, moderately long setae that are shorter in the center and longer and incurved on the periphery. The size of specimens is given in the original description as 1.6–1.8 mm. The additional specimens at hand range in size from 1.4 to 1.8 mm.

Pityophthorus costatulus Wood

Pityophthorus costatulus Wood, 1976, Great Basin Nat. 26, p. 351; Bright, 1981, Mem. Ent. Soc. Canada 118:73; Wood, 1982, Great Basin Nat. Mem. 6:1120.

This species was previously known from Jalisco and Oaxaca from *Thevetia* sp. A series of seven specimens bearing the labels: "Chilapa, Guerrero, 23.II.82, S-344, 1640 msnm, col. Atkinson y Equihua" and a series of seven specimens labeled: "Cuauhtenango, GRO., 23.II.82, S-344, Atkinson-Equihua" were seen.

Pityophthorus diligens Wood

Pityophthorus diligens Wood, 1976, Great Basin Nat. 36:363; Bright, 1981, Mem. Ent. Soc. Canada 188:77; Wood, 1982, Great Basin Nat. Mem. 6:1132.

This species was previously known only from Hidalgo from a desert shrub with bluish leaves. Mixed in a series of 25 specimens of *P. ablusus* was one specimen that is probably this species. It bears the labels: "Pachuca, Edo. de Hidalgo, S-461, 21.V.82, 2400 m, col. A. Equihua M"/"*Zexmenia* sp. (Compositae)."

SECOND NESTING RECORD AND NORTHWARD ADVANCE OF THE GREAT-TAILED GRACKLE (*QUISCALUS MEXICANUS*) IN NEVADA

Jennifer A. Holmes[1], David S. Dobkin[1,2], and Bruce A. Wilcox[1]

ABSTRACT.— The second nesting record for the Great-tailed Grackle (*Quiscalus mexicanus*) in Nevada is reported from the central part of the state approximately 240 km north of the previous record. Since 1912 this species has undergone a dramatic northward extension of its previous range in the United States, presumably as a result of increased agricultural irrigation in areas that were previously desert or short-grass prairie.

Range expansion of the Great-tailed Grackle (*Quiscalus mexicanus*) into Nevada is of relatively recent occurrence. Linsdale's surveys of the Nevada avifauna made no mention of the species (Linsdale 1936, 1951). The first published record for Nevada is from April 1973 in southeast Nevada near Las Vegas, Clark Co. (Oberholser and Kincaid 1974). Since then the species has been recorded from several localities in Clark, Lincoln, and Nye counties in the southeastern part of the state (Kingery 1980, 1984) and due north of there in the Ruby Valley area, Elko Co. (Kingery 1978, 1981, 1982, 1984). The first record outside these two areas was recently reported for central Nevada between Tonopah and Austin, Nye Co., during the summer of 1983 (Kingery 1984). Despite this plentitude of observations, there is only one record of nesting by this species in Nevada: a single active nest found in 1980 at Beatty, Nye Co., in southern Nevada (Kingery 1980). In this report we document the second Nevada nesting record for this species approximately 240 km north of the previous nesting record for the state.

During the first week of June 1983, a female Great-tailed Grackle was seen carrying nest material to a small stand of narrowleaf cottonwoods (*Populus angustifolia*) surrounding a shallow pond at Carver's ranch in Carvers, Nye Co., elevation 1715 m. This locality is in Big Smokey Valley approximately midway between Tonopah and Austin and is probably the basis for the observation record reported by Kingery (1984). In mid-July we observed an adult male, adult female, and a fledgling in the same stand of trees. The area used by the birds is typical of nesting areas for this species: close to water, human habitations, and agricultural land (Skutch 1958). Between 22 May and 15 July 1984, we observed adult male and female grackles at this same location, although we did not ascertain whether they nested there. Our observations were made incidental to a broad ecological analysis of riparian avifaunas of the Toiyabe Range (Dobkin and Wilcox, in press); we have never seen more than a single adult of each sex at the Carver's location at any time.

Prior to 1912 the Great-tailed Grackle ranged only as far north as southern Texas, New Mexico, and Arizona (Oberholser and Kincaid 1974). In recent years this species has expanded its range northward into Colorado (Stepney 1975), Nebraska (Faanes and Norling 1981), Utah (White et al. 1983), California (Small 1974), and Oregon (Littlefield 1983), as well as Nevada. We agree with Littlefield's assessment that the increased introduction of mechanized sprinkler irrigation systems into newly created agricultural areas within former deserts is the most likely factor enabling the Great-tailed Grackle to expand its range northwestward from southern Arizona. The north/south axes of the isolated mountain ranges in the Great Basin provide valley corridors with scattered agricultural "oases" containing suitable nesting habitat for this species. In the coming decade we should expect

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to see increased nesting by Great-tailed Grackles in the area extending from southern Nevada northward to southeastern Oregon.

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NEW SPECIES OF *TALINUM* (PORTULACEAE) FROM UTAH

N. Duane Atwood[1] and Stanley L. Welsh[2]

Abstract.— Named and described is *Talinum thompsonii* Atwood & Welsh. The species is evidently most closely allied to *T. validulum* Greene from northern Arizona. The new species is known from the Cedar Mountain region of Emery County, Utah.

In the late summer of 1970 the authors, accompanied by Dr. Glen Moore, visited the summit of Cedar Mountain in Emery County, Utah. The mountain summit is protected from excessive erosion by the Buckhorn Conglomerate Formation of Jurassic age. Rounded siliceous pebbles mark the surface, which is clothed by a pinyon-juniper woodland, interspersed here and there with ponderosa pine. Crevices in the conglomerate provide habitats where water accumulates from the impervious surface. The crevices are vegetated by those plants capable of survival through long drought periods, and it is there that we discovered a species of *Talinum*. The plants consisted of fleshy-leaved rosettes 2–4 cm broad, projecting only a few centimeters above the surface. Bright pink flowers were helpful in the discovery. The season was very dry, and few plants were found. Subsequent collections demonstrated that larger material was not exceptional when moisture was more abundant. The plants flower very late in the season, when most taxonomists have returned to other pursuits. This accounts, in part, for the long interval between initial discovery and this publication.

Attempts at identification were thwarted by lack of similar material in Utah and Arizona herbaria and by the real lack of information in contemporary keys to the Portulacaceae. Tentatively we settled on an identification as *T. validulum* Greene? Ultimate disposition of the plants as a new taxon awaited location of the type of that species at US. The type was taken in the Tusayan (now Kaibab) Forest Reserve, Coconino Co., Arizona, at 2013 m, 11 August 1912 by R. R. Hill. The type was borrowed, through the kindness of the curator at the Smithsonian Institution, and compared with our material. The plants are strikingly similar but differ in stamen number, leaves that average longer, and larger flowers. The type specimens of *T. validulum* consist of three specimens and a slide containing a mounted, dissected flower. A note on the sheet indicates that there are 12 stamens, not 10, as in our specimens. The Cedar Mountain talinum is described as follows:

Talinum thompsonii Atwood & Welsh, sp. nov.

Planta similis *T. validulo* Greene in radices, caudices, et staturas sed in folius et floribus majoribus et staminibus (10 nec 12) differt.

Type.— USA: Utah: Emery Co., Cedar Mountain, east of Castle Dale, T19S, R12E, S18, pinyon-juniper-ponderosa pine community, on conglomeritic rock, at 2288 m elev., 19 July 1981, N. D. Atwood & R. Thompson 8056 (Holotype BRY; isotypes NY, POM, US).

Perennial glabrous herbs from a fusiform or cylindric, reddish, tuberous root and a short perennating rootcrown bearing branches of the season; stems spreading, rosettelike, forming caespitose clumps to 10 cm wide; leaves 0.8–3.2 cm long, fleshy, cylindroid, to 3 mm wide when pressed, with auriculate, clasping base; flowers (1) 3–6 in cymes, ca 1 cm wide; petals pink; sepals 4.3–4.8 mm long, ovate, reticulately veined, greenish or brownish, with scarious margins, abruptly acuminate apically, tardily deciduous; stamens 10; capsules 6–6.5 mm long, 3.2–3.8 mm wide,

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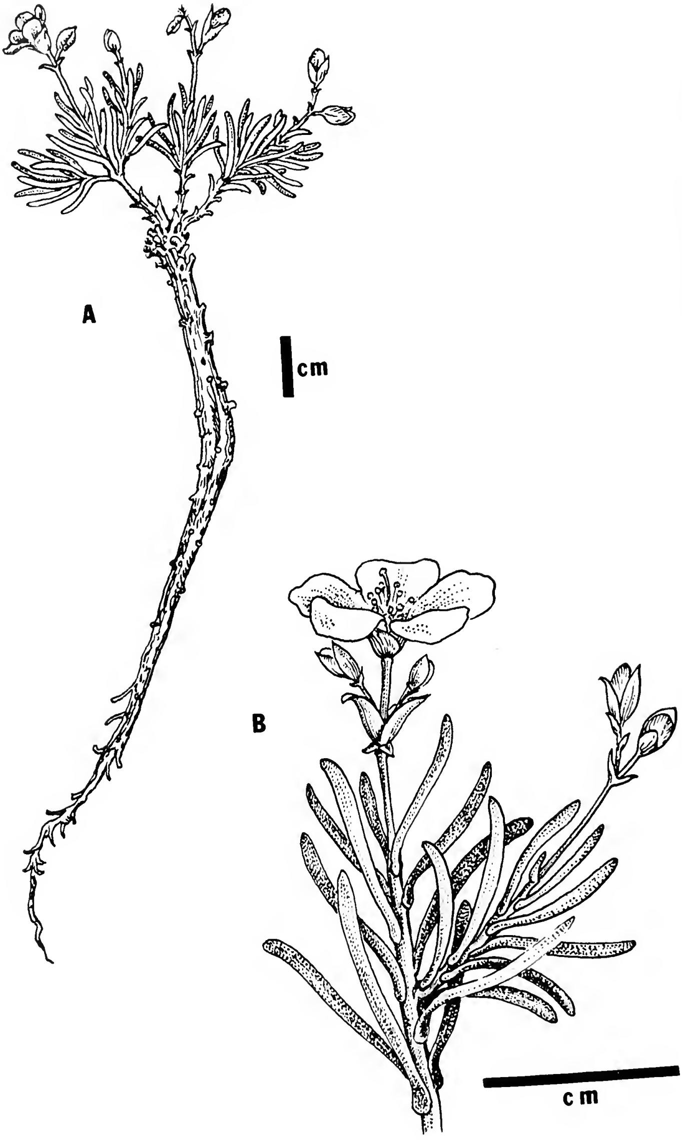

Fig. 1. *Talinum thompsonii* Atwood & Welsh. A, Habit. B, Detail of leaves and inflorescence.

keeled along the sutures apically; seeds grayish black, 1.2–1.3 mm long.

Additional collections.— Utah. Emery Co., summit of Cedar Mt., ca 50 km SSW of Price, T19S, R11E, S13, Pinyon-juniper woods on conglomerate, 31 August 1970, S. L. Welsh, N. D. Atwood, & G. Moore 10781 (BRY); Ca 35 km due SE of Huntington, T19S, R12E, S7, 2166 m, S. L. Welsh & S. Clark 16134, 16166 (BRY).

This low, clump-forming fleshy plant with beautiful pink flowers occurs on fused silicious conglomeratic gravel of the Buckhorn Conglomerate Formation. It occurs with another rarity, *Hymenoxys depressa* (T. & G.) Welsh & Reveal, which is known from other sites in Emery County. However, the physical features of the summit of Cedar Mountain are hardly matched by any other in the vicinity. The substrate is present over a large region, but it does not occur in the same context or at the same elevation in any other area. The extent of the formation on Cedar Mountain is relatively large, standing above the north rim of the San Rafael Swell proper. It is difficult to predict where the plant might be found elsewhere.

The plant is named for Robert (Bob) Thompson, long-time collector and botanical enthusiast, who works for the U.S. Forest Service in Price, Utah.

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TYPES OF NEVADA BUCKWHEATS (*ERIOGONUM*: POLYGONACEAE)

James L. Reveal[1]

ABSTRACT.— The types and type specimens of Nevada species and varieties of *Eriogonum* (Polygonaceae) are alphabetically listed. Appropriate lectotypes are selected as necessary.

The growing need for type information of Nevada plants for various projects, and especially that by A. Tiehm, makes necessary the publication of critical type data of *Eriogonum* (Polygonaceae), one of the state's largest genera. The format followed here is similar to that used by Welsh (1982). The entries are arranged alphabetically by basionym. A number of Gandoger names proposed for Nevada buckwheats in 1906 and reported by Heller 1907 have been shown to be invalid (Reveal 1980). Readers are referred to Reveal (1985) for a taxonomic treatment of the genus of the state.

Eriogonum anemophilum Greene, Pittonia 3:199. 1897. Pershing Co.: Windswept summits at the north end of the West Humboldt Mts., probably on Star Peak, Jul 1894, *Greene s.n.* Holotype, NDG! Isotype, NY!

Eriogonum angulosum Benth. var. *flabellatum* Gand., Bull. Soc. Roy. Bot. Belgique 42:187. 1906. Washoe Co.: near the Central Pacific Railroad entrance into the Virginia Mts., 16 Jun 1894, *Hillman s.n.* Holotype, LY! Isotype, NESH! = *E. maculatum* A. A. Heller.

Eriogonum angulosum Benth. var. *patens* Gand., Bull. Soc. Roy. Bot. Belgique 42:187. 1906. Washoe Co.: Wadsworth, 7 Aug 1899, *Hillman s.n.* Holotype, LY! Isotype, NESH [as 9 Jul 1899]! = *E. maculatum* A. A. Heller.

Eriogonum angulosum Benth. var. *pauciflorum* Gand., Bull. Soc. Roy. Bot. Belgique 42:187. 1906. Washoe Co.: Reno, 25 Jun 1895, *Hillman s.n.* Holotype, LY! Isotypes, DS! NESH! UC! = *E. maculatum* A. A. Heller.

Eriogonum argophyllum Reveal, Phytologia 23:168. 1972. Elko Co.: In sandy washes on crusty mineralized sand below Sulphur Hot Springs, 7 Jul 1969, *Holmgren & Kern 3661*. Holotype, US! Isotypes, ID! IDS! KANS! MIN! MSC! NY! OKL! RM! RSA! UBC! UC! UTC!

Eriogonum aridum Greene, Pittonia 3:200. 1897. Elko Co.: Holborn, 16 Jul 1896, *Greene s.n.* Lectotype selected here, NDG! Duplicate of the lectotype, NDG! = *E. umbellatum* Torr. var. *dichrocephalum* Gand.

Eriogonum azaleastrum Greene, Pittonia 5:67. 1906. Pershing Co.: Black Canyon, West Humboldt Mts., 29 Jul 1895, *Greene s.n.* Holotype, NDG! Isotype, NY! = *E. umbellatum* Torr. var. *aureum* (Gand.) Reveal.

Eriogonum baileyi S. Wats. var. *porphyreticum* Stokes ex Jones, Contr. W. Bot. 11:17. 1903. Eureka Co.: Palisades, 6 Aug 1881, *M. E. Jones s.n.* Lectotype, POM! Duplicate of the lectotype, DS! = *E. baileyi* S. Wats. var. *baileyi*.

Eriogonum beatleyae Reveal, Aliso 7:415. 1972. Nye Co.: About 0.9 mi N of U.S. Hwy. 6, 5.3 mi W of Salisbury Wash Rd., about 18 mi E of Tonopah, 26 Jun 1971, *Reveal et al. 2498*. Holotype, US! Isotypes, ARIZ! ASC! ASU! BRY! CAS! G! GH! K! MICH! MO! NY! OSC! OKL! RENO! RM! RSA! SD! SMU! TEX! UC! UTC! WTU!

Eriogonum bifurcatum Reveal, Aliso 7:357. 1971. Nye Co.: Pahrump Valley, 13 Jun 1970, *Reveal 2283*. Holotype, US! Isotypes, ARIZ! ASC! ASU! BRY! CAS! COLO! G! GH! K! KANU! KSC! MICH! MO! NCU! NTS! NY! OKL! OSC! P! RM! RSA! SD! SMU! UC! UTC! WIS! WT! WTU!

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Eriogonum cernuum Nutt. var. *multipedunculatum* S. Stokes, Leafl. W. Bot. 2:48. 1937. Lander Co.: 40 mi W of Austin, 25 Aug 1931, *J. T. Howell 7988*. Holotype, CAS! Isotypes, GH! NY! US! = *E. watsonii* Torr. & Gray.

Eriogonum cernuum Nutt. var. *purpurascens* Torr. & Gray, Rept. Explor. Surv. Ascert. Pract. Econ. Route Railroad Miss. River to Pacific Ocean 2:124. 1855. Washoe Co.: Mud Lake Valley, 16 Jun 1854, *Snyder s.n.* Holotype, NY! Isotypes, GH! MO! = *E. nutans* Torr. & Gray var. *nutans*.

Eriogonum cernuum Nutt. var. *tenue* Torr. & Gray, Proc. Amer. Acad. Arts 8:182. 1870. Elko Co.: East Humboldt [now Ruby] Mts., 1869, *Watson 1036*. Lectotype selected here, GH! Duplicates of the lectotype, K! PH! = *E. cernuum* Nutt. var. *cernuum*.

Eriogonum cernuum Nutt. subsp. *viminale* S. Stokes, Gen. Eriog. 41. 1936. Elko Co.: 44 mi SW of Wendover, 24 Aug 1931, *J. T. Howell 7952*. Holotype, CAS! Isotype, GH! = *E. cernuum* Nutt. var. *viminale* (S. Stokes) Reveal in Munz.

Eriogonum chrysocephalum A. Gray subsp. *desertorum* Maguire, Leafl. W. Bot. 3:11. 1941. Elko Co.: Foothills of dry gravelly lake bar, 8 mi W of Wendover, 5 Jun 1939, *Holmgren & Lund 163*. Holotype, UTC! Isotypes, NY! OKL! UC! US! = *E. desertorum* (Maguire) R. J. Davis.

Eriogonum collinum Stokes ex Jones, Contr. W. Bot. 11:15. 1903. Washoe Co.: Reno, 19 Jun 1900, *Stokes s.n.* Lectotype, UC!, vide Madroño 18:169. 1966. Duplicates of the lectotype, DS! MIN [as 20 Jun 1900]! NY! SD! US!

Eriogonum commixtum Greene ex Tidestrom, Proc. Biol. Soc. Wash. 36:181. 1923. Carson City Co.: Eagle Valley, 31 Jul 1902, *Baker 1402*. Holotype, US! Isotypes, B! GH! MO! MSC! NY! POM! UC! = *E. baileyi* S. Wats. var. *praebens* (Gand.) Reveal

Eriogonum comosum (M. E. Jones) M. E. Jones var. *playanum* M. E. Jones, Contr. W. Bot. 11:16. 1903. Clark Co., Mica Springs, 14 Apr 1894, *M. E. Jones 5064bc*. Lectotype selected here, POM! = *E. pusillum* Torr. & Gray.

Eriogonum concinnum Reveal, Bull. Torrey Bot. Club 96:476. 1969. Nye Co.: Buckboard Mesa Rd., near Cat Canyon and Timber Mtn., 5 Jul 1968, *Reveal 1501*. Holotype, UTC! Isotypes, ARIZ! BRY! CAS! CS! DS! GH! IDS! ISC! KSC! MIN! MO! MSC! NTS! NY! OKLA! RENO! RM! RSA! TEX! UC! UT! UTC! WIS! WTU!

Eriogonum cusickii Gand. var. *californicum* Gand., Bull. Soc. Roy. Bot. Belgique 42:193. 1906. Elko Co.: Little Lakes Canyon, near Stampede, 1 Jul 1902, *Kennedy 543*. Holotype, LY, not found at LY. Isotypes, NESH! RM! UC! = *E. strictum* Benth. subsp. *proliferum* (Torr. & Gray) S. Stokes var. *proliferum* (Torr. & Gray) Reveal.

Eriogonum deflexum Torr. in Sitgr. var. *nevadense* Reveal, Phytologia 25:206. 1973. Nye Co.: Near Lunar Crater, 18 Jul 1972, *Reveal & Reveal 2785*. Holotype, US! Isotypes, ARIZ! ASC! ASU! BRY! CAS! COLO! G! GH! ISC! K! MO! NY! OKL! OSC! P! RENO! RM! RSA! SD! SMU! TEX! UC! UTC! WIS! WT! WTU!

Eriogonum elatum Dougl. ex Benth. var. *erianthum* Gand., Bull. Soc. Roy. Bot. Belgique 42:188. 1906. Elko Co.: Little Lakes Canyon near Stampede, 14 Jul 1902, *Kennedy 563*. Holotype, LY! Isotypes, NESH! RM! UC! = *E. elatum* Dougl. ex Benth. var. *elatum*.

Eriogonum esmeraldense S. Wats., Proc. Amer. Acad. Arts 24:85. 1889. Esmeralda Co.: Miller Mtn., Jul 1888, *Shockley 581*. Lectotype selected here, GH! Duplicates of the lectotype, DS! JEPS! K! POM [as *381*]! UC!

Eriogonum esmeraldense S. Wats. var. *toiyabense* J. T. Howell, Leafl. W. Bot. 6:178. 1952. Lander Co.: Majogany Canyon, Toiyabe Mts., *Linsdale & Linsdale 550*. Holotype, CAS!

Eriogonum exaltatum M. E. Jones, Contr. W. Bot. 15:61. 1929. Clark Co.: Riverside, 2 Jul 1927, *M. E. Jones s.n.* Holotype, POM! Isotypes, GH! NDG! US! = *E. insigne* S. Wats.

Eriogonum eximium Tidestrom, Proc. Biol. Soc. Wash. 36:181. 1923. Washoe Co.: near Franktown, 16 Aug 1912, *Heller 10649*. Holotype, US! Isotypes, CAS! CI! DS! DUKE! E! F! G! GH! LA! MO! NESH! POM! = *E. ovalifolium* Nutt. var. *eximium* (Tidestrom) J. T. Howell.

Eriogonum gracile Benth. var. *effusum* Torr. & Gray, Proc. Amer. Acad. Arts 8:178.

1870. Carson City Co.: Near Empire City, 1865, *Torrey 439*. Lectotype selected here, GH! Duplicate of the lectotype, NY! = *E. baileyi* S. Wats. var. *baileyi*.

Eriogonum heermannii Dur. & Hilg. var. *clokeyi* Reveal, Phytologia 34:437. 1976. Clark Co.: Lee Canyon, Spring Mts., 10 Aug 1966, *Holmgren & Reveal 2990*. Holotype, US! Isotypes, ARIZ! BRY! CAS! CS! DAO! DS! IDS! ISC! KSC! MIN! MO! MSC! NY! OKL! OSC! RM! RSA! UC! US! UT! UTC!

Eriogonum heermannii Dur. & Hilg. subsp. *humilius* S. Stokes, Gen. Eriog. 90. 1936. Humboldt Co.: E of Golconda, Hot Springs Range, 22 Jul 1930, *Keck 937*. Holotype, CAS! Isotypes, DS! MO! RSA! UC! = *E. heermannii* Dur. & Hilg. var. *humilius* (S. Stokes) Reveal.

Eriogonum heracleoides Nutt. var. *virde* Gand., Bull. Soc. Roy. Bot. Belgique 42:190. 1906. Washoe Co.: Peavine foothills, 15 Jun 1894, *Hillman s.n.* Holotype, LY! Isotype, NESH! = *E. umbellatum* Torr. var. *nevadense* Gand.

Eriogonum holmgrenii Reveal, Leafl. W. Bot. 10:184. 1965. White Pine Co.: W base of Pyramid Peak N of Johnson Lake, Snake Range, 10 Aug 1964, *Holmgren & Reveal 1576*. Holotype, UTC! Isotypes, ARIZ! BRY! CAS! DS! GH! IDS! K! KSC! MARY! MIN! MO! MSC! NY! OKL! OSC! PH! RENO! RM! RSA! UC! US! UT! UTC! WIS!

Eriogonum howellii S. Stokes, Gen. Eriog. 91. 1936. Eureka Co.: 34 mi W of Eureka, 24 Aug 1931, *J. T. Howell 7963*. Holotype, CAS! = *E. heermannii* Dur. & Hilg. var. *argense* (M. E. Jones) Munz.

Eriogonum inflatum Torr. & Frem. var. *contiguum* Reveal, Aliso 7:221. 1970. Nye Co.: E of Ash Meadows, 3 Jun 1969, *Reveal & Matthews 2157*. Holotype, US! Isotypes, BRY! CAS! MICH! MO! NTS! NY! OKL! RENO! RM! RSA! SD! UC! UTC! WIS! = *E. contiguum* (Reveal) Reveal.

Eriogonum kingii Torr. & Gray, Proc. Amer. Acad. Arts 8:165. 1870. Elko Co.: East Humboldt [now Ruby] Mts., Jul 1868, *Watson 1020*. Lectotype selected here: GH! Duplicates of the lectotype: BM! K! NY! UC! US!

Eriogonum lactum S. Stokes, Gen. Eriog. 23. 1936. Pershing Co.: Near Humboldt, 24 May 1901, *George 9*. Holotype, CAS! = *E. rubricaule* Tidestrom.

Eriogonum lemmonii S. Wats., Proc. Amer. Acad. Arts 12:266. 1877. Washoe Co.: Sand hills between Wadsworth and Reno, 1875, *Lemmon 861*. Holotype, GH! Isotypes, ARIZ! ISC! NY! ?UC [as "Lava ridge, 1874"]! US!

Eriogonum leucocladum Gand., Bull. Soc. Roy. Bot. Belgique 42:189. 1906. Washoe Co.: Reno, Jun 1898, *Hillman s.n.* Holotype, LY! = *E. baileyi* S. Wats. var. *praebens* (Gand.) Reveal.

Eriogonum lewisii Reveal, Great Basin Nat.[2] 45. 1985. Elko Co.: White Elephant Butte, S of Elk Mtn., 30 Jul 1976, *Reveal & Reveal 4596*. Holotype, US! Isotypes, BRY! CAS! F! MARY! MEXU! MICH! MO! OKL! RSA! TEX! UTC!

Eriogonum microthecum Nutt. subsp. *intermedium* S. Stokes, Gen. Eriog. 75. 1936. White Pine Co.: near Ely, 24 Aug 1931, *J. T. Howell 7956*. Holotype, CAS! Isotypes, GH! US! = *E. microthecum* var. *simpsonii* (Benth in DC.) Reveal.

Eriogonum microthecum Nutt. var. *lapidicola* Reveal, Brigham Young Univ. Sci. Bull., Biol. Ser. 13(1):28. 1971. Nye Co.: N end of Rainier Mesa at the S end of the Belted Range at the head of The Aqueduct, 25 Aug 1968, *Reveal & Holmgren 1926*. Holotype, UTC! Isotypes, ARIZ! BRY! CAS! CS! DS! GH! MO! MSC! NTS! NY! OKLA! RENO! RM! TEX! UT! WIS!

Eriogonum monticola S. Stokes, Gen. Eriog. 123. 1936. Esmeralda Co.: S of Queen Mine, White Mts., 4 Sep 1926, *Ferris 6753*. Holotype, DS! Isotype, POM! = *E. latens* Jepson.

Eriogonum nevadense Gand., Bull. Soc. Roy. Bot. Belgique 42:188. 1906. Washoe Co.: Near Reno, 1878, *Hillman s.n.* Holotype, LY! = *E. ochrocephalum* S. Wats. var. *ochrocephalum*.

Eriogonum nutans Torr. & Gray var. *brevipedicellatum* S. Stokes, Gen. Eriog. 43. 1936. Eureka Co.: 30 mi W of Eureka, 25 Aug 1931, *J. T. Howell 7974*. Holotype, CAS! Isotype, GH! = *E. nutans* Torr. & Gray var. *nutans*.

Eriogonum nutans Torr. & Gray var. *glabratum* Reveal, Madroño 18:172. 1966. Elko Co.: 1 mi W of the Deeth turnoff, 20 Jun

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[2] All abbreviations follow those recommended by B-P-H Botanico-periodicum-huntianum except that for Great Basin Naturalist.

and 14 Jul 1964, *Holmgren & Reveal 1037*. Holotype, UTC! Isotypes, ARIZ! BRY! CAS! DS! GH! KSC! MO! MSC! NY! OKL! RENO! RM! RSA! SMU! UC! US! UTC! WIS!

Eriogonum ochrocephalum S. Wats. in Brewer & Wats., Bot. Calif. 2:480. 1880. Washoe Co.: "Valleys of Northwestern Nevada," likely from near Pyramid Lake, sin date, *Lemmon s.n.* (perhaps *91*). Holotype, GH! Isotype, NY!

Eriogonum ochrocephalum S. Wats. var. *alexanderae* Reveal, Great Basin Nat. 45:000. 1985. Lyon Co.: Wilson Canyon between Smith and Mason, 12.8 mi NE of Smith, 21 Jun 1978, *Reveal et al. 4737*. Holotype, US! Isotypes, BRY! CAS! DUKE! F! MARY! MEXU! MICH! MO! OKL! RSA! TEX! UTC!

Eriogonum ovalifolium Nutt. var. *caelestinum* Reveal, Great Basin Nat. 32:115. 1972. Nye Co.: South Fork of Pine Creek, Toquima Range, 23 Jul 1964, *Reveal 629*. Holotype, US! Isotypes, ARIZ! BRY! DS! GH! MIN! MO! NY! OKL! OKLA! RENO! RM! RSA! UC! UT! UTC! WTU!

Eriogonum ovalifolium Nutt. var. *nevadense* Gand., Bull. Soc. Roy. Bot. Belgique 42:193. 1906. Washoe Co.: Hills near the Truckee River, 4 May 1901, *Kennedy s.n.* Holotype, LY! Isotypes, MIN! NESH! RENO! RM! UC!

Eriogonum ovalifolium Nutt. var. *williamsae* Reveal, Brittonia 33:446. 1981. Washoe Co.: Steamboat Springs, 7 Jun 1979, *Williams & Tiehm 79-71*. Holotype, US! Isotypes, MARY and to be distributed.

Eriogonum praebens Gand. var. *divaricatum* Gand., Bull. Soc. Roy. Bot. Belgique 42:196. 1906. Washoe Co.: Peavine foothills, 27 Sep 1893, *Hillman s.n.* Holotype, LY! = *E. baileyi* S. Wats. var. *praebens* (Gand.) Reveal.

Eriogonum puberulum S. Wats. var. *venosum* S. Stokes, Gen. Eriog. 35. 1936. Eureka Co.: 34 mi E of Eureka, 24 Aug 1931, *J. T. Howell 7962*. Holotype, CAS! = *E. puberulum* S. Wats.

Eriogonum pusillum Torr. & Gray, Proc. Amer. Acad. Arts 8:184. 1870. Churchill Co. or Pershing Co.: Foothills of the Trinity Mts., May 1868, *Watson 1037*. Holotype, GH! Isotypes, K! NY! US!

Eriogonum reliquum S. Stokes, Leafl. W. Bot. 2:52. 1937. Clark Co.: Clarleston Park, Spring Mts., 9 Aug 1937, *Clokey 7491*. Holotype, CAS! Isotypes, AHFH! ARIZ! B! BALT! BM! BRY! CAN! CAS! CI! DAO! DS! DUKE! F! G! GH! IA! IDS! IND! ISC! K! LA! LCU! MARY! MICH! MIN! MO! MSC! NEB! NESH! NY! OKL! OKLA! ORE! OSC! P! PAC! PENN! PH! POM! RENO! SD! TEX! UC! US! UT! UTC! WILLU! WIS! WS! WTU! = *E. panamintense* Morton var. *panamintense*.

Eriogonum reniforme Torr. & Frem. var. *asarifolium* Gand., Bull. Soc. Roy. Bot. Belgique 42:196. 1906. Washoe Co.: Reno, 9 Aug 1894, *Hillman s.n.* Holotype, LY! Isotype, NESH! = *E. pusillum* Torr. & Gray.

Eriogonum reniforme Torr. & Frem. var. *comosum* M. E. Jones, Proc. Calif. Acad. Sci. II, 5:719. 1895. Clark Co.: Near Hole in the Rock, 10 mi above Stone's Ferry, 12 Apr 1894, *M. E. Jones 5036ao*. Lectotype, POM! = *E. reniforme* Torr. & Frem.

Eriogonum restioides Gand., Bull. Soc. Roy. Bot. Belgique 42:199. 1906. Washoe Co.: Reno, 9 Aug 1894, *Hillman s.n.* Lectotype, LY! Duplicate of the lectotype, NESH! = *E. baileyi* S. Wats. var. *baileyi*.

Eriogonum revolutum Goodding, Bot. Gaz. 37:54. 1904. Clark Co.: In low mountains near the Virgin River near Bunkerville, 9 May 1902, *Goodding 753*. Holotype, RM! Isotypes, F! G! GH! ISC! LY! MO! NEB! NESH! NY! P! POM! RM! UC! US! UT! UTC! = *Eriogonum fasciculatum* Benth. var. *polifolium* (Benth. in DC.) Torr. & Gray.

Eriogonum rhodanthum Nels. & Kenn., Proc. Biol. Soc. Wash. 19:35. 1906. Washoe Co.: Mt. Rose, 17 Aug 1905, *Kennedy 1184*. Holotype, RM! Isotypes, NESH! NY! UC! = *E. ovalifolium* Nutt. var. *nivale* (Canby in Cov.) M. E. Jones.

Eriogonum robustium Greene, Bull. Calif. Acad. Sci. 1:126. 1885. Storey Co.: Geiger Grade, NW of Virginia City, Jul 1884, *Curran s.n.* Holotype, CAS! Isotypes, BM! F! GH! = *E. lobbii* Torr. & Gray var. *robustium* (Greene) M. E. Jones.

Eriogonum rosense Nels. & Kenn., Proc. Biol. Soc. Wash. 19:36. 1906. Washoe Co.: Summit of Mt. Rose, 17 Aug 1905, *Kennedy 1180*. Holotype, RM! Isotypes, NDG! NESH! UC!

Eriogonum rubricaule Tidestrom, Proc. Biol. Soc. Wash. 36:181. 1923. Churchill Co.:

Near Lahontan, 21 May 1916, *Headley 4*. Holotype, US! Isotype, RENO!

Eriogonum rupinum Reveal, Aliso 7:226. 1970. Nye Co.: below Rose Spring, Cedar Pass, southern Kawich Range, 9 Aug 1969, *Beatley 9458*. Holotype, US! Isotypes, ARIZ! ASC! ASU! BRY! COLO! DUKE! G! GH! ISC! K! KANU! KSC! MICH! MO! NCU! NTS! NY! OKL! OSC! P! RM! RSA! SMU! SD! TEX! UC! UT! UTC! WTU!

Eriogonum saxatile S. Wats. subsp. *multicaule* S. Stokes, Leafl. W. Bot. 3:201. 1943. Esmeralda Co.: Gold Mtn., 5 Jul 1941, *Alexander & Kellogg 2478A*. Holotype, UC! Isotype, CAS! = *E. saxatile* S. Wats.

Eriogonum sericoleucum Greene ex Tidestrom, Proc. Biol. Soc. Wash. 36:182. 1923. Carson City Co.: King's Canyon, 4 Jun 1902, *Baker 984*. Holotype, US! Isotypes, B! F! GH! MO! MSC! NY! POM! RM! VT! = *E. caespitosum* Nutt.

Eriogonum shockleyi S. Wats., Proc. Amer. Acad. Arts 18:194. 1883. Mineral Co.: Candelaria, Jun 1882, *Shockley 248*. Holotype, GH! Isotypes, DS! ISC! JEPS! MICH! NY! P! POM! UC! US!

Eriogonum tenellum Torr. ex Benth. in DC. var. *sessiliflorum* Gand., Bull. Soc. Roy. Bot. Belgique 42:198. 1906. Washoe Co.: Reno, Sep 1894, *Hillman s.n.* Holotype, LY! Isotype, NESH! = *E. microthecum* Nutt. var. *laxiflorum* Hook.

Eriogonum thurberi Torr. var. *acutangulum* Gand., Bull. Soc. Roy. Bot. Belgique 42:198. 1906. Washoe Co.: Virginia Mts., 27 Aug 1894, *Hillman s.n.* Holotype, LY! = *E. maculatum* A. A. Heller.

Eriogonum tiehmii Reveal, Great Basin Nat. 45:493–519. 1985. Esmeralda Co.: Silver Peak Range N of the road from Silverpeak to Fish Lake Valley, 1.2 air mi NNW of Cave Springs, sec. 27, T1S, R37E, 1830 m elevation, 18 May 1983, *Tiehm et al. 8534*. Holotype, US! Isotypes, BRY! CAS! MARY! NY! RENO! RSA! UTC! and to be distributed.

Eriogonum umbellatum Torr. var. *californicum* Gand., Bull. Soc. Roy. Bot. Belgique 42:199. 1906. Washoe Co.: Peavine foothills, 11 Jun 1894, *Hillman s.n.* Holotype, LY! Isotype, NESH! = *E. umbellatum* Torr. var. *nevadense* Gand.

Eriogonum umbellatum Torr. var. *juniporinum* Reveal, Great Basin Nat. 45. 1985. White Pine Co.: Sacramento Pass, N of the Snake Range, 13 Aug 1975, *Reveal & Reveal 3925*. Holotype, US! Isotypes, BRY! CAS! MARY! OKL! TEX!

Eriogonum umbellatum Torr. var. *nevadense* Gand., Bull. Soc. Roy. Bot. Belgique 42:198. 1906. Washoe Co.: Huffakers, near Reno, 27 May 1893, *Hillman s.n.* Holotype, LY! Isotype, NESH!

Eriogonum umbellatum Torr. var. *subaridum* S. Stokes, Leafl. W. Bot. 2:53. 1937. Clark Co.: Kyle Canyon, Spring Mts., 17 Jul 1937. *Clokey [& Clokey] 7492*. Holotype, CAS! Isotypes, B! BALT! BR! BRY! CAN! CAS! CI! DS! DUKE! GH! IA! ILL! IND! K! KANU! LA! LAM! LL! MICH! MIN! MO! MSC! NESH! NY! OKL! OKLA! P! PAC! PENN! PH! POM! RM! TEX! UC! US! UTC! VT! WIS! WVA!

Eriogonum umbellatum Torr. var. *vernum* Reveal, Great Basin Nat. 28:157. 1968. Nye Co.: N end of Shoshone Mtn. along Buckboard Mesa Rd., 1 mi W of Tippipah Spring, 4 Jun 1968, *Reveal 1139*. Holotype, UTC! Isotypes, ARIZ! BRY! CAS! CS! DS! GH! IDS! KSC! MIN! MO! MSC! NTS! NY! OKLA! RENO! RSA! TEX! US! UT! UTC! WIS!

Eriogonum viscidulum J. T. Howell, Leafl. W. Bot. 3:138. 1942. Clark Co.: Virgin River Bridge, Riverside, 8 May 1941, *Eastwood & Howell 9031*. Holotype, CAS! Isotype, CAS!

Eriogonum watsonii Torr. & Gray, Proc. Amer. Acad. Arts 8:182. 1870. Elko Co.: East Humboldt [now Ruby] Mts., 1865, *Torrey 450*. Lectotype, NY! Duplicates of the lectotype, NY! US!

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ANNOTATED KEY TO *ERIOGONUM* (POLYGONACEAE) OF NEVADA

James L. Reveal[1]

ABSTRACT — Seventy-three species of *Eriogonum* (Polygonaceae) are reported for Nevada. A key is provided for the identification of these species along with brief notes on their distribution in the state and elsewhere.

The genus *Eriogonum* is a prominent member of the Nevada flora, and, except for the treatment of the genus by Tidestrom (1925), no key for the native species is available. The present treatment has been prepared for a doctoral dissertation by John Kartesz, a graduate student at the University of Nevada, who is writing a manual on the flora of Nevada. New entities discussed in this treatment may be found in a companion paper (Reveal 1985).

The key is followed by a comment section. The arrangement of the species in the key is largely artificial and should not be taken as representative of natural affinities. In the comment section species are arranged in a sequence that may be regarded as more natural. The distribution data given for Nevada is detailed, but that for adjacent states or regions is more generalized.

1. Plants perennial, not annual, but see *E. inflatum* with its inflated stems and yellow, hirsute flowers 2

— Plants annual, or if perennial then stems inflated and flowers yellow, hirsute, and in pedunculated involucres 41

2(1). Flowers not stipelike at the base 3

— Flowers stipelike at the attenuated base, sometimes weakly so 33

3(2). Plants distinctly shrubby or subshrubby, woody above the basal caudex and not dying back completely to the ground after each year 4

— Plants herbaceous, cespitose or pulvinate perennials, not at all shrubby or subshrubby 9

4(3). Flowers pubescent without, 2.5–3 mm long, white to pink; low shrubs; Esmeralda, Nye, Lincoln, and Clark cos. .... 6. *E. fasciculatum*

— Flowers glabrous without 5

5(4). Stems and branches smooth, glabrous to tomentose, not angled or scabrellous; inflorescences with involucres arranged in loose to compact terminal cymes or racemosely along the straight branches, the branches not zigzag 6

— Stems and branches angled or ribbed, or if smooth then obviously scabrous, or, if smooth and tomentose, then inflorescences of zigzag branches 8

6(5). Inflorescences cymose throughout with involucres dichotomously arranged even at the tips of the branches; leaves less than 8 mm wide, or, if broader, then flowers yellow 7

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— Inflorescences large with numerous branches and branchlets bearing racemosely arranged involucres at their tips; flowers white; White Pine and Lincoln cos. westward across central Nevada to Esmeralda, Mineral, and Ormsby cos. . . . . . . 2. *E. nummulare*

7(6). Leaf-apices acute, the blade less than 8 mm wide; flowers white, or, if yellow, then plants of western Nevada; widespread and common throughout the state . . . . . . 1. *E. microthecum*

— Leaf-apices rounded, the blades 5–15 mm wide; flowers yellow; local, near Las Vegas, Clark Co. . . . . . . 3. *E. corymbosum*

8(5). Stems and branches angled, ribbed or smooth and scabrous; involucres 0.7–2 mm long; throughout the lower two-thirds of the state . . . . . . 4. *E. heermannii*

— Stems and branches tomentose; involucres 2–2.5 mm long; rare, southernmost Clark Co. . . . . . . 5. *E. plumatella*

9(3). Plants cespitose or pulvinate perennials with a terminal, capitate cluster of involucres. 10

— Plants upright herbs with open, often elongated or much-branched inflorescences 27

10(9). Tepals monomorphic, glabrous or pubescent. 11

— Tepals strongly dimorphic, the outer tepals broader than inner tepals, or, if only slightly dimorphic, then the plants with oval to rotund leaf-blades 2–8 mm long and wide and restricted to the high mountains; common nearly throughout the state . . . . . . 28. *E. ovalifolium*

11(10). Flowers glabrous or glandular without, not pubescent with long hairs 12

— Flowers hairy pubescent without, not glabrous or glandular 26

12(11). Involucres rigid and distinctly tubular 13

— Involucres membranaceous and indistinctly forming a tube, mostly 2–3.5 mm long, glandular or glandular-hairy without 23

13(12). Scapes glabrous or tomentose, not glandular or glandular-hairy 14

— Scapes glandular-hairy or glandular, not glabrous or tomentose 22

14(13). Scapes glabrous 15

— Scapes tomentose to floccose 16

15(14). Leaves ovate to obovate, 1–2 cm long, 5–10 mm wide; scapes 1–2 dm long; involucres floccose without; clay hill or flats, Storey, Lyon and Washoe cos. . . . . . . 8. *E. ochrocephalum*

— Leaves spathulate to oblanceolate, 0.4–0.8 (1) cm long, 2–3 (4) mm wide; scapes 0.2–0.8 dm long; involucres glabrous or with a few hairs on the teeth; volcanic slopes and outcrops in northern Washoe Co. . . . . . . 9. *E. prociduum*

16(14). Flowers bright yellow 17

— Flowers pale yellow or more often whitish with a reddish midrib, 2–3 mm long; involucre 2–5 mm long 20

17(16). Involucres 3.5–5 mm long, floccose over the upper half of the tube; leaf-blades oblong to lanceolate, (1) 1.5–2.5 cm long, the petioles 1.5–3 cm long; scapes (0.6) 1–1.5 cm long; Lyon Co. northward to southern Washoe and Pershing cos. . . . . . . 8. *E. ochrocephalum*

— Involucres 2–3 mm long 18

18(17). Leaf-blades 1.5–2.5 (3) cm long, 5–9 mm wide; scapes densely tomentose; involucres tomentose without; flowers 2.5–3 mm long; Elko Co. south to northern White Pine Co. and westward to adjacent northern Eureka Co., 1700–2630 m elev. . . . . 7. *E. desertorum*

— Leaf-blades less than 1.5 cm long and 7 mm wide; scapes floccose; involucres floccose without and then mainly on the upper half of the tube; flowers mostly less than 2.5 mm long 19

19(18). Flowers (2) 2.5–3 mm long; involucres 2.5–3 mm long; leaf-blades 4–7 mm wide; high elevation rocky slopes in Elko Co. . . . . 10. *E. lewisii*

— Flowers 1.5–2 mm long; involucres 2–3 mm long; leaf-blades 1.5–4 (5) mm wide; low elevation clay outcrops in Humboldt Co.. 11. *E. crosbyae*

20(16). Involucres 2–2.5 mm long, floccose without; leaf-blades broadly elliptic to obovate or suborbicular, (7) 9–13 (15) mm long, 5–9 (11) mm wide; flowers glabrous; Lander, Pershing, and southwestern Humboldt cos. . 14. *E. anemophilum*

— Involucres 4–5 mm long, sparsely floccose without; leaf-blades elliptic to oblong, (8) 12–25 mm long, 5–8 (10) mm wide; flowers sparsely glandular without; Esmeralda Co. . . . . 15. *E. tiehmii*

21(13). Involucres tomentose without, 3–4 mm long; leaf-blades 1–2 cm long; flowers 2–2.5 mm long; scapes 0.7–2 dm long; clay hills mainly in Washoe Co., mostly below 2000 m elev. . . . . 8. *E. ochrocephalum*

— Involucres glandular-hairy or glandular, not tomentose; plants above 2000 m elev. or, if at lower elevations, then not of northwestern Nevada 22

22(21). Leaves oblanceolate, 4–15 mm long, 2.5–5 (6) mm wide; involucres more or less turbinate, 2.5–3 mm wide with (5) 6–8 teeth; achenes 1.5–2 mm long; montane forests and alpine areas in the Sierra Nevada and adjacent ranges of Esmeralda Co. northward to Washoe Co. mostly 2440–3300 m elev. . . . . 12. *E. rosense*

— Leaves elliptic, 10–25 mm long, 5–16 mm wide; involucres campanulate, 3–4 mm wide with 5 teeth; achenes (2.5) 3–3.5 mm long; clay hills and slopes in Lander, Eureka, Mineral, Nye, and Churchill cos., 1700–2750 m elev. . . . . 13. *E. beatleyae*

23(12). Flowers greenish yellow or pale yellow, not white or rose 24

— Flowers white to rose or red, not greenish yellow or pale yellow. 25

24(23). Involucres (2.8) 3–3.5 mm long; petioles 4–12 (15) mm long, thinly tomentose; flowers (2.5) 3–3.5 mm long, glabrous; rocky outcrops at high elevations, 2250–3250 m, East Humboldt and Ruby mts., Elko Co. and Cherry Creek Range, northern White Pine Co. . . . . 16. *E. kingii*

— Involucres 2–2.5 mm long; petioles 0.5–1 (1.5) mm long, densely tomentose; flowers 2.5–3 mm long, sparsely glandular; clay flat near Sulphur Hot Springs, 1850 m, Ruby Valley, Elko Co. . . . . 17. *E. argophyllum*

25(23). Leaves 1–2 cm long, densely white-tomentose below, less so and white above; scapes 3–8 cm long, glandular, not floccose; inflorescences of 5–7 involucres; pedicels glandular at the tips; high elevation sandy to granitic outcrops, White Mts., Esmeralda Co. . . . . 18. *E. gracilipes*

— Leaves 0.3–1 cm long, densely white-tomentose and greenish below, less so and greenish above; scapes up to 3 cm long, floccose and glandular; inflorescences of 2–4 involucres; pedicels glabrous except for a few scattered glands at the base; high elevation limestone and quartzite outcrops, Snake Range, White Pine Co. . . . . 19. *E. holmgrenii*

26(11). Ovaries and achenes glabrous; plants loosely cespitose with 10–20 rosettes; branches prostrate to weakly erect, 2–8 cm long; inflorescences cymose-umbellate to more or less capitate; local and infrequent on limestone gravel, Eureka, Nye, White Pine, and Lincoln cos. . . . . 20. *E. villiflorum*

— Ovaries and achenes pubescent; plants densely cespitose with 15–50 or more rosettes; branches erect, up to 3 cm long; inflorescences capitate; common on clay to gravel flats and slopes from Esmeralda to Nye and Clark cos. eastward to Elko and Lincoln cos. . . . . 21. *E. shockleyi*

27(9). Tepals monomorphic; plants not with elliptic leaves 5–15 mm long and tomentose stems 28

— Tepals dimorphic; plants 1–3 dm tall, the branches and stems tomentose; leaves mostly elliptic, 5–25 mm long, 5–15 mm wide, tomentose on both surfaces; flowers white or yellow; northern and northwestern Nevada . . . . 29. *E. strictum*

28(27). Inflorescences with involucres racemosely arranged along the branches, involucres solitary 29

— Involucres with involucres in cymes with usually clustered involucres dichotomously arranged throughout the inflorescence 32

29(28). Plants suffrutescent and branched at the base; leaves many, oblanceolate to elliptic, 0.5–1 cm long, 2–5 mm wide; involucres turbinate, 2–2.5 mm long; flowers white; rare and local in southern Clark Co. or common from Mineral Co. northward . . . . 22. *E. wrightii*

— Plants not suffrutescent at the base; basal leaves few, more than 1 cm long and 5 mm wide 30

30(29). Basal leaves roundish to broadly ovate, the leaf-blades 1.5–4 cm long, on petioles 1–5 cm long; plants with branched and woody spreading caudices; involucres and flowers 3–5 mm long; dry rocky slopes of Esmeralda Co. southeastwardly to the Spring Mts. and Sheep Range of Clark Co. . . . . 23. *E. panamintense*

— Basal leaves oblong, cordate, ovate or elliptic, the leaf-blades (2) 3–10 cm long, on petioles 3–10 cm long; plants arising from a single, woody, mostly unbranched caudex; involucres 2–5 mm long; flowers 2–4 mm long; Mineral and Nye cos. eastward to White Pine, Lincoln, and northern Clark cos. 31

31(30). Inflorescences cymose with 3–5 racemostly arranged involucres at the ends of the branches; plants 3–5 dm high with 3–7 stems arising from the caudex, rarely with 7–20 stems on somewhat more spreading caudices in some; involucres 2–3.5 mm long; widespread and common from Mineral and Esmeralda cos. across the central portion of the state to Lander and Nye cos. . . . . 24. *E. rupinum*

— Inflorescences cymose with 5–20 or more racemosely arranged involucres at the end of the branches; plants 3–10 dm high with 1–3 (5) stems arising from the compact caudex; widespread and locally common in Lincoln, White Pine, Nye, and northern Clark cos. . . . . 25. *E. racemosum*

32(28). Leaves tomentose below, somewhat less so above, the leaf-blades spreading with apices mostly obtuse; flowers glabrous; along the western edge of the state from Douglas and Carson City cos. northward . . . . 26. *E. nudum*

— Leaves villous and green on both surfaces, the leaf-blades erect, with acute apices; flowers thinly pubescent; rather common throughout the northern half of the state . . . . 27. *E. elatum*

33(2). Flowers with a long, tubular, more or less winged stipe at the base of white flower, together (3) 5–7 mm long, glabrous, the tepals dimprohic; leaves broadly obovate to roundish, 1–2 cm long, 1–1.5 cm wide, lanate to tomentose on both surfaces; flowering branches 5–10 cm long; inflorescences 0.5–1.5 dm long; rare and local in Clark, Nye, and Esmeralda cos. . . . . .30. *E. saxatile*

— Flowers abruptly stipitate, the stipe sometimes obscure and never winged; flowers generally yellow or cream 34

34(33). Involucres with lobes at least half as long as the tube, the lobes usually reflexed or spreading, never erect and toothlike 35

— Involucres with lobes much shorter than the tube, toothlike and erect or nearly so. 39

35(34). Flowers glabrous without 36

— Flowers pubescent without 37

36(35). Flowering stems not bracteated near the middle; leaf-blades oblong to elliptic; inflorescences umbellate to once or twice compoundly umbellate; common throughout the state . . . . 31. *E. umbellatum*

— Flowering stems bracteated near the middle; leaf-blades linear to oblanceolate; inflorescences compoundly umbellate three to several times; common across the northern half of the state. . . . . 32. *E. heracleoides*

37(35). Flowering branches with a whorl of subtending bracts at the base of the umbel or near the middle of the ray. 38

— Flowering branches without subtending bracts and with a solitary, terminal involucre; widespread and common throughout the Great Basin portion of the state . . . . 35. *E. caespitosum*

38(37). Involucres more than 1, umbellate, subtended by (2) 3–several leafy bracts below the umbel, or, if seemingly in the middle of the flowering branch, then the leaves glabrate above; leaves 1–3 (4) cm long; flowers 5–9 mm long; Carson City north and eastward to western Elko Co. . . . . 33. *E. sphaerocephalum*

— Involucres solitary, terminal, not immediately subtended by leafy bracts, the flowering branches with a whorl of bracts near the middle; leaves densely tomentose on both surfaces; flowers 5–8 mm long; Peavine Mtn. area of southern Washoe Co. . . . . 34. *E. douglasii*

39(34). Flowers pubescent without, cream to pale yellow, 5–6 mm long; leaves short-pilose to subglabrous, 1–3 cm long; White Mountains, Esmeralda Co. . . 37. *E. latens*

— Flowers glabrous without; leaves tomentose at least on the lower surface 40

40(39). Flowering branches erect, thinly tomentose; involucres 2–3 mm long; flowers unisexual, the male flowers yellow, 1.5–3 mm long, the female flowers yellow to lemon yellow, 4–7 mm long; infrequent, Carson City, Washoe, and Humboldt cos. . . . . 36. *E. marifolium*

— Flowering branches prostrate to weakly erect, usually densely tomentose; involucres 5–15 mm long; flowers perfect, white to rose or red, 5–9 mm long; locally frequent in Washoe, Storey, Lyon, and Carson City cos. . . . . 38. *E. lobbii*

41(1). Involucres smooth, not ribbed or angled, usually distinctly peduncled, or if sessile then involucres not vertically appressed to the stems; annuals except for *E. inflatum*. 42

— Involucres angled to strongly ribbed, usually tightly appressed to the stem and always sessile; strictly annuals 68

42(41). Leaves basal, not cauline, occasionally the leaves sheathing up the base 43

— Leaves basal and cauline at the lower nodes. 66

43(42). Leaves glabrous, pilose, hispid or villous on one or both surfaces, not densely tomentose at least on the lower surface; flowers mostly yellow 44

— Leaves densely tomentose to floccose-tomentose on one or both surfaces; flowers mostly white, glabrous or glandular-puberulent 52

44(43). Flowers pubescent without 45

— Flowers glabrous without 49

45(44). Plants glabrous, or, if glandular, the glands infrequent and restricted to the base and lower nodes of the stems and branches 46

— Plants glandular, the glands dense and frequent throughout the plant 48

46(45). Involucres 5-toothed 47

— Involucres 4-toothed; plants strictly annual; flowering stems glabrous or hirsute at the base, green to yellowish; widespread and common in southern Nye and Lincoln cos. and throughout Clark Co. . . . . 41. *E. trichopes*

47(46). Flowering stems glabrous and glaucous or with a few hirsute hairs at the base, grayish or green; plants first-year flowering perennials; widespread and common in the southern third of the state . . . . 39. *E. inflatum*

— Flowering stems glandular at the base and occasionally at the lower nodes, otherwise glabrous above, reddish; plants strictly annual; low desert valleys and foothills in extreme southern Nye and northern Clark cos. . . . . 40. *E. contiguum*

48(45). Flowers yellow, 1–1.5 (2) mm long; involucres turbinate-campanulate, 1.3–2 mm long on erect peduncles 3–10 mm long; achenes 1.5–1.8 mm long; Nye Co. eastward to Lincoln, White Pine and Elko cos. mostly on volcanic or limestone ranges . . . . 42. *E. howellianum*

— Flowers white, 1–1.8 mm long; involucres narrowly turbinate, 0.8–1.2 (1.5) mm long on deflexed peduncles 2–5 mm long; achenes 1–1.3 mm long; southwestern Nye and northern Clark cos. on low limestone desert ranges . . . . 43. *E. glandulosum*

49(44). Involucres long peduncled at least at the lower nodes 50

— Involucres sessile or the lowermost short-pedunculate, the tube campanulate, 2–2.5 mm long, 2.5–3 mm wide; flowers pink to rose, 1.5–2 mm long; clayey foothills and flats in northwestern Nevada . . . . 47. *E. lemmonii*

50(49). Flowers white to greenish white; involucres turbinate; peduncles descending 51

— Flowers pale yellow to yellow; involucres campanulate, 2.5–3 mm long and wide; peduncles 2–3 cm long, erect; volcanic ranges in northwestern Nevada . . . . 46. *E. rubricaule*

51(50). Peduncles slender to filiform, 2–15 mm long, spreading to deflexed; leaves obovate to round-obovate with tapering leaf-bases; involucres narrowly turbinate, 0.8–1.8 mm long, 0.5–1.2 mm wide; flowers white to pink or red; gravelly slopes from Humboldt and Mineral Co. south to Nye Co. eastward to Lander and Eureka cos. . . . . 44. *E. esmeraldense*

— Peduncles slender, (0.5) 1–2.5 mm long, sharply deflexed; leaves subcordate with cordate leaf-bases; involucres turbinate, 1.2–1.6 mm long, 1–1.4 mm wide; flowers white to greenish white; clayey or sandy-clay soils in southwestern Nye Co. . . . . 45. *E. concinnum*

52(43). Outer tepals cordate or subcordate at the base, mostly oblong to orbicular 53

— Outer tepals truncate to obtuse at the base 58

53(52). Involucres deflexed, sessile or on peduncles up to 25 mm long 54

— Involucres erect on peduncles less than 5 mm long 57

54(53). Stems and branches glabrous 55

— Stems and branches glandular, stoutish and usually short, the crowns flat-topped; peduncles up to 15 mm long; involucres turbinate to campanulate, 1–2.5 mm long; common throughout the southern half of the state . . . 51. *E. brachypodum*

55(54). Involucres narrowly turbinate to turbinate-campanulate; peduncles up to 25 mm long; tepals as long as to longer than wide, white to pink 56

— Involucres campanulate or hemispheric, 1–2 mm long; peduncles lacking; flowers yellow to reddish yellow; scattered throughout much of central Nevada . . . . 50. *E. hookeri*

56(55). Involucres 1.5–3 mm long; plants variously branched; flowers not gibbous at the base; common throughout the southern two-thirds of the state . . . . . 48. *E. deflexum*

— Involucres 1–1.5 mm long; plants branched in a series of layers one above the other so as to be pagodalike; flowers gibbous at the base when mature; infrequent in extreme southern Nye Co. . . . . 49. *E. rixfordii*

57(53). Flowering branches short, less than 3 cm long; plants 1–4 dm high, 3–15 dm across, the crown spreading and flat-topped; extreme southern Nye Co. and Clark Co. . . . . 52. *E. bifurcatum*

— Flowering branches long, 2–20 cm long; plants 2–12 dm high, 1–5 dm across, the crowns erect and strict; southern Nye and Clark cos. . . . . 53. *E. insigne*

58(52). Flowers smooth or saccate, glabrous or glandular, not strongly pustulose 59

— Flowers strongly pustulose without; northwestern Nevada 65

59(58). Tepals monomorphic, mostly oblong to ovate 60

— Tepals dimorphic, or, if similar, then glandular-pubescent, pandurate to flabellate or ovate 61

60(59). Plants glabrous; involucres 2–3 mm long, 5-toothed; peduncles deflexed, slender; flowers white, 2–2.5 mm long; local in northwestern and northcentral Nevada . . . . 54. *E. watsonii*

— Plants minutely viscid; involucres 1–1.2 mm long, 4-toothed; peduncles erect, filiform; flowers yellow, 1.3–2 mm long; rare and local in Clark Co. . . . . 60. *E. viscidulum*

61(59). Flowers glabrous without, not glandular 62

— Flowers glandular without 63

62(61). Peduncles glabrous, cernuous to ascending, straight or nearly so, lacking in var. *viminale*; involucres turbinate, 1–1.5 mm wide; flowers white, the outer tepals pandurate, crisped along the margin; common throughout nearly all of the state . . . . 55. *E. cernuum*

— Peduncles glandular, or, if glabrous, then curving downwardly; involucres campanulate, 1.5–2.5 mm wide; flowers white to rose, the outer tepals oblong to oval, not crisped along the margin; infrequent and local across the northern half of the state . . . . 56. *E. nutans*

63(61). Outer tepals saccate-dilated at the base, usually white when mature; involucres 0.6–1.2 mm long, glabrous; southern Nye, Lincoln, and Clark cos. . . 57. *E. thomasii*

— Outer tepals smooth; involucres 1–2 mm long, glabrous or glandular without; flowers yellow 64

64(63). Tepals and outer involucral surface glandular-puberulent; bracts glandular on the outer surface; western and southern Nevada . . . . 58. *E. pusillum*

— Tepals glandular-puberulent without; involucres glabrous on the outer surface; bracts villous on the outer surface; Churchill Co. southward through the southern half of the state. . . . . 59. *E. reniforme*

65(58). Upper involucres peduncled, the peduncles curving upwardly, 1–5 cm long, the involucral tube (1.5) 2–3 mm long; flowers white to yellow, 1–2.5 mm long; achenes 2–2.5 mm long; Washoe, Douglas, and Lyon cos. northward to Humboldt Co. . . . . 61. *E. collinum*

— Upper involucres sessile, erect, the peduncles at the lower nodes 1–5 mm long, the involucral tube 1.5–2 mm long; flowers white to rose, 1.2–1.8 mm long; achenes 1.6–2 mm long; rare, Humboldt Co. . . . . 62. *E. salicornioides*

66(42). Involucres glabrous to hispid or villous without 67

— Involucres glandular-puberulent without; tepals dimorphic, the outer tepals inflated at the base and middle, white to rose, often with a large purplish spot on the outer tepals; common throughout most of the state. . . . . 65. *E. maculatum*

67(66). Tepals distinctly dimorphic, the outer whorl oblong-ovate and bisaccate, yellow; infrequent, Lincoln Co. . . . . 63. *E. pharnacoides*

— Tepals essentially monomorphic, not saccate, white; northwestern Nevada. . . . . 64. *E. spergulinum*

68(41). Leaves tomentose on one or both surfaces; stems and branches glabrous to tomentose 69

— Leaves puberulent to villous or sericeous; stems puberulent to villous, with spreading hairs 74

69(68). Involucres 2–4 mm long; stems and lower branches thinly floccose or rarely glabrous; flowers 1.5–2 mm long, white to pink; local and often common from Carson City Co. north and eastward to Washoe, Humboldt, and Elko co. . . . . 67. *E. vimineum*

— Involucres 1–2 mm long; stems and branches glabrous to densely tomentose, or, if sparsely tomentose, then the flowers yellow to yellowish red 70

70(69). Stems glabrous, or, if tomentose, then the tepals glandular and the outer whorl not fan shaped 71

— Stems tomentose to floccose; tepals fan shaped, white or yellow 73

71(70). Involucres at the tips of slender branchlets and at the node of dichotomous branchlets or branches, not appressed to the stems, the tube turbinate-campanulate, smooth, 1.5–2 mm long; flowers 1–1.5 mm long with large, roundish, greenish, or, more commonly, reddish bases and white tepal tips; rare and local in Mineral Co. . . . . 66. *E. ampullaceum*

— Involucres scattered along and appressed to the stems, the tube narrowly turbinate and slightly angled, 1–1.5 (2) mm long; flowers 0.6–1.5 mm long, yellow, or, if white, then glandular, the base slender and never roundish; common 72

72(71). Flowers white, 1.5–2 mm long; stems and branches glabrous or tomentose; common throughout the Great Basin portion of western Nevada. . . . . . 68. *E. baileyi*

— Flowers yellow, 0.6–1 mm long; stems and branches glabrous; infrequent to locally common in western half of the state south to Nye Co. . . 69. *E. brachyanthum*

73(70). Flowers yellow to red; plants rather densely branched; involucres 1 mm long; widely scattered throughout much of the state. . . . . 70. *E. nidularium*

— Flowers white or rarely pale yellow; plants open with few branches; involucres 1.5–2 mm long; widely scattered throughout most of the southern two-thirds of the state . . . . 71. *E. palmerianum*

74(69). Outer tepals oblong to narrowly ovate, not hooded, white to red, 1–1.5 mm long, glabrous to hispidulous; involucres 4-toothed, 1–1.5 mm long; local but often common on volcanic soils in east central and southern Nevada . . . 72. *E. puberulum*

— Outer tepals fan shaped and hooded, pale yellow to pink, 1.5–2 mm long, hirtellous; involucres 5-toothed, 2–2.5 mm long; rare and local on clayey soils in Nye and White Pine cos. . . . . 73. *E. darrovii*

1. ***Eriogonum microthecum* Nutt.** A highly variable shrubby species common throughout the state mainly on gravelly, clayey, or sandy soils, occasionally on rock outcrops and ledges, 1160–3200 m, mostly in sagebrush communities. Flowering from June through October. Widespread in the western United 2.5 States.

Great Basin buckwheat. Low subshrubs and shrubs with white or yellow flowers; represented in Nevada by the following varieties:

1. Flowers white, not yellow or yellowish 2

— Flowers yellow; shrubs and subshrubs to 5 dm high; western Nevada from Esmeralda Co. northward to Washoe and Humboldt cos. . . . . var. *ambiguum*

2(1). Tomentum whitish; plants shrubs or well-formed subshrubs; common 3

— Tomentum brownish to reddish; plants low, compact subshrubs less than 1.5 dm high; southern Great Basin from Esmeralda and Nye cos. eastward to southern White Pine Co. and Lincoln Co. . . . . var. *lapidicola*

3(2). Leaves plane; stems and inflorescences floccose to glabrous; shrubs or subshrubs mostly 2–4 dm high; mainly in the Great Basin portion of the state . . . var. *laxiflorum*

— Leaves revolute; stems and inflorescences densely lanate to tomentose; shrubs mostly 4–15 dm high; mainly in the Mojave Desert portion of the state . . . . var. *simpsonii*

The most common expression in the state is **var. *laxiflorum* Hook.** [*E. confertiflorum* Benth. in DC.; *E. microthecum* var. *confertiflorum* (Benth. in DC.) Torr. & Gray; *E. tenellum* Torr. var. *sessiliflorum* Gand.; *E. microthecum* subsp. *laxiflorum* (Hook.) S. Stokes; *E. microthecum* subsp. *confertiflorum* (Benth. in DC.) S. Stokes; *E. microthecum* var. *spathulare* S. Stokes] occurs mainly in the Great Basin section of Nevada. It is found mostly above 1500 m on slopes and ridges. The **var. *simpsonii* (Benth. in DC.) Reveal** [*E. simpsonii* Benth. in DC.; *E. effusum* var. *foliosum* Torr. & Gray. *E. microthecum* var. *rigidum* Eastw.; *E. friscanum* M. E. Jones; *E. nelsonii* L. O. Williams; *E. effusum* subsp. *simpsonii* (Benth. in DC.) S. Stokes; *E. effusum* subsp. *nelsonii* (L. O. Williams) S. Stokes; *E. microthecum* subsp. *rigidum* (Eastw.) S. Stokes; *E. microthecum* subsp. *intermedium* S. Stokes; *E. microthecum* var. *friscanum* (M. E. Jones) S. Stokes; *E. microthecum* var. *foliosum* (Torr. & Gray) Reveal] is the common expression in the Mojave Desert region of the state but extends northward into the Great Basin portions of Esmeralda, Lander, Eureka, northern Nye, and White Pine cos. It occurs mostly below 2150 m on flats and slopes. The name var. *simpsonii* replaces var. *foliosum* used previously for this entity (Reveal 1971, 1983). The **var. *lapidicola* Reveal** is a dwarfed polygamodioecious subshrub mainly of rocky outcrops and ledges. It is found in Esmeralda, Nye, White Pine, and Lincoln cos. A Jaeger collection (POM) from Potosi Mtn., Clark Co., probably is representative of this variety. A closely related form from Eureka Co. may represent an undescribed expression (see *Ripley & Barneby 9330* and *9333*—CAS). The yellow-flowered expression in Nevada is now restricted to the **var. *ambiguum* (M. E. Jones) Reveal in Munz** [*E. tennelum* var. *erianthum* Gand.; *E. microthecum* var. *expansum* S. Stokes] that occurs in western Nevada from Esmeralda Co. northward into Washoe and Humboldt cos. It is a plant of slopes and ridges in the mountain in the southern part of its range, but of flats and foothills in the northern part of the state. The reference to var. *microthecum* (Reveal 1971) in Humboldt Co. is now considered an error, and these plants should be referred to var. *ambiguum*. It is not unusual to find var. *laxiflorum* and var. *ambiguum* growing together.

2. ***Eriogonum nummulare* M. E. Jones** [*E. kearneyi* Tidestrom; *E. nodosum* var. *kearneyi* (Tidestrom) S. Stokes; *E. dudleyanum* S. Stokes; *E. nodosum* subsp. *monoense* S. Stokes; *E. kearneyi* var. *monoense* (S. Stokes) Reveal; *E. kearneyi* subsp. *monoense* (S. Stokes) Munz ex Reveal]. Kearney's buck-

wheat. A large shrub of sandy places, 1130–1850 m elevation, in saltbush and sagebrush communities, eastern California eastward across the Great Basin portion of Nevada to western Utah, then southward into northwestern Arizona. In Nevada the plant occurs in Esmeralda, Mineral, and Ormsby cos., then eastward to Humdoldt, Nye, and Lincoln cos. As now defined, *E. kearneyi* and its var. *monoense* are reduced to synonymy under *E. nummulare*. Plants similar to the var. *monoense* are found in scattered locations in west central Nevada.

3. *Eriogonum corymbosum* Benth. in DC. Corymb-flowered buckwheat. A widespread and variable shrub from Nevada and Arizona to Colorado and New Mexico represented in Nevada by **var. *aureum* (M. E. Jones) Reveal** [*E. aureum* M. E. Jones; *E. aureum* var. *glutinosum* M. E. Jones; *E. fruticosum* A. Nels.; *E. crispum* L. O. Williams; *E. microthecum* subsp. *aureum* (M. E. Jones) S. Stokes; *E. microthecum* var. *crispum* (L. O. Williams) S. Stokes; *E. corymbosum* var. *glutinosum* (M. E. Jones) Reveal] that is a large yellow-flowered shrub of sandy places of southern Utah and northern Arizona, with a disjunct population near Las Vegas, Clark Co., Nevada. It is in flower from July to mid-October. The name var. *aureum* must now be used over the more familiar var. *glutinosum* because of a recent change in the International Code (Reveal 1983). A specimen of *E. jonesii* S. Wats. gathered by Wheeler (US) is labeled "Nevada" and "1872," no doubt an error because this plant is restricted to northern Arizona, where it is infrequent.

4. *Eriogonum heermannii* Dur. & Hilg. A variable shrub found nearly throughout Nevada except for the extreme northwestern part, on sandy, clayey, or rocky soils often of a limestone origin, 940–2200 m. Flowering from April to October. A desert shrub from southern California eastward through Nevada to Utah and northern Arizona.

Heermann's buckwheat. A large shrub to densely branched subshrub with green, glabrous or sometimes floccose, scabrellous or smooth branches that can be smooth, angled, or ribbed; represented in Nevada by the following varieties:

1. Stems smooth, not scabrous or angled, glabrous or floccose 1
— Stems scabrous or angled, not smooth or glabrous. 4
2(1). Involucres at the tips of the branches not racemosly arranged or only the last two or three so disposed, the inflorescence diffuse, glabrous; northern two-thirds of the state from Nye and Lincoln cos. northward to Humboldt and Elko cos. . . . . var. *humilius*
— Involucres at the tips of the branches racemosely arranged, the inflorescence open, glabrous or floccose 3
3(2). Branches glabrous; common in Clark Co. and adjacent southwestern Nye Co. . . . . var. *clokeyi*
— Branches floccose; rare, McCullough Mts., Clark Co. . . . . var. *floccosum*
4(1). Stems scabrellous but not sharply and deeply angled; mainly in the Great Basin portion of Nevada from Esmeralda and Nye cos. eastward to Eureka, White Pine, and Lincoln cos. . . . . var. *argense*
— Stems scabrellous to scabrous, sharply and deeply angled; mainly in the Mojave Desert portion of Nevada from southern Nye Co. and Clark Co. eastward to southern Lincoln Co. . . . . var. *sulcatum*

The most common expression in Nevada is **var. *humilius* (S. Stokes) Reveal** [*E. heermannii* subsp. *humilius* S. Stokes] that occurs in the Great Basin portion of the state from Nye and Esmeralda cos. north and east to Washoe, Humboldt, and southern Elko cos. It occurs on a variety of soils, but mainly those of volcanic origins. In the Mojave Desert portion of the state is **var. *clokeyi* Reveal**. It is found in southern Nye Co. and Clark Co. and occurs mainly on limestone foothills and slopes. In the McCullough Mts. of southern Clark Co. is

var. *floccosum* Munz [*E. heermannii* subsp. *floccosum* (Munz) Munz]. All of these varieties are well-defined shrubs and usually occur on gravelly soils. The **var. *argense* (M. E. Jones) Munz** [*E. howellii* S. Stokes; *E. heermannii* subsp. *argense* (M. E. Jones) Munz] occurs mainly in the Great Basin region, occurring from Esmeralda and Nye cos. eastward to Eureka, White Pine, and Lincoln cos. The **var. *sulcatum* (S. Wats.) Munz & Reveal** [*E. sulcatum* S. Wats.; *E. heermannii* subsp. *sulcatum* (S. Wats.) S. Stokes] is found mainly in the Mojave Desert region of southern Nye and Lincoln cos. and in Clark Co. The var. *argense* is a small shrub or subshrub, and var. *sulcatum* is a densely branched subshrub. Both occur mainly on limestone cliffs and rocky outcrops.

5. *Eriogonum plumatella* Dur.& Hilg. [*E. palmeri* S. Wats.; *E. nodosum* var. *jaegeri* Munz & Johnst.; *E. plumatella* var. *jaegeri* (Munz & Johnst.) Stokes ex Munz]. Flat-topped buckwheat. A small shrub with glabrous or tomentose branches. Infrequent in extreme southern Clark Co., 1000–1220 m. Flowering from June to November. The species ranges from southern California eastward to extreme southwestern Utah and western Nevada.

6. *Eriogonum fasciculatum* Benth. California buckwheat. Common in the arid Southwest and northwestern Mexico with only **var. *polifolium* (Benth. in DC.) Torr. & Gray** [*E. polifolium* Benth. in DC.; *E. revolutum* Goodding; *E. fasciculatum* subsp. *polifolium* (Benth. in DC.) S. Stokes; *E. fasciculatum* var. *revolutum* (Goodding) S. Stokes] found in Nevada. A low shrub mainly of the Mojave Desert of California and northern Baja California, Mexico, eastward across southern Nevada to southwestern Utah and western Arizona. Flowering throughout the year. The variety occurs from southern Esmeralda Co. eastward across southern Nye Co. to southern Lincoln Co. on the edge of the Great Basin southward to Clark Co., 520–1800 m elev. Flowering from late March to September.

7. *Eriogonum desertorum* (Maguire) R. J. Davis [*E. chrysocephalum* subsp. *desertorum* Maguire; *E. brevicaule* Nutt. var. *desertorum* (Maguire) Welsh] Cold desert buckwheat. A compact cespitose perennial with tomentose scapes and yellow flowers of desert ranges and flats in northeastern Nevada and adjacent northwestern Utah, 1700–2330 m elev. Flowering from late May to mid-July. In Nevada the species is found in Eureka, White Pine, and Elko cos. where it often occurs on clay slopes and flats.

8. *Eriogonum ochrocephalum* S. Wats. Ocher-flowered buckwheat. A compact cespitose perennial with glabrous, glandular, or tomentose scapes and yellow flowers of northwestern Nevada and adjacent northeastern California northward into southeastern Oregon and southern Idaho. Flowering from May to late June at lower elevations and to early September at higher elevations. The **var. *ochrocephalum*** [*E. nevadense* Gand.] is locally common on clayey outcrops and flats of Lyon and Storey cos. northward through Washoe Co. to the Oregon line. This variety occurs 1310–2470 m elevation, reaching its highest elevations on Peavine Mtn. The scapes of this variety are mainly glabrous, but occasional specimens in Washoe Co. have glandular scapes. The newly proposed **var. *alexanderae* Reveal,** characterized by its floccose scapes, occurs mainly east of var. *ochrocephalum*, being found from Mineral Co. northward to Washoe and Pershing cos. It occurs on clay outcrops 1430–2070 m elevation and flowers from late May to early July.

9. *Eriogonum prociduum* Reveal Austin's buckwheat. A compact cespitose perennial with glabrous scapes and yellow flowers known only from northern Washoe Co., Nevada, and adjacent Lassen Co., California, northward to Lake Co., Oregon, 1400–2450 m elevation. Flowering from May to early July. The Nevada site is vouchered by *Tiehm 8056* (MARY). It is mentioned in the latest installment of the rare and endangered species report for Nevada (Pinzl 1983).

10. *Eriogonum lewisii* Reveal Lewis' buckwheat. A compact cespitose perennial with floccose scapes and yellow flowers known only from northeastern Nevada and adjacent northwestern Utah. In Nevada the species is known from the high mountains of Elko Co. where it occurs above 2400 m elevation. It flowers from late June to early September.

11. *Eriogonum crosbyae* Reveal Crosby's buckwheat. A compact cespitose perennial with floccose scapes and yellow flowers known only from northwestern Nevada and adjacent southeastern Oregon. In Nevada the species occurs on clay outcrops in northern Washoe and extreme southern Humboldt cos., where it occurs 1600–1700 m elevation. It flowers from late May through July. This species, previously known only from Oregon (Reveal 1981), was first discovered by *Tiehm & Birdsey 5013* (MARY) in Humboldt Co. and more recently in Washoe Co. by Tiehm alone (*8040, 8043*—MARY).

12. ***Eriogonum rosense*** **Nelson & Kennedy** [*E. ochrocephalum* var. *agnellum* Jeps.; *E. ochrocephalum* subsp. *agnellum* (Jeps.) S. Stokes]. Mt. Rose buckwheat. A compact cespitose perennial with glandular scapes and yellow flowers common in the Sierra Nevada, and Sweetwater and White mountains of California northward into Nevada from Esmeralda Co. northward to Washoe Co., where it occurs (2000) 2440–3300 m elevation. It flowers from July to early September.

13. ***Eriogonum beatleyae*** **Reveal** Beatley's buckwheat. A compact cespitose perennial with glandular and eglandular villous scapes and yellow to cream-colored flowers of extreme east central California and Nevada. Local and scattered on clayey soils in west central and central Nevada from northern Nye Co. northward to Eureka and Lander cos., then westward to Churchill and Mineral cos. 1700–2320 (2750) m elevation. It flowers from May to August. Since this species was described (Reveal 1972), *E. beatleyae* has been found in a variety of sites in Nevada. For the most part the species is found at elevations lower than that of *E. rosense*, but a recent collection (*Ertter & Strachan 2804*—MARY) from the north end of the Monitor Range at 2750 m elevation is probably best referred to *E. beatleyae* rather than *E. rosense* as I originally annotated the collection. Cream-colored specimens of *E. beatleyae* occur in Nye, Churchill, Lander, and Eureka cos.

14. ***Eriogonum anemophilum*** **Greene** Wind-loving buckwheat. A compact cespitose perennial with floccose scapes and white flowers endemic to Nevada; restricted to the West Humboldt Mts. of Pershing Co. and the Jackson Mountains and Sonoma Range of Humboldt Co. 2500–2800 m elevation. Flowering from June to August.

15. ***Eriogonum tiehmii*** **Reveal** Tiehm's buckwheat. A compact cespitose perennial with floccose scapes and cream-white glandular flowers endemic to Nevada; restricted to white clay hills near Cave Springs, Esmeralda Co., 1830 m elevation. Flowering from early May to late July. This new species may be quickly recognized by its glandular tepals and its longer, acutely toothed involucres. The floccose scapes distinguishes Tiehm's buckwheat from the cream-colored specimens of *E. beatleyae*.

16. ***Eriogonum kingii*** **Torr. & Gray** King's buckwheat. A compact cespitose perennial with floccose to glabrous scapes and greenish yellow to pale yellow flowers endemic to the Ruby Mts. and East Humboldt Range of Elko Co., and in the Cherry Creek Range of northern White Pine Co., Nevada, 2400–3170 m elevation. It flowers from June to August.

17. ***Eriogonum argophyllum*** **Reveal** Sulphur Hot Springs buckwheat. A compact perennial with floccose scapes and yellow flowers endemic to mineralized soil at Sulphur Hot Springs, Elko Co., Nevada. It occurs at 1850 m elevation and flowers from June to July.

18. ***Eriogonum gracilipes*** **S. Wats.** [*E. kennedyi* subsp. *gracilipes* (S. Wats.) S. Stokes; *E. ochrocephalum* var. *gracilipes* (S. Wats.) J. T. Howell]. White Mountain buckwheat. A compact perennial with glandular-hairy scapes and white to reddish flowers of the White Mountains and adjacent portions of the Sierra Nevada of east central California and adjacent Esmeralda Co., Nevada. It is found 3000–4000 m elevation, but in Nevada it is at 3200 m. The plant flowers from July to September.

19. ***Eriogonum holmgrenii*** **Reveal** Holmgren's buckwheat. A compact perennial with floccose and stipitate-glandular scapes and white to reddish flowers endemic to the Snake Range of White Pine Co., Nevada, where it occurs 2870–3700 m elevation. It flowers from July to September.

20. ***Eriogonum villiflorum*** **A. Gray** Shaggy-haired buckwheat. A compact perennial of 10–20 rosettes, prostrate villous flowering stems, and densely pilose white flowers with glabrous achenes. Local and infrequent in western Utah and eastern Nevada on gravelly flats and slopes 1900–2200 m elevation. In Nevada the species is known only from White

Pine, Lincoln, Nye, and Eureka cos. It flowers from May to early June.

21. *Eriogonum shockleyi* S. Wats. A variable species rather common throughout the Intermountain Region and along its immediate borders in the western United States, mostly on gravelly, clayey or sandy soils, or on rocky outcrops and ledges, 730–2750 m elevation. Flowering from May through August.

Shockley's buckwheat. Cespitose to pulvinate perennials with up to a hundred or more rosettes with erect, floccose to tomentose stems, and white, reddish or yellow densely pilose flowers and pubescent achenes. The **var. *shockleyi*** [*E. villiflorum* var. *candidum* M. E. Jones; *E. acaule* var. *shockleyi* (S. Wats.) M. E. Jones; *E. pulvinatum* Small; *E. shockleyi* subsp. *candidum* (M. E. Jones) S. Stokes] is common in Nevada and ranges from Mineral and Esmeralda cos. eastward across Nye Co. to Lincoln Co., and northeastwardly to Elko Co. This plant occurs mainly on gravelly to clayey soils throughout this range 1500–2100 m elevation. Both white- and yellow-flowered specimens belong to this variety. A population at Baking Powder Flat in Spring Valley, White Pine Co., is on deep moving sand, and the resulting plants are large, open, loose mats (*Emmel 199*—CAS; *Reveal 4845*—MARY, US and elsewhere). This may prove to represent a new and as yet undescribed variety. A M. E. Jones collection (POM) gathered at Pioche, Lincoln Co., 31 August 1912, is similar to *E. soredium* Reveal which is now known only from Beaver Co., Utah. Attempts to rediscover specimens similar to the Jones collection have failed, and the extant specimen is not suitable to adequately determine its identity.

22. *Eriogonum wrightii* Torr. ex Benth. in DC. A highly variable cespitose to subshrubby or shrubby perennial of western and southern Nevada on sandy to gravelly soil, 1280–2450 m. Flowering from late June to early November. Widespread in North America from northern California and western Nevada southward to Baja California, Mexico, eastward through Arizona and New Mexico to western Texas southward to central Mexico.

Wright's buckwheat. Low shrubs or subshrubs with small elliptic leaves and white flowers. The **var. *wrightii*** is locally common in the McCullough Mts. and infrequent to rare in the Spring Mts., Clark Co. It is a distinct shrub and occurs from extreme southeastern California eastward across southern Nevada and southwestern Utah to Texas southward to central Mexico. The **var. *subscaposum* S. Wats.** [*E. wrightii* subsp. *subscaposum* (S. Wats.) S. Stokes] is a low subshrub of the mountains of western Nevada from the Sweetwater Mts. of Mineral Co. (and to be expected in the Nevada portion of the White Mts.) northward to southern Washoe Co. Other varieties are found in California and adjacent western Mexico.

23. *Eriogonum panamintense* Morton An erect herbaceous perennial with large leaves and white flowers on loam to gravelly soil in the desert ranges of southwestern Nevada and adjacent southeastern California, 1830–2600 m. Flowering from mid-June through September.

Panamint buckwheat. The **var. *panamintense*** [*E. reliquum* S. Stokes; *E. racemosum* var. *desertorum* S. Stokes] with numerous solitary involucres and large elliptic to ovate or obovate leaves is rather common in the mountains of southwestern Nevada from Mineral and extreme western Nye Co. southward to the Spring Mts. and Sheep Range of Clark Co. This variety is similar to *E. rupinum*. The **var. *mensicola* (S. Stokes) Reveal in Munz** [*E. panamintense* subsp. *mensicola* (S. Stokes) Munz] with few solitary involucres and generally rotund leaves is restricted to the Sheep Range of Clark Co., Nevada, and the Death Valley region of Inyo Co., California.

24. *Eriogonum rupinum* Reveal Canyon buckwheat. A stout erect perennial herb with large, oblong to elliptic leaves and 3–5 solitary involucres racemosely arranged at the tips of the branches, on gravelly to sandy (rarely clayey) soil on the foothills and canyon bottoms 1830–2600 (3489) m, in the mountains of central Nevada to eastern California. Flowering mainly from July to early October. In Nevada, the species occurs mostly below 3100 m from Lander and Nye cos. westward to Mineral and Esmeralda cos. It is a stouter plant than *E. panamintense*.

25. *Eriogonum racemosum* Nutt. [*E. orthocladon* Torr. in Sitgr.; *E. obtusum* Benth. in DC.]. Redroot buckwheat. An erect, graceful perennial herb with large, variably shaped leaves on sandy to gravelly soil from northwestern New Mexico and southwestern Colorado westward across northern Arizona and most of Utah to central Nevada. Mostly 1220–2500 m, and flowering from June to October. In Nevada the species is rather common in the desert ranges of Nye, White Pine, and Lincoln cos., but infrequent and local in the Sheep Range, Clark Co.

26. *Eriogonum nudum* Dougl. ex Benth. A highly variable perennial herb with numerous varieties. Widespread and common in the Pacific coast states from Washington to Baja California Norte eastward to western Nevada from sea level to 3400 m. Flowering from April through September.

Naked-stemmed buckwheat. Erect perennial herbs with small, variably shaped leaves and glabrous to tomentose stems; currently represented in Nevada by four poorly defined varieties. The montane expression is the **var. *deductum* (Greene) Jeps.** [*E. deductum* Greene] characterized by glabrous stems and solitary involucres. It occurs from Mineral Co. northward in the Sierra Nevada and adjacent ranges to southern Washoe Co. The **var. *nudum*** [*E. latifolium* subsp. *nudum* (Dougl. ex Benth.) S. Stokes] is rare in Nevada. It is known only from two old Nevada collections (*Kennedy* 962 and *Peterson* 279—NESH) gathered near Verdi, Washoe Co. This variety occurs from Washington and Oregon southward into northern California. It is characterized by clustered involucres and glabrous stems. The distinction between the two variants in low elevation populations is generally blurred in the Sierra Nevada, and the difficulties are repeated in Nevada. The **var. *oblongifolium* S. Wats.** [*E. harfordii* Small; *E. sulphureum* Greene; *E. capitatum* A. A. Heller; *E. latifolium* subsp. *sulphureum* (Greene) S. Stokes] occurs from Douglas Co. northward to southern Washoe Co. This variant ranges from southern Oregon to northern California and adjacent Nevada. It is characterized by a tomentose stem and pubescent flowers. The poorly differentiated **var. *pubiflorum* Benth. in DC.** occurs in northern Washoe Co. and southwestern Humboldt Co. It differs from var. *oblongifolium* in having glabrous stems along with its pubescent flowers. At present only the yellow-flowered expression of var. *pubiflorum* has been discov ered in Nevada. The **var. *gramineum* (S. Stokes) Reveal** is to be sought in the warm desert mountain ranges of extreme southwestern Nye Co. that border Death Valley. It has inflated, glabrous stems and yellow, pubescent flowers, and it is found on limestone outcrops. All occur 1500–2500 m elevation in Nevada and flower from June through September.

27. *Eriogonum elatum* Dougl. ex Benth. A tall, erect, perennial herb with large lanceolate to lance-ovate leaves and slightly pubescent flowers of Washington and Idaho south to central California and central Nevada 1200–2900 m. Flowering mainly from May through August.

Tall buckwheat. The **var. *elatum*** [*E. elatum* var. *erianthum* Gand.] occurs in the mountains and foothills of Nevada from Nye Co. northward. It is often locally common, although individual populations can be rather scattered. The **var. *villosum* Jeps.**, characterized by its pubescent stems, is restricted in Nevada to the foothills of the Sierra Nevada from Douglas Co. northward to southern Washoe Co. It is rather infrequent.

28. *Eriogonum ovalifolium* Nutt. A widespread and highly variable, compact perennial herb of many ecological niches found in the Nevada and throughout the western United States and southwestern Canada, 920–3700 m. Flowering from April to August.

Cushion buckwheat. A compact to cespitose herb with pubescent scapes and white to yellow or reddish, strongly dimorphic tepals (except in some high elevation expressions) in capitate terminal inflorescences mostly in the sagebrush communities throughout the state; consisting of the following varieties:

1. Leaves mostly more than 1 cm long; scapes 5–30 (or more) cm long; involucres (3.5) 4–7 mm long, turbinate; flowers (3) 4–7 mm long; plants mostly below 2450 m 2

— Leaves mostly less than 1 cm long; scapes up to 6 (10) cm long; involucres 2.5–4.5 mm long, turbinate-campanulate; flowers 2.5–4 mm long; plants mostly above 2450 m except in the Mt. Rose area of west central Nevada 3

2(1). Flowers white .... var. *ovalifolium*
— Flowers yellow .... var. *nevadense*

3(1). Flowers white 4
— Flowers yellow; endemic to the Toquima and Toiyabe ranges of Nye Co. .... var. *caelestinum*

4(3). Leaves without brown-edged margins; plants mainly of high elevation sites 5
— Leaves with distinct brown-edged margins; plants mainly of low elevation sites 6

5(3). Leaves densely white-tomentose on both surfaces; widespread and common .... var. *nivale*
— Leaves greenish white pubescent at least on the upper surface; infrequent, Elko Co. .... var. *depressum*

6(4). Leaves densely lanate tomentose on both surfaces, the tomentum brownish, the brown edge pronounced; plants of the Mt. Rose area in Carson City and southern Washoe cos. .... var. *eximium*
— Leaves white-tomentose on both surfaces, the tomentum whitish, the brown edge thin; plants endemic to the Steamboat Springs area of southern Washoe Co. .... var. *williamsiae*

The **var. *ovalifolium*** [*E. purpureum* (Nutt.) Benth. in DC.; *E. davisianum* S. Stokes] is the low elevation expression with white flowers, and **var. *nevadense* Gand.** [*E. orthocaulon* Small; *E. ovalifolium* var. *celsum* A. Nels.; *E. ovalifolium* var. *orthocaulon* (Small) C. L. Hitchc.] has yellow flowers. The var. *ovalifolium* is widespread throughout the Intermountain Region section of Nevada, and var. *nevadense* occupies essentially the same area although it is more common in the north than in the south. Two other low elevation variants are **var. *eximium* (Tidestrom) J. T. Howell** [*E. eximium* Tidestrom; *E. ovalifolium* subsp. *eximium* (Tidestrom) S. Stokes] and **var. *williamsae* Reveal.** Both are found in the Mt. Rose area of southern Washoe Co. and adjacent Carson City Co., with var. *williamsae* restricted to the Steamboat Springs area, Washoe Co. The former has larger leaves with distinctly brown-edged leaf-blades, and the latter has small leaves arranged in densely compact mats. Three high-elevation variants occur in Nevada. The most common phase is **var. *nivale* (Canby in Cov.) M. E. Jones** [*E. nivale* Canby in Cov.; *E. rhodanthum* Nels. & Kenn.] which has densely white-tomentose leaves and white flowers. It is rather common throughout the state. The **var. *depressum* Blank.,** with its greenish white tomentose leaves and white flowers, is infrequent in Elko Co. The high elevation yellow-flowered variety is the **var. caelestinum Reveal**, that is restricted to the Toquima and Toiyabe ranges of northern Nye Co.

29. *Eriogonum strictum* Benth. A branched, erect perennial herb with white or yellow dimorphic tepals ranging from northern Washington south to northern California, and eastward to western Montana south to northern and northwestern Nevada mainly below 2600 m. Flowering from May through August.

Blue Mountain buckwheat. Erect perennial herbs with branched inflorescences bearing white or yellow dimorphic tepals; represented in Nevada by two varieties of **subsp. *proliferum* (Torr. & Gray) S. Stokes** differing chiefly on flower color. The **var. *anserinum* (Greene) R. J. Davis** [*E. anserinum* Greene; *E. strictum* subsp. *anserinum* (Greene) S. Stokes; *E. ovalifolium* subsp. *flavissimum* S. Stokes; *E. strictum* var. *flavissimum* (S. Stokes) C. L. Hitchc.; *E. proliferum* subsp. *anserinum* (Greene) Munz] has yellow flowers and is the common expression. It is found from western Elko Co. across Humboldt Co. to Storey and Washoe cos. The **var. *proliferum* (Torr. & Gray) Reveal** [*E. proliferum* Torr. & Gray; *E. cusickii* Gand. var. *californicum* Gand.] is white flowered and occurs in Elko Co., although a Kennedy collection (*1381*—NESH, UTC) presently referred to this variety has been found at Broncho Creek in Washoe Co. This species differs from *E.*

ovalifolium in having branched rather than capitate inflorescences.

30. *Eriogonum saxatile* S. Wats. [*E. bloomeri* Parish; *E. stokesae* M. E. Jones; *E. saxatile* var. *stokesae* (M. E. Jones) S. Stokes ex Jones; *E. saxatile* subsp. *multicaule* S. Stokes]. Rock buckwheat. A low, loosely to densely matted perennial herb with broadly obovate to rotund leaves and white to cream flowers on elongated, winged stipes of sandy, decomposing soil in desert ranges of southern California and adjacent Nevada, 1220–3400 m. Flowering from May to late July. In Nevada the species is rather local in Nye and southern Esmeralda cos.

31. *Eriogonum umbellatum* Torr. A large and exceedingly complex species found throughout most of western North America from southern Canada to near the Mexican border on a wide variety of habitat and from near sea level to nearly 4000 m. Flowering from May to October. The species is composed of more than 30 varieties, several of which have as yet to be described formally. In Nevada the following variants are known:

1. Primary branches of the inflorescences simple, not branched 1

— Primary branches of the inflorescences branched 9

2(1). Flowers bright yellow 3

— Flowers mostly whitish to red, occasionally pale yellow; plants subshrubs (see also the shrubby var. *vernum*) 7

3(2). Leaves pubescent at least below on plants in full anthesis 4

— Leaves glabrous on both surfaces on plants in full anthesis 6

4(3). Leaves densely tomentose on the lower surface even in fruiting plants; plants low, spreading subshrubs; Elko Co. . . . . var. *umbellatum*

— Leaves sparsely pubescent on both surfaces or only glabrate on the upper surface on plants in full anthesis; plants upright to spreading subshrubs or shrubs 5

5(4). Flowers less than 7 mm long, always sulphur yellow; involucral tubes 2–3.5 mm long; plants late spring to summer flowering subshrubs or small shrubs, common throughout nearly all of Nevada except for Elko, Clark, and perhaps White Pine cos. . . . . var. *nevadense*

— Flowers 6–10 mm long, sulphur yellow or infrequently cream colored; involucral tubes 1.5–2.5 mm long; plants spring flowering shrubs endemic to Nye Co. . . . . var. *vernum*

6(3). Inflorescences umbellate or merely subcapitate; widespread at lower elevations from eastern Humboldt Co. south to Nye Co., then eastward to Elko and White Pine cos. . . . . var. *aureum*

— Inflorescences capitate or nearly so; rare in subalpine and alpine habitats in the Ruby and East Humboldt mts. . . . . var. *porteri*

7(2). Leaves sparsely tomentose to glabrous on both surfaces or with the tomentum slightly more below than above; flowers 3–8 mm long, whitish, cream-colored, or pale yellow to reddish brown to rose or pink with large, colored midribs 8

— Leaves densely tomentose below, bright green to olive-green and floccose to glabrous above; flowers cream colored, 3–7 mm long; to be expected in Elko Co. but currently unknown for Nevada . . . . var. *majus*

8(7). Flowers cream colored to pale yellow with tannish midribs; mostly northern Nevada from Nye Co. northward. . . . . var. *dichrocephalum*

— Flowers reddish brown to pink with reddish to purplish midribs; Spring Mts., Clark Co., and northward to extreme southern Nye Co. and adjacent southwestern Lincoln Co. . . . . var. *versicolor*

9(1). Flowers yellow or strongly yellowish 10

— Flowers cream colored or reddish brown to rose or pink, not bright yellow 11

10(9). Leaves densely tomentose below, thinly floccose or more commonly glabrous and green above; flowers bright yellow, (5) 6–8 mm long; Sierra Nevada from Lake Tahoe area northward to southern Washoe Co. . . . . var. *furcosum*

— Leaves evenly thinly pubescent to glabrous on both surfaces; flowers bright yellow, 6–7 mm long; desert ranges from Esmeralda Co. south to Clark Co. eastward to Lincoln and White Pine cos. . . . . var. *subaridum*

11(9). Flowers cream colored or whitish; plants forming low shrubs or subshrubs up to 8 dm tall; Lincoln and White Pine cos. . . . . var. *juniporinum*

— Flowers reddish brown to rose or pink with large reddish or purplish midribs; plants forming low, spreading, matted subshrubs mostly less than 2 dm tall; Spring Mts., Clark Co. . . . . var. *versicolor*

Sulphur-flower. The Rocky Mountain expression, **var. *umbellatum***, occurs in Nevada only in the high mountains of Elko Co., it being found typically in the Ruby and East Humboldt mts., but only infrequently in the mountains to the north. More widespread in the state is the glabrous-leaved expression **var. *aureum* (Gand.) Reveal** [*E. neglectum* Greene; *E. azaleastrum* Greene] that differs from the typical variant only in this single feature; it is generally found at a lower elevation than var. *umbellatum*. The var. *aureum* occurs from eastern Humboldt Co. south to northern Nye Co. eastward. The high elevation expression related to var. *aureum* is **var. *porteri* (Small) S. Stokes** [*E. porteri* Small] that occurs in the East Humboldt and Ruby mts. generally above 2750 m elevation. All three variants are more common in the Rocky Mountains to the east and reach their most westward point of distribution in Nevada.

The most common phase of *Eriogonum umbellatum* in Nevada is the western **var. *nevadense* Gand.** [*E. reclinatum* Greene; *E. heracleoides* var. *virde* Gand.; *E. umbellatum* var. *californicum* Gand.]. It is found throughout the Great Basin portion of Nevada from Nye Co. northward. It flowers mainly in the summer, forming well-defined subshrubs in most populations and is typically found at 1400–2900 m elevation. The variety is common in the mountains of western Nevada, but it becomes less frequent in the central and eastern portions of the state. At times, in Elko Co. for example, the differences between var. *umbellatum* and var. *nevadense* are obscured. The early spring-flowering expression related to var. *nevadense* is the northern Mojave Desert–southern Great Basin expression **var. *vernum* Reveal.** This plant, typically a large and well-defined shrub, is in full anthesis in May and continues to blossom into June. Bright yellow-flowered plants are common, but on the Nevada Test Site scattered populations are dominated by pale yellow-flowered individuals. At higher elevations, and mainly in the northern half of the state, is the cream-colored expression close to var. *nevadense*, the **var. *dichrocephalum* Gand.** [*E. aridum* Greene; *E. umbellatum* subsp. *aridum* (Greene) S. Stokes; *E. umbellatum* var. *aridum* (Greene) C. L. Hitchc.]. Unlike the subshrubby var. *nevadense*, the var. *dichrocephalum* is often more similar in habit to the spreading and mat-forming var. *umbellatum*. The var. *nevadense* occurs from the Sierra Nevada of California northward to southern Oregon and eastward across Nevada, and the var. *vernum* is endemic to Nye Co., Nevada. Both are found mostly below 2440 m elevation. The var. *dichrocephalum*, on the other hand, ranges from southeastern Oregon southward in the Sierra Nevada to Inyo Co., California, then eastward across Nevada and Utah to extreme western Colorado. This variety can occur above 3100 m but is most common 2200–2800 m elevation. Yet to be discovered in Nevada is the widespread, northern expression, **var. *majus* Hook.** [*E. subalpinum* Greene; *E. umbellatum* subsp. *majus* Piper; *E. umbellatum* subsp. *subalpinum* (Greene) S. Stokes; *E. umbellatum* var. *subalpinum* (Greene) R. J. Davis]. This is a mat-forming perennial with pale, cream-colored tepals, and olive-green leaves that are glabrous (or nearly so) on the upper surface. The var. *majus* occurs from British Columbia, Canada, southward to southern Oregon, then eastward across Idaho to Alberta and southward in the Rocky Mts. to Colorado.

The remaining variants of *Eriogonum umbellatum* differ from those mentioned above in having branched flowering inflorescences with each node subtended by a whorl of bracts. The majority of these expressions are found in the southern part of the state. The one exception is the **var. *furcosum* Reveal** that is restricted to the Sierra Nevada portion of Nevada in the Lake Tahoe region. This expression was previously referred in the literature to the more northern and less shrubby **var. *ellipticum* (Nutt.) Reveal** [*E. stellatum* Benth.; *E. ellipticum* Nutt.; *E. umbellatum* var. *stellatum* (Benth.) M. E. Jones; *E. umbellatum* subsp. *stellatum* (Benth.) S. Stokes] (see Reveal 1983). The most common expression in southern Nevada is the **var. *subaridum* S. Stokes** [*E. biumbellatum* Rydb.; *E. ferrissii* A. Nels.; *E. umbellatum* subsp. *ferrissii* (A. Nels.) S. Stokes; *E. umbellatum* subsp. *subaridum* (S. Stokes) Munz]. It differs from the var. *furcosum* in the degree of pubescence on the leaves. The var. *subaridum* ranges from Esmeralda Co. eastward across the state to Eureka and White Pine cos., then southward to Lincoln and Clark cos. In Clark Co., the var. *subaridum* is restricted to the Sheep and Spring mts. The variety occurs at 1830–2800 m elevation. A cream-colored expression related to the var. *subaridum* is the newly proposed **var. *juniporinum* Reveal,** which occurs in Lincoln and White Pine cos. and reappears again in the desert ranges of San Bernardino Co. in southeastern California. In Nevada var. *juniporinum* occurs at 1830–2500 m elevation. Also in the southern desert ranges is the rose to pink- or reddish-tepaled var. *versicolor* S. Stokes, a montane phase that may or may not have a compound inflorescence. It ranges from northern Clark and southern Nye cos., Nevada, westward to eastern Inyo and southern Mono cos., California. It occurs at 1980–2750 m elevation.

32. ***Eriogonum heracleoides* Nutt.** Wyeth's buckwheat. A matted perennial herb with branched flowering inflorescences, cream or whitish yellow flowers, and a whorl of bracts about midlength along the pubescent, erect, flowering stem. The species occurs from southern British Columbia, Canada, southward to northern California, then east to western Montana, Wyoming, and Colorado. Common in the mountains of northern Nevada from northern Washoe Co. eastward to Elko Co. and southward into Lander and northern White Pine Co. at 1740–3100 m elevation. Flowering from June through August. A Stokes collection (OKL) from Verdi, Washoe Co., is likely mislabeled.

33. ***Eriogonum sphaerocephalum* Dougl. ex Benth.** A variable species of the northwestern United States from Washington and Idaho southward to northern California and northern Nevada.

Round-headed buckwheat. A low, woody subshrub with yellow or ochroleucous, villous-tomentose flowers and achenes with a slightly pubescent beak; mostly on volcanic soils 920–2140 m elevation. Flowering from May to mid-July. The yellow-flowered expression is the **var. *sphaerocephalum*.** It occurs from Washoe Co. southward to the Carson City area (*M. E. Jones s.n.*—POM) eastward across Humboldt and Eureka cos. to Elko Co., mostly at 1430–1950 m elevation. The pale-flowered expression, **var. *halimoides* S. Stokes,** is restricted to northern Washoe Co., northwestern Humboldt Co., and northern Elko Co. It occurs mostly at 1740–2130 m elevation.

34. ***Eriogonum douglasii* Benth. in DC.** Douglas' buckwheat. Low, spreading, matted, and cespitose perennial herbs with yellow to ochroleucous, densely to sparsely villous-tomentose flowers, a pubescent, 3-angled beak, and a whorl of leaves about midlength along the flowering stems. The species ranges mostly in the sagebrush and woodland communities of central Washington south to east central California and western Nevada; it occurs at 610–2450 m elevation. The Nevada expression is the yellow-flowered **var. *douglasii*** [*E. caespitosum* var. *douglasii* (Benth. in DC.) M. E. Jones; *E. caespitosum* subsp. *douglasii* (Benth. in DC.) S. Stokes]. It is known only from the Peavine area of Washoe Co., where it occurs at 1600–2140 m elevation. Flowering mainly from April to late July.

35. ***Eriogonum caespitosum* Nutt.** [*E. andinum* Nutt., *E. sericoleucum* Greene ex Tidestrom; *E. sphaerocephalum* var. *sericoleucum* (Greene ex Tidestrom) S. Stokes]. Cespitose buckwheat. Low, compact, cespitose peren-

nial herbs with a single involucre atop the scapose flowering stem bearing yellow, densely pilose to villous-pubescent flowers, and glabrous to sparsely pubescent achenes. Widespread and common from eastern California across Nevada to northern Utah and northwestern Colorado, and north to southeastern Oregon, southern Idaho, western Montana, and western Wyoming. In Nevada the species is common throughout the Intermountain Region portion of the state. It occurs at 1400–3400 m elevation. Flowering from May through August.

36. *Eriogonum marifolium* Torr. & Gray Marum-leaved buckwheat. Low, spreading, loosely matted, dioecious perennial herb with green to olive-green leaves and numerous nonrooting caudices, the flowers yellow, glabrous, with those of the male plants smaller than the female plants. Common in sandy or pumice soils in the Sierra Nevada of California northward to central Oregon, and eastward to Humboldt Co., Nevada, mostly 1070–3400 m elevation. Flowering from June to August. In Nevada the species occurs in the Sierra Nevada portion of the state and is isolated on the Pine Forest Range of western Humboldt Co., mostly 2000–2930 m elevation. The closely related Gray-leaved buckwheat, *E. incanum* Torr. & Gray, which is characterized with densely pubescent leaves, is not known to occur in Nevada but is to be expected in the Sierra Nevada portion of the state.

37. *Eriogonum latens* Jeps. [*E. monticola* S. Stokes]. Onion-flowered buckwheat. Low, compact perennial herbs with short-pilose leaves and an erect, slender, essentially glabrous flowering scape bearing a single cluster of involucres with numerous cream to pale yellow flowers. Local and infrequent in the White Mts. of Esmeralda Co., Nevada, southward to the Inyo Mts. of Inyo Co., California, and along the eastern Sierra Nevada in northern Inyo Co., mostly 2000–3400 m elevation. Flowering from late June to late August.

38. *Eriogonum lobbi* Torr. & Gray A variable species of the numerous soil types in the mountains of northern and eastern California, and in western Nevada, that occurs mostly at 1310–3700 m elevation. Flowering from June through August.

Lobb's buckwheat. Low, spreading, small to robust, compact to densely matted perennial herbs with stoutish caudex branches bearing prostrate to decumbent or weakly erect flowering stems with large (5–15 mm long), solitary involucres bearing white to rose, glabrous flowers. The high elevation phase in Nevada is **var. *lobbii*** [*E. lobbii* var. *minus* Torr. & Gray] that occurs in the Sierra Nevada portion of the state in Washoe Co. The plant may be found at approximately 2150–2870 m elevation on granitic soils. The more common expression in Nevada is the endemic **var. *robustum* (Greene) M. E. Jones** [*E. robustum* Greene]. This phase is much more robust, with larger leaves, involucres, and flowers and erect or nearly so flowering stems. It occurs on altered andersite soils in Storey and Washoe cos. at 1310–2440 m elevation.

39. *Eriogonum inflatum* Torr. & Frem. Desert trumpet. A highly variable plant of arid regions of western North America from California eastward to Colorado southward to northwestern Mexico mostly on sandy, volcanic soils below 2100 m elevation. Flowering nearly throughout the year but mostly from March to October. Our expression, **var. *inflatum*,** is an annual or perennial herb with inflated stems and branches bearing numerous, erect, filiform to capillary peduncles of 5-toothed involucres and yellow, pubescent flowers. The variety is the common expression in Nevada; it may be found nearly throughout the state except the northernmost tier of counties. In southern Arizona southward is the **var. *deflatum* I. M. Johnston.** In northeastern Utah and adjacent states is the **var. *fusiforme* (Small) Reveal.** The first two varieties are first-year flowering perennials, but the latter is strictly an annual.

40. *Eriogonum contiguum* (Reveal) Reveal [*E. inflatum* var. *contiguum* Reveal]. Ash Meadow buckwheat. Erect annual herbs with slender, basally glandular stems and branches bearing numerous erect to spreading capillary peduncles bearing 5-toothed involucres and yellow, pubescent flowers. The species is restricted to the Mojave Desert region from Ash Meadows southward to the Pahrump Valley area of southern Nye Co., Nevada, then westward to the Death Valley region south to Tecopa, Inyo Co., California. It is found from near sea level to 762 m elevation. Flowering from April to late June.

41. *Eriogonum trichopes* Torr. Little trumpet flower. Erect annual herbs with slender or inflated, glabrous or occasionally basally glandular stems and branches bearing numerous, erect capillary peduncles of 4-toothed involucres and yellow, pubescent flowers. The species ranges from southern California, Nevada, and Utah southward to northwestern Mexico and eastward to southern New Mexico. It occurs from below sea level to 2000 m elevation and flowers throughout the year. In Nevada the **var. *trichopes*** [?*E. cordatum* Torr. & Frem.; *E. trichopodium* Torr. ex Benth.; *E. trichopodium* var. *minor* Benth. in DC.; *E. trichopes* subsp. *cordatum* (Torr. & Frem.) S. Stokes] occurs mainly in the Mojave Desert portion of the state from southern Nye and Lincoln cos. southward to Clark Co., 300–1770 m elevation. Flowering mainly from late March to early July. The Fremont collection of *E. cordatum*, described prior to that of *E. trichopes*, has been lost and the description is not clear enough to determine its actual identity. It is possible this is an early name for *E. trichopes* or *E. contiguum*. It is not likely an earlier name for *E. glandulosum*. All three species occur in the eastern Mojave Desert area of California where the type of *E. cordatum* was gathered.

42. *Eriogonum howellianum* Reveal Howell's buckwheat. Low, spreading, pilose-hirsutulous and glandular annual herbs with ascending peduncles bearing turbinate-campanulate involucres with dense pilose, yellow flowers. Local and rare on dry sandy soil in the desert ranges of the Great Basin from western Utah eastward across Nevada from Elko, White Pine, and Lincoln cos. to Nye and north central Clark cos., mostly 1500–1900 m elevation. Flowering from late June through August.

43. *Eriogonum glandulosum* (Nutt.) Nutt. ex Benth. in DC.[*E. trichopes* subsp. *glandulosum* (Nutt.) S. Stokes; *E. glandulosum* var. *carneum* J. T. Howell; *E. carneum* (J. T. Howell) Reveal in Munz]. Gambel's buckwheat. Low, spreading, pilose-hirsutulous and glandular annual herbs with deflexed peduncles bearing narrowly turbinate involucres with dense pilose, white to pinkish flowers. Local and rare on sandy soil in the desert ranges of the northern Mojave Desert from southwestern Nye and northwestern Clark cos., Nevada, westward into eastern Inyo Co. and northeastern San Bernardino cos., California. The species occurs at 880–1600 m elevation. Flowering from June through August.

44. *Eriogonum esmeraldense* S. Wats. A species of arid mountain ranges and foothills in the western portion of Nevada and adjacent eastern California, mostly at 1770–3170 m elevation. Flowering from June to late August.

Esmeralda buckwheat. Diffusely branched, erect, annual herbs with slender to filiform peduncles bearing small, narrowly turbinate, 5-toothed involucres with white, glabrous flowers. The **var. *esmeraldense*** is the widespread and common phase being found in Nevada in Humboldt, Esmeralda, Mineral, and Nye cos. The endemic var. ***toiyabense* J. T. Howell** is restricted to the Toquima and Toiyabe ranges in Lander and northwestern Nye cos. It differs from var. *esmeraldense* in having scattered glands at the very base of the stem.

45. *Eriogonum concinnum* Reveal Darin's buckwheat. Erect annual herb with slender to fistulose, glabrous stems bearing erect or spreading peduncles with narrow involucres and white, glabrous flowers. Endemic to the Nevada Test Site regions of southern Nye Co., occurring at 1480–2050 m elevation. Flowering from late May through August.

46. *Eriogonum rubricaule* Tidestrom [*E. laetum* S. Stokes; *E. trichopes* var. *rubricaule* (Tidestrom) S. Stokes]. Lahontan Basin buckwheat. Erect annual herbs with slender to fistulose, glabrous stems bearing erect peduncles with broad involucres and pale yellow to yellow, glabrous flowers. Endemic to the Lahontan portion of the western Great Basin of Nevada from Mineral and Nye cos. northward to Humboldt Co., mostly 1290–1830 m elevation. Flowering from late May to early August.

47. *Eriogonum lemmonii* S. Wats. Lemmon's buckwheat. Erect annual herbs with slender to slightly fistulose, glabrous stems bearing sessile or shortly peduncled, campanulate involucres with pinkish to dark red, glabrous flowers. Endemic to west central Nevada from Lyon to southern Washoe cos. eastward to Churchill and extreme southern Pershing cos., mostly 1280–1460 m elevation. Flowering from May to early July.

48. *Eriogonum deflexum* Torr. in Ives A widespread and highly variable species ranging from northern Nevada and Utah southward through southern California and Arizona to northwestern Mexico and southwestern New Mexico, mostly below 2300 m elevation. Flowering throughout the year but mainly from May through October.

Skeleton weed. Annual, glabrous herbs with erect to spreading branches bearing deflexed peduncles with narrowly turbinate to turbinate involucres and white flowers. The following varieties are found in Nevada.

1. Involucres turbinate, 1.5–2 mm long; peduncles up to 5 mm long; stems not inflated 2

— Involucres narrowly turbinate, (2) 2.5–3 mm long; peduncles 3–15 mm long; stems often inflated; desert ranges on the southern margin of the Intermountain Region and the adjacent edge of the Mojave Desert . . . . var. *baratum*

2(1). Tepals obtuse basally; plants of the Intermountain Region portion of the state . . . . var. *nevadense*

— Tepals cordate basally; plants of the Mojave Desert portion of the state . . . . var. *deflexum*

The Intermountain Region phase of the species is the **var. *nevadense* Reveal** which occurs throughout that portion of the state except for Eureka and Elko cos. The plant is often found on volcanic soils. It is generally restricted to the valley bottoms and foothills, where it occurs nearly always above 1300 m elevation. In the Mojave Desert portion of the state the **var. *deflexum*** is the common phase. It differs from the more northern expression in having distinctly cordate tepal bases as opposed to the obtuse tepal bases of the flowers in var. *nevadense*. The var. *deflexum* is restricted to southern Nye and Lincoln cos. and Clark Co., where it generally occurs below 1100 m elevation (some populations may occur as high as 1900 m in the Spring Mts.). The taller, more erect, and inflated stem phase of the species, **var. *baratum* (Elmer) Reveal** [*E. baratum* Elmer; *E. deflexum* subsp. *baratum* (Elmer) Munz], occurs in the mountains along the interface between the Intermountain Region and the Mojave Desert. In general, var. *baratum* occurs from Esmeralda Co. eastward across southern Nye Co. to west central Lincoln Co., where it is found at 1350–2050 m elevation.

49. *Eriogonum rixfordii* S. Stokes [*E. deflexum* subsp. *rixfordii*(S. Stokes) Munz]. Pagoda buckwheat. Erect glabrous annual herbs with inflorescence branches arranged in numerous tiers of horizontally arranged branches forming a pagodalike crown, with sessile, deflexed involucres bearing small, white flowers. Local and occasionally weedy in the Death Valley region of Inyo Co., California, and just entering Nevada in the Beatty area northward onto the eastern foothills of the Grapevine Mts. in extreme southern Nye Co. at 990–1600 m elevation. Flowering from late June to October.

50. *Eriogonum hookeri* S. Wats. [*S. deflexum* subsp. *hookeri* (S. Wats.) S. Stokes]. Hooker's buckwheat. Spreading glabrous annual herbs with sessile, deflexed involucres bearing yellow flowers. Widespread from east central California eastward across Nevada to eastern Idaho, Utah, western Colorado, northern Arizona and extreme northwestern New Mexico. Rather common in the Intermountain Region portion of Nevada except in Washoe and Humboldt cos., at 1250–2000 m elevation. Flowering from July to October.

51. *Eriogonum brachypodum* Torr. & Gray [*E. parryi* A. Gray; *E. deflexum* var. *brachypodum* (Torr. & Gray) Munz; *E. deflexum* subsp. *brachypodum* (Torr. & Gray) S. Stokes; *E. deflexum* subsp. *parryi* (Torr. & Gray) S. Stokes]. Parry's buckwheat. Low, spreading, glandular annual herbs forming a flat-topped inflorescence with sessile or peduncled, deflexed, involucres bearing white flowers. Widespread and locally common mainly on the Mojave Desert from southeastern California across southern Nevada to southwestern Utah and western Arizona. In Nevada the species occurs in the Lahontan Trough (Reveal 1980) as far north as Churchill and Pershing cos. and along the southern edge of the Intermountain Region from Mineral and Esmeralda cos. eastward across southern Nye Co. to southern Lincoln Co. southward throughout Clark Co., at 180–1900 m elevation. Flowering from March to October.

52. ***Eriogonum bifurcatum*** **Reveal** Pahrump Valley buckwheat. Low spreading glabrous annual herbs with erect peduncles bearing narrow involucres with white flowers. Local and restricted in the Pahrump and Stewart Valley area of Inyo Co., California, and adjacent Nye Co., Nevada, southward to Mesquite Valley in California and the Las Vegas area of Clark Co., Nevada, at 300–800 m elevation. Flowering from late April to late June.

53. ***Eriogonum insigne*** **S. Wats.** [*E. exaltatum* M. E. Jones; *E. deflexum* var. *insigne* (S. Wats.) M. E. Jones; *E. deflexum* subsp. *insigne* (S. Wats.). S. Stokes; *E. deflexum* subsp. *exaltatum* (M. E. Jones) S. Stokes]. Exalted buckwheat. Tall, erect, glabrous annual herbs with elongated, whiplike inflorescences bearing erect, sessile, or short-peduncled involucres with white flowers. Local and infrequent from southwestern Utah westward across southern Nevada to southern California. In Nevada the species is most common in the Bunkerville area southwestwardly to the Hoover Dam area in Clark Co.; infrequent elsewhere as on and near the Nevada Test Site in southern Nye Co. and in the Panaca area in Lincoln Co., mostly 300–1480 m elevation. Flowering from late June through October.

54. ***Eriogonum watsonii*** **Torr. & Gray** [*E. deflexum* subsp. *watsonii* (Torr. & Gray) S. Stokes; *E. cernuum* var. *multipedunculatum* S. Stokes; *E. deflexum* var. *watsonii* (Torr. & Gray) R. J. Davis; *E. deflexum* var. *multipedunculatum* (S. Stokes) C. L. Hitchc.]. Watson's buckwheat. Low, spreading, glabrous annual herbs with slender, deflexed peduncles bearing long, narrowly turbinate involucres with white flowers. Widespread in the Intermountain Region from southeastern Oregon and southern Idaho southward to northwestern and northern Nevada. In Nevada the species ranges from northern Nye Co. northward to Pershing, Churchill, and Lander cos. and northeastwardly through Eureka Co. to Elko Co., at 1400–2200 m elevation. Flowering from late May to early September.

55. ***Eriogonum cernuum*** **Nutt.** Widespread and common throughout much of temperate western North America from southwestern Canada southward on the western edge of the Great Plains to northern New Mexico and westward to southeastern Washington, eastern Oregon, and the mountains of eastern California; found up to 3300 m elevation. Flowering from June through October.

Nodding buckwheat. The **var. *cernuum*** [*E. cernuum* var. *tenue* Torr. & Gray; *E. cernuum* subsp. *tenue* (Torr. & Gray) S. Stokes]. Annual herbs with straight, cernuous peduncles bearing turbinate involucres and white flowers with crisped or wavy margins. Widespread and common throughout most of the Intermountain Region portion of Nevada and the higher mountain ranges in the Mojave Desert portion of the state; mostly 1200–3100 m elevation and flowering from June through September. The **var. *viminale* (S. Stokes) Reveal in Munz** [*E. cernuum* subsp. *viminale* S. Stokes] is similar to var. *cernuum* except the involucres are sessile. The var. *viminale* is rather frequent on the desert floors of the Intermountain Region ranging from Elko and Eureka cos. southward to Lincoln Co., then westward to Lander and Nye cos. The variety occurs at 1500–2400 m elevation and flowers from late July to early September.

56. ***Eriogonum nutans*** **Torr. & Gray** Drooping buckwheat. A low, often slightly spreading annual herb with curved, cernuous peduncles bearing campanulate involucres and white, rose, or red flowers ranging from western Utah eastward across Nevada to extreme eastern California and southeastern Oregon, mostly 1350–2000 m elevation. Flowering from May to September. The **var. *nutans*** [*E. cernuum* var. *purpurascens* Torr. & Gray; *E. rubriflorum* M. E. Jones; *E. nutans* var. *brevipedicellatum* S. Stokes] is the most common expression of this relatively rare species and in Nevada is found from Elko and White Pine cos. westward to Mineral, Esmeralda, and Washoe cos. It is characterized by glandular peduncles. The **var. *glabratum* Reveal** is restricted in Nevada to Elko Co., where it occurs along Interstate Highway 80 from near Elko to Wells. It differs from var. *nutans* in

having glabrous peduncles. The var. *glabratum* has been found near Hirschdale, Nevada Co., California, also on Interstate Highway 80, where it was likely introduced as a result of highway traffic.

57. *Eriogonum thomasii* Torr. Thomas' buckwheat. Low, spreading, often diffusely branched, annual herbs, glabrous throughout except for a few scattered glands near the base of the flowering stems, the spreading, capillary peduncles bearing small involucres of yellow to white or rose, short-hispidulous flowers with the cordate base of the outer tepals distinctly saccate-dialated at full anthesis. Widespread and often common on the warm deserts of northwestern Mexico northward through southern California and southern Nevada to southwestern Utah and western Arizona, where it occurs from below sea level to 1400 m elevation. Flowering from March through June. In Nevada the species is restricted to the Mojave Desert portion of the state in southern Nye and Lincoln cos. and Clark Co.

58. *Eriogonum pusillum* Torr. & Gray [*E. comosum* var. *playanum* M. E. Jones; *E. reniforme* var. *asarifolium* Gand.; *E. reniforme* subsp. *pusillum* (Torr. & Gray) S. Stokes; *E. reniforme* var. *playanum* (M. E. Jones) S. Stokes]. Puny buckwheat. Spreading annual herbs, glabrous throughout except for glands near the base of the flowering stems, the spreading, slender peduncles bearing broad, glandular involucres with yellow to reddish yellow, glandular flowers. Widespread and often common on the warm deserts of southern California northward through the Lahontan Trough of western Nevada to southeastern Oregon and southwestern Idaho and eastward across southern Nevada to southwestern Utah and western Arizona, where it occurs from near sea level to 1800 (rarely 2600) m elevation. Flowering from March through June. In Nevada, the species ranges from the Mojave Desert portion of the state in Clark, southern Lincoln, and Nye cos. northward through the Lahontan Trough (Reveal 1980) to Washoe Co., occurring at 680–1900 m elevation.

59. *Eriogonum reniforme* Torr. & Frem. [*E. reniforme* var. *comosum* M. E. Jones; *E. comosum* (M. E. Jones) M. E. Jones]. Kidney-leaved buckwheat. Spreading annual herbs, glabrous throughout except for a few scattered hairs near the base of the flowering stems, the spreading, slender to capillary peduncles bearing broad, glabrous involucres with yellow to yellowish red, glandular flowers. Widespread and often infrequent and local from northern Baja California, Mexico, and southern California eastward to western Arizona and north to southern and southwestern Nevada from near sea level to 1600 m elevation. Flowering from March through June. In Nevada the species occurs throughout the Mojave Desert portion of the state and extends up the Lahontan Trough to Churchill Co. It differs from the related *E. pusillum* (see no. 58) in the nature of its leaf pubescence and its glabrous, often glaucous involucres.

60. *Eriogonum viscidulum* J. T. Howell Clammy buckwheat. Tall, erect, diffusely branched, minutely viscid annual herbs with erect, filiform peduncles bearing small, narrow involucres with small yellow flowers. Endemic and rare along the Virgin River, Clark Co., Nevada, mostly 300–475 m elevation. Flowering from April to late June.

61. *Eriogonum collinum* Stokes ex Jones Hilly buckwheat. Low to tall and erect, essentially glabrous annual herbs with open inflorescences of upwardly curved peduncles bearing glabrous involucres of white to yellowish flowers with pustulose tepals. Local and widely scattered from northwestern Nevada and adjacent northeastern California northward to southeastern Oregon, occurring at 1300–2000 m elevation. Flowering from June to mid-September. In Nevada the species ranges from southern Wahoe Co. and Lyon Co. northward to west central Humboldt Co.

62. *Eriogonum salicornioides* Gand. [*E. demissum* S. Stokes; *E. demissum* var. *romanum* S. Stokes; *E. vimineum* var. *salicornioides* (Gand.) S. Stokes]. Glasswort buckwheat. Low, spreading, glabrous annual herbs with sessile or short-peduncled involucres bearing small white flowers with pustulose tepals. Rare and infrequent in heavy clay soil of southeastern Oregon and southwestern Idaho, just bearly entering Nevada in northern Humboldt Co. (*Train s.n.*—PAC) at 1000–1400 m elevation. Flowering from late April to mid-August.

63. *Eriogonum pharnaceoides* Torr. in Sitgr. Ginseng buckwheat. Erect villous herbaceous annual herbs with green, basal, and sheathing leaves, the slender and erect peduncles with campanulate involucres bearing 5 lanceolate lobes 1–3 mm long and white or yellow flowers with saccate-dialated tepals. Widespread and infrequent from southeastern Nevada and adjacent southern Utah south to northern Arizona and western New Mexico, mostly at 1350–2500 m elevation. Flowering from August through October. The Nevada expression is the yellow-flowered **var. *cervinum* Reveal** that is known in Nevada only from the Deer Lodge area of Lincoln Co. It also occurs in southwestern Utah (Iron and Washington cos.) and northern Mohave Co., Arizona. The **var. *pharnaceoides*** is restricted to Arizona and New Mexico.

64. *Eriogonum spergulinum* A. Gray Spurry buckwheat. Prostrate to spreading or erect hispid and often glandular annual herbs with basal and sheathing leaves, the filiform peduncles with turbinate involucres bearing 4 erect teeth and white, glabrous or sparsely pubescent flowers. Widespread and occasionally weedy from southern and eastern California northward to southeastern Oregon and southwestern Idaho, mostly 1450–3450 m elevation. Flowering from June to late September. The Nevada expression is the widespread and common **var. *reddingianum* (M. E. Jones) J. T. Howell** [*E. spergulinum* subsp. *reddingianum* (M. E. Jones) Munz ex Reveal] that occurs throughout the range of the species. In Nevada the variety ranges from Mineral Co. northward to Washoe and Humboldt cos., where it occurs at 1500–2800 m elevation. Other variants of the species are restricted to the Sierra Nevada of California.

65. *Eriogonum maculatum* A. A. Heller [*E. angulosum* var. *rectipes* Gand.; *E. angulosum* var. *pauciflorum* Gand.; *E. angulosum* var. *flabellatum* Gand.; *E. angulosum* var. *patens* Gand.; *E. thurberi* var. *acutangulum* Gand.; *E. angulosum* subsp. *maculatum* (A. A. Heller) S. Stokes; *E. cernuum* subsp. *acutangulum* (Gand.) S. Stokes]. Spotted-flowered buckwheat. Low, spreading, tomentose annual herbs with sheathing leaves, the filiform, spreading peduncles bearing campanulate involucres with white to yellow or pink to red, glandular-puberulent flowers, the outer tepals often with a single large purplish spot. Widespread and common in the desert regions of extreme northern Baja California, Mexico, northward through southern and eastern California to southern Washington, and eastward to southern Idaho, western Utah, and western Arizona, from just above sea level to 2450 m elevation. Flowering from April to November. In Nevada the species occurs essentially throughout the state at 510–2100 m elevation and flowers from late April through September.

66. *Eriogonum ampullaceum* J. T. Howell [*E. mohavense* var. *ampullaceum* (J. T. Howell) S. Stokes]. Bottle-shaped buckwheat. An erect slender annual with strictly basal leaves, sessile involucres, and minute flowers with enlarged, roundish, reddish bases and white tepal tips. Rare and infrequent in Mono Co., California, and in adjacent Mineral Co., Nevada, at 1980–2105 m elevation. Flowering from late June through August. In Nevada this species is known only from Alkali Valley on the north side of Alkali Lake (*Tiehm & Lavin 8143*—MARY). This represents a new record for the state.

67. *Eriogonum vimineum* Dougl. ex Benth. [*E. shoshonense* A. Nels.; *E. vimineum* var. *shoshonense* (A. Nels.) S. Stokes]. Wicker buckwheat. Erect glabrous to floccose annual herbs with basal leaves and occasional smaller cauline leaves, the involucres sessile and strongly angled, bearing white to rose or yellow glabrous flowers. Widespread and common in the Pacific Northwest from Washington and Idaho southward to central California and northwestern Nevada, 30–2400 m elevation. Flowering from June through September. In Nevada the species occurs from the Carson City area northward to Washoe, Humboldt, and Elko cos. at 1500–2400 m elevation.

68. *Eriogonum baileyi* S. Wats. Erect glabrous or tomentose annual herbs with basal leaves, sessile and small involucres, and white, glabrous or, more commonly, glandular-puberulent flowers. Widespread and often rather common from eastern California northward to Washington and eastward across Nevada and Idaho to western Utah, mostly 460–2250 m elevation. Flowering from May through September.

Bailey's buckwheat. In Nevada the common expression is **var. *baileyi*** [*E. gracile* var. *effusum* Torr. & Gray; *E. baileyi* var. *por-*

phyreticum Stokes ex Jones; *E. restioides* Gand.; *E. vimineum* subsp. *baileyi* (S. Wats.) S. Stokes; *E. vimineum* var. *restioides* (Gand.) S. Stokes; *E. vimineum* var. *porphyreticum* (Stokes ex Jones) S. Stokes; *E. vimineum* var. *baileyi* (S. Wats.). R. J. Davis] that is found nearly throughout the state (except Clark Co.). It occurs at 1300–2250 m elevation. The **var. *praebens* (Gand.) Reveal** [*E. leucocladum* Gand.; *E. praebens* Gand.; *E. praebens* var. *divaricatum* Gand.; *E. commixtum* Greene ex Tidestrom; *E. vimineum* var. *commixtum* (Greene ex Tidestrom) S. Stokes; *E. baileyi* var. *divaricatum* (Gand.) Reveal in Munz] differs from var. *baileyi* in having tomentose rather than glabrous branches and stems. The var. *praebens* ranges from eastern California northward into western Nevada. In Nevada the variety is common from Douglas Co. northward to central Washoe Co., then eastward to Humboldt and Eureka cos. (where rare).

69. *Eriogonum brachyanthum* Coville [*E. baileyi* var. *brachyanthum* (Coville) Jepson; *E. baileyi* subsp. *brachyanthum* (Coville) S. Stokes]. Short-flowered buckwheat. Low, rounded, glabrous annual herbs with basal leaves, sessile involucres, and minute yellow flowers. Common on the desert valley floors and foothills from southern California northward to Nevada at 610–1900 m elevation. Flowering from May through August. In Nevada the species ranges from Nye Co. northward to Washoe Co., then eastward to western Humboldt and Lander cos., 1250–1900 m elevation.

70. *Eriogonum nidularium* Coville [*E. vimineum* subsp. *nidularium* (Coville) S. Stokes]. Bird-nest buckwheat. Low, spreading, tomentose to floccose annual herbs with numerous incurved branches and basal leaves, the involucres minute and sessile, bearing yellow to reddish flowers. Common on the desert valley floors and foothills of southern California eastward to Arizona and northward to Oregon and Idaho, from near sea level to 2150 m elevation. Flowering April through October. In Nevada the species is found throughout the state, mainly at 1300–2150 m elevation.

71. *Eriogonum palmerianum* Reveal in Munz [*E. plumatella* var. *palmeri* Torr. & Gray; *E. baileyi* var. *tomentosum* S. Wats.]. Palmer's buckwheat. Low, spreading, tomentose to floccose annual herbs with few to many spreading branches and basal leaves, the involucres minute and sessile, bearing white flowers. Common on the desert valley floors and foothills of southern California eastward to extreme southwestern New Mexico, and northward to Nevada, Utah, and southwestern Colorado, mostly 670–2680 m elevation. Flowering from June through October. In Nevada the species is common nearly throughout all the state except the northwestern corner, 1300–2300 m elevation.

72. *Eriogonum puberulum* S. Wats. [*E. puberulum* var. *venosum* S. Stokes]. Puberulent buckwheat. Low, spreading, silky-puberulent, reddish annual herbs with basal leaves, the involucres divided to near the base into 4 lobes, with white to bright red, glabrous or hispidulous flowers. Local and infrequent mainly on volcanic soils of Inyo Co., California, eastward across Nevada to southwestern Utah, mainly 1300–2850 m elevation. Flowering from May through August. In Nevada the species is found in Nye, Eureka, White Pine, Lincoln, and extreme eastern Clark cos.

73. *Eriogonum darrovii* Kearney Darrow's buckwheat. Low, spreading, sericeous annual herbs with several to many compact branches bearing basal and cauline leaves, the involucres minute and 5-lobed with pale yellow to pink and white-hirtellous flowers. Rare and infrequent in northwestern Arizona and southeastern Nevada, mostly 1650–1880 m elevation. Flowering from late June to early September. In Nevada the species is known only from near Sunnyside, Nye Co., and south of Major's Place, White Pine Co. The latter locality was reported by Barneby (1947) as *E. divaricatum* Hook., a species not known to occur in Nevada.

INDEX TO NAMES

The following index is to entities of *Eriogonum* mentioned in the above treatment. Those marked by an asterisk (*) indicate basionyms established on type material gathered in Nevada (see Reveal 1985b for more details). Synonyms are printed in italics.

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HIGH RATES OF PHOTOSYNTHESIS IN THE DESERT SHRUB *CHRYSOTHAMNUS NAUSEOSUS* SSP. *ALBICAULIS*

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ABSTRACT.— Basic aspects of photosynthesis were investigated in white rubber rabbitbrush (*Chrysothamnus nauseosus* (Pallas) Britt. ssp. *albicaulis*), a common C_3 deciduous shrub native to arid regions of the western U.S. Under favorable field conditions, net photosynthesis (P_n) ranged from 36 to 73 mg $CO_2 \cdot dm^{-2} \cdot hr^{-1}$, which is relatively high for a woody species. The leaves from the actively growing flowering shoots exhibited higher P_n than those on the vegetative shoots. P_n also varied according to the age of the leaves and the location of the plants. P_n did not light saturate even at quantum flux densities (QFD) equivalent to full sunlight. The light compensation point was relatively high (ca 100 $\mu mol \cdot m^{-2} \cdot S^{-1}$), perhaps due to the presence of a tomentose vestiture on the leaf surface. At high QFD's, the stomatal conductance was high (ca 520 $mmol \cdot m^2 \cdot s^{-1}$) for a woody species. RUBP-carboxylase content of the leaves ranged from 20 to 22 mg per gram F.W., which is similar to that found in most C_3 crop species. These results suggest that rabbitbrush is able to maintain high rates of P_n, at least under nonstressed conditions.

The genus *Chrysothamnus* (rabbitbrush) consists of deciduous subshrubs or shrubs endemic to western North America in open plains, valleys, foothills, and mountains (McArthur et al. 1979). Like other species of the genus, *Chrysothamnus nauseosus* (Pallas) Britt. (rubber rabbitbrush) is an excellent plant for soil stabilization because of its deep roots, heavy litter, and ability to establish on severe sites. It can grow in the cold deserts of the Colorado plateau, the Great Basin plateau, and the warm deserts of the southwestern U.S. In fact, *Chrysothamnus* is able to survive and grow vigorously from Mexico to Canada, an area that represents a very wide range of environmental conditions.

Recently there has been a renewed surge of interest in rabbitbrush as a nontraditional source of rubber. Acquisitions containing up to 6% rubber per unit dry weight have been reported (Ostler 1980). As a part of an on-going project on the potential of *Chrysothamnus* as a rubber source, we became interested in evaluating factors controlling rubber production. Very little information is available on the photosynthetic potential and physiological characterization of rabbitbrush. This paper describes some basic aspects of the photosynthetic characteristics of this potentially important plant.

MATERIALS AND METHODS

For initial experiments, rates of net photosynthesis (P_n) were measured during September and October 1984 on vigorous, healthy, white rubber rabbitbrush plants growing in the Range Plant Garden at Brigham Young University (elevation approximately 1500 m) using the in situ CO_2 depletion technique (Ehleringer and Cook 1980). The cuvette was clamped onto the shoots for 45 sec. The CO_2 analysis system consisted of a Beckman 865 Infrared Analyzer through which N_2 gas was flowing. Samples were injected into the gas stream, and sample peaks were printed out by a Hewlett-Packard Model 3390-A Reporting Integrator. The rate of CO_2 exchange was calculated from the CO_2 depletion rate based on the chamber volume, using the ideal gas equation. Plants were about three years old and had been irrigated periodically throughout the summer. For comparative purposes, P_n was also measured on healthy, vigorous plants of several additional woody species growing under similar environmental conditions. P_n was also measured on rabbitbrush plants growing on three native sites in Utah County, Utah. These plants had received considerable rainfall about five days prior to measurement. Rates of P_n were expressed on leaf area, dry weight, and chlorophyll bases. Leaf

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area was determined using Li-Cor model LI-3000 and LI-3100 area meters. Because of the narrowness of rabbitbrush leaves, it was found that the LI-3000 area meter underestimated leaf area by 45%. Hence leaf area data obtained by the LI-3000 area was multiplied by 1.82 to correct for this error. Chlorophyll content was determined using the method of Lichtenthaler et al. (1982), and the dry weights were determined by oven drying at 70 C for at least 16 hours.

To determine the response of rabbitbrush P_n to light, shoots from plants growing in the Range Plant Garden were excised under water and placed in an open gas exchange system as described in detail by Ehleringer (1983). Shoots were first exposed to a quantum flux density (QFD) of 2650 μmol · m^{-2} · S^{-1}. The QFD was then lowered in steps down to 80 μmol · m^{-2} · S^{-1}. Shoots remained at a given QFD until a stable photosynthetic rate was achieved (usually about 45 min.). Leaf temperature was held constant at 25 C, and CO_2 concentration was about 350 μl · l^{-1} during the measurements. Stomatal conductance and intercellular CO_2 concentrations were calculated as described previously (Ehleringer 1983).

For enzyme assays, fully expanded leaves were collected from young vigorous shoots. One-gram samples were each ground in 5 ml buffer (0.1 M Tris-Cl, pH 8.2 (25 C), 20 mM $MgCl_2$, 4 mM ethylendiaminetetraacetic acid, 4 mM dithiothreitol, and 5% acid and deionized H_2O-washed polyvinylpolypyrrolidone (Sigma). Assay and activation of ribulose bisphosphate carboxylase (RuBPCase) followed the method of Lorimer et al. (1977). Concentration of $NaH^{14}CO_3$ was 10 mM in the activation and assay media. Concentration of ribulose-1,5-bisphosphate was a 0.4 mM with $MgCl_2$ at 20 mM in the activation and assay media. Determination of amount of enzyme followed the Beckman Model-E ultracentrifuge method of Andersen et al. (1970) using the Schlieren optical system at a bar angle of 50°. Amount of enzyme as mg · ml^{-1} extract was determined by dividing the 15× magnified area of the Schlieren peak by a factor of 4.107.

For scanning electron microscopy (SEM), leaf tissue was fixed in glutaraldehyde-acrolein (Hess 1966). After dehydration to acetone, tissue was critical-point dried and sputter coated with gold.

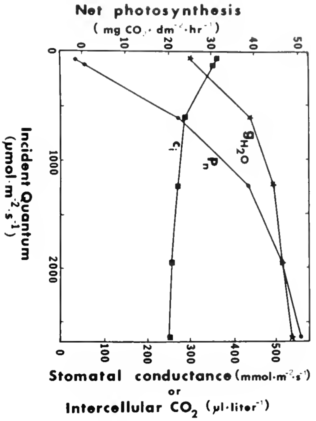

Fig. 1. Response of net photosynthesis (P_n), stomatal conductance (gH_2O), and intercellular CO_2(C_i) of rabbitbrush to incident quantum flux.

RESULTS

White rubber rabbitbrush consistently exhibited high P_n rates for a woody species (Fig. 1; Tables 1–4). Rates obtained with intact shoots in the field using the CO_2 depletion technique compared favorably with those obtained with excised shoots in the open gas exchange system. On a leaf area basis, the P_n in this plant was considerably higher than that of the other woody C_3 species (Table 1). Even on a dry weight basis, the P_n in rabbitbrush equaled that of *Atriplex canescens*, a C_4 species, and was nearly twofold or more than that of the other C_3 species. When calculated on chlorophyll basis, only the C_4 *A. canescens* exhibited a higher P_n rate than that of rabbitbrush. The P_n rates in plants growing on the nonirrigated native sites were found to be somewhat lower than those recorded for the plants maintained at the Range Plant Garden (Table 2).

In rabbitbrush the stem is also photosynthetic, and leaf senescence progresses acropetally. To assess the contribution of stem photosynthesis in overall P_n as well as to evaluate the role of leaf senescence, additional

TABLE 1. Net photosynthetic rates (P_n) of *Chrysothamnus nauseosus* ssp. *albicaulis* and six other woody species under similar environmental conditions. All plants were growing outdoors under irrigated conditions except for *A. tridentata*, which was measured on a native site after a heavy rainfall. Plus/minus values indicate standard of error of the mean (n = 4).

	P_n			Environmental conditions	
Species	$mgCO_2 \cdot dm^{-2} \cdot hr^{-1}$	$mgCO_2 \cdot g^{-1} D.W. \cdot hr^{-1}$	$mgCO_2 \cdot mg^{-1} Chl \cdot hr^{-1}$	QFD ($\mu mol.m^{-2} \cdot s^{-1}$)	Temp. (°C)
Chrysothamnus nauseosus	45.9±1.2	31.3±1.8	5.9±0.3	1050	20
Acer saccharinum	16.8±1.9	21.0±2.4	6.4±0.7	1700	24
Artemisia cana	26.8±2.9	17.4±2.3	3.1±0.4	1150	20
Artemisia tridentata	30.0±3.8	13.9±1.0	5.3±0.4	1600	26
Atriplex canescens	55.8±2.7	30.2±2.0	8.3±0.6	1050	20
Ephedra viridis	—*	5.2±0.5	3.7±0.4	1600	20
Malus domestica "Red Delicious"	23.1±2.1	18.9±1.7	4.0±0.4	1800	26

*This species has photosynthetic stems and bears no leaves. Hence P_n on a leaf area basis was not calculated.

TABLE 2. Net photosynthesis by *Chrysothamnus nauseosus* at three native locations in Utah County, Utah. Plus/minus values indicate standard error of the mean (n = 4). All measurements made at QFD of 1800 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and on nonflowering shoots.

	P_n	
Location	$mg\ CO_2 \cdot dm^{-2} \cdot hr^{-1}$	$mg\ CO_2 \cdot g^{-1} D.W. \cdot hr^{-1}$
1. Provo Canyon—partially shaded, southern slope, near Provo River (temp. = 20 C)	39.5±4.3	42.0±4.6
2. Provo Canyon—open field, flat, full sun (temp. = 20 C)	36.1±2.1	28.7±1.6
3. Mouth of Rock Canyon—slight western slope, full sun (temp. = 26 C)	40.9±2.2	28.6±1.6

TABLE 3. Net photosynthesis rates (P_n) of nonflowering and flowering shoots of *Chrysothamnus nauseosus* with and without leaves. Plus/minus values indicate standard error of the mean (n = 5).

	P_n		
Shoot type	$mgCO_2 \cdot dm^{-2} \cdot hr^{-1}$	$mgCO_2 \cdot g^{-1} D.W. \cdot hr^{-1}$	$mgCO_2 \cdot gChl^{-1} \cdot hr^{-1}$
Nonflowering, leaves intact	54.3±3.7	45.2±3.1	10.5±0.7
Flowering, leaves intact	73.3±6.7	61.5±5.6	16.8±1.5
Nonflowering, leaves removed	—	3.1±1.2	2.7±1.0
Flowering, leaves removed	—	4.7±1.6	4.3±1.5

TABLE 4. Net photosynthesis of the terminal 10 cm and the adjacent 10 cm below *Chrysothamnus nauseosus* shoots. Plus/minus values indicate standard error of the mean (n = 4). Environmental conditions during measurement: QFD = 1700 $\mu mol \cdot m^{-2} \cdot s^{-1}$, Temp. = 20 C.

	P_n		
Shoot location	$mgCO_2 \cdot dm^{-2} \cdot hr^{-1}$	$mgCO_2 \cdot g^{-1} D.W. \cdot hr^{-1}$	$mg \cdot mgChl^{-1} \cdot hr^{-1}$
Upper 10 cm	18.2±8.2	28.1±4.6	9.2±1.3
Section between 10 and 20 cm below apex	28.4±7.2	13.9±4.8	6.8±2.3

measurements of P_n were undertaken. The results indicate that stem P_n, on a dry weight basis, was only about 7% of that observed for leaves on both flowering and nonflowering shoots (Table 3). Leaves on flowering shoots at anthesis exhibited about a 35% higher P_n than

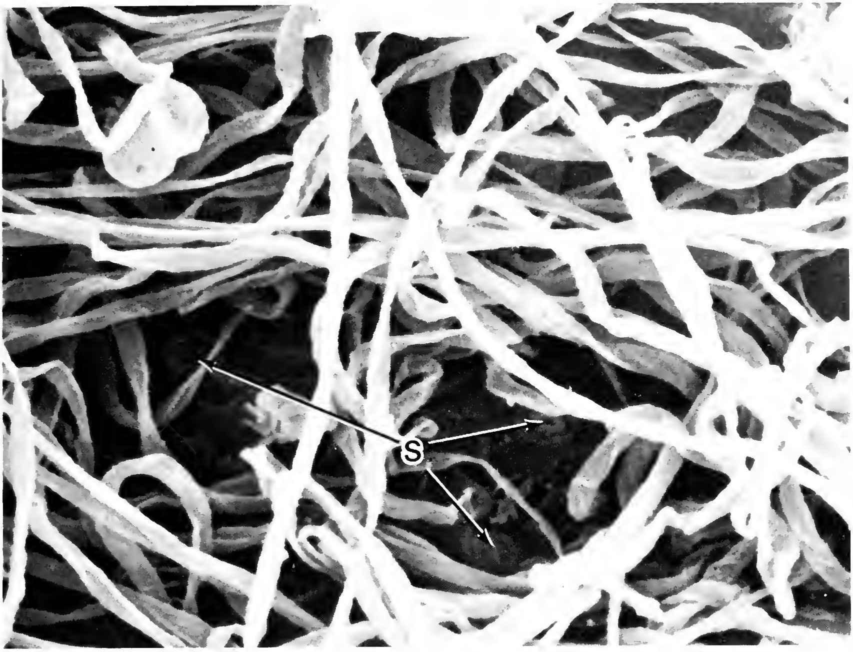

Fig. 2. Scanning electron micrograph of rabbitbrush leaf surface (X300) showing pubescence. Arrows point to stomata(s).

the leaves on nonflowering shoots on the same plant.

Results relating to the effect of leaf senescence on P_n are presented in Table 4. The leaves on the terminal 10 cm of rabbitbrush shoots exhibited a P_n rate that was about twofold higher that observed on the same shoots just 10 cm below the terminal section that had senescing leaves.

In this plant P_n did not light saturate at QFD's near full sunlight (Fig. 1). The light compensation point was also found to be relatively high (ca 100 μmol · $m^{-2} \cdot S^{-1}$). A SEM of the leaf surface revealed that rabbitbrush leaves are covered with a dense pubescence (Fig. 2). High P_n rates in rabbitbrush were accompanied by high stomatal conductance values (Fig. 1). The intercellular CO_2 concentrations in rabbitbrush leaves were similar to those found in other C_3 drought-deciduous shrubs that exhibit high P_n and stomatal conductance (Ehleringer and Björkman 1978, Comstock and Ehleringer 1984).

RuBPCase content and catalytic activities at V_{max} were measured for separate extractions of six samples of fully expanded leaves from actively growing shoots. Amount of RuBPCase was 21 ± 1.25 mg · g^{-1} F.W., 12.93 ± 0.74 mg · mg^{-1} chlorophyll, and 1.07 ± 0.06 mg · cm^{-2} leaf area. The catalytic activities of RuBPCase at V_{max} levels of substrate were 712 ± 96 nmol $^{14}CO_2$ · mg^{-1} enzyme · min^{-1}, 9.66 ± 0.87 μmol $^{14}CO_2$ · mg^{-1} chlorophyll · min^{-1}, and 761 ± 102 nmol $^{14}CO_2$ · cm^{-2} · min^{-1}.

DISCUSSION

Desert ecosystems are inhabited by a variety of plant life forms including ephemerals, drought-deciduous and desiccation-tolerant evergreen shrubs and herbaceous perennials (Walter and Stadelmann 1974, Ehleringer and Mooney 1983). Moisture stress is a continual limiting factor for the photosynthetic process in most desert plants. Therefore, it is not surprising to note that desert plants adapt the photosynthetic apparatus to desiccation tolerance and/or drought avoidance. It appears that white rubber rabbitbrush has resorted to drought avoidance in its photosynthetic adaptation. Like ephemerals (Mooney et al. 1976), this deciduous shrub is able to maintain high rates of P_n during nonstress periods. In fact, the rates of P_n exhibited by rabbitbrush were found to be similar to those observed in well-watered, drought-deciduous shrubs of warm deserts that typically exhibit very high P_n rates for woody species (Ehleringer and Mooney 1983). The rates of P_n in rabbitbrush even compared well with those found in many herbaceous C_3 crop species (Leopold and Kriedemann 1975). Rates of P_n were particularly high in flowering shoots at anthesis. The reason for this is not clear, but the presence of reproductive sinks is known to stimulate P_n in at least some plants (Milthorpe and Moorby 1974).

The higher amounts of RuBPCase per unit leaf area in rabbitbrush could also be a significant factor contributing to high rates of P_n in this species. In seedling leaves of *Pisum sativum* and in fully expanded leaves of *Medicago sativa*, the estimated amounts of RuBPCase were 11 and 21 mg · g^{-1} F.W., respectively (Gordon et al. 1978, Meyers et al. 1982). Thus, on a fresh weight basis, the amount of enzyme in rabbitbrush leaves is similar to that found in C_3 crop species. Based upon mass of enzyme per unit leaf area, however, RuBPCase in rabbitbrush is relatively high (1.07 mg · cm^{-2}). Some of the highest amounts of this enzyme on a leaf area basis (0.5 mg · cm^{-2}) for C_3 species have been measured in desert winter annuals (Seemann et al. 1980). Depending upon leaf age, RuBPCase amounts in soybean were 0.1 to 0.4 mg · cm^{-2} (Wittenbach et al. 1980). Similarly, in fully expanded leaves of spinach the amount of this enzyme was 0.3 mg · cm^{-2} (Seemann and Berry 1981). The amount of RuBPCase on a leaf area basis measured in our study of rabbitbrush exceeds the extremes of these values by more than twofold. However, on the bases of chlorophyll or fresh weight, rabbitbrush values are similar to those in other C_3 species. The carboxylation activities for rabbitbrush per mg RuBPCase or per mg chlorophyll are also similar to that found in other C_3 species (Koivuniemi et al. 1980, Seemann et al. 1980, Seemann and Berry 1981). However, carboxylation activities in rabbitbrush at V_{max} were high on a leaf area basis compared to other C_3 species showing high RuBPCase activities per unit leaf area (Mooney et al. 1976).

Among the different desert life forms, the highest photosynthetic rates and leaf conductances have been recorded for ephemerals (Mooney et al. 1976, Mooney and Ehleringer 1978, Ehleringer et al. 1979). Some of the drought-deciduous shrubs and herbaceous perennials, which are active for somewhat longer periods than ephemerals, also have high P_n rates (Ehleringer and Björkman 1978). High P_n rates in rabbitbrush were also accompanied by high stomatal conductance. However, it should be pointed out that these high conductance values were measured on well-watered plants. Under more dry native conditions, such high values may not be observed. Even the intercellular CO_2 concentrations in rabbitbrush leaves were found to be similar to C_3 drought-deciduous shrubs, which exhibit high P_n and high stomatal conductance (Ehleringer and Mooney 1983).

Leaves of many desert plants are pubescent. The presence of pubescence not only modulates leaf spectral characteristics and leaf boundary layer resistance, but it also reduces leaf absorptance resulting in reduced heat load, lower leaf temperatures, and lower transpiration rates (Ehleringer and Björkman 1978, Ehleringer and Mooney 1978) and may have adaptive significance. In rabbitbrush the shoot is covered with a green, yellow-green, gray-green to white, feltlike tomentum, and the leaves are clothed with a tomentose vestiture. A characteristic feature of P_n in rabbitbrush is that it is not light saturated at QFD's near full sunlight. In addition, the light compensation point is relatively high. Similar responses of P_n to light have also been recorded in some C_3 species native to the Sonoran desert (Ehleringer and Björkman 1978). In *Encelia farinosa*, the high light saturation point has been attributed to the pubescent nature of the leaf surface. It is likely that the nonsaturation of P_n at near full sunlight and the high light compensation point in rabbitbrush is due to its tomentose vestiture.

In conclusion, this study indicates that rabbitbrush is capable of maintaining high photosynthetic rates during nonstress periods. Thus, at least under favorable environmental conditions, a potential exists for high rates of dry matter accumulation per unit of biomass. The extent to which the dry matter production can be partitioned into rubber as well as an elucidation of the factors promoting rubber production should be a worthwhile subject for future investigation. It will also be of interest to determine how P_n responds on a seasonal basis to water stress and other environmental parameters.

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FOOD HABITS OF THE WESTERN WHIPTAIL LIZARD (*CNEMIDOPHORUS TIGRIS*) IN SOUTHEASTERN NEW MEXICO

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ABSTRACT.— This study presents the first food habit assessment for the western whiptail lizard (*Cnemidophorus tigris*) in the shinnery oak–mesquite habitat (*Quercus havardii–Prosopis glandulosa*) of southeastern New Mexico. Short-horned grasshoppers, termites, antlions, beetles, and spiders formed the major portion of the diet during the four-year study. Discriminant analyses were used to evaluate annual, seasonal (monthly), and sexual variation. Incidental food categories were responsible for most of the annual and seasonal variation. Dominant foods varied little between months and years. Sexual variation was more evident; it may act to reduce intraspecific competition for food resources and may be associated with secondary sexual size dimorphism.

Food habits of the western whiptail lizard (*Cnemidophorus tigris*) have been studied in several areas of the western United States (e.g., Pack 1923, Milstead 1957a, 1958, 1961, 1965, Johnson 1966, Echternacht 1967, Medica 1967, Milstead and Tinkle 1969, Pianka 1970, Bickham and MacMahon 1972, Scudday and Dixon 1973, Vitt and Ohmart 1977, Mitchell 1979, Best and Polechla 1983). Some of these investigators have examined intraspecific variation: e.g., Johnson (1966) found that the diet of immature whiptails was similar to that of adults, and Johnson (1966) and Pianka (1970) found little difference in diet between sexes. Conversely, there is considerable geographic (Milstead and Tinkle 1969, Pianka 1970), seasonal (Johnson 1966, Milstead and Tinkle 1969, Pianka 1970, Vitt and Ohmart 1977, Mitchell 1979), and annual variation (Milstead 1965, Medica 1967, Milstead and Tinkle 1969, Mitchell 1979).

In southeastern New Mexico, Best and Polechla (1983) reported diet data for *C. tigris* in their study of *C. gularis*, but their sample of *C. tigris* was small and the habitat where they collected specimens was quite different from where those examined herein were obtained. Subsequently, Best and Gennaro (1984) studied *Uta stansburiana* from the shinnery oak–mesquite habitat of southeastern New Mexico using specimens collected in sympatry with the *C. tigris* reported herein. In view of the previous studies of food habit variation and because no extensive studies of *C. tigris* have been conducted in the shinnery oak–mesquite association of southeastern New Mexico, the present study was initiated. Our objectives were to assemble a listing of food items consumed in that area and to examine annual, seasonal (monthly), and sexual variation.

MATERIALS AND METHODS

From 1976 through 1979, 174 *C. tigris* were collected approximately 40 km E of Carlsbad in Eddy and Lea counties, New Mexico (within an 8-km radius of drill hole ERDA 9, SE corner, Sec. 20, T22S, R31E). Specimens were fixed in 10% formalin and stored in 40% isopropyl alcohol. Stomach contents were later removed, placed into individual vials, and identified. Arthropod taxonomy follows Borror et al. (1981).

Two separate data sets were used in the analyses. One contained the number of individuals in each arthropod order. The second included the number of individuals identified to family except where identification was impossible (e.g., unidentified Coleoptera were entered as Coleoptera, Buprestidae was another character, Cleridae another, etc.). Discriminant analyses (Nie et al. 1975) were used to test for annual, seasonal (monthly), and sexual variation in food habits. Best and Gennaro (1984) presented a summary of this tech-

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TABLE 1. Food items found in 174 western whiptail lizards (*Cnemidophorus tigris*). Sample sizes are given in parentheses and occurrence data are presented as: number of lizards containing a food category; total items observed.

Food category	1976(10)	1977(42)	1978(69)	1979(53)	Combined(174)
Arthropoda				1;1	1;1
ARACHNIDA				1;1	1;1
Scorpionida	1;1	1;1	7;7	5;5	14;14
Araneae		5;8	13;18	13;17	31;43
Solifugae			8;9	3;3	11;12
CHILOPODA		1;1			1;1
HEXAPODA			4;5		4;5
Orthoptera (9)[1]	7;9	32;61	61;146	46;82	146;298
Isoptera (3)		14;299	19;509	23;487	56;1295
Psocoptera (1)			2;2		2;2
Hemiptera (5)	1;1	13;18	2;2	5;5	21;26
Homoptera (5)	2;3	6;14	5;10	1;1	14;28
Neuroptera (2)	1;2	15;22	19;29	4;5	39;58
Coleoptera (9)	4;4	23;62	38;85	13;20	78;171
Lepidoptera (4)	1;1	13;29	20;48	15;22	49;100
Diptera (2)		2;4	7;8	2;2	11;14
Hymenoptera (4)	1;1	7;156	16;24	16;22	40;203
MISCELLANEOUS					
Insect eggs				1;18	1;18
Lizards				2;2	2;2
Sand				2;2	2;2
Empty stomachs				1;1	1;1

[1] Minimum number of families represented

nique in relation to lizard feeding ecology studies. Analyses were conducted using the IBM computer system at University of New Mexico. Specimens and their stomach contents were deposited in the Eastern New Mexico University Natural History Museum in Portales.

Lizards were collected in a shinnery oak–mesquite association (*Quercus havardii–Prosopis glandulosa*). Although shinnery oak and mesquite did not have the greatest plant density on our study area, they were among the most obvious plant taxa. Extensive vegetation analyses of this noncultivated region are given in Best and Jackson (1982).

Results

Food items found in the stomachs of the 174 *C. tigris* are presented in Table 1. In addition, one platyhelminth was found in July 1978, and 12 nematodes were found in seven 1978 specimens. Arthropods represented by the highest frequencies of occurrence (number of specimens containing a food category/total number of specimens × 100) were: Orthoptera, 84%; Coleoptera, 45%; Isoptera, 32%; and Lepidoptera, 28%. Except for the lack of isopterans in 1976, these categories were represented in each of the four annual samples. Other consistently occurring arthropods were Scorpionida, Hemiptera, Homoptera, Neuroptera, and Hymenoptera. Although the Orthoptera represented at least nine families, there were about 10 times as many Acrididae as any of the others. Their frequency of occurrence was 78%, with 242 acridids being counted. The Coleoptera were more evenly distributed among the nine families identified, but Scarabaeidae, Tenebrionidae, Elateridae, and Curculionidae had 11%–17% frequencies of occurrence, respectively. Other coleopteran families occurred at frequencies less than three percent. In addition, there was an 8% frequency of unidentified coleopterans (18 beetles). There were at least three families of Isoptera; Termitidae was the most common and occurred at a frequency of 4%. Half the lepidopterans were unidentified, and most of the remainder were Geometridae (14% frequency).

The results of the discriminant analysis between years (sexes combined), using the number of arthropods in each order as characters, are shown in Table 2. Only 47% of the *C. tigris* were classified correctly, indicating little difference between years. The analyses using all arthropod taxa (orders, suborders, super families, families) classified 69% of the specimens correctly. In decreasing order of impor-

TABLE 2. Discriminant analyses between years and months for *Cnemidophorus tigris*.

	Actual group	n	Predicted group membership			
Years (1976–1979)[1,2]			1976	1977	1978	1979
	1976	10	7(70.0%)	2(20.0%)	1(10.0%)	0
	1977	42	11(26.2%)	21(50.0%)	7(16.7%)	3(7.1%)
	1978	69	19(27.5%)	7(10.1%)	32(46.4%)	11(15.9%)
	1979	53	19(35.8%)	3(5.7%)	9(17.0%)	22(41.5%)
Months (1977–1979)[3]			May	June	July	August
	May	31	13(41.9%)	8(25.8%)	10(32.3%)	0
	June	60	15(25.0%)	16(26.7%)	25(41.7%)	4(6.7%)
	July	59	6(10.2%)	3(5.1%)	48(81.4%)	2(3.4%)
	August	14	0	1(7.1%)	6(42.9%)	7(50.0%)
Months—1977[4]			May	June	July	
	May	9	5(55.6%)	2(22.2%)	2(22.2%)	
	June	14	1(7.1%)	9(64.3%)	4(28.6%)	
	July	19	2(10.5%)	0	17(89.5%)	
Months—1978[5]			May	June	July	August
	May	14	4(28.6%)	4(28.6%)	6(42.9%)	0
	June	26	4(15.4%)	14(53.8%)	7(26.9%)	1(3.8%)
	July	20	1(5.0%)	1(5.0%)	17(85.0%)	1(5.0%)
	August	9	0	0	4(44.4%)	5(55.6%)
Months—1979[6]			May	June	July	August
	May	8	3(37.5%)	0	5(62.3%)	0
	June	20	2(10.0%)	5(25.0%)	13(65.0%)	0
	July	20	0	0	20(100%)	0
	August	5	0	0	3(60.0%)	2(40.0%)

[1] The data in subsequent footnotes are given as: percent of the specimens that were correctly classified, in decreasing order of importance, the variables accounting for most or all of the differences.

[2] 47.1%; Hemiptera, Coleoptera, Orthoptera, Homoptera, Neuroptera, Araneae, Solifugae, Chilopoda, Hexapoda, and lizards.

[3] 51.2%; lizards, Lepidoptera, Isoptera, Scorpionida, Coleoptera, Psocoptera, Diptera, Orthoptera, Hemiptera, and Araneae.

[4] 73.8%; Lepidoptera, Coleoptera, Hemiptera, Homoptera, and Scorpionida.

[5] 58.0%; Diptera, Hexapoda, Coleoptera, Psocoptera, Araneae, Lepidoptera, Scorpionida, and Isoptera.

[6] 56.6%; lizards, Orthoptera, Scorpionida, and Solifugae.

tance, the variables separating years were Gryllacrididae, Acanalonidae, Coleoptera, Coreidae, Hemiptera, Cydnidae, Curculionidae, Orthoptera, and Lepidoptera. This analysis indicated there was some variation between years. However, most of the variability was in food categories that were incidental (occurred at very low frequencies) or that were abundant during only one or two of the four years. The major food categories occurred every year, but fluctuated in frequency and total number of items observed.

Discriminant analysis was performed between months (May through August) combining sexes and data for 1977 through 1979 (Table 2); 51% of the specimens were classified correctly. Using all arthropod taxa, 64% were classified correctly. Variables contributing the most to the classification were lizards (juvenile *Phrynosoma*), Termitidae, Scorpionida, Coleoptera, Asilidae, Psocoptera, and Elateridae. These analyses showed some variation between months, but most of the variability was associated with incidentally occurring food categories.

When months were considered for individual years, discriminant analyses using arthropod orders as characters showed greater differences between months than when data were combined (Table 2). Analyses using all arthropod taxa correctly classified 88, 75, and 72% of specimens to month for 1977, 1978, and 1979, respectively. For 1977 variables accounting for the most differences were Hymenoptera, Sphingidae, Cicadellidae, Lepidoptera, Acrididae, Coleoptera, and Elateridae. For 1978 Mantidae, Curculionidae, Isoptera, Gryllacrididae, Elateridae, Psocoptera, and Gryllidae accounted for the most differences. For 1979 variables accounting for the most differences between months were lizards, Acrididae, Pentatomidae, Geometridae, Blattoidea, Lepidoptera, and Tenebrionidae. For each of the three years, the separa-

TABLE 3. Discriminant analyses between sexes for *Cnemidophorus tigris*.

	Actual group	n	Predicted group membership	
			Male	Female
1978–1979[1,2]	Male	64	51(79.7%)	13(20.3%)
	Female	58	22(37.9%)	36(62.1%)
1978[3]	Male	37	34(91.9%)	3(8.1%)
	Female	32	11(34.4%)	21(65.6%)
1979[4]	Male	27	20(74.1%)	7(25.9%)
	Female	26	6(23.1%)	20(76.9%)
May 1978[5]	Male	9	9(100%)	0
	Female	5	1(20.0%)	4(80.0%)
June 1978[6]	Male	13	12(92.3%)	1(7.7%)
	Female	13	2(15.4%)	11(84.6%)
July 1978[7]	Male	11	10(90.9%)	1(9.1%)
	Female	9	2(22.2%)	7(77.8%)
August 1978[8]	Male	4	4(100%)	0
	Female	5	0	5(100%)
May 1979[9]	Male	5	5(100%)	0
	Female	3	0	3(100%)
June 1979[10]	Male	12	12(100%)	0
	Female	8	0	8(100%)
July 1979[11]	Male	6	4(66.7%)	2(33.3%)
	Female	14	2(14.3%)	12(85.7%)

[1] The data in subsequent footnotes are given as: percent of the specimens that were correctly classified, in decreasing order of importance, the variables accounting for most or all of the differences.

[2] 71.3%, Neuroptera, Hemiptera, Orthoptera, Coleoptera, Isoptera, Solifugae, Psocoptera, Araneae, Scorpionida, and lizards.

[3] 79.7%, Neuroptera, Solifugae, Orthoptera, Psocoptera, Isoptera, and Hexapoda.

[4] 75.5%, Hemiptera, Lepidoptera, Orthoptera, sand, Solifugae, Coleoptera, Araneae, and Isoptera.

[5] 92.9%; Neuroptera, Solifugae, Homoptera, and Coleoptera.

[6] 88.5%, Neuroptera, Isoptera, Coleoptera, Solifugae, Orthoptera, Hemiptera, Diptera, Hexapoda, and Scorpionida.

[7] 85.0%, Neuroptera, Hemiptera, Solifugae, Homoptera, and Araneae.

[8] 100%, Coleoptera, Isoptera, Homoptera, Orthoptera, and Neuroptera.

[9] 100%, Scorpionida, Araneae, and Coleoptera

[10] 100%, Hymenoptera, Isoptera, Neuroptera, Hemiptera, Lepidoptera, Coleoptera, insect eggs, Scorpionida, Diptera, and sand.

[11] 80.0%, Araneae, Hymenoptera, and Arthropoda.

tion of months was primarily based upon incidental occurrences. Thus, monthly-seasonal variation was evident but was mostly reflected by incidentally occurring food categories. This was the same type of variation observed between years.

The sex of each lizard was determined in 1978 and 1979, and discriminant analyses were used to assess sexual variation for these years. When 1978 and 1979 males were combined and compared to females, there were differences between sexes (Table 3). Except for Hemiptera, Solifugae, and Psocoptera, food categories accounting for the most differences were represented in both sexes (Table 4). Analysis using all arthropod taxa provided 79% correct classifications; Myrmeleontidae, Isoptera, Noctuidae, Hymenoptera, Solifugae, Psocoptera, Araneae, Scorpionida, and Rhopalidae contributed the most to the differences. Of these, Myrmeleontidae, Isoptera, and Araneae were the most consistently occurring food categories.

Each year was then examined separately. For 1978, 80% of the lizards were classified correctly to sex (Table 3). Psocoptera and Hexapoda were the only variables accounting for differences that could be considered as incidental (Table 4). Considering all arthropod taxa, 90% were classified correctly, and Myrmeleontidae, Solifugae, Tettigoniidae, Hymenoptera, Cicadellidae, Psocoptera, and Elateridae accounted for the differences. Of these, Myrmeleontidae, Solifugae, and Tettigoniidae were the only consistently occurring food categories. For 1979, 76% of the specimens were classified correctly (Table 3). Except for Hemiptera, sand, and Solifugae, the variables accounting for the differences represented some of the most consistently occurring food categories (Table 4). Eighty-three percent of the lizards

TABLE 4. Food items in *Cnemidophorus tigris* collected during 1978 and 1979. See Table 1 for data presentation format.

Food category	Year and month of collection									
	1978									
	May (14)		June (26)		July (20)		August (9)		Total (69)	
	♂♂(9)	♀♀(5)	♂♂(13)	♀♀(13)	♂♂(11)	♀♀(9)	♂♂(4)	♀♀(5)	♂♂(37)	♀♀(32)
ARACHNIDA										
Scorpionida	1;1	1;1	1;1	4;4					2;2	5;5
Araneae	2;3	2;2	3;4	4;7		1;1	1;1		6;8	7;10
Solifugae		2;2		2;3		2;2	1;1	1;1	1;1	7;8
HEXAPODA	1;1		2;3	1;1					3;4	1;1
Orthoptera (6)	6;9	5;19	11;27	12;37	9;16	9;16	4;9	5;13	30;61	31;85
Isoptera (3)	2;10		3;7	5;95	2;37	3;139	1;48	3;173	8;102	11;407
Psocoptera (1)	1;1						1;1		2;2	
Hemiptera (1)			1;1			1;1			1;1	1;1
Homoptera (3)		1;2				2;6		2;2		5;10
Neuroptera (2)		2;3	2;2	6;15	1;1	4;4	1;1	3;3	4;4	15;25
Coleoptera (6)	6;21	4;9	9;21	6;12	4;8	6;10		3;4	19;50	19;35
Lepidoptera (3)	2;10	2;4	6;15	7;14	2;4	1;1			10;29	10;19
Diptera (1)	1;1		1;2	1;1			1;1	3;3	3;4	4;4
Hymenoptera (3)	2;2	3;3	3;11	3;3	1;1	1;1	1;1	2;2	7;15	9;9

	1979									
	May (8)		June (20)		July (20)		August (5)		Total (53)	
	♂♂(5)	♀♀(3)	♂♂(12)	♀♀(8)	♂♂(6)	♀♀(14)	♂♂(4)	♀♀(1)	♂♂(27)	♀♀(26)
Arthropoda					1;1				1;1	
ARACHNIDA					1;1				1;1	
Scorpionida		2;2		2;2			1;1		1;1	4;4
Araneae	1;1	1;1	1;1	2;2		7;10	1;2		3;4	10;13
Solifugae			3;3						3;3	
HEXAPODA										
Orthoptera (5)	4;6	2;6	10;14	7;13	5;8	13;23	4;9	1;3	23;37	23;45
Isoptera (2)		1;57	4;22	6;195	3;42	6;84	3;87		10;151	13;336
Hemiptera (3)		2;2		2;2		1;1				5;5
Homoptera (1)			1;1						1;1	
Neuroptera (1)		1;1		1;1		1;2	1;1		1;1	3;4
Coleoptera (4)	2;2		3;3	1;4	2;3	3;5	2;3		9;11	4;9
Lepidoptera (3)	1;1	2;4	2;3	3;3	2;2	5;9			5;6	10;16
Diptera (1)			1;1			1;1			1;1	1;1
Hymenoptera (2)	1;1		1;1	4;6	3;5	5;6	2;3		7;10	9;12
MISCELLANEOUS										
Insect eggs				1;18						1;18
Lizards							2;2		2;2	
Sand			2;2						2;2	
Empty stomachs	1;1								1;1	

were classified correctly using all arthropod taxa. In decreasing order of importance, the variables contributing the most to the differences were Araneae, lizards, Scorpionida, Sphingidae, Rhopalidae, Solifugae, Acrididae, and Polyphagidae. Only Araneae and Acrididae occurred with consistency between sexes for 1979. The degree of sexual differences between years were similar (Table 3).

Subsequent analyses concentrated on the differences between sexes for each monthly sample during 1978 and 1979. For May 1978, 93% of the specimens were classified correctly to sex (Table 3). Of the variables accounting for the differences, only Coleoptera were found in both sexes; the others were in females only (Table 4). When all arthropod taxa were considered, 93% of the specimens were classified correctly, with Solifugae, Myrmeleontidae, and Cicadellidae accounting for the differences. All of these occurred in females only. For June 1978, 89% of the specimens were classified correctly to sex (Table 3). Of the variables accounting for the differences, all except Solifugae and Hemiptera were present in both sexes (Table 4). Using all arthropod taxa, 96% of the specimens were classified correctly, with Myrmeleontidae, Solifugae, Isoptera, Tenebrionidae, Scorpionida, Araneae, Hymenoptera, and Coleoptera accounting for the most differences. Solifugae, Hymenoptera, and Coleoptera occurred in females only, and the others were found in both sexes. For July 1978, 85% of the specimens were classified correctly to sex (Table 3). Of the variables accounting for the differences, all but Neuroptera occurred in females only (Table 4). Using all arthropod taxa, 90% were classified correctly, with Elateridae, Solifugae, Termitidae, Tettigoniidae, Myrmeleontidae, and Noctuidae accounting for the differences. Except for Myrmeleontidae, all of these variables occurred in female stomachs only. The August 1978 analysis correctly classified 100% of the lizards to sex (Table 3). Coleoptera and Homoptera were found in females only (Table 4). Considering all arthropod taxa, 100% were classified correctly with Coccoidea, Termitidae, Gryllidae, Scarabaeidae, Myrmeleontidae, and Asilidae accounting for the differences. Myrmeleontidae and Asilidae were in both sexes, and the others were in females only.

For May 1979, 100% of the specimens were classified correctly to sex (Table 3). Of the three variables accounting for the differences, only Araneae was found in both sexes (Table 4). When all arthropod taxa were used in the analysis, 100% of the specimens were classified correctly. The variables accounting for the differences were Pentatomidae, Geometridae, and Araneae. Pentatomidae occurred in males only, and the other two were in both sexes. For June 1979, 100% of the specimens were classified correctly to sex (Table 3). Of the variables accounting for the most differences, only Hymenoptera, Isoptera, Lepidoptera, and Coleoptera occurred in both sexes (Table 4). Considering all arthropod taxa, 100% of the lizards were classified correctly. In decreasing order of importance, variables accounting for the differences were Isoptera, Sphingidae, Termitidae, Rhopalidae, Myrmeleontidae, Formicidae, Scorpionida, and Blattidae. None of these occurred in both sexes. For July 1979, 80% of the lizards were classified correctly (Table 3). Of the three variables accounting for the differences, only Hymenoptera was present in both sexes (Table 4). Considering all arthropod taxa, 85% of the specimens were classified correctly, with Araneae, Elateridae, Arthropoda, Formicidae, and Lepidoptera accounting for the differences between sexes. Elateridae, Formicidae, and Lepidoptera occurred in both sexes. Because of the small sample for August 1979, discriminant analyses were not performed.

DISCUSSION

In his examination of geographic variation in the diet of *C. tigris*, Pianka (1970) found the same major food items as in previous studies, but there was a pronounced latitudinal shift in diet. His southern lizards consumed large numbers of termites, but northern lizards relied on other foods. He indicated that this could possibly be because there were simply fewer termites in his Great Basin flatland desert habitats. Additionally, Pianka (1970) observed that food species diversities reflected the latitudinal change in diet. Our results were similar to previous studies in that Orthoptera, Coleoptera, Isoptera, and Lepidoptera were among the most abundant food categories. The diversity of food categories found in our specimens is as great or greater than any of the previous *C. tigris* food habit studies. This may indicate a greater diversity of food organisms was available for consumption by our lizards, that a greater diversity was taken by our lizards, that there were varying degrees of expertise in identifying the stomach contents, or that different taxonomic levels have been used in identifying the food categories.

Several previous investigators have noted the presence of annual diet variation in *C. tigris* (Milstead 1965, Medica 1967, Milstead and Tinkle 1969, Mitchell 1979). Our findings also indicated some annual variation was present. However, the differences we found between years were primarily the result of incidentally occurring food categories. The consistency of the major food categories between years indicated that *C. tigris* was not a completely opportunistic feeder. The species takes certain arthropod taxa very regularly from year to year (i.e., Orthoptera, Coleoptera, Isoptera, and Lepidoptera) and is opportunistic only in the sense of taking other taxa that may fall into, for example, the proper size, taste, or behavioral category. *Cnemidophorus tigris* takes foods within its normal "requirements" in greater abundance when they are available in greater abundance. We believe a completely opportunistically feeding species is one that takes food as it more or less randomly encounters it, such as is done by coyotes (e.g., Best et al. 1981). The consistency of various food categories in the diet of *C. tigris* indicated that some selection must have been taking place. From Best and Gennaro's (1984) study of *Uta stansburiana* on the same study area, we know that large numbers of ants (Formicidae) and true bugs (Hemiptera) were also available as food items. However, possibly because of different foraging habits (e.g., Milstead 1957b, Pianka 1970, Vitt and Ohmart 1977, Parker and Pianka 1977) or selection of foods, ants and certain other arthropods were rarely found in *C. tigris* stomachs. During times of environmental adversity, we expect that *C. tigris* would take food species that may not be "preferred" just to survive.

The presence of seasonal variation in the diet of *C. tigris* has been addressed by some previous workers (Johnson 1966, Milstead and Tinkle 1969, Pianka 1970, Vitt and Ohmart 1977, Mitchell 1979). We found varying degrees of separation between months. This seasonal variation was probably caused by the taking of a variety of temporarily abundant arthropods as the growing seasons progressed. In the Chihuahuan desert of south central New Mexico the seasonal rainfall pattern as well as total amount of rainfall affects the primary productivity and hence the availability of arthropods as foods for lizards (Whitford and Creusere 1977).

Sexual differences in diet of *C. tigris* have been examined by Johnson (1966) and Pianka (1970). They noted there were only slight differences between sexes. Our data from southeastern New Mexico indicated there was a great deal of difference between sexes. Sexual differences have also been shown for *Anolis* (Schoener 1967, 1968); they differed dramatically in size and ate quite different foods. Sexual differences have been found in *U. stansburiana* (Parker and Pianka 1977, Best and Gennaro 1984). Best and Gennaro (1984) postulated these differences may be related to secondary sexual size dimorphism. Since *C. tigris* also shows secondary sexual size dimorphism (e.g., Medica 1967), we expect that the sexual diet differences reported herein may also be related to size variation. Diet differences between sexes would act to reduce intersexual competition for food resources—an adaptation that is known for other vertebrates (e.g., birds, Selander 1966).

Our study of the feeding ecology of *C. tigris* in southeastern New Mexico has shown the presence of a small amount of annual and seasonal variation, and a considerable amount of sexual variation. The annual and seasonal variation was attributed to the temporary abundance of a variety of arthropod taxa that were taken as available. Sexual differences in diet were possibly related to differences in secondary sexual size dimorphism and may be acting to reduce intraspecific competition for food in the semidesert environment of southeastern New Mexico.

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VEGETATION PATTERNS IN RELATION TO SLOPE POSITION IN THE CASTLE CLIFFS AREA OF SOUTHERN UTAH

Jack D. Brotherson[1] and William J. Masslich[1]

ABSTRACT.— Vegetation patterns in relation to slope position were studied on four foothill knolls in the Castle Cliffs area of Washington County, Utah. Study plots were established at four different slope positions: ridge top, upper slope, lower slope, and floodplain. Exposed rock was highest on the ridge top; exposed soil was highest on the floodplain; soil depth increased downslope. Plant life form varied with respect to slope position. Grass, annuals, and cryptogamic crust cover was highest on the ridge top and shrubs were most prominent on the midslope. Forb cover gradually increased downslope. Succulents were restricted to the ridge top or floodplain. Species distribution was distinct and strongly correlated to slope position. Two sets of congeneric species showed strong patterns of niche separation. The vegetation of the slopes is highly distinct at the ridge top and floodplain and grades toward the midslope from both ends.

Vegetation composition and its relationship to slope position has been of interest to researchers for many years. The majority of work reported has been conducted in areas with moderate climates and annual precipitation exceeding 15 inches. Foothill knolls in the Castle Cliffs area of southern Utah provide an opportunity to study such relationships in a more arid and extreme climate.

Moretti and Brotherson (1982) examined vegetation and soil factors in relation to slope position on foothill knolls in the Uintah Basin of Utah. They reported that differences in plant life-form composition, plant cover, and wind-adapted growth forms were significant between the top and bottom of the slopes. Plant diversity was also found to vary with slope position.

In a study of vegetation on windswept ridges in south central Wyoming, Anderson et al. (1976) found that mat-forming plants were more predominant on areas subjected to strong winds. Less windy areas were occupied by sagebrush-grass communities.

In the montane steppes of central Utah, England (1979) also found vegetation patterns varied with slope position. Both life form and species composition changed from the ridge top to the base of the slope, with grasses dominating the base of the slope and shrubs dominating the ridge top. Plant moisture stress was also found to vary with slope position.

Moisture relationships associated with slope position also provide an opportunity to detect correlations between ecological variations in the habitat and plant morphology. Anderson's (1977) studies of several cactus groups suggested that the surface area to volume ratio (S/V) of various species of cacti can be correlated to moisture and temperature stress associated with climatic conditions in the area they inhabit. He indicates that the S/V ratio would be expected to increase as moisture and temperature stress decrease. Microclimates (soil and moisture differences) associated with topographical differences with respect to desert knolls may therefore be similarly linked with differences in morphology among species of cacti.

The objective of this study was to determine differences in vegetative patterns with respect to slope position in a desert ecosystem and to identify possible correlations of slope position to variations in life form, cactus morphology, and species niche specialization.

STUDY SITE

The study site is located 16 km north of the Utah-Arizona state line along Highway 91 in Castle Cliffs Wash (Fig. 1). The area lies in a transition zone between the hot Mohave desert and the cold Great Basin desert. Soils are shallow and well drained and have from 0% to 10% slopes. Parent materials are mixed

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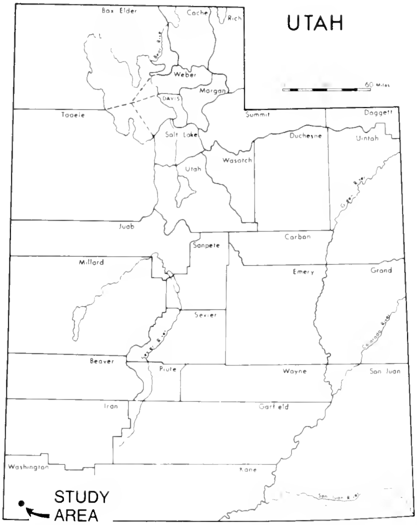

Fig. 1. Map of study site location in Castle Cliffs Wash area of Washington County, Utah.

limestone, gneiss, schist, sandstone, and basalt (Bowns 1973). Altitude of the study area is about 1420 m. The average annual precipitation in the area is 29.6 cm (Hodges and Riechelderfer 1962). Annual temperatures range from 47 C to −23 C (Eubank and Brough 1979).

Materials and Methods

Four slopes of southwest exposure near Castle Cliffs Wash were selected for study. Elevation differences from top to bottom of the slope varied from 30 to 50 m. Slope steepness varied between 16% and 20%. Each slope was sampled with four 10 × 10 m (0.01 ha) study plots. The plots were established at four different slope positions; ridge top, upper slope, lower slope, and floodplain. Each plot was randomly subsampled with 10-quarter-meter-square quadrats. Vascular plant cover was estimated for each species (Daubenmire 1959) at each quadrat. In addition, cover contributed by rock, litter, and cryptogamic crusts was estimated. Soil depth was measured with a penetrometer within five of the 10-quarter-meter-square quadrats (Greenwood and Brotherson 1978). Total living plant cover, plant cover by life form (i.e., trees, shrubs, perennial forbs, perennial grasses, annuals, cryptogams, succulents) were ocularly estimated from each quadrat following a procedure suggested by Ostler (1980).

Cluster analysis techniques (Sneath and Sokal 1973) were applied to similarity index values (in percent) computed via the formula: SI = Σmin (XiYi) / Σmax (XiYi) where SI is the similarity index between two study sites: the Σmin (XiYi) represents the sum of the minimum values from the paired relative abundance figures across all species found in stands (XY), and the Σmax (XiYi) represents a similar figure for the maximum values of the same two stands (Ruzicka 1958). Clustering the above indices employed unweighted pair/group clustering procedures (Sneath and Sokal 1973). This method computes the average similarity of each unit to the cluster, using arithmetic averages. It is widely used and has been found to introduce less distortion than other methods (Kaesler and Cairns 1972). Using this technique we expected to cluster those study plots that were most alike together and thus aid in uncovering relationships existent between them.

Means were calculated for all biotic and abiotic data. In addition, niche breadth and overlap indicies (Colwell and Futuyma 1971) were computed for all species found in the study area. Species were clustered from niche overlap values. Plant nomenclature follows Welsh and Moore (1973) for the dicotyledons and Cronquist et al. (1977) for the monocotyledons.

In an attempt to compute surface area to volume ratios for each cactus species encountered, individual plants in each plot were measured. Barrel cactus (*Ferocactus acanthoides*) was measured for height and width; numbers of flutes on each plant were recorded, and average depth of the flutes was determined. Measurements of buckhorn cholla (*Opuntia acanthoecarpa*) included the length and width of the individual segments on the plant and the total number of segments for each plant.

Results and Discussion

As shown in Table 1, soil depth was greatest at the base of the slope and decreased with

TABLE 1. Mean values for the environmental factors (biotic and abiotic) for the slopes of the Castle Cliffs area of southern Utah.

	Slope position			
Environmental factors	Ridge top	Upper slope	Lower slope	Floodplain
ABIOTIC FACTORS				
Soil depth (dm)	0.8	2.1	4.1	5.8
Rock cover (%)	70.4	7.3	10.6	13.6
Bare ground (%)	7.8	56.5	38.2	60.3
SSMI	1.3	2.0	2.7	3.3
Litter cover (%)	8.2	5.1	8.3	8.1
BIOTIC FACTORS				
Average vegetation height (dm)	4.9	5.9	5.2	5.0
Total living cover (%)	28.9	34.8	39.6	29.7
Tree cover (%)	4.2	0.0	0.0	0.5
Shrub cover (%)	14.8	27.5	39.5	15.9
Forb cover (%)	1.4	2.0	2.2	3.8
Grass cover (%)	5.8	1.8	3.5	3.4
Annual cover (%)	5.7	3.3	3.1	3.4
Cryptogam crust cover (%)	5.1	3.2	0.9	0.1
Succulent cover (%)	3.7	0.0	0.0	4.4
Yucca species cover (%)	0.1	2.8	0.4	11.2

TABLE 2. Mean cover (%) of plant species in relation to position in the Castle Cliffs area of southern Utah.

	Slope position			
Species	Ridge top	Upper slope	Lower slope	Floodplain
Cersium species	0.3			
Coleogyne ramosissima	12.8	70.5	15.6	1.2
Cowania mexicana	1.7		0.9	0.4
Dalea fremontii	0.4			
Ephedra nevadensis	9.1	8.7	8.9	16.5
Eriogonum microthecum	3.0	0.3		3.6
Ferocactus acanthodes	12.9			
Gutierrezia microcephala	2.5	1.8	65.6	11.6
Gutierrezia sarothrae	47.3	0.3	1.7	
Hymenochlea salsola			1.0	
Juniperus osteosperma	0.3			
Lithospermum multiflorum	3.0			0.9
Opuntia acanthocarpa			4.5	9.6
Opuntia polyacantha		0.8		2.1
Prunus fasciculata			0.4	
Senecio longilobus			4.5	20.1
Yucca baccata	0.5	17.5	1.2	
Yucca brevifolia	2.3	0.3	0.5	11.6

elevation, reaching a minimum at the ridge top. This is probably the result of soil movement downslope by water, wind, and gravity. Exposed rock was highest on the ridge top. Rock outcroppings on the tops of knolls are a prominent feature of the area and reflect the high values of exposed rock. Habitat conditions on the slopes of the knolls (i.e., exposed rock, varying soil depths, exposure to wind, etc.) create a moisture gradient downslope (England 1979). Ridge tops are characterized as being the most zeric, with moisture stress decreasing downslope. Therefore, the most mesic conditions exist at the slope base. Total vegetation cover and litter cover were sparse over the entire area and may therefore have little significant effect on water runoff or soil stabilization on the slopes.

Plant life forms showed significant variation in relation to slope position (Table 2). Cover of cryptogamic crusts was highest on the ridge top and steadily decreased downslope. In midslope areas the velocity of water movement over the ground may prevent establishment of cryptogams. The near absence of cryptogams at the base of the slope may be

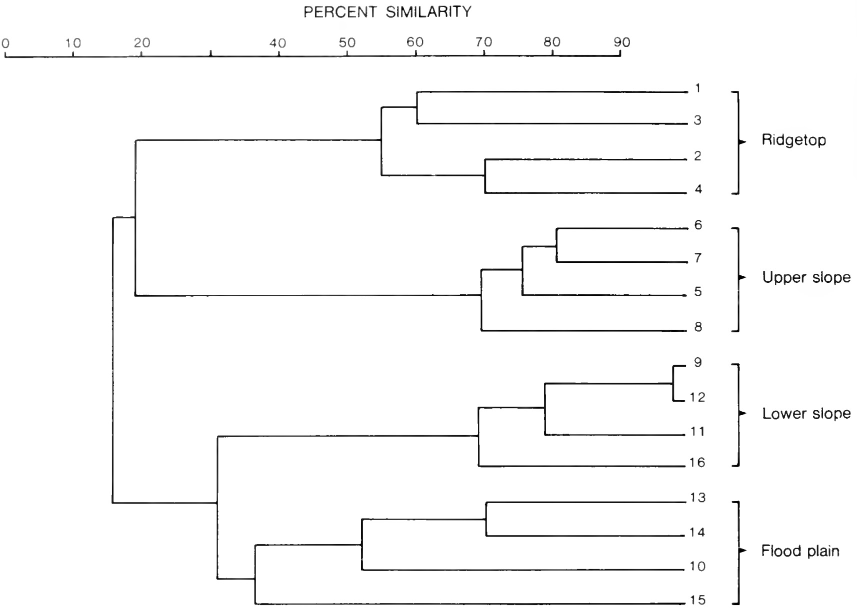

Fig. 2. Cluster analysis dendrogram of 16 study sites with respect to slope position. Clustering based on similarity of vegetative cover.

due to flooding and soil movement that occur during thunderstorms in the area. Shrub cover was highest in the midslope positions, decreasing upslope and downslope. Forb cover generally increased downslope, and perennial grasses and annuals were most prominent at the ridge tops but were found at all slope positions. Succulents (Cacti) were restricted to the ridge top and floodplain sites. This may be due to competition from the elevated levels of shrub cover at the midslope positions (Table 1). Yucca cover was most predominant on the floodplain sites.

Cluster analysis was used to group the study sites on the basis of similarity in vegetative cover (Fig. 2). As shown, four groups emerged. With the exception of two sites (10 and 16), the clustering correlated well with slope position. Patterns were strong, with most stands clustering above the 55% level. The floodplain group clustered more loosely (at the 32% level), indicating greater variability in the vegetation of those sites.

The high level of clustering in the groups suggests a causal effect for the occurrence of dominant species that characterize each slope position (Table 2). The ridge top and upper slope sites appear to be more similar to each other vegetatively than they are to the lower slope and floodplain sites. The reverse is also true. The vegetation on the slopes can be described as being highly distinct at the ends of the slope gradient (i.e., ridge top and floodplain) and grading toward the midslope from both ends.

A list of important plant species was developed for each slope position (Table 2). Threadleaf snakeweed (*Gutierrezia microcephcela*), blackbrush (*Coleogyne ramosissima*), Nevada ephedra (*Ephedra nevadensis*), and Joshua tree (*Yucca brevifolia*) were found at all slope positions and therefore are apparently adapted to tolerate a wide range of environmental conditions. However, differences in cover values at the four slope positions indicate that each species has optimum

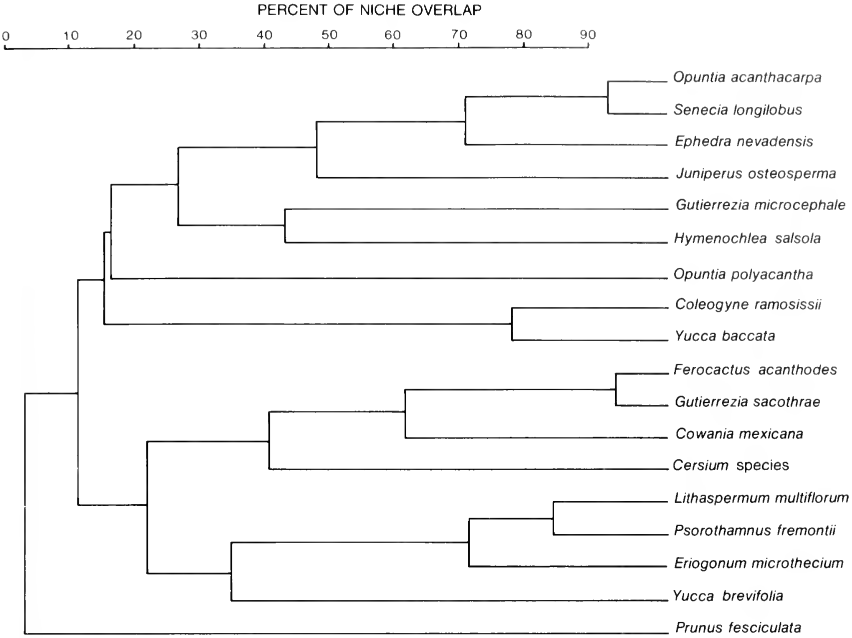

Fig. 3. Cluster analysis dendrogram of species. Clustering based on niche overlap values.

growing conditions at only one position along the slope. Seventy percent of the blackbrush cover is at the upper-slope position, 96% of threadleaf snakeweed's cover occurred at the lower-slope position, and 79% of Joshua tree's cover and 38% of Nevada ephedra's cover occurred in the floodplain. Cover values for other species also showed restricted distribution patterns. Thistle (*Cersium* sp.), cliffrose (*Cowania mexicana*), Fremont Dalia (*Dalea fremontii*), and barrel cactus (*Ferocactus acanthodes*) had significantly higher cover values on the ridge top; Datil yucca (*Yucca baccata*) was higher at the upper slope. Nevada ephedra (*Ephedra nevadensis*), slenderbush eriogonum (*Eriogonum microthecum*), threadleaf groundsel (*Senecio longilobus*), prickly pear (*Opuntia polyacantha*), buckhorn cholla (*Opuntia acanthocarpa*), and Utah juniper (*Juniperus osteosperma*) are highest on the floodplain.

To help clarify relationships between these patterns of distribution, the species were clustered on the basis of niche overlap values (Fig. 3). As shown, there are four distinct cluster groups. The groups generally reflect distribution patterns of species that correlate with slope position. For example, blackbrush and Datil yucca are species restricted to the upper midslope sites. Broom snakeweed and barrel cactus are the most closely associated species. Both occurred predominantly on the ridge top and therefore appear best adapted to the more xeric areas of the study site. A strong association also exists between the distribution patterns of the blackbrush and Datil yucca. Optimum growing conditions for these species seem to be present on the upper slopes of the arroyos. The cluster containing buckhorn cholla, threadleaf groundsel, Nevada ephedra, and Utah juniper also suggests similar habitat preferences. These species occurred mainly on the floodplain in the study area. Joshua tree showed no strong associations with any other species on the site. This is probably due to its occurrence at all slope positions with only a slight preference for the floodplain. Other associations in the cluster

TABLE 3. Correlation coefficients of biotic and abiotic factors with respect to each other and to slope position. Correlation coefficients of above .468 are significant at the 0.05 level, above .588 are significant at the .01 level, and above .708 are significant above the .001 level.

Factor	Bare ground	Soil depth	Rock	Litter
Gutierrezia sarothrae	−.777	.545	.879	
Ferocactus acanthoides	−.766	.565	.881	
Opuntia acanthocarpa		.786		
Senecio longilobus		.599		
Coleogyne ramosissima				−.576
Yucca baccata				−.632
Grasses	−.645		.750	
Forbs		.804		
Annuals	−.617		.686	
Cryptogams		−.546	.514	
Soil depth	.537			
Rock	−.818			
Total living cover			−.653	

are due to the relatively low cover contributed by each species.

The plant life forms, species cover values, and environmental factors were subjected to correlation analyses (Table 3), from which several significant correlations developed. Most of the correlations appear related to slope effect. For example, grasses as a life form are negatively correlated with bare ground and positively correlated with rock. Since ridge tops had large areas of exposed rock, the floodplain had large areas of bare ground, and grasses were predominant on the ridge tops and less important downslope; the implied relationships appear valid. The same holds true for cryptogamic crusts that were negatively correlated with soil depth and positively correlated with rock. All factors examined seem to exhibit patterns with respect to slope.

Disjunct distribution patterns of two sets of congeneric species, (1) Datil yucca and Joshua tree and (2) Broom snakeweed and threadleaf snakeweed, are conspicuous. All four species are known to be widely distributed in the Mojave desert, but Broom snakeweed and Datil yucca extend further north into the Great Basin desert. On the study sites Datil yucca and broom snakeweed were primarily restricted to the ridge tops and upper slopes, and Joshua tree and threadleaf snakeweed were most predominant on the floodplain and lower slopes.

Since the study site lies in a transition zone between the Great Basin desert on the north and the Mojave Desert on the south, differences in the habitat requirements of these congeneric species are more easily recognized. The effects of slope on the overall environmental complex allows for the geographical separation of species in localized areas while having in common distribution patterns across large geographical areas.

Also, the disjunct distribution patterns of barrel cactus and buckhorn cholla (both of the Cactaceae) provide us opportunity to examine variations in plant morphology that may be related to habitat differences. Anderson (1977) suggests that surface area to volume ratios of various cactus species may be correlated with differential temperature and moisture conditions of their habitats. According to his theory, the surface area to volume ratios would be expected to increase as moisture and temperature stress decrease. Although our data were inconclusive because of difficulties we experienced in measuring surface area and volume in these cacti, the cacti exhibit very different morphologies. The buckhorn cholla that occupies the most mesic part of the study site is tall and highly branched. Barrel cactus, on the other hand, is short and unbranched and occupies the most xeric parts of the study area. If the morphological differences in these two species is related to environmental stress and/or other habitat differences, the causal relationships are not readily apparent. Further work is presently underway to investigate this phenomena.

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INVASION AND STABILIZATION OF RECENT BEACHES BY SALT GRASS (*DISTICHILIS SPICATA*) AT MONO LAKE, MONO COUNTY, CALIFORNIA

Jack D. Brotherson[1] and Samuel R. Rushforth[1]

ABSTRACT.— Invasion of plant species onto recently exposed beaches of Mono Lake, California, was documented. Three vegetation zones were evident on these beaches. The first was formed entirely of annual species. The second was composed of annuals mixed with salt grass, and the third was formed entirely of salt grass. Stabilization of these beaches was accomplished by the aggressive growth of salt grass rhizomes.

Present-day Mono Lake is a saline remnant of Pleistocene Lake Russell. Mono Lake lies in Mono Basin with no outlet drainage (Fig. 1). The lake is fed by five major tributary streams flowing off the east slope of the Sierra Nevada. Until recently, this flow had been sufficient to maintain the lake at or near presettlement elevation and salinity. However, in recent years the demand for water created by population growth in southern California has led to the construction of the Los Angeles Aqueduct and Tunnel System. This water capture system has tapped four of the five tributary streams of Mono Lake and has led to significant dewatering. This hás resulted in increased salinity and a corresponding 13.5-m (44-foot) drop in water level since 1941 (Young 1981). This drawdown has left large areas of former lake bottom to become exposed beaches. One such new beach on the northwest part of the lake between Black Point and Niget Island is composed of black lava sands originating from volcanic explosions during the quite recent past.

Since the drawdown of Mono Lake during the last 40 years, a significant invasion of these new beaches by vascular plant species has occurred. The objectives of the present study were twofold. First, we wanted to determine what species were important in invasion, and, second, we wanted to document the invasion process and resultant stabilization of the beaches.

METHODS

Twenty 0.25-m quadrats were randomly located in each vegetation zone 27 August 1981. Cover for all plant species encountered as well as for litter and bare ground was estimated following the cover class category method suggested by Daubenmire (1959). Three soil samples were taken from the root zone (top 20 cm of soil) in each vegetational type and later pooled for laboratory analyses of abiotic soil factors.

Soil analyses were performed by the Soil Analysis Laboratory, Department of Agronomy, Brigham Young University, following standard methods. Plant nomenclature is after Munz (1959).

RESULTS AND DISCUSSION

The beach between Black Point and Niget Island exhibited three prominent vegetation zones that seemed to mirror three stages in the beach invasion process. The three zones included one dominated by annual species (Figs. 1, 2), a second dominated by the perennial *Distichilis spicata* (salt grass) (Figs. 5, 6), and a transition zone under invasion by *Distichilis* (Figs. 3, 4). A total of six vascular plant species was encountered in the three vegetation zones (Table 1). These species included only a single perennial and five annuals.

The general pattern of invasion of the new beach appeared to be first by the annuals and later by *Distichilis*. Establishment of saltgrass is not uniform but appears at random points across the beach. Once the saltgrass becomes established, it spreads dramatically by rhizomes (Figs. 3, 4) until it completely dominates the vegetation (Figs. 5, 6) and crowds out the annuals (Table 1). We measured some

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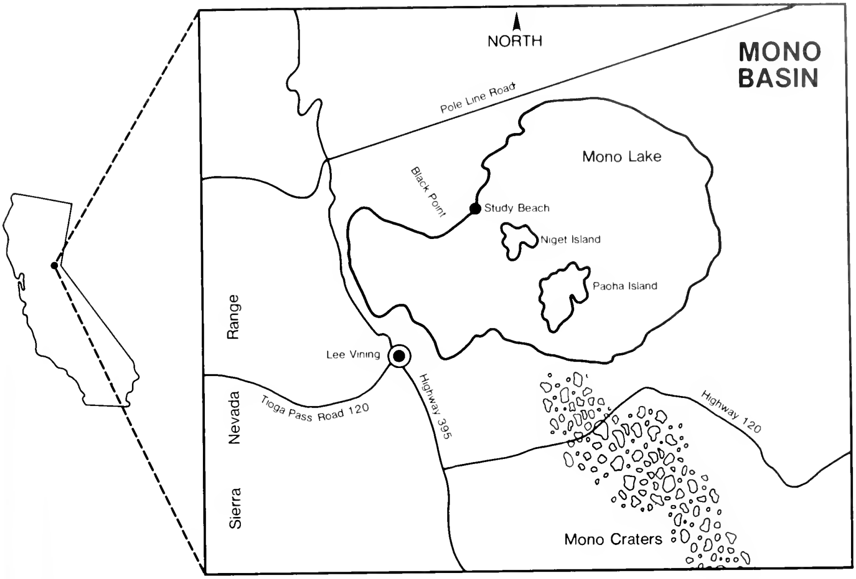


Fig. 1. Reference map showing study area at the edge of Mono Lake in Mono Basin, California.

TABLE 1. Percent cover of vascular plant species, bare ground, and litter in three zones on the beach between Black Point and Niget Island at the edge of Mono Lake, Mono County, California.

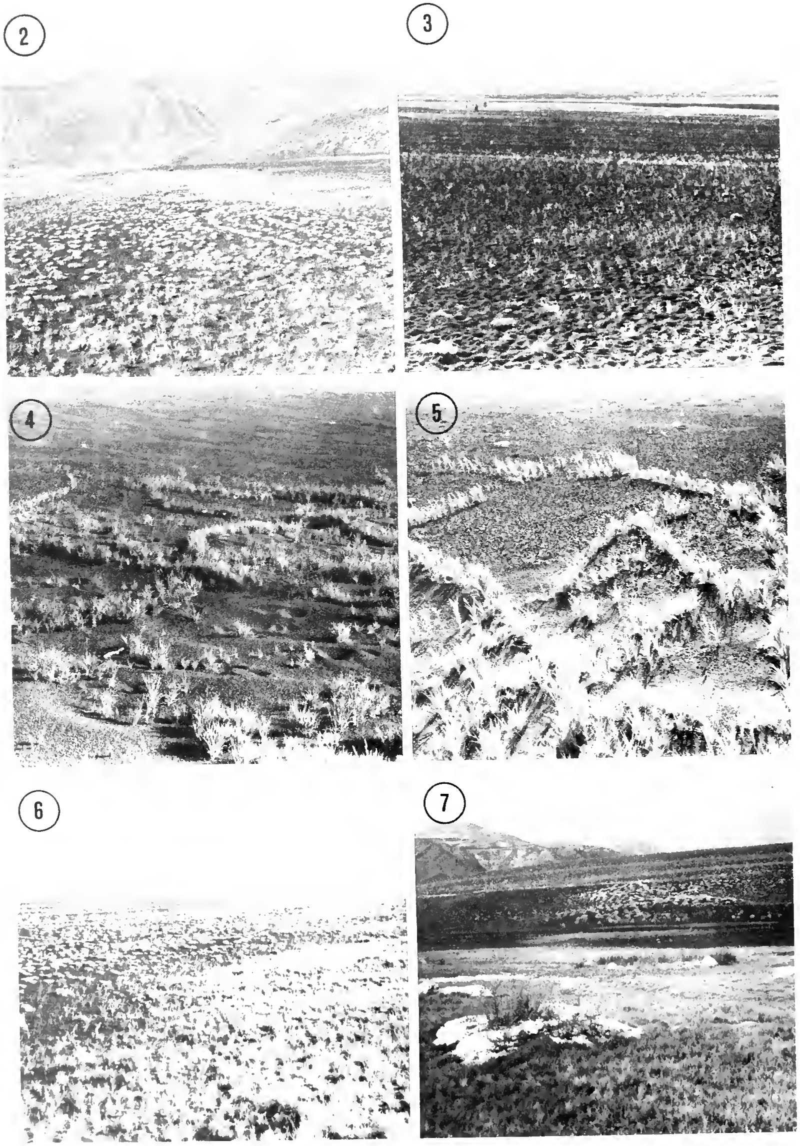
	Zones		
Species	Established *Distichilis*	Invasion zone	Annual zone
Bare ground	52.8	81.8	86.8
Litter	2.5	0.0	0.0
Psathyrotes annua	0.5	3.8	7.8
Distichilis spicata	47.3	11.3	0.0
Kochia scoparia	0.8	0.0	0.3
Mentzelia torreyi	0.0	0.5	4.3
Oenothera boothii	0.3	5.0	6.8
Salsola iberica	0.3	0.5	0.0

TABLE 2. Important physical and chemical factors in three zones of beach soils between Black Point and Niget Island at the edge of Mono Lake, Mono County, California.

	Zones		
Soil Factor	Established *Distichilis*	Invasion zone	Annual zone
Sand (%)	96.0	91.0	93.0
Silt (%)	3.0	4.0	3.0
Clay (%)	1.0	4.0	4.0
Conductance (μmhos)	760	400	420
Soluble salts	38000	20138	20138
pH	7.0	7.3	7.0
Nitrogen (%)	0.005	0.006	0.005
Phosphorus (ppm)	2.27	2.76	2.27
Calcium (ppm)	78.0	68.5	85.0
Magnesium (ppm)	3.0	2.5	4.5
Potassium (ppm)	312.5	295.0	421.0
Sodium (ppm)	112.0	208.0	624.0
Zinc (ppm)	0.58	0.54	0.56
Copper (ppm)	0.09	0.08	0.06
Manganese (ppm)	0.80	0.92	1.00
Iron (ppm)	4.10	5.32	3.68

of these rhizomes at more than 20 m long. In late stages in the invasion process, rhizomes proliferate and entangle until saltgrass cover reaches as high as 87%.

To assess whether vegetational zones may be delineated by edaphic factors, several important soil parameters were measured (Table 2). Noteworthy differences in parameters occurred only in soluble salts, conductance, and sodium. We believe these differences to be related to the fact that *Distichilis* has glands that secrete salts (Hansen et al. 1975) that would likely contribute salts to the soils where it grows. No major differences in other soil factors were evident between the three zones,



Figs. 2–7. Views of the beach between Niget Island and Black Point, Mono Lake, California: 2–3, Annual zone; 4–5, Transition zone showing long rhizomes of salt grass, 6–7, Salt grass zone.

suggesting that vegetation differences are due to invasional phenomena rather than soil factors.

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GRASS SPIDER MICROHABITAT USE IN ORGAN PIPE CACTUS NATIONAL MONUMENT, ARIZONA

Mark Robert Deutschman[1]

ABSTRACT.— The grass spider (*Agelena naevia*), commonly found in Organ Pipe Cactus National Monument, Arizona, uses rodent burrows located under a shrub canopy more frequently for web construction than burrows located in the open. The average number of prey available in canopy microhabitat was greater than in open microhabitat, and unequal prey abundance may explain spider microhabitat use.

Fixed-web foragers must assess prey abundance when selecting a web site (Riechart 1979). Locomotion, silk production, and respiration while waiting for prey all require energy (Ford 1977). When selecting a web site, spiders might choose a microhabitat that maximizes prey availability. Turnbull (1964) reported that *Achaearanea tepidariorum* (Koch), a web-building spider, used prey availability as an index to determine web location. Webs were placed where wind currents maximized prey availability and minimized web damage. Horton and Wise (1983) found web location in two species of orb-web-building spiders to be affected by the degree of environmental stress. Turnbull assumed (1964) that solar radiation and wind velocity influence web location.

The grass spider (*Agelena naevia*), common to the Sonoran Desert, constructs webs in the openings of rodent burrows. Therefore, microhabitat use may be a consequence of burrow location. Because prey capture should be maximized, microhabitat preference may also be determined by prey abundance. In this paper, I seek to determine whether or not the distribution of *Agelena naevia* is independent of burrow location and whether food availability may be a possible explanation for the preferential use of canopy microhabitat.

MATERIAL AND METHODS

This study was conducted on the desert flats of Organ Pipe Cactus National Monument, Arizona, in late March 1982. The number of rodent burrows, with and without webs built in the burrow opening, were counted in a 3- by 50-m transect in two microhabitats. Burrows were located in canopy microhabitat if below the downward projection of a bush canopy (normally *Larrea tridentata* or *Ambrosia deltoidea*); otherwise, burrows were in open microhabitat. All animal burrows were considered available for spider occupancy, and I made no attempt to distinguish if rodent burrows were currently being used.

Twelve plastic boards ($10\ \text{cm}^2$) covered with Tanglefoot were used to assess insect availability. Twelve boards were placed in each microhabitat on each of two successive days. Boards in canopy microhabitat were randomly placed either north, south, east, or west of the bush under the edge of the canopy. Boards in open microhabitat were arbitrarily placed at least 2 m from a bush canopy.

Spider body length (front of head to tip of abdomen) was also measured in each microhabitat using a vernier caliper while randomly searching for webs.

RESULTS

Spider distribution was related to burrow location ($X^2 = 5.37$, $p = .02$). Spiders occupied 33.4% of the burrows in the canopy microhabitat and 4.8% of the burrows in the open microhabitat.

The number of prey were also different between microhabitats (ANOVA, $F = 8.79$, $p < .01$); an average of 1.16 ± 0.9 insects/day were caught in the open microhabitat, and 2.42 ±

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1.1 insects/day were caught in the canopy microhabitat.

Significantly larger spiders occurred in the canopy microhabitat ($F = 4.14$, $p < .05$). The mean spider body length was 0.66 ± 0.19 cm ($n = 22$) in the open microhabitat and 0.76 ± 0.19 cm ($n = 29$) in the canopy microhabitat.

DISCUSSION

Greater food abundance may explain the preferential use of canopy microhabitat by *Agelena naevia*. However, other hypotheses include: (1) lower environmental stress in the canopy microhabitat, (2) more suitable strata for web construction in the canopy microhabitat, (3) rodent burrows may not be equally available as sites for web construction in canopy and open microhabitats. These hypotheses are discussed below.

Although Castillo and Eberhard (1983) reported that artificial webs were inaccurate in assessing the exact species composition of prey captured by webs, they do conclude that artificial webs are effective in comparing different properties of the environment (e.g., relative insect abundance). Trapping with sticky plastic boards indicated a greater number of potential prey in the canopy microhabitat. If microhabitat use was based solely on prey abundance, burrows located in canopy microhabitat would be used more often. Increased prey consumption may allow greater growth and reproductive success (Calow 1981).

Less severe environmental conditions may characterize canopy microhabitat. A diminishing of the intense solar radiation of summer should be beneficial in maintaining body temperature at an optimal level. Shrub branches and litter may also provide better physical strata for web construction, resulting in less web destruction and energy for web repair. Eisner and Nowicki (1983) suggested that web destruction resulted not only in the loss of time spent in web repair, but in the loss of valuable proteinaceous silk.

Spiders may choose to establish webs only in inactive (or active?) rodent burrows. If true, then spider residency in a microhabitat is a consequence of the distribution of rodents and the location of inactive rodent burrows. I assumed all burrows were available for spider use and made no distinction with respect to the degree of rodent activity.

At the time of spring hatching, spiders may be seeking burrows. If burrows were limited and canopy microhabitat preferred, competition for web sites might occur. The difference in average spider body length may be evidence of intraspecific competition (Schoener 1974).

ACKNOWLEDGMENTS

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NEW SPECIES OF *PRIMULA* (PRIMULACEAE) FROM UTAH

Ronald J. Kass[1] and Stanley L. Welsh[1]

Abstract.— Named as a new species from the House Range of Millard County, Utah, as *Primula domensis* Kass & Welsh.

The House Range in west central Millard County, Utah, is famous for its massive limestone and dolomite sequence, which exposes cliffs with a relief of more than 1280 m on its western flank. Drainage plunges steeply on the western side, more gently so on the eastern side of the range. The foot slopes are clothed sparsely by mixed desert shrub vegetation, with pinyon-juniper woodland becoming important at about the 2135 m contour. The range is arid, despite its high elevation, and has only a few truly mesic sites.

Collections of plants have been taken from the House Range for almost a century, but no intensive study had been undertaken until the present time. Beginning in 1981 a study of the flora of the House Range was undertaken by the senior author (Kass 1983) as partial fulfillment of the requirements for completion of a master of science degree at Brigham Young University. Those collections, consisting of some 366 species, were routine for the most part, yielding few surprises. An exception among the specimens taken is a dwarf primrose species, whose characteristics, in combination, are unique among the primroses of the west.

Except for the rather widely distributed *Primula parryi* Gray and *P. specuicola* Rydb., the only other primulas known from Utah are rare and restricted (Welsh 1985). *Primula incana* Jones is known from Daggett County and, until 1982, only from its historic type locality in western Garfield County, and *P. maguirei* L. O. Williams is known only from Logan Canyon in Cache County. During 1982 *P. incana* was rediscovered in Garfield County by E. S. Nixon and in 1984 by Sherel Goodrich, presumably neither locality far removed from where it was initially discovered by Marcus E. Jones in 1894. Thus, the discovery of a primrose in the House Range was unexpected. However, *P. nevadensis* N. Holmgren is known from the Mt. Washington area of the Snake Range in White Pine County, Nevada, only 80 km distant from the newly discovered population of primrose growing in the House Range. Relationships of the House Range primrose apparently lie most closely with *P. maguirei* and *P. nevadensis* and more remotely with *P. cusickiana* Gray, a plant of eastern Oregon and Idaho.

***Primula domensis* Kass & Welsh,** sp. nov. Species habitu cum *Primula maguirei* L. O. Williams sed in corollae tubis calyce sub 1.5 longioribus (nec 1.5–2) et corollae lobis latioribus (4–12 nec 4–5 mm) et foliis plus dentatibus differt; ab *Primula nevadensis* N. Holmgren in inflorescentia foliis superans differt; similis *Primula cusickiana* Gray in habitu calyce et corollae tubis ad calyce statura sed in foliis plus dentibus et majoribus et plantis majoribus differt.

Type.— USA: Utah: Millard Co., Sawtooth Canyon, House Range, T19S, R14W, S23, 2590 m, limestone cliff faces, in *Cercocarpus intricatus–Ephedra viridis* community, 4 June 1982, R. and J. Kass 884 (Holotype BRY; isotypes NY, RM, POM).

Plants 7–15 cm tall, from a short, rhizomatous caudex, this clothed with persistent, brown leaf bases; leaves 2–8 (11) cm long, 5–22 mm wide, oblanceolate to spatulate, dentate to subentire, tapering to a broad petiole, green and more or less glandular on both sides; bracts usually 3, 1.5–10 mm long, lanceolate, not swollen at the base, glabrous or mealy; peduncle apex glabrous or somewhat

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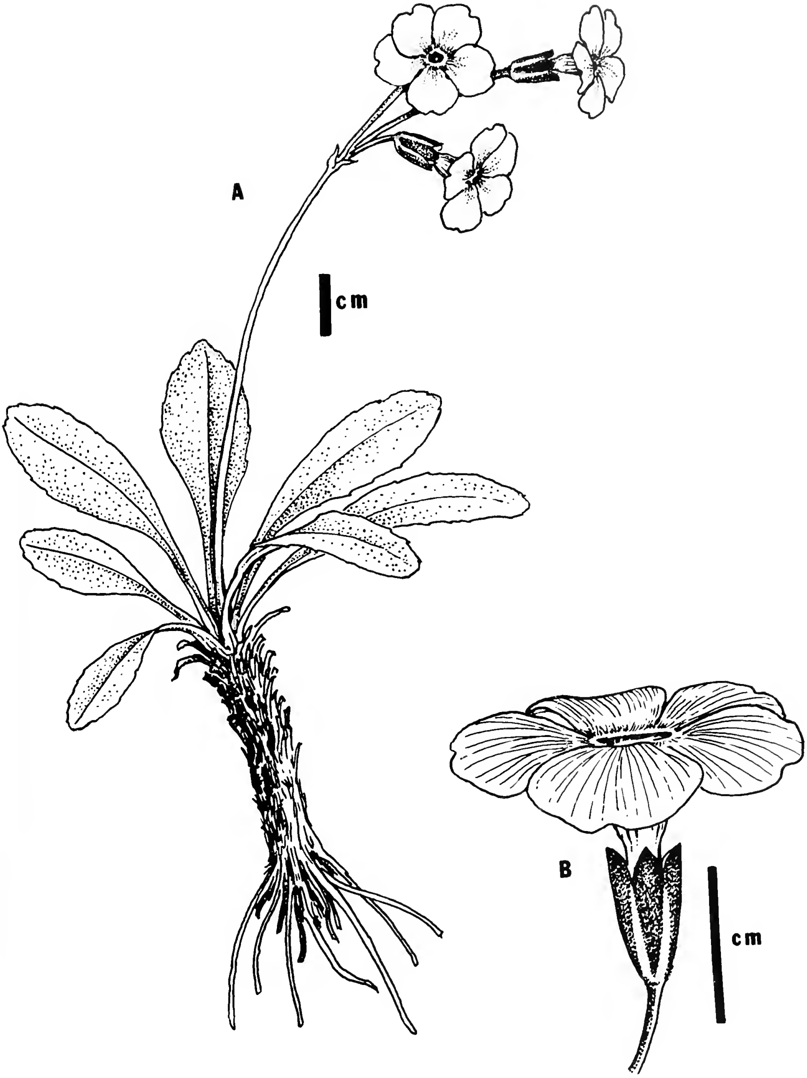

Fig. 1. *Primula domensis* Kass & Welsh. A, Habit. B, Detail of flower.

mealy; umbels 1- to 5-flowered, the pedicels 5–22 mm long; calyx 8–12 mm long, mealy or glabrous, the teeth shorter than the tube, more or less accrescent in fruit; corolla rose to lavender, the tube surpassing the calyx, but less than twice its length, the limb 12–25 mm wide, the lobes shorter than the tube, 4–12 mm wide; capsule to 8 mm long, not surpassing the calyx.

ADDITIONAL SPECIMENS.— Utah: Millard Co., House Range, Notch Peak, T19S, R14W, S23, moist limestone cliffs at 2623 m, 22 May 1981, R. Kass 289 (BRY); Ibid., T19S, R14W, S22, limestone cliffs at 2745 m, 27 June 1981, R. Kass & S. White 473 (BRY; UT, UTC).

The House Range primrose is most closely similar to *P. nevadensis* and *P. maguirei*, between whose ranges it occurs. It differs from the former in the inflorescence to leaf proportions (leaves are overtopped by the inflorescence) and leaf shape (leaves spatulate to oblanceolate, not cuneate) and from the latter in the corolla tube to calyx proportions, mostly broader corolla lobes, and more consistently toothed leaves. It seems probable that each of these geographically and genetically isolated microspecies would be treated best as portions of an expanded *P. cusickiana*, the first named of the group. However, no such combination is intended or implied herein.

The specific epithet is taken from the word "house" (*domus* in Latin) from the House Range.

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NEW SPECIES OF *ASTRAGALUS* (LEGUMINOSAE) FROM SOUTHEASTERN UTAH

Rupert C. Barneby[1] and Stanley L. Welsh[2]

ABSTRACT.— Named and described is *Astragalus piscator* Barneby & Welsh, a species of sect. Argophylli subsect. Missourienses. The species occurs in Grand and San Juan counties, Utah.

For several years the authors have been aware of an undescribed species of *Astragalus* masquerading within the specimens designated as *A. amphioxys* and *A. cymboides* from Grand and San Juan counties in southeastern Utah. The plants begin flowering in late March and are in fruit by mid-May. Few collections represent flowering material, possibly due to the earliness of anthesis. Relationship of flowering to fruiting materials has only recently become apparent. The species is described as follows:

Astragalus (sect. *Argophylli* subsect. *Missourienses*) *piscator* Barneby & Welsh, sp. nov., inter arcte affines *A. musiniensem* M. E. Jones, *A. chamaeleucem* A. Gray, *A. amphioxyn* A. Gray necnon *A. cymboidem* M. E. Jones ambigens, tam a prima, facie foliolisque ellipticis acutis simili, quam a secunda, foliolis obovatis obtusis distantiori, leguminis valvulis maturis chartaceis nec spongiosi-alveolatis diversa, a tertia imprimis leguminis longitrorsus bicariniti sutura dorsali tota longitudine acuta, nec depressa, et ab *A. cymboide* legumine simpliciter per rostrum hiantem dehiscenti valvularum epicarpio haud ab endocarpio exfolianti diagnoscenda.—UTAH. San Juan Co.,: Salt Canyon, above jump, T31S, R20E, S31/32, +/− 1700 m, 2 June 1964 (fr), S. L. Welsh (with G. Moore and S. G. Canter) 2979.—Holotype, BRY; isotype, NY.

Acaulescent or subacaulescent herbs from vertical taproot, perennial of short duration flowering the first year, the leaves and scapiform peduncles arising from root-crown at soil level, this more or less clothed with a persistent thatch of leaf bases, strigose throughout with appressed dolabriform hairs, the leaflets yellow-green above, gray beneath; stipules ovate-acuminate 3–9 mm, usually closely imbricated, strigose dorsally, persistent; leaves (3)4–10(16) cm; leaflets of most leaves 5–11(13), elliptic or lance-elliptic, acute or subobtuse (5)7–17(32) × 2–4(6) mm, those of some eophylls only 1–3 and rhombic ovate; peduncles (1)2–6(9) cm, ascending at anthesis, procumbent in fruit, the pods humistrate; racemes shortly loosely 3–10-flowered, the axis becoming 4–15(20) mm in fruit; calyx 11–14.5 mm, either black- or partly white-strigose, the cylindric tube 8.5–11 × 3–4 mm, the linear-subulate teeth 2–3.5(4) mm; corolla of *A. amphioxys*, the banner 18–24 mm, the obtuse keel 16–18 mm; ovary strigulose, the ovules +/− 40; pod ascending, sessile, deciduous from receptacle, in profile lance-elliptic, shallowly lunate-incurved, obtuse at base, acuminate distally, 24–40 × 8–15 mm, somewhat laterally compressed but the valves dilated near middle into an obtuse longitudinal ridge, both sutures becoming sharply prominulous at maturity, the moderately fleshy, densely strigose, purplish mottled valves becoming stiffly chartaceous or subcoriaceous (but not pithy) and +/− 0.5 mm thick when dry, dehiscent after falling through the gaping beak.

In sandy soils of valley benches and in gullied foothills, on Moenkopi, Cutler, and White Rim formations, 1550–1750 m, known only from the lower Grand River Valley in SE Grand and N San Juan counties, Utah.—Fl. late March to early June.

ADDITIONAL SPECIMENS EXAMINED: UTAH. Grand Co.: foothills east of Moab, 28 March 1967, J. Pederson 15 (BRY); Castle Valley, T25S, R23E, 5 June 1970, S. L. Welsh & N. D. Atwood 9952 (BRY, NY), 9953 (BRY); along Fisher Valley road up Onion Creek, 8.4 mi E of Utah Hwy 128, below summit of road at Fisher Valley, 1 July 1975, J. L. Reveal

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[2] Life Science Museum and Department of Botany and Range Science, Brigham Young University, Provo, Utah 84602.

3850 (BRY; NY); ibid., 20 May 1982, R. Barneby 17808 (BRY, NY, US); about half a mile E of Castle Rock, T25S, R23E, S9, 28 April 1984, S. L. Welsh & D. Trotter 22716 (BRY, NY, ISC, RM, CAS, RSA, UT, UTC, COLO). San Juan Co.: Chesler Park, T31S, R19E, S5, 1 June 1964, S. L. Welsh, G. Moore, & S. G. Canter 2899 (BRY); Canyonlands National Park, Virginia Park, northeast of entrance, in grassy flat, 14 May 1965, G. Moore 316 (BRY).

Astragalus piscator is a critical species closely related to *A. musiniensis* M. E. Jones, *A. cymboides* M. E. Jones, *A. chamaeleuce* A. Gray, and *A. amphioxys* A. Gray but is distinguished by a regrouping of foliage and pod characters not previously encountered. In habit and mostly elliptic acute leaflets it resembles *A. musiniensis*, but the lateral compression of the ripe pod is reminiscent rather of *A. cymboides*. The pod valves are, however, only moderately fleshy, as in *A. amphioxys*, and do not become alveolate-pithy as in *A. musiniensis* and *A. cymboides*. The fully ripe pod of the last mentioned is remarkable for the exfoliating epicarp of the valves, a character unique to this one species. Although the pod of *A. piscator* resembles that of *A. amphioxys* in texture and curvature, it differs in the permanently prominent dorsal suture and consequently elliptic transverse section. On Onion Creek *A. piscator* and *A. amphioxys* were encountered in close proximity and were there instantly perceived as different in foliage and flower color, the petals of the new species being pale lilac, not vivid pink-purple.

Because of the distinctive fruit, this species was regarded as belonging to *A. missouriensis* by Welsh following initial collections taken in June 1964. However, it was the robust material taken by Welsh and Atwood from Castle Valley in 1970, and by Reveal from Onion Creek in 1975, that called our attention to *A. piscator*. Among the specimens taken in 1970 and 1975 are relatively gigantic plants, with leaves up to 17 cm long and pods up to 14 mm in diameter. Specimens bearing flowers and young pods, collected from what is believed to be the same part of the Onion Creek population in the unfavorable spring of 1982, show a gradation in stature down to a diminutive plant only 4 cm diameter. A longer set of flowering plants from nearby Castle Rock obtained in 1984 is essentially similar to the last. Although this material was being analyzed for the Intermountain Flora, a collection, cited above as type of *A. piscator*, was retrieved from the herbarium at NY, where it had lain for twenty years misidentified as a varient of *A. chamaeleuce* (the specimen exchanged as *A. missouriensis* by Welsh). Subsequent review of specimens identified at BRY as *A. amphioxys*, *A. cymboides*, and *A. missouriensis* yielded the other specimens cited above. The *Argophylli* are notoriously sensitive and adaptable to annual fluctuation of rainfall, and we believe the extremes of variation allowed for in our description of *A. piscator* are acceptable within any species of this group.

The epithet "piscator" refers to Fisher Towers, a notable geological feature of the Grand Valley near the main body of the species. The species will be illustrated in a forthcoming volume of the Intermountain Flora.

NEW *SCLEROCACTUS* (CACTACEAE) FROM NEVADA

Stanley L. Welsh[1] and Kaye Hugie Thorne[1]

Abstract.— Described is *Sclerocactus blainei* Welsh & Thorne, sp. nov. from Nye County, Nevada.

Studies of rare plant species in portions of Nevada were undertaken in 1980 when many of the valleys were under consideration as possible sites for location of long-range guided missile launching sites. The studies yielded many records of rare plant species, among them specimens identified initially as *Sclerocactus polyancistrus* (Engelm. & Bigel.) Britt. & Rose. Specimens were discovered by members of two field crews 3 and 4 June in Railroad, Ralston, and Hot Creek valleys. Three separate discoveries were made, including a mature plant in full flower, a juvenile plant, and a moderately mature, fruiting plant with 5 large, whorled stems around a dead base of a mature plant. The extent of the known range exists along a northeast-southwest axis of more than 160 km. The collecting crews consisted of Kaye Hugie Thorne and Blaine Tree Welsh in Railroad Valley and Dr. Elizabeth Neese and Susan White in Ralston and Hot Creek valleys.

Revision of the Cactaceae for the flora of Utah (Welsh 1984) stimulated examination of Nevada materials as well. It became apparent that the materials from Nye County matched neither the large-flowered specimens with numerous glabrous, long, central spines from Esmerelda and southern Nye counties designated as *S. polyancistrus* nor the small-flowered specimens of *S. pubispinus* (Engelm.) L. Benson with fewer central spines and puberulent juvenile or even mature spines from eastern White Pine County. They were remarkable in sharing some features of both the extreme types. However, the plants were intermediate in such features as central spine number. Thus, the unique combination of characteristics dictated that the plants require formal taxonomic recognition.

Sclerocactus blainei **Welsh & Thorne**, sp. nov. Plantis similis *Sclerocacto pubispino* (Engelm.) L. Benson sed in spinis pubescentibus et floribus majoribus differt et similis *Sclerocacto polyancistro* (Engelm. & Bigel.) Britt. & Rose in staturis et floribus sed in spinis paucioribus, brevioribus, et pubescentibus (inter alia) differt.

Type.— USA: Nevada: Nye Co., T10N, R58E, 1.6 km NE of Currant, 1617 M elev, 23 May 1981, S. L. Welsh 20580 (Holotype BRY).

Plants solitary or sometimes colonial, depressed-hemispheric, obovoid, ovoid, or cylindric, 3–15 cm tall or more; ribs mainly 6–12, tuberculate; areoles circular to elliptic, villous, juvenile spines and often mature ones (in part) densely to sparingly white-puberulent to villous, finally glabrate; central spines 1–6, some or all of them hooked, mainly 1.8–5.5 cm long, straight or curved, the upper central spine (at least) usually pale and flattened (or trigonous) and more or less ribbon-like, 0.5–6 cm long, 1–1.8 (2.1) mm wide, erect; radial spines 10–16 or more; flowers 8–10 cm long in anthesis; sepaloids greenish, margined with rose-purple; petaloids pink or violet; fruit immature, green, not scaly; seeds unknown.

Additional specimens.— Nevada. Nye Co., same locality and another bud of the same plant as the type, 3 June 1980, K. H. Thorne and B. T. Welsh 960A (BRY); Nye County, T2N, R45E, 1830 m elev, 4 June 1980, E. Neese & S. White 8872 (BRY, and 3 duplicates distributed previously as S.

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[1] Life Science Museum and Department of Botany and Range Science, Brigham Young University, Provo, Utah 84602.

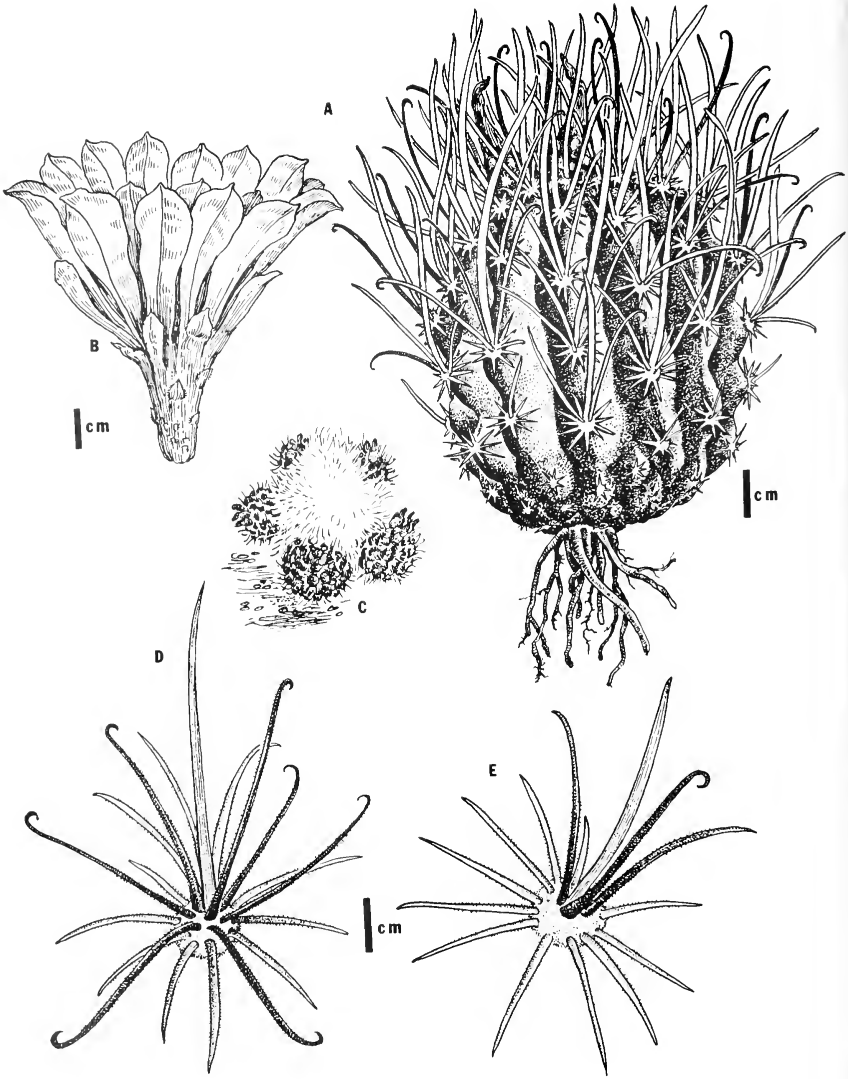

Fig. 1. *Sclerocactus blainei* Welsh & Thorne. A, Detail of the plant. B, Flower. C, Habit of the type specimen, with five buds surrounding the base of a single dead stem. D, Detail of spines at an areole on a mature plant. E, Detail of an areole on an immature plant.

polyancistrus; T4N, R51E, 4 June 1980, E. Neese & S. White 8857 (BRY, a juvenile plant).

The plants grow in greasewood, galleta, rabbitbrush, shadscale, and sagebrush communities at 1586 to 1830 m elevation in limestone and igneous gravel with a clay matrix.

REFERENCES

BENSON, L. 1982. The Cacti of the United States and Canada. Stanford University Press, California. 1044 pp.

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SUCCESSION IN PINYON-JUNIPER WOODLANDS FOLLOWING WILDFIRE IN THE GREAT BASIN

Susan Koniak[1]

ABSTRACT.— Twenty-one areas in pinyon (*Pinus monophylla*)-juniper (*Juniperus osteosperma*) woodlands burned by wildfire from approximately 1 to 60 years prior to sampling and adjacent unburned mature woodland stands were studied in Nevada and California to determine successional patterns and individual species responses to burning and to changing plant communities through time. One year after burning, all late successional woodland species were present in postburn plant communities except tree species. Increases in both cover and occurrence of annual and perennial forbs resulted in their dominance on early successional sites. Shrubs and annual grasses dominated midsuccessional sites, subsequently giving way to tree, shrub, and perennial grass dominance in late succession. North and east slopes generally supported high cover and occurrence of shrubs, perennial grasses, and perennial forbs, and south and west slopes generally supported high cover and occurrence of annual forbs and annual grasses. The ability to group species according to preferential occurrence on various aspects and successional stages can be used to predict plant community composition in time and space in the pinyon-juniper woodlands.

Fire is a natural component of the pinyon-juniper woodland and a primary cause of secondary succession. Everett and Ward (1984) and Klebenow and others (1977) described patterns of early succession following prescribed burns on sites in eastern Nevada. Barney and Frischknecht (1974) examined 28 Utah sites primarily in juniper-dominated woodlands burned by wildfire from 3 to over 100 years ago. Within the framework of a larger study, Stager (1977) described plant species variation among wildfire sites in Great Basin woodlands dominated by both pinyon and juniper. Seven sites were studied, ranging in postburn age from 2 to 115 years. The ability to predict postfire plant and plant community response in the pinyon-juniper woodland depends upon a broader data base than is currently available.

This study was designed to increase our knowledge of individual species response to fire in Great Basin pinyon-juniper woodlands and subsequent changes in cover and occurrence through time. Variations of species cover and occurrence among aspects and differences in the successional cycle between aspect groups were also examined.

FIELD METHODS AND DATA ANALYSIS

In 1981 and 1982 we found 21 areas burned by wildfire from approximately 1 to 60 years ago in pinyon-juniper woodlands in Nevada and California (Table 1). Eight of the burns had been seeded following burning (Koniak 1983). Four successional stages were apparent among the burns: early succession (1-year-old burns), early midsuccession (4- to 8-year-old burns), midsuccession (15- to 17-year-old burns), and late midsuccession (22- to 60-year-old burns). Adjacent to each burned area, unburned pinyon-juniper represented the late successional stage. Study sites were limited to areas that had had a minimum 100 trees per hectare.

On each burn, the entire area or a representative part of the burn was surveyed to determine the plant communities present. A sample stand or relevé was established in each plant community, with size varying with the size of the sampled community. Relevé size generally ranged from 20 m^2 to 100 m^2. Each relevé had to be large enough to contain all species in the plant community and had to have uniform aspect and slope and homogeneous plant cover. On each relevé all species were recorded, and canopy cover for each individual species as well as each growth form (i.e., annual forb, perennial forb, annual grass, perennial grass, shrub, tree) was estimated according to the Braun-Blanquet cover abundance scale (Mueller-Dombois and El-

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TABLE 1. Description of 21 pinyon-juniper burned areas in Nevada (NV) and California (CA) studied to determine successional patterns.

Study areas	Date of burn	Location description	Average elevation (m)	Average annual precipitation (cm)
Double Springs (NV)	1920's	T11N R21E Sec 31, 32	1975	33
June Ellen (NV)	1950's	T15N R21E Sec 35	2060	33
Jumbo (NV)	7-57	T17N R20E Sec 23,26	1900	33
War Canyon (NV)	8-58	T20N R36E Sec 25	2160	30
Jake Hill (NV)	7-59	T11N R21E Sec 5	1665	20
Big Creek #1 (NV)	8-64	T17N R43E Sec 10,15,16	2220	30
Gabbs (NV)	8-64	T12N R37E Sec 29	2135	30
Bald Mountain (NV)	7-65	T23N R57E Sec 4,9	2190	32
Wichman Canyon (NV)	7-65	T 8N R27E Sec 19,20,30	2050	24
Bennett Crossing (NV)	5-66	T12N R22E Sec 20	2025	33
Milk Ranch (NV)	8-70	T 8N R65E Sec 19,20	2100	33
Pine Nuts (NV)	8-73	T11N R22E Sec 7,18,19,30 T11N R23E Sec 13,24,25,36	2060	33
Rock Creek (CA)	7-73	T 8N R23E Sec 17,24	1920	24
China Gardens (CA)	7-74	T 7N R23E Sec 4,5 T 8N R23E Sec 28,29,32,33	1910	24
Mt. Wilson (NV)	7-74	T 4N R68E Sec 1–3,10–15 Sec 21–28	2185	33
Geiger Grade (NV)	9-74	T18N R20E Sec 35,36	1797	33
Miller (NV)	7-76	T19N R61E Sec 24–26	2110	31
Big Creek #2 (NV)	8-77	T17N R43E Sec 9	2110	30
Rock Springs (NV)	7-81	T19N R61E Sec 34,35	2230	31
Austin (NV)	8-81	T19N R43E Sec 25,36 T19N R44E Sec 30,31	2020	30
Slater Mine (NV)	8-81	T12N R21E Sec 4–8	2230	31

lenberg 1974). Elevation, slope, and aspect were recorded.

Unburned pinyon-juniper stands were sampled by the same methods used for sampling the burned stands. Several tree cores were taken in each of the 21 areas, with the average age for each area ranging from 72 to 159 years. Approximately one unburned relevé was sampled for every four burned relevés. A total of 546 relevés, 433 burned and 113 unburned, were sampled. There were 187 species in the entire sample.

Chi-square tests were used to delineate the relationships of individual species to aspect and age of stands and to compare the eight seeded burns and 13 nonseeded burns.

RESULTS AND DISCUSSION

Big sagebrush (*Artemisia tridentata*) was the only species found on all 21 burns sampled (Table 2). All the following were found on 75% or more of the burns sampled: rubber rabbitbrush (*Chrysothamnus nauseosus*), low rabbitbrush (*Chrysothamnus viscidiflorus*), antelope bitterbrush (*Purshia tridentata*), desert gooseberry (*Ribes velutinum*), cheatgrass (*Bromus tectorum*), Sandberg bluegrass (*Poa secunda*), bottlebrush squirreltail (*Sitanion hystrix*), prickly poppy (*Argemone munita*), tapertip hawksbeard (*Crepis acuminata*), and tailcup lupine (*Lupinus caudatus*). All except prickly poppy were also present on mature woodlands. These species occurred over a wide range of successional stages and locations, indicating a wide ecological amplitude. Individual species cover was generally less than 1% on most releves. Only 19 understory species had ≥ 5% cover on more than 5% of the relevés where the species occurred (Table 3). Cover will only be discussed if it varies substantially from occurrence values (occurrence = number of sites where a species occurred per total number of sites).

First-Year Postfire Species Response

Initial responses to fire were determined by comparing occurrence and cover of individual species on mature woodlands and on one-

TABLE 2. Plant species that occur on ≥ 5 (24%) of the 21 burns sampled.

Scientific name[1]	Common name	Constancy[2]
Trees and shrubs		
Pinus monophylla	Single leaf pinyon	33
Amelanchier alnifolia	Saskatoon serviceberry	29
Artemisia tridentata	Big sagebrush	100
Ceanothus velutinus	Snowbrush ceanothus	24
Chrysothamnus nauseosus	Rubber rabbitbrush	86
Chrysothamnus viscidiflorus	Low rabbitbrush	95
Ephedra viridis	Green ephedra	67
Opuntia spp.	Prickly pear	33
Prunus andersonii	Anderson peachbrush	43
Purshia tridentata	Antelope bitterbrush	76
Ribes velutinum	Desert gooseberry	95
Sambucus cerulea	Blueberry elder	52
Symphoricarpos oreophilus	Mountain snowberry	57
Tetradymia canescens	Gray horsebrush	38
Xanthocephalum sarothrae	Broom snakeweed	24
Grasses		
Agropyron spicatum	Bluebunch wheatgrass	29
Bromus tectorum	Cheatgrass brome	95
Elymus cinereus	Great Basin wild rye	52
Festuca idahoensis	Idaho fescue	24
Oryzopsis hymenoides	Indian ricegrass	57
Poa fendleriana	Mutton bluegrass	52
Poa secunda	Sandberg bluegrass	95
Sitanion hystrix	Bottlebrush squirreltail	90
Stipa comata	Needle-and-thread	43
Stipa speciosus	Desert needlegrass	24
Stipa thurberiana	Thurber needlegrass	71
Perennial forbs		
Antennaria rosea	Rose pussytoes	29
Arabis holboellii	Holboell rockcress	67
Arenaria nuttallii	—	24
Argemone munita	Hedgehog prickly poppy	76
Astragalus beckwithii	Beckwith milkvetch	43
Astragalus filipes	—	29
Astragalus purshii	Pursh locoweed	52
Balsamorhiza hookeri	Hooker balsamroot	24
Balsamorhiza sagittata	Arrowleaf balsamroot	52
Calochortus nuttallii	Segolily	33
Castilleja chromosa	Indian paintbrush	38
Chaenactis douglasii	Douglas chaenactis	71
Crepis acuminata	Tapertip hawksbeard	76
Cryptantha flavoculata	Roughseed cryptantha	24
Delphinium andersonii	Anderson larkspur	28
Erigeron aphanactis	Hairy fleabane	33
Eriogonum elatum	—	29
Eriogonum umbellatum	Sulphur eriogonum	52
Galium multiflorum	Shrubby bedstraw	29
Lithosperum ruderale	Wayside gromwell	24
Lomatium nevadense	Nevada lomatium	29
Lupinus caudatus	Tailcup lupine	76
Lygodesmia spinosa	Thorn skeleton plant	67
Machaeranthera canescens	Hoary aster	71
Penstemon deustus	Scabland penstemon	29
Penstemon speciosus	Royal penstemon	48
Phacelia hastata	—	57
Phlox hoodii	Hood's phlox	38
Phlox spp.	—	57
Phoenicaulis cheiranthoides	Wallflower phoenicaulis	24

TABLE 2. continued.

Scientific name[1]	Common name	Constancy[2]
Senecio integerrimus	Lambstongue groundsel	29
Senecio multilobatus	Lobeleaf groundsel	29
Zigadensus paniculatus	Foothill deathcamas	24
Annual forbs		
Collinsia parviflora	Little flower collinsia	29
Cryptantha spp.	—	38
Descurainia spp.	Tansy mustard	38
Eriastrum sparsiflorum	Eriastrum	43
Eriogonum spp.	—	33
Erodium cicutarium	Alfileria	33
Gayophytum spp.	Groundsmoke	38
Gilia spp.	—	43
Lactuca serriola	Prickly lettuce	33
Lappula occidentalis	Annual stickweed	33
Mentzelia albicaulis	White stem mentzelia	48
Microsteris gracilis	—	24
Nicotiana attenuata	Coyote tobacco	24
Salsola iberica	Saltwort	29
Sisymbrium altissimum	Tumble mustard	62
Seeded species		
Agropyron cristatum	Fairway wheatgrass	33
Agropyron intermedium	Intermediate wheatgrass	29

[1] According to Holmgren and Reveal (1966).

[2] Constancy is defined as the number of burns a species occurred on divided by the total number of burns.

TABLE 3. Occurrence (percent of relevés a species occurs on) and cover (percent of the relevés a species occurs on that has ≥ 5% cover) of species[1] on five successional stages.

	Occurrence Successional stages					Cover[2] Successional stages				
	Early	Early mid	Mid	Late mid	Late	Early	Early mid	Mid	Late mid	Late
Tree species										
Juniperus osteosperma	0^{c}	0^{c}	2^{c}	27^{b}	56^{a}	0^{b}	0^{b}	0^{b}	0^{b}	100^{a}
Pinus monophylla	0^{c}	$.5^{c}$	5^{c}	80^{b}	100^{a}	0^{b}	0^{b}	0^{b}	5^{b}	100^{a}
Shrub species										
Artemisia tridentata	9^{c}	74^{b}	79^{b}	98^{a}	88^{ab}	0^{d}	15^{c}	36^{b}	88^{a}	30^{b}
Chrysothamnus nauseosus	2^{b}	66^{a}	63^{a}	65^{a}	8^{b}	0^{b}	10^{b}	49^{a}	32^{a}	0^{b}
Chrysothamnus viscidiflorus	37^{c}	54^{b}	75^{a}	44^{bc}	22^{d}	6^{c}	21^{b}	33^{a}	0^{c}	0^{c}
Ephedra viridis	17^{b}	52^{a}	68^{a}	60^{a}	51^{a}	—	—	—	—	—
Prunus andersonii	1^{d}	35^{b}	67^{a}	31^{b}	13^{c}	—	—	—	—	—
Purshia tridentata	28^{c}	60^{b}	61^{b}	83^{a}	73^{a}	0^{c}	3^{c}	15^{c}	45^{a}	24^{b}
Ribes velutinum	25^{c}	72^{a}	48^{b}	59^{ab}	56^{b}	—	—	—	—	—
Sambucus cerulea	45^{ab}	28^{b}	30^{b}	63^{a}	4^{c}	—	—	—	—	—
Symphoricarpos oreophilus	39^{a}	27^{ab}	22^{ab}	38^{a}	20^{b}	6^{bc}	47^{a}	18^{ab}	0^{c}	29^{a}
Tetradymia canescens	8^{b}	37^{a}	10^{b}	4^{b}	13^{b}	0^{b}	22^{a}	0^{b}	0^{b}	0^{b}
Grasses										
Bromus tectorum	42^{c}	86^{a}	61^{b}	60^{b}	49^{bc}	13^{c}	76^{a}	71^{b}	48^{b}	7^{c}
Festuca idahoensis[3]	44^{a}	—	—	—	19^{b}	0^{b}	—	—	—	33^{a}
Oryzopsis hymenoides	12^{bc}	22^{b}	56^{a}	16^{bc}	8^{c}	—	—	—	—	—
Poa fendleriana	4^{c}	7^{c}	7^{bc}	31^{a}	17^{ab}	—	—	—	—	—
Poa secunda	75^{a}	19^{c}	39^{b}	49^{b}	63^{a}	—	—	—	—	—
Sitanion hystrix	43^{c}	58^{b}	49^{bc}	90^{a}	44^{c}	3^{b}	15^{a}	28^{a}	0^{b}	0^{b}
Stipa thurberiana	33^{b}	12^{c}	37^{ab}	57^{a}	34^{b}	0^{bc}	9^{b}	23^{a}	21^{a}	3^{bc}
Perennial forbs										
Arabis holboellii	19^{b}	9^{c}	26^{b}	26^{b}	50^{a}	—	—	—	—	—

TABLE 3. continued.

	Occurrence					Cover[2]				
	Successional stages					Successional stages				
	Early	Early mid	Mid	Late mid	Late	Early	Early mid	Mid	Late mid	Late
Argemone munita	44^{ab}	56^{a}	26^{b}	31^{b}	0^{c}	2^{b}	8^{a}	0^{b}	0^{b}	0^{b}
Astragalus purshii	14^{b}	6^{b}	33^{a}	14^{b}	8^{b}	—	—	—	—	—
Balsamorhiza sagittata	21^{a}	29^{a}	20^{ab}	11^{b}	19^{ab}	—	—	—	—	—
Chaenactis douglasii	8^{a}	7^{a}	16^{a}	13^{a}	7^{a}	—	—	—	—	—
Crepis acuminata	40^{a}	24^{b}	29^{b}	36^{ab}	13^{c}	5^{ab}	6^{ab}	16^{a}	0^{b}	0^{b}
Eriogonum umbellatum	5^{ab}	4^{b}	11^{a}	5^{ab}	10^{a}	—	—	—	—	—
Lupinus caudatus	46^{a}	20^{c}	32^{ab}	25^{ab}	19^{bc}	9^{ab}	7^{ab}	0^{b}	13^{a}	0^{b}
Lygodesmia spinosa	31^{a}	32^{a}	19^{ab}	27^{a}	13^{b}	—	—	—	—	—
Machaeranthera canescens	18^{a}	15^{a}	19^{a}	28^{a}	6^{b}	—	—	—	—	—
Phacelia hastata	47^{a}	36^{a}	48^{a}	15^{b}	3^{c}	—	—	—	—	—
Phlox hoodii	66^{a}	6^{c}	45^{b}	0^{c}	32^{b}	—	—	—	—	—
Phlox spp.	26^{a}	13^{b}	23^{ab}	31^{a}	12^{b}	—	—	—	—	—
Annual forbs										
Collinsia parviflora	56^{a}	1^{d}	0^{d}	6^{c}	27^{b}	—	—	—	—	—
Cryptantha spp.	56^{a}	12^{b}	0^{b}	0^{b}	11^{b}	11^{a}	0^{b}	0^{b}	0^{b}	0^{b}
Descurainia spp.	37^{a}	7^{b}	3^{bc}	0^{c}	23^{a}	—	—	—	—	—
Eriogonum spp.	1^{c}	33^{a}	8^{ab}	0^{c}	6^{b}	—	—	—	—	—
Erodium cicutarium	0^{b}	25^{a}	25^{a}	20^{a}	0^{b}	0^{b}	3^{b}	0^{b}	60^{a}	0^{b}
Gayophytum spp.	57^{a}	10^{c}	11^{bc}	29^{b}	6^{c}	—	—	—	—	—
Gilia spp.	65^{a}	4^{c}	2^{c}	46^{ab}	34^{b}	58^{a}	0^{b}	0^{b}	0^{b}	0^{b}
Lactuca serriola	25^{a}	7^{b}	10^{b}	0^{b}	0^{b}	—	—	—	—	—
Mentzelia albicaulis	32^{a}	35^{a}	0^{c}	8^{b}	2^{bc}	—	—	—	—	—
Nicotiana attenuata	38^{a}	4^{b}	0^{b}	0^{b}	0^{b}	—	—	—	—	—
Sisymbrium altissimum	7^{b}	46^{a}	35^{a}	12^{b}	4^{b}	0^{b}	35^{a}	21^{a}	0^{b}	0^{b}

[1] Species that occurred on ≥ 20% of the total relevés or ≥ 20% of the relevés in any one of the categories examined

[2] Only species that occurred on ≥ 5% of the actual relevés the species occurs on with ≥ 5% cover were examined

[3] Chi square test inclnding all successional stages was not valid, therefore, only early and late stages were compared.

year-old burns (Table 3). Tree species were essentially eliminated by burning. Shrubs such as big sagebrush and bitterbrush, which regenerate by seed, were easily killed by burning but began to reoccupy some burned sites within one year. Reestablishment of big sagebrush appeared to occur through migration and germination of seed from adjacent unburned areas or germination of on-site soil seed reserves. Bitterbrush reestablished primarily by germination of rodent caches (pers. obs.). Ecotypes of bitterbrush that can resprout were not found on the study sites. Both species had negligible cover on one-year-old burns.

Although some individual plants were killed, all root-sprouting species studied remained part of the postburn plant community. This is consistent with other studies (Wright et al. 1979). Occurrence of rubber rabbitbrush and horsebrush (*Tetradymia canescens*) was not significantly different between mature woodland stands and one-year-old burns. One-year-old wildfire sites had significantly higher occurrences of blueberry elder (*Sambucus cerula*), mountain snowberry (*Symphoricarpos orephilus*), and low rabbitbrush than did mature woodlands and significantly lower occurrences of Mormon tea (*Ephedra viridis*), desert gooseberry, and Anderson peachbrush (*Prunus andersonii*). Only mountain snowberry and low rabbitbrush occurred on early postburn sites with cover values ≥ 5%. Even though occurrence of mountain snowberry was significantly greater on the one-year-old burns than on the woodland stands, the percent of these relevés with cover ≥ 5% was significantly less on one-year-old burns. The differences were not significant between the two successional stages for low rabbitbrush.

Root crowns of most perennial grasses can survive wildfire, continuing growth when conditions are favorable (Wright et al. 1979, White and Currie 1983). Comparison of one-year-old burns and mature woodlands showed that only the occurrence of one species, mutton bluegrass (*Poa fendleriana*), was significantly reduced. Occurrence of other perennial grasses remained the same or increased slightly. For most perennial grasses, high cover values (≥ 5%) were not found on either one-year-old burns or mature woodlands. Idaho fescue (*Festuca idahoensis*) occurred on the highest number of relevés, all on mature woodlands, with cover ≥ 5%. Cheatgrass, an annual grass, was killed by wildfire but regained postburn levels of occurrence and cover within one year from germination of either soil seed reserves or seed from adjacent areas (Young and others 1976, Merrill and others 1980).

Most perennial forbs occurred more frequently on one-year-old burns than on mature woodlands. Only Holboell rockcress (*Arabis holboellii*) had significantly lower occurrence on the early successional stage than on the late stage. Few relevés had cover values ≥ 5% for any perennial forb species. No significant differences occurred between cover values of the two stages, although cover tended to be higher on one-year-old burns.

Annual forbs are killed by burning but rapidly reoccupy most sites by germination of seed from adjacent unburned areas or on site soil seed reserves (Koniak and Everett 1982). Occurrence of most annual forbs was significantly greater on one-year-old burns than on mature woodlands. Only gilia (*Gilia* spp.) and cryptantha (*Cryptantha* spp.) occurred with cover ≥ 5% and only on the one-year-old burns.

Occurrence and cover of understory species in pinyon-juniper woodlands generally remained the same or increased after burning. High postfire occurrence or cover of perennial species may be attributed to a combination of high tolerances to burning, increased visibility of plants from either increased size or elimination of litter or duff, and increased germination, survival, and growth following release from competition from late successional species. High postfire occurrence or cover of annual species may result from increased germination and growth of on-site seed or seeds from adjacent unburned sites.

Several shrub species and Holboell rockcress decreased substantially after fire. The decrease may be attributed to a high susceptibility to fire-related injury and death, to the inability to compete with early successional species or, for woody species, to the slow accumulation of biomass. Wildlife grazing may also contribute to the decline in a number of browse species.

Species Variation over Five Successional Stages

Annual forbs displayed the greatest variation in distribution patterns among successional stages (Table 3). Some species occurred most frequently on early successional sites, others occurred most frequently on midsuccessional sites, and still others had higher occurrence on early and late sites than on midsuccessional sites. Most perennial forbs were found on a disproportionately higher number of early and midsuccessional sites than on late sites. Hood's phlox (*Phlox hoodii*) had significantly greater occurrence on the early successional stage than on later stages, but occurrence was also high during midsuccession and late succession. Holboell rockcress was the only nontree species that occurred more frequently on late successional sites than at other stages.

Perennial and annual grasses were consistently found on more mid-successional sites than on early or late sites. A notable exception was Sandberg bluegrass, whose high occurrence on early and late successional sites paralleled the distribution patterns of several annual forbs.

All shrubs, except blueberry elder and mountain snowberry, had relatively low occurrence on early successional sites compared to midsuccessional sites. Occurrence of all root sprouting shrubs, except desert gooseberry and Mormon tea, decreased between midsuccession and late succession. Big sagebrush and antelope bitterbrush, shrub species that regenerate by seed, maintained high occurrence throughout midsuccession and late succession. Unlike occurrence, cover of antelope bitterbrush and big sagebrush decreased significantly from midsuccession to late succession. Apparently, as tree species dominated a site, the resources available to understory species rapidly diminished and cover was greatly reduced.

Tree species began to reestablish 20 to 30 years after fire, but cover was minimal even 60

TABLE 4. Aspects on which species[1] occurred most frequently.

Species	Aspect			
	North	East	South	West
Shrubs				
* *Artemisia tridentata*	X	X		X
Chrysothamnus nauseosus				X
* *Chrysothamnus viscidiflorus*	X	X		
Ephedra viridis			X	X
* *Prunus andersonii*		X		
* *Purshia tridentata*	X	X		X
* *Ribes velutinum*	X	X		
* *Symphoricarpos oreophilus*	X	X		
* *Tetradymia canescens*	X	X		X
Grasses				
* *Bromus tectorum*				X
* *Festuca idahoensis*	X	X		
Oryzopsis hymenoides		X		
* *Poa fendleriana*		X		
Poa secunda		X	X	XX[2]
Sitanion hystrix		X	X	XX
* *Stipa thurberiana*		X		
Perennial forbs				
Argemone munita	X	X	X	X
* *Arabis holboellii*	X			
Astragalus purshii	X	X	X	X
* *Balsamorhiza sagittata*	X	X		
* *Crepis acuminata*	X	X		
Eriogonum elatum	X	X		
* *Eriogonum umbellatum*	X	X		
* *Lupinus caudatus*	X	X		
Lygodesmia spinosa	X	X		
* *Machaeranthera canescens*	X	X		
* *Phacelia hastata*			X	X
Phlox hoodii	X	X		X
Phlox spp.	X	X	X	X
Annual forbs				
Collinsia parviflora		X		
Cryptantha spp.	X	X	X	X
* *Descurainia* spp.			X	X
Eriogonum spp.	X	X		
* *Erodium cicutarium*			X	X
Gayophytum spp.			X	X
* *Gilia* spp.			X	X
Lactuca serriola			X	X
Mentzilia albicaulus			X	X
Nicotiana attenuata	X	X	X	X
* *Sisymbrium altissimum*			X	X

[1] Species that occurred on ≥ 20% of the relevés in any one of the categories investigated (i.e., north, south, east, west).

[2] Occurrence of species with X's in all categories was not significantly different among aspects.

*Differences are significant at $P < .05$.

years after burning. Recent work (Tausch and West, in prep.) indicates that at this point trees rapidly increase in density and cover, dominating a site 100 to 150 years after burning.

Species with high occurrence in early succession apparently survived wildfire as seeds on the burned site or on adjacent unburned sites, or as buds at the root crowns, or both. They were able to rapidly take advantage of the increased availability of water, nutrients, and light in the postfire environment. Limited occurrence of species in midsuccessional or late stages may be related to several factors (Barbour et al. 1980). Seed may germinate most effectively after fire scarification. As shrubs and later tree species overtop the low-growing herbaceous forbs, reducing the light intensity at the soil level, photosynthesis is reduced and shade-intolerant plants will not survive. Competition with midsuccessional or late species for water and nutrients may limit occurrence of some species. Plants prominent in later stages of succession may produce allelopathic chemicals that may inhibit growth of other plants. Increase in occurrence of perennial species in midsuccession may be correlated to the attainment of the critical biomass necessary for seed production or to the increase in ground cover providing a favorable microsite for seed germination and plant survival.

Reentry of tree species into the plant community depends upon perennial nurse plants associated with midsuccessional and late stages (Everett and Ward 1984). Nontree species with high occurrence on late stages can successfully compete with other late species and may actually benefit from the combination of shade and relative lack of ground cover. However, many of these species exhibit a substantial reduction in cover with increasing tree dominance.

Common factors may explain similar species occurrence on two seemingly dissimilar sites, one-year-old burns (early succession) and mature woodlands (late succession): an abundance of bare ground and a lack of competition for resources in the upper soil horizons. Species in this group appear to be tolerant of late successional conditions (shade, tree competition, alleopathy) but cannot compete with species that have high cover in midsuccessional stages.

A number of species, although often occurring more frequently in specific successional stages, exhibited high occurrence (≥ 20%) in all stages. These species could be a major component of a plant community at any point in the successional cycle and include cheatgrass, bottlebrush squirreltail, Sandberg bluegrass, tailcup lupine, mountain snowberry, low rabbitbrush, bitterbrush, and desert gooseberry.

Species Variation with Aspect

Species can be grouped according to differences in occurrence on the various aspects. Many root-sprouting shrubs and perennial forbs typically had higher occurrence on north and east aspects (Table 4). Other species associated with east slopes included Indian ricegrass (*Oryzopsis hymenoides*), mutton bluegrass, Thurber needlegrass (*Stipa thurberiana*), and Anderson peachbrush. Holboell rockcress occurred most frequently on north aspects. Many annual forbs were more prominent on south and west slopes than on north and east slopes. Rubber rabbitbrush and cheatgrass exhibited significantly higher occurrence on west slopes than on north or east slopes. South slopes had medium occurrence of these species. Shrubs that regenerate by seed (i.e., big sagebrush and bitterbrush), Hood's phlox (*Phlox hoodii*), and horsebrush (*Tetradymia canescens*) tended to occur least frequently on south slopes and with equal occurrence on other slopes. Most other species, including the two most frequently occurring perennial grasses, Sandberg bluegrass and bottlebrush squirreltail, had no significant differences among aspects.

North and east slope conditions appear to favor the establishment of perennial species. These slopes generally have better moisture relations, less variation in temperature, and generally less harsh conditions than south and west slopes. Conditions limiting the occurrence of annual species may range from reduction of their soil seed reserves from long-term preburn competition by perennial species to the prolonging of the winter dormancy of many winter annuals (Baskin and Baskin 1981), by cooler temperatures and longer snow cover on north and east slopes.

Other site factors appear to determine the establishment patterns on south and west aspects. On these sites, large daily temperature and moisture differentials, especially in spring and early summer, can easily damage susceptible seedlings. Annual species appear to survive these fluctuations better than most perennial species (Evans and Young 1982, Young and Evans 1982). Species that showed no marked preference for aspect appear to germinate and survive equally well under a variety of environmental conditions.

Variation of the Successional Cycle among Aspects

Canopy cover by growth forms reflected and summarized individual species cover

TABLE 5. Percent of relevés with cover values ≥ 5% for five growth forms, two aspect groups, and five successional stages.

	North and east aspects					South and west aspects				
	successional stages									
Growth forms	Early	Early mid	Mid	Late mid	Late	Early	Early mid	Mid	Late mid	Late
Shrubs	${}_{w1}18^{d2}$	${}_{v}71^{b}$	${}_{x}79^{b}$	${}_{x}97^{a}$	${}_{x}49^{c}$	${}_{x}0^{e}$	${}_{w}53^{c}$	${}_{x}76^{b}$	${}_{x}90^{ab}$	${}_{v}47^{c}$
Annual forbs	${}_{v}38^{b}$	${}_{x}2^{d}$	${}_{x}3^{d}$	${}_{y}0^{d}$	${}_{x}4^{d}$	${}_{x}65^{a}$	${}_{x}35^{b}$	${}_{x}11^{c}$	${}_{wx}25^{bc}$	${}_{x}2^{d}$
Perennial forbs	${}_{vw}35^{a}$	${}_{x}20^{b}$	${}_{w}16^{b}$	${}_{x}0^{c}$	${}_{x}6^{c}$	${}_{w}22^{ab}$	${}_{x}20^{ab}$	${}_{x}13^{bc}$	${}_{x}5^{bc}$	${}_{x}3^{c}$
Annual grasses	${}_{x}0^{f}$	${}_{w}56^{b}$	${}_{w}24^{cd}$	${}_{x}16^{de}$	${}_{x}2^{f}$	${}_{x}9^{ef}$	${}_{x}80^{a}$	${}_{w}55^{b}$	${}_{w}45^{bc}$	${}_{x}3^{f}$
Native perennial grasses	${}_{wx}15^{bc}$	${}_{x}19^{b}$	${}_{w}26^{ab}$	${}_{w}42^{a}$	${}_{w}25^{ab}$	${}_{x}0^{d}$	${}_{z}9^{cd}$	${}_{x}32^{a}$	${}_{x}15^{bc}$	${}_{w}14^{bc}$

[1]Percents in a column preceded by the same letters v, w, x, y, or z do not differ significantly at $P < .05$

[2]Percents in a row followed by the same letters a, b, c, d, e, or f do not differ significantly at $P < .05$

among successional stages and aspects (Table 5). Early succession on all slopes was dominated by perennial and annual forb cover, with higher perennial forb cover on north and east slopes and higher annual forb cover on south and west slopes. In addition, north and east slopes had high cover of shrubs and native perennial grasses. Early midsuccession brought a sharp increase on all aspects in the number of relevés with shrub and annual grass cover ≥ 5% and a sharp decrease in the same measure for annual forbs. Annual forbs remained an important component on south and west slopes throughout midsuccession, but not on north and east aspects. During all stages of midsuccession, annual grass cover was significantly greater on south and west slopes than on north and east aspects, and perennial grasses tended to be higher on north and east slopes. By late succession, the number of relevés with perennial and annual forb and annual grass cover ≥ 5% decreased on all aspects to less than 6%.

Perennial grass and shrub cover also decreased by late succession but still maintained relatively high cover on all aspects. North and east slopes tended to support higher cover of perennial grasses than did the south and west slopes, but the difference was not significant. Differences between aspect groups were even less for other growth forms. Different moisture, temperature, and light regimes on the different aspects appear to determine the species and subsequently the growth forms that can establish and survive, as well as the speed with which a species or vegetational group becomes prevalent or diminishes. This in turn controls the successional pattern.

Affect of Seeding on Other Species

Eight of the 21 burns were seeded. Dominant seeded species included crested wheatgrass (*Agropyron desertorum*), intermediate wheatgrass (*Agropyron intermedium*), and smooth brome (*Bromus inermis*). Seven of the eight seeded burns were identified as early midsuccessional and midsuccessional stages. The eighth seeded burn, which was only one year old, will not be discussed because seeded species generally appeared only in trace amounts. No consistent pattern emerged when comparing occurrence of shrubs on seed and nonseeded burns (Table 6). Three species had higher occurrence on nonseeded burns, one had higher occurrence on seeded burns, and three exhibited no significant difference between the two groups.

All nonseeded grass species occurred significantly less on seeded burns. This would be expected because most seeded species were grasses selected for their competitive ability. Cheatgrass, however, is a highly competitive grass whose decrease on seeded burns appears to be limited to north and east slopes and high elevation sites, where seeded species have a competitive edge (Koniak 1983). Occurrence of perennial forbs was generally not affected by seeding. Only two species, sulfur buckwheat (*Eriogonum umbellatum*) and Hood's phlox, occurred less frequently on seeded burns. These species are relatively woody and often classified as half-shrubs. Only five annual species occurred on enough midsuccessional sites to examine. Tumble mustard and alfileria occurred less frequently on seeded burns than on nonseeded. The other species showed no significant difference

TABLE 6. Effect of seeding on naturally occurring species.[1]

Species with significantly higher occurrence on nonseeded sites than on seeded sites	Species with no significant differences in occurrence between seeded and nonseeded sites or with greater occurrence (*) on seeded sites
Shrubs	Shrubs
Artemisia tridentata	*Ephedra viridis*
Chrysothamnus nauseosus	*Purshia tridentata* (*)
Chrysothamnus viscidiflorus	*Ribes velutinum*
	Symphoricarpos oreophilus
Grasses	Grasses
Bromus tectorum	None
Oryzopsis hymenoides	
Poa fendleriana	
Poa sandbergii	
Sitanion hystrix	
Stipa thurberiana	
Agropyron spicatum	
Forbs	Forbs
Eriogonum umbellatum	*Arabis holboellii*
Phlox hoodii	*Argemone munita* (*)
Sisymbrium altissimum	*Crepis acuminata*
Erodium cicutarium	*Lupinus caudatus*
	Lygodesmia spinosa (*)
	Machaeranthera canescens
	Phacelia hastata
	Astragalus purshii
	Chaenactis douglasii
	Phlox spp. (perennial species)
	Penstemon speciosus
	Gilia spp. (annual species)
	Mentzelia albicaulis
	Eriogonum spp. (annual species)

[1]Species that occurred on at least two seeded and two nonseeded burns in early midsuccession and midsuccession.

between occurrence on seeded and nonseeded sites.

Seeding appears to be detrimental to a number of naturally occurring species. This should be taken into account when examining the results of this study. However, if percent occurrence in early midsuccession and midsuccession from Table 3 were adjusted to compensate for apparent losses due to seeding, the changes would generally be less than 10%. In addition, other factors may be confounding the apparent decrease in species occurrence correlated to seeding because the burns are of different years and locations. Because of the difficulty in isolating the cause of decreased occurrence on seeded sites and the relatively small decrease involved, it was not considered worthwhile to analyze seeded burns separately from nonseeded.

CONCLUSIONS

Plant succession following wildfire within the pinyon-juniper type has previously been described as relay floristics (Arnold and others 1964, Erdman 1970, Barney and Frischknecht 1974), a sequential migration of later successional species into a site (Egler 1954). Everett and Ward (1984), however, have indicated that initial floristics, the sequential dominance of a site by species on the burn immediately after wildfire (Egler 1954), may be of equal or even greater importance. This study supports the latter hypothesis. Species that became dominant in midsuccession and late succession were present in the early stage. Slow growth or establishment rates precluded early dominance. Tree species, which rely on nurse plants for establishment and survival, were the only exceptions.

Within the pinyon-juniper woodlands, postburn succession may follow multiple pathways (Everett and Ward 1984). Successional patterns varied with aspect and associated preburn species composition. To increase the predictability of postburn plant and community response, effects of elevation, soil type, seeding, postburn climate, and severity and timing of disturbance should also be considered and studied at greater length.

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USE OF RADIO TRANSMITTER IMPLANTS IN WILD CANIDS

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ABSTRACT.— Twelve adult and five juvenile coyotes and 20 adult kit foxes were implanted with radio transmitters using relatively simple surgical procedures. Four foxes were successfully implanted in the field. None of the animals implanted exhibited noticeable behavioral effects, and no deaths were confirmed to result from implantation. Implants were attached to the peritoneum in adult coyotes and kit foxes and were left free-floating within the abdominal cavity of the coyote pups. Both procedures produced satisfactory results. Radio signals transmitted from implants had less range than those from traditional neck collar transmitters. Implants offered benefits unavailable with traditional collar transmitters: no external packaging to influence behavior, ability to radio monitor small or juvenile animals, and ability to acquire various physiological data on free-ranging individuals.

Implantable radio transmitters have beenused to monitor physiological parameters and movements of numerous mammals (primates, Stone et al. 1972; canids, Golightly and Ohmart 1983; ursids, Jessup and Koch 1984; mustelids, Melquist and Hornocker 1979, Melquist et al. 1981, Garshelis and Siniff 1983, Eagle et al. 1984; sciurids, Eagle et al. 1984, Golightly and Ohmart 1978; castorids, Davis et al. 1984; and others, Folk et al. 1971). Implants may offer advantages over externally attached transmitters such as a decreased effect on animal behavior, ability to instrument small or juvenile animals, and ability to acquire physiological data. One disadvantage of implantation is surgical risk to the animal. Techniques of implantation have been described for several species, yet there is a lack of detail concerning the implantation procedure and effectiveness of implants for monitoring physiological parameters and movements of canids.

In this paper we report the results of two independent studies using implants in wild canids. In one study (authors JSG, SLL, and BRL) implants were used to monitor the movements of juvenile coyotes (*Canis latrans*), and in the other (author RTG) implants were used in adult coyotes and adult kit foxes (*Vulpes macrotis*) to monitor body temperature (Golightly and Ohmart 1983) and location (Golightly 1981).

STUDY AREAS AND METHODS

Coyote Pups

Five pups (two male, three female) were obtained from two captive litters in two 65-ha enclosures at the U.S. Sheep Experiment Station, Clark County, Idaho. Pups were 100–136 days old and weighed 3.7–5.8 kg. Each pup was pretranquilized with 2.2 mg/kg xylazine (Rompun) intramuscularly and 0.05 mg/kg atropine sulfate subcutaneously. Induction and surgical anesthesia were obtained by administering 16 mg/kg thiamylal sodium intravenously until a desired plane of anesthesia was reached. Each pup was placed in dorsal recumbency and its abdomen shaved from the xyphoid process to the pubis. This area was washed, and a 4-cm incision through the skin was made caudal to the umbillicus. The peritoneal cavity was entered through the linea alba by a short incision made with a scalpel and extended with blunt-tipped scissors. Each transmitter (22 g cylinder, 6 cm long, 2 cm diameter; Telonics, 932 E. Impala, Mesa, AZ 85204) was presoaked for approximately 15 minutes in a disinfectant solution (Nolvasan) and inserted into the peritoneal cavity.

The peritoneum and internal and external rectus sheaths were sutured with a simple interrupted pattern using size 00 chromic gut.

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The superficial fascia and skin were repositioned with a simple interrupted pattern of 0 chromic gut. Each pup was given a prophylactic injection of 150,000 units of procaine penicillin G and 150,000 units of benzathine penicillin G (1 cc Benza-Pen) intramuscularly. Two days later the pups were given a second 1-ml dose of the antibiotic and released into the enclosures.

From August 1982 through May 1983 performance of the implanted transmitters was compared with that of 10 collar-mounted transmitters (weight 290 g; Telonics) on adult coyotes concurrently within the enclosures. Coyotes were observed from an elevated (9 m) observation booth located at a boundary common to both enclosures. Signals were received with a phase-combined stacked array of two 5-element beams, 15.5 m above the ground. Maximum distance from transmitter to receiver was 1.14 km. Signals were classified as good (signal strong, direction easily determined), fair (signal of medium strength, direction difficult to determine), poor (signal audible, unable to determine direction), or no signal.

The implants were recovered when the coyotes were recaptured nine months following implantation. The surgical procedure for removal of the implants was similar to the implanting procedure.

Coyote Adults

In 1977, 12 adult coyotes (10 male, 2 female) weighing 9.1–12.7 kg were captured near Phoenix, Maricopa County, Arizona, and immobilized with a mixture of 1.25 mg/kg ketamine hydrochloride (Ketaset), 0.5 mg/kg Rompun, 0.12 mg/kg Acepromazine, and 0.006 mg/kg atropine sulfate administered intramuscularly. A surgical plane of anesthesia resulted in 5–7 minutes. The peritoneum was opened in a manner similar to that described for pups, and a temperature-sensitive transmitter (13 g, 5.7 by 2.4 by 1.7 cm; J. Stuart Enterprises, Grass Valley, CA 95965) was inserted. A length of size 0 Vetafil ligature was run through a loop of Vetafil attached to the transmitter, and both ends of the ligature were held by clamps outside the incision. The ligature was then tied to the peritoneum 1 cm lateral to the superior end of the incision, thus securing the transmitter to the peritoneal wall. The peritoneum and the linea alba were closed with a running suture of size 0 chromic gut. Powdered Furacin was applied to the sutured incision. The skin was then closed with mattress sutures of size 0 Vetafil, and Betadine ointment was applied to the suture line. Following surgery, 75,000 units of Bicillin were administered intramuscularly. Coyotes were confined to cages for 12 hours before being released into a 0.13 ha enclosure at Arizona State University.

To remove an implant, an incision was made similar to the one described previously. The ligature was located, clamped, and cut, the implant was removed, and closure was accomplished as described previously.

Kit Foxes

In 1978 and 1979, 12 kit foxes (five male, seven female) were captured near Apache Junction, Pinal County, Arizona, implanted with transmitters, and released in a 0.13-ha enclosure at Arizona State University. Eight additional kit foxes (three male, five female) were captured and released into the wild following placement of an implant and a conventional neck-collar radio transmitter (110 g, Telonics). Body weights of kit foxes ranged from 1.4 to 2.4 kg.

Kit foxes were immobilized with a mixture of 2 mg/kg Ketaset, 0.25 mg/kg Rompun, 0.25 mg/kg Acepromazine, and 0.012 mg/kg atropine sulfate administered intramuscularly. Anesthesia resulted in 3–5 minutes. The implant and implantation procedure as previously described for adult coyotes was used. Following surgery, 25,000 units of Bicillin were administered to each animal intramuscularly. Kit foxes were released into their dens or into the enclosure 6–8 hours following surgery. Four of the foxes released into the wild were implanted in the field; otherwise, all surgeries were performed in a laboratory.

RESULTS AND DISCUSSION

Coyote Pups

We did not observe any behavioral changes or mortality resulting from implanting coyote pups. Implants provided an advantage over collars in that we were able to equip each pup with a transmitter at a young age. This made capture more efficient and less stressful to the animal since young pups usually retreated to a den from which they were dug, and older animals usually ran until cornered or exhausted. Also, data on sex, weight, physical measurements, and movement were obtained earlier than if coyotes had been captured after they reached adult size when conventional radio collars could be used. (Expandable neck collar transmitters may also be used on juveniles.)

Three disadvantages of implants were recognized. The transmitted signals from the implants (58% rated good, 21% fair, 7% poor, 14% no signal, n=254) were not as strong as those of the collars (93% good, 5% fair, 1% poor, 1% no signal, n=630). However, the implants were usually adequate for identifying location or direction of the pups. Second, use of a motion-sensing option with the implant would have necessitated attachment of the implant to the abdominal wall (probably more extensive than the attachment described previously for adult coyotes and kit foxes). We were unsure of the risk (e.g., internal complications) involved with such a procedure. Third, the implants had an approximately two-thirds shorter operational life than collar transmitter packages (based on data from Telonics).

When the time came to remove the implants from the coyote pups, three of the four implants were floating freely within the abdominal cavity and the fourth was encased within a thin membrane. There was no evidence of trauma or irritation of tissue adjacent to the site of implantation.

Although coyote pups were implanted at 3.5 and 4.5 months of age, implanting comparably sized transmitters would likely be possible in coyote pups as young as 2–2.5 months.

Coyote Adults

From 1977 to 1980, 21 transmitter implantations were performed on 12 adult coyotes. Each implantation procedure lasted approximately 30–35 minutes. Postsurgical infection requiring medical attention developed in only one instance. All coyotes appeared healthy and fed normally during the 2–4 month experimental periods following implantation. One female successfully produced a litter of two pups while carrying an implant.

Serial implantations (replacement of an implant in each of six coyotes) resulted in moderate scar tissue and made final retrieval surgeries slightly more difficult.

The ligature attachment did not cause apparent damage to internal organs or to the peritoneum, and it facilitated retrieval of the implant through a relatively small incision. Some experimental conditions (e.g., where public visibility is a concern or in heat exchange studies) necessitate that a small surgical site be prepared, thus potentially making retrieval of a free-floating implant difficult. Attachment of the implant to the peritoneum reduced time in surgery and trauma during recovery or replacement of implants. This might be an important consideration with rare species or animals that are difficult to obtain.

The attachment also provided a consistent location for measurement of body temperature. Some experiments require accurate measurement of relatively small differences in body temperature with implanted transmitters (Golightly 1981). Body temperature varied at locations within the abdominal cavity of mammals during arousal from hibernation (Lyman et al. 1982), and body temperature of normothermic mammals may vary at different locations within the body. It would be particularly important to attach implanted transducers for measuring heart or respiration rate.

The transmitters were effective in providing information on body temperature to remote receiving locations outside the enclosure. Signals were routinely received with a hand-held Yagi antenna at a distance of 70–100 m from the animal despite the presence of physical barriers (i.e., brick walls, rock piles) between the transmitter and the receiver.

Kit Foxes

Sixteen transmitters were implanted into foxes in the enclosure, including four serial exchanges (two implants in each of four foxes). The surgery lasted approximately 20–35 minutes. The kit foxes were observed every 2 or 3 days, and infections were not evident. The animals maintained weight and appeared healthy. One female died of undetermined causes while carrying the implant. No pathology was evident upon necropsy, and the tissue around the implant appeared normal.

Two males developed hernias at the site of incision several months following implantation. The transmitter may have physically stressed the site of incision and caused or contributed to the hernia. Both foxes had received replacement implants. One fox had continued problems with the hernia following repair of the surgical site. Because kit foxes have a thin peritoneum compared with that of coyotes, we suspect that the serial implantations precipitated the hernias. Four of the eight free-ranging kit foxes died during the study but none from transmitter-related causes.

All foxes appeared to feed normally and maintain weight, and some moved substantial distances at night (maximum distance of approximately 21 km in a single night, Golightly 1981). No infections were observed. One free-ranging female was implanted early in pregnancy and carried the implant for four months while successfully whelping and rearing a litter of three pups.

A signal transmitted from an implant normally could be received 75–100 m away from foxes in dens (1–2 m underground), whereas transmitters affixed by neck collars could be received 500–700 m. Outside dens, signals from implants and collars were received at 200+ m and 1,000–2,000 m, respectively.

Implants were useful for obtaining body temperature data and for determining movement within a den after the fox was located with the signal from the neck collar. Implants were not useful as a sole means of locating kit foxes. However, kit foxes should be able to accommodate the larger implant described previously for coyote pups, which would perhaps increase their range of transmission.

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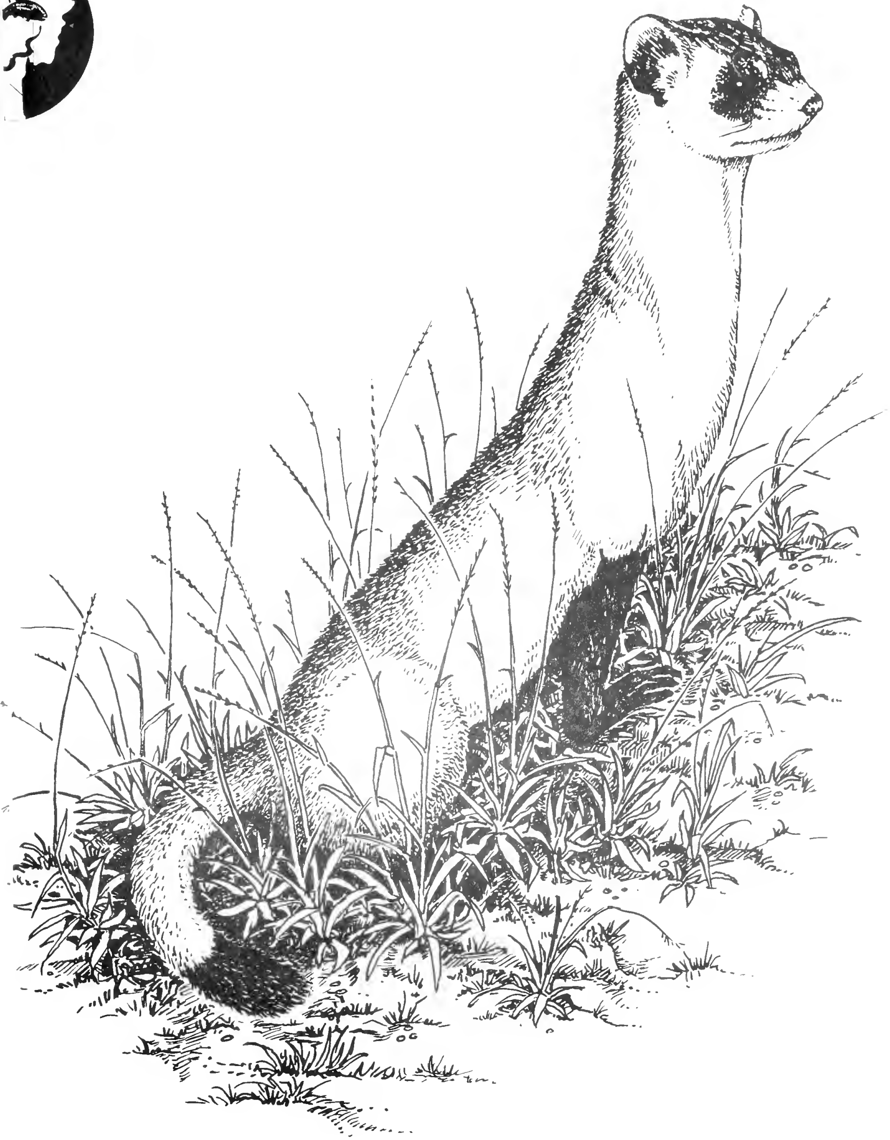

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LIFE HISTORY OF THE CUI-UI, *CHASMISTES CUJUS* COPE, IN PYRAMID LAKE, NEVADA: A REVIEW

William F. Sigler[1], Steven Vigg[2], and Mimi Bres[3]

ABSTRACT.—The cui-ui, *Chasmistes cujus* Cope, a member of the sucker family and endemic to Pyramid Lake, Nevada, is listed as endangered by the U.S. Fish and Wildlife Service. Cui-ui was once a major source of sustenance for native Americans, who have inhabited the Lahontan region for at least 11,000 years. The Northern Paiutes developed sophisticated fishing technology to harvest this resource. The original distribution of cui-ui was the ancient Lake Lahontan complex, but as a result of climatic changes it was restricted to the Pyramid-Winnemucca-Truckee system by the turn of the 20th century. Transbasin water diversions (1905 to present) have resulted in further restrictions of habitat. The species is now limited to Pyramid Lake and the lower Truckee River. Reproduction is from hatcheries as well as limited natural reproduction. Females produce more than 40,000 2–mm eggs per year. The normal development is described from the unfertilized egg through 912 hours post-hatching, when the fry are actively feeding and approaching adult body form. The unusual feature of adult cui-ui morphology is the relatively large ventro-terminal mouth, with thin and obscurely papillose lips. Cui-ui grow slowly and may live 18 years or possibly much longer; females generally live longer and attain a greater size than males. The highest adult mortality probably occurs during spawning runs. At this time they are vulnerable to predation, stress, and sometimes environmental degradation. The highest larval mortality probably occurs from predation when they are planted or migrate into the lake. The trophic ecology of the species is poorly understood, but they are known to ingest algae and zooplankton. Spawning behavior is documented. At present, natural reproduction is probably still the limiting factor for the cui-ui population. Cui-ui composed less than one percent of the total fish in Pyramid Lake during 1975–1977. During 1982 the largest cui-ui spawning run (13,000) in recent years occurred. The activity of cui-ui in the lake closely resembles that of the Tahoe sucker being most active during the spawning season each spring. Cui-ui inhabit the inshore-benthic zone and the pelagic waters of Pyramid Lake (<46 m).

The cui-ui, *Chasmistes cujus* Cope, a member of the sucker family (Catostomidae), is present only in Pyramid Lake and the affluent lower Truckee River, Nevada (Fig. 1). Because of its limited range and depleted numbers, it is listed as endangered (Federal Register, Vol. 32/48, 11 March, 1967). Cui-ui until recently was an important food source for Northern Paiute, the native Americans who have inhabited the region for at least 11,000 years. Prehistorically the habitat of cui-ui consisted of the Lake Lahontan system, which reached its maximum size of about 22,300 km^2 some 13,000 years before present (BP) and inundated a large portion of northwestern Nevada. The cui-ui was present in Winnemucca Lake until the late 1920s or early 1930s (Fig. 2).

There is general agreement that the ecological devastation of the cui-ui's lake and river environment was caused in part by the Newlands Reclamation Irrigation Project (NRIP), which was authorized by the U.S. Congress in 1903. In 1905 Derby Dam was dedicated, and

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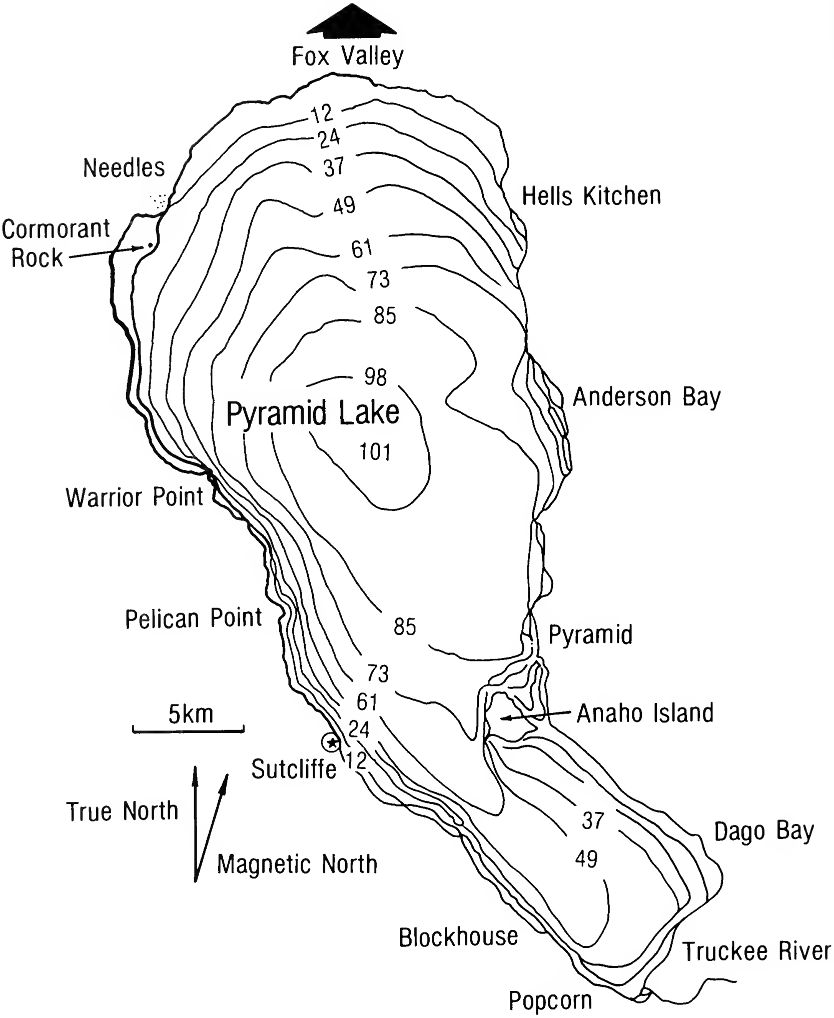

Fig. 1. Bathymetric map of Pyramid Lake, Nevada, depth contours are in meters at elevation 1154.9 m.

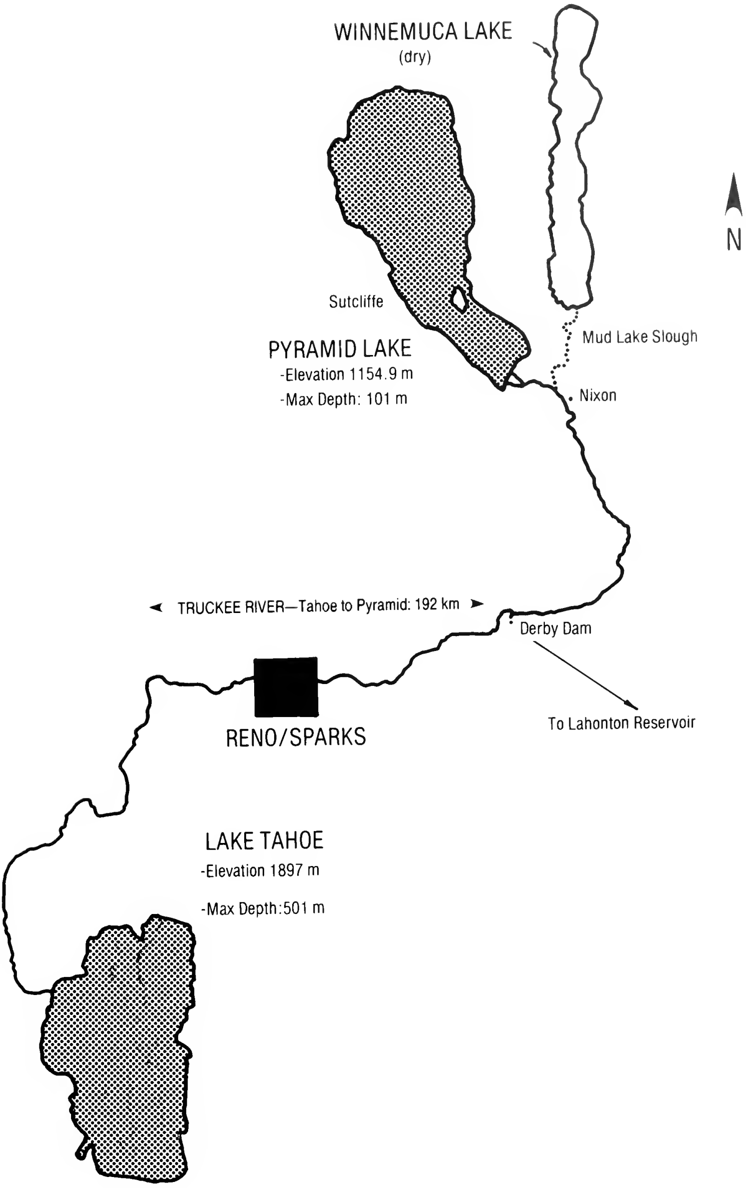

Fig. 2. The Truckee River–Pyramid Lake Ecosystem.

transbasin water diversion from the Truckee River to the Carson River system began. Lahontan Dam on the Carson River was completed in 1915, creating Lahontan Reservoir—the water storage impoundment for the NRIP. From 1915 to 1970 as much as half or more of the total flow of the lower Truckee River was diverted to the NRIP. Because of droughts and diversions, the level of Pyramid Lake declined more than 24.4 m from 1909 to 1968, Pyramid Lake increased in total dissolved solids (TDS) from about 3500 to 5500 mg/l, and Winnemucca Lake disappeared in 1938. A delta developed at the mouth of the Truckee River in the early 1930s that was virtually impassable to spawning migrations of cui-ui. Natural reproduction in the Truckee River was very limited for about 50 years (until the new Marble Bluff dam and the fishway became functional for cui-ui in 1982). However, during years of exceptionally high flow, natural reproduction may have been possible. Upstream, Siphon dam (washed out in 1958), and about 1 mile below it the original Marble Bluff dam (washed out in 1950) were also barriers to migrating cui-ui. Neither of these obstructions had functional fish ladders. The original Numana Dam also barred cui-ui migration.

It is our objective to synthesize information collected during the Pyramid Lake Ecological Study, conducted by W. F. Sigler & Associates Inc. during 1975–1978, with available data from agency reports and research publications to present an overview. It is hoped this paper will contribute to the knowledge of the cui-ui, and that its deficiencies will point out areas where additional research is needed.

HISTORICAL OVERVIEW

Cope (1883) first diagnosed and revised the genus *Chasmistes* and named a new species *C. cujus* from Pyramid Lake. In 1918, Snyder published the first life history information on *C. cujus* and other fishes of the Lahontan System; even at this early date Snyder considered the fate of the cui-ui to be uncertain. Sumner (1940) collected environmental and fishery data from Pyramid Lake and the Truckee River, compiled a chronology of the fishery, and stated that the major cause of the decline of the fishery was the transbasin diversion of Truckee River water.

T. J. Trelease, the first fishery biologist for the Nevada Department of Fish and Game (NFG), did preliminary work on the diet and reproduction of cui-ui (La Rivers 1962). Jonez (1955) and Johnson (1958) (both NFG biologists) worked with cui-ui during the 1950s conducting evaluations of cui-ui behavior and habitat. La Rivers made many observations over the years and developed a life history for cui-ui, incorporating information from previous workers.

Koch (1972, 1973) supplied information on life history, reproductive characteristics, and spawning behavior of cui-ui, Koch and Contreras (1973) advanced artificial hatching techniques, and Koch (1976) summarized available life history information. The U.S. Fish and Wildlife Service operated a cui-ui hatchery in 1974–75. Pyramid Lake Fisheries (PLF) has operated the David L. Koch Cui-ui Hatchery since 1977 and has further refined hatching and rearing techniques.

In 1971 the U.S. Department of the Interior (DI) reported the classification status of the cui-ui. Federal restoration of the species began in 1973 by the U.S. Fish and Wildlife Service (FWS) cui-ui recovery team. This team completed a Draft Cui-ui Recovery Plan in 1977 (Pyle et al. 1977). The 1982 revision of the original Cui-ui Recovery Plan was approved by the FWS and reviewed by DI (U.S. Fish and Wildlife Service 1983).

In 1975 the U.S. Bureau of Indian Affairs (BIA) funded studies on the fisheries of the Truckee River and Pyramid Lake. The results of the Pyramid Lake Ecology Studies, including data on cui-ui ecology, are presented in Sigler and Kennedy (1978). The results of the Truckee River studies are in preliminary FWS reports. McConnell, Galat, and Hamilton-Galat (1978) and Galat and McConnell (1981) discuss Pyramid Lake fish production in relation to potential changes in total dissolved solids (TDS).

In the early 1960s the NFG developed plans for a fishway that would enable upstream migrating fish to bypass the delta and enter the lower Truckee River. The plans were submitted to the Fleischmann Foundation, Reno, Nevada, but the facility was not funded because the Foundation could be given no assurance of a water right. The NFG, along with the FWS and the U.S. Bureau of Reclamation

(BOR), then developed plans for a larger and more elaborate facility. The NFG also lobbied with state and national agencies for the Washoe Project Act, which made funding possible (T. J. Trelease personal communication 1984). The Washoe Project Act was made much more salable by the earlier development, largely by NFG, of highly successful Lahontan cutthroat trout, *Salmo clarki henshawi*, fishery.

In 1975 BOR completed the Marble Bluff Fishway. The FWS operates the Marble Bluff facility and monitors spawning migrations of cui-ui and Lahontan cutthroat trout. Data collected by FWS on cui-ui spawning populations in the lake and fishway are presented by U.S. Fish and Wildlife Service, Nevada Department of Fish and Game, California Department of Fish and Game (1976), Ringo and Sonnevil (1977), and Sonnevil (1977a, 1977b, 1978, 1981). The age structure of cui-ui in 1978 was determined by Robertson (1979). Scoppettone et al. (1981, 1983, and G. Scoppettone personal communication 1983) studied the spawning behavior and habitat requirements of cui-ui in a natural side channel of the lower Truckee River.

Research on the habitat and ecology of fish species in Pyramid Lake was conducted by Vigg (1978a). Vertical distribution patterns and relative abundance are reported (Vigg 1978b, 1980, 1981).

Research on the effects of increasing levels of TDS on cui-ui was initiated by Earl Pyle of FWS during 1975–1978. Chatto (1979) presented preliminary data on hatching success of cui-ui eggs in various proportions of Pyramid Lake water. Lockheed Ocean Sciences Laboratories (LOSL) (1982) studied the effects of various levels of TDS on the embryos, larvae, and juveniles of cui-ui.

T. J. Trelease first reared larvae in 1947, and Kay Johnson and Ivan Young (all NFG personnel) raised them to adult size—about 31 cm. Koch et al. (1979) estimated 91.6% hatching success in controls during nitrogen-species bioassays. However, they were unable to obtain definitive results on toxicity because of high mortality in all treatments and controls. Koch (1981) conducted preliminary temperature tolerance studies of cui-ui embryos and larvae.

Various morphological studies have been conducted on catostomid fishes, including cui-ui. Nelson (1948, 1949, 1961) studied the comparative morphology of the Weberian apparatus, the opercular series, and the swim bladder, respectively. Miller and Evans (1965) studied the external morphology of the catostomid brain and lips. Snyder (1981a, 1981b, 1983) studied larval development of cui-ui, mountain sucker (*Catostomus platyrhynchus*), and Tahoe sucker (*Catostomus tahoensis*) and prepared a key for their identification. Miller and Smith (1967, 1981) discuss the paleohistory, systematics, distribution, evolution, and status of each species of *Chasmistes*.

Donald R. Tuohy, Nevada State Museum, Carson City, has conducted extensive archaeological studies within the Pyramid Lake region; however, the data are largely unpublished. Archaeological finds at Pyramid Lake are reported by Ting (1967) and Tuohy and Clark (1979). Hattori (1982) studied the archaeology of the Winnemucca Lake area and relates the importance of aquatic resources, including cui-ui, to human prehistoric habitation. The importance of the fishery, especially cui-ui, to the native Americans is discussed by Bath (1978). The ethnographic record of Pyramid Lake Northern Paiute fishing is presented by Fowler and Bath (1981). Follett (1963, 1974, 1977, 1980, 1982) has studied cui-ui remains in aboriginal deposits. Stewart (1941) discusses the culture element distributions of the Northern Paiute.

PROCEDURES

Cui-ui were captured with variable mesh bottom-set gill nets in Pyramid Lake and at the Marble Bluff facility on the Truckee River. Vigg (1981) presents a description of fish sampling design and methodology. For age and growth data, fish were weighed to the nearest gram, measured (nearest mm), and sexed internally, except at spawning time. Scales, opercula, otoliths, and fin rays were taken to compare accuracy of aging using different bony parts. The length-weight relationship is expressed by the formula $W = aL^b$ (Sigler 1951), where W = weight (g), L = fork length (cm), and a and b are constants. The value of the constants (a and b) are calculated by the method of least squares using log transformations of weight and length (log W = log a + log b length). Validity of the aging method was determined by criteria suggested by Van Oosten (1923, 1929, 1944) and Hile (1941). To avoid possible bias, scales and other bony parts were first read without knowledge of the size of the fish. They were read at least three times. The length of body–bony part relationship was calculated according to Tesch (1971). The condition factor $K = Wx10^5/L^3$ was calculated according to Carlander (1969), where W = weight (g) and L = fork length (mm). Age and growth calculations were accomplished using a computer program (Nelson 1976).

Cui-ui eggs and embryos used in this study were obtained from the David L. Koch Fish Hatchery. They were collected at regular intervals postfertilization and preserved in both Bouin's solution and Puckett's fixative. Serial sections of the entire embryo were cut at 8–10 micrometers and stained with hematoxylin and eosin and Mallory's Triple Stain. Embryos to be sectioned were chosen from among the best preserved of 12–15 specimens from each sample. In addition to sectioned material, whole mounts were also used, ranging in age from 9 to 912 hours post-hatching (Bres 1978).

There were 19 water sampling stations located along 4 transects designed to represent the horizontal areas of the lake and to facilitate measuring the influence of the river upon the system. Stations were sampled on a monthly basis from November 1975 through October 1977. Conductivity, oxygen, pH, temperature, and turbidity in relation to time, depth, and location were measured in the field with an InterOcean probe (Model 513D). Measurements were taken at 2-m intervals from the surface to 22 m and at 5-m intervals from 25 m to the bottom. Conductivity measurements were standardized to 25 C. Water samples were collected for analysis of major chemicals and trace elements the third week of every month from January through December 1976 and again in April and September 1977. Samples to be tested for nutrients were collected at least once a month from January 1976 through December 1977. Water samples were collected at the surface (1m), middepth, and bottom levels at the midpoint of each of three transects (Lider 1978). Analyses were done by the Desert Research Institute Water Chemistry Laboratory.

RANGE AND DISTRIBUTION

Four recent species of *Chasmistes* are known: *C. cujus* Cope, *C. liorus* Jordan, *C. brevirostris* Cope, and *C. muriei* Miller and Smith; the latter species, known from a single collection, is now extinct. Two additional extinct species, *C. batrachops* Cope and *C. spatulifer* Miller and Smith, are known only from the fossil record. Miller and Smith (1981) discuss the distribution and evolution of the various forms of *Chasmistes* (Table 1).

Chasmistes is a lacustrine sucker; all living species and most extinct forms are associated with lake systems. However, the oldest known form, *Chasmistes* sp. from the fluvial beds of the Miocene Deer Butte Formation in Oregon, is an exception (Miller and Smith 1981).

The Pyramid Lake cui-ui population is the last remaining pure species of the genus; the other species have considerable hybridization and introgression with *Catostomus* spp. (Miller and Smith 1981). Cui-ui inhabited Lake Lahontan during the late Pleistocene period (Fig. 3). At its maximum extent, approximately 12,000 years BP, Lake Lahontan covered about 22,300 km^2 and received drainage from about 117,000 km^2 (Russell 1885). Fossil cui-ui have been discovered in the Carson Desert, which was once contained in the largest basin of Lake Lahontan; additional *Chasmistes* sp. fossils have been found in the Honey Lake basin to the northwest (Miller and Smith 1981). As Lake Lahontan desiccated during the last 10,000 years, its contiguous basin became nine remnant lakes. Cui-ui persisted for variable lengths of time in these remnant waters until desiccation caused extinction of most populations. Cui-ui was not present in Walker Lake during historical times. This idea is confirmed by the work of Spencer (1977) and Benson (1978a), which indicated Walker Lake was dry sometime during the period 9050 to 6400 years BP.

During historic times cui-ui lived in both Pyramid and Winnemucca lakes and spawned in the Truckee River as far upstream as just below Reno (Snyder 1918). When Derby Dam was completed in 1905, spawning cui-ui

TABLE 1. The geographic distribution of recent and fossil species of *Chasmistes* (Miller and Smith 1981).

RECENT SPECIES

Common name	*Scientific name*	*Drainage basin*	*Present range*
Cui-ui	*C. cujus* Cope	Lahontan	Pyramid Lake, Nevada
June sucker	*C. liorus* Jordan[A] *C. l.* *C. l. mictus*	Bonneville	Utah Lake, Utah
Shortnose sucker	*C. brevirostris* Cope	Klamath River	Upper Klamath Lake, Oregon
Snake River sucker	*C. muriei* Miller and Smith	Snake River	Extinct[B]

FOSSIL SPECIES

Scientific name	*Geologic epoch*	*Geologic formation*	*Paleohabitat*
Chasmistes sp.	Miocene	Deer Butte, OR	Fluvial
C. spatulifer Miller & Smith	Pliocene and Pleistocene-Recent	Glenns Ferry, ID to Adrian, OR	Lake beds
Chasmistes sp.	Pliocene	Glenns Ferry, ID	Lake beds
Chasmistes sp.	Pliocene	Secret Valley, CA	Lake beds
Chasmistes sp.	Pliocene	Honey Lake sediments	Lake Lahontan
Chasmistes sp.	Pliocene	Calcareous sands	Mono Lake
Chasmistes sp.	Pliocene	Teevimom, WY	——
C. batrachops Cope	Pleistocene - Recent	Fort Rock Basin, OR	Fossil lake
Chasmistes cf. *C. batrachops*	Pleistocene - Recent	White Hills, CA	China Lake
C. batrachops	Pleistocene - Recent	Duck Valley, NV	Pleistocene Lake
Chasmistes cf. *C. liorus*	Pleistocene - Recent	Black Rock Canyon, UT	Lake Bonneville
C. cujus	Pleistocene - Recent	Pleistocene gravels, Fallon, NV	Lake Lahontan
C. brevirostris	Pleistocene - Recent	Indian middens, Klamath Lake, OR	Klamath Lake

A. *Catostomus fecundus* *Chasmistes liorus* × *Catostomus ardens*
B. Based on a single collection from the Snake River below Jackson Lake Dam

were restricted to the river below that point. As water was diverted to the NRIP via the Truckee Canal, the water level in Winnemucca and Pyramid lakes dropped. Winnemucca Lake dried in 1938. Pyramid Lake and the affluent lower river is the only remaining habitat for cui-ui.

EMBRYOLOGY

Koch (1972, 1976) did limited work on the larval development of cui-ui, finding many similarities to the development of the white sucker, *Catostomus commersoni*, as described by Stewart (1926). Long and Ballard (1976) document the stages of embryonic development of the white sucker and cite diagnostic structural characteristics for each stage. They also review previous work on embryology of other fishes within the order Cypriniformes. Snyder (1983) found that sequences of developmental events are nearly equal for cui-ui, Tahoe sucker, and mountain sucker and typical at least for the tribe Catostomini. However, the latter two species, at any given size, are slightly more developed than cui-ui. The following is a detailed discussion of the embryological development of the cui-ui in a 13 C environment (Bres 1978).

Egg-Embryos

The unfertilized egg of the cui-ui is about 2 mm in diameter and is surrounded by a noncellular chorion. It has one micropyle at the animal pole. After fertilization, during a process known as water hardening, the eggs

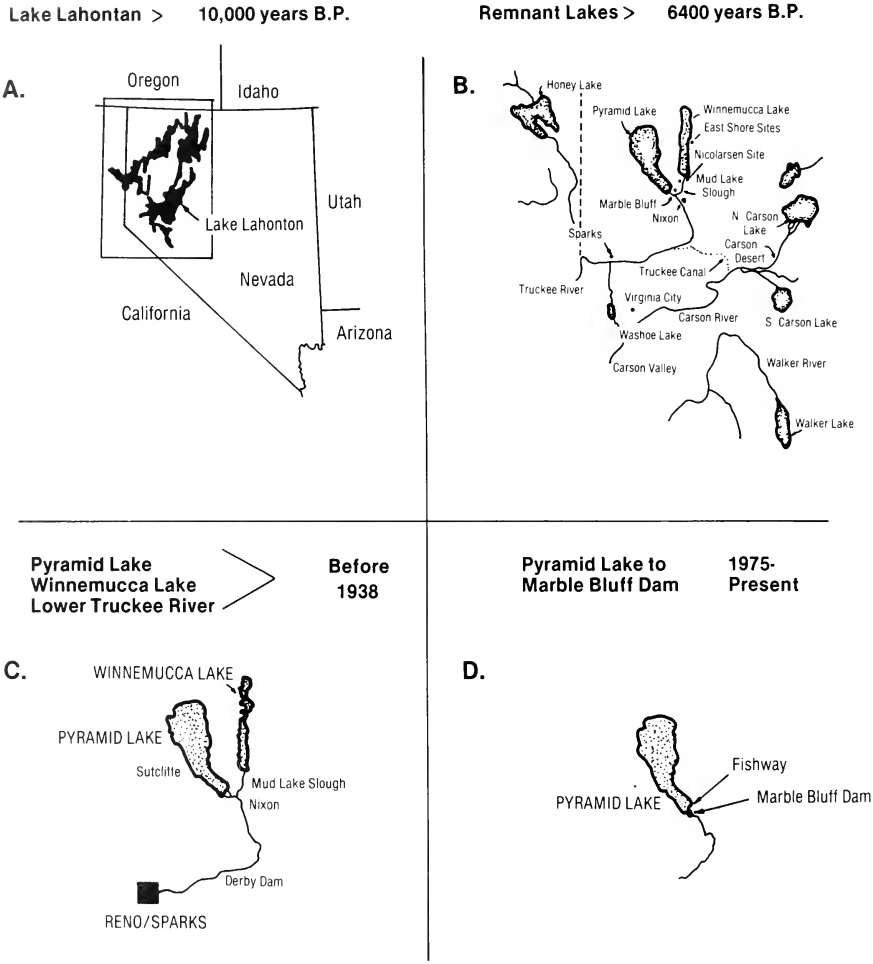

Fig. 3. Decrease in the range of the cui-ui from Lake Lahonton times to the present.

imbibe water and swell to 3 mm. Koch (1976) recorded an 83% increase in egg volume during water hardening, which took 39 minutes. Trelease (personal communication 1984) recorded 75% increase during water hardening and a time of 60 to 75 minutes. The blastodisc appears at 6 hours postfertilization, 0.5 mm in diameter, and is elevated above the surface of the egg at the animal pole. By 18 hours postfertilization, 8 blastomeres are present, with an exponential increase in number thereafter. After 19 hours, "giant" nuclei are seen associated with the syncytial cells of the yolk sac. The marginal periblast is at the periphery of the blastoderm.

At 48 hours postfertilization, the first distinction between the three germ layers is apparent. The neural plate has formed, along with a thickened precursor to the neural tube. The notochord and somites are present.

At 96 to 120 hours, the neural tube and notochord are well developed. Myotomes have differentiated from somites, and the dorsal fin fold has begun to develop. The pronephric ducts are formed anteriorally but are undifferentiated posteriorally. The gut has no lumen and is incomplete posteriorally, and the cloaca has not yet formed.

Anterior neural crest migration occurs at 144 to 168 hours. The diencephalon exhibits cruciform shape. The optic vesicles have developing lenses, and the opticoel joins the diocoel. Auditory vesicles are also present. Myoblasts the length of one somite can be seen. The coelomic cavity is developing between the somatic and splanchnic mesoderm.

At 192 hours cranial ganglia V, VII, and X are visible. Presumptive medulla is developing, and the lateral ventricles are present. The pronephric duct has increased in length, and tubule development is beginning. The liver diverticulum and developing gut are visible. Vitelline circulation is well developed, and the dorsal aorta and postcardinal veins are visible. Precursors of the pigmented retina (a single layer of cells) and the neural retina are forming in the eye. At 13 C hatching occurs at 216 hours.

Larvae

At hatching cui-ui are white and threadlike in appearance, 6 to 7 mm in length, without functional vision, and have only limited powers of locomotion (Table 2 and Fig. 4).

TABLE 2. Time sequence of cui-ui development at 13 C.

AGE (Hours postfertilization)	DEVELOPMENTAL STAGE
0	Unfertilized ovum
6	Formation of blastodisc
18	Eight-cell stage
19	Early blastula
48	Early neurulation, somites present
96 to 120	Neurulation complete, organ development begins
192	Well-developed circulation, appearance of retinal pigment
216	Hatching
(Hours post-hatching)	
9	S-shaped heart
26 to 31	4 pairs of gill arches, optic chiasma forms, secondary reopening of gut begins
51 to 56	6 pairs of gill arches, recanalization progresses to foregut
72	Extensive nerve development, spinal cord differentiated, internal melanophore development
84	Development of lateral line system and external melanophores
120	Begin directional swimming
312	Functional mesonephros, 5 functional gill arches
384	Mouth open, eyes functional, first development of swim bladder
672	Yolk completely absorbed, functional gut
912	Fry actively feeding, approaching adult body form

Central Nervous System.—The anterior curvature of the brain is noted 26 to 36 hours (post-hatch). Considerable nerve development has occurred by 72 hours. The cerebellum is still relatively small compared to the large medulla. The neural tube has differentiated into a spinal cord, and both gray and white matter are present. At 84 hours the potential neurohypophysis of the pituitary is developing in the brain. The III and IV ventricles are present, with the Aqueduct of Sylvius connecting them; the region of the epiphysis is also beginning to develop. Spinal ganglia

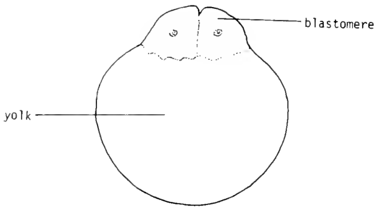

Fig. 4a. 6 hours postfertilization

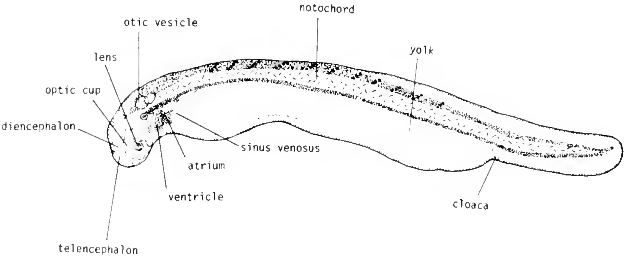

Fig. 4b. 9 hours post-hatching

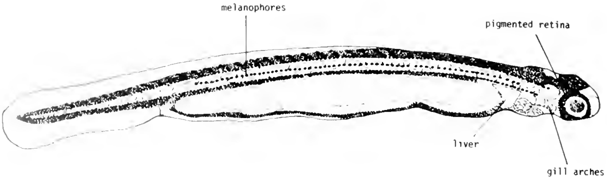

Fig. 4c. 4.5 days post-hatching

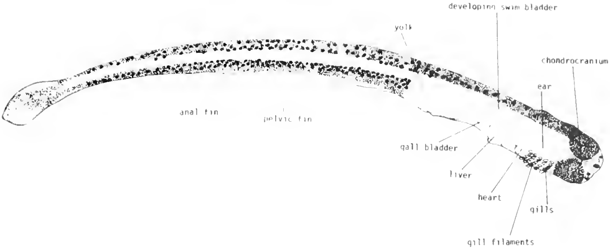

Fig. 4d. 21 days post-hatching

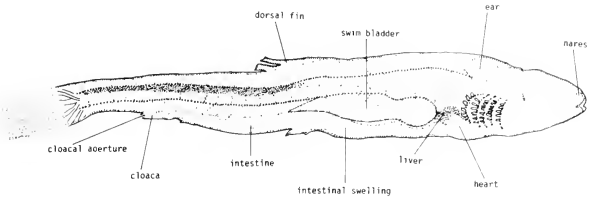

Fig. 4e. 38 days post-hatching

Fig. 4. Embryonic stages of development of the cui-ui.

are visible along the spinal cord. At 384 hours the epiphysis continues to develop. The pituitary and hypothalamus are visible, although no differentiation has occurred in the pituitary. Motor neurons are well developed in the mesencephalon. At 504 hours the developing chondrocranium is visible.

Eye.—The optic cup and retina continue to develop after hatching occurs. The optic chiasma is first observed at 26 to 31 hours (post-hatch), with the optic nerve connected to the retina. The horseshoe-shaped retina, derived from the optic cup, is apparent at 51 to 56 hours. At this time the oculomotor nerve is visible, extending from the brain to the eye region. By 72 hours the lens is present and the pigmented retina is represented by a thin layer; however, no differentiation has occurred in the sensory portion of the retina. Presumptive cornea has formed by 84 hours, and differentiation in layers of sensory retina has occurred. The optic nerve is attached to the retina. Extrinsic ocular muscles are well developed. By 120 hours, heavy pigmentation has been laid down on the retina. After 384 hours the pigmented iris, cornea, lens, and many sensory layers of the retina are visible. The eyes are functional and capable of movement.

Ear and Lateral Line.— Seventy-two hours post-hatching, the otic vesicle, the rudiment of the inner ear, begins to develop. The first complete distinction between the dorsal sacculus and the central utriculus takes place in the otic vesicle at 84 hours post-hatching. At this time the first indication of lateral line system development occurs. By 168 hours the otic vesicle is well developed. After 384 hours of larval development, the otic capsule has divided into 3 parts, the latter part being completely closed off. Otoliths are visible in the inner ear, and the cranial nerves that supply the ear are visible. The vestibular ganglia has developed outside the otic capsule from the stato-acoustic nerve (VIII).

Olfactory Sense and Taste Buds.—By 20 hours the olfactory placodes are well developed in the anterior portion of the head. The neural connection of the nasal placode to the brain (olfactory nerve) is visible by 26 to 31 hours. By 168 hours the olfactory organ has developed from the nasal placode. By 384 hours indentations are forming at the site of the future external nares. The mouth is open, and developing taste buds are visible in the mouth and gills by 384 hours. These are very abundant on the head, mouth, and gills of adults and compensate for incomplete development of the internal nares.

Gills.—Four pairs of gill arches are visible at 26 to 31 hours. The aortic arches leave the center of the gill arch to fuse together and open into the conus arterious. At 51 to 56 hours six pairs of gill arches are present and the gill cleft is developing. By 60 hours each of the six pairs of well-developed gill arches has a central core, the aortic arch. By 72 hours the aortic arch has increased substantially in size. At 84 hours the first gill cleft has opened. By 312 hours the 6 primitive gill arches have been reduced to 5 functional gill arches, the definitive adult condition. Each arch has at least 3 filaments composed of loops of capillaries. After 384 hours of development, gill filaments are evident, as are gill cartilages associated with muscles for moving the gills.

Heart.—The S-shaped heart is visible 9 hours post-hatching. After 20 hours the endocardial cushion, which is the precursor to valve development, is forming in the atrioventricular canal. Separation between endocardium and myocardium is pronounced by 56 hours post-hatching. The heart and associated vessels are well developed by 72 hours. Cardiac jelly is visible after 82 hours. After 120 hours all 4 chambers of the heart and the atrio-ventricular canal are visible. After 312 hours the muscular wall of the heart is well developed and the ventricle has become trabeculated. By 384 hours all blood vessels contain eosinophilic plasma.

Muscle.—Myotomes and myocommata are well developed by 9 hours. By 26 to 31 hours connective tissue is present in the myocommata. At 72 hours myofibrils appear as ribbons around the periphery of the muscle cells; this conforms to the standard configuration of the adult fish.

Skeleton.—After 20 hours the sites of the future chondrification of the ribs are visible as individual swellings along the dorso-lateral intersegmental myosepta. By 51 to 56 hours condensation is beginning to form the initial skeletal elements. The trabeculae of the chondocranium are visible, although they are not true cartilage but simply condensations of the mesenchyme. After 312 hours a large number of caudal rays are present. At 384 hours cartilage is present in the gill arches, opercula, and the roof of the mouth (precursor to palate).

Liver and Pancreas.—The liver primordium is well developed by 20 hours. At 26 to 31 hours the sinus venosus has been displaced to a crescent shape at the side of the liver. The liver primordium is well developed by 84 hours; a pancreatic rudiment is visible next to the intestinal swelling. The liver has an adult pattern of organization and is functional by 384 hours. The pancreas is forming lobules that will later spread out forming the adult diffuse pancreas. The gall bladder is visible; bile and pancreatic ducts are separate and fuse together at the entrance to the gut.

Kidney.—At 9 hours the pronephric ducts join with the intestine posteriorally to form the cloaca. By 26 to 31 hours, ciliated nephrostomes, the opening of the kidney tubule to the coelom, have developed in the pronephros, and coelomic fluid is pumped into the tubule. After 72 hours of larval development, kidney tubules are well developed in the pronephros. For the first time, the mesonephros and mesonephric tubules are visible. At 84 hours the mesonephric duct is visible, opening into the mesonephros and contacting the cloaca. By 312 hours the mesonephros has greatly enlarged, is very well developed, and has reached a functional state. At 672 hours the mesonephric duct and anus empty together into the cloacal aperture.

Alimentary Canal.—The pronephric ducts join with the intestine posteriorly to form the cloaca 9 hours post-hatching. The tiny, solid gut begins to form the loop of the intestinal swelling at about 20 hours. The larval cui-ui, like the adults, do not have a true stomach since it contains no glands. At 26 to 31 hours the secondary reopening of the gut begins, small in the liver mass but enlarging in the midgut region posterior to the liver. Mesenteries supporting the gut are visible. Absorptive cells are apparent in the yolk sac, and the mouth cleft is present. Further recanalization of the foregut is occurring at 51 to 56 hours. At

72 hours there are many secondary openings in the foregut. Also the lumen of the gut has greatly increased from 1 to 2 to 10 to 15 micrometers in diameter. At 84 hours the loops of the gut are beginning to form; early differentiation of the intestinal swelling and visceral cavity occurs. The pharyngeal cavity is open at 120 hours. After 384 hours the mouth is open, and many mucous-secreting cells are visible in the oral cavity. Material present in the pharynx suggests feeding, although some parts of the pharynx are still undifferentiated. The gut is broadly open and has developing longitudinal folds. From 384 to 504 hours the yolk sac is greatly diminishing in size. After 672 hours of larval development, the yolk is absent and the gut is functional, with food present in the intestine. By 840 hours the larvae are 20 to 25 mm long (Koch 1976). After 912 hours fry are actively feeding and the digestive tract is filled with food.

Integument and Pigmentation.—By 20 hours lateral fin folds are well developed, and many mucous secreting cells are visible in the ectoderm. Connective tissue is present in the dermis of the skin at 26 to 31 hours. After 72 hours the epithelium is still simple, and many secretory cells are present. Melanophore development is beginning internally. At 84 hours goblet cells are observed in the epithelium. Granular cells, filled with eosinophilic granules, are present, characteristic of the adult condition. Both small and large external melanophores are visible by 120 hours posthatching. At 384 hours mucous-secreting goblet cells are present in the skin.

Swimming.—After 18 hours the larvae are 8 to 9 mm long, and sudden bursts of energy constitute their initial swimming attempts; at 192 to 240 hours the larvae are 12 to 14 mm in length and continually swim at the surface (Koch 1976). Between 240 to 360 hours they swim to keep their position in the water column (Koch 1976). After 384 hours the pneumatic duct enters the gut from the developing swim bladder, and at 504 hours the swim bladder is clearly visible. The swim bladder has increased in size during 672 hours.

Identification.—Larval and juvenile cui-ui are sometimes difficult to identify in Pyramid Lake; they are easily confused with another resident catostomid, the Tahoe sucker. This may, in part, account for the fact that relatively few cui-ui less than 300 mm in length have been identified. Ramsey (letter to E. A. Pyle, 16 September, 1974) offers the following points of contrast between the two larvae:

> *Ventral-Pigmentation*: A consistent character for distinguishing larval stages of Tahoe sucker from larval cui-ui is the presence of a superficial row of melanophores on the midventral skin posterior to the pectoral basis. This abdominal pigmentation is generally absent in cui-ui, although a row of melanophores sometimes is present but confined to the breast anterior to the pectoral bases. The row of midventral melanophores in larval Tahoe suckers is still present at age 66 days (17 to 19 mm total length).
>
> *Intestinal Coiling*: At age 66 days the intestine of the Tahoe sucker loops far anterior in contrast to the cui-ui, where it is either straight or has a left twist.
>
> *Mouth*: The lips of the Tahoe sucker are thicker and the mouth is placed further ventrally than in the cui-ui.
>
> *Other*: A character sometimes useful at ages earlier than 66 days is the presence in cui-ui of a depigmented "one to one" on top of the head, just posterior to the eyes. There is considerable occluding of this pigmentation by age 66 days.

Snyder (1981a, 1981b, 1983) studying larval development of cui-ui in comparison to the other catostomids that spawn in the Truckee River system, i.e., Tahoe sucker and mountain sucker, developed a taxonomic key that separates the larvae and early juveniles of the three species. Snyder concludes the larvae can be separated on the basis of midventral pigmentation, peritoneal pigmentation, gut-loop formation, and mouth characters.

The following differential characteristics are included to complement previous descriptions of larval development and morphology (Snyder 1983). At a total length (TL) of 11 to 21 mm, cui-ui are characterized by absence of midventral melanophores on the head or abdomen anterior to the bases of pelvic fin or their precursors and anterior to the vent. If midventral melanophores exist, they are present as a short line only in the branchial and heart regions between and anterior to pectoral fin bases. Mesolarvae have a straight gut until about 19 mm TL; metalarvae to 21 mm may develop a primary loop extending forward less than two-thirds of the length of the stomach and not crossing over the stomach. Metalarvae have peritoneal pigmentation largely restricted to the dorsal and dorsalateral visceral cavity.

The following characteristics apply to metalarvae > 21 mm and juveniles < 50 mm. The pigmentation of the peritoneum is mostly lim-

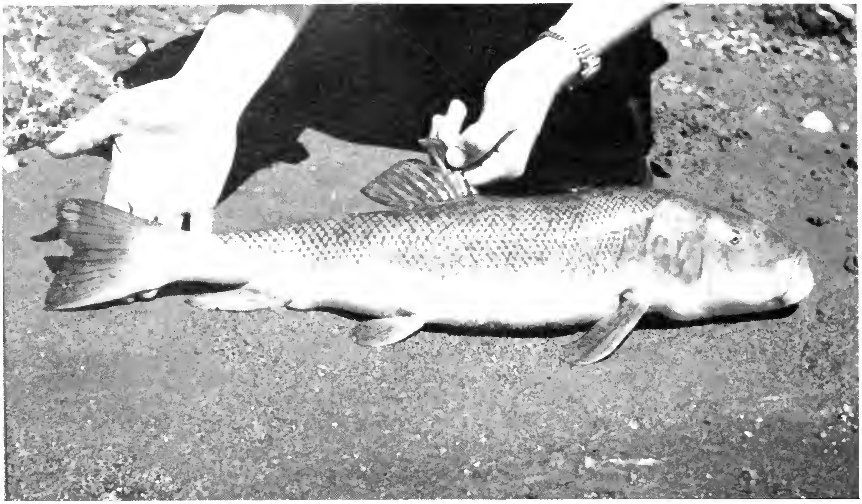

Fig. 5. Adult female cui-ui. Photo by Thomas J. Trelease.

ited to the dorsal and dorsalateral visceral cavity. The primary loop of the gut is relatively straight along the left side of the stomach until about 30 mm TL, at which size secondary loops cross the stomach in an S-shape, persisting through 50 mm TL. The mouth is terminal—usually slightly oblique but sometimes very low and almost horizontal, approaching a subterminal condition.

ADULT MORPHOLOGY

Description

The cui-ui is a large, big-mouthed sucker. The head is wide and somewhat round in cross-section. Its interorbital space is greater than half the length of the head. The mouth is unsuckerlike with a ventro-terminal position. The lips are thin and obscurely papillose. The lower lip is somewhat pendant and divided by a wide median notch. The cui-ui is coarsely scaled, with counts of 13 to 14 above the lateral line, 59 to 66 along the lateral series and 22 to 26 around the caudal peduncle. The total body length is 9 times that of the dorsal fin base. The length of the anal fin, from the insertion to the tip, is about one sixth the total body length. Fin ray counts are: dorsal, 10 to 12; anal, 7; and caudal, 8 or less. The caudal is weak to moderately forked. The caudal peduncle is thick, with the smallest depth going 12 times into standard body length (SL). In triangular section, the pharyngeal teeth are delicate. The last pharyngeal arch bears a row of more than 10 comblike teeth confined to a single row. The swim bladder is 2–celled; the peritoneum is nearly black. Each gill raker is branched like broccoli (Fig. 5).

Sexual Dimorphism

Breeding males display a brilliant red to brassy color on the sides; in general they are black or brown above, fading into flat white below. Females have a bluish gray cast year-round. Female cui-ui attain greater length and heavier weight than males. During the spawning season the vent of females becomes swollen and extended, whereas males develop nuptial tubercles on their fins. Apparent sexual dimorphism exists in the meristics associated with fin size (Table 3). The length of the base of the dorsal and anal fins, the height of the dorsal and anal fins, and the length of the pectoral, pelvic, and caudal fins are all proportionally greater for males. Snyder (1918) refers to differences between the sexes:

> The females are more stocky than the males, and with their huge heads, large rounded bodies, and relatively

TABLE 3. Meristics of *Chasmistes cujus* from near the mouth of the Truckee River (Snyder 1918).

Morphological characteristic	Mean measurement Males n=11	Females n=7
Standard length (mm) ***	427.1	487.3
range	(410–444)	(445–538)
Percent of body length		
Length head	28.0	27.8
Depth body *	21.1	22.4
Depth caudal peduncle	8.5	8.2
Length caudal peduncle	15.8	15.2
Length snout	12.9	13.2
Diameter eye	3.1	2.9
Interorbital width	12.4	12.5
Depth head	18.7	18.6
Snout to occiput	22.3	22.0
Snout to dorsal	51.3	50.5
Snout to ventral	58.1	58.4
Length base of dorsal ***	15.1	13.3
Length base of anal ***	9.4	8.1
Height dorsal	12.9	12.5
Height anal ***	19.9	15.6
Length pectoral **	18.9	17.5
Length pelvic ***	13.8	11.6
Length caudal ***	20.4	18.4
Dorsal rays	11.1	10.7
Anal rays	7.2	7.0
Scales lateral line	62.1	61.6
Scales above lateral line	13.6	13.9
Scales below lateral line	10.4	10.1
Scales before dorsal	31.6	30.3

* Significant differences between sexes, $P<0.05$.
** $P<.01$
*** $P<.001$

short fins are very ungainly looking fish. The scales and fins are without tubercles.

Snyder (1918) describes the differential coloration patterns between the sexes. He also reports that Indians could differentiate cui-ui from Pyramid and Winnemucca lakes by the grayer color of the Winnemucca cui-ui, although he was unable to detect any difference.

Comparative Morphology

The ventro-terminal position of the mouth is a diagnostic characteristic of *Chasmistes* spp. It is so exceptional among the usually ventral-mouthed sucker family that it has been regarded as an extreme specialization; however, certain primitive suckers (e.g., *Amyzon* and *Ictiobus cyprinellus*) and presumed sucker ancestors are also characterized by relatively terminal mouths (Miller and Smith 1981). Cui-ui is the largest living species of *Chasmistes*. Snyder (1918) collected specimens ranging from 410 to 670 mm in SL.

Of various adult meristic data summarized from the literature, Snyder (1983) determined that lateral series scale counts prove to be diagnostic in separating cui-ui (59 to 66) from mountain sucker (75 to 100) and Tahoe sucker (79 to 95). For juveniles, Snyder found this character useful only when squamation is complete, usually by 35 to 50 mm TL.

The comparative morphology of Catostomidae has been studied with reference to the swim bladder (Nelson 1961), the opercular series (Nelson 1949), the Weberian apparatus (Nelson 1948), and the brain and lips (Miller and Evans 1965). *Chasmistes* spp. have a two-chambered swim bladder that is characteristic of all catostomids except *Moxostoma*, which has a three-chambered structure. It is the posterior chamber in catostomids that regulates buoyancy. The usual catostomid swim bladder is 35 to 45% of the SL of the fish (7% by volume); however, the cui-ui swim bladder is only 32.1% of SL (Nelson 1961).

Nelson (1949) presents a generalized composite of the catostomid opercular series, which consists of a large operculum, relatively small suboperculum and interoperculum, and invariably three branchiostegal rays. On the basis of the opercular series, the genera of Catostomidae can be arranged into three well-defined groups; *Chasmistes* belongs to the group including *Catostomus* and *Xyrauchen* (Nelson 1949).

The Weberian apparatus of catostomids includes the first four vertebrae and associated structures that form two separate functional units. *Chasmistes* has the same general morphological pattern as *Catostomus* and *Xyrauchen*; however, it differs in having enlarged esophageal supports and obliterated second to third intervertebral space (Nelson 1948). Based on the comparative morphology of the Weberian apparatus, Nelson concludes *Chasmistes* is an early divergent of the catostomid stock.

Miller and Evans (1965), studying the morphology of the brain and lips in catostomids, conclude:

> Their principal value probably lies in providing a basis for making inferences about the life history, and especially the habitat preferences and feeding behavior of little-known species.

Thus, morphological evidence may shed light on aspects of the ecology of cui-ui about which there has been much speculation. The facial lobe of the brain is associated with taste buds on the lips and skin, whereas the vagal lobes receive fibers from taste buds in the mouth and pharynx. The brain morphology of cui-ui is unique in several ways: the optic lobes are small and separated, the postcerebellar medulla is elongated, and the vagal lobes are well developed but located more posteriorly than is usual in catostomids. The overall pattern suggests a well-developed "mouth tasting" apparatus (Miller and Evans 1965). Suckers that have large vagal lobes are characteristic of lotic habitats, and mouth tasters probably sort food within the oral cavity. Thus the cui-ui is probably not a sight-feeder in surface waters but may use the oral cavity to sort out food (e.g., algae and invertebrates). Other genera with well-developed vagal lobes include *Xyrauchen*, *Ictiobus*, and *Carpiodes*.

AGE AND GROWTH

The cui-ui is a slow-growing, long-lived fish, living 18 or more years (Robertson 1979). Scoppettone (report to Desert Fishes Council 1983) stated it may live much longer (≥ 40). Growth in length is rapid for the first 4 to 5 years and slower thereafter. Annuli in older fish are formed between June and August; in younger fish it may occur the first week of June.

Back-calculated fork length (FL) at scale formation is 46.0 mm for known age fish (I to III), from the NFG Washoe Rearing Station, Reno. The calculated FL was skewed substantially higher when advanced age groups (IV and VI) from Pyramid Lake were added. In aquarium-reared fish, E. Pyle (personal communication 1977) found they started forming scales at 49.0 mm FL, and fish 50 mm had from 3 to 7 scales at the base of the caudal peduncle.

Scales are judged not to be reliable for aging cui-ui older than age VI. Other bony parts, otolith, opercula, and fin ray, are more nearly reliable. No technique is reliable when there is no, or almost no, growth and no discernible annulus. This is a definite possibility in older cui-ui. There is reasonably good agreement between fin rays and otoliths and excellent agreement between otoliths and operculum through age XIII (Table 4). There was generally good agreement for otolith, opercula, and scale in age I to IV. Data from opercula were chosen because it is reliable and easy to collect and process. Since growth differences were not significant, sexes are combined (Table 5). The absolute growth is in good agreement with calculated growth (Fig. 6). The body fork length-opercula (X) relationship, sexes combined, is: FL = 229.2 + 7.0 x (r^2 = 0.92).

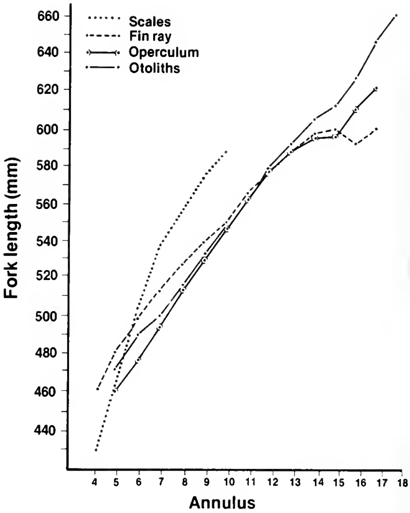

Fig. 6. Absolute growth rates using four methods of age assignment (scales, fin rays, operculum, and otoliths) for cui-ui collected from Pyramid Lake, Nevada, 1978 (Robertson 1979).

The body length–bony part radius regressions are highly correlated: fin ray (r^2 = 0.93), opercula (r^2 = 0.92), otolith (r^2 = 0.80), and scales (r^2 = 0.63) (Robertson 1979).

The drop in numbers of fish older than age XV may be attributed largely to natural mortality or no growth, but the low numbers of fish in some of the younger age groups are, in part, a result of moderate to weak year classes (Table 6). Sonnevil (1978) suggests reduced spawning populations and consequent weak year classes can be attributed to reduced river flows at the time cui-ui spawn.

There appears to be good correlation between strength of year classes and flow levels of the river for 5 of the 12 years and poor correlation for 3 of the 12 years (Table 7).

TABLE 4. Comparison of assigned age by various aging methods for 28 cui-ui, sexes combined. Collected April to July 1978 from Pyramid Lake, Nevada.

	Methods of age assignment					
ID#	Fork length (mm) at capture	Scale age	Fin ray age	Operculum age	Otolith age	Centrum age
32A	599	8	10	11	10	—
33A	587	8	11	11	11	—
36A	612	8	12	13	13	—
17A	638	8	13	13	14	—
14B	584	8	—	11	11	—
16B	615	8	11	11	11	—
YY−3	565	8	11	—	12	—
24A	604	8	11	11	11	—
17	578	8	12	12	12	—
24	633	8	15	14	15	—
31	607	8	11	12	12	—
33	618	8	11	12	12	—
9B	588	8	—	11	11	—
20A	618	8	—	14	13	—
21A	615	8	—	12	12	—
28A	591	8	12	12	12	—
8B	588	8	7	12	12	—
4B	620	8	—	13	13	—
27A	648	9	14	14	14	—
38A	632	9	12	13	13	—
19A	609	9	—	11	12	—
AA	610	9	—	12	12	—
F	573	9	—	10	11	10
E	638	9	—	16	16	—
2B	598	—	—	10	10	—
ZZ-B	575	—	—	11	—	—
3B	601	—	—	12	12	—
23	632	—	13	13	13	—

TABLE 5. Calculated average fork length and annual growth increments using opercula of 79 cui-ui, sexes combined. Collected April 1978 to July 1978 from Pyramid Lake, Nevada (Robertson 1979).

Age	Number of	Mean calculated fish length (FL-mm) at each annulus												
group	fish	5	6	7	8	9	10	11	12	13	14	15	16	17
V	13	466												
VI	12	465	490											
VII	3	453	481	499										
X	6	451	470	485	511	527	468							
XI	10	455	477	499	518	539	559	576						
XII	17	453	471	494	512	530	547	563	583					
XIII	10	447	468	492	511	523	546	562	579	596				
XIV	4	455	478	493	515	531	547	566	580	594	611			
XV	1	453	474	495	508	522	529	536	553	564	578	599		
XVI	1	418	440	460	484	508	522	543	564	578	585	599	613	
XVII	2	440	457	471	488	507	524	540	550	564	583	596	610	624
Total number		79	66	54	51	51	51	45	35	18	8	4	3	2
Grand average (mm) calculated fork length		459	475	493	512	530	548	564	578	589	597	598	611	624
Range (mm) in calculated length		418–488	439–529	467–536	484–533	484–571	495–592	515–606	522–634	536–634	553–620	564–627	578–641	592–655
Length increments (mm)		459	16	18	19	18	18	16	14	11	8	1	13	13

TABLE 6. Age and year class composition of 665 cui-ui sampled in Pyramid Lake, Nevada, 1978 (Robertson 1979).

Age class	Year class	% Composition	Number of fish
IV	1974	6.0	37
V	1973	32.0	211
VI	1972	22.0	149
VII	1971	7.0	49
VIII	1970	5.0	34
IX	1969	3.0	18
X	1968	2.0	16
XI	1967	2.0	14
XII	1966	4.0	27
XIII	1965	4.0	28
XIV	1964	3.0	21
XV	1963	6.0	41
XVI	1962	2.0	13
XVII	1961	0.9	6
XVIII	1960	0.2	1

There appears to be good correlation between strength of year classes and flow levels of the river for 5 of the 12 years and poor correlation for 3 of the 12 years (Table 7).

TABLE 7. Discharge in cubic feet per second (cfs), of the Truckee River near Nixon, Nevada, for the calendar years 1962–1973 (USGS 1962–1973) and year class–levels of flow relationship.

Year	Age group	Mean flows (cfs) by month April	May	June	July	Strength of year class*	Level of river flows*
1962	XVI	315.0	229.0	31.3	18.8	1	3
1963	XV	183.0	1391.0	926.0	53.7	1	2
1964	XIV	53.4	93.2	48.3	26.2	3	3
1965	XIII	580.0	1325.0	515.0	62.2	2	1
1966	XII	64.6	61.4	47.0	33.2	2	1
1967	XI	5.9	7.5	11.4	31.7	3	3
1968	X	321.0	67.9	52.4	38.8	3	3
1969	IX	3392.0	3454.0	3469.0	430.0	3	1
1970	VIII	530.0	212.0	291.0	445.0	2	2
1971	VII	770.0	1234.0	1744.0	451.0	2	1
1972	VI	236.0	249.0	110.0	43.3	1	3
1973	V	854.0	991.0	453.0	321.0	1	1

*Rated on a 1 to 3 scale, where 1 is strong and 3 is weak.

Although 1969 was a high water year, a weak year class resulted. According to Robertson (1979), this appears to contradict the hypothesis of high flows and successful cui-ui spawning; however, it is pointed out this was the year of exceptionally high suspended sediment discharges, which may have been lethal to fertilized eggs.

Koch (1972) reports the mean age of spawning cui-ui in 1971 and 1972 as 7.5 and 7 years, respectively. These represent the strong year classes produced in high water years of 1963 and 1965. Koch also found a low number of fish representing ages IV, V, and VI in 1971 and 1972.

Robertson (1979) determined the length-weight relationship for 139 females, ranging from 453 to 653 mm FL, and for 147 males, ranging from 448 to 577 mm FL. Only spawned fish were included in these data. The relationships for males and females are: males $\log_{10} W = 3.4725 + 2.4639 (\log_{10} L) (r^2 = 0.77)$; females $\log_{10} W = 4.5046 + 2.8485 (\log_{10} L) (r^2 = 0.93)$. Males weighed less than females of equivalent length and age. This is in agreement with Johnson (1958) and Koch (1972). The length-weight relationship in the 1975 to 1977 Pyramid Lake study (Robertson and Koch 1978) was: $\log_{10} W = -1.240 + 2.5738 (\log_{10} L)$; this is in agreement with work done by Robertson (1979) in 1978–1979.

The condition factor, or general robustness of the fish, K(FL) for spent (spawned out) fish ranged between 1.08 and 1.64, with a mean of 1.21 for females and 0.81 to 1.61 and a mean of 1.20 for males (Robertson 1979). The condition factor decreases moderately with an increase in length, and the decrease is higher for males than females. Condition factors for the 1976 to 1977 study showed similar trends (Table 8).

FOOD AND FEEDING

The diet of cui-ui is not well known; however, we made some observations under artificial conditions. Koch (1972, 1976) reports larval cui-ui, older than 20 days, readily consume zooplankton introduced into an aquar-

TABLE 8. Length, weight, and condition factors $K = W \times \frac{10^5}{FL^3}$ for cui-ui, sexes combined, Pyramid Lake, Nevada, 1976 to 1977 (Robertson and Koch 1978).

Fork length (mm)	Weight (g)	K factor
378	566	1.04
401	659	1.02
424	761	0.99
447	872	0.97
472	1002	0.95
495	1133	0.93
518	1273	0.91
544	1444	0.89
589	1771	0.86

ium of lake water. He reports the zooplankter *Moina hutchinsoni* is most preferred by larvae, presumably because it has limited mobility, whereas *Diaptomus sicilis* is the least preferred zooplankter (Fig. 7). We have observed aquaria-reared larvae and juvenile cui-ui grazing on periphyton growing on rocks. Since zooplankton is not abundant in the river habitat of larval cui-ui, periphyton is probably important in their diet. When young cui-ui first enter the lake, they may feed both on periphyton and zooplankton. In the David L. Koch Hatchery larval and juvenile cui-ui feed on algae on the sides of the tanks, as well as on commercial fish feed (A. Ruger personal communication 1983).

Snyder (1918) found spawning adults do not feed; he states: "The stomachs of all specimens examined were devoid of food." Koch (1972) reports cui-ui examined during spawning migrations of 1971 and 1972 had not recently fed. Examination of fish during the spawning migration at the Marble Bluff facility also confirm these observations.

Johnson (1958) reports that, of 46 adult cui-ui examined, 43 had eaten zooplankton (93.5% occurrence), 4 sand and mud (8.7% occurrence), 2 unidentified material (4.3% occurrence), and 1 insects (2.1% occurrence). La Rivers (1962) reports T. J. Trelease examined specimens taken in commercial net hauls and found a mixture of algal filaments with zooplankton fragments. From this information La Rivers (1962) concludes, "It seems probable that most of the feeding is done about rocks where thick algae coatings are heavily populated with micro-crustacea." Based on the cui-ui's fine and numerous gill rakers, La Rivers hypothesized, "The strong possibility exists that they can extract useable quantities of micro-crustacea from the open lake waters." T. J. Trelease (personal communication 1984) observed cui-ui in large doughnut-shaped schools near the surface over deep water and far from shore first in 1954. He assumed they were feeding since tui chub form similarly shaped schools when they are feeding. He saw these schools somewhat frequently as late as 1968. Vigg (1978a, 1980) documented that adult cui-ui primarily inhabit the shallow benthic areas and not the limnetic water column. It may be that when they inhabit the benthic zone they generally feed further off the bottom than species of suckers with ventral mouths.

Fig. 7. An adult copepod, *Diaptomus sicilis*, a common food of cui-ui.

REPRODUCTION

Migration

Snyder (1918) and Scoppettone et al. (1981, 1983) made detailed observations on cui-ui spawning migrations. Snyder observed the annual cui-ui spawning run begins about April 15, depending on the condition of the river. La Rivers (1962) states it is about a month later than in Snyder's time as a result of river conditions: it extends from mid-May to early June. However, Trelease (1971) reports cui-ui may spawn as early as April and as late as July, when a surge of fresh water often triggers the spawning run. The cui-ui apparently homes fresh water, including springs. Scoppettone et al. (1981) also found a sudden heavy surge of very turbulent water often triggered spawning activities, even in the daytime. The cui-ui prefers depths of water for spawning that range from 9 to 43 cm, velocities that range from 23 to 87 cm/sec, and substrate with about 60% gravel.

Historically, cui-ui spawning runs up the Truckee River only occasionally reached downtown Reno, a distance of over 100 km (Snyder 1918). Today they generally run no farther upstream than 15 to 20 km, although they can go further. Koch and Contreras (1972) report spawn-laden cui-ui reach exhaustion in 18, 10, 2, and 0.5 hours at velocities of 1.2, 1.8, 4.6 and 5.2 m/s, respectively.

Spawning Behavior

Spawning cui-ui often choose the head of gravel bars, where the flow is rapid and the substrate relatively free of silt (McGarvey 1974). At times the dorsal fins of the cui-ui project above the water, and in very shallow places, where there is much crowding, the entire backs of the fish are exposed (La Rivers 1962). Trelease (1971) notes the numbers of cui-ui at the mouth of the Truckee River in past years were so immense at spawning time that fish near the surface were literally forced out of the water, and during periods of peak activity schools of fish covering 0.4 ha or more would form a mass of writhing fish on the surface of the water. Some runs of cui-ui were so extensive that, as fish worked their way upstream in dense schools, their numbers actually blocked the flow of water and diverted it around them. As a result, a new channel was sometimes cut through the sandy delta, leaving large numbers of fish stranded.

Migrating and spawning cui-ui are more active at night than in daytime (Snyder 1918). Scoppettone et al. (1983) found that peak spawning occurs between the hours 2000 and 0600 over a 3–day period and postulate that nocturnal spawning lessens egg predation. Adhesive eggs are broadcast over a large area (Koch 1973). One spawning act, lasting from 3 to 6 seconds, is participated in by 1, or occasionally 2, females and from 2 to 4 males; although a typical spawning act has 1 female and 2 males. Scoppettone et al. (1983) found the most active male spawned 294 times, the most active female 114 times. The length of the spawning run for individual males was 3 to 5 days, for females 2.5 to 4 days.

Just prior to spawning, two males position themselves on either side of a female, the heads of the males just aft of the female's head. With bodies touching and quivering, the female deposits eggs, followed by the males expelling sperm. The cupping and vibration of the male's caudal, along with the female's caudal, creates an eddy preventing the eggs from drifting away before they are fertilized (Scoppettone et al. 1983). Although the cui-ui does not build a nest, the fanning of the caudal fins serves to clear the area of silt.

Optimum Hatching Temperature

In an 8–day period when temperatures ranged from 13.8 to 20.8 C, with a mean of 16.7 C, mean viability of the embryos was 47% (Scoppettone et al. 1981). Koch (1981) found 13.9 C optimum for cui-ui egg incubation; embryos incubated at 17.8 C had a 60% survival to hatching, whereas embryos incubated at 21.7 C had a 30% survival. High temperatures cause preemergence of larva, and a lower rate of survival (Lockheed Ocean Sciences Laboratories 1982).

Larval Migration

Larval peak downstream migration is 14 or more days after hatching (Scoppettone et al. 1983). Hatchery-reared larval cui-ui, 15 to 18 days old, released in 3 areas of the Truckee River, began migrating downstream immediately. The peak migration occurred the night of release followed by several days' lull. All three groups showed a tendency for immediate outmigration (Scoppettone et al. 1981). It should be noted that our embryological studies show that larvae are not developed well enough to feed or swim actively before 21 to 18 days at 13.6 C. It may be that early migrations (< 28 days) greatly reduce chances of survival.

Lake Spawning

There are several reports of cui-ui spawning in the freshwater–lake saline interface. Snyder (1918) reports, "On May 1, 1913 large numbers of cui-ui were found depositing eggs along the shallows near some springs on the southwest shore." Johnson (1958) observed ready-to-spawn cui-ui around the periphery of the lake. Koch (1973) documented the spawning behavior of cui-ui near the inflow of freshwater springs (0.014 cms) in 17.3 C lake

TABLE 9. Number of cui-ui eggs taken at the Marble Bluff facility, 1978–1983 (Source: Alan Ruger, Pyramid Lake Fisheries director).

	Number of spawners		Number of eggs	Eggs per female
	Male	Female		
1978	188	226	4,838,660	21,410
1979	112	92	2,706,308	29,416
1980	333	320	12,140,480	37,939
1981	166	158	5,437,886	34,417
1982	422	436	17,707,268	40,613
1983	184	244	13,706,700	56,175
Totals and weighted average	1,405	1,476	56,537,197	38,304

water in the Hell's Kitchen area, which is approximately 29.5 km north of the Truckee River. Most biologists agree that cui-ui spawn in the lake (> 5000 mg/l TDS) as well as in the river (< 600 mg/l TDS), but the success of the lake spawning is not known. Observed lake spawning has been in the vicinity of fresh water, e.g., springs or stream-lake interfaces (Koch 1973). T. J. Trelease (personal communication 1984) lists seven places around the lake where he observed cui-ui spawning over the years. Experiments by LOSL (1982) and Chatto (1979) indicate that eggs must be water hardened in fresh water (< 600 mg/l TDS), or they will either not hatch or the larvae will not survive in lake water. The issue then revolves around the question, Is there enough fresh water in these lake microhabitats for cui-ui eggs to produce healthy larvae? This is a difficult question. According to Chatto (1979), from 2 to 3 days are required if hatching is to be successful. LOSL (1982) declare freshly fertilized eggs are intolerant of 5,897 mg/l of TDS, but within a day the embryos have acquired considerable resistance.

Fecundity

Koch (1972) found cui-ui become sexually mature in their fifth or sixth year and produce 20,000 to 30,000 eggs per year. Frazier and Ferjancic (1977) estimated the average-sized female produced 35,700 eggs. Mean number of eggs per female taken at the Marble Bluff facility from 1978 to 1983 was 36,662 (Table 9). This is a nearly linear increase in the number of eggs/female. This may be due to increased efficiency in egg-taking caused by such factors as riper females, better water conditions, better fish-holding facilities, increased use of hormone injections, and/or increased experience of workers (A. Ruger personal communication 1983). The 1983 value of over 55,000 eggs/female may be more indicative of the actual mean fecundity of the species than lower estimates. The 1983 run was quite different from previous years in timing and size of females. Possibly more large females increased the average number of eggs taken. It is understood that, in the wild, a female would have to spawn several times to reach this number, and realistically this may not happen.

MORBIDITY AND MORTALITY

Large, long-lived cypriniform fishes (such as cui-ui) with relatively small eggs and high fecundity usually experience extremely high mortality rates in their early life stages. At present recruitment is derived from both artificially and naturally reared cui-ui. The hatching success is moderate in the PLF operation, e.g., 75.2% in 1983 (A. Ruger personal communication 1984).

Cui-ui mortality can be divided into five stages: spawning adults, eggs (embryos), larvae, juveniles, and maturing adults. Each stage has differing levels of vulnerability and causes of death. Spawning adults are adversely affected by low flows, high temperatures, and predation. Egg mortality is affected by condition of spawners, high temperatures, and silt. Larvae survival is determined by a complex of factors during their early life in the river, including temperature, flow, food availability, parasites, disease, and predation. In the lake the mortality of juvenile cui-ui is determined by food availability, salinity change, competition, and predation. Nonspawning adults are subject only to mortality factors in the lake environment. Predation there is minimal; therefore, if food supplies are adequate, then parasites, disease, and senility are probably the most significant adverse factors.

Egg and Larvae Mortality

If the Truckee River spawning habitat were optimal, one would expect high hatching success from the river-spawning cui-ui. However, using the fecundity of 35,700 eggs per female estimated by Frazier and Ferjancic (1977), Scoppettone et al. (1981) projected that if 21 females deposited 750,000 eggs only 20,000 larvae would be produced. Their estimated survival rate to emergence is 2.7%, this was attributed to high temperatures, poor egg viability, and predation by Lahontan redsides, *Richardsonius egregius*.

Adult Mortality

The highest adult mortality probably occurs during the spawning season, when cui-ui are most vulnerable to predation. Historically fishing mortality may or may not have been significant; it continued at low levels, as a snag fishery of spawners on and near the Truckee River Delta, until recent years. Since 1979 all fishing for cui-ui, even by tribal members, is prohibited. Death of adults as a result of spawning, as well as handling mortality during and following egg taking at the Marble Bluff and the PLF facilities occurs at unknown levels. Snyder (1918) reports a few dead individuals along the Truckee River after each spawning season, and high mortality regularly occurred at the mouth of Winnemucca Lake. Fish-eating birds, primarily white pelicans, *Pelecanus erythrorhynchos*, double-crested cormorants, *Phalacrocorax auritus*, and California gulls, *Larus californicus*, can wound or kill adult cui-ui. Although large numbers of white pelicans and cormorants were observed on the Truckee River Delta during the 1976 and 1977 cui-ui spawning migration, Knopf and Kennedy (1980) found no evidence that these birds fed on cui-ui. Common carp, *Cyprinus carpio*, and tui chub, *Gila bicolor*, composed over 97% of the diet of the pelican. T. J. Trelease (personal communication 1984) states he has observed pelicans catch and swallow adult cui-ui. The pelicans then had great difficulty taking off with so heavy a load. He also states he has seen several, but not a great many, cui-ui remains on Anahoe Island. He believes the major damage done by birds is pecking out eyes and gills. Pelicans preyed on adult cui-ui during the large run of 1982 (M. LaFever personal communication 1983). This phenomenon was also observed by D. L. Galat in recent years (personal communication 1984). Snyder (1918) reports that when cui-ui migrate in dense schools considerable numbers are crowded into shallow water and even stranded out of water on sand bars:

> Cormorants, gulls, and pelicans in great numbers were attacking them, and many still wriggling fishes had lost their eyes and strips of flesh had been torn from their sides.

Disease

Pathological studies of the wild cui-ui populations have not been conducted; therefore, the effect of internal and external parasites, fungal infestation, and viral and bacterial disease is unknown.

Effects of TDS on Eggs, Larvae, and Juveniles

Bioassay tests conducted by LOSL (1982) demonstrate the intolerance of fertilized and/or water-hardened cui-ui eggs to TDS concentrations above 525 mg/l. Embryos placed in 525 mg/l water (i.e., Truckee River water) for 24–96 hours survived when transferred to Pyramid Lake water (5897 mg/l), although some abnormalities were found. Embryos placed in 5897 mg/l water immediately after fertilization in 525 mg/l water, were atypical within 24 hours. An average 90% mortality occurred in the 5897 mg/l TDS concentration by the third day, and an average of only 8.3% of the embryos in this concentration produced apparently normal fry.

One-day-old cui-ui larvae placed in test concentrations of either 5781 or 3503 mg/l showed differential mortality; 20% and 13.3% of the test fish died in the respective concentrations within 72 hours. Three day old cui-ui larvae placed in test concentrations of 350 and 5781 mg/l had 100% survival in the first 96 hours. After 192 hours there was no mortality in the 350 mg/l level, but the 5781 mg/l level had 7% mortality and an additional 8% abnormalities.

Chronic 180–day tests indicate that reduced survival of juvenile cui-ui, across a broad range of TDS levels extending from 3620 to

5225 mg/l, represents only 33% to 48% of the 96–hour median tolerance limit (LC50). This indicates that, although LC50 tests may show acute toxicity resulting in death only at high TDS levels, lower TDS levels may cause death or abnormalities when fish are exposed for extended periods of time (LOSL 1982).

HABITAT AND ECOLOGY

Physical

At an elevation of 1154.9 m above mean sea level, Pyramid Lake is approximately 40.8 km long and from 5.8 to 17.3 km wide, with a north-south axis (Fig. 1). At this elevation it has a surface area of 437 km^2, a volume of 25.3 km^3, a mean depth of 57.9 m, and a maximum depth of 100.6 m (Harris 1970). The only significant inflow into the lake most years is the Truckee River, which originates 193 km upstream at Lake Tahoe in the Sierra Nevada. During 1976 and 1977 mean surface temperatures ranged from 6.1 to 23.1 C; the lake is monomictic, thermally stratifying in summer and mixing physically during winter. The most characteristic feature of Pyramid Lake is its high TDS—about 5,350 mg/l during 1976–1977. Although sodium chloride is the dominant salt in the TDS (over 70%), the lake is high in bicarbonate alkalinity that is probably important to the ecosystem. Since the baseload of TDS is relatively constant, the TDS of the lake varies with its volume (Benson 1978b).

Temperature

The maximum surface (0 to 1 m) water temperature in Pyramid Lake was 21.4 and 23.1 C in July 1976 and August 1977, respectively (Lider 1978). The lake is thermally stratified from June through December; wind-generated mixing occurs from January through May. A metalimnion forms at depths ranging from 16 to 22 m. The euphotic depth averaged 11 m for 1976 and 1977, which resulted in a trophogenic zone of about 4.67 km^3 (Galat et al. 1981). Dissolved oxygen (DO) at the surface is always near saturation, about 8 mg/l. Metalimnetic and hypolimnetic DO depletion occurs beginning in July, following stratification and algal decomposition. Maximum DO deficits occur in the profundal zone just prior to fall mixing (Sigler et al. 1983).

Plankton

Diatoms *Cyclotella* sp. and *Stephanodiscus* spp. dominate the phytoplankton community during winter; the most abundant chlorophyte, *Crucigenia* sp., attains its maximum abundance in spring. Blue-green algae are by far the dominate phytoplankton in Pyramid Lake (> 74%). *Nodularia spumigena* is the most abundant blue-green algae. Its bloom begins as early as July and last as late as October. Following spring increases of algal growth, orthophosphate and nitrate are depleted and remain at low levels throughout the summer. Silica, in addition to nitrate, probably limits diatom production in Pyramid Lake (Galat et al. 1981). Chironomids are the lake's most abundant macroinvertebrates, followed by oligochaetes, which are especially abundant in the profundal zone (Robertson 1978). Two euryhaline amphipods, *Gammarus lacustris* and *Hyallela azteca*, are associated with tufa and rocks. La Rivers (1962) reports the Mormon creeper, *Ambrysus mormon*, common among the rocks around the periphery of the lake.

The zooplankton community is composed of five cladocerans, three copepods, and four rotifers (Lider and Langdon 1978). The cladoceran, *Diaptomus sicilis*, is a perennial species and the most abundant zooplankton throughout the year.

Factors Affecting Fish Activity

The cui-ui is the least abundant of the four major fish species native to Pyramid Lake. The other three species in increasing order of abundance are Lahontan cutthroat trout, Tahoe sucker, and tui chub. Vigg (1981) estimates cui-ui compose 0.03% by numbers and 0.47% by weight of the fish population. The mean cui-ui catch/gill net set slightly declined from 1976 to 1977 (1.29 to 0.95). This is not a statistically significant decrease ($P = .21$). During 1982 the largest spawning run in five years ascended the Marble Bluff fishway—13,807 cui-ui (Scoppettone personal communication 1983). Although it is not known what proportion this spawning migration represents of the total adult population, now that the fishway is operational at a near constant efficiency, the magnitude of future spawning

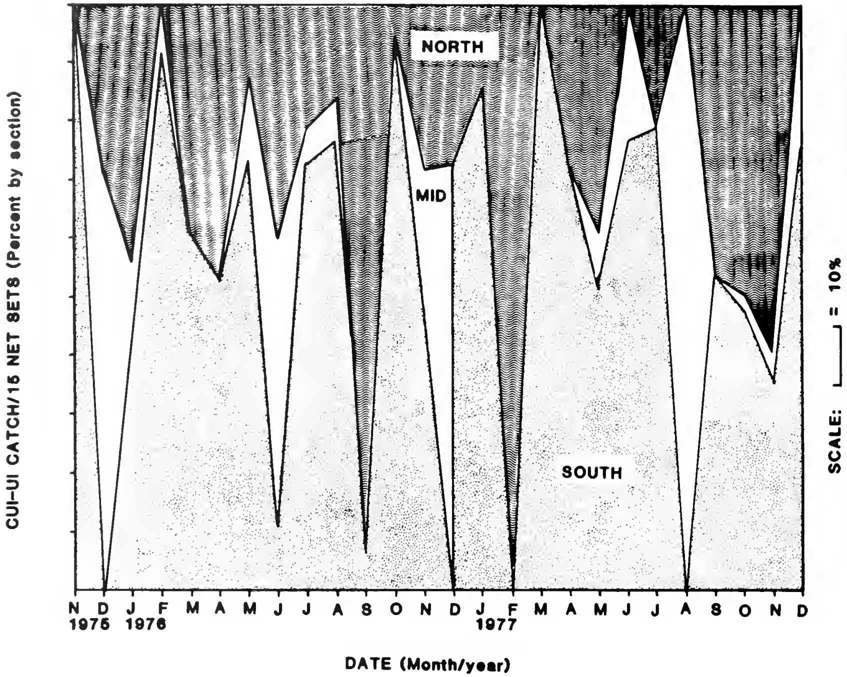

Fig. 8. Proportion of the catch from 15 bottom-set gill nets per month taken in the north (wavy lines), middle (clear), and south (dotted) sections of Pyramid Lake, Nevada, from November 1975 through December 1977.

migrations during years of similar flow regimes will give an indication of cui-ui population trends.

During 1976 and 1977 elevated net catch rates of cui-ui occurred during the spring. There was a concentration in the southern third of the lake during February to May 1976 and March to July 1977 (Fig. 8). Periods of increased proportional catches in the southern section corresponded to a decrease in the relative contribution of the middle third of the lake, with relatively little effect on the catch in the north end. The percent of total was 30, 10, and 60 for the north, middle, and south sections, respectively. The Truckee River delta produced the highest catch rates: 26/net (38.1 m) in May 1976 and 8/net in June 1977. These maxima correspond to the historical spawning period (April to June) and undoubtedly reflect spawning-related activity.

It is a complex of environmental parameters, not just a single variable, that triggers year-round cui-ui activity patterns in Pyramid Lake. We would also expect a multivariate factor to trigger cui-ui spawning runs. Tahoe suckers exhibit a very similar response to the environmental complex in terms of temporal activity (Fig. 9); about 30% of the monthly cui-ui catches can be explained statistically by comparable Tahoe sucker catches ($N = 26$, $P < .01$). This relationship is even more convincing when the spatial effect is included; i.e., 373 individual net samples of the two species in benthic habitats throughout the lake were significantly correlated ($r = .404$, $p < .001$). Thus these two native catostomids are associated in terms of seasonality and habitat.

Environmental variables that can be hypothesized to affect the activity of cui-ui in-

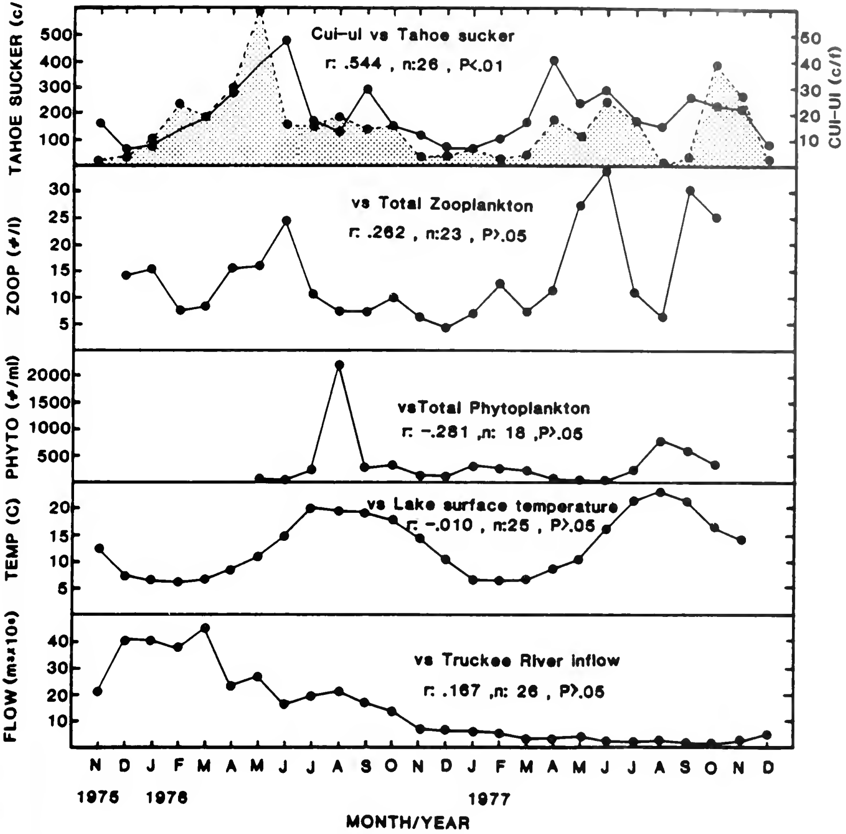

Fig. 9. Comparison of monthly cui-ui catches (shaded) with Tahoe sucker catches, total zooplankton density, lake surface temperature, and monthly Truckee River inflow from November 1975 through December 1977.

clude zooplankton, phytoplankton, lake temperature, and river inflow (Fig. 9). The general pattern of total zooplankton abundance was quite similar to cui-ui activity—unimodal in the spring of 1976 and bimodal in the spring and fall of 1977. The maxima did not correspond exactly, however, and the overall correlation ($r = .262$) was not statistically significant ($P > .05$). Peak phytoplankton concentrations, primarily *Nodularia spumigena*, occurred in June 1976 and August 1977; during these months low numbers of both zooplankton and cui-ui occurred in the samples. The overall correlation between cui-ui and phytoplankton is negative ($r = -.281$) but again not significant. Limited data suggest that cui-ui feed on benthic zooplankton, and *Nodularia* blooms may depress zooplankton populations; therefore these two trophic-related variables may have a cause-effect relationship with cui-ui activity.

It is reasonable to hypothesize that Truckee River inflows affect river spawning-related cui-ui behavior and thus their lakeside activity. The relationship between these variables, however, is very weak ($r = .167$, $P > .05$). The flow regime of 1976 was relatively normal compared to the constant and extremely low flows of 1977. This situation provides an illuminating comparison: in 1976 peak cui-ui ac-

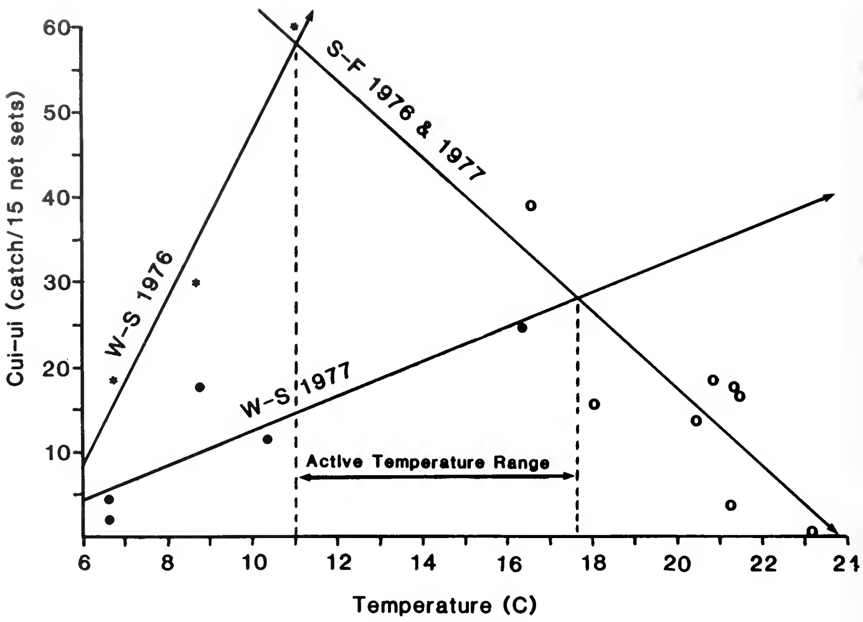

Fig. 10. Direct linear relationships ($P<.05$) between cui-ui catches and surface lake temperature during the winter-spring (W-S) periods of 1976 (asterisks) and 1977 (solid circles) compared to the inverse linear relationships ($p<.05$) during the summer-fall (S-F) periods of 1976 and 1977 combined (open circles).

tivity in the lake occurred in May as flows began to subside after four months of high flows. In 1977 cui-ui activity again peaked in the spring in spite of the fact that river flows had been negligible for over seven months. This limited observation may illustrate that cui-ui have an innate response to spring environmental conditions that is not totally dependent on high river flows. It is notable, however, that the magnitude of the 1977 cui-ui activity peak was much less than 1976 and had a different pattern (bimodal).

Water temperature is another variable that is generally associated with the activity of spring-spawning fishes. There was no linear correlation, however, with lakewide cui-ui activity and the surface temperature of the lake ($r = -.010$, $P > .05$). The explanation for this apparent anomaly is that the relationship is quadratic, not linear. During spring, as water temperature increases from winter minima, cui-ui activity increases in a direct relationship. As temperature continues to increase during the summer past a threshold value, cui-ui catches decline. This relationship is illustrated by Fig. 10; the temperature threshold was 11.0 C in 1976 and 17.6 in 1977. Thus the temperature range of maximum cui-ui activity during the winter-spring period of increase and summer-fall maximum temperature decrease regime was 11.0 to 17.6 during 1976–1977. Photoperiod may also have an (unmeasured) effect on the prespawning migration of cui-ui.

Cui-ui catches varied significantly by season and depth for both 1976 and 1977 ($P < .001$). Maximum densities of cui-ui occurred in the inshore benthic zone from 0 to 15 m in depth, i.e., 2.0 fish/net (Table 10). Catch/effort progressively decreased in benthic areas at depths of 23 and 46 m. No cui-ui was captured at depths 46 m, nor at the surface inshore, nor in the deep water column offshore. These distribution patterns are similar to the Tahoe

TABLE 10. Distribution of 421 adult cui-ui captured in six depth-stratified habitats of Pyramid Lake with experimental gill nets from November 1975 through December 1977 (Vigg 1980).

	Depth (m)	Number of samples	Cui-ui	
			Number	Catch/effort
Inshore benthic:	0–15	199	400	2.01
	23	35	10	0.29
Offshore benthic:	46	152	11	0.07
	46–100	72	0	0
Surface inshore:	0–2	35	0	0
Water column offshore:	0–46	18	0	0

sucker, but according to net catches the cui-ui is apparently more inshore oriented (Vigg 1978a, 1978b, 1980). This does not overlook the fact that in the past large schools of surface-feeding cui-ui were observed over deep water and away from shore.

IMPORTANCE TO NATIVE AMERICANS

Native Americans inhabited the Lake Lahontan ecosystem from at least 11,250 ± 250 radiocarbon years BP, as indicated from artifacts in the Winnemucca Lake basin (Hattori 1982). When the Indians arrived, Lake Lahontan occupied much of western Nevada (Russell 1885, Benson 1978a). Follett (1982) identified remains of four fish species at the Falcon Hill archaeological site, northwest of Winnemucca Lake: cui-ui, Tahoe sucker, Lahontan cutthroat trout, and tui chub; the earliest materials associated with fish remains were radiocarbon dated at 9540 ± 120 radiocarbon years BP. D. R. Tuohy, curator of archaeology, Nevada State Museum, conducted extensive studies of human habitation in the Pyramid Lake basin; his data indicate that between 9500 and 500 BP at least 3 different prehistoric human cultures inhabited the region. The latest culture, the Northern Paiute, live in the vicinity of Pyramid Lake.

The cui-ui at one time constituted the principal food of the Northern Paiute around Pyramid and Winnemucca lakes (Powers 1877). The fact that the Pyramid Lake Paiutes were called kuyuidikadi or kuyuitakuda (eaters of cui-ui) indicates the importance of this fish to the tribe's culture and sustenance. Snyder (1918) reports Pyramid Lake Indians preferred cui-ui to trout. Bath (1978) reports cui-ui were preferred because, unlike trout, they could be dried in the sun and thus preserved for later use. Information collected by Stephen Powers (cited by Fowler and Bath 1981) indicate Tahoe suckers were also eaten regularly, but they were not as favored as cui-ui or trout. For example, a collection from Thea Heye Cave near the southern end of Pyramid Lake contained the desiccated remains of nine or more cui-ui but only one Tahoe sucker (Follett 1977). Pyramid Lake Indians made elaborate adaptations to various components of their wetlands, but they concentrated on the capture of Lahontan cutthroat trout and cui-ui (Harner 1974). The Pyramid Lake Paiutes resisted all attempts by the federal government to turn them into irrigation agriculturalists and instead actively pursued subsistence fishing (Knack 1982).

Elaborate techniques were utilized by Indians to capture fish (Fowler and Bath 1981). Fishing was a year-round subsistence activity at Pyramid Lake and could be separated into river and lake fishing (Bath 1978). River fishing could be further subdivided into (1) exploitation of spawning runs (high water) and (2) low-water fishing. Lake fishing was an individual enterprise practiced during the summer and early fall and accomplished with set lines (for trout), gill nets, harpoons, and spears (Fowler and Bath 1981). However, baited hooks were probably not used for cui-ui. Large treble hooks were utilized at one time to snag cui-ui congregated at the delta.

Cui-ui were caught in large quantities and played an important role in the historic economy of the Pyramid Lake Tribe as a trade item. Follett (1980) reports cui-ui remains at the Karlo Site, about 24 km north of Honey Lake, California. Archaeological sites in Nevada where cui-ui remains have been found include: Humboldt Cave and Humboldt Sink (Hubbs and Miller 1948, Heizer and Krieger

1956), Fishbone Cave and Winnemucca Lake (Orr 1956), Lovelock Cave and Humboldt Sink (Follett 1967, 1970), the Nicolarsen Site at Winnemucca Lake (Follett 1974), Thea Heye Cave at Marble Bluff, Pyramid Lake (Follett 1977), and Falcon Hill (Follett 1982). The Pyramid Lake Tribe was the most widely known band of Northern Paiute. The Paiute name was familiar to Indians from Burns, Oregon, to Owens Lake, California, a distance of more than 805 km (Stewart 1939).

T. J. Trelease (personal communication 1984), who talked to many of the older Paiutes and other local people (some whose observations date back to 1906), believes the cui-ui and trout were taken by Indians in large numbers only during spawning runs. These harvests were so plentiful that they lasted for many months. The tui chub, however, was captured year-round, except during the more severe winter weather, and was a staple in the diet. It was taken from the lake in sagebrush bark nets and by hook and line. Some of the informants Trelease mentioned were Phil Orr, Margaret (Peggy) Wheat and L. W. Morgan.

Spawning runs of cui-ui during high water were fished using platforms with lifting nets, with or without weirs (Fowler and Bath 1981). Sturdy winter platforms were built by several men who shared trout fishing privileges. Spring and summer platforms operated by individuals were less substantial. During summer and early fall, as well as winter, when flow was low and the water clear, harpoons and spears were used (Fowler and Bath 1981). Trelease (personal communication 1984), quoting L. W. Morgan, describes an Indian family fishing expedition sometime between 1906 and 1910 as follows: the father, using a gaff-hook fastened to a long pole, stood in waist-deep water and snagged cui-ui, which were tossed up on the bank. Mother and children built drying racks, cleaned the fish, and put them out to dry. Sometimes platforms were used in conjunction with weirs that directed fish over an area of river bottom paved with white rocks to improve visibility; the lighter bottom also facilitated night fishing.

The fishing technology used by the Walker Lake Northern Paiutes, and at least to some degree by the Carson Lake and Humboldt Basin groups was similar to that of the Pyramid Lake Indians (Speth 1969). Fowler and Bath (1981) conclude native Americans in the western Great Basin have been involved in fishing complexes of various orders and varying degrees for several millenia.

Knack (1982) reports that efficient methods utilized by the Pyramid Lake Paiutes to capture cui-ui and Lahontan cutthroat trout during their spawning runs were unacceptable to the Nevada legislature, which "imposed a definition of appropriate sporting technique, which was derived from the Anglo-European cultural past." Knack (1982) summarized the fishing laws the state of Nevada passed affecting the Indians:

> For over one hundred years, the state of Nevada attempted to impose its laws on the Northern Paiutes of Pyramid Lake. It declared which fish could be caught and where, as well as the techniques to be used. At first, the state tried simply to assume jurisdiction over Indians living on reservations, and then it employed a series of circumventions. Indians were cut off from sales markets and arrested as soon as they left federal trust land. Indian agents were encouraged to enforce state law on the reservation itself. The opportunity to commercialize the one productive resource of the reservation was denied Paiutes by the imposition of state law; economic development was thereby blunted, prosperity stopped, and the local economy allowed to stagnate. Meanwhile, Anglo economic developments, dependent on water diversions to agriculture, mining, and urban areas, produced drastic changes in the fishery population. The state defined fish as a luxury suitable only for sport, and subsequent Anglo actions assured that this would be so.

Trelease (personal communication 1984) strongly disagrees with Knack. He believes the state had only the welfare of the resource in mind, and the federal government, whose responsibility it was, did nothing.

Townley (1980) documents the historical devastation of the Truckee River, the Pyramid Lake trout and cui-ui fishery, and the attitudes of the various sides of the controversy. Snyder (1918) enunciated the attitude of those who believed that the fishery, so important to the livelihood of the Pyramid Lake Indians, could not stand in the way of white man's progress:

> A discussion of the economic value of the fishes of this region and any consideration of methods of propagation and protection must begin and end with the assumption that agricultural and manufacturing interests are of paramount importance. A considerable and constantly increasing amount of the flowing water must be used first for power and then for irrigation, and when any measure intended for the protection of fishes is found to seriously interfere with the working of power plants or the demands of agriculture it will have to be abandoned.

Fortunately for fishery resources in general and the cui-ui in particular, society is evolving a philosophy more compatible with the maintenance of renewable natural resources. Through federal laws, especially the Endangered Species Act, the cui-ui is deemed to be important to society as a whole.

MANAGEMENT

The primary management objective for the cui-ui is the restoration of a stable, naturally reproducing population, thereby allowing its removal from the endangered and threatened species list. This can best be done by increasing numbers substantially and by improving habitat. Ongoing programs designed to reduce man-induced threats to the cui-ui population in Pyramid Lake include: (1) maintenance of water temperatures ≤ 13.9 C during spawning, made possible by maintaining adequate flows and shading of the river; (2) renovation of the lower Truckee River so that it has a stable meandering channel and riparian habitat of trees and shrubs; (3) artificial propagation; (4) use of the Marble Bluff Dam and Fishway for monitoring the spawning population, collecting eggs, and providing spawner access to the Truckee River; (5) maintenance of the fishway at Numana Dam to provide spawning access further upriver; (6) continuation of life history studies.

The lower Truckee River temperatures fluctuate with flow, time of day, season, and year. The optimum temperature for cui-ui spawning and egg hatching is 13.9 C. The lower river has a scouring, braided, exposed channel; the need is for a meandering, stable channel and banks that stand firm, with trees and shrubs for shading (Gregory 1982). The impoundment above Marble Bluff Dam has a population of predatory fish including sunfishes and one or more species of catfish. This poses a problem for larval cui-ui that migrate downstream primarily at night. Removal or depletion of predators is a possible answer. In very low water years these larvae may also become disoriented in the impoundment.

The tribe's Pyramid Lake Fisheries organization is rearing millions of cui-ui fry annually, some stocked in Pyramid Lake and in the Truckee River. In 1982, a high water year, more than 11,000 adult cui-ui went up the fishway to spawning sites in the river (13,807 reached the trapping facility). Life history studies have and are exploring stages in the life of the fish and their current and optimum habitat. Artificial propagation should be continued until the number of adult cui-ui in Pyramid Lake is at or near their optimum, if not historic, numbers. Barring disaster, the natural runs should then be able to maintain adequate numbers.

The base load of TDS is essentially static in Pyramid Lake (Benson 1978b). This means the concentration varies inversely with the volume of the lake. The concentration of TDS in Pyramid Lake should not be allowed to increase appreciably; current levels are at or above optimum for cui-ui. The lake levels should not fluctuate beyond a range of plus or minus 3 m except in high water years. Nutrient loading should not be increased from municipal, industrial or agricultural sources.

SUMMARY

The cui-ui, once so abundant that it was a staple in the diet of the Pyramid Lake Paiute Indians and an item of trade, is today endangered. It is a slow-growing, long-lived fish, reaching a length of > 70 cm. Cui-ui eggs must be water-hardened in relatively fresh water. It may or may not be able to spawn successfully in the Truckee River-Pyramid Lake interface, in temporary streams of high water years, or in springs in Pyramid Lake. Biologists are not in firm agreement on these points. Upriver spawning migrations are often, but apparently not always, triggered by surges of fresh water. Spawning starts from mid-April to May and extends through June or, rarely, July.

Modification of the Marble Bluff Fishway provides upstream passage for cui-ui, especially during low water years. Eggs are taken from part of the spawning population; others are allowed to move upstream. Spawning success depends largely on acceptable temperatures and flows. Mortality, primarily from predation, is presumably high on both embryos and larvae in the stream. Once in the lake, young cui-ui undoubtedly face heavy predation. In addition to natural reproduction, millions of larvae are released each year from the David L. Koch Fish Hatchery, Sutcliffe, Nevada.

Cui-ui feed on zooplankton, benthic invertebrates, and algae. They inhabit shallow to medium depth water (< 46 m) in the lake, where they are most active in spring and fall. Adults move into fresh water only to spawn; young cui-ui generally remain in the river for a few weeks after they are hatched.

CONCLUSIONS

The cui-ui is endangered today because of a progressive population decline resulting from transbasin water diversion, failure on the part of the federal government to originally protect the Indians' resources, upstream water use, and early adverse legal and political decisions. Percent of total river flow diversions that began in 1905 reached a climax in the early 1930s, when the combination of low river flows and dropping lake levels caused a delta to form at the mouth of the river. The cui-ui could no longer migrate upstream to spawn; thereafter numbers of adults dropped sharply. To date the population has not stabilized or recovered. Artificial propagation and restoration of river spawning are providing an interim solution. The long-term answer is acceptable spawning habitat: an adequate flow of ≤ 13.9 C water from early to mid-April through June, a stabilized, nonbraided river bed with spawning gravels, and reestablishment of shaded raparian habitat.

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HELMINTH PARASITES OF THE WHITE-TAILED JACKRABBIT, *LEPUS TOWNSENDI*, FROM NORTHWESTERN COLORADO AND SOUTHERN WYOMING

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ABSTRACT.—Helminth parasites of white-tailed jackrabbits, *Lepus townsendi*, were surveyed from southern Wyoming and northwestern Colorado. A total of eight helminth species were identified, including two species of adult cestodes, *Mosgovoyia pectinata* and *M. varabilis*; three species of larval cestodes, *Multiceps serialis*, *Taenia pisiformis*, and *Taenis sp.*; and three species of nematodes, *Dermatoxys veliger*, *Passalurus ambiguus*, and a filariid, *Micipsella brevicauda*. In addition, eggs of an unidentified species of *Nematodirus* were found in pooled fecal samples. The cysticercus larva of *Taenia sp.* is a species new to science and will be reported elsewhere. *Mosgovoyia varabilis* and *Micipsella brevicauda* are new records for the white-tailed jackrabbit.

The helminth parasites of the white-tailed jackrabbit are not well known throughout most of its range. Only in North Dakota has any attempt at a survey been made (Voth and James 1965). Additional reports such as those of Honess and Winter (1956) and Thomas and Honess (1962) indicate that helminths occur occasionally in this host but give no information on number of hosts examined or percent of infection.

MATERIALS AND METHODS

The hosts for this study were collected from three locations, i.e., near Meeker, Colorado; 20 miles north of Baggs, Wyoming; and 30 miles north of Medicine Bow, Wyoming. All were collected using firearms. Standard parasitological techniques were used for the recovery of helminths. Selected examples of all adult helminths were deposited in the United States National Museum Helminthological Collection (USNM#).

RESULTS

A total of eight helminth species were found infecting white-tailed jackrabbits examined in this study. They consisted of five species of cestodes and three species of nematodes. A comparison of hosts from the three study areas is shown in Table 1. For the sake of clarity each species will be considered separately.

Mosgovoyia pectinata (Goeze, 1782).—This is the only cestode found in jackrabbits from all areas of collection. It has been reported previously from Albany County, Wyoming (Honess 1982), and from southwestern North Dakata as *Cittotaenia* by Voth and James (1965). It is found in the small intestine of the definitive host (USNM# 77145).

Mosgovoyia varabilis (Stiles, 1895) Beverridge, 1978.—This species was found in only one host from northwestern Colorado. It has been reported previously from the cottontail rabbit, *Sylvilagus nuttalli*, examined from southern Wyoming (Honess and Winter 1956) as *Cittotaenia varabilis*. This cestode, like *M. pectinata*, is a double-pored species that occurs in the small intestine. It may be distinguished from the former by the arrangement of the testes, which are enclosed between the ovaries instead of extending to the longitudinal excretory canals (USNM# 77144).

Multiceps serialis Gervalis, 1847.—One host collected north of Baggs, Wyoming, contained a 5-cm coenurus of this species. It was located in the posterior abdominal cavity in association with the psoas muscle. This species has been reported previously in the cottontail rabbit from Carbon County, Wyoming (Honess 1982), and in white-tailed jackrabbits in North Dakota (Voth and James 1965).

Taenia pisiformis Bloch, 1780.—Cysticerci of this cestode were found encysted in the intestinal mesenteries of two hosts collected

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TABLE 1. A comparison of the helminths of white-tailed jackrabbits from three study areas. Percentages indicate percent infected in that locality.

Species	30 miles north Medicine Bow, Wyoming (n = 10)	20 miles north Baggs, Wyoming (n = 11)	Meeker, Colorado. (n = 8)
Mosgovoyia pectinata	4 (40%)	1 (9%)	1 (12%)
M. varabilia	—	—	1 (12%)
Multiceps serialis	—	1 (9%)	—
Taenia pisiformis	—	2 (18%)	—
Taenia sp.	—	1 (9%)	—
Passalurus ambiguus	—	—	1 (12%)
Dermatoxys veligera	6 (60%)	2 (18%)	—
Micipsella brevicauda	—	5 (45%)	—

north of Baggs, Wyoming. This larval cestode, commonly found encysted in the viscera of cottontail rabbits from the same area (Shults, unpublished data) is a parasite of coyotes, *Canis latrans*, and bobcats, *Lynx rufus*. It has been reported from white-tailed jackrabbits in North Dakota (Voth and James 1965) and cottontail rabbits from Carbon and Fremont counties, Wyoming (Honess and Winter 1956).

Taenia sp.—One host from the Baggs, Wyoming, site was found to be infected with visceral cysts of an undescribed species of this genus. Similar cysts have been found in cottontail rabbits. Descriptions of this new species will be published elsewhere.

Passalurus ambiguus (Rudolphi, 1819) Dujardin, 1845.—This species was found in the caecum of one host collected in northwestern Colorado. Thomas and Honess (1962) indicated that this species has been found in cottontail rabbits in Wyoming (USNM# 77146).

Dermatoxys veligera (Rudolphi, 1819) Schneider, 1866.—These caecal nematodes were found in hosts collected from Wyoming sites. They have also been reported from the white-tailed jackrabbit in Albany County, Wyoming, by Honess and Winter (1956) (USNM# 77147).

Micipsella brevicauda Lyons & Hansen, 1961.—Only hosts collected from near Baggs, Wyoming, were infected with this filariid nematode. The adults were found free in the abdominal cavity, and microfilaria were recovered from the circulating blood. Morphological comparisons with other species of this genus indicate that our specimens most closely resemble those of *M. brevicauda* described from black-tailed jackrabbits, *Lepus californicus*, in Kansas by Lyons and Hansen (1961). Voth and James (1965) found microfilaria in blood smears from white-tailed jackrabbits collected in North Dakota but did not assign them to any genus, although they suggested that they might be *M. brevicauda* (USNM# 77148).

In addition to the above species, pooled fecal samples from each of the study areas revealed ova of *Nematodirus sp.* No adults of this genus were found. It is possible that the specimens were *N. neomexicanus*, which has been reported from black-tailed jackrabbits in Colorado and cottontails in Wyoming (Thomas and Honess 1962).

DISCUSSION

Helminth parasites found in the present study differ somewhat from those found in a similar study by Voth and James (1965). They found only the microfilaria of a filariid nematode present in their survey, whereas two cecal nematode species and the filariid *Micipsella brevicauda* were found in our study. In addition, ova of *Nematodirus sp.* was found by fecal flotation.

In our study only the adult cestodes *Mosgovoyia pectinata* and *M. varabilis* were found. This is in contrast to data from both Voth and James (1965) and Honess (1982), who found *Raillietina sp.* in the white-tailed jackrabbit. Honess (1982) stated that this species occurs more often in hosts from an arid or semiarid area, and *Mosgovoyia* is most commonly found in hosts living along streams or in foothills and forests. This was not the case in the present study; *Raillietina sp.* was not found in any area, arid or otherwise.

Mosgovoyia variabilis has not previously been reported from white-tailed jackrabbits, although Honess (1982) stated that this cestode is "probably a parasite of all wild rabbits and hares" in Wyoming.

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THERMAL ECOLOGY AND ACTIVITY PATTERNS OF THE SHORT-HORNED LIZARD (*PHRYNOSOMA DOUGLASSI*) AND THE SAGEBRUSH LIZARD (*SCELOPORUS GRACIOSUS*) IN SOUTHEASTERN IDAHO

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Abstract—A mark-recapture study of the short-horned lizard (*Phrynosoma douglassi*) and the sagebrush lizard (*Sceloporus graciosus*) was performed from 1976 to 1977 in southeastern Idaho. Both species had mean cloacal temperatures of approximately 33 C. However, *P. douglassi* had more variable cloacal temperatures, particularly during morning and evening periods. This was caused by differences in sleeping sites chosen by the two species. Adults of both species were active from mid-April through late August, with peak activity in June. Juvenile *P. douglassi* displayed a seasonal activity pattern similar to that of adults. Juvenile *S. graciosus* were most active later in the year (August), when adults were disappearing. In both species, young-of-the-year appeared in early to mid-August. Adult and juvenile *P. douglassi* were active during all daylight hours and displayed no activity peaks, whereas young-of-the-year displayed a bimodal activity pattern. Adult and juvenile *S. graciosus* were active over all daylight hours but had peak activity between 1200 and 1500 h. Ants (*Pogonomyrmex*) were the lizard's principle prey. However, only young-of-the-year *P. douglassi* had activity patterns that paralleled that of ants on their mounds.

This study was conducted to determine aspects of thermal ecology and seasonal, daily, and reproductive activity patterns for the short-horned lizard (*Phrynosoma douglassi*) and the sagebrush lizard (*Sceloporus graciosus*) near the northern edge of their distributions. Thermal activity is a commonly studied aspect of lizard ecology (Brattstrom 1965, Heath 1965, Pianka and Parker 1975, Prieto and Whitford 1971 for *P. douglassi*, and Brattstrom 1965, Burkholder and Tanner 1974, Mueller 1969 for *S. graciosus*), whereas activity patterns are much less commonly reported (Pianka and Parker 1975, for *P. douglassi* and Burkholder and Tanner 1974, and Stebbins 1944 for *S. graciosus*). Our results are compared to studies of *P. douglassi* from Utah (Pianka and Parker 1975) and *S. graciosus* from Utah (Burkholder and Tanner 1974, Woodbury and Woodbury 1945, Tinkle 1973), Wyoming (Mueller and Moore 1969), and California (Goldberg 1975, Stebbins 1944).

Methods

The study was conducted on the Idaho National Engineering Laboratory (INEL) site in southeastern Idaho during June to October 1976 and April to October 1977. This area is ca 1500 m in elevation, is characterized vegetatively as a sagebrush-desert community (McBride et al., 1978), and is composed geologically of Recent lava flows covered by wind and waterborne deposits. The climate is characterized by short, hot summers (average maximum and minimum temperatures 30.5 and 10.0 C, respectively) and long, cold winter (average maximum and minimum −2.7 and −16.1 C, respectively). The average yearly precipitation is 21.6 cm, mostly in the form of spring rains.

Much of the data were collected on a 1-ha grid system with stakes placed 10 m apart. This grid system and the surrounding area were dominated vegetatively by big sagebrush (*Artemisia tridentata*), rabbitbrush (*Chrysothamnus nauseosus*), halogeton (*Halogeton glomeratus*), and squirreltail grass (*Sitanion hystrix*). Lizards were captured by hand or noose and were marked permanently by toe-clip and for field identification by color marks on their legs. Individuals were sexed and measured snout-to-vent (nearest mm), from which age and sex groups were determined. Five age and sex groups were recognized: young-of-the-year (YOY, 23–30 mm SVL), juvenile males (30–50 mm SVL), juvenile females (30–60 mm SVL), adult males (>50 mm SVL), and adult females (>60 mm SVL). Cloacal temperatures were measured

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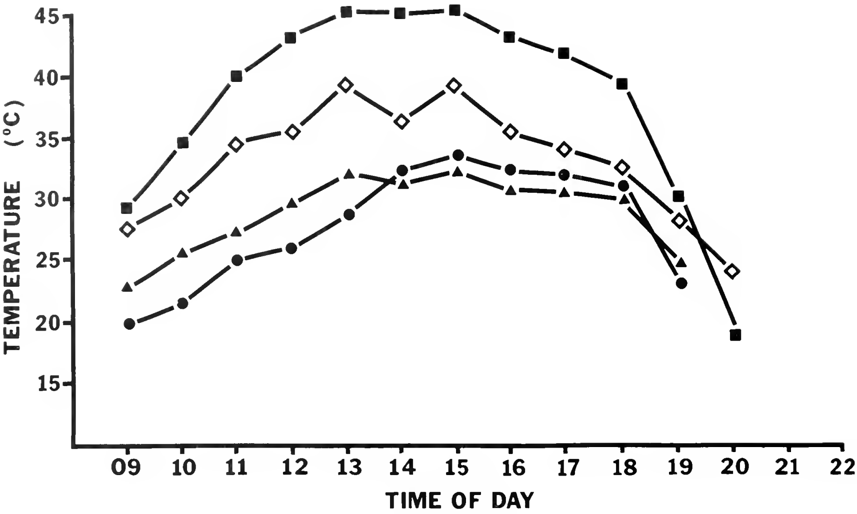

Fig. 1. The relationship between mean environmental temperatures on cloudless days and time of year. Solid squares are soil temperatures in sun, open diamonds are air temperatures in sun, solid triangles are air temperatures in shade, and open circles are soil temperatures in shade.

to the nearest 0.2 C with a Schulteis quick-reading thermometer, except for YOY, which could not accept the bulb without injury. Handling time for individuals was generally less than 5 minutes, and temperatures were taken within the first minute of capture. Time and location where the animals were first sighted were recorded as were the following environmental temperatures: air temperature in sun (ATS), soil temperature in sun (STS), air temperature in shade (ATSh), and soil temperature in shade (STSh). All soil temperatures were taken with the bulb barely covered with loose soil, and all air temperatures were taken with the bulb 1 cm from the soil surface. Each day's observations averaged 5 h and starting times were rotated so that observations occurred during all daylight hours.

Ants (principally *Pogonomyrmex*) were the most abundant insects on the grid. Since ants are important prey of both lizards (Knowlton and Baldwin 1953, Knowlton et al. 1946, Burkholder and Tanner 1974), ant activity was monitored in 1977 to determine if lizard activity paralleled ant activity. All *Pogonomyrmex* mounds on the grid were mapped. During each grid sampling, each mound was visited. To index ant activity, we recorded active mounds (>20 active ants) and inactive mounds (<20 active ants.)

All data used to analyze activity patterns were from lizards seen on the grid. Temperature data were collected from lizards on the grid as well as lizards marked in surrounding areas (Guyer 1978).

RESULTS

Environmental temperatures increased parabolically from 0800 to 1500 h followed by a parabolic decline from 1500 to 2100 h (Fig. 1). The hottest microenvironment during all hours except 2000 to 2100 h was STS, and STSh was the coolest microenvironment until late afternoon (1400–1900 h), when ATSh was coolest. The peak for STSh was shifted to the right relative to curves of the other three microenvironments indicating a lag period involved with heating and cooling the soil.

Mean cloacal temperatures (± 1 SD) were 33.4 ± 4.4 C for *P. douglassi* (N = 84) and 33.9 ± 2.4 C for *S. graciosus* (N = 61). Since

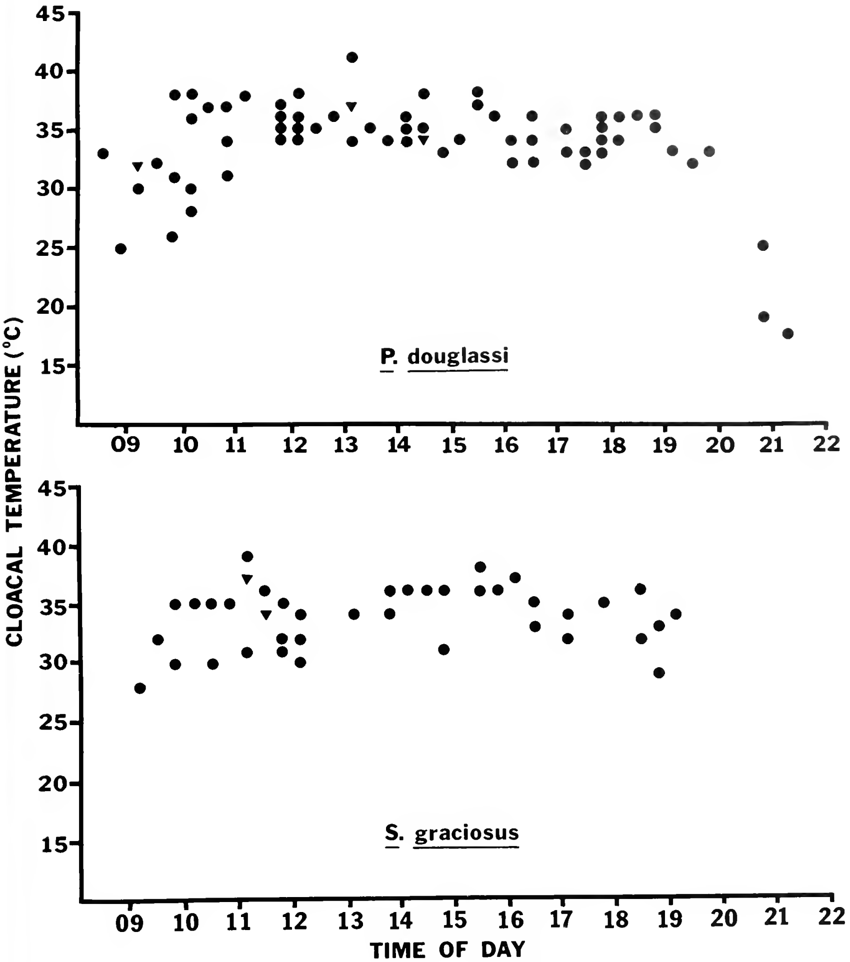

Fig. 2. The relationship of cloacal temperatures of *Phrynosoma douglassi* and *Sceloporus graciosus* and time of day. Circles are single observations, and triangles are double observations.

animals captured on overcast days were much cooler than those captured on sunny days, only lizards caught on cloudless days were used to test for trends among age and sex groups. No differences were found in the distribution of cloacal temperatures among age and sex groups for either species (Kruskal-Wallis test; $p < 0.05$ for both species), so data were pooled within each species.

Cloacal temperatures of *P. douglassi* during daylight hours could be separated into three thermoregulatory periods (Fig. 2): a morning period (0800–1100 h), a midday period (1100–1800 h), and an evening period (1800—2200 h). The morning period was characterized by rising temperatures at each successive hour and wide variability. The midday period was characterized by relatively stable temperatures and reduced variability, and the evening period was characterized by falling and widely variable temperatures. During midday *P. douglassi* were found more frequently in shade than in direct sun (68 of 158 in direct sun), whereas during morning (58 of 70 in sun) and evening (23 of 36 in sun) periods lizards were found more often in direct sun. There was a significant association between thermoregulatory period and location of *P. douglassi* (Chi-square test of association; $p < 0.05$). However, there was no difference in location of individuals between morning and evening periods (Chi-square test; $p > 0.05$). One thermoregulatory period was found in *S. graciosus*, corresponding to the midday period of *P. douglassi* (Fig. 2). No major shifts in cloacal temperature occurred during daylight hours. Because *S. graciosus* escaped at distances prohibiting the determination of original microhabitat, locations with respect to sun or shade could not be analyzed.

Adult *P. douglassi* were first sighted 12 April 1977, and juveniles were first sighted 23 April 1977. Fieldwork was begun too late in the season to determine time of emergence in 1976. Seasonal patterns of activity were similar between years so these data were pooled. Adults and juveniles had similar seasonal activity patterns, with greatest activity occurring from June to July and declining activity from July to September (Fig. 3). Adults were last seen 29 August 1976 and 3 September 1977, and juveniles were last seen 18 September 1976 and 11 September 1977.

One copulation of *P. douglassi* was observed 10 May 1977. Young-of-the-year of this species were first seen 5 August 1976 and 10 August 1977. This group was encountered increasingly more often until their sudden disappearance in mid- to late September (Fig. 3). Individuals from this age class were last sighted 25 September 1976 and 12 September 1977.

The earliest emergence of *S. graciosus* adults was 16 April 1977, whereas juveniles were first seen 31 May 1977. Again, seasonal patterns of abundance did not differ, so data for the two years were pooled. Monthly activity of adults and juveniles differed in that adult activity peaked during May and declined from June through September, whereas juveniles peaked in August and declined through September (Fig. 3). Adults were last seen 29 August 1976 and 28 August 1977, whereas juveniles were last seen 29 August 1976 and 17 September 1977.

We estimated time of mating for *S. graciosus* using the intensity of orange, the nuptial coloration in females that indicates ovulation (Burkholder and Tanner 1974). In 1977 orange color was most intense 3–8 June 1977 with some color persisting through 21 June 1977, implying an early June mating season. Young-of-the-year were first seen 28 August 1976 and 14 August 1977. This group was active throughout August and September (Fig. 3) and was last seen 25 September 1976 and 1 October 1977.

Daily activity patterns of adult and juvenile *P. douglassi* were uniform throughout all daylight hours (Fig. 4). This pattern did not shift during the study period so data for all months and both years were pooled. Daily activity of young of the year followed a bimodal pattern with decreased activity during the hottest part of the day (Fig. 4). Because insufficient captures were made of *S. graciosus* juveniles and YOY, their daily activity patterns were not analyzed. Adults showed uniform daily activity patterns, with peak activity occurring from 1100 to 1500 h (Fig. 4). The daily activity of *Pogonomyrmex* on their mounds was bimodal (Fig. 4), with activity depressed during the hottest part of the day. This pattern was similar for all months sampled, so data were pooled.

DISCUSSION

Mean cloacal temperatures of both species agree with those reported from other populations (Brattstrom 1965, Pianka and Parker 1975 for *P. douglassi*, and Brattstrom 1965, Burkholder and Tanner 1974 for *S. graciosus*). *Sceloporus graciosus* had similar cloacal temperatures throughout the daylight hours. However, *P. douglassi* temperatures differed during the day, with reduced temperatures during early and late hours of the day. This difference appears to be related to daily activity patterns and sleeping sites utilized. *Phrynosoma douglassi* were never observed using rodent burrows or burrowing under loose soil. Several individuals were followed

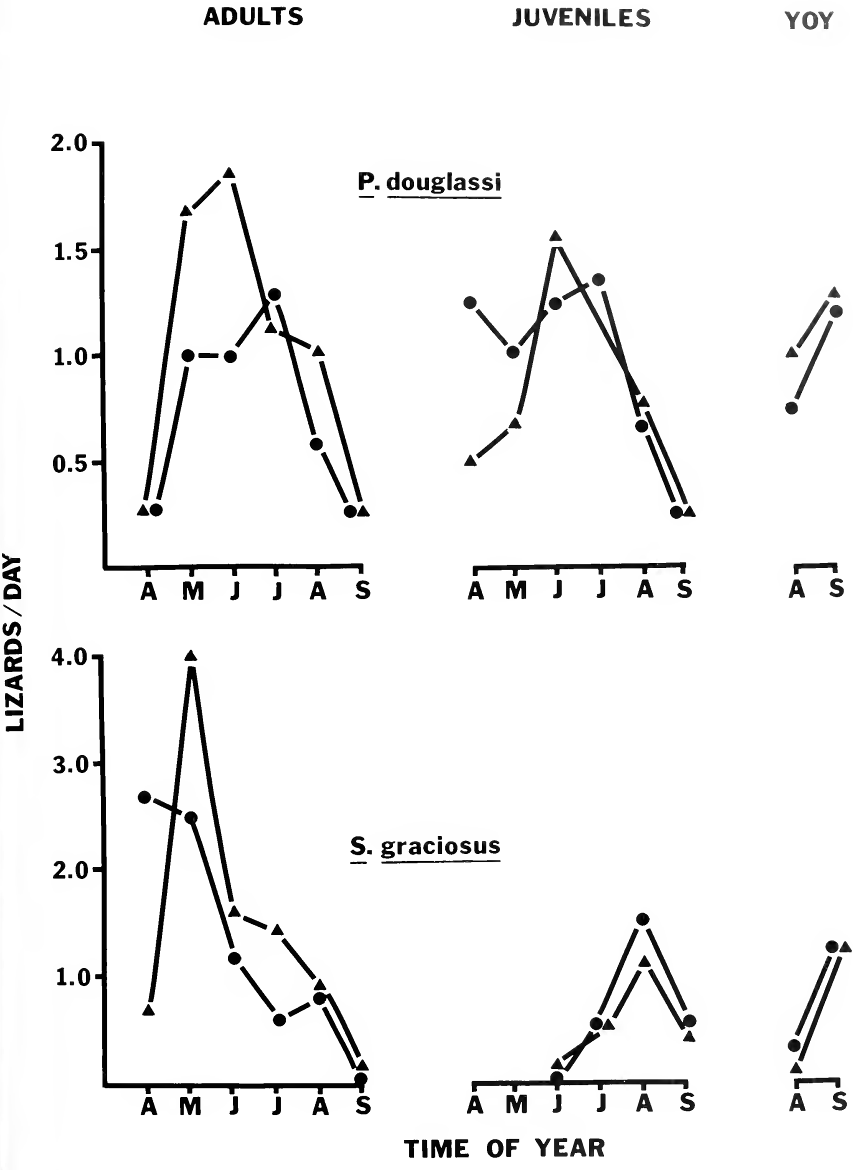

Fig. 3. The relationship between mean number of lizards seen per sample period and time of year. Circles are males, and triangles are females.

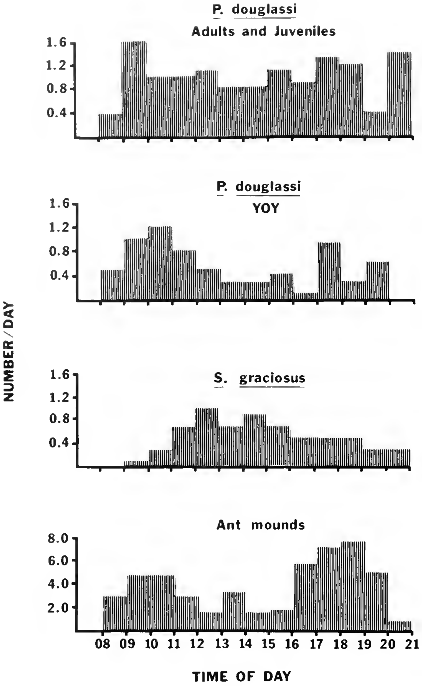

Fig. 4. Mean number of lizards and active ant mounds seen per sample period and time of day.

until they became inactive during evening hours and were relocated early the next morning before becoming active. All were observed to spend the night above ground. On several occasions sluggish individuals were captured during cool, early-morning hours. In contrast, *S. graciosus* were often observed using rodent burrows for escape and were found at burrow entrances during early-morning hours. These sites were apparently used overnight. Sluggish individuals were never observed. The fact that cloacal temperatures of *S. graciosus* were uniform throughout all daylight hours over which lizards were observed indicates that this species does not emerge until body temperatures reach levels at which activity takes place and that this level is maintained throughout the hours over which activity occurs. The morning and evening periods of low cloacal temperatures seen in *P. douglassi* apparently result from the location of these animals above ground during all hours of the day. *Phrynosoma douglassi* expedite their morning rise in cloacal temperature by locating in the warmest and fastest heating microhabitat (STS), a conclusion supported by Heath (1965). Maintenance of a relatively constant cloacal temperature throughout midday hours, when environmental temperatures continue to fluctuate, is probably accomplished by shuttling between sun and shade and may indicate the level preferred for daily activity. Cloacal temperatures were maintained until STS dropped below this preferred level. Cloacal temperatures then decreased at a rate similar to STS. This cooling during evening hours may be delayed by relocating in sunny areas.

Pianka and Parker (1975) found variability of cloacal temperature in *Phrynosoma* to be greater than that of any other North American iguanid. They attribute this to relaxed thermoregulation. In this study both species had approximately equal mean cloacal temperatures, but the variation about the mean was approximately two times greater in *P. douglassi* than in *S. graciosus*. However, the increased variability of *P. douglassi* was due to lizards captured during morning and evening periods, when few *S. graciosus* were observed. If *S. graciosus* could have been captured at these times, it is likely that similar variability would have been seen. During midday hours both species maintained relatively constant and similar cloacal temperatures. Thus, during comparable periods of activity *P. douglassi* probably does not exhibit wider thermal variability than *S. graciosus*.

Seasonal activity of juveniles differed between the two species. Activity of *P. douglassi* juveniles was similar to that of adults, whereas activity of juvenile *S. graciosus* was inversely related to that of adults. The reduced activity of juvenile *S. graciosus* early in summer was due primarily to the low numbers of juveniles encountered, but this was confounded by poor capture success of smaller lizards. These results differ from those of Burkholder and

Tanner (1974), who found activity patterns to be similar for *S. graciosus* adults and juveniles in Utah. These authors did show that the level of activity maintained by juveniles was below that of adults until August, when adults began hibernating. Whitford and Creusere (1977) showed an inverse relationship between adult and juvenile activity for *P. cornutum* and *S. magister* in New Mexico.

Seasonal activity patterns for adults of both species were similar, with emergence occurring in mid-April and hibernation beginning in late August to early September. Peak activity of adults occurred approximately one month earlier in *S. graciosus* (May) than in *P. douglassi* (June). The duration of adult seasonal activity was shorter than that reported for southern populations of the same two species (Goldberg 1971, 1975, Burkholder and Tanner 1974) due to later emergence and earlier hibernation. The active season reported for *S. graciosus* adults in this study is similar to that reported for northern populations (Stebbins 1944, Mueller and Moore 1969). A similar pattern of adult seasonal activity has been found for *P. douglassi* in Alberta, Canada (G. Larry Powell, personal communication).

Mating occurred at different times of the year in the two species. This is probably due to the difference in reproductive method of the two species. *Phrynosoma douglassi* is ovoviviparous and gestation is approximately three months (Goldberg 1971), whereas *S. graciosus* is oviparous and gestation is approximately two weeks (Goldberg 1975). The time of mating predicted or observed in this study compares favorably with that found by Goldberg (1971) for *P. douglassi* and by Burkholder and Tanner (1974) for *S. graciosus*.

Young-of-the-year appeared at approximately the same time of year (early August) in both species. The time of hatching is similar to that reported by Goldberg (1971) and Pianka and Parker (1975) for *P. douglassi* and by Woodbury and Woodbury (1945), Mueller and Moore (1969), Tinkle (1973), Burkholder and Tanner (1974), and Goldberg (1975) for *S. graciosus*. Because these studies were done in a variety of geographic locations, there seems to be little geographic variation in timing of the first clutch in either species.

Bimodal activity patterns, particularly in the hot months of July and August, have been reported commonly for southern populations of *Phrynosoma* (Parker 1971, Tanner and Krogh 1973, 1974, Baharav 1975) and *S. graciosus* (Burkholder and Tanner 1974). This pattern was observed only in *P. douglassi* YOY during this study. Bimodality seen in southern populations appears to provide an escape from high midday temperatures. In this study at least one microhabitat was available at all times that was lower than and one that was higher than or at least equal to the cloacal temperature maintained by the two species. This may explain the absence of bimodality seen in this study. Because of this absence of midday decline in activity, northern populations may have a longer daily activity pattern than southern populations. The bimodal pattern of *P. douglassi* YOY may be a result of more rapid heating and cooling of small ectotherms (Brattstrom 1965). Because the duration of seasonal activity is much longer in southern than in northern populations, it has been suggested that southern populations are exposed to predation for longer periods of time. This is thought to be an important factor causing the short life span of southern populations (Tinkle 1973). However, because southern populations may have reduced daily activity compared to northern populations, the effects of seasonal and daily activity may cancel each other between northern and southern populations. Thus, speculation about the relative role of predation in northern versus southern lizard populations must account for not only the effect of differences in seasonal activity patterns (Nussbaum and Diller 1976) but the effect of daily activity patterns as well.

Ant activity on the grid was bimodal. However, activity patterns of both lizard species were not directly related to that of ants. This differs from the observations of Baharav (1975), who found that *P. solare* in Arizona tracked ant activity. The fact that *P. douglassi* activity did not track that of ants may be related to the broader diet of this species compared to *P. solare* (Pianka and Parker 1975), or it may indicate that the relationship between *Phrynosoma* activity and ant activity in Arizona is not a causal one. Instead both lizards and ants may require escape from high midday temperatures in Arizona, whereas lizards in Idaho require no such escape.

Acknowledgments

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SNAKES OF WESTERN CHIHUAHUA

Wilmer W. Tanner[1]

ABSTRACT.—This is a report on the snakes of western Chihuahua that were taken at intervals from 1956 to 1972. At no time did we attempt to collect east of Highway 45, rather expending our time in the foothills, valleys, and desert ranges east of the mountains and in the highlands of the Sierra Madre Occidental.

Reference is made to reports on the geological and ecological aspects of the area as a whole, but without a major attempt to duplicate previous studies. A brief gazetteer and a map are included as guides. To provide orientation to the area traversed by the John Cross expeditions, a map of the lower Rio Urique and Rio San Miguel is also included.

From the area studied, 28 genera and 51 species are listed, with three new subspecies described: two worm snakes (*Leptotyphlops humilis chihuahuaensis* and *Leptotyphlops dulcis supraocularus*) and a garter snake (*Thamnophis rufipunctatus unilabialis*). For a number of species it became necessary to expand the study into populations from adjoining states in Mexico and the United States. Such species as *T. rufipunctatus* and *R. hesperia* are examples. Where data were available systematic relationships were implied, as well as ecological and biological data.

This study is an outgrowth of a series of herpetological investigations and a number of conversations with individuals who have spent many years in various parts of Mexico. I was constantly enthused with the idea of spending time in Mexico, and, upon my arrival at the University of Kansas in 1946, where I became associated with Dr. Edward H. Taylor, I was even more motivated by his constant references to the fabulous herpetological fauna of this neighboring country to the south. My association with the plethodontid salamanders, which through the courtesy of Dr. Taylor served as the subject of my dissertation, demonstrated there were new species and subspecies to be discovered. The thrill of discovering the new genus *Lineatriton* left little doubt in my mind that someday I must visit the area and become more involved in understanding the herpetological faunas of this fascinating republic.

I remember distinctly a conversation with Dr. Taylor during my visit to the University of Kansas in 1952, at which time I was trying to prepare for my first adventures into Mexico. After we discussed some of the problems that seemed pertinent to my understanding of the faunas extending from Mexico into the southwestern U.S., he advised me emphatically to not worry about getting into the central and southern parts of Mexico, but to start collecting as soon as I had crossed the Mexican border. He suggested that perhaps one of the areas most neglected was the state of Chihuahua.

Preliminary studies from the small collection that then existed at Brigham Young University (BYU) indicated there were a number of relationships, particularly as I understood them in the serpents, that must yet be understood not only from the standpoint of taxonomy, but also from the standpoint of geographical distribution. Also, a small collection made by Dr. D Eldon Beck in 1931 included a juvenile skink from the vicinity of Colonia Garcia. It was not possible to key this specimen to any of the materials described and discussed by Taylor (1936) and others, and it was eventually found to represent a new species (Tanner 1957). My visits with some of the students from the Mormon colonies in northern Chihuahua convinced me they were familiar with a fauna that was unique to that area, and certainly not one that was commonly understood by most of the herpetologists with whom I had visited. Thus, in May 1956, in company with Mr. Verl Allman and my oldest son, Lynn, we spent a month in northern Chihuahua, spending most of our time in the area of Nuevo Casas Grandes and Colonia Juarez, with one trip into the mountains of western Chihuahua at Three Rivers (Tres Rios) on the Río Bavispe.

Each year, from then until 1972, trips were

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made into Chihuahua at various times during the summer from May into October. My companion in 1957 and on through the next three years was Dr. Gerald W. Robison. Perhaps the three most noteworthy trips were made in 1957, 1958, and 1960, during which times much of the mountain area west of Colonia Juárez and west of Ciudad Chihuahua was visited. The trip in 1958 reached its climax at the mining town of Urique on the Río Urique in the Barranca del Cobre.

In 1960 an extended trip was made into the barranca country, where we visited the mining town of Maguarichic, and thus were in the vicinity of the area collected by Dr. Irving W. Knobloch (Taylor and Knobloch 1940). Other trips will be mentioned as it becomes important to do so, but it should be noted that the emphasis on our biological surveys was to cover as best we could in the time available to us the area west of Highway 45 that extends from Ciudad Juárez south to Parral. The only important area that we were not able to visit was the area southwest of Parral across the headwaters of the Río Conchos and into the headwaters of the Río San Miguel, and the tableland area near Guadalupe y Calvo. We were, however, fortunate in having received a collection from Mr. John Cross as he traversed the area southeast of Guachochic and then boated down the Río Verde and San Miguel rivers to their junction with the Río Urique. Mr. Cross also provided some specimens from the Urique River north of the town of Urique. Figure 8 indicates the extent of his travels.

The state of Chihuahua is 245,612 square km and is the largest state in the Mexican republic. Its territory is approximately 12.5% of the total area of Mexico. Within the state are many diverse ecological habitats ranging from deserts in the eastern and central areas to subtropical areas in the southwest barrancas. As should be expected, the vegetation is very diverse, from desert and dune floras in the eastern deserts to the pine-oak forests in the western mountains. Between these extremes are the multitude of ecological niches that change with the seasons from dry, rocky, scrub, brush foothills to fields of waving grasses and other flowering plants after the summer rains have renewed the area. For a more complete study and review of the Chihuahuan Desert see Morafka (1977).

Ecologists have established various life zones in northern Mexico that have included the state of Chihuahua. Perhaps the report compiled by Leopold (1950) and summarized by Knobloch and Correll (1962) gives a general overview useful to an understanding of the diverse biotic zones encountered in this state.

Knobloch and Correll (1962) summarized these zones as follows:

1. Boreal forest: rare, found only at 3000–3200 m (Cerro Mohinara).
2. Pine-oak forests: ranging from pure pine forests to mixed pine/oak and scrub oak.
3. Chaparral: mostly shrubs and small trees other than oak.
4. Mesquite-grassland: the short grass plains, mesquite shrubs and grasslands east of the Sierras.
5. Desert: cactus-euphorbia-yucca and creosote bush.
6. Tropical deciduous forests: short thorn forests of the western barrancas.

Chihuahua may best be considered a steppe desert, in which there is no certainty as to when or how much precipitation may occur in any given year or at any locality. At times during July and August, heavy rains occur, producing heavy runoff in local streams, but this is not always widespread nor constant. Thus, Chihuahua has much dry terrain and there are many small or intermittent streams during most of the year. During the rainy season streams may be in flood for a short time, requiring traffic in local areas to wait for the streams to recede. We encountered these conditions several times, but usually for only a few hours or, at most, a day.

The heavy runoff in the desert valleys and mountains rutted the roads, most of which were dirt, exposing rock and making travel off the main highways difficult and hazardous. Because of the rugged Sierra Madre Occidental, which extends through most of western Chihuahua,, few roads are available, and these often in poor condition. Roads in the mountains were passable, particularly where mining or lumber companies were operating; however, if these companies closed or moved, the roads soon deteriorated. Furthermore, most traffic was from the mountains eastward since the abrupt escarpment and the deep canyons on the west limited travel to means other than a car.

It was not until the 1960s that the railroad from Ciudad Chihuahua to Creel and on to Los Mochis, Sinaloa, was completed, providing for the first time a route across the mountains. Prior to this, travelers going westward from eastern Chihuahua had to first go north, usually into the U.S., and then into Sonora, or go south to Durango. Our trip to Urique took advantage of the newly built railroad grade (then used as a road) from Creel to Cuiteco, but we were three hours going seven miles from Cuiteco to Cerocouhui and from there to Urique, a nine-hour trip by mule.

GEOLOGY AND PHYSIOGRAPHY OF CHIHUAHUA

The state of Chihuahua has been part of an area of extensive mountain building that has occurred throughout much of western Mexico, extending northward through most of western Chihuahua. The Sierra Madre Occidental uplift reaches its highest elevation in the south central part of Chihuahua, where the Cerro Mohinara perhaps serves as the highest elevation, reaching to at least 3200 m (10,500 ft). There is a gradual reduction in elevation from south to north, with the mountains terminating in low passes of about 1500 m (5000 ft) near the border of Chihuahua and the states of Arizona and New Mexico. The uplift provided for a steep escarpment on the west side, resulting in heavy erosion cutting deeply into the mountains and developing the deep canyons and barrancas. To the east the escarpment is less severe, owing to the erosion that filled the adjoining valleys with sediments in the form of many large and extensive alluvial fans.

According to geological reports of scientists who have explored the Sierra Madre (Rothwell, Raymond, and Hobart 1901, Knobloch and Correll 1962, Goldman 1951, Hovey 1907, West Texas Geological Soc. 1964, and 1974), Chihuahua is underlain primarily with Cretaceous limestone that has been capped in many localities by rhyolite and basaltic flows in numerous areas along the major fault lines both to the east and west of the uplift. According to Forrest Shreve (1939), the state can logically be divided into five physiographical zones:

1. The bajados, gentle slopes in the eastern section of the country, including the lower portion of the Río Conchos and the large area to the east and northeast.

2. The enclosed basins, particularly of the northwest, which are referred to as Bolsons and have no outlets except into the stagnant lakes such as the Guzman and Santa María. These lake beds are filled with sandy silt and usually possess shallow water with a high salt content.

3. The elevated plains, the central portion of the state, extending, for the most part, through the central part of Chihuahua, and including the lower desert ranges and valleys immediately east of the Sierra Madre uplift.

4. The Sierra Madre region, the mountainous western part of the state. Through this area winds the Continental Divide, separating such streams as the Río Conchos and the Río Fuerte, whose headwaters immediately east of Guachochic are divided by a relatively narrow ridge. It is, however, in the western part of the Sierra Madre region that the deep barrancas have been formed—in contrast to the more gentle canyons and streambeds east of the Continental Divide.

5. From the standpoint of a herpetologist, a fifth region, which may be referred to as the barranca area, provides a distinct biological zone. The zone fingers into the mountainous areas from west to east and provides in the deep canyons (such as the Barranca del Cobre) a series of subtropical habitats not found in any other part of Chihuahua. The floor of these deep canyons are of reduced elevation, such as at Urique, to about 600 m (2000 ft), and thus the thorn forests of northern Sinaloa have extended far into these narrow canyons. It is estimated that the height of the barranca rim above and west of Urique is at least 1800 m (5800 ft).

The sediments, occurring in much of western Chihuahua, consist of limestones capped in many areas by a large outflow of tuft and other loose, volcanic materials. Such formations have been subject to rapid erosion, resulting in the deep canyons along the western escarpment of the Sierra Madre. Only below the headwaters of such streams as the Río Urique and the Río Conchos occur waterfalls and severe rapids where the streams have encountered more resistant sediments. It should be noted that during the rainy season the streams may become torrents and deepen rapidly these steep, deep canyons (Shreve 1944). Because of the rapid erosion through the various stratifications of the Sierra Madre uplift, deposits of minerals have been exposed, primarily silver and associated lead. However, copper is also exposed in various areas and has been responsible for the name "Barranca del Cobre." Because of the numerous ore deposits, areas in Chihuahua that would not otherwise be explored biologically may be reached by roads built to the mines.

The mountainous area varies in width from about 130 to 160 km (80 to 100 miles) in the south, that is, west of Parral and from 65 to 80 km (40 to 50 miles) west of Colonia Juárez. Within these areas there may be many comparatively flat park and meadow areas as well as gentle slopes with considerable timber. Most of the headwaters of such streams as the Bavispe, the Papagochic, the Conchos, and some of the tributaries of the Urique and Oteros drain these highland meadows and parks, and it is not until the streams reach near the west or east escarpments that the terrain is cut into deep canyons or barrancas.

Perhaps the most noted of the barrancas is that of the Barranca del Cobre, in which the Río Urique flows; it is not a swiftly flowing stream in its canyon toward the headwaters, but downstream it soon becomes a series of waterfalls and rapids, in some areas deeply undercutting the lateral canyon walls, in turn resulting in much shearing of the steep walls in the riverbed below—even to the point of permitting the river to flow among and under great masses of boulders. It was this type of terrain that made our river running trip in 1963 a failure (Fig. 9).

Considerable publicity about this trip occurred in Chihuahua and the southwestern United States. Actually, we descended the river for about 16 km (10 miles); during this time, several rapids and waterfalls were encountered. These did not stop us, but later, when the river partly or totally disappeared under large, granite boulders for great distances, it became impossible to continue. The next year John Cross and his associates did enter the Barranca del Cobre near the Divisidero, and they ran the Río Urique to the Río El Fuerte. They also entered the Río San Miguel south of Guachochic and ran it to the El Fuerte. During these river running trips, Mr. Cross made collections that included several genera and species not previously known to occur in Chihuahua. The Cross collections (three trips) are deposited in the BYU herpetological collection.

PREVIOUS HERPETOLOGICAL SURVEYS

Perhaps the first significant herpetological survey of Chihuahua was that of Edward A. Goldman (made under the direction of Dr. E. W. Nelson). Although his work was done from the fall of 1898 into October of 1899, his study was not published until July 1951.

Much of his report is concerned with the geography, geology, and flora of various localities, but herpetological specimens were obtained and deposited in the U.S. National Museum. It should also be noted that the Goldman-Nelson travels in Chihuahua did not cover much of the central part of the state but were confined to the northern area, Nuevo Casas Grandes and areas to the north and west, and the southern area from Parral westward across the mountains to Batopilas and the Barranca del Cobre.

During the 1930s and early 1940s, Dr. Irving W. Knobloch investigated the fauna and flora of the west central mountains of Chihuahua in the vicinity of Majorachic. This collection was reported by Taylor (1940) and by Taylor and Knobloch (1940). Several other biological surveys have also been made into Chihuahua; the one by Dr. James D. Anderson was confined largely to the Sierra del Nido area, and his material is primarily deposited at the University of California at Berkeley.

In 1942 Dr. Hobart M. Smith briefly reviewed Mexican and Central American *Thamnophis* and described as new the subspecies *T. ordinoides errans*. He also spent time studying the herpetological fauna along the Río Santa María and its environs.

Other field trips originating at the University of Kansas, the University of Illinois, and the University of Texas at El Paso have added to the specimens available for study. A collection from Yepómera was made by members of the University of Arizona, and a special study of *Thamnophis* and *Natrix* was conducted by Dr. Roger Conant. A trip by Kenneth L.

Williams, Edward O. Moll, Francois Vuilleumier, and John E. Williams (Smith et al. 1963) down the Conchos River in August 1962 was one of few that has attempted to collect in the desert areas east of the main highway. Reynolds and Scott (1982) reported on a series of 20 species taken along Highway 16 between Villa Aldama and El Pastor. This was a study of food and habitat selection in northeastern Chihuahua from 1975 to 1977. There undoubtedly have been other collections made, but those indicated above apparently represent the most important collections.

GAZETTEER

Some of the localities from which many of our specimens were collected are listed below with various comments concerning their location and general habitat (Fig. 1).

Colonia Juárez

This is a Mormon colony established before 1900 and serving since then as headquarters for the colonists. It is basically a farming community with a considerable emphasis in recent years on orchards, with apples and some pears and peaches the primary crops. It is located along the Río Piedras Verdes which flows directly eastward from the mountains west of the colony.

From its eastern border one looks toward the east at the old settlement listed on maps as San Diego. Rolling hills surround the town, with the escarpment of the Sierra Madre Occidental showing sharply to the southwest. To the north and northeast are rolling hills and a relatively broad, open canyon known as the Tinaja extending westward into the mountains. To the northeast of the mouth of the Tinaja are some rolling hills that have been productive in our collecting program. The environs of Colonia Juárez support a herpetological fauna in which not only the more desert species occur along the base of the escarpment, but also species more commonly found in the mountains descend into the mouth of the canyons and along the streams.

The climate in this part of Chihuahua is relatively dry from September through the winter months and into June. The summer rains usually begin in late June and continue intermittently through July, August, and early September. This part of Chihuahua is a steppe desert, receiving much of the moisture from the southeast as the tradewinds circle into the area from the Gulf of Mexico, but with some storms being initiated from the southwest. The winters are mild, but with some precipitation in the form of snow and an adequate period of cold to favor temperate zone vegetation.

Some of the summer precipitation is heavy, producing considerable runoff and, at times, closing roads and flooding the lowlands. When the first heavy rains come in July, the desert flats east of Colonia Juárez and N. Casas Grandes are alive with amphibians; in fact, in some areas they become so numerous that it is impossible to drive the roads without a continual popping sound as the inflated individuals are mashed on the road. In this area and throughout some of the valleys to the east, the dry season provides an opportunity for collecting mainly lizards, with only a small population of snakes extant. During the rainy season, there is a greater percentage and a greater variety of snakes to be found along the roads and under rocks and other debris throughout the area.

Ciudad Chihuahua

The basin in which Ciudad Chihuahua is located drains from the northwest toward the east. Our collecting was done primarily northwest of the city; this area was actually a lower, southern end of the Sierra del Nido. We were concerned with the foothill areas and did not move into the higher elevations of this range. The eastern sloping foothills and their alluvial fans provided a habitat in which the scrub brush and cacti were separated so as to provide no difficulty in walking through the terrain. Also, there were a number of rocky outcroppings and boulder-strewn flats providing an opportunity for collecting, particularly during the rainy season that brought the more secretive burrowing forms to the surface. Extending westward from Ciudad Chihuahua for many miles, almost to Cuauhtemoc, is a terrain similar to these foothills.

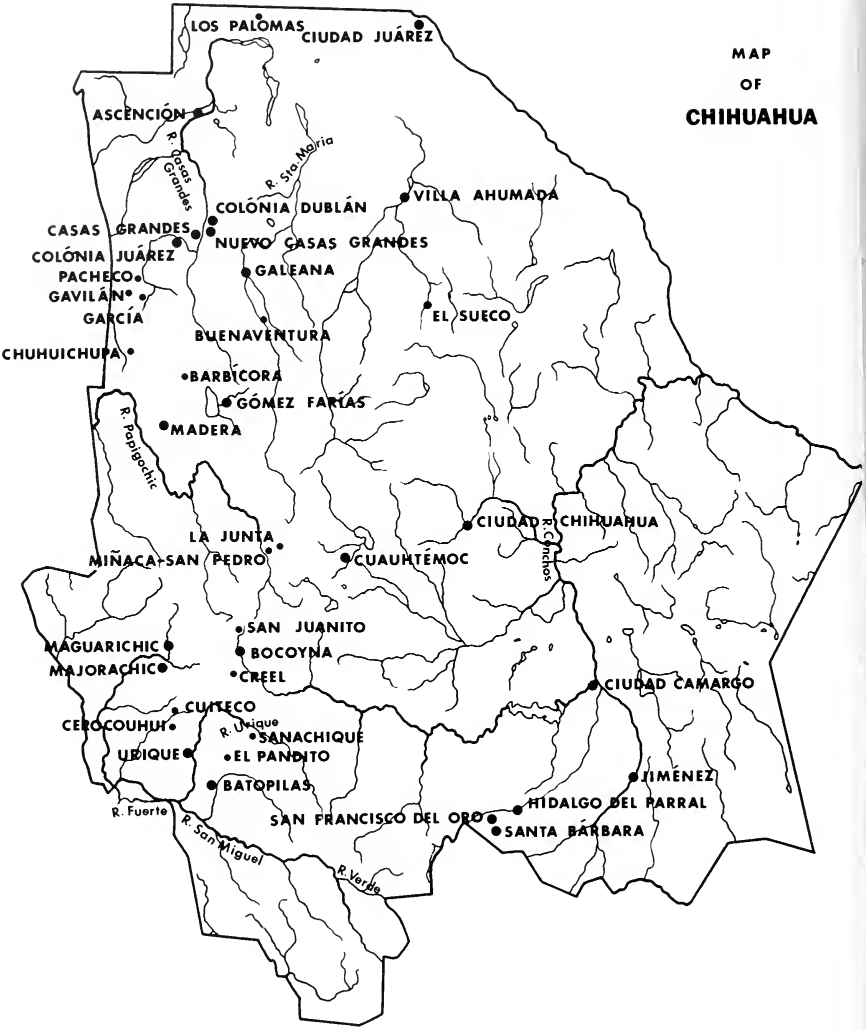

Fig. 1. Map of Chihuahua.

Maguarichic

Maguarichic is located on a bluff overlooking the deep canyon of the Río Oteros. It is a mining town and was at one time a thriving community. We were there for three days during the rainy season of 1958 and were successful in securing a number of specimens, some of species not previously reported by Taylor and Knobloch (1940) from Majorachic. We attempted to visit Majorachic, but the roads were so muddy that we were unable to ascend some of the hills leading into the town.

We did, however, remain in the general area a few miles southeast of it. The entire area here was covered with vegetation, a long leaf pine, oak, madrone, and other trees and shrubs. This area is on the high, mountainous plateau and drains southwestward into the smaller tributaries of the Río Oteros. The area between San Juanito and Maguarichic is the high, mountainous area lying mostly to the west of the Continental Divide that lies a few miles west of San Juanito; thus, there are in this generally mountainous area not only pines, but also Douglas-fir and Chihuahua spruce, particularly on the northern sloping ridges.

Cuiteco-Cerocouhi Area

We left Creel and traveled along the railroad grade which, in 1958, was serving as a highway while the Mexican government built the railroad on through the mountains to Los Mochis in northern Sinaloa. The grade had been finished to Cuiteco, and we were privileged to stay in some government-owned cabins while we organized for the short run to Cerocouhi. The latter was only seven miles from Cuiteco by road but required over two hours to traverse. At Cerocouhi we were housed in some government buildings that had been used as a headquarters during a mosquito abatement survey. It adjoined the Catholic church and a nunnery. We spent two days there while Dr. Knobloch arranged for a mule train to take us to Urique. The area in and around Cuiteco and Cerocouhi was on small tributaries of the Río Oteros, and during much of the time that we were there the streams were at flood stage. The area to the east of these towns was forested with oak, madrone, and scattered (particularly on the higher ridges) pine. Much of the area in and around Cerocouhi had been overgrazed, but in the small canyons to the east across the main stream were boulder-strewn alluvial fans mixed with some oak forests that provided suitable habitat for a number of amphibians and reptiles.

Urique

Urique is a mining town that has been largely abandoned as far as mining is concerned. We discovered here the same situation that occurred in other almost-abandoned mining towns where the inhabitants were left stranded after the mines closed; although Urique had been a very prosperous mining settlement, only a few people were working the mining area at the time we were there, and any ores mined were hauled out by burro packtrains.

The town is located on the Urique River at the bottom of the Barranca del Cobre. The vegetation there is subtropical. We stayed in a large building next to the dwelling of the "Presidente," and to the side of the building were mangos, wild figs, and other subtropical trees and shrubs. A short distance away from the river on the slopes were thorn forests with the leguminous cat claw predominating and serving as a real deterrent to one wishing to hurry through.

Although we were forced to select areas where we could collect without vegetational hindrances, we found a few areas of rocky outcroppings along the river. We were led by some of the Mexican children to the old stone wall around the cemetery, where we secured a number of iguanids and other rock-dwelling species. It may be of interest to note that in some of the old graves the deceased were not fully buried but placed in crypts and could now be seen through the cracks as skeletons. Many of these tombs had been elaborately constructed during the height of the mining boom of Urique.

Three Rivers Area

The Tres Rios area of western Chihuahua and eastern Sonora derives its name from the junction of three streams that form the Río Bavispe. These streams (Chuhuichupa Creek, Trout Creek, and Black Canyon Creek) flow northwest as does the Bavispe. We collected along the stream, in the small side canyons, and on the sides of the main canyon. Although the canyon has steep slopes, there are ledges and talus to provide for a variety of habitats. Oak was dominant on the lower slopes, with some long leaf pine on the higher ridges. Along the streams were sycamore, cottonwoods, and willows. This area was visited in May 1956 and in June 1958.

Chuhuichupa

This Indian name refers to the mist that forms in the valley on the cool mornings following afternoon or evening thunderstorms. The few American inhabitants used the term "valley of the mists" to explain the term. The valley lies in a high mountain basin, draining to the north and then west to join with other streams (Black Canyon and Trout Creek) at Three Rivers to form the Río Bavispe.

Above the town of Chuhuichupa is a series of large springs that are the major sources of Chuhuichupa Creek. To the west through a low pass is Black Canyon Creek, which flows northward in a parallel canyon to join Chuhuichupa Creek at Tres Rios. The headwaters of these streams are in open basins with gentle slopes and meadow pastures. The steeper slopes and ridges surrounding these basins are forested; thus, these areas provide a variety of habitats for a large number of species.

Creel

The city of Creel is located in a high basin just north of the Barranca del Cobre. During our work in this area, this was the terminus of the railroad that has since been extended across the mountains to Los Mochis, Sinaloa. The area around Creel is a series of rolling hills and basins with slow-flowing streams. As one moves south, the canyons deepen as streams join the deep canyon of the Río Urique. Besides being a railroad junction, Creel serves as a road junction for travel to the south and west. The La Bufa Road connected Creel to the headwaters of the Río Urique and to Batopilas and ore mines south of the west-flowing Río Urique.

The area of Creel and north to San Juanito is in the higher mountain valleys, with the Continental Divide lying between them. Thus, the roads into these valleys were difficult and, during the rainy season, often impassable.

La Bufa Road

This area about 25 miles southeast of Creel on a small, south-flowing stream with low, boulder-strewn hills was a very productive area. We were there in July during the rainy season. Low-growing trees (oak and madrona) and shrubs mixed with grass provided the general habitat. This area is on the plateau north of the Barranca del Cobre.

LIST OF GENERA AND SPECIES

The serpent fauna of the state of Chihuahua is rich, primarily because of the diverse habitats that occur in various areas of the state. Of the various faunas that have invaded the state of Chihuahua from practically all sides, we can now recognize from the Smith-Taylor checklist (1945) a total of 18 genera and 39 species and a total species-subspecies of 43. Their list has been modified by the deletion of some species, such as *Crotalus semicornutus*, and by altering the status of others, such as placing *Lampropeltis knoblochi* as a subspecies of *L. pyromelana*. A number of genera and species have been added so that there are now at least 28 genera and 51 species plus an additional 6 subspecies.

To understand the serpent fauna of Chihuahua, it became necessary to review specimens from those states (Mexican and United States) adjoining Chihuahua (Sonora, Sinaloa, and Durango and Texas, New Mexico, and Arizona). The strategic location of Chihuahua lends itself well to the reception of numerous species into diverse habitats within the state, which necessitated this review. Throughout Chihuahua there are only a few species and subspecies that may be considered endemic to the state. Several of these inhabit the mountainous area of western Chihuahua and represent subspecifically distinct linear extensions of species into the narrow mountainous corridor.

In an attempt to understand such species as *Thamnophis rufipunctatus*, which extends throughout Chihuahua and into the adjoining states to the north and south, I have taken the liberty to investigate again the basic characteristics of this wide-ranging species and to interpret, from the data available, the variations in the populations as I have encountered and understood them. It should, therefore, be understood that where deemed necessary consideration is given to the geographical overlap of adjacent populations of various species and subspecies.

Family Leptotyphlopidae

Two species of the genus *Leptotyphlops* have been found in Chihuahua. The first one treated below was reported by Cope (1879) from a collection made by Edward Wilkinson, Jr., at Batopilas, a small mining town located on a tributary of the Río San Miguel, itself a tributary of the Río El Fuerte (see Smith and Mittleman 1943, 1944, Cope 1896, 1900). Except for the summer rains, this area is dry and slopes to the southwest (Goldman 1951).

The second record was recently reported by Murphy (1975) from 5 km (3 mi) NW of Chilmahma, a suburb of Chihuahua City. We have collections from 9 to 11 km (6 to 7 mi) NW of Chihuahua City and from Colonia Juárez. The area northwest of Chihuahua City is an eastward-sloping alluvial plain, strewn with rocks and with rocky hills extending onto the plain from the higher hills to the west. Specimens were taken in late July and early September from under rocks while the soil was moist. Those taken at Colonia Juárez were collected by children in the school yard. Presumably all specimens were on the surface and all were collected during April and May, which is usually the dry season.

The species of *Leptotyphlops* apparently inhabit the foothills on the eastern edge of the Sierra Madre Occidental. The records now available suggest that a comparatively narrow area, extending from north (Colonia Juárez–Casas Grandes) to south (Chihuahua City–Cuauhtemoc) and undoubtedly on southward, supports worm snake populations. In these foothills, we have worked numerous sidehills and driven numerous hours night collecting, with only limited success. What is seemingly true for the eastern foothills is also apparently the case for the western foothills. In the west, however, the foothills are mostly in the states of Sonora and Sinaloa, so the only suitable habitat in western Chihuahua is on the edge of the low river valleys of the Río Fuerte and its tributaries.

Leptotyphlops humilis dugesii (Bocourt)

Catodon dugesii Bocourt, 1881, Bull. Soc. Philom. 7(6):81. Colima, Mexico.

Leptotyphlops humilis dugesii Klauber, 1940a. Trans. San Diego Soc. Nat. Hist. 9:129.

No specimen from Chihuahua is available. The listing of this subspecies is based on the report of Cope (1879), reiterated by Klauber (1940a), of a specimen from Batopilas in southwestern Chihuahua. Bogert and Oliver (1945) reported a specimen from Alamos, Sonora, and Hardy and McDiarmid (1969) listed several records for Sinaloa. It is thus suspected that if specimens are taken along the Río Fuerte and its tributaries they would be *L. h. dugesii* (Hahn, 1979a).

In 1966, we received three specimens (BYU 23913–15) of this subspecies from 15.9 km (9.4 mi) W of Autlán, Jalisco. The following scale characters are significant: 14 rows around body, 12 rows around tail, 212–236 in dorsal row, prefrontal a little longer than the frontal but not wider, 5th dorsal enlarged and wider than other dorsals. There are 7 rows of dorsals with heavy pigmentation.

In contrast to the data presented by Klauber (1940a), there are fewer dorsals, 212–236 (Klauber gives 235–257), and the enlarged prefrontal may be unique to the western *humilis* subspecies. These specimens extend the lower extreme in the dorsals and indicate that total variation in the cline for the dorsals in *humilis* may be as much as 100 scales, with the known range 212–309.

A specimen from west of Autlán (BYU 23914) was preserved with its mouth fully opened. There are only 3 infralabials on each side of the mental (Fig. 2A), and the 2nd and 3rd infralabials are pigmented nearly as heavily as the lateral and dorsal head scales. The other two specimens have the mouth closed but do show some pigmentation on the same scales. I have noted this pigmented characteristic in no other specimens of *humilis*.

The color pattern in the Jalisco specimens shows 9 rows of dorsals with dark brown pigmentation, 7 rows completely pigmented, and the 2 adjoining lateral rows with half the scales pigmented.

Leptotyphlops humilis chihuahuaensis, n. subsp.

Holotype.—BYU 17000, adult male from 10.7 km (6.7 mi) NW of Ciudad Chihuahua (west of Highway 45), collected by W. W. Tanner and W. G. Robison, 21 July 1960.

Paratypes.—BYU 15211 and 16999, topotypes; MVZ 57331, 5 km (3 mi) NW of

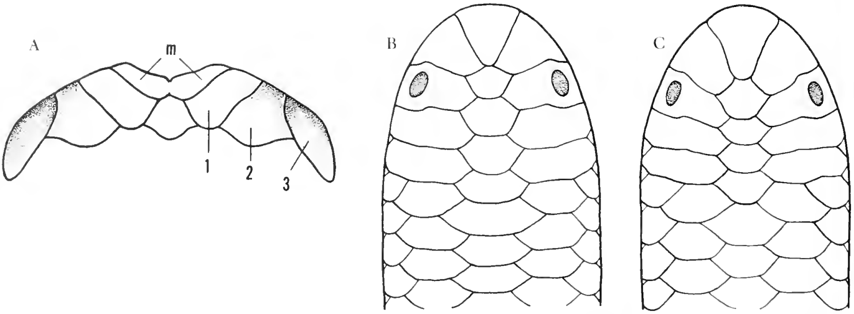

Fig. 2. A, Lower lip of *Leptotyphlops humilis dugesii* in specimen BYU 23914; M mental, 1-2-3 lower labials. B, Dorsal head scales in BYU 23929, same subsp. C, Dorsal head scales *L. h. chihuahuaensis*, BYU 17000.

Chilmahma, a northwestern suburb of Chihuahua City, Mexico.

DIAGNOSIS.—A subspecies of *L. humilis* having only 10 scale rows around the tail, whereas all others, except *h. segregus* and probably *h. tenuiculus*, have 12. From *L. h. segregus* it is distinguished by having a low number of dorsal scales (253–257), and the first 4 dorsals of approximately equal size, the 5th greatly enlarged (compare Figs. 2B and C).

DESCRIPTION.—Body cylindrical, head only slightly if at all distinct from body, tail slightly reduced and with the characteristic terminal spine. Snout rounded and extending beyond the lower jaw. From the ocular caudad the head merges into the body with no apparent deviation, so that from a dorsal view the head is not distinct from the body. The longest specimen (the type) is 158 mm in total length, with a tail of 19 mm from tip of spine to posterior edge of the vent. The paratypes are 133 and 112 mm, respectively, in total length, with tail lengths of 8 and 6 mm.

The body has 14 rows of smooth, imbricate scales, uniform in size except for those on or near the head. There is a reduction to 12 rows a few scales anterior to the vent, and a final reduction to 10 rows at or just posterior to the vent. The anal scale is single and triangular in shape. The middorsal scale count is 253, not counting the rostral and tail spine. There are 17 subcaudals in the type. The paratypes, both females, have 256 and 257 dorsals and 16 and 17 subcaudals.

The rostral curves over the snout between the 2 large nasals to contact the prefrontal, which is in contact laterally with the nasals and oculars and posteriorly with the frontal. Nasal is divided through the nostril, with the upper nasal largest and the lower nasal forming the lateral edge of the snout between the rostral and first supralabial. Ocular large, extending from lip to contact the prefrontal and frontal dorsally, eye spot near middle of scale and above the level of the nostril. Posterior supralabial large, narrowing dorsally to contact the parietal below the level of the eye. Parietals and occipitals are elongate scales extending from the dorsals laterally to be partially separated by the temporal, wedging between them at their lateral ends. The first 4 dorsals are of approximately the same size, with the lateral edges forming nearly straight lines to the 5th dorsal, which is much enlarged laterally and is the largest scale in the dorsal series.

The mental is broad and narrow, joined laterally by 3 infralabials on each side, with the posterior scale the largest; a single chin shield contacts the mental and divides the first infralabials.

The middorsal scale row and the three adjoining lateral body and tail rows on each side are finely pigmented, but the next lateral rows show a reduction of pigmentation near the middle of each scale and the ventral 1/4 to 1/2 of the scale row without pigmentation. This color pattern extends from the head posteriorly to the tail spine. Below the dorsal pigmentation the sides and ventral scales are light cream or a light buff.

REMARKS.—The relationship of *chihuahuaensis* is with *segregus* primarily because of the 10 rows of scales on the tail and its geographical nearness. The occurrence of *segregus* in south Texas and adjoining eastern Coahuila, and the fact that the Chihuahua basin (type locality) lies in the drainage of the Río Conchos, which drains to the Rio Grande in southwest Texas, supports this assumption. These facts suggest that these two subspecies had a common ancestry. Whether the desert areas of eastern Chihuahua and western Coahuila have served as an isolation barrier is as yet unknown, since no specimens are available and little collecting has been done in these areas. Hahn (1979) cites two localities (on map) for Chihuahua. The one from central Chihuahua must be from 5 km (3 mi) NW Chihuahua (Murphy 1975). The one from south central Chihuahua may also belong to this subspecies.

A specimen of *segregens* from Coahuila, Mexico (USNM 93593), has 286 ventrals, 12 caudals, prefrontal larger than frontal and interparietal, and the 5th dorsal enlarged. Klauber (1940a) lists the dorsals for *segregus* as 261(271)275; a larger series from Coahuila would probably increase the known average for dorsals and add credence to the uniqueness of the Chihuahua population.

In preserving the type of *L. h. chihuahuaensis*, the mouth was opened so that the infralabials were exposed. In most preserved specimens the mouth is closed and the lower lip scales are partially, if not entirely, covered. This is particularly the case for the most posterior infralabial scale. In most of the literature (Klauber 1940a, Taylor 1939c) I have found a listing of 4 infralabial scales. Klauber believes there are 4 in *L. h. segregus* and other subspecies of *humilis*. Murphy (1975) also lists 4 for *h. lindsayi* and *h. levitoni*, stating that the first lower labial is very small. I have not seen Murphy's specimens, but those *humilis* available to me do not have a small scale by the mental. In fact, there appears to be but 3 infralabials in *humilis*, with the 3rd, the largest, wedged back to the corner of the mouth and with only the lower edge exposed when the mouth is closed. One or two scales may appear to be infralabials, but they contact the larger 3rd infralabial beneath the large, overlapping posterior upper labial and do not reach the inner margin of the lip. A *humilis* specimen from Jalisco (BYU 23913) was in pre-ecdisis condition, and the scales from around the lower lip were removed intact. After staining in eosin to show more clearly the sutures between the scales, it was apparent that there were only 3 scales on each side of the mental. Other *humilis* specimens were examined with the same results. The mental scale is grooved on each side, giving the appearance of a small lateral scale, but I could not see any suture to indicate an additional scale.

During preservation, the hemipenes of the type were everted. They are elongate tubular structures without spines, but with numerous grooves and irregularities.

Leptotyphlops dulcis supraocularis, n. subsp.

HOLOTYPE.—BYU 30426, an adult taken at Colonia Juárez, Chihuahua, México, by Virginia and Herman Hatch during April 1965.

PARATYPES.—BYU 1421, 19131, 30427–28, and 32417, topotypes.

DIAGNOSIS.—A subspecies of *L. dulcis*, with the anterior supralabial divided as in *dulcis dissectus* but differing from *dissectus* in having the supraoculars elongate and wedging between the prefrontal and frontal to enclose or nearly enclose the prefrontal. The interparietal (3rd scale in dorsal row) is much larger than either the frontal (2nd) or the interoccipital (4th) and is approximately equal in size to the enlarged 5th scale. Prefrontal noticeably larger than frontal. The occipital is not divided.

DESCRIPTION.—The body is cylindrical from head to tail. Head only slightly distinct from body, with the snout slanting forward and downwards, beginning at about the prefrontal. Tail short and terminating in a sharp spine. Total length 219 mm, snout-vent length 208 and tail length 11 mm. The topotypes range in total length from 105–257 mm. The ratio of the body length (S-V) to the midbody diameter in four specimens averages .02. The tail length is approximately 5.0% of the total length.

There are 14 rows of smooth, imbricate scales on the body from just posterior to the occipitals to about 5–7 scales anterior to the vent, where the rows are reduced to 12; just posterior to the vent the rows are reduced to 10 on the tail. The anal is single and triangular, followed by 14 subcaudals that range in the paratypes from 13 to 15. There are 237 middorsal scales, beginning with the prefrontal and counting to, but not including, the tail spine. Type and paratype series range from 231(238) to 246.

The rostral is the largest head scale and curves from the underside of the lip dorsally and posteriorly to contact the prefrontal at about the level of the eye. The rostral is only slightly narrowed from the snout between the nasals and has a rather broad, rounded contact with the prefrontal. On the upper lip are 5 scales extending posteriorly from the rostral: nasal, divided through the nostril to form an upper and a lower scale; first supralabial, divided into 2 scales by a vertical suture; ocular, with the eye spot just above the level of the nostril; and a large posterior labial that overlaps the posterior infralabials. Of this series, only the rostral, nasal, and ocular contact the dorsal head scales.

The supraoculars are elongate (Fig. 3), extending from their contact between the nasal and ocular posteriorly and medially to contact the parietal and to wedge between the prefrontal and frontal. In two paratypes, the 2 supraoculars are in contact, thus separating the frontal and prefrontal. The supraoculars are about the same size as the prefrontal, which is larger than the frontal; the interparietal is larger than either the frontal or interoccipital, and approximately equal in size to the 5th dorsal. In none of the series are the first 4 dorsals of about equal size. From smallest to largest they are: frontal-interoccipital-prefrontal-interparietal. The 5th dorsal is enlarged and is equal in size to the interparietal or slightly larger.

The mental is broad and short with 3 infralabials on each side. The posterior infralabial is large and extends under the overlapping posterior supralabial to the corner of the mouth. A scale just posterior and lateral to the posterior infralabial appears to be a 4th infralabial. It is overlapped by the supralabial so that its true relationship to the 3rd infralabial and the lip cannot be seen as it joins the posterior infralabial, but it does not reach the lip.

COLOR PATTERN.—The 5 dorsal rows of scales are finely pigmented, and the dorsal edges of the adjoining rows show some pigmentation. The snout, including the most anterior part of the rostral and extending laterally to include the area surrounding the nostril, is not pigmented. Those parts of the rostral, nasal, and ocular that are pigmented have small papillae, but these do not appear on the nonpigmented areas. Those scales on the lateral and ventral parts of the head and body are not pigmented.

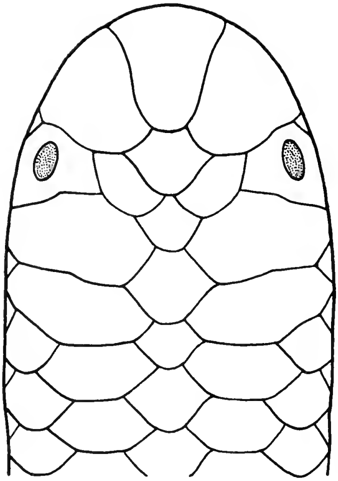

Fig. 3. Dorsal head scales of *Leptotyphlops dulcis supraocularis* (BYU 30427).

REMARKS.—An attempt to key the Chihuahua specimens (Klauber 1940a, Taylor 1939c) did not satisfy the key characters. The supraoculars were shaped more as in *L. albifrons* than in the figures by Klauber (1940a) and *dissectus* specimens available. In fact, the first specimen collected in Colonia Juárez (1959) had the supraoculars completely separating the prefrontal from the frontal, and the occipitals are not divided. As additional specimens became available, it was obvious that this supraocular character was apparently unique and not represented in either *d. dulcis* or *d. dissectus*. A comparison of Figure 2 with those presented by Klauber (1940a) illustrates this basic difference in the dorsal head scales.

I have not examined as many specimens from Texas, New Mexico, and Arizona as did Klauber; however, those seen from southern Texas are *dissectus* as described by Klauber.

A specimen from 4 km (2.5 mi) NW of Glenwood, Catron County, New Mexico, has approximately the same head characters as the Chihuahua series except that the interparietal is not greatly enlarged. Although this locality is northwest of the type locality of *L. dulcis dissectus* (near Lake Valley, Sierra County, New Mexico), it is west of the Continental Divide and in the Gila River drainage.

A specimen from Thatcher, Graham County, Arizona, has characteristics of *dissectus* and *supraocularis*; that is, the supraoculars are elongate, but the occipitals are divided and the interparietal is not greatly enlarged.

The terrain favors intergradation of the populations in southwestern New Mexico, southeastern Arizona, and the area directly south in northwestern Chihuahua. Specimens in Arizona and New Mexico west of the Continental Divide are thus expected to show intergrading characters between *d. dissectus* and the Chihuahua subspecies *d. supraocularis*, particularly those representing populations from the Gila River drainage to the west, and from the desert ranges to the south and into extreme northwestern Chihuahua.

A specimen (KU 44264) from Rancho San Francisco in the extreme northwest corner of Chihuahua has all the characteristics of *dulcis dissectus*. The prefrontal is noticeably smaller than the frontal, and the supraoculars are equal in size to the prefrontal and not elongate and thus permit a wide contact between the frontal and prefrontal. This may be the specimen cited (map) by Hahn (1979b).

A specimen (BYU 41893) from Monterrey, Nuevo Léon, is heavily pigmented, with the dorsal rows dark brown and the more lateral and ventral scales a light slate color. The supraoculars are not curved to enclose the prefrontal, and the following scales (frontal, supraoculars, interparietal, and interoccipital) are of approximately equal size. There are 230 dorsal scales, and the prefrontal is the smallest of the series.

Small series of *d. dulcis* (19), *d. dissectus* (15), and *d. supraocularis* (7) provide the following data for the dorsals: *d. dulcis* 212(224)239; *d. dissectus* 206(229.35)239; *d. supraocularis* 231(237.7)246. There is overlapping in all subspecies; however, a cline is evident from east to southwest.

Family Colubridae

The colubrid fauna of Chihuahua is large and diverse primarily because of the many different habitats existing from the deserts to the foothills and into the mountains. This diversity increases the number of available ecological niches and supports a home for 24 genera and at least 40 species, with 5 additional subspecies in the state. Although the greater part of the state has been traversed by collectors and a number of collections made other than those of which I have been a participant, there are yet additions to be made to this large and interesting fauna. In view of the limited collecting in the desert areas east of Highway 45 and in the rugged barranca terrain in which the west coastal thorn forest has invaded the deep canyons, these areas undoubtedly contain additional genera and species for the state of Chihuahua. *Salvadora g. bairdi*, among others now occurring in northeastern Sinaloa but not yet reported for Chihuahua, may occur there.

The colubrid fauna of Chihuahua is composed of genera and species with strong affinities to the desert habitats that surround the state to the east, north, and northwest, permitting an invasion to occur from the deserts into eastern and northern Chihuahua and a major movement of the central Mexican species through the mountains from the south into the western highlands. It is important to note the species and subspecies that inhabit the central plains and foothills, extending from the area near Nuevo Casas Grandes south along the eastern foothills to the state of Durango. In this area some species and subspecies appear to have been isolated since the recent Pleistocene. This isolation has been intensified by the persistence of the desert areas to the north and east, and in turn these desert areas, extending as they do through northern Chihuahua into southern Arizona and New Mexico, have limited the northern movement of the montane species such as *Thamnophis melanogaster* and *Storeria storerioides*. Therefore, one investigating the colubrid fauna of Chihuahua should take into account more than the great diversification of the habitats resulting primarily from changes in elevation from the northeast to the southwest. The geological past has contributed to the changing habitat conditions and has resulted in some isolation as well as permitting certain species to expand their ranges into the various ecological areas in western and southwestern Chihuahua.

Arizona elegans expolita Klauber

Arizona elegans expolita Klauber, 1946, San Diego Soc. Nat. Hist. 10(17):340–343.
- 2.2 mi SE N. Casas Grandes, 1 (BYU 15254).
- Tinaja Valley, 2 mi S of highway, 2 (BYU 13899, 14334).
- 1 mi S Sueco, 1 (BYU 17105).
- 3 mi W Galeana, 1 (BYU 17106).
- 17 mi N Chihuahua City, 4 (BYU 15293, 15299, 15342, 15346).
- 10 mi S Chihuahua City on Route 45, 1 (BYU 32041).
- 12 mi S Los Nieves, Durango, 1 (BYU 14073).
- 7.4 mi N Moctezuma, 1 (UTEP 4099).
- 12 mi from Chihuahua City, 1 (MVZ 43656).
- 1 mi W Ojo de Laguna, 1 (MVZ 73030).
- 20 mi SE Ciudad Camargo, 1 (MVZ 80001).

The original description cited a type and two paratypes (not examined). With the present series and including data for the types, 17 specimens are available for study.

In all, scale and color patterns, range, and variation in scalation have been increased, although the averages are not appreciably changed.

The scale rows at midbody are 27 in all except one specimen from 27 km (17 mi) N Chihuahua City with 26 rows. The variation occurs anteriorly with 25–29 rows and before the vent with 17–20 rows. Two rows adjacent to the ventrals have larger (wider) scales than those near the dorsum. The head scales show little variation: supralabials 8-8, infralabials 12 or 13, loreals 1-1 except for one with 1-2, preoculars 1-1, postoculars 2-2, and temporals 2-3 or 2-4. Ventrals range from 192 to 207. The males are 192–203, and females 198–207. Caudals are 39–51, with males 50–51, and females 39–49. When ventrals and caudals are combined for males (246.8) and females (247.3), the averages are nearly equal. The total length/tail length ratios were: males 14.2, 14.6, 14.7, 14.8, and 15.1; females 12.7, 13.8, and 13.9. The male from Durango is 15.0.

The color pattern consists of a series of irregular dorsal brown spots ranging from 44 to 54 (47.74) on the body, and from 15 to 23 (18.25) on the tail. Between the darker dorsal spots, the scales are flecked with brown on a cream background. Between the dorsal spots and the ventrals is a row of small spots alternating with the dorsal spots. The ventrals and caudals are without any spots or flecks.

This subspecies, based on available records, occurs in the valleys and foothills east of the Sierra Madre Occidental into the desert valleys at least a short distance east of the main highway (45) and south from north central Chihuahua into Durango. Banta and Leviton (1961) report a DOR specimen from 1.6 km (1 mi) S Juan Batista, Aguascalientes, 12 September 1957, and Dixon, Sabbath, and Worthington (1962) report 4 male specimens from 9 to 32 km (6 to 20 mi) SE of Nombre de Dios, Durango. These have ratios, tail to total length, of 12.4% to 13.6%. If there is justification for recognizing the subspecies *australis*, it is not supported by the northern Durango specimen. The specimen from 19 km (12 mi) S of Los Nieves, Durango, is near the mean for the Chihuahua series in all characters, and is thus considered to be an extension of the Chihuahua population into Durango.

Dixon and Fleet (1976) have mapped the approximate distribution of this species in Chihuahua; also, they show *A. e. elegans* in northeastern Chihuahua and *A. e. philipi* occurring in extreme north central Chihuahua. Two specimens (BYU 15431-2) of *philipi* 5 km (3.4 mi) N of Columbus, New Mexico, are similar to the Chihuahua series in scalation but differ in color pattern with 61 and 64 dorsal body spots.

Conopsis nasus labialis Tanner

Conopsis nasus Günther, 1858, Catalogue of the snakes in the British Mus., p. 6.

Conopsis nasus Taylor & Smith, 1942, Univ. Kansas Sci. Bull. 28(2)15:329–333.

Conopsis nasus labialis Tanner, 1961, Herpetologica 17:13–18.
- 2 mi SE Creel, 4 (BYU 14295–8).
- 1 mi W La Laja (6 mi E of Majorachic), 2 (BYU 16854–5).
- 22.5 mi SE Creel, 1 (BYU 16952).
- 25 mi SE Creel (by La Bufa Road), 7 (BYU 16856–62).

Since the report of Tanner (1961), no additional data on scale and color pattern variations have been obtained. A field note reference to their habitat is as follows: south of

Creel these snakes were found under rocks in moist to wet soil and in the crumbled volcanic gravel. Some were taken under loose rocks at the base of a small ledge from which water was issuing, keeping the base materials wet. In this area, three small individuals were taken, each of which showed large umbilical scars, suggesting that they were recent hatchlings (total length 101–124 mm), recorded 18 July 1960.

Diadophis punctatus regalis Baird and Girard

Diadophis regalis Baird and Girard, 1853, Cat. N. Amer. Rept. Pt. I, p. 115.

Diadophis punctatus regalis Gehlbach, 1965, Proc. U.S. Nat. Mus. 116:300–307.

10 mi W San Francisco del Oro, 1 (BYU 14251).

Approximately 2 mi E Cerocouhui, 1 (BYU 14243).

Yepomera, 2 (UAZ 34398 and 34792).

Only two specimens were taken in the years we worked Chihuahua, and these seemed to have come from very different populations. The one from San Francisco del Oro lacks a light neck ring and has a very high ventral count (243); the specimen is otherwise very similar to the *regalis* specimens I have seen from New Mexico, Arizona, Utah, and Nevada. This female specimen was taken alive as it crossed a road, along the margins of which were numerous boulders. Gehlbach (1965) placed it in with the subspecies *regalis*.

A second specimen from Cerocouhui is very different, with a wide neck ring and only 195 ventral scutes. The two specimens are from approximately the same latitude but on opposite sides of the Sierra Madre Occidental. The latter specimen is a male, and this may account for some of the differences in the number of ventral scutes; however, a difference of 48 seems a rather wide margin to retain it in the same subspecies.

Although I have not attempted to examine a large series (27 specimens) of the subspecies *regalis*, the Cerocouhui specimen does not fit the basic color and scale patterns I have come to associate with the *regalis* populations in Idaho, Utah, and Nevada. Furthermore, in southwestern Chihuahua it is associated with the high mountainous habitats extending southward through Durango and into central Mexico. These areas do not provide the same foothill or xeric conditions I have associated with the subspecies *regalis*; for this reason, it seems that the *dugesii* subspecies may well extend as far north as the high mountain habitats of southern Chihuahua. This geographic pattern would be in keeping with the distribution of several other species that have extended their range northward throughout the high mountain habitats from Durango and into south and south central Chihuahua. It is more logical to include it in the subspecies *dugesii*. Gehlbach (1965) considered it a *regalis-dugesii* intergrade.

The Cerocouhui specimen was taken after heavy rains in a boulder-strewn alluvial fan at the mouth of a small canyon and was taken in company with *Eumeces callicephalus*, *Crotalus lepidus klauberi*, and the Hylactophrine frog *Eleutherodactylus tarahumaraensis*. If it is indeed a representative of *D. p. dugesii*, it not only represents an extension of its range but also a new record for Chihuahua.

The two female specimens taken at Yepomera have wide distinct nuchal collars but were similar to the specimen from San Francisco del Oro in scalation (ventrals more than 240). Since *regalis* may or may not have a nuchal collar, these specimens are, on the basis of scalation, retained in the subspecies *regalis*. Eleven male specimens (at BYU) from southwestern United States (states listed above) and Chihuahua have the following ventral and caudal counts: ventrals 211(215.2)222, caudals 69(74.5)81; 15 females, ventrals 219(231.1)243, caudals 57(66.4)72. There is an indicated clinal increase from north to south if the Cerocouhui specimen is excluded.

Drymarchon corais rubidus Smith

Drymarchon corais rubidus Smith, 1941a, Jour. Wash. Acad. Sci. 31(11):474–476.

Hardy and McDiarmid, 1969, Univ. Kansas Publ. Mus. Nat. Hist. 18(3):159–160.

Approximately 2 mi S Urique, near river, 1 (BYU 14245).

Along San Miguel River, just below Arroyo Ciénega, 1 (BYU 23708).

Smith (1941a) reported the type series as having the ventrals ranging from 190 to 203, and the caudals as 69–78. Hardy and McDiarmid (1969) reported the range in ventrals as 187–197 for 17 specimens from Sinaloa. The two Chihuahua specimens (both males) have 199 and 196, respectively, in ventrals, and one has 72 caudals. In both specimens there are 8-8 supralabials; however, one (23708) has 9-9 infralabials, and in both the 6th supralabial contacts the 1st lower temporal but is widely separated from the lower postocular. Both are adult males measuring 1457 and 1987 mm in total length, with the latter having lost approximately half of its tail.

The color pattern is more nearly as described by Smith (1941a) for the type series; that is, the dorsum is black and the head markings are essentially the same color. One difference is noted: the ventrals anterior to those that are black have the posterior edge in black. This black edging becomes thin anteriorly until the median divides, leaving thin, dark margins extending laterally along the edges of the ventrals to within 15–20 ventrals before the gulars. The ventral color of the specimen from the San Miguel River is a deep, almost ruby, red. The Urique specimen was a salmon pink (Tanner and Robison 1960).

This is another extension of the coastal thorn forest fauna extending its range into the deep valleys of southwestern Chihuahua. McCranie (1980) lists a record for southwestern Chihuahua.

Elaphe guttata emoryi (Baird & Girard)

Scotophis emoryi Baird & Girard, 1853, Smithsonian Institution, part I, p. 157.

Elaphe guttata emoryi Dowling, 1952, Occ. Papers Mus. Zool. Univ. Michigan 540:2.

12 mi SE Nuevo Casas Grandes, 1 (BYU 13918).
11.7 mi W Ricardo Flores Magón, 1 (BYU 15347).

The scale and color patterns are normal for the subspecies, and the distribution is within the limits established by previous reports. Both specimens are males with 204 and 208 ventrals; one (14547) has 74 caudals, and the dorsal body spots are 43 and 37, respectively.

In spite of extensive collecting in the area, only two specimens were found. This is surprising, since none were seen as DOR specimens on roads. We attempted not only daytime collecting along roads in the valleys or on the hillsides, but we also did considerable road running during the evenings and early mornings. We have concluded that this is either a rare or very secretive species of Chihuahua.

Elaphe subocularis (Brown)

Coluber subocularis Brown, 1901, Proc. Acad. Nat. Sci. Philadelphia 53:492.

Elaphe subocularis Stejneger and Barbour, 1917, Checklist, p. 84.

Elaphe subocularis Worthington, 1980, Cat. Amer. Amph. and Rept., p. 268.

12 to 39 mi NE Aldama on Chihuahua Road 16, 9 (Carnegie Mus. Nat. Hist. 59917–23, 49926 and 61792).
18 mi SE Ciudad Chihuahua, 1 (NMMZ 9307).
17.7 mi E Coyame, 1 (TCWC 44005).

The distribution of this species in Chihuahua is far from being fully understood. The present records place it primarily in the eastern part of the state; however, some records from central Chihuahua indicate that it could occur in much of the lower foothills and ranges lying east of the Sierra Madre Occidental.

We did not collect east of Highway 45, and the records listed above (kindly provided by Dr. Richard D. Worthington) are all from localities east of the highway.

Elaphe triaspis intermedia (Boettger)

Coluber triaspis Cope, 1879, Proc. Amer. Philos. Soc. 18:261–277.

Pityophis intermedius Boettger, 1883, Ber. Offenbach. Ver. Naturk 22/23:148.

Elaphe triaspis intermedia Mertens & Dowling, 1952, Senckenbergiana 33:201.

I am aware of only one specimen from Chihuahua, previously reported by Taylor and Knobloch (1940), and now number 17681 in the University of Illinois Natural History Museum.

Based on the records reported for Sonora (Bogert and Oliver 1945) and Sinaloa (Hardy and McDiarmid 1969), this species is obviously more common in the western lowlands than in any part of western Chihuahua. Its occurrence at or near Majorachic is undoubtedly the extreme eastern extension of its range and represents another species that has ascended the valleys of the Río Fuerte, this time via its western tributary, the Oteros.

Geophis aquilonaris Legler

Geophis aquilonaris Legler, 1959, Univ. Kansas Publ. Mus. of Nat. Hist. 11(4):327–334.

Maguarichic, 2 (BYU 16912, 16913).

Both specimens (females) were taken 13 July 1960. One was underneath a rock, and the other was taken as it moved in leaves under low growing shrubs. When the speciman was collected, the ground was wet and the temperature hot and humid.

The scalation and color pattern are generally within those of other *G. aquilonaris*, but a few counts extend the known variation (Legler 1959). One specimen (BYU 16912) has only 170 ventrals but 66 caudals. Thus, the ventral range for females is now 170–183 and the caudals 55–66. The color pattern is within the limits previously described for the species.

Gyalopion canum Cope

Gyalopion canum Cope, 1860, Proc. Acad. Nat. Sci. Philadelphia 12:241, 243.

Ficimia cana Garman, 1883, Mem. Mus. Comp. Zool. 8(3):82.

Gyalopion canus Leviton & Banta, 1960, Occ. Pap. California Acad. Sci. 26:1–4.

5.5 mi NE of Colonia Juárez, 1 (BYU 15257).

Scalation and color pattern as reported by Cope (1900). Ventrals 138, caudals 30, scale rows 17. The specimen was taken on a warm and humid night about 10:00, just after a light rain, 3 September 1959 on the road between Colonia Juárez and Casas Grandes. When the specimen was picked up, it produced several rather loud, sharp, popping noises.

In spite of many hours of night driving during all types of weather, this is the only specimen seen DOR or otherwise. The range is now definitely within Chihuahua and may be expected throughout most of the foothill area on the eastern front of the Sierra Madre Occidental. Hardy (1976) cites (map) a record for central Chihuahua.

Heterodon nasicus kennerlyi Kennicott

Heterodon kennerlyi Kennicott, 1860, Proc. Acad. Nat. Sci. Philadelphia 12:336.

Heterodon nasicus kennerlyi Cope, 1900, Ann. Rept. U.S. Nat. Mus. 1898:773. Smith 1943. Proc. U.S. Nat. Mus. 93(3169):432–433.

Tinaja Valley, 1 mi S of highway to Colonia Juárez, 7 (BYU 13900, 14315, 15337, 15816, and 16106–8).

3 to 5 mi SE N Casas Grandes (along highway), 4 (BYU 15250, 17101, 17103–4).

54 mi S Juárez City, DOR on Highway 45, 1 (UTEP 4696).

Smith (1943) lists three specimens from the following localities: Progreso, 27 km (17 mi) W Carmen, and Corralitos.

The scalation and color pattern are not different from those provided by previous authors. In all, there are 23-23-19 scale rows; 131–146 ventrals, males 131–136, females 139–146; caudals 29–40, males 37–40, females 29–33.

Smith (1943) lists a specimen for Tlajualilo, Durango. This indicates that the range in Chihuahua undoubtedly extends south throughout the desert valleys of central Chihuahua. We were fortunate to have half our collection given to us by Mr. Herman Hatch, who found them in his cultivated field a mile east of Colonia Juárez. The only specimens we found were on or along the highways.

Once arriving in the Colonia Juárez/Casas Grandes area and letting it be known that we were interested in reptiles, we were introduced to a number of snake stories. One concerned the species at hand. It was referred to as a deadly adder that feigned death only to get you to pick it up or get close enough for it to strike. In 1959 we were fortunate to find a live adult a few miles SE of N. Casas Grandes, and it was possible to demonstrate that it was completely harmless. We soon found that many were afraid of reptiles, and before we engaged any help from the locals, we had to educate them that the only good snake is not a dead one.

Genus *Hypsiglena*

In 1860 Cope described two species of the genus *Hypsiglena*: *ochrorhyncha* from Cape San Lucas and *chlorophaea* from Fort Buchanan, Arizona. Most authors have placed the latter species as a synonym under *ochrorhyncha*, even though there are at least two subspecies geographically between Cape San Lucas in Baja California and the populations in Arizona and northern Sonora. Now that adequate material is seemingly available, it does seem appropriate, on the basis of the ventral counts and combining the ventral-caudal counts and color pattern, that we recognize *chlorophaea* as a distinct subspecies and indicate its description and distribution in central and northern Sonora and in most, if not all, of Arizona. The material from Chihuahua is, in several respects, more nearly similar to the Cape San Lucas population than to the Arizona-Sonora populations.

An analysis of the available material from southern Sonora, northern Sinaloa, and southwestern Chihuahua indicates that intergradation of the *torquata* type (having a light nape band followed by a large, dark band) with the *ochrorhyncha* type (or *chlorophaea*) to the north has produced several head and nape color pattern combinations. It does appear that the light cream band on the nape of the *torquata* material is gradually replaced in the intergrading specimens to the north by forward movement of the broad, dark band, which in turn is responsible in part

TABLE 1. Ventral and caudal variation in *Hypsiglena*.

Region	No.	Sex	Ventrals	Caudals	Ventral-Caudals
Cape San Lucas	13	M	166(170.8)176	42(49.5)53	212(220.5)224
and environs	8	F	173(178.4)188	44(45.8)48	218(225.7)235
Sonora	11	M	161(173.57)189	49(61.6)65	232(238.7)250
	10	F	178(183.8)188	52(55)58	231(238.3)244
Arizona	19	M	175(179.6)193	51(55.7)66	222(230.9)248
	29	F	175(185.2)190	44(47.8)53	223(233.5)241
Chihuahua	4	M	164(168.3)171	48(52.3)56	216(220.7)227
	3	F	170(172.0)175	41(44.2)49	211(216.2)221

for eliminating at least the posterior portion of the cream-colored band. The anterior part of the white band becomes pigmented and spotted like the dorsum of the head. To further reduce the prominence of the light band, a medial dark stripe two or three scales wide extends from the dark band to or within a scale of the parietals, and the orbital stripes are extended caudad to contact laterally the dark nuchal band. The elimination of the cream band is followed by a reduction in the size of the dark nape band, which becomes incised dorsolaterally, and, as the reduction in the length of the dark nape band continues, the dorsolateral indentations separate the nape band into a median spot posterior to the parietals and two lateral spots extending dorsad to the orbit. This intergradation of color pattern is more apparent than perhaps in any other subspecies thus far examined, and is, of course, the criterion that induced Dunn (1936) to suggest only one species existed in the genus.

An examination of 32 specimens from the cape region of Baja California (that is, the area south of La Paz and in the cape area) suggests that the material from the type locality of *ochrorhyncha* and the general area north from the Cape to near the La Paz area represents a population quite distinct from any other in the Baja California peninsula. Specimens taken a short distance north of La Paz show a substantial increase in the number of ventrals and caudals, and a substantial increase in the number of dorsal spots, providing the basic characteristics of the midpeninsular subspecies *venusta*. A comparison of the material in the Loreto/Comondu area to that of the Cape shows an increase of approximately 10–15 scales in the ventrals and an increase of approximately 10 in the caudals, so that a combination of the ventral-caudals results in an average increase in the *venusta* population of 15–20 ventral-caudal scutes. Immediately north of the *venusta* subspecies, in the area of San Felipe and on into the Great Basin area of southern California, Nevada, and Utah, and as far north as British Columbia, the subspecies *deserticola* provides an even higher number of ventrals and caudals, with a combination of the ventral-caudal scutes exceeding 240 scales. Thus, the populations at the cape and those populations in Arizona-Sonora have, until now, been referred to as disjunct populations of *ochrorhyncha*. On the basis of statistical analysis, the Arizona-Sonora populations should be separated and placed in a distinct subspecies. An examination of the Arizona-Sonora populations (85 specimens examined) indicates that the average ventral-caudal scales in these populations range from 232 to 239, in contrast to an average of approximately 220 in the typical *ochrorhyncha* population of the Baja cape. There is also an increase of approximately 10 dorsal body spots in the Arizona-Sonora populations, averaging 57–60 spots in contrast to the 50–52 in the cape population (Table 1). It is thus proposed that the Arizona-Sonora populations be recognized as distinct and placed in the subspecies *Hypsiglena torquata chlorophaea* Cope.

Hypsiglena torquata texana Stejneger

Hypsiglena texana Stejneger, 1893, N. Amer. Fauna 7:205.

Hypsiglena ochrorhyncha texana Stejneger & Barbour, 1917, Checklist N. Amer. Amph. Rept., p. 93.

Colonia Juárez, 4 (BYU 14300–3).
9 mi NE Colonia Juárez, 1 (BYU 15373).
Casas Grandes (in ruins), 1 (BYU 16988).
24 mi E Buenaventura, 1 (BYU 15260).
6.5 mi N Chihuahua City, 1 (BYU 16989).
5 mi N Cerro Campaña, 2 (MVZ 70995–6).

Ojo de Laguna (25 mi S Gallego), 2 (MVZ 73012–3).
16 mi N Durango City, Durango, 1 (MVZ 59299).
0.5 mi S Matachic on highway 16, 1 (UAZ 34420).

The Chihuahua *Hypsiglena* that have, in recent studies, been referred to as part of the *H. t. ochrorhyncha* complex are more comparable in scale patterns to the Baja cape population than to any other subspecies referred to above. For example, the mean ventrals in the males (7) is 168.3 in contrast to the cape males (22) at 170.5. The females are equally similar in that the total of ventral caudal scutes is almost identical in the two populations, as is also the number of dorsal spots in both sexes. However, a comparison of the Chihuahua population samples to a series of specimens from southeastern New Mexico and Texas suggests that the central and eastern Chihuahua material should be associated with the subspecies *t. texana* rather than retained in the subspecies *t. ochrorhyncha* or *t. chlorophaea*. Thus, the *Hypsiglena* of Chihuahua can best be assigned to two subspecies: those east of the Sierra Madre Occidental in the area of Colonia Juárez and south into Durango to *texana*, and those on the west, at least in the Río El Fuerte basin, on the basis of the material now available, to the subspecies *chlorophaea*.

A female specimen (16 mi N Cd. Durango, MVZ 59299) has 174 ventrals and 51 caudals (225 V-C) and should perhaps be included in this subspecies.

Hypsiglena torquata chlorophaea Cope

Hypsiglena chlorophaea Cope, 1860, Proc. Acad. Nat. Sci. Philadelphia p. 246.
Urique, 1 (BYU 14313).

There is a real possibility that the population of the El Fuerte basin in extreme southwestern Chihuahua may also have representatives of *t. torquata*, since adjacent southern Sonora and northern Sinaloa represent the area where intergradation seemingly occurs. I would, therefore, expect to find specimens with the *t. torquata* pattern entering from Sinaloa into southwestern Chihuahua.

The specimen from Urique has a broad, dark, nape band 5 scales long with a median extension of 5 scales to the parietals. At the anterior edges of the dark band (on each side of the median) are light brown areas. This nape pattern is similar to that of a specimen from Colima (BYU 23962) except that, in the Urique specimens, the areas anterior to the dark band and on each side of the median nape stripe are cream colored. This pattern seems to be a further indication of changes in pigmentation pattern that have occurred because of intergradation between *H. t. torquata* and *H. t. chlorophaea*.

Summary for *Hypsiglena*

The taxonomic arrangement of *Hypsiglena*, indicated above, seems the most logical interpretation, based on geographical distribution and statistics. For a long time the Arizona-Sonora-Chihuahua material represented a taxonomic problem. With the material now available, there seems to be little justification for not recognizing Cope's subspecies described from Fort Buchanan, Arizona, in 1860. Averages provide ample key characters to serve the purpose of separating the two widely separated populations.

The climatic changes that have occurred during the last 15,000–20,000 years may have subjected this widely dispersed genus to substantially changing environments. The cape area of Baja California and the Arizona-Sonora area may not have changed as radically as did the area between (that is, central and northern Baja California and the lower regions of the Great Basin). The area thus retains ancestral characteristics in these populations while necessitating a more radical change in the external color pattern and scalation characteristics of the populations in the intervening desert areas. Therefore, the primary difference that has developed in the Arizona–Sonora–southwestern Chihuahua populations has been an increase in the ventral-caudal scutes, with no major alteration in the basic color pattern except for an increase in the number of dorsal spots.

The parameters of intergrading populations are, as yet, not well defined, but general areas as given above can now be indicated. They are as follows:

a. *H. t. torquata–t. chlorophaea*: northern Sinaloa, southern Sonora, and perhaps southwestern Chihuahua.

b. *H. t. ochrorhyncha–t. venusta*: areas near La Paz and immediately north of Bahia de La Paz but not extending far beyond the Arroyo Salado.

c. *H. t. venusta–t. deserticola–t. klauberi*: *venusta* in the area south of San Felipe and along the gulf coastal areas, with more typical *deserticola* ranging northward into southeastern California, and *klauberi* extending westward to the coast and north into southwestern California.
d. *H. t. deserticola–t. chlorophaea*: not as clearly defined, but occurring to a limited degree along the edges of the Colorado River to Glen Canyon Dam.
e. *H. t. chlorophaea–t. texana*: apparently occurring in extreme eastern Arizona, southwestern New Mexico, and northwestern Chihuahua.

Lampropeltis getulus splendida (Baird & Girard)

Ophibolus splendidus Baird & Girard, 1853, Cat. of N. Amer. Reptiles, p. 83.
Lampropeltis splendida Cope, 1860, Proc. Acad. Nat. Sci. Philadelphia, p. 255.
Lampropeltis getulus splendidus Wright & Bishop, 1915, Proc. Acad. Nat. Sci. Philadelphia 67:168.
2.3 mi N Chihuahua City, 2 (BYU 15182–15283).
28 mi W Chihuahua City, 1 (BYU 14138).
Río Santa María at bridge W of Galeana, 1 (BYU 13515).
14.5 mi E Buenaventura, 1 (BYU 15252).
1 mi SW Casas Grandes, 1 (BYU 17691).
7 mi N El Sueco, 1 (UTEP 4018).

Literature citations are for San Diego (Blanchard 1921, AMNH 3752) and Río Santa María and San Diego (Smith and Taylor 1945).

Based on the available records, it appears that this species ranges in the area west of Highway 45, extending west through the valleys and low ranges to the east base of the Sierra Madre Occidental. Records are available from the desert areas of eastern Chihuahua (Reynolds and Scott 1977).

The scale counts of examined specimens are slightly higher than those listed by Blanchard (1921) and are as follows: scale rows 23-23-19 or 23-25-19, with 4 of the 7 having 25 rows at midbody; ventrals 209–217, males 204–213 (210.3), females 210–217 (213.3); caudals 51–58; other variation as previously reported.

Three of the specimens are juveniles and show a decided series of large dorsal spots, clearly divided by narrow, light lines. In the adults, an increase of dorsal dark pigment obscures this spotted pattern. The dorsum of the head and the nape are black, with this pattern extending for 15 scales posterior from the parietals. The ventrals are mostly black, but with light spots on the edges.

There appears to be a strong influence of the subspecies *nigrita* in the specimens I have seen from Chihuahua. Blaney (1977) found intergradation in northern Sonora and south and eastern Arizona. This was based not only on color pattern, but also on the increase of dorsal scale rows to 25 in some specimens. As noted above, 4 of 7 specimens have 25 scale rows, and there is, in live specimens, a decided melanistic color pattern. I do not have enough specimens to establish a zone of intergradation but suggest only that a closeness in basic characters does exist between the subspecies *splendida* and *nigrita*.

Lampropeltis triangulum sinaloae Williams

Lampropeltis triangulum nelsoni Blanchard, 1920 (part), Occ. Pap. Mus. Zool. Univ. Michigan 81:6.
Lampropeltis triangulum sinaloae Williams, 1978, Milwaukee Public Mus., Publ. in Biol. and Geol. 2:167.

A single specimen is available from Piedras Verde, Chihuahua (BYU 22482). This locale is near the junction of the Río Urique and the San Miguel, which in turn is a tributary of the Río El Fuerte.

This is an extension of the known range of *L. t. sinaloae* and represents a new record as well as an addition to the herpetofauna of Chihuahua.

Lampropeltis pyromelana pyromelana (Cope)

Ophibolus pyromelana Cope, 1866, Proc. Acad. Nat. Sci. Philadelphia 18:305.
Lampropeltis pyrrhomelaena Blanchard, 1921, U.S. Nat. Mus. Bull. 114:231–236.
Lampropeltis pyromelana pyromelana Stejneger and Barbour, 1917, Checklist N. Amer. Amph. and Rept., p. 88.
Black Canyon, approximately 8 mi W Chuhuichupa, 1 (BYU 14210).
Top of mountain on road to Pacheco, 2 (BYU 13389 and 19132).
5 mi below Rancho Verde on Río Gavilán, 1 (BYU 32418).
For additional records, see Tanner 1983 (Cat. of Amer. Amph. and Reptiles).

In the northern mountains (north of the Río Papigochic) of Chihuahua is one of several isolated populations of *L. p. pyromelana*. Because of the many mountain islands in the total distribution of this species, we find very little evidence of intergradation between the subspecies. This may also be the result of an incomplete understanding of its distribution, since few specimens are available.

Both Blanchard (1921) and Smith and Taylor (1945) list a specimen from San Diego

(AMNH 3716). In the early days San Diego was an important Rancho. It is located east of Colonia Juárez and south of Casas Grandes, and this is not a montane locality. Those who have seen *pyromelana* report them to be only in the mountains much to the west of Colonia Juárez. I suspect that the San Diego specimen was also taken in the mountains but reported from the then-recognized locality. The scale counts listed by Blanchard for this San Diego specimen are within a few scales of those examined from the mountains to the west.

Specimens reported from Guerrero (Smith and Taylor 1945) and from Yepómera (Van Devender and Lowe 1977) in west central Chihuahua include its range in the Río Papigochic basin. There is a strong indication that *pyromelana* has entered Chihuahua by ascending the tributaries of the Río Yaqui from northwestern Sonora, since both the Bavispe and Papigochic drain the northern and central regions of the Sierra Madre Occidental.

Lampropeltis pyromelana knoblochi Taylor

Lampropeltis knoblochi Taylor, Copeia 1940:253.
Lampropeltis pyromelana knoblochi Tanner, 1953, Great Basin Nat. 13:47–66.
25 mi S Creel (La Bufa Road), 2 (BYU 16864–5).

The only other specimens known are the types from Majorachic (FMNH 23016–17), two specimens from Yecora, Sonora (UAZ 25131 and 28177), and a specimen in the British Museum from Yoquiro, Chihuahua.

This subspecies shows the greatest departure from the basic characteristics of *L. pyromelana*. The color pattern is unique in that the red is not constricted dorsally by the black bands, nor does the red reach the ventrals. Thus, the red is combined to large, dorsal spots surrounded by narrow, black bands dorsally and laterally and by an irregular, light stripe ventrally between the black-edged red blotches and the ventral scales. In the other subspecies the red reaches the ventrals in some or all triads. The length of the triads is shorter than in other subspecies, and thus there is an increase in the number of white bars and/or triads (transverse white bars 63-(74)-85). The white bars terminate laterally by becoming a part of the lateral, irregular, light line; such bars equal or exceed the total number of caudals.

This subspecies is not ringed or banded but has a series of red spots extending across the dorsum from the 3rd or 5th scale rows on each side. There is an increase in ventrals 225–238 and in caudals 64(67)74.

The two specimens taken south of Creel were on a rocky hill above a small stream. Heavy rains the day before left the habitat wet; both were found under rocks.

The distribution of *knoblochi* is not fully known. Those records indicated above are all from the high mountains of southwestern Chihuahua and extreme southeastern Sonora. Since most of the area to the south has not been studied, it is suspected that this subspecies may range south into the Guadalupe y Calvo area and even into northern Durango.

Leptodeira splendida ephippiata
Smith & Tanner

Leptodeira ephippiata Smith & Tanner, 1944. Copeia 3:131. Type locality, 13.3 km (8.3 mi) WNW of Alamos, Sonora.
Leptodeira splendida ephippiata Duellman, 1958. Bull. Amer. Mus. Nat. Hist. 114:82.
Approximately 15 mi upstream from Divisadero Trail, Urique River, 1 (BYU 22658).

A juvenile or subadult male 277 mm in total length and with a tail/body ratio of 0.267, less than that reported for juveniles by Duellman (1958) at 0.365. The scale rows are 21-21-17, ventrals 179, caudals 92, supralabials 7-8, infralabials 10-10, preoculars 3-3, postoculars 1-2, loreals 1-1 and temporals 0-2 on right side (with first temporal fused to the parietal) and 1-2 on the left side. The range of the caudals is increased from 78-85 (Duellman 1958) to 78-92 in males.

There are 26 spots on the body, and 20 on the tail. The first body blotch is connected to the nuchal stripe, which extends as a narrow, uniform streak to the posterior tip of the parietals. The area between the parietals and the first body spot is a light cream color, providing a noticeable contrast between the mottled head and the first body spot. The postorbital stripe fades on the posterior temporals and appears only as a stippling from the posterior supralabial on one row of scales to the first body spot. Otherwise, the color and scale patterns are as has been described by Duellman (1958), Hardy and McDiarmid (1969), and Taylor (1939a).

The importance of this specimen is not that it varies appreciably from specimens taken in Sinaloa, but primarily in that it was found at such a distance up the Urique River, suggesting that there may well be a sizeable population inhabiting the Río El Fuerte basin (at least as far as the coastal thorn woodland habitat extends into the barrancas). The specimen had recently eaten an adult *Hyla* and several arthropods, the latter not easily recognized since they were fragmented.

The reduced ratio between body and tail and the increase in caudals suggest that this species, as with others that inhabit the deep, narrow canyons, is sufficiently isolated there to have evolved distinctive variations. This specimen is also a new record for Chihuahua.

Leptophis diplotropis diplotropis (Günther)

Ahaetulla diplotropis Günther, 1872, Ann. Mag. Nat. Hist. 4(9):25–26.
Leptophis diplotropis Günther, 1894, Biologia Centrali-Americana, Rept., p. 130.
Arroyo Cienaga Prieta, approximately 35 mi below Guachochic, 1 (BYU 22484).

A single female specimen represents the first to be taken in the Río El Fuerte basin of southwestern Chihuahua. It has a higher ventral count (188) than specimens examined from nearby Sinaloa as reported by Oliver (1948) and Hardy and McDiarmid (1969). Oliver (1948) also lists four specimens (MCZ 43268–43271) from Guasaremos, Chihuahua, a locale on the Río Mayo. In these, the ventral counts range from 181 to 184. The average of the five available specimens from Chihuahua is 183.4. The ventral counts of Chihuahua specimens (181–188) are similar to those occurring in specimens from the Tres Marías Islands (185–186) and may, therefore, justify the retention of the island population within the nominal subspecies *diplotropis*. Otherwise, the scale counts are approximately the same as those observed by previous authors cited above. The color pattern is as described by Oliver (1948) and as figured by Bogert and Oliver (1945), except that the dorsolateral stripe does not involve the 4th–5th rows and the anterior half of the 7th supralabial.

The scales in the 1st and 8th (middorsal) scale rows are noticeably larger than other scales in the intermediate scale rows. Faint keels occur only on the paravertebral rows of the body, but not on the tail. The differences in the size and shape of the body scales is very noticeable, with rows 3 to 6 on each side elongate, and with a diagonal position in contrast to the other more uniformly positioned rows.

An increase in ventrals and differences in color pattern from south to north in western Mexico is apparent, but whether the northern populations can be considered to be subspecifically distinct from those in southern Sinaloa southward must await a much larger series of specimens.

Masticophis flagellum lineatulus Smith

Coluber flagellum Shaw, 1802, General Geol. or Systematic Nat. Hist., p. 615.
Masticophis flagellum Ortenburger, 1928, Occ. Pap. Mus. Zool. Univ. Michigan 139:2.
Masticophis flagellum lineatulus Smith, 1941, J. Wash. Acad. Sci. 31(9):394.
13 mi S Acensión, 1 (BYU 17102).
22 mi S Gallego, 1 (BYU 13975).
1 mi W Sueco, 1 (BYU 15360).
9 mi W Sueco, 1 (BYU 15339).
2 mi S Sueco, 1 (BYU 42244).
38 mi S Ahumada, 1 (BYU 15340).
3.5 mi E Buenaventura, 1 (BYU 15358).
Colonia Juárez, 1 (BYU 15468).
8 mi NW Colonia Juárez, 1 (BYU 15461).
Lower Tinaja near Colonia Juárez, 1 (BYU 15341).
4 mi NE Colonia Juárez, 1 (BYU 17697).
25 mi N Cd. Chihuahua, 1 (BYU 30381).

Aside from the type (11 mi S of Buenaventura), Smith lists four additional paratype specimens from Chihuahua (USNM 14279, 14283 Chihuahua, and USNM 104675–6, Río Santa Maria, near Progreso). In the UTEP collection are the following: 2519, Sierra del Nido; 3582 0.8 mi NW Zavalza, Durango (near Chihuahua border); 4097, 72 mi N Cd. Chihuahua and 4228, 6 mi NE Janos.

The scale counts are as follows: ventrals, males 194(198.6)201, females 191(193.5)195; caudals, males 98(104.6)113, females 98(98.8)100; scale rows 17 reducing to 12 or 13 before the vent; supralabials 8, and infralabials 9 or 10.

The color pattern does not vary from Smith's (1941) original description. Adult specimens preserved 25 years ago still show the brilliant, deep, salmon-red color. This alone is a remarkable distinction for this subspecies. A few specimens from northern Durango (12 mi S Los Nieves, BYU 14071 and 1 mi N Zarca, BYU 14072) have also retained this unique color and color pattern.

Wilson (1973) indicates by map two and possibly three subspecies in Chihuahua. The subspecies *testaceus* enters northeastern Chihuahua from Coahuila, and *piceus* intergrades with *lineatulus* in the northwestern corner. There is reason to suspect that *cingulum* may occur in southwestern Chihuahua by entering through the El Fuerte Basin. None of the specimens we have taken in central Chihuahua, west of Highway 45, show any intergrading of characters.

Masticophis mentovarius striolatus (Mertens)

Coluber striolatus Mertens, 1934, Zoologica 32:190.
Masticophis s. striolatus Zweifel & Norris, 1955, Amer. Midl. Nat. 54:242.
Masticophis mentovarius striolatus Johnson, 1982, Cat. Amer. Amph. and Rept., p. 295.

Cueva Creek near Tres Rios, 1 (BYU 17112). This locality is just east of the Sonora border and is a small creek draining into the Bavispe River.

This female has the following scale counts: scale rows 17-17-13, ventrals 177, caudals 109, supralabials 8-8, infralabials 9-10, preoculars 2-2, postoculars 2-2, loreals 1-1 and temporals 2-2-3. An examination of specimens from Sonora and those reported from Sonora by Bogert and Oliver (1945) show, from the limited material available, lower ventral counts than those reported from farther south. Hardy and McDiarmid (1969) list the total range for Sinaloa specimens as 178–189. Specimens available to me, and those reported in the literature, give the range in ventrals as 177–195. Scale rows at midbody are 17 and at vent 13. The color pattern is unique in adults, with the dark spots on the tips of the scales forming fine, broken, diagonal stripes across the dorsal scale rows.

Johnson (1977 and 1982) reviewed the taxonomy and distribution of the whipsnake *Masticophis mentovarious* (Duméril, Bibron, & Duméril), recognized five subspecies, and placed *striolatus* as the northern subspecies. The Chihuahua specimen is well within both the scale counts and color patterns provided in the studies by Johnson.

Masticophis taeniatus girardi Stejneger & Barbour

Masticophis ornatus Baird & Girard, 1853, Cat. N. Amer. Reptiles, pp. 102–103.
Masticophis taeniatus ornatus Schmidt & Smith, 1944. Publ. Field Mus. Nat. Hist. Zool. Ser. 29:90.
Coluber taeniatus girardi Stejneger & Barbour, 1917, Checklist, p. 89.
Masticophis taeniatus girardi Parker, 1982, Cat. Amer. Amph. and Rept., p. 304.
48 mi W Ciudad Chihuahua, 1 (BYU 14128).
7.5 mi E Buenaventura, 1 (BYU 15256).
6 mi E Ricardo Flores Magón, 1 (BYU 19134).
Bridge at Río Urique on La Bufa Road, 1 (BYU 22700).
Sierra del Nido, 1 (UTEP 2519).
72 mi N Ciudad Chihuahua, 1 (UTEP 4097).
6 mi NE Janos, 1 (UTEP 4228).

Smith and Taylor (1945) list the range of this species in México as extending north from central Zacatecas through extreme eastern Chihuahua to western Texas. The records listed above indicate that most of Chihuahua may be a part of its range. While on the Río Urique in September 1963, a large specimen was seen approximately four miles downstream from the bridge. Unfortunately it escaped, but it does establish its occurrence in western Chihuahua.

Ortenburger (1928) recognized the subspecies *girardi* and extended the range south from the south central United States through adjoining central and eastern Chihuahua to Guanajuato.

The scale counts are normal for the subspecies. Ventrals range from 199 to 205, the caudals 125 to 168. The single male has 168 caudals, and the females vary from 125 to 147. All have 15 dorsal rows at midbody and 11 or 12 before the vent.

In adults the lateral light stripe fades into the general body color a short distance before the vent. However, in young and juveniles the light stripe is present, extending onto the tail and involving at the vent only the 3rd and 4th rows. The fading of the light stripes in adults is a character distinguishing *girardi* from the subspecies *taeniatus*.

Opheodrys vernalis blanchardi Grobman

Colubes vernalis (Harlan) 1827. J. Acad. Nat. Sci., Phila., 5:361.
Opheodrys vernalis Schmidt and Necker 1936. Herpetologica, 1(2):63.
Opheodrys vernalis blanchardi Grobman 1941. Misc. publ., Mus. Zool. Univ. Michigan 50:11–37.
1.6 mi N Pederhales (24 mi SE Guerrero, on Highway 16), 1 (UAZ 34416).

The occurrence of the green snake is added evidence that the recent past did indeed have a climate and thus ecological conditions permitting a wide dispersal of many species. The passed distribution of this species must have extended throughout much of the intermountain area from Wyoming, Colorado, Utah, New Mexico, and northwestern Chihuahua. There is reason to believe that its distribution was halted by the deserts of the Great Basin extending from the Snake River in southern Idaho and south through central Utah. The slow desiccation during the last 10,000 to 20,000 years has driven this species as well as others (a good example is *Lampropeltis pyromelana*) into more suitable habitats in mountains (6000 ft) well above the desert valleys. The numerous disjunct areas suggest that there may be other mountainous areas not yet discovered in what appears to have been its past area of distribution.

Oxybelis aeneus auratus (Bell)

Dryinus aeneus Wagler, 1824, Serpentum Brasiliensum Species Novas, p. 12.
Dryinus auratus Bell, 1825, Zool. Jour. 2:324–326.
Oxybelis aeneus auratus Bogert & Oliver, 1945, Bull. Amer. Mus. Nat. Hist. 83:381.
Arroyo Santa Anita, 1 (BYU 22485).
Rio San Miguel, 1 (BYU 38338).

These female specimens were taken in the drainage basin of the Río San Miguel in southwestern Chihuahua; it is another species that has entered the state by way of the El Fuerte River basin.

The scale counts are within the limits set forth by Bogert and Oliver (1945) for the species in México; however, the ventrals at 201 and 202 and caudals up to 185 are more than for the Sinaloa female specimens (183–195 and 175–176) reported by Hardy and McDiarmid (1969) but are within the range reported for Sonora (Bogert and Oliver 145:387). On the right side of specimen 22485 there are 2 preoculars, one being formed from a division of the upper posterior (orbital) part of the normal preocular.

These are new records for the state of Chihuahua.

It is obvious that the 1-2 preocular pattern is an anomaly in this specimen. An examination of a few specimens in our collection from Venezuela, Costa Rica, and western México indicates that throughout the greater range of this species the normal preocular formula is 1-1; however, the occurrence of 2 preoculars, as reported by Taylor (1941) in his description of *Oxybelis potosiensis*, may not have been an anomaly. Bogert and Oliver (1945) did not see the type specimen or others from or near the type locality.

Keiser (1970:227) provides a key to the species of the genus *Oxybelis*. His catalogue report (1982) provides a complete synonomy for *Oxybelis aeneus* (Wagler). The map for the species includes the edge of southwestern Chihuahua, but it is not clear as to whether a collecting locality is within the state.

Pituophis melanoleucus affinis (Hallowell)

Pityophis affinis Hallowell, 1852, Proc. Acad. Nat. Sci. Philadelphia 6:181.
Pituophis melanoleucus affinis Smith & Kennedy, 1951, Herpetologica 7:93–96.
2 mi E Colonia Dublán, 2 (BYU 13878–9).
6 mi SE N Casas Grandes, 1 (BYU 15324).
16.4 mi SE N Casas Grandes, 1 (BYU 15359).
23.3 mi SE N Casas Grandes, 1 (BYU 15369).
Eastern limits of Casas Grandes, 1 (BYU 15370).
8 mi NE Colonia Juárez, 1 (BYU 15374).
Galeana, 1 (BYU 15255).
1.5 mi S Galeana, 1 (BYU 15258).
12.5 mi S Galeana, 1 (BYU 15353).
21 mi E Buenaventura, 1 (BYU 15354).
23.9 mi SE N Casas Grandes, 1 (BYU 15355).
2 mi W Sueco, 1 (BYU 42245).
18 mi W Sueco, 1 (BYU 15352).
25 mi W Sueco, 1 (BYU 15336).
Colonia Juárez, 2 (BYU 15430 and 18249).
3 mi S Palomas, 1 (BYU 14651).
4 mi W San Francisco del Oro, 1 (BYU 15378).
1 mi W Chuhuichupa, 1 (BYU 13877).
21.7 N Ciudad Chihuahua, 1 (BYU 15323).
46.7 mi W Ciudad Chihuahua, 1 (BYU 22686).
23.5 mi N Ciudad Chihuahua, 1 (BYU 32042).
48 mi W Ciudad Chihuahua, 1 (BYU 13881).
4 mi E Cuauhtemoc, 1 (BYU 15385).
25 mi E Cuauhtemoc, 1 (BYU 15428).
5 mi W Miñaca, 1 (BYU 17083).
60 mi S Ciudad Chihuahua on Highway 45, 2 (BYU 15772 and 41339).

Aside from the locality records listed above, DOR snakes were seen along Highways 45 and 10 and from Ciudad Chihuahua west to La Junta. Most were badly mashed and were not kept. The records do, however, place this species throughout central and western Chihuahua.

None of the Chihuahua specimens reach the upper limits of the ventrals set by Klauber (1947:220–251). Ventrals range in males from 213 to 232 (225.1); females range from 223 to 238 (228.7). Caudals in males range from 62 to

69 (64.66), and females range from 52 to 61 (55.28). In both sexes the caudal ranges varied less than 10 scales. The range in the ventrals was greater but showed a lower mean than was projected by Klauber for specimens studied from the entire geographical area occupied by *affinis*. In the preoculars, 16 had 1-1, 7 had 2-2, and 3 had 1-2. Postoculars were 3 or 4 in nearly equal numbers, and the scale rows were 29 to 33 at midbody, with 31 rows being the usual number. With few exceptions, the rows at the vent were 23. Sixteen specimens had 8-8 supralabials, with others having 8-9 or 9-9. Infralabials were usually 12-12, but with 12-13 or 13-13 occurring frequently.

The scale counts are generally lower than those obtained from specimens seen from Sonora and areas from the western part of the *affinis* range.

Dorsal spots on the body range from 26 to 56, average 42.7. Klauber lists the range as 34–63 with an average of 48. The male specimen with 26 spots came from the western mountains near Chuhuichupa; its spots are large, round, and without the usual convexity so common in most specimens. The next lowest number is the specimen from Miñaca with 32 spots. Otherwise, the specimens are within the recorded range of variation in scale and color patterns.

Klauber (1947) gives the ratio of the length of the tail to the total length as about 0.136 in males and 0.125 in females. He obtained these ratios from western specimens and states that the more eastern population would have shorter tails. This is not borne out from the smaller series from Chihuahua in which the males range from 0.129 to 0.157 (.143), and the females from 0.120 to 0.144 (.132). Perhaps the present series (29) from Chihuahua is more representative of the eastern populations than material seen by Klauber. His intrasubspecific trends are, except for ratios, seemingly valid; and, yet, an in-depth study of the *affinis* complex, including a more balanced distribution of specimens, would provide a better understanding of the variation in this widely dispersed subspecies.

Rhadinaea hesperia hesperioides Smith

Rhadinaea hesperia Bailey, 1940, Occ. Pap. Mus. Zool. Univ. Michigan 412:8–10.

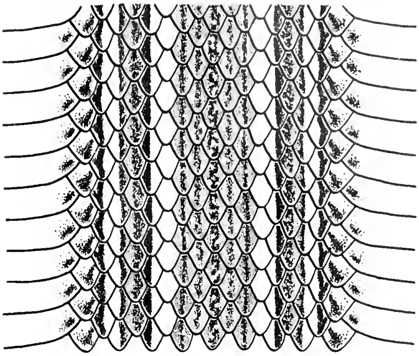

Fig. 4. Color pattern of *R. h. hesperioides* as seen in specimen from south of Guachochic (BYU 22483).

Rhadinaea hesperia hesperioides Smith, 1942a, Proc. Biol. Soc. Washington 55:186.

Rhadinaea hesperia Myers, 1974, Bull. Amer. Mus. Nat. Hist. 153:81.

30 mi (by road) S Guachochic, 1 (BYU 22483).

This female specimen, taken in the Río San Miguel Valley in southwestern Chihuahua, is a new record for the state. Based on published records available, it is at least 250 miles north of the previous records at Plomosas and Santa Lucía in southern Sinaloa. The specimen was taken in the lower edge of the pine forest well above the lowlands along the Río San Miguel. Except that the ventrals (159) are more than any specimen thus far reported for Sinaloa (149–154), the scale counts are similar: 17-17-17 scale rows, 121 caudals, 8-8 supralabials, 10-10 infralabials, 1-1 preoculars and 1-1 presuboculars, 2-2 postoculars, 1-1 loreals and 1-2 temporals. The specimen is a subadult, 250 mm total length and, of this, 90 mm is tail (36% of total length). The high ventral count may be an indication of a south to north cline, a reversal of the north-south clinal trend from west central Mexico (Jalisco-Michoacán) into Guerrero and Oaxaca.

The color pattern is in variance to the description of Myers (1974) for specimens from southern Sinaloa (Fig. 4). At midbody the dorsolateral stripe is on rows 5-6-7, with only the edges of rows 5 and 7 involved, but with more of row 5 included than row 7. On each scale of row 5 below the light stripe is a series of dark spots involving most of the ventral part of the scale and forming, in contrast to the light stripe, a broken dark line. There are no discernible dark stripes on rows 7 or 8. The dorsal area between the dorsolateral stripes is pigmented with brown and with dark flecking in the center of row 9, but without a distinct solid, dark stripe. A distinct, light line on the adjacent halves of rows 2 and 3 is clearly visible and is bordered both below and above by narrow, dark stripes. The area between this lateral stripe and the dorsolateral stripe is pigmented as the dorsal rows (8 and 9). The supralabials are edged above with dark stripe, but also with a series of irregular, dark spots near their ventral center, forming a broken line extending to the spots on the edge of the ventrals. The temporal stripe is distinct and extends only to the nasal scale. This stripe is two plus scales anterior from the dorsolateral stripe.

Although the color pattern differs from both *hesperia* and *hesperioides* as described by Myers (1974), it does conform closely to the latter as described by Smith (1942a). A series from southwestern Chihuahua and/or northern Sinaloa is needed before a final judgment can be made as to the final disposition of the subspecies *hesperioides*. Smith (1942a), in describing *hesperioides*, makes the following statement: "A light stripe, most distinct anteriorly, on adjacent halves of second and third scale rows." This, along with other characteristics, seemingly places not only this specimen in the subspecies *R. h. hesperioides* but also seems to justify the recognition of *hesperioides* as a valid taxon.

A review of the literature (Smith 1942a, Hardy and McDiarmid 1969, Myers 1974) indicated that I should at least examine some specimens from Sinaloa for comparisons before concluding this species report. The three KU specimens (75629, 80870–1) seen, figured, and discussed by Myers were examined. In both 80871 and 75629, the lateral, light line on rows 2-3 (noted by Smith in the type series of *hesperioides*) is clearly evident. Myers (1974, Fig. 11-L) illustrates the body color pattern of KU 80871 but represents it as not having a lateral, light stripe on rows 2-3. However, the stripe is present not only on KU 80871 but also on KU 75629, and it extends the length of the body. In the larger specimen (KU 80870) from 12.3 km (by Highway 40) SW of Santa Lucía, the lateral line is faint but discernible. The question arises as to whether there is a fading or blending of the lateral pattern in older individuals. In any event, the few specimens available from Sinaloa and Chihuahua suggest that the subspecies *R. h. hesperioides* should be recognized based on its distinct color pattern (Fig. 3).

Rhinocheilus lecontei tessellatus Garman

Rhinocheilus lecontei tessellatus Garman, 1883, Mem. Mus. Comp. Zool. 8(3):74.

Rhinocheilus lecontei tessellatus Medica, 1975, Cat. Amer. Amph. and Rept., p. 175. Type locality, Monclova, Coahuila; Klauber, 1941. San Diego Soc. Nat. Hist. 9(29):302–308; Smith and Taylor, 1945. Bull. U.S. Nat. Mus. 187:121.

6.7 mi NW Chihuahua City, 2 (BYU 15284 and 15318).
33 mi N Chihuahua City, 1 (BYU 15285).
37 mi N Chihuahua City, 1 (BYU 15286).
17 mi S Sueco, 1 (BYU 15343).
9 mi N El Sauz, 1 (UTEP 1309).
3 mi W Jiménez, 1 (UTEP 4096).
13 mi NW Jiménez, 1 (UTEP 4227).
18 mi S Villa Ahumada, 1 (UTEP 4545).
6 mi S Moctezuma, 1 (UTEP 4546).

The scale counts and color patterns were consistently within the range limits listed by Klauber (1941) for this subspecies. One specimen (BYU 15318), compared with Ridgeway color Plate 1, was nearly equal to the color listed as Geranium Pink.

Unfortunately, most of the specimens were DOR. However, the distribution records do place this species within the central part of Chihuahua from south of Juarez City along Highway 45 to the Durango border. The greatest concentration seems to be between Villa Ahumada and Ciudad Chihuahua. Why, with our many trips from El Sueco to Casas Grandes, we did not see this species is not explainable; it is suspected to be present in most of the desert valleys between the western mountains and the eastern deserts.

Salvadora g. grahamiae Baird & Girard

Salvadora grahamiae Baird and Girard, 1853, Cat. N. Amer. Rept. pt. 1:104.

Salvadora g. grahamiae Bogert, 1939. Publ. Univ. California Los Angeles 1(10):186–189.

7 mi from Highway 10 up Tinaja Canyon, 1 (BYU 13850).
27 km SW Colonia Juarez, 1 (BYU 15462).
2.2 mi NE Hidalgo del Parral, 1 (UAZ 26183).
Los Leones, 18.4 km Yepomera, 1 (UAZ 34417).

Bogert (1939) lists four specimens from Chihuahua (possibly USNM 8225), Presidio del Norte (USNM 2080), Barranca del Cobre (R. T. Moore, No. 24), and Batopilas (USNM 46505). Smith (1943) lists the specimen from Batopilas (USNM 46505) as *S. h. deserticola*.

The two specimens from north central Chihuahua (BYU 13850 and 15462) have the same basic characters seen in specimens from New Mexico and Texas. Ventrals 186 in a male and 197 in one female; caudals 103 in male, female tail incomplete. The head of the female is badly mashed, but the male has the following head scales: supralabials 8-9 with the 2nd contacting the 1st section of the nasal on one side; 2nd supralabial in contact with loreals; loreals 1-1; preoculars 4-4; postoculars 2-2; temporals 1-3-2; infralabials 9-9; posterior chin shields shorter than anterior and divided by two small scales. Color pattern is as illustrated by Schmidt (1940:145).

The above data are a close approximation to the description of the type as reported by Schmidt. Both specimens were collected at about 1700-1800 m (5500-6000 ft), well above the desert valleys to the east, corresponding to the habitat reported for the species in the Huachuca Mountains of Arizona and the Chisos Mountains of western Texas. The habitat in Chihuahua (as we observed it) is in the scrub oak between the desert valleys and the longleaf pine habitats.

Bogert and Oliver (1945) identified the specimen from the Barranca del Cobre (RTM 24) as *S. bairdi*. Smith (1943) lists a specimen (USNM 46505) from Batopilas as *S. h. deserticola*. Hardy and McDiarmid (1969) list both species as occurring in Sinaloa, and it is thus possible that both occur in southwestern Chihuahua, where many species have ascended the river valleys from the coastal lowlands.

A comparison of the data presented by Schmidt (1940), Smith (1943), Bogert and Oliver (1945), Hardy and McDiarmid (1969) and the data available to me suggest that there is a close relationship between *bairdi* and *grahamiae*. There is little or no basic difference in the scalation between *grahamiae* and *bairdi*. An overlapping of scale patterns occurs or the patterns do not vary. The head and body proportions are the same and the rostral scale is the same in both. The only real variation occurs in the color patterns. Sinaloan specimens examined (BYU 37929, KU 68753) and those reported by Hardy and McDiarmid (1969) have a dark lateral stripe on the 3rd scale row. Specimens of *S. g. grahamiae* usually do not have this stripe but do have a dark spot at the base of each scale on the third row. These spots vary in size, with some individuals having small ones and others much enlarged ones forming a dotted stripe. This remnant may be the modified stripe so apparent in *bairdi*.

The two specimens from central and southern Chihuahua (UAZ 34417 and 26183) are similar in scalation but show variation in the color and color pattern. Specimens from Coyotes, Durango (UAS 28077 and 37737), have similar scalation to those from Chihuahua but vary in the color pattern. This variation ranges from a light, tannish brown to a darker brown lateral to the middorsal stripe. The lateral stripe may be present on row 3 or rows 3 and 4 as in UAZ 34417, 28077, and 37737, or it may be represented as a series of spots at the base of each scale on row 3 as in UAZ 26183 and BYU 13850 and 15462.

A specimen from Arroyo El Noghlito, west side of Sierra La Madera, 10 mi E Cumpas (UAZ 44947), and one from the west slope of San Luis Mts (UAZ 26182), Sonora, are also with distinct spots at the base of each scale but in these on row 4. These specimens extend the range of *grahamiae* into central and northeastern Sonora.

The distribution of *S. grahamiae* in Mexico is at least in the foothills of Chihuahua east of the mountains and extending south along the eastern escarpment to Zacatecas. Although specimens are not available from Northwest Chihuahua, the specimens from Sonora (east of Cumpas) suggest that the distribution includes those suitable habitats surrounding the Sierra Madre in northern Chihuahua and eastern Sonora.

With the geographical ranges coming ever closer in Sonora, and since there is little or no basic difference in scalation between *grahamiae* and *bairdi*, and since they share a similar color pattern, I am persuaded to include *bairdi* as a subspecies of *Salvadora grahamiae*. Thus, in Chihuahua there are the following: on the eastern foothills of the Sierra Madre and possibly extending at least around the northern end of these mountains into Sonora is *Salvadora grahamiae grahamiae*

Baird and Girard. On the western front of the Sierra Madre in southern Sonora, southwestern Chihuahua, and Sinaloa is *Salvadora grahamiae bairdi* (Jan).

Salvadora deserticola Schmidt

Salvadora hexalepis deserticola Schmidt, 1940, Publ. Field Mus. Nat. Hist. Zool. Ser. 24:146.

Salvadora deserticola Smith & Brodie, 1982, A Golden Field Guide, Western Publishing Co., p. 194.

2 mi N Colonia Juárez, 3 (BYU 13351, 15465 and 16109).
14 mi N Colonia Dublán, 1 (BYU 13978).
4 mi SE N Casas Grandes, 1 (BYU 13851).
6 mi NE Colonia Juárez, 1 (BYU 15372).
2 mi N Galeana, 1 (BYU 15357).
5 mi NW Galeana, 1 (BYU 15280).
23 mi E Buenaventura, 1 (BYU 15259).
6.7 mi N Chihuahua City, 2 (BYU 15287–8).
12 mi from Chihuahua (probably the City), 1 (MVZ 43656).
1 mi W Ojo Laguna, 1 (MVZ 73030).
20 mi SE Ciudad Camargo, 1 (MVZ 80001).
3 mi W Ciudad Camargo, 1 (UTEP 1318).
Río Santa María near Progreso, 6 (USNM 104668–73).
Near Balleza, 1 (USNM 46504).
Casas Grandes, 2 (USNM 46375–6).
Batopilas, 1 (USNM 46505 not seen).
Chihuahua, 2 (USNM 14255 and 14295).
Cd. Chihuahua, 1 (USNM 46451).
Lake Santa María, 1 (USNM 46594).

All of the specimens examined by me from Chihuahua were taken in the desert valleys between Highway 45 and the western mountains, except for those taken by Nelson and Goldman and reported by Goldman (1951: 118–9). All were taken in central Chihuahua except the Batopilas specimen and at elevations up to 1800 m (6,000 ft). This species does occur west of the mountains in Sonora and Sinaloa, and does also range into the lower valleys of southwestern Chihuahua.

Twenty-nine specimens from Chihuahua and the adjoining states of Sonora (2) and one each from New Mexico and Texas have the following scale counts: ventrals, males 179(186.3)202, females 183(189.6)204; caudals, males 76(80.0)103, females 68(71.0)74. Supralabials 9-9 in all (except one with 9-10), and infralabials usually 9-9 but also with 10 or 11 occasionally occurring on one or both sides. Preoculars usually 2-2 (1-1 in two, 1-2 and 2-3 in one), postoculars 2-2, and temporals 2-3 or 2-2. Scale rows are 17 at midbody and 13 before the vent. In the Chihuahua series, the infralabials are usually 10 on at least one side but with an occasional individual with 9-9 or 9-10.

The two specimens from the vicinity of Navojoa, Sonora, both have ventral counts that exceed 200 (202–204). None of the Chihuahua specimens exceed 197, and they average 189 (179–197). A larger series from the entire range may indicate the significance of these and other variations within this species.

Bogert and Oliver (1945:404) reported a specimen from Ahome, Sinaloa, with 205 ventrals. The two specimens listed above from Sonora (a male and female) indicate that the number of ventrals in northern Sinaloa and Sonora may average higher than in eastern Chihuahua.

Sonora semiannulata Baird and Girard

Sonora semiannulata Baird and Girard, 1853, Cat. N. Amer. Rept., p. 117.

Sonora semiannulata isozona Stickel, 1943, Proc. Biol. Soc. Washington 56:120.

Sonora semiannulata Frost, 1983, Cat. Amer. Amph. and Rept., p. 333.

6.5 mi N (by road) and 1.5 mi W of Chihuahua City, 14 (BYU 14203–6, 15289–91, 17001–7).
3.7 mi (by road) N Chihuahua City, 1 (BYU 15292).
11.5 mi SE Nueva Casas Grandes, 3 (BYU 13852, 14246, 17692).
Mezquite, approximately 17 mi SW Chihuahua City, 1 (KU 56228).

A series of 20 specimens is available from an area extending from Casas Grandes south to 25 km (16 mi) south of Chihuahua City. Within the populations that have been sampled, and particularly those 9 km (6 mi) northwest of Chihuahua City, all have the color variations previously reported for the subspecies *isozona* (Stickel 1943, Tanner and Jorgensen 1963). The plain grey, the normal bicolored, and the various modifications in between range from one specimen with bright, scarlet red (without dark bars) on the scale rows to those with red lines the length of the body and without any trace of black bands and those with a more uniform orange on the more dorsal scale rows and grey extending from the ventrals onto the first few rows of dorsals. The specimens seen from Idaho through Utah, southern Nevada, and Arizona have also exhibited this complete range of color patterns, and there is little variation that has not been encountered throughout the very broad range of the species *semiannulata*.

The major differences between the Chihuahua specimens and a large series from southern Utah and Nevada is to be found in the number of ventrals and occurrence of the standard bicolored pattern in the Utah population. The 9 males from Chihuahua show an average of 151.5 (148–154) ventrals and 53 (52–54) caudals whereas the Utah specimens average 164 (159–168) ventrals and 55.4 (50–61) caudals. The females in Chihuahua average 162 (160–168) and in the Utah series 175 (168–178), with caudals 47.8 (45–51) and 45.3 (42–49), respectively.

Although Stickel (1938) gave considerable general information concerning the subspecies of *Sonora semiannulata*, some of the details, particularly with reference to the subspecies *blanchardi*, are lacking. The available information suggests that the Chihuahua population may be more closely associated with Stickel's *blanchardi* than to either *s. semiannulata* or *s. isozona*. Tanner and Jorgensen (1963) discussed the many color patterns that occur in this species, and I have since concluded that pattern is not a useful character to be used in the identification of the subspecies of *semiannulata*. Apparently there is an increasing cline from southeast to northwest in the number of ventrals, all of which raises a question as to the justification for recognizing the several subspecies occurring between Chihuahua, western Texas, and the areas extending westward through New Mexico, Arizona, Utah, Nevada, and Idaho. The color patterns and scalation patterns seem to justify not recognizing subspecies at this time, as recommended by Frost (1983) also.

Storeria storerioides (Cope)

Tropidoclonion storerioides Cope, 1865, Proc. Acad. Nat. Sci. Philadelphia 17:190–191.
Storeria storerioides Garman, 1883, Mem. Mus. Comp. Zool. 8(3):29.
26 mi W San Juanito (by road), 1 (BYU 16955).

This specimen was taken 12 July 1960 from among rocks and litter under a rotten spruce log on the north side of a wet, rocky slope.

Anderson (1960) reported on two specimens he collected at Yaguirachic, a locality almost directly west of La Junta and approximately 128 km (80 mi) north of the specimen taken west of San Juanito. These specimens were taken in moist or wet habitats and in pine or fir forests.

A comparison of the scale patterns of the three Chihuahua specimens to those reported by Cope (1900), Taylor and Smith (1938), and Duellman (1961) do not indicate any important variations except that the ventrals seem to be fewer, perhaps representing the lower end of a north-south cline. The ventrals are 124–127, caudals 37–49 and the scale rows are 15-15-14. Other scale and color characters do not seemingly vary from data available from specimens taken in central Mexico and from those reported by Anderson (1960). Perhaps the most remarkable fact concerning these records is that they represent a northern extension of the range into central Chihuahua, a distance of more than 480 km (300 mi) from records in Durango and Sinaloa.

Sympholis lippiens rectilimbus Hensley

Sympholis lippiens rectilimbus Hensley, 1966, Herpetologica 22:48–55.
Urique, 3 (KU 56229–31).

The three specimens have scale and color patterns that are well within the limits set by Hensley (1966) except for the female (KU 56230), which has 17 caudals, and KU 56231, which has a light spot on the parietals rather than the cream-colored band covering the entire posterior area of the head. Hensley described the pattern but did not identify the specimen. This is another species that has entered Chihuahua from Sinaloa by way of the deep barrancas cut by tributaries of the Río Fuerte.

These three specimens, by the way, have an interesting history. Before leaving Urique in August 1958, we left with the Presidente a gallon jar containing 10% formalin and instructed him to put any small snake in it. We also left a few tags that were apparently lost. Dr. William E. Duellman has been so kind as to provide the field notes of Sydney Anderson, which are as follows: "Above specimens collected in August 1959 by Mexican in Urique who had jar of formalin given him by American last August." The date in Anderson's field catalog is 11 May 1960.

Because adequate material was not available to determine variation in certain characters, both scutellation and color patterns, Hardy and McDiarmid (1969) refrained from recognizing the subspecies *rectilimbus*. I have examined only five specimens—three from Chihuahua (KU 45229–31), one from Sonora (11 mi WSW of Alamos, BYU 41197), and one from Sinaloa (11.6 mi S of Rio Piaxtla, DOR on Highway 15, BYU 23927). Although none of these were reported by Hardy and McDiarmid (1969) and three are paratypes of *S. l. rectilimbus* Hensley, a brief discussion seems warranted.

Three areas concerning this subspecies need further investigation: (a) there is a clinal increase in the ventrals and caudals from south to north, with the higher counts occurring in the north; (b) the dark bands may be as broad as 7–12 scales across and the light bands as narrow as 1 and 1/2–3 scales (according to previous published reports, the dark bands are narrower and the white bands up to 5 scales across); (c) the head and nape pattern is variable, showing at least three distinct arrangements of the white nape pattern. Two are described and figured by Hensley (1966), and in a third the usual wide, light nape band is restricted to a small spot completely surrounded by the dark of the frontal, temporal, and the first dark body band. One of the Chihuahua specimens and the one from Sonora have this pattern.

Considerably more specimens must be studied before one can determine which pattern or patterns represent the subspecies *S. l. rectilimbus*.

The material I have seen, though variable and with indications of subspeciation, does need a study of a much larger series than has been available thus far. Until such a study is made, I prefer to retain the subspecies *Sympholis lippiens rectilimbus* Hensley.

Tantilla nigriceps Kennicott

Tantilla nigriceps Kennicott, 1860, Proc. Acad. Nat. Sci. Philadelphia 12:328.

Tantilla nigriceps nigriceps Smith, 1938, Copeia (3):150.

Foothills east edge of Colonia Juárez, 2 (BYU 14299 and 16105, both females).

Chihuahua City, 1 (BYU 14340) (badly damaged).

Only the scale counts for the Colonia Juárez specimens are available. The ventrals are 163 and 156, respectively, and the caudals in the latter are 47. In all three specimens the head cap is 3–5 scales posterior to the parietals and is angular shaped in one and pointed in two.

The specimen from Chihuahua City was given to me while at a motel in the northern part of the city. It had been killed and was partly eaten by ants. The only real characters for identification are the extension of the head cap at least four scales posterior to the parietals and the wide separation by the first pair of infralabials of the mental from the anterior pair of genials. Cole and Hardy (1981) list five specimens from Chihuahua along Highway 45 (S Samalayuca and Villa Ahumada) and west along Highway 10 into the Nuevo Casas Grandes area.

According to Cole and Hardy (1981), the geographic ranges of *T. nigriceps* and *T. hobartsmithi* broadly overlap in Chihuahua. I have not found this to be the case, nor are there actual distributional data in their report (1981 or 1983) to support such a conclusion. Their range map places *T. hobartsmithi* well to the east of any known locality records for *T. nigriceps* if we base their conclusions on the data presented. There may be an overlapping of ranges in this area, but as yet this has not been demonstrated.

In view of the wide range of *T. nigriceps*, it would be more convincing if additional data would have been presented to justify the extremely narrow extension of *T. hobartsmithi* into eastern Chihuahua. Based on the data they presented, females from that area could belong to either species. Reynolds and Scott (1977) list three specimens of *T. nigriceps* from along Highway 16.

Tantilla wilcoxi Stejneger

Tantilla wilcoxi Stejneger, 1902, Proc. U.S. Nat. Mus 25:156. Ft. Huachuca, Arizona.

Red Rock, 12 mi up Tinaja Canyon, 2 (BYU 13847–8).

50 mi W Chihuahua City (Highway 30), 1 (BYU 13849).

25 mi SE Creel (La Bufa Road), 1 (BYU 16863).

The following data apply to the specimens listed above. Males: ventrals 149–158, females 153–159. Only one male and one female had a complete tail, with 72 and 69 caudals, respectively. By including the data of four specimens reported by Taylor and Knobloch (1940), the following range for three males and five females is: ventrals 149(154)158 and 153(158.8)164. The caudals in two males are 62 and 72 and in three females 64, 67, and 69. Head scales are uniform and there are 15 dorsal rows in all specimens.

Color pattern in the four specimens listed above is uniform. The nape ring involves the tips of the parietals and one or two posterior scales.

Only a few specimens of *Tantilla wilcoxi* have been collected in Chihuahua. Taylor and Knobloch (1940) reported four specimens from the Sierra Madre Occidental, presumably taken in the vicinity of Majorachic. In a recent study by Cole and Hardy (1981), a single specimen is listed from the vicinity of Stacíon Barbara. During the years spent in Chihuahua, four additional specimens were collected (as listed above). The specimen taken south of Creel represents the most southern extent of the known range in Chihuahua. There is little variation in the scale or color patterns exhibited by the specimens taken over the rather wide range in Chihuahua. Those on each side of the Continental Divide show little variation in contrast to some of the other species listed in this report.

Since the above was written, the catalog account by Liner (1983) appeared; it does not include those records listed above from central and northern Chihuahua. Liner's distribution map and the new records in this report suggest that this species may occur in the mountains of central and western Chihuahua from the northern end of the Sierra Madre Occidental south through at least western Chihuahua to perhaps extreme eastern Sonora, Sinaloa, and into most of Durango. Our records indicate a habitat in Chihuahua above 1500 m (5000 ft) and in the area of the foothills on the eastern edge of the Sierra Madre above the desert valleys and extending into the forested areas above 2250 m (7500 ft).

Tantilla yaquia Smith

Tantilla yaquia Smith, 1942, Zoologica 27:41.

Only the type specimen (MCZ 43274, not examined) has been taken in Chihuahua (Guasaremos, Río Mayo). The foothills extending south and then perhaps eastward into the barrancas of the Río El Fuerte may also be included in its geographical distribution.

Thamnophis Fitzinger

Except for the crotalids, the garter snakes are represented in Chihuahua by more species than any other group of serpents. We collected six species with three additional subspecies, and the literature (Smith and Taylor 1945, Fitch 1965) cites a seventh. Since the report by Smith and Taylor (1945), a number of studies dealing with this genus have appeared (Bogert and Oliver 1945, Thompson 1957, Tanner 1959a, Conant 1963, Fitch 1965, Webb 1966, Hardy and McDiarmid 1969, Rossman 1971, and others).

In none of the studies listed above are all the species of *Thamnophis*, known to occur in Chihuahua, examined as a group and their distribution and variations considered.

Thamnophis rufipunctatus (Cope)

In recent years this species has been reviewed by several authors, each adding new data. However, the problems of generic designation and the possibility of subspecies within this widespread species warrants additional consideration. The reexamination of its generic position is again evaluated, based on additional material from most of the known areas of distribution. I have examined for this report 148 specimens and have reviewed data by others. Field notes, based on extensive work in Chihuahua and limited travels in Arizona and Durango, provide data on habits and habitats.

As data were evaluated, it became apparent that the species *T. rufipunctatus* has, for reasons of isolation and/or dispersal, developed significant character modifications that warrant the recognition of subspecies. This was most obvious when comparisons were made between *T. nigronuchalis* of Durango and the populations of *T. rufipunctatus* in Chihuahua, as well as the isolated population of the latter in Arizona and New Mexico. These comparisons aided materially in a better understanding of the relationships between the northern, isolated segment of the species and those populations occurring in Mexico. Although *Thamnophis rufipunctatus* is widely dispersed, it has maintained a surprising uniformity in most characters. The scale rows, number of loreals, preoculars, postoculars, labials, and, to a degree, ventrals and caudals, are rather uniform. Only in size and position of some scales is variation present. Color pattern also shows some variation and is with certain scale variations discussed below.

TABLE 2. Ventral and caudal variation in *Thamnophis rufipunctatus*.

Subspecies	No.	Sex	Ventrals	Caudals	Ventral-Caudals
Rufipunctatus	32	M	159(171.0)179	76(81.93)88	240(253.45)263
	25	F	156(164.68)171	67(70.21)79	232(239.1)243
Unilabialis	37	M	155(161.51)169	71(76.2)82	232(239.68)249
	27	F	151(156.68)163	65(69.95)76	219(226.43)239
Nigronuchalis	14	M	157(161.92)167	68(72.54)77	225(234.63)240
	15	F	152(156.53)160	62(66.57)72	215(223.25)230

A comparison of data for the Arizona–New Mexico, Chihuahua, and Durango populations indicates that three subspecies exist. In each case, these populations occur in widely separated drainage systems, with the Arizona and New Mexico specimens coming primarily from tributaries of the Salt River Basin extending along the southern edge of the Mogollon Rim and draining to the south and west. Between this population and that of Chihuahua lie the desert flats, extending from west of Phoenix east and south past Tucson and into southwestern New Mexico. The distance between these two populations is approximately 320 km (200 or more mi). The geographical differences between the Chihuahua *rufipunctatus* and Durango (*nigronuchalis*) populations are not as readily apparent, but they seemingly intergrade with each other somewhere in the highlands of northwestern Durango and/or southwestern Chihuahua.

Data now available clearly indicate that the Chihuahua and northeastern Durango populations represent a distinct group from either those in Arizona or west central Durango. Based on scalation (Table 2) and other characters, these subspecies are distinguished and described below.

Thamnophis rufipunctatus rufipunctatus (Cope)

Chilopoma rufipunctatum Cope, 1875, In Yarrow, Wheeler's Rept. Geog. Geol. Expl. Surv. W. 100th Mer. Zool. 5:544. Type locality, southern Arizona.

Eutaenia angustirostris Kennicott, 1860, Proc. Acad. Nat. Sci. Philadelphia 12:332.
Type locality, Parras, Coahuila, Mexico.

Thamnophis angustirostris Ruthven, 1908, Bull. U.S. Nat. Mus. 61:120.

Atomarchus multimaculatus Cope, 1883, Amer. Nat., p. 1300. Type locality, San Francisco River, New Mexico.

Thamnophis rufipunctatus Smith, 1942c, Zoologica 27(3–4):120.

Natrix angustirostris Lowe, 1955, Copeia 1955(4): 307–309.

Thamnophis rufipunctatus Thompson, 1957. Occ. Pap. Mus. Zool. Univ. Michigan 584:1–10; Tanner, 1959a, Herpetologica 15(4):165; Conant, 1963, Copeia 3:480.

DIAGNOSIS.—A moderate- to large-sized subspecies usually with 21-21-17 scale rows, head elongate and compressed laterally; 1 loreal, 2 preoculars, usually 3 postoculars with the inferior one being narrowly separated from or barely contacting the 4th supralabial in 75% of the specimens; 2 or occasionally only 1 supralabial entering orbit; ventrals 156 to 179, caudals 67–88, ventral-caudals average 239 ♀, 254 ♂; (Table 2); ground color brown to olive brown, with 6 rows of dark brown or rust colored spots.

DISTRIBUTION.—Central Arizona east from Yavapai County into west central New Mexico.

SPECIMENS EXAMINED.—*Arizona:* UAZ 26543, 30944, 31384, 41344, Oak Creek Canyon; 26454–55, Big Bonito Creek at bridge to Maverick, Navajo Co.; 26456, Eagle Creek School, Greenlee Co.; 26457, East Fork of White River, 3 mi E Fort Apache, Navajo Co.; 26458, Point of Pines, Graham Co.; 26459, 15 mi SW Flagstaff, Coconino Co.; 26460, Black River at Diamond Fork, Greenlee Co.; 30951, Slide Park, Oak Creek Canyon, Coconino Co.; 30955, Oak Creek 1/2 mi up from Slide Rock; 31392, 31396 and 41343, East fork of Black River at Diamond Rock Camp, Apache Co.; 34157, 23 mi S Flagstaff; 37035 S of Sedona; 37824, Oak Creek 5–7 mi N Sonoma; 41342, 7 mi S Noury Ranch, Yavapai Co.; 41345–47, Kitbridge, Oak Creek Canyon; 41348–51, 18–20 mi S Flagstaff; 41352–55, 8–9.7 mi above Sedona; 44775, 2 mi by river below white crossing, Apache Co.; BYU 11465, Black Canyon, Yavapai Co.; ASU 10542, Gila Co.; NMMZ 8465, McNary fish cultural station; "17923, Black range at 10 of diamond ranch"; 13567–9, FAI, reservation, Black River at old military crossing, Apache Co. *New Mexico:* NMMZ 387, Río San Francisco, 2 mi above Frisco Hot Springs; 385–6, Beaver Creek, Catron Co.; 7442, near Gila Cliff Dwellings Nat. Park, Grant Co.; 4582, Mogollon Mts. 2.5 mi W Wall Lake, Middle fork of Gila; 4616–7, 6023, E of Luna, Wall Dake; 6809, E of Luna, Glenwood Canyon; 10832, approx. 5 mi E Glenwood; 32017, Pleasanton E of Luna; 41625, West fork of Gila River 9 mi upstream from Gila Cliff Dwellings, Catron Co.

REMARKS.—In this subspecies, as in the Chihuahua form, only rarely does the midbody scale rows vary from 21. When variation occurs, an increase is to 22 or 23 rows (two specimens of each). In 53 specimens (106 counts), there are 2–5 postoculars with 80 having 3, 21 having 4, 4 with 2 and one with 5; those with only 2 postoculars have 2 supralabials widely contacting the orbit. In those with 3-3 postoculars, approximately 75% have a narrow contact of the 5th supralabial and the eye on one or both sides (Fig. 5A), or only reaching the 4th labial (Fig. 5B).

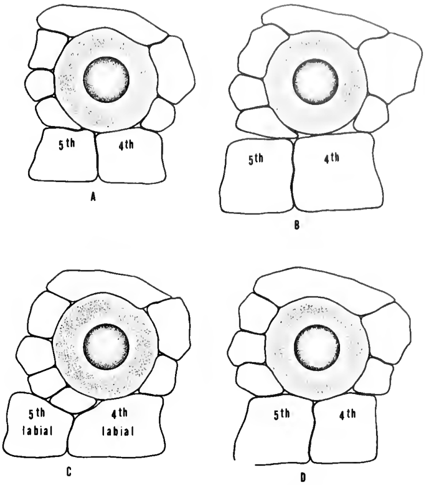

Fig. 5. The relationship of the supralabials and lower postoculars to the orbit in: A, (AUZ 31392); and B, (NMMZ 6023) relationship as seen in *Thamnophis r. rufipunctatus;* C, (BYU 14218) as seen in the Chihuahua–northeastern Durango populations (*Thamnophis r. unilabialis*); and D, (UTEP 3654 or LSUMZ 16450) as seen in *Thamnophis r. nigronuchalis* from west central Durango.

There is a distinct difference between *T. r. rufipunctatus* and specimens of the species from Chihuahua, the former having a greater number of both ventrals and caudals. There is only a slight overlap in ventral count and noteworthy differences when these scale counts are combined and averaged (Table 2).

In the subspecies *rufipunctatus*, the divided anal variation occurs primarily in populations of Oak Creek in Yavapai Co., Arizona, whereas this variation occurs in the Chihuahua and Durango subspecies only rarely. I am aware of only two specimens, AUZ 26465 from García, Chihuahua, and LSUMZ 16459 from 8.3 mi W El Salto, Durango.

Lowe (1955) placed *T. rufipunctatus* in the genus *Natrix*, based on the divided anal in some specimens of the Arizona population and on habits, color pattern, and its "water snake"–like habitude. Thompson (1957) reexamined the series seen by Lowe and included 14 additional specimens, in which 7 of the series had divided or partly divided anals (25% of the series). From these data he chose to retain *rufipunctatus* in the genus *Thamnophis*. Tanner (1959a) examined 52 specimens from Chihuahua and concurred with Thompson in retaining *rufipunctatus* in the genus *Thamnophis*. Conant (1963) also reviewed the previous studies, examined additional specimens from Chihuahua and Durango, and concurred in retaining *rufipunctatus* in the genus *Thamnophis.* Smith (1955) placed *Thamnophis multimaculatus* Cope, which was given species status by Taylor and Knobloch (1940), as a synonym of *T. rufipunctatus.* Thompson (1957) also reviewed the synonymy associated with *rufipunctatus* and, after examining four specimens from Parras, Coahuila, concluded that the type series of *T. angustirostris* Kennicott was in fact more closely related to *T. marcianus* than to Cope's *T. rufipunctatus.* He states that the name *angustirostris* was misapplied by Ruthven (1908) and should now belong in the synonymy of *T. marcianus.*

The placing of *rufipunctatus* in the genus *Natrix*, as suggested by Lowe (1955), is seemingly based primarily on the occurrence of a divided anal in some Arizona specimens. That anomaly has also been reported for *T. e. vagrans* (Tanner, 1950). The divided anal was brought to my attention when students began classifying specimens of our local *Thamnophis* (Provo, Utah) in the genus *Natrix*. There is no question that *rufipunctatus* is an unusual species within the genus; with the elongate snout and narrow head, it appears to have become adapted for feeding on small, aquatic vertebrates—particularly fish and tadpoles. However, other species in the genus that are aquatic have not evolved the same head modification, indicating only that great flexibility exists within the genus *Thamnophis*.

Considering all of these factors, it would seem unjustifiable to place this species in a different genus based on a few anomalous specimens found in localized populations. I have seen 37 specimens from Arizona, and of these 5 have divided anals and 3 show a grooving. This is 21.6% with divided or grooved anals in contrast to a population in central Utah that reached 30%. A series of 25 specimens from eastern Arizona (Apache, Graham, Greenlee, and Navajo counties) and Grant and Catron counties in New Mexico do not have divided anals. Those with this character are generally confined to the local populations in Oak Creek and its tributaries in Yavapai and Gila counties of Arizona.

There may be other characteristics that relate *T. rufipunctatus* to the genus *Nerodia*. An in-depth study may reveal this relationship and justify a taxonomic adjustment as suggested by Lowe (1955). Such a study is beyond the scope of this report, even though it seems an important step. One character not included in previous studies is the structure of the hemipenis. Everted hemipenes of *T. rufipunctatus* are capitate. I note that the hemipenis of one of the spotted *Nerodia* (*harteri*), figured by Trapido (1941), is bilobate and appears from the figure to have a similar spine arrangement; that is, the enlarged spines on the proximal part of the structure occur in two series, with the sperm duct lying between them. Three specimens of *rufipunctatus* were examined (UTEP 3386, UAZ 34158, and LSUMZ 16451), and in each the organ is basically capitate and has two enlarged spines on the outer anterior edge and three on the posterior edge. It is a much different structure than that of *N. harteri*. A comparison of other *Thamnophis* (*elegans*, *cyrtopsis*, and *eques*) to *rufipunctatus*, and the figure for *N. harteri*, suggest a much closer overall structural relationship to *Thamnophis* than to the figure of *Nerodia harteri*. If, as indicated by Cole and Hardy (1981), the structure of the hemipenis is an important taxonomic character, then perhaps the generic status of *rufipunctatus* will not be satisfactorily resolved until an extensive comparative study is made for both *Thamnophis* and *Nerodia*.

Another character peculiar to *T. r. rufipunctatus* is the small, azygous scale separating the rostral from the internasals (Fig. 6). This scale appears randomly throughout most, if not the entire range and may be considered to be a unique character, particularly in the Arizona and some Chihuahua populations. The type of *T. multimaculatus* Cope (type locality San Francisco River, New Mexico) was stated to have this preinternasal scale, and it occurs randomly in specimens from Arizona, New Mexico, and Chihuahua. In the series from Arizona and New Mexico (53 specimens), 40% have the azygous preinternasal. In Chihuahua populations, only 24% of 67 specimens show this character, and the percentage is lower in Durango. Also, more specimens seen from Arizona have 10 infralabials (80.14%), as is also the case for most Chihuahua specimens. Excepted are those from San Pedro on the Papagochic and Bocoyna, which have 9 infralabials in 77.5% of the 20 specimens examined. This is in contrast to a series of 26 from Yepomera (about 80 km or 50 mi N and also on the Rio Papagochic), in which nearly 80% (43 of 52) have 10 infralabials.

The Chihuahua to northeastern Durango populations have both scale and color pattern variations that are different from those in Arizona and southwestern Durango, and compose a new subspecies described as follows.

Thamnophis rufipunctatus unilabialis, n. subsp.

HOLOTYPE.—BYU 14217, an adult female from .5 mi SW of Bocoyna, Chihuahua, Mexico. Collected 11 July 1958 by W. W. Tanner and W. G. Robison.

PARATYPES.—*Chihuahua*: BYU 14213–16, 14218, 14224, 17085–6, topotypes; 14368–14375 and 14485–6, San Pedro on Río Pa-

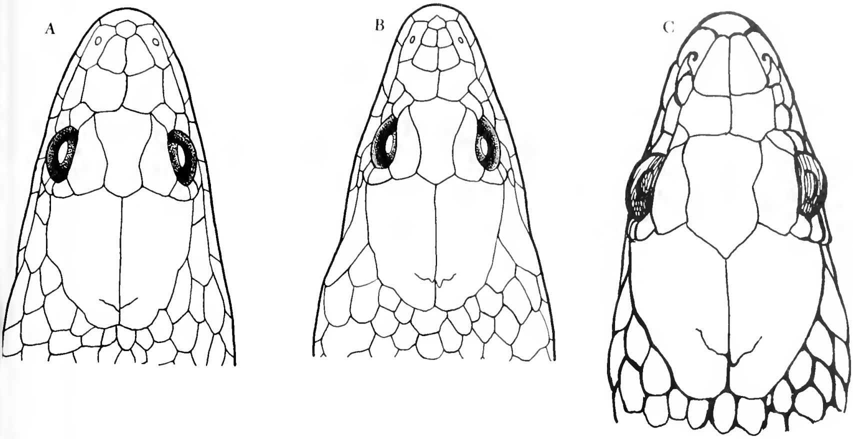

Fig. 6. Relationship of preinternasal scale to nasal and internasals: A, single azygous scale (BYU 14220); B, paired and azygons scales (BYU 13797); and C, usual pattern (BYU 14214).

pagochic; BYU 13797, 2 mi N Chuhuichupa; BYU 14219–20, Black Canyon, 8 mi W Chuhuichupa; BYU 14207, Río Bavispe, below Three Rivers; ASU 5304–6 and 5334–6, 3.8 mi SSE Galeana; ASU 17042, Río Tutuaca; AUZ 26461–2, 35922 and 36290, 4.5 mi SE Galeana; UAZ 34158–63, 34265–79, Yepómera; AUZ 35236, El Norte, 3 mi N Chuhuichupa; AUZ 26463–5, García; AMNH 73754–5, Noragachic; NMMZ 31256, Willys on Río Piedras Verdes; NMMZ 33463–5, ojo de Los Reyes; NMMZ 33478, 4.7 mi SE Galeana. *Sonora*: UAZ 35235, Yecora. *Durango*: UTEP 9078, 6 mi SW Los Frailes.

DIAGNOSIS.—A subspecies of *rufipunctatus* that differs from both *r. rufipunctatus* and *r. nigronuchalis* in having only the 4th supralabial contacting the eye by reason of the lower postocular having a firm contact with the 4th labial; ventrals reduced and ventral-caudal averages 13–15 scales fewer than in *r. rufipunctatus*. Ventral color pattern with anterior margins of scales usually pigmented, forming alternating dark and light transverse bands.

DESCRIPTION OF TYPE.—Head and body length 412 mm; tail at 96 mm, 21.8% of total length; head elongate and compressed laterally, dorsal head scales normal for the species; no azygous preinternasal scale, loreal single, preoculars 2-2, postoculars 3-3, temporals 1-3, scale rows 21-21-17, ventrals 156, caudals 67, anal single, lower postocular with a firm contact on 4th supralabial (Fig. 5C). A longitudinal series in six rows of light rust or dark brown spots (rust spots faded to light spots in preservative) on a dark grey ground color; ventrals and caudals with dark pigmentation on anterior margins, forming dark and light cross bars on ventrals; caudals with reduced pigment forming a dark speckling on a light grey gound color; dorsal head plates dark greyish brown, grading to lighter shades on labials; latter with dark stripes crossing upper third or half of each scale and forming a dark, posterior margin on all but the last 2 supralabials; lower labials with posterior margins edged in dark brown; gulars light grey and without spots.

VARIATION.—In this subspecies, there is little variation among scale and color pattern in the specimens examined. The 67 specimens seen show a small variation of only 8 to 14 scales difference in ventral plus caudal counts, with the greatest variation occurring in the ventrals of males. The one noticeable difference is in the presence of the preinternasal azygous scale, which is seemingly present in most, if not all individuals in the headwaters of the Río Bavispe. Five specimens from Chuhuichupa and its environs all have this scale in several variations (Fig. 6), whereas few specimens on the east side of the Continental Divide and those in the Río Papagochic and Río El Fuerte drainage do not (3 of 45 specimens).

The most noticeable variation in the color pattern is the light, rust-colored spots in some specimens, whereas in others the spots are a dark brown; this difference persists in preserved specimens as faded light spots. Conant (1963), referring to the field notes of R. G. Zweifel, indicates that the live snakes at Miñaca had "reddish spots." The population at San Pedro also had individuals with bright spots, but we determined them to be a bright yellowish rust, quite in contrast to the red colors seen in kingsnakes or bicolored *Sonora*. That this color pattern was not observed in all specimens collected or seen may suggest an expression of a seasonal or sex-induced character.

In a few specimens, the two dorsal rows of spots anteriorly contact each other dorsally, giving the appearance of only 5 rows. The *rufipunctatus* in northern and eastern Durango, Chihuahua, and Arizona have a divided nuchal blotch. This is best seen in young or juvenile specimens in which the nape has a narrow (usually one or a fraction of a scale) light stripe extending from the parietals to divide the dark, irregular blotches. In older specimens, there is a fading or perhaps a blending of the nape color pattern, making it more difficult to identify the divided blotches, especially in preserved specimens. In the young, the spots on the body are dark and readily noted. Posterior to the nuchal blotches in the young is a series of 1–3 dark, middorsal spots. The spots posterior to this series usually divide, forming two rows of dorsolateral spots and thus leaving the normal number of six rows of spots at midbody. In most specimens, the anterior margins of the ventrals are heavily pigmented, but with the posterior much lighter. This produces an even or an irregular cross-barring pattern of dark and light pigment.

On the basis of other studies and our observations, it is obvious that this subspecies occurs throughout the Sierra Madre Occidental of central and western Chihuahua. It is found primarily along streams or in ponds or meadows where fish, tadpoles, and presumably other small, aquatic or semiaquatic vertebrates are foraged. At San Pedro (near Miñaca), we observed a subadult catch a small minnow. When we visited this locality (10 July 1958), the stream was low and clear and the small fish were abundant in the pools along the rocky stream bed. It was also evident that the snakes were feeding on the fish from the fish odor we encountered when the snakes were handled.

At a pond 8 km (5 mi) SW of Bocoyna, this species was feeding on tadpoles. The pond was formed between the road and railroad grades with rocks forming the walls around the pond. Along the water's edge, large numbers of snakes were seen; when disturbed, they descended into the rock pile or the water. When they were handled, the fish odor was not present.

The following information, noted as the series was examined, may be of interest. Specimen UAZ 26461 collected 7 December 1958 at Yepómera was heavily infested with Acanthocephala. Their spiny heads protruded from between the scales, presumably an attempt to escape the preservative solutions. Two males from Bocoyna (BYU 14213 and 17085) and one from San Pedro (BYU 14368), Chihuahua, had everted hemipenes. In each case there were three large spines on the base of the lateral surface and two on the posterior surface. Small spines, but descending in size, covered the organ from the large proximal spines to the enlarged capitate distal end. Specimen UAZ 26460 from Black River at Diamond Fork, Greenlee County, Arizona, did not differ in this character. Specimen UAZ 34335 from Yepómera, Chihuahua, was gravid, with 7 or 8 nearly mature young. It was taken 17 July 1971.

Thamnophis rufipunctatus nigronuchalis Thompson

Thamnophis nigronuchalis Thompson, 1957, Occ. Pap. Mus. Zool. Univ. Mich. 584:1–10.

DIAGNOSIS.—A subspecies of *rufipunctatus* with supralabials 4 and 5 having a wide contact with the eye and with a single, dark, median nuchal spot.

DISTRIBUTION.—Type locality San Luis, Durango. Specimens examined: UTEP 3386–7, 6 mi SW El Salto; UTEP 3653–4, 1.5

mi W San Luis; UAZ 37709, 17 mi N Coyotes; MVZ 59235, 33 mi ENE El Salto; LSUMZ 11637, 6 mi SW El Salto; LSUMZ 16488–16460, 8.3 mi W El Salto; LSUMZ 33100, 8 mi WSW El Salto; LSUMZ 40830–40834, 40849, 5.6 mi W El Salto; NMMZ 32511, 0.3 mi W El Salto, Durango.

REMARKS.—The above series is unusual in having few variations. The scale rows were 21-21-17 in most, the only variation occurring at the neck, where 5 specimens had 23 and 3 had 22 rows; supralabials 8-8 in most, but with 9-9 or 9-8 in a few; infralabials usually 10-10 and a few with 9-9 or 9-10; loreals 1-1; preoculars 2-2, rarely 3; postoculars 3-3 in all specimens examined; temporals 1-2 or 1-3 in about equal numbers.

The color pattern consists of a single nape blotch usually wider than long, lying just posterior to the parietals. Posterior to the nape blotch is a series of smaller, middorsal spots that may separate toward midbody in two rows of dorsolateral spots; if this occurs, there are 6 rows of spots, otherwise only 5 rows. Thompson (1957) states that there are 5–10 rows of spots. With some fusions and others splitting, one may at one point across the body count more than 6 rows. An examination of the spots along the entire body indicates that the basic number of rows is 6, reduced to 5 when the two dorsal rows remain fused.

The range of this subspecies suggests that it is confined to the high altitude basins that flow from near the Continental Divide westward. Considerably more material must be obtained before its total range will be known and also whether it occurs only west of the Continental Divide and/or if it intergrades with *r. unilabialis* in drainage basins north and east of the Continental Divide in Durango.

SUBSPECIES RELATIONSHIPS AND VARIATION.—The recognition of three subspecies in *T. rufipunctatus* is based primarily on variation in color pattern, ventral-caudal scale counts, and the relationship of the 4th or 5th labials contacting the eye (Fig. 5). There is little variation in the color pattern except that, in *T. r. nigronuchalis*, a single, large, nuchal blotch is present, whereas the northern subspecies have a divided blotch, at least in the young. When the spotting is apparent, there are usually 5 or 6 rows of body spots, and the head is similarly patterned and colored in all three subspecies. In some specimens of each subspecies, there are bright, yellowish rust spots. In the subspecies *nigronuchalis*, the two most dorsal rows of spots are often fused at least anteriorly, thus reducing the number of rows to 5, whereas in the other subspecies, the usual number of rows is 6. The five-row pattern is apparently a continuation along the dorsum of the central nape spot pattern in contrast to the divided nape spot pattern in the northern subspecies. The spotting in all subspecies is more apparent in the young and subadults, with some adults having a faded and less apparent spotted appearance, especially in preserved specimens.

There is some variation in the ventral color pattern. In the Chihuahua subspecies, the anterior edges of the ventrals are usually margined with dark pigment forming dark cross bars. In *r. rufipunctatus,* the ventral pigmentation tends to form two rows of ventrolateral spots, with only small amounts of pigmentation midventrally and in areas between the spots that are not pigmented. At least the barring effect is not obvious as in *r. unilabialis*. In the series of *nigronuchalis* from 8.9 km (5.6 mi) W of El Salto, there is no discernible ventral pattern. On about the anterior third of the body the ventrals are only flecked, but posterior ventrals show more and larger spots. In this series of specimens there isn't a uniform spotting or bar pattern.

Variation in the ventrals and caudals is indicated in Table 2, and the variation in the labial-eye character is seen in Figure 5. In all specimens of *r. nigronuchalis* examined, there is a wide contact between the 4th and 5th supralabials and the eye, whereas in *r. rufipunctatus*, about 25% of the specimens have the lower postocular making contact with the 4th labial and thus excluding the 5th labial from narrowly contacting the orbit. However, in most specimens of the latter, there is usually not a firm or broad contact between the lower postocular and the 4th labial, leaving a small area of contact between the 5th labial and the eye or merely with the tip of the lower postocular touching the 4th labial. In both subspecies (*nigronuchalis* and *rufipunctatus*), there are usually 3 postoculars. Only in the subspecies *rufipunctatus* and *unilabialis* have I observed 4 postoculars (in *rufipunctatus*, 16 of 74 counts, 21.6%). An increase in postoculars occurs in the Chihuahua subspecies (43 of 128 counts, 33.6%). However, it is not the number of postoculars that prevents the 5th labial from contacting the orbit, but the size of the postocular scales. In Chihuahua specimens, the lower postocular, whether it is the 3rd or 4th scale, extends around the eye to form a firm contact with the 4th labial, thus permitting only the 4th to enter the orbit (Fig. 5). In specimens with only 2 postoculars, there are always 2 supralabials (4 and 5) that enter the orbit. In the series from Arizona and Chihuahua, 7 specimens (of 101) had 2 postoculars on one or both sides.

There are, however, small populational segments that do not fit all characteristics of these subspecies. An example is seen in the divided anal scale in the Oak Creek population of *r. rufipunctatus*. In *r. unilabialis*, a population in and around Galeana, Chihuahua has some individuals with a ventral color pattern similar to individuals in New Mexico. Also, the few specimens seen south of the Río San Miguel near the Durango-Chihuahua border have a ventral-caudal count noticeably higher than the other Chihuahua specimens. In each case, these small populations are widely separated from the main populations.

Each of these allopatric subspecies occurs in a separate drainage basin. *T. r. rufipunctatus* is primarily in the Gila River Basin, occurring principally in the tributaries draining the Mogollon Rim and the headwaters in east central Arizona and adjoining New Mexico. The greatest departure is in Chihuahua and northeastern Durango, in which such basins as the Río Bavispe, Río Papagochic, and Río El Fuerte drain from the Continental Divide to the west and the Río Conchos and other mainly northern small streams drain to the east. There is little variation in the populations that inhabit these basins, seemingly because they occur in the headwaters where contact, across the open basins on each side of the Continental Divide, is possible. There is, however, wide separation between the populations in Arizona and Chihuahua. Specimens from the headwaters of the Río Bavispe resemble the northern subspecies in that a high percentage of specimens have the azygous preinternasal scale. Since the Bavispe flows north and is part of the drainage basin in southern Arizona north from Douglas, the high frequency of this scale character in northern Chihuahua may represent a recent past contact with populations northward in east central Arizona and adjoining western New Mexico.

The distribution of the subspecies *nigronuchalis* is as yet not well defined. Records available seem to place it primarily in the upper basin of the Río Presidio, draining to the west. Intergrading specimens are not available. Some character variation, such as in the azygous scale of *rufipunctatus* and *unilabialis*, were not observed in *nigronuchalis*.

Conant (1963) states that the azygous scale character is present in two specimens from the Río Nazas drainage; however, in these, there is seemingly an anomalous condition where corners of internasals are cut off to form an extra scale. The azygous scale as described above is not a fragment, but it represents a median scale fitted in between the rostral and the anterior ends of the two internasals. As far as is known, this character (Fig. 6) does not occur in any Durango population, including *T. r. nigronuchalis*.

A specimen (UAZ 37709) from 37 km (17 mi) N of Coyotes has all the characters of *nigronuchalis* except that the nuchal blotch is lobate, that is, divided anteriorly but with the lobes connected posteriorly. In some specimens of *unilabialis*, the nape spots are narrowly divided, with only a fraction of a scale between them showing a light color. Specimens throughout the entire distribution of the species show color pattern similarities except for the single nape blotch in *r. nigronuchalis* and the ventral bar character in *r. unilabialis*. Only in a few characters is the variation sufficient to permit a separation into subspecies. Data available suggest that subspeciation is recent, perhaps occurring after the last pluvial period when isolation between the northern (Arizona–New Mexico) and the southern (Chihuahua and Durango) segments of the species occurred (Fig. 7).

Key to the Subspecies

1. A large, single nuchal blotch and two supralabials (4 and 5) widely contacting orbit . . . . *r. nigronuchalis*

Fig. 7. Distribution map indicating the approximate distribution of the subspecies of *Thamnophis rufipunctatus*: A, *T. r. rufipunctatus*; B, *Thamnophis r. unilabialis*; and C, *T. r. nigronuchalis*.

— Nuchal blotch divided, two supralabials may or may not contact the orbit 2

2(1). Lower postocular forming a firm contact with the 4th supralabial (Fig. 5C); ventral + caudal averages less than 240; ventrals with anterior margin pigmented to form a series of dark crossbars .... *r. unilabialis*

— Lower postocular not forming a firm contact with the 4th supralabial, usually with one or both sides failing to contact the 4th supralabial; ventral + caudal averages more than 239; ventrals spotted but rarely with anterior margins evenly pigmented to form light and dark cross bands. .... *r. rufipunctatus*

Thamnophis melanogaster chihuahuaensis Tanner

Tropidonotus melanogaster Peters, 1864, Monatsb. Acad. Wiss. Berlin, pp. 389–390.

Thamnophis melanogaster melanogaster Smith, 1942 (part), Zoologica 27:116–120.

Thamnophis melanogaster chihuahuaensis Tanner, 1959a, Herpetologica 15:170–172.

Bavispe River below Three Rivers, Chihuahua-Sonora line (BYU 14197, type specimen; BYU 13451, 13505–6, 13493, 13496, 13371, 13373, 14198–14202, 14208–9, topotypes-paratypes).
Cuiteco (BYU 14293).
6 mi SE Maguarichic (BYU 16914).
Río Urique approx. 10 mi below La Bufa Bridge (BYU 22696, 22698).
Río San Miguel (BYU 38331–37).

Since the original description (Tanner 1959a), 10 specimens have been added to our series: 1 (BYU 16914), taken 6 mi SE of Maguarichic; 2 (BYU 22696 and 22698) from the Urique River approximately 10 mi below the La Bufa Road Bridge, and 7 from the junction of the Río Verde and Río Loera west to the junction of the Río San Miguel and the Río Urique. Nine are females, one the largest of the entire series at 862 mm, and one the smallest at 204 mm. The small one taken on 1 October 1963 is undoubtedly a newborn and exhibits on each side three rows of alternating spots that are separated by a dark brown dorsal area. In none is there a middorsal light stripe. The larger specimens are a uniform olive brown dorsally and light slate with no dark spots ventrally.

The scalation and color pattern are well within parameters listed for the type series. Conant (1963) discusses at length the subspecies *T. m. canescens* from Durango and Zacatecas. His material from the Río Nazas and the Río Florida in northern Durango indicates that *canescens* may occur in southeastern Chihuahua in the southern tributaries of the Río Conchos. All specimens of *T. m. chihuahuaensis* have been taken in the Bavispe and El Fuerte River basins, both of which drain to the west. If intergrading populations occur, it will seemingly be in the headwaters of the Nazas southwest of Hidalgo del Parral or west in the upper tributaries of the Río San Miguel.

This species is found along permanent streams or ponds, not very far from water. Its aquatic habits were first observed as we collected the type series below Three Rivers on the Bavispe River. The snakes would climb onto the lower branches of a willow that hung over the river; any disturbance and they would fall into the water. We succeeded in catching them by getting into the river near the overhanging willows, and, as the snakes came up for air, we could catch them. Fortunately, the river was riled from recent rains—an aid, since the snakes could not see us. The large specimen from the Río Urique had eaten a fish.

Thamnophis cyrtopsis cyrtopsis (Kennicott)

Eutaenia cyrtopsis Kennicott, 1860, Proc. Acad. Nat. Sci. Phila. 12:333. Type locality, Rinconada, Coahuila, Mexico.

Thamnophis cyrtopsis cyrtopsis Smith, 1951, Copeia 1951:140.

Thamnophis cyrtopsis cyrtopsis Webb, 1980, Cat. Amer. Amph. and Rept., p. 245. Bavispe River below Three Rivers and near the Sonora-Chihuahua line, 11 (BYU 13367, 13370, 13372, 13583, and 14471–77).
Black Canyon 8 mi W Chuhuichupa, 1 (BYU 14222).
4.5 mi NE Colonia Juárez, 2 (BYU 14509 and 15464).
30 mi NNW Colonia Juárez (Tinaja Canyon), 1 (BYU 13443).
Colonia Juárez, 1 (BYU 17696).
22 mi S Creel, 2 (BYU 16953–4).
25.5 mi S Creel, 4 (BYU 17687–90).
Cuiteco, 2 (BYU 14269 and 15666).
6 mi S Hidalgo del Parral, 1 (BYU 13925).
Maguarichic, 3 (BYU 16909–11).
4.5 mi SE Maguarichic, 1 (BYU 17073).
10 mi SE Nuevo Casas Grandes, 2 (BYU 15316 and 17111).
14 mi W San Francisco del Oro, 1 (BYU 15711).
Tejabán, on rim of Barranca del Cobre near air strip, 1 (BYU 32038).
Río San Miguel, 5 (BYU 38339–43).

Webb (1966) lists 22 specimens from Chihuahua, 12 from Durango, 5 from Sonora, and 4 from Zacatecas. The range from Zacatecas north through Durango and Chihuahua is primarily in the mountains, the foothills, and the high plains to the east of the mountains. Only in the north does its range reach the Gulf Coast in Sonora. In the north it ranges into New Mexico, Arizona, western Texas, southern Colorado, and the upper basin of the Colorado River in eastern Utah.

This species was reviewed by Webb (1966), who listed three subspecies distributed in the southwestern United States and Mexico. The subspecies *cyrtopsis* is found throughout Chihuahua, except for the deep canyons of the southwest and is one of, if not the most, widespread and common snakes. Although it is commonly found along streams and mesic areas, it does occur in rather remote desert areas where springs occur.

Scale counts are based on 38 Chihuahua specimens taken from most areas west of

Highway 45. Ventrals range from 164 to 185, with the males averaging 177.3 and the females 171.1. Caudals range from 73 to 105, with the males averaging 97.1 and the females 86.5. These averages are approximately four scales higher than those reported by Webb (1966). Some of this discrepancy may have resulted from the fact that most of our specimens were secured in the higher elevations, where it is noted that scale counts are higher. The dorsal rows are consistently 19-19-17, except for one specimen from 4.5 mi SE of Maguarichic, which has 21-21-19 rows. This specimen is otherwise quite average for other mountain specimens. There is little variation in the head scales, there being with few exceptions 1 loreal; 1 preocular; 3 postoculars, with 2 or 4 occurring occasionally; temporals 1-2 or 1-3; supralabials 8, rarely 7 or 9; infralabials usually 10 but with 9 out of 80 counts having 11.

The color pattern is variable and fits generally the description given by Webb (1966). The middorsal stripe may be on one row, or it may involve the para-vertebral rows to as much as one-half of each scale. Anteriorly this stripe reaches to the parietals or terminates 1 or 2 scales posteriorly. If it reaches the parietals, the dark nape spot is divided by it. A wide middorsal stripe may involve 3 or 4 rows just posterior to the nape spot. Nevertheless in those specimens with only 1 row involved, little or no increase in size occurs at any point from nape to tail. Specimens with the narrow middorsal stripe may be dark between the lateral and dorsal stripes, thus resembling the mountain forms of *Thamnophis eques*. In such specimens only the reduced scale rows (19) and the lateral stripe on rows 2 and 3 serve to distinguish them from *eques*. Specimens vary not only in the width of the dorsal stripe, but also in the amount of pigment between the dorsal and lateral stripes (Webb 1980). As noted above, this may result in some misidentifications. Whether this dark color pattern is genetically or altitudinally (environmentally) induced convergence in *eques virgatenuis* or *c. cyrtopsis* is an interesting yet unsolved speculation.

In those specimens with distinct wide stripes and lighter ground color, a distinct spotting occurs above as well as below the lateral stripe. This is particularly true for young and juvenile specimens. In all specimens the sutures of the supralabials are edged with pigment. The sutures of the infralabials may or may not be edged with pigment, but never to the same extent as with the supralabials.

Thamnophis cyrtopsis collaris (Jan)

Tropidonotus collaris Jan, 1863, Elenco Sist. Ofidi, p. 69.
Thamnophis cyrtopsis cyclides Smith, 1951, Copeia 1951(2):140.
Thamnophis cyrtopsis collaris Webb, 1966, Tulane Studies in Zoology 13(2):55–70.
12 mi above Pitahaye, 1 (BYU 22685).
30 mi below (S) Guaruchic, 1 (BYU 22684).
2 mi N Cerocouhui, 3 (BYU 14478, 14595, 15651).
10 mi down Urique River from La Bufa Road Bridge, 2 (BYU 22690 and 22699).
Piedras Verdes, (near mouth of Río San Miguel) 1 (BYU 22683).
Webb (1966) lists 5 specimens from Urique.

The most distinguishing character is the dark (nearly black) nape band, which is not divided by the middorsal stripe (Webb 1980). In specimens from Cerocouhui, the dorsal stripe indents the collar but is several scales from the parietals. There is an increase in the caudals 91(101.2)110, based on 5 male specimens. This is 4 more than is present in 10 male Chihuahua specimens of *cyrtopsis*. Otherwise, the scalation is similar.

Specimens taken on the high plateau areas, that is, out of the deep barrancas, are *cyrtopsis*. This suggests that *collaris* is generally confined to the low canyon habitats of southwestern Chihuahua.

Thamnophis marcianus marcianus (Baird and Girard)

Eutaenia marciana Baird and Girard, 1853, Cat. N. Amer. Reptiles, pp. 36–37.
Thamnophis marciana Ruthven, 1908, U.S. Nat. Mus. Bull. 61:849–852.
Thamnophis marcianus marcianus Rossman, 1971, Occ. Papers Mus. Zool. Louisiana State Univ. Bull. 41:11.
Colonia Juárez, 2 (BYU 15466–7).

Only two juvenile specimens were collected from Juárez Creek, a tributary of the Río Casas Grandes. Distribution of this species in Chihuahua is apparently restricted to the northeastern part of the state, and seemingly in the drainage of those streams flowing northward and at present terminating in the desert lakes (now playas) in northern Chihuahua. It is assumed that their occurrence in this area is an extension of their range southward from Texas and New Mexico.

The scalation and color pattern fit within the ranges established by Rossman (1971) for both male and female specimens. However, the ground color and spotting is identical to specimens seen from Brewster and Jim Hogg counties in Texas. The light, parietal spot edged in black is very prominent and is thus in contrast to a series from Charleston, Cochise County, Arizona, a further indication that the Chihuahua population is an extension of the Texas population during the last Pluvial Period. The mesic areas between the closed basins in northern Chihuahua and the Rio Grande basin has been ecologically divided since perhaps the late Pleistocene.

Thamnophis elegans errans Smith

Thamnophis ordinoides errans Smith, 1942c, Zoologica 27:112.

Thamnophis ordinoides Fitch, 1948 (part), Copeia 1948:121–126.

Thamnophis elegans errans Tanner, 1959a, Herpetologica 15:168.

Thamnophis elegans errans Webb, 1976, Nat. Hist. Mus. of Los Angeles County Bull. 284:1–13.

Bocoyna, 1 (BYU 15742).

Black Canyon, 8 mi W of Chuhuichupa, 1 (BYU 14225).

Colonia Chuhuichupa, 21 (BYU 13889–96, 13921–23, 14479–81, 14492–95, 14501, 14505, 15721, and 15776).

2 mi S Creel, 5 (BYU 14381, 14511, 15644, and 17076–7).

The series listed above was seen by Webb (1976). His review of this *elegans* subspecies cannot be added to at this time, except to note that Tanner (1959a) arrived at essentially the same conclusion, namely that *errans* was indeed a southern subspecies of the widespread species *Thamnophis elegans*.

Tanner (1959a) and Webb (1976, 1980) discussed the characteristics of the specimens available from northwestern Chihuahua, that is, areas north of the Río Papigochic. Specimens from this northern area show considerable overlap in characters with *T. elegans vagrans* in Arizona, New Mexico, and Utah. This is particularly evident in the dorsal scale rows, which may be 21-21-17 or 19-19-17 or a combination. South of the Río Papigochic the scale row formula is 19-19-17 and there is an increase in the caudals (Creel area 89.75 and Chuhuichupa area 82.66). A reexamination of the BYU *errans* specimens suggests a strong relationship to the *elegans vagrans* population in central and southern Arizona. Although no *T. elegans* are known from the intervening area, the terrain is favorable for contact through the Bavispe River and its tributaries extending from southern Arizona (near Douglas) south, by way of the Río Bavispe, into western Chihuahua (Chuhuichupa area). Fitch (1948) raised *errans* to a full species on the basis of the reduced scale rows (19) and the reduced infralabials (9-9). Both these scale patterns occur in many, if not most, populations of *vagrans*, and, since the ventral-caudal counts are essentially the same, there are no scale character differences sufficient for considering *errans* to be other than a disjunct subspecies of *elegans*.

In addition the color patterns are similar, but with the southern populations of *vagrans* (central Arizona) and *errans* having a more distinct dorsal stripe, usually involving three dorsal rows, and with little or no invasion of the middorsal row by dark spots. The stripe is thus more uniform and distinct and unlike the undulating stripe in *elegans vagrans* from central Utah.

Fitch (1980) considered again the status of *Thamnophis elegans errans*. I would add only two additional comments. First, the species *Thamnophis elegans* is widely dispersed and as such has developed clinal variations because of its wide dispersion and isolation in some of the desert basins. The color pattern of the populations in the upper Colorado River basin of southeastern Utah is clearly distinct from those seen in the Little Colorado basin of Arizona. Specimens from Joseph City and near Holbrook, Arizona, have a wide dorsal stripe in which three rows of scales are involved; no dark spots invade it—or at least they do not disrupt the stripe as they do in the upper basin specimens. The color patterns in *errans* is thus similar to the Arizona *T. e. vagrans*. Fitch (1983) did not include *errans* in his report and distribution map of *Thamnophis elegans*, choosing to include only those populations north of Mexico.

A perusal of my field notes indicates that *errans* has essentially the same wandering habits as does *vagrans*. We found them along streams or ponds, in meadows, and in fields during the rainy season. The distribution of *Thamnophis elegans* in southeastern Utah, Arizona, and Chihuahua is somewhat similar to that of *Lampropeltis pyromelana*, that is, in disjunct populations. *Thamnophis elegans* occurs in separate basins with wide desert areas separating them. In Chihuahua the extent of the deserts, particularly between those in Arizona and Chihuahua, has required the populations either to inhabit streamside habitats or to move into cooler, moist, mountain areas where habitat restrictions are not as severe.

The wide desert areas between *errans* and *vagrans* suggest again that, in the recent geological past, more favorable climatic conditions existed, permitting *T. elegans* to be widely dispersed over areas now desert and uninhabitable. However, as a consequence of this former distribution, those populations in northern Chihuahua would be expected to show remnants of intergrading or intermediate characteristics with those in Arizona not only in scalation, but also in color pattern. These factors suggest that the contact between them has been in the recent past. As indicated above, the population of *errans* south of the Río Papigochic has apparently been sufficiently isolated to have developed the basic characteristics of the subspecies. Nevertheless, on the basis of the material available to me, the type series (Smith 1942c) and the report by Webb (1976), it now appears that the more typical *errans* are found on the east side of the Continental Divide in northern Chihuahua (Garcia area) and south of the Papigochic River in southwestern Chihuahua and Durango, with the population in the headwaters of the Bavispe River (Chuhuichupa area) showing intergrading characteristics with the *elegans vagrans* to the north.

In 1957 and 1958 collecting was done during July (7-20), and each year the large females were gravid. Two (BYU 14493 and 15721) from Chuchuichupa had 6 and 7 nearly mature embryos, and two (BYU 17076 and 17077) from Creel had 10 and 8 embryos. The latter two specimens were 590 and 498 mm in total length. The largest specimen in the series is a female, 635 mm in total length.

Thamnophis eques megalops (Kennicott)

Eutaenia megalops Kennicott, 1860, Proc. Acad. Sci. Phila. 12:330–331.

Thamnophis macrostemma megalops Smith, 1939, Publ. Field Mus. Nat. Hist., Zool. Ser. 24:30–31.

Thamnophis eques megalops Smith, 1951, Copeia 1951:139–140. Conant, 1963, Copeia 1963:487.

Basiguare, 1 (BYU 22701).
Black Canyon, 8 mi W of Chuhuichupa, 6 (BYU 14221, 14223, 15744–46 and 15769).
Colonia Dublán, 1 (BYU 13731).
Colonia Juárez, 2 (BYU 243 and 1134).
5 mi S Gomez Farias, 1 (BYU 15747).
Guachochic at spring, 1 (BYU 22687).
10 mi S of Hidalgo del Parral, 1 (BYU 13924).
2 mi N Casas Grandes, 2 (BYU 14136–37).
4.5 mi S of Palomas, 1 (BYU 14504).
2 mi SE La Junta, 1 (BYU 17084).
San Pedro on Río Papigochic, 2 (BYU 14376 and 14487).

Conant (1963) listed 10 additional specimens from the areas west and south of Hidalgo del Parral, and the following are at the University of Texas at El Paso: El Sauz, Río Sauz, UTEP 3648; Ricardo Flores Magón, 3659–60; and Yepómera, 2053.

I have examined only the specimens available to me at BYU. These (19) vary little in scalation from that of Conant (1963:488) and are as follows: ventrals males 166(168.7)170; females 160(164.4)171; caudals males 83(84.8)87; females 69(73.5)78. Scalation of the head is similar in all details to that indicated by Conant for both subspecies *megalops* and *virgatenuis*.

I have not undertaken a systematic review of this species covering its entire area of distribution, although such a study is clearly warranted as suggested by Conant (1963:488). The color pattern varies on an altitudinal cline, with the wide, middorsal stripe occurring at low altitudes, that is, the low valleys and foothills primarily to the east of the western mountains. The narrow, one-scale-wide, middorsal stripe occurs only in populations at the higher elevations.

There is, based on the above series, a gradual reduction in the width of the dorsal stripe from those specimens from low elevations (formula 1/2-1-1/2) to the point that some specimens in the highlands (Bocoyna and Chuhuichupa) have an invasion of pigment into the middorsal scale row, reducing the stripe to a fraction of the row (–1–) (Conant's formula, 1963:490). If we consider any pigment encroachment into the paravertebral part of the middorsal stripe as an indication of intergradation between the subspecies, then a wide area in Chihuahua would lie in the zone of intergradation. We find "true" *megalops* only in the lower valleys and *virgatenuis* only in the highest elevations.

There are two color pattern variables: first the size of the middorsal stripe depends on the degree of involvement of the paravertebral rows in the dorsal stripe, and second the melanistic pigment gradually increases to produce a nearly uniform dark pattern between the ventrolateral stripes and the middorsal stripe. All the variations figured by Conant (1963) are present in the Chihuahua specimens, but the above color pattern phenomenon is most noticeable in those specimens from the area of 6000 feet and higher. A few specimens from Black Canyon just west of Chuhuichupa and at about the same elevation range from little involvement of the paravertebral rows to a full one-half scale row involvement. There is little variation in color pattern between the Black Canyon and Chuhuichupa specimens, perhaps a little less involvement of the paravertebral rows in the latter. However, Conant (1963) considered the Chuhuichupa specimens to belong to the subspecies *virgatenuis* even though the formula for this population would be +1+ in all specimens. In both populations the area between the dorsal stripe and the lateral stripes is also nearly black, with only fine, light flecks. Apparently the only useful key characters to differentiate *virgatenuis* from *megalops* are for the dorsal stripe to occur only on the middorsal row and for the color between the lateral and dorsal stripe to be black or nearly so, with fine, white flecks showing between the scales.

Thamnophis eques virgatenuis Conant

Thamnophis eques virgatenuis Conant, 1963, Copeia 1963:490.

Bocoyna, 12 (BYU 14377–9, 15735–41, 17087–90).
4 mi S Bocoyna, 6 (BYU 17091–95, 14380).
1 mi S Chuhuichupa, 2 (BYU 13919–20).
Chuhuichupa, 7 (BYU 13896–97, 14482, 14497–500).
2 mi SE Creel, 5 (BYU 15641–43, 17074–75).
16 mi NE San Juanito, 2 (BYU 17028–29).
San Juanito, 1 (BYU 32039).
Colonia García, 1 (BYU 246).
5 mi WSW Colonia García, 1 (UTEP 4850).

Conant (1963) also lists 1 from Bocoyna (AMNH 74465) and 2 from Sisoguichi (AMNH 57389–90).

Although there is considerable intergradation in the color and color patterns of the populations of *Thamnophis eques* in Chihuahua and little variation in their scalation and body proportions, it is seemingly wise at this time to let the subspecies *T. e. virgatenuis* stand pending a detailed study of the species. The color pattern changes in the Chihuahua populations are gradual, with specimens taken between 6000 and 8000 feet showing the variants one might consider to represent the area as well as the range of intergradation. In a few specimens from Bocoyna, there is an invasion of the middorsal stripe by pigment to the point of reducing the stripe to only a fraction of a scale row. In this character, the evolutionary process may thus be moving to eliminate the middorsal stripe. At least the effect of the color pattern changes is toward a sustained though gradual reduction of the size of the middorsal stripe.

Specimens with the *virgatenuis* color pattern were not found south of Creel in the Barranca del Cobre and adjoining areas. It now appears that the population in the Bocoyna area is not only separated from the highland populations in Durango, but it is also separated from the Chuhuichupa population by the low areas in the basin of the Rio Papigochic. Thus, in Chihuahua, we now recognize two highland islands of the subspecies *T. eques virgatenuis*, both of which are surrounded by the subspecies *T. eques megalops* in the lower mountains, foothills, and valleys of western and southwestern Chihuahua, and with intergrading population in between.

The highlands of southern Chihuahua and northern Durango are not well known and may hold the answers to many distribution patterns not only for the several species of *Thamnophis*, but also for other species.

Thamnophis sirtalis dorsalis Baird & Girard

Eutaenia dorsalis Baird and Girard, 1853, Cat. N. Amer. Reptiles, p. 31.

Eutaenia ornata Baird, 1859, Rep. U.S. and Mex. Boundary Surv. 2:1–35.

Thamnophis sirtalis ornata Fitch and Maslin, 1961, Univ. Kansas Publ. Nat. Hist. 13(5):297–299.

Thamnophis sirtalis dorsalis Fitch, 1980, Cat. Amer. Amph. and Rept., p. 270.

6.2 km SE Galeana, Ojo de los Reyes 2 (UAZ 32780 and 36291).
0.8 km N Nuevas Casas Grandes 1 (UAZ 34434).
Yepomera vicinity 13, (UAZ 34066–71, 34149, 34230, 34399, 34879–82).

The specimen taken at Casas Grandes by Nelson and Goldman (USNM 46371) was reported by Smith (1942c), and a brief description was included. It is a female with the following scale counts: 19-19-17 scale rows, 152 ventrals, tail incomplete, 7-7 supralabials, 10-11 infralabials, 1-1 preoculars, and 3-3 postoculars. A specimen from New Mexico (E. D. Flaherty, no. 560, 1 mi W and 1/2 mi S of Isleta, Bernalillo County) reported by Fitch and Maslin (1961) is stated as having only 8-8 infralabials. This seems most unusual for any specimen of *sirtalis*. Of 114 counts (57 specimens) of *s. sirtalis* and *s. parietalis* (from Utah and Kansas), only one had a count of 8-9; all others were 9, 10, or 11, with 10 being the predominant count. Based on the characteristics of the few specimens previously reported, the normal lepidosis for this subspecies remains obscure or wanting for additional data.

An examination of the scalation and color patterns of the series reported by Van Devender and Lowe (1977) suggests that the population in the two northern valleys (Río Casas Grande and Rio Santa María) corresponds closely to those specimens previously reported by Smith (1942c) and Fitch and Maslin (1961). There are still two few specimens to establish basic data for this southern population. The two specimens from near Galeana (UAZ 32780 and 36291) have fewer ventrals than the other specimens (from N Casas Grande and Yepómera) and are similar in scalation (ventrals 151 and 152, labials 7-7 and 10-10) to the one reported by Smith (1942c) from Casas Grandes. Since Nelson and Goldman collected extensively north and east of Casas Grande but returned to that city or San Diego, where they reorganized for further trips, it is possible that the specimen (USUM 46371) was taken in the drainage of the Río Santa María. It has the basic characteristics of those seen from near Galeana. The single specimen from N Casas Grandes is a male with 166 ventrals and 84 caudals. These characters relate it to the Yepómera population and justify the suggestion of Van Devender and Lowe (1977) that the Yepómera population came into its present habitat by way of the Río Casas Grande.

The Yepómera population has developed a few characters not seen in most other populations of *sirtalis*. These will be discussed in a forthcoming study.

The occurrence of *sirtalis* in the valleys of northern Chihuahua is not surprising and is, undoubtedly, a relict population isolated after the desiccation following the last ice age severed the former water courses directly connected with the Río Grande. This is yet another example of the effects of the desiccation that occurred as the Pluvial Lakes such as Palomas disappeared and rendered the lowlands uninhabitable. We can now assign such species as *Lampropeltis pyromelana*, *Opheodreys vernalis*, *Thamnophis elegans*, and now *Thamnophis sirtalis* as relict populations.

Genus *Trimorphodon*

There are two species that occur in Chihuahua, with only one specimen of *b. vilkinsoni* and one of *b. lambda* having been collected; their distribution in the state is poorly documented. The secretive and nocturnal habits may account for the scarcity of collected specimens. *Trimorphodon tau* occurs in southwestern Chihuahua, inhabiting the deep canyons of the barrancas.

Trimorphodon biscutatus vilkinsoni Cope

Trimorphodon vilkinsoni Cope, 1886, Proc. Amer. Philos. 23:285–286; Taylor, 1939, Univ. Kansas Sci. Bull. 25:361–363; Smith, 1941b, Proc. U.S. Nat. Mus. 91:151–167.

Trimorphodon biscutatus vilkinsoni Gehlbach, 1971, Herpetologica 27:209.

Trimorphodon biscutatus vilkinsoni Scott and McDiarmid, 1984a, Cat. Amer. Amph. and Rept. 353:1–4.

Ciudad Chihuahua, 1 (USNM 14268, type specimen).

A description of the type is in the report by Taylor (1939b), and Smith ((1941b) provides a diagram of the possible phylogeny of the genus. The above reports dealt with only one or two specimens. Klauber (1940b) reported on three, Reynolds and Scott (1977) list three taken on Chihuahua Highway 16 between Villa Aldama and El Pastor, and Banicki and Webb (1982) have described in detail a series of 22 specimens from the Franklin Mountains in El Paso, Texas. However, the scarcity of specimens for Chihuahua still exists. Our many trips into Chihuahua produced no specimens, but we do have one additional female specimen from Green Gulch, Chisos Mountains, Brewster County, Texas. It has the following scalation: scale rows 21-23-17, ventrals 231, caudals 74, supralabials 9-9, infralabials 12-13, loreals 2-2, preoculars 3-3, postoculars 2-3, and temporals 2-2-3 and 3-3-4. There are 24 body spots and 9 on the tail. These patterns correspond closely to those reported by Klauber (1940b) and Banicki and Webb (1982), but they do indicate that additional specimens from central Chihuahua may provide more variation than that seen in the specimens now available.

Trimorphodon biscutatus lambda Cope

Trimorphodon lambda Cope, 1886, Proc. Amer. Philos. 23:285–286.
Trimorphodon biscutatus lambda Gehlbach, 1971, Herpetologica 27(2):208.
Maguarachic, 1 (UMMZ 118926).

This female specimen has an unusually high ventral count for this subspecies. Other scale counts and the color pattern are, however, well within the limits of the subspecies. The scale counts are as follows: ventrals 255, caudals 67, anal divided, dorsal scale rows 19-23-16, supralabials 9-9, infralabials 12-12, preoculars 3-3, loreals 3-3, postoculars 3-4, and temporals 3-4. There are 26 dorsal body spots and 12 on the tail. At or near midbody the dorsal spots involve 12–15 rows of scales, with a dark spot extending from the lateral point of the spot to the first row above the ventrals.

REMARKS.—Using only the specimens available to me in the Monte L. Bean Life Science Museum (BYU), I find the series from Utah, Nevada, Arizona, and Sonora (16 specimens) to have a ventral range of 218-(221)-226 in males 227-(232.57)-246 in females. By adding the ventrals and caudals, the eight southern Arizona and Sonoran specimens and the Chihuahua specimen average 320 and range from 303 to 322, but the more northern specimens range from 292 to 301. This emphasizes the clinal decrease in these counts from south to north. All the specimens listed under *T. biscutata* have the chevron head pattern and a similar body pattern.

Hardy and McDiarmid (1969) list *Trimorphodon lambda paucimaculata* as occurring in northern Sinaloa. An examination of our series of *Trimorphodon* from Sonora (12) and Sinaloa (2), and 10 specimens from Arizona, Nevada, and Utah, suggests that only two species of *Trimorphodon* occur in Sonora and perhaps also in Sinaloa, *T. biscutatus* and *T. tau*. Two male specimens from southern Sinaloa (6.7 mi N Río Quelite) are *T. b. biscutatus* and have low ventral counts (192–197), suggesting a reversed cline from south to north. It is also suspected that any specimen previously identified as *lambda* or perhaps *paucimaculata* actually belongs to either the species *T. biscutatus* or *T. tau* (see Scott and McDiarmid 1984b:353, 1984:354).

Trimorphodon tau tau Cope

Trimorphodon tau Cope, 1869 (1870), Proc. Amer. Phil. Soc. 11:152.
Trimorphodon tau McDiarmid & Scott, 1970, Contributions in Sci., Los Angeles County Museum, no. 179:29.
Trimorphodon tau tau Scott & McDiarmid, 1984b, Cat. Amer. Amph. and Rept. 354:1–2.
Batopilas, 1 (USNM).

Only a single specimen is listed for Chihuahua. The species was collected by Edward Wilkinson and reported by Cope (1900:1105). The reports by McDiarmid and Scott (1970, 1984b) cite the locality on their range maps.

The occurrence of *T. tau* in Chihuahua is to be expected, since a number of specimens have been taken in northeastern Sinaloa only a few miles from Chihuahua. Additional collecting in the low valleys of southwestern Chihuahua will undoubtedly provide additional material.

Since this report was written, the catalog reports by Scott and McDiarmid (1984b) confirm the distribution of the above species in southwestern Chihuahua, Sinaloa, and Sonora.

Family Elapidae

On the basis of published reports (Cope 1900:1126, Bogert and Oliver 1945:407, Smith and Taylor 1945:169, Hardy and McDiarmid 1969:211, Zweifel and Norris 1955:245–8), there are seemingly only three records of elapids for Chihuahua. Both genera (*Micruroides* and *Micrurus*) occur in the southwestern part of the state, with their ranges extending westward into Sinaloa and Sonora.

Micruroides euryxanthus australis Zweifel & Norris

Elaps euryxanthus Kennicott, 1860, Proc. Acad. Nat. Sci. Philadelphia, p. 336.
Micruroides euryxanthus australis Zweifel and Norris, 1955, Amer. Midl. Nat. 54:245–248.
Batopilas, 1 (USNM 8850 - Wm. Grant, collector).

Cope's record from Batopilas is referred to the subspecies *e. australis* by Zweifel and Norris (1955) and Roze (1974). This designation is most logical because of the nearness of Batopilas to the type locality (Guirocoba, Sonora), and because both are in the drainage of the Río El Fuerte.

The record (USNM 8566) from the northwest corner of Chihuahua is recorded as *M. e. euryxanthus* by Zweifel and Norris (1955:246) and Roze (1974:163). The subspecies referred to above undoubtedly have a wider distribution in western and northwestern Chihuahua. They are poorly represented in collections primarily because little collecting has been done in the fringe areas of their distribution.

Micrurus distans distans (Kennicott)

Elaps distans Kennicott, 1860, Proc. Acad. Nat. Sci. Philadelphia, 12:338.
Micrurus diastema distans Schmidt, 1933, Publ. Field Mus. Nat. Hist., Zool. Ser. 20:39.
Batosegachic (= Batosegachie of Smith and Taylor 1945), 1 (USNM 1144).

This locality is in southwestern Chihuahua, west of Cuiteco and approximately half the distance from Cuiteco to the Sonoran line. It is in the drainage of the Río Oteros, a northern tributary of the Río El Fuerte. Roze (1983) gives the distribution as southwestern Chihuahua and southern Sonora to Sinaloa and northwestern Nayarit, intergrading with the subspecies *zweifeli* in central Nayarit, Mexico.

The few records now available for the two genera of coral snakes indicate that they have overlapping ranges in southwestern Chihuahua and the adjoining terrain in eastern Sonora and northeastern Sinaloa.

Family Crotalidae

Seven species of this family are known to occur in Chihuahua. Four species or their subspecies occur in the lower valleys and foothills of central Chihuahua, with four species or their subspecies more commonly found in the western mountains. The single published record for *C. v. viridis* is for a specimen taken in the 1850s and is apparently valid. A second specimen, CAS-SU 14361 collected by Figg-Hoblyn et al. on 24 August 1950, 25 km (16 mi) E Chihuahua-Sonora border on the road between the towns of Bavispe (Sonora) and Nuevo Casas Grandes, is a confirmation of the distribution of *Crotalus v. viridis* occurring in northwestern Chihuahua. It is actually a slight extension southward of the range indicated by Klauber (1936). Intensive collecting in northern Chihuahua and Sonora may extend the range of *viridis* farther south and west.

If additional species of this family are in Chihuahua, the most likely area would be in river valleys extending into the mountains of southwestern Chihuahua. Other species may occur in the low valleys of the Urique, El Fuerte, and Oteros rivers that are not found elsewhere and represent species ascending these valleys from the coastal plains. We might expect that *C. basiliscus* will be found in one or all of these valleys.

In summary, there are seven rattlesnake species in the state of Chihuahua, and of these four are more commonly found in the mountains; that is, *willardi*, *pricei*, *lepidus*, and *molossus*. Of these, *lepidus* and *molossus* (Price 1982) do reach the desert foothills east of the mountains, but *atrox* and *scutulatus* are seemingly restricted to the deserts east and north of the mountains.

Crotalus molossus molossus Baird & Girard

Crotalus molossus Baird & Girard, 1853, Cat. N. Amer. Rept., p. 10.
Crotalus molossus molossus Gloyd, 1936a, Occ. Papers, Mus. Zool. Univ. Michigan 325:2.
23 km SW Colonia Juárez (on road to Chuhuichupa), 2 (BYU 13875–6).
3 mi N Chuhuichupa, 5 (BYU 13873–4 and 15382–4).
3 mi E Colonia García, 2 (BYU 15380–1).
11.3 mi W R. F. Magón, 1 (BYU 15251).
11 mi S Creel (on La Bufa Road), 1 (BYU 15399).
Head of Arroyo Guachochic (southwestern Chihuahua), 1 (BYU 22688).

Gloyd (1940) lists the following localities: Colonia García, District of Guerrero, Pacheco, and San Blas Mountains.

The series available to me does not suggest that, contrary to the distribution maps of Price (1980), *C. m. nigrescens* occurs in Chihuahua.

There is no doubt that the color (dark brown to black on tail and posterior one-fourth to one-third of body) indicates a modification of the color pattern in contrast to most specimens seen from Arizona and New Mexico. However, the scalation of the Chihuahua series does not fit that of *m. nigrescens*. The summary of scale rows, ventrals, and caudals fits well within those listed for *C. m. molossus* by Gloyd (1940) and by Klauber (1952, 1956).

The scale rows are consistently 27 or 29 at midbody in contrast to 23 or 25 in *m. nigrescens* south in Durango. Ventrals are 185–194, with males averaging 188 and females 193, much higher than in *m. nigrescens*, but average for *m. molossus*. A key based only on color pattern would place some of the specimens from the western mountains either as *m. nigrescens* or as intergrades of *molossus* x *nigrescens*, depending on the specimen at hand. A key based on scalation would place all Chihuahua specimens we have taken with *m. molossus*.

All indications are that the color and color pattern show intergradation between the subspecies *molossus* and *nigrescens* in the mountains of southwestern Chihuahua, but with scalation remaining as in *m. molossus*. A series from northern Durango may indicate where the scale variation approaches that of *nigrescens* and thus establish the area of intergradation. It now appears that intergradation is occurring over a much wider area than has been indicated by previous studies, perhaps in extreme southern Chihuahua and northern Durango. However, most specimens we have collected in southwestern Chihuahua (Chuhuichupa and south) do not show consistently the closed blotches above the ventrals as indicated by Klauber (1936, Fig. 64). Quite to the contrary, most have the dark edge of the blotches extending to the ventrals (his Fig. 63). Price (1980) indicates by map that a finger-shaped zone of intergradation extends north from Durango into the mountains of western Chihuahua. This area of intergradation would include Creel and north to near Chuhuichupa. We have collected six specimens from these areas, all of which are *m. molossus*. Only the specimen from Arroyo Guachochic in southwestern Chihuahua (near Río San Miguel) could be considered an intergrade, and this is based only on the increased pigmentation on the posterior third of the body. All scalation in this male also remains with the subspecies *molossus*: scale rows at midbody 27, ventrals 190, and labials 18-19 and 17-17.

Based on literature records (Gloyd 1940, Klauber 1936, 1952, Hardy and McDiarmid 1969) and the series available (at BYU), it is surmised that the area of intergradation is south of the Río San Miguel in Chihuahua, in northern Durango, and perhaps in the mountains of northeastern Sinaloa.

Crotalus pricei pricei Van Denburgh

Crotalus pricei Van Denburgh, 1895, Proc. California Acad. Sci., Ser. 2, 5:856.

Crotalus triseriatus Amaral, 1927, Bull. Antivenin Inst. Amer. 1:52.

Crotalus pricei pricei Smith, 1946, Univ. Kansas Sci. Bull. 31(1)(3):79.

3 mi N Chuhuichupa, 6 (BYU 15773–5, 15389, 13796 and 13888).
4 mi SW Chuhuichupa, 1 (BYU 15415).
16 mi SW Creel, 1 (BYU 14470).
12 mi W San Juanito, 1 (BYU 17082).
22.5 mi S of Creel on La Bufa Road, 1 (BYU 16951).

Gloyd (1940) lists specimens for the following localities: Casas Grandes, Colonia García, Guadalupe y Calvo, Galeana, 24 km (15 mi) N of Chuhuichupa, Guerrero, Miñaca, Pacheco, Río Piedras Verdes, Samachique, and San Blas Mountains.

This small, spotted species is seemingly common along the rocky crests of the riverbanks south and north of Chuhuichupa. Aside from those taken, several were seen disappearing in the porous rock formations.

The scalation is all within the limits of variation set forth by Gloyd (1940) and McCranie (1980). For the 10 specimens, the ventrals were 150(158.4)162 in males and 155(159.4)161 in females, caudals in males 24(26)30 and 19(22.2)24 in females. In 20 supralabial counts, 12 were 9, 6 were 10, and 2 were 8; the infralabials were 13 with 10, 5 and 9, and 2 with 11. The color and color patterns do not vary from the description given by Gloyd (1940).

Two specimens (BYU 15773–4), from 5 km (3 mi) N of Chuhuichupa, taken 27 August 1957, were gravid. The embryos were fully formed and numbered 5 in each clutch.

Crotalus lepidus klauberi Gloyd

Caudisona lepida Kennicott, 1861, Proc. Acad. Nat. Sci., Philadelphia 13:206.
Crotalus lepidus Cope, 1883, Proc. Acad. Nat. Sci., Philadelphia 35:13.
Crotalus lepidus klauberi Gloyd, 1936b, Occ. Papers, Mus. Zool. Univ. Michigan 337:2.
2 mi W Colonia Juárez, 1 (BYU 13416).
5.5–6.5 mi NE Colonia Juárez, 3 (BYU 14247, 15281–2).
Pacheco, 1 (BYU 33614).
2 mi E Cerocouhui, 1 (BYU 14244).
25.5 mi SE Creel (on road to La Bufo), 1 and 6 mature embryos (BYU 17114 and 37241–6).
Majorachic, 1 (EHT-HMS 23014).
On road to Sierra del Nido, 1 (UTEP 2570).
5 km S Yepómera, 1 (UTEP 2541).

This report includes 14 specimens seen from Chihuahua, 9 of which were taken in the mountains of western Chihuahua. Because there are considerable variations in color and color pattern between those taken in the mountains and those from the foothills on the eastern front, and because the systematics of *Crotalus semicornutus* is not fully resolved, the data on variation in this series may be of interest.

All specimens were taken west of Highway 45, with those from the foothills west of Nuevas Casas Grandes and near Colonia Juárez having the color and pattern of typical *C. l. klauberi* (Klauber 1956:56, Fig. 2:281). The montane specimens from Pacheco and south, to near the Barranca del Cobre, are darker in color with secondary spots and numerous flecks between the primary dark cross bars. Most are surprisingly similar in the body pattern to that figured by Klauber (1956:67, Fig. 2:27) for *C. l. lepidus*, except that the parietal-nape spot is single and large, and the crossbars are large and dark as in *l. klauberi*. An adult female taken 40.8 km (25.5 mi) SE of Creel has the nape spot single, but with divided posterior extensions and the anterior-cross bars showing some dorsal enlargement. A clutch of six nearly mature young and one infertile egg were removed from her; all color patterns are mature and resemble the adult.

A specimen from 3 km (2 mi) E of Cerocouhui (approximately 120 km or 75 mi SW of Creel) is, except for the darker color, a typical *l. klauberi*. We failed to secure specimens from the Majorachic-Maguarichic area. Those taken from south of the type locality of *Crotalus semicornutus* Taylor (1944) do not show the pattern of *semicornutus*, retaining the basic pattern of *klauberi*, with the strong secondary spots and flecking of *l. lepidus*.

A comparison of the scalation shows great similarity. Ventrals 158-170; males 159-163.3-170 and females 158-161-169. Caudals 19-28; males 19-25-28 and females 19-21.6-25. Scale rows are consistently 23 at midbody, and the head scales are consistent except that the loreals may vary from 1 to 5. When these variations are compared to the averages of the larger series reported by Gloyd (1940) and Klauber (1956), no difference is apparent. The number of transverse body blotches is also approximately the same, at 17.5.

When our data and those presented by Gloyd (1940) and Klauber (1956) are compared to the characters reported for *Crotalus semicornutus* Taylor, it is seemingly apparent that *C. semicornutus* is a pattern variant of *C. l. klauberi* Gloyd. The large vertebral spots in the type of *semicornutus* and the increase in pigmentation and secondary spotting between the body blotches of other montane specimens does suggest that the population in the mountains of western Chihuahua does have color pattern deviations from that of typical *C. l. klauberi*, as was observed in specimens from near Colonia Juárez.

Except that the specimen taken south of Creel has a single nape spot, it could pass as a *C. l. lepidus*. The strong *lepidus* influence in the mountain populations from southwestern Chihuahua to Jalisco is now apparent and was suggested by Klauber (1952). Furthermore, *C. l. maculosus* (Tanner, Dixon, and Harris 1972), with its dark pigmentation and divided nape spot, is apparently more easily derived from *lepidus* than from *klauberi*.

As indicated above, there appears to be a strong color and pattern influence of *l. lepidus* remaining in the mountain populations of western Chihuahua. The presence of secondary spotting, the dark pigmentation both dorsal and ventral, and apparently the geographic isolation (separated from *l. lepidus* by typical *l. klauberi* along the eastern foothills of the Sierra Madre) may have led Taylor to describe *C. semicornutus*.

One may speculate that *C. l. klauberi* is a recent, vigorous form now extending its range southward and replacing *C. l. lepidus*, or that perhaps the influence of *lepidus* has been extended northward from the area of intergradation, now occurring apparently in the southern areas of their distribution. It may also be possible that *lepidus* is less easily displaced in the mountains than along the foothills, and thus the residual color pattern. The evidence of a retention of *lepidus* characters, particularly color and color pattern, is best exhibited in *C. l. maculosus*. The narrow crossbars, often broken on the sides in *lepidus*, the divided nape spot, and the dark pigmentation can be related to *lepidus* but not to *klauberi*. The present data give strong evidence that *lepidus* was present in the western mountains of Chihuahua before *klauberi* arrived and seemingly is slowly being replaced by a more vigorous form. Or is it possible that the color patterns and coloration is influenced by the environment and that the scalation in the subspecies *lepidus* and/or *klauberi* is more meaningful in determining taxa? Vincent (1982) examined a large series of two populations from western Texas and observed that significant differences in ground color and color patterns occurred. He concluded that these color and pattern differences resulted from the dominant substrate colors that differ between ranges. His conclusion appears true of the series from Chihuahua, with no real difference in scalation and with color and color pattern showing localized variation that places, for the present, all *C. lepidus* specimens from Chihuahua in the subspecies *klauberi*. Thus, *Crotalus semicornutus* Taylor is apparently only a color morph within the subspecies *C. l. klauberi*.

All our specimens have been taken on rocky hillsides and usually from under rocks. On one occasion a specimen (BYU 15281) was disturbed while out foraging; at least it was disturbed while not under cover, and immediately it began rattling and moved rapidly down the hill, parting the grass as it moved (12 September 1959). I have observed many rattlesnakes in the open, but never before one with such speed and agility.

Crotalus scutulatus scutulatus Kennicott

Caudisona scutulata Kennicott, 1861, Proc. Acad. Nat. Sci., Philadelphia, p. 207.
Crotalus scutulatus Klauber, 1930, Trans. San Diego Soc. Nat. Hist. 6:1–17.
Crotalus scutulatus scutulatus Price, 1982, Cat. Amer. Amph. and Rept., p. 291.
1 mi W Sueco, 1 (BYU 19133).
9 mi E Ricardo Flores Magón, 1 (BYU 17109).
4 mi E Ricardo Flores Magón, 1 (BYU 15351).
4 mi E Buenaventura, 1 (BYU 15314).
24.5 mi W Sueco, 1 (BYU 15313).
23 mi E Buenaventura, 1 (BYU 15261).
11.5 mi N Colonia Dublán, 2 (BYU 13872 and 15479).
6.8 mi SE Nueva Casas Grandes, 1 (BYU 15350).
11 mi SE Nueva Casas Grandes, 3 (BYU 13871, 15349 and 15371).
25 mi N Ciudad Chihuahua, 1 (BYU 21717).
28 mi S Sueco, 1 (BYU 15344).
38 mi N Ciudad Chihuahua, 1 (BYU 15296).
5-6 mi N Ciudad Chihuahua, 7 (BYU 15295, 15297, 15320–1, 15345, 16987 and 17113).
17 mi N Ciudad Chihuahua, 1 (BYU 17108).
10 mi W San Francisco del Oro, 1 (BYU 15678).
13.5 mi N Jiménez, 1 (BYU 14074).

Records provided by Dr. Robert Webb (UTEP) list six specimens taken along Highway 45 from south of Villa Ahumada to 32 km (20 mi) W of Jiménez. Gloyd (1940) and Klauber (1956) show distribution by map shading rather than by locality.

Distribution based on the above localities establishes *C. s. scutulatus* in the low, rolling hills and desert valleys extending east from the mountains. Price (1982) lists localities that are apparently in the montane areas of western Chihuahua. I did not find them in the western mountains.

We found *C. scutulatus* on the rocky hillsides and *C. atrox* in the brushy valleys; thus, these two species occur widely in the low desert ranges and valleys, but there is seemingly a difference in the habitat niche that each occupies. The only other species we have taken in this general habitat area is *C. m. molossus*. The single specimen taken in a rocky arroyo, 17 km (11 mi) W of R. F. Magón, does not suggest that *molossus* represents an important competitor for the more common species *C. atrox* and *C. scutulatus*. Color pattern and scalation do not vary from those listed by Gloyd and Klauber.

Crotalus atrox Baird and Girard

Crotalus atrox Baird and Girard, 1853, Cat. N. Amer. Rept., p. 5.
20 mi S Palomas, 1 (BYU 13869).
Sueco, 1 (BYU 15338).
15 mi W Sueco, 1 (BYU 17107).
17.7 mi E Ricardo Flores Magón, 1 (BYU 15356).
12 mi E Buenaventura, 1 (BYU 15299).

9 mi SE Galeana (N of Buenaventura), 2 (BYU 13870 and 15342).
14 mi N Colonia Dublán, 1 (BYU 13866).
5 mi SE Nueva Casas Grandes, 2 (BYU 13867–8).
11 mi SE Nueva Casas Grandes, 2 (BYU 15261 and 15278).
7 mi SE Nueva Casas Grandes, 1 (BYU 15322).
6 mi N Chihuahua City, 3 (BYU 15294, 15298, and 15319).

Neither Gloyd (1940) nor Klauber (1952) list locality records. Records provided by Dr. Robert Webb show five localities from 20 mi S of Ciudad Juárez along Highway 45 to 10 km (6 mi) N of El Sueco. All other records available indicate that *C. atrox* occurs in the desert valleys and foothills of northern and eastern Chihuahua. All locality records listed above are below 1800 m (6000 ft), and range from approximately 1300 to 1700 m (4500 to 5500 ft).

We found them to be common along the roads and in the valleys between El Sueco and Colonia Juárez. A few badly mashed ones were seen along the road to Chihuahua City. In spite of our many trips into the mountains of western Chihuahua, none have been found above 1800 m (6000 ft). If our records are indicative of the range of this species in Chihuahua, then the species does not occur over much of western Chihuahua, as was indicated by the range map of Klauber (1956, Fig. 2:1). The wide range of this species does extend across the lower plainlands from Arkansas to California, but it does not apparently include the high elevations of the various mountain ranges in western Chihuahua, preferring to live (to quote Klauber 1952) "in dry—even arid—country, such as brush-covered plains, dry washes, sandstone outcrops, or mesquite crowned dunes." This is a good description of the terrain south of Ciudad Juárez on both sides of Highway 45 to southern Chihuahua, and westward in the low valleys to the mountain foothills.

We soon discovered that *C. atrox* was temperamental and, at times, aggressive. On 20 August 1957, while riding horses in a brushy pasture about 8 km (5 mi) SE of Nueva Casas Grandes, a medium-sized (805 mm) *C. atrox* sprang full length, barely missing the hind legs of the horse just in front of me. That same evening, while road running, a smaller one sprang at me as I approached it. Other species either took a defensive position or moved away to cover. We soon noted whether we were dealing with *atrox* or *scutulatus*, the latter in our experience being much less aggressive. The color pattern and scalation conform closely to those published previously by Gloyd (1940) and Klauber (1930 and 1952).

Crotalus viridis viridis (Rafinesque)

Crotalus viridis Rafinesque, 1818, Amer. Month. Mag. Crit. Rev., 4:41.
Crotalus viridis viridis Klauber, 1936, Trans. San Diego, Soc. Nat. Hist. 8:194.
El Espía, reported by Smith and Taylor, 1945, 1 (USNM 264. See Klauber 1952, 26:103).
16 mi E of Chihuahua-Sonora border on the Bavispe to Nueva Casas Grandes Road, 1 (CAS-SU 14361).

Our collecting south of Ciudad Juárez, Las Palomas, and Antelope Wells (across the border south of Lordsburg) has not provided a specimen of *viridis*. The California Academy specimen does establish an authentic record verifying the earlier USNM specimen taken in the 1850s. The full extent of the range of *viridis* in Chihuahua must yet be established. For the present, it is expected to be found only in the northwestern corner of Chihuahua, perhaps from the vicinity of Las Palomas westward in the foothills and into extreme northeastern Sonora.

Crotalus willardi amabilis Anderson

Crotalus willardi amabilis Anderson, 1962, Copeia 1:160–163.

The type and 10 paratypes, all from the Sierra del Nido, are deposited in the Museum of Vertebrate Zoology (68895–68900, 71015–71016 and 66177, 68894 and 68893). This series was seen, but not examined. The Sierra del Nido are east of the Sierra Madre Occidental and extend from an area slightly southwest of Gallego to just northwest of Ciudad Chihuahua. The principal drainage is from the western slopes into the basin of the Río Santa Clara, which flows north to terminate in the desert basin near Villa Ahumada. This range has an elevation above 2400 m (8000 ft), and thus provides for isolation from the western highlands.

The fieldwork of Dr. James D. Anderson provides material that is not only indicative of isolation but also of some species not yet known to occur in the western mountains.

Crotalus willardi silus Klauber

Crotalus willardi Meek, 1905, Fld. Col. Mus. Pub. 104, Zool. Ser. 7(1):18.

Crotalus willardi silus Klauber, 1949, Trans. San Diego Soc. Nat. Hist. 11(8):128.

Type locality on Río Gavilán, 7 mi SW of Pacheco (MVZ 46694).

Red Rock, Tinaja Canyon, 12 mi W highway between Casas Grandes and Colonia Juárez, 4 (BYU 13843–6).

Upper fork of Nutria Creek (tributary of the Río Bavispe near Chihuahua-Sonora border), 1 (BYU 13487).

On rim trail approximately halfway between Urique and Cerocouhui, 1 (BYU 14596).

Chuhuichupa, 1 (BYU 15480).

1 mi W Chuhuichupa, 3 (BYU 15720, 15722–3).

5 mi W Colonia García, 1 (BYU 15388).

Gloyd (1940) lists specimens for the following localities: Colonia García, Dist. Guerrero, Río Piedras Verdes (head of canyon), Sierra Madre, Tamarino, and Majorachic. Klauber (1949) lists the following new localities: Río Gavilán 11 km (or 7 mi SW of Pacheco) and halfway between Majuarachic and Las Varas.

The most southern locality previously reported was Majorachic. The specimen (BYU 14596) taken near the canyon rim west of Urique is the most southern *C. w. silus* available to me. Its color pattern, and particularly that of the head, does not vary from those seen from northern localities.

Two specimens (BYU 15480 and 15722) each had recently eaten a small rodent, and two (BYU 15388 and 15720) had large oviducal eggs, 7 and 6, respectively.

Scale and color patterns do not vary appreciably from published reports by Gloyd (1940) and Klauber (1972). The only significant variation occurs in the caudals, which average higher than those listed by Klauber (1972, Table 2:7): caudals, males (5), 31-32-35; females (6), 27-29.7-34.

Harris and Simmons (1976) list the subspecies *C. w. obscurus* as occurring in the Sierra de San Luis of Northwestern Chihuahua. This is based on a single specimen (UA 27943) from the west slope of that range. We did not collect in these mountains and assume the specimen to represent an addition to the fauna of Chihuahua. In their report is a lengthy and useful discussion of the habitats within the range of the species *C. willardi* and their understanding of the isolation factors that have resulted in the subspeciation within the species. A table of meristic characters for the *willardi* subspecies is provided, as well as a suggested phylogeny.

ACKNOWLEDGMENTS

I am indebted to a number of individuals and families who assisted during the fieldwork conducted in various parts of Chihuahua. We were accepted not only by the American colonists, but also by the Mexican and Indian individuals with whom we came in close contact upon numerous occasions.

At Colonia Juárez we were fortunate in having an opportunity to stay at the homes of Mr. and Mrs. David Johnson and Mr. and Mrs. Irvin Romney. Mr. George Turley was also very helpful, but perhaps those most understanding of our aims in the gathering of material were the Hatch brothers, Herman, Roy, and Seville. We were particularly grateful to the Herman Hatch family, who not only permitted us to bed down under the old apple tree at any hour of the day or night, but offered us their hospitality and served as information agents for our travels in much of northern and central Chihuahua.

Our first trip into the mountains was with the Colonia Juárez Scout troop to the Río Bavispe (just below Three Rivers), and the next year with Amilio Borgous to Chuhuichupa. These trips introduced us to the mountains and prepared us, so we thought for the barrancas of southwestern Chihuahua

In Colonia Dublán Mr. Alma Jarvis, who was the postmaster, provided us with valuable information concerning areas for which he was well informed, and Mr. and Mrs. Keith Bowman upon a number of occasions provided us with meals and a place to stay.

In Ciudad Chihuahua, we were fortunate in becoming acquainted with Mr. Harold Pratt who was the Chihuahua agent for the Allis-Chalmers Equipment Company. Mr. and Mrs. Pratt opened their door to us, provided an opportunity for us to recoup after having been in the mountains for a time, and also gave us an opportunity to reassemble our collections in preparation for the trip home. Also, it was from their estate that we were able to spend collecting time in the Ciudad Chihuahua area. We were also fortunate to have met a friend, Mr. Ray Thane, in San Francisco

del Oro, who provided us with information and an opportunity to visit with a Mexican family.

During the years spent in Mexico, I had the good fortune of having as companions a number of capable faculty and graduate students. The first trip (1956) involved Mr. Verle Allman, a biology teacher, and my son Lynn. For the next four years I had as my companion Dr. Gerald W. Robison. We were accompanied upon one occasion (1958) by Dr. and Mrs. Irving W. Knobloch, he a professor of botany from Michigan State University, and upon another occasion with Dr. Stephen L. Wood, an entomologist from BYU, and his graduate student Dr. Jay B. Karran.

The trip to Urique with Dr. Knobloch was a highlight, as was the trip with Dr. Wood to Maguarichic. Each trip added to our species list and seemed to compel us to plan the next trip. In October 1963 I was a member of the John Cross expedition into the Barranca del Cobre. Although we could not run the river as planned, we did get considerable publicity in both Chihuahua and U.S. newspapers and had the opportunity to secure additional material and data. Mr. John Cross is an accomplished adventurer and river runner, having been interested in commercial river expeditions during much of his life. His interest in the rivers of southwestern Chihuahua was thus not only a part of his vocation but also an adventure for him into a new river system. Mr. Cross made at least two additional trips into the barrancas of southwest Chihuahua: one down the Rio Urique, from just above the Divisadero to Urique (Figs. 8 and 9A–F), and one from the Rio Verde, south of Guachochic into the Rio San Miguel and to the junction of the Rio Urique. Although herpetology was not their prime interest, a number of new records for Chihuahua were obtained and deposited in the BYU collection. During the next few years I had as my companions either Dr. Glen T. Moore, a botany professor at BYU, or Dr. Kenneth R. Larson, a graduate student at that time.

Upon occasion we solicited the aid of some of the Mexican people, particularly when we were short-handed in the mountain areas. We found them to be very cooperative, and at no time were we ever made to feel unwelcome. For example, when we were at Creel the La Bufa mining superintendent helped us to secure the necessary fuel to complete our trip into the southeastern barranca area. At Cerocouhui we parked our truck and all of our contents by the side of the Catholic church, where it remained for over a week totally unmolested. We found that the Mexican people in the mountains were not only friendly, but very trustworthy.

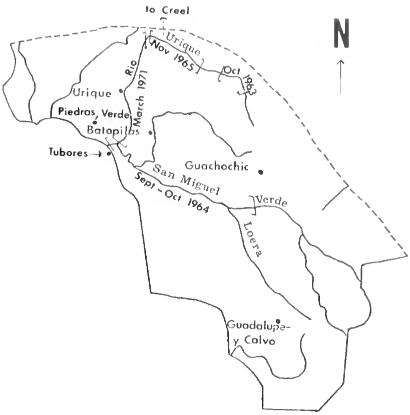

Fig. 8. Map of the area traversed by J. L. Cross during his river-running expeditions in southwest Chihuahua.

SPECIMEN MATERIALS

Except for a few exchanges made with other museums and university collections, the materials gathered during the 15 years of collecting are deposited in the herpetological collection at Brigham Young University. We have sent a few specimens to the University of Mexico, and have, in all of our collecting trips, tried to observe the collecting regulations set forth by the Mexican government. During our collecting it was not our intent to take large samples of any one species at any one locality, but we were interested primarily in determining, as far as possible, the species and subspecies that actually occur within the state of Chihuahua.

For the loan of comparative specimens, I am indebted to the following individuals and institutions: Dr. Charles C. Carpenter, University of Oklahoma (UO); Dr. William G. Degenhardt, Dr. Roger Conant, and Mr. Lee

Fig. 9. A series of photographs from southwestern Chihuahua showing the rugged terrain in and around the Barranca del Cobre and the Rio Urique.

A. Looking northwest across the Barranca del Cobre toward the Divisadero. Tarahuniara dwelling is in the foreground.

Fitzgerald, Museum of Southwestern Biology, University of New Mexico (NMMZ); Dr. William E. Duellman and Joseph T. Collins, Museum of Natural History, University of Kansas (KU); Dr. M. J. Fouquette, Jr., Arizona State University (ASU); Dr. Arnold G. Kluge, University of Michigan, Museum of Zoology (UMMZ); Dr. Alan Leviton and Dr. Robert C. Drewes, California Academy of Sciences (CAS and CAS-SU); Dr. Charles H. Lowe, University of Arizona (UAZ); Dr. Roy W. McDiarmid, U.S. National Museum (USNM); Dr. Douglas A. Rossman, Museum of Zoology, Louisiana State University (LSUMZ); Dr. David B. Wake, Museum of Vertebrate Zoology, University of California (MVZ); Dr. Robert G. Webb, University of Texas at El Paso (UTEP); and Monte L. Bean Life Science Museum, Brigham Young University (BYU).

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I am indebted to Mr. John L. Cross for his kindness in permitting me to accompany him on one of his trips in southwestern Chihuahua (October 1963) and for the use of his field journals from his other trips into the Rio Urique Barranca and the valley of the Rio San Miguel. From his interest in our project, a number of genera (*Leptodeira*, *Leptophis*, *Oxybelis*, and *Rhadinaea*) were added to the fauna. Other specimens extended ranges and helped in a better understanding of systematic relationships. I was also the recipient of his entire herpetological collection, without which this study would have been greatly wanting for material from southwestern Chihuahua.

The drawings are by Mrs. Diane Mellor, library and reference work was done by Mrs. Jody Chandler, and the manuscript was typed by Mrs. Colleen Taylor. To each I am indeed grateful for their help.

B. Looking north from south rim of Barranca del Cobre.

The manuscript was reviewed by Dr. Hobart M. Smith and Dr. Carl S. Lieb.

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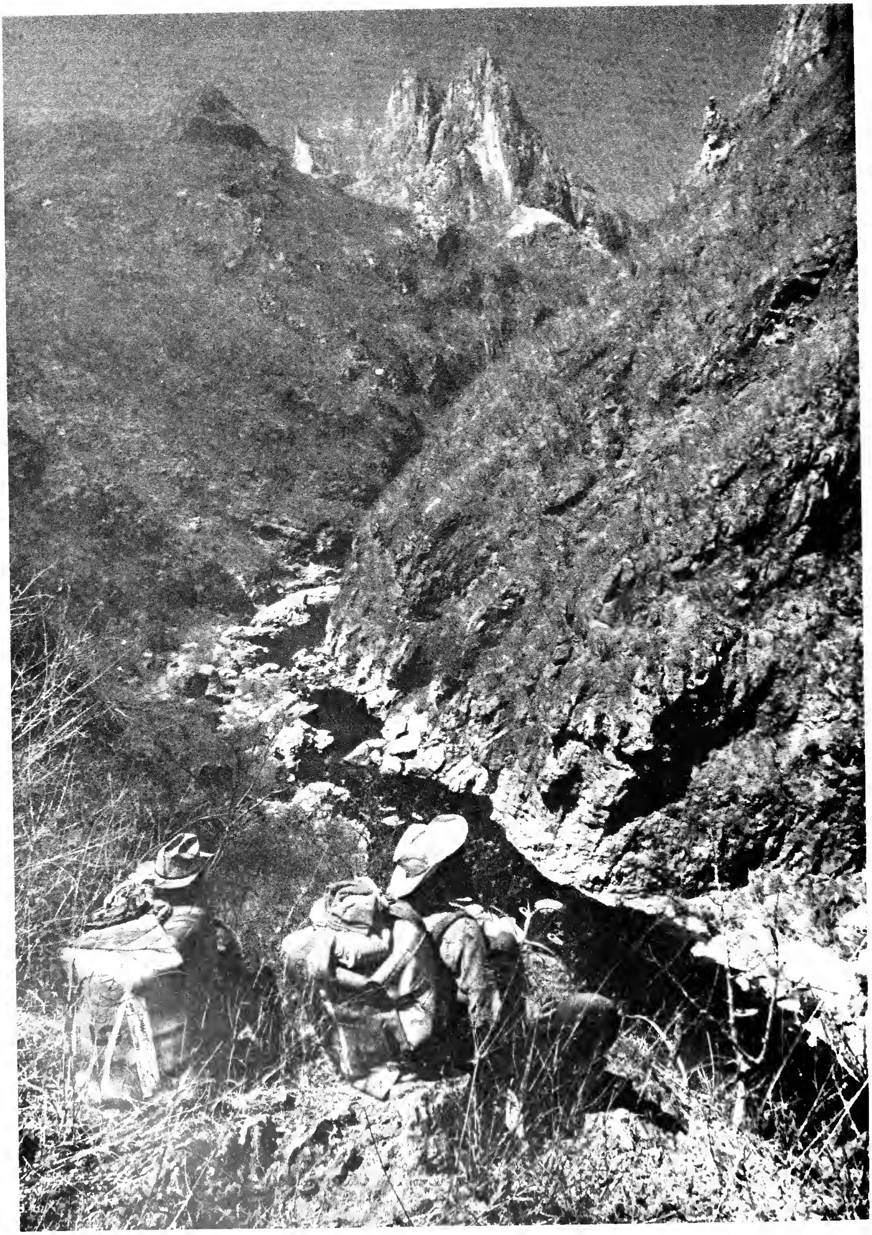
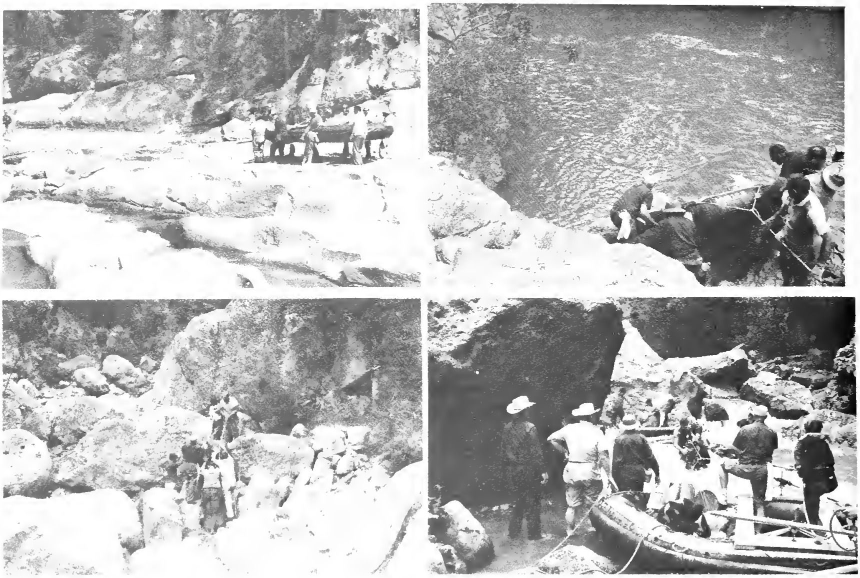


C. Just below the Divisadero looking north up the Rio Urique. Part way up the slope and looking down at the boats in the river below.

D. Rio Urique just below Divisadero, looking downstream.



E. Photographs showing our attempt to run the Rio Urique. Top photos showing portage around two waterfalls. Bottom photos showing the boulder-filled channel.

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ELECTROPHORETIC STUDY OF CUTTHROAT TROUT POPULATIONS IN UTAH

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ABSTRACT.—Thirty-nine Utah streams were sampled for cutthroat trout. Of these, 31 contain cutthroat or cutthroat/rainbow hybrid populations. By using starch gel electrophoresis, these populations were segregated into three groups. One group consisted predominately of fish from the Sevier River (of the Bonneville Basin) and Colorado drainages. A second was primarily populations from the Bear River Drainage (Bonneville Basin) as well as some scattered populations along the Wasatch Front (Bonneville Basin). The third consisted of Wasatch Front populations and populations that have hybridized with rainbow trout. Since different subspecies of cutthroat trout are native to the Colorado and Bonneville drainages, one would expect the populations from within the Bonneville Basin to be more similar to one another and less similar to the Colorado River populations. That this did not occur raises questions concerning the evolutionary relationships of the subspecies and the populations. It is clear that at least a northern (Bear River) and southern (Sevier River) form of the Bonneville cutthroat exists. The Wasatch Front may represent an intermediate zone where these two forms intergrade.

Salmo clarki, the cutthroat trout, had the most extensive continental distribution of the western North American native trout (Salmonidae, *Salmo*). Behnke (1981) tentatively recognized 15 subspecies of cutthroat trout associated with three major phyletic groups: a coastal cutthroat trout, *S. clarki clarki*, characterized by 68 to 70 chromosomes (Gold et al. 1977); an interior cutthroat trout, *S. c. lewisi*, native to the upper Columbia River, upper Missouri River, and the South Saskatchewan drainages, characterized by 66 chromosomes (Loudenslager and Thorgaard 1979); and a group of subspecies derived from the Yellowstone cutthroat trout, *S. c. bouvieri*, which inhabit the upper Snake River, Yellowstone River, the Great Basin, Colorado River, South Platte River, and Rio Grande drainages. These are characterized by 64 chromosomes (Loudenslager and Thorgaard 1979).

Utah's waters originally supported three cutthroat trout subspecies—the Yellowstone, *S. c. bouvieri*, the Colorado River, *S. c. pleuriticus*, and the Bonneville, *S. c. utah*. The Yellowstone cutthroat is native in the Raft River drainage of northwestern Utah but has now been introduced throughout Utah. The headwaters of the Colorado River Basin (the Green River) downstream to the Dirty Devil River, Utah, on the west and the San Juan drainage of Colorado, New Mexico, and Arizona on the east composed the original range of the Colorado River cutthroat (Fig. 1). This trout has been severely impacted by man and is now considered threatened (Miller 1972). The Bonneville Basin (Fig. 1), situated on the eastern edge of the Great Basin, represents the drainage basin of Pleistocene Lake Bonneville. This basin comprises the original range of the Bonneville cutthroat trout, *S. c. utah*. Until recently the Bonneville cutthroat was thought to be extinct or so hybridized with introduced trout that it was unrecognizable. However, Hickman (1978) located 15 relict populations in Utah, Nevada, and Wyoming, and a sizable sport fishery has now been developed on what may be a native population in Bear Lake at the Utah-Idaho border.

The present distribution of cutthroat trout within the Bonneville Basin is restricted to isolated lakes and tributaries where suitable habitat remained following the desiccation of pluvial Lake Bonneville. Three morphologically and ecologically differentiated groups of populations, associated with the Snake Valley region on the Nevada-Utah border, the Bear River drainage in Wyoming, Idaho, and Utah, and the central Bonneville Basin proper, are currently recognized (Hickman and Duff 1978, Behnke 1981). In addition to the ecological and morphological differentiation of these

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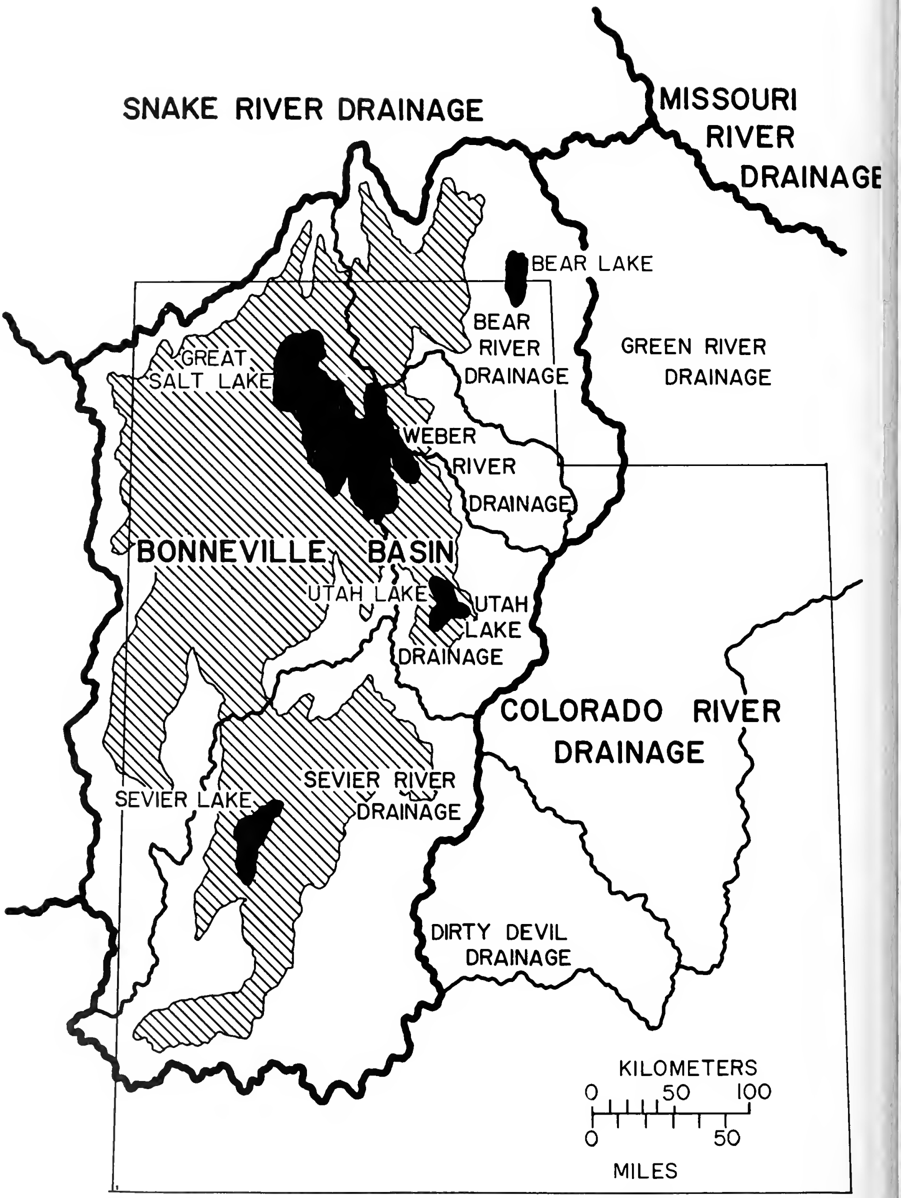

Fig. 1. Major drainage basins in the Utah area. The cross-hatched area represents the Bonneville stage of Lake Bonneville during the Wisconsin glacial period.

population groups, there is evidence of genetic divergence. Klar and Stalnaker (1979) reported a distinctive LDH allele in the Snake Valley population group. Gall and Loudenslager (1981), using 36 protein loci, compared three populations from the Bear River drainage and four populations from the Snake Valley with each other and representative *S. c. bouvieri*, *S. c. pleuriticus*, and *S. c. henshawi*. They reported little genetic differentiation within the Bear River or Snake Valley population groups but substantial differentiation between them. Moreover, the Bear River populations were more similar genetically to *S. c. bouvieri*, and the Snake Valley populations were more similar to *S. c. pleuriticus* than the Bear River and Snake Valley groups were to each other.

In this paper we present results of an electrophoretic analysis of Utah cutthroat trout populations from drainage systems not previously surveyed, using the protein systems that distinguish Snake Valley and Bear River cuttthroat trout from each other and rainbow trout, *S. gairdneri* (Gall and Loudenslager 1981). The objectives were to evaluate the genetic relatedness of these populations and identify hybridization between native cutthroat and introduced rainbow trout.

Methods

Thirty-nine Utah streams located in the Wasatch-Cache, Uinta, Manti-La Sal and Fish Lake National Forests were examined (Fig. 2, Table 1). Both electrofishing and hook and line were used to collect fish. Eight streams lacked cutthroat trout populations. A total of 550 trout from the remaining 31 streams were examined. Fish were frozen in the field on dry ice and returned to Brigham Young University for processing. Following processing, specimens were preserved in formalin and stored in 40% isopropyl alcohol.

Tissue samples were homogenized in 0.25 M sucrose and centrifuged at 30,000 x g for 15 minutes. The resulting supernatant was analyzed with horizontal starch-gel electrophoresis. Four protein systems encoded by six loci were examined: tripeptide aminopeptidase (LGG; EC 3.4.11.4) from muscle tissue, isocitrate dehydrogenase (IDH-3,4; EC 1.1.1.42) from liver tissue, malic enzyme (ME; EC 1.1.1.40) from liver tissue, and sorbitol dehydrogenase (SDH-1,2; EC 1.1.1.14) from liver tissue (Gall and Loudenslager 1981).

Loci are designated using the nomenclature of Allendorf and Utter (1978). An abbreviation that corresponds to the name of a protein designates each locus. Multiple forms of a protein are designated with the least anodally migrating locus as −1, the next −2, and so on. Allelic variants are designated according to the relative mobility of their products, with the most common allele in *S. gairdneri* designated 100.

Allelic frequencies were determined from the protein bands. A matrix of similarities between populations based on Nei's genetic identity index (Nei 1972) was clustered with the NTSYS statistical package. The unweighted pair-group method using arithmetic averages (UPGMA), cluster algorithm was used (Sneath and Sokal 1973).

Results and Discussion

Polymorphism was found in five of the six loci examined: GCP, IDH-3, ME, and SDH-1,2. Allelic frequencies for these loci are given in Table 2. All of the polymorphisms have been previously described in cutthroat trout (Loudenslager and Gall, 1980; Gall and Loudenslager, 1981).

Evidence of hybridization with hatchery rainbow trout, Salmo gairdneri.— If parental species are monomorphic for different alleles at a locus, or are polymorphic but share no alleles, then that locus can be used to distinguish the parental species and their hybrids (Gall and Loudenslager 1981). Two loci, GCP and ME, examined in the present study can be used to distinguish cutthroat trout, rainbow trout, and their hybrids. The GCP locus had two alleles, GCP (160) and GCP (100). The GCP (160) allele was previously reported to be: monomorphic in *S. c. bouvieri*, *S. c. utah*, and *S. c. pleuriticus* and absent in *S. gairdneri* (Gall and Loudenslager 1981), whereas the GCP (100) allele is the common allele in hatchery *S. gairdneri* (Gall and Loudenslager 1981). Similarly, the ME locus had two alleles, ME (125) and ME (100). ME (125) is monomorphic in *S. c. bouvieri*, *S. c. utah*, and *S. c. pleuriticus* and absent in hatchery *S. gairdneri*, whereas ME (100) is the common

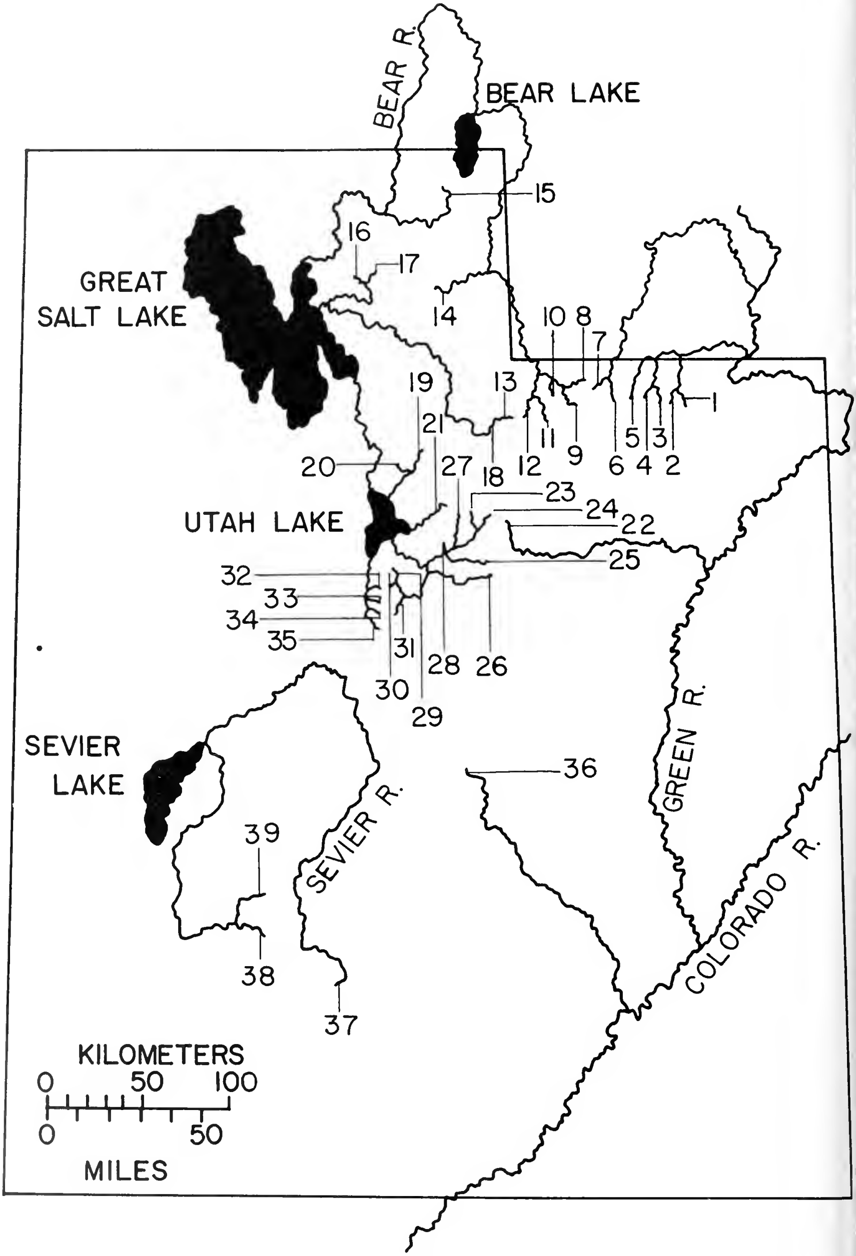

Fig. 2. Location of the 39 streams examined in this study. See Table 1 for the stream name and drainage basin.

TABLE 1. Localities and numbers of trout collected.

Sample number	Sample site	Drainage	Major drainage	Number of specimens
1.	Kabell Creek	Green River	Colorado River	4
2.	Thompson Creek	Green River	Colorado River	16
3.	M. Fk. Beaver Creek	Green River	Colorado River	9
4.	W. Fk. Beaver Creek	Green River	Colorado River	20
5.	Joulious Creek	Green River	Colorado River	17
6.	M. Fk. Blacks Creek	Green River	Colorado River	24
7.	Brush Creek	Green River	Colorado River	22
8.	McKenzie Creek	Bear River	Bonneville Basin	12
9.	Mill Creek	Bear River	Bonneville Basin	22
10.	Carter Creek	Bear River	Bonneville Basin	17
11.	Boundary Creek	Bear River	Bonneville Basin	20
12.	Meadow Creek	Bear River	Bonneville Basin	19
13.	Moffit Creek	Weber River	Bonneville Basin	18
14.	Sugarpine Creek	Bear River	Bonneville Basin	19
15.	Bunchgrass Creek	Logan River	Bonneville Basin	19
16.	Durfee Creek	Ogden River	Bonneville Basin	0
17.	Greetsen Creek	Ogden River	Bonneville Basin	3
18.	Red Pine Creek	Weber River	Bonneville Basin	18
19.	N. Fk. Amer. Fk. River	Utah Lake	Bonneville Basin	5
20.	Silver Creek	Utah Lake	Bonneville Basin	0
21.	L. Fk. Hobble Creek	Utah Lake	Bonneville Basin	21
22.	Strawberry River	Green River	Colorado River	60
23.	Shinglemill Creek	Spanish Fork	Bonneville Basin	16
24.	Chase Creek	Spanish Fork	Bonneville Basin	4
25.	Fifth Water Creek	Spanish Fork	Bonneville Basin	11
26.	Indian Creek	Spanish Fork	Bonneville Basin	0
27.	Wanrhodes Creek	Spanish Fork	Bonneville Basin	11
28.	Little Diamond Creek	Spanish Fork	Bonneville Basin	17
29.	Tie Fork Creek	Spanish Fork	Bonneville Basin	0
30.	Holman Creek	Spanish Fork	Bonneville Basin	27
31.	Nebo Creek	Spanish Fork	Bonneville Basin	23
32.	Mendenhall Creek	Utah Lake	Bonneville Basin	0
33.	North Creek	Utah Lake	Bonneville Basin	0
34.	Bear Canyon Creek	Utah Lake	Bonneville Basin	0
35.	Willow Creek	Utah Lake	Bonneville Basin	0
36.	Muddy Creek	Dirty Devil River	Colorado River	5
37.	Deep Creek	Sevier River	Bonneville Basin	16
38.	Hy Hunt Creek	Sevier River	Bonneville Basin	25
39.	N. Fk. North Creek	Sevier River	Bonneville Basin	30

allele in hatchery *S. gairdneri*. Individuals representative of the parental species will be homozygous for their respective diagnostic alleles, F_1 hybrids will be heterozygous for both loci, and F_2 or backcross individuals will possess a mixture of heterozygous and homozygous diagnostic loci. Evidence for hybridization cannot be based on allele frequencies alone but requires classification of individuals based on a composite biochemical phenotype. This is because composite phenotypes could indicate the presence of both parental species without hybridization.

Of the Utah cutthroat trout populations sampled, seven were found that had an apparent introgression of rainbow trout alleles: Thompson, Mill, Boundary, Bunchgrass, Wanrhodes, Nebo, and Hy-Hunt Creeks. Using the composite enzyme phenotype, no sample included rainbow trout, *Salmo gairdneri*.

Genetic differentiation and relationships among Utah cutthroat trout populations.— An inspection of allelic frequencies (Table 2) indicates that the SDH-1 locus is primarily responsible for differences among Utah cutthroat trout populations (after hybridization with rainbow trout is considered). Cutthroat trout populations in the Colorado River drainage are dichotomous for SDH-1 allele frequencies. Middle Fork Beaver, West Fork Beaver, Joulious, Middle Fork Blacks, and

TABLE 2. Allelic frequencies of 6 loci for 31 trout populations.

Locus		Kabell 1	Thompson 2	M. Fk. Beaver 3	W. Fk. Beaver 4	Joulious 5	M. Fk. Blacks 6	Brush 7	McKenzie 8
SDH-1	100	—	—	—	—	—	—	—	—
	40	0.63	—	0.05	0.02	0.18	0.12	0.02	1.00
	0	0.37	1.00	0.95	0.98	0.82	0.88	0.98	—
SDH-2	250	—	—	—	—	—	—	—	—
	100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
IDH-3	170	—	—	—	—	—	—	—	—
	100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	60	—	—	—	—	—	—	—	—
IDH-4	140	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
LGG	160	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	100	—	—	—	—	—	—	—	—
ME	125	1.00	0.97	1.00	1.00	1.00	1.00	1.00	1.00
	100	—	0.03	—	—	—	—	—	—

Table 2 continued.

Locus		Mill 9	Carter 10	Boundary 11	Meadow 12	Moffit 13	Sugarpine 14	Bunchgrass 15	Greetsen 17
SDH-1	100	—	—	—	—	—	—	—	—
	40	0.55	1.00	1.00	1.00	0.03	1.00	1.00	0.17
	0	0.45	—	—	—	0.97	—	—	0.83
SDH-2	250	—	—	—	0.13	—	—	—	—
	100	1.00	1.00	1.00	0.87	1.00	1.00	1.00	1.00
IDH-3	170	—	—	0.11	0.03	0.08	—	—	—
	100	1.00	1.00	0.89	0.97	0.92	1.00	0.97	1.00
	60	—	—	—	—	—	—	0.03	—
IDH-4	140	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
LGG	160	0.95	1.00	0.68	1.00	1.00	1.00	1.00	1.00
	100	0.05	—	0.32	—	—	—	—	—
ME	125	1.00	1.00	0.75	1.00	1.00	1.00	0.97	1.00
	100	—	—	0.25	—	—	—	0.03	—

Brush creeks have a high frequency of the SDH-1 (0) allele ($\bar{x} = 0.922$), whereas Kabell Creek, Strawberry River, and Muddy Creek have intermediate frequencies of the SDH-1 (0) allele ($\bar{x} = 0.49$). Gall and Loudenslager (1981) sampled *S. c. pleuriticus* from two locations in Wyoming and found the populations monomorphic for the SDH-1 (0) allele. The intermediate frequency of SDH-1 (40) in Kabell Creek, Strawberry River, and Muddy Creek could be due to natural selection, genetic drift, or hybridization with stocked cutthroat trout. Since Yellowstone cutthroat trout, *S. c. bouvieri*, are monomorphic for SDH-1 (40) (Loudenslager and Gall 1980), hybridization is a probable cause. The Strawberry River is also a major source of cutthroat eggs for stocking operations throughout the

Table 2 continued.

		Streams Stream number							
Locus		Red Pine 18	N. Fk. Am. Fk. 19	L. Fk. Hobble 21	Strawberry 22	Shinglemill 23	Chase 24	Fifth Water 25	Wanrhodes 27
SDH-1	100	—	—	—	—	—	—	—	—
	40	0.25	0.25	1.00	0.50	0.97	1.00	0.50	0.36
	0	0.75	0.75	—	0.50	0.03	—	0.50	0.64
SDH-2	250	—	—	—	—	—	—	—	—
	100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
IDH-3	170	—	—	—	0.01	—	—	—	—
	100	1.00	1.00	1.00	0.99	1.00	1.00	1.00	0.95
	60	—	—	—	—	—	—	—	0.05
IDH-4	140	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
LGG	160	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.91
	100	—	—	—	—	—	—	—	0.09
ME	125	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.91
	100	—	—	—	—	—	—	—	0.09

Table 2 continued.

		Streams Stream numbers						
Locus		Little Diamond 28	Holman 30	Nebo 31	Muddy 36	Deep 37	Hy Hunt 38	N. Fk. North 39
SDH-1	100	—	—	—	—	—	—	—
	40	0.35	0.85	0.54	0.40	—	0.20	—
	0	0.65	0.15	0.46	0.60	1.00	0.80	1.00
SDH-2	250	—	—	—	—	—	—	—
	100	1.00	1.00	1.00	1.00	1.00	1.00	1.00
IDH-3	170	—	—	—	—	—	0.04	—
	100	1.00	1.00	1.00	1.00	1.00	0.96	1.00
	60	—	—	—	—	—	—	—
IDH-4	140	1.00	1.00	1.00	1.00	1.00	1.00	1.00
LGG	160	1.00	1.00	0.87	1.00	1.00	0.80	1.00
	100	—	—	0.13	—	—	0.20	—
ME	125	1.00	1.00	0.91	1.00	1.00	0.86	1.00
	100	—	—	0.09	—	—	0.14	—

state of Utah. The stocking of fish from this population could change allele frequencies in native populations.

Within the Bonneville Basin, cutthroat trout populations were sampled from the Bear River drainage, along the Wasatch Front (Weber and Utah lake drainage), and the Sevier River drainage (Fig. 1). The four Bear River drainage populations not influenced by rainbow trout hybridization were monomorphic for the SDH-1 (40) allele. This supports previous observations that Bear River drainage cutthroat trout were monomorphic for SDH-1 (40) (Gall and Loudenslager 1981). In contrast, both the Deep Creek and North Fork of North Creek populations from the Sevier River drainage were monomorphic for the SDH-1 (0) allele. The SDH-1 allele frequen-

TABLE 3. Genetic identity and distance values for pairwise comparisons of the 31 trout populations sampled. Identity values are above the diagonal, and distance values are below the diagonal.

Stream	No.	1	2	3	4	5	6	7	8	9	10	11	12	13
Kabell	1	—	.931	.942	.936	.964	.954	.936	.977	.998	.977	.942	.973	.936
Thompson	2	.071	—	.999	1.00	.995	.998	1.00	.832	.947	.832	.790	.825	.999
M. Fk. Beaver	3	.060	.001	—	1.00	.997	.999	1.00	.848	.956	.848	.805	.842	.999
W. Fk. Beaver	4	.066	.000	.000	—	.996	.998	1.00	.839	.951	.839	.796	.833	.999
Joulious	5	.037	.006	.003	.004	—	.999	.996	.885	.975	.885	.843	.879	.995
M. Fk. Blacks	6	.047	.003	.001	.002	.001	—	.998	.869	.967	.869	.826	.862	.998
Brush	7	.066	.000	.000	.000	.004	.002	—	.839	.951	.839	.796	.833	.999
McKenzie	8	.023	.184	.164	.175	.122	.141	.175	—	.965	1.00	.972	.997	.840
Mill	9	.002	.054	.045	.050	.025	.034	.050	.035	—	.965	.934	.960	.951
Carter	10	.023	.184	.164	.175	.122	.141	.175	.000	.035	—	.972	.997	.840
Boundary	11	.060	.235	.217	.229	.171	.191	.229	.029	.069	.029	—	.967	.797
Meadow	12	.028	.192	.172	.183	.129	.148	.183	.003	.041	.003	.034	—	.833
Moffit	13	.067	.001	.001	.001	.005	.003	.001	.175	.051	.175	.227	.183	—
Sugarpine	14	.023	.184	.164	.175	.122	.141	.175	.000	.035	.000	.029	.003	.175
Bunchgrass	15	.024	.186	.167	.177	.124	.143	.177	.000	.036	.000	.027	.003	.177
Greetsen	17	.038	.005	.002	.004	.000	.000	.004	.125	.026	.125	.174	.132	.005
Red Pine	18	.026	.011	.007	.009	.001	.003	.009	.101	.017	.101	.148	.108	.010
N. Fk. Am. Fk.	19	.026	.011	.007	.009	.001	.003	.009	.101	.107	.101	.148	.108	.010
L. Fk. Hobble	21	.023	.184	.164	.175	.122	.141	.175	.000	.035	.000	.029	.003	.175
Strawberry	22	.003	.044	.036	.040	.018	.026	.040	.044	.001	.044	.084	.049	.041
Shinglemill	23	.020	.173	.154	.165	.113	.131	.165	.000	.031	.000	.029	.003	.164
Chase	24	.023	.184	.164	.175	.122	.141	.175	.000	.035	.000	.029	.003	.175
Fifth Water	25	.003	.044	.036	.040	.018	.026	.040	.044	.001	.044	.084	.049	.041
Wanrhodes	27	.017	.024	.019	.022	.008	.012	.022	.077	.009	.077	.104	.084	.022
Lt.* Diamond	28	.014	.021	.015	.019	.005	.009	.019	.075	.008	.075	.119	.081	.019
Holman	30	.008	.132	.116	.125	.082	.097	.125	.004	.016	.004	.035	.007	.125
Nebo	31	.006	.055	.047	.052	.028	.036	.052	.040	.002	.040	.058	.047	.053
Muddy	36	.010	.028	.021	.025	.009	.014	.025	.064	.005	.064	.107	.070	.025
Deep	37	.071	.000	.000	.000	.005	.002	.000	.182	.054	.182	.237	.191	.001
Hy Hunt	38	.047	.014	.012	.014	.010	.010	.014	.132	.032	.132	.144	.141	.014
N. Fk. North	39	.071	.000	.000	.000	.005	.002	.000	.182	.054	.182	.237	.191	.001

cies for Wasatch Front populations were highly variable: Moffit Creek had the highest frequency of the SDH-1 (0) allele (0.97), wheras Chase Creek and the Left Fork Hobble Creek were monomorphic for SDH-1 (40). The remaining populations had SDH-1 (0) allele frequencies ranging from 0.03 to 0.83.

A pattern in the SDH-1 allele frequencies is discernible if one includes Loudenslager and Gall's (1980) and Gall and Loudenslager's (1981a, b) findings of populations monomorphic for the SDH-1 (0) allele in four populations native to or derived from the Snake Valley area in western Utah. Populations inhabiting the south and west extremes of the Bonneville Basin are monomorphic for SDH-1 (0), and those in the northeastern region are monomorphic for SDH-1 (40). A zone of intergradation in allele frequency occurs along the Wasatch Front.

Genetic identity and distance were computed (Nei 1972) for all pairwise comparisons of the 31 populations using the six loci surveyed (Table 3). The genetic identity index is an estimate of the proportion of sampled alleles that are identical between paired populations. Genetic distance is an estimate of the net codon differences and a measure of the accumulated allele differences per locus between two populations. Genetic identity in pairwise comparisons of populations ranged from 1.00 in several comparisons to 0.826 between Meadow Creek and North Fork of North Creek. The average genetic identity for pair-wise comparisons of Utah's cutthroat trout was 0.944.

The genetic identity matrix was also used to calculate the mean genetic identity between groups of populations inhabiting different drainage systems (Table 4). In this analysis, populations thought to be hybridized with rainbow trout or Yellowstone cutthroat trout were excluded. Within the Bear River, Colorado River, and Sevier River drainages, genetic identity among localities was high: I = 0.998; 0.998; and 1.00, respectively. In con-

Table 3 continued.

14	15	17	18	19	21	22	23	24	25	27	28	30	31	36	37	38	39
.997	.976	.963	.974	.974	.977	.997	.981	.997	.997	.984	.986	.992	.995	.990	.932	.955	.932
.832	.831	.995	.989	.989	.832	.957	.842	.832	.957	.977	.979	.876	.946	.975	1.00	.986	1.00
.848	.847	.998	.993	.993	.848	.965	.857	.848	.965	.982	.985	.890	.951	.979	1.00	.988	1.00
.839	.838	.996	.991	.991	.839	.961	.848	.839	.961	.979	.982	.882	.949	.976	1.00	.986	1.00
.885	.885	1.00	.999	.999	.885	.982	.893	.885	.982	.992	.995	.922	.973	.992	.995	.990	.995
.869	.867	1.00	.997	.997	.869	.975	.877	.869	.975	.988	.991	.908	.965	.986	.998	.990	.998
.839	.838	.996	.991	.991	.839	.961	.848	.839	.961	.979	.982	.882	.949	.976	1.00	.986	1.00
1.00	1.00	.883	.904	.904	1.00	.957	1.00	1.00	.957	.926	.928	.996	.961	.938	.833	.876	.833
.965	.964	.974	.983	.983	.965	.999	.970	.965	.999	.991	.992	.984	.998	.996	.948	.969	.948
1.00	1.00	.883	.904	.904	1.00	.957	1.00	1.00	.957	.926	.928	.996	.961	.938	.833	.876	.833
.972	.974	.840	.862	.862	.972	.920	.971	.972	.920	.902	.887	.965	.944	.899	.789	.866	.789
.997	.997	.876	.898	.898	.997	.953	.997	.997	.952	.919	.922	.993	.955	.933	.827	.869	.827
.840	.838	.996	.991	.991	.840	.960	.848	.840	.960	.978	.981	.882	.948	.975	.999	.986	.999
—	1.00	.883	.904	.904	1.00	.957	1.00	1.00	.957	.926	.928	.996	.961	.938	.833	.876	.833
.000	—	.881	.902	.902	1.00	.956	1.00	1.00	.956	.926	.926	.996	.960	.937	.831	.876	.831
.125	.127	—	.999	.999	.883	.981	.890	.883	.981	.991	.994	.919	.972	.991	.995	.990	.995
.101	.103	.001	—	1.00	.904	.989	.911	.904	.989	.995	.998	.937	.981	.996	.990	.990	.990
.101	.103	.001	.000	—	.904	.989	.911	.904	.989	.995	.998	.937	.981	.996	.990	.990	.990
.000	.000	.125	.101	.101	—	.957	1.00	1.00	.957	.926	.928	.996	.961	.938	.833	.876	.833
.044	.045	.019	.011	.011	.044	—	.962	.957	1.00	.993	.996	.978	.996	.998	.957	.972	.957
.000	.000	.116	.094	.094	.000	.039	—	1.00	.962	.932	.934	.998	.965	.944	.842	.884	.842
.000	.000	.125	.101	.101	.000	.044	.000	—	.957	.926	.928	.996	.961	.938	.833	.876	.833
.044	.045	.019	.011	.011	.044	.000	.039	.044	—	.993	.996	.978	.996	.998	.957	.972	.957
.077	.077	.009	.005	.005	.077	.007	.071	.077	.007	—	.997	.954	.993	.997	.976	.992	.976
.075	.077	.006	.002	.002	.075	.004	.069	.075	.004	.003	—	.956	.989	1.00	.980	.985	.980
.004	.004	.084	.065	.065	.004	.022	.002	.004	.022	.047	.045	—	.979	.964	.877	.912	.877
.040	.041	.029	.019	.019	.040	.005	.036	.040	.004	.007	.011	.021	—	.992	.946	.976	.946
.064	.065	.009	.004	.004	.064	.002	.058	.064	.002	.003	.000	.036	.008	—	.973	.982	.973
.182	.185	.005	.010	.010	.182	.044	.172	.182	.044	.024	.021	.131	.056	.027	—	.985	1.00
.132	.133	.010	.011	.011	.132	.028	.123	.132	.028	.008	.015	.092	.025	.018	.015	—	.985
.182	.185	.005	.010	.010	.182	.044	.172	.182	.044	.024	.021	.131	.056	.027	.000	.015	—

trast, genetic identity among localities along the Wasatch Front was only 0.928. Pair-wise comparisons of populations from different drainages indicated a high identity between the Sevier River drainage populations and Colorado River populations (I = 0.998). Identity between Bear River drainage populations and either Sevier River drainage samples (I = 0.831) or Colorado River drainage samples (I = 0.855) was much lower. The Wasatch population group had mean identities of 0.940 with the Bear River sites, 0.930 with the Sevier River sites, and 0.941 with the Colorado River sites. These data are similar to those of Loudenslager and Gall (1980b). In addition, they demonstrated a genetic identity of 0.996 between the Bear River Bonneville and Yellowstone cutthroat trout.

The clustering of the genetic identity matrix resulted in three distinct clusters (Fig. 3). Populations in the first cluster were polymorphic for the SDH-1 locus with intermediate frequencies of the (0) and (40) alleles. Included in this cluster were populations hybridized with rainbow and cutthroat populations from the zone of intergradation along the Wasatch Front. The second cluster contained populations from the Colorado River, Sevier River, and Wasatch Front with a high frequency of the SDH-1 (0) allele. The third cluster contained populations from the Bear River drainage and Wasatch Front with a high frequency of the SDH-1 (40) allele.

The similarity between the Colorado and Sevier River Bonneville and between the Bear River Bonneville, and Yellowstone cutthroat strains could be due to common ancestry (closely related) or it could be a result of convergence or drift. However, the dissimilarity between the Bear River and Sevier River forms of the Bonneville cutthroat is definitive. That is, the occurrence of different allelic frequencies must be due to divergent histories of the populations. For example, the headwaters of Meadow Creek (Bear River drainage) and Moffit Creek (Weber River drainage) are less than a kilometer apart, yet the cutthroat populations have SDH-1 (0) frequencies of 0.00 and 0.97, respectively.

Interpretation of the populations along the Wasatch Front is problematic. Urbanization in

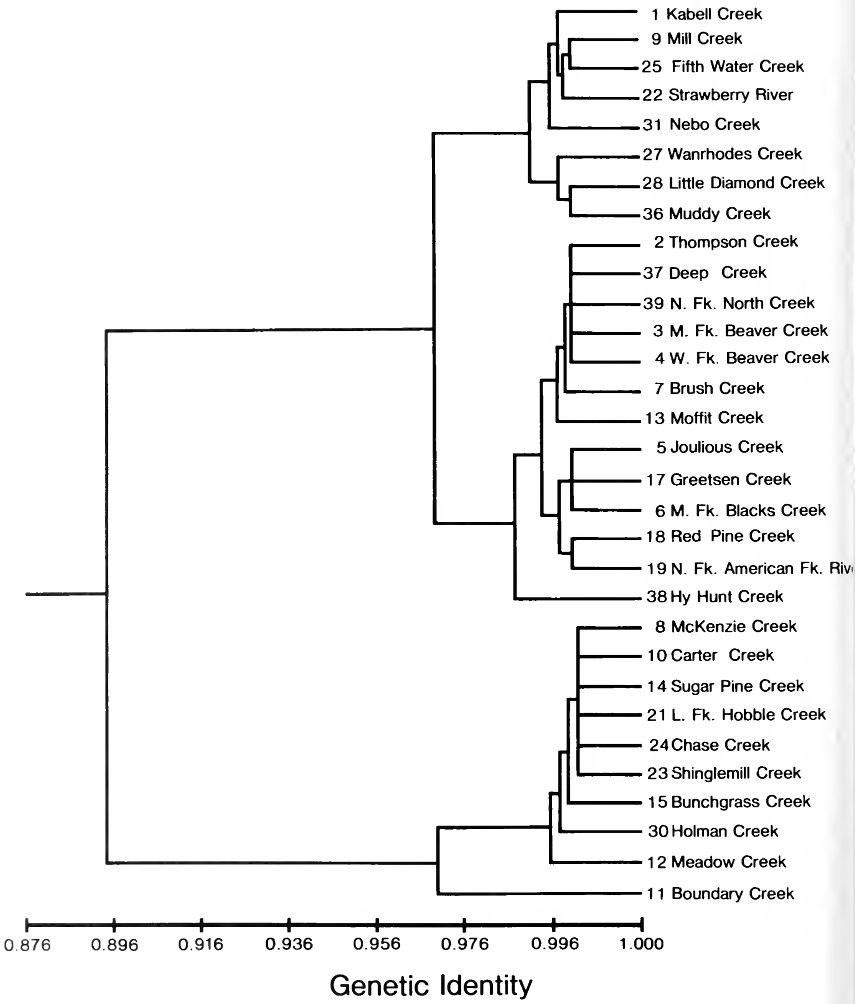

Fig. 3. Cluster dendrogram based on UPGMA clustering of the genetic identity matrix.

TABLE 4. Matrix of genetic identity among cutthroat trout populations from drainages within the Bonneville Basin and Colorado River. The number of sample locations for each drainage is in parenthesis, and within drainage population identity is on the diagonal.

	1	2	3	4
1. Bear R. (4)	.998	.831	.940	.855
2. Sevier R. (2)		1.000	.930	.998
3. Wasatch Front (10)			.928	.941
4. Colorado River (5)				.998

Utah is concentrated along the Wasatch Front. The stocking of nonnative trout has been intense in this area. Although we can reliably identify hybridization with rainbow trout, we are unable to confidently assess hybridization with nonnative cutthroats because of the close genetic relationship between native Bonneville Basin trout and cutthroats from contiguous basins. Whether these populations were originally polymorphic or monomorphic for SDH-1 is unknown.

Several populations in the Bonneville Basin near Utah Lake had high SDH-1 (40) frequencies. These fish are similar to the Yellowstone cutthroat trout and may have resulted from stocking. The highly polymorphic populations in the area are also likely to have been influenced by the activities of man. For instance, the Diamond Fork drainage (Bonneville basin) receives water diverted from the Strawberry River (Colorado River) drainage. This would allow colonization by Yellowstone-Colorado cutthroat from the Strawberry River into the Diamond Fork drainage and could influence allele frequencies.

Because determining the original geographical variation of the native Utah cutthroat is difficult, all streams that contain cutthroat trout that have not hybridized with rainbow should be given special management consideration. Such streams need not contain monomorphic populations since monomorphism may represent only the extremes of the species variability of the subspecies. Polymorphic populations may still represent the native stocks as long as rainbow hybridization is not evident. This study has advanced our knowledge of the native cutthroat, but much remains to be investigated. One focal area should be the Wasatch Front, where the gradation between the northeastern and southwestern Bonneville forms occurs. Another topic that warrants study is the identification of additional protein systems that separate the Yellowstone from the Bear River Bonneville form and the Snake Valley Bonneville form from the Colorado River cutthroat. These will be instrumental in understanding the taxonomic relationships and variability of the native inland cutthroat trout.

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SEXUAL SELECTION AND MATING SYSTEM VARIATION IN ANURAN AMPHIBIANS OF THE ARIZONA-SONORAN DESERT

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ABSTRACT.—Mating system variation in anuran amphibians of the Arizona-Sonoran Desert was reviewed. Male density and breeding period duration were negatively correlated in seven bufonids and pelobatids. Variation in male mating behavior and ability of females to freely select their mates unhindered by active-searching males also was related directly to male density. These observations support hypotheses relating ecological factors to mating system organization. It is suggested that male calling behavior, and anuran lek mating sytems in general, may be significantly influenced by predation on vocalizing males.

The Arizona-Sonoran Desert boasts a surprising diversity of frogs and toads: seven bufonids, three pelobatids, three ranids, two hylids, one microhylid, and one leptodactylid. As expected, the breeding biology of these anurans is significantly influenced by the xeric climate. Most of these species have short, or "explosive," (Wells 1977) breeding periods during the summer rainy season, although a few have relatively extended, or "prolonged" breeding periods during the spring (Sullivan 1982a, 1983a, 1984, Sullivan and Sullivan 1985). As suggested by Wells (1977), the mating behavior of anurans such as those of the Arizona-Sonoran Desert appears related to breeding period duration. For example, Woodhouse's toad (*Bufo woodhousei*) forms low-density breeding aggregations at sources of permanent water throughout the spring, and all males within these choruses call to attract females (Sullivan 1982a). In contrast, the Great Plains toad (*B. cognatus*) forms high density aggregations at temporary rain pools for only a few nights each summer. Within these short-lived choruses some males adopt satellite positions near vocalizing males and attempt to intercept females approaching the calling males (Sullivan 1982b).

This diversity in breeding period duration and reproductive behavior provides an excellent opportunity for evaluating hypotheses of sexual selection and mating system theory (Trivers 1972, Emlen and Oring 1977, Wells 1977). It is generally hypothesized that duration of breeding period should directly influence opportunities for female mate selection and, hence, male behavior. Wells (1977) argued that for explosive-breeding anurans female choice should be restricted as a result of: (1) temporal constraints limiting time available for mate selection and (2) high male densities and corresponding alternative male mating tactics that typically reduce the ability of females to move freely in breeding aggregations. Conversely, in species with prolonged breeding periods and lower male densities, females should be capable of freely selecting their mates and constitute a potentially significant evolutionary force (e.g., Arnold 1983). The variation in breeding biology of anurans of Arizona allows direct test of these hypotheses. Here I summarize recent studies of sexual selection in pelobatids and bufonids of Arizona and, following Emlen and Oring (1977), document the existence of predictable relationships between the ecology, mating systems, and reproductive behavior of these species. I also examine species recognition and acoustic competition among these anurans. Lastly, I discuss the evolution of anuran lek mating sytems.

GENERAL METHODS

Methods employed in the studies reviewed here have been described in detail elsewhere (Sullivan 1983c, 1984, Sullivan and Sullivan 1985); a brief summary follows. Observations at anuran breeding aggregations in southern Arizona were made with a six-volt headlamp

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TABLE 1. Mean male density (number of males) and breeding period duration (days) for seven anurans (*Bufo* and *Scaphiopus*) of southern Arizona (N = number of breeding aggregations).

	Density		Duration		Source
Species	x̄	N	x̄	N	
S. multiplicatus	43.6	7	1.6	7	Sullivan and Sullivan, 1985
S. bombifrons	26.7	6	1.8	6	Sullivan and Sullivan, 1985
B. cognatus	25.2	8	2.6	10	Sullivan, 1983c
S. couchi	23.3	3	1.0	3	Sullivan and Sullivan, 1985
B. debilis	11.4	5	2.6	5	Sullivan, 1984
B. woodhousei	5.4	5	19.8	10	Sullivan, 1982a
B. punctatus	3.0	5	20.0	5	Sullivan, 1984

during the evening in the spring and summer from 1980 to 1984. Toads were captured by hand at breeding aggregations and individually marked by toe-clipping. Snout-vent length was measured to the nearest mm with a plastic rule, and density of males at breeding aggregations was determined by direct count on each night of breeding activity. Male mating success was defined as the number of females a male was observed in amplexus with during a season since amplectant males were never displaced by single males (Sullivan 1983c, 1984, Sullivan and Sullivan 1985).

Focal animal sampling techniques were used to observe behavior of individual males and females in breeding aggregations (Sullivan 1983a, 1983b, 1984). Male advertisement calls were recorded in the field and analyzed in the lab with a Kay 6061B Sonagraph. Determination of pulse rate and frequency of individual calls followed standard methodology as outlined in Sullivan (1982c).

DENSITY, ALTERNATIVE MALE MATING TACTICS, AND FEMALE CHOICE

There is considerable range in breeding period durations of Arizona anurans (Table 1). Mean male density at breeding aggregations is negatively correlated ($\tau = -0.71$, $\underline{P} = 0.01$) with duration of breeding period for seven bufonids and pelobatids. All the species with high density aggregations utilize temporary rain pools for breeding. Presumably, in these explosive-breeding forms the limited temporal availability of water restricts local populations to a pattern of more or less synchronous breeding.

Wells (1977) postulated that temporal constraints and high male densities should promote the adoption of alternative mate-locating tactics by males of explosive-breeding anurans. Sullivan (1982b) corroborated Wells' hypothesis: in breeding aggregations of *B. cognatus* the proportion of noncalling, satellite males "parasitizing" calling males is correlated with chorus size. These satellite males will begin vocalizing if male density decreases. Similar satellite, as well as active-searching behavior, has been observed in two of the pelobatids of Arizona (Sullivan and Sullivan 1985). It seems clear that density is the primary factor influencing male adoption of alternative tactics, especially in light of the intraspecific variation in *B. cognatus*. Furthermore, in those anurans that form low density breeding aggregations no noncalling male tactics have been observed independent of breeding period duration (Sullivan 1982a, 1984). Other bufonids and pelobatids of North America also exhibit active-searching and satellite behaviors (Wells 1977). As expected, all these forms are characterized by explosive breeding periods and high male densities.

Active-searching and satellite males have been observed successfully amplexing females in high density breeding aggregations of two Arizona anurans, *B. cognatus* (Sullivan 1982b), and *Scaphiopus multiplicatus* (Sullivan and Sullivan 1985). These observations support the notion that females are limited in their ability to freely select mates in high density aggregations in part as a result of some males adopting noncalling, mate-locating tactics. Another line of evidence suggesting that mating is random with respect to male phenotype in explosive-breeding anurans is the lack of relationship between male size and mating success among these forms (Table 2). Many investigators have suggested that female

TABLE 2. Relationships between male size and mating success in five anurans (*Bufo* and *Scaphiopus*) of southern Arizona.

	Snout-vent length (mm)								
	Mating males		Nonmating males			Positive assortative mating			Source
Species	x̄	N	x̄	N	P	r	N	P	
S. couchi	71.0	6	70.0	6	>.05*	0.07*	12	=.50	Sullivan and Sullivan, 1985
	74.1	10	71.1	18	>.05	0.07*	20	=.43	
	74.4	5	69.2	18	>.05*	−0.40*	10	=.24	
S. multiplicatus	50.9	21	51.3	28	>.05	0.05	21	>.05	Sullivan and Sullivan, 1985
	51.2	12	50.0	15	>.05	—	—	—	
	48.0	6	48.0	11	>.05*	—	—	—	
B. cognatus	78.6	24	77.2	150	>.05	0.09	24	>.05	Sullivan, 1983a
B. debilis	41.3	6	42.3	16	>.05*	0.20*	6	>.05	Sullivan, 1984
B. woodhousei	84.1	18	85.4	43	>.05	0.23	47	>.05	Sullivan, 1983b

*For small samples (<10) a Mann-Whitney *U* test or Kendal's tau was calculated

anurans should select large males as mates if size is an indicator of fitness (Wilbur et al. 1978, Fairchild 1981). Others have argued that females might benefit from selecting a male similar in size to themselves if fertilization success is related to the size difference between mating males and females (Licht 1976, Davies and Halliday 1979). Analysis of male size and mating success in four explosive-breeding anurans of Arizona has not supported either of these hypotheses (Table 2.)

Male size is positively correlated with mating success in some explosive-breeding bufonids and pelobatids of the United States (Gatz 1981, Woodward 1982). However, in these forms large males might achieve greater mating success as a result of size advantages during direct struggles for possession of females (Sullivan 1983a). Davies and Halliday (1979) and Lamb (1985) determined that large male bufonids are more successful in taking over females during male-male disputes. For these species a mating advantage for large males may be independent of any female preference. Woodward (1982) documented a large-male mating advantage in one of four *S. couchi* and one of two *S. multiplicatus* breeding aggregations in central New Mexico. This interspecific variation suggests that a number of variables such as density and alternative mating tactics of males influence the outcome of sexual selection in nature.

Male mating success in prolonged-breeding anurans is often correlated with the number of nights a male participates in chorus activity (Kluge 1981, Woodward 1981, Ryan 1983). For prolonged-breeding *B. woodhousei* in Arizona male mating success is weakly correlated ($R^2 = 0-25\%$) with participation in chorus activity (Fig. 1). However, this result is expected since many males are only observed at a chorus for one night: a correlation occurs because any male who mates two or three times must be present at the chorus for at least as many nights. Further, many males who are unattractive as mates (low call rate males) are active at choruses for many nights without obtaining any matings. Hence, for this anuran male persistance in chorus activity is not an important determinant of mating success.

Female mate selection has been observed in breeding aggregations of the three Arizona bufonids with low-density choruses (Sullivan 1983a, 1984). In all of these forms, females initiate amplexus by making physical contact with a calling male and are able to move freely through breeding choruses to select their mates from among the calling males. In *B. woodhousei* male mating success is correlated with call rate, suggesting that females prefer high call rate males as mates (Sullivan 1983a). Males within a chorus retain a consistent, relative ranking in call rate within and between nights, and there is significantly more variation in call rate between than within males (Sullivan 1983a, Sullivan and Leek in review). Females prefer speakers broadcasting calls at the higher rate in simple two-speaker discrimination experiments, further supporting the female preference hypothesis. Proximately, female choice of high call rate males could be passive if they merely locate such males more readily, or active if genetically determined

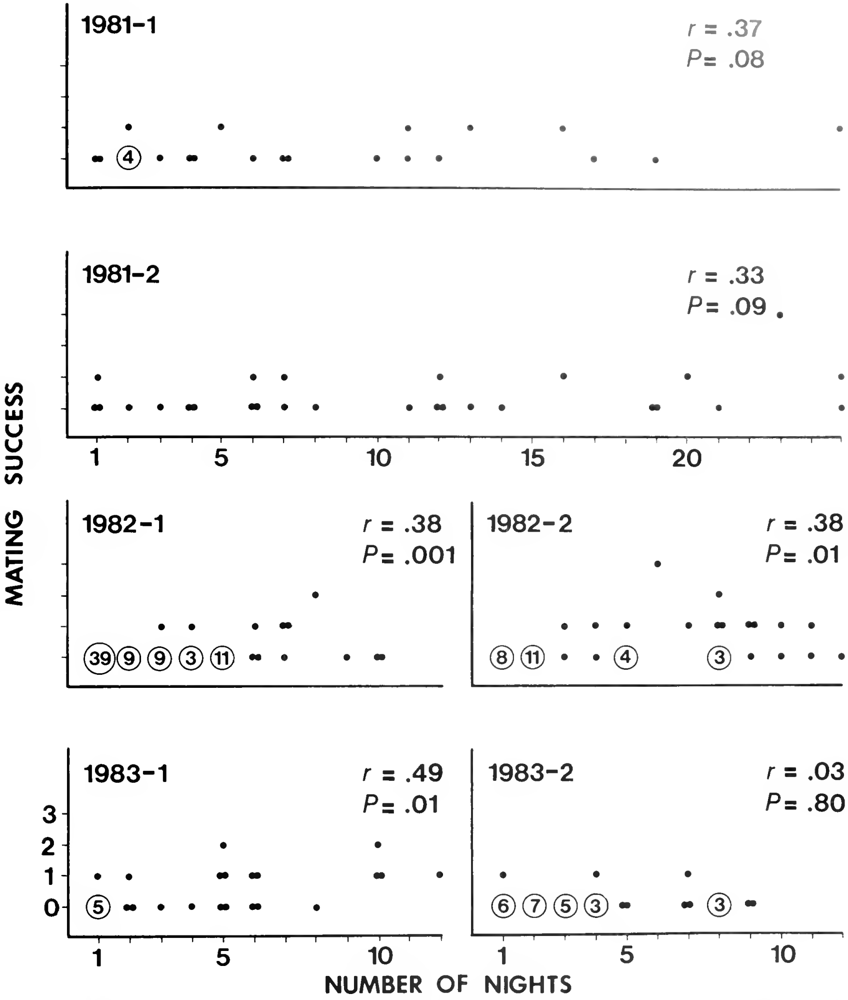

Fig. 1. Male mating success (number of matings) against number of nights of participation in chorus activity for six aggregations of *Bufo woodhousei* (number of concordant observations given inside circle).

preferences exist (Parker 1982, Arak 1983). In *B. woodhousei* female behavior is consistent with the latter alternative since they often pass by low call rate males when moving through a chorus toward a high call rate male (Sullivan 1983a). However, the ultimate significance of these alternatives is indistinguishable: high call rate males derive fitness benefits through increased mating success, and females, although deriving no immediate benefits, may benefit via increased offspring survivorship or mating success, or both (Lande 1981, Kirkpatrick 1982, Arnold 1983). The importance of these benefits to females would be determined by the heritability of male call rate and its relation to offspring survivorship and mating success. In any event, mating is clearly nonrandom with respect to male phenotype and female behavior in *B. woodhousei*.

These observations on male behavior and mate selection by females reveal that the prolonged-breeding species (*B. punctatus* and *B. woodhousei*), and at least some of the explosive-breeding forms (*B. cognatus* and *B. debilis*), have lek-like mating systems (Sullivan 1983c). Females typically select their mates freely from among aggregations of displaying males, and males provide only sperm to their mates. Females mate disproportionately often with males possessing high call rates in both *B. cognatus* and *B. woodhousei* (Sullivan 1983c); for the other species it is unknown whether females discriminate between conspecific males on the basis of male phenotype (Sullivan 1984). The explosive-breeding pelobatids exhibit a typical male-dominance mating system in which mate selection by females is somewhat limited (Emlen and Oring 1977). Males may obtain multiple matings within a breeding season if they participate in breeding aggregations following every rainstorm each summer (Sullivan 1983b). Although generally consistent with the hypothesis of Emlen and Oring (1977) concerning the significance of breeding period duration to mating system structure, these observations indicate clearly that male density, through its impact on female choice and regardless of breeding period length, influences sexual selection and the organization of the mating systems of these desert anurans.

SPECIES RECOGNITION AND ACOUSTIC COMPETITION

An important component of female mate selection concerns proper species recognition. For anurans it is generally assumed that interspecific call differences allow sympatrically breeding species to avoid hybridization (e.g., Hodl 1977, Drewry and Rand 1983, Duellman and Pyles 1983). For example, among hylid and bufonid forms, rate of amplitude modulation (pulse rate) of the male advertisement call is apparently the primary call parameter separating closely related sympatric species (Gerhardt 1982, Rose and Capranica 1983, Sullivan and Leek, in review). Discrimination experiments have revealed that female tree frogs (Hylidae) can discriminate between two acoustic stimuli differing only in pulse rate, and they prefer stimuli similar to advertisement calls of conspecific males (Loftus-Hills and Littlejohn 1971, Straughan 1975).

All pelobatids and most bufonids occurring in southern Arizona have been observed in mixed-species breeding aggregations, providing the potential for heterospecific interactions (Fig. 2). The ranges in pulse rate and dominant frequency of advertisement calls of these anurans are given in Figure 3. As expected, advertisement calls of the closely related forms, *S. bombifrons* and *S. multiplicatus*, and *B. microscaphus* and *B. woodhousei*, are clearly dissimilar in pulse rate but not frequency. In the pelobatids, hybrid offspring are sterile; hence, there is presumably strong selection against females who select heterospecific mates. The divergence in advertisement calls of these two species in southeastern Arizona suggests that species recognition has been a significant selective force acting on female mate choice. Hybridization has also been documented between the two bufonids, but nothing is known concerning the evolutionary significance of this interaction (Sullivan 1986b). Sympatrically breeding bufonids in Texas have also been found to differ in pulse rate and frequency (Blair 1956). Advertisement call variation in two other Arizona anurans is also compatible with the species recognition hypothesis: the closely related but allopatric bufonids *B. debilis* and *B. retiformis* do not differ dramatically in pulse rate. Presumably, selection has not favored divergence in advertisement call structure in the absence of an opportunity for heterospecific interactions.

Aspects of intra- and interspecific acoustic competition between anuran males have recently received considerable attention (reviewed by Sullivan, 1985). A number of workers have argued that male anurans increase their locatability for selecting females by calling asynchronously with neighboring conspecifics as well as heterospecifics. In Arizona *B. woodhousei* follows this pattern: males reduce their calling activity in response to play-

SYMPATRICALLY BREEDING ANURANS IN ARIZONA

	Sb	Sc	Sm	Ba	Bc	Bd	Bm	Bp	Br	Bw
Sb	—									
Sc	●	—								
Sm	●	●	—							
Ba	●	●	●	—						
Bc	●	●	●	●	—					
Bd	●	●	●	●	●	—				
Bm							—			
Bp	●	●	●	●	●	●	●	—		
Br		●	●	●	●			●	—	
Bw		●			●	●	●	●		—

Fig. 2. Anurans (*Bufo* and *Scaphiopus*) observed breeding sympatrically (●) in southern Arizona (Sb = *S. bombifrons*, Sc = *S. couchi*, Sm = *S. multiplicatus*, Ba = *B. alvarius*, Bc = *B. cognatus*, Bd = *B. debilis*, Bm = *B. microscaphus*, Bp = *B. punctatus*, Br = *B. retiformis*, Bw = *B. woodhousei*).

back of conspecific advertisement calls as well as a variety of synthetic stimuli (Sullivan 1985, Sullivan and Leek, in review). Proximately, males avoid calling during playback of any acoustic stimuli with a freqency close to the mean frequency of the species-typical call (Sullivan and Leek, in review). However, male *B. punctatus* do not avoid overlap with broadcast of conspecific advertisement calls (Sullivan 1985). These bufonids possess relatively long calls ($\bar{x}$ = 7.0 sec) and appear to prefer to call synchronously with nearby calling males. Such interspecific variation suggests that male calling behavior is influenced by factors other than those associated with locatability for females alone. It may be that males of some species call synchronously to reduce the risk of predation; predators who locate anurans acoustically have difficulty capturing synchronously chorusing forms (Ryan and Tuttle 1982). Below I develop the hypothesis that predation has shaped the evolution of anuran lek mating systems in general.

EVOLUTION OF ANURAN LEK MATING SYSTEMS

The evolution of lek mating systems has recently received much attention (Bradbury 1981, Loiselle and Barlow 1978, Wrangham 1980). Lek mating systems, in which females select mates based on male phenotype or dominance position on a display arena, have been described for a variety of organisms, including two Arizona bufonids (Sullivan

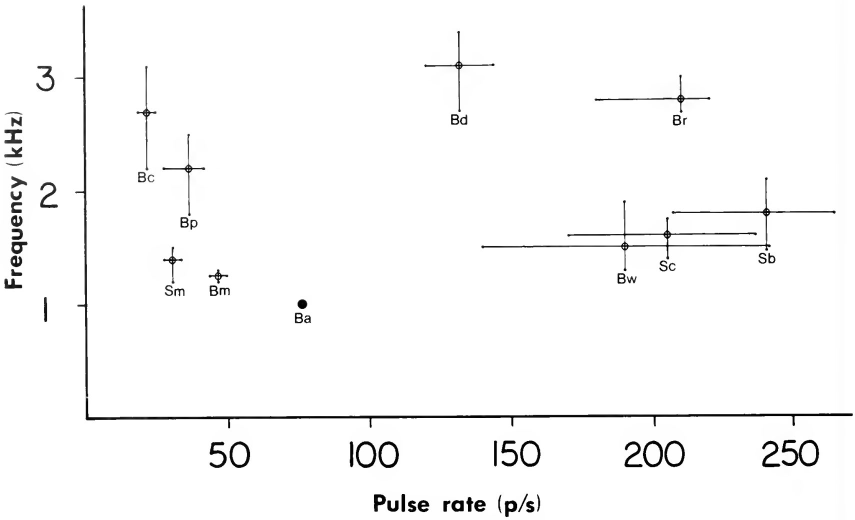

Fig. 3. Range in dominant frequency against range in pulse rate for bufonids and pelobatids of Arizona (see Fig. 1 for abbreviations).

1982a, 1983b). However, there has been considerable controversy concerning evolutionary origins of such female choice systems in which females receive no material benefits from their mates (Lambert et al. 1981, Taylor and Williams 1982). Most authors have argued that female preference for communally displaying males is a necessary condition for the evolution of a lek mating system (e.g., Alexander 1975, Bradbury 1981). It is suggested that when selecting a mate females save time and energy by sampling males in aggregations. Females might also benefit by selecting their mate from a group of males if a wider range of males (in terms of genetic quality) is available in larger aggregations (Bradbury 1981). A prediction of these hypotheses is that females should prefer the largest aggregation of males available since time and energy savings, and availability of high quality mates, should increase with aggregation size (Alexander 1975).

Many anurans have lek mating systems (Alexander 1975, Emlen 1976, Sullivan 1982a, 1983b, Wells 1977). Populations of *B. cognatus* and *B. woodhousei* in Arizona clearly possess lek mating systems (Sullivan 1982a, 1983b). In both of these bufonids, males aggregate in discrete areas of ponds, and females freely select their mates based on male behavior (calling activity). Males do not defend resources of interest to females or their offspring, because oviposition occurs away from the calling site of the male. Hence, females obtain no material benefits from their mates. These two toad species provide an opportunity for direct test of the hypothesis concerning female preference for larger aggregations because male choruses in both species often occur in close proximity to other conspecific aggregations. Models of lek evolution predict that female *B. cognatus* and *B. woodhousei* will visit large aggregations when selecting a mate. That is, the relationship between nightly operational sex ratio (OSR) or the proportional number of females available and number of males present (chorus size) should be positive.

For both *B. cognatus* and *B. woodhousei* OSR (no. of females/no. of males) and chorus size were not significantly correlated (*Bc*: $r = -0.35$, $P > 0.05$, $N = 19$; *Bw*: $r = 0.04$, $P > 0.05$, $N = 144$). Females were afforded the opportunity to select between aggregations of different sizes since for both species there were always from 1 to 4 choruses simultaneously active near the study chorus (<0.5 km) on the night of observation (some females even visited more than one chorus). It is important to note that in this analysis the assumption of independence of variables is violated since OSR is in part derived from chorus size; however, the results indicate clearly that for these aggregations OSR does not increase with chorus size. Hence, females do not prefer to visit larger choruses when selecting their mates. Observations on the intensity of sexual selection in *B. woodhousei* further support the hypothesis that anuran females do not prefer to visit larger aggregations of males when selecting a mate. Sullivan (1986a) documented that the intensity of sexual selection increases with chorus size (male density) in *B. woodhousei*. That is, the proportional number of females decreases as male density increases: proportionally fewer males obtain matings in larger choruses.

This result suggests that females do not derive any benefits by selecting their mate from among larger groups of displaying males. I suggest that benefits accruing to individual males who display communally are the primary factors influencing anuran lek behavior. For example, many authors have suggested that males who participate in aggregations suffer less predation than males who display in isolation (see reviews in Alexander 1975, Bradbury 1981, Loiselle and Barlow 1978, Wrangham 1980). Recently Ryan et al. (1981) substantiated this claim by showing that in a neotropical leptodactylid frog individual predation risk decreases for males as chorus size increases. Ryan et al. (1981) found that at least three predators located males acoustically; hence males might benefit greatly by displaying communally. Predation may only be important to males since they participate in choruses night after night: most anuran females visit choruses only on the night they oviposit and are inconspicuous while present in breeding aggregations (e.g., Sullivan 1982a, Wells 1977).

If males derive substantial benefits by displaying communally, and females incur no (or insignificant) costs by selecting their mate from among such groups, then it is conceivable that females play no active role in the evolutionary maintenance of lek behavior. Of course, female choice of individual males within aggregations would remain an important aspect of sexual selection in species with lek mating systems.

Observations on mate selection by females also suggest that the spatial distribution of males within a chorus is unaffected by female behavior. For example, some workers have suggested that in lek breeding forms females prefer males positioned at the center of the display area. The linear, shoreline choruses of *B. woodhousei* can be readily partitioned into three equal areas with respect to the distribution of males within the aggregations to test this hypothesis. Analysis of mating success and chorus location for all males on 18 nights of chorus activity reveals there was no position effect: centrally located males did not achieve a disproportionate number of matings ($\underline{X}^2 = 0.33$, $\underline{P} > 0.05$, df $= 2$). Thus, within choruses females do not appear to favor the clustering of males.

Under the extremely arid conditions of the Arizona-Sonoran Desert the lek-like mating systems and acoustic courtship behaviors employed by anurans seem efficient means of rapidly bringing the sexes together. However, this review indicates that some diversity in mating systems can occur under these severe ecological constraints. It is clear that environmental factors influencing breeding period duration shape mating system organization as a result of corresponding variation in male density and behavior. Continued study will be necessary to further elucidate the precise action of sexual selection in relation to mating system variation in breeding aggregations of these desert anurans.

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THREE NEW SAUROPOD DINOSAURS FROM THE UPPER JURASSIC OF COLORADO

James A. Jensen[1]

ABSTRACT.—From 1972 to 1982 three exceptionally large sauropod scapulocoracoids and other equally large sauropod bones were collected from the base of the Brushy Basin Member of the Upper Jurassic, Morrison Formation, in western Colorado. Two of the scapulae are conspecific, but the third represents a second genus and possibly a new family. The two conspecific specimens are described here as: *Supersaurus vivianae*; the second genus is described as *Ultrasaurus mcintoshi*, and a large, robust anterior dorsal vertebra of unique form is described as *Dystylosaurus edwini*. Various miscellaneous elements are referred to the three genera.

Historical

The genus *Brachiosaurus*, named by E. S. Riggs (1903), was part of an articulated skeleton from the Upper Jurassic Morrison Formation within the present city limits of Grand Junction in western Colorado. Riggs believed the genus represented a land-dwelling animal, rather than one preferring an aquatic habitat.

No one took him seriously at the time, but modern interpretations of sauropod habits and paleoenvironments agree with him. The brachiosaurs are now considered to be the largest terrestrial animals to have lived on earth.

The first uranium boom during World War II triggered the discovery of the second known North American brachiosaur; it was found by prospectors Eddie and Vivian Jones who were looking for uranium, circa 1943, when they collected a brachiosaur humerus from the Uncompahgre Upwarp and donated it to the Smithsonian Institution, where it was put on display. However, no credit was given to the collectors.

That display led to the discovery of the Uncompahgre fauna and the materials described herein. The author saw the Jones humerus in 1958 and later in Colorado found the Jones family, who took him to the location on Potter Creek. They also took him to three other major fossil localities on the Uncompahgre Upwarp that together produced a relatively new dinosaur fauna, described as the Uncompahgre fauna (Jensen, in preparation). The author later returned to Potter Creek and collected additional brachiosaur material (being described elsewhere).

Dry Mesa Quarry

Three large sauropod scapulocoracoids were collected from one of the Jones localities near Dry Mesa, Mesa County, 35 miles west of Delta, Colorado. Over a period of 10 years the site proved to be very productive, yielding many tons of field blocks and packages of dinosaur material. It was named after Dry Mesa and is located near the base of the Brushy Basin member of the Morrison Formation and, consequently, is not easily confused with the overlying Lower Cretaceous, Cedar Mountain Formation when making simple stratigraphic determinations. The top of the Morrison Formation is easy to follow cross-country because the superior Cedar Mountain sediments are set-back above it, forming a prominent shoulder from 100 to 500 m wide. Sag-ponds are a characteristic feature of this shoulder, being produced by land-flow and slumping that crush and mutilate fossils contained in the moving sediments. Its bentonitic clays and mudstones, interbedded with soft sandstones, grits, and fine gravels, respond actively to cyclic wet/dry stressing, accelerating the deterioration rate of fossil

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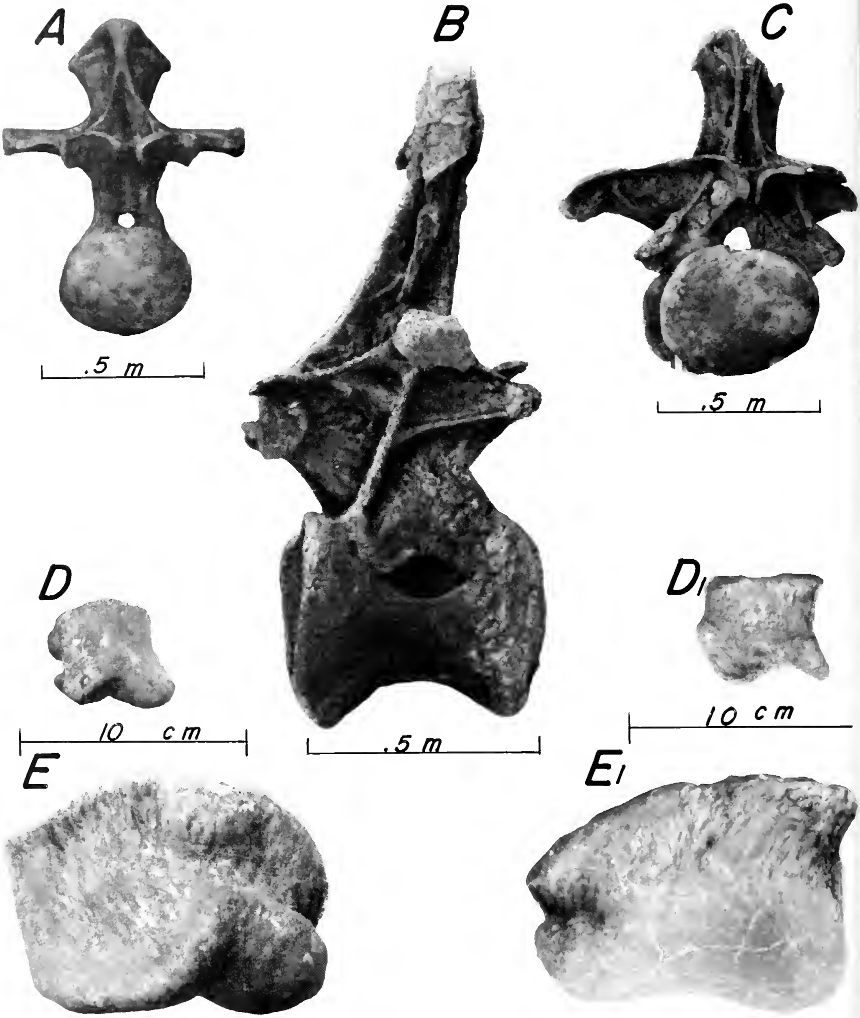

Fig. 1. A, *Brachiosaurus* sp., dorsal vertebra. B, Holotype, *Ultrasaurus macintoshi*, posterior dorsal vertebra, BYU 5000. C, Holotype, *Dystylosaurus edwini*, anterior dorsal vertebra, BYU 5750. D, E1, unidentified manual phalanges.

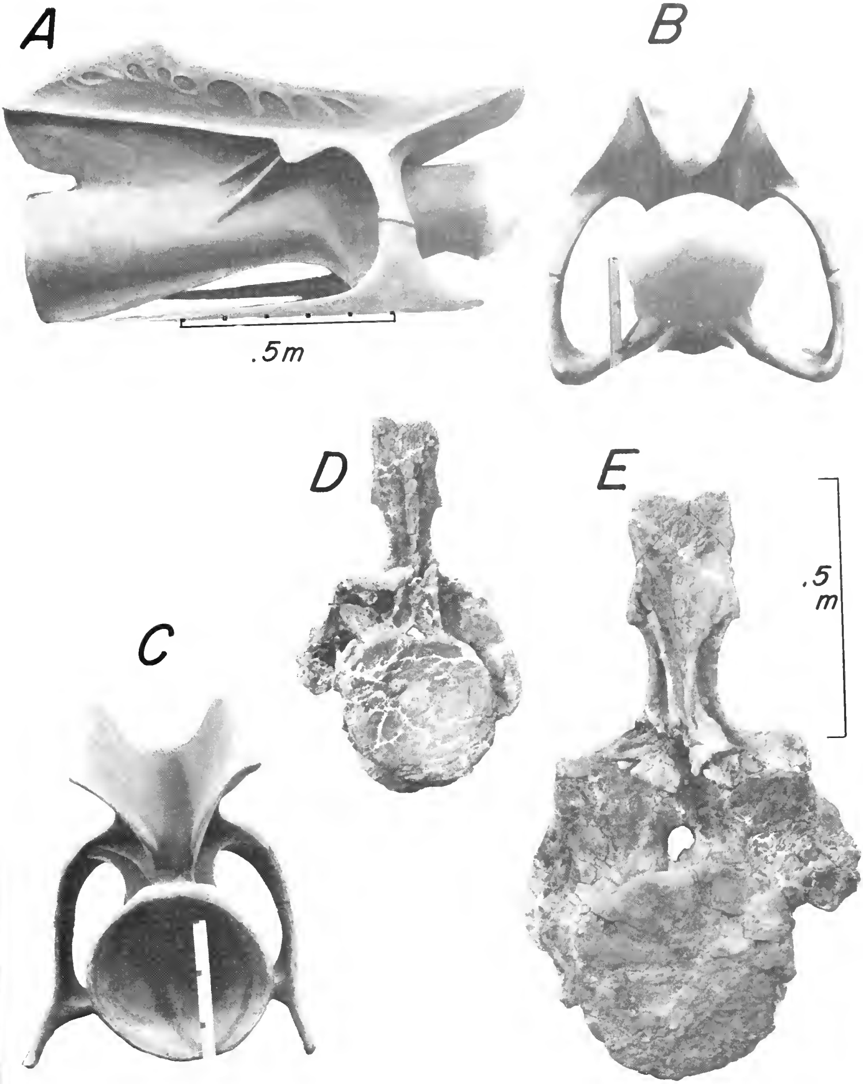

Fig. 2. A–C, Model of referred specimen, *Ultrasaurus macintoshi*, midcervical vertebra: A, right lateral view. B, anterior view. C, posterior view. D–E, Referred specimen, *Ultrasaurus macintoshi*, anterior caudal vertebra. D, anterior view. E, posterior view.

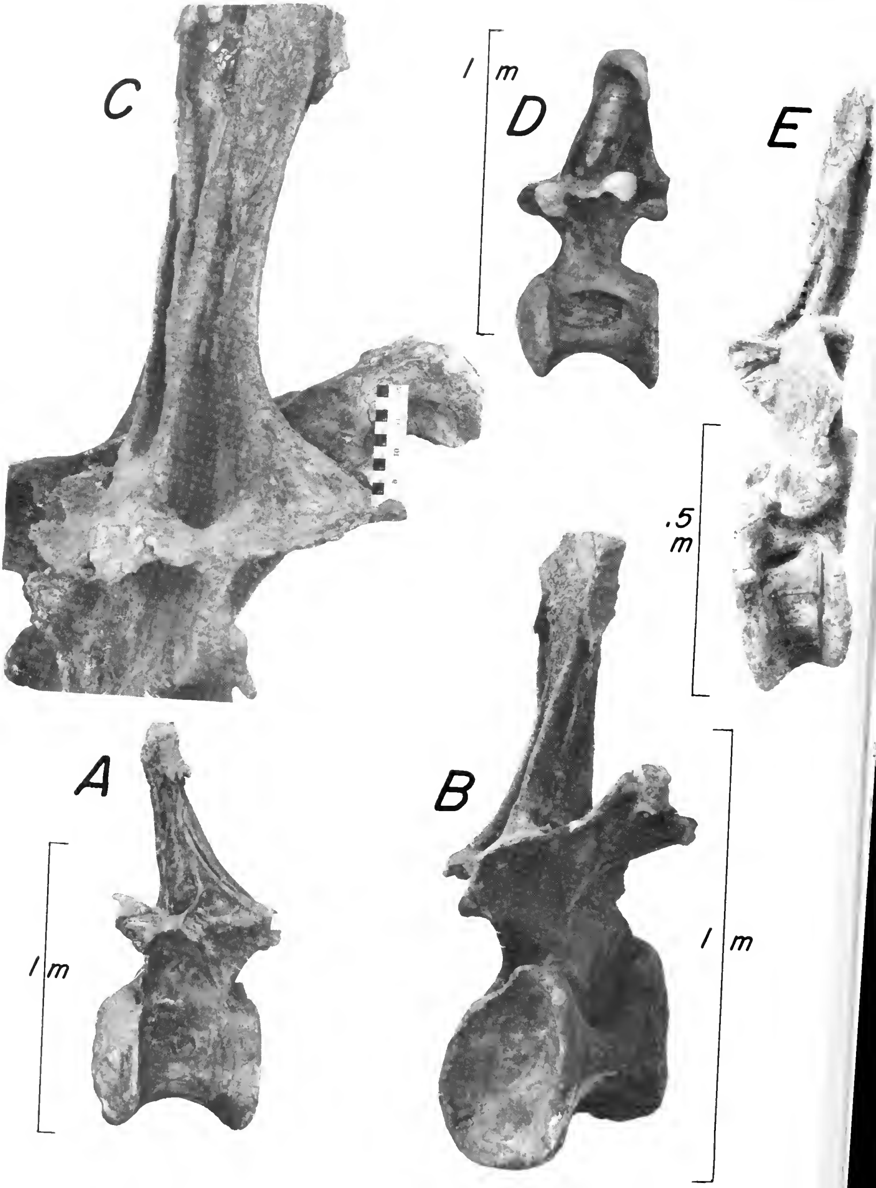

Fig. 3. A–C, Holotype, *Ultrasaurus macintoshi*, posterior dorsal vertebra: A, left lateral view. B, oblique posterior view. C, detail of neural spine. D, *Brachiosaurus* sp., dorsal vertebra, left lateral view. E, *Ultrasaurus macintoshi*, referred specimen, anterior caudal vertebra, left lateral view.

materials beyond that of calcified sandstone or limestone preservations.

One of the most important problems yet to be solved is that of the exact age of the Dry Mesa sediments. It is mapped as Morrison Formation, but the fauna does not match taxa of classical Morrison localities. The assemblage is not only very diverse but contains many taxa previously unknown in the Upper Jurassic of North America.

The author believes the Morrison sediments exposed along the eastern monocline of the Uncompahgre Upwarp are younger than the Morrison in previously described localities, and that the Uncompahgre fauna may represent the last expression of Jurassic dinosaur evolution.

Class Reptilia
Order Saurischia
Suborder Sauropodomorpha
Infraorder Sauropoda
Family indeterminate
Supersaurus vivianae, n. gen., n. sp.

ETYMOLOGY.—*Supersaurus*, internationally published vernacular name; *vivianae*, after Vivian Jones, co-discoverer of all the important Late Jurassic fossil localities on the Uncompahgre Upwarp.

HOLOTYPE.—BYU 5500, scapulocoracoid 2.44 m (8') long.

REFERRED MATERIAL.—BYU 5501, scapulocoracoid 2.70 m (8,10") long; BYU 5502, ischium; BYU 5503, medial caudal vertebra; BYU 5504, 12 articulated caudal vertebrae.

TYPE LOCALITY.—Dry Mesa quarry; E 1/2, Section 23: T 50N, R 14W, NMPM.

HORIZON.—Near the base of the Brushy Basin Member of the Upper Jurassic Morrison Formation, Mesa County, Colorado.

COLLECTOR.—James A. Jensen 1979.

CLARIFICATION.—Sauropod scapular terminology in the literature is not uniform (Hatcher 1903, Mook 1921, Gilmore 1936), resulting in some confusion. This paper describes the scapula in a somewhat normal orientation; using an external view with the glenoid cavity down and the coracoid on the right end, the right scapula will be described. Descriptive terminology used: narrow midsection is the "shaft"; left end is the "distal" end; upper edge is the "superior border"; lower edge is the "inferior border"; ventral projection of glenoid area is the "glenoid process"; ridge separating the two muscular fossae and running on a curved diagonal line up from the glenoid process to the maximum scapular width is the "transverse ridge." This ridge and the shaft-axis form an angle that varies in different sauropod genera. The great depressions to the left (above) and right (below) of the transverse ridge are the "superior fossa" and "inferior fossa," respectively.

DESCRIPTION.—(Holotype BYU 5500; right scapulocoracoid) Scapula long but not robust; distal end expanding moderately; shaft not severely constricted in midsection.

A shallow outward curve in inferior border slightly proximad to greatest width of scapula, at top of transverse ridge, indicates origin of a ligament, possibly M. scapulohumeralis. This process also present on *Diplodocus*, occurring considerably higher up on *Cetiosaurus* and most prominently developed on *Ultrasaurus*, but absent or insignificant in *Brachiosaurus*, *Apatosaurus*, and *Camarasaurus*. Inferior border of scapula forming a gentle curve from glenoid process to distal end, resembling *Apatosaurus* and *Diplodocus* rather than *Brachiosaurus* or *Camarasaurus*. Inferior fossa not broadly expanded as in *Brachiosaurus* and longer than wide, contrasting with opposite design in *Apatosaurus* and *Camarasaurus*. Coracoid with a subrectangular profile.

REFERRED MATERIAL.—BYU 5501, scapulocoracoid 2.70m (8' 10") long. Description same as Holotype, BYU 5500.

BYU 5502, 12 articulated caudal vertebrae: each approximately 30 cm long, collected but not yet prepared for study. They were examined closely in the field by the author, and a decision was made to refer them to *Supersaurus* on the basis of their massive size and general morphology. They were found parallel to, and near the *Supersaurus* scapula; however, location is not a criterion for association in the Dry Mesa quarry because of the extensive fluvial transport of all elements prior to final burial.

BYU 5503, ischium (Fig. 7A): straight shaft, more robust than *Diplodocus*; distal end expanded dorsally, truncated ventrally. Very similar to *Diplodocus*.

BYU 5504, two medial caudal vertebrae (Figs. 7C, D, D1). C, double-keeled, diplo-

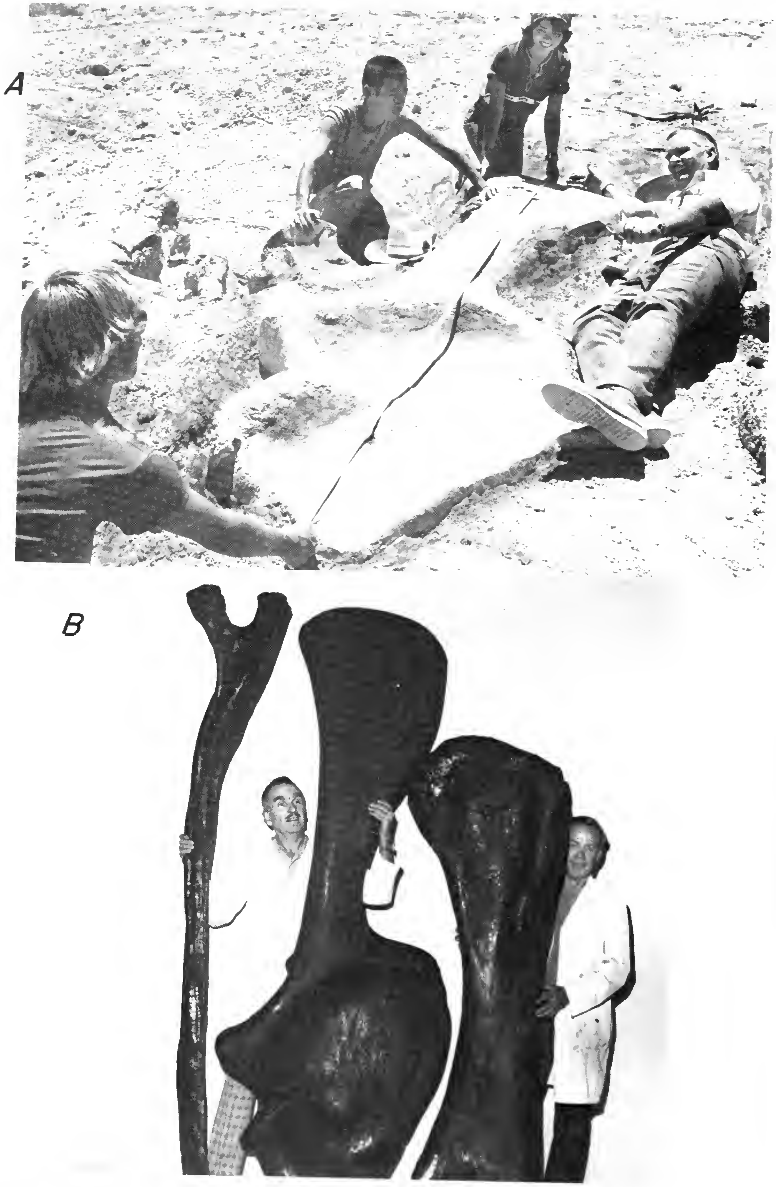

Fig. 4. A Measuring *Ultrasaurus macintoshi* scapulocoracoid at discovery site. Author lying beside specimen. Three reproductions: left, *Brachiosaurus* sp. rib 2.75 m (9') long, middle, *Ultrasaurus macintoshi* right scapulocoracoid; right, left humerus of *Brachiosaurus* sp. from Potter Creek. J. A. Jensen (left) and Adrian M. Bouche (right).

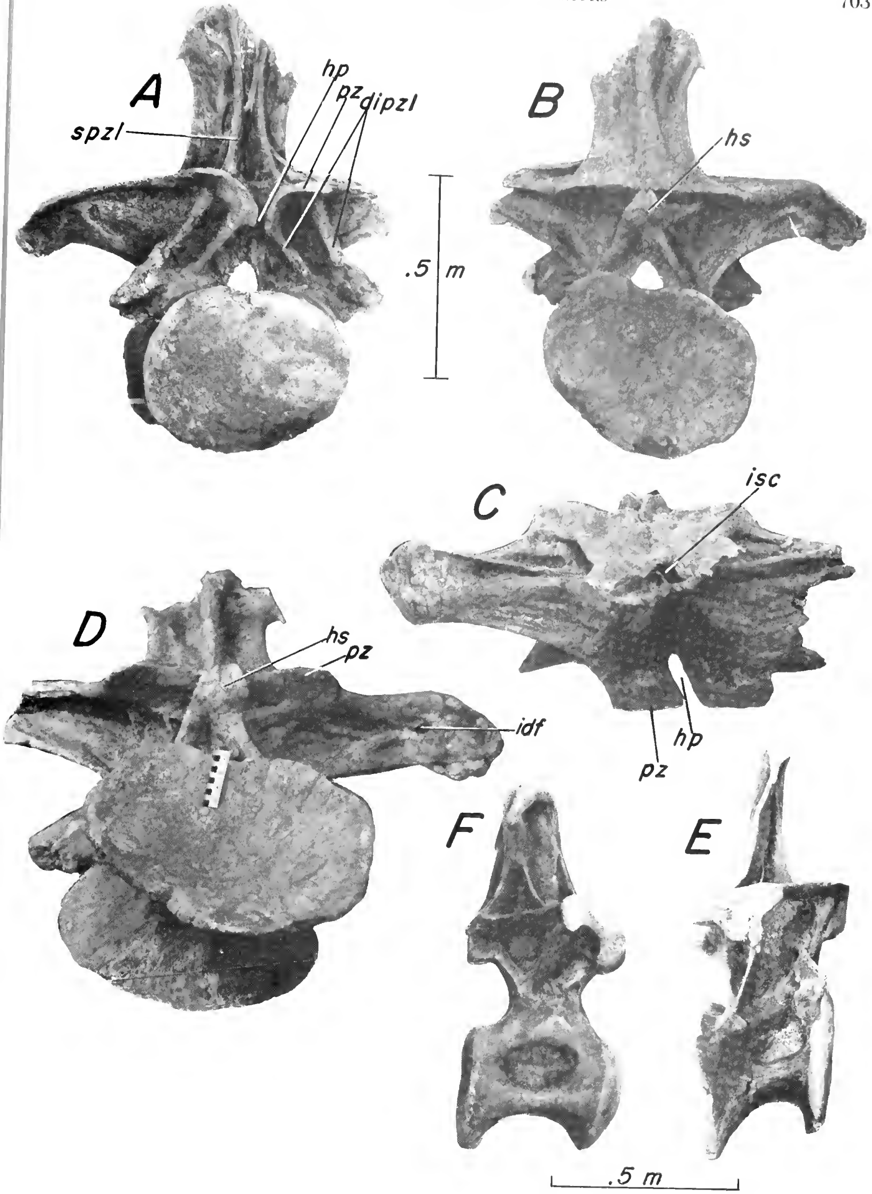

Fig. 5. A–E, Holotype, *Dystylosaurus edwini*, anterior dorsal vertebra: A, anterior view. B, posterior view. C, superior view. D, posteroventral view. E, right, lateral view. F, *Brachiosaurus* sp. from Potter Creek. Abbreviations: dipzl-diagonal infraprezygapophysal lamina hs-hyposphen; hp-hypantrum; idf-intradiapophysal foramina; isc-intraspinal cavity; pz-presygapophysis; spzl-supraprezygapophysal lamina.

coid caudal with broad ventral channel; D, D1, double-keeled diplocoid caudal with transveısely thick neural spine that is expanded dorsoventrally at its summit. The caudal neural spines of *Diplodocus* are thin, narrow, and unexpanded at the summit; caudal rib missing, no pleurocoel but a short channel exists below base of caudal rib. Proportion of diameter-to-length would place the specimen as number 12 in a *Diplodocus* caudal series, but the reduction of the neural arch would place it much further back in the same series.

Order Saurischia
Suborder Sauropodomorpha
Infraorder Sauropoda
Family Brachiosauridae
Ultrasaurus macintoshi, n. gen., n. sp.

ETYMOLOGY.—*Ultrasaurus*, internationally published vernacular name; *macintoshi*, in honor of John S. McIntosh, an enthusiastic, indefatigable student of sauropods who encourages everyone to greater effort in their behalf.

HOLOTYPE.—BYU 5000, posterior dorsal vertebra.

REFERRED MATERIAL.—BYU 5001, scapulocoracoid; BYU 5002, anterior caudal vertebra; BYU 5003, medial cervical vertebra;

TYPE LOCALITY.—E 1/2 Section 23, T 50N, R 14W, NMPM, Mesa County, Colorado.

HORIZON.—Base of Brushy Basin Member of the Upper Jurassic, Morrison Formation.

COLLECTOR.—James A. Jensen 1979.

DIAGNOSIS.—A sauropod differing from other brachiosaur genera in having a scapula with a moderately expanded distal end; dorsal vertebrae with anteroposteriorly narrow neural spines; midcervical vertebrae lacking pleurocoels; posterior dorsal vertebrae with high neural spines; anterior caudal vertebrae with high neural spines.

DESCRIPTION.—Posterior dorsal vertebra (Figs. 1B; 3A, B, C). A long centrum characteristic of brachiosaurs: ratio of length to diameter, 1.2; Potter Creek brachiosaur, 1.3; *Brachiosaurus altithorax* (Riggs 1903), 1.07. *Ultrasaurus* shares the family characteristic of a long dorsal centrum with *Brachiosaurus*, but in other features it has no parallel with that genus. The Potter Creek *Brachiosaurus*, collected by Jones and Jensen (description in preparation by the author) appears to be *altithorax* (see Figs. 1A, B; 3A-D).

Figure 3C is a detail of the base of the neural spine and postzygapophyses of BYU 5000. The form of the suprapostzygapophysal laminae is greatly altered by assymetry, with the right side being more robust than the left. The vertebra is crushed transversely, making an anterior view nearly useless. The neural spine is tall and buttressed posteriorly by suprapostzygapophysal laminae 2/3 the height of the spine (Fig. 3B). In contrast, the supraprezygapophysal laminae are almost nonexistent. The general structure of the neural spine is fragile compared to the Potter Creek specimen (Fig. 1A) and *altithorax* (Riggs 1903). Pleurocoels are present, their length being less than twice their height.

REFERRED MATERIAL.—BYU 5001, scapulocoradoid. The inferior fossa is broader than in *Supersaurus* (Figs. 4A, B); glenoid process projects beyond the inferior border of the shaft as in *Brachiosaurus*; overall length approximately 2.70 m (8' 10"); dorsoventrally, midshaft is constricted to 23 cm (9"). A tabular process occurs on the inferior border, slightly above the transverse ridge and slightly below the minimum dorsoventral diameter of the flattened shaft (Fig. 4A). The function of this tabular process is unknown but appears to support the origin of an intercostal muscle or possibly an m. humeroscapularis. The process is not a gentle convexity below the inferior border, as in *Supersaurus*, but instead is a distinct tab erupting from the inferior border with a base approximately 100 mm in length, extending approximately 50 mm ventrally from the edge of the scapula (Fig. 4B).

BYU 5002, anterior caudal vertebra (Figs. 2D, E, 3E).

This is probably No.3 caudal with a spine taller than those on anterior brachiosaur caudals. All zygapophyses are damaged by crushing, but two infraprezygapophysal laminae support the anterior pair. The suprapostzygapophysal laminae diverge about midway up the spine, expanding to expose a broad, rugose development of the postspinal lamina. Viewed anteriorly the upper half of the spine presents a modified rectangular profile. Like BYU 5000 dorsal vertebra, there are no supraprezygapophysal laminae. The supradiapophysal laminae form a wide border enclos-

Fig. 6. A, Measuring *Supersaurus vivianae* scapulocoracoid. D. E., Vivian Jones; J. A. Jensen. B, The author, 6'3" tall beside *Supersaurus vivianae* scapulocoracoid.

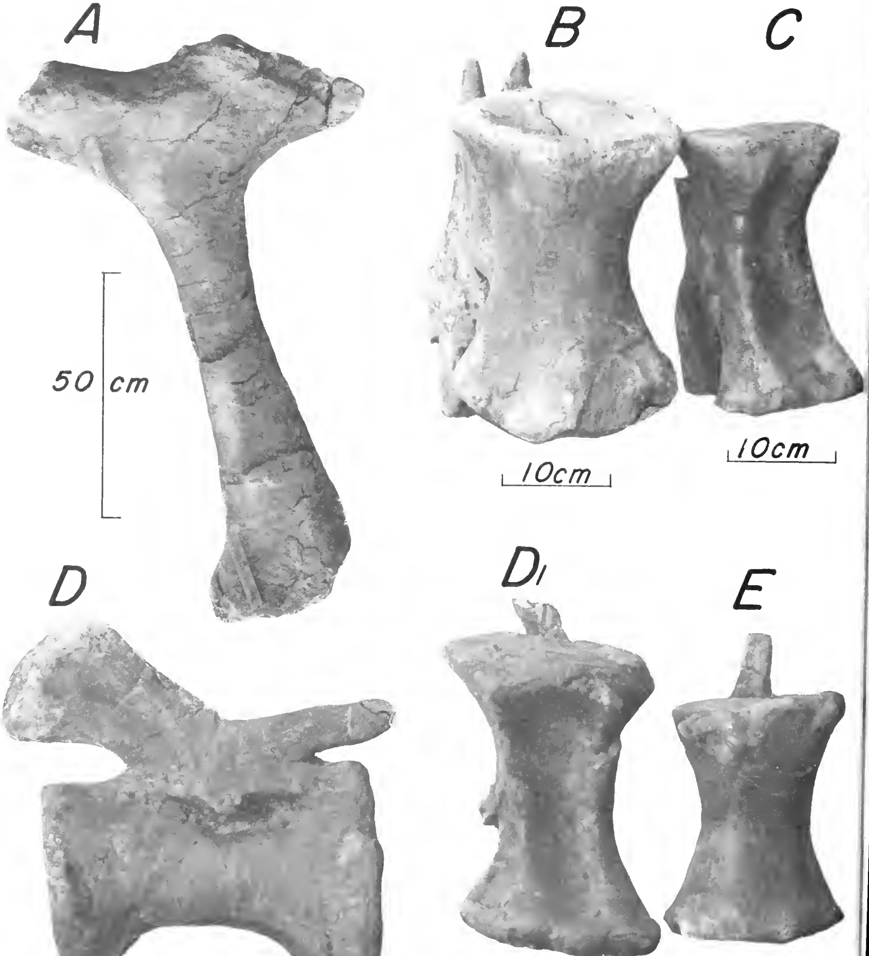

Fig. 7. A, BYU 5503, referred specimen, *Supersaurus vivianae* ischium. B, Ultrasaurus caudal vertebra. C, BYU 5503, *Supersaurus vivianae*, referred specimen, ischium. D, D1, BYU 5504, *Supersaurus vivianae*, referred specimen, caudal vertebra. E, unidentified caudal vertebra.

ing a narrow, but prominent, prespinal lamina. A small pleurocoel is present and the centrum is not procoelous but both ends are nearly flat.

BYU 5003, medial cervical Vertebra (Fig. 2A, B, C). The original referred specimen is not illustrated. What is seen is a life-sized model of BYU 5003, constructed from careful measurements taken from the crushed original. All brachiosaur cervical vertebrae are extremely fragile in construction and generally found badly crushed. The cervical rib is arbitrary, but the vertebra was modeled as carefully as possible from the original. One remarkable feature is the absence of pleurocoels, so radically developed in some sauropod families, such as that of the *Diplodocidae*. Also, the postdiapophysal, or horizontal, laminae are missing. The spine is single, being slightly lower than the summit of the supraprezygapophysal laminae, which align with the elevated suprapostzygapophysal laminae to provide a channel for the long cervical flexor muscles. The anterior convexity is exaggerated approximately 5%, and the postzygapophysal articular facets were not modeled.

Order Saurischia
Suborder Sauropodomorpha
Infraorder Sauropoda
Family indeterminate
Dystylosaurus edwini, n. gen., n. sp.

ETYMOLOGY.—Greek: *di*, two; *stylos*, beam; *sauros*, lizard; *edwini*, in honor of the late Daniel Edwin (Eddie) Jones, who, with his wife, Vivian, brought more new dinosaur taxa to science than any other two amateurs while providing 20 years of logistic support for fieldwork on the Uncompahgre "Plateau."

HOLOTYPE.—BYU 5750, anterior dorsal vertebra.

TYPE LOCALITY.—E 1/2, Section 23; T 50N, R 14W, NMPM.

HORIZON.—Near the base of the Brushy Basin Member of the Upper Jurassic Morrison Formation.

COLLECTOR.—James A. Jensen 1972.

DIAGNOSIS.—A sauropod differing from all described North American sauropod genera in having two parallel, diagonal infraprezygapophysal laminae supporting each hypantrozygapophysal arch in anterior dorsal vertebrae; lower half of neural arch massive, the neurocentral suture occupying nearly 7/8 the length of the centrum; neural spine fragile, being transversely broad but anteroposteriorly thin; supraprezygapophysal laminae not convergent at midshaft as in *Brachiosaurus*; neural arches of dorsal vertebrae completely pneumatic, including spine, transverse processes, and zygapophyses.

DESCRIPTION.—The location of the parapophyses at the neurocentral suture and the presence of a strongly developed hyposphen/hypantrum articulation locates the vertebra anterior to No. 3. Lower half of neural arch massive, being characterized on its anterior face by four diagonal infraprezygapophysal laminae, two below each zygapophyses. Each pair of these diagonal supports are spaced well apart and more or less parallel, supporting the hypantrozygapophysal arch on each side (Fig. 5A). The hypantrum consists of two opposing articular faces formed by the down-turned, medial edges of the prezygapophyses. Each zygapophysis thus specialized forms an arch termed a hypantrozygapophysal arch. The ventral ends of these four laminae rise from the anterior surface of the parapophyses; internal lamina of each pair supports the ventral end of the hypantrum; external pair supports the prezygapophyses. No other sauropod family displays such a well-designed mechanical arrangement for supporting the hypantrozygapophysal arches. Thin supradiapophysal laminae rise to the lateral spur near the summit of the neural spine, making the spine transversely broad (5A). However, viewed laterally (5E), the spine is very slender and fragile when compared to the lower half of the neural arch. By comparison the neural spine of *Brachiosaurus* (5F, E) is deep and robust anteroposteriorly, but the base of the neural arch occupies no more than 2/3 the length of the centrum; the neurocentral suture on *Supersaurus* extends approximately 7/8 the length of the centrum. The zygapophyses are small and weak, but the hyposphen/hypantrum structure is as strongly developed as it is in the anterior dorsal vertebrae of *Barosaurus* (Lull 1919).

This vertebra bears little resemblance to any described genus and no doubt represents a new sauropod family. Many elements belonging to it were probably collected from the

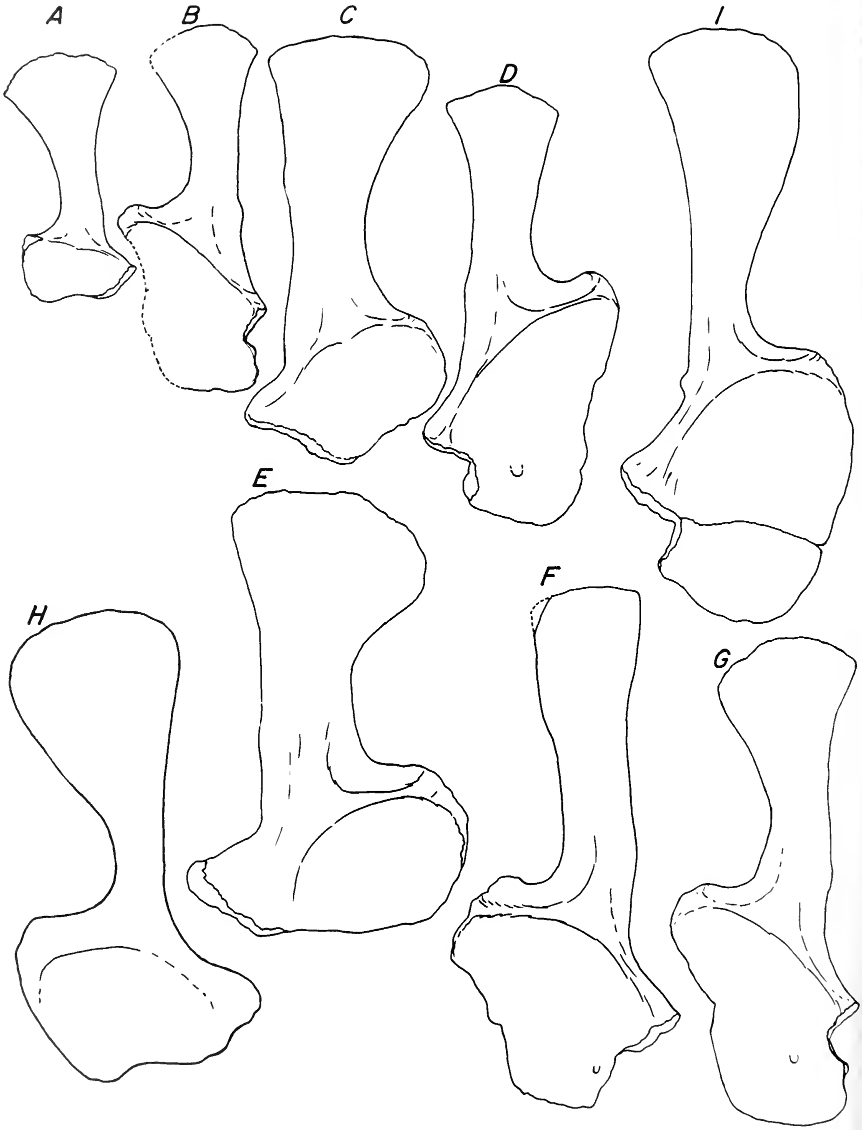

Fig. 8. For comparison only; not to scale. Profiles of various sauropod scapulae and scapulocoracoidae: A, C, E, G, scapulae; B, D, F, H, I, scapulocoracoidae. A, *Haplocanthosaurus* sp. B, *Supersaurus vivianae*, first specimen. C, *Cetiosaurus* sp. D, *Diplodocus longus*. E, *Camarasaurus supremus*. F, *Apatosaurus louisae*. G, *Supersaurus vivianae* second specimen. H, *Brachiosaurus brancai*. I, *Ultrasaurus macintoshi*. B is 2.44 m (8') long; G is 2.74 m (8'10") long.

Dry Mesa quarry, but correct association is difficult when dealing with masses of disarticulated elements belonging to undescribed genera.

DISCUSSION.—In 1983 the unprepared dinosaur materials collected by the author for the Earth Science Museum at Brigham Young University amounted to approximately 100 tons. This mass of material will require many years of careful preparation and, as of this writing, only a very small part of it had been prepared for study. The Uncompahgre fauna came from massive deposits of disarticulated bones, except two more or less complete articulated sauropod skeletons from the Dominguez/Jones quarry, and it will be difficult, if not impossible, to properly associate many of the elements into generic sets. One paper including a faunal list is in press, and a second much larger paper is in preparation illustrating most of the prepared material and giving some brief descriptions.

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UNCOMPAHGRE DINOSAUR FAUNA: A PRELIMINARY REPORT

James A. Jensen[1]

ABSTRACT.—A diverse late Jurassic dinosaur fauna, discovered in western Colorado in 1963, contains many undescribed taxa that may represent evolutionary trends at the generic level not previously reported from the Morrison Formation. A preliminary faunal list is given. Bones of the largest known dinosaur, *Ultrasaurus*, are present as are a variety of small animals, including Pterosaurs, in which one sacrum displays avianlike fused sacral neural spines. A new family, the *Torvosauridae*, erected, based on the genus *Torvosaurus* that is redescribed.

One of the most diverse Jurassic dinosaur faunas in North America was found on the Uncompahgre Upwarp in western Colorado in 1963. This fauna contains more undescribed taxa than has been encountered in any other North American Jurassic assemblage in this century. The first vertebrate fossil collecting on the upwarp was by the author in 1964 and continued for the next 20 years. More than 50 tons of dinosaur bone and matrix were collected from an area stretching 35 miles along the upwarp's eastern monocline.

Very little systematic work was done during those two decades of collecting for several reasons: (1) all available funds were used for collecting; (2) the most productive quarries being worked contained masses of disarticulated bones that could not be separated with confidence into specific sets; (3) the author thinks that any attempt to sort and describe extensive deposits of disarticulated material before the largest possible sample is taken will not produce the most comprehensive results; and (4) the collecting program was so productive that it acquired more material each season than could be prepared for study in five or more years. However, many representative specimens were prepared for study, and one unique carnosaur was described and named *Torvosaurus tanneri* (Galton and Jensen 1979).

The author believes the fauna will demonstrate substantial evolution at the generic level when compared to classical Morrison assemblages. Dodson et. al. (1980) state that their field investigations "failed to find any convincing evidence of evolution at the generic level within the Morrison Formation." There are familiar forms in the Uncompahgre fauna, but there is also consistent evidence of change, or "evolution at the generic level" as demonstrated by: (1) giganticism in more than one sauropod family; (2) at least a 100% increase in carnosaur genera; (3) the presence of the first relatively abundant pterosaur elements, previously known in the North American Jurassic from one phalangial fragment from Como Bluff; (4) undescribed variations in sauropod skeletal morphology, particularly the axial skeleton; and (5) the presence of ornithischians above the Morrison average, plus various other novel differences.

A problem of identification in this diverse Uncompahgre fauna is focused on the question "How far must an evolving genus move from parent stock, i.e., change morphologically, before it qualifies as a new genus?" Satisfactory criteria to deal with this question do not exist.

Other Morrison quarries today generally produce specimens that can be confidently identified with described material in genera that are comfortably distinct from one another. The Uncompahgre fauna displays so many variations on classical morphology that it probably represents either an advanced or younger fauna. It contains many specimens that look familiar, as if they are closely related, yet vary enough in structure to qualify as new taxa. They may represent evolution at the generic level.

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Detailed studies of the Uncompahgre fauna may at least provide a new window on dinosaur evolution and possibly shed some light on the time-transgressive evolution of Jurassic dinosaurs into Cretaceous forms.

The Uncompahgre fauna will be discussed further and illustrated in a larger paper, "New and Undescribed Dinosaurs of the Southwestern Colorado Plateau," now in preparation.

TAXONOMIC REVISION

Romer (1956) listed four carnosaur families: Palaeosauridae, Teratosauridae, Megalosauridae, and Tyrannosauridae. A conservative modern interpretation of the infraorder Carnosauria, as used by Russell (1984), retains the Megalosauridae and Tyrannosauridae but discards the other two families and adds Ceratosauridae, Allosauridae, Aublysodontidae, and Dryptosauridae.

Galton and Jensen (1979) placed the genus *Torvosaurus* in the family Megalosauridae, but subsequent laboratory work has doubled the number of elements available for study, revealing a number of diagnostic features in *Torvosaurus* not seen in the Megalosauridae. Although unique morphological characteristics of this genus set it apart from the families listed by Russell, it shares a few common features with the Megalosauridae. In contrast, *Allosaurus* and *Tyrannosaurus*, representing two different families, share common characteristics to a much greater degree than either one resembles *Torvosaurus*.

The genus *Torvosaurus* is best characterized as being a theropod with both primitive and advanced characteristics: the pubis and ischium are of the prosauropod, brachyiliac type; the ilium is of the coelurosaurian, dolichoiliac type. This combination has not been seen in any North American theropod (Galton and Jensen 1979) and may be the only example from any age.

Torvosauridae, new family

The new family Torvosauridae is proposed to receive the genus, species, *Torvosaurus tanneri*, Order Saurischia, Suborder Theropoda, Infraorder Carnosauria, New Family Torvosauridae.

DIAGNOSIS.—Characterized by robust long bones; skull short, massive, and moderately low; forelimb very short with ratio of maximum length of humerus to radius at more than 2; lachrymal with a 90-degree angle between maxillary and jugal rami; very distinctive pelvic girdle with ilium dolichoiliac; pubis and ischium brachyiliac; pubis with closed obturator foramen. Pubis with an almost continuous median symphysis; very small non-weight-bearing pubic foot.

TYPE GENUS.—*Torvosaurus* Galton & Jensen 1979.

Revised description of *Torvosaurus*: A large, heavily built theropod with a short skull and a total body length of at least 10 m. Three premaxillary teeth with no rectilinear grooves (Figs. 2D, D_1); 10 maxillary teeth (Fig. 1, B_1); open foramina along superior border of fused interdental plates exposing germinal teeth; short dentary with 10 teeth (Figs. 3A-B); unsutured median symphysis; no meckelian groove on medial surface (Fig. $3A_1$). Lachrymal horn absent (Fig. $1A_1$); lachrymal vacuity opening forward (Fig. $1A_1$). Dorsoventrally broad jugal with narrow preorbital ramus. Forelimb with heavy humerus and short forearm with ratios of maximum length of humerus to radius at 2.2; humerus straight with large deltopectoral crest, broad distal and proximal ends (Fig. 4D); proximal end of ulna massive with ratio of maximum length to maximum proximal width at 2.1; metacarpal I with square proximolateral corner; first phalanx of digit I stout, short, and helically twisted along its length; metacarpal II short but extremely massive with ratio of maximum length to maximum proximal width at 1.5; metacarpal III massive, ratio 2.2. Ilium heavy with low dorsal blade, broad brevis shelf and transversely wide acetabular surface. Pubis with closed obturator foramen and a nearly continuous median symphysis on both pubis and ischium. Pubis with no horizontal weight-bearing ventral plane. Astragalus massive, ascending ramus thick and truncated toward calcaneum. (See Galton and Jensen 1979 for previously published figures). Metatarsals massive with no distal lateral or medial pits. Cervical vertebrae with subcircular ball-and-socket joints, the vertical axes being shorter than the horizontal axes; large pleurocoels openly communicating with internal pneu-

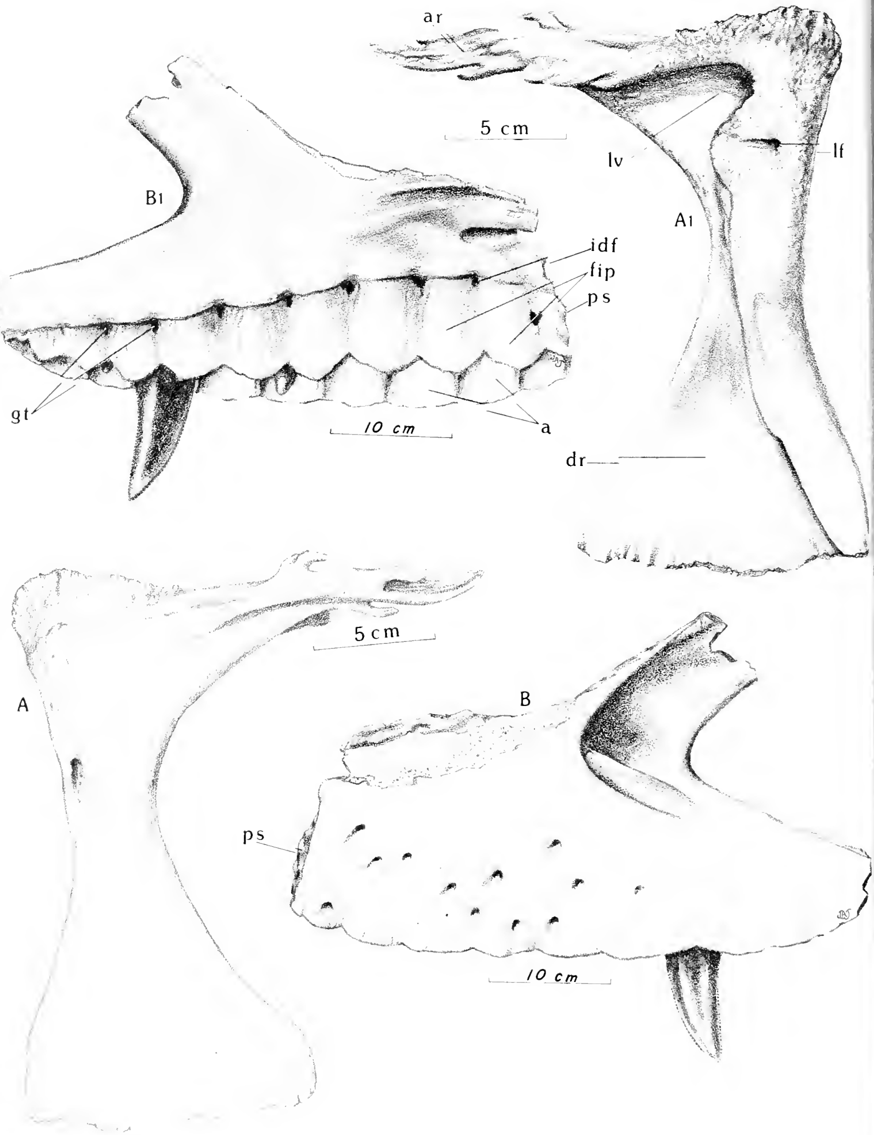

Fig. 1. A–A1, *Torvosaurus tanneri*, left lachrymal: A, medial view. A1, lateral view. B–B1, *Torvosaurus tanneri*, left maxilla. B, lateral view. B1, medial view.

Abbreviations: a, alveoli; ar, anterior ramus; dr, descending ramus; fip, fused interdental plates; idf, interdental foramen; lf, lachrymal foramen; lv, lachrymal vacuity; ps, premaxillary suture.

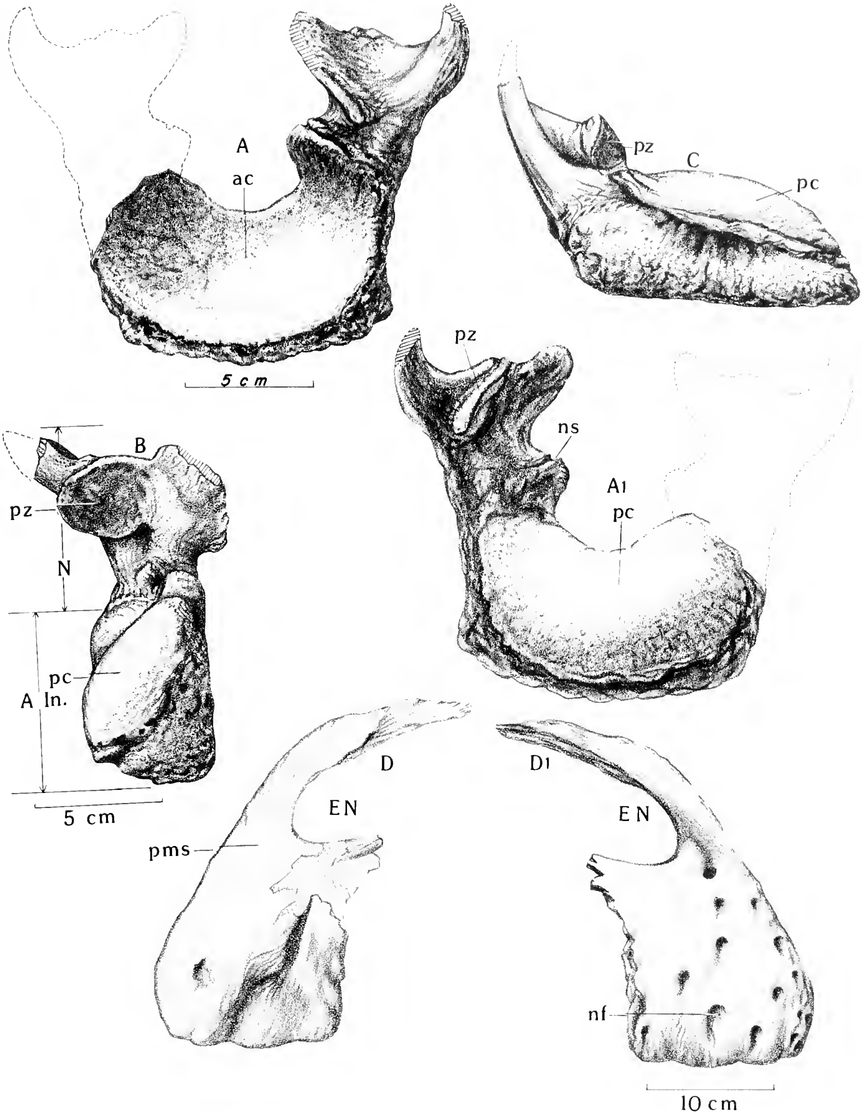

Fig. 2. A–A1, *Torvosaurus tanneri* atlas intercentrum with coossified left neuropophysis. A, anterior view. A1, posterior view. B, right lateral view. C, ventral view. D–D1, *Torvosaurus tanneri* right premaxilla. D, medial view. D1, right, lateral view.

Abbreviations: A In, atlas intercentrum; N, neuropophysis; ac, anterior concavity; en, external naris; nf, nutrient foramen; ns, neurocentral suture; pc, posterior convexity; pms, premaxillary symphysis; pz, postzygapophysis.

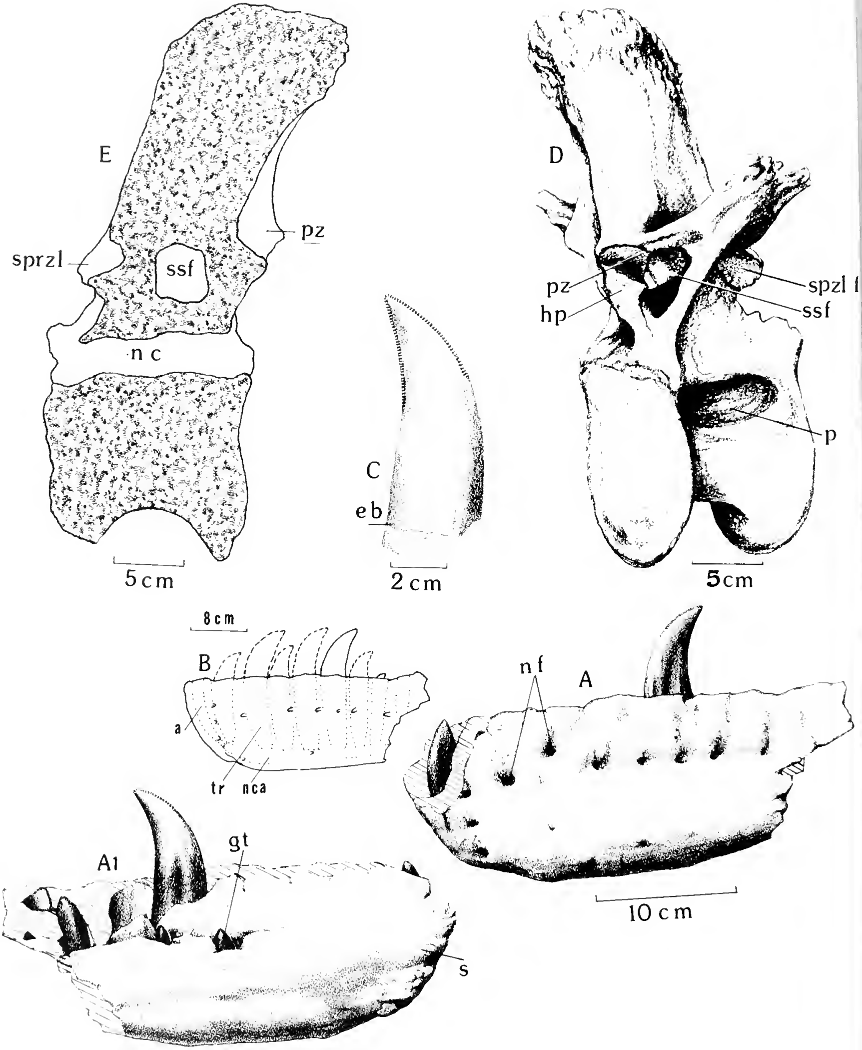

Fig. 3. *Torvosaurus tanneri*: A-A1, left dentary: A, lateral view. A1, medial view. B, simplified tooth diagram, germinal teeth not shown. C, unidentified carnivore tooth. D, *Torvosaurus tanneri* posterior dorsal vertebra. E, median cross section of torvosaur dorsal vertebra.

Abbreviations: a, alveoli; eb, enamel bases; gt, germinal tooth; hp, hypantrum; nc, neural canal; nca, nutrient canal; nf, nutrient formamina; pz, postzygapophyses; s, symphysis; spzl, supraprezygapophyses; spzl f, supraprezygapophysal flange; ssf, subspinal fenestra; tr, tooth root.

matic structure of centrum; anterior ends of centrae with radial flange, or collar, around subspherical convexity; posterior ends of centrae with subcircular concavity deeper than length of anterior convexity. Dorsal vertebrae with transverse, subspinal fenestrae passing transversely, anterior to and isolating hyposphenal pillar; expanded bases of supraprezygapophysal laminae on posterior dorsal vertebrae intruding onto posterior, superior surfaces of prezygapophyses with no fusion between ventral surface of intrusion and superior surface of prezygapophyses (Figs. 3D, 4B, B_1). Caudal vertebrae with transverse processes backswept approximately 30 degrees (Fig. $4C_1$). Chevrons more subquadrangular than bladelike in cross-section (Fig. 4F).

TYPE SPECIES: *Torvosaurus tanneri* Galton and Jensen 1979.

UNCOMPAHGRE FAUNAL LIST

This list is intended to provide a general view of the diversity of the Uncompahgre fauna. It is not certified as being comprehensive, correct, or complete. Identifications, for the most part, are tentative. With the exception of one described theropod, very few genera are listed because the comparative research necessary to work below the family level will not, and cannot, be done by the author. Additional taxa are doubtless present, but the nature of the specimens and the great amount of material awaiting preparation precludes their recognition at the present time.

Class OSTEICHTHYES

- Subclass Lepidosauria
- Order RHYNCHOCEPHALIA
  - Family Sphenodontidae
    - Undescribed genus, species
- Subclass Archosauria
- Order DIPNOI
  - Family Ceratodontidae
    - ? Ceratodus sp.

Class REPTILIA

- Order CHELONIA (TESTUDINATA)
  - Family Pleurosternidae
    - ? *Glyptops* sp.
    - Undescribed genus and species
- Order CROCODILIA
  - Family Crocodylidae
    - Crocodylinae
- Order SAURISCHIA
  - Suborder THEROPODA
    - Infraorder COELUROSAURIA
      - Coeluridae
      - Undescribed family
    - Infraorder CARNOSAURIA
      - Allosauridae
        - new genus, species
      - Torvosauridae
        - *Torvosaurus tanneri*
      - One or more undescribed families
    - Infraorder Ornithomimosauria
      - Ornithomimidae
  - Suborder SAUROPODMORPHA
    - Infraorder Sauropoda
      - Brachiosauridae
        - *Ultrasaurus*
        - *Brachiosaurus ? altus*
        - undescribed genera
      - Camarasauridae
        - undescribed genera
      - Diplodocidae
        - undescribed genera
      - One or more undescribed families
- Order ORNITHISCHIA
  - Suborder ORNITHOPODA
    - Hypsilophodontidae
      - *Laosaurus*
        - indeterminate species
      - *Othnelia*
        - indeterminate species
    - Iguanodontidae
      - *Camptosaurus*
        - unidentified species
  - Suborder STEGOSAURIA
    - Stegosauridae
      - *Stegosaurus*
        - indeterminate species
- Order PTEROSAURIA
  - Suborder PTERODACTYLOIDEA
    - Pterodactylidae
      - unidentified genera and species
  - Undescribed? suborder (avianlike fused sacral neural spines)

Class MAMMALIA

Incertae sedis: distal half of humerus
(Probably multituberculate or triconocont)

The Uncompahgre fauna includes some of the most spectacular fossil bones ever found. Their size equals or exceeds that of the dinosaurs from Tendaguru Hill in Tanganyika (Tanzania), Africa, which produced the skeleton of the great *Brachiosaurs brancai*, long displayed as the world's largest dinosaur in the Museum für Naturkunde in Berlin. It stands 11.87 m tall and 22.65 m long. The British Museum of Natural History also collected material from Tanzania, but specula-

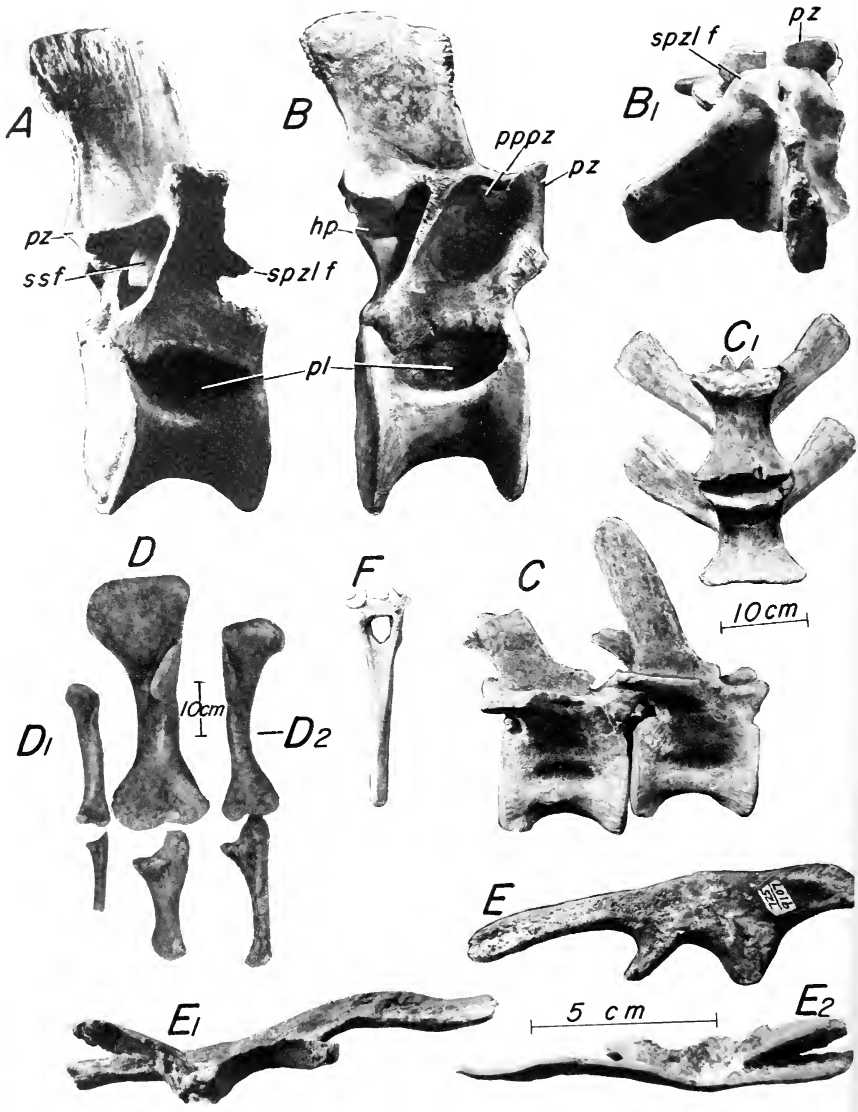

Fig. 4. *Torvosaurus tanneri*, A–F: A, posterior dorsal vertebra, right lateral view. B–B1, posterior dorsal vertebra. B, right lateral view. Bl, superior view. C–Cl, articulated medial caudal vertebrae. C, right lateral view. C1, ventral view. F, posterior view of chevron, articulates with C, C1. D–D2, three theropod forelegs representing three families: D, Torvosauridae, *Torvosaurus tanneri*. D1, Tyrannosauridae, undescribed genus, species. D2– Allosauridae, *Allosaurus* sp. E–E2, *Othnelia* sp. ilium: E, left lateral view. El, ventral view. E2, medial view.

Abbreviations: hp, hypantrum; pl, pleurocoel; pppz-posterior process of prezygapophysis; poz, postzygapophysis; pz, prezygapophysis; spzl f, supraprezygapophysal laminar flange; ssf, subspinal fenestra.

tion as to which locality produced the largest dinosaur is put to rest by the presence of a cervical and a dorsal vertebra, both nearly 4′6″ (1.36 m) long and two scapulocoracoids 8′10″ (2.70 m) long from Dry Mesa.

Because of perpetual universal interest in dinosaurs, the discovery of these materials was given wide exposure by the international news media. The first such discovery was that of a sauropod scapulocoracoid eight feet (2.44 m) long in 1972. It was given the popular name "Supersaurus" by an article in the domestic and all international editions of the *Reader's Digest* (George August 1973).

A larger scapulocoracoid, 8′10″ (2.70 m) long, was collected from Dry Mesa the same year but was not prepared until several years later, thus remaining unknown to the news media. It displays diplodocid affinities.

In 1979, during the filming of a Japanese Television Workshop documentary at the Dry Mesa quarry, a second scapulocoracoid 8′10″ (2.7 m) long was discovered and received extensive international publicity as the "world's largest dinosaur" under the popular name "Ultrasaurus." At the time of the discovery, and in response to persistent questions from the news media asking what the huge creature would be called, the author replied that, since it was probably the ultimate in size for a land animal, unofficially he would name it Ultrasaurus.

Subsequent universal usage of this name, applied to the huge dinosaur bones from Dry Mesa, has established it as the "world's largest dinosaur" in many publications such as various textbooks; documentary films; science pamphlets for school children; popular books written by scientists, e.g., *Dinosaurs, an Illustrated History* by Dr. Edwin H. Colbert; books by popular writers, such as *Dinosaurs of North America* by H. R. Sattler, *The New Dinosaur Dictionary* by Donald Glut, and *Dinosaurs Discovered* by John Gilbert; and various other hardcover publications, all of which cite Ultrasaurus as being the world's largest dinosaur.

The Ultrasaurus scapulocoracoid represents a family unlike that of the other two large specimens. It is characterized by a constricted central shaft 9″ wide (23 cm) and a prominent tabular process on the lower anterodorsal border, and it is not greatly expanded dorsoventrally at the distal end as is the case in *Brachiosaurus*.

This huge bone was protected only by a shallow layer of loose dirt and rocks when discovered, having been subjected to deterioration from plant-root raiding, frost action, and water leaching for a long time. Its extremely fragile condition suggested a plaster mold be made of the first side exposed to preserve all dimensions in case of mishaps during collection and transportation. A model was subsequently developed from the mold, and a cast of it has been circulated internationally as part of "Ultrasaurus, the world's largest dinosaur."

Additional large bones were collected that obviously belong to one of the three large scapulocoracoids, but they cannot be correctly matched up; e.g., a cervical vertebra nearly 4′6″ (1.36 m) long was collected, but there is no way to relate it to a particular scapula.

Other unusually large sauropod elements collected include: a posterior dorsal vertebra 4′6″ (1.36 m) tall; a very robust median dorsal vertebra 1 m tall; several cervical vertebrae more than 1 m long; an unusually large anterior caudal vertebra; an articulated posterior caudal series 12 feet (3 m) long; an ischium; various rib materials, including a rib head 18″ (45 cm) across the capitulum/tuberculum dimension; and a pedal phalange. No large sauropod cranial elements or appropriately large limb bones were found.

Theropods

At least four genera and more than one unidentified family are represented by theropod humeri. An equal number of novel forms can be identified in caudal vertebrae, but since humeri and caudal vertebrae do not articulate there is no way to properly match them up.

One humerus displays an anomaly involving the distal half of the shaft. A massive abnormal growth of bone penetrated by random vascular burrows indicates a serious pathological condition in life. The elbow joint was destroyed and the forearm was completely useless, if not severely atrophied. The proximal half of the bone is moderately robust, with a straight shaft, a moderate expansion of the proximal articular surfaces, and a short deltoid crest. It belongs to an undescribed genus in an

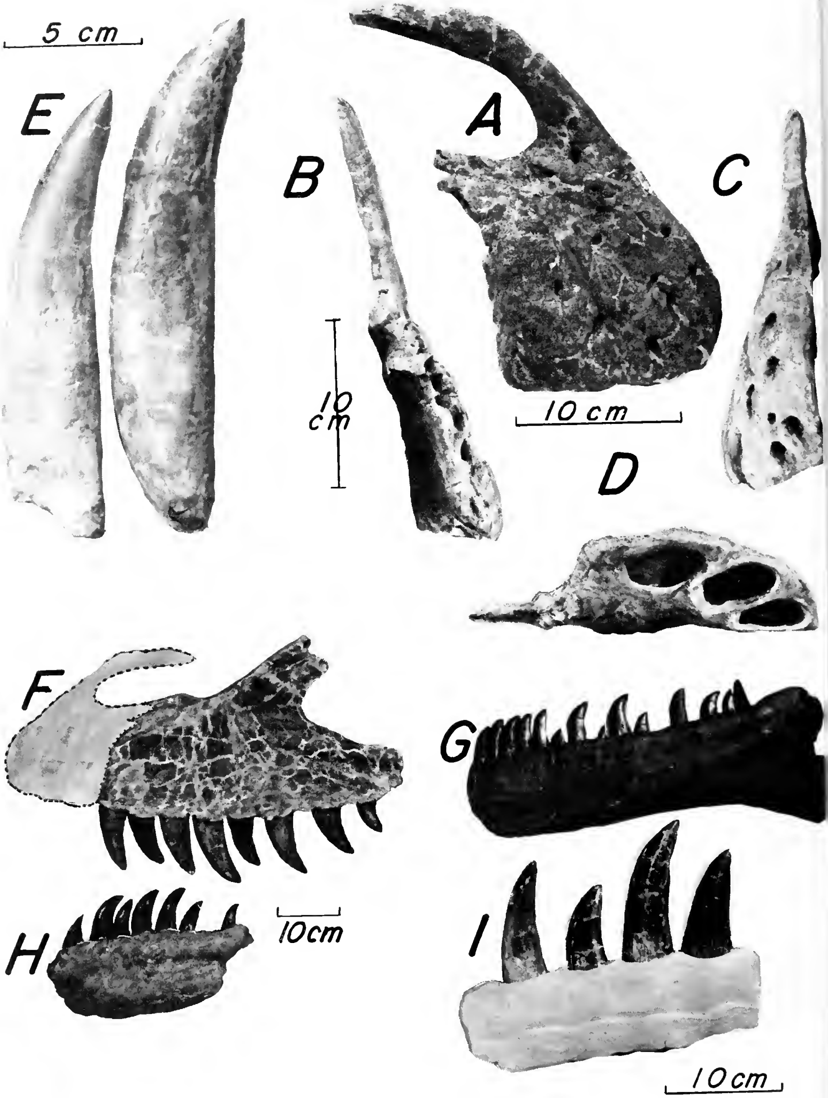

Fig. 5. A–D, *Torvosaurus tanneri* right premaxilla: A, lateral view. B, maxillary contact, or posterior edge. anterior edge. E, two shed teeth,? *Torvosaurus tanneri*. F, H, I, *Torvosaurus tanneri*: F, left maxilla with outline premaxilla. H, left dentary. I, four shed teeth in clay model for contrast with G, left dentary of *Allosaurus* sp.

unidentified family. Other abnormal conditions occurring on elements in the fauna include various excellent examples of gnawed bones.

A Remarkable Carnosaur

The genus and species *Torvosaurus tanneri* was erected on the holotype elements consisting of the left humerus, radius, and ulna. A matching right forelimb was found nearby but not in close association. The holotype and all referred materials were used in the familial and generic diagnoses.

The referred material was selected because it matched the very robust nature of the genus and because there was no evidence of a second robust carnosaur genus present in the deposit.

Based on a comparison of a dozen metatarsals and an apparent enigma in the distribution of diagnostic characteristics in the vertebral column, the author feels there may be two torvosaur species present in the fauna. That possibility may be considered by future workers.

Small Dinosaurs

There is an interesting variety of single elements from small dinosaurs in the fauna. Small, proximally compressed metatarsals are characteristic of both coelurosaurid and ornithomimid genera making the identification of incomplete pedal elements guesswork. No small cranial elements have been recovered to date, but one very important diagnostic pelvic element was recently uncovered in a plastered block in the laboratory.

An *Othnelia* sp. ilium (Fig. 4E) was found marking another occurrence of this characteristically European genus in North America. Galton and Jensen (1975) incorrectly identified the locality producing the first known North American *Othnelia* skeleton as being in the Lower Cretaceous. Instead, the skeleton was collected by the author from the base of the Brushy Basin Member, Upper Jurassic Morrison Formation, near an important fossil plant locality (Chandler 1966) in central Utah.

This small ornithopod belongs to a suborder widely distributed in the Upper Jurassic of North America but poorly known, partly because of a paucity of good study specimens. Its infraorder, Hypsilophodontia, has undergone various revisions in recent years and at present is in a state of mild confusion. Because of this and the incomplete nature of ornithopod materials from Dry Mesa, miscellaneous small specimens such as centrae and random fragments of small bones can only be listed as unknown ornithopod or theropod.

Pterosaurs

Pterosaurs were previously known from the Jurassic of North America by one short phalangial fragment from Como Bluff. Dry Mesa produced the first significant Jurassic pterosaur material, which includes a sacrum with avianlike fused neural spines and a very reduced caudosacral vertebra. The tail was extremely small, with no important function. The neural spines contrast with all described forms that display short, well-separated spines of equal height. One procoelous dorsal vertebra is present, together with three humeri, various more or less complete manual elements, a nearly complete scapulocoracoid, a tiny femur with a spherical head set on a stem nearly parallel to the femoral shaft, and a tiny unidentified cervical vertebra that may be pterosoaurian.

ACKNOWLEDGMENTS

Interested students and aspiring paleontologists who worked on the Uncompahgre fauna project over two decades include Lee Perry, Dennis Belnap, Kevin Maley, Michael Fracasso, Michael Scheetz, Rodney Scheetz, Brooks Britt, Dee Hall, Richard Erickson, and others. Funding for the project came from a regular Brigham Young University, Earth Science Museum budget plus contributions from private sources such as the National Geographic Society, the Sierra Club, small donations from hundreds of children, and, in particular, the Kenneth Thomson family of Toronto. Logistic and social support were consistently supplied by the late Daniel ("Eddie") Jones and his wife, Vivian, of Delta, Colorado, who directed the author to the best fossil localities worked. The author expresses his sincere thanks to them for knowing where to look and for demonstrating for 20 years an enthusiastic determination to get there. Their contribution to science is invaluable.

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FOOD HABITS AND DIETARY OVERLAP OF NONGAME INSECTIVOROUS FISHES IN FLINT CREEK, OKLAHOMA, A WESTERN OZARK FOOTHILLS STREAM[1]

C. Stan Todd[2] and Kenneth W. Stewart[2]

ABSTRACT.—Insectivorous fishes were sampled from March, 1983 to February 1984, in Flint Creek, Delaware Co., Oklahoma. There was insignificant habitat segregation between *Etheostoma spectabile* and *E. punctulatum* and seasonal habitat partitioning between *Cottus carolinae* and both darters. Mature *E. spectabile* ate primarily chironomids and mayflies, whereas juveniles fed primarily on microcrustaceans. Mature *E. punctulatum* consumed fewer *Ephemerella* and *Leptophlebia* than *E. spectabile*, feeding on *Stenonema* and other crustaceans. Juvenile *E. punctulatum* fed mainly on amphipods and mayflies, and juvenile *E. spectabile* ate primarily microcrustaceans. *Cottus carolinae* elected primarily mayflies in spring-summer and chironomids in January-February. Coefficients of dietary overlap were highest between larger *E. spectabile* and juvenile *E. punctulatum* and lowest between immature *E. spectabile* and mature *E. punctulatum*. Overlap between the two darters was significantly correlated with differences in mean prey size ($p<0.0005$). Overlap between sizes of *E. spectabile* was also significantly correlated to differences in mean prey sizes. *Etheostoma spectabile* generally preferred smaller prey than *E. punctulatum*. All three species avoided *Stenelmis*. *Cottus carolinae* avoided microcrustaceans. The study showed that resource partitioning among these three insectivorous fishes is affected by complex interactions of habitat and prey electivity, and prey size selectivity.

Darters and other nongame insectivorous fishes, such as sculpins and madtoms, are often found coexisting in the same stream (Diaber 1956, Braasch and Smith 1967, Page and Smith 1970, 1971, Novak and Estes 1974, Page 1974, Flynn and Hoyt 1979, Matthews et al. 1982, Wynes and Wissing 1982). In such systems, resource partitioning by coexisting species is expected (Gause 1934, Zaret and Rand 1971). Smart and Gee (1979), Matthews et al. (1982) and Wynes and Wissing (1982) have shown varying degrees of segregation of food and habitat use in coexisting darter species. Northcote (1954) studied the ecology of two sculpin species, and Daiber (1956) compared the feeding habits of the mottled sculpin and the fantail darter. Ecological segregation has also been shown among several other groups of sympatric freshwater fishes (Zaret and Rand 1971, Moyle 1973, Mendelson 1975, Werner and Hall 1976, Surat et al. 1980, Baker and Ross 1981).

Several factors may influence competition for food between cohabiting fishes. These include primarily: (1) the utilization of different habitats, (2) prey size selectivity, and (3) the selection of specific prey species.

Spatial segregation by stream fishes is difficult to assess, and studies based on seine hauls may be deceptive, since the method of capture potentially disturbs them to the point where their distribution may no longer represent natural activities, or the sampling area is so large that important differences in microhabitat usage are obscured.

The food habits of some darters and sculpins change as they mature (Koster 1937, Bailey 1952, Daiber 1956, Braasch and Smith 1967, Page and Smith 1970, 1971, Scalet 1972, Page 1974, Flynn and Robert 1977, Schenec and Whiteside 1977, Layzer and Reed 1978). This suggests an age-related change in the strategies of food partitioning. Different size classes of a species are often found in different habitats. This potentially reduces both interspecific and intraspecific competition. The selection of different prey or different prey sizes may be influenced by many factors such as morphological, physiological, and behavioral characteristics of both the predator and prey.

Preliminary studies of darter food habits in Flint Creek, Oklahoma, suggested a difference in the magnitude of dietary overlap, depending on the size classes of fishes compared. Although Smart and Gee (1979) separated fish into age groups, most studies have reported indices of overlap without sub-

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dividing the population into size classes, possibly overlooking some very important aspects of darter ecology.

At times during the life histories of game fishes there may be competition with noneconomic fishes for the available food resources. To better comprehend these relationships, it is necessary to understand the resource requirements of the noneconomic species. In Flint Creek, Delaware County, Oklahoma, insectivorous fishes that are in potential competition with the primary game fish, the smallmouth bass (*Micropterus dolomieui* Lacepede), are the orangethroat darter (*Etheostoma spectabile* Agassiz), the stippled darter (*Etheostoma punctulatum* Agassiz), the banded darter (*Etheostoma zonale* Cope), the fantail darter (*Etheostoma flabellare* Rafinesque), the greensided darter (*Etheostoma blennioides* Rafinesque), and the banded sculpin (*Cottus carolinae* Gill).

The food habits and life histories of many darters and sculpins have been studied (Koster 1937, Dineen 1951, Bailey 1952, Braasch and Smith 1967, Page and Smith 1970, 1971, Scalet 1972, Novak and Estes 1974, Page 1974, Flynn and Hoyt 1979, Cordes and Page 1980). Neither the food habits of the orangethroat darter, the stippled darter, or the banded sculpin nor the relationships between these species have been reported. Therefore, the objectives of this study were: (1) to describe the food habits of the three most abundant insectivorous fishes in Flint Creek, Oklahoma, *E. spectabile*, *E. punctulatum*, and *C. carolinae*; (2) to determine the magnitude of dietary overlap between various sizes of the two darter species and the banded sculpin; (3) to conduct field and laboratory studies to determine if the darters and sculpins of each size class are selecting prey items.

MATERIALS AND METHODS

STUDY AREA.— Flint Creek is a third order stream running southeasterly through Delaware County, Oklahoma, to its confluence with the Illinois River. The study area was a 1-km section approximately 4-km upstream from Oklahoma Highway 33. At this point the stream passes through an open valley with occasional riparian trees. The stream consists of many pools separated by as many riffles. The substrate ranges from detritus and silt to gravel and rubble, with gravel being most common. During summer months, a large portion of the stream becomes covered with water willow (*Justicia americana*) and water primrose (*Ludwigia* spp.).

HABITAT USAGE.— Fishes were captured monthly from March 1983 to February 1984 using a kick-net placed downstream of habitats to be sampled, with the substrate disturbed to dislodge fish. A total of 50 kick-sets were made monthly in each of four general habitats: (1) open pools, (2) open riffles, (3) pools with submerged and/or emergent cover, and (4) riffles with submerged and/or emergent cover. The standard length in mm was measured for each fish. An analysis of co-dispersion was made incorporating a log-likelihood ratio test. Although sampling efficiencies may have differed in each habitat, an ANOVA was run to test for differences in the average length of each species between the four habitats followed by a Student-Newman-Keuls multiple comparison.

STOMACH ANALYSIS.—In habitats where two or more species were captured, five fish in as many 10-mm size classes as possible were preserved in 10% formalin for stomach analysis. Roberts and Winn (1962) and Daughtery et al. (1976) found that visual stimuli were necessary for normal feeding responses of darters. Several researchers have found darters to exhibit diurnal feeding patterns, with peak feeding occurring in midday or afternoon, with maximum gut content later in the day (Mathur 1973, Schenec and Whiteside 1977, Layzer and Reed 1978, Cordes and Page 1980, Matthews et al. 1982). Preliminary studies indicated the two darter species under study both fit this pattern; therefore, all fish were captured between 12:00 noon and 5:00 p.m.

Stomach contents of the preserved darters were identified to the lowest possible taxon (genera for most insects). The head capsule width (HCW) of insects or the maximum diameter of other taxa was measured with an ocular micrometer.

FOOD AVAILABILITY.—Within the same habitats where darters were collected for stomach analyses, three 0.05 m^2 Hess samples were taken at the same monthly sampling times and preserved in 70% isopropanol for determination of prey availability. Additional benthic organisms were collected, and their HCW or maximum diameter measured. These organisms were then killed in 4% formalin, immediately dried for 24 hours at 105 C, and their dry weight was measured to the nearest 0.1 mg. Regression lines were developed from these data and were used to estimate the live dry weight of the prey consumed.

DIETARY OVERLAP.—Dietary overlap was determined with an index of association $C\lambda$ (Horn 1966) which is calculated:

$$C\lambda = \frac{2\sum_{i=1}^{s} x_i y_i}{\sum_{i=1}^{s} x_i + \sum_{i=1}^{s} y_i}$$

where:

s = total number of food taxa

x_i = proportion of the total diet of species x taken from taxa i

y_i = proportion of the total diet of species y taken from taxa i

This index ranges from 0.0 to 1.0, with a value of 0.0 indicating no overlap, and 1.0 indicating complete overlap. An index of overlap was calculated for both numbers and biomass of each prey taxa.

PREY SELECTION.—A linear index of food selection L (Strauss 1979) was used. It is calculated:

$$L_i = r_i - p_i$$

where:

r_i = the relative abundance of item i in the gut

p_i = the relative abundance of item i in the environment

This index ranges from −1.0 to 1.0, with positive values indicating preference and negative values indicating avoidance and/or inaccessibility. A Students t-test was used to test the null hypothesis of no difference in L from zero.

An index of selectivity assesses differences in the proportions of a specific prey item in the diet relative to proportions available in the environment. These indices may or may not express actual election or avoidance of a prey item. The real availability of prey items is usually not known; therefore, unavailability may be mistaken as avoidance.

The following experiment was conducted in June 1984 to gain some further insight into selectivity by darters in a situation where no prey had protective cover. Five 18.9-l aquaria were placed in the stream to minimize stress on the darters during the experiment. A selected group of prey, representative of the stream population and in sufficient numbers (n=70) to allow feeding without greatly affecting the proportions of the prey, were counted into the aquaria. Fish were placed in the aquaria after dark as follows: (1) two mature *E. spectabile* in each of three aquaria and (2) two mature *E. punctulatum* in each of two aquaria. This allowed adjustment to confinement prior to dawn, when normal feeding should begin. The darters were allowed to feed until noon, when they were preserved for stomach analysis.

SIZE SELECTIVITY.—Size selectivity was assessed by comparing mean widths of prey consumed by each species in each size class. A one-way ANOVA followed by a Student-Newman-Keuls multiple range test was used to test for differences in mean widths of prey consumed between different size classes of fishes.

RESULTS AND DISCUSSION

SEASONAL ABUNDANCE.—A total of 992 darters and sculpins were captured over the 12-month study period. *Etheostoma spectabile* was most abundant (n=543), followed by *Cottus carolinae (n=275), E. punctulatum* (n=157), and *E. zonale* (n=17). Their seasonal abundance from March 1983 to February 1984 is illustrated in Figure 1, and numbers of *E. spectabile* and *C. carolinae* generally followed expected survivorship, except in August when dense macrophytic vegetation may have impaired sampling efficiency. These two species are spring and summer spawners, and their numbers were greatest, as expected, during these periods of recruitment. *Etheostoma zonale* was low in abundance over the entire year, with the greatest number captured (n=6) occurring in August. The efficiency of seining as a method of sam-

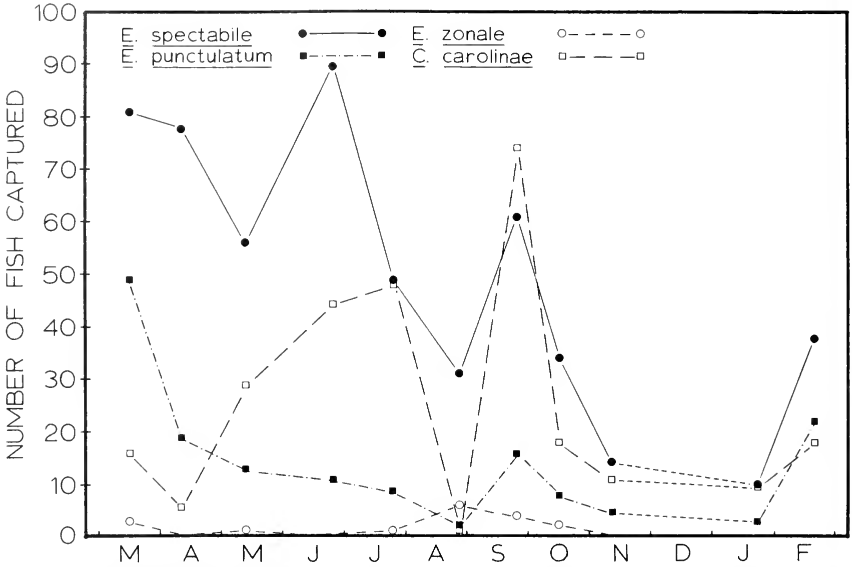

Fig. 1. Seasonal abundance of the four most abundant noneconomic insectivorous fishes in Flint Creek, Oklahoma, March 1983 to February 1984.

pling darters and sculpins is questionable, because of their ability to avoid capture by hiding under rocks and in crevices. The use of kicknets in this study probably gave a more discrete sample.

HABITAT USAGE.—An analysis of co-dispersion for *E. spectabile* and *E. punctulatum* revealed no significant habitat segregation. Significant ($p<0.05$) positive co-dispersion (overlap) was observed in June and September 1983. All values for co-dispersion were positive except in November 1983 and January 1984, when numbers collected were low (19 and 13, respectively).

Areas sampled can greatly affect the results of an analysis of co-dispersion. Small sampling areas tend to give negative values, whereas large sampling areas tend to result in positive values. Kick-netting resulted in a large percentage of kick-sets capturing no fish. The positive values for co-dispersion and a low capture rate suggests that the two darters did not separate themselves on the basis of habitat selection alone.

Similar analyses with *C. carolinae* and both darters showed relatively more habitat segregation between mature banded sculpins and both darters during spring (March, April), with significant negative co-dispersion between *C. carolinae* and *E. punctulatum* in April. Significant ($p<0.05$) overlap was shown between *C. carolinae* and *E. spectabile* in May, coinciding with the hatching and recruitment of both species. Mature *C. carolinae* were absent from the four habitats sampled from May to September, when juvenile fish were abundant, probably reducing intraspecific and interspecific competition.

On a yearly basis, an ANOVA revealed a significant difference in the average body lengths of both *E. spectabile* and *E. punctulatum* between habitats ($p<0.0001$), whereas no significant difference in the mean lengths of *C. carolinae* were found. A Student-Newman-Keuls multiple comparison showed *E. punctulatum* with a significantly larger mean length in riffles with submerged and/or emergent cover than in open pools, 62.3 and 43.5 mm, respectively ($p<0.05$). *Etheostoma spectabile* had a significantly higher mean length in riffles with and without submerged and/or emergent cover (51.6 and 50.3 mm,

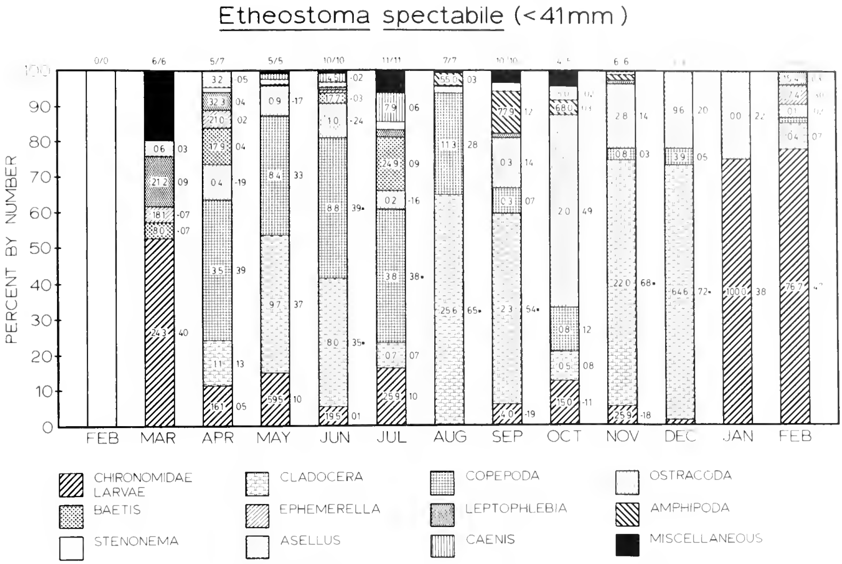

Fig. 2. Food habits of *Etheostoma spectabile* <41 mm February 1983 to February 1984. In this figure and Figures 3–6, each bar equals the percent by number of each selected prey item, numbers above bars are equal to the ratio of fed to total guts examined, numbers within bars are equal to the percent by dry weight of food items, and numbers right of major food categories are equal to the Strauss Selectivity Index. Asterisks with Strauss Index are equal to significance (p<0.05).

respectively) than in pools with and without submerged and/or emergent cover (42.3 and 40.8 mm, respectively) (p<0.05). Although not significant, both species were larger in riffles with submerged and/or emergent cover and pools with submerged and/or emergent cover than in open riffles and open pools, respectively. The presence of different sizes of fishes in different habitats may be important in the reduction of intraspecific competition. Since roughly similar size classes of the two darters were found in similar habitats, the segregation of habitat alone by different size classes probably had little effect on interspecific competition; however, the combination of habitat selection, temporal segregation of spawning times, prey selection, and differences in prey size probably resulted in lowered competition between *E. spectabile* and *E. punctulatum*.

FOOD HABITS.—In both darters a major dietary shift could be related to maturation, and therefore separation of fish sizes for discussion of food habits was made on this basis. *Etheostoma spectabile* and *E. punctulatum* were therefore respectively separated into <41 and >40, and <51 and >50 mm sizes (Figs. 2–5).

The stomachs of 244 *E. spectabile* contained 35 different prey taxa. Both juveniles and adults fed heavily on chironomids during winter and early spring (January–March, Figs. 2,3). Chironomids continued to constitute 16.1%–59.5%, by dry weight, of juvenile fish diets in April to July, as they increased feeding on microcrustaceans and small mayflies (Fig. 2). This shift to planktonic prey items coincided with recruitment of darter fry. In August, diets of these smaller fish were exclusively composed of microcrustaceans, particularly Cladocera and Copepoda, and for the rest of the year microcrustaceans and amphipods continued to make up the major percentages by number and dry weight, into December (Fig. 2). Mayfly nymphs (*Baetis*, *Stenonema*, *Ephemerella*, *Leptophlebia*, and *Caenis*) made up 49.1%–77.3%, by dry weight, of mature *E. spectabile* diets in spring

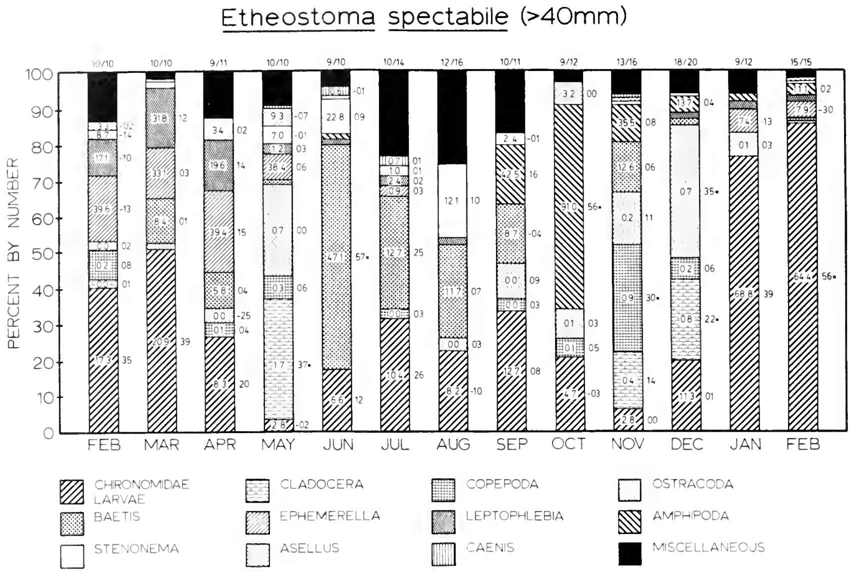

Fig. 3. Food habits of *Etheostoma spectabile* >40 mm February 1983 to February 1984.

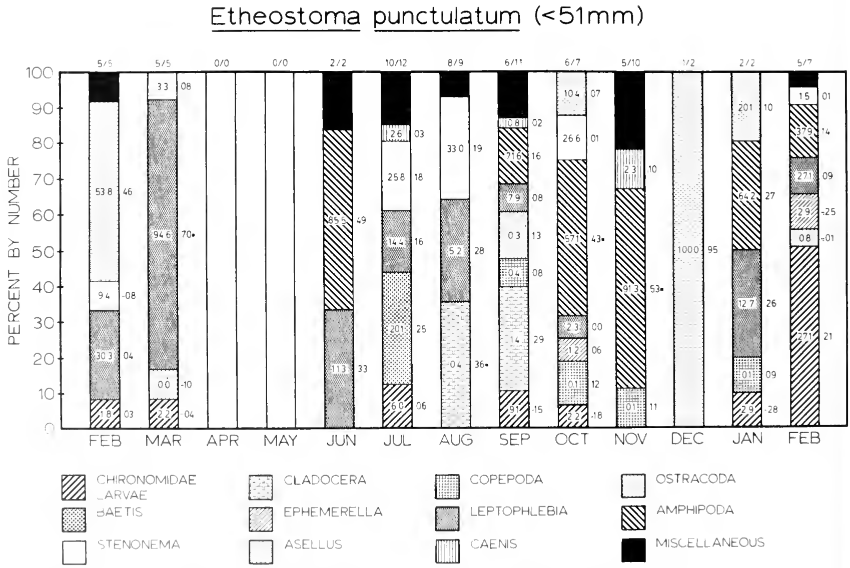

Fig. 4. Food habits of *Etheostoma punctulatum* <51 mm February 1983 to February 1984.

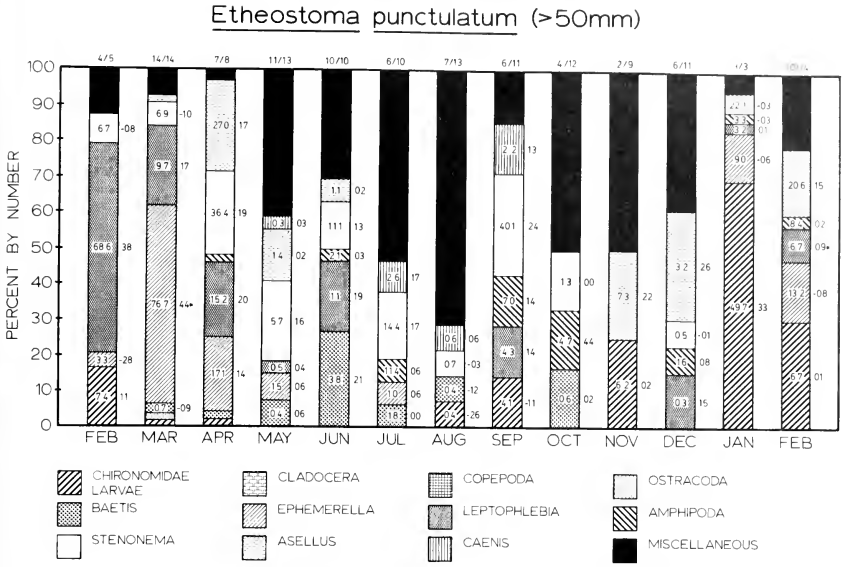

Fig. 5. Food habits of *Etheostoma punctulatum* >50 mm February 1983 to February 1984.

and early summer until June (Fig. 3), corresponding with the emergence and recruitment of these insects. They were ingested at lower levels for the rest of the summer, and none were eaten by 12 fish in October (Fig. 3). Unlike juveniles, mature fish fed on chironomids at levels less than 11% by dry weight from April to July, and microcrustacea were not present in mature fish guts in late spring and summer in amounts above 3.1% by dry weight (June, August). Amphipods appeared in diets of mature orangethroat darters at levels of 42.5% and 91.0% (dry weight), respectively, in September and October, when ingestion of amphipods generally decreased and chironomid feeding increased in November and December until winter, when chironomids again predominated in guts. Mature fish relied more heavily on larger items such as *Baetis*, *Ephemerella*, *Leptophelebia*, *Stenonema*, and amphipods as these items were available.

Stomachs of 205 *E. punctulatum* contained 30 different prey taxa. Both classes of *E. punctulatum* utilized chironomids in the coldest months, January and February (Figs. 4, 5), but relied much less on them in those months, and generally throughout the year, than did *E. spectabile* (Figs. 2, 3). Feeding by *E. punctulatum* during these months was less concentrated on chironomids than in *E. spectabile*, in favor of diverse feeding on mayflies, *Asellus*, and amphipods (Figs. 4, 5).

Few juvenile *E. punctulatum* were captured in spring (March–May). The five fed fish taken in March fed almost exclusively on the mayfly *Leptophlebia* (94.6% by dry wt.), apparently segregating themselves from small *E. spectabile* that spread their feeding predominately over chironomids (24.3% by dry wt.), *Ephemerella* (18.1%), and *Leptophlebia* (21.2%). During summer months (June–September) and into November, juvenile stippled darters fed mainly on amphipods and the mayflies *Stenonema*, *Baetis*, and *Leptophlebia*, further suggesting segregation of themselves from smaller *E. spectabile* that were feeding more on microcrustaceans during that time. The single fed immature fish captured in December had only *Asellus* in the gut (Fig. 4). Mature *E. punctulatum* showed little pattern in feeding, except in January to March, when chironomids, *Leptophlebia*, and *Ephemerella* were ingested in high vol-

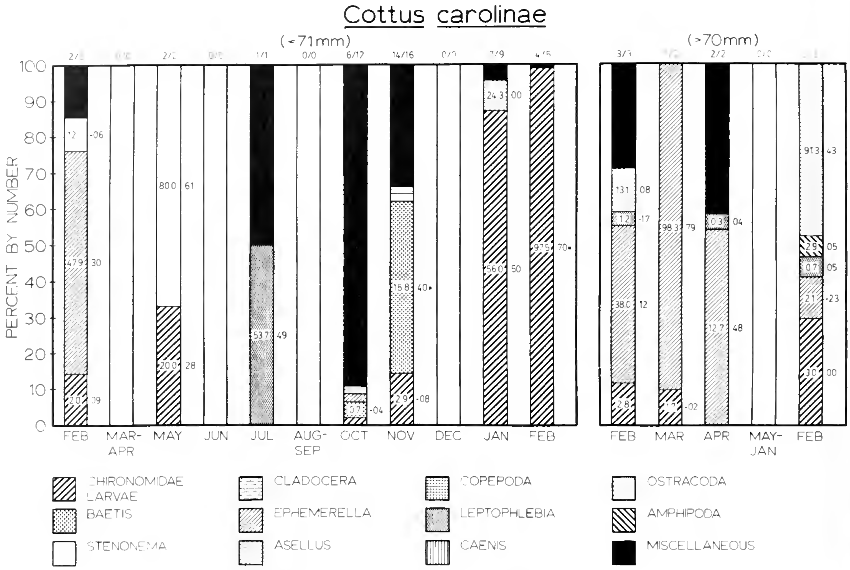

Fig. 6. Food habits of *Cottus carolinae* February 1983 to February 1984.

umes (Fig. 5). During these months larger *E. spectabile* were feeding predominately on chironomids and the mayflies *Ephemerella* and *Leptophlebia*. Ingestion of *Stenonema* and miscellaneous organisms was greater and more seasonally distributed (Fig. 5) than in larger *E. spectabile* (Fig. 3), indicating partitioning of available food resources by the mature fish of both species. The seemingly erratic pattern of prey ingestion (Figs. 4, 5) was generally closely related to the relative abundance of the various prey in the environment.

A few taxa which were not consumed in sufficient numbers to be important items in the annual diet of both darter species composed a large percentage of the diet in months when these items were available. In March 1983 fish eggs made up 25.6%, by dry weight, of the diet of juvenile *E. spectabile*. In mature fish the following prey made up an important part of the diet: February 1983, *Prostoia* (12.8%); April 1983, fish eggs (18.3%), *Isoperla* (5.1%); August 1983, *Isonychia* (35.4%). The diet of smaller *E. punctulatum* contained such important prey as: July 1983, *Neoperla* (16.2%), *Stenacron* (9.8%); August 1983, *Corydalus* (61.4%); September 1983, *Leptohyphes* (5.2%). The following items were important at times in the diet of mature *E. punctulatum*: May 1983, *Isonychia* (39.1%), oligochaeta (27.3%), *Psephenus* (8.2%), *Acroneuria* (15.2%); June 1983, decapoda (20.8%), *Acroneuria* (38.6%), *Corydalus* (16.4%); July 1983, *Neoperla* (17.9%), *Psephenus* (27.9%), decapoda (18.8%); August 1983, *Corydalus* (47.9%), decapoda (34.2%), *Psephenus* (13.7%); September 1983, *Psephenus* (42.4%); October 1983, *Argia* (15.2%), *Corydalus* (78.2%); November 1983, *Psephenus* (86.5%); December 1983, oligochaeta (94.3%).

Two size classes of sculpins were selected with similar reasoning as with the two darter species. These size classes were <71 and >70 mm (Fig. 6).

During the initial months of the study (February–April), it was not known whether sufficient sculpins could be sampled for food habits analysis; therefore, young sculpins were returned to the stream. In the fall, fish were collected for stomach analysis, and 42 specimens were taken during the period October–February (Fig. 6). Mature fish were not collected in the study area of the stream during May–September, and very few were captured until February, possibly because of migration into unsampled habitats such as deep pools. Therefore, food habits were determined from a relatively small sample of nine fish during February–April 1983 and February 1984 (Fig. 6). While studying the movements of sculpins, Bailey (1952) found that, although they usually remained within a radius of 46 m, some moved up to 144 m from the point of initial capture. Deep pools were always within this range in the study area.

Stomachs of 53 *C. carolinae* contained 18 prey taxa. Cladocerans, copepods, and ostracods were absent in the diets of both size classes of *C. carolinae*, suggesting segregation of this species from juvenile *E. spectabile* during August–December, when the latter fed heavily on these items. Both size classes of *C. carolinae* fed on *Ephemerella* (47.9% and 38.0%, by dry weight) during February 1983, as did mature *E. spectabile* (Figs. 3, 6). Mature *C. carolinae* continued to feed on *Ephemerella* through April, when no juveniles were collected. At this time, mature *E. spectabile* and *E. punctulatum* were observed feeding on the mayfly *Ephemerella* (Figs. 3, 5).

In May and July the three small fish collected fed on chironomids (May, 20.0% by dry weight) and small mayflies, *Stenonema* (May, 80.0%), and *Leptophlebia* (July, 53.7%) (Fig. 6); in July *Hydroptila* was also taken (46.3%). During October and November small mayflies such as *Baetis* (0.7% and 15.8%, respectively, by dry weight) were taken, with large numbers of *Psephenus* (2.5%), decapods (63.2%), and *Corydalus* (29.8%) in October. In November *Corydalus* (59.0%) and *Psephenus* (16.6%) made up a large percentage of the diet. Heavy feeding by small *C. carolinae* on chironomids was observed in January (56.0%), increasing to 97.5%, by dry weight, in February (Fig. 6). Although the larger size class consumed some chironomids in this month, *Asellus* made up 91.3% of the diet of the mature fish (Fig. 6). Only mature *E. punctulatum* also fed on *Asellus* at this time in amounts higher than 2 percent (Fig. 5).

Dietary overlap.—Monthly values for dietary overlap between different size classes of darters and sculpins were highly variable, ranging from 0.00 to 0.99 for numeric data and 0.00 to 0.97 for dry weight data (Table 1). Based on numeric data, the lowest average monthly overlap value was between immature *E. spectabile* and mature *E. punctulatum* (0.22), whereas the highest average monthly overlap value was between larger *E. spectabile* and juvenile *E. punctulatum* (0.45). Variations in monthly overlap values may be attributed to differences in prey availability, gape size differences, or differences in prey size. No significant correlation between overlap values and prey availability, or differences in gape were shown; however, a significant ($p<0.0005$) correlation between the difference in mean prey sizes of the groups being compared and overlap values was found. This indicates that prey size selection is important in regulating possible competition for food between these insectivorous fishes in Flint Creek.

Indices of dietary overlap between the two size classes of *E. spectabile* were significantly correlated ($p<0.05$) to the difference in the mean size of prey selected by the two groups. Although mean prey size selection may be important in reducing intraspecific competition for *E. spectabile*, the indices of dietary overlap between the two size classes of *E. punctulatum* were not correlated with the differences in the mean prey size selected by the two size classes. This suggests that the regulation of dietary overlap between the two size classes of *E. punctulatum* is dependent on some factor besides prey size, such as actual election of specific prey items.

Dietary overlap was generally high (.81–.99) only between small banded sculpins and both classes of the orangethroat darters in January–February 1984, since both species fed heavily on chironomids (Table 1). Overlap values between the banded sculpin and *E. punctulatum* were generally low. A value of .96 by number, .93 by dry weight (Table 1), however, was found in January between juvenile *C. carolinae* and mature *E. punctulatum*, when both species were feeding on chironomids.

Size selectivity.—The selection of prey on the basis of size is important in the partitioning of Flint Creek food resources by orangethroat and stippled darters. During most

TABLE 1. Coefficients of dietary overlap of different size classes of *Etheostoma spectabile*, *E. punctulatum*, and *Cottus carolinae* from February 1983 to February 1984. Upper values are based on numeric data. Lower values are based on dry weights data.

Comparison		Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb
E. spectabile	<41 mm	—	.33	—	—	.01	.40	.58	.84	.16	.03	.00	.17	.87
E. punctulatum	<51 mm	—	.37	—	—	.00	.49	.02	.97	.88	.63	.00	.04	.55
E. spectabile	<41 mm	—	.20	.19	.01	.05	.16	.00	.13	.07	.04	.00	.92	.61
E. punctulatum	>50 mm	—	.40	.48	.00	.09	.06	.00	.20	.08	.04	.00	.76	.17
E. spectabile	>40 mm	.29	.38	—	—	.03	.75	.27	.46	.88	.35	.00	.21	.85
E. punctulatum	<51 mm	.28	.53	—	—	.05	.25	.12	.80	.84	.55	.00	.13	.63
E. spectabile	>40 mm	.47	.38	.53	.18	.63	.22	.25	.44	.34	.06	.04	.98	.58
E. punctulatum	>50 mm	.43	.67	.44	.12	.25	.20	.01	.15	.06	.00	.85	.87	.21
E. spectabile	<41 mm	—	.94	.42	.73	.08	.55	.01	.22	.29	.44	.62	.97	.99
E. spectabile	>40 mm	—	.78	.76	.18	.51	.60	.03	.77	.94	.47	.07	.92	.96
E. punctulatum	<51 mm	.48	.37	—	—	.31	.46	.10	.33	.40	.15	.48	.25	.75
E. punctulatum	>50 mm	.49	.13	—	—	.04	.41	.69	.15	.06	.05	.03	.33	.27
C. carolinae	<71 mm	—	—	—	.12	—	.03	—	—	.01	.02	—	.94	.96
E. spectabile	<41 mm	—	—	—	.23	—	.04	—	—	.00	.02	—	.81	.95
C. carolinae	<71 mm	.55	—	—	.12	—	.04	—	—	.01	.33	—	.98	.99
E. spectabile	>40 mm	.67	—	—	.14	—	.04	—	—	.00	.06	—	.87	.90
C. carolinae	>70 mm	—	.17	.09	—	—	—	—	—	—	—	—	—	.50
E. spectabile	<41 mm	—	.31	.07	—	—	—	—	—	—	—	—	—	.04
C. carolinae	>70 mm	.64	.32	.43	—	—	—	—	—	—	—	—	—	.50
E. spectabile	>40 mm	.74	.54	.12	—	—	—	—	—	—	—	—	—	.06
C. carolinae	<71 mm	.89	—	—	—	—	—	—	—	—	—	—	—	.44
C. carolinae	>70 mm	.87	—	—	—	—	—	—	—	—	—	—	—	.03
C. carolinae	<71 mm	.06	—	—	—	—	.25	—	—	.01	.04	—	.21	.77
E. punctulatum	<51 mm	.03	—	—	—	—	.23	—	—	.00	.01	—	.15	.42
C. carolinae	<71 mm	.15	—	—	.43	—	.00	—	—	.05	.32	—	.96	.50
E. punctulatum	>50 mm	.06	—	—	.10	—	.00	—	—	.42	.25	—	.93	.11
C. carolinae	>70 mm	.32	.01	—	—	—	—	—	—	—	—	—	—	.55
E. punctulatum	<51 mm	.25	.00	—	—	—	—	—	—	—	—	—	—	.04
C. carolinae	>70 mm	.22	.85	.38	—	—	—	—	—	—	—	—	—	.80
E. punctulatum	>50 mm	.08	.96	.05	—	—	—	—	—	—	—	—	—	.36

months there were significant differences ($p<0.05$) in the mean prey widths selected by *E. spectabile* and *E. punctulatum* (Table 2). Also, during many months there were significant differences in prey widths selected by the different size classes of each darter species (Table 2.). Differences in morphology may be partially responsible for these differences. *Etheostoma punctulatum* has the larger gape of the two species. However, in both species the mean prey size selected was not significantly correlated with gape size ($p>0.05$). In months when *C. carolinae* were sampled for stomach analysis, the size of prey selected by this species was generally similar to that consumed by immature *E. punctulatum*. During January and February 1984, when both *C. carolinae* and *E. spectabile* were electing chironomids, prey size for these two groups were similar, possibly indicating a period of higher competition.

SELECTIVITY.—For each class of fishes, monthly electivity for particular prey items were variable; however, some trends are evident (Figs. 2–6). All classes of fishes avoided *Stenelmis*. A preference for specific prey items coincided with months when those prey items were abundant. *Etheostoma spectabile* generally preferred smaller items such as cladocerans and chironomids, whereas *E. punctulatum* generally preferred larger items such as mayflies, *Corydalus*, decapods, and oligochaetes. *Cottus carolinae* showed negative selection for microcrustaceans such as os-

TABLE 2. Mean prey size (mm) of different size classes of *Etheostoma spectabile*, *E. punctulatum*, and *Cottus carolinae* from February 1983 to February 1984.

Month	*E. spectabile* immature	*E. spectabile* mature	*C. carolinae* immature	*C. carolinae* mature	*E. punctulatum* immature	*E. punctulatum* mature
Feb	—	0.74	1.40	1.14	1.45	1.09
Mar	0.54	0.67	—	1.29	1.31	1.35
Apr	0.28	0.92	—	1.47	—	1.38
May	0.11	0.36	0.98	—	—	2.30
Jun	0.13	0.68	—	—	0.84	1.49
Jul	0.23	0.55	0.55	—	0.93	2.14
Aug	0.07	0.65	—	—	0.83	2.73
Sep	0.21	0.35	—	—	0.36	1.66
Oct.	0.19	0.58	1.33	—	0.80	1.37
Nov	0.08	0.25	1.41	—	0.82	2.63
Dec	0.05	0.19	—	—	1.15	1.47
Jan	0.24	0.39	0.36	—	0.81	0.52
Feb	0.32	0.38	0.30	1.21	0.54	0.89

tracods and cladocerans, preferring mayflies, oligochaetes, and decapods.

Several researchers have suggested that changes in the diets of darters occur in response to changing prey densities (Braasch and Smith 1967, Page and Smith 1971, Page and Burr 1976, Schenck and Whiteside 1977). The results of this study support this conclusion. However, changes in either morphology or behavior, or both, as darters mature may also contribute to shifts in the diet. For example, the greater and more seasonally distributed ingestion of *Stenonema* and other miscellaneous organisms by mature *E. punctulatum* (Fig. 5) than by mature *E. spectabile* (Fig. 3), and other instances of positive electivity (Figs. 2–5), cannot be totally rationalized on the basis of those food items becoming more available at certain times.

IN-STREAM AQUARIA EXPERIMENTS.—A group of natural prey, totaling 70 individuals in each aquarium, was used for assessing darter selectivity under the condition of no protective cover. Specific potential prey and their predetermined compositions (by number) were *Cheumatopsyche* (14.3%), *Atherix* (28.6%), *Neoperla* (28.6%), *Stenelmis* larvae (7.1%), *Psephenus* (7.1%), *Isonychia* (7.1%), and *Stenonema* (7.1%). Under these conditions in June 1984, prey selection by the mature fish of each species generally corroborated selectivity indices calculated from field studies in June 1983. Positive election for mayflies and negative selection for *Psephenus* continued. Both species continued to avoid *Stenelmis*, and none were consumed. *Atherix*, which was not abundant in the stream in June 1983, was also completely avoided. *Etheostoma spectabile* had a higher selectivity index for *Cheumatopsyche* (.11) and *Neoperla* (.13) than in the field studies (.01 and −.00, respectively). *Etheostoma punctulatum* also showed a higher index for *Neoperla* (.21) than in the field (−.00). The inaccessibility of *Cheumatopsyche* and *Neoperla*, because of their cryptic nature and the fact that the experimental array of prey was not exactly the same as in the field, may have resulted in altered electivities.

CONCLUSIONS

Several factors influence the degree of overlap in the diet of cohabiting fishes. Differences in the diets of *E. spectabile*, *E. punctulatum*, and *C. carolinae* in Flint Creek, Oklahoma, are related to a complex of factors, including the utilization of different habitats, prey size selection, and the selection of specific prey items.

The absence of mature *C. carolinae* during the summer and fall suggests their movement into unsampled areas, thereby exhibiting habitat partitioning. Analyses of co-dispersion further revealed partitioning of habitat between the banded sculpin and both darters during months when mature sculpins were captured in the study area. Habitat partitioning probably reduces both intraspecific and interspecific competition.

An analysis of co-dispersion between the two darters showed no habitat segregation: however, different lengths of both darter species were found in different habitats. This not only may reduce intraspecific competition, but, together with temporal segregation of spawning times, may reduce interspecific competition.

The selection of prey on the basis of size was found to be an important factor in explaining overlap in the diets of insectivorous fishes. Other researchers have shown prey size to be consistent with gape (Northcote 1954, Daiber 1965, Matthews et al. 1982), and the results of this study support this. However, no correlations between mean prey size and gape were found. No significant ($p<0.05$) correlation was found between differences in gape and dietary overlap between corresponding fish groups. This suggests that gape may be important in prey size range, but other ethological or morphological factors are involved in the determination of the degree of dietary overlap between species. The selection of prey on the basis of size may reduce both intraspecific and interspecific competition. Although difference in dietary overlap between age groups of *E. spectabile* are correlated with differences in mean prey size, differences in dietary overlap between age groups of *E. punctulatum* and mean prey size are not.

Etheostoma spectabile generally fed upon smaller prey than *E. punctulatum*. Although the selection of prey items may be due to the election of a specific prey size, some selection of specific prey items regardless of size was noted. Both species selected prey at times when the particular item was abundant.

The management of stream game fishes is dependent on a knowledge of the species to be managed and their potential competitors. The resources available for management are dependent on the entire food web in the stream, and the resource requirements of noneconomic fishes are often overlooked, obscuring an important factor in total stream management. This study reveals food and potential habitat resource use by, and interactions between, nongame fishes in an Ozark stream. These findings not only provide new basic knowledge for these fishes, but they should be helpful reference data for future assessments of resource use, partitioning, and consequent development of management strategies for stream fishes.

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CHECKLIST OF VASCULAR PLANTS FOR THE BIGHORN CANYON NATIONAL RECREATION AREA, WYOMING AND MONTANA

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Abstract.—The checklist of vascular plants of Bighorn Canyon National Recreation Area is presented based on field collections and herbarium specimens. The checklist treats 656 taxa from 73 families.

Bighorn Canyon National Recreation Area (BCNRA) is located near the northern end of the Bighorn Mountains in Wyoming and Montana, and occupies 25,911 ha (64,000 acres). The vegetation ranges from desert shrubland to lower montane forest.

Previous to this study, the area had only been collected infrequently by several botanists. Therefore, the lack of knowledge about this area warranted further botanical collections. The objectives of this study were threefold: (1) to conduct an intensive inventory of the flora of BCNRA, (2) to bring together existing herbarium data on the plants of the area, and (3) to compile a checklist of the flora.

METHODS

The fieldwork was conducted during the summer of 1983, with collecting trips taking place monthly from May through August. Approximately 1750 collections, in triplicate, were made from throughout the BCNRA. One set of specimens has been deposited in the Rocky Mountain Herbarium (Department of Botany, University of Wyoming) and another set is at the BCNRA Visitor Center (Lovell, Wyoming).

Specimens were identified during the autumn of 1983. To ensure proper identification, most specimens were compared to material in the Rocky Mountain Herbarium (RM). In addition to field collections, several herbaria and knowledgeable botanists in the region were consulted for information. The RM and two small herbaria at BCNRA were checked for species location data, and Dr. Robert Dorn, who has made many collecting trips to the area, provided a list of species he had collected there.

MAJOR FLORISTIC ELEMENTS

The flora of BCNRA is composed of the Rocky Mountain, Great Basin, and Great Plains floristic elements (Porter 1962, Dorn 1977). The Great Basin element is the major component of the flora, which includes the following prominent species: *Juniperus osteosperma*, *Artemisia spinescens*, *Atriplex confertifolia*, *Cercocarpus ledifolius*, *Tetradymia spinosa*, *Sarcobatus vermiculatus*, *and Agropyron spicatum*. This element is approaching the northern edge of its range in the BCNRA. The Rocky Mountain element is the second major component of the BCNRA flora, primarily because of the close proximity to the Bighorn and Pryor mountains. Some of the species associated with this element are *Abies lasiocarpa*, *Picea engelmannii*, *Pinus ponderosa*, *Mahonia repens*, *Arnica cordifolia*, and *Calypso bulbosa*.

The smallest element of the flora represents the Great Plains region. This element is found in the northeast portion of the area and includes *Amorpha canescens*, *Calylophus serrulatus*, *Andropogon gerardii*, *Bouteloua curtipendula*, *Echinacea angustifolia*, *Liatris punctata*, and *Petalostemon purpureum*.

The distribution of the three floristic elements is correlated to some extent with climatic patterns. The south end of the recreation area is the most arid and is dominated by

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he Great Basin flora, whereas the Rocky Mountain element dominates at cooler, higher elevations from near the south end to Bull Elk Basin. Coniferous forests dominate he higher north slopes. In the area of Fort Smith, the flora is more representative of the Great Plains element, with higher summer precipitation. The average annual precipitaion ranges from 18 cm (7 inches) at the south end (Lovell) to 50 cm (20 inches) at Fort Smith on the north end (BCNRA, personal communication).

NOVELTIES OF THE FLORA

Because of the representation of three maor elements in the area and numerous endemics located within the Bighorn Mounains, the checklist for BCNRA has some taxa warranting recognition. Also, these taxa of inerest include species on the edge of their ranges. A list of these species follows.

Near or Regional Endemics

Penstemon caryi Penn.
Sullivantia hapemanii (Coult. & Fish.) Coult.
Musineon vaginatum Rydb.
Townsendia spathulata Nutt.
Erigeron allocotus Blake
Cryptantha cana (A. Nels.) Pays.
Eritrichium howardii (Gray) Rydb.
Kelseya uniflora (Wats.) Rydb.
Eriogonum brevicaule Nutt. spp. *canum* (Stokes) Dorn
Astragalus hyalinus Jones
Stanleya tomentosa Parry

Peripheral Species

Ligusticum porteri Coult. & Rose
Logfia arvensis (L.) Holub.
Polystichum lonchitis (L.) Roth.
Triodanis leptocarpa (Nutt.) Niewl.
Lilium philadelphicum L.
Smilax herbacea L.

THE CHECKLIST

Families, genera, and species are listed in alphabetical order, and the nomenclature follows Dorn (1977), Hitchcock and Cronquist (1973), and Cronquist, Holmgren, Holmgren, and Reveal (1972, 1977). A total of 73 families of vascular plants occur in the BCNRA with 320 genera and 656 taxa of specific or subspecific rank. Because this checklist is based largely on one summer of fieldwork, additional species should be expected with additional collections.

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EQUISETACEAE
- *Equisetum*
  - *arvense* L.
  - *hyemale* L.
  - *laevigatum* A. Br.

POLYPODIACEAE
- *Cheilanthes*
  - *feei* T. Moore
- *Cystopteris*
  - *fragilis* (L.) Bernh.
    - var. *fragilis*
- *Pellaea*
  - *occidentalis* (E. Nels.) Rydb.
- *Polystichum*
  - *lonchitis* (L.) Roth
- *Woodsia*
  - *scopulina* D.C. Eat.

SELAGINELLACEAE
- *Selaginella*
  - *densa* Rydb.

CUPRESSACEAE
- *Juniperus*
  - *communis* L.
    - var. *depressa* Pursh
  - *osteosperma* (Torr.) Little
  - *scopulorum* Sarg.

PINACEAE
- *Abies*
  - *lasiocarpa* (Hook.) Nutt.
    - var. *lasiocarpa*
- *Picea*
  - *engelmannii* Parry ex Engelm.

- *Pinus*
  - *flexilis* James
  - *ponderosa* Dougl. ex P. & C. Lawson
- *Pseudotsuga*
  - *menziesii* (Mirb.) Franco
    - var. *glauca* (Beissn.) Franco

ACERACEAE

- *Acer*
  - *glabrum* Torr.
  - *negundo* L.
    - var. *interius* (Britt.) Sarg.

AMARANTHACEAE

- *Amaranthus*
  - *blitoides* Wats.

ANACARDIACEAE

- *Rhus*
  - *glabra* L.
  - *trilobata* Nutt.
    - var. *trilobata*
- *Toxicodendron*
  - *rydbergii* (Small ex Rydb.) Greene

APIACEAE

- *Berula*
  - *erecta* (Huds.) Cov.
    - var. *incisa* (Torr.) Cronq.
- *Bupleurum*
  - *americanum* Coult. & Rose
- *Conium*
  - *maculatum* L.
- *Cymopterus*
  - *acaulis* (Pursh) Raf.
- *Heracleum*
  - *sphondylium* L.
- *Ligusticum*
  - *filicinum* Wats.
- *Lomatium*
  - *cous* (Wats.) Coult. & Rose
  - *dissectum* (Nutt.) Math. & Const.
    - var. *multifidum* (Nutt.) Math. & Const.
  - *foeniculaceum* (Nutt.) Coult. & Rose
  - *orientale* Coult. & Rose
  - *triternatum* (Pursh) Coult. & Rose
    - ssp. *platycarpum* (Torr.) Cronq.
- *Musineon*
  - *divaricatum* (Pursh) Nutt. ex T. & G.
  - *vaginatum* Rydb.
- *Osmorhiza*
  - *chilensis* H. & A.
  - *depauperata* Phil.
  - *longistylis* (Torr.) DC.
- *Perideridia*
  - *gairdneri* (H. & A.) Math.
    - ssp. *borealis* Chaung & Const.
- *Pteryxia*
  - *terebinthina* (Hook.) Coult. & Rose
    - var. *calcarea* (Jones) Math.
- *Sanicula*
  - *marilandica* L.

APOCYNACEAE

- *Apocynum*
  - *androsaemifolium* L.
  - *cannabinum* L.

ASCLEPIADACEAE

- *Asclepias*
  - *speciosa* Torr.

ASTERACEAE

- *Achillea*
  - *millefolium* L.
    - var. *lanulosa* (Nutt.) Piper
- *Agoseris*
  - *glauca* (Pursh) Raf.
    - var. *dasycephala* (T. & G.) Jeps.
    - var. *glauca*
    - var. *laciniata* (D.C. Eat.) Smiley
- *Ambrosia*
  - *artemisiifolia* L.
    - var. *elatior* (L.) Desc.
  - *psilostachya* DC.
    - var. *coronopifolia* (T. & G.) Farw.
  - *trifida* L.
    - var. *trifida*
- *Antennaria*
  - *alpina* (L.) Gaertn.
    - var. *media* (Greene) Jeps.
  - *microphlylla* Rydb.
  - *parvifolia* Nutt.
  - *racemosa* Hook.
- *Arctium*
  - *minus* (Hill) Bernh.
- *Arnica*
  - *cordifolia* Hook.
  - *fulgens* Pursh
  - *latifolia* Bong.
  - *rydbergii* Greene
  - *sororia* Greene
- *Artemisia*
  - *biennis* Willd.
  - *campestris* L.
    - ssp. *borealis* (Pall.) Hall & Clem.
      - var. *scouleriana* (Bess.) Cronq.
  - *cana* Pursh
    - ssp. *cana*
  - *dracunculus* L.
  - *frigida* Willd.
  - *ludoviciana* Nutt.
    - var. *ludoviciana*
  - *nova* A. Nels.
  - *spinescens* D. C. Eat.
  - *tridentata* Nutt.
- *Aster*
  - *chilensis* Nees
    - ssp. *adscendens* (Lindl.) Cronq.
  - *ciliolatus* Lindl.
  - *eatonii* (Gray) Howell
  - *falcatus* Lindl.
  - *foliaceus* Lindl. ex DC.
  - *hesperius* Gray

Balsamorhiza
- *incana* Nutt.
- *sagittata* (Pursh) Nutt.

Bidens
- *cernua* L.

Brickellia
- *grandiflora* (Hook.) Nutt.
  - var. *grandiflora*

Centaurea
- *maculosa* Lam.
- *repens* L.

Chaenactis
- *douglasii* (Hook.) H. & A.

Chrysanthemum
- *leucanthemum* L.

Chrysothamnus
- *nauseosus* (Pall. ex Pursh) Britt.
- *viscidiflorus* (Hook.) Nutt.
  - ssp. *viscidiflorus*
    - var. *latifolius* (D.C. Eat.) Rydb.
    - var. *viscidiflorus*

Cichorium
- *intybus* L.

Cirsium
- *arvense* (L.) Scop.
- *flodmanii* (Rydb.) Arthur
- *tweedyi* (Rydb.) Petr.
- *undulatum* (Nutt.) Spreng.
- *vulgare* (Savi) Tenore

Conyza
- *canadensis* (L.) Cronq.

Crepis
- *acuminata* Nutt.
  - ssp. *acuminata*
- *atrabarba* Heller
- *intermedia* Gray
- *modocensis* Greene
  - ssp. *modocensis*
- *runcinata* (James) T. & G.

Echinacea
- *pallida* Nutt.
  - var. *angustifolia* (DC.) Cronq.

Erigeron
- *allocotus* Blake
- *caespitosus* Nutt.
- *compositus* Pursh
- *corymbosus* Nutt.
- *glabellus* Nutt.
  - var. *glabellus*
- *ochroleucus* Nutt.
  - var. *ochroleucus*
  - var. *scribneri* (Canby ex Rydb.) Cronq.
- *pumilus* Nutt.
  - ssp. *pumilus*
- *speciosus* (Lindl.) DC.
- *strigosus* Muhl. ex Willd.

Eupatorium
- *maculatum* L.

Gaillardia
- *aristata* Pursh

Grindelia
- *squarrosa* (Pursh) Dunal

Gutierrezia
- *sarothrae* (Pursh) Britt. & Rusby

Haplopappus
- *armerioides* (Nutt.) Gray

Helianthella
- *quinquenervis* (Hook.) Gray

Helianthus
- *annuus* L.
- *nuttallii* T. & G.
- *petiolaris* Nutt.
  - ssp. *petiolaris*
- *rigidus* (Cass.) Desf.
  - var. *subrhomboideus* (Rydb.) Cronq.

Heterotheca
- *villosa* (Pursh) Shinners

Hieracium
- *albiflorus* Hook.
- *cynoglossoides* Arv.-Touv.

Hymenopappus
- *filifolius* Hook.
  - var. *filifolius*
  - var. *polycephalus* (Osterh.) Turner

Hymenoxys
- *acaulis* (Pursh) Parker
- *torreyana* (Nutt.) Parker

Iva
- *axillaris* Pursh
- *xanthifolia* Nutt.

Lactuca
- *ludoviciana* (Nutt.) Ridd.
- *oblongifolia* Nutt.
- *serriola* L.

Liatris
- *punctata* Hook.
  - var. *punctata*

Logfia
- *arvensis* (L.) Holub

Lygodesmia
- *juncea* (Pursh) D. Don

Machaeranthera
- *grindelioides* (Nutt.) Shinners
  - var. *grindelioides*
- *tanacetifolia* (H.B.K.) Nees

Malacothrix
- *sonchoides* (Nutt.) T. & G.
- *torreyi* Gray

Microseris
- *nutans* (Hook.) Schultz-Bip.

Nothocalais
- *cuspidata* (Pursh) Greene

Picradeniopsis
- *oppositifolia* (Nutt.) Rydb. ex Britt.

Platyschkuhria
- *integrifolia* (Gray) Rydb.
  - var. *integrifolia*

Ratibida
columnifera (Nutt.) Woot. & Standl.

Rudbeckia
laciniata L.
var. *ampla* (A. Nels.) Cronq.

Senecio
canus Hook.
eremophilus Richards.
integerrimus Nutt.
paupereulus Michx.
plattensis Nutt.
serra Hook.
streptanthifolius Greene

Solidago
canadensis L.
var. *salebrosa* (Piper) Jones
gigantea Ait.
var. *serotina* (Kuntze) Cronq.
missouriensis Nutt.
rigida L.
var. *humilis* Porter
spathulata DC.
var. *nana* (Gray) Cronq.

Sonchus
asper (L.) Hill
oleraceus L.
uliginosus Bieb.

Sphaeromeria
capitata Nutt.

Stephanomeria
runcinata Nutt.

Taraxacum
laevigatum (Willd.) DC.
officinale Weber

Tetradymia
canescens DC.
spinosa Hook & Arn.

Townsendia
hookeri Beaman
incana Nutt.
parryi D.C. Eat.
spathulata Nutt.

Tragopogon
dubius Scop.

Wyethia
scabra Hook.
var. *scabra*

Xanthium
strumarium L.

Berberidaceae
Mahonia
repens (Lindl.) G. Don

Betulaceae
Betula
occidentalis Hook.

Boraginaceae
Asperugo
procumbens. L.

Coldenia
nuttallii Hook.

Cryptantha
cana (A. Nels.) Pays.
celosioides (Eastw.) Pays.
flavoculata (A. Nels.) Pays.
kelseyana Greene

Cynoglossum
officinale L.

Eritrichium
howardii (Gray) Rydb.

Hackelia
deflexa (Wahlenb.) Opiz
var. *americana* (Gray) Fern. & I. M. Johnst.
floribunda (Lehm.) I. M. Johnst.

Lappula
redowskii (Hornem.) Greene

Lithospermum
incisum Lehm.
ruderale Dougl. ex Lehm.

Mertensia
ciliata (James ex Torr.) G. Don
var. *ciliata*
oblongifolia (Nutt.) G. Don
viridis (A. Nels.) A. Nels.

Onosmodium
molle Michx.
var. molle
var. *occidentale* (Mack.) I. M. Johnst.

Brassicaceae
Alyssum
alyssoides (L.) L.
desertorum Stapf

Arabis
demissa Greene
var. *languida* Roll.
glabra (L.) Bernh.
hirsuta (L.) Scop.
holboellii Hornem.
var. *pendulocarpa* (A. Nels.) Roll.
var. *retrofracta* (Grah.) Rydb.
lignifera A. Nels.
microphylla Nutt.
var. *saximontana* Roll.
nuttallii Robins.
sparsiflora Nutt.

Barbarea
orthoceras Ledeb.

Camelina
microcarpa Andrz. ex DC.

Capsella
bursa-pastoris (L.) Medic.
var. *bursa-pastoris*

Cardaria
chalepensis (L.) Hand.-Mazz.
pubescens (C.A. Mey.) Jarmol.

Chorispora
tenella (Pall.) DC.

Descurainia
pinnata (Walt.) Britt.
sophia (L.) Webb ex Prantl

Draba
crassifolia Grah.
var. *crassifolia*
nemorosa L.
oligosperma Hook.
praealta Greene
reptans (Lam.) Fern.
ssp. *reptans*
stenoloba Ledeb

Erysimum
asperum (Nutt.) DC.
var. *asperum*
cheiranthoides L.
ssp. *altum* Ahti
inconspicuum (Wats.) MacM.
var. *inconspicuum*

Hesperis
matronalis L.

Lepidium
densiflorum Schrad.
perfoliatum L.

Lesquerella
alpina (Nutt.) Wats.
ssp. *alpina*
ludoviciana (Nutt.) Wats.

Malcolmia
africana (L.) R. Br.

Nasturtium
officinale R. Br.

Physaria
acutifolia Rydb.
var. *acutifolia*
didymocarpa (Hook.) Gray
vary. *didymocarpa*

Rorippa
calycina (Engelm.) Rydb.
curvipes Greene
sinuata (Nutt.) Hitchc.

Sisymbrium
altissimum L.
loeselii L.
linifolium (Nutt.) Nutt. ex T. & G.

Smelowskia
calycina (Steph. ex Willd.) C.A. Mey
var. *americana* (Regel & Herd.) Drury & Roll.

Stanleya
pinnata (Pursh) Britt.
tomentosa Parry

Streptanthella
longirostris (Wats.) Rydb.
var. *longirostris*

CACTACEAE
Opuntia
polyacantha Haw.

Pediocactus
simpsonii (Engelm.) Britt. & Rose
var. *simpsonii*

CAMPANULACEAE
Campanula
rotundifolia L.

Triodanis
leptocarpa (Nutt.) Nieuwl.
perfoliata (L.) Nieuwl.
var. *perfoliata*

CANNABACEAE
Humulus
lupulus L.
var. *neomexicanus* Nels. & Ckll.

CAPPARACEAE
Cleome
lutea Hook.
var. *lutea*
serrulata Pursh

Polanisia
dodecandra (L.) DC.
ssp. *trachysperma* (T. & G.) Iltis

CAPRIFOLIACEAE
Lonicera
utahensis Wats.

Sambucus
canadensis L.
var. *canadensis*
cerulea Raf.
var. *cerulea*
racemosa L.
ssp. *pubens* (Michx.) House
var. *melanocarpa* (Gray) McMinn

Symphoricarpos
albus (L.) Blake
var. *albus*
occidentalis Hook.
oreophilus Gray
var. *utahensis* (Rydb.) A. Nels.

CARYOPHYLLACEAE
Arenaria
congesta Nutt.
hookeri Nutt.
nuttallii Pax
ssp. *nuttallii*
obtusiloba (Rydb.) Fern.

Cerastium
arvense L.
nutans Raf.
var. *nutans*

Lychnis
alba Mill.

Paronychia
sessiliflora Nutt.

Silene
menziesii Hook.
var. *viscosa* (Greene) Hitchc. & Maguire

- *Stellaria*
  - *media* (L.) Vill.

CHENOPODIACEAE
- *Atriplex*
  - *argentea* Nutt.
    - ssp. *argentea*
      - var. *argentea*
  - *canescens* (Pursh) Nutt.
  - *confertifolia* (Torr. & Frem.) Wats.
  - *gardneri* (Moq.) D. Dietr.
  - *heterosperma* Bunge
  - *rosea* L.
- *Ceratoides*
  - *lanata* (Pursh) J. T. Howell
    - var. *lanata*
- *Chenopodium*
  - *berlandieri* Moq.
    - var. *zschackei* (J. Murr.) J. Murr.
  - *leptophyllum* (Moq.) Wats.
- *Corispermum*
  - *hyssopifolium* L.
- *Grayia*
  - *spinosa* (Hook.) Moq.
- *Halogeton*
  - *glomeratus* (Bieb.) C. A. Mey.
- *Kochia*
  - *americana* Wats.
  - *scoparia* (L.) Schrad.
- *Monolepis*
  - *nuttalliana* (Schult.) Greene
- *Salsola*
  - *kali* L.
    - var. *tenuifolia* Tausch.
- *Sarcobatus*
  - *vermiculatus* (Hook.) Torr.
    - var. *vermiculatus*
- *Suaeda*
  - *fruticosa* (L.) Forsk.
  - *torreyana* Wats.

COMMELINACEAE
- *Tradescantia*
  - *bracteata* Small ex Britt.
  - *occidentalis* (Britt.) Smyth
    - var. *occidentalis*

CONVOLVULACEAE
- *Convolvulus*
  - *arvensis* L.
- *Ipomoea*
  - *leptophylla* Torr.

CORNACEAE
- *Cornus*
  - *stolonifera* Michx.

CRASSULACEAE
- *Sedum*
  - *lanceolatum* Torr.

CYPERACEAE
- *Carex*
  - *aquatilis* Wahlenb.
  - *elynoides* Holm
  - *filifolia* Nutt.
  - *heliophila* Mack.
  - *hoodii* Boott
  - *interior* Bailey
  - *lanuginosa* Michx.
  - *microptera* Mack.
  - *nebraskensis* Dewey
  - *oederi* Retz
  - *parryana* Dewey
    - var. *parryana*
  - *praegracilis* W. Boott
  - *raynoldsii* Dewey
  - *rostrata* Stokes ex With.
  - *sprengelii* Dewey ex Spreng.
  - *viridula* Michx.
  - *vulpinoidea* Michx.
- *Eleocharis*
  - *palustris* (L.) R. & S.
- *Scirpus*
  - *pallidus* (Britt.) Fern.
  - *pungens* Vahl
  - *validus* Vahl

ELAEAGNACEAE
- *Elaeagnus*
  - *angustifolia* L.
- *Shepherdia*
  - *argentea* (Pursh) Nutt.
  - *canadensis* (L.) Nutt.

ERICACEAE
- *Pyrola*
  - *asarifolia* Michx.
  - *secunda* L.

EUPHORBIACEAE
- *Euphorbia*
  - *cyparissias* L.
  - *esula* L.
  - *glyptosperma* Engelm.
  - *robusta* (Engelm.) Small

FABACEAE
- *Astragalus*
  - *adsurgens* Pall.
    - var. *robustior* Hook.
  - *agrestis* Dougl. ex G. Don
  - *bisulcatus* (Hook.) Gray
  - *canadensis* L.
    - var. *canadensis*
  - *ceramicus* Sheld.
    - var. *filifolius* (Gray) F. J. Herm.
  - *chamaeleuce* Gray
  - *crassicarpus* Nutt.
  - *drummondii* Dougl. ex Hook.
  - *gilviflorus* Sheld.
  - *hyalinus* Jones
  - *kentrophyta* Gray
  - *lotiflorus* Hook.

- *miser* Dougl. ex Hook.
  - var. *decumbens* (Nutt.) Cronq.
- *missouriensis* Nutt.
  - var. *missouriensis*
- *oreganus* Nutt.
- *purshii* Dougl. ex Hook.
  - var. *purshii*
- *spatulatus* Sheld.

- *Glycyrrhiza*
  - *lepidota* Pursh

- *Hedysarum*
  - *boreale* Nutt.
  - *sulphurescens.* Rydb.

- *Lupinus*
  - *argenteus* Pursh
    - var. *argenteus*
  - *sericeus* Pursh
  - *wyethii* Wats.

- *Medicago*
  - *lupulina* L.
  - *sativa* L.

- *Melilotus*
  - *alba* Medic.
  - *officinalis* (L.) Pall.

- *Oxytropis*
  - *besseyi* (Rydb.) Blank.
    - var. *besseyi*
    - var. *fallax* Barneby
  - *campestris* (L.) DC.
  - *deflexa* (Pall.) DC.
  - *lagopus* Nutt.
  - *sericea* Nutt.

- *Petalostemon*
  - *occidentale* (Heller ex Britt. & Kearn.) Fern.
  - *purpureum* (Vent.) Rydb.

- *Psoralea*
  - *esculenta* Pursh
  - *lanceolata* Pursh
  - *tenuiflora* Pursh
    - var. *tenuiflora*

- *Sphaerophysa*
  - *salsula* (Pall.) DC.

- *Thermopsis*
  - *rhombifolia* (Nutt. ex Pursh) Nutt. ex Richards.

- *Trifolium*
  - *hybridum* L.
  - *pratense* L.

- *Vicia*
  - *americana* Muhl. ex Willd.
    - var. *minor* Hook.

FUMARIACEAE
- *Corydalis*
  - *aurea* Willd.

GENTIANACEAE
- *Frasera*
  - *speciosa* Dougl. ex Griseb.

GERANIACEAE
- *Erodium*
  - *cicutarium* (L.) L'Her.

- *Geranium*
  - *viscosissimum* Fisch. & Mey. ex Mey.
    - var. *viscosissimum*

GROSSULARIACEAE
- *Ribes*
  - *americanum* Mill.
  - *aureum* Pursh
    - var. *aureum*
  - *cereum* Dougl.
    - var. *inebrians* (Lindl.) C. L. Hitchc.
  - *setosum* Lindl.

HYDROPHYLLACEAE
- *Phacelia*
  - *glandulosa* Nutt.
  - *hastata* Dougl. ex Lehm.
  - *ivesiana* Torr.
  - *linearis* (Pursh) Holz.
  - *sericea* (Grah. ex Hook.) Gray

IRIDACEAE
- *Iris*
  - *missouriensis* Nutt.

- *Sisyrinchium*
  - *angustifolium* Mill.
  - *montanum* Greene

JUGLANDACEAE
- *Juglans*
  - *cinerea* L.

JUNCACEAE
- *Juncus*
  - *balticus* Willd.
    - var. *montanus* Engelm.
  - *ensifolius* Wikstr.
  - *longistylis* Torr.
    - var. *longistylis*
  - *parryi* Engelm.
  - *regelii* Buch.
  - *tenuis* Willd.
    - var. *dudleyi* (Wieg.) F. J. Herm.
    - var. *tenuis*
  - *torreyi* Cov.

LAMIACEAE
- *Hedeoma*
  - *drummondii* Benth.

- *Mentha*
  - *arvensis* L.
    - var. *glabrata* (Benth.) Fern.

- *Monarda*
  - *fistulosa* L.
    - var. *menthaefolia* (Grah.) Fern.

- *Nepeta*
  - *cataria* L.

- *Scutellaria*
  - *galericulata* L.

- *Stachys*
  - *palustris* L.
    - var. *pilosa* (Nutt.) Fern.

LENTIBULARIACEAE
- *Utricularia*
  - *vulgaris* L.

LILIACEAE
- *Allium*
  - *brevistylum* Wats.
  - *geyeri* Wats.
  - *textile* Nels. & Macbr.
- *Asparagus*
  - *officinalis* L.
- *Calochortus*
  - *gunnisonii* Wats.
  - *nuttallii* T. & G.
- *Disporum*
  - *trachycarpum* (Wats.) Benth. & Hook.
- *Fritillaria*
  - *pudica* (Pursh) Spreng.
- *Leucocrinum*
  - *montanum* Nutt. ex Gray
- *Lilium*
  - *philadelphicum* L.
    - var. *andinum* (Nutt.) Ker
- *Smilacina*
  - *racemosa* (L.) Desf.
  - *stellata* (L.) Desf.
- *Smilax*
  - *herbacea* L.
    - var. *lasioneuron* (Hook.) A. DC.
- *Yucca*
  - *glauca* Nutt.
    - var. *glauca*
- *Zygadenus*
  - *elegans* Pursh
    - ssp. *elegans*
  - *venenosus* Wats.
    - var. *gramineus* (Rydb.) Walsh ex Peck

LINACEAE
- *Linum*
  - *lewisii* Pursh
    - var. *lewisii*

LOASACEAE
- *Mentzelia*
  - *albicaulis* (Dougl. ex Hook.) T. & G.
  - *decapetala* (Pursh ex Sims) Urban

MALVACEAE
- *Malva*
  - *parviflora* L.
- *Sphaeralcea*
  - *coccinea* (Nutt.) Rydb.

NYCTAGINACEAE
- *Abronia*
  - *fragrans* Nutt. ex Hook.
- *Mirabilis*
  - *linearis* (Pursh) Heimerl

ONAGRACEAE
- *Calylophus*
  - *serrulatus* (Nutt.) Raven
- *Camissonia*
  - *andina* (Nutt.) Raven
  - *minor* (A. Nels.) Raven
  - *scapoidea* (T. & G.) Raven
    - ssp. *scapoidea*
- *Circaea*
  - *alpina* L.
    - var. *alpina*
- *Epilobium*
  - *angustifolium* L.
  - *ciliatum* Raf.
    - ssp. *ciliatum*
    - ssp. *glandulosum* (Lehm.) Hoch & Raven
  - *paniculatum* Nutt. ex T. & G.
- *Gaura*
  - *coccinea* Nutt. ex Pursh
  - *parviflora* Dougl. ex Hook.
- *Gayophytum*
  - *ramosissimum* T. & G.
- *Oenothera*
  - *albicaulis* Pursh
  - *caespitosa* Nutt.
  - *depressa* Greene
  - *pallida* Lindl.
    - ssp. *trichocalyx* (Nutt. ex T. & G.) Munz & Klein

ORCHIDACEAE
- *Corallorhiza*
  - *maculata* Raf.
  - *striata* Lindl.
- *Goodyera*
  - *oblongifolia* Raf.
- *Piperia*
  - *unalascensis* (Spreng.) Rydb.
- *Platanthera*
  - *dilatata* (Pursh) Lindl. ex Beck
  - *hyperborea* (L.) Lindl.

OROBANCHACEAE
- *Orobanche*
  - *uniflora* L.

PLANTAGINACEAE
- *Plantago*
  - *major* L.
  - *patagonica* Jacq.

POACEAE
- *Agropyron*
  - *cristatum* (L.) Gaertn.
  - *elongatum* (Host) Beauv.
  - *repens* (L.) Beauv.
  - *riparium* Scribn. & Sm.
  - *smithii* Rydb.
  - *spicatum* (Pursh) Scribn. & Sm.
    - f. *spicatum*
  - *trachycaulum* (Link) Malte ex Lewis

Agrostis
- *alba* L.
  - var. *palustris* (Huds.) Pers.
- *exarata* Trin.
- *scabra* Willd.

Andropogon
- *gerardii* Vitman
- *scoparius* Michx.
  - var. *scoparius*

Aristida
- *fendleriana* Steud.
- *longiseta* Steud.

Bouteloua
- *curtipendula* (Michx.) Torr.
  - var. *curtipendula*
- *gracilis* (H. B. K.) Lag. ex Griffiths
  - var. *gracilis*

Bromus
- *carinatus* H. & A.
- *ciliatus* L.
- *commutatus* Schrad.
- *inermis* Leys.
- *japonicus* Thunb.
- *tectorum* L.

Calamagrostis
- *purpurascens* R. Br.

Calamovilfa
- *longifolia* (Hook.) Scribn.
  - var. *longifolia*

Dactylis
- *glomerata* L.

Deschampsia
- *cespitosa* (L.) Beauv.
  - var. *cespitosa*

Distichlis
- *spicata* (L.) Greene
  - var. *stricta* (Torr.) Scribn.

Echinochloa
- *crusgalli* (L.) Beuav.
  - var. *crusgalli*

Elymus
- *canadensis* L.
  - var. *canadensis*
- *cinereus* Scribn. & Merr.
- *glaucus* Buckl.
  - var. *glaucus*
- *virginicus* L.
  - var. *submuticus* Hook.

Festuca
- *idahoensis* Elmer
- *octoflora* Walt.

Glyceria
- *striata* (Lam.) Hitchc.
  - var. *stricta* (Schribn.) Fern.

Hordeum
- *jubatum* L.

Koeleria
- *macrantha* (Ledeb.) Schult.

Leucopoa
- *kingii* (Wats.) W. A. Weber

Melica
- *subulata* (Griseb.) Scribn.
  - var. *pammelii* (Scribn.) C.L. Hitchc.

Muhlenbergia
- *racemosa* (Michx.) B. S. P.

Oryzopsis
- *hymenoides* (R. & S.) Ricker ex Piper
- *micrantha* (Trin. & Rupr.) Thurb.

Phalaris
- *arundinacea* L.

Phleum
- *pratense* L.

Phragmites
- *australis* (Cav.) Trin. ex Steud.

Poa
- *alpina* L.
  - var. *alpina*
- *arida* Vasey
- *bulbosa* L.
- *compressa* L.
- *cusickii* Vasey
- *fendleriana* (Steud.) Vasey
- *glaucifolia* Scribn. & Williams ex Williams
- *interior* Rydb.
- *pratensis* L.
- *sandbergii* Vasey

Polypogon
- *monspeliensis* (L.) Desf.

Setaria
- *viridis* (L.) Beauv.

Sitanion
- *hystrix* (Nutt.) J. G. Sm.

Spartina
- *pectinata* Link

Sphenopholis
- *obtusata* (Michx.) Scribn.
  - var. *major* (Torr.) K. S. Erdm.

Sporobolus
- *airoides* (Torr.) Torr.
- *cryptandrus* (Torr.) Gray

Stipa
- *columbiana* Macoun
- *comata* Trin. & Rupr.
- *lettermanii* Vasey
- *viridula* Trin.
- *williamsii* Scribn.

Trisetum
- *spicatum* (L.) Richt.

POLEMONIACEAE

Gilia
- *leptomeria* Gray
- *pinnatifida* Nutt. ex Gray
- *tweedyi* Rydb.

Ipomopsis
pumila (Nutt.) Grant
spicata (Nutt.) Grant

Leptodactylon
caespitosum Nutt.
pungens (Torr.) Nutt.
ssp. *pungens*

Linanthus
septentrionalis Mason

Phlox
bryoides Nutt.
hoodii Richards.
multiflora A. Nels.

Polemonium
occidentale Greene
var. *occidentale*
pulcherrimum Hook.
var. *pulcherrimum*
viscosum Nutt.

POLYGONACEAE
Eriogonum
annuum Nutt.
brevicaule Nutt.
ssp. *canum* (Stokes) Dorn
flavum Nutt.
var. *flavum*
ovalifolium Nutt.
var. *ovalifolium*

Polygonum
achoreum Blake
aviculare L.
bistortoides Pursh
lapathifolium L.

Rumex
crispus L.
triangulivalvis (Danser) Rech. f.
venosus Pursh

PORTULACACEAE
Claytonia
lanceolata Pursh
var. *lanceolata*

Lewisia
rediviva Pursh
ssp. *rediviva*

Montia
perfoliata (Donn) Howell
var. *perfoliata*

Portulaca
oleracea L.

POTAMOGETONACEAE
Potamogeton
filiformis Pers.

PRIMULACEAE
Androsace
septentrionalis L.

Dodecatheon
pulchellum (Raf.) Merr.

Lysimachia
ciliata L.

RANUNCULACEAE
Actaea
rubra (Ait.) Willd.

Anemone
cylindrica Gray
multifida Poir.
patens L.

Clematis
columbiana (Nutt.) T. & G.
var. *tenuiloba* (Gray) J. Pringle
ligusticifolia Nutt.
var. *ligusticifolia*

Delphinium
bicolor Nutt.

Ranunculus
cymbalaria Pursh
var. *cymbalaria*
macounii Britt.
pensylvanicus L. f.
testiculatus Crantz
uncinatus D. Don ex G. Don
var. *uncinatus*

Thalictrum
dasycarpum Fisch. et al.
fendleri Engelm. ex Gray
var. *fendleri*
occidentale Gray
var. *palousense* St. John

ROSACEAE
Agrimonia
gryposepala Wallr.

Amelanchier
alnifolia (Nutt.) Nutt.

Cercocarpus
ledifolius Nutt.

Crataegus
douglasii Lindl.

Fragaria
vesca L.
var. *bractreata* (Heller) R. J. Davis
virginiana Duchn.
var. *glauca* Wats.

Geum
aleppicum Jacq.
macrophyllum Willd.
var. *perincisum* (Rydb.) Raup
triflorum Pursh
var. *triflorum*

Ivesia
gordonii (Hook.) T. & G.

Kelseya
uniflora (Wats.) Rydb.

Petrophytum
caespitosum (Nutt.) Rydb.

Physocarpus
malvaceus (Greene) Kuntze
monogynus (Torr.) Coult.

Potentilla
anserina L.
biennis Greene
diversifolia Lehm.
var. *diversifolia*
fissa Nutt.
fruticosa L.
gracilis Dougl. ex Hook.
var. *glabrata* (Lehm.) C. L. Hitchc.
norvegica L.
ssp. *monspeliensis* (L.)
Asch. & Graebn.

ovina Macoun
paradoxa Nutt.
pensylvanica L.

Prunus
americana Marsh
virginiana L.
var. *melanocarpa* (A. Nels.) Sarg.

Rosa
acicularis Lindl.
ssp. *sayi* (Schwein.) W. H. Lewis
sayi Schwein.
woodsii Lindl.

Rubus
idaeus L.
ssp. *sachalinensis* (Levl.) Focke
var. *gracilipes* Jones

Spiraea
betulifolia Pall.
var. *lucida* (Dougl. ex Hook.)
C. L. Hitchc.

RUBIACEAE

Galium
boreale L.
trifidum L.
triflorum Michx.

SALICACEAE

Populus
x *acuminata* Rydb.
alba L.
angustifolia James
deltoides Marsh.
ssp. *monilifera* (Ait.) Echenw.
tremuloides Michx.

Salix
amygdaloides Anderss.
boothii Dorn
drummondiana Barr. ex Hook.
exigua Nutt.
lutea Nutt.
monticola Bebb

SANTALACEAE

Comandra
umbellata (L.) Nutt.
var. *pallida* (A. DC.) Jones

SAXIFRAGACEAE

Boykinia
heucheriformis (Rydb.) Rosend.

Conimitella
williamsii (D. C. Eat.) Rydb.

Heuchera
parvifolia Nutt. ex T. & G.

Lithophragma
parviflorum (Hook.) Nutt. ex T. & G.

Parnassia
palustris L.
var. *montanensis* (Fern. & Rydb.)
C. L. Hichc.

Saxifraga
rhomboidea Greene

Sullivantia
hapemanii (Coult. & Fish) Coult.
var. *hapemanii*

SCROPHULARIACEAE

Besseya
wyomingensis (A. Nels.) Rydb.

Castilleja
angustifolia (Nutt.) G. Don
chromosa A. Nels.
linariaefolia Benth.
miniata Dougl. ex Hook.
pulchella Rydb.
sessiliflora Pursh

Collinsia
parviflora Lindl.

Mimulus
guttatus DC.
ssp. *guttatus*
suksdorfii Gray

Pedicularis
cystopteridifolia Rydb.

Penstemon
aridus Rydb.
caryi Penn.
confertus Dougl.
var. *procerus* (Dougl. ex Grah.) Cov.
eriantherus Pursh
var. *eriantherus*
glaber Pursh
humilis Nutt. ex Gray
var. *humilis*
laricifolius H. & A.
nitidus Dougl. ex Benth.
radicosus A. Nels.

Verbascum
thapsus L.

Veronica
americana Schwein. ex Benth.
peregrina L.
var. *xalapensis* (H. B. K.)
St. John & Warren

SOLANACEAE

Physalis
heterophylla Nees
var. *heterophylla*

- *Solanum*
    - *dulcamara* L.
    - *triflorum* Nutt.

TAMARICACEAE
- *Tamarix*
    - *chinensis* Lour.

TYPHACEAE
- *Typha*
    - *angustifolia* L.
    - *latifolia* L.

ULMACEAE
- *Celtis*
    - *occidentalis* L.
- *Ulmus*
    - *pumila* L.

URTICACEAE
- *Parietaria*
    - *pensylvanica* Muhl. ex Willd.
- *Urtica*
    - *dioica* L.

VALERIANACEAE
- *Valeriana*
    - *dioica* L.
        - var. *sylvatica* (Richards.) Wats.
    - *edulis* Nutt. ex T. & G.
        - var. *edulis*

VERBENACEAE
- *Verbena*
    - *bracteata* Lag. & Rodr.
    - *hastata* L.

VIOLACEAE
- *Viola*
    - *adunca* Sm.
        - var. *adunca* Harrington
    - *canadensis* L.
        - var. *canadensis*
    - *nuttallii* Pursh
    - *vallicola* A. Nels.

VITACEAE
- *Vitis*
    - *riparia* Michx.

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PRESETTLEMENT VEGETATION OF PART OF NORTHWESTERN MOFFAT COUNTY, COLORADO, DESCRIBED FROM REMNANTS

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ABSTRACT.—A general botanical inventory of a part of northwestern Moffat County, Colorado, resulted in the location of "remnants" of the presettlement vegetation spectrum that are largely unaltered by grazing, logging, or other recent human-related land uses. The 69 samples taken from these remnants were classified into 22 plant associations. Composition, structure, environmental location, geographical range, and response to disturbance are discussed for each association, and a photograph of each is presented. Seven of the 22 associations are apparently restricted to the study area. Restricted associations occur in the more extreme environments of the study area, such as on calcareous substrata or very xeric sites. More mesic sites along ephemeral creeks, on north-facing slopes, or on sandstones support plant associations that have much wider ranges, many of them extending across the northern Great Basin.

The vegetation that occupied the landscape in the western United States prior to settlement has been effectively extirpated in some areas by conversion to cultivation or by urban development. In most of the remainder, other kinds of land use have resulted in alteration of the presettlement composition and structure. The most pervasive and most consequential of these other land uses are domestic livestock grazing and logging, though mining and recreation have had substantial effects in more localized areas. Also pervasive has been the replacement of native plant species by exotics. Additional effects have resulted from fire control, loss or modification of native herbivore populations, exotic diseases, air pollution, and acid precipitation. In some parts of the western United States, and in many parts of the eastern United States, the composition and structure of the presettlement vegetation can only be known now by reference to historical accounts, early photographs, and other secondary records. Vale (1982) reviewed methods of analyzing these sources. Nevertheless, in parts of the West it is still possible to locate remnants of the presettlement vegetation, which have essentially escaped alteration, though such remnants are exceedingly rare at lower elevations or on very productive sites and are disappearing as land uses continue or accelerate.

These remnants have been widely used in the forested parts of the western United States to develop "habitat type" classifications (Pfister 1982). Such classifications are irreplaceable records of the detailed composition and structure of the presettlement vegetation. Some of these remnants, occurring on federal lands, have been protected from further alteration or loss by designation as Research Natural Areas under regulations and policies of the U.S. Department of the Interior, Department of Agriculture, and other departments. Perpetuation of remnants in such designated Research Natural Areas means that they will be available in the future for more extensive study. Very few opportunities are available for the study of ecosystem function on unaltered sites. Without such studies it is difficult for land managers to know how to most efficiently manage land uses on similar lands for maximum benefit with minimum alteration. Such protected remnants also serve an important role in the long-term perpetuation of their component plants and animals.

The natural vegetation of some parts of Colorado is nearly unknown (Baker 1982a), particularly at lower elevations. An earlier report characterized some of the presettlement vegetation of the Piceance Basin occurring on Green River and Uinta formations (Baker 1983). This report extends that earlier report to include additional areas of Green River Formation (Fm.) and other geologic substrata occurring in a part of northwestern Moffat

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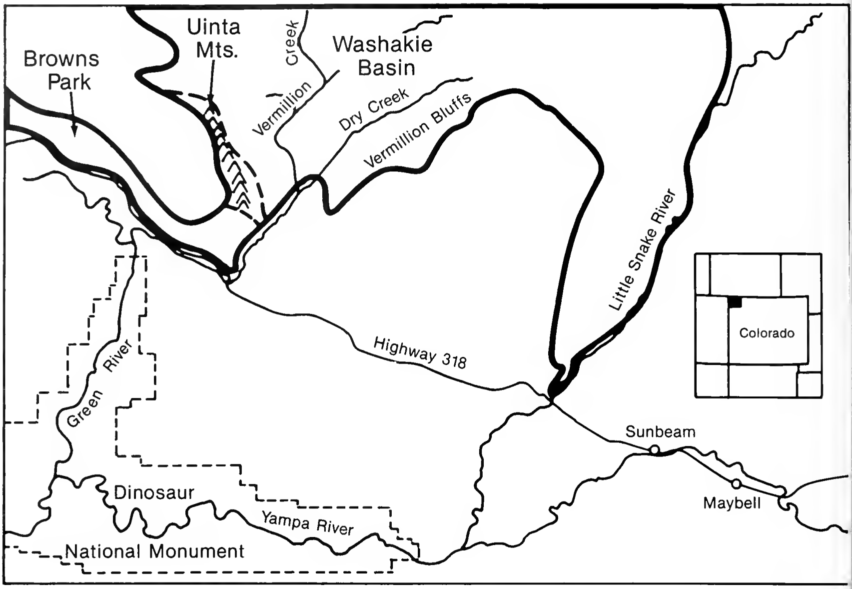

Fig. 1. Map of the study area.

County, Colorado (Fig. 1), again based on remnants located during a general botanical inventory (Peterson and Baker 1983) of this area.

STUDY AREA

The study area (Fig. 1) includes part of northwestern Moffat County north of Highway 318 and west of the Little Snake River. Excluded from study within this area are the Sand Wash Basin and the forested summits of Cold Spring Mountain, Middle Mountain, and Diamond Peak. The study area includes parts of Browns Park, the eastern Uinta Mountains, and the Washakie Basin. Concentrated study was made of the Limestone Ridge, Vermillion–Dry Creeks, and Vermillion Bluffs area. Elevations in the study area range from about 1830 to 2600 m.

The stratigraphy of exposed rocks in the study area is complex. The most comprehensive geologic map is Rowley et al. (1979). Additional mapping is available in Sears (1924), Nightingale (1930), and Bradley (1964). In the Uinta Mountains section of the study area, exposures of pre-Tertiary rocks predominate. These consist primarily of sandstones (Mesa Verde Group, Dakota, Entrada, Glen Canyon, Weber, Morgan, Lodore formations) and shales and siltstones (Mancos, Morrison, Chinle, Moenkopi formations), though Limestone Ridge is capped by Madison limestone and other minor beds in the above formations may contain limestone. In the Washakie Basin section of the study area, Eocene rocks of the Green River Formation and Wasatch Formation predominate (Bradley 1964), though along the base of the Uintas and throughout Browns Park the Browns Park Formation is common, and localized Quaternary alluvial and colluvial deposits may occur. The Green River Formation in this area consists of two members (Wilkins Peak, Laney), and two tongues (Tipton, Luman). The Wilkins Peak Member, consisting of a sequence of thin beds of marlstone, mudstone, and oil shale, is composed of a greater abundance of saline minerals and dolomite than any other beds in the Green River Formation (Bradley 1964). The Laney Member is muddy marlstone and brown to light ash gray shale. The Tipton

Tongue consists of sandstone beds and beds of greenish gray shale and gray mudstone. The Luman Tongue consists of shell marl, sandstone, and conglomerate. The Wasatch Formation occurs as the main body, consisting primarily of fluviatile sandy mudstone, and two tongues (Niland, Cathedral Bluffs). The Niland Tongue consists of mudstone, shale, and lenticular tuff, and the Cathedral Bluffs Tongue consists of pink and red-layered gray mudstone that forms badland slopes (Bradley 1964). The Miocene Browns Park Formation consists primarily of soft, well-bedded chalk-white sandstone (Nightingale 1930), though there are local beds of tuff, limestone, and volcanic materials (Rowley et al. 1979).

Climatic data are available from Craig, Colorado (Gale Research Co. 1980), about 50 km southeast of the study area, at about the same elevation as the lowest elevations in the study area. Mean annual precipitation there is 338 mm, distributed fairly evenly throughout the year. Mean January temperature is −7.7 C, with mean July temperature 19.4 C.

There have been no studies or general descriptions of vegetation in the study area. Though Lindauer et al. (1982) reviewed the literature on the broad area of northwestern Colorado and discussed some general vegetation types, their study was not concerned with presettlement conditions. In adjoining Utah, Woodbury et al. (1960) sampled vegetation in the Flaming Gorge area but did not present a classification, presented minimal understory data, and did not attempt to characterize presettlement conditions. Svihla (1932) described vegetation zones in the Uinta Mountains, recognizing a sagebrush zone from 1765 to 2745 m, a cedar-pinyon minor belt from 2130 to 2440 m, and several zones above these. Graham (1937), in his study of the Uinta Basin, revised Uinta Mountain zonation to include a mixed desert shrub zone from 1370 to 1675 m, a juniper-pinyon zone from 1675 to 2130 m, a submontane shrub zone from 2130 to 2440 m, and several zones above these. In the Uinta Mountain portion of the study area, Graham's zonation scheme requires modification. The mixed desert shrub zone occurs up to or occasionally above about 1825 m, the juniper-pinyon zone extends from 1825 to 2375 m, and above this elevation the submontane shrub zone extends to about 2560 m. In the adjoining Washakie Basin part of the study area, this zonation scheme does not accurately describe vegetation patterns. Most elevations in this area are between 1980 and 2285 m. In this elevational band, plant associations dominated by saltbushes and sagebrush occur in a mosaic. Juniper occurs only in a few areas on steep slopes or above 2130 m.

METHODS

Field Methods

Remnants of natural vegetation occur on sites that either have not been grazed by domestic livestock or have been grazed lightly, have not been logged, mined, cultivated, or subjected to other surface disturbances, and are free of obvious effects of fire control, acid rain, air pollution, or other postsettlement human-related disturbances. In an area such as the study area, where the predominant current land use is domestic livestock grazing, remnants are most often found in areas removed from water, or on steep slopes, or in areas that have escaped heavy use because of accidents of fencing or use patterns. Cattle and sheep eat primarily grass and forbs in addition to some of the more edible shrubs, so that effects of grazing are often most pronounced in the understory of most vegetation types in the study area. Decline in understory density can result in an increase in shrub or overstory density over time. Domestic livestock also alter vegetation by trampling, which results in breakage of shrub stems and changes in soil surface morphology. A soil surface layer dominated by cryptogams is well known to disappear under the effects of trampling by domestic livestock (Anderson et al. 1982a, 1982b). Methods of locating and identifying remnants, using these and other criteria, are described in detail in Baker (1982b, 1983) and Daubenmire (1970).

Located remnants were sampled quantitatively using a temporary 375 m^2 circular plot method. This method has been widely utilized in the western United States for habitat typing (e.g., Pfister et al. 1977). Within the plot, canopy coverage of all vascular plant species was estimated to the nearest 1% (below 15%) or 5% (above 15%). Species with less than .5% cover were recorded as having trace cover (abbreviated "tr" in the tables). Tree species within the plot were tallied by 2 in dbh size classes. Seedlings are considered to be those individuals less than 1 m tall and less than 1 in dbh; saplings are greater than 1 m tall and less than 1 in dbh. Diameter at breast height (dbh) was in actual practice measured below the major point of branching on *Juniperus* and *Pinus* stems, as these trees often lack a single stem at actual breast height.

Reported responses to domestic livestock grazing were derived by examining fenceline contrasts and by comparing located remnants with areas currently being grazed at various levels. These observations were compared with those reported in the scientific literature for similar vegetation.

Soils

Soil samples from the upper 15 cm of the profile were taken from near the center of the sampling plot, air-dried in the field, and removed to the laboratory for analysis. All samples were passed through a 2-mm sieve (Richards 1954) prior to analysis. Electrical conductivity (soluble salts) and pH values were determined according to methods described by Soltanpour and Workman (1981). An Orion Model 21 Digital pH meter and probe were used to obtain readings from each saturated soil paste. A Lab-Line Lectro Mho-Conductivity Meter (Model Mc-1, Mark IV) was used to obtain electrical conductivity values (millimhos/cm) of saturation extracts at 25 C.

Nomenclature

The plant associations named here follow the vegetation nomenclature detailed in Baker (1984). Plant species nomenclature follows Kartesz and Kartesz (1980). Questionable plant specimens were identified by Dr. Dieter Wilken, curator of the herbarium, Colorado State University. Certain taxonomic separations were found to be difficult to apply consistently during field sampling. *Gilia sinuata* may include some other annual *Gilia* species. *Agropyron smithii* may occasionally include *Agropyron dasystachyum*. *Opuntia polyacantha* may include other *Opuntia* species. The common low-growing *Atriplex* in the study area may in some populations consist of a mixture of specimens of both *Atriplex cuneata* and *Atriplex gardneri* (Wilken, personal communication), with some indication of possibly intermediate individuals. The complex is here called by the name *Atriplex gardneri*.

Natural Vegetation Concept

Natural vegetation is that vegetation that existed prior to the changes that have accompanied European settlement, essentially the presettlement vegetation. This concept is similar in many respects to the habitat type concept pioneered by Daubenmire (1952, 1970) and now widely used in the western United States (e.g., Pfister et al. 1977). The differences between this concept and Daubenmire's are discussed in detail in Baker (1984).

It is important to recognize that the remnants located represent, as well as is still possible within the study area, the composition and structure of the presettlement vegetation. Most of these remnants, however, now contain a minor component of exotic plant species that was not present in the association prior to settlement. The actual presettlement composition must be inferred to some degree, perhaps by subtracting these exotic species and increasing slightly the coverage of native species. In some instances an individual stand may lack species it contained prior to settlement, because of either natural population fluctuations or loss from postsettlement land uses that have left no other lasting evidence within the stand.

RESULTS AND DISCUSSION

Plant Associations

1. *Juniperus osteosperma/Agropyron spicatum*.—This association occurs on any aspect, and on several parent materials (Green River Fm.–Laney Member, Madison Limestone, Weber Sandstone, and others) from 1920 to 2250 m in elevation often on steep slopes, but also on flats. Soils, which are moderately well developed but may be very rocky, have an average pH of 7.79 and an electrical conductivity of .48 mmhos/cm (Table 1).

The association has a savanna appearance (Fig. 2), with the shrub layer generally nearly

TABLE 1. Percent cover and constancy of shrubs and herbs, plot locations, and physical parameters. Plant association numbers correspond to those in the text. 1 = *Juniperus osteosperma/Agropyron spicatum*, 2 = *Juniperus osteosperma–Pinus edulis/Artemisia nova/Agropyron spicatum*, 3 = *Juniperus osteosperma–Pinus edulis/Cercocarpus ledifolius* var. *intricatus*. Table entries under each plot are percent canopy cover. Tr = trace quantities (less than .5% cover). Table entries under Cov/Con are average percent canopy cover for all the plots in the association on the left of the slash and percent constancy to the right of the slash. 100% is abbreviated to 99. Soil EC is soil electrical conductivity; its measurement is discussed in the text.

Township	10 N	10 N	10 N	10 N		10 N	11 N		10 N	10 N	10 N	10 N	
Range	101W	101W	99W	100W		101W	101W		101W	101W	101W	100W	
Section	S23	S15	S9	S27		S34	S32		S15	S14	S25	S30	
Elevation (meters)	2060	2160	2170	2080		1890	2290		2190	2070	1890	1900	
Aspect	SW	E	NE	S		W	SE		W	NE	W	E	
Slope (degrees)	30	20	15	5		20	20		10	5	5	10	
Soil pH	7.95	7.85	7.70	7.65	Avg 7.79	7.75	7.95	Avg 7.85	8.15	7.90	7.65	8.00	Avg 7.93
Soil EC (mmhos/cm)	.37	.86	.33	.36	Avg .48	.34	.34	Avg .34	.27	.34	.40	.29	Avg .33
Plant association number	1					2			3				
Plot number	1	2	3	4	Cov/Con	1	2	Cov/Con	1	2	3	4	Cov/Con
SHRUBS													
Ephedra viridis	2	tr			.6/50				1	tr			tr/50
Artemisia tridentata ssp. *wyomingensis*		tr	tr		tr/50								
Atriplex confertifolia			tr		tr/25								
Opuntia polyacantha				tr	tr/25						tr		tr/25
Pediocactus simpsonii				tr	tr/25								
Artemisia nova						10	8	9.0/99			tr	2	.6/50
Cercocarpus montanus							tr	tr/50					
Symphoricarpos oreophilus							tr	tr/50					
Cercocarpus ledifolius var. *intricatus*									22	15	15	10	15.5/99
Chrysothamnus nauseosus									tr	tr	tr	tr	tr/99
Chrysothamnus viscidiflorus									tr				tr/25
Fendlerella utahensis									tr				tr/25
Purshia tridentata										tr			tr/25
GRAMINOIDS													
Agropyron spicatum	25	20	20	20	21.3/99	10	17	13.5/99				tr	tr/25
Poa sandbergii	2		1	1	1.0/99		3	1.5/50	tr	tr	tr	tr	tr/99
Poa fendleriana	2	3	7	1	3.3/99								
Oryzopsis hymenoides	tr	tr	tr		tr/75	tr	1	.8/99	tr	tr	tr		tr/75
Bromus tectorum	tr	2			.6/50	tr	2	1.3/99	tr			tr	tr/50
Sitanion hystrix		tr			tr/25		tr	tr/50					
Koeleria cristata			1		tr/25		2	1.0/50					
Poa canbyi			tr		tr/25								
Carex filifolia				tr	tr/25						1	2	.8/50
Carex pityophila							tr	tr/50	2				tr/25
FORBS													
Physaria acutifolia	tr	tr		tr	tr/75	1	1	1.0/99		tr		tr	tr/50
Cryptantha flavoculata	tr	tr	1	tr	.6/99		1	tr/50					
Erigeron sp.	tr				tr/25								
Descurainia richardsonii	tr	tr	1	tr	.6/99	1	tr	.8/99	tr	tr	1	tr	.6/99
Phlox hoodii	1		1	1	.8/75	1		tr/50		tr	1	tr	tr/75
Hedeoma drummondii	tr				tr/25								
Gilia sinuata	tr	tr			tr/50							tr	tr/25
Eriogonum ovalifolium	tr		tr	tr	tr/75								
Caulanthus crassicaulis		tr		tr	tr/50	tr	tr	tr/99				tr	tr/25
Conringia orientalis		tr			tr/25								
Agoseris glauca		tr			tr/25		tr	tr/50					
Arabis demissa		tr	tr	tr	tr/75	tr	tr	tr/99	tr	tr		tr	tr/75
Schoenocrambe linifolia		tr		tr	tr/50		tr	tr/50					
Balsamorhiza hookeri var. *hispidula*		tr	3	1	1.1/75		2	1.0/50					
Mertensia oblongifolia		tr	2		.6/50		1	tr/50					
Crepis occidentalis		tr	tr		tr/50								
Senecio integerrimus		tr			tr/25								
Haplopappus acaulis		tr	1	tr	tr/75	1	3	2.0/99	tr				tr/25
Cryptantha fendleri		tr		1	tr/50		tr	tr/50					
Lappula redowskii		tr		tr	tr/50								
Phlox longifolia			tr		tr/25								
Astragalus tenellus			2		tr/25								
Trifolium gymnocarpon			tr		tr/25								
Astragalus convallarius			1	tr	tr/50								
Arenaria fendleri			tr		tr/25								
Eriogonum umbellatum			1		tr/25		tr	tr/50					
Erigeron eatonii			tr		tr/25								
Penstemon fremontii			tr	tr	tr/50		tr	tr/50				tr	tr/25
Cryptantha sericea			tr		tr/25								
Castilleja chromosa			tr		tr/25								
Chaenactis douglasii			tr		tr/25								

Table 1 continued.

Township	10 N	10 N	10 N	10 N		10 N	11 N		10 N	10 N	10 N	10 N	
Range	101W	101W	99W	100W		101W	101W		101W	101W	101W	100W	
Section	S23	S15	S9	S27		S34	S32		S15	S14	S25	S30	
Elevation (meters)	2060	2160	2170	2080		1890	2290		2190	2070	1890	1900	
Aspect	SW	E	NE	S		W	SE		W	NE	W	E	
Slope (degrees)	30	20	15	5		20	20		10	5	5	10	
Soil pH	7.95	7.85	7.70	7.65	Avg 7.79	7.75	7.95	Avg 7.85	8.15	7.90	7.65	8.00	Avg 7.93
Soil EC (mmhos/cm)	.37	.86	.33	.36	Avg .48	.34	.34	Avg .34	.27	.34	.40	.29	Avg .33
Plant association number	1					2			3				
Plot number	1	2	3	4	Cov/Con	1	2	Cov/Con	1	2	3	4	Cov/Con
Astragalus detritalis			tr		tr/25								
Eriogonum sp				tr	tr/25	tr		tr/50				tr	tr/25
Ipomopsis congesta				tr	tr/25								
Lupinus brevicaulis				tr	tr/25								
Haplopappus armerioides				tr	tr/25								
Atriplex sp				tr	tr/25								
Hymenoxys acaulis						tr		tr/50					
Trifolium longipes ssp *pygmaeum*						2		1.0/50					
Eriogonum tumulosum						tr		tr/50			1		tr/25
Lesquerella alpina						tr		tr/50					
Penstemon yampaensis						tr		tr/50					
Machaeranthera grindeloides						tr		tr/50					
Cymopterus sp							tr	tr/50					
Petradoria pumila							1	tr/50					
Calochortus nuttallii							tr	tr/50					
Erigeron flagellaris							tr	tr/50					
Petrophytum caespitosum									3				.8/25
Cryptantha sp.									1				tr/25
Erigeron nematophyllus										tr	tr		tr/50
Astragalus spatulatus											2	1	.8/50
Cryptantha flava										tr			tr/25
Erysimum asperum											tr	tr	tr/50
Cryptantha caespitosa											tr		tr/25
Arabis pulchra											tr		tr/25
Oxytropis sericea											tr	tr	tr/50
Stanleya pinnata												tr	tr/25
Vicia americana												tr	tr/25
Nemophila breviflora												tr	tr/25
Cymopterus fendleri												tr	tr/25
Lesquerella ludoviciana												tr	tr/25
Arenaria fendleri												tr	tr/25
Lappula redowskii												tr	tr/25

absent. *Agropyron spicatum* forms a dense sward in stands that are in good condition (Table 1). Stands usually consist of a moderately dense (320—510 trees/ha) overstory of pure *Juniperus osteosperma* (Table 2). *Pinus edulis*, when present, consists primarily of seedlings, but an occasional larger stem may occur. Many stands consist of only large stems (9–35 in dbh), with very few smaller stems or seedlings and saplings.

Domestic livestock grazing results in decreases in *Agropyron spicatum* and *Poa fendleriana* and increases in shrubs, herbs, and the exotic grass *Bromus tectorum*. Several stands were observed with *Poa sandbergii* dominant and only trace quantities of *Agropyron spicatum* remaining. Another grazing-induced successional stage has *Artemisia tridentata* ssp. *wyomingensis* dominant in the understory, with only small amounts of grass present. On very flat sites *Haplopappus acaulis* may become very abundant.

This association is limited in Colorado to northern and western Moffat County. It has been observed in Utah in Dinosaur National Monument (Welsh 1957) and in western Wyoming (DeSpain 1973, Wight and Fisser 1968). In the study area it is the most common pinyon-juniper woodland, though a large percentage of stands have been altered by domestic grazing or by woodcutting.

2. *Juniperus osteosperma–Pinus edulis/Artemisia nova/Agropyron spicatum.*—This association occurs on a variety of aspects on several parent materials (e.g., Browns Park Fm., Morgan Fm.) on steep slopes (15–25 degrees) from 1830 to 2375 m in elevation. Soils are similar to those of the *Juniperus osteosperma/Agropyron spicatum* association, having an average pH of 7.85 and an electrical conductivity of .34 mmhos/cm (Table 1).

It consists of a moderately dense (400–500 trees/ha) stand of *Juniperus osteosperma* and *Pinus edulis* (Table 2, Fig. 2). *Juniperus* stems

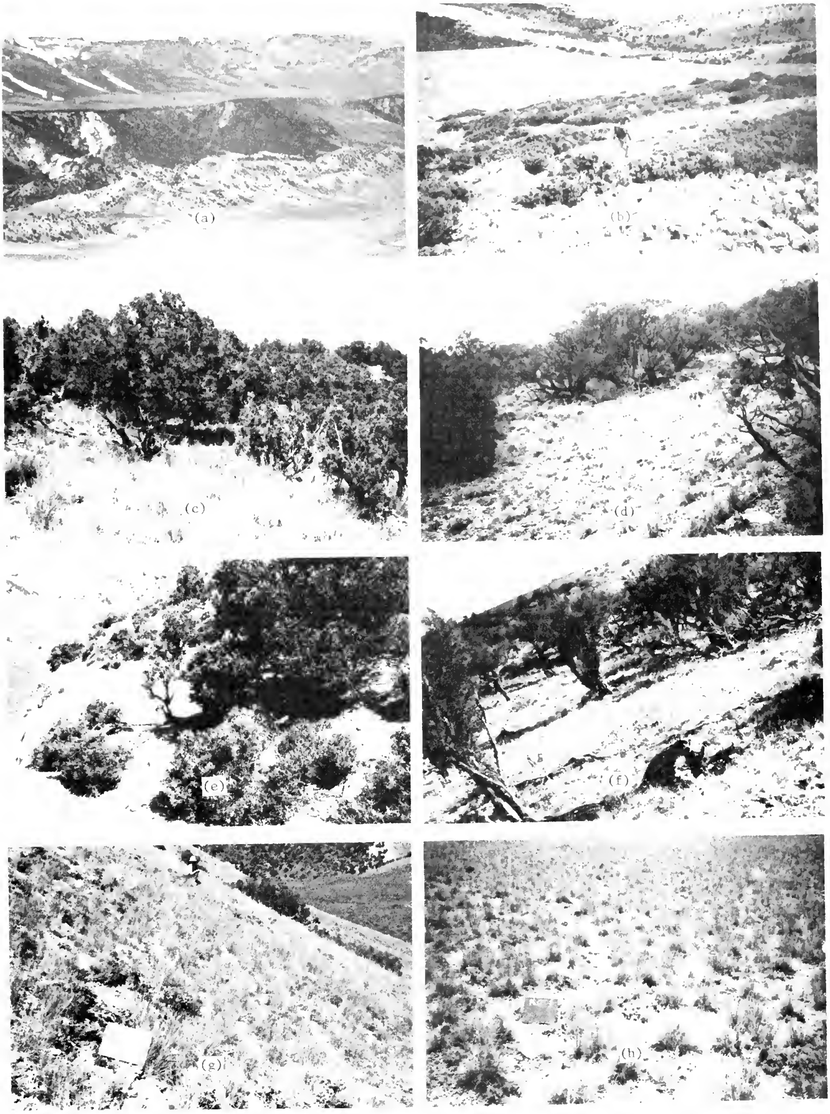

Fig. 2. (a) Limestone Ridge and part of the study area, (b) *Juniperus osteosperma* "krummholz," (c) *Juniperus osteosperma/Agropyron spicatum*, (d) *Juniperus osteosperma–Pinus edulis/Artemisia nova/Agropyron spicatum*, (e) *Juniperus osteosperma–Pinus edulis/Cercocarpus ledifolius* var. *intricatus*, (f) *Cercocarpus ledifolius/Artemisia tridentata* ssp. *wyomingensis–Symphoricarpos oreophilus/Agropyron spicatum*, (g) *Artemisia nova/Agropyron spicatum*, (h) *Artemisia nova/Stipa comata*.

TABLE 2. Tree diameter size distribution. Tree diameters were measured by 2″ size class at breast height (dbh). Seedlings are less than 1″ dbh and less than 1 m tall. Saplings are less than 1″ dbh and greater than 1 m tall. Size classes are listed by the midpoint of the size class. Entries are the number of stems in each size class within the 375 m² plot.

Plot No.	Species	Seedlings	Saplings	2	4	6	8	10	12	14	16	18	20	22	24	26	28	30	31+
Juniperus osteosperma/Agropyron spicatum																			
1	*Juniperus osteosperma*	2	1	1	1	1	4	1	1	1	1								
	Pinus edulis	5	1					1											
2	*Juniperus osteosperma*	3						3		4	2		1		1			2	
	Pinus edulis	8						1	1										
3	*Juniperus osteosperma*	1		3	3			1		1	1	1	2	1	1	1		1	3 (34,35,35)
4	*Juniperus osteosperma*							1	1	1	2		3	2	1	1			
Juniperus osteosperma–Pinus edulis/Artemisia nova/Agropyron spicatum																			
1	*Juniperus osteosperma*	8		2	2	1		1		1		1	1	1	1	1			
	Pinus edulis	10	3	4		1													
2	*Juniperus osteosperma*	4	1	1	1	1	1	2		1			2	1			1		1 (35)
	Pinus edulis	2	2	4			1												
Juniperus osteosperma–Pinus edulis/Cercocarpus ledifolius var. *intricatus*																			
1	*Juniperus osteosperma*	3	1	3	2		2		1										
	Pinus edulis	4	5	4	3	4	1	1											
2	*Juniperus osteosperma*			1			1	1	1		1								
	Pinus edulis		1	1		4	2	4		1									
3	*Juniperus osteosperma*	2	3					1	1		1				1		1		1 (35)
	Pinus edulis					1	2	3	1										
4	*Juniperus osteosperma*			1	1		1	1			2	1	1						
	Pinus edulis	2	1		2	1													
Cercocarpus ledifolius/Artemisia tridentata ssp. *wyomingensis–Symphoricarpos oreophilus/Agropyron spicatum*																			
1	*Cercocarpus ledifolius*	5	1	1		1	1	1		1	1						1		1 (34)
	Juniperus scopulorum		2																
	Pinus edulis	1																	
2	*Cercocarpus ledifolius*	16	1		1	1	2	2		2	2							1	
	Juniperus scopulorum			1															
	Pinus edulis		2																
3	*Cercocarpus ledifolius*	14	7	8	7	5													
	Juniperus scopulorum	1	2							1									
	Pinus edulis	1																	

may be more abundant and often larger than *Pinus* stems. Both species typically have abundant small stems. The shrub layer is sparse (Table 1), with 8%–10% cover of *Artemisia nova*, which may be nearly hidden by dense *Agropyron spicatum* (Fig. 2).

Domestic livestock grazing results in an increase in *Poa sandbergii*, *Haplopappus acaulis*, *Balsamorhiza hookeri* var. *hispidula*, and the exotic *Bromus tectorum*. *Agropyron spicatum* may decrease and is often nearly absent on heavily grazed sites. *Artemisia nova* does not appear to increase appreciably.

This association was first located in Colorado during this study. It occurs within the study area in only two locations near Limestone Ridge. Data collected in Dinosaur National Monument suggest it may also occur there (S. Wathen, personal communication). It is probably limited in Colorado to northwestern Moffat County but has been reported from southeastern Idaho about 600 km northwest of the study area (Johnson and Pfister 1982), and probably occurs in the intervening areas in southwestern Wyoming and northeastern Utah.

3. *Juniperus osteosperma–Pinus edulis/Cercocarpus ledifolius* var. *intricatus*.—This association is found exclusively on sandstone outcrops of several formations (Weber Sandstone, Glen Canyon Sandstone, Entrada Sandstone, and Mesa Verde Group Sandstone) in the study area, typically occurring on rocky ridge tops or abrupt sandstone outcrops where bedrock is extensively exposed and somewhat cracked and jointed. Aspects are variable, slopes range from 0° to 30°, and the association may occur from 1825 to 2300 m in elevation. Soils are poorly developed, but where there is soil it is similar in average pH (7.93) and electrical conductivity (.33 mmhos/cm) to that of the other pinyon-juniper associations in the study area (Table 1).

The association consists of a moderately dense (290–560 trees/ha) stand of *Juniperus osteosperma* and *Pinus edulis* (Table 2, Fig. 2). Most trees are less than 20 in dbh. *Juniperus* often has more and larger stems than *Pi-*

nus. No clear pattern in regeneration potential is apparent, with some stands lacking seedlings and saplings of one or both trees. The trees and the shrub layer, characterized by 10%–25% cover of *Cercocarpus ledifolius* var. *intricatus*, commonly grow out of cracks and joints in the bedrock. The herb layer consists of about 30 species, which have low constancy and cover (Table 1). Total herb cover rarely exceeds 5%.

It is unlikely that the association receives much use for domestic grazing, which would have little effect in any event because of lack of forage. The exotic *Bromus tectorum* now exists in some stands.

In Colorado the association has been observed in western Moffat County in the study area and in Dinosaur National Monument, as well as in adjoining northwestern Rio Blanco County. It has been reported from Wayne County, Utah, about 250 km southwest of the study area (Dixon 1935) and very likely occurs in other parts of eastern Utah. In the study area the association is limited to the upturned sandstone outcrops east of Limestone Ridge and Irish Canyon.

4. *Cercocarpus ledifolius/Artemisia tridentata* ssp. *wyomingensis-Symphoricarpos oreophilus/Agropyron spicatum*. —This association was found in the study area over a narrow elevational range, above the upper limit of pinyon-juniper woodlands from 2440 to 2560 m. It occurs exclusively on Madison Limestone on steep (25°–35°) slopes on a variety of aspects. Some stands occur as long bands on a slope following a particular layer in the Madison Limestone. Soils are not very different from those of adjoining pinyon-juniper woodlands in terms of average pH (7.36) and electrical conductivity (.43 mmhos/cm) (Table 3).

The association consists of a sparse to moderately dense (185–530 trees/ha) stand of *Cercocarpus ledifolius* (Table 2). Although *Cercocarpus ledifolius* may only reach shrub stature in some areas, it definitely forms woodlands in the study area. Stems as large as 34 in dbh have been observed. *Juniperus scopulorum* and *Pinus edulis* are often present as seedlings or saplings and occasionally as trees. There are generally numerous *Cercocarpus* seedlings and saplings (Table 2). The shrub layer has 10%–25% total cover, with *Artemisia* and *Symphoricarpos* co-dominant. *Agropyron spicatum* dominates the herb layer with 5%–15% cover (Table 3).

Domestic livestock grazing may reduce the amount of *Agropyron spicatum*, resulting in increases in the amount of *Artemisia tridentata* and herbs.

The association is currently not known outside the study area, where it has been located

TABLE 3. Percent cover and constancy of shrubs and herbs, plot locations, and physical parameters. Plant association number corresponds to that in the text. 4 = *Cercocarpus ledifolius/Artemisia tridentata* ssp. *wyomingensis–Symphoricarpos oreophilus/Agropyron spicatum*. Table entries under each plot are percent canopy cover. Tr = trace quantities (less than .5% cover). Table entries under Cov/Con are average percent canopy cover left of the slash, and percent constancy right of the slash. 100 is abbreviated to 99. Soil electrical conductivity (soil EC) is discussed in the text.

Township	10 N	10 N	10 N	
Range	101W	101W	101W	
Section	S9	S16	S16	
Elevation (meters)	2470	2460	2560	
Aspect	NE	E	SW	
Soil pH	7.30	7.15	7.65	Avg = 7.36
Soil EC (mmhos/cm)	.37	.45	.48	Avg = .43
Plant association number	4			
Plot number	1	2	3	Cov/Con
SHRUBS				
Artemisia tridentata ssp. *wyomingensis*	6	15	15	12.0/99
Symphoricarpos oreophilus	4	5	7	5.3/99
Artemisia nova	tr			tr/33
Cercocarpus montanus	1		tr	tr/67
Ribes cereum	1	tr	2	1.2/99
Amelanchier utahensis		tr		tr/33
Fendlerella utahensis		tr		tr/33

Table 3 continued.

Township	10 N	10 N	10 N	
Range	101W	101W	101W	
Section	S9	S16	S16	
Elevation (meters)	2470	2460	2560	
Aspect	NE	E	SW	
Soil pH	7.30	7.15	7.65	Avg=7.36
Soil EC (mmhos/cm)	.37	.45	.48	Avg= .43
Plant association number	4			
Plot number	1	2	3	Cov/Con
Chrysothamnus viscidiflorus			2	.7/33
Pediocactus simpsonii		tr		tr/33
GRAMINOIDS				
Agropyron spicatum	6	10	10	8.7/99
Poa fendleriana	3	2		1.7/67
Oryzopsis hymenoides		2	tr	.8/67
Bromus tectorum		tr		tr/33
Poa sandbergii			1	tr/33
Agropyron smithii			tr	tr/33
Sitanion hystrix			tr	tr/33
Carex pityophila		tr		tr/33
FORBS				
Claytonia lanceolata	5	tr		1.8/67
Balsamorhiza hookeri var. *hispidula*	3	2	2	2.3/99
Mertensia oblongifolia	4	2	2	2.7/99
Senecio integerrimus	4	2	1	2.3/99
Petradoria pumila	1	tr		tr/67
Collinsia parviflora	3	3	tr	2.1/99
Erigeron eatonii	tr			tr/33
Heuchera parvifolia	tr		tr	tr/67
Lithofragma glabrum	1	tr		tr/67
Lomatium triternatum	1	tr		tr/67
Androstephium breviflorum	tr	tr		tr/67
Antennaria dimorpha	tr			tr/33
Sedum stenopetalum	tr	tr		tr/67
Erysimum asperum	tr	tr		tr/67
Linum lewisii	tr			tr/33
Eriogonum sp.	tr	tr	tr	tr/99
Eriogonum umbellatum	tr	tr	tr	tr/99
Penstemon humilus	tr			tr/33
Agoseris glauca	tr	tr	1	.7/99
Lomatium orientale	tr			tr/33
Selaginella densa	tr			tr/33
Phlox hoodii	tr			tr/33
Castilleja chromosa	tr			tr/33
Petrophytum caespitosum	tr			tr/33
Arabis sp.	tr	tr		tr/67
Haplopappus armerioides		4		1.3/33
Lithospermum ruderale		tr		tr/33
Schoenocrambe linifolia		tr		tr/33
Zigadenus paniculatus		tr		tr/33
Delphinium nuttallianum		tr		tr/33
Erigeron nematophyllus		tr		tr/33
Comandra umbellata		1		tr/33
Descurainia richardsonii			tr	tr/3
Cryptantha flavoculata			2	.7/3
Arabis lignifera			tr	tr/3
Hymenopappus filifolius			tr	tr/3
Stellaria jamesiana			tr	tr/3
Penstemon moffattii			tr	tr/3

only on the upper slopes of Limestone Ridge. *Cercocarpus ledifolius* stands occur across the northern Great Basin to southeastern Oregon. Many of these have been classified as belonging to a *Cercocarpus ledifolius/Agropyron spicatum* association.

Cercocarpus ledifolius was observed to occur mixed with *Pinus ponderosa* in the Douglas Mountain area, south of the study area. A single stand was located (T11N R101W S19 NE4) that has an overstory of *Cercocarpus ledifolius* with an understory of *Cercocarpus montanus*. Scattered individuals of *Cercocarpus ledifolius* var. *intricatus* also occur in the stand. Because this was the only stand of this sort observed, and no reference to similar vegetation could be found in the literature, it was not described as a separate association.

5. *Artemisia nova/Agropyron spicatum*. — This association occurs exclusively on relatively calcareous parent materials (Browns Park Fm., Madison Limestone). It occupies a wide elevational range from 1700 to 625 m, occurring primarily on northerly facing slopes that are often steep (up to 35°). It occurs at lower elevations on mesa sides and the sides of draws, and at higher elevations it may occur in a broad band above the pinyon-juniper zone. Soils, in spite of developing on a calcareous parent material, have an average pH (7.94) and electrical conductivity (.38 mmhos/cm) not much different from those in pinyon-juniper woodlands on noncalcareous substrata (Table 4).

The association consists of a low shrub layer of sparse (8%–20% cover) *Artemisia nova* (Table 4). At lower elevations (below about 1900 m) *Atriplex confertifolia* may commonly occur and occasionally be abundant. The herb layer, with 15%–30% cover of *Agropyron spicatum*, often overtops the *Artemisia nova*, giving the association a grassland appearance (Fig. 2).

In many stands with abundant domestic livestock grazing signs *Koeleria cristata*, or occasionally *Poa sandbergii*, is much more

Table 4. Percent cover and constancy of shrubs and herbs, plot locations, and physical parameters. Plant association numbers correspond to those in the text. 5 = *Artemisia nova/Agropyron spicatum*, 6 = *Artemisia nova/Stipa comata*. Table entries under each plot are percent canopy cover. Tr = trace quantities (less than .5% cover). Table entries under Cov/Con are average percent canopy on the left of the slash and percent constancy to the right of the slash. 100 is abbreviated to 99. Soil EC is soil electrical conductivity; its measurement is discussed in the text.

Township	9 N	10 N	9 N	10 N		10 N	9 N	11 N	9 N	
Range	102W	101W	101W	101W		101W	101W	101W	101W	
Section	S12	S14	S5	S9		S34	S2	S28	S3	
Elevation (meters)	1730	2070	1860	2340		1915	1900	2100	1910	
Aspect	N	NE	N	NE		S	S	—	S	
Slope (degrees)	35	5	30	10		2	3	0	2	
Soil pH	8.10	7.85	8.05	7.75	Avg=7.94	8.00	7.90	7.75	7.75	Avg=7.85
Soil EC (mmhos/cm)	.38	.39	.34	.42	Avg= .38	.42	.37	.73	.36	Avg= .47
Plant association number	5					6				
Plot number	1	2	3	4	Cov/Con	1	2	3	4	Cov/Con
Shrubs										
Artemisia nova	8	17	17	20	15.5/99	12	10	8	10	10.0/99
Atriplex confertifolia	1		tr		tr/50					
Ceratoides lanata	tr		tr	tr	tr/75	tr			1	tr/50
Gutierrezia sarothrae		tr			tr/25					
Pediocactus simpsonii	tr	tr		tr	tr/75			tr		tr/25
Artemisia tridentata ssp. *wyomingensis*						tr	tr	tr		tr/75
Tetradymia spinosa							tr			tr/25
Opuntia polyacantha								tr	tr	tr/50
Chrysothamnus viscidiflorus								tr	tr	tr/50
Graminoids										
Agropyron spicatum	25	20	18	20	20.8/99					
Poa sandbergii	5	3	3	2	3.3/99		tr	2	3	1.4/75
Vulpia octoflora	tr				tr/25					
Oryzopsis hymenoides	tr		tr	tr	tr/75	tr	tr	1	tr	.6/99
Koeleria cristata		3	1	4	2.0/75					
Agropyron smithii				tr	tr/25			tr	1	tr/50

Table 4 Continued.

Township	9 N	10 N	9 N	10 N		10 N	9 N	11 N	9 N	
Range	102W	101W	101W	101W		101W	101W	101W	101W	
Section	S12	S14	S5	S9		S34	S2	S28	S3	
Elevation (meters)	1730	2070	1860	2340		1915	1900	2100	1910	
Aspect	N	NE	N	NE		S	S	—	S	
Slope (degrees)	35	5	30	10		2	3	0	2	
Soil pH	8.10	7.85	8.05	7.75	Avg=7.94	8.00	7.90	7.75	7.75	Avg=7.85
Soil EC (mmhos/cm)	.38	.39	.34	.42	Avg= .38	.42	.37	.73	.36	Avg= .47
Plant association number	5					6				
Plot number	1	2	3	4	Cov/Con	1	2	3	4	Cov/Con
Stipa comata						30	25	20	25	25.0/99
Bromus tectorum						1	tr	tr	tr	.6/99
Sitanion hystrix						tr		tr	1	tr/75
FORBS										
Phlox hoodii	4	tr	2	3	2.4/99	tr	tr	2	2	1.3/99
Arenaria hookeri	1				tr/25			tr		tr/25
Astragalus spatulatus	tr				tr/25					
Arenaria fendleri	tr				tr/25					
Erigeron pumilus	tr	tr	tr	tr	tr/99					
Allium textile	tr				tr/25					
Haplopappus acaulis	tr		1	1	.6/75					
Townsendia incana	tr				tr/25			tr		tr/25
Cymopterus fendleri	tr				tr/25					
Zigadenus paniculatus	tr		tr		tr/50					
Crepis occidentalis	tr				tr/25					
Arabis pulchra	tr				tr/25					
Castilleja chromosa	tr			1	tr/50					
Eriogonum tumulosum	tr				tr/25					
Astragalus missouriensis	tr				tr/25					
Erysimum asperum	tr		tr		tr/50		1			tr/25
Physaria acutifolia	tr	tr	tr		tr/75					
Penstemon yampaensis		1			tr/25		tr	1	tr	tr/75
Astragalus chamaeleuce		tr	tr		tr/50		tr			tr/25
Cryptantha flava				tr	tr/25					
Hymenoxys acaulis		tr			tr/25					
Linum lewisii		tr		tr	tr/50					
Penstemon osterhoutii		tr	tr		tr/50					
Caulanthus crassicaulis		tr			tr/25		tr			tr/25
Agoseris heterophylla			tr		tr/25					
Antennaria dimorpha			tr		tr/25					
Lesquerella alpina			tr	1	tr/50					
Schoenocrambe linifolia			tr		tr/25			tr		tr/25
Crepis modocensis			tr		tr/25					
Sedum stenopetalum				tr	tr/25					
Arabis demissa				tr	tr/25					
Eriogonum sp.				tr	tr/25			tr		tr/25
Townsendia incana				tr	tr/25					
Petradoria pumila				tr	tr/25					
Androstephium breviflorum				tr	tr/25					
Descurainia richardsonii						1	2	tr	tr	1.0/99
Lappula redowskii						tr	tr	tr	tr	tr/99
Sphaeralcea coccinea						1	1	1	tr	.9/99
Allium textile						tr	tr	tr		tr/75
Gilia sinuata						tr				tr/25
Delphinium nuttallianum						tr	tr			tr/50
Ipomopsis pumila						tr				tr/25
Eriogonum ovalifolium								1		tr/25
Penstemon fremontii								tr	tr	tr/50
Lesquerella ludoviciana								tr		tr/25
Orobanche fasciculata								tr	tr	tr/50
Cymopterus purpureus									tr	tr/25

abundant than *Agropyron spicatum*. Other species that tend to increase under livestock grazing include *Vulpia octoflora*, *Haplopappus acaulis*, and many other herbs. Moderately grazed sites with lower grass cover tend to have more herbs.

In Colorado the association has been observed only in western Moffat County (the study area), where it occurs from Browns Park north to near the Wyoming border. The association occurs across the northern Great Basin from Wyoming (Thatcher 1959, Tweit and Houston 1980) to northern Nevada (Zamora and Tueller 1973), southern Idaho (Hironaka 1978, Johnson and Pfister 1982, Passey et al. 1982, Sharp and Sanders 1978), and California (Barbour and Major 1977).

6. *Artemisia nova/Stipa comata*. —This association occurs from 1890 to 2165 m in elevation on nearly flat surfaces primarily on the Browns Park Fm. It may also occur on other parent materials on benches, mesa tops, and flat plains. Soils are similar to those of the *Artemisia nova/Agropyron spicatum* association in terms of average pH (7.85) and electrical conductivity (.47 mmhos/cm) (Table 4).

The association consists of a sparse stand of *Artemisia nova* (Table 4) scattered through a dense grass matrix of *Stipa comata* (Fig. 2).

Domestic livestock grazing decreases *Stipa comata* and results in increases in *Poa sandbergii*, *Bromus tectorum*, and forbs. Most stands now have *Poa sandbergii* dominant. though others have dense *Artemisia nova* with very little grass present, or no grass at all.

The association has been observed in Colorado only in western Moffat County, where it has been located only in the vicinity of Limestone Ridge, and in North Park in Jackson County some 200 km east of the study area. It is known to occur across the northern Great Basin to Nevada (Blackburn et al. 1969 a,b,c, Zamora and Tueller 1973) and California (Barbour and Major 1977).

7. *Artemisia tridentata* ssp. *tridentata/Elymus cinereus*.—This association occurs only on relatively flat stream floodplains with or without permanent surface water. Elevations range from about 1980 to 2200 m, though the association has been observed at lower elevations outside the study area. The substrate is Quaternary alluvium. Soils are clayey, with an average pH of 7.75 and electrical conductivity of .44 mmhos/cm (Table 5).

The association (Fig. 3, Table 5) consists of a tall stand of *Artemisia tridentata* ssp. *tridentata*, with 15%–25% cover. *Elymus cinereus*, with 20%–40% cover, dominates the herb layer. *Agropyron smithii*, with 2%–5% cover, is usually present.

The association is prone to invasion by exotic species. Those commonly present now include *Poa pratensis*, *Bromus tectorum*, *Thlaspi arvense*, *Malcomia africana*, and *Melilotus officinalis*. Domestic livestock grazing decreases *Elymus cinereus* and results in increases in the density of *Artemisia tridentata* and these exotic herbs. The environment occupied by the association may be modified from a relatively wide and shallow floodplain to a deep, steep-sided gully if land uses in the stream catchment area result in changes in the timing and intensity of runoff.

The association occurs in scattered locations throughout the study area. It is known to occur in scattered locations throughout Moffat and Rio Blanco counties (Baker 1982b) in Colorado and occurs across the northern Great Basin in Utah (Pammel 1903), northern Nevada (Blackburn et al. 1971, Young et al. 1975), southern Idaho (Hironaka 1978, Johnson and Pfister 1982), to California (Barbour and Major 1977), Oregon, and Washington (Hironaka 1978).

8. *Artemisia tridentata* ssp. *vaseyana/Agropyron spicatum*. —This association occurs only above about 2125 m in elevation in the study area, where it occupies upper slopes and ridge tops, occurring on the Laney Member of the Green River Fm. on flat to moderately steep slopes.

Though many stands of this association were observed in the study area, only one stand was located that was sufficiently free of grazing effects to be usable for sampling. For this reason, this description must be considered preliminary, but because the association is well known and well described in the literature from other parts of its range, it was felt that inclusion of even minimal data from the study area would be beneficial. The association (Table 5, Fig. 3) consists of about 15% cover of *Artemisia tridentata* ssp. *vaseyana*, with minor amounts of *Ceratoides lanata* and *Opuntia polyacantha* present. *Agropyron*

TABLE 5. Percent cover and constancy of shrubs and herbs, plot locations, and physical parameters. Plant association numbers correspond to those in the text. 7 = *Artemisia tridentata* ssp. *tridentata*/*Elymus cinereus*, 8 = *Artemisia tridentata* ssp. *vaseyana*/*Agropyron spicatum*, 9 = *Artemisia tridentata* ssp. *wyomingensis*/*Agropyron smithii*, 10 = *Artemisia tridentata* ssp. *wyomingensis*/*Agropyron spicatum*, 11 = *Artemisia tridentata* ssp. *wyomingensis*–*Atriplex confertifolia*–*Grayia spinosa**/*Stipa comata*. Table entries under each plot are percent canopy cover. Tr = trace quantities (less than .5% cover). Table entries under Cov/Con are average percent canopy cover for all the plots in the association on the left of the slash and percent constancy to the right of the slash. 100 is abbreviated to 99. Soil electrical conductivity (soil EC) is discussed in the text.

Township	12 N	11 N		10 N	10 N	10 N		10 N	10 N	10 N		9 N	9 N	9 N	
Range	98W	97W		97W	101W	101W		99W	100W	100W		101W	101W	101W	
Section	S34	S3		S3	S12	S2		S9	S27	S35		S12	S18	S17	
Elevation (meters)	2100	2030		2220	1885	2060		2165	2130	2100		1750	1790	1790	
Aspect	NE	N		N	NE	W		NE	SE	SE		NE	SW	SW	
Slope (degrees)	2	1		15	3	4		5	5	2		3	2	3	
Soil pH	7 70	7.80	Avg 7.75	7.95	8 05	7.85	Avg 7.95	7.80	7 80	7.65	Avg 7 75	8 15	8 20	7.70	Avg = 8.02
Soil EC (mmhos/cm)	45	42	Avg 44	43	19	.17	Avg 18	40	31	30	Avg 34	33	.37	40	Avg .37
Plant association number	7			8	9			10				11			
Plot number	1	2	Cov/Con	1	1	2	Cov/Con	1	2	3	Cov/Con	1	2	3	Cov/Con
SHRUBS															
Artemisia tridentata ssp. *tridentata*	15	25	20 0/99												
Chrysothamnus nauseosus	5	1	3.0/99									tr			tr/33
Sarcobatus vermiculatus	tr		tr/50												
Chrysothamnus viscidiflorus	4	tr	2 3/99		tr		tr/50								
Opuntia polyacantha		tr	tr/50	tr					tr	1	tr/67	tr	tr		tr/67
Artemisia tridentata ssp. *vaseyana*				15											
Ceratoides lanata				tr	tr	1	8/99						tr		tr/33
Artemisia tridentata ssp *wyomingensis*					8	14	11 0/99	10	17	20	15.7/99	20	10	14	14.7/99
Tetradymia spinosa					2	tr	1 3/99								
Atriplex confertifolia					2	tr	1 3/99	2			7/99	4	4	3	3.7/99
Artemisia spinescens					tr		tr/50								
Atriplex gardneri					tr		tr/50								
Grayia spinosa												3	tr	3	2.3/99
GRAMINOIDS															
Elymus cinereus	40	20	30 0/99												
Poa pratensis	tr	1	8/99												
Agropyron smithii	2	5	3.5/99	tr	20	15	17.5/99	3		tr	1.2/67				
Bromus tectorum		tr	tr/50									6	tr	1	2.5/99
Sitanion hystrix		tr	tr/50		tr		tr/50		tr		tr/33	1	tr	tr	.7/99
Oryzopsis hymenoides		tr	tr/50	tr		tr	tr/50		1	tr	tr/67	tr		tr	tr/67
Agropyron spicatum				20				15	20	25	20 0/99				
Poa sandbergii				3	1	2	1.5/99	3	4	4	3.7/99	2	tr	1	1.2/99
Koeleria cristata				tr				2			.7/33				
Stipa comata						tr	tr/50					12	25	25	20.7/99
Poa fendleriana										tr	tr/33	tr			tr/33
Vulpia octoflora												4	tr	5	3.2/99
FOBBS															
Thlaspi arvense	3	tr	1.8/99												
Cirsium vulgare	tr		tr/50												
Cryptantha flavoculata	tr		tr/50					tr	tr		tr/67				
Mertensia oblongifolia	3	tr	1.8/99												
Schoenocrambe linifolia	1		tr/50						tr		tr/33				
Descurainia sophia	tr	1	8/99												
Taraxacum officinale	tr		tr/50												
Atriplex sp	tr	tr	tr/99												
Malcomia africana	tr	tr	tr/99												
Melilotus officinalis	tr		tr/50												
Grindelia sp	3		1 5/50												
Penstemon fremontii	tr		tr/50	tr		tr	tr/50								
Ipomopsis congesta	tr		tr/50											tr	tr/33
Vicia americana		tr	tr/50												
Stanleya pinnata		tr	tr/50												
Thelypodiopsis elegans		tr	tr/50												
Allium textile				tr	tr	tr	tr/99	tr			tr/33	tr			tr/33
Eriogonum ovalifolium				1					tr		tr/33				
Arenaria fendleri				tr											
Linum lewisii				tr											
Commandra umbellata				tr											
Haplopappus acaulis				1				3	tr		1.2/67				
Phlox hoodii				2	tr	1	8/99	tr	tr	2	1 0/99			tr	tr/33
Draba oligosperma				tr											
Astragalus spatulatus				tr											
Eriogonum sp				tr	tr		tr/50								
Astragalus purshii				tr				tr	tr	tr	tr/99				
Townsendia incana				tr	tr	tr	tr/99								

Table 5 continued.

Township	12 N	11 N		10 N	10 N	10 N		10 N	10 N	10 N		9 N	9 N	9 N	
Range	98W	97W		97W	101W	101W		99W	100W	100W		101W	101W	101W	
Section	S34	S3		S3	S12	S2		S9	S27	S35		S12	S18	S17	
Elevation (meters)	2100	2030		2220	1885	2060		2165	2130	2100		1750	1790	1790	
Aspect	NE	N		N	NE	W		NE	SE	SE		NE	SW	SW	
Slope (degrees)	2	1		15	3	4		5	5	2		3	2	3	
Soil pH	7.70	7.80	Avg 7.75	7.95	8.05	7.85	Avg 7.95	7 80	7.80	7 65	Avg 7.75	8.15	8.20	7.70	Avg 8 02
Soil EC (mmhos/cm)	.45	.42	Avg .44	.43	19	17	Avg .18	10	31	.30	Avg .34	.33	.37	40	Avg .37
Plant association number	7			8	9			10				11			
Plot number	1	2	Cov/Con	1	1	2	Cov/Con	1	2	3	Cov/Con	1	2	3	Cov/Con
Phlox longifolia				tr				tr		tr	tr/67				
Arabis demissa				tr											
Erysimum asperum				tr											
Sphaeralcea coccinea				tr	tr		tr/50						tr		tr/33
Castilleja chromosa				tr	tr		tr/50	1			tr/33				
Descurainia richardsonii					tr	tr	tr/99		tr	tr	tr/67		tr	1	tr/67
Cymopterus bulbosus					tr	tr	tr/99								
Zigadenus paniculatus					tr		tr/50								
Astragalus chamaeleuce					tr	tr	tr/99								
Lappula redowskii					tr		tr/50					tr		tr	tr/67
Physaria acutifolia						tr	tr/50								
Cryptantha sp.						tr	tr/50								
Chaenactis douglasii						tr	tr/50								
Arabis pulchra						tr	tr/50								
Crepis modocensis						tr	tr/50								
Xylorhiza venusta						tr	tr/50								
Machaeranthera grindelioides						tr	tr/50								
Astragalus detritalis								2			.7/33				
Trifolium gymnocarpon								1	tr	tr	.7/99				
Lomatium sp.								tr			tr/33				
Crepis occidentalis								tr	tr	tr	tr/99				
Balsamorhiza hookeri var. *hispidula*									4		1.3/33				
Erigeron divergens									tr	tr	tr/67				
Astragalus megacarpus									tr		tr/33				
Cordylanthus ramosus										tr	tr/33				
Delphinium nuttallianum												tr			tr/33
Ipomopsis pumila												tr	tr	tr	tr/99
Agoseris heterophylla												tr		tr	tr/67
Erigeron pumilus												tr			tr/33
Lepidium densiflorum													tr	1	tr/67
Camissonia contorta														tr	tr/33
Mentzelia albicaulis														tr	tr/33

spicatum, with about 20% cover, dominates the understory. *Poa sandbergii* commonly has 2%–3% cover.

Domestic livestock grazing has altered the composition of nearly all stands in the study area, resulting in the decline or loss of *Agropyron spicatum* and widespread replacement by *Poa sandbergii*, accompanied by increased density of *Artemisia tridentata* ssp. *vaseyana*. Herb density may also be very high.

The association has been located in Colorado only in the study area and in Middle Park, Grand County (Terwilliger and Tiedeman 1978). It is known to occur from western Wyoming (Beetle 1961) to Idaho (Hironaka 1978, Johnson and Pfister 1982) and Oregon (Hironaka 1978). In the study area it has been observed primarily in the Vermillion Bluffs and Sevenmile Ridge area.

9. *Artemisia tridentata* ssp. *wyomingensis*/*Agropyron smithii*.—This association occurs on slight convexities on flat to gently rolling plains formed in shales of the Mancos Fm., Green River Fm., or Wasatch Fm. It occurs in the study area from 1830 to 2130 m in elevation. Soils have an average pH of 7.95 and electrical conductivity of .19 mmhos/cm (Table 5). Over a broad area the association occurs in an alternating mosaic with the *Atriplex gardneri*/*Oryzopsis hymenoides* association, which occurs on more saline, more clayey soils, often in gentle concavities, on the rolling plains. Boundaries between these two associations may be very abrupt, apparently reflecting abrupt changes in soil properties.

The association consists of a sparse stand of *Artemisia tridentata* ssp. *wyomingensis* (Table 5, Fig. 3) scattered through a grass matrix. *Agropyron smithii* has 15%–20% cover. *Poa sandbergii* commonly has 1%–2% cover.

Domestic livestock grazing may decrease *Agropyron* and result in increases in

Fig. 3. (a) *Artemisia tridentata* ssp. *tridentata/Elymus cinereus*, (b) *Artemisia tridentata* ssp. *vaseyana/Agropyron spicatum*, (c) *Artemisia tridentata* ssp. *wyomingensis/Agropyron smithii*, (d) *Artemisia tridentata* ssp. *wyomingensis/Agropyron spicatum*, (e) *Artemisia tridentata* ssp. *wyomingensis–Atriplex confertifolia–Grayia spinosa*/Stipa comata*, (f) *Atriplex confertifolia/Agropyron spicatum*, (g) *Atriplex confertifolia/Elymus salina*, (h) *Atriplex confertifolia/Stipa comata*

Artemisia density, but, in general, probably due to the rhizomatous growth form of *Agropyron smithii*, the association is moderately resistant to alteration from domestic grazing. Many stands, however, have lost *Agropyron smithii* dominance completely and now have the less palatable grass *Poa sandbergii* as the understory dominant.

This is a very common association within the study area, but it is found only north and east of the Browns Park Formation area that occurs in the vicinity of Limestone Ridge and in Browns Park. It has been located in Colorado in the Piceance Basin in Rio Blanco County (Baker 1982b) and in Middle Park in Grand County (Terwilliger and Tiedeman 1978), and it probably occurs in other areas of northwestern Colorado. It also occurs in western Wyoming (Johnson and Pfister 1982) and in western New Mexico (Donart et al. 1978). It has not been reported from other western states.

10. *Artemisia tridentata* ssp. *wyomingensis*/*Agropyron spicatum*.—This association may occur in the study area from about 1980 to 2440 m in elevation, on gently rolling slopes and flat benches, on a variety of parent materials including the Laney Member of the Green River Fm. and the Browns Park Fm. Soils have an average pH of 7.75 and an electrical conductivity of .34 mmhos/cm (Table 5).

The association consists of about 10%–20% cover of *Artemisia tridentata* ssp. *wyomingensis* (Table 5, Fig. 3), with an understory of 15%–25% cover of *Agropyron spicatum*. *Poa sandbergii* typically has 3%–5% cover.

Domestic livestock grazing may decrease *Agropyron spicatum* and result in increases in *Poa sandbergii*, *Bromus tectorum*, and *Tetradymia spinosa*. Many stands now have *Poa sandbergii* dominant and appear superficially similar to overgrazed stands of the *Artemisia tridentata* ssp. *wyomingensis*/*Agropyron smithii* association. Usually it will be possible to find some plants of *Agropyron smithii* or *Agropyron spicatum* in even the most altered stands, allowing identification of the appropriate former association. These observations on the effect of domestic grazing are similar to those reported for the association in other areas (Mueggler and Stewart 1980, Tweit and Houston 1980).

The association is known in Colorado from northern Larimer County (Hess 1981), North Park in Jackson County (Smith 1966), Middle Park in Grand County (Terwilliger and Tiedeman 1978), and the study area in northern Moffat County and has been observed by the senior author in southern Routt County. Within the study area it was observed primarily along Vermillion Bluffs and north toward Powder Wash. The association occurs across the northern Great Basin from western Wyoming (Tweit and Houston 1980) and Montana (Mueggler and Stewart 1980) to Idaho (Hironaka 1978, Johnson and Pfister 1982) and Oregon (Hironaka 1978).

11. *Artemisia tridentata* ssp. *wyomingensis*–*Atriplex confertifolia*–*Grayia spinosa**/*Stipa comata*.—This association is restricted to sandy soils formed in the Browns Park Fm. It occurs on gently rolling hills, flat benches, and plains from 1700 to 1980 m in elevation. It may also occur on sandy hummocks and convexities in an area of finer-textured soils. Soils have an average pH of 8.02 and an electrical conductivity of .37 mmhos/cm (Table 5).

The association consists of a mixed shrub layer (Table 5, Fig. 3), with *Artemisia tridentata* ssp. *wyomingensis* generally most abundant (10%–20% cover) but *Atriplex confertifolia* usually co-dominant. *Grayia spinosa* may be uncommon or very abundant, but it is always present. The herb layer is dominated by *Stipa comata*, with 12%–25% cover.

Domestic livestock grazing decreases *Stipa comata* and results in increases in the exotic grass *Bromus tectorum* and other annual weeds. Most stands in the range of the association now are dominated by *Bromus tectorum*. A soil cryptogam layer, which has about 5% cover on relatively ungrazed sites, is absent on more grazed sites, probably due to trampling.

The association is currently known only from Browns Park in western Moffat County, Colorado. It may extend into Utah in Browns Park. It was, prior to livestock grazing, the predominant vegetation type in Browns Park, occurring over a large area.

12. *Atriplex confertifolia*/*Agropyron spicatum*.—This association occurs in the study area from about 1950 to 2200 m in elevation, most often on northerly facing slopes, but also on other aspects. Slopes are shallow to moder-

ately steep (up to about 25°). It occurs on side-slopes of draws and on gently sloping benches on two parent materials in the study area: the Cathedral Bluffs Tongue of the Wasatch Fm. and the Laney Member of the Green River Fm. Soils have an average pH of 7.90 and an electrical conductivity of .31 (Table 6).

The association has a sparse shrub layer composed of 4%–8% cover of *Atriplex confertifolia* (Table 6, Fig. 3) and often a small amount of *Ceratoides lanata*. *Agropyron spicatum* dominates the herb layer with 15%–30% cover, giving the association a grassland appearance.

Domestic livestock grazing decreases *Agropyron spicatum*, resulting in increases in *Poa sandbergii* and *Tetradymia spinosa*. Many of the stands of this association have been grazed primarily by sheep. Often, sheep-grazed stands have low forb density and *Atriplex confertifolia* plants have very poor vigor, with part of the crowns dead. *Agropyron spicatum* plants tend to have better vigor and greater cover on most sheep-grazed areas than on cattle-grazed sites.

The association has not been reported to date from outside the study area, where it is found only in the northern part of the area between Vermillion Creek and the Little Snake River. Since the association occurs within a few miles of Wyoming, and similar habitat occurs there, it is likely that it will eventually be found in Sweetwater County.

13. *Atriplex confertifolia/Elymus salina*. —This association occurs from 1950 to 2130 m in elevation in the study area on shallow to steep slopes with a northerly aspect. Parent materials include the Cathedral Bluffs Tongue of the Wasatch Fm. and the Laney Member of the Green River Fm. Soils are the most saline observed in the study area, with an average electrical conductivity of 1.16 mmhos/cm and pH of 7.77 (Table 6). Soils characteristically are shaley, with a surface layer of sandstone fragments. This sandstone surface layer commonly occurs throughout the range of the association.

The association contains a sparse shrub layer dominated by *Atriplex confertifolia* with 5%–10% cover (Table 6). *Sarcobatus vermiculatus*, *Artemisia tridentata* ssp. *wyomingensis*, and *Ceratoides lanata* are often present in small quantities. *Elymus salina* dominates the herb layer with 20%–30% cover. When flowering, this grass may obscure the shrub layer, giving the association a grassland appearance (Fig. 3).

Domestic livestock grazing decreases *Elymus salina* and results in increases in *Atriplex confertifolia* and *Poa sandbergii*.

The association is now known to occur in Colorado in scattered localities from northern Montrose County and Delta and Mesa counties, where it occurs at the boundary between Mancos shale and Mesa Verde Group sandstones (Baker, unpublished data) to the Piceance Basin in Rio Blanco County on Green River Fm. (Baker 1982b) and north to the study area. Within the study area it occurs in the area between Vermillion Creek and the Little Snake River. It has not been reported outside Colorado to date, but it has been observed by the senior author in eastern Grand

TABLE 6. Percent cover and constancy of shrubs and herbs, plot locations, and physical parameters. Plant association numbers correspond to those in the text. 12 = *Atriplex confertifolia/Agropyron spicatum*, 13 = *Atriplex confertifolia/Elymus salina*, 14 = *Atriplex confertifolia/Stipa comata*. Table entries under each plot are percent canopy cover. Tr = trace quantities (less than .5% cover). Table entries under Cov/Con are average percent canopy cover for all the plots in the association on the left of the slash and percent constancy to the right of the slash. 100 is abbreviated to 99. Soil electrical conductivity (soil EC) is discussed in the text.

Township	10 N	10 N	10 N	10 N	10 N		10 N	10 N	10 N		12 N	12 N	12 N	12 N	
Range	99W	99W	100W	100W	96W		100W	100W	96W		99W	98W	98W	96W	
Section	S5	S6	S22	S13	S7		S15	S22	S7		S25	S30	S25	S20	
Elevation (meters)	2070	2050	1960	2190	2090		1965	1980	2065		2100	2090	2120	2170	
Aspect	NNE	NW	NE	NW	NE		NE	NW	NE		—	—	NE	N	
Slope (degrees)	5	10	20	20	15		20	25	5		—	—	5	3	
Soil pH	7.95	7.95	7.90	7.80	—	Avg 7.90	7.85	7.75	7.70	Avg 7.77	7.95	8.05	7.85	7.75	Avg 7.90
Soil EC (mmhos/cm)	.25	.28	.38	.34	—	Avg .31	1.43	.36	1.70	Avg 1.16	.34	.32	46	.03	Avg .29
Plant association number	12						13				14				
Plot number	1	2	3	4	5	Cov/Con	1	2	3	Cov/Con	1	2	3	4	Cov/Con
SHRUBS															
Atriplex confertifolia	5	5	6	6	5	5.4/99	7	8	5	6.7/99	5	4	5	4	4.5/99
Tetradymia spinosa	tr	1	tr	1		6/80	tr	tr		tr/67					
Artemisia pedatifida	tr					tr/20							tr		tr/25
Atriplex gardneri	tr					tr/20		tr	tr	tr/67	tr	tr		tr	tr/75
Ceratoides lanata		tr	tr		tr	tr/60		tr		tr/33	tr	2	2	tr	1.3/99

Table 6 continued.

Township	10 N	10 N	10 N	10 N	10 N		10 N	10 N	10 N		12 N	12 N	12 N	12 N	
Range	99W	99W	100W	100W	96W		100W	100W	96W		99W	98W	98W	96W	
Section	S5	S6	S22	S13	S7		S15	S22	S7		S25	S30	S25	S20	
Elevation (meters)	2070	2050	1960	2190	2090		1965	1980	2065		2100	2090	2120	2170	
Aspect	NNE	NW	NE	NW	NE		NE	NW	NE				NE	N	
Slope (degrees)	5	10	20	20	15		20	25	5				5	3	
Soil pH	7.95	7.95	7.90	7.80	—	Avg 7.90	7.85	7.75	7.70	Avg 7.77	7.95	8.05	7.85	7.75	Avg 7.90
Soil EC (mmhos/cm)	.25	.28	.38	.34	—	Avg .31	1.43	.36	1.70	Avg 1.16	.34	.32	.46	.03	Avg .29
Plant association number	12						13				14				
Plot number	1	2	3	4	5	Cov/Con	1	2	3	Cov/Con	1	2	3	4	Cov/Con
Artemisia frigida					1	tr/20									
Opuntia polyacantha					tr	tr/20			tr	tr/33	tr		tr		tr/50
Sarcobatus vermiculatus							tr		tr	tr/67					
Artemisia tridentata ssp. *wyomingensis*								tr	tr	tr/67					
Chrysothamnus viscidiflorus									tr	tr/33	tr		1	1	6/75
Artemisia spinescens												tr	tr		tr/50
GRAMINOIDS															
Agropyron spicatum	28	25	20	27	22	24.4/99									
Hilaria jamesii	3	3				7/20					1				tr/25
Poa sandbergii	2	1	1	1	4	1.8/99	2	2	3	2.3/99	4	5	4	1	3.5/99
Stipa comata	tr					tr/20					20	17	25	17	19.8/99
Sitanion hystrix		tr			tr	tr/40		tr	tr	tr/67					
Bromus tectorum		tr				tr/20									
Oryzopsis hymenoides		tr	tr	tr		tr/60		tr	tr	tr/67	2	2	3	6	3.3/99
Elymus salina			8		2	2.0/40	22	28	25	25.0/99					
Agropyron smithii											tr	1	4		1.4/75
Carex filifolia											tr				tr/25
FORBS															
Arenaria fendleri	1	1	tr			tr/60		tr		tr/33					
Crepis occidentalis	1	tr				tr/40									
Phlox hoodii	3	2	1	1	2	1.8/99	2	1	2	1.7/99	2		1	1	1.0/75
Erigeron compactus var. *consimilis*	1	tr	tr	tr	tr	tr/99	1			tr/33					
Balsamorhiza hookeri var. *hispidula*	1					tr/20									
Machaeranthera grindelioides	tr	tr	1	tr	tr	tr/99									
Physaria acutifolia	tr	tr	tr			tr/60			tr	tr/33					
Haplopappus armerioides	2	1	1			8/60	tr		tr	tr/67					
Astragalus detritalis	tr					tr/20									
Lygodesmia grandiflora	1	tr				tr/40									
Ipomopsis congesta	tr	1				tr/40								tr	tr/25
Thelypodiopsis elegans	tr					tr/20			tr	tr/33					
Arenaria hookeri	1		tr	2	3	1.3/80		tr		tr/33				tr	tr/25
Haplopappus acaulis	tr	tr		tr		tr/60									
Townsendia incana	tr	tr		tr		tr/60						tr	tr		tr/50
Penstemon fremontii	tr	tr	tr			tr/60		tr		tr/33					
Stanleya pinnata	tr		tr			tr/40	tr	tr		tr/67					
Hymenoxys richardsonii		tr		tr		tr/40									
Descurainia richardsonii		tr				tr/20					2	tr	tr		8/75
Lappula redowskii		tr				tr/20			tr	tr/33	tr	tr	tr		tr/75
Cymopterus acaulis		tr			tr	tr/40									
Astragalus chamaeleuce		tr		tr	tr	tr/60	tr			tr/33	tr			tr	tr/50
Arabis demissa		tr				tr/20									
Chaenactis douglasii		tr				tr/20									
Castilleja chromosa			tr			tr/20									
Eriogonum umbellatum			tr			tr/20									
Sphaeralcea coccinea				tr		tr/20	tr			tr/33			1		tr/25
Calochortus nuttallii							tr			tr/33					
Xylorhiza glabriuscula							1			tr/33					
Camissonia scapoidea							tr			tr/33					
Allium textile								tr	tr	tr/67	1		tr	tr	tr/75
Cryptantha sericea								tr	tr	tr/67					
Schoenocrambe linifolia									tr	tr/33			tr		tr/25
Descurainia sophia									tr	tr/33					
Cordylanthus ramosus									tr	tr/33					
Phlox longifolia									tr	tr/33					
Lesquerella ludoviciana											tr			1	tr/50
Gilia leptomeria											tr				tr/25
Nemophila breviflora											tr				tr/25
Eriogonum sp.											tr			tr	tr/50
Arabis pulchra											tr				tr/25
Oenothera pallida											tr				tr/25
Ipomopsis pumila											tr				tr/25
Eriogonum ovalifolium											tr				tr/25
Cymopterus bulbosus												tr			tr/25
Erigeron pumilus													tr		tr/25

County, Utah, in the Grand Valley. The total range of *Elymus salina* and, consequently, the maximum potential range of this association are now known to be essentially the upper Colorado River Basin in eastern Utah, western Colorado, and southwestern Wyoming (Barkworth and Atkins 1984).

14. *Atriplex confertifolia/Stipa comata.* — This association occurs in the study area from 2070 to 2200 m in elevation, where it occupies relatively flat or gently sloping uplands. Parent materials include the Cathedral Bluffs Tongue of the Wasatch Fm. and the Laney Member of the Green River Fm. Soils have a sandier texture than other *Atriplex confertifolia* associations in the study area, but average soil pH (7.90) and average electrical conductivity (.29 mmhos/cm) are not very different (Table 6).

The association has a sparse shrub layer (Table 6, Fig. 3) dominated by *Atriplex confertifolia*, with 4% or 5% cover. *Ceratoides lanata* is often present but may have only trace cover. *Stipa comata* dominates the herb layer, with 15%–30% cover. *Oryzopsis hymenoides* and *Poa sandbergii* are always present, generally with 2%–6% cover each.

Domestic livestock grazing generally decreases *Stipa comata* and results in increases in *Poa sandbergii*. Many stands of this association have been grazed primarily by sheep. In these stands there may be very low forb cover and diversity, and *Atriplex confertifolia* plants may have very low vigor, often with parts of the crown dead. *Stipa comata* often retains better cover and vigor in sheep-grazed than in cattle-grazed stands.

The association has not currently been reported from outside the study area, where it occurs in the area between Vermillion Creek and the Little Snake River. Because it occurs within a few miles of the Wyoming border and similar habitat extends into Wyoming, it may eventually be documented from Sweetwater County.

15. *Atriplex gardneri/Elymus salina.* — The association occurs in the study area from 1890 to 2130 m in elevation on flat to very gently sloping benches, ridges, and saddles. Parent materials include the Bridger Fm. and the Laney Member of the Green River Fm. Soils often are very clayey and have an average pH of 8.01 and electrical conductivity of .35 mmhos/cm (Table 7).

The association (Table 7, Fig. 4) has a sparse and low shrub layer dominated by *Atriplex gardneri*, with 4%–6% cover. *Ceratoides lanata* is always present, but usually has less than 1% cover. The herb layer consists of 20%–30% cover of *Elymus salina*, as well as small amounts of *Poa sandbergii* and *Oryzopsis hymenoides*.

Domestic livestock grazing decreases *Elymus salina* and results in increases in *Poa sandbergii*, *Sitanion hystrix*, and weedy forbs such as *Descurainia* and *Lappula*.

In Colorado the association occurs on north-facing Mancos shale hills in western Mesa County (Baker, unpublished data) and in the study area, where it was located only on the ridges immediately west of the Little Snake River from Highway 318 north to near the Wyoming state line. It has not been reported from Utah or Wyoming to date, though it occurs near both state lines.

16. *Atriplex gardneri/Oryzopsis hymenoides.* —This association occurs in the study area from 1980 to 2200 m in elevation on flat to gently sloping mesa tops, plateaus, rolling plains, and gentle hills. Parent materials are the Luman Tongue of the Green River Fm. and the Niland and Cathedral Bluffs Tongues of the Wasatch Fm. Soils are very clayey, and have an average pH of 8.01 and electrical conductivity of .39 mmhos/cm (Table 7).

The association (Table 7, Fig. 4) consists of a sparse shrub layer dominated by the low-growing shrub *Atriplex gardneri*, with 6%–8% cover, lesser amounts (trace to 2% cover) of *Artemisia spinescens*, and often small amounts of *Ceratoides lanata*. *Oryzopsis hymenoides* dominates the herb layer, with 10%–25% cover. *Sitanion hystrix*, with trace%–4% cover, and *Poa sandbergii*, with trace%–4% cover, are regular components of the association. The forb component is very sparse and variable. But, because none of the sampled stands were entirely free of some signs of grazing, the variability of the forb component may be a reflection of past grazing history more than presettlement conditions.

Grazing by domestic livestock tends to result in the loss of *Oryzopsis hymenoides*. Either *Sitanion hystrix* or *Poa sandbergii* or

TABLE 7. Percent cover and constancy of shrubs and herbs, plot locations, and physical parameters. Plant association numbers correspond to those in the text. 15 = *Atriplex gardneri/Elymus salina*, 16 = *Atriplex gardneri/Oryzopsis hymenoides*. Table entries under each plot are percent canopy cover. Tr = trace quantities (less than .5% cover). Table entries under Cov/Con are average percent canopy cover on the left of the slash and percent constancy on the right of the slash. 100 is abbreviated to 99. Soil electrical conductivity (soil EC) is discussed in the text.

Township	9 N	9 N	8 N	10 N	11 N		12 N	12 N	11 N	11 N	11 N	11 N	
Range	97W	97W	97W	96W	96W		101W	101W	101W	100W	99W	97W	
Section	S25	S35	S3	S8	S17		S24	S20	S9	S21	S1	S3	
Elevation (meters)	2010	1980	1915	2050	2110		2125	2135	2090	2050	2085	2025	
Aspect	S	SSW	WNW	S	N		—	—	SW	S	SE	W	
Slope (degrees)	3	2	3	4	1		1	0	4	4	3	2	
Soil pH	8.30	7.90	7.85	8.15	7.85	Avg 8.01	7.65	8.00	8.00	8.15	8.05	8.20	Avg 8.01
Soil EC (mmhos/cm)	.38	.36	.28	.39	.34	Avg .35	.36	.34	.45	.39	.41	.37	Avg .39
Plant association number	15						16						
Plot number	1	2	3	4	5	Cov/Con	1	2	3	4	5	6	Cov/Con
SHRUBS													
Atriplex gardneri	6	5	5	6	5	5.4/99	8	7	8	7	6	6	7.0/99
Ceratoides lanata	tr	1	tr	tr	tr	.6/99	tr	2	5			1	1.4/67
Artemisia spinescens			tr			tr/20	tr	3	1	1		2	1.3/83
Atriplex confertifolia			tr		tr	tr/40	tr						tr/17
Opuntia polyacantha	tr		1		tr	tr/60				tr			tr/17
Artemisia pedatifida								tr					tr/17
Chrysothamnus sp.											1		tr/17
GRAMINOIDS													
Elymus salina	27	30	22	25	25	25.8/99							
Poa sandbergii	2	2	2	4	5	3.0/99	1	4		2	tr	4	1.9/83
Oryzopsis hymenoides	tr	2	3	1	tr	1.4/99	10	10	20	15	12	25	15.3/99
Sitanion hystrix	tr	1	1	2		.9/80	4	3	tr	3	3	3	2.8/99
Bromus tectorum	tr					tr/20				1			tr/17
Agropyron smithii											tr	tr	tr/33
X *Stiporyzopsis* X *bloomeri*												tr	tr/17
FORBS													
Phlox hoodii	2	tr	3	1	2	1.7/99	tr	1		tr		tr	tr/67
Descurainia sophia	1	1	1	tr		.7/80							
Lappula redowskii	tr	1	tr	1	tr	.7/99	tr		tr	6	tr	2	1.6/83
Phlox longifolia	tr		tr	tr		tr/60							
Calochortus nuttallii	tr					tr/20							
Cymopterus acaulis	tr					tr/20							
Allysum desertorum	tr					tr/20							
Allium textile	tr		tr	tr	tr	tr/80	tr	tr				tr	tr/50
Camelina microcarpa		1	tr			tr/40							
Lepidium perfoliatum		tr				tr/20							
Trifolium gymnocarpon			tr			tr/20							
Camissonia scapoidea				1		tr/20				tr	tr		tr/33
Nemophila breviflora				tr		tr/20							
Cymopterus bulbosus				tr		tr/20	tr				tr		tr/33
Monolepis nuttalliana				tr		tr/20						1	tr/17
Thelypodiopsis elegans				tr		tr/20					tr		tr/17
Ipomopsis congesta					tr	tr/20							
Arabis lignifera					tr	tr/20							
Astragalus chamaeleuce					tr	tr/20							
Erigeron compactus var. *consimilis*					tr	tr/20							
Townsendia incana					tr	tr/20	tr	tr					tr/33
Haplopappus acaulis					tr	tr/20							
Lesquerella ludoviciana					tr	tr/20							
Descurainia richardsonii							1	tr	tr				tr/50
Sphaeralcea coccinea							tr	tr		tr			tr/50
Halogeton glomeratus							tr			tr		tr	tr/50
Eriogonum ovalifolium								tr					tr/17
Ipomopsis pumila										tr			tr/17
Xylorhiza venusta										tr			tr/17
Vicia americana											1		tr/17
Stanleya pinnata											tr		tr/17
Rumex sp.											tr		tr/17

both will tend to replace *Oryzopsis*. All but a very small percentage of the range of this association now is dominated by one or both of these grasses. In many of these stands *Oryzopsis* can still be found in very small quantities. These surviving *Oryzopsis* plants are nearly always of very poor vigor, with dead centers, no litter, no flower stalks, and short and sparse foliage. Two other grazing-induced forms of this association occur. In one, the exotic *Halogeton glomeratus* dominates in the absence, or near absence, of perennial grass.

Fig. 4. (a) *Atriplex gardneri*/*Elymus salina*, (b) *Atriplex gardneri*/*Oryzopsis hymenoides*, (c) *Cercocarpus ledifolius* var. *intricatus*/*Agropyron spicatum*, (d) *Cercocarpus montanus*/*Agropyron spicatum*, (e) *Agropyron smithii* Great Basin Grassland, (f) *Agropyron spicatum*–*Arenaria hookeri*[+], (g) *Carex aquatilis* Wetland, (h) *Eleocharis palustris* Wetland.

In the other, a nearly pure stand of *Atriplex gardneri* occurs, with only a few annual weeds present.

The association has currently been described only from the study area, where it formerly covered a wide area primarily on the plateaus and benches adjoining Vermillion Creek and Dry Creek. The degraded forms of the association, with either *Sitanion hystrix* or *Poa sandbergii* dominant, have been observed by the senior author in southern Sweetwater County, Wyoming, but it is not known whether good condition stands are still extant in Wyoming, or how far north the association formerly occurred.

17. *Cercocarpus ledifolius* var. *intricatus*/*Agropyron spicatum*.—This association occurs above the pinyon-juniper zone, from about 2375 to 2550 m in elevation. It occupies very rocky ridge tops and upper slopes (Fig. 4) on exposures of Madison Limestone and Morgan Fm. Slopes range from 0° to 15°. Aspects are often northerly. Soils are very rocky and have an average pH of 7.80 with an electrical conductivity of .41 (Table 8).

The association has a dense shrub layer, with 35%–40% cover of *Cercocarpus ledifolius* var. *intricatus* and a small amount (less than 2% cover) of *Cercocarpus montanus*. The herb layer is dominated by *Agropyron spicatum*, with 5%–10% cover. *Carex pityophila*, with 5%–10% cover, and *Koeleria cristata*, with trace %–3% cover, are generally present.

Domestic livestock grazing may decrease *Agropyron spicatum* and result in increases in forbs and in *Cercocarpus* density. Most known sites are, however, far from water and generally poor in forage, so that heavy grazing is unlikely.

The association has not been described from outside the study area. It occurs within the study area only on Limestone Ridge, where it covers considerable area.

18. *Cercocarpus montanus*/*Agropyron spicatum*.—This association commonly occurs on steep northerly facing slopes between 1830 and 2130 m elevation in the study area. It occurs on Browns Park Fm. as well as several other parent materials.

Though many stands of the association were observed in the study area, only one stand could be located that was sufficiently undisturbed to be usable for sampling. The description and data are thus tentative, though the association is well known to the north in Wyoming. The association (Table 8, Fig. 4) in the study area contains a moderately dense shrub layer dominated by *Cercocarpus montanus*, with about 20% cover. *Agropyron spicatum* dominates the herb layer, with about 15% cover. Other commonly associated grasses include *Poa fendleriana* and *Poa sandbergii*.

The association occurs in scattered locations in western Wyoming. It is probably at or near its southern range limit in Moffat County, where it was located primarily in the area north of Limestone Ridge and west of Vermillion Creek, extending north to the Wyoming border.

19. *Agropyron smithii* Great Basin Grassland.—This association occurs in flat to gently sloping basins and along ephemeral creeks, between 1980 and 2130 m in elevation in the study area. Soils are very clayey and have an average pH of 7.78 and electrical conductivity of .32 mmhos/cm (Table 9). The parent material is Quaternary alluvium.

The association consists primarily of a dense stand of *Agropyron smithii*, with about 50% cover. Associated forbs and grasses are very variable.

Domestic livestock grazing has been reported (Christensen and Welsh 1963) to be capable of converting this association to solid sagebrush in as little as seven years of grazing. Livestock grazing may also enable the establishment of annual exotic weeds, such as *Conringia orientalis*, *Polygonum aviculare*, and *Lappula redowskii*.

The association has been observed in Colorado by the senior author in eastern Moffat County along Fortification Creek north of Craig. It also occurs in central Utah (Christensen and Welsh 1963, Christensen and Johnson 1964); in northeastern Nevada (Miller et al. 1982), where it occurs in a similar topographic position on saline soils; and in northeastern Arizona (Nichol 1937), where it occurs on "heavy gumbo soils."

20. *Agropyron spicatum*–*Arenaria hookeri**.—This association occurs exclusively on rocky exposures of Madison Limestone on open, wind-exposed summits that are alpine-like (Fig. 4) in that they are above the upper pinyon-juniper treeline and are on windy

TABLE 8. Percent cover and constancy of shrubs and herbs, plot locations, and physical parameters. Plant association numbers correspond to those in the text. 17 = *Cercocarpus ledifolius* var. *intricatus*/*Agropyron spicatum*, 18 = *Cercocarpus montanus*/*Agropyron spicatum*. Table entries under each plot are percent canopy cover. Tr = trace quantities (less than .5% cover). Table entries under Cov/Con are average percent canopy cover on the left of the slash and percent constancy on the right of the slash. 100 is abbreviated to 99. Soil electrical conductivity (soil EC) is discussed in the text.

Township	11 N	11 N	11 N		11 N
Range	101W	101W	101W		101W
Section	S19	S29	S19		S35
Elevation (meters)	2375	2530	2550		1995
Aspect	N	N	S		NNE
Slope (degrees)	10	2	4		30
Soil pH	7.95	7.85	7.60	Avg = 7.80	7.95
Soil EC (mmhos/cm)	.40	.38	.44	Avg = .41	.35
Plant association number	17				18
Plot number	1	2	3	Cov/Con	1
SHRUBS					
Cercocarpus ledifolius var. *intricatus*	40	35	35	36.7/99	
Cercocarpus montanus	2	tr	tr	1.0/99	20
Artemisia nova	1			tr/33	
Artemisia frigida	tr			tr/33	
Symphoricarpos oreophilus	tr			tr/33	
Chrysothamnus viscidiflorus			tr	tr/33	
Artemisia tridentata ssp. *wyomingensis*					tr
GRAMINOIDS					
Agropyron spicatum	7	6	5	6.0/99	15
Carex pityophila	2	1	2	1.7/99	
Koeleria cristata	3	tr		1.2/67	
Oryzopsis hymenoides	2	tr	tr	1.0/99	
Poa sandbergii	tr		tr	tr/67	2
Carex filifolia		tr		tr/33	
Agropyron smithii		tr		tr/33	
Poa fendleriana					5
FORBS					
Haplopappus acaulis	4	2	2	2.7/99	
Cryptantha flavoculata	tr		tr	tr/67	tr
Erigeron nematophyllus	2	tr	1	1.2/99	
Phlox hoodii	2	2	2	2.0/99	2
Draba oligosperma	1	tr	tr	.7/99	
Arenaria hookeri	tr	1	1	.8/99	
Astragalus spatulatus	tr		tr	tr/67	
Eriogonum sp.	tr	tr	tr	tr/99	
Physaria acutifolia	tr			tr/33	
Senecio werneriifolius	tr	1	1	.8/99	
Petrophytum carspitosum	tr		tr	tr/67	
Descurainia richardsonii	tr			tr/33	3
Hymenoxys acaulis	tr	tr	1	.7/99	
Arenaria fendleri	tr	tr		tr/67	
Machaeranthera grindeloides		1	tr	tr/67	
Erigeron flagellaris		tr		tr/33	
Linum lewisii		tr		tr/33	
Townsendia incana		tr	tr	tr/67	
Lesquerella alpina		tr	tr	tr/67	
Castilleja chromosa		tr	tr	tr/67	
Sedum stenopetalum			tr	tr/33	
Cryptantha gracilis					1
Lappula redowskii					tr
Arabis lignifera					tr
Pteryxia hendersonii					1
Haplopappus armeroides					tr

TABLE 9. Percent cover and constancy of shrubs and herbs, plot locations, and physical parameters. Plant association numbers correspond to those in the text. 19 *Agropyron smithii* Great Basin Grassland, 20 *Agropyron spicatum–Arenaria hookeri**. Table entries under each plot are percent canopy cover. Tr trace quantities (less than .5% cover). Table entries under Cov/Con are average percent canopy cover on the left of the slash and percent constancy on the right of the slash. 100 is abbreviated to 99. Soil electrical conductivity (soil EC) is discussed in the text.

Township	11 N	10 N		10 N	10 N	11 N	11 N	
Range	101W	101W		101W	101W	101W	101W	
Section	S21	S10		S16	S22	S30	S29	
Elevation (meters)	2105	2025		2500	2440	2460	2560	
Aspect	—	—		NW	N	N	SE	
Slope (degrees)	0	0		7	5	15	10	
Soil pH	7.70	7.85	Avg 7.78	8.05	7.85	7.85	7.85	Avg 7.90
Soil EC (mmhos/cm)	.31	.32	Avg .32	.45	.37	.44	.38	Avg .41
Plant association number		19				20		
Plot number	1	2	Cov/Con	1	2	3	4	Cov/Con
SHRUBS								
Artemisia nova				tr	tr			tr/50
Pediocactus simpsonii				tr				tr/25
Ceratoides lanata					tr			tr/25
Artemisia frigida				tr	2	tr		.8/75
Cercocarpus ledifolius var. *intricatus*							tr	tr/25
GRAMINOIDS								
Agropyron smithii	50	50	50.0/99	tr		tr		tr/50
Bromus tectorum	tr	tr	tr/99					
Sitanion hystrix	tr		tr/50					
Bromus inermis		tr	tr/50					
Agropyron spicatum				6	7	5	6	6.0/99
Koeleria cristata				1	1	1	tr	.9/99
Poa sandbergii						tr	tr	tr/50
Oryzopsis hymenoides						tr		tr/25
FORBS								
Polygonum aviculare	3	tr	1.8/99					
Monolepis nuttalliana	1		tr/50					
Atriplex argentea	1	tr	.8/99					
Plagiobothrys scouleri	1		tr/50					
Cryptantha kelseyana	tr		tr/50					
Descurainia sophia	tr		tr/50					
Conringia orientalis		2	1.0/50					
Descurainia richardsonii		tr	tr/50					
Iva axillaris		10	5.0/50					
Lappula redowskii		tr	tr/50					
Grindelia sp.		tr	tr/50					
Arenaria hookeri				3	4	3	2	3.0/99
Astragalus spatulatus				1	tr	2	1	1.1/99
Lesquerella alpina				4	3	tr	tr	2.0/99
Paronychia sessiliflora				1	tr	2	1	1.1/99
Phlox hoodii				3	5	4	4	4.0/99
Townsendia incana				1	2	1	tr	1.1/99
Draba oligosperma				1	tr	1	tr	.8/99
Hymenoxys acaulis				1	3	5	1	2.5/99
Erigeron sp.				tr	1	1	tr	.8/99
Lomatium orientale				tr	tr			tr/50
Haplopappus acaulis				tr		tr		tr/50
Petrophytum caespitosum				tr	1		2	.9/75
Machaeranthera grindeloides					tr		tr	tr/50
Sedum stenopetalum					tr	tr	tr	tr/75
Cryptantha sericea						tr		tr/25
Senecio werneriifolius						tr	tr	tr/50
Potentilla ovina						tr		tr/25
Cryptantha flavoculata							tr	tr/25
Selaginella densa							tr	tr/25

ridge tops probably blown free of snow in the winter. Similar habitats in the true alpine of the southern Rocky Mountains also have cushion plants of the same genera (*Arenaria, Paronychia, Phlox, Draba*) but different species. To add to the comparison, the upper tree line in the Limestone Ridge area where this association occurs sometimes has a very dwarfed "krummholz" appearance (Fig. 2). Elevations range from 2400 to 2560 m. The association occurs on any aspect but is most often missing on lee slopes with easterly exposure. Soils have an average pH of 7.90 and electrical conductivity of .41 mmhos/cm (Table 9).

The association consists of a very sparse collection of graminoids and "cushion plants," or low-growing forbs. Total cover averages 20%–25%. Rocks and lichens are conspicuous (Fig. 4). The shrub layer is almost nonexistent, though *Artemisia frigida* often occurs in small amounts. *Agropyron spicatum*, with 5%–7% cover, and *Koeleria cristata*, with trace %–1% cover are consistently present. Cushion plants always present, with 1%–5% cover each, include *Arenaria hookeri, Astragalus spatulatus, Draba oligosperma, Hymenoxys acaulis, Lesquerella alpina, Paronychia sessiliflora, Phlox hoodii*, and *Townsendia incana*. There are no clear dominants among this set of species. Relative amounts of each species vary from site to site. *Arenaria hookeri*'s presence distinguishes this association from other *Agropyron spicatum* associations that have been described in the western United States.

The association occurs in the study area only on Limestone Ridge. It very likely also occurs on similar Madison Limestone exposures that occur on the southern part of Douglas Mountain south of the study area, and it may occur in Dinosaur National Monument or in the eastern Uinta Mountains in Utah. Other cushion plant assemblages have been observed in southwestern Wyoming, as well as on the Great Plains (R. Lichvar, personal communication 1982), but it is not known if these are the same association.

21. *Carex aquatilis* Wetland.—This association occurs on the saturated soils alongside streams, creeks, and ponds on alluvial parent materials, generally above 2285 m in elevation in the study area. It often occurs below springs that originate in isolated aspen stands, in an area otherwise dominated by sagebrush. Slopes are variable, ranging from 0°–20°. Soils have an average pH of 7.20, the lowest observed in the study area, and an electrical conductivity of .47 mmhos/cm (Table 10).

The association is very common in the study area, but only two stands could be located that were relatively undisturbed. The description is thus somewhat tentative. *Carex aquatilis* dominates the association (Table 10, Fig. 4), with about 40% cover. *Juncus balticus* and *Eleocharis palustris* are important subdominants, each regularly having 5%–10% cover. *Carex rostrata* or *Equisetum arvense* may have 5%–10% cover in some stands or be absent entirely.

Domestic livestock grazing results in declines in *Carex aquatilis*, which may result in increases in the exotic *Poa pratensis* or in weedy natives, such as *Iris missouriensis*.

The association occurs above about 2285 m in elevation in scattered localities throughout the western two-thirds of Colorado. It also occurs in Oklahoma (Penfound 1953), Wyoming (Knight and Thilenius 1975, Billings and Mooney 1959), Canada (Looman 1982), and in other scattered localities throughout the western United States.

22. *Eleocharis palustris* Wetland.—This association occurs on the bottom of ephemeral ponds or playas at about 1830 m in elevation. The parent material is Quaternary alluvium. Soils have a heavy clay content, an average pH of 7.80, and an electrical conductivity of .76 mmhos/cm (Table 10).

Only one occurrence of this association was located in the study area, but, because the association is well-known elsewhere, it seems appropriate to add data from the study area to the available knowledge. The one occurrence was sampled in two separate areas. *Eleocharis palustris* dominates the association, with 45%–50% cover. Other commonly associated graminoids include *Hordeum jubatum* and *Agropyron smithii*.

Domestic livestock grazing may tend to result in increases in *Hordeum jubatum, Polygonum aviculare*, and *Kochia scoparia*.

The association occurs in the study area at only one location, adjacent to Irish Lakes. It occurs in scattered localities throughout Colorado from 1525 to 2750 m in elevation. It also

TABLE 10. Percent cover and constancy of shrubs and herbs, plot locations, and physical parameters. Plant association numbers correspond to those in the text. 21 *Carex aquatilis* Wetland, 22 *Eleocharis palustris* Wetland. Table entries under each plot are percent canopy cover. Tr trace quantities (less than .5% cover). Table entries under Cov/Con are average percent canopy cover on the left of the slash and percent constancy on the right of the slash. 100 is abbreviated to 99. Soil electrical conductivity (soil EC) is discussed in the text.

Township	12 N	11 N		10 N	10 N	
Range	103W	102W		101W	101W	
Section	S36	S8		S10	S10	
Elevation (meters)	2500	2375		2020	2025	
Aspect	W	E		—	—	
Slope (degrees)	4	8		0	0	
Soil pH	7.70	6.70	Avg 7.20	7.75	7.85	Avg 7.80
Soil EC (mmhos/cm)	.37	.56	Avg .47	.51	1.01	Avg .76
Plant association number	21			22		
Plot number	1	2	Cov/Con	1	2	Cov/Con
SHRUBS						
Salix bebbiana	tr		tr/50			
Potentilla fruticosa	tr		tr/50			
GRAMINOIDS						
Carex aquatilis	40	40	40.0/99			
Juncus balticus	10	5	7.5/99			
Eleocharis palustris	5	4	4.5/99	50	45	47.5/99
Deschampsia cespitosa	1	1	1.0/99			
Equisetum arvense	7		3.5/50			
Carex aurea	tr		tr/50			
Poa pratensis	tr	3	1.8/99			
Carex rostrata		10	5.0/50			
Carex microptera		3	1.5/50			
Muhlenbergia filiformis		tr	tr/50			
Sitanion hystrix				tr		tr/50
Hordeum jubatum				1	5	3.0/99
Agropyron smithii				1	1	1.0/99
Bromus tectorum					tr	tr/50
FORBS						
Dodecatheon pulchellum	2		1.0/50			
Viola nephrophylla	3		1.5/50			
Taraxacum officinale	1	tr	.8/50			
Trifolium longipes	tr	tr	tr/99			
Cirsium arvense	tr		tr/50			
Antennaria microphylla	tr		tr/50			
Erigeron sp.	2		1.0/50			
Sisyrinchium idahoense var. *occidentale*	tr		tr/50			
Epilobium ciliatum	tr		tr/50			
Iris missouriensis	tr		tr/50			
Ranunculus cymbalaria		2	1.0/50			
Veronica americana		tr	tr/50			
Rorippa sinuata				5	3	4.0/99
Polygonum aviculare				2	1	1.5/99
Grindelia sp.				tr		tr/50
Rumex salicifolius				1	tr	.8/99
Atriplex argentea				1	1	1.0/99
Sesuvium verrucosum					tr	tr/50
Chenopodium glaucum					2	1.0/50
Kochia scoparia					tr	tr/50
Sisymbrium altissimum					tr	tr/50

occurs from Nevada (Billings 1945) to Oklahoma (Penfound 1953).

Other Vegetation Types Not Sampled

A single stand was located (T10N R101W S9 SE4) that appears to represent the *Juniperus osteosperma–Pinus edulis/Purshia tridentata/Poa fendleriana* association, which is common in southwestern Colorado in the Mesa Verde region (Baker 1984), though the stand would be very disjunct and may simply represent an anomaly.

A single stand of what appears to have been a *Juniperus osteosperma–Pinus edulis/Cercocarpus montanus/Agropyron spicatum* association was located on the northwestern lower slopes of Limestone Ridge. Fragments of this association were observed in other areas, but they were either insufficiently large or too disturbed to be sampled. A stand similar to this was also observed in Dinosaur National Monument in 1983 (S. Wathen, personal communication 1983).

An area in T11N R101W S29 SE4 contains an open apparently wind-trimmed stand of prostrate *Juniperus osteosperma* (Fig. 2). The authors know of no other reports of "krummholz" growth form in pinyon-juniper woodlands. This stand does occur near the upper tree limit on Limestone Ridge, but other upper tree limit areas in the vicinity lack this phenomenon.

Several small stands of the *Artemisia tridentata* ssp. *wyomingensis–Symphoricarpos oreophilus/Elymus cinereus* association described by Baker (1982b, 1983) were observed along the north end of Vermillion Bluffs, but none were sufficiently undisturbed to be usable for sampling.

Several stands of *Sarcobatus vermiculatus* were observed in the study area. Without exception, they contain understories dominated by annual exotic weeds (e.g., *Bromus tectorum, Chorispora tenella, Malcomia africana, Halogeton glomeratus*). It is likely that prior to livestock grazing the understory of these stands was dominated by the native perennial grass *Distichlis spicata* var. *stricta*.

Occurring on dry lakebeds (e.g., Fonce Lake) are large, nearly monospecific stands of *Iva axillaris*. It is not known at this time if such stands occurred as a natural part of the presettlement vegetation spectrum.

Distribution of the Plant Associations in the Study Area

From an examination of the soils data presented in Tables 1–10, it is clear that soil pH and electrical conductivity are not sufficiently different among the plant associations to fully explain their environmental differences. It is likely that additional data on soil chemical and physical properties would help clarify the differences among associations, but collection of those data was beyond the scope of this study. Instead, the general arrangement of the plant associations in the landscape can be clarified in most cases by simple reference to topographic setting, aspect, and parent material. The arrangement of plant associations differs between the three geographic subdivisions of the study area.

In the Uinta Mountains section of the study area below 2375 m northerly facing slopes on calcareous substrata have the *Artemisia nova/Agropyron spicatum* association, whereas similar flat areas have the *Artemisia nova/Stipa comata* association. Southerly facing calcareous slopes may have the *Juniperus osteosperma–Pinus edulis/Artemisia nova/Agropyron spicatum* association, and rocky slopes on sandstones have the *Juniperus osteosperma/Agropyron spicatum* association. Very rocky sandstone ridges have the *Juniperus osteosperma–Pinus edulis/Cercocarpus ledifolius* var. *intricatus* association. Low-elevation rolling areas or flats that are noncalcareous have the *Artemisia tridentata* ssp. *wyomingensis/Agropyron smithii* association, whereas finer-textured soils have the *Agropyron smithii* Great Basin Grassland. In the northern part of the Uinta Mountains area, *Cercocarpus montanus/Agropyron spicatum* occurs on northerly facing noncalcareous substrata. Low-elevation ephemeral ponds and playas have the *Eleocharis palustris* Wetland association. Above 2375 m *Artemisia nova/Agropyron spicatum* occurs on calcareous slopes, and the *Cercocarpus ledifolius* var. *intricatus/Agropyron spicatum* association occurs on rocky calcareous ridge tops, with the *Agropyron spicatum–Arenaria hookeri** association occupying similar but more wind-exposed sites. The *Cercocarpus ledifolius/Artemisia tridentata* ssp. *wyomingensis–Symphoricar-pos oreophilus/Agropyron spicatum* association occurs in bands on slopes or in slight draws. The *Carex aquatilis* Wetland occupies areas below springs and along creeks. There are also forested areas dominated by *Populus tremuloides*, *Pinus contorta*, and *Pseudotsuga menziesii*. These upper-elevation forests were not sampled during this study.

In the Washakie Basin part of the study area, the rolling plateaus along Vermillion and Dry creeks below 2375 m contain an alternating mosaic of two associations, the *Artemisia tridentata* ssp. *wyomingensis/Agropyron smithii* association on coarser-textured, less saline soils, often on slightly convex sites, and the *Atriplex gardneri/Oryzopsis hymenoides* association on finer-textured, more saline soils, often on slightly concave sites. On more dissected sloping uplands, the *Atriplex confertifolia/Agropyron spicatum* association occurs on benches and ridges, whereas the *Atriplex confertifolia/Elymus salina* association occupies steep, rocky, northerly facing slopes. Above 2375 m the *Artemisia tridentata* ssp. *wyomingensis/Agropyron spicatum* association occurs on flat to gently sloping plateaus or as openings in *Juniperus osteosperma/Agropyron spicatum* woodlands. *Artemisia tridentata* ssp. *vaseyana/Agropyron spicatum* occupies windy sites on shallow soils on ridge tops in a few areas along Vermillion Bluffs. The *Atriplex confertifolia/Stipa comata* association occurs on flat to gently rolling uplands in the Powder Wash area. Further south on the southern end of Sevenmile Ridge, the *Atriplex gardneri/Elymus salina* association occurs on flat ridges on soils with a high clay content.

Browns Park contains a large area of the *Artemisia tridentata* ssp. *wyomingensis–Atriplex confertifolia–Grayia spinosa*/Stipa comata* association. A few north-facing slopes have the *Artemisia nova/Agropyron spicatum* association.

Status of the Plant Associations

Seven (numbers 4, 11, 12, 14, 16, 17, and 20) of the 22 plant associations described here are not known from outside the study area, based on currently available data. Three of these (4, 17, and 20) are restricted to Madison Limestone. The Madison Limestone occurs in adjoining Utah in the Uinta Mountains, but the vegetation of that area is currently largely undescribed. The other restricted associations occur on Browns Park, Green River, or Wasatch formations. These geologic strata and similar topographic situations occur in adjacent Utah and Wyoming, and it is likely that, as the vegetation of these adjoining regions becomes better known, the ranges of some of these associations will be expanded; but it is possible that this may not be so. On the basis of current knowledge, the study area has about as high a percentage of "endemic" plant associations as the Piceance Basin (Baker 1982b), the other major area of Green River Fm. exposures in Colorado. As in that area, the more extreme environments and uncommon geologic strata in the study area contain plant associations with restricted ranges, whereas mesic situations, northerly facing slopes, and sandstones have more wide-ranging associations. Many of these wider-ranging associations in the study area extend across part or all of the northern Great Basin.

Only a very small percentage of the study area still contains vegetation that retains to a substantial degree the composition and structure it had prior to the introduction of domestic livestock grazing and other recent land uses. Although records such as these of that presettlement composition and structure offer a permanent record valuable for rehabilitation and reclamation, it is of vital importance to the future understanding of the functioning of these ecosystems that the few extant remnants be perpetuated for additional research.

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WINTER PREFERENCE, NUTRITIVE VALUE, AND OTHER RANGE USE CHARACTERISTICS OF *KOCHIA PROSTRATA* (L.) SCHRAD

James N. Davis[1] and Bruce L. Welch[1]

ABSTRACT.—A cafeteria-style study was conducted during the winter for two years with tame mule deer to determine if there were preferential differences between accessions of forage kochia (*Kochia prostrata*). Deer consumed significantly more of P.I. numbers 314929, 330708, and 356826 than any of the other accessions. Other plant adaptive characteristics and nutritive qualities are also reported.

Forage kochia or perennial summer cypress (*Kochia prostrata*) is a widely distributed shrub native to the arid and semiarid regions of southern Europe and from northern Africa to Manchuria (Moghaddam 1978). Forage kochia was first introduced into the United States from Russia during the early 1960s (Keller and Bleak 1974). In its native Russia, it is commonly associated with *Agropyron*, especially crested wheatgrass (*A. cristatum*) (Balyan 1972).

There is an increasing interest in forage kochia as a desirable half-shrub for revegetation work on many arid and semiarid western ranges.

Ecotypic variation has been noted by many researchers (Balyan 1972, Francois 1976, Keller and Bleak 1974, McArthur and others 1974). Chromosome work indicates that the accessions we worked with included diploids, tetraploids, and hexaploids. The P.I. number 314929 was a diploid (McArthur 1984, personal communication). This same accession has recently been released as "Immigrant" forage kochia for forage and erosion control on greasewood-shadscale, sagebrush-grass, and pinyon-juniper rangelands of the Intermountain West (Stevens et al., in press).

Differential preference of wintering mule deer among accessions of big sagebrush (*Artemisia tridentata*) and black sagebrush (*A. nova*) has been reported by Welch et al. (1981). Also, Van Epps and McKell (1978) reported differential preference of domestic sheep for accessions of fourwing saltbush (*Atriplex canescens*).

The purpose of this study was twofold: first to determine the preference of tame mule deer for 13 accessions of *K. prostrata* grown in a uniform garden, and second to report the results of research concerned with the nutritive value and use of *K. prostrata*.

METHODS

Four tame mule deer (one buck and three doe) were used in a cafeteria-style preference study for two winters, 1978 and 1979. The second year, three of the four deer were the same as the first year. Throughout the study, the deer were given free choice of their specially formulated and pelleted feed, alfalfa hay, rolled barley, and water.

Selected accessions of forage kochia (Table 1) were air dried and clipped into 6 to 10 cm lengths. Samples were randomly assigned to 1 gal plastic buckets placed in a row in a rack in the deer pen. After 24 hours, each bucket was weighed and refilled with 120 g of clipped forage and again randomly placed in the rack. The test ran for 10 consecutive days each winter.

Analysis of variance was used to determine if there were significant differences between treatment means. Newman-Keuls multiple means test was used to determine the significant differences between individual means.

RESULTS

Deer consumed significantly more of some accessions than others (Table 1). Deer pre-

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TABLE 1. Deer preference for selected accessions of *Kochia prostrata*, plant introduction numbers, soil types, and origin of *K. prostrata* accessions used in this study.

Grams/day	P.I. number	Soil type	Location
53.9^{a}*	314929	**	Stavropol, Russia
43.4^{a}	330708	**	Tehran, Iran
39.4^{a}	356826	Salty	Actobinsk, Ural Mountains, Russia
13.3^{b}	**	**	Yun Dudar, Russia
13.2^{b}	356818	Clay	Actobinsk, Aral Sea, Russia
12.8^{b}	356819	Salty	Actobinsk, Aral Sea, Russia
8.6^{b}	356823	Sandy	Actobinsk, Russia
6.8^{b}	356822	Clay	Ural Mountains, Russia
3.4^{b}	356825	Clay	Actobinsk, Russia
2.8^{b}	356820	Sandy	Actobinsk, Aral Sea, Russia
0.9^{b}	356817	Salty	Actobinsk, Aral Sea, Russia
0.9^{b}	356824	Salty	Actobinsk, Russia
0.1^{b}	356821	Salty	Actobinsk, Aral Sea, Russia

*Values sharing the same letter superscript are not significantly different at the 95% level.
**Information not available.

ferred P.I. numbers 314929, 330708, and 356826 over the other 10 accessions. These 3 accessions did not differ significantly. The less preferred group of 10 accessions also failed to show significant differences in their means. It should be noted that P.I. numbers 356817, 356824, and 356821 received less than a gram of use per day. Data indicate that preference by tame mule deer for accessions of forage kochia is highly variable. We have no reason to believe that preference of wild and tame mule deer for accessions of *Kochia* differs significantly (Wallmo and Neff 1970). Highly preferred accessions (P.I. 314929, P.I. 330708, and P.I. 356826) are the ones that should be used in reseeding efforts where grazing is one of the management objectives.

DISCUSSION

Because of great ecotypic variation, forage kochia appears to be a useful range plant for improvement of our semiarid ranges. Some forage kochia ecotypes are quite salt tolerant. Francois (1976) tested two accessions for three years and found both to be salt tolerant, but one was significantly more productive at all salinity levels. The highest salinity level was twice that normally found in a greasewood community (Gates et al. 1956).

Forage kochia is drought tolerant. Moghaddam (1978) describes transplanting it into areas of Iran where annual precipitation was only 150 mm. He further reported that forage kochia's productivity and persistence was superior to fourwing saltbush. In Russia forage kochia is cut as "cypress hay" and fed to sheep, goats, and horses in regions having as little as 165 mm annual precipitation (Balyan 1972).

The nutritive value of forage kochia has received some attention. Davis (1979) reported that the oxalate—a potential animal poison—level in forage kochia was lower than levels in fourwing saltbush and winterfat (*Ceratoides lanata*). Welch and Davis (1984) reported the mean in vitro digestibility of the 13 accessions used in this study was 32.2% of dry matter (Table 2). In comparison to other winter forages, forage kochia ranks low in digestibility. Seasonal crude protein content was also determined for the accessions of forage kochia (Table 3). Mean crude protein was highest during July (14.4%) and November (10.7%) for "upper" stems. For the "lower" stems, highest mean protein was May (12.8%) and July (14.0%). Table 4 lists the average winter levels of crude protein of *Kochia* compared to other range plants. Forage kochia tends to green up earlier in the spring than many other range plants. Crude protein levels in new spring growth ranged from 12.1% to 21.8% (Davis and Welch 1984).

Forage kochia could be an important and useful subshrub on saline, and alkaline soils of our arid and semiarid ranges in the western United States. It grows well on a wide range of soil textural classes, sandy to fine clays. It is well adapted to areas occupied by juniper-pinyon, big sagebrush, greasewood, and shadscale. It grows fairly rapidly, usually producing seed the first year. Forage kochia could provide important sources of protein

TABLE 2. In vitro digestibility of winter range forages.

Winter forage	Dry matter digestibility/%	Range	Reference*
Aspen	57.4		1
Big sagebrush	57.3	(49.9–67.0)	2, 3, 4, 5, 6, 7, 10
Bud sagebrush	57.0		8
Woods rose	54.5		1
Sand dropseed grass	53.2		8
Black sagebrush	53.7	(53.1–54.0)	3, 8, 14
Rose hips	51.1		6
Indian ricegrass	50.0	(45.7–54.2)	8, 10
Bluestem wheatgrass	45.5		10
Curl-leaf mountain mahogany	49.1	(44.7–53.5)	4, 6
Galleta	48.2		8
Needle-and-thread	47.0		10
Bluebunch wheatgrass	45.5		10
Common winterfat	44.7		8
Rubber rabbitbrush	44.4		10
Shadscale	43.4		8
Western snowberry	41.0		1
Chokecherry	38.8	(26.3–51.3)	1, 11
Fourwing saltbush	38.3		9
Cliffrose	37.6		12
Desert bitterbrush	35.8		12
Forage kochia (P.I. 330708)	32.4		13
Forage kochia (mean)	32.2	(24.2–36.1)	13
Forage kochia (P.I. 314929)	31.0		13
Apache-plume	29.8		12
Forage kochia (P.I. 356826)	28.3		13
Gambel oak	28.1		2
Antelope bitterbrush	25.4	(19.8–30.0)	4, 6, 10, 12
True mountain mahogany	24.3	(20.0–28.5)	4, 6

*1. Dietz 1972
2. Kufeld et al. 1981
3. Sheehy 1975
4. Urness et al. 1977
5. Wallmo et al. 1977
6. Welch and Pederson 1981
7. Pederson and Welch 1982
8. Welch et al. 1983b
9. Welch and Monsen 1984
10. Ward 1971
11. Uresk and Messner 1975
12. Welch et al. 1983a
13. Welch and Davis 1984
14. Behan and Welch, in press

TABLE 3. Crude protein content of "upper" and "lower" parts of the same stems of *Kochia prostrata* through a year. Data expressed as percent of dry matter. Each data point is a mean of 13 accessions.

	Month							
Stem part	Dec.	Jan.	Feb.	Mar.	Apr.	May	July	Nov.
Upper	5.9^{a}*	6.1^{a}	6.1^{a}	5.2^{a}	5.7^{a}	5.8^{a}	14.4^{b}	10.7^{b}
Lower	8.2^{a}	8.3^{a}	8.7^{a}	8.1^{a}	9.8^{a}	12.8^{b}	14.0^{b}	8.6^{a}

*Values sharing the same letter superscript are not significantly different at the 95% level

and carotene (Davis 1979, Davis and Welch 1984) and help introduce variety to many monoculture seedings of crested wheatgrass. Otsyina (1983) reported that during a fall grazing study sheep showed a high preference for forage kochia in shrub-grass pastures. He also reported that crude protein contents of sheep diets on forage kochia-crested wheatgrass pastures were significantly higher than sheep diets on pure crested wheatgrass (10.6% vs. 1.5%). Forage kochia shows its greatest potential for use with grass ranges in the fall and

Table 4. Winter crude protein content of selected range plants.

Range plant	Crude protein (% dry matter)	Range	Reference*
Crested wheatgrass (green regrowth)	15.0		16
Black sagebrush	11.7		13
Big sagebrush	11.4	(9.9–14.2)	1, 2, 3, 4, 6, 8, 9, 10, 13, 16, 19
Curlleaf mountain-mahogany	10.1	(9.6–10.6)	3, 7
Fourwing saltbush	9.6		12
Forage kochia (P.I. 330708)	8.9		20
Chokecherry	8.7	(7.6–9.9)	3, 5, 11, 17
Cliffrose	8.6	(8.4–8.8)	5, 14
Desert bitterbrush	8.5	(8.0–9.0)	3, 14
Rocky mountain juniper	8.4		1
Forage kochia (P.I. 314929)	8.4		20
Antelope bitterbrush	7.8	(6.7–9.1)	1, 3, 4, 7, 8, 9, 11, 14
True mountain-mahogany	7.8	(7.2–8.4)	1, 5, 9
Rubber rabbitbrush	7.8	(5.9–7.8)	1, 11
Shadscale	7.7		10
Forage kochia (P.I. 356826)	7.3		20
Gardner saltbush	7.2		10
Forage kochia (mean)	7.1		20
Utah juniper	6.6	(5.9–7.6)	3, 5, 7
Saskatoon serviceberry	5.9	(5.5–6.2)	3, 11
Woods rose	5.8	(5.4–6.1)	17, 18
Gambel oak	5.3	(5.1–5.4)	5, 19
Apache-plume	4.8		14
Crested wheatgrass	3.9		11
Native grass	3.6		3
Wildrye	3.2		15
Indian ricegrass	3.0	(2.5–3.5)	11, 15

*1. Dietz et al. 1962
2. Welch and McArthur 1979
3. Tueller 1979
4. Bissell et al. 1955
5. Smith 1957
6. Smith 1950
7. Smith 1952
8. Trout and Thiessen 1973
9. Medin and Anderson 1979 (data converted to dry matter basis)
10. National Academy of Sciences 1975
11. National Academy of Sciences 1958
12. Welch and Monsen 1981
13. Sheehy 1975
14. Welch et al. 1983a
15. National Academy of Sciences 1964
16. Urness et al. 1983
17. Dietz 1972
18. Welch and Andrus 1977
19. Kufeld et al. 1981
20. Davis and Welch 1984

would improve forage quantity and quality on extensive crested wheatgrass seedlings in the Intermountain West.

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AGE, GROWTH, AND FOOD HABITS OF TUI CHUB, *GILA BICOLOR*, IN WALKER LAKE, NEVADA

James J. Cooper[1]

ABSTRACT.—At Walker Lake, Nevada, tui chub were collected 1975–1977 for analysis of age, growth rate, and food habits. The fork length (FL)–scale radius (SR) relationship was linear and described by the equation FL = 4.44 + 3.17 (SR). Age I, II, III, and IV chub were 116, 176, 218, and 242 mm fork length, respectively. Maximum longevity was six years. The length weight relationship was defined by the log transformed linear equation log weight = -4.65 + 2.93 (log FL). Chub collected from pelagic regions ate mostly zooplankton, whereas chub collected from littoral areas had a diet of zooplankton and benthic organisms.

Tui chub, *Gila bicolor*, is the most abundant of the three species of fish currently found in Walker Lake, Nevada. It is common to the Walker, Carson, Truckee, and Humboldt river systems of the Lahontan basin (La Rivers 1962). Various subspecies of tui chub occur in other endorheic basins in the drainages of pluvial lakes Railroad, Toiyabe, and Dixie, and lakes in the White Mountains in west central Nevada. Other forms occupy lake basins in California, southeastern Oregon, and southeastern Washington (Hubbs et al. 1974). In Walker Lake tui chub are an important component of the ecosystem bioenergetics and are preyed upon heavily by the piscivorous Lahontan cutthroat trout, *Salmo clarki henshawi* (Cooper and Koch, 1984). The vast number of fish-eating birds that annually visit the lake are also predators of tui chub.

Most of the life history information reported in the literature for the Lahontan form of tui chub has been collected from Eagle Lake, California, and Pyramid Lake, Nevada. Kucera (1978) and Kennedy (1983) studied the reproductive biology and growth of Pyramid Lake tui chub. Kimsey (1954) described the life history of the Eagle Lake tui chub population. Cooper (1978, 1982), working on Walker Lake, described various aspects of tui chub life history. Notes on the species can be found in other articles (Snyder 1917, La Rivers 1962, Vigg 1978, 1980, 1981, Galat et al. 1981, Galat and Vucinich 1983a, 1983b). The objectives of this study are to present data on the age, growth rate, and diet of tui chub from Walker Lake.

STUDY AREA

Walker Lake, a remnant of pluvial Lake Lahontan, is in west central Nevada 209 km southeast of Reno. The lake has a surface area of 15,000 ha, is 25 km long and 9 km wide, and has a maximum and mean depth of 33 and 20 m, respectively. It is the second largest remnant of Lake Lahontan. The lake's drainage basin is endorheic and receives water from the eastern Sierra Nevada via the Walker River. Because Walker is a terminal lake, it has a relatively high total dissolved solids (TDS) content of 12,500 mg/l that has increased rapidly in historic times. During the past 45 years the lake has had an average increase in TDS of 152 mg/l per year, and the cutthroat trout sport fishery appears to be in jeopardy. The primary factor responsible for the increasing salinity has been surface evaporation exceeding tributary inflow; since 1915 the lake's elevation has dropped at an average rate of 0.58 m per year (Cooper and Koch, 1984). Agricultural and urban diversion of the Walker River is hastening desiccation of the lake.

METHODS

The scale method was used to analyze the age of tui chub at various sizes (Ricker 1971, Everhart et al. 1975). Scales were taken from the left side of the body above the lateral line and below the dorsal fin. In the laboratory scales were placed between two plastic slides and run through a roller press to form an impression. Scales were read using an Eber-

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TABLE 1. Mean calculated fork length and mean calculated annual growth increments for tui chub collected June–November 1976, Walker Lake, Nevada.

Age class	No. of fish	Calculated fork length at end of each year of life (mm) 1	2	3	4
I	46	113			
II	16	124	187		
III	31	117	172	220	
IV	8	111	165	214	242
Grand mean		116	176	218	242
Increments of growth		116	60	42	24
Number of fish		101	55	39	8

bach microprojector and the distance from the focus to each annulus and from the focus to the scale radius recorded. All age and growth calculations were performed using the computer program SHAD II (Nelson 1976).

Stomach contents were analyzed two ways: percent occurrence and percent composition. In the former the number of stomachs in which each item occurred was recorded and expressed as a percentage of the total number examined. In the second method a representative sample of a stomach content was placed in a Sedgewick Rafter counting chamber and strip counts made of individual food items at 40X magnification. Percent composition of each food item identified in the counts were calculated for the total sample. Comparisons were made between the feeding habits of fish collected from pelagic surface (midlake) areas versus collections from littoral (< 5 m) regions of the lake. Tui chub stomachs appear as an enlargement in the anterior portion of the digestive tract, and it was at this point the contents were removed for food analysis. Fish were collected using multipaneled experimental gill nets with meshes of 3.8, 5.1, 6.4, 7.6, 8.9, and 10.2 cm stretched mesh measure. A more complete description of the methods is given in Cooper (1978).

RESULTS AND DISCUSSION

Age and Growth

Scale samples from 101 tui chub were examined for age and growth determinations. The fork length (FL) - scale radius (SR X 24) relationship was linear (Fig. 1) and described by the regression equation FL = 4.44 + 3.17 (SR) (r = 0.93). Scale formation begins to occur in Walker Lake tui chub between 25 and 30 mm in length. Kimsey (1954) reported that scale formation occurred in tui chub from Eagle Lake, California, when the fry reached 20 to 25 mm in length.

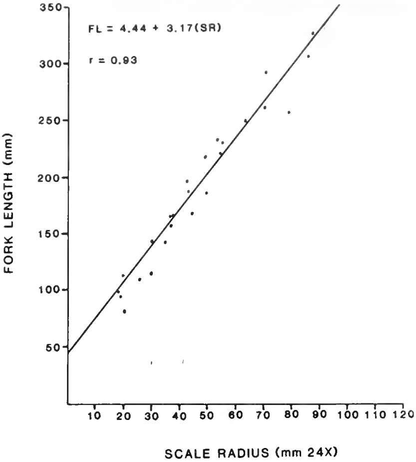

Figure 1. Fork length–scale radius relationship for Walker Lake, Nevada, tui chub.

Annual growth of tui chub were analyzed from summer hatch to four years (Table 1). The major growth in length is achieved during the first year of life. Young of the year chub captured in late August at approximately 2 to 3 months of age ranged in length from 72 to 115 mm and averaged 91 mm. Kucera et al. (1978) reported that by two months of age Pyramid Lake chub were 48 mm long and by September had attained a length of 122 mm. Eagle Lake young of the year only reach a length of 22–41 mm by September (Kimsey 1954). Following this rapid growth during the first year of life, annual growth increments become progressively smaller.

Table 2. Tui chub growth rates in five selected waterbodies.

Location	Fork length at end of each year of life (mm) 1	2	3	4	Reference
Walker Lake, Nevada	116	176	218	242	This study
Pyramid Lake, Nevada	123	172	215	259	Kucera et al. (1978)
Eagle Lake, California*	74	125	187	242	Kimsey (1954)
Big Sage Reservoir, California	58	103	140	157	Kimsey and Bell (1955)
East Lake, Oregon	43	75	114	149	Bird (1975)

* Standard length converted to fork length by a factor of 1.12

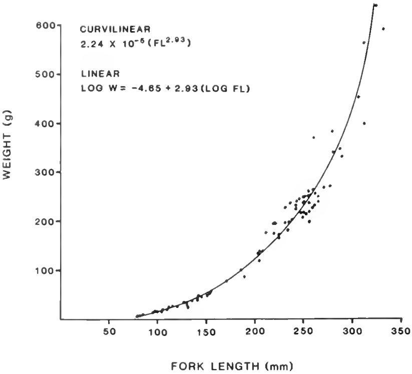

Figure 2. Length-weight relationship for Walker Lake, Nevada, tui chub.

Maximum growth at an immature age can be explained by the fact that this age group does not contend with reproduction and thus all energy is expended in growth. Furthermore, maximum growth in length at an early age with a subsequent decline could be advantageous because most Lahontan cutthroat trout can only ingest smaller sized chub.

Growth rates of tui chub in Walker and Pyramid lakes are higher than other nonterminal lakes (Table 2). First-year growth in the two terminal lakes is over three times that of the relatively unproductive, high elevation East Lake, Oregon (Bird 1975). Eagle Lake chub exhibit slow growth their first year but by year IV are the same size as Pyramid and Walker fish. This too may be related to the lake's trophic state because Walker and Pyramid are the more productive (Huntsinger and Maslin 1976, Cooper and Koch 1984, Galat et al. 1981). Temperature may also be a factor because winter temperatures are about 6 C warmer in Pyramid and Walker, which do not experience ice cover.

Longevity of tui chub from Walker Lake is probably near four or five years of age. Maximum age of 102 fish collected for age examination was one six-year-old individual. This is similar to data collected from Pyramid Lake, where a sample size of 322 produced six age five, one age six, and one age seven (Kucera et al. 1978).

The length-weight relationship can best be described by the linear log transformed equation $\log W = -4.65 + 2.93 (\log FL)$, where W = weight in grams and FL = fork length in millimeters (Fig. 2). Chub used for length-weight analysis ranged in size from 72 to 324 mm in length and 6.3 to 636.8 g in weight. The largest individual caught was a female (324 mm, 636.8 g) that had a young-of-the-year tui chub in its stomach.

Walker tui chub are heavier in weight per unit length than Pyramid chub (Kucera et al. 1978), although there was only a slight difference in length at any given age. This was corroborated by the higher mean coefficient of condition (K) of Walker (1.51) versus Pyramid (1.31) fish. Kimsey (1954) reported a mean K value of Eagle Lake tui chub of 1.92, the highest of all three lakes.

Food

Food items identified from 103 stomachs revealed Walker Lake tui chub to be omnivorous and highly opportunistic. Zooplankton was the most important item in the diet of chub captured in pelagic water by both occurrence (97.4%) and composition (94.4%) (Table 3). Fish captured in littoral regions also fed on zooplankton but took significant quantities of benthic material. The attached alga (*Cladophora*), Chironomidae larvae, and the gammarid *Hyalella azteca* were evidence of benthic feeding activity in the littoral catch. Zooplankton were the most important organ-

TABLE 3. Food of tui chub by percent frequency of occurrence and percent gut composition collected from two habitats in Walker Lake, Nevada, in 1976 and 1977*.

Food item	Occurrence %		Composition %	
	Pelagic	Littoral	Pelagic	Littoral
Zooplankton	97.4	63.9	94.4	30.6
Cladophora sp.	10.3	88.5	2.5	44.5
Chironomidae	5.1	29.5	0.5	12.9
Hyalella azteca	0	0	0	2.9
Bottom substrate	0	27.9	0	9.1
Gila bicolor	2.6	0	2.6	0

* Pelagic n = 41
Littoral n = 62

isms in the diet of these fish, probably due to the small amount of littoral habitat in Walker Lake.

These findings are consistent with the literature in categorizing tui chub as opportunistic omnivores (Kimsey 1954, La Rivers 1962, Bird 1975, Langdon 1979, Galat and Vucinich 1983b), although the data suggest zooplankton may be more important in the diet of Walker Lake fish. Gill raker counts of Walker chub indicate an abundance of the fine-rakered *pectinifer* form, with only a small representation of an intermediate between *pectinifer* and the course-rakered *obesa* form (Cooper 1978, Vigg and Cooper, unpublished data). In Pyramid Lake both forms are abundant and exhibit differences in feeding behavior (Langdon 1979, Galat and Vucinich 1983a); fine-rakered chub consume more zooplankton and course-rakered chub more macroinvertebrates. However, as in this study, Langdon (1979) found little similarity in the diet of *pectinifer* sampled at the surface and bottom. It seems that *obesa* is more dependent on a bottom-feeding strategy than *pectinifer* is on pelagic feeding. This theory is supported by Pyramid Lake data showing that only *pectinifer* are found in open water, but both forms can be caught inshore on the bottom (Vigg 1978, Langdon 1979). Although there is little gill raker variation in Walker Lake chub, for whatever reason, *pectinifer* appear to have successfully filled the trophic niche unoccupied by *obesa*. When compared to lakes supporting *obesa* populations, Walker chub are, in general, feeding on the same food items and can modify their feeding strategy in accordance with food availability. This suggests that feeding strategy in lentic Great Basin chub populations may be just as dependent on behavioral and ecological characters as it is on morphological variation.

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NEW VARIETY OF *YUCCA HARRIMANIAE* (AGAVACEAE) FROM UTAH

Elizabeth Neese[1] and Stanley L. Welsh[1]

ABSTRACT.—*Yucca harrimaniae* var. *sterilis* Neese & Welsh is named and described from the Uinta Basin of Utah. The plant is strongly rhizomatous, evidently sterile, and has limber, sparingly filiferous leaves that tend to recline on the ground.

During field investigations in the Uinta Basin of Utah in the late 1970s and early 1980s, a phase of *Yucca harrimaniae* Trel. was brought to our attention by Mr. Dan Gardner of the Bureau of Land Management in Vernal, Utah, who had observed the plants in the Pariette Bench vicinity of the basin.

Several occurrences of this peculiar entity were discovered thereafter by the authors and by other collectors in the region. The plants are characterized by being strongly rhizomatous, with the rosettes more or less widely spaced; the leaves are limber and sparingly, if at all, filamentous marginally, and tend to recline in curved fashion on the ground. These characters contrast strongly with typical material of *Yucca harrimaniae* as it occurs in the Uinta Basin and elsewhere. Furthermore, the plants with sprawling, sparingly filamentous, flaccid leaves are not known to produce fruit, even though some populations have been observed over a period of several years, nor has fruit from previous years, often observable in the typical material, been found by us. In typical plants the rosette leaves are stiffly erect-ascending and marginally filamentous, the rosettes are clumped to narrowly spaced, and fruit is produced routinely. The species is treated as follows.

***Yucca harrimaniae* Trel.** Harriman Yucca. [*Y. harrimaniae* var. *gilbertiana* Trel., type from Juab County; *Y. gilbertiana* (Trel.) Rydb]. Plants acaulescent, forming densely to widely spaced rosettes; leaves falcate or straight, lanceolate to spatulate-lanceolate, concavo-convex, deeply striate, rather thick and rigid or limber, pale green, pungent apically, 1–5 dm long, 0.7–4 cm wide, the margins white or brown, in age more or less filiferous, the fibers, when present, somewhat coarse and curly; inflorescence 3.5–7 dm tall, racemose or rarely with a few short branchlets, extending from within the foliage to well above; flowers broadly campanulate, pendant, yellowish or greenish yellow to cream, tinged with purple, the segments 4–5 (6) cm long, 1.6–3.5 cm broad; ovary 1.5–2 cm long, pale green; style 9–11 mm long, bright green; capsule cylindric, with a short attenuate beak, 3.7–5 (6) cm long, usually deeply constricted toward the center and flaring open when dried, or not developed. Two more or less distinctive varieties are present in this species.

1. Leaves of basal rosette stiffly erect-ascending, conspicuously filamentous along the margin; rosettes often clumped; plants not strongly rhizomatous, routinely forming capsules . . . . *Y. harrimaniae* var. *harrimaniae*

— Leaves of basal rosette flaccid, often reclining on the ground, typically curved, not especially filamentous marginally; rosettes often widely spaced; plants strongly rhizomatous, not known to form fruit . . . . *Y. harrimaniae* var. *sterilis*

Var. *harrimaniae*. Warm desert shrub, grasslands, sagebrush, pinyon-juniper, and mountain brush communities at 1200 to 2700 m in Beaver, Carbon (type from near Helper), Duchesne, Emery, Garfield, Grand, Iron, Juab, Millard, Piute, Sevier, San Juan, Uintah, and Wayne counties; Nevada, Colorado, Arizona, and New Mexico; 42 (xii).

Var. *sterilis* Neese & Welsh, var. nov. Similis *Y. harrimaniae* var. *harrimaniae* in floribus et staturis generalis sed in foliis flaccidis et floribus sterilis differt. TYPE: USA Utah. Uintah Co., T6S, R22E, Sec 14, ca 8 km S of Jensen, at mouth of Walker Hollow, at 1470 m elev., Salt desert shrub community, on bluff

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margin, alluvium over Uinta Formation, 31 May 1979, S. L. Welsh 18461 (Holotype BRY; Isotypes 4, distributed previously as *Yucca*). Additional specimens: Utah. Uintah Co., 19 km due SSW of Naples, 14 May 1980, S. White & E. Neese 133 (BRY); mouth of Walker Hollow, 31 May 1979, Neese et al. 7479 (BRY); 41 km S of Roosevelt, 29 June 1978, E. Neese & L. England 5899 (BRY); ca 3 km NW of Gusher, 8 June 1979, E. Neese & B. Welsh 7542, 8 June 1979 (BRY). Duchesne Co., ca 11 km NNW of Roosevelt, 19 June 1979, E. Neese 7663 (BRY).

LITERATURE CITED

HIGGINS, L. C., AND S. L. WELSH. 1985. Utah flora: Agavaceae. Brigham Young University. Unpublished manuscript. 8 pp.

REVISION OF THE *PHLOX AUSTROMONTANA* (POLEMONIACEAE) COMPLEX IN UTAH

Stanley L. Welsh[1]

ABSTRACT.—The taxa centering around *Phlox austromontana* Coville are revised. Named as a new variety is *P. austromontana* var. *lutescens* Welsh from eastern Garfield County, Utah. A new combination is provided as *P. austromontana* var. *jonesii* (Wherry) Welsh.

Taxa within the genus *Phlox* have been reviewed preparatory to completion of the Utah flora, a summary revision of all indigenous, adventive, and commonly cultivated plant species for Utah. Observations made during that review demonstrated the need for modification of contemporary concepts within the complex of forms centering around the concept of *Phlox austromontana* sensu lato. The species has been interpreted by contemporary authors as consisting of a single polymorphic taxon, or of a closely allied species pair, i.e., *P. austromontana* and *P. jonesii*.

Transitional morphological features tend to obscure the populations, which are often more or less geographically or topographically correlated. This is a general problem in the genus, and *P. austromontana* merely exemplifies that problem. Thus, it is not surprising that the various taxa represented in herbaria previously should have been subjected to differential treatment. Some named portions of the variation have been reduced to synonymy, when the transitional morphology was interpreted as taxonomically negligible. *Phlox austromontana* var. *prostrata* consists of sprawling plants with long internodes and occurs in much of the middle elevation portions of Washington County, Utah. The calyces of this variety are ordinarily conspicuously hairy. The *jonesii* phase is similar to the prostrata phase in having sprawling stems with long internodes, but the calyces are glabrous in extreme examples. Where the two phases meet in Zion Canyon, the type locality for the *jonesii* phase, there is a mixing of characters. Brightly colored pink flowers characteristic of the *jonesii* phase have either glabrous calyces or hairy ones like the *prostrata* materials. The overlapping characteristics seem to indicate variation that should be recognized within a species in this genus. Therefore, the *jonesii*, *prostrata*, and *austromontana* phases are treated at varietal level.

Examination of the large series of specimens in this species at the herbarium of Brigham Young University demonstrated the existence of a robust, subligneous specimen taken from crevices in the Cedar Mesa Sandstone along the margin of Cataract Canyon in eastern Garfield County, Utah. The specimen had creamy yellowish flowers when collected, and, because of its growth habit and flower color, was initially determined as a *Leptodactylon*. The leaves are simple, however, not digitate as in that genus. The flowers have dried a lemon yellow color and are thickly cartillaginous, unlike any other portions of the *austromontana* complex, but other features, including lax stems, long leaves, and carinate intercostal membranes of the calyx, indicate affinity with *P. austromontana*. The species is, therefore, revised as follows.

Phlox austromontana **Coville** Desert Phlox. Plants caespitose, cushion or matlike, from a pluricipital caudex and taproot, mainly 0.5–3 dm wide; herbage pilose-puberulent to subglabrous or the calyx glabrous to villous externally; leaves opposite, mainly 5–20 mm long, simple, linear-subulate; flowers solitary, sessile or subsessile at branch tips; calyx urceolate to campanulate, glabrous to villous, the intercostal membranes carinate, the lobes vil-

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lous internally; corolla white, blue, pink, lavender, or yellowish, the tube 8–15 mm long; styles 2–9 mm long. This is a complex assemblage of variants, some sufficiently distinctive and sufficiently geographically correlated as to warrant taxonomic recognition. The morphology is, however, wholly confluent. Trends within the diversity are recognized at varietal level.

1. Plants more or less open, the internodes typically apparent; plants of western Kane and much of Washington counties 2
— Plants variously open to compact; distribution various 3
2(1). Calyx usually glabrous, the leaves (or some of them) 20–35 mm long; corollas usually bright pink; morphology transitional to the next. . . . . *P. austromontana* var. *jonesii*
— Calyx at least moderately villous, the leaves typically 10–22 mm long; corolla commonly white . . . . *P. austromontana* var. *prostrata*
3(2). Flowers yellowish (fading lemon yellow); leaves 10–25 mm long; calyx campanulate . . . . *P. austromontana* var. *lutescens*
— Flowers white, pink, or lavender (sometimes fading to cream in color); leaves mostly less than 15 mm long; calyx turbinate to subcylindric. . . . . *P. austromontana* var. *austromontana*

Var. *austromontana* [*P. densa* Brand, type from Frisco]. Mixed desert shrub, salt desert shrub, pinyon-juniper, sagebrush, mountain brush, and ponderosa pine communities at 1525 to 3050 m in Beaver, Carbon, Duchesne, Emery, Garfield, Iron, Juab, Kane, Millard, Piute, Sanpete, Sevier, Tooele, Uintah, Washington (type from Beaverdam Mountains), and Wayne counties; Nevada, California, and Arizona; 159 (xxiii).

Var. *jonesii* (Wherry) Welsh, comb. nov. [based on: *Phlox jonesii* Wherry Notul. Nat. Acad. Nat. Sci. Philadelphia 146: 8. 1944; holotype—Washington County, Zion Canyon, 7 May 1923, M. E. Jones sn US!]. Ponderosa pine, pinyon-juniper, and mountain brush communities at 1435 to 2600 m in Kane and Washington counties; endemic; 12 (ii). This variety forms intermediates with both var. *prostrata* and var. *austromontana*. It is partially sympatric with both.

Var. *lutescens* Welsh, var. nov. Affinis et similis *Phlox austromontana* Coville var. *austromontana* sed in corollis lutescentibus et plus crassis et calycibus campanulatis differt. TYPE: USA Utah. Garfield Co., T33S, R14#, SW 1/4 S1, along Orange Cliffs Rd, E of Hwy 95, 1373 m elev., rimrock-blackbrush, ash, squawbush community, 11 May 1983, S. L. Welsh, B. Welsh, M. Chatterley 21972 (Holotype BRY; isotypes 4, distributed previously as *Leptodactylon watsonii* [Gray] Rydb.). The specimens collected were taken from a large population of suffrutescent, rounded, cushions growing in crevices in rimrock of Cedar Mesa Sandstone, and, because of the peculiar flower color and growth habit, were mistaken for the superficially similar *Leptodactylon watsonii*.

Var. *prostrata* E. Nels. Mountain brush and pinyon-juniper communities at 1220 to 2135 m in Washington (type from Silver Reef!) County; endemic (?); 14 (0).

LITERATURE CITED

WELSH, S. L. 1985. Utah flora: Polemoniaceae. Brigham Young University. Unpublished manuscript. 48 pp.

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The genera, species, and other taxa described as new to science in this volume appear in bold type in this index.

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