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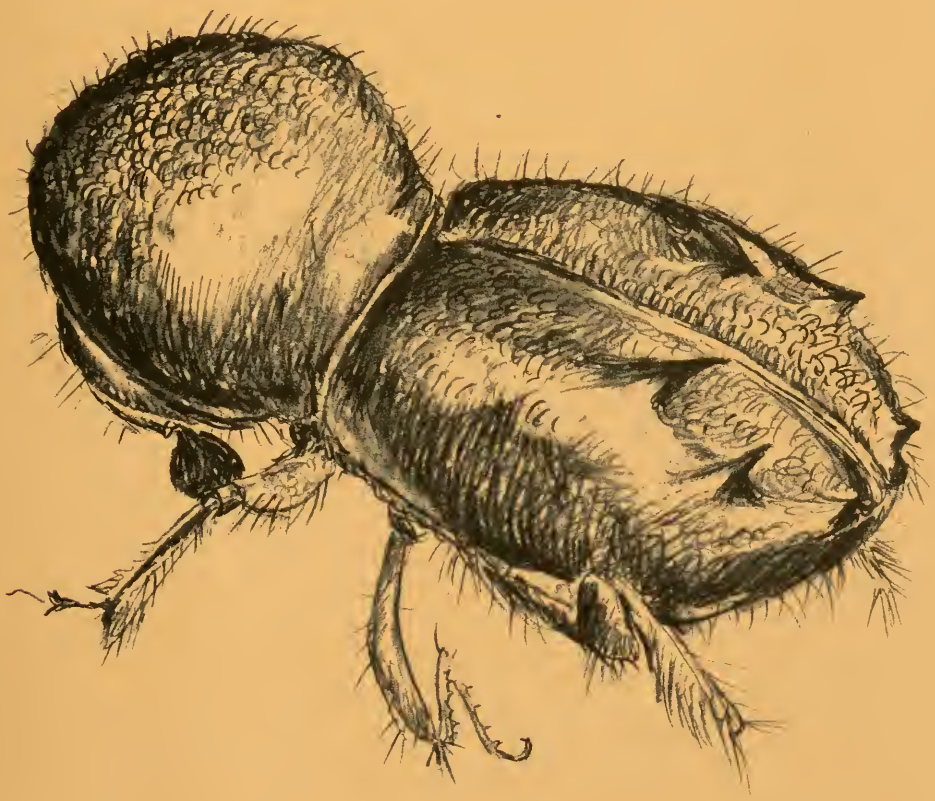

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SEASONAL CHANGES OF SELECTED SECONDARY PLANT PRODUCTS IN *CHRYSOTHAMNUS NAUSEOSUS* SSP. *TURBINATUS*

D. F. Hegerhorst[1], R. B. Bhat[1], D. J. Weber[1], and E. D. McArthur[2]

ABSTRACT.—Previously, physiological studies of rubber and resin production during the growing season of *Chrysothamnus nauseosus* ssp. *turbinatus* indicated a negative correlation between rubber and resin content. The resin was highest in the spring and lowest in the summer, whereas rubber was highest in the summer and lowest in the spring. Individual compounds were followed during the growing season to see if they correlated with the rubber or resin trend. The total compounds in the cyclohexane fraction followed the resin pattern. Individual compounds varied in their changes during the growing season. Limonene, for example, was negatively correlated with rubber production, whereas β cubebene was positively correlated. The possible metabolic pathways between resin and rubber are discussed.

Recently there has been increased interest with respect to the availability and possible commercialization of rubber rabbitbrush (*Chrysothamnus nauseosus*) for natural rubber (Pierson 1975, Weber et al. 1985, Ostler et al. 1986). Some of the subspecies contain levels of natural rubber similar to those of guayule (Ostler et al. 1986, Hegerhorst et al., Resin and rubber, 1987). Additional uses of rabbitbrush, such as a winter forage and as a revegetation shrub, increase its potential as a commercially beneficial crop (McArthur et al. 1979, Weber et al. 1985). Because of the vast environmental and geographical latitude in which rubber rabbitbrush grows, the potential advantages of growing rubber rabbitbrush for a commercial source of natural rubber and other plant products become more obvious. *Chrysothamnus nauseosus* ssp. *turbinatus* is of particular interest because levels of natural rubber reported exceed 6.5% (dry wt) (Hegerhorst et al., Resin and rubber, 1987). Commercialization of rabbitbrush relies on understanding plant habitat, genetic variability, rubber accumulation in the plant, seedling characteristics, and many other aspects of plant development (Hegerhorst et al., Chemical analysis, 1987). A deeper understanding of the parameters influencing rubber synthesis will help us possibly control its accumulation. Recent results (Hegerhorst et al., Seasonal changes, 1987) show that a strong negative correlation exists between rubber and resin production in selected subspecies of rubber rabbitbrush. The purpose of this study is to better understand the relationship between resin and rubber production within the plants by following seasonal changes in selected secondary plant products.

MATERIALS AND METHODS

Plant material from rubber rabbitbrush (*Chrysothamnus nauseosus* ssp. *turbinatus* [Jones] Hall & Clem.) was collected 1.6 km west of Goshen, Utah (USA), during the

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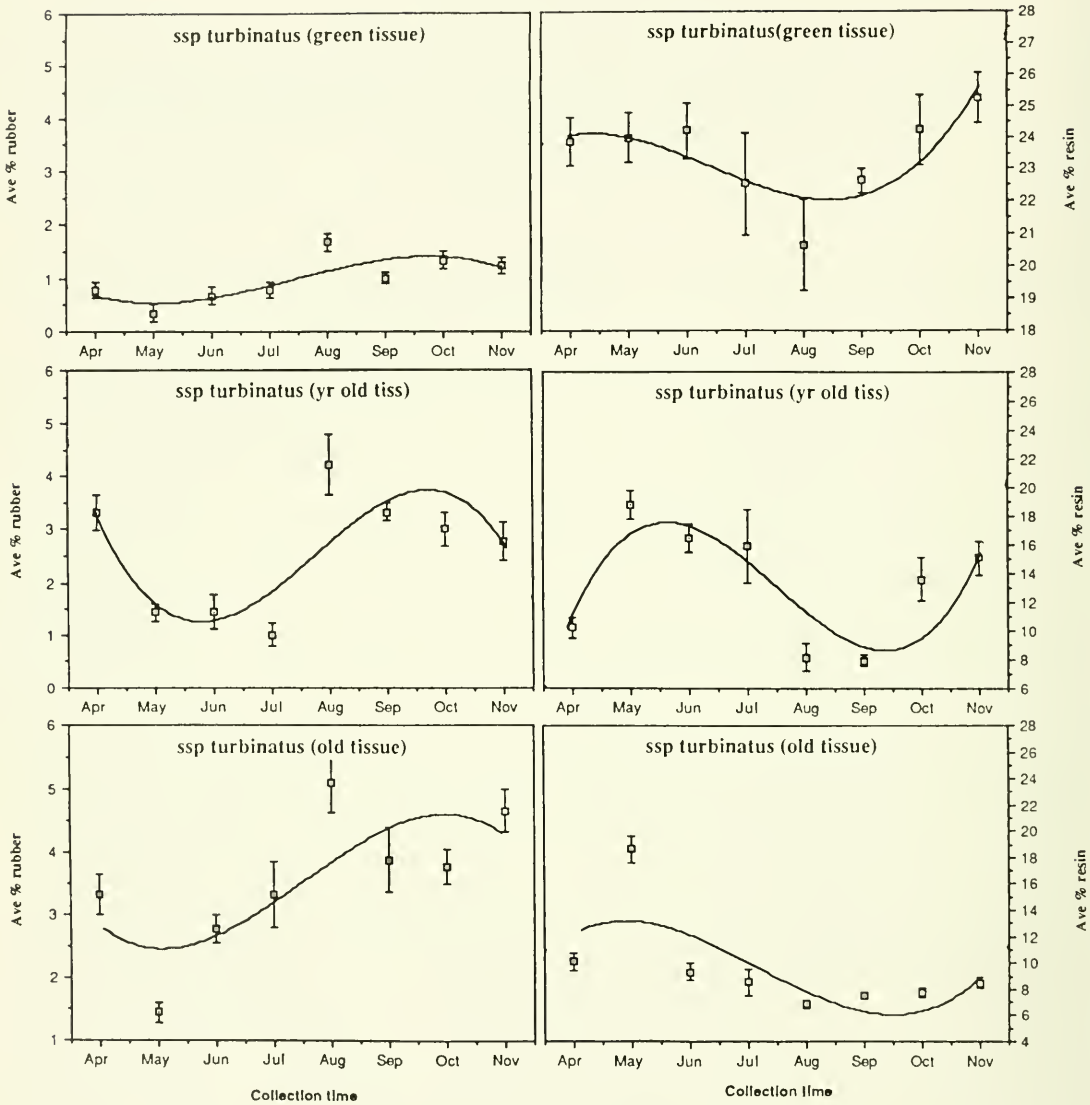

Fig. 1. Left: The average percentage of rubber in green tissue, year-old tissue, and several-years-old tissue of *Chrysothamnus nauseosus* ssp. *turbinatus* during the growing season at Goshen, Utah. The vertical lines are standard error bars. Right: The average percentage of resin in green tissue, year-old-tissue, and several-years-old tissue of *Chrysothamnus nauseosus* ssp. *turbinatus* during the growing season at the Goshen, Utah, site. The vertical lines are standard error bars (Hegerhorst et al., Seasonal changes, 1987).

months of April through November 1986. The plants are in a dormant state during the winter months because of the cold, and often freezing, temperatures. The temperature and precipitation were recorded by the state weather station of Goshen, Utah. Random samples of new growth (current growth), one-year-old tissue, and tissue older than one year were clipped from three different plants each month. The samples were bagged and taken to the laboratory where they were frozen at −20 C. Following the last collection period, all of the samples were ground in liquid nitrogen using a motorized steel mortar and pestle. Liquid nitrogen grinding was used to prevent the loss of volatile compounds due to enzyme hydrolysis during the grinding process. Compounds of interest were extracted from 2 g of tissue using three portions of cyclohexane. The tissue was extracted in a 125-ml

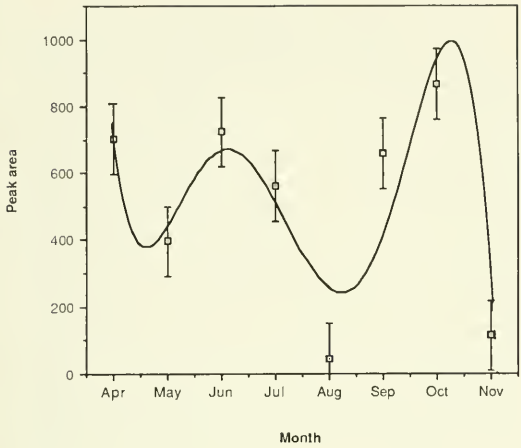

Fig. 2. Total compounds from *Chrysothamnus nauseosus* ssp. *turbinatus* during the growing season at Goshen, Utah. The vertical lines are standard error bars (Hegerhorst et al., Seasonal changes, 1987).

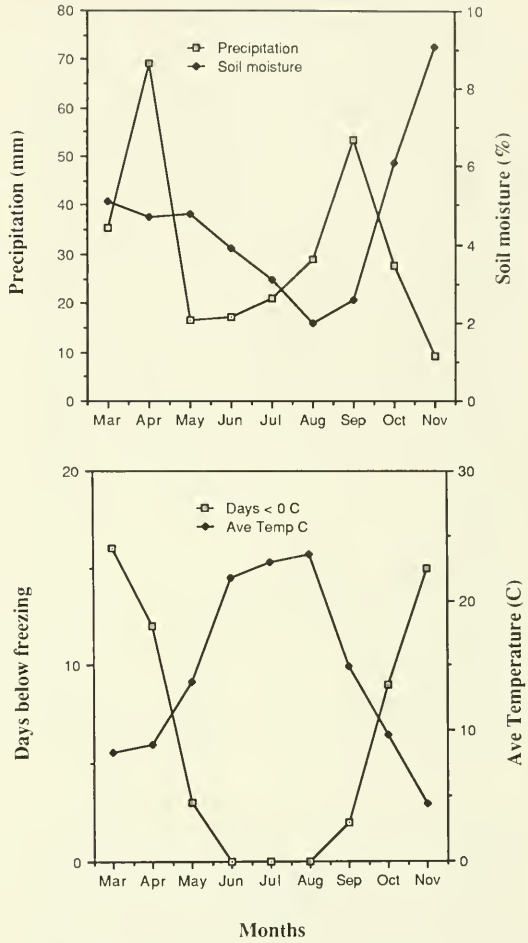

Fig. 3. The precipitation (mm) and soil moisture (upper figure), and average temperature (C) and days below freezing (lower figure) during the growing season at Goshen, Utah (Hegerhorst et al., Seasonal changes, 1987).

Erlenmeyer flask on a rotary shaker for 30 minutes at 160 rpm. The samples were filtered using a coarse, sintered glass funnel. The filtrate was reduced to 5 ml under nitrogen, and 50 μl of gamma terpinene (internal standard at 1 mg/ml) was added to 150 μl of sample. Analysis was carried out with a Hewlett Packard 5995C gas chromatograph-mass spectrometer (GC-MS). Partial identification of the compounds was done by comparing the mass spectral data to a library of about 87,000 compounds, using a Hewlett Packard HP 1000 computer linked with the GC-MS system (Hewlett Packard 1986). A cross-linked methyl silicon capillary column (0.20 mm) was used with a splitless injection system and a capillary-direct interface with the MS. Carrier flow was adjusted to 1.5 ml per minute, and the temperature gradient went from 35 to 290 C with a 10 C per minute ramp. The data from the triplicate runs were statistically analyzed. Chemical standards were also used to identify some of the compounds.

RESULTS AND DISCUSSION

A previous study (Hegerhorst et al., Seasonal changes, 1987), using the same plants collected at the same site, found a strong negative correlation between resin and rubber in rubber rabbitbrush ($r^2 = -.64$, $p = .03$). Figure 1 represents the changing pattern of rubber and resin content through the growing season. As resin content increased, rubber content showed a decrease. This could be significant if the energy used to synthesize these compounds could be directed into rubber. In this research we investigated specific resinous compounds and their relationship to rubber production. In the cyclohexane extraction the compounds were identified by GC-MS using the large computer spectra library (Hewlett Packard 1986). Figure 2 is a graph representing the sum of all the compounds, as determined by GC-MS, for each month in the growing season. The resin pattern in Figure 1 and the total compounds in Figure 2 are not identical, but they have similar patterns, with

TABLE 1. Compounds present in *Chrysothamnus nauseosus* ssp. *turbinatus* as determined by GC-MS and their GC retention time.

Name of the compound	Retention times	% of total
Sabinene	6.8	7.40
Myrcene	7.1	1.60
Cymene	7.6	11.5
Limonene	7.7	15.2
β cubebene	14.5	0.76
Δ cadinene	15.1	9.80
Cyclohexanol, 3 ethenyl-3-methyl-2-(1 methylethenyl-6-)	15.7	5.20
Unknown A	15.9	0.99
Epi-bicyclosesquiphellandrene	16.4	8.80
Unknown B	16.4	2.80
Unknown C	16.6	3.20
Unknown D	17.1	7.00
Unknown E	17.5	2.40
β elemene	17.6	1.60
Unknown F	17.9	0.78
Unknown G	18.3	3.20
Unknown H	18.7	0.56
C-27 branched hydrocarbon	26.2	0.34
C-28 branched hydrocarbon	27.6	0.46
Nonacosane C-29	27.9	1.70
C-29 branched hydrocarbon	28.5	0.41
Triacontane C-30	28.7	0.25
C-30 branched hydrocarbon	29.4	0.38
Hentriacontane C-31	29.8	1.30

the highest content in June and the lowest in August. Some of the difference between the graphs can be attributed to the variation in solubility of compounds between cyclohexane used in this experiment and the acetone-water mixture used in the crude resin extraction.

The resin content and the total monthly precipitation have limited similarity, with higher values in the spring and fall (Fig. 3). In the case of precipitation and rubber content it can be inferred from the data (Figs. 1 and 3) that a decrease in precipitation resulted in an increase in rubber content. This subspecies of rubber rabbitbrush grows in a very sandy soil and would be sensitive to high temperatures and low moisture (Fig. 3), which would cause water stress in the plant.

The compounds detected and their average concentration over the growing period in the cyclohexane fraction are listed in Table 1. Six compounds, sabinene, cymene, limonene, Δ cadinene, epi-bicyclosquiphellandrene, and 3 ethenyl-3-methyl-2-(1 methylethenyl-6-) cyclohexanol, represented 58% of the concentration of compounds detected. Limonene was the highest with 15.2% of the total.

There are also some interesting patterns that can be seen with specific compounds as compared with the rubber and resin content in rubber rabbitbrush during the growing season. For example, Figure 4a is the graph of a typical hydrocarbon. It is high at the beginning of the growth season (April) and increases more in May. The compound then decreases steadily through the remainder of the season. When we used a similar extraction and GC-MS analyses of callus tissue from rubber rabbitbrush, we found that the major secondary plant products being produced in the rapidly dividing callus cells were simple hydrocarbons. This seems to suggest that early in the season, as new shoots and leaves are rapidly expanding, the major secondary plant products are predominantly simple hydrocarbons.

The terpenes extracted in our analysis show a varied correlation in relation to the pattern for rubber content shown in Figure 1. Limonene is an example of a terpene that is negatively correlated with that of rubber production (Fig. 4b). On the other hand, β cubebene is an example of a terpene that is positively correlated with rubber production (Fig. 4d). Sabinene was low in the spring, had a peak in June, decreased in August, and was high in November, which was similar to resin production (Fig. 4c).

The changes in the individual compounds from rubber rabbitbrush for each month were rated and compared with the changing pattern of rubber and resin content. A similarity value was calculated using Statview 512+ (1986), and the compounds were grouped in relationship to rubber (Table 2) or resin (Table 3). The rubber pattern had the greatest similarity to the sesquiterpene cyclohexanol, 3 ethenyl-3-methyl-2-(1-methylethenyl-6-), which was also the compound that was the least similar to the resin pattern. In contrast, compounds that had a high similarity to the resin pattern were sabinene, limonene, unknown C, and unknown E (Table 3). All of these compounds were rated as having little similarity to the rubber pattern (Table 2). A rather interesting observation is that four of the patterns of the straight-chained and branched-chained hydrocarbons had little similarity to either rubber or resin (Tables 2 and 3). These compounds could be associated with cuticle and wax formation of the leaves.

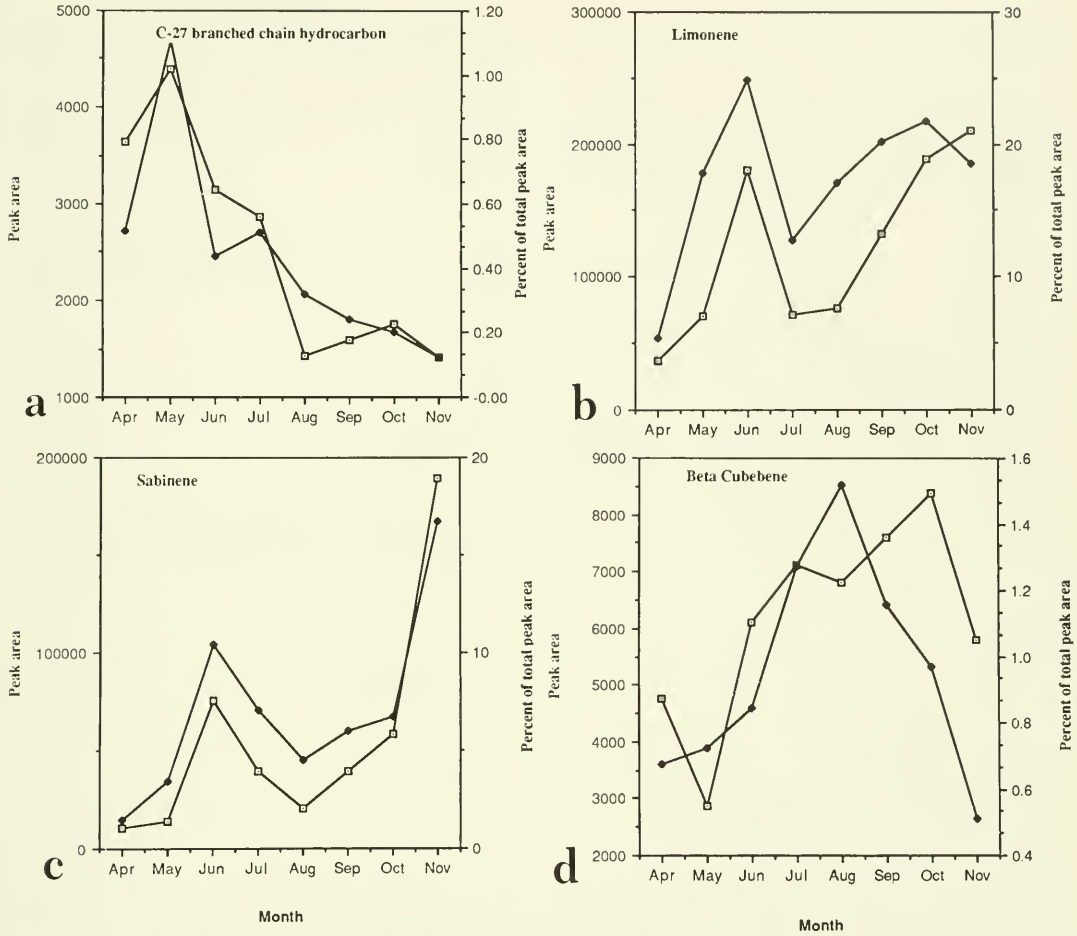

Fig. 4. Changes in C–27 branched hydrocarbon (a), limonene (b), sabinene (c), and β cubebene (d) from *Chrysothamnus nauseosus* ssp. *turbinatus* during the growing season at Goshen, Utah. The line with squares is based on the peak area, and the line with the black spots is based on the percentage of the compound in relation to the total area of the compounds.

Three of the sesquiterpenes, β cubebene, Δ cadinene, and epi-bicyclosesquiphellandrene, were common to both rubber and resin patterns at the intermediate similarity classification (Tables 2 and 3).

A correlation matrix and factor analysis of individual compounds to each other was determined by Statview 512+ (1986). A high correlation value indicated that the two compounds had a similar pattern during the growing season and could possibly be synthesized by the same pathway. Factor analyses of the data (Statview 512+, 1986) indicated that six factors were involved. The compounds in the six factors are listed in Table 4. Factor 1 contains long-chain hydrocarbons that form a group seemingly independent of the other compounds. The synthetic pathway to waxes is considered to be different from the rubber and resin pathways (Robinson 1983). Factor 3 had three compounds, including 3 ethenyl–3-methyl–2-(1-methylethenyl–6-) cyclohexanol, which all have a high correlation with the rubber content pattern. Factor 6 contains monoterpenes, which have a high correlation with the resin synthesis. The outlined pathway (Robinson 1983) in Figure 5 shows a pathway to monoterpenes. There is a branch point at isopentenyl pyrophosphate between monoterpenes and the pathways to the sesquiterpenoids, diterpenoids, and rubber. Rubber synthesis is considered to involve isopentenyl pyrophosphate and perhaps diterpenoids or similar compounds (Robinson

TABLE 2. Similarity of individual compounds over the growing season in *Chrysothamnus nauseosus* ssp. *turbinatus* in relation to total rubber content as determined by Statview 512+.

Compounds that are very similar to rubber pattern
Cyclohexanol, 3 ethenyl-3-methyl-2-(1 methylethenyl-6-)
Compounds that have some similarity to rubber pattern
Myrcene
β cubebene
Δ cadinene
Unknown A
Epi-bicyclosesquiphellandrene
Unknown G
Unknown D
C-28 branched hydrocarbon
C-30 branched hydrocarbon
Hentriacontane C-31
Compounds that have little similarity to rubber compounds
Sabinene
Cymene
Limonene
Unknown B
Unknown C
Unknown E
β elemene
Unknown F
Unknown H
C-27 branched hydrocarbon
Nonacosane C-29
C-29 branched hydrocarbon
Triacontane C-30

TABLE 3. Similarity of individual compounds over the growing season in *Chrysothamnus nauseosus* ssp. *turbinatus* in relation to total resin content as determined by Statview 512+.

Compounds that have high similarity to resin pattern
Sabinene
Limonene
Unknown C
Unknown E
Compounds that have some similarity to resin pattern
Myrcene
Cymene
β cubebene
Δ cadinene
Epi-bicyclosesquiphellandrene
Unknown D
Unknown F
Unknown G
Unknown H
Compounds not similar to resin pattern
Cyclohexanol, 3 ethenyl-3-methyl-2-(1 methylethenyl-6-)
Unknown A
Unknown B
β elemene
C-27 branched hydrocarbon
C-28 branched hydrocarbon
Nonacosane C-29
C-29 branched hydrocarbon
Triacontane C-30
C-30 branched hydrocarbon
Hentriacontane C-31

1983). Benedict (1986) used isopentenyl pyrophosphate as the substrate for rubber synthesis in guayule (*Parthenium argentatum*). While more investigations are needed to determine the synthesis pathways of the different compounds in rubber rabbitbrush, our results provide some support for the concept that rubber and resin synthesis pathways are different (Fig. 5).

Benedict (1986) found that the enzymatic synthesis of rubber was induced by cool temperatures and that the enzymatic incorporation of isopentenyl pyrophosphate occurs on the surface of subcellular rubber particles. The rubber synthesis did not begin until the cool months of October and November (Bucks et al. 1986). The enzymatic activity of cis isopolyisoprene polymerase was related to the number of hours at 13 C and below. While the process of rubber synthesis in rubber rabbitbrush has not been studied as it has been in guayule, it is obvious that regulatory genes for the cis isopolyisoprene polymerase in rubber rabbitbrush would have to function in response to heat or stress signals rather than cool temperatures. Although not clearly demonstrated, evidence suggests that the pathway from mevalonic acid to cis-isoprene is more closely tied to the formation of some terpenes than others. Figure 5 gives a diagrammatic explanation of the possible relationship between terpene formation and that of natural rubber from cis-isoprene. While the changes in rubber and resin content imply an interconversion, radioactive tracer studies are needed to verify the concept. The significance of elucidating the exact relationship that exists between the resin and rubber formation is in controlling the flow of energy from terpene production into natural rubber. If environmental signals such as high temperature, low moisture levels, and water stress could be imitated, it may be possible to favor the conversion from mevalonic acid and certain terpenes to natural rubber, rather than to monoterpenoids.

TABLE 4. Individual compounds present in the factors as determined by factor analyses by Statview 512+ in relation to each other over the growing season in *Chrysothamnus nauseosus* ssp. *turbinatus*.

Factor 1
C-27 branched hydrocarbon
C-28 branched hydrocarbon
Nonacosane C-29
C-29 branched hydrocarbon
Triacontane C-30
C-30 branched hydrocarbon
Hentriacontane C-31
Factor 2
Δ cadinene
Unknown D
Unknown F
Unknown B
Unknown H
Factor 3
Cyclohexanol, 3 ethenyl-3-methyl-2-(1 methylethenyl-6-)
Epi-bicyclosesquiphellandrene
Unknown C
Factor 4
Unknown A
Unknown E
β elemene
Unknown F
Factor 5
β cubebene
Factor 6
Sabinene
Myrcene
Cymene
Limonene

ACKNOWLEDGMENT

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LITERATURE CITED

BENEDICT, C. R., ED. 1986. Biochemistry and regulation of cispolyisoprene in plants. NSF Workshop, Texas A & M University, College Station. 251 pp.

BUCKS, D. A., F. S. NAKAYAMA, AND S. G. ALLEN. 1986. Regulation of guayule rubber content and biomass by water stress. Pages 161–173 *in* C. R. Benedict, ed., Biochemistry and regulation of cispolyisoprene in plants. NSF Workshop, Texas A & M University, College Station.

HEGERHORST, D. F., D. J. WEBER, AND E. D. MCARTHUR. 1987. Resin and rubber content in *Chrysothamnus*. Southwestern Naturalist (in press).

HEGERHORST, D. F., D. J. WEBER, E. D. MCARTHUR, AND A. J. KHAN. 1987. Chemical analysis and comparison of subspecies of *Chrysothamnus nauseosus* and related species. Biochemical Systematics and Ecology 15: 201–208.

HEGERHORST, D. F., D. J. WEBER, R. B. BHAT, T. D. DAVIS, S. C. SANDERSON, AND E. D. MCARTHUR. 1987. Seasonal changes in rubber and resin in *Chrysothamnus nauseosus* ssp. *hololeucus* and ssp. *turbinatus*. Biomass. (In press.)

HEWLETT PACKARD. 1986. RTE–6 VM data system manual. Hewlett Packard.

MCARTHUR, E. D., A. C. BLAUER, A. P. PLUMMER, AND R. STEVENS. 1979. Characteristics and hybridization of important intermountain shrubs. III. Sunflower family. USDA Forest Service Research Paper. INT–220. 82 pp.

OSTLER, W. K., C. M. MCKELL, AND S. WHITE. 1986. *Chrysothamnus nauseosus:* a potential source of natural rubber. Pages 389–394 *in* E. D. McArthur and B. L. Welch, comps., Proceedings—symposium on the biology of *Artemisia* and *Chrysothamnus*. USDA Forest Service, Gen. Tech. Rept. INT–200. Ogden, Utah.

PIERSON, R. M. 1975. Use of natural rubber. *In:* W. G. McGinnies and E. F. Haase, eds., An international conference on the utilization of guayule. Office of Arid Lands Studies, University of Arizona, Tucson.

ROBINSON, T. 1983. The organic constituents of higher plants: their chemistry and interrelationships. 5th ed. Cordus Press. 352 pp.

STATVIEW 512+. 1986. Statistical methods for the Macintosh. Brainpower, Inc., Calabasas, California. 180 pp.

WEBER, D. J., T. D. DAVIS, E. D. MCARTHUR, AND N. SANKHLA. 1985. *Chrysothamnus nauseosus* (rubber rabbitbrush): multiple-use shrub of the desert. Desert Plants 7: 180, 208–210.

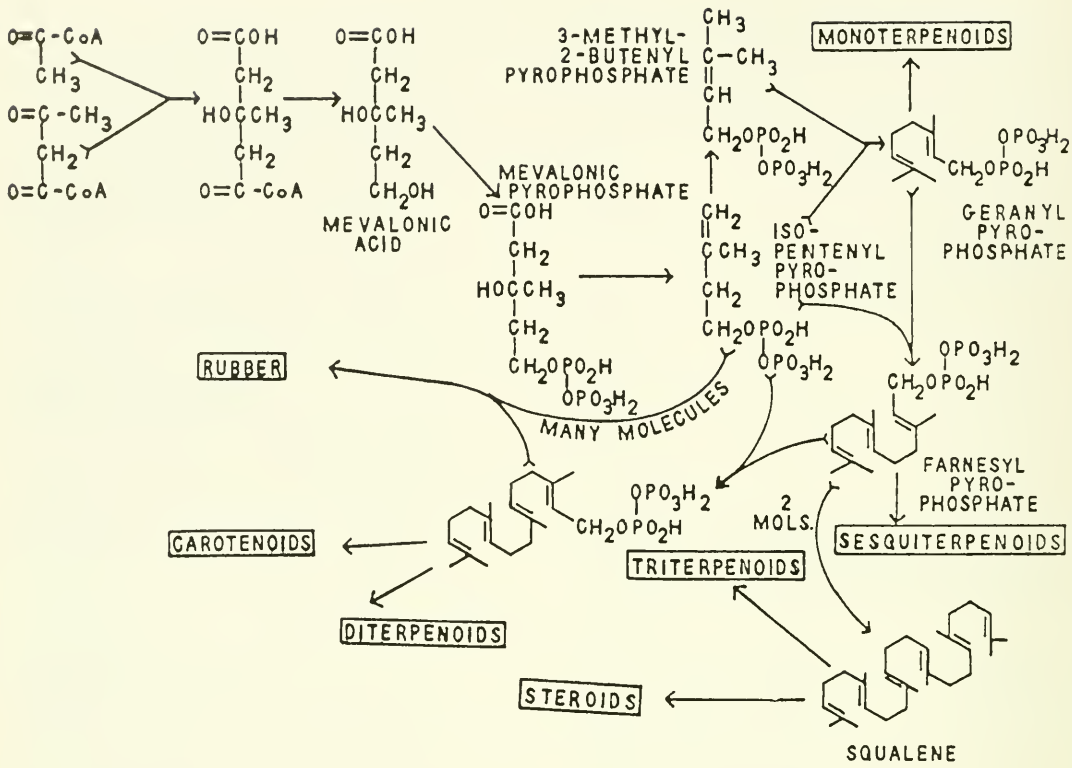

Fig. 5. Simple diagram of mevalonic acid pathways to hydrocarbons and rubber. Modified from Robinson (1983).

UTAH BOTANICAL EXPLORER CHARLES CHRISTOPHER PARRY (28 AUGUST 1823–20 FEBRUARY 1890)

Stanley L. Welsh[1]

ABSTRACT.—The Utah botanical contributions of Charles Christopher Parry are discussed. Especial emphasis is on his trips to Utah in 1874 and 1875. Plants taken during those years, which were subsequently listed as type-specimens, are listed. Insight is gained into this window in Utah botanical history through his letters to Dr. George Engelmann and limited correspondence from Engelmann and Joseph Ellis Johnson.

When medical doctor and professional botanist Charles Christopher Parry arrived in St. George on 5 April 1874 (Parry letter BRY), Utah's Dixie was essentially unexplored botanically. Prior to his trip, this part of the Southwest had been visited by John Charles Fremont in 1844 (Fremont 1845), French naturalist J. Remy in 1855 (Parry 1875a), and Dr. Edward Palmer in 1870 (McVaugh 1956, Parry 1875a), each of whom had collected plants in or near present-day Washington County.

It is not certain that Fremont collected in southern Utah specifically, but it is known that he took plants from immediately south of Utah near present-day Littlefield on 9 May 1844. He traversed the region quickly from the Virgin River to Mountain Meadows, where he remained for one day, resting from his harrowing trip across the Mohave (Fremont 1845). Parry (1875a) notes that in 1855 "a French naturalist, named J. Remy, passed over this route from Salt Lake to Los Angeles, and made a scanty collection of plants on the journey, which were afterwards deposited in the Paris Museum." In his letter dated 8 October 1874, Parry enquired of Dr. George Engelmann at St. Louis Missouri if he knew anything about the Frenchman J. Remy, "who collected plants on the way from Salt Lake to S. California and Virgen valley sometime in 1854? Specimens deposited in the Paris Mus. Did he publish anything? and what date, &c &c &c????." The questions anticipated Parry's (1875) publications in the American Naturalist (Amer. Naturalist 9: 14–21; 139–146; 199–205; 267–273; 346–351).

Doctor Palmer, a friend of Parry's employed by the Department of Agriculture and the Smithsonian Institution, came to St. George in the spring of 1870 at the suggestion of Parry (Parry 1875a). Palmer collected plants in the St. George vicinity for only about 10 days prior to leaving for St. Thomas, Nevada. During that trip he collected the types of seven Utah plant taxa. In 1877 he returned and collected the types of some 51 additional taxa from Utah, many of them from the southern part (Welsh 1982).

Parry's sojourn in the St. George vicinity in 1874 resulted in the collection of 37 of a total of 38 type-specimens recognized by various authors as requiring description (Welsh 1982). The solitary type taken during 1875 was that of *Festuca dasyclada* Hackel ex Beal. He named only three plant taxa from Utah during the period (Welsh 1982), depending on others to name plants of his taking. The plants named by Parry are *Oenothera johnsonii* Parry, *Gilia filiformis* Parry ex Gray, and *Shepherdia rotundifolia* Parry. The latter is based on material collected "on bare clay soil in the upper valley of the Virgen, A. L. Siler, 1873." The others are based on Parry's own collections.

The life of Parry has been summarized in several publications, the most important of which are Biographical Sketch of Dr. C. C. Parry (Preston 1897), Charles Christopher Parry (Malone 1962), and Utah Plant Types—Historical Perspective 1840 to 1981—Annotated List and Bibliography (Welsh 1982).

Parry was born 28 August 1823 in Admington, Gloucestershire, England, the son of Joseph and Eliza Parry. His family moved to

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the United States in 1832, settling on a farm in Washington County, New York, when Charles was nine years old. He obtained an A.B. degree in 1842 from Union College and went to graduate school at Columbia College, where he took an M.D. degree in 1846. At Columbia he came under the influence of John Torrey, professor of chemistry, but in reality a pioneer plant taxonomist. Following completion of graduate studies, Parry settled in Davenport, Iowa.

Following 1849, Parry devoted nearly 40 years to botanical exploration of western states and territories, either privately or as a member of some governmental expedition. He was the first person to serve as botanist for the United States Department of Agriculture. Parry was at the Smithsonian Institution from 1869 to 1871, organizing collections from government-sponsored expeditions.

Parry spent much time in Colorado, where he discovered *Picea engelmannii* and named peaks for Asa Gray and John Torrey. California became something of an obsession to him. He visited there more and more in the 1870s and 1880s, where he became interested in chaparral, finally publishing on *Manzanita* and *Ceanothus*. Many new taxa were discovered by him during the course of almost 40 years of collecting. He died at his home in Davenport, Iowa, on 20 February 1890.

Parry's herbarium and papers are at Iowa State University (ISC); they were sold to the university by his widow in 1895.

Parry was in Utah during portions of 1874, 1875, and 1877 (with Palmer). The main year of exploration was 1874, when he visited St. George and worked out of the home of Joseph Ellis Johnson in Washington. In 1875, Parry worked out of Spring Lake, Utah, where he lived at the home of Benjamin F. Johnson (brother of Joseph Ellis Johnson). Originals of letters written by Parry to George Engelmann, and from George Engelmann and Joseph Ellis Johnson to him, are in the library at Iowa State University. Copies of some of the letters are at the herbarium of Brigham Young University.

Insights into Parry's days of collection at St. George in 1874 especially are to be found in those letters. They are filled with botanical discussions and other information about the aspirations and expectations of the lives of the participants. While most of the letters are from Parry to George Engelmann, and must have been returned following receipt by Engelmann, additional letters to Asa Gray and other correspondents are hinted at.

The selected letters are too long to be reproduced here in their entirety, and much of the information is not of botanical importance. I have selected for reproduction two complete letters and portions of others that might add insight to the botanical understanding of the period and to the personality of the characters involved. They afford a window into a time no one now living has experienced. The extracts are reproduced as exactly as possible from the handwritten pages, except for underlining of scientific words. Words misspelled are indeed spelled that way in the letters; after all, the letters were not edited and not intended for publication. Within the letters, scientific names were often written without underlining. I have chosen to underline them routinely, so as to avoid the inevitable "sic" quotation. Parry chose to spell Virgin as Virgen. I have not changed his original spelling. Notations in brackets are my editorial notes.

Knowledge of the flora of the region around St. George was strictly limited. The nature of the vegetation was largely a mystery. Botanists in the East were grasping for any material possible to clarify the thin line of specimens, often mere fragments, then available for study. Parry and his correspondents used each other as sounding boards to test the understanding of the taxonomy of the time. They discussed the taxa, offered more complete descriptions, and traded (or sold) specimens. The evolution of taxonomic thought was advanced by their discussions.

Dr. George Engelmann, of St. Louis, Missouri, was interested in many groups of plants, but especially in conifers, cacti, and other succulents (including *Yucca*), and woody plants generally. Parry sent him specimens of these and many more. The Parry correspondence reproduced or quoted here is exclusively to Engelmann, accounting for the many references to the same kinds of plants.

Letters from Parry to Engelmann are addressed to "My Dear Dr." That dated 14 April 1874, which is reproduced here in its entirety, was sent from St. George (actually Washington, where Johnson's home was situated) and notes that he:

Reached here 5th inst just in time to hear Brighams farewell address to the faithful. Since then I have [been] tramping over hill and dell, walking and gathering up the many strange things that came in my way. I am in time to catch all early plants, the season being 3 weeks late (for my accomodation). Best news of all *Yucca brevifolia*, fide mail rider, is in full flower 30 miles from here, & [he] will bring it up on excursion next monday. Imagine my exultation, say tuesday, 21st, I can hardly wait. Not many varieties of cacti just about here. *O[puntia] rutilla* [probably *O. erinacea* var. *ursina* Parish] is here most common. I do not yet meet *E.* [*Echinocactus*, now *Neolloydia*] *johnsonii*. There is a large Turks head [*Ferocactus acanthodes*] near here, that I do not recognize. Am watching it. The Mormons individually call *Y[ucca] brevifolia* 'Joshua.' We have here Mesquite & *Larrea* near the north limits. I do not yet get sight of *Agave utahensis*. Glad to hear you think *Juniperus Utahensis* distinct from *J. occidentalis*. I am just now out of the range of *Juniperus* but will be in it again back & forth & send occasional 'instruction' specimens. I do not yet notice a uniform color to the fruit. The riper appear to assume a dull brown, though that may be the result of abortive seeds. I have occasionally seen a tendency to a dull blue with slight bloom. The trunk has a shreddy bark. Heart wood is dull red, slightly fragrant. Will get a section, usual size, of full grown trees — 20 ft? — in a clumpy shape — branching low down. It is a very common fire wood of the country. Where does it range? I send you today a branch from a woodpile that seems to show male fl. I also saw a fruited *Mamillaria*. There are hosts of nice things coming on. I am now giving special attention to the evanescent annuals before they take their leave. This is a wonderfully rich fruit district. All temperate & subtropical plants in abundance. I have never seen such a profusion of blossom. There is danger of late spring frosts, else I do not see what they cannot raise. Grapes [two words illegible] the California. As they say will be 100 degrees F. I see a common wild species [of grape]. So much to try of beginning — send in your ??? hooks. Yours truly C C Parry.

The Parry letter was answered by Engelmann as follows:

St. Louis Apr 24 1874. My Dear Parry: Your different packages have, I think all come to hand, the last were *Opuntia rutila* and today a trashy fragment without fl & fr of *Junip Utah*, but good as illustrating locality — firewood?, good!, harder, more compact than our cedar? Well, you will find *J. occid.* also and examine its wood and bark and perhaps *J. pachyphloea*, which you know. It comes from Prescott & Fort Whipple — wood, bark, ripe berries. Of course you can not now say anything about the (in the fall) ripe berries. I divide all our Junipers as such with red brown (glaucous bloom) dryish berries of fibrous texture, and such with bluish black (also bloom) juicy or pulpy berries, number of seeds variable in each:

I. Larger brown fibrous berries: 1) *osteosperma* with *Utahensis*, 2) *pachyphloea*

II. Smaller blue pulpy berries: 3) *occidentalis*, 4) *Virginiana*, 5) *Sabina*.

But with *Mamillaria*, you missed it! Why that is your old friend and early discovery *Mam. phellosperma*. First time that I see it fresh. Lord, but — the plant was too fresh and juicy, with the pride and pleasure of spring and [two words illegible]. Mail back [here] squeezed it to death — try again! Guaranteed there were good seed in those berries.

So you are among Joshua's Army, I hope they don't take you for a Philistine and pierce you with their daggers. But don't forget for heaven's sake, that these plants make suckers, which can be sent, ought to be sent. How would it do to send a whole box full of such young plants here — also of *Agave* and of *Y[ucca] baccata*. Or is this season not favorable, which I doubt, then Johnson might plant there and send in fall or early spring — smaller suckers by mail! Shall I send you a lot of stamps? A sort of inducement to use them well and use them soon.

My *Ech. Johnsoni* did not winter, it was never vigorous. Your Turk's head may be *Lecontei* or *Emoryi*.

You will recognize easily *Agave Utahensis* by the inflorescences (I saw flower stalks of last year) being spiked, flowers in pairs or 4s [?]. You know it does sprout.

Dr. [McClechamp?] keeps sending flowering oaks and I hope soon to set matters right and reconstruct/restore some of these condemmed scattered species.

Hope you send me flowers of *Yucca brevifolia* at once by mail. My article [?] of *Yucca* is now in printers hands with notes of *Yucca globosa* fruit etc. Of course you will look out for fruit of last year — gather as much as you can and find out about the position of the fruit — pendulous or erect.

Gilbert of Lieut. Wheelers Exped. has last fall collected *Arceuthobium* but I have written to you all about it on *Ab. douglasii [Pseudotsuga menziesii* (Mirb.) Franko], *Ab. Engelm.* & look out! Any oaks? in flower?

You ask about the range of *Junip. Utahensis* — Utah, Arizona, Nevada, and S. California [illegible word]. But the plant is not really distinct from *osteosperma* (*tetragona* var. *osteosperma* Torr.) which grows in California but ranges east to Zuni.

Don't forget to collect that wild grape — male flowers and fruit.

A few bundles of spms of that large Turk's head would be more acceptable to me [by] U.S. Mail I suppose.

I wish you could satisfy me about that 'fibrous bark of Juniper.' It would be a bad sell if I print the damned investigation and then some fellow comes and says it is all closet botany — old universe herbarium specimens — nothing like it is native! Some Mexican Junipers belong to one — another to the other class.

Now my best wishes for Johnson and yourself.

Yours ever. G. Engelmann.

Even though Engelmann formalized the name *Juniperus californica* var. *utahensis* in 1877 (Trans. Acad. Sci. St. Louis 3: 588), the discussion of *Juniperus osteosperma* versus *J. utahensis* would not be settled for many decades (Leafl. W. Bot. 5: 125. 1948). The combination of Torrey's var. *osteosperma* at specific rank under the genus *Sabina* by Antoine (Cupress.-Gatt. 51. 1857–60) provided an obstacle to later use of the specific epithet "*utahensis*," aside from the consideration of an earlier use of the name *Juniperus californica* var. *utahensis* by Vasey (Cat. Forest Trees U.S. 37. 1876).

Parry wrote to Engelmann on 21, 24, and 29

May. In his letter to Engelmann dated 3 June 1874, Parry indicated receipt of information that Engelmann had received "Joshua tree," and sent a sketch of flowers of *Yucca brevifolia* and actual flowers of *Y. angustifolia* [probably *Y. utahensis*], with a bug "which may do the fertilizing though I have not seen it in the *act*." Parry goes on to state that he had selected some yucca plants near his lodgings with the Joseph Ellis Johnson family for observation. "The plants were ruthlessly broken down by boys or cows?" Parry then looks forward to the possibility of joining Engelmann in Colorado.

In spite of the close of the spring-flowering season, Parry was still in St. George on 19 June. He chastises Engelmann for his interest in oaks. He opens his letter to Engelmann on that date with the following:

If I had you within reaching distance I should be strongly tempted to use an instructive cudgel of *Quercus emoryi* [*Q. turbinella* Greene] — to keep bothering me with the nasty things! As if it was not enough to loose the seat of my pants in scrambling over them to find old fruit & new flowers!!! Well the disaster above referred to is measureably repaired & now I am in better humor. I recognize here only the 2 oaks (evergreen) *Q. emoryi*, very variable, & deciduous leaved *Q. douglasii?* [*Q. gambelii* Nutt.].

Parry also indicated that he had taken *Vitis arizonica*, including male and female flowers and young fruit, for shipment to Engelmann. Also, Engelmann seems to have been interested in having more complete material of *Lewisia brachycalyx* Engelm. ex Gray, which had been published earlier (Proc. Amer. Acad. 7: 400. 1868). Parry writes:

I enclose in this [letter] a scrap of *Lewisia brachycalyx* Engelm., of which I have ample material to [amend] the characters. Petals in fully opened specimens have the length of the sepals, 1' [line] broad, whitish satin color with pink streaks. The plant is not very showy. The individual (- post fl.) buds being massed in the center of a circle of spathulate oblong leaves on the ground. Grows in boggy spring places. Pine Valley. 8000 ft!

Parry further states: "About Cacti, our common arborescent species is *O. echinocarpa* Engelm. & Big., a horrid thing with greenish yellow fls." And, further:

I have had some conversation with [Joseph Ellis] Johnson in reference to collecting plants & seeds for sale. He is anxious to do something in that way. He is pretty much broken down himself but has an active promising boy Charles who I hope will do some good work. I have given him some training and he is apt. They will make it a business to collect "Joshua," Agave, Cacti, to ship this fall. Johnson is very hard up & poor? (too much polygamy). It would be quite an encouragement if you could advance him say $20. He is perfectly reliable and will send everything to you to be disposed of to the best advantage so you will run little risk.

On 23 June 1874, Parry sent his "last flash" from St. George. He stated: "I am now packed & ready to leave in the morning for Cedar City or as you would have it *Juniperus osteosperma* var. *Utahensis* [city]." Parry includes a statement to Engelmann clarifying the location of "Beaver Dam." "It is the next SW tributary to the Virgen, was a frontier Mormon settlement till surveys showed it to be within the boundaries of Nevada [actually Arizona] and was then abandoned, also St. Thomas further south on the Muddy. I suppose Powell's maps will give latest geographical data, or Wheeler's. The Beaver Dam Mts. are the high range between here [St. George] and Beaver Dam Creek. I do not know their elevation."

A single letter dated 9 July 1874 from Parry to Engelmann is extant from Cedar City. Following a preliminary discussion on future plans to go to Davenport and return to Colorado with Mrs. Parry to meet the Engelmanns, Parry launches into his first love:

Now a word on botany. I sent you in paper a sprig of *J. utahensis* (July 4th). The fruit seems well formed but hardly mature enough for seed. I shall arrange here to have seed collected & sent on later. Did the berries reach you in their natural color — light green with glaucous bloom? I judge from specimens that they soon turn purple to brown. I send with this fr. & leaf of *Y[ucca] angustifolia* var. *latifolia!* as it grows here, fr. disturbed by the worms. *Op. rutilla* Nutt. looks different from St. George, fewer (coarse) spines & thin growth. Charlie Johnson will fill you out with *Op. echinocarpa* Engelm., seed & fr. Ask him for the common tree species and tell him what you want. Send postage stamps (not too large 6 & 14 cts). There will be a difficulty in getting ripe cones of *A[bies] concolor*. It must be watched closely & gathered within a week or less.

Parry notes that the Johnsons can "manage *Y. brevifolia* seed by the bushel if desired." Engelmann is told to "write encouraging to Johnson, but do not send money at first. Let him say what he will do."

Almost as an aside Parry indicates: "I met here by accident A. L. Siler, an odd specimen. He is collecting seeds and plants. I have advised him to send pines & oaks to you. He is living in a very choice mountain district east of here, is poor, shiftless, & lazy (fide Johnson), will need postage stamps. He gave me some seeds. I enclose a few of a remarkable Eleagnaceae."

Andrew Lafayette Siler, a Mormon rancher, lived at a place called "Ranch," reputedly near Kanab, but actually near the head of the Sevier River, between present-day Long Valley Junction and Hatch near the Kane-Garfield county line. Siler collected plants in Kane and adjacent Mohave (Arizona) counties. He was interested in cacti and took a collection of a low depressed-hemispheric ball-cactus, which was named by Engelmann as *Echinocactus sileri* (later *Utahia sileri* [Engelm.] Britton & Rose; now *Pediocactus sileri* [Engelm.] L. Benson). The cactus was later found in Utah. His most important find appears to be *Shepherdia rotundifolia* Parry. Jones (Contr. W. Bot. 16: 46–47. 1930) says of Siler: "He was about seven feet tall and slim as a rail, and wore about a No. 14 shoe. He was awkward and uncouth, but a real man."

Following his contact with Parry in Cedar City, Siler corresponded with both Engelmann and Parry. He collected seeds of various plants for sale to Engelmann and others. Parry notes the collection of 50 pounds of *Abies concolor* seed for sale by Siler, and in another place he wrote that Siler expected to make a thousand dollars that year selling seeds and specimens. Both Parry and Engelmann scoffed at the idea; they sent him stamps and occasional payments of a dollar.

The reference to the seeds of the "remarkable Eleagnaceae" were to be the subject of discussion in several of Parry's letters to Engelmann during the last months of 1874 and much of 1875. They turned out to represent *Shepherdia rotundifolia* Parry.

Parry found himself somewhat of a celebrity upon his return to Davenport. He had, after all, returned from among the Mormons, with their peculiar polygamous life-style. Parry's letter of 23 February 1875 to Dr. Engelmann notes: "I am through with my lecture 'Utah & the Mormons.' So I can't sympathize with you. It netted our Acad. Sciences $2.50????" Evidently, preparation for his Mormon lecture had led him to enquire of the events surrounding the Mountain Meadows Massacre, which had taken place in 1857 some 25 miles due north-northwest of St. George. His source of information was Joseph Ellis Johnson, who wrote to him on 30 January 1875. Johnson opens the letter with greetings and then recounts family and neighborhood happenings. The temple was under construction and "up to middle of the first story." Johnson had his "wine and curing house up and closed in." Finally, having put off the question for as long as possible, he states:

> Well I have written everything I can think of and will now change subject to the subject of your lecture. The M.M.M. [Mountain Meadows Massacre] occurred in that exciting period when Johnson's army was striving to enter S L Valley, the people off here 350 miles south from settlements on the road — no mail facilities — nervously guarding and watching for a part of the army to come, Via New Mexico, Colorado or California — All uncertainty & excitement — Indians highly excited against 'Americats' (white emigrants) who from the time of Fremont's visit, who shot 8 indians near here, and generally after they (Emigrants) have shot Indians at sight — Then the company from Ark. [Arkansas] while at Corn Creek lost an ox & the Indians Eat of it & 8 died immediately — These Indians followed and raised all others on the route — and no doubt under the excitement some of our vengeful ones might have joined — we don't *know*, but so I believe and the deed was done — The Indian Chief at Parowan was advised by the Bishop not to go — he stayed[?], but was brought two yoke of oxen by his men.

Johnson then defended the Mormon church and its officials, stating that it was the policy at the time to "cripple the enemy in means but not in men. . . . They sent an express to B. Y. [Brigham Young], asking shall we protect them or fight them? The answer came by swift messenger 2 days too late — 'protect & pass them safely through the country' from B. Young."

It would be interesting to know how the information was used in the Parry lecture on the Mormons, whose polygamous life-style impressed him negatively.

There are two letters from Parry to Engelmann from Spring Lake, Utah, in the summer of 1875. The first is dated 8 July 1875. In it Parry discusses *Abies concolor*, other plant species, and the nature of Utah Lake. Of the latter, Parry says, "I have been over on a trip to the head of Lake Utah, a nice sheet of water but poor in botany." He had anticipated going to St. George in the autumn but decided to go to California instead. He discusses some of the forest trees of Utah and gives their common names as follows: "*Abies concolor* is called here 'Black balsam' and is cut for R R ties, considered good timber. *A. grandis* [probably *A. lasiocarpa*] is 'White balsam' and considered worthless. 'Red pine' is *A. douglasii* & 'White pine' *A. Engelmannii*."

A portion of the 1875 season was spent in a mountain cabin remote from Spring Lake, but

there is no reference to where collections were actually made, except for Mt. Nebo and vicinity.

In the letter dated 28 August 1875, Parry notes: "I expect Mrs. Parry next week, will go to meet her at Salt Lake, bring her down here to introduce her to the polygamists &c & leave for California about 20th Sept."

Thus, Parry closes out his second trip to Utah.

List of C. C. Parry Type-Specimens

Arctomecon humilis Cov., Proc. Biol. Soc. Washington 7: 67. 1892.
Washington Co., Utah, near St. George, Parry sn 1874 (US!; NY!).
Papaveraceae.

Parry (1875b) says, in reference to this plant:

Amid the more unusual forms of undergrowth, made familiar in my rambles near St. George, my attention was drawn at a single locality to a showy Papaveraceous plant, with nodding white flowers, in which I was delighted to recognize the *Arctomecon Californicum* Torr. (No. 6), collected only by Fremont thirty years ago, and figured and described in his report from a single specimen. The present collection, since supplemented by mature fruiting specimens, furnishes the means of completing the description of this interesting plant, which seems to differ from the original figure in its less hairy leaves, four (not six) valved capsule and more caespitose habit. The fruiting specimens show marcescent petals, persisting after the maturity of the seed, and an eversion of the upper third of the triangular valves, leaving the placental ribs connected at the summit with the united stigmas forming a basket in which the shining black seeds lie loosely like so many eggs. The plant is apparently biennial, with deep tap roots, the broken stem and leaves giving out a yellowish sap. In the two localities where found it grew in a loose marly soil, strongly impregnated with Gypsum.

The protologue of *Arctomecon* and its only species, *A. californicum*, in the appendix of the second Fremont expedition included the descriptions of the petals "about an inch long, yellow" (Fremont 1845). The discrepancy seems to have been lost on Parry, but with only the description by Torrey for comparison, it is not easy to now fault Parry.

The species was not published until two years following Parry's death.

Asclepias leucophylla Engelm. in Parry, Amer. Naturalist 9: 348. 1875.
Washington Co., Utah, near St. George, Parry 207, 1874 (MO). Asclepiadaceae *A. erosa* Torr.

In Parry's letter to George Engelmann dated 23 February 1875 is a comment on his specimen No. 207. Parry says: "But there is something in your line. I am not quite clear about No. 207, which Gray says is near *Asclepias eriocarpa* Benth. I doubt this, as the habitat and location is quite familiar, grows 4–6 feet. What do you say?" The answer is not present among the correspondence examined, but obviously Engelmann agreed that specimen No. 207 was not *Asclepias eriocarpa*. In another letter to Engelmann, dated 27 March 1875, Parry says: "I have nothing to help out *Asclepias eriocarpa*, No. 207, grows in dry sandy washes of the Virgen, 3–5 feet, curious mottled leaves. I do not think it is either of the California sp." On 29 April 1875, in another letter to Engelmann, Parry further states: "I have seen *Asclepias* here [he was writing from Brooklyn, New York, and had visited the Torrey herbarium] & at Philadelphia, including several specimens of *A. eriocarpa* and *A. vestita*, confirming your diagnosis of *A. leucophylla*, but yesterday at Torrey herb I saw an unmarked specimen from Vera Cruz (Hatsted), the exact counterpart of ours? I send some flowers to compare, not having any specimen of *A. leucophylla* here. If it agrees, is not the taller likely to prove a descended Mexi[can] sp.?"

Astragalus eremiticus Sheld., Bull. Geol. & Nat. Hist. Surv. Minnesota 9: 161. 1894.
Washington Co., Utah, Beaver Dam Mountains, C. C. Parry 45, 8 May 1874 (MINN; US!).
Leguminosae

Parry (1875b) notes that No. 45 (identified as *Astragalus arrectus*) was taken "at our nooning place [Beaver Dam Mts.], having reached an elevation of not less than one thousand feet above the valley of the Virgen, a deep gorge in the limestone rocks afforded a scant supply of water." *Astragalus eremiticus*, the hermit milkvetch, remained unnamed until four years following Parry's death.

The opportunity to travel to the Beaver Dam Mountains is reported by Parry (1875b). He describes the route as crossing the Santa Clara near its mouth (confluence with the Virgin) and proceeding up one of the "dry washes" leading more directly toward the mountain slope. The site of the "nooning" is not known, but could be the head of Cedar Pocket Wash, which is crossed by the historic road between St. George and Las Vegas. Other plants cited by Parry as being collected with *Astragalus arrectus* are *Oenothera*

[Camissonia] pterosperma Watson (No. 70), a tall *Phacelia* of a climbing habit with foliage resembling *P. tanacetifolia* (probably *P. vallis-mortae*), *Phacelia ramosissima* Benth. (No. 184), and a robust, showy form of *Eriogonum ovalifolium* Nutt. (No 241).

The numbers of the specimens are not traditional collection numbers. Instead, they are exiccatae numbers assigned as the specimens were placed in sets for distribution.

Astragalus megacarpus (Nutt.) Gray var. *parryi* Gray ex Wats., Bot. California 1: 148. 1876.
Iron Co., Utah, near Cedar City, Parry 51, 1974 (GH; US!; NY!).
Leguminosae

"After spending a few days very pleasantly in the rude homes of these hospitable herders, I returned to Cedar city, by a very direct trail, leading down the steepest part of the mountain slope. On this route I was fortunate in securing good fruiting specimens of *Astragalus megacarpus* Gray (No. 51), hitherto only known from Nuttall's original specimens" (Parry 1875c).

Parry wrote last to Engelmann on 23 June 1874, noting: "This is my last flash from St. George. I am now packed & ready to leave in the morning for Cedar City or as you would have it *Juniperus osteosperma* var. *Utahensis* [city]!!!" He must have arrived there within the next few days, possibly as early as 25 or 26 June. Only one letter from Parry to Engelmann, dated 9 July 1874, is from Cedar City. That letter looks forward to a trip later that year to Colorado, where Parry expected to be joined by Engelmann.

Cordylanthus parryi Wats. in Parry, Amer. Naturalist 9: 346. 1875.
Washington Co., saline marshes in valley of the Virgen, Parry 155, 1874 (US!; NY!).
Scrophulariaceae = *C. maritimus* ssp. *canescens* (Gray) Chuang & Heckard

Cuscuta denticulata Engelm. in Parry, Amer. Naturalist 9: 348. 1875.
Washington Co., St. George (on *Coleogyne*, *Biscutella* [*Dithyraea*]), Parry 205, 1874 (US!; NY!).
Cuscutaceae

Parry (letter from Davenport, Iowa, dated 8 October 1874) pressed Engelmann: "I want you to look again at the *Cuscuta* parasitic on *Coleogyne*. It cannot be a form of *C. californica*, will look for more advanced plants." Possibly this need to have Engelmann "look again" led to the publication of *C. denticulata*.

Eremocarya muricata Rydb., Bull Torrey Bot. Club 36: 677. 1909.
Southern [probably Washington Co.] Utah, Parry 164, 1874 (NY).
Boraginaceae = *Cryptantha micrantha* (Torr) Johnst.

The collection was properly identified at the time (Parry 1875d) as *Eritrichium micranthum* Torr., the basionym of *Cryptantha micrantha*.

Eriogonum parryi Gray, Proc. Amer. Acad. 10: 76. 1874.
Washington Co., Utah, rocky slopes near St. George, May 1874 (US!; NY!).
Polygonaceae = *E. brachypodum* T. & G.

Eriogonum spathulatum Gray, Proc. Amer. Acad. 10: 76. 1874.
Sevier (?) Co., "Lower valley of the Sevier," Parry 245, July 1874 (GH).
Polygonaceae

This was likely taken on his return trip from Beaver to Salt Lake City.

Eriogonum subreniforme Wats., Proc. Amer. Acad. 12: 260. 1877.
Washington Co., Virgin River valley, Parry 237, 1874 (ISC!).
Polygonaceae

Eritrichium barbigerum Gray, Synop. Fl. N. Amer. 2(1): 194. 1878.
Washington Co., St. George, Parry 171, 1874 (NY?).
Boraginaceae = *Cryptantha barbigera* (Gray) Greene

Eritrichium pterocaryum Torr. var. *pectinatum* Gray, Proc. Amer. Acad. 10: 61. 1874.
Southern [probably Washington Co.] Utah, Parry sn 1874 (NY!).
Boraginaceae = *Cryptantha pterocarya* var. *pterocarya*

Parry (1875e) cites two collections of *Eritrichium pterocaryum* Torr., numbers 168 and 169.

Euphorbia parryi Engelm. in Parry, Amer. Naturalist 9: 350. 1875.
Washington Co., Utah, "St. George, in loose drifting sand," Parry 247, 1874 (MO).
Euphorbiaceae

Festuca dasyclada Hack. ex Beal, Grasses N. Amer. 2: 602. 1896.
Utah, Parry 93, 1875 (US!; ISC!; NY!).
Gramineae

This curious grass was taken by Parry in 1875 while he was a resident at the home of Benjamin F. Johnson. Parry was concentrating on collecting conifers for shipment to Dr. Engelmann. He made forays to Mt. Nebo, and possibly penetrated as far as the Strawberry Ridge or to the Wasatch Plateau. The

species in Utah is currently known from the margin of Strawberry Ridge near the Utah-Wasatch county line, the Wasatch Plateau, and the Table Cliff Plateau. This grass, named some six years following Parry's death, remained obscure for a long time, partially because of its remote habitats, but primarily because of its resemblance to *Stipa hymenoides*, which it simulates in growth form and habit of branching of the inflorescence. The *Stipa* is a common species through much of Utah and coexists with *Festuca dasyclada* on high-elevation Tertiary limestones and calcareous shales. Each plant must be examined with care to note the differences. This festuca is also known from Tertiary shales in Rio Blanco and Garfield counties, Colorado.

Gaillardia acaulis Gray, Proc. Amer. Acad. 10: 73. 1874.
Iron Co., "gypseous clay hills near Cedar City," C. C. Parry 120, July 1874 (NY!).
Compositae = *G. parryi* Greene, not Pursh

The name *Gaillardia acaulis* Gray is a later homonym of *G. acaulis* Pursh, the basionym of *Hymenoxys acaulis* (Pursh) Parker, hence *G. parryi* Greene.

Gilia filiformis Parry ex Gray, Proc. Amer. Acad. 10: 75. 1874.
Washington Co., Utah, "rocky slopes near St. George," C. C. Parry 187, April 1874 (NY!).
Polemoniaceae

Gray (1875a) cites the type locality as "Southern Utah, on the detritus of volcanic rocks, Dr. Parry."

Gilia latifolia Wats. in Parry, Amer. Naturalist 9: 347. 1875.
Washington Co., Utah, "Valley of the Virgen, near St. George," Parry 188, 1874 (GH; US!; CAS!; NY!; BRY).
Polemoniaceae

This plant is almost at the margin of its range at the type locality. The species extends into Utah in two areas: along the Virgin River into Washington County, and along the canyons of the Colorado into Kane, San Juan, and Wayne counties. Otherwise its distribution is through southern Nevada, northern Arizona, and southern California. *Gilia latifolia* is especially well adapted to growth on gravelly alluvial fans warmed early by spring sunshine and watered late by summer and winter rains.

Gilia scopulorum var. *deformis* Brand, Pflanzenr. 4. Fam. 250: 109. 1907.
Washington Co., Utah, "Sud Utah; Ohne nahere Angabe," Parry 198, 1874 (?).
Polemoniaceae = *G. scopulorum* Jones?

Parry (1875e) identifies his No. 198 as *Gilia inconspicua* Gray. The same identification is indicated for his No. 199, but he notes (1875e, p. 348): "Apparently distinct from the above form" (i.e., No. 198.).

Hamosa atratiformis Rydb., Bull. Torrey Bot. Club 34: 48. 1907.
Washington Co., Utah, Pine Valley Mts. (Parry 1875c, pp. 200–201), on "the lower dividing ridge to the north and west," Parry 47, 8 or 9 June, 1874 (NY!).
Leguminosae = *A. straturensis* Jones

This species was initially identified by Parry (l.c.) as *Astragalus atratus* Watson. Marcus E. Jones (1898) subsequently named the plant *A. straturensis*.

Langloisia setosissima var. *campyloclados* Brand, Pflanzenr. 4. Fam. 250: 171. 1907.
Washington Co., Utah, near St. George, C. C. Parry 190, May 1874 (US!).
Polemoniaceae = *L. setosissima* (T. & G.) Greene

Number 190 in the Parry list is identified as *Gilia setosissima* Gray. Parry (1875e) says of the plant that it is "a very neat and ornamental species, abundant on rocky slopes near St. George, May."

Lepidium georginum Rydb., Bull. Torrey Bot. Club 30: 253. 1903.
Southern Utah (Washington Co.?), C. C. Parry 19, 1874 (NY!).
Cruciferae = *L. lasiocarpum* var. *georginum* (Rydb.) C. L. Hitchc.

Parry's No. 19 was originally identified as *L. wrightii* Gray.

Lesquerella gordonii var. *sessilis* Wats., Proc. Amer. Acad. 23: 253. 1888.
Washington Co., near St. George (?), C. C. Parry sn 1874 (GH).
Cruciferae = *L. tenella* A. Nels.

Lupinus rubens Rydb., Bull. Torrey Bot. Club 34: 45. 1907.
Washington Co., near St. George, C. C. Parry 41, 1874 (NY!; ISC!).
Leguminosae = *L. pusillus* Pursh

Mammillaria chlorantha Engelm. in Wheeler, Rep. U.S. Geogr. Surv. W. 100th Meridian 6: 127. 1878.
Washington Co., Beaver Dam Mountains, C. C. Parry sn, 1874 (MO).
Cactaceae = *Coryphantha viripara* var. *deserti* (Engelm.) W. T. Marshall

The narrative of Parry's report (1874b) includes a solitary mention of this species. He

left St. George on 8 May 1874 on an excursion to the Beaver Dam Mountains, and, "On reaching a higher elevation on a continuous upward grade there was brought to view a greater profusion of plants and shrubbery, conspicuous among which may be noted *Audibertia incana* [probably *Salvia dorrii*] *Coleogyne ramosissima*, and a caespitose yellow-flowered *Mammillaria* (*M. chlorantha* Engelm., ined.)." Various authors have cited the type locality as "Southern Utah, east of St. George." The pale-flowered plants are currently known only from the Beaver Dam Mountains.

"*Mam. chlorantha* is forming seed but not yet in proper condition. I send in this parcel what I like to be *M. arizonica*, apparently distinct enough" (Parry letter of 23 June 1874 from St. George).

Specimens of an unnumbered *Mammillaria* are in the Parry herbarium at ISC (duplicate BRY). They were annotated as *Coryphantha vivipara* var. *arizonica* (Engelm.) W. T. Marshall by Lyman Benson in 1967. Possibly these are the basis of the reference to *M. arizonica*.

Mimulus parryi Gray, Proc. Amer. Acad. 11: 97. 1876.
Washington Co., Utah, near St. George, C. C. Parry 147, 1874 (NY!; US; BRY!).
Scrophulariaceae

The citation for No. 147 in Parry's (1875e) list is as follows: "*Eunanus* ——? A slender, large flowered showy annual, growing abundantly on gravelly hills near St. George; flowers mostly bright yellow. A light pink variety(?) was also met with later in the season."

Notholaena parryi D. C. Eaton, Amer. Naturalist 9: 351. 1875.
Washington Co., Utah, "Crevices of basaltic rocks near St. George," C. C. Parry 263, April 1874 (US!; BRY!).
Polypodiaceae.

Oenothera albicaulis var. *decumbens* Wats. ex Parry, Amer. Naturalist 9: 270. 1875.
Washington Co., Utah, "common in dry, sandy soil, near St. George, C. C. Parry 63, 1874 (GH?).
Onagraceae = *Oe. deltoides* ssp. *ambigua* (Wats.) W. Klein

Oenothera brevipes var. *parviflora* Wats. in Parry, Amer. Naturalist 9:271. 1875.
Washington Co., Utah, near St. George, C. C. Parry 74, 1874 (GH; MO; F).
Onagraceae = *Camissonia multijuga* (Wats.) Raven

Oenothera johnsonii Parry, Amer. Naturalist 9: 270. 1875.
Washington Co., Utah, near St. George, C. C. Parry 64, 1874 (ISC!).
Onagraceae = *Oe. primiveris* Gray

Parry (1875d) notes: "Common on all dry hills near St. George. Dedicated to J. E. Johnson, Esq."

Oenothera parryi Wats. ex Parry, Amer. Naturalist 9: 270. 1875.
Washington Co., Utah, "near St. George," C. C. Parry 72, May 1874 (US!; NY!; BRY!).
Onagraceae = *Camissonia parryi* (Wats.) Raven

"Abundant in bare gypseous clay hills near St. George; fl. May" (Parry 1875d).

Petalonyx parryi Gray, Proc. Amer. Acad. 10: 72. 1877.
Washington Co., Utah, near St. George, C. C. Parry 75, 1874 (NY!; BRY!).
Loasaceae

Parry (1874b) discusses this species as follows:

Among the rarities of this section must be noted a well marked new species of the peculiar southwestern genus *Petalonyx*, characterized by Prof. Gray as *P. Parryi* n.sp. (No. 75), this making a second recent addition to the genus. Of this only a single plant was met with, forming a low bush with remains of dead stalks, especially conspicuous at a distance from the faded leaves of the previous season's growth, exhibiting a pure pearly white. The delicate cream-colored blossoms, with exserted style and stamens, reminded one of *Lonicera*, but the polypetalous flowers and the peculiar hairy brittle leaves designated it at once as belonging to the Loasaceae. A diligent search over the dry gravelly and alkaline soil, where it was found associated with the common 'grease woods' of this region, failed to bring to light any other plants, so that this single locality, precariously situated within a stone's throw of the great Mormon temple, does not encourage the hope of a prolonged existence for the benefit of future botanists.

The plant from which the type material was taken has long since been eradicated. The species is, however, locally common on the Moenkopi Formation east of Washington, Utah.

Peucedanum parryi Wats., Proc. Amer. Acad. 11: 143. 1876.
Southern Utah (Washington? Co.), C. C. Parry 85, 1874 (NY!).
Umbelliferae = *Lomatium parryi* (Wats.) Macbr.

Phacelia cephalotes Gray, Proc. Amer. Acad. 10: 325. 1875.
Washington Co., Utah, near St. George, C. C. Parry 179, May 1874 (NY!; US!; BRY!).
Hydrophyllaceae

According to Parry (1875e), this species occurred "on bare clay soil in the valley of the Virgen." The label information on Parry 179 at BRY is "rock crevices, near St. George."

Phacelia pulchella Gray, Proc. Amer. Acad. 10: 326. 1875.
Washington Co., Utah, near St. George, C. C. Parry 182, May 1874 (GH; POM!; NY!; US!; BRY!).
Hydrophyllaceae

"Abundant on gypseous clay hills near St. George" (Parry 1875e). The species is referred to in the text (Parry 1875a) as *P. crassifolia* Torr. Of the species, he (l.c.) notes: "Hardly less showy [than *P. fremontii* Torr.] is the *Phacelia crassifolia* Torr. (No. 182), with flowers of an intense blue shade, thickly scattered over gypseous clay knolls. This latter species frequently becomes dwarfed in exposed places, and spreads out in the form of purple patches over the bare soil."

Platystemon remotus Greene, Pittonia 5: 190. 1903.
Washington Co., Utah, "Upper Santa Clara," C. C. Parry 8, 1874 (CAS!).
Papaveraceae = *P. californicus* Benth.

This is correctly identified in Parry's (1875d) list.

Platystemon rigidulus Greene, Pittonia 5: 167. 1903.
Washington Co., Utah, near St. George, C. C. Parry 8a, 1874 (CAS!).
Papaveraceae = *P. californicus* Benth.

Thelesperma subnudum Gray, Proc. Amer. Acad. 10: 72. 1874.
Iron Co., Utah, near Cedar City, C. C. Parry 109, 1874 (US!; ISC!; BRY!).
Compositae

Parry (1874c) notes: "Along the gravelly margins of Cedar Creek was found . . . *Thelesperma subnudum* Gray, n. sp." Gray (l.c.) cites the type locality as "St. George, Southern Utah, Dr. Parry." That error, having been copied from Gray, is perpetuated in Welsh (1982).

Trifolium confusum Rydb., Bull. Torrey Bot. Club 34: 46. 1907.
Iron Co., Utah, near Cedar City, C. C. Parry 35, 1874 (NY!; BRY!).
Leguminosae = *T. longipes* var. *brachypus* Wats.

This plant, called *Trifolium eriocephalum* Gray by Parry (1875d), is indicated as having been collected on the "Sheep range, Cedar City. July." Parry (l.c.) notes: "Having soon exhausted this scanty flora [near Cedar City], my attention was directed to the high mountain range of the Wahsatch, rising abruptly to the East, and overlooking the southern extension of the great interior basin. An ascent of about 3,000 feet in a distance of three miles, brings us to the outer crest of the range, which extends eastward in an irregular series of undulations to the upper Sevier valley." He further states: "Four miles back towards the interior of the range, the country expands into wide grassy slopes, and frequent springs and running streams bordered by snow drifts, give unwonted freshness to the pastoral scenery. Here is located the summer sheep range, and dairy farms of this district, of which the only apparent drawback to their attractive and productive features, is the annoying prevalence of blood-thirsty flies."

The flies are still there during the summer months.

LITERATURE CITED

FREMONT, J. C. 1845. Report of the exploring expedition to the Rocky Mountains in the year 1842, and to Oregon and north California in the years 1843–1844. House Rep. Doc. 199.

GRAY, A. 1875a. Contributions to the botany of North America. II. Proc. Amer. Acad. 10: 39–78.

———. 1875b. A conspectus of the North American Hydrophyllaceae. Proc. Amer. Acad. 10: 312–332.

JONES, M. E. 1898. Contributions to western botany. No. 8. Contr. W. Bot. 8: 1–43.

MCVAUGH, R. 1956. Edward Palmer. Plant explorer of the American West. University of Oklahoma Press, Norman. 430 pp.

MALONE, D., ED. 1962. Dictionary of American biography. 7: 261–262.

PARRY, C. C. 1875a. Botanical observations in southern Utah, in 1874. I. Amer. Naturalist 9: 14–21.

———. 1875b. Botanical observations in southern Utah. II. Amer. Naturalist 9: 139–146.

———. 1875c. Botanical observations in southern Utah. No. 3. Amer. Naturalist 9: 199–205.

———. 1875d. Botanical observations in southern Utah. No. 4. Amer. Naturalist 9: 267–273.

———. 1875e. Botanical observations in southern Utah. No. 5. Amer. Naturalist 9: 346–351.

PRESTON, C. H. 1897. Biographical sketch of Dr. C. C. Parry. Proc. Davenport Acad. Nat. Sci. 6: 35–45.

WELSH, S. L. 1982. Utah plant types—historical perspective 1840–1981—annotated list, and bibliography.

AGONISTIC BEHAVIOR OF THE CALIFORNIA GROUND SQUIRREL, *SPERMOPHILUS BEECHEYI*, AT AN ARTIFICIAL FOOD SOURCE

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ABSTRACT.—Occurrence of agonistic behavior patterns in *Spermophilus beecheyi* at a concentrated artificial food source was studied. Our data from 851 encounters are compared with previously published information from unmanipulated populations. Eight new behavior patterns (rump block, kick, forward shove, pounce, displacement grooming, circle fight, roll fight, and boxing fight) are described.

Because of the diversity of life-styles exhibited and habitats occupied by its member species, the squirrel family Sciuridae has provided biologists with a rich source of information on the evolution of mammalian sociality. Aspects of this work with ground squirrels have been discussed by, among others, Armitage (1981) and Michener (1983). A recent volume (Murie and Michener 1984) deals extensively with the biology of ground squirrels, including sociality. Biologists generally accept, however, that successful analysis of the evolution of behavior and sociality depends upon the prior cataloging of the behavioral repertoire of each species as an ethogram (Lehner 1979). Only when the extent and context of each behavioral action is understood can its adaptiveness be fully appreciated. For this reason, many works on the behavior of squirrels have been at least partially devoted to descriptions of behavioral actions.

Among the highly social ground squirrels, agonistic behavior has received considerable attention. Descriptions of postures and actions associated with agonism have been published for several species, among them *Spermophilus undulatus* (Watton and Keenleyside 1973, Steiner 1974), *S. armatus* (Balph and Stokes 1963, Clark and Russell 1977), *S. richardsonii* (Sheppard and Yoshida 1971), *S. columbianus* (Betts 1976, Steiner 1974), and *Ammospermophilus leucurus* (Fisler 1976). For the California ground squirrel, *Spermophilus beecheyi*, Owings et al. (1977) have described many agonistic behavior patterns, and Dobson (1983) has provided information on the timing, pattern, and form of agonism in this species. The purpose of this paper is to describe eight agonistic actions previously unreported in this species, all observed among individuals feeding at artificial, concentrated food sources; we also provide additional information concerning the context and frequency of agonistic actions previously described.

STUDY AREA

Two populations about 880 m apart were observed in the Santa Susana Mountains, north of Chatsworth, Los Angeles Co., California, from 27 July 1975 until 29 April 1976. Site 1 was relatively flat, at the head of a steep canyon (920 m elevation); Site 2 was a south-facing hillside (985 m elevation). Predominant vegetation at both sites was wild oats (*Avena fatua*), heavily grazed by cattle. The only other vegetation was a single, small coast live oak (*Quercus agrifolia*) and a small stand of California sagebrush (*Artemisia californica*) at Site 1. Grasslands of this sort are common habitats of *S. beecheyi* in southern California. The locality studied is well within the range of *S. b. beecheyi* (Hall 1981).

METHODS

Squirrels were live-trapped, sexed, weighed, toe-clipped for permanent identification, and dye-marked with Rodol-A. Trapping was continued sporadically throughout the study and toe-clipped animals re-dyed as necessary. Forty-eight animals (17♂, 31 ♀) were marked at Site 1, 44 (23♂, 21♀) at site 2. At Sites 1 and 2, respectively, 15 and 4

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animals were adults when first captured; all others at capture were young-of-the-year (hereafter termed young). By spring, all animals had attained adult size. No exchange of individuals between the two sites was noted.

Of the 50 observation days, 29 were in the fall prior to winter inactivity (3 September–4 December), 18 were in the spring mating, gestation, and lactation period (3 February–29 April), and 3 were in summer (13 July–19 August). Observations were made, sometimes with binoculars, from a car.

To encourage and intensify interactions, we filled four or five enclosed wooden boxes (20 × 20 × 25 cm) with seed (wild-bird mix) and placed them in various locations within the colony each observation day. Seeds fell into a 5 × 5-cm feeding tray on one side of each box where only one squirrel could feed at a time. Interactions among squirrels at each box were then recorded over a 3–4-hr period.

Most observations were made on 15 marked animals (7♂, 8♀) at Site 1 and 18 (11♂, 7♀) at Site 2; both adults and young were included. To avoid including animals of unknown biological and social status, we limited our analysis to interactions between two dye-marked squirrels. Kinship among animals was not known, but male-female pairs sometimes were identified.

RESULTS

New Behavioral Patterns

Behavior patterns previously unnoted in this species are described below. Where applicable, we use terminology applied by Fisler (1976).

RUMP BLOCK: A shifting of the rump position by a feeding animal so as to block another individual's approach.

KICK: A raising of and pushing with the rear legs against the flank of another animal.

FORWARD SHOVE: A pushing action with the forelegs while in an upright posture.

POUNCE: The leaping of one animal onto another so that all four of its feet are momentarily in contact with the back of the animal being attacked.

BOXING FIGHT: An action in which two animals stand briefly on their hind legs, face to face, and bat each other vigorously with their forepaws.

ROLL FIGHT: An intense fight in which two individuals roll over and over in a tight ball, frequently with considerable clawing and biting.

CIRCLE FIGHT: An intense fight in which two squirrels chase each other in a tight circle.

"DISPLACEMENT" GROOMING: A very brief (4–5 sec), elaborate "washing" motion, starting with a vigorous rubbing action with both forepaws on the face and ears, then proceeding rapidly down the entire body to the tail tip. Because the action appears out of context, typically interspersed among intense agonistic encounters, we interpret it to be "displacement" behavior.

Occurrence of Behavior Patterns

Here we consider the context and frequency of occurrence of agonistic behavior patterns seen in our study. Where appropriate, we compare our findings with those of Owings et al. (1977). Data for all 851 encounters observed by us are summarized in Table 1.

CHASE.—As did Owings et al. (1977), we found chase the most common type of agonistic interaction (27.5% of all encounters), with males chasing more frequently than females (167 of 234 chases; 71.4%). In contrast to their findings, however, we observed males chasing females more frequently than they did other males, 1.34X as frequently among adults in spring and 1.65X as often overall. Females were the chasers 67 (28.6%) times, chasing other females 52 times, males only 15. One young female accounted for 13 of the 15 chases of seven males (six young, one adult), five of which were larger than she by 50–150 g. Two other females were also seen to chase a male once each; in one instance both animals were young, and in the other both were adults.

On seven occasions in spring, two adult males engaged in bouts of reciprocal chasing after meeting at a box. First one chased the other 2–3 m from the box. Reversing roles, the pair then ran past the box 2–3 m in the opposite direction. Typically the roles reversed repeatedly, in one case eight times, before an encounter terminated. We believe such behavior to be the result of repeated dominance reversals across a territorial boundary. As evidence, we cite the fact that such behavior could be induced only at certain locations; moving the box as little as 1 m to either side caused agonistic encounters to

TABLE 1. Frequency of behavior patterns by sex and age in dyadic encounters. All encounters involving young occurred in fall. All encounters between two adults were seen in spring, except for two rump blocks, one roll fight, and one flank push between two females, and the four male-female flank pushes in which males did the pushing. In male-female encounters, frequency of male wins and frequency of female wins, respectively, are separated by a slash. Asterisks identify newly described behaviors.

Agonistic	Age and sex										
Behavior	Two adults			Two young			Adult-young			N	%
	♂-♂	♀-♀	♂-♀	♂-♂	♀-♀	♂-♀	♂-♂	♀-♀	♂-♀[a]		
Chase	32[b]	25	42/1[c]	26	27	54/13	5		8/1	234	27.5
Supplant	13	14	25/0	25	45	43/3	11[d]	2	37/0	218	25.6
Stare			12/1		6	3/2		2	3/0	29	3.4
Rump block*		6	0/1[e]		28	1/1[e]				37	4.3
Kick*		2			24	1/0				27	3.2
Forward shove*					19	1/0				20	2.4
Flank push	3	4	4/4	1	37	6/3	1	13	8/0	84	9.9
Lateral approach	21	2	1/0	3	31	3/1			6/0	68	8.0
Pounce*	2		1/1							4	0.5
Boxing fight*			1/0	2	15	2/2			2/0	24	2.8
Circle fight*	1				2					3	0.4
Roll fight*	7	2	4/0	2	16	3/2			1/0	37	4.3
Displacement groom*	20									20	2.4
Cheek-back rub	30									30	3.5
Cheek rub	8									8	0.9
Dusting	8									8	0.9
Totals	145	55	90/8	59	250	127/27	17	17	65/1	851	100.0

[a]All encounters involved an adult male and a young female; none involving adult female and young male were seen.
[b]Includes 19 chases in 4 bouts of reciprocal chasing.
[c]Includes 4 redirected chases.
[d]In 2 of 11, young supplanted adult
[e]Female attempted to block male, but was forced out.

cease, with one male having exclusive use. This observation conforms with Dobson's (1983) finding that "dominance [is] at least partially site-specific" among adult male *Spermophilus beecheyi*.

In four instances, a chase of an adult female by an adult male was apparently the result of redirected aggression. In each case, one of two males engaged in an agonistic encounter at a territorial boundary turned quickly to chase a female not previously involved.

SUPPLANT.—As did Owings et al. (1977), we found supplanting—the causing of another animal to move away—to be almost as common as chasing. However, in contrast to their findings, in our study males were the most common supplanters (154 cases; 70.6%), usually of females. Females supplanted others only 64 times (29.4%); all but three of the supplanted animals were also females. No adult male was ever supplanted by a female, but twice adult males were seen to retreat at the approach of a smaller, young male.

"BLOCKING" ACTIONS.—A feeding squirrel tended to retain its position at a box when approached by another animal by lifting its head and directing its gaze at the intruder (stare of Owings et al. 1977, passive displacement of Fisler 1967), by a rump block, by kicking, by a forward shove, or by a combination of these behaviors.

Stare was used to block approaching females 26 times (89.6%), males only 3 (10.4%). Eighteen times a male did the blocking, 8 times a female. A female blocked a male with a stare on only 3 occasions; in the one encounter involving two adult animals, the female was pregnant and shared a burrow with the male. Although Owings et al. (1977) reported staring among males, we saw no male-male stares.

Rump block was used exclusively by females, usually against other females. In the only two instances when a female attempted to block a male in this manner, the male supplanted the female.

On 27 of the 37 occasions when a rump block was seen, the action was followed by a kick. Twenty-six kicks were delivered by females against other females (96.3%), mainly young; only once was a male, a young, seen to

deliver a kick (3.7%) against a young female.

Frequently, forward shoves were interspersed with kicking. This action was seen 20 times, 19 of them involving two young females. All but two forward shoves occurred coincidentally with kicking.

DISPLAYS.—During intense agonistic encounters two animals often showed a lateral approach display (Owings et al. 1977), their bodies parallel, either head to head or head to flank, their backs arched, their heads slightly up and oriented toward the opponent, their tails elevated, and the tail hairs erect. Although Owings et al. (1977) reported such action mainly among males, of the 68 lateral approaches we saw, only 24 (35.3%) involved two males; 33 (48.5%) cases involved a male and a female, 11 (16.2%) two females.

Owings et al. (1977) reported that lateral approaches often ended in flank pushes or slams, but we found they most commonly terminated simply by separation (20 cases; 43.5%); 10 (21.7%) ended with a chase, 6 with a kick, 6 in fights (13% each), and only 4 (8.7%) in flank pushes. Furthermore, the display was not always initiated in a side-to-side orientation; 38 times (55.8%) we saw this behavior begin as two animals approached head-on, often when 3–4 m apart. Only as they closed on each other in a slow, stiff-legged gait did they assume the typical lateral position.

PUSHES.—Whenever two animals approached a box simultaneously, or when one tried to enter while another fed, flank pushing (side-shove match of Fisler 1976) was common. An animal at the box when the encounter began typically initiated the pushing, usually after an attempted rump block failed. Two males engaged in such matches only 5 times (6.0%) compared to 54 (64.3%) such interactions between two females and 25 (29.8%) between a male and a female. Of the 25 male-female encounters, the male retained or attained control of the box in 19 (76%). The vigorous flank slams described from film by Owings et al. (1977) were not seen.

MARKING BEHAVIOR.—Three behavior patterns described by Owings et al. (1977) and probably involved in scent marking occurred among our squirrels. Cheek-back rubbing was most common, with cheek rub and dusting seen only about 25% as often. All were exclusively actions of adult males in spring, usually occurring when two males met at a box on their common territorial boundary. Typically, a lateral approach display was followed by a brief period of ambivalence as first one, then the other, approached the box. One animal would then turn away to rub either its cheek (cheek rub) or its whole side from mouth to flank (cheek-back rub) on a nearby stake or log, or in the dust (dusting). Frequently such behavior was repeated many times in succession.

In one case a cheek-back rub occurred with only one male immediately involved. While one adult male was in a trap, another advanced 5 or 6 m into the trapped male's territory where it cheek-back rubbed a stake three times before retreating.

FIGHTS.—Several gradations of fighting behavior occurred. Least vigorous was the pounce. Twice an adult male pounced on another adult male feeding at their common territorial boundary. In a third instance a male pounced on a female, apparently causing her to relinquish a box. In a fourth encounter a pregnant female, without obvious preliminaries, leaped onto a male (with whom she shared a burrow) while he was feeding in the grass. He gave no obvious response and continued feeding as she began feeding also.

Boxing fights occurred 24 times. This action was most common between two young (21 times; 87.5%), usually females (15 times; 62.5%). Only once did two adults, a male and a female, engage in such an action. Each encounter lasted only 3–5 sec.

Both roll and circle fights were usually intense, often involving clawing and biting. Roll fights, the more common of the two, occurred among both mature and immature animals. In 2 of the 10 roll fights between a male and a female (both young), the female won the encounter and retained the box.

Of the 68 fights of all sorts, roll fight and boxing fight were most common (54.3% and 35.3%, respectively); pounce accounted for only 5.9% of the fights and circle fight only 4.5%. Forty-six (67.6%) fights were between two young animals, and 33 (48.5%) involved two young females.

DISPLACEMENT GROOMING.—This action was seen only during high-intensity encounters between adult males on territorial boundaries. It was observed in six encounters and in each was repeated many times. Each

time the behavior was seen it was interspersed among bouts of lateral approach, flank push, fights, and marking behavior. Typically a male would break off an agonistic encounter, engage in displacement grooming, then either renew the encounter with its adversary or mark a nearby stake.

We occasionally shifted the action from one member of a dyad to the other by moving the feeding box 0.5–1 m toward the territory of the animal that had previously been "grooming." Consequently, our subjective opinion is that the grooming animal is the one most "ill at ease" at the moment. We have not seen such action among adult males in any other context, nor among females or immature males.

DISCUSSION

Our study differs from that of Owings et al. (1977) in that most interactions we saw took place at a concentrated food source. Presumably the level of antagonism at such a locale is higher than among individuals interacting where resources are more widely scattered. This difference in procedure probably accounts for most of the differences observed in frequency and context of behavior patterns. It probably also accounts for our observations of several previously unreported fight patterns and displacement grooming, thereby allowing an extension of the ethogram for *Spermophilus beecheyi*.

Some behavior patterns, (e.g., chase, supplantation, flank push, lateral approach) are common to both sexes and all ages. Indeed, if one assumes a 1:1 ratio among the sexes in the populations, the frequency of occurrence of the first two behaviors approximates the 1:2:1 ratio expected on the basis of likelihood of male-male, male-female, or female-female contacts. The frequencies of occurrence of the flank push and lateral approach, on the other hand, are clearly skewed, the former much more common among females than males, the latter mainly utilized when the two animals are of the same sex.

Other behaviors are more restricted in occurrence. Almost half of the fights were between young females, perhaps animals still sorting out hierarchical relationships. Stare and rump block were never seen between two males of any age, although both were common when two females or a male and a female interacted. Kick and forward shove, typically associated with stare and rump block, were almost totally restricted to young females. They occurred only rarely in a young male-female encounter and never between two males of any age. Among adult males, the more intense agonistic action of lateral approach appears largely to replace the milder actions of rump block, stare, kick, and forward shove, although it is not restricted to this context.

Four behavior patterns—displacement grooming and three marking actions—occurred only during intense boundary interaction between two adult, territorial males. Owings et al. (1977) also reported cheek rub and cheek-back rub to be mainly a male action, although they saw these actions among females occasionally. The predominance of marking actions among males is not surprising since such actions are presumed to be related to identification and reinforcement of territorial boundaries; evidence that adult males are territorial during the breeding season is strong, but clearcut indications of territoriality among females is lacking (Dobson 1983). The role of displacement grooming is not clear.

As evidenced by the "winner" in all categories of agonistic behavior but one (rump block), male dominance is characteristic in this species, even among young and among adults in the nonbreeding season. This conforms generally with the findings of Dobson (1983) and Fitch (1948). Male dominance may be related both to sex-related hormonal differences and to the generally larger size of males. However, the possibility that factors other than sex and size are also involved is suggested by the fact that among Richardson's ground squirrels (*S. richardsonii*) the larger males do not dominate females after the breeding season (Michener 1983). Even in the California ground squirrel male dominance is not invariable, as indicated by a young female that at various times chased seven different males, all but two larger than she, and by a pregnant female that attacked a larger male in whose territory she lived (her mate?) with apparent impunity on a few encounters. Clearly the degree of aggressiveness among females differs and may temporarily be increased relative to certain males during

pregnancy. Dobson (1983) also found females to occasionally dominate males, at least nonresident ones.

Our observations also confirm the findings of Dobson (1983) that male California ground squirrels frequently are territorial, at least during the breeding season. Using artificial food sources, we had no difficulty identifying the territorial borders between adjacent males and found them to be stable throughout the breeding period. We suggest that this technique, though manipulative, may prove useful with other squirrels for verifying the existence of territoriality and for delineating boundary locations.

Finally, we note that the majority (92%) of the agonistic encounters seen appear to involve little energy output and entail little physical risk. The four fight categories, those behaviors presumed bioenergetically most expensive and potentially most harmful, comprised only 8% of the encounters observed.

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LITERATURE CITED

ARMITAGE, K. B. 1981. Sociality as a life-history tactic of ground squirrels. Oecologia 48: 36–49.

BALPH, D. F., AND A. W. STOKES. 1963. On the ethology of a population of Uinta ground squirrels. Amer. Midl. Nat. 69: 106–126.

BETTS, B. J. 1976. Behaviour in a population of Columbian ground squirrels, *Spermophilus columbianus columbianus*. Anim. Behav. 24: 652–680.

CLARK, T. W., AND C. RUSSELL. 1977. Agonistic behavior in Uinta ground squirrels. Northwest Sci. 51: 36–42.

DOBSON, F. S. 1983. Agonism and territoriality in the California ground squirrel. J. Mamm. 64: 218–225.

FISLER, G. F. 1967. Nonbreeding activities of three adult males in a band of free-ranging monkeys. J. Mamm. 48: 70–78.

———. 1976. Agonistic signals and hierarchy changes of antelope squirrels. J. Mamm. 57: 94–102.

FITCH, H. S. 1948. Ecology of the California ground squirrel on grazing lands. Amer. Midl. Nat. 39: 513–596.

HALL, E. R. 1981. The mammals of North America. John Wiley and Sons, New York. 2 vols. 1,181 pp.

LEHNER, P. 1979. Handbook of ethological methods. Garland STPM Press, New York. 403 pp.

MICHENER, G. R. 1983. Kin identification, matriarchies, and the evolution of sociality in ground-dwelling sciurids. Pages 528–572 *in* J. F. Eisenberg and D. F. Kleiman, eds., Recent advances in the study of mammalian behavior. Spec. Publ. Amer. Soc. Mamm. No. 7. 753 pp.

MURIE, J. O., AND G. R. MICHENER, EDS. 1984. Biology of ground-dwelling squirrels: annual cycles, behavioral ecology, and sociality. University of Nebraska Press, Lincoln. 459 pp.

OWINGS, D. H., M. BORCHERT, AND R. VIRGINIA. 1977. The behavior of California ground squirrels. Anim. Behav. 25: 221–230.

SHEPPARD, D. H., AND S. YOSHIDA. 1971. Social behavior in captive Richardson's ground squirrels. J. Mamm. 52: 793–799.

STEINER, A. L. 1974. Body-rubbing, marking, and other scent-related behavior in some ground squirrels (Sciuridae), a descriptive study. Canadian J. Zool. 52: 889–906.

WATTON, D. G., AND M. H. A. KEENLEYSIDE. 1974. Social behaviour of the arctic ground squirrel, *Spermophilus undulatus*. Behaviour 50: 77–99.

MIGRATING MORMON CRICKETS, *ANABRUS SIMPLEX* (ORTHOPTERA: TETTIGONIIDAE), AS FOOD FOR STREAM FISHES

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ABSTRACT.—Migrating bands of Mormon crickets (*Anabrus simplex*) were observed crossing the Green and Yampa rivers in Dinosaur National Monument, Colorado and Utah, in 1986 and 1987. Swimming crickets were swept downstream and eaten by four endemic and seven introduced fish species. Included were two endangered fishes, Colorado squawfish (*Ptychocheilus lucius*) and humpback chub (*Gila cypha*). Direct and indirect effects to aquatic food webs associated with application of pesticides for Mormon cricket control may pose a threat to these fishes and to man.

The Mormon cricket (*Anabrus simplex* Haldeman) occurs only in western North America where it is generally regarded as an agricultural pest (Wakeland 1959). This flightless, long-horned grasshopper is primarily solitary in low-density subpopulations but becomes gregarious and migratory with high densities, moving from its mountain breeding areas to plague croplands (Capinera and MacVean 1987). Earliest records of this insect date to Mormon pioneers in the Salt Lake Valley in 1847 and to the legendary cricket plague of 1848 (Bancroft 1889, Whitney 1892).

Although most reports stress the detrimental effects of Mormon cricket outbreaks, Mormon crickets potentially provide an abundant and high-quality food source (Defoliart et al. 1982). Predation by terrestrial animals includes about 50 species of birds, mammals, and reptiles; however, references to predation by aquatic animals are few (Wakeland 1959). Mormon crickets swim readily (LaRivers 1956), as do other Orthoptera, and reference to their movements into Utah streams and lakes dates to 1848 (Bancroft 1889). Swimming crickets would be exposed to aquatic predators during migrations, but we found no reference to predation on this species by fishes.

Annual Mormon cricket outbreaks and migrations in Dinosaur National Monument (DNM), Colorado and Utah (Fig. 1), have renewed an old controversy about control of crickets by aerial spraying of pesticides (Capinera and MacVean 1987), U.S. Fish and Wildlife Service 1986, 1987). A part of this controversy concerns Park Service policy to treat crickets with natural controls, if needed (National Park Service 1986), since aerial spraying could adversely affect endangered species in DNM. The objectives of this study are to evaluate fish predation on Mormon crickets in DNM, discuss possible significance to fishes of a periodic, massive, and seasonal food supply, and comment on possible impacts of cricket controls on fishes, aquatic communities, and man.

METHODS

The availability of Mormon crickets in streams and predation on them by fishes were evaluated by visual observations, use of crickets as bait, and direct inspection of stomachs of nonnative species taken by angling, trammel nets, and electrofishing. Angling included bottom-fishing with weighted hooks and surface-fishing with floats. Mormon crickets were hooked through the thorax and abdomen. Weekly trips through the Green and Yampa rivers in 1986 and 1987 (May through July) included the season when crickets were present.

Average weights of late instar and adult Mormon crickets were obtained in 1987 by weighing 20–50 individuals from several large bands. All crickets in a 5–30-m section of road were collected and weighed on a 1,000 × 2-g platform scale. Crickets were placed in previously tared plastic bags, and subsamples were separated by sex. Cricket bands were located on Harpers Corner Road in DNM from 19 July to 14 August 1987.

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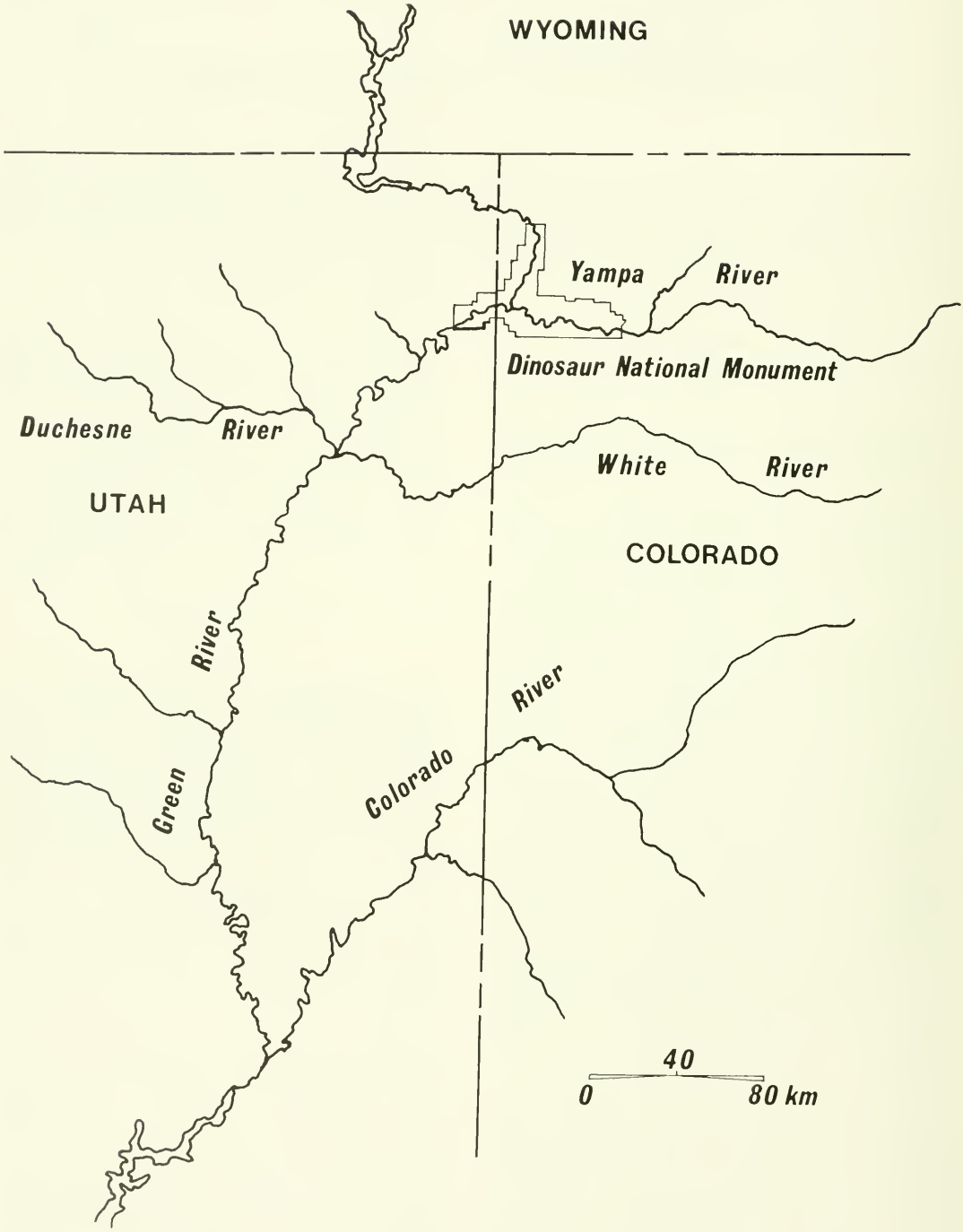

Fig. 1. Map of upper Colorado and Green river basins, Colorado and Utah.

RESULTS

Migratory Mormon crickets formed a unique and substantial organic input to the Green and Yampa rivers in DNM in 1986 and 1987. Young crickets were first observed on

TABLE 1. Numbers of fish captured using Mormon cricket, *Anabrus simplex*, as bait or fish whose stomachs contained crickets. All fish were captured in DNM 1986–1987 ([—] indicates no records kept).

Family	Species	Status	Number of individuals 1986	1987
Cyprinidae	*Cyprinus carpio*	introduced	2	12
	Gila cypha	endemic	16	29
	Gila robusta	endemic	134	185
	Ptychocheilus lucius	endemic	1	3
Catostomidae	*Catostomus latipinnis*	endemic	1	9
Ictaluridae	*Ameiurus melas*	introduced	—	8
	Ictalurus punctatus	introduced	—	161
Salmonidae	*Salmo clarki*	introduced	0	1
	Salmo gairdneri	introduced	0	4
	Salmo trutta	introduced	0	20
Cottidae	*Cottus bairdi*	native	0	1

roads in early May, and huge bands of late instars and adults migrated into river canyons in early June through July. All Mormon crickets observed encountering streams ultimately entered the water; we saw no individual turn from the water's edge for more than a few minutes. Crickets entrained in river currents varied from a few individuals per hour to concentrations of over 50 individuals/m^2 of water surface. Entrained crickets remained on the surface and continued to swim for long periods. Live, moribund, and dead individuals accumulated in eddies and remained at or near the surface for hours. Downstream from shorelines where migrating bands were entering the river, numbers averaged 10–20 individuals/m^2. Largest numbers were observed where a tributary creek intersected a migration and carried the crickets in large numbers to the mainstream. In this instance, 50 individuals/m^2 is a conservative estimate. Highest numbers were observed in eddies where crickets accumulated. In such instances, their abundance exceeded the last value, and, in minutes, hundreds of crickets climbed aboard our rafts.

A total of 430 Mormon crickets were weighed from 12 collections taken in 1987. Average weight per cricket was 3.03 g. A subsample of 112 males averaged 2.84 g (range 2.30–3.02 g), and 141 females averaged 3.12 g (range 3.07–3.27 g). Although we could not reliably estimate the biomass of crickets, we observed several bands of 1 km^2 or more entering the Green River. At 10–20 individuals/m^2, one of these bands could weigh 30–60 metric tons.

Eleven fish species, in five families (Table 1), fed on Mormon crickets from 18 May to 1 August 1987. A total of 587 fish were captured by angling in 1986 and 1987 with Mormon crickets as bait, or had crickets in their digestive systems. Included were four endemic Colorado River fishes: roundtail chub, *Gila robusta;* humpback chub, *Gila cypha;* Colorado squawfish, *Ptychocheilus lucius;* and flannelmouth sucker, *Catostomus latipinnis*. Roundtail chub and the endangered humpback chub were voracious feeders on Mormon crickets. Although bait records for 1986 were incomplete, these two species comprised 53% (N = 210) of fish captured in 1987 (N = 399) with cricket-baited hooks (Table 1). Three Colorado squawfish were captured using crickets for bait, and a fourth attempted to eat a cricket but was not landed.

When Mormon crickets were present, all fish species large enough to eat them had done so. Small individuals of aggressive, omnivorous species (channel catfish, *Ictalurus punctatus*, and black bullhead, *Ameiurus melas*) dismembered and devoured even the largest crickets. Remarkable numbers were present in some digestive tracts, distending stomachs and intestines and, in some cases, filling buccal cavities and protruding from mouths. Channel catfish and carp (*Cyprinus carpio*) were observed at the water surface feeding on crickets in eddies whenever crickets were present. The most striking example of point input and opportunistic feeding was observed 28 May 1987 at the confluence of the Green River and a small tributary in DNM. Nineteen of 21 brown trout (*Salmo trutta*), 1 of 3 rainbow trout (*Salmo gairdneri*), and 1 cutthroat trout (*Salmo clarki*) taken immediately below the inflow were gorged with crickets. However, no Mormon crickets were observed

upstream of the confluence (13-km reach), and none of 25 individuals of the same three species collected there had consumed crickets.

DISCUSSION

Mormon Crickets and Stream Ecology

The movements of large bands of Mormon crickets into the Green and Yampa rivers in DNM in 1986 and 1987 provided a substantial and high-quality organic input to this system. This must have been the case in other years of major outbreaks, such as from 1980 to 1987 in DNM (Capinera and MacVean 1987, National Park Service 1986). Mormon cricket availability may be important to the ecology of both native and nonnative fishes. This is especially true in DNM, which contains the only known spawning site for the endangered humpback chub in the Green River Basin, and one of the two confirmed spawning sites for the endangered Colorado squawfish (Tyus et al. 1987).

Various investigators have studied Green River fishes (Holden and Stalnaker 1975, Miller 1964, Miller et al. 1982, Vanicek and Kramer 1969) with emphasis on rare, native species listed or considered for listing as threatened or endangered (U.S. Department of the Interior 1985). The fauna also includes numerous nonnative fishes introduced for sport, forage, food, or by accident (Tyus et al. 1982). Food habits of native fishes are generally known (Vanicek and Kramer 1969, Jacobi and Jacobi 1982), but their seasonal use of terrestrial animals is not. Foods of nonnative species are described for other rivers (e.g., Carlander 1977), but few data exist in DNM.

Mormon cricket movements into rivers in DNM in spring provide food for stream fishes. This is a time when flooding, scouring, and annual insect emergence reduce food availability. High-water turbidity presumably reduces visual feeding efficiency of predatory fishes, yet large numbers of crickets at or near the water surface are vulnerable to aquatic predators. Cricket availability coincides with prereproductive periods for some native species, including roundtail and humpback chubs, flannelmouth sucker, and Colorado squawfish. As reported by Defoliart et al. (1982), adult Mormon crickets have a mean crude protein content of 58% and a fat content of 16.5%. Such abundant and high-quality food might enhance fish reproductive success, postreproductive recovery, or both.

We do not advocate that native fishes time reproductive behavior to cricket input. However, a demonstrable relationship between nutrition and reproductive success in these fishes would be of interest, and long-lived fishes could incorporate such unpredictable major outbreaks to advantage in life-history strategies (Smith 1981, Tyus 1986). Longevities of endemic Colorado River fishes studied to date indicate long life is an exceptional attribute of this fauna. Bonytail chub (*Gila elegans*) older than 40 years have been reported, razorback sucker (*Xyrauchen texanus*) commonly reach 30 to 40 years, and Colorado squawfish that formerly achieved 1.8 m in length must have lived even longer (McCarthy and Minckley 1987, Rinne et al. 1986). Periodic outbreaks of Mormon crickets could contribute significantly to nutrition, directly or indirectly, for a number of consecutive or disjunct years during such a long period of life.

High flows and seasonal flooding in the mainstream Green River are now reduced by dams (Joseph et al. 1977). This alters or precludes floodplain inundation and removes particulate organics through reservoir entrapment (e.g., Minckley and Rinne 1986). Flooded lowlands were formerly expansive during sustained high flows, which often exceeded mean discharge (181 m^3/second, based on an 86-year record at Jensen, Utah) by more than an order of magnitude during snowmelt (Remilliard et al. 1986). Floodplain communities were thus made available to predation by riverine fishes, as observed elsewhere (Welcomme 1979). In the Green River, Colorado squawfish and razorback sucker have been radiotracked to flooded lowlands, where they presumably feed (Tyus 1987, Tyus et al. 1987). Flood reduction and loss of allochthonous inputs may make seasonal inputs of terrestrial animals, including Mormon crickets, more important now than historically.

Mormon Cricket Control

In their natural grassland or sagebrush-dominated habitats, Mormon crickets prefer to feed on succulent, herbaceous vegetation. Damage to range grasses is considered so slight that they are not generally considered a

serious livestock competitor (Capinera and MacVean 1987, Corkins 1923, Cowen 1932). Bands of crickets migrating into croplands have resulted in economic damage that is legendary. However, reports of flying grasshoppers in early accounts (Bancroft 1889), indicate Mormon crickets did less than all the damage. Psychological effects of hordes of large, black insects invading gardens and dwellings during periodic outbreaks were nonetheless sufficient to stimulate severe countermeasures. Mechanical barriers, poisoned baits, aerial application of pesticides, and biological controls have all been used (Animal and Plant Health Inspection Service 1986, Capinera and MacVean 1987, Swain 1944, Wakeland 1959).

As mentioned, Mormon crickets provide food for many terrestrial and aquatic animals. They are also potentially valuable to man. Defoliart et al. (1982) found that dried Mormon crickets contained 2,800 Kcal/kg and valued the powder at $300/metric ton. A small (1 km^2) band of crickets (10–20 crickets/m^2) would be worth about $3,000-$7,000 based on these values. Mormon crickets are also beneficial because they feed on other insect pests, including aphids (Ueckert and Hanson 1970), and are known to scavenge on feces or carrion, converting these energy sources into food more readily usable by higher predators. Control may therefore conflict with perpetuation and management of desirable species, either through direct poisoning or indirectly through reduction in the terrestrial and aquatic food supply (Capinera and MacVean 1987, Mont and Oehme 1981).

Although government agencies currently utilize pesticides of relatively low toxicity to vertebrates (i.e., carbaryl, malathion), these chemicals can cause adverse impacts to the avifauna (Moulding 1976) and to aquatic invertebrates (Mont and Oehme 1981). Private citizens may employ even more dangerous chemicals. Direct impacts of pesticides (e.g., blow-over, accidental spraying, or washing of poisons into aquatic habitats) may be minimized by enforcement of regulations (U.S. Fish and Wildlife Service 1986, 1987). Yet pesticide contamination remains a possibility if applied near aquatic systems. If direct poisoning of nontarget animals does not occur, indirect effects, such as reduction in foods, may affect fishes.

Contamination of aquatic habitats may further occur through mass movements of pesticide-laden Mormon crickets into streams, and entrainment of other contaminated animals. If crickets consumed by fishes contain pesticides, the large number eaten by fishes suggests that substantial amounts of pesticides could likewise be consumed. This would result in death or physiologic impairment. Coincidence of cricket outbreaks, pesticide application, and fish reproduction may result in potential pesticide influence on gamete production, gametes, or young. A high incidence of vertebral anomaly (lordosis) in roundtail chub in DNM has been tentatively linked to pesticide applications (Haynes and Muth 1985).

Lastly, streams within and near DNM are renowned for sport fishing. Substantial harvests are recorded for trouts in the Green River below Flaming Gorge Dam and channel catfish throughout the upper Green River Basin. Other carnivorous fishes, including northern pike (*Esox lucius*), are also taken and eaten. If pesticides are bioaccumulated by sport fishes, an avenue exists for direct transfer of potentially damaging substances to the public.

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LITERATURE CITED

ANIMAL AND PLANT HEALTH INSPECTION SERVICE. 1987. Biological assessment for the Rangeland Grasshopper Cooperative Management Program. U.S. Dept. Agric., Washington, D.C.

BANCROFT, H. H. 1889. History of Utah. *In:* The works of Hubert Howe Bancroft, Vol. 26. The History Company, San Francisco. (Reprinted 1964 by Bookcraft, Inc., Salt Lake City, Utah).

CAPINERA, J. AND C. MACVEAN. 1987. Ecology and management of Mormon cricket, *Anabrus simplex* Haldeman. Final Report to the National Park Service. Department of Entomology, Colorado State University, Fort Collins.

CARLANDER, K. D. 1977. Handbook of freshwater fishery biology. Vols. 1 and 2. Iowa State University Press, Ames.

CORKINS, C. L. 1923. Mormon cricket control. Colorado Office State Ent., Circular 40.

COWEN, F. T. 1932. Mormon cricket control in Colorado. Colorado Office State Ent., Circular 57.

DEFOLIART, G. R., M. D. FINKE, AND M. L. SUNDE. 1982. Potential value of the Mormon cricket (Orthoptera: Tettigoniidae) harvested as a high-protein food for poultry. J. Econ. Ent. 75: 848–852.

HAYNES, C. M., AND R. T. MUTH. 1985. Lordosis in *Gila*, Yampa River, Colorado. Proc. Desert Fish. Counc. 13(1981): 83–84.

HOLDEN, P. B., AND C. B. STALNAKER. 1975. Distribution and abundance of mainstream fishes of the middle and upper Colorado River Basin 1967–1973. Trans. Amer. Fish. Soc. 104: 217–231.

JACOBI, G. Z., AND M. D. JACOBI. 1982. Report No. 9, Fish stomach content analysis. Pages 284–324 *in* Part 3, Colorado River Fishery Project Final Report, Contracted Studies. U.S. Fish Wildl. Serv. and Bureau Reclam., Salt Lake City, Utah.

JOSEPH, T. W., J. A. SINNING, R. J. BEHNKE, AND P. B. HOLDEN. 1977. An evaluation of the status, life history, and habitat requirements of endangered and threatened fishes of the upper Colorado River system. U.S. Fish and Wildlife Service Report FWS/OBS 24. Natl. Ecol. Center, Fort Collins, Colorado.

LARIVERS, I. 1956. Aquatic Orthoptera. Page 154 *in* R. L. Usinger, ed., Aquatic insects of California. University of California Press, Berkeley.

MCCARTHY, M. S., AND W. L. MINCKLEY. 1987. Age determination for imperiled razorback sucker (Pisces: Catostomidae) from Lake Mohave, Arizona-Nevada. J. Arizona-Nevada Acad. Sci. 21: 87–97.

MILLER, W. H., H. M. TYUS, AND C. A. CARLSON. 1982. Fishes of the upper Colorado River system: present and future. Amer. Fish. Soc. (WD), Bethesda, Maryland.

MINCKLEY, W. L., AND J. N. RINNE. 1986. Large woody debris in hot-desert streams: an historical review. Desert Plants 7(1985): 142–153.

MONT, M. E., AND F. W. OEHME. 1981. Carbaryl: a literature review. Residue Rev. 80: 1–64.

MOULDING, J. D. 1976. Effects of a low-persistence insecticide on forest bird populations. Auk 93: 692–708.

NATIONAL PARK SERVICE. 1986. General management plan. Dinosaur National Monument. U.S. Nat. Park Serv., Dinosaur, Colorado.

REMILLIARD, M. D., G. C. ANDERSEN, G. A. BIRDWELL, AND G. W. SANDBERG. 1986. Water resource data for Utah, water year 1985. U.S. Geol. Surv., Water-data Report UT-85-1.

RINNE, J. N., J. E. JOHNSON, B. L. JENSEN, A. W. RUGER, AND R. SORENSON. 1986. The role of hatcheries in the management and recovery of threatened and endangered fishes. Pages 271–285 *in* R. H. Stroud, ed., Fish culture in fisheries management. Amer. Fish. Soc., Bethesda, Maryland.

SMITH, M. L. 1981. Late Cenozoic fishes of the warm deserts of North America: reinterpretation of desert adaptations. Pages 11–38 *in* R. J. Naiman and D. L. Soltz, eds., Fishes in North American deserts. John Wiley and Sons, New York.

SWAIN, R. B. 1944. Nature and extent of Mormon cricket damage to crop and range plants. U.S. Dept. Agric. Tech. Bull. 866.

TYUS, H. M. 1986. Life strategies in the evolution of the Colorado squawfish (*Ptychocheilus lucius*). Great Basin Nat. 46: 656–661.

———. 1987. Distribution, reproduction, and habitat use of the razorback sucker in the Green River, Utah, 1979–1986. Trans. Amer. Fish. Soc. 116: 111–116.

TYUS, H. M., B. D. BURDICK, R. A. VALDEZ, C. M. HAYNES, T. A. LYTLE, AND C. R. BERRY. 1982. Fishes of the upper Colorado River: distribution, abundance, and status. Pages 12–70 *in* W. H. Miller, H. M. Tyus, and C. A. Carlson, eds., Fishes of the upper Colorado River system: present and future. Amer. Fish. Soc. (WD), Bethesda, Maryland.

TYUS, H. M., R. L. JONES, AND L. A. TRINCA. 1987. Green River rare and endangered fish studies, 1982–1985. Final Report, Colorado River Fishes Monitoring Project, U.S. Fish Wildl. Serv., Vernal, Utah.

UECKERT, D. N., AND R. M. HANSON. 1970. Seasonal dry weight composition in diets of Mormon crickets. J. Econ. Ent. 63: 96–98.

U.S. DEPARTMENT OF THE INTERIOR. 1985. Endangered and threatened wildlife and plants; notice of completion of review for 1978 and a five-year review of species listed before 1976, and in 1979 and 1980. Fed. Reg. 50: 29900–29909.

U.S. FISH AND WILDLIFE SERVICE. 1986. Biological opinion FA/SE/APHIS—Mormon cricket control. Letter report to the Animal and Plant Health Inspection Service. U.S. Fish Wildl. Serv., Denver, Colorado.

———. 1987. Biological opinion FA/SE/APHIS (6-RO-87-F-004). Letter report to the Animal and Plant Health Inspection Service. U.S. Fish Wildl. Serv., Denver, Colorado.

USINGER, R. L. 1956. Aquatic insects of California. University of California Press, Berkeley.

VANICEK, C. D., AND R. H. KRAMER. 1969. Life history of the Colorado squawfish, *Ptychocheilus lucius*, and the Colorado chub, *Gila robusta*, in the Green River in Dinosaur National Monument, 1964–1966. Trans. Amer. Fish. Soc. 98: 193–208.

WAKELAND, C. 1959. Mormon crickets in North America. U.S. Dept. Agric. Tech. Bull. 1202.

WELCOMME, R. L. 1979. Fisheries ecology of floodplain rivers. Longman, London.

WHITNEY, O. F. 1892. The cricket plague. History of Utah. George Q. Cannon and Sons, Salt Lake City, Utah.

NOMENCLATURAL CHANGES AND NEW SPECIES OF SCOLYTIDAE (COLEOPTERA)

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ABSTRACT.—New replacement names for junior homonyms are presented as follows: *Acanthotomicus tuberculifer* for *A. (Mimips) tuberculatus* Schedl 1967, *Chaetoptelius versicolor* for *C. (Acrantus) tricolor* Schedl 1958, *Hylesinopsis angolanus* for *H. (Aridiamerus) angolensis* Schedl 1982, *Hylurgops tuberculifer* for *H. tuberculatus* Schedl 1947, *Pseudothysanoes spinatifer* for *P. spinatus* Wood 1956, *Scolytodes aterrimus* for *S. ater (Hylocurosoma atrum* Eggers) 1941, *Scolytodes boliviensis* for *S. (Prionosceles) bolivianus* Eggers 1928, *Scolytodes brasilianus* for *S. (Hexacolus) brasiliensis* Schedl 1935, *Scolytodes discriminatus* for *S. discedens* Eggers 1943, *Scolytodes elongatissimus* for *S. elongatus (Hylocurosoma elongatum* Eggers) 1943, *Scolytodes gennaeus* for *S. genialis* Wood 1978, *Scolytodes laevigatulus* for *S. (Hexacolus) laevigatus* Schedl 1962, *Scolytodes laevicorpus* for *S. laevis (Hylocurosoma laeve* Eggers) 1943, *Scolytodes majus* for *S. major* Eggers 1943, *Scolytodes medialis* for *S. medius* Eggers 1943. New synonymy is reported for *Dactylipalpus niger* Schedl (= *D. unctus* Wood), *Dendroctonus armandi* Tsai & Li (= *D. prosorovi* Kurenzov & Kononov), *Sinophloeus porteri* Brèthes (= *S. destructor* Eggers). Species new to science include: *Acacicis bicornis* (New Guinea), *Acacicis zeylanicus* (Sri Lanka), *Sphaerotrypes bengalensis* (India), *Sphaerotrypes costatus* (North Andaman Island), *Sphaerotrypes cristatus* (Sri Lanka), *Sphaerotrypes pentacme* (Burma), *Sphaerotrypes ranasinghei* (Sri Lanka), *Xylechinus ongeiniae* (India), *Xylechinus padus* (India).

On the following pages 15 new names are presented as replacements for newly discovered junior homonyms, 3 new cases of synonymy are reported, and 9 species new to science are described. These items are necessary nomenclatural housekeeping discovered during the preparation of a new world catalog of Scolytidae and are published here to facilitate citation for the catalog. The new names affect species from Angola (1) and Zaire (1) in Africa; USA and Mexico (1) in North America; Argentina (1), Bolivia (7), Brazil (1), and Venezuela (1) in South America; New Zealand (1); and Baltic amber from Europe (1). The new synonymy affects species from Chile (1), China (1), and the Philippine Islands (1). The species new to science are from the Andaman Islands (1), Burma (1), India (3), New Guinea (1), and Sri Lanka (Ceylon) (3).

NEW NAMES

Part of the task of preparing a new world catalog of Scolytidae is the review of all available names. My review of the genera (Wood 1986, Great Basin Naturalist Memoir No. 10) included considerable generic synonymy that resulted in the formation of a number of secondary homonyms. This has made it necessary to rename those junior homonyms when synonyms are not available to fill this need. Fifteen new names are presented below.

Acanthotomicus tuberculifer, n. n.

Mimips tuberculatus Schedl, 1967, Opusc. Zool. Budapest 7(1):230 (Holotype, male; Bouenza cataract, Congo; Budapest Nat. Mus.), preoccupied

When *Mimips* became a synonym of *Acanthotomicus*, it was necessary to transfer *M. tuberculatus* Schedl 1967:230 into *Acanthotomicus*. Because *Ips tuberculatus* Eggers 1927:79 had previously been transferred into that genus, Schedl's name became a junior homonym. The new name *tuberculifer* is proposed as a replacement for the junior homonym as indicated above.

Chaetoptelius versicolor, n. n.

Acrantus tricolor Schedl, 1958, Ann. Mag. Nat. Hist. (13)1:560 (Holotype, sex?; Nelson, New Zealand; British Mus. [Nat. Hist.]), preoccupied

The holotype of *Leperisinus tricolor* Schedl 1938:34 was examined and was found to be a member of the genus *Chaetoptelius*. Because the genus *Acrantus* has been placed in synonymy under *Chaetoptelius* (Wood 1986:42),

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the name *Acrantus tricolor* Schedl 1958:560 became a junior homonym of Schedl's 1938:34 name and must be replaced. The new name *versicolor* is proposed as a replacement for this junior homonym.

Hylesinopsis angolanus, n. n.

Aridiamerus angolensis Schedl, 1982, Ann. Transvaal Mus. 33(15):284 (Holotype, sex?; Angola; Schedl Collection in Wien Museum), preoccupied

As indicated above, the genus *Aridiamerus* Schedl 1982 is a junior synonym. Its type-species, *angolensis* Schedl, therefore, is transferred to *Hylesinopsis*, where it becomes a junior homonym of *angolensis* Schedl 1959:24. The new name *angolanus* is proposed as a replacement for this junior homonym.

Hylurgops tuberculifer, n. n.

Hylurgops tuberculatus Schedl, 1947, Zentralbl. Gesampt. Ent. 2(1):28 (Holotype, sex?; fossil in Baltic amber; Geol.-Paleont. Inst. Albertus-Univ., Konigsburg), preoccupied

Schedl 1947:28 named *Hylurgops tuberculatus*, a fossil from Baltic amber; however, this name was preoccupied by Eggers 1933:98. The new name *tuberculifer* is proposed as a replacement for the junior homonym, *tuberculatus* Schedl.

Pseudothysanoes spinatifer, n. n.

Pseudothysanoes spinatus Wood, 1956, Canadian Ent. 88:154 (Holotype, male; 27 km W. Tehuantepec, Oaxaca, Mexico; University of Kansas Collection), preoccupied

When the genus *Bostrichips* became a junior synonym of *Pseudothysanoes* (Wood 1986:63), the name *P. spinatus* Wood 1956:154 became the junior homonym of *B. spinatus* Schedl 1951:21. The new name *spinatifer* is proposed as a replacement for this junior homonym.

Scolytodes aterrimus, n. n.

Hylocurosoma atrum Eggers, 1943, Mitteilungen Münchner Ent. Ges. 33:371 (Holotype, sex?; Bolivia, Cochabamba; Paris Museum), preoccupied

When *Hylocurosoma atrum* Eggers was transferred to *Scolytodes*, the change in gender of the genus required that spelling of the specific name be changed to *ater*. This name thus became a junior homonym by page priority of *Prionosceles ater* Eggers 1943:365 (now in *Scolytodes*) that was validated in the same article. The new name *Scolytodes aterrimus* is proposed as a replacement for the junior name cited above.

Scolytodes boliviensis, n. n.

Prionosceles bolivianus Eggers, 1928, Arch. Inst. Biol. São Paulo 1:88 (Lectotype, sex?; Bolivia, Cochabamba; U.S. National Museum, designated by Anderson and Anderson, 1971, Smithsonian Contrib. Zool. 94:7), preoccupied

The transfer of *Prionosceles bolivianus* Eggers 1928:88 to *Scolytodes* caused this name to become a junior homonym by page priority of *Scolytodes bolivianus* Eggers 1928:86 that was validated in the same article. The new name *boliviensis* is proposed as a replacement for the junior name.

Scolytodes brasilianus, n. n.

Hexacolus brasiliensis Schedl, 1935, Stylops 4:274 (Holotype, sex?; Brazil; Schedl Collection in Wien Museum), preoccupied

The transfer of both *Prionosceles brasiliensis* Eggers 1928:89 and *Hexacolus brasiliensis* Schedl 1935:274 to *Scolytodes* caused the Schedl name to become a junior homonym. The new name *brasilianus* is proposed as a replacement for the junior name.

Scolytodes discriminatus, n. n.

Scolytodes discedens Eggers, 1943, Mitteilungen Münchner Ent. Ges. 33:360 (Holotype, sex?; Bolivia, Cochabamba; Paris Museum), preoccupied

The transfer of *Hexacolus discedens* Eggers (1940, Arb. Morph. Taxon. Ent. Berlin 7:133) to *Scolytodes* created a junior homonym of *Scolytodes discedens* Eggers 1943:360 cited above. The new name *discriminatus* is proposed as a replacement for the junior name.

Scolytodes elongatissimus, n. n.

Hylocurosoma elongatum Eggers, 1943, Mitteilungen Münchner Ent. Ges. 33:369 (Holotype, sex?; Bolivia, Cochabamba, Paris Museum), preoccupied

The transfer of *Hylocurosoma elongatum* Eggers 1943:369 to *Scolytodes* required that spelling of the specific name be corrected to

elongatus. This action made Eggers name a junior homonym of *Scolytodes elongatus* Schedl (1935, Stylops 4:273). Although the Schedl name is a junior synonym of *S. trispinosus* Eggers 1934, it is an available name and requires that *elongatus* Eggers be replaced. The new name *elongatissimus* is proposed as a replacement for this junior homonym.

Scolytodes gennaeus, n. n.

Scolytodes genialis Wood, 1978, Great Basin Nat. 38(4):403 (Holotype, female; 30 km N Merida, Merida, Venezuela; Wood Collection), preoccupied

The name of *Scolytodes genialis* Wood 1978:403 is preoccupied by *Scolytodes genialis* Wood 1975:27 and must be replaced. The new name *gennaeus* is proposed as a replacement for this junior homonym.

Scolytodes laevigatulus, n. n.

Hexacolus laevigatus Schedl, 1962, Mitteilungen Münchner Ent. Ges. 52:98 (Holotype, male; Argentina, Missiones, Dept. Concept., Sta. Maria; Schedl Collection in Wien Museum), preoccupied

The transfer of *Hexacolus laevigatus* Schedl 1962:98 to *Scolytodes* made the Schedl name a junior homonym of *Scolytodes laevigatus* Ferrari. The new name *laevigatulus* is proposed as a replacement for this junior homonym.

Scolytodes laevicorpus, n. n.

Hylocurosoma laeve Eggers, 1943, Mitteilungen Münchner Ent. Ges. 33:367 (Holotype, sex?; Bolivia, Cochabamba; Eggers Collection, on loan to Schedl), preoccupied

The transfer of *Hylocurosoma laeve* Eggers 1943:367 to *Scolytodes* and the change in gender of the generic name dictates that spelling of the specific name be changed to *laevis*. That action caused the name *laevis* (Eggers 1943: 367) to become a junior homonym when *Prionosceles laevis* Eggers 1928:88 was also transferred to *Scolytodes*. The new name *laevicorpus* is proposed as a replacement for this junior homonym.

Scolytodes majus, n. n.

Scolytodes major Eggers, 1943, Mitteilungen Münchner Ent. Ges. 33:361 (Holotype, sex?; Bolivia, Cochabamba; U.S. National Museum)

The transfer of *Prionosceles major* Eggers 1928:86 to *Scolytodes* caused *Scolytodes major* Eggers 1943:361 to become a junior homonym. The new name *majus* is proposed as a replacement for this junior homonym.

Scolytodes medialis, n. n.

Scolytodes medius Eggers, 1943, Mitteilungen Münchner Ent. Ges. 33:359 (Holotype, male; Bolivia, Cochabamba; Paris Museum), preoccupied

The transfer of *Prionosceles medius* Eggers 1928:89 to *Scolytodes* caused *Scolytodes medius* Eggers 1943:359 to become a junior homonym. The new name *medialis* is proposed as a replacement for this junior homonym.

NEW SYNONYMY

In order to provide a basis for listing names in synonymy for the new world catalog of Scolytidae, the following proposals are presented.

Dactylipalpus niger Schedl

Dactylipalpus niger Schedl, 1961 (March?), Philippine J. Sci. 90(1):87 (Luzon, Laguna, Mt. Makiling, 2,000 ft; Schedl Collection in Wien Museum)

Dactylipalpus unctus Wood, 1961 (May), Great Basin Nat. 21:8 (Holotype, female; Mt. Makiling, Laguna, Philippine Islands; British Museum, [Nat. Hist.]). *New synonymy*

When I received a series of this species from the California Academy of Science, I was told that one specimen might have been sent to Schedl. An inquiry to Schedl brought the response that only one species of *Dactylipalpus* occurred in the Philippines and that if I had another I should name it and he would refrain from doing so should the specimen mentioned in my letter reach him. One can only speculate as to what happened either before or after that letter with respect to this species. His specimen quite clearly was sent to him by the California Academy of Science from the same series sent to me, but their ownership was not acknowledged and the specimen resides at the Wien Museum. The holotype of *niger* and a paratype of *unctus* were compared directly; both the specimens and their locality labels are identical.

Dendroctonus armandi Tsai & Li

Dendroctonus armandi Tsai & Li, 1959, K'un chung hsueh chi K'an (Opera Entomologic), Peking, p. 80 (Holotype, sex?; North China; Institute of Zoology, Academia Sinica, Beijing)

Dendroctonus prosorovi Kurenzov & Kononov, 1966, Pages 29–33 *in* A. I. Cherepanow, Instit. Biol., Acad. Sci., Siberian Br., (Holotype, sex?; Yunnan Province, China; Lab. Ent. Coll. Inst. Soil Biol., Far Eastern Br., Academy of Science, USSR). *New synonymy*

My series of *Dendroctonus armandi* Tsai & Li was compared by H. F. Yin to the holotype. Authentic specimens of *armandi* were sent to Kurenzov before his death and he agreed that they were the same species, but he apparently never published that information. I have talked to or have a letter from two other workers who also claim to have seen the type of *prosorovi* and agree on the synonymy, but I have not yet located the type. In view of the fact that both types came from *Pinus armandii*, that *prosorovi* was taken within the known distribution of *armandi*, that the descriptions and illustration do not disagree, and that only one species of small *Dendroctonus* is known from China, it is concluded that these names are synonymous as indicated above.

Sinophloeus porteri Brèthes

Sinophloeus porteri Brèthes, 1922, Rev. Chilena Hist. Nat. 25:434 (Holotype, male; Province de Cautin, Chile sur *Nothophagus oblique*; Brèthes Collection)

Sinophloeus destructor Eggers, 1942, Zool. Anzeiger 139:15 (Holotype, female; Chile [Chillan]; Hamburg Museum [lost], 2 cotypes in Eggers Collection). *New synonymy*

Several years ago Dr. G. Kuschel sent a pair of *Sinophloeus porteri* Brèthes 1922:434 to me that he had compared to the holotype. Since then I have compared a series of this species to the Eggers cotypes of *S. destructor* Eggers 1942:15 and to the Kuschel specimens and find no characters that distinguish these taxa except for secondary sexual characters. All specimens are from *Nothophagus*. The Eggers name must, therefore, be placed in synonymy as indicated above.

NEW TAXA

Acacicis bicornis, n. sp.

This species is unique in the genus in frontal, pronotal, and elytral sculpture and in vestiture as described below.

MALE.—Length 1.4 mm (paratypes 1.4–1.6 mm), 1.4 times as long as wide; color black, vestiture pale.

Frons deeply concave from eye to eye from epistoma to upper level of eyes, this sulcus continuing to broadly flattened area from upper level of eyes to vertex; lateral margins at upper level of eyes armed by a pair of prominent tubercles; surface minutely rugose-reticulate, punctures not clearly evident, minute; vestiture in lower concavity at least partly bifid, those above stout, sparse, short, not divided.

Pronotum 0.62 times as long as wide, widest at base, sides rather strongly, arcuately converging to strong constriction just behind anterior margin; surface rugose-reticulate, unarmed except for two or three small tubercles near anterior margin; punctures minute, rather abundant. Vestiture on sides and posterior third of disc with pale, rather long, bifid hair, remaining area of disc with mostly undivided, darker setae.

Elytra 0.91 times as long as wide; sides weakly arcuate and subparallel on basal third, then arcuately converging to declivital tubercles, posterior margin between tubercles almost straight; feeble impressions indicate position of striae, but punctures not evident; surface smooth, shining, punctures small, distinct, close, confused. Declivity beginning one-third of elytral length from base, moderately steep, very broadly convex; sculpture as on disc except prominent subtuberculate prominences at posterior end of interstriae 5 (a generic character). Vestiture of abundant, short, apparently bifid, almost scalelike setae, and erect, hairlike setae twice as long as short setae.

FEMALE.—Similar to male except frons almost convex, somewhat flattened on lower half.

TYPE MATERIAL.—The male holotype, female allotype, and two damaged male paratypes were taken near Bulolo, Morobe District, New Guinea, 6 August 1972, from the bark of a partly uprooted tree seedling, by me.

The holotype, allotype, and paratypes are in my collection.

Acacicis zeylanicus, n. sp.

The small size and numerous, widely

distributed pronotal asperities distinguished this species from all other previously named members of the genus.

MALE.—Length 1.4 mm (paratypes 1.3–1.5 mm), 1.4 times as long as wide; color almost black, vestiture pale.

Frons moderately concave on lower two-thirds of area below upper level of eyes, slightly convex above; surface finely, somewhat obscurely rugose-reticulate, punctures not evident, upper half with sparse, fine granules; vestiture of moderately abundant, coarse, rather long hair.

Pronotum 0.65 times as long as wide; widest at base, arcuately, strongly converging toward anterior margin; surface smooth, shining, anterior three-fourths rather uniformly armed by small, rather numerous tubercles, posteromedian area with small, distinct punctures. Vestiture of uniformly distributed, short, stout hair.

Elytra 0.93 times as long as wide; sides almost straight and parallel on basal third, then arcuately converging to broadly rounded posterior margin, declivital major tubercle projecting slightly at posterolateral angles; basal crenulations low, forming a distinct marginal row, a submarginal row also present; striae distinctly, narrowly impressed, punctures in rows, distinct, very small; interstriae distinctly convex, almost smooth, surface dull, setiferous punctures small, three-ranked. Declivity beginning one-third elytral length from base, rather steep, very broadly convex; sculpture much as on disc except interstriae 1 strongly narrowed toward apex, a large, blunt tubercle at apex of 5 (a generic character), interstriae 2–9 each with a few low tubercles toward apex. Vestiture hairlike, three-ranked on each interstriae, middle rank slightly longer and distinctly coarser.

FEMALE.—Similar to male except frons more evenly convex.

TYPE MATERIAL.—The male holotype, female allotype, and 115 paratypes were taken at Buttala, Sri Lanka, 6 June 1975, elevation 50 m, No. 147, from a liana 3 cm in diameter, by me.

The holotype, allotype, and half of the paratypes are in the U.S. National Museum; the remaining paratypes are in my collection.

Sphaerotrypes bengalensis, n. sp.

This species is allied to *tsugae* Tsai & Yin, from China; they share the large size and shape, and nine rows of setae on the antennal club; this species is distinguished from *tsugae* by the finer sculpture and by the unique arrangement of elytral setae.

MALE.—Length 3.3 mm (paratypes 3.4–3.6 mm), 1.4 times as long as wide; tenneral color light brown, vestiture apparently dark.

Frons weakly impressed on lower half, flattened above, lateral areas of lower half with a few lateral tubercles, a weak median carina on lower third; vestiture of abundant, multiply divided setae, surface largely obscured. Antennal club with nine transverse rows of setae.

Pronotum outline as for genus; punctures coarse, very close, interspaces much less than one-fourth diameter of a puncture; vestiture all of one kind of suberect scale, each about three times as long as wide, short, close, rather abundant.

Elytra about as wide as long; striae abruptly, deeply, narrowly impressed, punctures rather coarse, very close; interstriae rather weakly convex, three to four times as wide as striae, small crenulations restricted to near base. Declivity gradual, beginning on basal fourth, broadly convex, sculpture as on disc; interstrial punctures confused, rather small, very deep, some with posterior margin feebly subcrenulate. Vestiture all of one kind, small, erect scales at posterior bottom of puncture, each scale about twice as long as wide, of uniform length throughout.

FEMALE.—Similar to male except frons more distinctly convex.

TYPE MATERIAL.—The male holotype and female allotype were taken at Samsingh, Kalimpong, Bengal, India, III-1934, by Mohan Lall, from sahaje jahara; 2 male paratypes bear similar data except they were taken on 5-X-1933.

The holotype and allotype are at the Forest Research Institute, Dehra Dun; the paratypes are in my collection.

Sphaerotrypes costatus, n. sp.

This species is distinguished from *cristatus* Wood by the very different sculpture of the elytral declivity.

MALE.—Length 2.2 mm (paratypes 2.3–2.4 mm), 1.4 times as long as wide; mature color dark brown.

Frons as in *cristatus*.

Pronotum as in *cristatus* except several larger punctures with their lateral margin very weakly crenulate.

Elytra 1.03 times as long as wide; sides straight and subparallel on more than basal half, broadly rounded, then sinuate between interstriae 3; striae narrowly, abruptly, deeply impressed, punctures very small, rather close; interstriae six times as wide as striae, surface rugose, crenulations very small except on basal margin and submargin and on base of declivity. Declivity beginning rather abruptly one-fourth elytral length from base, rather steep, very broadly convex; as in *cristatus* except crenulations obsolete except on interstriae 7 (these larger, 6 in number), 8 more strongly costate, this costa extending farther toward base and apex continuing to and slightly up 3; interstriae on base of declivity each with about three coarse crenulations, each about two-thirds as wide as an interstriae. Vestiture as on *cristatus* except erect scales wider, each about three times as long as wide.

FEMALE.—As in male.

TYPE MATERIAL.—The male holotype and female allotype are from North Andaman [Island], 11-III-1930, C. F. C. Beeson, from *Dipterocarpus turbinatus;* 3 male paratypes bear the same data except they were taken 18-XII-1928.

The holotype and allotype are in the Forest Research Institute, Dehra Dun; the paratypes are in my collection.

Sphaerotrypes cristatus, n. sp.

This species is distinguised from *siwalikensis* Stebbing by the larger size and by the very different elytral sculpture as described below. This species was cited as *vateriae* Beeson, nomen nudum.

MALE.—Length 3.0 mm (paratypes 3.0–3.5 mm), 1.4 times as long as wide; color brown to very dark brown.

Frons convex, a feeble impression on lower half and near vertex; a short, feeble, median carina indicated on lower third; surface apparently smooth, shining, and finely, closely punctured, largely obscured by short bifid hair and small scales; eyes separated by 1.4 times width of an eye.

Pronotum as in *ranasinghei* except some setae in ground cover bifid.

Elytra 1.1 times as long as wide; sides almost straight and parallel on basal half then arcuately converging to rather narrowly rounded posterior margin; striae strongly, abruptly, rather deeply impressed, punctures very small, rather close; interstriae moderately convex, four times as wide as striae, basal fourth of 1–4 with a row of coarse crenulations, these abruptly decrease in size and become obsolete on declivity, on 5 and 6 crenulations attain middle of elytra, on 7 they extend to apex. Declivity rather gradual, beginning on basal fourth, broadly convex; interstriae narrower, sculpture as on posterior disc, 8 very strongly, acutely costate on mesal margin from base of declivity to interstriae 3, 9 similarly but very weakly costate. Vestiture of ground cover of very minute scales, and rows of longer, erect scales, each erect scale four times as long as wide and one-fourth as long as width of an interstriae.

FEMALE.—As in male except for segmentation of abdomen.

TYPE MATERIAL.—The male holotype and five paratypes were taken at Gilmale, Rat. Distr., Sri Lanka, 17 May 1975, No. 19, from *Callophyllum* sp., by me; the female allotype and six paratypes are from Weddagala, Rat. Dist., Sri Lanka, 19 May 1975, No. 37, from *Doona cordifolia*, by me; 4 paratypes are from Thandikela, Ratnapura, Sri Lanka, 2000, 28-XII-1934, *Vateria copalifera*.

The holotype, allotype, and six paratypes are in the U.S. National Museum, 2 paratypes are in the Forest Research Institute, Dehra Dun, and the remaining paratypes are in my collection.

Sphaerotrypes pentacme, n. sp.

This species is distinguished from *quadrituberculatus* Sampson by the more strongly impressed basal half of the striae, by the more narrowly rounded interstriae, and by other characters described below.

MALE.—Length 2.8 mm (paratypes 2.8–3.0 mm), 1.4 times as long as wide; color dark brown, vestiture pale.

Frons shallowly impressed on lower half, somewhat flattened between eyes; surface smooth, shining, covered by abundant setae multiply divided to their bases, carina absent, small tubercles apparently in lateral areas; antennal club with six rows of setae.

Pronotum typical of genus; surface smooth, shining, punctures very small, abundant, a

few larger ones intermixed posteriorly; ground vestiture of abundant, minute hair, and a few erect, longer scales.

Elytral outline similar to *quadrituberculatus*, striae on posterior half of disc much more strongly impressed, much wider; interstriae almost as wide as striae, rather narrowly convex, 3, 5, and 7 with crest undulating, one or two undulations forming a coarse tubercle on these interstriae. Declivity moderately steep, broadly convex, beginning at middle of elytra; interstriae 3 and 5 each with three widely spaced, coarse tubercles, 7 weakly elevated and with tubercles indicated but less definite and closer, junction of 2 and 9 with a coarse tubercle as in *quadrituberculatus*. Ground vestiture not evident, each interstriae with an indefinite row of erect scales, each scale about twice as long as wide and spaced within a row by length of a scale.

FEMALE.—Similar to male except frons more strongly convex and discal interstriae more broadly convex.

TYPE MATERIAL.—The male holotype, female allotype, and one male and one female paratype were taken at Mohnyin Res., Myitkyina (Burma), 9-X-1928 (26-VII or 12-VIII-1928), C. F. C. Beeson, from *Pentacme suavis*.

The holotype and allotype are in the Forest Research Institute, Dehra Dun; the paratypes are in my collection.

Sphaerotrypes ranasinghei, n. sp.

This species is distinguished from *coimbatorensis* Sampson (based on examination of the type; Schedl confused no less than three species under this name) by the smaller size, by the much more narrowly separated upper eyes, by the near absence of a frontal carina, and by other characters described below.

MALE.—Length 1.6 mm (paratypes 1.5–1.8 mm), 1.4 times as long as wide; color very dark brown, vestiture pale on pronotum.

Frons convex, except slightly impressed just above epistomal margin on median third; a fine, weak, median carina except just above epistoma; surface rugose-punctate, largely obscured by erect scalelike setae; upper eyes narrowly separated by a distance less than width of an eye.

Pronotum typical of genus, without any crenulations; surface smooth, dull, densely, rather finely punctured, interspaces equal to about half width of a puncture; a pair of larger punctures near base separated by one-third width of pronotum bear a pair of long, stout setae; vestiture of scales, mostly short, recumbent, a few twice as large.

Elytra as long as wide; arcuate almost from base; striae shining, strongly, narrowly impressed, punctures very small, widely spaced; interstriae six times as wide as striae, closely punctured, each with a row of narrow, sharply pointed tubercles. Declivity rather steep, evenly convex; sculpture as on disc except interstriae become narrower. Ground vestiture of small, dark scales, each as wide as long, and rows of lighter, erect scales, each twice as long as ground cover.

FEMALE.—As in male, except for segmentation of abdomen; frontal carina usually obsolete.

TYPE MATERIAL.—The male holotype, female allotype, and 22 paratypes were taken at Kanneliya, Sri Lanka, 22 May 1975, 250 m, No. 54, from an unidentified log, by me.

The holotype, allotype, and 10 paratypes are in the U.S. National Museum, and the remaining paratypes are in my collection.

Xylechinus ougeiniae, n. sp.

This species is distinguished from *darjeelingi* Schedl by the smaller size, by the uniseriate interstrial tubercles, by the sparse ground setae, and by coarser, erect, interstrial bristles.

FEMALE.—Length 1.5 mm (paratypes 1.6–1.7 mm), 2.1 times as long as wide; color light brown, vestiture pale.

Frons similar to *padus* except punctures much larger, shallower, closer.

Pronotum 0.84 times as long as wide, widest at base, sides very feebly arcuate, converging toward almost imperceptible constriction near anterior margin; surface smooth, shining; punctures coarse, very close, moderately deep except indefinite, rather small and obscure on anterior fifth; vestiture of short, fine, moderately abundant hair.

Elytra 1.4 times as long as wide, 1.9 times as wide as pronotum; sides almost straight and parallel on basal two-thirds, rather broadly rounded behind; striae weakly impressed, punctures coarse, deep, close; interstriae slightly wider than striae, weakly convex, smooth, shining, each armed by a row of

rather closely set tubercles of moderate size. Declivity convex, steep. sculpture essentially as on disc. Vestiture of rows of fine strial hair and interstriae with sparse ground setae and erect, close bristles; bristles moderately stout, extending on all rows from base to apex, each slightly shorter than distance between rows. Abdomen rises slightly to meet elytra.

TYPE MATERIAL.—The female holotype and two female paratypes are labeled Asan R., Dehra Dun, M. Bose, 17-VIII-1928, S.E's No. 531, RRD930, B.C.R. 297, Cage 1001 ex *Ougeinia dalbergioides.*

The holotype is in the Forest Research Institute; the paratypes are in my collection. There are 13 additional specimens in the Forest Research Institute.

Xylechinus padus, n. sp.

This species was designated as *Auiphagus padus* (nomen nudum) in Beeson's 1941 (second printing) Ecology and Control of the Forest Insects of India and the Neighboring Countries, p. 285. Although it has been cited several times in the literature, the name has not previously been validated.

This species is larger than other Indian *Xylechinus*, it has very different vestiture, and it has declivital interstriae 1 and 3 distinctly elevated.

FEMALE(?).—Length 2.7 mm (paratypes 2.7–3.0 mm), 2.4 times as long as wide; color very dark brown, vestiture pale.

Frons broadly convex, a feeble median impression on lower half, pre-epistomal margin rather abrupt on median two-thirds; surface smooth and shining, feeble reticulation becoming slightly stronger laterally, much stronger toward vertex; punctures rather small, distinct, moderately coarse; vestiture of sparse, fine, rather short hair.

Pronotum 0.95 times as long as wide; sides on basal half almost parallel, very weakly constricted on anterior half; surface smooth, shining, punctures moderately large, very close, rather deep, interspaces equal to less than one-third diameter of a puncture. Vestiture of moderately abundant, fine, rather short hair.

Elytra 1.6 times as long as wide, 2.1 times as long as pronotum; striae slightly impressed, punctures moderately impressed, close, those on 1 and 2 usually with a small tubercle arising from their interior, lateral punctures often with a similar tubercle; interstriae distinctly wider than striae (about 1.5 times), distinctly convex, 1 and 3 slightly more strongly elevated on posterior half of disc, 1 and 3 each with a row of small, subcrenulate tubercles throughout, others usually with smaller tubercles near base. Declivity convex, steep; odd-numbered interstriae distinctly elevated, elevation of 3 joins 9 then continues almost to 1; odd-numbered interstriae each with a few to many small tubercles, others unarmed. Vestiture of moderately abundant, short, almost hairlike setae throughout; odd-numbered interstriae on posterior half of disc and declivity each with a row of erect, slender bristles, each as long as width of an interstriae.

MALE.—The only identifiable male is as in female, except frons without median impression.

TYPE MATERIAL.—The female(?) holotype and one paratype are labeled Mundali, 8,500′, Chakrata, U.P., C. F. C. Beeson, 17-VI-1924, ex *Prunus padus;* 2 paratypes, U. Mundali, 7,200′, Pir Panjal, Kashmir, 10-V-1928, C. F. C. Beeson, ex *Prunus padus;* one paratype Baghi 8,500′, Simla Hills, C. F. C. Beeson, ex *Xammor;* one paratype Talrathachi, 10,500′, Tharoch, Simla, Punjab, 27-V-1924, C. F. C. Beeson, *Prunus padus.*

The holotype and one paratype are in the Forest Research Institute, and the remaining paratypes are in my collection. In addition to these, 44 other specimens are in the Forest Research Institute.

COMPARISON OF REGRESSION METHODS FOR PREDICTING SINGLELEAF PINYON PHYTOMASS

Robin J. Tausch[1] and Paul T. Tueller[1]

ABSTRACT.—Succession, nutrient cycling, production, and competition studies in plant communities require estimation of plant biomass. This is often accomplished by relating weight to easily measured plant dimensions via allometric equations. Dimensions of basal area and crown volume were used to predict phytomass of singleleaf pinyon (*Pinus monophylla* Torr. & Frem.). Two regression methods for fitting the allometric equation to data for phytomass prediction were tested. These methods were the more commonly used logarithmic transformation of both data variables followed by linear regression analysis and an iterative nonlinear analysis without data transformation. The first was consistently less effective for predicting both individual tree and total plot phytomass for pinyon. Basal area was a better predictor of phytomass on a site than was crown volume. Prediction equations were highly site specific. Age of the trees in the stand used to derive the equations significantly affected the phytomass estimates. Other site and stand factors also appear to affect the phytomass-allometric parameter relationship.

Detailed studies of succession, nutrient cycling, production, and competition in plant communities often require estimates of plant biomass and production. Procedures have been developed for making these estimates by relating biomass or production to easily measured plant dimensions. Examples include the prediction of surface area and biomass relationships of woody plants in deciduous forests (Whittaker and Woodwell 1967, Pastor et al. 1983) and prediction of the aboveground biomass and wood volume of western conifers (Cochran 1982, Hatchell et al. 1985) and eucalyptus species (Stewart et al. 1979). Biomass predictions from plant dimensions have also been used for shrubs, grasses, and forbs (Tausch 1980, Hymphrey 1985, Alaback 1986, Hughes et al. 1987). The most commonly used plant dimensions are stem or trunk diameter, plant height, and crown volume.

Various types of regression analysis techniques are used for these procedures. Usually they involve some type of regression fit to the allometric equation: $Y = aX^b$, where Y = weight and X = the dimension measured (Sprent 1972). The allometric equation describes the constant specific or relative growth rates between measurements of plant size and shape (Batschelet 1973). Commonly the equation is fit to specific data sets through linear regression of logarithmically transformed data known as log-log or power regression (Grove and Malajczuk 1985). Log-log regression has the form: $\ln(Y) = a + b \ln(X)$. Its preferred use is the result of a more precise fit to the transformed data as indicated by higher values for the coefficient of determination (R^2), and lower values for the standard errors of the estimate ($S_{y.x}$) (Stewart et al. 1979, Huges et al. 1987).

Such transformation of data has been demonstrated to sometimes introduce bias into the results (Baskerville 1972, Lee 1982, Sprugel 1983). Theoretically this bias represents the introduction of an underestimate of individual plant biomass values resulting from the log-antilog transformations. In some studies this bias appeared to make only a small difference (Madgwick and Satoo 1975, Turner and Long 1975, Pastor and Bockheim 1981), and a proposed correction factor (Lee 1982, Sprugel 1983) has been shown to result in overestimation of plant biomass in some instances (Westmann and Rogers 1977). Transformation can also result in difficulties in appropriate evaluation by the usual measures of goodness of fit such as the coefficient of determination (R^2) and standard error of the estimate. This occurs because they apply only to the logarithmically transformed data (Payandeh 1981, Chiyenda and Kozak 1982). Previous attempts at using the allometric equation for biomass determination in woodlands dominated by singleleaf pinyon and Utah juniper

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(*Juniperus osteosperma* [Torr.] Little) did not consider the bias problem (Tausch 1980).

Avoidance of the potential introduction of bias into the results of regression analyses for biomass estimation by the allometric equation is possible by using untransformed data in an iterative nonlinear regression technique (Payandeh 1981, Chiyenda and Kozak 1982). Determination of the possible presence of bias is best accomplished by the simultaneous use of both log-log and nonlinear regression techniques and comparison of the results (Schlaegel 1981, Brand and Smith 1985).

The first objective of this study was a comparison of the use of log-log and iterative nonlinear regression for the estimation of leaf biomass or phytomass of singleleaf pinyon. The second objective was the comparison of measurements of basal area and crown volume for predicting the phytomass of both individual trees and entire stands. Regression results were also evaluated for how they were affected by different ages of the trees in a stand.

STUDY SITE DESCRIPTION

Tree data used for most of the analyses were associated with four locations in the pinyon-juniper woodlands of the Sweetwater Mountains in western Nevada, first sampled by Meeuwig (1979) and Meeuwig and Budy (1979). These locations ranged in elevation from just over 2,000 m to 2,300 m (Table 1). All four sites were in woodlands that were fully stocked or fully tree-occupied as described by Meeuwig and Budy (1979). Some juniper was present in plot S4, but plots S1, S2, and S3 contained only singleleaf pinyon. Data from four additional sites (Table 1) in central Nevada from Meeuwig (1979) plus data from a site in southwestern Utah from Tausch (1980) were included in one analysis. All five additional sites were closed-stand woodlands with mixed pinyon and juniper.

TABLE 1. Elevation, slope, and aspect for eight plots from Meeuwig (1979) and one plot from Tausch (1980). Mountain ranges represented are the Sweetwater Mountains of Nevada and California (S), Paradise Range of central Nevada (P), Monitor Range of central Nevada (M), and the Needle Range of southwestern Utah (UT).

Plot number	Aspect (degrees)	Slope (degrees)	Elevation (meters)
S1	80	3	2210
S2	40	11	2100
S3	120	8	2300
S4	345	20	2020
P1	354	3	2060
P2	55	9	2040
P3	85	3	2190
M1	60	11	2220
UT	285	2	2015

METHODS

Sampling Procedures

The Sweetwater Mountains plots from Meeuwig (1979) and Meeuwig and Budy (1979) were 30 × 30 m in size. All trees in the four plots were measured for height, average crown diameter, and basal diameter. All trees were harvested and a subsample was used for the determination of bole, bark, branch, twig, and foliage wet and dry biomass. Multiple regression techniques were used to derive the reported total dry weight of the components for each tree. Paradise and Monitor Range plots from Meeuwig (1979) were sampled in a similar manner. Tree data from the Needle Range, southwestern Utah, were sampled following the Sweetwater Mountains procedures but on a 0.1-ha plot.

A random sample of 12 singleleaf pinyon, stratified by age class, was harvested adjacent to each of the previously sampled plots, S1, S3, and S4, in an area with the same site and stand conditions. Plot S2 (Table 1) did not have a suitable adjacent area. Age classes were determined as described by Blackburn and Tueller (1970). A baseline was located in the adjacent area parallel to, and 10 m from, the side of each plot, and the selected trees were those closest to a random point on that line. Each tree was measured for average crown diameter, tree height, and basal diameter. Basal diameter measurements were just above the root crown and about 15 cm above the ground surface. Where multiple trunks branched below this point, each trunk was individually measured and an average basal diameter determined as described by Meeuwig and Budy (1979).

The harvested trees were sampled by two methods depending on tree size. All green foliage was collected on trees with basal trunk diameters up to about 15 cm. A trunk cross section was collected at the point of basal diameter measurement. The relationship of

sapwood area to phytomass has been shown to remain linear throughout the crown for several species of conifers (Long et al. 1981, Kaufmann and Troendle 1981). This relationship was used to subsample trees with basal trunk diameters greater than 15–18 cm. Two subsamples were collected, one from the main stem and one from a random major branch in the middle one-third of the tree. Main stem and branch subsamples were cut at a diameter of about 12 cm. A cross section was collected from the base of each stem and branch subsample, and a trunk cross section was collected from the base of the tree. All green foliage was collected from each stem and branch subsample during the first week of August.

Analysis Techniques

Crown volume was computed for each harvested tree from the average crown diameter and tree height using the formula for one-half of an ellipsoid (Tausch 1980). Crown volumes in plots S1 through S4 were computed from the average crown diameter and tree height data provided by Meeuwig (1979) and Meeuwig and Budy (1979). Basal diameter measurements were converted to basal area.

Trunk, stem, and branch cross sections from the subsampled trees were measured for heartwood and sapwood area with a dot grid. Sapwood areas and phytomass data from the two subsamples of each tree were combined and an overall ratio of kg of phytomass per cm^2 of sapwood area determined. This ratio was multiplied by the sapwood area of the trunk cross section to estimate the total phytomass of the tree.

Two prediction relationships were used at each site, one using basal area and the other using crown volume, to predict phytomass. Both log-log regression and nonlinear regression were used to derive prediction equations for each relationship for a total of four equations for each site. For nonlinear regression the parameters *a* and *b* were determined by an iterative least-squares technique.

Regression results were compared for each prediction relationship on each plot. Log-log regression results were converted back to arithmetic form (anti-log) prior to comparison with results from nonlinear regression analyses. Because R^2 from log-log analysis applies only to transformed data, it cannot be used for direct comparison with nonlinear regression results (Payandeh 1981). Results from the two types of analyses were compared on the basis of a Fit Index (FI) and a standard error of the estimate ($S_{y.x}$) computed from untransformed data for both analyses as recommended by Payandeh (1981) and Brand and Smith (1985). The term *Fit Index* is from Brand and Smith (1985). The FI is a measure of the variation in Y explained by the variation in X:

$$FI = 1 - (\Sigma(\hat{Y}_i - Y_i)^2/\Sigma(Y_i - \bar{Y})^2).$$

The FI and R^2 are equivalent for linear regression without data transformation. For the log-log and nonlinear regression analyses the maximum value for FI is also 1.0, but unlike R^2 it can be negative (Payandeh 1981). The standard errors of the estimate for all analyses were computed as the square root of the sums of deviations squared (based on untransformed data) divided by the number of observations minus 2 (Steel and Torrie 1960).

Equations derived from the trees collected next to plots S1, S3, and S4 were used to predict the total pinyon phytomass of the respective adjacent plot. All four possible combinations of regression techniques and prediction relationships were used for each site. Basal areas and crown volumes used on these plots were derived from data provided by Meeuwig (1979) and Meeuwig and Budy (1979). Predicted biomass values were then compared with the published values.

The nonlinear regression results for the basal area and crown volume to phytomass relationships for plots S1, S3, and S4 were used to predict the total plot phytomass for plot S2. This provided a test of how accurately an equation derived for one plot could predict total plot phytomass on a different plot. The results were then evaluated on the basis of differences in singleleaf pinyon age between predicting and predicted sites. Average tree ages for sampled plots from Meeuwig (1979) and Meeuwig and Budy (1979) were computed from individual tree age data they provided.

The effects of average pinyon age in a stand on biomass prediction were further evaluated by comparing the differences over nine sites with trees of different ages. Eight of the sites are from Meeuwig (1979) and one is from Tausch (1980). Nonlinear regression was used

TABLE 2. Basal area (cm^2) to tree phytomass (g) log-log and nonlinear regression equation parameters for trees harvested adjacent to three plots studied by Meeuwig (1979) and Meeuwig and Budy (1979) on the Sweetwater Mountains. Plot designations are described in Table 1.

	Log-log regression					Nonlinear regression			
Plot number	a	b	R^2	Fit index	Standard error (g)	a	b	Fit index	Standard error (g)
S1	11.75	1.235	0.98	0.83	9159.1	85.85	0.921	0.88	7806.5
S3	14.82	1.170	0.98	0.90	4299.4	56.63	0.958	0.92	3934.2
S4	14.88	1.139	0.96	0.12	14592.2	397.61	0.620	0.93	4193.9

TABLE 3. Crown volume (m^3) to tree phytomass (g) log-log and nonlinear regression equation parameters for trees harvested adjacent to three plots studies by Meeuwig (1979) and Meeuwig and Budy (1979) on the Sweetwater Mountains. Plot designations are described in Table 1.

	Log-log regression					Nonlinear regression			
Plot number	a	b	R^2	Fit index	Standard error (g)	a	b	Fit index	Standard error (g)
S1	852.48	0.988	0.96	0.58	14563.2	3896.0	0.568	0.82	9486.0
S3	912.78	0.935	0.99	0.89	4619.5	1851.5	0.739	0.91	4088.5
S4	462.44	1.068	0.97	0.87	5555.6	698.0	0.950	0.88	5412.1

to derive equations predicting phytomass from basal area for all nine sites. The estimated phytomass of a tree on each site with a basal area equivalent to a basal diameter of 25.4 cm (10 in) was determined. The 25.4-cm (10-in) diameter is the one most commonly used for site comparisons in singleleaf pinyon (Chojnacky 1986). These tree phytomass values and the average pinyon ages in the plots were used in the regression analysis.

RESULTS

Nonlinear regression consistently provided a better fit for the basal area to tree phytomass relationship for harvested trees from each site than log-log regression with transformed data (Table 2). This is evident in both higher Fit Index values (closer to 1.0) and lower standard error of the estimate values. Results were similar for the crown volume to tree phytomass relationships in Table 3. Fit Index values from each log-log regression are always lower than the respective R^2 (coefficient of determination) from the same analysis. This reflects the unreliability of the R^2 values based on transformed data. Differences are particularly evident for plot S4 in Table 2 and plot S1 in Table 3 where high R^2 values from log-log regression are associated with low Fit Index values and poor standard errors computed from untransformed (anti-log) data.

Crown volume was consistently less precise than basal area in predicting tree phytomass. This appears related to variability of density and distribution of phytomass in the tree crowns, thus making these measurements more variable than those from basal area. Values of the regression parameter *b* are nearly always lower for the nonlinear regression method (Tables 2, 3).

Equations for trees harvested adjacent to plots S1, S3, and S4 were used to estimate the total pinyon phytomass of their respective plots as a direct check on predictability (Table 4). Estimates of total phytomass in the three plots by nonlinear regression had average errors of +0.5 % for prediction by basal area and +5.7% for prediction by crown volume. The equivalent figures for log-log regression were +39.3% and +35.3%. A substantial overestimate related to the bias associated with data transformation for power regression was evident. The error, however, is opposite that usually reported in the literature. Application of a correction factor to the log-log regression results (Lee 1982, Sprugel 1983) would further increase the overestimate, similar to the results reported by Westmann and Rogers (1977).

Prediction of total tree phytomass from basal area on the test plot S2 by nonlinear regression equations from plots S1, S3, and S4 (Table 2) revealed an inverse relationship

TABLE 4. Prediction of total pinyon phytomass from crown volume and basal area of individual trees on three plots studied by Meeuwig and Budy (1979) and Meeuwig (1979) and comparison with the published values. Plot designations used are those from Meeuwig (1979). Nonlinear and log-log regression equations used are for data from trees randomly collected adjacent to the plots.

	Computed by nonlinear regression equations				Computed by log-log regression equations			
Test plot	Phytomass from crown volume (1)	Percent error	Phytomass from basal area (2)	Percent error	Phytomass from crown volume (1)	Percent error	Phytomass from basal area (2)	Percent error
S1	1171.6	+11.5	1052.8	+0.2	1608.3	+53.0	1257.3	+19.6
S3	1300.2	+2.5	1284.2	+1.2	1701.6	+34.1	1729.4	+36.3
S4	878.6	+3.2	851.4	+0.05	1101.8	+18.9	1378.6	+62.0
Average error		+5.7		+0.5		±35.3		+39.3

[1]Equations used from Table 3
[1]Equations used from Table 2

TABLE 5. Estimation of total plot phytomass for test plot S2 from Meeuwig (1979) by equations based on trees harvested adjacent to sample plots S1, S3, and S4 in Table 1. Equations were derived from nonlinear regression analyses for the basal area to tree phytomass relationship. Average pinyon age data are from Meeuwig (1979).

Plot used for estimation equation	Estimated phytomass for plot S2 (kg)	Deviation from actual phytomass (%)	Estimated average tree age (yrs)
S1	1623	+12.6	88.2
S3	1364	−5.4	122.4
S4	1064	−26.2	242.7
Actual S2	1441	0	128.6

between the average tree age on the plot used to develop the equation and estimated total tree phytomass for plot S2 (Table 5). The equation from plot S4, with trees older than the test plot, underestimated actual total tree phytomass of S2. The equation from plot S1, with younger trees, overestimated actual phytomass. Plot S3, with an average tree age the most similar to S2, came the closest to predicting its actual total tree phytomass.

Effects of age on the basal area to phytomass relationship were further investigated using the data from the eight plots from Meeuwig (1979) and the plot from Tausch (1980). A regression analysis between the average age of the trees on each plot and the respective phytomass of a tree with a basal area equivalent to a diameter of 25.4 cm (10 in) was significantly negative (Fig. 1). The variability in Figure 1 indicates that other environmental and stand differences are involved in the estimation errors between sites. These could include differences in site potential, tree size, competing species, and edaphic and topographic conditions between sites.

DISCUSSION

The more commonly used log-log regression was consistently the poorest performer in both precision and prediction accuracy. Nonlinear regression provided better equations for predicting tree biomass for singleleaf pinyon on the sites studied. Differences in the equations between the two regression methods stem from an interaction between logarithmic transformation of the data and the distribution of tree sizes in a stand. There is a skewed distribution with more small trees than large ones. Smaller trees also generally have denser crowns with more foliage biomass per unit of crown volume or unit of basal area than the larger trees. Larger trees, however, usually contribute most of the total tree phytomass in a plot. Logarithmic transformations used for power regression decrease the values for the larger trees more than for the smaller trees. As a result, the smaller trees with their denser crowns have greater weight in the log-log than in the nonlinear regression analyses.

The effects of data transformation on the resulting equations are evident in the higher values of the regression parameter b for log-log than for nonlinear regression (Tables 2, 3). Consistent overestimation of the phytomass values for the largest trees and for the total tree phytomass in the individual plots is the result. Each tree contributes to the regression result more in proportion to its size with nonlinear regression, thus tending to reduce or eliminate the overestimation. For this type of

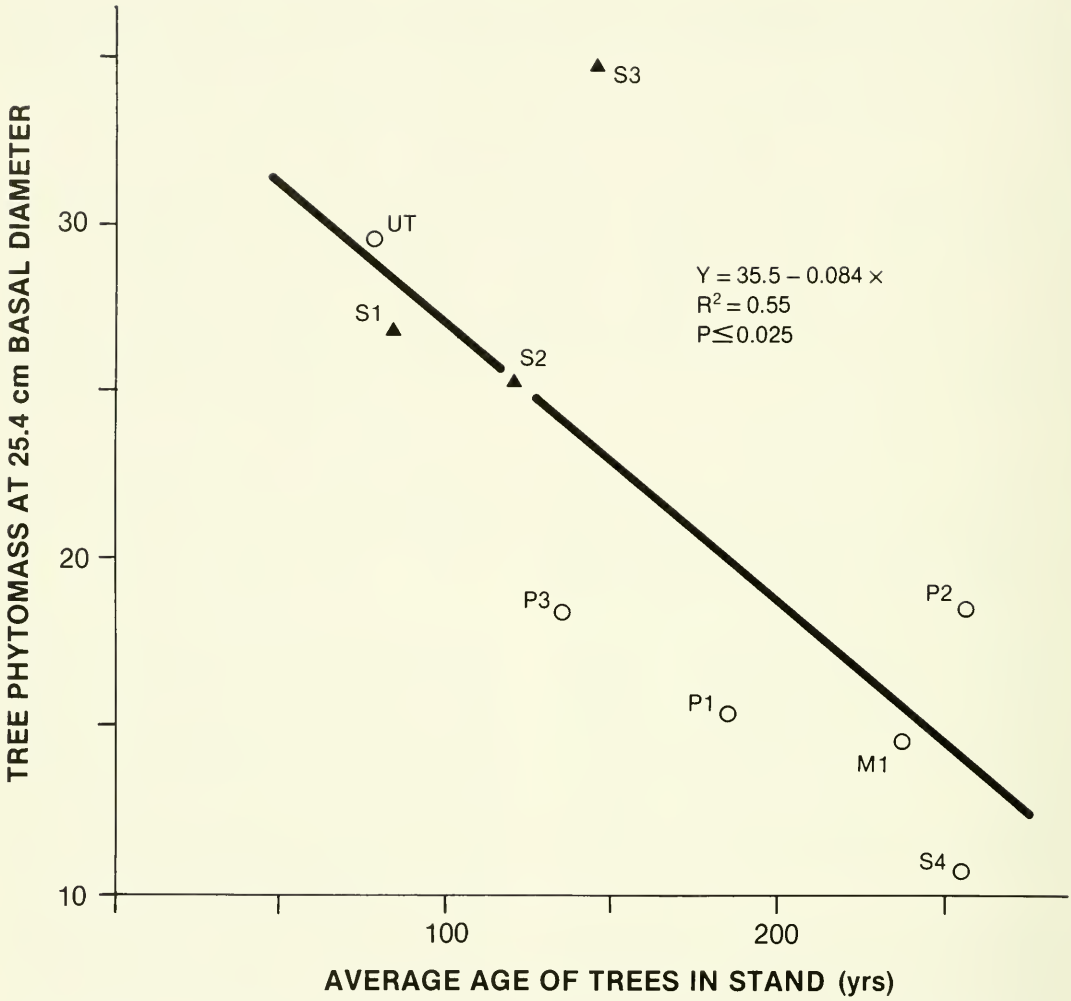

Fig. 1. Regression analysis between the average age of a tree in a stand and the estimated average phytomass of a tree with a basal diameter of 25.4 cm (10 in). Tree phytomass was determined from a nonlinear regression analysis between basal area and tree phytomass for all the trees on each site. Plot definitions are in Table 1.

data, nonlinear regression provides more accurate estimates on an individual tree and total plot basis than the more commonly used log-log regression.

The highly site-specific nature of tree age on analysis results is apparently related to growth characteristics of trees of semiarid climates. Studies of semiarid sites in Australia have shown that the phytomass of mature trees becomes constant after a certain size is reached (Sharpe et al. 1985). Basal area continues to increase after phytomass has become constant, however, resulting in a decline in the ratio of phytomass to basal area with increasing age of the trees. Because younger trees have higher phytomass to basal area ratios, equations developed from plots with younger trees overestimate the phytomass of plots with older trees. Conversely, equations developed from plots with older trees, with their lower ratios, underestimate plots with younger trees. In most instances new equations should be developed for each site where biomass estimates are needed.

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LITERATURE CITED

ALABACK, P. B. 1986. Biomass regression equations for understory plants in coastal Alaska: effects of species and sampling design on estimates. Northwest Sci. 60: 90–103.

BASKERVILLE, G. L. 1972. Logarithmic regression in the estimation of plant biomass. Canadian J. For. Res. 2: 49–53.

BATSCHLET, E. 1973. Introduction to mathematics for life sciences. Springer-Verlag, New York. 495 pp.

BLACKBURN, W. H., AND P. T. TUELLER. 1970. Pinyon and juniper invasions in black sagebrush communities in east central Nevada. Ecology 51: 841–848.

BRAND, G. J., AND W. B. SMITH. 1985. Evaluating allometric shrub biomass equations fit to generated data. Canadian J. Bot. 63: 64–67.

CHIYENDA, S. S., AND A. KOZAK. 1982. Some comments on choosing regression models for biomass prediction equations. For. Chron. 58: 203–204.

CHOJNACKY, D. C. 1986. Pinyon-juniper site quality and volume growth equations for Nevada. USDA For. Serv. Res. Pap. INT–372.

COCHRAN, P. H. 1982. Estimating wood volumes for douglas-fir and white fir from outside bark measurements. Forest Sci. 28: 172–174.

GROVE, T. S., AND N. MALAJCZUK. 1985. Biomass production by trees and understory shrubs in an age-series of *Eucalyptus diversicolor* F. Muell. Stands. For. Ecol. and Manage. 11: 59–74.

HATCHELL, G. E., C. R. BERRY, AND H. D. MUSE. 1985. Nondestructive indices related to aboveground biomass of young loblolly and sand pines on ectomycorrhizal and fertilizer plots. For. Sci. 31: 419–427.

HUGES, H. G., L. W. VARNER, AND L. H. BLANKENSHIP. 1987. Estimating shrub production from plant dimensions. J. Range Manage. 40: 367–369.

HUMPHREY, L. D. 1985. Use of biomass predicted by regression from cover estimates to compare vegetation similarity of sagebrush-grass sites. Great Basin Nat. 45: 94–98.

KAUFMANN, M. R., AND C. A. TROENDLE. 1981. The relationship of leaf area and foliage biomass to sapwood area in four subalpine forest tree species. For. Sci. 27: 477–482.

LEE, C. Y. 1982. Comparison of two correction methods for the bias due to the logarithmic transformation in the estimation of biomass. Canadian J. For. Res. 12: 326–331.

LONG, J. N., F. W. SMITH, AND D. R. M. SCOTT. 1981. The role of douglas-fir stem sapwood and heartwood in the mechanical and physiological support of crowns and development of stem form. Canadian J. For. Res. 11: 459–464.

MEEUWIG, R. O. 1979. Growth characteristics of pinyon-juniper stands in the western Great Basin. USDA For. Serv. Res. Pap. INT–238. 22 pp.

MEEUWIG, R. O., AND J. D. BUDY. 1979. Pinyon growth characteristics in the Sweetwater Mountains. USDA For. Serv. Res. Pap. INT–227. 26 pp.

PASTOR, J., AND J. G. BOCKHEIM. 1981. Biomass and production of an aspen mixed hardwood-spodosol ecosystem in northern Wisconsin. Canadian J. For. Res. 11: 132–138.

PASTOR, J., J. D. ABER, AND J. M. MELILLO. 1983. Biomass prediction using generalized allometric regressions for some northwest tree species. For. Ecol. and Manage. 7: 265–274.

PAYANDEH, B. 1981. Choosing regression models for biomass prediction equations. For. Chron. 57: 229–232.

SCHLAEGEL, B. D. 1981. Testing, reporting, and using biomass estimation models. Pages 95–112 *in* Proceedings of 1981 Southern Forest Biomass Workshop, June 11, 12, 1981, Clemson University, Clemson, South Carolina. USDA For. Serv. S. For. Exp. Sta., New Orleans.

SHARPE, P. J. H., J. WALKER, L. K. PENDRIDGE, AND H. WU. 1985. A physiologically based continuous-time markov approach to plant growth modelling in semi-arid woodlands. Ecol. Model. 29: 189–213.

SPRENT, P. 1972. The mathematics of size and shape. Biometrics 28: 23–27.

SPRUGEL, D. G. 1983. Correcting for bias in log-transformed allometric equations. Ecology 64: 209–210.

STEEL, R. G. D., AND J. H. TORRIE. 1960. Principles and procedures of statistics. McGraw-Hill Book Co., New York.

STEWART, H. T. L., D. W. FLINN, AND B. C. AEBERLI. 1979. Above-ground biomass of a mixed eucalypt forest in eastern Victoria. Australian J. Bot. 27: 725–740.

TAUSCH, R. J. 1980. Allometric analysis of plant growth in woodland communities. Unpublished dissertation, Utah State University, Logan.

TURNER, J., AND J. N. LONG. 1975. Accumulation of organic matter in a series of douglas-fir stands. Canadian J. For. Res. 5: 181–190.

WESTMANN, W. E., AND R. W. ROGERS. 1977. Biomass and structure of a subtropical eucalypt forest, north Stradbroke Island. Australian J. Bot. 25: 171–191.

REPRODUCTIVE CHARACTERISTICS OF TWO KOKANEE STOCKS IN TRIBUTARIES TO FLAMING GORGE RESERVOIR, UTAH AND WYOMING

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ABSTRACT.—The characteristics of kokanee (*Oncorhynchus nerka*) spawning stocks in the Green River and Sheep Creek (tributaries to Flaming Gorge Reservoir) are described as observed in fall 1985 and spring 1986: the time of spawning; length, age, and sex structure of the stocks; fecundity and egg retention; density of eggs in redds; and the timing of downstream drift of emerging fry. The time of spawning, length-frequency distributions of spawning fish, and egg density in redds differed between the two stocks, but other differences were not observed.

The kokanee (*Oncorhynchus nerka*), the landlocked form of sockeye salmon, have been widely introduced into reservoirs of the western United States as both a sport and forage fish (Wydoski and Bennett 1981). Despite the widespread stocking of kokanee by fishery managers, there is little published information on the dynamics of spawning stocks that migrate from reservoirs or lakes into streams to spawn. Past studies include descriptions of stocks that migrate from Flathead Lake (Hanzel 1964, Fraley and McMullin 1984) and Lake Koocanusa (Huston 1984) in Montana, Porcupine Reservoir in Utah (Janssen 1983), Priest and Upper Priest lakes in Idaho (Bjornn 1961), Lake Tahoe in California (Cordone et al. 1971), and Nicola Lake in British Columbia (Lory and Northcote 1965).

From 1963 to 1983, 2.2 million kokanee were stocked in Flaming Gorge Reservoir on the Green River in Wyoming and Utah (Wengert 1985). Natural reproduction of kokanee occurred in two tributaries to the reservoir—the Green River in Wyoming and Sheep Creek in Utah. The objective of the present study, from 1 October to 19 November 1985 and from 1 March to 27 May 1986, was to describe the characteristics of the kokanee spawning stocks in these two streams including the time of spawning; length, age, and sex of the spawning fish; fecundity and egg retention; density of eggs in redds; and the time of downstream drift of emerging fry.

STUDY AREA

Flaming Gorge Reservoir is on the Green River in Sweetwater County, southwest Wyoming, and Daggett County, northeast Utah. The dam was closed and the reservoir began filling in November 1962. At full pool the reservoir is 145 km long and has a surface area of 17,000 ha.

The Green River originates in the Wind River Mountains of Wyoming. Fontenelle Dam, 115 km upstream from Flaming Gorge Reservoir, creates a barrier to upstream fish movement, and its hypolimnetic discharge provides cold water to support a salmonid fishery downstream to Flaming Gorge Reservoir. Kokanee spawning is concentrated over the 3.5-km reach of the Green River immediately downstream from Fontenelle Dam. Over this reach the river had an average wetted width of 68 m (range 33–121 m) and a constant discharge of 24 m^3/second during fall 1985.

Sheep Creek is a small, high-gradient stream that enters Flaming Gorge Reservoir from the west in Utah. Most of the discharge originates from a large spring 9.6 km upstream from the reservoir. Kokanee spawning occurs 1–7 km upstream from the creek mouth. Mean wetted width over this reach was 8.4 m (range 2.9–23.9 m) during fall 1985, and average discharge was 1.6 m^3/second over the same period.

METHODS

Kokanee adults were collected from both streams to determine the timing of migration; length, age, and sex structure of the stocks; and fecundity and egg retention by females.

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In the Green River, fish were sampled from angler catches and with an electrofishing boat between 0.5 and 3.5 km downstream from Fontenelle Dam during fall 1985. A trap installed across the mouth of Sheep Creek in September prevented fish from passing upstream without being caught. The trap was checked at about 1000 and 1800 hrs each day.

Total lengths were measured to the nearest millimeter. Otoliths were removed by the method of Schneidervin and Hubert (1986), and age was determined by three independent readers using a dissecting scope. Estimated age was the modal value or the median value of the three readings (Hubert et al. 1987). The fish were sexed by morphological differences. Ovaries were removed and placed in Gilson's fluid to break down ovarian tissue and harden the eggs for counting (Snyder 1983). Dead females were collected, and all eggs remaining in the body cavity were removed and counted to determine egg retention.

We used a modified Hess sampler to excavate redds and estimate egg deposition (Usinger 1956). The sampler was placed over a portion of the redd, and rocks were removed and water stirred to lift eggs into the current to be carried into the catch bucket. Excavation continued to a depth of 20–25 cm at different locations until the entire redd had been sampled.

The downstream drift of emergent fry was measured with drift nets (0.25-m^2 mouth, 4-mm mesh Ace netting), 7.2 km downstream from Fontenelle Dam on the Green River and 50 m upstream from the high-water mark of Flaming Gorge Reservoir on Sheep Creek. Samples were collected about once a week at 1-hr intervals after sundown in spring 1986. Flowmeters (General Oceanics, Miami, Florida) were mounted in the nets to measure the water volume sampled. Stream discharge estimates for the Green River at Fontenelle Dam were obtained from the U.S. Bureau of Reclamation and were made by the float method (Buchanan and Somers 1969) for Sheep Creek.

RESULTS

Time of Migration and Spawning

On the Green River, anglers were first observed snagging kokanee within the initial 1.5 km downstream from Fontenelle Dam on 1 October 1985. The fish were seen over shallow riffles on 15 October, and the first redd was observed on 22 October. Intensive spawning continued over the next two weeks. Water temperatures during the spawning period ranged from 4 to 7 C. Moribund kokanee were observed until 19 November, when sampling was terminated.

Mature, reddish orange kokanee were observed jumping in Sheep Creek Bay of Flaming Gorge Reservoir on 27 August. The first kokanee was observed in Sheep Creek on 5 September and migration peaked on 12 September 1985. The first redd was observed on 13 September; new redds were found over the following nine days. Water temperatures ranged from 7 to 15 C during the spawning period.

TABLE 1. Length-frequency distributions of kokanee in samples from the Green River and Sheep Creek, fall 1985.

	Green River		Sheep Creek	
Length (mm)	Male	Female	Male	Female
261–280	0	0	2	0
281–300	0	0	2	0
301–320	0	0	1	0
321–340	0	0	1	3
341–360	2	3	0	5
361–380	3	23	6	9
381–400	21	104	15	20
401–420	45	158	24	52
421–440	73	46	42	33
441–460	47	7	48	17
461–480	12	0	21	2
481–500	0	0	6	0
501–520	0	1	2	0

TABLE 2. Age structure for kokanee spawners in samples from the Green River and Sheep Creek, fall 1985.

Estimated	Green River		Sheep Creek	
age (years)	Male	Female	Male	Female
2	1	3	2	2
3	40	35	21	29
4	53	43	50	44
5	2	1	3	4

Spawning Stock Structure

Length frequencies of 545 kokanee (204 males, 341 females) from the spawning run in the Green River and 311 (170 males, 141 females) from the run in Sheep Creek are shown in Table 1. Length-frequency distributions

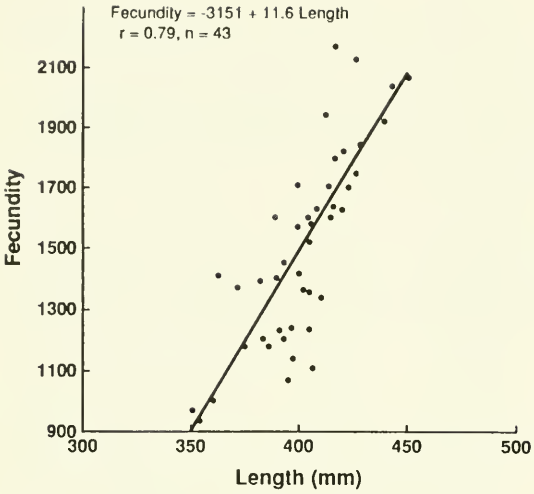

Fig. 1. Absolute fecundity versus total length of female kokanee from the Green River, fall 1985.

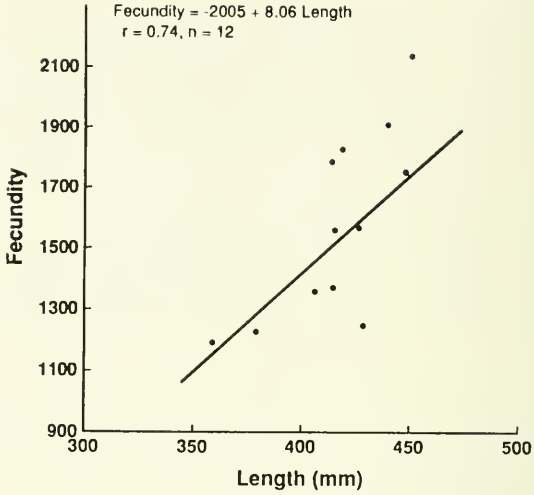

Fig. 2. Absolute fecundity versus total length of female kokanee from Sheep Creek, fall 1985.

differed significantly between the Green River and Sheep Creek for both males (Kolmogorov-Smernov test, $p = .015$) and females ($p = .001$). Average total length of male kokanee was 427 mm in Green River and 431 mm in Sheep Creek. Females averaged 405 mm in Green River and 412 mm in Sheep Creek.

Age structure of both male and female kokanee was similar in the two streams (Table 2). Fish of age 4 made up more than 50% of the fish of both sexes in both streams. The male to female ratio was 1.5:1 (not determined for the Green River).

Fecundity and Egg Retention

Absolute fecundity—the number of ripening eggs in the female before spawning—was estimated for fish from both the Green River and Sheep Creek (Figs. 1, 2). Log transformations and multiple regressions based on both length and age as independent variables did not significantly increase the variance accounted for in either stream sample. Regression equations were not significantly different between streams.

An average of 1,370 eggs per female ($n = 328$) were stripped from Sheep Creek fish by Wyoming Game and Fish Department personnel in 1985. Examination revealed an average of 136 (SD = 43) eggs remained in the body cavity of artificially spawned fish ($n = 12$). The average number of residual eggs in 83 dead females from Sheep Creek was 71 (SD = 136).

Egg Deposition

Excavations of redds yielded an average of 406 (SD = 303, range 0–1,058) eggs in 16 redds in the Green River and 113 (SD = 153, range 0–447) eggs in 12 redds in Sheep Creek. A Mann-Whitney test indicated that the Green River redds contained significantly more eggs than Sheep Creek redds.

Downstream Drift of Emergent Fry

Drifting kokanee fry were sampled in the Green River from 22 March to 22 May 1986 (when sampling was terminated due to high discharges of 250 m^3/second). Discharges during the sampling period were 41–160 m^3/second. A total of 65 kokanee fry were captured during 16 sampling nights; the largest number (13) was taken on 22 May, when an estimated 1,800 fry drifted past the sampling site during the four-hour sampling period. Total estimated fry drift between 22 March and 27 May was 31,000.

Kokanee fry sampling in Sheep Creek was conducted from 1 March to 17 May, when discharge increased to over 2.5 m^3/second. During the sampling interval discharge was 0.8–2.4 m^3/second. A total of 658 kokanee fry were captured during 32 sampling nights. The peak catch of 164 fry was made on 24 April. An estimated 6,800 fry drifted past the sampling site between 1 March and 17 May.

On five dates we collected samples in Sheep Creek for 24-hour periods. Fry were

TABLE 3. Comparison of predicted kokanee fecundity from length-fecundity equations for four waters.

Length (mm)	Green River	Sheep Creek	Lake Huron[a]	Lake Stevens[b]
300	329*	413*	590	1024
325	619*	615*	753	1163*
350	909	816	943	1321*
375	1199	1018	1162	—
400	1489	1219	1414	—
425	1779	1420	1700	—
450	2069	1622	2022	—
475	2359*	1823*	2382	—

*Predicted fecundity outside the range of lengths used to develop the equations.
[a]Collins (1971)
[b]Pfeifer (1978)

captured exclusively between sunset and 0200 hrs, except that two fry were taken between 1400 and 1700 hrs on 20 March. Fry catch was not related to either discharge or water temperature in either stream during the sampling period.

DISCUSSION

Coloration of kokanee spawners differed distinctly between the Green River and Sheep Creek. Green River fish were drab, whereas Sheep Creek fish were bright reddish orange. Information on various kokanee strains suggests that the Green River fish were descendants of the Flathead Lake, Montana, strain, and the brightly colored Sheep Creek fish were descendants of the Kootenay Lake, British Columbia, strain.

Kokanee generally spawn between August and January, the exact timing depending upon the genetic background of the stock and the lake environment (Seeley and McCammon 1966). The differences in spawning time between the Green River (late October and early November) and Sheep Creek (September) further suggested that the stocks had differing genetic backgrounds.

Population structure was similar in the Green River and Sheep Creek. Age at maturity in Kokanee ranges from 2 to 7 years (Seeley and McCammon 1966). A 4-year life cycle tended to predominate in the present study. Most of the kokanee spawners in both streams were estimated to be 4 years old (range 2–5 years). The frequency of aging errors was unknown, but some errors were likely.

As shown in Table 3, the fecundity of females from the Green River and Sheep Creek was similar to that of fish migrating from Lake Huron (Collins 1971) and Lake Stevens, Washington (Pfiefer 1978). Kokanee from Sheep Creek retained an average of 4.5% of their eggs; elsewhere retention rates were 1.5% (Pfiefer 1978) and 6.2% (Janssen 1983).

The density of eggs in redds differed between the Green River and Sheep Creek. Access to spawning sites in Sheep Creek was generally blocked by the trap across the creek, but 328 females were released after being stripped of eggs and allowed to move upstream. Redd building after being stripped of eggs has been reported in other salmon (Belding 1934, Hoover 1936) and could explain the lower egg densities observed in Sheep Creek.

Despite probable genetic differences, as well as differences in the timing of migration, length-frequency distributions, and egg density in redds, between the Green River and Sheep Creek kokanee, the two stocks showed little difference in such adult population features as age composition, fecundity, and egg retention.

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LITERATURE CITED

BELDING, D. D. 1924. The cause of the high mortality in the Atlantic salmon after spawning. Transactions of the American Fisheries Society 64: 219–222.

BJORNN, T. C. 1961. Harvest, age structure, and growth of game fish populations from Priest and Upper Priest lakes. Transactions of the American Fisheries Society 90: 27–31.

BUCHANON, T. J., AND W. P. SOMERS. 1969. Discharge measurements at gaging stations. Book 3, Chap. 8A *in* Techniques of water resources investigations of the U.S. Geological Survey. U.S. Government Printing Office, Washington, D.C.

COLLINS, J. J. 1971. Introduction of kokanee salmon (*Oncorhynchus nerka*) into Lake Huron. J. Fish. Res. Bd. Canada 28: 1857–1871.

CORDONE, A. J., S. J. NICOLA, AND P. H. BAKER. 1971. The kokanee salmon in Lake Tahoe. California Fish and Game 57: 28–43.

FRALEY, J. J., AND S. L. MCMULLIN. 1984. Monitoring kokanee salmon escapement and spawning in the Flathead River system. Fisheries Research and Special Projects Bureau, Montana Department of Fish, Wildlife, and Parks, Kalispell, Montana.

HANZEL, D. A. 1964. Evaluation of kokanee spawning and population density in Flathead Lake and tributaries. Job Completion Report F-7-R-12, Job II. Montana Department of Fish and Game, Kalispell, Montana.

HOOVER, E. E. 1936. Contributions to the life history of the chinook and landlocked salmon in New Hampshire. Copeia 36: 193–198.

HUBERT, W. A., G. T. BAXTER, AND M. HARRINGTON. 1987. Comparisons of age determinations based on scales, otoliths, and fin rays for cutthroat trout from Yellowstone Lake. Northwest Science. 61: 32–36.

HUSTON, J. E., P. HAMLIN, AND B. MAY. 1984. Lake Koocanusa fisheries investigations final completion report. Montana Department of Fish, Wildlife, and Parks, Helena, Montana.

JANSSEN, P. J. 1983. Investigation of selected aspects of kokanee ecology in Porcupine Reservoir, Utah, with management implications. Unpublished thesis, Utah State University, Logan.

LORZ, H. W., AND T. G. NORTHCOTE. 1965. Factors affecting stream location, and timing intensity of entry by kokanee (*Oncorhynchus nerka*) into an inlet of Nicola Lake, British Columbia. J. Fish. Res. Bd. Canada 22: 665–687.

PFEIFER, R. L. 1978. Evaluation of the natural reproduction of kokanee salmon (*Oncorhynchus nerka*) in Lake Stevens, Washington, as related to lake limnology and basin. Unpublished thesis, University of Washington, Seattle.

SCHNEIDERVIN, R. W., AND W. A. HUBERT. 1986. A rapid technique for otolith removal from salmonids and catostomids. North Amer. J. Fish. Manage. 6: 287.

SEELEY, C. M., AND G. W. MCCAMMON. 1966. Kokanee. Pages 274–293 *in* A. Calhoun, ed., Inland fisheries management. California Department of Fish and Game, Sacramento, California.

SNYDER, D. E. 1983. Fish eggs and larvae. Pages 165–197 *in* L. A. Nielson and D. L. Johnson, eds., Fisheries techniques. American Fisheries Society, Bethesda, Maryland.

USINGER, R. L. 1956. Aquatic insects of California. University of California Press, Berkeley.

WENGERT, M. W. 1985. Flaming Gorge Reservoir fisheries management investigations six year completion report (1977–1983). Wyoming Game and Fish Department, Fish Division, Cheyenne, Wyoming.

WYDOSKI, R. S., AND D. H. BENNETT. 1981. Forage species in lakes and reservoirs of the western United States. Trans. Amer. Fish. Soc. 110: 764–771.

SEM ANALYSIS OF UTAH *EQUISETUM* STEMS (EQUISETACEAE)

Robert B. Warrick[1]

ABSTRACT.—The Utah taxa of *Equisetum* were observed with the scanning electron microscope to test for taxonomic significance of stem morphology. The four Utah species of *Equisetum* were compared. Stem morphology was shown to be taxonomically significant in most cases. The hybrid *E.* x *ferrissii*, recognized in the literature as being extant in Utah but heretofore unrecognized in Utah herbaria, was shown to be present in the flora of the state.

Certain species of *Equisetum* have long been difficult to positively identify. Easily keyed species often have intermediate forms with characteristics of two species. This paper attempts to resolve some of these problems by observing stem characteristics, including siliceous tubercle dimensions, position of stomata, and ridge morphology, to test for taxonomic significance.

The stems of *Equisetum* are longitudinally striated, forming a series of furrows and ridges. The two most obvious characteristics of *Equisetum* stems are the stomata and siliceous tubercles. Stomatal arrangement has been used to divide the genera of *Equisetum* into two subgenera (Emons 1986). Stems of *Equisetum* are heavily impregnated with silicon, forming various-sized tubercles. The literature is replete with confusing terms for different-sized tubercles, with little or no uniformity among writers. The tubercles have been called silica nobs, rosettes, bands, bars, bodies, nodules, pustules, spicules, papilla, mamillae, pilulae, etc. (Kaufman et al. 1971, Pant and Kidwai 1968). On all specimens observed, siliceous tubercles were of three sizes. For simplicity, they are designated here as "microtubercles," "mesotubercles," and "megatubercles" (Fig. 1). Microtubercles appear as small white specks, much smaller than the stomata. Mesotubercles are rounded, sometimes coalescing tubercles smaller than the stomata but larger than the microtubercles. Megatubercles, located on the ridges, are larger than the stomata.

METHODS AND MATERIALS

Ten specimens of each species were observed (where possible) from random locations in Utah. For species not well represented in Utah, specimens from random locations throughout the United States were observed for comparison. All specimens were from dry herbarium mounts located in the Brigham Young University Herbarium (BRY). An attempt was made to observe a section of each stem from the second node below the strobilus. All samples were from mature, fertile stems, with the exception of *E. arvense*, where sections from both fertile and sterile stems were observed.

Samples were prepared for scanning electron microscopy (SEM) by mounting on aluminum stubs with double-sided tape, then carbon coating followed by gold sputter coating (Dawes 1971). Specimens were neither fixed nor critical-point dried before mounting on stubs.

RESULTS

***Equisetum arvense* L.** This species is unique among the species of *Equisetum* found in Utah, being dimorphic, with both fertile and sterile growth forms. The siliceous tubercles of sterile *E. arvense* (Fig. 2) are predominantly microtubercles. Megatubercles are lacking. Mesotubercles may be present either singly or coalescent with other mesotubercles. *Equisetum arvense* is in many ways unique when compared with the remaining

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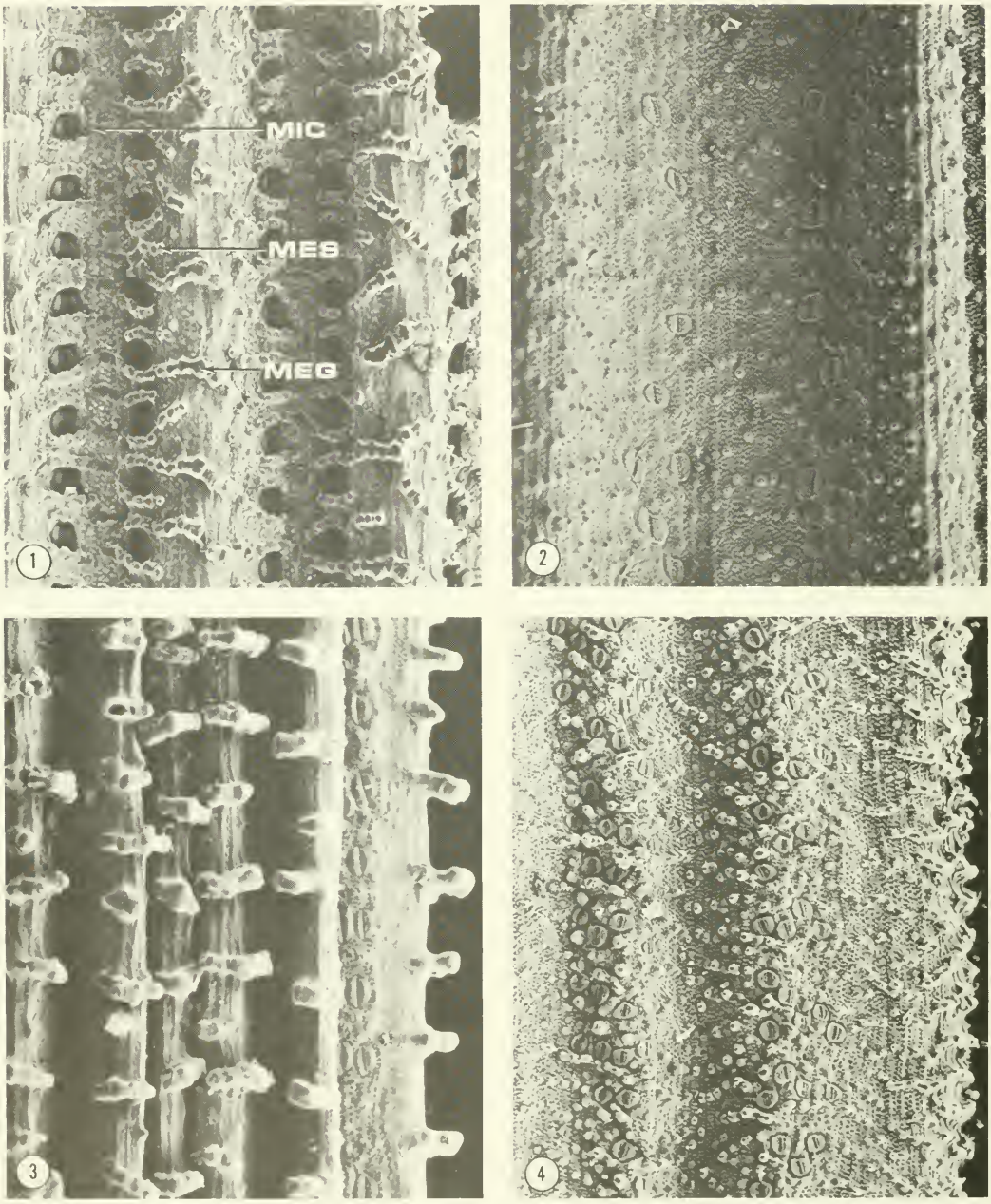
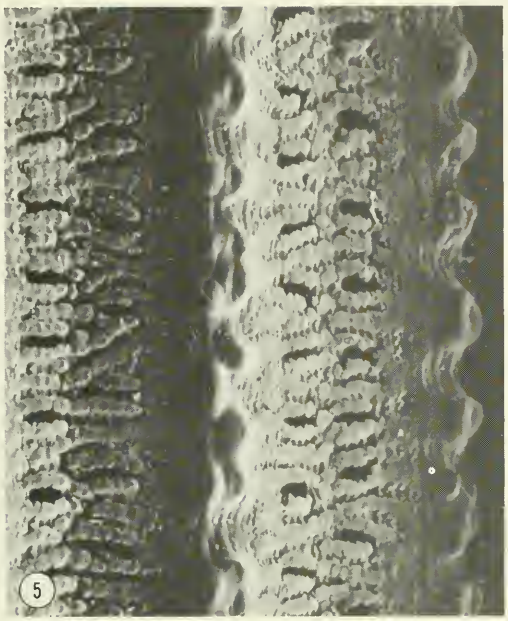
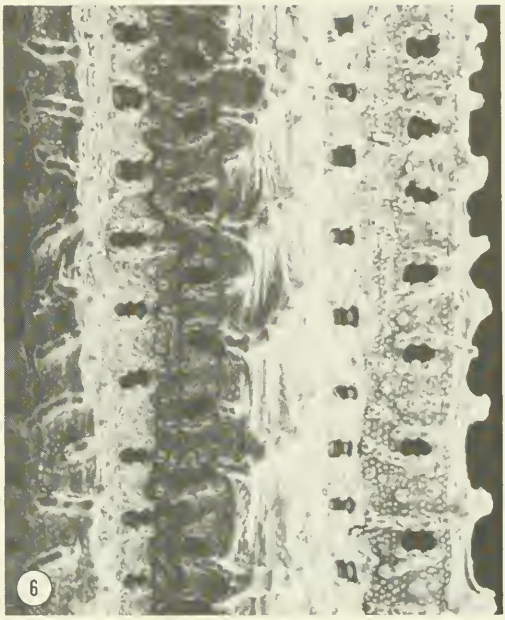


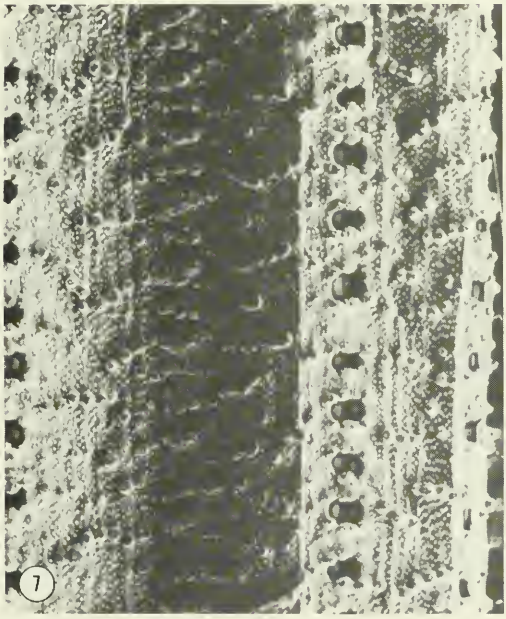
Fig. 1. *Equisetum* stem showing microtubercles (mic), mesotubercles (mes), and megatubercles (meg).
Fig. 2. Sterile stem of *Equisetum arvense* (100X).
Fig. 3. Sterile stem of *Equisetum pratense* from Palmer, Alaska (100X).
Fig. 4. Fertile stem of an atypical *Equisetum arvense* (100X).

species in Utah. The stomata, instead of forming two neat, parallel rows, form uneven, scattered rows, referred to by Hauke (1963) as bands. On specimens observed, bands are often as many as four stomata wide. The stomata are not sunken as in other species, lack a border of mesotubercles, and are generally taller than wide. Tubercles are altogether lacking on fertile stems.

A species similar in appearance to *E. arvense* is *E. pratense*. Both are dimorphic and somewhat small in stature (Welsh 1974).







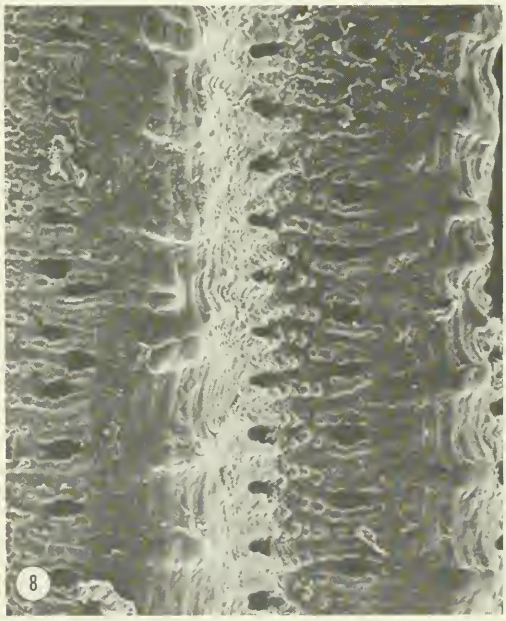


Fig. 5. *Equisetum hyemale* stem (100X).
Fig. 6. Immature *Equisetum laevigatum* stem (110X).
Fig. 7. Mature *Equisetum laevigatum* stem (100X).
Fig. 8. *Equisetum* x *ferrissii* stem (100X).

Where the two overlap in distribution, field identification is difficult by sight alone. *Equisetum pratense* was historically represented in Utah on the basis of a few herbarium sheets, generally collected in the northern part of the state. All were annotated to *E. arvense* previous to this study, but one specimen collected along the Logan River in Cache County remained slightly enigmatic. This specimen was carefully scrutinized with the SEM (Fig. 3) and compared with a collection of *E. pratense* from Alaska (Fig. 4) and *E. arvense* from Utah

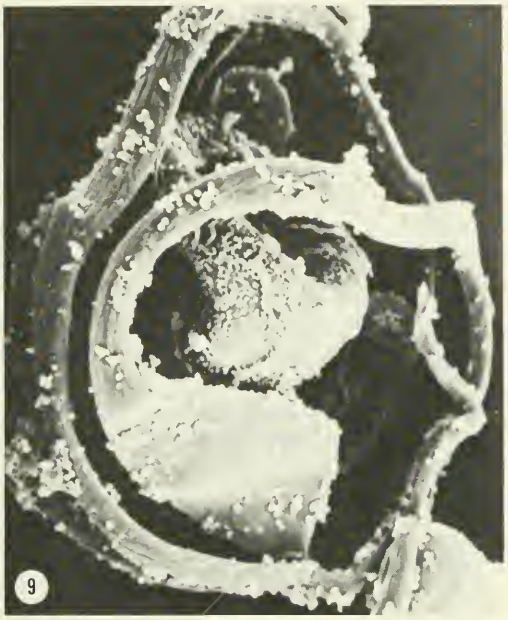
(Fig. 2). As shown in Figure 3, the megatubercles of *E. pratense* are taller than wide and arranged in a very regular pattern along the ridges. The stomata are also grouped into neat rows and mesotubercles are very few in number. When the Logan River collection of "*E. pratense*" was compared with the Alaskan *E. pratense* and a Utah collection of *E. arvense*, it readily correlated with *E. arvense*, albeit with some differences. Unequivocal specimens of *E. pratense* are not currently known from Utah.

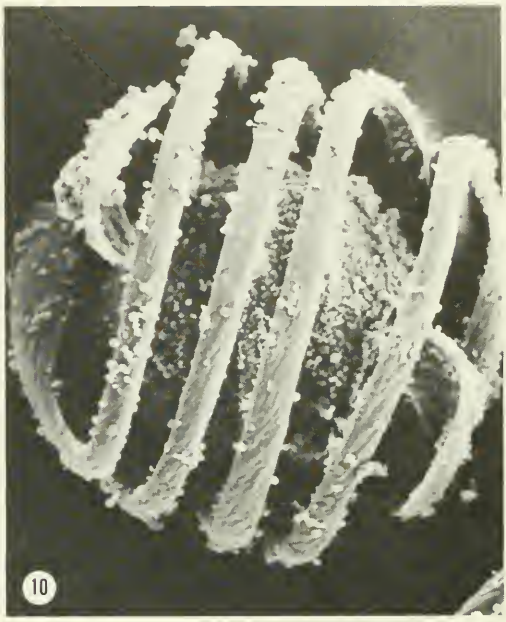
***Equisetum hyemale* L.** This species is the most robust of the *Equisetum* taxa occurring in the state, usually possessing an ash gray band near the top of each sheath, and with apiculate cones. The surface characters of *E. hyemale* (Fig. 5) are very distinct. Microtubercles are very few on mature stems. Mesotubercles are numerous but are usually coalesced. Most form short bars running perpendicular to the furrows, with groups of three or four forming borders around the stomata, causing a "doubly sunken" condition (Dayanandan and Kaufman 1973). The stomata are arranged in two even, closely spaced, parallel rows, and are wider than tall. The megatubercles are very prominent on the narrow ridges and appear to form two parallel rows on each ridge. Megatubercles are wider than tall.

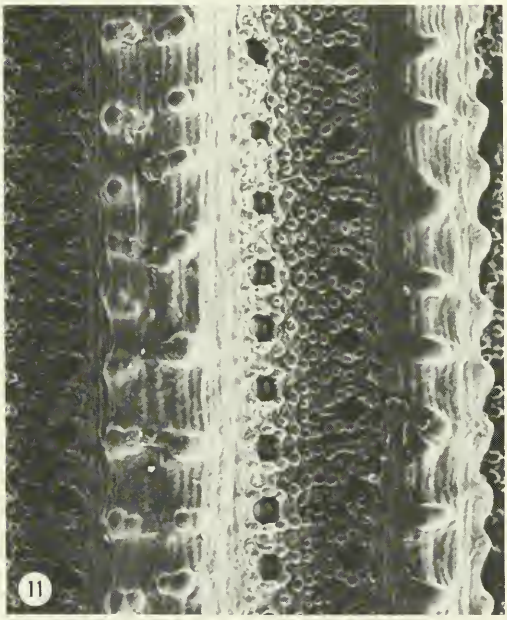
***Equisetum laevigatum* A. Br.** This taxon is readily identifiable unless the specimens are small or otherwise depauperate. *Equisetum laevigatum* tends to branch from the caudex, as does *E. variegatum*, whereas *E. hyemale* and *E. arvense* rarely exhibit this feature. Small or immature specimens (Fig. 6) may resemble *E. variegatum* (Fig. 12) and vice versa. The surface characters of *E. laevigatum* (Fig. 7) show the tubercles to be predominantly microtubercles, with megatubercles nonexistent to very few (hence the common name, "smooth scouring rush"). The ridges range from being obscure with no special arrangement of tubercles to prominent with perpendicular bars of small megatubercles. Mesotubercles are scattered throughout, both as single units and as groups coalesced into bars perpendicular to the furrows. Stomata are sunken beneath the epidermis and bordered by three connivent mesotubercles above and below. The stomata are wider than tall and arranged in widely spaced, parallel rows. The rows tend to be equidistant between the row in the same furrow and the row in the adjacent furrow.

***Equisetum* x *ferrissii* Clute (= *E. hyemale* x *E. laevigatum*).** This hybrid is widespread in the United States and has been reported for Utah (Hauke 1963, Raven et al. 1981). It should occur frequently since both parents are abundant throughout the state (Welsh et al. 1987). While there are no collections labeled as such, several sheets at BRY look like intermediates between *E. hyemale* and *E. laevigatum* and could possibly be designated as the hybrid *E.* x *ferrissii* (Fig. 9). Both collections examined appear similar with the SEM. Microtubercles, mesotubercles, and megatubercles are all common. Stomata are deeply sunken and spaced as in *E. hyemale*. Ridge prominence and shape of stomata are about intermediate between the two putative parents.

***Equisetum variegatum* Schleich.** This taxon is poorly represented in the herbaria of the state because of its rarity. Many of the herbarium sheets labeled as *E. variegatum* appear to be misidentified. Only two of the six collections labeled as *E. variegatum* at BRY have cones. From external appearance, five of the six, including the four lacking cones, could very well be immature specimens of *E. laevigatum*. For this reason, several collections of *E. variegatum* from throughout the United States were observed and photographed (Fig. 11) for comparison with the Utah material. Results showed that the collections from outside of Utah, though spaced over 3,000 miles, are strikingly similar to one another in external stem morphology. The ridges are prominent and tend to be as wide as the furrows. Microtubercles are present but not especially common. Mesotubercles are prominent in the furrows but nonexistent on the ridges, while the reverse is true for the megatubercles, thus forming distinct rows on the ridges. The Utah material, however, lacks evident megatubercles. Tubercles on the ridges are borderline megatubercles, appearing more like slightly large coalesced mesotubercles. They are not appreciably larger than the mesotubercles found in the furrows. Microtubercles are much more common in the Utah collection. The only Utah *E. variegatum* which could be







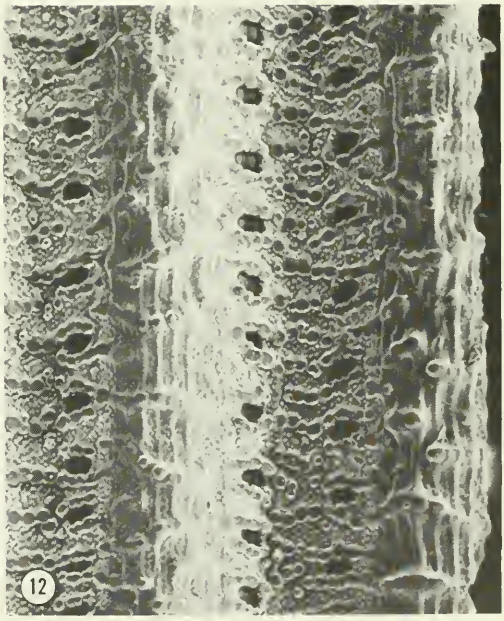


Fig. 9. Aborted spore of *Equisetum* x *ferrissii* (1,350X).
Fig. 10. Developed spore of *Equisetum hyemale* (1,350X).
Fig. 11. *Equisetum variegatum* stem from Richland, Washington (100X).
Fig. 12. *Equisetum variegatum* stem from Navajo Lake, Utah (100X).

positively identified as such (Fig. 12) was collected near Navajo Lake. This site is only a few miles from Cedar Breaks, the Utah location frequently reported in the literature for this taxon (Cronquist et al. 1972, Hitchcock et al. 1969).

DISCUSSION

While some researchers doubt that stem characteristics such as those described above are worthy as taxonomic features (Kaufman et al. 1971), others feel that these characteristics

are analogous to the sculpturing of pollen grains and are thus important as diagnostic features (Page 1972, Larouche et al. 1970). These features, based upon this small study of Utah taxa of *Equisetum*, are useful taxonomically, at least for Utah species.

The species *E. arvense* and *E. hyemale* are very distinct and unmistakable when compared with other taxa occurring in the state. These are, however, not easily mistaken for anything else in the field, and it is unlikely that one would ever have to resort to tubercle morphology for identification. It has proven useful, nonetheless, to show beyond doubt that collections labeled as *E. pratense* were mislabeled and that this taxon has yet to be collected within Utah (see also Hauke 1978). It is interesting to note that while the Utah specimen identified as *E. pratense* is most closely allied to *E. arvense*, it does not match that taxon perfectly, possibly accounting for the misidentification. Several mature stems of fertile *E. arvense* from random sites in Utah were examined and no stomata or tubercles were observed. On fertile stems of "*E. pratense*," stomata and tubercles were observed to be as common as on the sterile stems of *E. arvense*. In his monograph of the *Equisetum* subgenus *Hippochaete*, Hauke (1963) states that a considerable amount of variability exists within the species. Others have noted that the horsetails are known to be plants of notoriously plastic morphology (Page 1972). All known taxa of *Equisetum* have 2n = 256 (Soltis 1986), a condition adding to the plasticity of this genus. Thus, while different, the Logan River collection of "*E. pratense*" fits into the spectrum of variation for *E. arvense*.

Within Utah, *E. laevigatum* and *E. variegatum* are distinct as mature adults, but when specimens are immature or depauperate, identification becomes difficult and tubercle morphology tends to resemble one another. This would seem to indicate relatedness, but, oddly enough, these are two of the most distantly related taxa in the subgenus Hippochaete (Hauke 1963). Since *E. laevigatum* and *E. variegatum* are distinct as mature adults and nearly impossible to distinguish when depauperate or immature, tubercle and stomata morphologies alone are not especially useful for these two taxa within Utah. The one certain collection of *E. variegatum* (Fig. 12) examined with SEM is somewhat distinct from collections of *E. variegatum* (Fig. 11) from other states. Based solely on tubercle and stomatal characteristics, this collection appears to be intermediate between *E. variegatum* and *E. laevigatum*. Since this specimen readily keys to *E. variegatum* using easily observable external features and looks like other collections of *E. variegatum* from all over the United States, I can only conclude that this specimen is within the range of expectations for tubercle morphology, but that a large enough sample was not examined. Again, the notoriously plastic morphology of this genus must be kept in mind. Inasmuch as the Utah populations represent the southwest extreme of the distribution of this species and are somewhat disjunct, it is not surprising to find this population slightly different from specimens from other states.

Prior to this study, *E.* x *ferrissii* was unrecognized in the herbaria of the state, though discussed in the literature (Hauke 1963, Hitchcock et al. 1969, Cronquist et al. 1972). Because the two specimens examined are intermediate in stomata and tubercles and also appear intermediate from gross morphological features used in the keys, these collections apparently fall safely within the concept of *E.* x *ferrissii*. The spores of *E.* x *ferrissii* all abort, and none are released from the strobilus (Hauke 1963), thus providing one of the best aids for identification (Wagner et al. 1986). Aborted spores from Utah collections of *E.* x *ferrissii* (Fig. 9) were compared with viable spores of *E. hyemale* (Fig. 10). This verifies the existence of *E.* x *ferrissii* in Utah.

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LITERATURE CITED

CRONQUIST, A. J., A. H. HOLMGREN, N. H. HOLMGREN, AND J. L. REVEAL. 1972. Intermountain Flora. Vol. 1. Hafner Publishing Company, Inc., New York.

DAYANANDAN, P., AND P. KAUFMAN. 1973. Stomata in *Equisetum*. Canadian J. Bot. 51: 1555–1564.

DAWES, C. 1971. Biological techniques for transmission and scanning electron microscopy. Ladd Research Industries, Inc., Burlington, Vermont.

EMONS, A. 1986. Cell wall texture in root hairs of the genus *Equisetum*. Canadian J. Bot. 64: 2201–2206.

HAUKE, R. 1963. A taxonomic monograph of the genus *Equisetum* subgenus *Hippochaete*. Beih. Nova Hedwigia, Heft 8: 1–123.

———. 1978. A taxonomic monograph of *Equisetum* subgenus *Equisetum*. Nova Hedwigia 30: 385–455.

HITCHCOCK, C. L., A. J. CRONQUIST, F. M. OWENBY, AND H. J. THOMPSON. 1969. Vascular plants of the Pacific Northwest. University of Washington Press, Seattle.

KAUFMAN, P., W. BIGELOW, R. SCHMID, AND N. GHOSHEH. 1971. Electron microprobe analysis of silica in epidermal cells of *Equisetum*. Amer. J. Bot. 58(4): 309–316.

LAROUCHE, J., C. GUERVIN, C. LACOQ, AND V. DAO. 1970. Interet taxonomique de la excretion siliceuse chez les Equisetacees. C. R. Acad. Sci. Paris, t. 270, serie D, pp. 2958–2960.

PAGE, C. 1972. An assessment of inter-specific relationships in *Equisetum* subgenus *Equisetum*. New Phytol. 71: 355–369.

PANT, D., AND P. KIDWAI. 1968. Development of stomata in *Equisetum*. Ann. Bot. (London) 32: 601–608.

RAVEN, P., R. EVERT, AND H. CURTIS. 1981. Biology of plants. 3d ed. Worth Publishers, New York.

SOLTIS, D. 1986. Genetic evidence for diploidy in *Equisetum*. Amer. J. Bot. 73(6): 908–913.

WAGNER, W., F. WAGNER, AND C. TAYLOR. 1986. Detecting abortive spores in herbarium specimens of sterile hybrids. Amer. Fern. J. 76(3): 129–140.

WELSH, S. L. 1974. Anderson's flora of Alaska and adjacent parts of Canada. Brigham Young University Press, Provo, Utah.

WELSH, S. L., N. D. ATWOOD, S. GOODRICH, AND L. C. HIGGINS. 1987. A Utah flora. Great Basin Nat. Mem. 9.

FIRE HISTORY OF THE PAUNSAUGUNT PLATEAU IN SOUTHERN UTAH

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ABSTRACT.—A fire history of the Paunsaugunt Plateau in southern Utah was developed using dendrochronological methods. Fire frequencies of individual ponderosa pine trees from three sites on the plateau varied from 19.5 to 47 years. Composite fire intervals for the three sites ranged from 15.2 to 18.4 years. The last recorded fires in these study areas occurred in 1892, 1902, and 1911, corresponding to the initiation of fire suppression policies in the West. The absence of fire since 1911 may be contributing to a recently documented decrease in ponderosa pine regeneration within the high-elevation, mixed-coniferous forests of the Paunsaugunt Plateau.

Fossil charcoal in both Tertiary and Carboniferous coal deposits testifies to natural fires from over 400 million years ago to the present (Komarek 1973). Before humans, lightning was the primary cause of fires. McCann (1942) has estimated that each year about 16 million thunderstorms occur on the earth, causing an average of 50 lightning strikes per second or a total of 2 billion strikes a year. Even though only a small percentage of these strikes ignites forest fuels, lightning causes about 50,000 wildland fires per year worldwide (Taylor 1974).

Historical evidence indicates that fires have always been an ecological and evolutionary force in ponderosa pine (*Pinus ponderosa* Laws.) forests (Cooper 1960, Weaver 1951). Fire in primeval ponderosa pine forest typically involved frequent surface fires spreading slowly through the forest (Biswell 1973, Wagener 1961). These fires had a significant effect on community structure and composition by reducing understory vegetation and thereby decreasing competition for water and nutrients, accelerating biogeochemical cycling, and controlling the encroachment of less fire-resistant tree species (Wright 1978, Weaver 1967b, Williams 1959). Fire enhanced ponderosa pine regeneration by creating small openings and by thinning the dense sapling thickets that developed (Wright 1978).

Ponderosa pine has characteristics that allow it to withstand frequent ground fires. These include thick bark, rapid juvenile growth, a moderately high and open crown, deep rooting habit, and open stand structure (Brown and Davis 1973). Mutch (1970) hypothesized that some fire-dependent plants might possess characteristics to enhance the spread of fire. The highly flammable, resinous needles that are dropped in great quantities each year by ponderosa pines may be a characteristic that supports Mutch's contention.

Dense thickets of crowded, spindly ponderosa pine and understories that have become invaded with more shade-tolerant species are now common in post-fire suppression forests (Weaver 1974, Biswell 1973). This leads to speculation that ponderosa pine would likely have a more restricted distribution were it not for frequent fires in the past (Wellner 1970).

In this study the fire history of an isolated plateau in southern Utah is quantified. Results are compared to other studies in the western United States.

STUDY AREA

The study was conducted on the Paunsaugunt Plateau, located within the Powell Ranger District of the Dixie National Forest and Bryce Canyon National Park. The Paunsaugunt Plateau is approximately 49 × 16 km (78,400 ha), occupying a position midway between 37 and 38 degrees North latitude, 16 km west of the 112th meridian. It slopes upward from about 2,100 m in the north to 2,870 m in the south. Ponderosa pine can be found in pure stands from 2,200 to 2,600 m. It begins

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to mix with Douglas-fir (*Pseudotsuga menziesii* Franco) at about 2,200 m on north- and east-facing slopes. Most of the higher elevations are covered with mixed coniferous forests including Douglas-fir, blue spruce (*Picea pungens* Engelm.), white fir (*Abies concolor* Lindl.), Engelmann spruce (*Picea engelmannii* Parre.), limber pine (*Pinus flexilis* James), subalpine fir (*Abies lasiocarpa* Nutt.), and quaking aspen (*Populus tremuloides* Michx.). Old individuals of ponderosa pine grow among the spruce and fir trees on the southern end of the Paunsaugunt Plateau, though very little regeneration occurs.

The mean monthly precipitation recorded at Bryce Canyon National Park Headquarters ranges from 1.5 cm in June to 5.6 cm in August with an annual mean of 40.9 cm. The mean maximum temperature is 2 C in January and 27 C in July. The mean minimum temperature is −12 C in January and 8 C in July.

The three study areas selected were Whiteman Spring, Seiler Mill, and Straight Canyon. Because the first two areas contained recent timber sales, cross sections could be easily obtained from stumps.

Materials and Methods

Cross sections were collected from 14 fire-scarred ponderosa pine trees. Each cross section was surfaced with progressively finer sandpaper (40–500 grit) until individual cells were readily visible with the aid of a dissecting microscope. Annual rings were dated using the skeleton plot technique (Stokes and Smiley 1968). These plots then were cross-dated with a master skeleton plot developed from cores of 20 trees growing in the same area as the fire-scarred trees. A master tree ring chronology developed in Bryce Canyon National Park and vicinity was also used (Tree Ring Laboratory, University of Arizona). Fire scars were identified from the 14 cross sections on the basis of the following criteria (Stokes 1980): (1) the presence of a break or gap within or along a tree ring boundary, (2) the presence of charred wood within the break or gap, (3) subsequent overlapping curvilinear growth over the break.

Fire scars were dated by determining the ring in which the fire scar appeared. When the scar occurred between the latewood of one ring and the earlywood of the next ring, the scar was dated to the year of the latewood growth.

Individual fire frequencies (mean fire intervals) were determined for each of the 14 fire-scarred ponderosa pines. This represents the mean interval between fires from the first to the last fire scar. A composite fire interval (mean interval for an area) was then constructed for each of the three study areas, which expresses the historical fire frequency for a particular area (Dieterich 1980).

Results and Discussion

Fire frequency and intensity vary among species. Fire patterns for any one species also vary over its geographic range. Prior to fire suppression, the average fire frequency of ponderosa pine forests in Arizona and New Mexico was between 4 and 12 years (Dieterich 1980, Weaver 1951). In Washington and Oregon, Weaver (1967a, 1959) showed that fire frequency varied from 6 to 47 years in a wide range of ponderosa pine communities. Arno (1980) reported an average fire frequency of between 6 and 12 years in the northwestern Rockies. Ponderosa pines have an average fire frequency of between 39 and 46 years in the Colorado Rocky Mountains (Laven et al. 1980, Rowdabaugh 1978), and between 8 and 14 years in California (McBride and Jacobs 1980, Warner 1980, Wagener 1961).

The fire history of the Paunsaugunt Plateau is presented in Figure 1. Fire frequencies of individual trees varied from 19.5 to 47 years. Composite fire intervals from the three study areas ranged from 15.2 to 18.4 years.

Though these observed fire frequencies are greater than those reported from the central Rocky Mountains, they are less than other reports in ponderosa pine stands. On the Paunsaugunt Plateau, understory growth and buildup of litter are slow due to the cool, dry climate, nutrient-poor soils, and short growing season (Stein 1983). Generally, fires are of small areal extent because of cool temperatures and the shortage of fuels. This pattern of fires is reflected by the rarity of fires that affected all trees sampled at a particular site (Fig. 1). Consequently, the composite interval for each area is much less than the fire intervals of the individual trees.

The last recorded fires in the three study areas occurred in 1892, 1902, and 1911 (Fig.

Outside ring		1980	1980	1980	1980	1980		1932	1968	1906	1968		1948	1980	1980	1980	1980	
Number of fires	15	9	3	8	8	5	17	10	5	7	3	12	5	2	4	5	3	
Mean fire interval	15.9	22.8	19.5	28.5	23.6	20.3	15.2	26.0	27.3	36.3	28.5	18.4	33.8	23.0	47.0	27.3	29.0	
1920																		1920
	1911	1911				1911												
1900							1902			1902								1900
	1888	1888		1888	1888	1888						1892				1892		
							1885		1885									
1880												1883		1883				1880
							1878	1878										
	1874					1874	1876	1876	1876	1876	1876							
												1871					1871	
1860												1860	1860	1860		1860	1860	1860
	1847	1847	1847	1847	1847	1847	1848				1848							
1840							1841		1841									1840
	1830					1830												
	1824	1824		1824	1824		1825		1825									
1820	1820		1820				1819	1819			1819							1820
							1817			1817		1814	1814					
												1813			1813	1813	1813	
1800	1808	1808	1808		1808									1807 C				1800
	1796	1796			1796		1795	1795	1795	1795		1794	1794					
												1789				1789		
1780	1777	1777		1777	1777													1780
							1774	1774				1773	1773		1773	1773		
							1766			1766								
	1763	1763		1763														
1760																		1760
	1749			1749	1749													
1740																		1740
	1729	1729		1729														
	1723				1723		1723	1723		1723		1725	1725			1728 C	1728 C	
1720																		1720
							1711	1711			1713 C							

YEAR

YEAR

Fig. 1. Paunsaugunt Plateau fire chronology based on dendrochronological analysis of fourteen fire-scarred *Pinus ponderosa* trees from the three study areas. The dates in each column represent the years fire scars were present for individual trees. The left-hand column for each study area displays the composite fire interval for that area.

1). These dates correspond to the initiation of fire suppression policies in the West around 1900, and the establishment of Dixie National Forest in 1905. The exclusion of forest fires on the Paunsaugunt Plateau by the Dixie National Forest and Bryce Canyon National Park has been effective since 1911. Before 1911, periodic ground fires were common. These fires may have created conditions that helped to establish fire-dependent ponderosa pines at higher elevations, where only scattered individuals remain today (Stein 1988).

Many inventories show a marked decrease in land dominated by ponderosa pine (Gruell et al. 1982, Eyre 1980, Barrett 1979, Schubert 1974, Weaver 1961, Cooper 1960). These and other authors have observed an anomalous size-class distribution of ponderosa pine in many stands, due to a lack of individuals in smaller size-classes. Both these changes have been documented on the higher elevations of the Paunsaugunt Plateau (Stein 1988). Fire suppression policies have probably made ponderosa pine regeneration difficult at higher elevations throughout its range, favoring the more competitive, shade-tolerant spruce and fir. This is somewhat ironic since ponderosa pine is the favored timber tree throughout much of the interior West. However, the Forest Service continues its policy of eliminating forest fires despite the major ecological and evolutionary role that fire has played in the establishment and persistence of ponderosa pine forests.

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LITERATURE CITED

ARNO, S. F. 1980. Forest fire history in the northern Rockies. J. For. 78: 460–465.

BARRETT, J. W. 1979. Silviculture of ponderosa pine in the Pacific Northwest: the state of our knowledge. USDA For. Serv. Rept. PNW-97.

BISWELL, H. 1973. Fire ecology in ponderosa pine-grassland. Proc. Tall Timbers Fire Ecol. Conf. 12: 69–96.

BROWN, A. A. AND R. P. DAVIS. 1973. Forest fire control and use. 2d. ed. McGraw-Hill Book Co., New York. 686 pp.

COOPER, C. F. 1960. Changes in vegetation, structure and growth of southwestern forests since white settlement. Ecol. Monogr. 39: 129–164.

DIETERICH, J. H. 1980. Chimney Spring forest fire history. USDA For. Serv. Res. Pap. RM-220. 8 pp.

EYRE, F. H. 1980. Forest cover types of the United States and Canada. Society of American Foresters. 148 pp.

GRUELL, G. E., W. C. SCHMIDT, S. F. ARNO, AND W. J. REICH. 1982. Seventy years of vegetal change in a managed ponderosa pine forest in western Montana—implications for resource management. Gen. Tech. Rept. INT-130. 42 pp.

KOMAREK, E. V. 1973. Ancient fires. Pages 219–240 *in* Proc. of the Tall Timbers Fire Ecol. Conf. 1972.

LAVEN, R. D., P. N. OMI, J. G. WYANT, AND A. S. PINKERTON. 1980. Interpretation of fire scar data from a ponderosa pine ecosystem in the central Rocky Mountains, Colorado. Proc. of the Fire History Workshop, Tucson, Arizona, 1980. USDA For. Serv. Gen. Tech. Rept. RM-81. 142 pp.

MCBRIDE, J. R., AND D. F. JACOBS. 1980. Land use and fire history in the mountains of southern California. Proc. of the Fire History Workshop, Tucson, Arizona, 1980. USDA For. Serv. Gen. Tech. Rept. RM-81. 142 pp.

MCCANN, G. D. 1942. When lightning strikes. Sci. Amer. 49: 23–25.

MUTCH, R. W. 1970. Wildland fires and ecosystems—a hypothesis. Ecology 51: 1046–1051.

ROWDABAUGH, K. M. 1978. The role of fire in the ponderosa pine–mixed conifer ecosystem. Unpublished thesis, Colorado State University, Fort Collins.

SCHUBERT, G. H. 1974. Silviculture of southwestern ponderosa pine: the status of our knowledge. USDA For. Serv. Res. Pap. RM-123. 71 pp.

STEIN, S. J. 1983. Reproductive failure and scattered distribution of aged ponderosa pine within a high elevation mixed coniferous forest of southern Utah. Unpublished thesis, University of Colorado, Boulder.

———. 1988. Explanations of the imbalanced age structure and scattered distribution of ponderosa pine within a high elevation mixed coniferous forest. For. Ecol. and Manage. In press.

STOKES, M. A. 1980. The dendrochronology of fire history. Proc. of the Fire History Workshop, Tucson, Arizona, 1980. USDA For. Serv. Gen. Tech. Rept. RM-81. 142 pp.

STOKES, M. A., AND T. C. SMILEY. 1968. Introduction to tree ring dating. University of Chicago Press, Chicago.

TAYLOR, A. R. 1974. Ecological aspects of lightning. Proc. of the Tall Timbers Fire Ecol. Conf. 1973.

WAGENER, W. W. 1961. Past fire incidence in the Sierra Nevada forests. J. For. 59: 739–747.

WARNER, T. E. 1980. Fire history in the yellow pine forests of Kings Canyon National Park. Proc. of the Fire History Workshop, Tucson, Arizona, 1980. USDA For. Serv. Gen. Tech. Rept. RM-81. 142 pp.

WEAVER, H. A. 1951. Fire as an ecological factor in southwestern ponderosa pine forests. J. For. 49: 93–98.

_____. 1959. Ecological changes of the ponderosa pine forest of Warm Springs Indian Reservation in Oregon. J. For. 57: 15–20.

_____. 1961. Ecological changes in the ponderosa pine forest of Cedar Valley in southern Washington. Ecology 42: 416–420.

_____. 1967a. Fire and its relationship to ponderosa pine. Proc. Tall Timbers Fire Ecol. Conf. 7: 127–149.

_____. 1967b. Fire as a continuing ecological factor in perpetuation of ponderosa pine forests in the western United States. Adv. Front. Plant Sci. 18: 137–154.

_____. 1974. Effects of fire on temperate forests: western United States. *In:* T. T. Kozlowski and C. E. Ahlgren, eds., Fire and ecosystems. Academic Press, New York.

WELLNER, C. A. 1970. Fire history in the northern Rocky Mountains. *In:* The role of fire in the Intermountain West, Proc. Symp. 1970. Missoula, Montana.

WILLIAMS, H. W., JR. 1959. The effect of understory competition on the growth rate of ponderosa pine in northcentral Oregon. J. For. 57: 852–853.

WRIGHT, H. A. 1978. The effect of fire on vegetation in ponderosa pine forests: a state of the art review. Texas Tech. University Range and Wildlife Series #2, Pub. 9-9-199.

USE OF INTERSTATE HIGHWAY OVERPASSES AND BILLBOARDS FOR NESTING BY THE COMMON RAVEN (*CORVUS CORAX*)

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ABSTRACT.—Common ravens are usually rather shy birds around their nests and avoid nesting too near human activity. We here report the use of overpasses along heavily traveled Interstate Highway 84 in Idaho and Utah for nest placement. Nests are within 6 m of passing vehicles.

The feral pigeon (*Columba livia*) is a common inhabitant of overpasses and underpasses along interstate highway systems. Also, throughout the Great Basin at least, the cliff (*Hirundo pyrrhonota*) and barn (*Hirundo rustica*) swallows frequently nest on these structures. The western kingbird (*Tyrannus verticalis*) has also built nests on overpasses. A thorough survey of over- and underpasses would probably reveal numerous bird species nesting on them.

The common raven (*Corvus corax*), while widespread and often common, tends to be a shy species and nests in remote areas, especially in the eastern United States (Hooper 1977, Knight and Call 1981). Although it is not as retiring in the Great Basin, it nonetheless nests in areas more or less removed from busy human activity, especially as compared to the American crow (*Corvus brachyrhynchos*) that may nest in woodlots surrounding homes. Prior to the arrival of settlers in the Great Basin, ravens doubtless primarily used cliffs for nesting. Since the arrival of settlers, many man-made structures have been used for nest placement (Knight and Call 1981), usually remote from excessive human activity. Currently, high-tension steel pylons for electric transmission line support or other power line poles are being used with increasing frequency by ravens for nesting (personal observation, Steenhof et al. 1985). For example, along Interstate Highway 80 north of Rye Patch, Nevada, we found 10 nests on power poles within a distance of 21.7 km. Seven of the nests had young or adults present. The closest 2 nests with pairs were 0.64 km apart. This may have resulted from the poles providing new nesting habitat in areas formerly nest-site limited but not food limited. The list of other man-made structures used by ravens for nest placement includes such things as buildings, windmills, and artificial platforms built for hawk nesting (Howard and Hilliard 1980, Knight and Call 1981, McBee 1927). A railroad bridge (Johnson 1899) was used formerly, the nest being located 0.6 m from the rails where a train passed four times daily.

Because overpasses structurally resemble cliffs, it is not surprising that ravens would use them. However, because of the retiring nature of ravens, it is noteworthy that they nested so close to busy vehicular traffic. This is the first report of which we are aware wherein ravens are documented nesting over interstate highways or freeways. We found seven raven nests on overpasses within a 466-km stretch of Highway I–84 between Boise, Idaho, and Brigham City, Utah, in 1986 and 1987. An additional nest was found in the same general area in 1978.

In the 466 km, 69 overpasses were examined. Of these, 12 were constructed in such a way that there were no ledges or other structures for nest placement. From the Wendall-Hagerman area south, to at least the Rupert-Declo area, the land is so intensively and extensively crop-farmed that ravens are not seen there (although nesting crows may be seen). Between these two areas there is one stretch of interstate along which native vegetation occurs, but a stretch of about 107 km is deemed not suitable for raven nesting. (The development of cropland, unless extreme,

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does not necessarily exclude ravens). There are 22 overpasses in this 107 km, a disproportionate number for the distance, but results because there are many more roads in developed areas. In the mixed native grass and brush vegetation areas one may travel long distances through which no roads cross the interstate. Twenty-four overpasses occur in areas we categorized as native vegetation of mixed grass and brush. Between the junction of I–84 and I–86 and Tremonton, Utah, we judged the habitat to be a complex mosaic of cropland and native vegetation. This area has many ravens, covers 166 km, and contains 22 overpasses and underpasses. Based on habitat and overpass structure, then, we judged only 25 overpasses available to ravens for nesting. We extended our survey to Brigham City, Utah, in spite of extensive crop development between Tremonton and Brigham City, because ravens nest on a steel electric power pylon 300 m from the interstate near Brigham City and could thus easily have used an overpass.

In May 1986 we found a raven nest on the Power Plant Road overpass (Exit 129) of I–84 at the Gooding-Elmore County line in Idaho. It was situated on the top of a pillar support of the overpass that was in the area between south- and northbound traffic lanes (Fig. 1). The nest was about 7.2 m from the nearest road edge and 5.5 m above the southbound traffic lanes. The intact condition of regurgitation pellets below the nest and the amount of fecal stain suggested that the nest was used in 1985 or, at the latest, 1984. The good construction and size of the nest suggested that it had been used more than one year. By May 1987 no pellets remained intact.

In May 1986 a second nest was found on the overpass at the Malta-York exit (Exit 228) of I–84, Cassia County, Idaho. Its location on the overpass, as shown in Figure 1, was about 1 m from the nearest road edge and 5.5 m above the traffic. It was not in use, its state of disrepair suggesting that it had not been used for three or four years. In September 1986 it showed further disrepair, and by May 1987 only a dozen or so sticks remained.

About 4.8 km further south (mile 230.5) another overpass (without an exit) crosses I–84. There was a partially constructed nest on the southbound traffic side in the same location as above. The nest consisted of about

Fig. 1. Nest on Power Plant overpass in Idaho showing position of nest relative to traffic. Overpasses with the type of pillar support shown were those types of construction most easily used by ravens in Idaho. The nest is indicated by the arrow.

15–20 sticks and a couple of mammal ribs (calf size?). In May 1987 a nest of similarly poor construction was on the opposite side of the overpass above the northbound traffic lane. These two nests and the one 4.8 km north may have been built by the same birds and, at least the latter two, were probably never used.

On 14 May 1987 a fifth nest was found above the northbound traffic at Exit 32 (Ranch Road) of I–84 in Box Elder County, Utah. The construction style of the overpass and, consequently, nest placement were different from the above four nests (Fig. 2). The nest was about 6 m to the left of the inside traffic lane and 6.1 m above the traffic. At least three young, approximately two weeks old, were in the nest. Wings of two fledgling meadowlarks (*Sturna neglecta*) were below the nest. On 23 May the three young were about one week from fledging. On 13 June at least two young had fledged.

At the Howell underpass (Exit 26) in Box Elder County, Utah, two more nests were

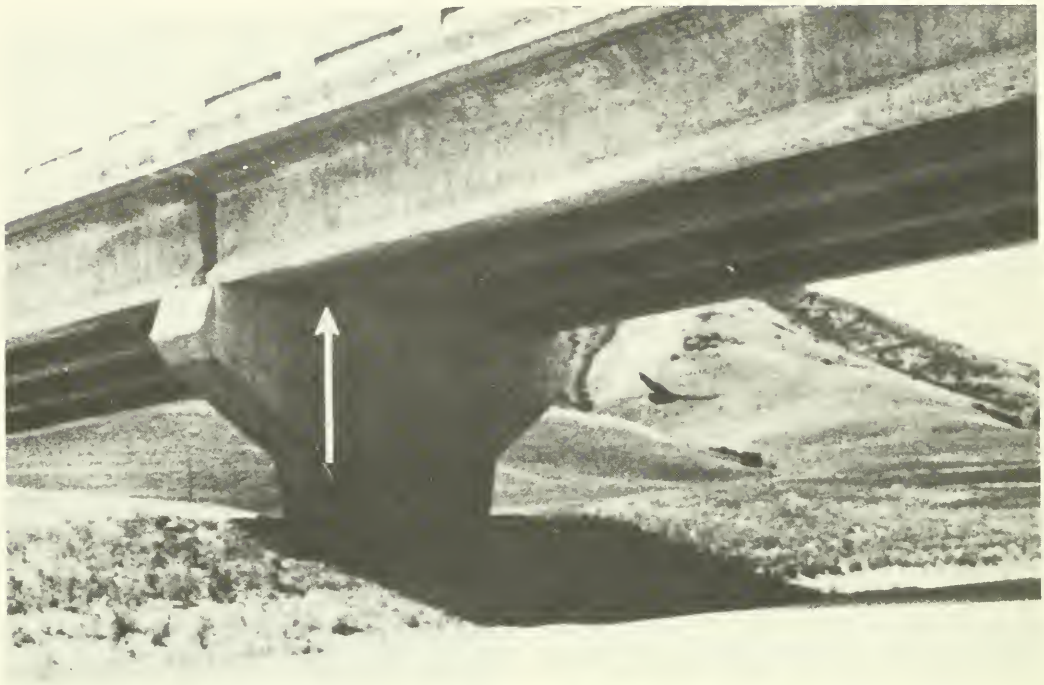

Fig. 2. Overpass construction mode in Utah used by ravens. This nest was used in 1987, and its location is indicated by the arrow in the upper figure (also shows an adult leaving the nest). In the lower figure, young nearly ready to fledge (23 May) are shown in the nest.

found on 22 August 1987. Both looked freshly built, but neither had been used beyond the incubation period, if at all. While one was well constructed, the other consisted of only 30–40 sticks. They faced each other on opposite sides of the underpass about 15 m apart. Used cliff or barn swallow nests were within 1 m of them.

Lastly, a nest was found in 1978 on a roadside billboard along Idaho State Highway 81 some 32 km due west of I–84. The nest, from which young fledged from at least 1978 to 1980, was 25 km south of Malta, Cassia County. The billboard, which had been torn down by 1984, was 26 m from the road. This was a dual-directional billboard, with advertisements facing both north- and southbound traffic. The south-facing billboard, about 4.5 m high, was connected to the north-facing sign, and both were supported by two "telephone polelike" poles with the tops of the poles about 3.6 m above ground. The nest was on top of one pole and, although between both signs, was easily accessible to the raven because the north-facing sign was also only about 3.6 m high.

If raven populations continue to increase at the rate shown by Robbins et al. (1986), it will be of interest to see how extensively this "interstate habitat" will be used. The fact that most cars do not stop along the highway and people remain in the cars has probably removed the human disturbance element from these nestings.

ACKNOWLEDGMENTS

We thank Karen Steenhof, Bureau of Land Management, U.S. Department of the Interior, Boise District, for help with the literature and discussion of ideas.

LITERATURE CITED

HOOPER, R. G. 1977. Nesting habitat of common ravens in Virginia. Wilson Bull. 89: 233–242.

HOWARD, R. P., AND M. HILLIARD. 1980. Artificial nest structures and grassland raptors. Raptor Res. 14: 41–45.

JOHNSON, H. C. 1899. Raven nesting on a railroad bridge. Condor 1: 71–72.

KNIGHT, R. L., AND M. W. CALL. 1981. The common raven. U.S. Bur. Land Manage., Tech. Note 344.

MCBEE, C. 1927. Unusual nesting sites for the American raven. Oologist 44: 58–59.

ROBBINS, C. S., D. BYSRAK, AND P. H. GEISSLER. 1986. The breeding bird surveys: its first fifteen years, 1965–1979. Resource Publ. 157. U.S. Fish and Wildlife Ser., Washington, D.C.

STEENHOF, K., M. H. KOCHERT, J. ROPPE, M. MULROONEY, AND D. RAMIREZ. 1986. Raptor and raven nesting on the PP&L Malin to Midpoint 500KV transmission line. Pages 21–35 *in* K. Steenhof and M. H. Kochert, eds., Snake River Birds of Prey Research Project, Annual Report, 1986. U.S. Dept. Int., Bur. Land Manage., Boise, Idaho.

FIELD OBSERVATIONS OF *IRBISIA PACIFICA* (HEMIPTERA: MIRIDAE): FEEDING BEHAVIOR AND EFFECTS ON HOST PLANT GROWTH[1,2]

James D. Hansen[3]

ABSTRACT —The interaction between a grass-feeding mirid, *Irbisia pacifica* (Uhler), and plant growth of intermediate wheatgrass, *Thinopyrum intermedium* (Host) Barkw. & D. R. Dewey, was examined on a field site in northern Utah in 1985. With egg hatch beginning in April, the bug completed its life cycle within two months. Ovarian development was completed by 11 June, a week after all bugs had become adults. The proportion of feeding damage per leaf (35.1%) peaked on the seventh week of the twelve-week study (18 July). Green leaf area per tiller decreased initially from bug feeding and then continued to decrease because of seasonal aging. All plants senesced within three months. Grass bugs predominantly attacked the second and third youngest leaves. Analyses of age-specific leaf cohorts demonstrated that the major effect of bug feeding was the loss of green leaf area and potential foliage production over time. Bug feeding may also exacerbate other physiological stresses on the host plants.

The grass bug, *Irbisia pacifica* (Uhler) (Hemiptera: Miridae), has the widest distribution among all species within the genus (Schwartz 1984). In this univoltine species, all five nymphal instars and the adult stage feed on an assortment of native and introduced grasses (Schwartz 1984, Hansen 1986). At times this insect is a pest of forage grasses in the Intermountain West (Knowlton 1951, 1967).

In spite of its economic importance, very little is known about the interaction between feeding by *I. pacifica* and its impact on host plants. Hansen and Nowak (1985) observed that although chlorophyll concentration in leaves of crested wheatgrass, *Agropyron desertorum* (Fisch. ex Link) Schult., decreased as feeding by *I. pacifica* intensified, specific leaf mass remained about the same. They also suggested that a compensatory response occurred with this feeding. Hansen (1987) showed that adult *I. pacifica* prefer the second and third youngest leaves and that feeding was greatest near the leaf tip. However, these studies did not examine the impact of feeding on plant growth and survival in the field.

The objectives of the present study were to determine in the field the effect of feeding by *I. pacifica* during its life cycle on spring growth of intermediate wheatgrass, *Thinopyrum intermedium* (Host) Barkw. & D. R. Dewey, and to obtain biological information on the development and population changes in *I. pacifica*.

MATERIALS AND METHODS

The study was conducted during the spring growing season of 1985 at an ungrazed pasture that contained a monoculture of intermediate wheatgrass. This site, ca 3 km NE North Logan, Utah, was selected because of its history of high populations of *I. pacifica*.

Along a fence row, 25 grass tillers (or plants) 50 cm apart were identified by colored wire rings. The plants were examined weekly from the time the insects became active (8 May) to full plant senescence (24 July). For every observation, all leaves on each marked plant were measured for length, width, condition, height from ground, and location on the plant. The amount (expressed as a proportion) of bug-feeding damage for each leaf was visually estimated as described by Hansen and Nowak (1985). Relative bug population densities were obtained by taking 10 full sweeps with a standard (38-cm-diameter) net in the pasture. Adult females were dissected to determine reproductive condition by using the technique of Kamm and Ritcher (1972).

Total leaf area was estimated by multiplying

[1]This paper presents the results of cooperative investigations of USDA-ARS and the Utah Agricultural Experiment Station, Logan, Utah 84322. Approved as Journal Paper No 3311.

[2]Mention of a commercial or proprietary product does not constitute endorsement by the U S Department of Agriculture.

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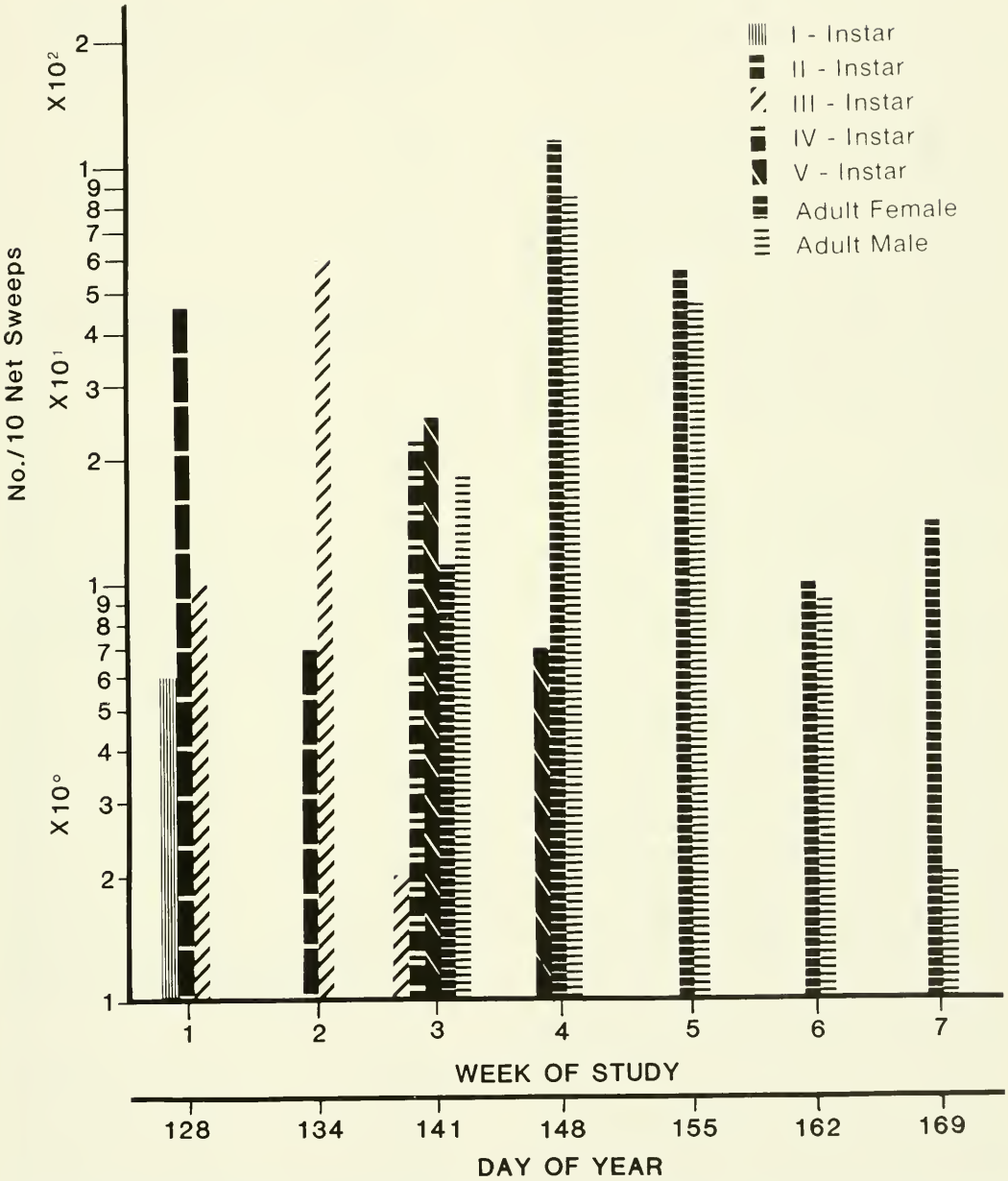

Fig. 1. Weekly collections from 8 May 1985 to 18 June 1985 of all life stages of *Irbisia pacifica* from an ungrazed pasture of intermediate wheatgrass, 3 km NE of North Logan, Utah.

length by width. Undamaged green leaf area (GLA) was estimated by subtracting the area damaged by feeding from total leaf area. Leaf size and relative position of cohorts (leaves of the same age) were followed throughout the study. For each weekly observation the youngest leaves were the most apical, while the oldest were the lowest on the plant.

Data analysis was done at the USDA Washington Computer Center with the Statistical Package SAS (Statistical Analysis System, SAS Institute Inc., SAS Circle, Box 8000, Cary, NC 27511-8000) using the procedure MEANS (SAS User's Guide: Basics,

1982 ed., p. 527). Linear correlation and Student's t-tests were conducted with a Hewlett-Packard HP-11C calculator.

RESULTS

Early instar nymphs of *I. pacifica* were already present when the field study began on 8 May (Fig. 1). Adults appeared in the third week (21 May), and metamorphosis was completed by the fifth week (4 June). The largest weekly collection was in the fourth week. Weekly adult sex ratios favored females, except for the collection during the third week when males outnumbered females by 63.6%. In the seventh week females exceeded males by 700%, and no bugs were found after this collection.

No eggs were found in the first dissection of adult females (week 3). By the fifth week, 87.3% of the adult females contained eggs, and females collected the next week had the greatest proportion of eggs (90.0%). In the last week that females were collected, the fecundity level remained high (78.6% with eggs).

Although some grass bugs were present at the start of the study, grass plants appeared uninjured (Fig. 2). The proportion of feeding damage on green leaves was initially low (7.1%) but increased very rapidly between the third and fourth weeks. After culminating on the seventh week (35.1%), the proportion of feeding damage steadily declined, thus indicating some form of recovery. Only one plant survived to the twelfth week, a factor that resulted in erratic values. Total GLA per tiller increased during the first few weeks of the study and then dropped consistently from the third week to the eleventh. The correlation between average GLA per leaf and week of collection was highly significant ($r^2 = .893$, slope $= -2.36$, $P < .01$). Total leaf area per tiller peaked a week after maximum GLA. Most of the grass plants endured to the tenth week, then senesced or died within the remaining two weeks. Seed head production was first observed in the seventh week and continued irregularly during the rest of the study. Only 44% of the plants grew seed heads.

Initially, all plants had at least three green leaves. In the second observation five plants had five green leaves, and in the fourth week one plant had six green leaves. Yet after the

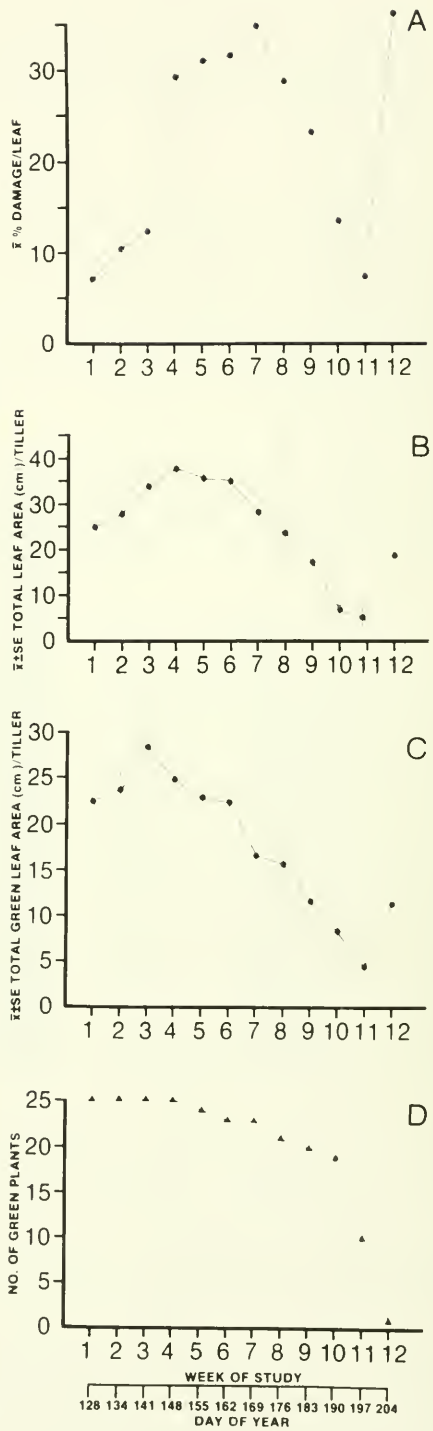

Fig. 2. Summary of weekly measurements of intermediate wheatgrass attacked by *Irbisia pacifica*: A, percent feeding damage/leaf of green leaves; B, total leaf area (cm^2)/tiller; C, total green leaf area (cm^2)/tiller; D, number of green plants.

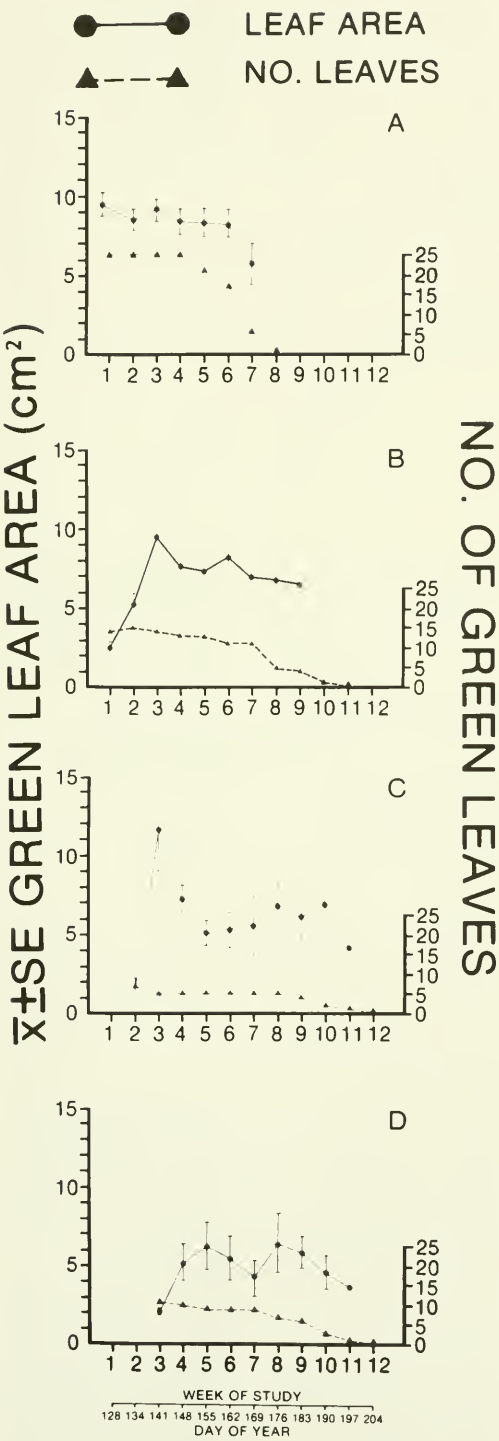

Fig. 3. Weekly green leaf area and number of green leaves of selected age-specific cohorts of intermediate wheatgrass: A, Cohort A; B, Cohort B; C, Cohort C; D, Cohort D.

seventh week, no plant had more than three green leaves.

The greatest damage by leaf position was to the third youngest leaf at the fifth week ($\bar{x} \pm SE = 49.1 \pm 4.2\%$). Excluding the last week, the greatest average damage among leaf-age categories for the entire study was to the second youngest leaf ($\bar{x} \pm SE = 28.4 \pm 4.4\%$), then the third youngest ($\bar{x} \pm SE = 24.4 \pm 5.1\%$), followed by the youngest ($\bar{x} \pm SE = 13.4 \pm 2.0\%$). Paired Student's t-tests showed no significant differences among the weekly damage values between the second and third youngest leaves ($t = 2.023$, $df = 10$), but significant differences between the youngest and the second youngest ($t = 5.125$, $df = 10$, $P < .01$), and the youngest and the third youngest ($t = 2.883$, $df = 10$, $P < .05$). For the remaining leaf positions, the average weekly damage for the fourth youngest leaf ($\bar{x} \pm SE = 19.6 \pm 5.0\%$, eight weeks) was greater than for the next oldest leaf ($\bar{x} \pm SE = 9.6 \pm 2.6\%$, seven weeks.).

The weekly average GLA in the cohorts clearly showed the seasonal changes in plant phenology and the effects of bug feeding (Fig. 3). At the start of the study, Cohort A was the second youngest, fully expanded leaf, while Cohort B was the youngest growing leaf. Two weeks later Cohort B reached maximum growth. By the seventh week, Cohort A was the oldest leaf in some plants (the bottom leaf); Cohort B was the oldest leaf in the ninth week. Cohort C appeared in the second week as the youngest expanding leaf, and Cohort D, also as the youngest growing leaf, in the third week. Cohort C took a week for maximum growth, while Cohort D required two weeks; both cohorts were gone by the end of the study.

Bug feeding affected each cohort differently (Figs. 3, 4). In Cohort A the amount of GLA decreased slightly up to the sixth week, then dropped suddenly. The rate of increase in percent feeding damage in Cohort A was lowest of the four cohorts. After leaf expansion, GLA in Cohort B gradually decreased. The rate of feeding damage increased rapidly for Cohorts C and D before reaching maximum levels at the fifth week.

DISCUSSION

In the intermountain region the single gen-

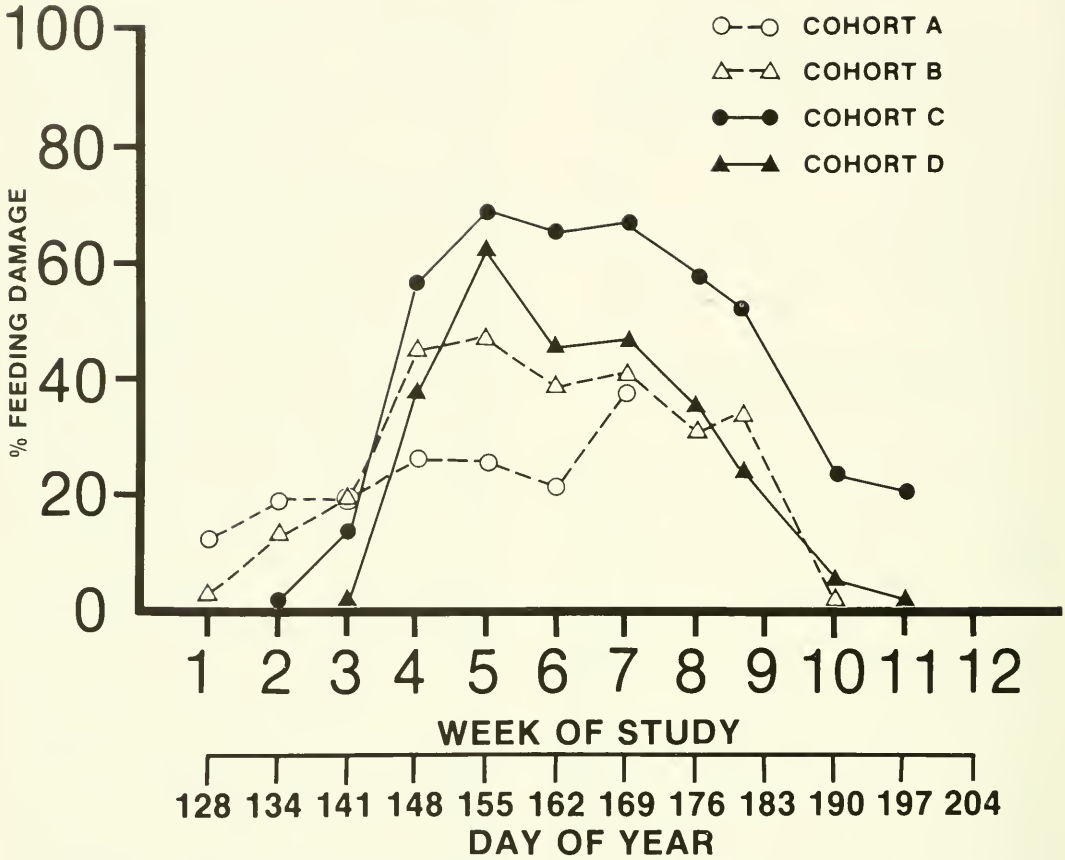

Fig. 4. Weekly percentage of feeding damage of four age-specific cohorts of intermediate wheatgrass.

eration of *Irbisia pacifica* occurs in late spring and early summer. At the study site, development of all nymphal stages was rapidly completed in about a month. Schwartz (1984) estimated the duration of nymphal development in *Irbisia* sp. from western Oregon to be four weeks. The population (Fig. 1) increased until peaking at the fourth week. More likely, however, this apparent increase resulted because either adults were more easily collected than nymphs or adults moved from the middle to the periphery of the pasture.

Female adults of *I. pacifica* generally outnumbered males (Fig. 1). Females also outlived males. These observations were similar to those of Schwartz (1984) for the genus *Irbisia*. Total adult life span at the study site was less than six weeks, but it may differ elsewhere. These insects appear highly sensitive to increased temperatures (Hansen 1987), and a cool summer may conceivably prolong life.

Females apparently required about a week after the adult molt for ovarian development. The oviposition period seemed short, peaking about a week after maximum female population level (28 May). Since most males were gone by the seventh week, mating presumably occurred early.

The amount of GLA is physiologically important to the plant. GLA is a good indicator of the potential for plant growth and maintenance. A leaf in good condition has a large GLA relative to its total size. GLA is also the primary food source for *I. pacifica*.

When GLA is compared to total leaf area, plant damage from different origins can be demonstrated. The greatest proportion of bug-feeding damage occurred between the third and fourth weeks, which coincided with the decline of GLA (Fig. 2). However, total area peaked one week later, suggesting that the grass bugs caused a premature drop in GLA. The percent of feeding damage per leaf declined after the seventh week because the

grass bugs were no longer present. Yet, the total GLA per tiller also declined, indicating that other physiological factors, such as drought stress, were also causing senescence. Other grass-feeding mirids and early instar nymphs of grasshoppers were on the study site during this time, but there were too few of these insects to be the primary cause of late-season decline of GLA. Senescence is a common characteristic of intermediate wheatgrass during dry periods. The decline in plant population after the tenth week was not directly due to bug feeding, but feeding damage may have contributed to plant mortality that occurred earlier in the growing season.

Grass bug feeding differed with leaf position. *Irbisia pacifica* clearly preferred the second and third youngest leaves. This feeding preference verified an earlier study on *I. pacifica* feeding-site selection on leaves of field-collected intermediate wheatgrass and other grass species (Hansen 1987). Reasons for this preference are still unknown.

The interrelationship between the host plants and grass bug feeding was best illustrated by the cohort data (Figs. 3, 4). Cohort A, which had mature leaves at the start of the study, was relatively unharmed by *I. pacifica*. As the season progressed and the grass bugs developed, the other cohorts were affected more. The leaves of Cohorts B, C, and D all had an opportunity to expand successfully because the youngest leaves present on a tiller are less preferred (Hansen 1987). Cohort B had less damage than Cohort C because more of the grass bugs were immature at the time of attack. The rapid increase in percent feeding damage for Cohorts B, C, and D between the third and fifth weeks occurred when the bugs became adults. All cohorts exhibited a reduction in GLA and eventual death due to normal aging. Yet, the greatly reduced GLA in the later cohorts (Cohorts C and D) suggested that meaningful damage from bug feeding reduced biomass production.

In summary, grass bug feeding resulted both in less GLA and in less potential foliage. Feeding may also cause presenescent stress that may weaken the grass plant physiologically. Although we did not examine it in this study, other researchers found that seed head production in intermediate wheatgrass was reduced by another grass-feeding mirid, *Labops hesperius* Uhler (Malecheck et al. 1977).

This study suggests several areas for future research with *Irbisia pacifica*. First, the nutritional quality of the host plants, particularly the nitrogenous compounds, should be examined to determine their effect on insect development and egg production (McNeill 1971, 1973). Does *I. pacifica* complete its life cycle before grass senescence because of an intrinsic mechanism, or is it due to nutrition? If nutrition is important, how can intermediate wheatgrass be developed as a good forage crop without encouraging *I. pacifica* population growth? How do grazing practices interact with growth of plants attacked by grass bugs? If monocultural stands of intermediate wheatgrass increase *I. pacifica* populations, what other forage species can be interspersed to reduce bug-feeding damage? Finally, the effect of *I. pacifica* feeding on growth of other host plants needs to be examined.

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LITERATURE CITED

HANSEN, J. D. 1986. Differential feeding on range grass seedlings by *Irbisia pacifica* (Hemiptera: Miridae). J. Kansas Entomol. Soc. 59: 199–203.

_____. 1987. Feeding site selection by *Irbisia pacifica* (Hemiptera: Miridae) on four cool-season western range grasses. J. Kansas Entomol. Soc. 60: 316–323.

HANSEN, J. D., AND R. S. NOWAK. 1985. Evaluating damage by grass bug feeding on crested wheatgrass. Southwestern Entomol. 10: 89–94.

KAMM, J. A., AND P. O. RITCHER. 1972. Rapid dissection of insects to determine ovarial development. Ann. Entomol. Soc. Amer. 65: 271–274.

KNOWLTON, G. F. 1951. Bugs damage grass in Utah. Bull. Brooklyn Entomol. Soc. 46: 74–75.

_____. 1967. Grass bugs: a serious range problem in 1966. Utah Acad. Sci., Arts, Letters 43: 20–21.

MALECHEK, J. C., A. M. GRAY, AND B. A. HAWS. 1977. Yield and nutritional quality of intermediate wheatgrass infested by black grass bugs at low population densities. J. Range Manage. 30: 128–131.

MCNEILL, S. 1971. The energetics of a population of *Leptopterna dolobrata* (Heteroptera: Miridae). J. Animal Ecol. 40: 127–140.

———. 1973. The dynamics of a population of *Leptopterna dolobrata* (Heteroptera: Miridae) in relation to its food resources. J. Animal Ecol. 42: 495–507.

SCHWARTZ, M. D. 1984. A revision of the black grass bug genus *Irbisia* Reuter (Heteroptera: Miridae). J. New York Entomol. Soc. 92: 193–306.

A CASE OF LEUCISM IN THE WESTERN BLUEBIRD (*SIALIA MEXICANA*)

Kevin L. Ellis[1] and Jimmie R. Parrish[2]

ABSTRACT.—Leucism in the western bluebird (*Sialia mexicana*) is reported from La Plata County, Colorado.

Leucism in birds is a condition resulting from a partial loss of pigment, affecting all the colors present and reducing them in intensity (Harrison 1985). Recently, Jehl (1985) estimated that the frequency of leucism is rare in eared grebes (*Podiceps nigricollis*). Occurrence overall is rare in birds, differing greatly among species (Sage 1963, Gross 1965). Herein, we report a case of leucism in a western bluebird (*Sialia mexicana*).

A study of nest site fidelity of western bluebirds was conducted in the vicinity of Durango, La Plata County, Colorado, from May to July 1986. A total of 32 nest boxes were checked for occupancy and presence of nestlings, and young birds were monitored throughout the nesting cycle. Adults and young were banded with U.S. Fish and Wildlife Service numbered leg bands. One particular nest box contained two young that differed considerably in early plumage color. One nestling appeared normally colored, while the other was very pale. The young bluebirds were approximately 15 days old when first observed, and remex and rectrix colors were not observable at that time. The nest box was visited 10 days later and both young appeared to have fledged successfully.

On 24 September 1986 at 1100 hrs, a leucistic western bluebird was seen feeding along a fence row approximately 6 km south of Durango, Colorado, in the company of normally colored bluebirds. The leucistic bluebird was collected and found to be the pale-colored individual banded as a nestling. Foot and eye color appeared normal. Head, breast, and back plumage was an uncharacteristic light brown, intermixed with white (Figs. 1A, 1B). Shoulder, upper wing, and tail coverts were lightly colored slate blue gray (Fig. 1A). The outer vane of the distal primary remiges was white, while the inner vane was light tan (Fig. 1A). The proximal remiges were colored white on both the inner and outer vanes. The ventral surfaces of remiges were virtually all white, with the exception of a few centrally located remiges that were light tan on the ventral surface (Fig. 1B). The outer vane on the dorsal surface of the rectrices was also white, while the inner vane was light tan (Fig. 1A). Upper tail coverts were slightly colored with a light blue–purplish wash, and one darker central rectrix was approximately half emerged (Fig. 1A). The ventral surfaces of the rectrices were white (Fig. 1B). In addition, leucistic feathers were overall somewhat translucent (Figs. 1A, 1B). Sex could not be determined.

At least 10 cases of albinism have been reported for the eastern bluebird (*Sialia sialis*) (Ross 1963). We found no previous record of albinism or leucism occurring in the western bluebird. Future population studies comparing eastern and western bluebirds should provide estimates of frequency and variation in expression of leucism.

ACKNOWLEDGMENTS

We thank Clayton M. White and Joseph H. Jehl, Jr., for helpful comments on earlier drafts of the manuscript. The specimen (No. 8356) is currently housed in the Monte L. Bean Life Sciences Museum at Brigham Young University.

LITERATURE CITED

GROSS, A. O. 1965. The incidence of albinism in North American birds. Bird Banding 36: 67–71.

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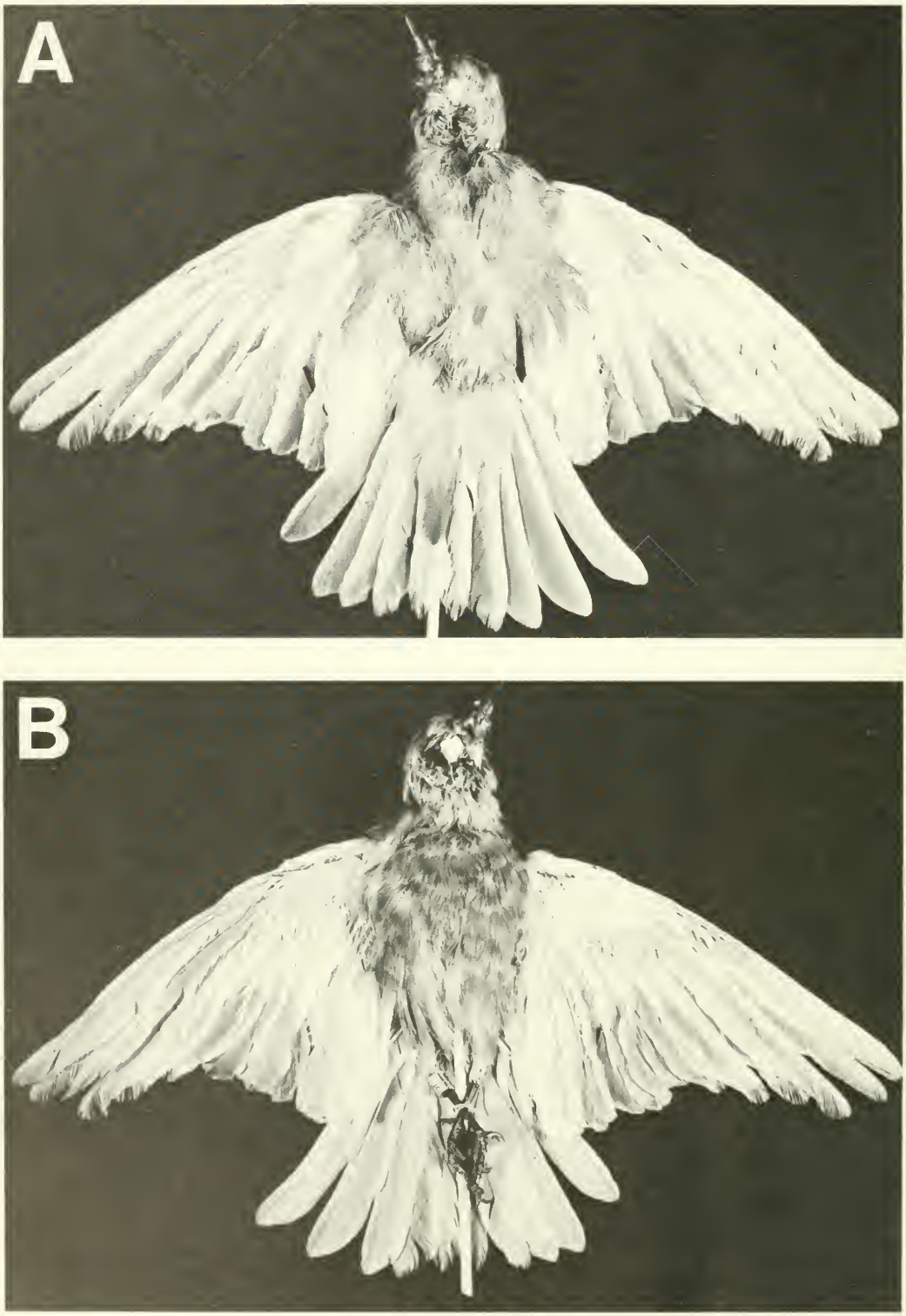

Fig. 1. Leucistic western bluebird collected in the vicinity of Durango, La Plata County, Colorado: A, dorsal view; B, ventral view.

HARRISON, C. J. O. 1985. Plumage, abnormal. Pages 472–474 *in* B. Campbell and E. Lack, eds., A dictionary of birds. Buteo Books, Vermillion, South Dakota.

JEHL, J. R., JR. 1985. Leucism in eared grebes in western North America. Condor 87: 439–441.

ROSS, C. C. 1963. Albinism among North American birds. Cassinia 47: 2–21.

SAGE, B. L. 1963. The incidence of albinism and melanism in British birds. Br. Birds 56: 409–416.

INFLUENCE OF PONDEROSA PINE OVERSTORY ON FORAGE QUALITY IN THE BLACK HILLS, SOUTH DAKOTA

Kieth E. Severson[1] and Daniel W. Uresk[2]

ABSTRACT.—Forage quality was assessed in pole and sapling ponderosa pine (*Pinus ponderosa*) stands growing at five stocking levels—0, 5, 14, 23, and unthinned (which approximated 40 m^2/ha basal area)—in the Black Hills of South Dakota. Crude protein, acid detergent fiber, acid detergent lignin, ash, calcium, and phosphorus were evaluated for cream peavine (*Lathyrus ochroleucus*), bearberry (*Arctostaphylos uva-ursi*), and timber oatgrass (*Danthonia intermedia*). Acid detergent fiber, acid detergent lignin, and ash showed some significant differences among growing stock levels for cream peavine growing in sapling stands. Crude protein content of timber oatgrass was different among growing stock levels in pole stands. In all cases, however, no trends or patterns relative to stocking levels were evident. When understory forage quality was compared within pole and sapling stands, only 4 of 18 possible comparisons were significant. In general, modifying the overstory of ponderosa pine in the Black Hills by clearcutting or thinning did not result in predictable changes in nutritional values of selected understory species.

Understory-overstory relationships have been studied extensively throughout North America (Ffolliott and Clary 1982), but most studies have focused on how understory production responds to alterations of overstory. Relatively few have examined nutritional changes in understory plants that may have resulted from overstory reduction or removal (Dealy 1966, Wolters 1973, Regelin et al. 1974, Hanley et al. 1987). Others have compared nutritional attributes of plants collected from beneath an overstory canopy and from adjacent natural openings (McEwen and Dietz 1965, Rickard et al. 1973, Barth and Klemmedson 1978).

It is generally recognized that understory production, particularly herbage, increases in a linear or curvilinear manner as overstory density, cover, and/or basal area decrease. It is also generally assumed that these increases in understory production are favorable to herbivores, especially large ungulates. Relationships between overstory and chemical content or nutritional quality of understory forage plants are not well defined, however.

The purpose of this study was to compare selected nutritive attributes in understory plant species from sapling and pole ponderosa pine (*Pinus ponderosa*) stands growing at five stocking levels ranging from clearcuts (0 m^2/ha basal area) to unthinned (40 m^2/ha basal area).

STUDY AREA

The Black Hills of South Dakota and Wyoming are dominated by ponderosa pine. White spruce (*Picea glauca*), paper birch (*Betula papyrifera*), quaking aspen (*Populus tremuloides*), and bur oak (*Quercus macrocarpa*) are common associates (Boldt et al. 1983). Common understory species include bearberry (*Arctostaphylos uva-ursi*), common chokecherry (*Prunus virginiana*), Oregon grape (*Berberis repens*), Saskatoon serviceberry (*Amelanchier alnifolia*), and snowberry (*Symphoricarpos spp.*). Herbs include roughleaf ricegrass (*Oryzopsis asperfolia*), timber oatgrass (*Danthonia intermedia*), Kentucky bluegrass (*Poa pratensis*), cream peavine (*Lathyrus ochroleucus*), and bluebell (*Campanula rotundifolia*). Ponderosa pine and quaking aspen subtypes have been delineated by Thilenius (1972) and Severson and Thilenius (1976), respectively.

The study was conducted on the Black Hills Experimental Forest about 30 km west of Rapid City, South Dakota. The Experimental Forest encompasses about 1,375 ha and elevations range from 1,620 to 1,800 m. The average annual precipitation is 55 cm, of which 70% falls from April to September. Soils are primarily gray wooded, shallow to moderately deep, and derived from metamorphic rock (Boldt and Van Deusen 1974).

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METHODS

Five growing stock levels (GSLs) of ponderosa pine were sampled. These were numerically designated as 0, 5, 14, 23, and unthinned. Growing stock indicates all living trees in a stand. The numerical designation of growing stock levels approximates, but may not equal, the actual basal area (m^2/ha) of the stand. Basal areas of unthinned pole stands ranged from 37 to 40 m^2/ha, while unthinned sapling stands ranged from 27 to 33 m^2/ha. Three replications of each of the five GSLs were established in each of two size classes of pine: saplings (8–10 cm diameter-breast-height [dbh]) and small poles (15–18 cm dbh). These tree size classes are common and extensive in second-growth forests of the Black Hills.

Replicate plots were randomly selected and installed for each of the four GSLs from 5 through unthinned in 1963; the clearcuts (0 GSL) were selected in 1966. Each of the 15 sapling plots was 0.10 ha, and each of 15 pole plots was 0.20 ha.

Three common understory species were collected on each plot in August 1976 for analysis. These included one grass, timber oatgrass; one forb, cream peavine; and a shrub, bearberry. Twelve 30 × 61-cm plots were clipped at ground level and bagged by species from each of the 30 GSL plots. Samples were oven-dried to a constant weight at 45 C. All specimens of the above three species from each plot were ground through a 1-mm screen Wiley mill, thoroughly mixed together, and composited by plot to obtain samples for analyses.

Standard analytical procedures (AOAC 1970) were used for analyses of duplicate subsamples for each plant species and plot. Moisture content was determined by oven-drying samples at 135 C for four hours, cooling in a vacuum desiccator, and reweighing to determine percent moisture. All results were corrected to a dry-weight basis. These samples were placed in a muffle furnace and ashed at 600 C for four hours. Samples were then cooled in a vacuum desiccator and reweighed to determine percent ash. Ash samples were further digested with hydrochloric acid and nitric acid. Calcium content was determined by titrating an aliquot of this mineral solution with ethylenediaminetetracetate acid (EDTA), using calcein indicator under ultraviolet light. Phosphorus content was determined by measuring optical density on a colorimeter at 440 mu with the addition of ammonium vanadate and sodium molybdate. Standard curves were prepared to correct optical density to milliequivalents of phosphorus per milliliter.

Crude protein was determined using micro-Kjeldahl procedures. Acid detergent fiber and acid detergent lignin were analyzed following procedures outlined in AOAC (1972).

The null hypothesis—no differences between tree size-classes or among GSLs in nutritional content of selected understory species—was tested with a 2 × 5 (tree size-class × GSL) analysis of variance with three replications per cell. All statistical inferences were made at $P = .05$. Where differences among GSLs were noted, or a significant tree size-class × GSL interaction was detected, size-classes were analyzed separately with one-way analysis of variance. Where differences were significant, means were separated using Tukey's HSD. Because percentage data were used, homogeneity of variances was tested with Bartlett's Box F. In all cases, Box F was not significant, and so data transformations were not applied. All analyses were done with SPSS/PC+ (Norusis 1986).

RESULTS AND DISCUSSION

Nutritive contents of understory species were not affected by the overstory 13 years after thinning treatments were applied (Table 1). Some significant differences were noted in the structural compounds (acid detergent fiber and lignin) and ash content of cream peavine from sapling stands, and crude protein content of timber oatgrass in pole stands. In these cases, however, no patterns or trends related to growing stock levels (basal area) were evident.

Similar results were noted when stands were compared; in only 4 of 18 possible comparisons were significant differences observed (Table 1). The structural compounds were both higher in bearberry growing under sapling stands. Phosphorus content was higher in both herbaceous species collected from pole-sized stands. However, there were no consistent differences, indicating that tree size, pole vs. sapling, does not have important

TABLE 1. Percentages (mean ± standard error) of six nutritive attributes found in three plant species growing under five different stocking levels of two size classes of ponderosa pine, Black Hills, South Dakota.

Attribute	Growing[1] stock level	*Lathyrus ochroleucus* Pole	*Lathyrus ochroleucus* Sapling	*Arctostaphylos uva-ursi* Pole	*Arctostaphylos uva-ursi* Sapling	*Danthonia intermedia* Pole	*Danthonia intermedia* Sapling
Crude protein	0	14.3 ± 0.1	15.1 ± 0.6	5.4 ± 0.1	5.9 ± 0.2	6.7 ± 0.9 ab	6.1 ± 0.1
	5	14.6 ± 0.3	15.1 ± 0.1	5.8 ± 0.3	5.6 ± 0.2	5.3 ± 0.2 a	5.6 ± 0.3
	14	15.2 ± 0.8	15.5 ± 0.1	5.6 ± 0.3	5.6 ± 0.4	8.4 ± 0.3 b	7.2 ± 0.1
	23	16.1 ± 0.9	15.4 ± 0.6	5.6 ± 0.3	5.6 ± 0.1	6.0 ± 0.3 ab	6.2 ± 0.5
	UT	15.5 ± 0.6	15.3 ± 0.9	5.1 ± 0.1	5.6 ± 0.2	5.9 ± 1.1 ab	6.2 ± 0.5
	$\bar{x}$	15.1 ± 0.3	15.3 ± 0.4	5.5 ± 0.1	5.7 ± 0.1	6.5 ± 1.3	6.3 ± 0.3
Acid detergent fiber	0	28.5 ± 0.3	26.7 ± 0.6 ab[2]	25.6 ± 0.7	26.7 ± 0.2	41.8 ± 1.0	41.1 ± 0.1
	5	26.6 ± 0.7	28.5 ± 0.4 b	25.9 ± 0.3	26.7 ± 0.4	43.5 ± 0.7	41.8 ± 0.4
	14	27.4 ± 0.5	28.0 ± 0.7 ab	27.9 ± 0.9	26.6 ± 0.5	41.8 ± 0.6	42.3 ± 0.6
	23	27.4 ± 0.5	28.0 ± 0.9 ab	25.4 ± 0.1	27.3 ± 0.8	42.2 ± 1.2	42.7 ± 0.7
	UT	26.4 ± 0.9	25.0 ± 0.6 a	24.4 ± 1.0	26.7 ± 0.2	41.8 ± 1.3	40.8 ± 1.3
	$\bar{x}$	27.3 ± 0.1	27.2 ± 0.2	25.8 ± 0.6 x[2]	26.8 ± 0.1 y	42.2 ± 0.3	41.7 ± 0.4
Acid detergent lignin	0	6.0 ± 0.3	5.8 ± 0.2 b	12.7 ± 0.5	14.1 ± 0.1	6.2 ± 0.3	5.1 ± 0.4
	5	5.6 ± 0.5	6.4 ± 0.1 c	12.0 ± 0.4	13.5 ± 0.5	7.2 ± 0.1	6.8 ± 0.4
	14	6.3 ± 0.2	6.2 ± 0.1 bc	13.3 ± 0.3	13.1 ± 0.2	6.4 ± 0.5	6.5 ± 0.2
	23	6.2 ± 0.1	6.2 ± 0.1 bc	13.0 ± 0.5	13.0 ± 0.6	5.5 ± 0.2	6.9 ± 0.2
	UT	5.8 ± 0.4	4.9 ± 0.1 a	11.9 ± 0.3	12.8 ± 0.5	5.4 ± 0.8	6.1 ± 0.6
	$\bar{x}$	6.0 ± 0.1	5.9 ± 0.3	12.6 ± 0.3 x	13.3 ± 0.2 y	6.1 ± 0.3	6.3 ± 0.3
Ash	0	5.83 ± 0.32	6.01 ± 0.14 ab	3.35 ± 0.02	2.98 ± 0.15	4.75 ± 0.15	5.06 ± 0.29
	5	6.94 ± 0.25	5.52 ± 0.06 a	3.23 ± 0.19	3.12 ± 0.37	6.22 ± 0.27	5.21 ± 0.19
	14	6.72 ± 0.26	6.30 ± 0.08 ab	3.22 ± 0.31	3.25 ± 0.07	6.19 ± 0.53	5.77 ± 0.33
	23	6.71 ± 0.17	6.40 ± 0.55 b	3.06 ± 0.24	3.29 ± 0.28	5.51 ± 0.30	5.25 ± 0.13
	UT	6.07 ± 0.45	6.40 ± 0.30 b	2.91 ± 0.35	2.77 ± 0.08	5.58 ± 0.19	5.36 ± 0.16
	$\bar{x}$	6.45 ± 0.21	6.13 ± 0.17	3.15 ± 0.55	3.08 ± 0.09	5.65 ± 0.27	5.33 ± 0.12
Calcium	0	1.70 ± 0.08	1.61 ± 0.9	0.63 ± 0.05	0.61 ± 0.04	0.25 ± 0.01	0.25 ± 0.02
	5	1.72 ± 0.05	1.67 ± 0.2	0.67 ± 0.03	0.60 ± 0.01	0.29 ± 0.02	0.25 ± 0.02
	14	1.71 ± 0.15	1.61 ± 0.3	0.65 ± 0.03	0.62 ± 0.06	0.27 ± 0.01	0.29 ± 0.01
	23	1.61 ± 0.05	1.69 ± 0.5	0.60 ± 0.01	0.58 ± 0.03	0.27 ± 0.02	0.27 ± 0.01
	UT	1.68 ± 0.02	1.63 ± 0.2	0.60 ± 0.02	0.59 ± 0.05	0.25 ± 1.01	0.28 ± 0.01
	$\bar{x}$	1.68 ± 0.02	1.64 ± 0.2	0.63 ± 0.01	0.60 ± 0.01	0.27 ± 1.01	0.27 ± 0.01
Phosphorus	0	0.21 ± 0.01	0.18 ± 0.1	0.14 ± 0.01	0.13 ± 0.01	0.19 ± 0.01	0.19 ± 0.01
	5	0.20 ± 0.01	0.18 ± 0.1	0.14 ± 0.01	0.14 ± 0.01	0.22 ± 0.01	0.18 ± 0.01
	14	0.19 + 0.01	0.17 ± 0.1	0.14 ± 0.01	0.14 ± 0.01	0.23 ± 0.01	0.20 ± 0.01
	23	0.20 + 0.01	0.18 ± 0.1	0.15 ± 0.01	0.14 ± 0.01	0.20 ± 0.01	0.19 ± 0.01
	UT	0.20 + 0.01	0.19 ± 0.1	0.14 ± 0.01	0.14 ± 0.01	0.20 ± 1.01	0.18 ± 0.01
	$\bar{x}$	0.20 ± 0.01 x	0.18 ± 0.1 y	0.14 ± 0.01	0.14 ± 0.01	0.21 ± 0.01 x	0.19 ± 0.01 y

[1]Approximate basal area (m^2/ha); UT = unthinned stands, which ranged from 27 to 33 m^2/ha for saplings and 37 to 40 m^2/ha for poles.
[2]Means ± standard errors followed by same letter indicate no significant differences ($P \geq .05$); abc notations used among GSLs, x and y between stands. Absence of letters indicates no significant differences ($P \geq .05$).

or predictable effects on nutritional quality of selected understory plants.

There was only one other study that had similar results. Regelin et al. (1974) found no differences in crude protein, moisture content, or digestible dry matter in forage collected from clearcuts and uncut strips in mixed-conifer forests of Colorado 15 years after cutting. Three other studies in coniferous forest areas noted variable results. McEwen and Dietz (1965), in the Black Hills, did not detect differences in crude protein or crude fat contents of Kentucky bluegrass growing in open meadows or under the ponderosa pine canopy. Ash and crude fiber content, however, were greater in plants from the understory, while nitrogen-free extract was higher in plants from meadows. Dealy (1966) compared bitterbrush (*Purshia tridentata*) growing in unthinned and thinned ponderosa pine stands in Oregon and found significantly more ash and less fiber under natural than under

thinned stands, but no differences in crude protein or crude fat. Wolters (1973) compared forage growing on longleaf (*P. palustris*) and slash pine (*P. elliottii*) plantations in Louisiana to that from cutover areas. While chemical contents were similar the year of treatment, crude protein and phosphorus contents were consistently higher under pine plantations than on cutover land during succeeding years. These differences grew larger as plantations developed (9 years). Nitrogen-free extract was significantly and inversely related to pine basal area during later years; there were no significant changes in crude fat, crude fiber, or calcium. Hanley et al. (1987) did not detect differences in digestible dry matter of two shrubs from very young stands (5–11 years) and adjacent older (80 and about 450 years) Sitka spruce (*Picea sitchensis*)–western hemlock (*Tsuga heterophylla*) forest, but did note that plants in young stands had greater astringency, phenolics, and total nonstructural carbohydrates. Those growing beneath older, well-developed overstories had greater concentrations of nitrogen.

Similar results have been found where shrubs are overstory. Rickard et al. (1973), for example, found no differences in foliar nitrogen of bluebunch wheatgrass (*Agropyron spicatum*) growing under and outside the canopy of big sagebrush (*Artemisia tridentata*). Nor did Barth and Klemmedson (1978) detect differences in nitrogen and carbon percentages in understory vegetation growing under velvet mesquite (*Prosopis juliflora*) and in the open. Conversely, foliar nitrogen percentage of cheatgrass (*Bromus tectorum*) collected from beneath canopies of greasewood (*Sarcobatus vermiculatus*) and spiny hopsage (*Grayia spinosa*) was higher than that collected from open areas (Rickard et al. 1973).

Examination of studies conducted on areas with a tree harvest treatment (this study, Dealy 1966, Regelin et al. 1974, Wolters 1973, Hanley et al. 1987) reveals considerable variation in response of nutritive attributes to overstory. Nitrogen, or crude protein, for example, was not affected by overstory in South Dakota (this study) and Oregon (Dealy 1966) ponderosa pine, or in Colorado mixed-conifer forest (Regelin et al. 1974), but was in Louisiana pine forests (Wolters 1973) and in Alaska spruce-fir (Hanley et al. 1987). Ash, or total mineral content, was not affected by overstory reduction in this study, but higher concentrations were noted in natural or unthinned stands by McEwen and Dietz (1965) and Dealy (1966). Crude fiber (obtained via proximate analysis) cannot be directly compared to acid detergent fiber, but both indicate the least digestible fractions. Responses of crude fiber and acid detergent fiber were extremely variable among studies. Crude fat, however, was not affected by overstory in all instances where it was considered.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Variable and inconsistent responses of nutrient concentrations in forage plants to changes in overstory indicate that overstory modification cannot be relied upon to obtain predictable changes in nutritional values of individual plant species within interior ponderosa pine forests. However, overstory reduction will increase forage production and forage diversity (Ffolliott and Clary 1982). Therefore, total nutrients can be altered by reducing the overstory, but this results from increased plant production, not from changes in forage quality. Increasing forage diversity creates more and better opportunities for herbivores to encounter higher quality plants or plant parts and thereby improve diet quality. Because ungulates, as a general rule, are selective feeders, by providing the maximum number of forage species, managers would be increasing the opportunities for animals to exercise this selectivity.

LITERATURE CITED

ASSOCIATION OF OFFICIAL AGRICULTURAL CHEMISTS (AOAC). 1970. Official methods of analysis. 11th ed. Washington, D.C.

ASSOCIATION OF OFFICIAL AGRICULTURAL CHEMISTS (AOAC). 1972. Changes in official methods of analysis. 3d suppl. to 11th ed. Washington, D. C.

BARTH, R. C., AND J. O. KLEMMEDSON. 1978. Shrub-induced spacial patterns of dry matter, nitrogen, and organic carbon. Soil Sci. Soc. Amer. J. 42: 804–809.

BOLDT, C. E., R. R. ALEXANDER, AND M. J. LARSON. 1983. Interior ponderosa pine in the Black Hills. Pages 80–83 *in* R. M. Burns, tech. comp., Silvicultural systems for the major forest types of the United States. USDA For. Serv. Handbook No. 445. USDA, Washington, D.C.

BOLDT, C. E., AND J. L. VAN DEUSEN. 1974. Silviculture of ponderosa pine in the Black Hills: the status of our knowledge. USDA For. Serv. Res. Pap. RM-124. Rocky Mt. For. and Range Expt. Sta., Fort Collins, Colorado.

DEALY, J. E. 1966. Bitterbrush nutrition levels under natural and thinned ponderosa pine. USDA For. Serv. Res. Note PNW-33. Pacific Northwest For. and Range Expt. Sta., Portland, Oregon.

FFOLLIOTT, P. F., AND W. P. CLARY. 1982. Understory-overstory vegetation relationships: an annotated bibliography. USDA Gen. Tech. Rept. INT-136. Intermountain For. and Range Expt. Sta., Ogden, Utah.

HANLEY, T. A., R. G. CATES, B. VAN HORNE, AND J. D. MCKENDRICK. 1987. Forest stand-age-related differences in apparent nutritional quality of forage for deer in southeastern Alaska. Pages 9–17 *in* Proceedings—Symposium on plant-herbivore interactions. USDA For. Serv. Gen. Tech. Rept. INT-222. Intermountain For. and Range Expt. Sta., Ogden, Utah.

MCEWEN, L. C., AND D. R. DIETZ. 1965. Shade effects on chemical composition of herbage in the Black Hills. J. Range Manage. 18: 184–190.

NORUSIS, M. J. 1986. SPSS/PC+ for the IBM PC/XT/AT. SPSS, Inc., Chicago, Illinois.

REGELIN, W. L., O. C. WALLMO, J. NAGY, AND D. R. DIETZ. 1974. Effect of logging on forage values for deer in Colorado. J. For. 72: 282–285.

RICKARD, W. H., J. F. CLINE, AND R. O. GILBERT. 1973. Soil beneath halophytes and its influence upon the growth of cheatgrass. Northwest Sci. 47: 213–217.

SEVERSON, K. E., AND J. F. THILENIUS. 1976. Classification of quaking aspen stands in the Black Hills and Bear Lodge Mountains. USDA For. Serv. Res. Pap. RM-166. Rocky Mt. For. and Range Expt. Sta., Fort Collins, Colorado.

THILENIUS, J. F. 1972. Classification of deer habitat in the ponderosa pine forest of the Black Hills, South Dakota. USDA For. Serv. Res. Pap. RM-91. Rocky Mt. For. and Range Expt. Sta., Fort Collins, Colorado.

WOLTERS, G. L. 1973. Southern pine overstories influence forage quality. J. Range Manage. 26: 423–426.

A REVIEW OF FLEA COLLECTION RECORDS FROM *ONYCHOMYS LEUCOGASTER* WITH OBSERVATIONS ON THE ROLE OF GRASSHOPPER MICE IN THE EPIZOOLOGY OF WILD RODENT PLAGUE

Rex E. Thomas[1]

ABSTRACT.—Published records of fleas collected from the northern grasshopper mouse, *Onychomys leucogaster*, indicate that these mice have a great deal of intimate environmental contact with other rodents or their burrows. Fifty-seven species of fleas have been collected from the omnivorous grasshopper mouse. The range of this mouse overlaps much of the distribution of plague, *Yersinia pestis*, in the western United States; and nearly one-half of the flea species collected from *O. leucogaster* are known to be of importance in the epizoology of plague. This article discusses the importance of the association of fleas with a hospitable secondary host in the maintenance and transmission of wild rodent plague.

Wenzel and Tipton (1966) defined host species that provide suitable conditions for a large ectoparasite fauna as *euxenous* or hospitable hosts. For example, certain hosts such as the opossum, *Didelphis marsupialis*, collect a disproportionately large number of ectoparasitic species in comparison to others. Such hosts play potentially important evolutionary and ecological roles by providing physical, behavioral, and/or physiological conditions adequate for a large number of ectoparasite species. Dissemination of ectoparasites between ecologically restricted populations of preferred hosts by carrier hosts benefits the parasites by providing opportunities for dispersal and colonization of new host populations or gene exchange with established populations. Wenzel and Tipton noted that since host species with large flea faunas must have contacts with many other host species or their immediate habitats, they are likely to acquire pathogens from ecologically more restricted hosts or their parasites and thus become carriers or reservoirs themselves.

The northern grasshopper mouse, *Onychomys leucogaster*, is an example of such an animal. Members of the genus *Onychomys* are unique among North American cricetine rodents in that they are true omnivores (Landry 1970). The range of *O. leucogaster* extends from Mexico to Canada in the arid plains and deserts of the western United States (Fig. 1). While much of their diet probably consists of arthropods, these mice will often kill and consume other small rodents (Flake 1973). Hubbard (1947) described them very colorfully as

> savage little brutes and murderous little carnivores whose marauding habits tell in their fleas, for upon them can be found all the desert species, fleas picked up from their victims as they pommel and kill them.

Traub (1985) credits the success of rodent fleas adapted to arid habitats as due to the survival strategies of remaining in the fur of the host or, when unattached, remaining wholly in the burrow. It would certainly be to the advantage of fleas on the victim of a grasshopper mouse to move, at least temporarily, onto the *Onychomys* to avoid a harsher second-order environment. As a species, northern grasshopper mice are certainly exposed to a variety of fleas due to their semi-carnivorous nature. This, however, is not adequate to explain the phenomenal flea fauna that published records collectively indicate *O. leucogaster* to have (Table 1).

HOST SPECIFICITY

In a survey of flea/host associations involved in the ecology of plague in the western United States, Eskey and Haas (1939) reported over 50 species of fleas from 30,000 small wild animals. They observed that all of the rodent flea species exhibited some degree of specificity, which limited them to one host species or a group of biologically related rodents. They

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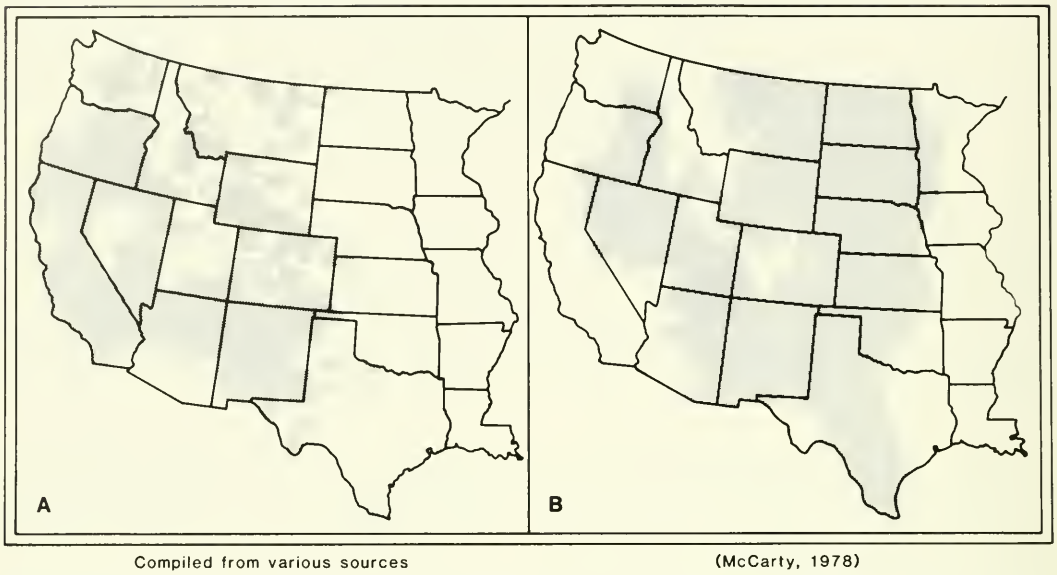

Fig. 1. The historical occurrence of human and animal plague in the United States (by county) from 1900 to 1986 (A), and the distribution of the northern grasshopper mouse, *Onychomys leucogaster*, in the United States (B).

also noted that among wild rodents having environmental contact with each other, some degree of flea interchange occurs constantly.

It is not uncommon for survey data to report collection of a flea species from other than its primary host. Collection records conventionally include the flea species recovered from various hosts in a restricted area over a relatively short period of time. As these data accumulate, the geographical and seasonal distribution of fleas on host species with which they are commonly associated are subject to analysis over their entire range. Stark (1986) has pointed out the difficulty of establishing reliable terminology to describe host associations. He suggests use of the terms "primary," "secondary," and "accidental" as used by Holland (1964), but notes the frequent use of "major" and "principal" as equivalent terms.

Collection of a flea from other than its primary host can be interpreted in two ways. Either the flea is physically and/or physiologically adapted to one species of host by specific habitat or blood-meal requirements (e.g., *Spilopsyllus caniculi* on *Oryctolagus cuniculus* [Rothschild 1965]), and records from other hosts are temporary associations; or the flea and the host depend on similar ecological requirements, and host ranges overlap in such a way that more than one species satisfies the flea's ecological needs (Holland 1958). Hopkins (1957) emphasized the physical conditions provided by the host in determining limitations to host utilization. Many fleas may be adapted more to nest conditions favorable to eggs and larvae than to other factors identified with a particular host (Hopkins 1957). Benton and Miller (1979) noted that *Peromyscopsylla h. hamifer* occurs over most of the range of its normal host, *Microtus* spp., but appears to be limited to flood plains where the soil type or soil moisture provides necessary requirements. Other flea species are climatically restricted, and climate changes with altitude (Barnes et al. 1977, Wenzel and Tipton 1966).

Ruffer (1965) described several types of burrows constructed by *O. leucogaster* in a test arena but quoted Bailey and Sperry (1929) as stating that it is questionable whether they dig their own burrows, use abandoned burrows, or use those of their prey. Bailey (1931) felt that they occupied any burrow found abandoned or from which they could evict the owner. If the host environment is a primary factor in determining host suitability, then grasshopper mice could satisfy some of the needs of many flea species by inhabiting the burrow from which the fleas were acquired. The flea collection data presented in Table 1

TABLE 1. Species of fleas collected from *Onychomys* spp., their normal hosts[1], location of collection (city, county, state), and collection reference.

Anomiopsyllus amphibolus	
Caliente, Lincoln, Nevada	(*Neotoma*, *Peromyscus* and other rodent genera–nest flea)
	(Barnes et al. 1977)
A. hiemalis	
____, ____, Texas	(*Neotoma*–nest flea)
	(Eads and Menzies 1948)
____, [several], Texas	(Eads 1950)
A. novomexicensis	
Roswell, Chaves, New Mexico	(*Neotoma*–nest flea)
	(Graves et al. 1974)
Las Cruses, Dona Ana, New Mexico	(Barnes et al. 1977)
Catallagia decipiens	
White Horse Ranch, Malheur, Oregon	(Small rodents esp. *Peromyscus*, *Microtus*, and *Clethrionomys*)
	(Lewis 1976)*
Ceylon, Saskatchewan, Canada	(Holland 1985)
Dactylopsylla bluei psilos (= *psila*)	
Mercury, Nye, Nevada*	(*Thomomys*)
	(Beck and Allred 1965)
D. comis	
____, ____, Utah	(*Thomomys*)
	(Beck 1955)
D. digitenua	
Matador, Motley, Texas	(*Geomys*)
	(Prince and Stark 1951)
D. neomexicana	
____, ____, ____,	(probably *Geomys*)
	(Smit 1983)
D. percernis	
____, [several], Texas	(*Cratogeomys* and *Thomomys*)
	(Eads and Menzies 1949)
____, [several], Texas	(Eads 1950)
Diamanus montanus	
____, ____, ____,	(*Spermophilus*)
	(Stark 1970)
Echidnophaga gallinacea	
Albuquerque, Bernalillo, New Mexico	(Birds, rodents, large insectivores and carnivores)
	(Williams and Hoff 1951)
Columbus, [Luna], New Mexico	(Traub and Hoff 1951)
	(Miles et al. 1952)
____, ____, Texas	(Graves et al. 1974)
Roswell, Chaves, New Mexico	(primarily *Peromyscus*)
Epitedia stanfordi	
Polacca, Navajo, Arizona	(Augustson 1955)
	(Morlan 1955)
____, Santa Fe, New Mexico	(Stark 1958)
____, ____, Utah	(University of Utah 1969)
Dugway Proving Ground, Utah	(primarily *Peromyscus*)
E. wenmanni	
Brigsdale, Weld, Colorado	(CDC 1985)
Foxella ignota	
____, Dawson, Texas	(*Geomys* and *Thomomys*)
	(Eads and Menzies 1949)
____, [Tooele], Utah	(Parker and Howell 1959)
____, Harney, Oregon	(Hansen 1964)
Natl. Reactor Testing Sta., Idaho	(Allred 1968)
____, Navajo, Arizona	(CDC 1981)
____, Coconino, Arizona*	(CDC 1983)
F. i. albertensis	
____, Albany, Wyoming	(*Geomys* and *Thomomys*)
	(Prince 1945)
____, Bowman, North Dakota	(Larson et al. 1985)
F. i. ignota	
____, Grant, Nebraska	(*Geomys* and *Thomomys*)
	(Prince 1945)
F. i. omissa	
____, ____, ____,	(*Geomys* and *Thomomys*)
	(Smit 1983)
F. i. recula	
Fields, [Harney], Oregon	(*Geomys* and *Thomomys*)
	(Hubbard 1941)
Narrows, ____, Oregon	(Hubbard 1941)
Ontario, [Malheur], Oregon	(Hubbard 1941)
Cody, Park, Wyoming	(Wiseman 1955)
F. i. utahensis	
____, Big Horn, Wyoming	(*Geomys* and *Thomomys*)
	(Prince 1945)
Great Salt Lake Desert, Utah	(Woodbury 1964)
Hoplopsyllus affinis = (*Eupholopsyllus glacialis*) *affinis*	
____, [several], Texas	(*Lepus* and *Sylvilagus*)
	(Eads and Menzies 1949)
____, [several], Texas	(Eads 1950)
H. anomalus	
Denio, [Humboldt], Nevada	(Ground squirrels and hares)
	(Hubbard 1947)

Table 1 continued.

Alamo, Lincoln, Nevada	(Hubbard 1949)
Searchlight, Clark, Nevada	(Hubbard 1949)
____, ____, Utah	(Allred 1952)
____, ____, Utah	(Beck 1955)
____, San Juan, Utah	(Stark 1958)
____, [Tooele], Utah	(Parker and Howell 1959)
Great Salt Lake Desert, Utah	(Woodbury 1964)
____, Coconino, Arizona	(CDC 1983)
Malaraeus sinomus	(*Peromyscus*)
Palm Springs, Riverside, California*	(Augustson 1943)
____, Riverside, California*	(Hubbard 1947)
Denio, [Humboldt], Nevada*	(Hubbard 1947)
____, Santa Fe, New Mexico	(Morlan 1955)
Mercury, Nye, Nevada*	(Beck and Allred 1965)
M. telchinus	(*Peromyscus*; also *Microtus*, *Clethrionomys*, and *Reithrodontomys*)
____, [Tooele], Utah	(Parker and Howell 1959)
____, Harney, Oregon	(Hansen 1964)
Great Salt Lake Desert, Utah	(Woodbury 1964)
Dugway Proving Ground, Utah	(University of Utah 1968)
Natl. Reactor Testing Sta., Idaho	(Allred 1968)
____, Colfax, New Mexico	(CDC 1982)
Megarthroglossus bisetis	(*Peromyscus* and *Neotoma*–nest flea, Eads and Campos 1977)
Roswell, Chaves, New Mexico	(Rail et al. 1969)
Roswell, Chaves, New Mexico	(Graves et al. 1974)
____, ____, New Mexico or Texas	(Tipton et al. 1979)
M. divisus	(*Tamiasciurus*)
____, Colfax, New Mexico	(CDC 1982)
Meringis altipecten	(*Dipodomys*)
Columbus, [Luna], New Mexico	(Traub and Hoff 1951)
____, Socorro, New Mexico	(Eads et al. 1987)
M. arachis	(*Dipodomys*)
____, Hidalgo, New Mexico	(Hubbard 1947)
Columbus, [Luna], New Mexico	(Traub and Hoff 1951)
____, Dona Ana, New Mexico	(Eads et al. 1987)
____, Hidalgo, New Mexico	(Eads et al. 1987)
M. bilsingi	(*Dipodomys* and *Onychomys*)
____, [several], Texas	(Eads and Menzies 1949)
____, [several], Texas	(Eads 1950)
Roswell, Chaves, New Mexico	(Rail et al. 1969)
Roswell, Chaves, New Mexico	(Graves et al. 1974)
____, ____, Texas	(Lewis 1974a)
____, ____, New Mexico	(Lewis 1974a)
Portales, Roosevelt, New Mexico	(Pfaffenberger and de Bruin 1986)
____, Lea, New Mexico	(Eads et al. 1987)
____, Dona Ana, New Mexico	(Eads et al. 1987)
____, Sandoval, New Mexico	(Eads et al. 1987)
M. californicus	(*Dipodomys*)
____, Kern, California*	(Eads et al. 1987)
____, Nye, Nevada*	(Eads et al. 1987)
M. dipodomys	(*Dipodomys* and many other small rodent genera)
Palm Springs, Riverside, California*	(Augustson 1943)
____, Riverside, California*	(Hubbard 1947)
St. George, Washington, Utah**	(Stark 1958)
____, Washington, Utah**	(Tipton and Allred 1951)
Mercury, Nye, Nevada*	(Beck and Allred 1965)
Roswell, Chaves, New Mexico	(Rail et al. 1969)
Dugway Proving Ground, Utah	(University of Utah 1969)
Dugway Proving Ground, Utah	(University of Utah 1970a)
Roswell, Chaves, New Mexico	(Graves et al. 1974)
____, Mohave, Arizona	(Eads et al. 1987)
____, Pima, Arizona	(Eads et al. 1987)
____, Nye, Nevada*	(Eads et al. 1987)
M. disparalis	(*Dipodomys*)
____, Dona Ana, New Mexico*	(Eads 1978)

Table 1 continued.

____, Luna, New Mexico*	(Eads 1978)
____, Dona Ana, New Mexico	(Eads et al. 1987)
M. facilis	*(Dipodomys)*
____, Bernalillo, New Mexico*	(Eads 1978)
____, Chaves, New Mexico*	(Eads 1978)
____, Valencia, New Mexico*	(Eads 1978)
____, Chaves, New Mexico	(Eads et al. 1987)
____, Bernalillo, New Mexico	(Eads et al. 1987)
M. hubbardi	*(Peromyscus, Perognathus,* and *Onychomys)*
Crane, [Harney], Oregon	(Hubbard 1947)
Denio, [Humboldt], Nevada	(Hubbard 1947)
____, Harney, Oregon	(Hansen 1964)
Natl. Reactor Testing Sta., Idaho	(Allred 1968)
____, ____, Utah	(Lewis 1974a)
White Horse Ranch, Malheur, Oregon	(Lewis 1975)
Idaho Falls, [Bonneville], Idaho	(Eads et al. 1987)
M. jamesoni	*(Perognathus* and *Dipodomys)*
____, Santa Fe, New Mexico	(Morlan 1955)
____, ____, North Dakota	(Genoways and Jones 1972)
M. nidi	*(Dipodomys)*
____, Santa Fe, New Mexico	(Morlan 1955)
Roswell, Chaves, New Mexico	(Rail et al. 1969)
Roswell, Chaves, New Mexico	(Graves et al. 1974)
____, Coconino, Arizona	(Eads et al. 1987)
M. parkeri	*(Dipodomys;* also *Onychomys* and *Perognathus)*
Crane, [Harney], Oregon	(Hubbard 1947)
Narrows, ____, Oregon	(Hubbard 1947)
____, Meade, Kansas	(Hubbard 1947)
____, [several], Texas	(Eads and Menzies 1949)
____, ____, Utah	(Tipton 1950)
____, [several], Texas	(Eads 1950)
Albuquerque, Bernalillo, New Mexico	(Williams and Hoff 1951)
____, Santa Fe, New Mexico	(Morlan 1955)
Dugway, Tooele, Utah	(Howell 1957)
Kanab, Kane, Utah	(Stark 1958)
____, Harney, Oregon	(Hansen 1964)
Great Salt Lake Desert, Utah	(Woodbury 1964)
Mercury, Nye, Nevada*	(Beck and Allred 1965)
Dugway Proving Ground, Utah	(University of Utah 1967)
Natl. Reactor Testing Sta., Idaho	(Allred 1968)
Dugway Proving Ground, Utah	(University of Utah 1969)
Dugway Proving Ground, Utah	(Ecodynamics 1971)
____, Bighorn, Montana	(Jellison and Senger 1973)
____, Custer, Montana	(Jellison and Senger 1973)
____, San Juan, New Mexico	(CDC 1981)
____, Coconino, Arizona	(CDC 1982)
____, Albany, Wyoming	(Eads et al. 1987)
____, Wichita, Kansas	(Eads et al. 1987)
M. rectus	*(Dipodomys)*
____, Santa Fe, New Mexico	(Morlan 1953)
____, Santa Fe, New Mexico	(Morlan 1955)
Roswell, Chaves, New Mexico	(Rail et al. 1969)
Roswell, Chaves, New Mexico	(Graves et al. 1974)
M. shannoni	*(Onychomys, Perognathus* and *Peromyscus)*
Crane, [Harney], Oregon	(Hubbard 1947)
Mabton, [Yakima], Washington	(Hubbard 1947)
A.L.E. Reserve, Benton, Washington	(O'Farrell 1975)
____, Grant, Washington	(Eads et al. 1987)
Monopsyllus exilis	*(Onychomys)*
____, Meade, Kansas	(Hubbard 1943)
____, Yavapai, Arizona	(Hubbard 1947)
Roggen (*sic* Rugger), Colorado	(Hubbard 1947)
____, Meade, Kansas	(Hubbard 1947)
Powderville, Powder River, Montana	(Hubbard 1947)

Table 1 continued.

Crane, [Harney], Oregon	(Hubbard 1947)
____, [several], Texas	(Eads and Menzies 1949)
____, ____, Utah	(Tipton 1950)
____, ____, Texas	(Miles et al. 1952)
____, Santa Fe, New Mexico	(Morlan 1955)
____, ____, Nebraska	(Kartman and Prince 1956)
____, Santa Fe, New Mexico	(Holdenreid and Morlan 1956)
Kanab, Kane, Utah	(Stark 1958)
St. George, Washington, Utah**	(Stark 1958)
____, [Tooele], Utah	(Parker and Howell 1959)
____, Finney, Kansas	(Poorbaugh and Gier 1961)
Great Salt Lake Desert, Utah	(Woodbury 1964)
Winnett, Petroleum, Montana	(Senger 1966)
Natl. Reactor Testing Sta., Idaho	(Allred 1968)
____, ____, North Dakota	(Genoways and Jones 1972)
____, Navajo, Arizona	(CDC 1981)
____, San Juan, New Mexico	(CDC 1981)
____, Colfax, New Mexico	(CDC 1982)
____, Jones, South Dakota	(Easton 1982)
____, Weld, Colorado	(CDC 1983)
____, Yavapai, Arizona	(CDC 1984)
Alpine, Brewster, Texas*	(CDC 1984)
Brigsdale, Weld, Colorado	(CDC 1984)
Brigsdale, Weld, Colorado	(CDC 1985)
Portales, Roosevelt, New Mexico	(Pfaffenberger and de Bruin 1986)
M. wagneri	*(Peromyscus)*
____, [several], Texas	(Eads and Menzies 1949)
____, Harney, Oregon	(Hansen 1964)
Natl. Reactor Testing Sta., Idaho	(Allred 1968)
____, Colfax, New Mexico	(CDC 1982)
____, Bowman, North Dakota	(Larson et al. 1985)
____, Mercer, North Dakota	(Larson et al. 1985)
M. w. ophidius	*(Peromyscus)*
____, Lamb, Texas	(Eads 1950)
M. w. systaltus	*(Peromyscus)*
Ceylon, Saskatchewan, Canada	(Holland 1985)
M. w. wagneri	*(Peromyscus)*
Boardman, [Morrow], Oregon	(Hubbard 1941)
Two Rivers, ____, Washington	(Hubbard 1941)
Crane, [Harney], Oregon	(Hubbard 1947)
Denio, [Humboldt], Nevada	(Hubbard 1947)
Mabton, [Yakima], Washington	(Hubbard 1947)
Steen Mountain Pass, [Harney], Oregon	(Hubbard 1947)
____, ____, Utah	(Allred 1952)
____, Santa Fe, New Mexico	(Morlan 1955)
____, ____, Utah	(Beck 1955)
____, ____, Utah	(Stark 1958)
____, [Tooele], Utah	(Parker and Howell 1959)
Great Salt Lake Desert, Utah	(Woodbury 1964)
Mercury, Nye, Nevada*	(Beck and Allred 1965)
Dugway Proving Ground, Utah	(University of Utah 1967)
Natl. Reactor Testing Sta., Idaho	(Allred 1968)
Dugway Proving Ground, Utah	(University of Utah 1969)
Opisocrostis hirsutus	*(Cynomys)*
____, [several], Texas	(Eads and Menzies 1949)
____, [several], Texas	(Eads 1950)
____, Navajo, Arizona	(CDC 1981)
O. labis	*(Spermophilus)*
Narrows, ____, Oregon	(Hubbard 1947)
Natl. Reactor Testing Sta., Idaho	(Allred 1968)
O. washingtonensis	*(Spermophilus)*
____, ____, ____	(Smit 1983)
Opisodasys keeni	*(Peromyscus)*
Dugway Proving Ground, Utah	(University of Utah 1970b)

Table 1 continued.

Orchopeas caedens	
Dugway Proving Ground, Utah	(University of Utah 1969)
O. leucopus	
____, ____, Utah	(*Tamiasciurus* and *Glaucomys*)
____, Santa Fe, New Mexico	(*Peromyscus*)
Moab, Grand, Utah	(Tipton 1950)
Alpine, Brewster, Texas*	(Morlan 1955)
Portales, Roosevelt, New Mexico	(Stark 1958)
O. sexdentatus	(CDC 1984)
____, [several], Texas	(Pfaffenberger and de Bruin 1986)
O. s. agilis	(*Neotoma*)
____, ____, Utah	(Eads and Menzies 1949)
____, Santa Fe, New Mexico	(*Neotoma*)
Kanab, Kane, Utah	(Beck 1955)
Oropsylla idahoensis	(Morlan 1955)
____, ____, ____	(Stark 1958)
Peromyscopsylla draco	(*Spermophilus* and other small rodents)
Roswell, Chaves, New Mexico	(Stark 1970)
P. hesperomys	(*Peromyscus*)
____, Dawson, Texas	(Graves et al. 1974)
____, Howard, Texas	(*Peromyscus*)
____, Coconino, Arizona	(Eads and Menzies 1949)
Portales, Roosevelt, New Mexico	(Eads and Menzies 1949)
P. h. adelpha	(CDC 1982)
____, Rosebud, Utah	(Pfaffenberger and de Bruin 1986)
____, San Juan, Utah	(*Peromyscus*)
____, [Tooele], Utah	(Johnson and Traub 1954)
Mercury, Nye, Nevada*	(Stark 1958)
Phalacropsylla allos	(Parker and Howell 1959)
Natl. Reactor Testing Sta., Idaho	(Beck and Allred 1965)
Pulex irritans	(*Neotoma*)
____, ____, Texas	(Allred 1968)
Rhadinopsylla (*Acthenophthalmus*) sp.	(Man and large carnivores)
____, Cochran, Texas	(Eads 1950)
____, Yoakum, Texas	
____, Cochran, Texas	(Eads and Menzies 1949)
____, Yoakum, Texas	(Eads and Menzies 1949)
R. fraterna	(Eads 1950)
Natl. Reactor Testing Sta., Idaho	(Eads 1950)
Rock Glen, Saskatchewan, Canada	(*Spermophilus*)
R. heiseri	(Allred 1968)
____, [Tooele], Utah	(Holland 1985)
Great Salt Lake Desert, Utah	(*Ammospermophilus lecurus*)
Mercury, Nye, Nevada*	(Parker and Howell 1959)
R. multidenticulata	(Woodbury 1964)
____, Santa Fe, New Mexico	(Beck and Allred 1965)
Dugway Proving Ground, Utah	(*Onychomys leucogaster*)
Roswell, Chaves, New Mexico	(Morlan and Prince 1954)
____, ____, Arizona	(University of Utah 1970b)
____, ____, New Mexico	(Graves et al. 1974)
____, ____, Texas	(Lewis 1974a)
R. (*Micropsylla*) *sectilis*	(Lewis 1974a)
Crane, [Harney], Oregon	(Lewis 1974a)
R. s. sectilis	(mainly *Peromyscus*)
Mercury, Nye, Nevada*	(Hubbard 1941)
Natl. Reactor Testing Sta., Idaho	(mainly *Peromyscus*)
Thrassis aridis	(Beck and Allred 1965)
Portales, Roosevelt, New Mexico	(Allred 1968)
Th. aridis campestris	(*Dipodomys*)
____, Mojave, Arizona	(Pfaffenberger and de Bruin 1986)
____, Hooker, Nebraska	(*Dipodomys*)
____, Cherry, Nebraska	(Hubbard 1947)
____, Hidalgo, New Mexico	(Hubbard 1947)
____, [several], Texas	(Hubbard 1947)
	(Hubbard 1947)
	(Eads and Menzies 1949)

Table 1 continued.

____, Cochran, Texas	(Eads 1950)
____, Terry, Texas	(Eads 1950)
____, ____, Texas	(Miles et al. 1952)
____, Santa Fe, New Mexico	(Morlan 1955)
Camel, Black Mountain, Utah	(Stark 1958)
____, [Tooele], Utah	(Parker and Howell 1959)
Roswell, Chaves, New Mexico	(Rail et al. 1969)
Roswell, Chaves, New Mexico	(Graves et al. 1974)
Th. a. hoffmani	(*Dipodomys*)
St. George, Washington, Utah**	(Tipton and Allred 1951)
Mercury, Nye, Nevada*	(Beck and Allred 1965)
Th. arizonensis	(*Neotoma*, *Spermophilus*, *Dipodomys*, *Ammospermophilus*, and *Onychomys*)
Palm Springs, Riverside, California*	(Augustson 1943)
Santa Rosa Mountains, California*	(Augustson 1943)
____, Riverside, California*	(Hubbard 1947)
Th. b. bacchi	(*Spermophilus*)
Dugway, Tooele, Utah	(Howell 1957)
____, Morton, North Dakota	(Larson et al. 1985)
Cheyenne, Laramie, Wyoming	(CDC 1985)
Th. b. caducus	(*Ammospermophilus* and *Spermophilus*)
____, Emery, Utah	(Stark 1958)
Th. b. consimilis	(*Ammospermophilus*, *Spermophilus*, and *Onychomys*)
Holbrook, Navajo, Arizona	(Stark 1957)
Winslow, Navajo, Arizona	(Stark 1957)
Th. b. gladiolus	(*Ammospermophilus*)
Searchlight, Clark, Nevada	(Hubbard 1949)
____, ____, Utah	(Tipton 1950)
Dugway Valley, Tooele, Utah	(Stark 1958)
____, Washington, Utah**	(Stark 1958)
____, [Tooele], Utah	(Parker and Howell 1959)
____, Harney, Oregon	(Hansen 1964)
Great Salt Lake Desert, Utah	(Woodbury 1964)
Mercury, Nye, Nevada*	(Beck and Allred 1965)
Dugway Proving Ground, Utah	(University of Utah 1970a)
Th. b. johnsoni	(*Lagurus*)
Juarez, Mexico*	(Traub and Hoff 1951)
Th. b. pansus	(*Spermophilus*, *Ammospermophilus*, and frequently *Onychomys*)
____, Brewster, Texas**	(Eads and Menzies 1949)
____, Brewster, Texas**	(Eads 1950)
Albuquerque, Bernalillo, New Mexico	(Williams and Hoff 1951)
____, Santa Fe, New Mexico	(Morlan 1955)
Bloomfield, San Juan, New Mexico	(Stark 1970)
Th. b. setosis	(*Ammospermophilus* and frequently *Onychomys*)
____, ____, ____	(Stark 1970)
Th. fotus	(*Spermophilus*)
____, Brewster, Texas**	(Prince 1944)
____, [several], Texas	(Eads and Menzies 1949)
____, [several], Texas	(Eads 1950)
____, ____, Texas	(Miles et al. 1952)
____, ____, Nebraska	(Kartman and Prince 1956)
Roswell, Chaves, New Mexico	(Rail et al. 1969)
Guyman, Texas, Oklahoma	(Stark 1970)
Eunice, Lea, New Mexico	(Stark 1970)
Loco Hills, Eddy, New Mexico	(Stark 1970)
Maljamar, Lea, New Mexico	(Graves et al. 1974)
Roswell, Chaves, New Mexico	(Stark 1970)
Wellington, Larimer, Colorado	(CDC 1984)
Brigsdale, Weld, Colorado	(CDC 1984, 1985)
Portales, Roosevelt, New Mexico	(Pfaffenberger and de Bruin 1986)
Th. francisi rockwoodi	(*Spermophilus*)
Blitzen, [Harney], Oregon	(Hubbard 1947)
Ontario, Malheur, Oregon	(Hubbard 1947)
Alamo, Lincoln, Nevada	(Hubbard 1949)

Table 1 continued.

Th. p. pandorae	(*Spermophilus*)
Denio, [Humboldt], Nevada	(Hubbard 1947)
Steen Mountain Pass, [Harney], Oregon	(Hubbard 1947)
Natl. Reactor Testing Sta., Idaho	(Allred 1968)
Th. petiolatus	(*Spermophilus*)
Boardman, [Morrow], Oregon	(Hubbard 1941)
Denio, [Humboldt], Nevada	(Hubbard 1941)
Two Rivers, ____, Washington	(Hubbard 1941)

[1]References to normal hosts are after Lewis (1972, 1974a, 1974b, 1975) except where otherwise noted.
*Collected from *Onychomys torridus*.
**Probably collected from *Onychomys torridus*.
+Personal collection data—no reference cited.
County records in brackets [ ] were either not in the original record and have been added in this review, were inferred from the original record, or the original record listed more than one county of collection and is noted by [several].

indicate that grasshopper mice frequently investigate or utilize burrows previously constructed by other rodents. This observation is supported by the number of fleas commonly associated with *Dipodomys*, *Spermophilus*, and geomyids collected from grasshopper mice. Members of these rodent genera are comparatively large and aggressive enough to be unlikely victims of *O. leucogaster* except as juveniles. By preying on these animals as juveniles, the grasshopper mouse would still be likely to enter a burrow of the prey species, which makes burrow investigation an avenue to interspecific parasitism.

Some species of fleas considered to have principal hosts other than *O. leucogaster* have developed what appear to be primary associations with grasshopper mice from secondary associations. This was observed by Graves et al. (1974) for *Meringis nidi*, *M. bilsingi*, and *M. dipodomys* in Roswell County, New Mexico, and by Morlan and Prince (1954) for *Rhadinopsylla multidenticulata*. Several of the flea species reported here from *O. leucogaster* are drawn from a single published reference. These may be interpreted as accidental or "trivial" collections that do not represent a flea/host association of any natural importance at present, but they may also represent rarely documented normal associations.

ONYCHOMYS, THEIR FLEAS AND PLAGUE

Twenty-six of the 57 nominate species of fleas collected from *O. leucogaster* are known to be potential or capable vectors of plague (Table 2). Beck (1955) defines a potential vector as one that demonstrates the presence of the etiologic agent in its body but has not been found to transmit the disease organisms either naturally or experimentally. He defined a capable vector as able to transmit the disease either naturally or experimentally. However, the experimental success or failure of a flea species tested for vector competency does not necessarily reflect its natural ability to transmit the disease. Jordan (1943) proposed that a priori every flea is a "potential" vector of plague.

TABLE 2. Plague vectoring capacities of 25 nominate species and six additional subspecies of fleas collected from *Onychomys leucogaster*.

Capable vectors	Potential vectors
Diamanus montanus[1]	*Anomiopsyllus amphibolus*[4]
Echidnophaga gallinacea[1]	*Catallagia decipiens*[1]
Hoplopsyllus anomalus[1]	*Epitedia wenmanni*[1]
Malaraeus telchinus[1]	*Enhoplopsyllus glacialis affinis*[1]
Opisocrostis hirsutus[1]	*Foxella ignota*[1]
O. labis[1]	*Meringis shannoni*[4]
Oropsylla idahoensis[1]	*Monopsyllus exilis*[4]
Thrassis a. arizonensis[1]	*Monopsyllus wagneri*[1]
Pulex irritans[1]	*M. w. wagneri*[2]
Thrassis bacchi johnsoni[3]	*Opisodasys keeni*[4]
Th. francisi rockwoodi[1]	*Orchopeas leucopus*[4]
Th. p. pandorae[1]	
O. sexdentatus[4]	
O. s. aqilis[1]	
Peromyscopsylla hesperomys adelpha[3]	
Thrassis b. bacchi[6]	
Th. b. caducus[6]	
Th. b. gladiolus[6]	
Th. b. pansus[5]	
Th. fotus[5]	
Th. petiolatus[1]	

[1]Beck 1955
[2]Egoscue 1960
[3]Kartman and Prince 1956
[4]Pollitzer and Meyer 1961
[5]Stark 1970
[6]Thorpe 1962

Individual grasshopper mice vary widely in the number of fleas that they carry. The average number of fleas per *Onychomys* (flea index) is often fairly low, and many are found to

TABLE 3. Flea index records from *Onychomys leucogaster* collections.

Number of *Onychomys*	Number of fleas	Flea index	Reference source
405	0	0.0	Haas et al. 1973
71	35	0.5	Miller et al. 1977b
405	368	0.9	Holdenreid and Morlan 1956
—	16,876	1.0	Wayson 1947
13	29	2.2	Miller et al. 1977a
88	202	2.3	Dugway 1964–1972*
57	191	3.4	Poorbaugh and Gier 1961
92	344	3.7	Pfaffenberger and de Bruin 1986
13	91	7.0	Hubbard 1941
62	545	8.8	CDC 1984–1985

*References for fleas collected from *O. leucogaster* during the University of Utah studies of the ecology and epizoology of the Great Salt Lake Desert are: (1) Woodbury 1964, (2) University of Utah 1967, 1968, 1969, 1970a, 1970b; (3) Ecodynamics, Inc. 1971, 1972.

have no fleas at all (Table 3). Haas et al. (1973) found no fleas on 405 *O. leucogaster* collected in north central New Mexico at one-month intervals over a one-year period; however, Hubbard (1941) collected 91 fleas from 13 *O. leucogaster*, none of which were free of fleas. He also notes that only 4 of the fleas were *Monopsyllus exilis*, a flea that Traub (1985) described as ultraspecific to grasshopper mice. Wayson (1947) stated that an index of less than one flea does not eliminate the probability of disseminating plague. One infected flea has transmitted the disease to each of several animals when afforded the opportunity experimentally. He adds that the dissemination of plague vectors to animals of different genera may be aided by the habits of a host such as the grasshopper mouse, whose burrow-utilization behavior leads to the spread of the several varieties of fleas it collects. Stark (1970) commented that although *O. leucogaster* are infrequently trapped, they and their fleas figure with surprising frequency in the plague records, and their relationship may play an important role in the transfer of plague in nature.

The high flea index reported for *O. leucogaster* by CDC (1984, 1985) is significant in interpreting the role of grasshopper mice in areas of enzootic plague. These mice were collected from the Pawnee National Grasslands in Weld County, Colorado, during and subsequent to a local plague epizootic. Thomas et al. (in press) found the *O. leucogaster* from this population to be very susceptible to infection with the plague bacillus, but resistant to mortality due to the disease. Nearly one-third of the fleas taken from grasshopper mice in this area were those normally associated with *Spermophilus tridecemlineatus*, *Peromyscus maniculatus*, *Geomys bursarius*, and *Dipodomys ordii*. The remaining 67% were *Monopsyllus exilis*. Two of the *O. leucogaster* collected on the Pawnee Grasslands carried 91 and 67 fleas, respectively, and remained healthy in a lab colony. Poorbaugh and Gier (1961) observed during their rodent collections in Kansas that flea infestations were generally higher when host populations were declining. During a reduction in host populations fleas apparently concentrate on remaining hosts. The reason for the high flea index observed in the *O. leucogaster* population in Colorado may well have been that the epizootic reduced the number of available hosts. Work by Rödl (1979) revealed that flea transfer in a rodent nest is a function of the number of fleas present in the nest and the period of time that the newly arrived host spends in the nest. He stated that in the absence of the normal occupant, flea transfer to a visiting host is intensive and often total. Following a plague epizootic, fleas can feed upon, infect or be infected by, and be dispersed by resistant grasshopper mice investigating and/or utilizing the burrow of a dead host.

The behavior of *O. leucogaster* most certainly accounts for their ability to act as a suitable host for a large flea fauna. This may, in turn, lead to selection for resistance to plague in enzootic areas as observed by Thomas et al. (in press). The selection pressure for development of resistance as a population character would be intensified due to the potential for infection by eating infected prey and using their burrows.

Northern grasshopper mice, due to their

omnivory and habit of secondary burrow use, appear to be likely participants in the maintenance of wild rodent plague. As hospitable temporary hosts, they are responsible for dispersing a variety of fleas of known importance in the epizoology of plague. The range of *O. leucogaster* extends into all of the foci of plague in the western United States described by Barnes (1982) (compare Fig. 1). In areas where populations of grasshopper mice have been associated with plague for a period of time, the selection pressures leading to a population resistance increase the ability of these mice to effectively maintain both the local flea populations and the enzootic character of this disease in nature.

TAXONOMIC TREATMENT

The purpose of this review is to report published flea collection records from members of the genus *Onychomys* and discuss the importance of their associations in the epizoology of plague. It is not my intent to address the validity of the current taxonomy of North American Siphonaptera. Smit (1983) has revised the superspecific taxonomy of fleas of the family Ceratophyllidae. Due to the nature of this article, I have adopted Holland's (1985) use of the conservative taxonomy in order to retain the generic names reported in the original literature. For determination of generic classification according to Smit, the reader is referred to Appendix 5 of Traub, Rothschild, and Haddow (1983). Johnson (1961) reduced the subspecific status of the geographic races of *Monopsyllus wagneri*. Again, in order to retain the original taxonomy reported in the collection records, I follow Holland (1985) in the use of the subspecific epithets.

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LITERATURE CITED

ALLRED, D. M. 1952. Plague important fleas and mammals in Utah and the western United States. Great Basin Nat. 12(1–4):67–75.

———. 1968. Fleas of the National Reactor Testing Station. Great Basin Nat. 28(2): 73–87.

AUGUSTSON, G. F. 1943. Preliminary records and discussion of some species of Siphonaptera from the Pacific southwest. Bull. So. California Acad. Sci. 42(2): 69–88.

———. 1955. Records of fleas (Siphonaptera) from the Pacific southwest. Bull. So. California Acad. Sci. 54(1): 36–39.

BAILEY, V. 1931. Mammals of New Mexico. N. Amer. Fauna No. 53. 412 pp.

BAILEY, V., AND C. C. SPERRY. 1929. Life history and habits of the grasshopper mice, genus *Onychomys*. U.S. Dept. Agric. Tech. Bull. No. 145. 19 pp.

BARNES, A. M. 1982. Surveillance and control of bubonic plague in the United States. Symp. Zool. Soc. London 50: 237–250.

BARNES, A. M., V. J. TIPTON, AND J. A. WILDE. 1977. The subfamily Anomiopsyllinae (Hystrichopsyllidae: Siphonaptera). I. A review of the genus *Anomiopsyllus* Baker. Great Basin Nat. 37(2): 130–206.

BECK, D. E. 1955. Distributional studies of parasitic arthropods in Utah, determined as actual and potential vectors of Rocky Mountain spotted fever and plague, with notes on vector-host relationships. Brigham Young Univ. Sci. Bull., Biol. Ser. 1(1): 1–64.

BECK, D. E., AND D. M. ALLRED. 1965. Siphonaptera (fleas) of the Nevada Test Site. Brigham Young Univ. Sci. Bull., Biol. Ser. 7(2): 1–27.

BENTON, A. H., AND D. H. MILLER. 1970. Ecological factors in the distribution of the flea *Peromyscopsylla h. hamifer*. Amer. Midl. Nat. 81: 301–303.

CDC. 1981–1985. Annual collection data. Plague Branch, Division of Vector-borne Viral Diseases, Centers for Disease Control, Fort Collins, Colorado 80522, USA. Unpublished manuscript.

EADS, R. B. 1950. The fleas of Texas. Control Div., Entomol. Bureau, Texas State Health Dept. 85 pp.

———. 1978. Two new species of fleas of the genus *Meringis* (Siphonaptera: Hystrichopsyllidae). Great Basin Nat. 38(4): 447–455.

EADS, R. B., AND E. G. CAMPOS. 1977. Notes on the flea genus *Megarthroglossus* (Siphonaptera: Hystrichopsyllidae: Anomiopsyllinae), with description of a new species. J. Med. Entomol. 14(1): 97–100.

EADS, R. B., E. G. CAMPOS, AND G. O. MAUPIN. 1987. A review of the genus *Meringis* (Siphonaptera: Hystrichopsyllidae). J. Med. Entomol. 24: 467–476.

EADS, R. B., AND G. C. MENZIES. 1948. An undescribed *Anomiopsyllus* Baker from the pack rat, *Neotoma micropus* Baird. J. Kansas Entomol. Soc. 21(4): 133–136.

———. 1949. A preliminary list of the Siphonaptera of Texas. Texas J. Sci. 1(4): 33–39.

EASTON, E. R. 1982. An annotated checklist of the fleas of South Dakota (Siphonaptera). Entomol. News 93(5): 155–158.

ECODYNAMICS, INC. 1971. Ecological studies in western Utah. 1970 Annual Report. Ecology and Epizoology Series No. 71-1, Salt Lake City, Utah. 116 pp.

———. 1972. Ecological studies in western Utah. 1971 Annual Report. Ecology and Epizoology Series No. 72-1. Salt Lake City, Utah. 111 pp.

EGOSCUE, H. J. 1960. Laboratory and field studies of the northern grasshopper mouse. J. Mammal. 41: 99–110.

ESKEY, C. R., AND V. H. HAAS. 1939. Plague in the western part of the United States. Infection in rodents, experimental transmission by fleas and inoculation tests for infection. Pub. Health Repts. 54: 1467–1481.

FLAKE, L. D. 1973. Food habits of four rodent species in a short-grass prairie in Colorado. J. Mammal. 54: 636–647.

GENOWAYS, H. H., AND J. K. JONES. 1972. Mammals from southwestern North Dakota. Occ. Pap. Mus. Texas Tech. Univ. No. 6.

GRAVES, G. N., W. C. BENNETT, J. R. WHEELER, B. E. MILLER, AND D. L. FORCUM. 1974. Sylvatic plague studies in southeast New Mexico. I. Flea-host relationships from six years' study. J. Med. Entomol. 4: 488–498.

HAAS, G. E., R. P. MARTIN, M. SWICKARD, AND B. E. MILLER. 1973. Siphonaptera-mammal relationships in northcentral New Mexico. J. Med. Entomol. 10(3): 281–289.

HANSEN, C. G. 1964. Ectoparasites of mammals from Oregon. Great Basin Nat. 24(2): 75–81.

HOLDENREID, R., AND H. B. MORLAN. 1956. A field study of wild mammals and fleas of Santa Fe County, New Mexico. Amer. Midl. Nat. 55(2): 369–381.

HOLLAND, G. P. 1958. Distribution patterns of northern fleas (Siphonaptera). Proc. Tenth Internatl. Congr. Entomol. 1: 645–658.

_____. 1964. Evolution, classification and host relationships of Siphonaptera. Ann. Rev. Entomol. 9: 123–146.

_____. 1985. The fleas of Canada, Alaska and Greenland (Siphonaptera). Mem. Entomol. Soc. Canada 130: 1–631.

HOWELL, J. F. 1957. Fleas associated with the nests of the desert wood rat. J. Parasitol. 43: 566–573.

HOPKINS, G. H. E. 1957. Host-associations of Siphonaptera. Pages 64–87 *in* First symposium on host specificity among parasites of vertebrates. Institute Zoologie, Universite de Neuchatel.

HUBBARD, C. A. 1941. The fleas of rare western mice. Pacific Univ. Bull. 37(9A): 1–4.

_____. 1943. Three new fleas from Kansas. Pacific Univ. Bull. 39(10): 1–2.

_____. 1947. Fleas of western North America. Iowa State College Press, Ames. 533 pp.

_____. 1949. Fleas of the state of Nevada. Bull. So. California Acad. Sci. 48(3): 115–128.

JELLISON, W. L., AND C. SENGER. 1973. Fleas of Montana. Montana Agric. Expt. Sta. Res. Rept. No. 29. 82 pp.

JOHNSON, P. T. 1961. A revision of the species of *Monopsyllus* Kolenati in North America. (Siphonaptera: Ceratophyllidae). U.S. Dept. Agric. Tech. Bull. No. 1227. 69 pp.

JOHNSON, P. T., AND R. TRAUB. 1954. A revision of the flea genus *Peromyscopsylla*. Smithsonian Misc. Pub. 123(4): 1–68.

JORDAN, K. 1943. Siphonaptera. Pages 202–223 *in* J. Smart, ed., A handbook for identification of insects of medical importance, British Museum of Natural History.

KARTMAN, L., AND F. M. PRINCE. 1956. Studies on *Pasturella pestis* in fleas. V. The experimental plague-vector efficiency of wild rodent fleas compared with *Xenopsylla cheopis*, together with observations on the influence of temperature. Amer. J. Trop. Med. Hyg. 5(6): 1058–1070.

LANDRY, S. O., JR. 1970. The Rodentia as omnivores. Quart. Rev. Biol. 45: 351–372.

LARSON, O. R., M. G. MCKENNA, AND N. R. FELLOWS. 1985. North Dakota fleas. IX. Siphonapterans of mammals in southwestern North Dakota. Prairie Nat. 17(4): 241–247.

LEWIS, R. E. 1972. Notes on the geographical distribution and host preferences in the order Siphonaptera. Part 1. Pulicidae. J. Med. Entomol. 9(6): 511–520.

_____. 1974a. Notes on the geographical distribution and host preferences in the order Siphonaptera. Part 3. Hystrichopsyllidae. J. Med. Entomol. 11(2): 147–167.

_____. 1974b. Notes on the geographical distribution and host preferences in the order Siphonaptera. Part 5. Ancistropsyllidae, Chimaeropsyllidae, Ishnopsyllidae, Leptopsyllidae and Marcopsyllidae. J. Med. Entomol. 11(5): 525–540.

_____. 1975. Notes on the geographical distribution and host preferences in the order Siphonaptera. Part 6. Ceratophyllidae. J. Med. Entomol. 11(6): 658–676.

MCCARTY, R. 1978. *Onychomys leucogaster*. Mammalian Species 87: 1–6.

MILES, V. I., M. J. WILCOMB, AND J. V. IRONS. 1952. Rodent plague in the Texas south plains 1947–1949, with ecological considerations. Pub. Health Monogr. No. 6, Part II, pp. 40–53.

MORLAN, H. B. 1953. *Meringis rectus* (Siphonaptera: Hystrichopsyllidae). A new ectoparasite of kangaroo rats. J. Parasitol. 39(6): 605–609.

_____. 1955. Mammal fleas of Santa Fe County, New Mexico. Texas Repts. Biol. Med. 13(1): 93–125.

MORLAN, H. B., AND F. M. PRINCE. 1954. Notes of the subfamily Rhadinopsyllinae Wagner 1930 (Siphonaptera: Hystrichopsyllidae) and description of a new species, *Rhadinopsylla multidenticulatus*. Texas Repts. Biol. Med. 12: 1037–1046.

O'FARRELL, T. P. 1975. Small mammals, their parasites and pathologic lesions on the Arid Lands Ecology Reserve, Benton County, Washington. Amer. Midl. Nat. 93(2): 377-387.

PARKER, D. D., AND J. F. HOWELL. 1959. Host-flea relationships in the Great Salt Lake Desert. J. Parasitol. 45(6): 597–604.

PFAFFENBERGER, G. S., AND D. DE BRUIN. 1986. Ectoparasitic overlap between sympatric *Dipodomys ordii* and *Onychomys leucogaster* (Rodentia) in eastern New Mexico, USA. J. Med. Entomol. 23(2): 201–207.

POLLITZER, R., AND K. F. MEYER. The ecology of plague. Pages 433–590 *in* J. M. May, ed., Studies in disease ecology. Hafner Publ. Co., New York.

POORBAUGH, J. H., AND H. T. GIER. 1961. Fleas (Siphonaptera) of small mammals in Kansas. J. Kansas Entomol. Soc. 34(4): 198–204.

PRINCE, F. M. 1944. Descriptions of three new species of *Thrassis* Jordan and the females of *T. bacchi* and *T. pansus*. Pan-Pacif. Entomol. 20(1): 13–19.

_____. 1945. Description of three new species of *Dactylopsylla* Jordan and one new species of *Foxella* Wagner, with records of other species in the genera (Siphonaptera). Canadian Entomol. 77: 15–20.

PRINCE, F. M., AND H. E. STARK. 1951. Four new species of fleas of the genus *Dactylopsylla* Jordan, 1929. Pan-Pacif. Entomol. 27(3): 128–139.

RAIL, C. D., D. L. FORCUM, J. R. WHEELER, AND B. E. MILLER. 1969. Wild mammals and fleas of Red Bluff Ranch, New Mexico. J. Med. Entomol. 6(1): 92–94.

RÖDL, P. 1979. Investigation of the transfer of fleas among small mammals using radioactive phosphorus. Folia Parasitologia 26(3): 265–274.

ROTHSCHILD, M. 1965. The rabbit flea and hormones. Endeavour 24 (93): 162–168.

RUFFER, D. G. 1965. Burrows and burrowing behavior of *Onychomys leucogaster*. J. Mammal. 46: 241–247.

SENGER, C. M. 1966. Notes of fleas (Siphonaptera) from Montana. J. Kansas Entomol. Soc. 39(1): 105–109.

SMIT, F. G. A. M. 1983. Key to the genera and subgenera of Ceratophyllidae. Pages 1–163 *in* R. M. Traub, M. Rothschild, and J. F. Haddow, The Rothschild Collection of fleas: the Ceratophyllidae. Academic Press Inc., London.

STARK, H. E. 1957. Five new fleas of the genus *Thrassis* Jordan 1929 (Ceratophyllidae: Siphonaptera), a genus of known importance in plague transmission. J. Parasitol. 43(3): 332–346.

_____. 1958. The Siphonaptera of Utah. U.S. HEW-PHS. 239 pp.

_____. 1970. A revision of the flea genus *Thrassis* Jordan 1933 (Siphonaptera: Ceratophyllidae), with observations on ecology and relationships to plague. Univ. California Pub. Entomol. 53: 1–184.

_____. 1986. Book review, The Rothschild Collection of fleas. The Ceratophyllidae: key to the genera and host relationships with notes on their evolution, zoogeography and medical importance. J. Med. Entomol. 23(3): 336–337.

THOMAS, R. E., A. M. BARNES, T. J. QUAN, M. L. BEARD, L. G. CARTER, AND C. E. HOPLA. 1988. Resistance and susceptibility to *Yersinia pestis* in two populations of the northern grasshopper mouse *Onychomys leucogaster*. J. Wildl. Dis. 24(2). In press.

THORPE, B. O. 1962. Summary status report on *Pasturella pestis*. Staff, Ecology and Epizoology Research, University of Utah. 110 pp.

TIPTON, V. J. 1950. New distributional records for Utah Siphonaptera. Great Basin Nat. 10(1–4): 62–65.

TIPTON, V. J., AND D. M. ALLRED. 1951. Distribution records of Utah Siphonaptera. Great Basin Nat. 11(3–4): 105–114.

TIPTON, V. J., H. E. STARK, AND J. A. WILDE. 1979. Anomiopsyllinae (Siphonaptera: Hystrichopsyllidae) II. The genera *Callistopsyllus*, *Chonorhinopsylla*, *Megarthroglossus* and *Stenistomera*. Great Basin Nat. 39: 351–418.

TRAUB, R. 1985. Coevolution of fleas and mammals. Pages 295–437 *in* K. C. Kim, ed., Coevolution of parasitic arthropods and mammals. John Wiley and Sons, New York.

TRAUB, R., AND C. C. HOFF. 1951. Records and descriptions of fleas from New Mexico (Siphonaptera). Amer. Mus. Novitates 1530: 1–23.

TRAUB, R., M. ROTHSCHILD, AND J. F. HADDOW. 1983. The Ceratophyllidae. Key to the genera and host relationships; with notes on their evolution, host relationships and medical importance. Academic Press Inc., London. 288 pp.

UNIVERSITY OF UTAH. 1967. A study of the ecology and epizoology of the Great Salt Lake Desert. Annual Report for 1966. Ecology and Epizoology Series No. 141. Staff, Ecol. Epizool. Res. Group. 313 pp.

_____. 1968. A study of the ecology and epizoology of the Great Salt Lake Desert. Annual Report for 1967. Ecology and Epizoology Series No. 144. Staff, Ecol. Epizool. Res. Group. 234 pp.

_____. 1969. A study of the ecology and epizoology of the Great Salt Lake Desert. Annual Report for 1968. Ecology and Epizoology Series No. 145. Staff, Ecol. Epizool. Res. Group. 116 pp.

_____. 1970a. A study of the ecology and epizoology of the Great Salt Lake Desert. Annual Report for 1969. Ecology and Epizoology Series No. 154. Staff, Ecol. Epizool. Res. Group. 256 pp.

_____. 1970b. A study of the ecology and epizoology of the Great Salt Lake Desert. Annual Report for 1970. Ecology and Epizoology Series No. 157. Staff, Ecol. Epizool. Res. Group. 36 pp.

WAYSON, N. E. 1947. Plague—field surveys in western United States during ten years (1936–1945). Pub. Health Repts. 62(22): 780–791.

WENZEL, R. L., AND V. J. TIPTON. 1966. Some relationships between mammal hosts and their ectoparasites. Pages 677–724 *in* R. L. Wenzel and V. J. Tipton, eds., Ectoparasites of Panama. Field Museum of Natural History.

WILLIAMS, L. A., AND C. C. HOFF. 1951. Fleas from the Upper Sonoran zone near Albuquerque, New Mexico. Proc. U.S. Natl. Mus. 101: 305–313.

WISEMAN, J. S. 1955. The Siphonaptera of Wyoming. Univ. Wyoming Pubs. Sci. 19(1–2): 1–28.

WOODBURY, A. M. 1964. Disease dissemination among biotic communities of the Great Salt Lake Desert. Bull. Univ. Utah 55(22): 1–282.

CHECKLIST OF THE ODONATA OF COLORADO

Mary Alice Evans[1]

ABSTRACT.—One hundred and one species of Odonata are recorded for Colorado, including 58 species of Anisoptera (of which 4 are new state records) and 43 Zygoptera (9 new state records). County records are indicated for each. Three major elements are recognized: predominantly eastern species occurring in the plains and mountain valleys east of the Rocky Mountains, Canadian Zone elements occurring principally above 2,440 m (8,000 ft) in the mountains, and Great Basin and western species occurring chiefly west of the mountains. The list is based primarily on the collections at Colorado State University and the University of Colorado, with additional records from the literature and from other collections.

Although various papers have been published listing Odonata from Colorado, no comprehensive checklist has been compiled. Colorado contains many different habitats, ranging from cold, wet alpine meadows to hot, dry areas that approach desert conditions, especially in late summer. In addition, altitudes range from a little over 915 m (3,000 ft) to well above 4,270 m (14,000 ft). On the accompanying map of Colorado (with the counties indicated), I have added the Continental Divide and the approximate 1,525-m (5,000-ft) contour lines on each side of it. Colorado's fauna is enriched by the movement of eastern species into its eastern plains, Great Basin species into the western counties, and northern species down the crest of the Rocky Mountains from Canada.

Of particular interest are the Canadian Zone representatives, i.e., those found between approximately 2,440 m (8,000 ft) and 3,355 m (11,000 ft). Of the 101 species here reported from Colorado, 18 Anisoptera and 13 Zygoptera were found at 2,440 m (8,000 ft) or above. Of those found above 2,745 m (9,000 ft), 8 were dragonflies and 5 damselflies, and above 3,050 m (10,000 ft), there were 5 of each. Of the dragonfly genera, two contain most of the high-altitude species, namely, *Somatochlora* and *Leucorrhinia*. In the genus *Sympetrum*, several species occur above 2,440 m (8,000 ft), but the genus is also well represented at lower altitudes. The highest altitude I have recorded is for *Libellula pulchella* at 3,263 m (10,700 ft). This species also has the widest range altitudinally of any odonate that I have observed in the state, over 2,135 m (7,000 ft). Of the damselflies, all major genera, except members of the family Calopterygidae, seem to have at least one species in the Canadian Zone; the highest flier I observed is *Coenagrion resolutum* at 3,141 m (10,300 ft).

Anisoptera, which occur throughout Colorado, except perhaps for the highest altitudes, are: *Ophiogomphus severus*, *Libellula pulchella* and *L. quadrimaculata*, *Sympetrum corruptum* and *S. occidentale;* and Zygoptera are: *Lestes disjunctus*, *Amphiagrion abbreviatum*, *Enallagma cyathigerum*, and *Ischnura perparva*.

Western species that barely enter the state are: *Cordulegaster dorsalis* and *Gomphus intricatus;* others penetrating further east but not to the eastern border of the state are: *Aeshna interrupta*, *A. palmata*, and *A. umbrosa*, *Sympetrum danae* and *S. pallipes*, *Lestes congener* and *L. dryas*, *Coenagrion resolutum*, *Enallagma boreale* and *E. cyathigerum*.

Eastern species barely entering the state are: *Celithemis eponina*, *Pachydiplax longipennis*, *Calopteryx maculata*, *Lestes rectangularis*, *Argia alberta* and *A. apicalis*, *Enallagma hageni* and *E. vesperum;* others reaching the foothills (more or less) are: *Progomphus obscurus*, *Libellula luctuosa* and *L. lydia*, *Sympetrum rubicundulum*, *Argia violacea*, and *Enallagma praevarum*.

Southern species that barely enter the southern border are: *Gomphus militaris*, *Epitheca cynosura* and *E. petechialis*, *Perithemis*

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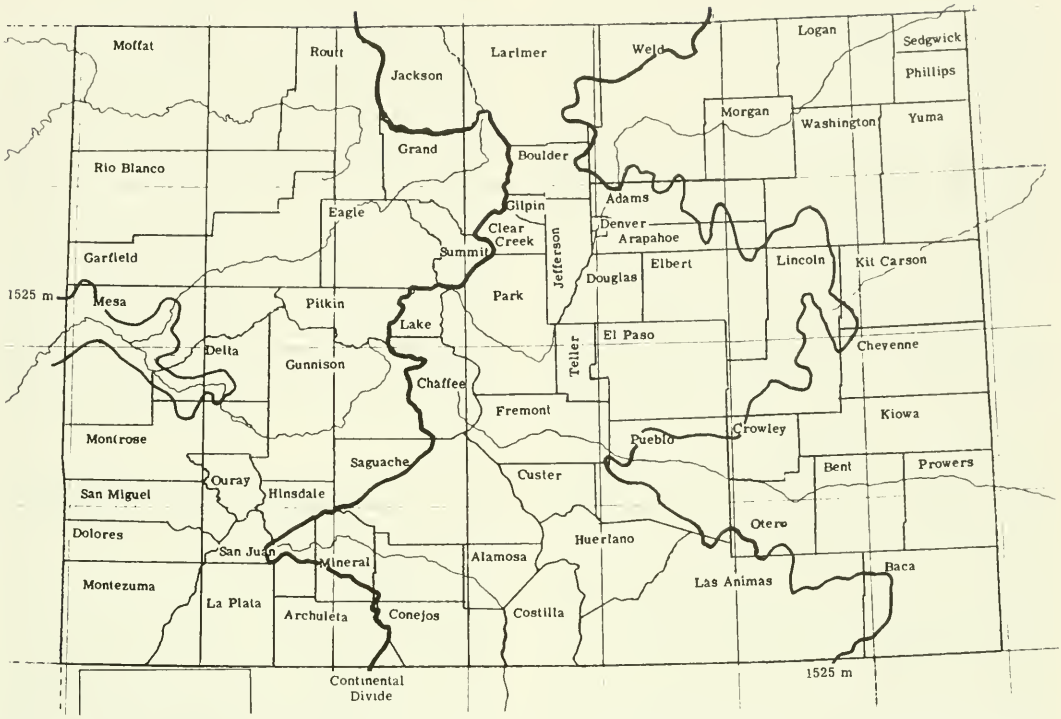

Fig. 1. Map of Colorado with the counties indicated. The approximate locations of the Continental Divide and the 1,525-m (5,000-ft) contour lines on each side are superimposed.

tenera, *Libellula nodisticta*, *Argia lugens*, *A. nahuana*, and *A. plana;* others reaching farther into the state are: *Libellula saturata* and *L. subornata*, *Tramea lacerata* and *T. onusta*, and *Pantala hymenea*. Some of these can be found further north in areas of hot springs.

In the following list I have given the literature citations first and then the specimen records (by county when possible). These records are based primarily on specimens in collections of the Department of Entomology at Colorado State University in Fort Collins and of the University of Colorado Museum at Boulder. Most of this material was identified by the author. Additional records have been taken from the following institutions (cited by abbreviations).

Florida State Collection of Arthropods (FSCA), Gainesville, Florida.

Museum of Comparative Zoology (MCZ), Harvard University, Cambridge, Massachusetts.

Museum of Zoology (UMMZ), University of Michigan, Ann Arbor, Michigan.

United States National Museum (USNM), Smithsonian Institution, Washington, D.C.

University of Nebraska State Museum (UNSM), Lincoln, Nebraska.

Also, indicated by one asterisk (*) are the thirteen new state records, and the few doubtful records, by two (**).

ANISOPTERA

Cordulegastridae

****Cordulegaster dorsalis* Hagen.** Moffat.

*****Cordulegaster erronea* Hagen.** Recorded as doubtful from Colorado by Montgomery (1968). Colorado is far to the west of the established range.

Gomphidae

***Progomphus borealis* McLachlan.** (Byers 1939).

***Progomphus obscurus* (Rambur).** El Paso (Hess 1940), Bent (G. H. Bick 1987, personal communication).

***Ophiogomphus severus* Hagen.** Costilla (Hagen 1874), "Buffalo, Platte Canyon" (Tucker 1907), Jefferson (Williamson 1913), El Paso (Hess 1940). Boulder, Delta, Denver (UMMZ), Elbert, Fremont (USNM), Huerfano, Jackson, Jefferson (UMMZ), Larimer, Las Animas, Mesa, Moffat, Montezuma, Montrose, Park (USNM), Rio Blanco, Rio Grande (UMMZ), Routt, Weld, Yuma.

*****Gomphus cornutus* Tough.** Recorded from Colorado by Needham and Westfall (1955), but its occurrence there is doubted by Montgomery (1968).

***Gomphus externus* Hagen.** (Montgomery 1968).

Gomphus intricatus **Hagen.** Mesa (Kormondy 1960). Mesa.

Gomphus militaris **Hagen.** Bent (Bick and Hornuff 1974). Baca, Lincoln.

Aeshnidae

Anax junius **(Drury).** El Paso and Pueblo (Hess 1940), Bent (G. H. Bick 1987, personal communication). Baca, Boulder (USNM), Larimer, Prowers, Rio Blanco, Weld.

Aeshna constricta **Say.** Archuleta (Hagen 1875). Grand.

Aeshna eremita **Scudder.** Boulder (Kormondy 1960). Boulder, Larimer.

Aeshna interrupta **Walker.** Gunnison (Bird and Rulon 1933), El Paso and Pueblo (Hess 1940), Routt (G. H. Bick 1987, personal communication). Archuleta, Boulder, Huerfano (UMMZ), Jackson (USNM), Larimer, Mesa.

Aeshna juncea **Linnaeus.** "Southeastern part," "Corfi" (Walker 1912), El Paso (Hess 1940). Boulder, Moffat.

Aeshna multicolor **Hagen.** Denver (Calvert 1905), El Paso (Tucker 1907), Weld (Walker 1912), Pueblo (Hess 1940). Arapahoe, Baca, Bent, Boulder, Fremont, Las Animas, Moffat, Prowers, Weld.

Aeshna palmata **Hagen.** Lake (Walker 1912), Gunnison (Bird and Rulon 1933), El Paso and Pueblo (Hess 1940), Moffat (G. H. Bick 1987, personal communication). Archuleta, Boulder, Chaffee, Grand, Jackson, Jefferson (UMMZ), Larimer, Las Animas, Mesa.

Aeshna umbrosa **Walker.** El Paso (Hess 1940). Archuleta, Boulder, Delta, Fremont, Garfield, Grand, Gunnison, La Plata, Larimer, Las Animas.

Corduliidae

Epitheca cynosura **(Say).** El Paso (Hess 1940). Baca, Bent.

Epitheca petechialis **(Muttkowski).** Lincoln (Bick and Hornuff 1974). Baca.

Somatochlora ensigera **Martin.** Jefferson (Williamson 1907), El Paso (Hess 1940).

Somatochlora hudsonica **(Selys).** Boulder, Teller, and "El Dora Lakes" (Walker 1925). Boulder.

****Somatochlora minor*** **Calvert.** Larimer.

Somatochlora semicircularis **(Selys).** Lake (Hagen 1874), Boulder, "Sulphide Flats," and "Arcad River" (Walker 1925), Gunnison (Bird and Rulon 1933), Mesa (G. H. Bick 1987, personal communication). Boulder, Routt, Summit.

Cordulia shurtleffi **Scudder.** (Needham and Westfall 1955). Boulder.

Libellulidae

****Perithemis tenera*** **(Say).** Baca.

Celithemis eponina **(Drury).** El Paso (Hess 1940). Yuma.

Libellula comanche **Calvert.** (Montgomery 1968).

Libellula forensis **Hagen.** Boulder (Cockerell 1927), El Paso and Pueblo (Hess 1940), Moffat (G. H. Bick 1987, personal communication). Archuleta, Boulder, Denver (UMMZ), Larimer, Mesa, Weld (USNM).

Libellula luctuosa **Burmeister.** El Paso and Pueblo (Hess 1940), Prowers (Kormondy 1960), Morgan and Washington (G. H. Bick 1987, personal communication). Baca, Bent, Boulder, Jefferson (UMMZ), Kiowa, Larimer, Las Animas, Prowers, Sedgwick, Weld, Yuma.

Libellula lydia **Drury.** Denver (Williamson 1906), Boulder (Cockerell 1927), El Paso (Hess 1940). Arapahoe, Archuleta, Bent, Boulder, Denver (UMMZ), Larimer, Lincoln, Weld, Yuma.

Libellula nodisticta **Hagen.** (Hagen 1874). Saguache.

Libellula pulchella **Drury.** Jefferson (Williamson 1913), Park (Cockerell 1927), El Paso and Pueblo (Hess 1940), Rio Blanco (G. H. Bick 1987, personal communication). Arapahoe, Archuleta, Baca, Bent, Boulder, Cheyenne, Denver (UMMZ), Grand, Kiowa, Larimer, Las Animas, Mesa, Moffat, Montezuma, Morgan, Saguache, Weld, Yuma.

Libellula quadrimaculata **Linnaeus.** El Paso (Hess 1940), Mesa and Rio Blanco (G. H. Bick 1987, personal communication). Archuleta, Boulder, Delta, Dolores, Fremont (USNM), La Plata, Larimer, Mesa, Montezuma, Park, Rio Blanco, Routt, Saguache, Weld, Yuma.

Libellula saturata **(Uhler).** Larimer (Calvert 1905), Pueblo (Cockerell 1927), El Paso (Hess 1940), Mesa (G. H. Bick 1987, personal communication). Baca, Bent, Las Animas.

Libellula subornata **(Hagen).** Denver and Larimer (Calvert 1905), Archuleta (Williamson 1906), El Paso and Pueblo (Hess 1940). Archuleta (UMMZ), Bent, Denver (UMMZ), Weld, Yuma.

Leucorrhinia borealis **Hagen.** Mesa (Bick and Hornuff 1974). Larimer.

****Leucorrhinia hudsonica*** **(Selys).** Boulder, Eagle, Grand, Larimer, Mesa.

Leucorrhinia intacta **Hagen.** El Paso (Hess 1940). Moffat (G. H. Bick 1987, personal communication). Archuleta, Boulder, Denver (UMMZ), Dolores, La Plata, Larimer, Morgan, Yuma.

Leucorrhinia proxima **Calvert.** Boulder (Calvert 1923). Moffat (G. H. Bick 1987, personal communication). Boulder, La Plata, Larimer.

Sympetrum atripes **(Hagen).** (Needham and Westfall 1955). Larimer.

Sympetrum corruptum **(Hagen).** El Paso and Denver (Tucker 1907), Jefferson (Williamson 1913), Arapahoe (Cockerell 1927), Pueblo (Hess 1940), Larimer and Prowers (Tai 1967), Garfield, Morgan, Rio Blanco, and Weld (G. H. Bick 1987, personal communication). Alamosa, Arapahoe, Archuleta, Baca, Bent, Boulder, Cheyenne, Crowley, Denver (UMMZ), Huerfano, La Plata (UMMZ), Larimer, Las Animas, Mesa, Moffat, Park (UMMZ), Prowers, Weld, Yuma.

Sympetrum costiferum **(Hagen).** Larimer (Tai 1967). Arapahoe, Larimer (USNM).

Sympetrum danae **(Sulzer).** Boulder (Cockerell 1927), El Paso (Hess 1940), Larimer (Tai 1967). Alamosa, Boulder, Chaffee (USNM, UMMZ), Denver (UMMZ), Grand, Gunnison (USNM), La Plata, Larimer, Park (UMMZ), Rio Blanco, Rio Grande (UMMZ), Routt, Saguache, San Juan (UMMZ).

Sympetrum internum **Montgomery.** Boulder, Costilla, Grand, Jefferson, Lake, Larimer, Rio Grande, and "Catal Spring" (Tai 1967). Alamosa, Arapahoe, Archuleta, Boulder, Chaffee (UMMZ), Eagle, Grand, Gunnison, Jackson, Jefferson (UMMZ), La Plata, Larimer, Moffat, Montezuma, Morgan, Ouray, Rio Blanco, Rio Grande (UMMZ), Routt, Saguache, Weld.

Sympetrum madidum **Hagen.** (Muttkowski 1910). Gunnison (FSCA).

Sympetrum obtrusum **(Hagen).** Larimer and Weld (Tai 1967), Moffat and Washington (G. H. Bick 1987, personal communication). Archuleta, Boulder, Gunnison,

Huerfano, Jefferson, Larimer, Mesa, Montrose, Sedgwick, Weld, Yuma.

Sympetrum occidentale **Bartenev.** Arapahoe, Denver, Huerfano, Jefferson, Mesa, Prowers, and Rio Grande (Walker 1951); Boulder, Larimer, Montezuma, and Weld (Tai 1967); Baca (G. H. Bick 1987, personal communication). Arapahoe, Bent, Boulder, Delta, Denver (MCZ, UMMZ), El Paso (MCZ), Fremont (USNM), Huerfano (UMMZ), Jefferson (UMMZ), Kiowa, La Plata, Larimer, Las Animas, Lincoln, Mesa, Montezuma, Montrose, Prowers (USNM), Pueblo, Weld, Yuma.

Sympetrum pallipes **(Hagen).** El Paso and Pueblo (Hess 1940), Jefferson, Larimer, and Platte Canyon (Tai 1967), Mesa (G. H. Bick 1987, personal communication). Archuleta, Boulder, Denver (UMMZ), Fremont (USNM), Huerfano, Jefferson (UMMZ), La Plata, Larimer, Las Animas, Weld.

Sympetrum rubicundulum **(Say).** El Paso (Hess 1940). Alamosa (USNM), Arapahoe, Boulder, Huerfano, Larimer, Weld, Yuma.

*****Sympetrum semicinctum*** **(Say).** El Paso (Tucker 1907), Jefferson (Williamson 1913), Pueblo (Hess 1940). These records are almost certainly in error. This is a northeastern species whose presence west of Minnesota has not been verified (Walker 1951, Tai 1967). Colorado records probably refer to *Sympetrum occidentale fasciatum* Walker (G. H. Bick 1987, personal communication).

Sympetrum vicinum **(Hagen).** Gunnison (Bird and Rulon 1933). Larimer.

Erythemis collocata **(Hagen).** Bent and Mesa (Bick and Hornuff 1974). Baca, Kiowa, Las Animas, Yuma.

Erythemis simplicicollis **(Say).** El Paso and Pueblo (Hess 1940). Baca, Larimer, Mesa, Yuma.

Pachydiplax longipennis **(Burmeister).** Pueblo (Hess 1940), Morgan (G. H. Bick 1987, personal communication). Baca, Prowers, Yuma.

Tramea lacerata **Hagen.** Pueblo (Hess 1940), Mesa, Morgan, and Washington (G. H. Bick 1987, personal communication). Baca, Boulder.

Tramea onusta **Hagen.** Denver (Cockerell 1927), El Paso (Hess 1940), Prowers (Kormondy 1960). Baca, Bent, Crowley, Prowers.

Pantala flavescens **(Fabricius).** Morgan (Bick and Hornuff 1974). Bent, Larimer, Las Animas, Weld.

Pantala hymenea **(Say).** Bent (Bick and Hornuff 1974). Weld.

ZYGOPTERA

Calopterygidae

Calopteryx aequabilis **Say.** Boulder (Cockerell 1913), Larimer (Kennedy 1918b).

****Calopteryx maculata*** **(Beauvois).** Yuma.

Hetaerina americana **(Fabricius).** Jefferson (Williamson 1913), Pueblo (Cockerell 1927), Bent (G. H. Bick 1987, personal communication). Arapahoe, Baca, Boulder, Denver (UMMZ), Huerfano, Kit Carson, Larimer, Las Animas, Logan, Mesa, Moffat (USNM), Rio Blanco, Yuma.

Lestidae

****Archilestes grandis*** **(Rambur).** Boulder, Fremont (USNM). Larimer, Mesa.

Lestes congener **Hagen.** (Hagen 1874). Alamosa, Arapahoe, Archuleta, Boulder, Denver (UMMZ), Jackson, Larimer, Mesa, Rio Grande (UMMZ), Weld.

Lestes disjunctus **Selys.** Gunnison (Bird and Rulon 1933), Boulder (Walker 1952), Rio Blanco and Routt (G. H. Bick 1987, personal communication). Arapahoe, Archuleta, Baca, Boulder, Conejos, Eagle, Huerfano, Jackson, La Plata, Larimer, Las Animas, Mesa, Moffat, Montezuma, Park (USNM), Prowers, Teller, Weld, Yuma.

Lestes dryas **Kirby.** Gunnison (Bird and Rulon 1933), Mesa and Rio Blanco (G. H. Bick 1987, personal communication). Alamosa, Archuleta, Boulder, Gunnison, Jackson, La Plata, Lake, Larimer, Las Animas, Moffat, Montezuma, Montrose, Morgan, Routt, Saguache, Weld.

Lestes forcipatus **Rambur.** (Hagen 1874). Weld.

****Lestes rectangularis*** **Say.** Baca, Lincoln, Yuma.

Lestes unguiculatus **Hagen.** Routt, Wash-ington and Weld (Bick and Hornuff 1974). Alamosa, Boulder, Routt, Sedgwick, Yuma.

Coenagrionidae

*****Argia agrioides*** **Calvert.** Tucker (1907) recorded this species from El Paso County, but Gloyd (1958) states that it is limited to Baja California.

Argia alberta **Kennedy.** El Paso (Kennedy 1918a), Bent (G. H. Bick 1987, personal communication). Bent (UMMZ), Prowers (UMMZ).

****Argia apicalis*** **(Say).** Baca, Bent, Lincoln, Yuma.

****Argia emma*** **Kennedy.** Boulder, Douglas, Huerfano (FSCA, UMMZ), Moffat (FSCA, UMMZ), Sedgwick, Yuma.

Argia lugens **(Hagen).** Baca (Bick 1978). Huerfano (UMMZ, USNM).

Argia moesta **(Hagen).** (Walker 1953). Baca, Bent, Las Animas, Lincoln, Mesa, Prowers, Routt (USNM).

Argia nahuana **Calvert.** Baca and Bent (Bick 1978). Prowers (UMMZ).

Argia plana **Calvert.** Baca (Bick and Hornuff 1974).

****Argia sedula*** **(Hagen).** Boulder, Moffat, Weld.

Argia violacea **(Hagen).** Baca (Bick and Hornuff 1974). Huerfano (UMMZ), Weld.

Argia vivida **Hagen.** Archuleta (Calvert 1902), Jefferson (Williamson 1913). Arapahoe, Archuleta, Baca, Bent, Boulder, Delta, Dolores, La Plata, Larimer, Las Animas, Lincoln, Mesa, Moffat, Montezuma, Montrose, Routt, Weld, Yuma.

Amphiagrion abbreviatum **(Selys).** El Paso (Tucker 1907); Jefferson (Williamson 1913 as *A. saucium*); Bent, Mesa, and Rio Blanco (G. H. Bick 1987, personal communication). Alamosa, Arapahoe, Archuleta, Boulder, Costilla, Delta, Denver, Dolores, Douglas, Fremont (USNM), Garfield, Grand, Gunnison, Huerfano, Kiowa, La Plata, Larimer, Las Animas, Lincoln, Mesa, Moffat, Montezuma, Montrose, Pueblo, Rio Blanco, Routt, Saguache, Weld, Yuma.

*****Amphiagrion saucium*** **(Burmeister).** El Paso (Tucker 1907), Jefferson (Williamson 1913). The range of this species is distinctly eastern, extending no further west than Minnesota and Wisconsin, whereas *A. abbreviatum* is distinctly western (Walker 1953); disregarding the possibility of an undescribed species for central U.S., it seems best for the present to refer all Colorado records of *A. saucium* to *A. abbreviatum* (G. H. Bick 1987, personal communication).

Coenagrion resolutum **(Hagen).** Gunnison (Bird and Rulon 1933), Garfield and Mesa (G. H. Bick 1987, personal communication). Boulder, Delta, Dolores, Jackson,

La Plata, Larimer, Mesa (USNM), Montezuma, Routt.

Enallagma anna **Williamson.** (Garrison 1984), Costilla (Garrison 1985, personal communication). Boulder.

Enallagma antennatum **(Say).** Bent and Larimer (Bick and Hornuff 1974). Larimer (USNM).

Enallagma basidens **Calvert.** Larimer (Bick and Hornuff 1974). Boulder.

Enallagma boreale **Selys.** Jefferson (Williamson 1913), Gunnison (Bird and Rulon 1933), Garfield, Mesa and Rio Blanco (G. H. Bick 1987, personal communication). Boulder, Gilpin, Grand, Jackson, Jefferson (UMMZ), Larimer, Moffat, Montezuma, Montrose, Routt, Teller, Weld.

Enallagma carunculatum **Morse.** Jefferson (Williamson 1913), Gunnison, Larimer, Mesa, Moffat, and Weld (Garrison 1984), Garfield (G. H. Bick 1987, personal communication). Alamosa, Archuleta, Baca, Boulder, Chaffee, Cheyenne, Costilla, Delta, Denver (UMMZ), Dolores, Eagle, Grand, Huerfano (UMMZ), Larimer, Montrose, Weld.

Enallagma civile **(Hagen).** El Paso (Calvert 1902), Jefferson (Williamson 1913), Huerfano, Larimer, Logan, Mesa, Morgan, Prowers, and Weld (Garrison 1984), Washington (G. H. Bick 1987, personal communication). Alamosa, Arapahoe, Baca, Bent, Boulder, Cheyenne, Crowley, Delta, Huerfano, La Plata, Larimer, Las Animas, Morgan, Prowers, Pueblo, Sedgwick, Weld.

Enallagma clausum **Morse.** El Paso (Tucker 1907), Jefferson (Williamson 1913), Gunnison (Bird and Rulon 1933). Alamosa, Boulder, Costilla, Eagle, Larimer, Yuma.

Enallagma cyathigerum **(Charpentier).** Garfield, Moffat, Rio Blanco and Routt (Bick 1978), Lake (Garrison 1984). Alamosa, Archuleta, Boulder, Chaffee, Conejos, Costilla, Crowley, Delta, Eagle, Gilpin, Grand, Gunnison, Huerfano, Jackson, La Plata, Lake (USNM), Larimer, Mineral, Moffat, Montezuma, Montrose, Park, Pueblo, Routt, Saguache, Weld.

Enallagma hageni **(Walsh).** Washington (Bick and Hornuff 1974).

Enallagma praevarum **(Hagen).** El Paso (Tucker 1907), Weld (Kumar et al. 1976), Baca and Larimer (Bick 1978). Baca, Boulder, Huerfano (UMMZ), Larimer, Las Animas, Prowers (UMMZ).

****Enallagma vesperum*** **Calvert.** Yuma.

Ischnura barberi **Currie.** (Muttkowski 1910).

Ischnura cervula **Selys.** Moffat, Rio Blanco, and Routt (Bick and Hornuff 1974). Arapahoe, Archuleta, Baca, Boulder, Conejos, Dolores, Eagle, Larimer, Mesa, Pueblo, Weld.

Ischnura damula **Calvert.** Denver (Calvert 1902), Jefferson (Williamson 1913), Mesa and Washington (G. H. Bick 1987, personal communication). Alamosa, Arapahoe, Baca, Bent, Boulder, Costilla, Crowley, Huerfano, La Plata, Larimer, Las Animas, Morgan, Prowers, Saguache, Weld, Yuma.

Ischnura demorsa **(Hagen).** Denver (Calvert 1903). Larimer (USNM), Prowers (UMMZ).

Ischnura perparva **Selys.** El Paso (Tucker 1907), Bent, Moffat, and Rio Blanco (G. H. Bick 1987, personal communication). Alamosa, Archuleta, Boulder, Delta, Dolores, Eagle, El Paso (UMMZ), Garfield, Huerfano, La Plata, Larimer, Las Animas, Lincoln, Mesa, Moffat, Montezuma, Montrose, Morgan, Pueblo, Routt, Saguache, Weld, Yuma.

Ischnura verticalis **(Say).** Morgan and Washington (Bick and Hornuff 1974). Larimer, Yuma.

****Hesperagrion heterodoxum*** **(Selys).** Boulder, Larimer.

****Anomalagrion hastatum*** **(Say).** La Plata.

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LITERATURE CITED

BICK, G. H. 1978. New state records of United States Odonata. Notul. Odonatol. 1(2): 17–19.

BICK, G. H., AND L. E. HORNUFF. 1974. New records of Odonata from Montana and Colorado. Proc. Entomol. Soc. Washington 76: 90–93.

BIRD, R. D., AND G. O. RULON. 1933. Dragonflies from high altitudes in Colorado (Odonata). Entomol. News 44: 44–45.

BYERS, C. F. 1939. A study of the dragonflies of the genus *Progomphus* (*Gomphoides*) with a description of a new species. Proc. Florida Acad. Sci. 4: 19–85.

CALVERT, P. P. 1901–1908. Biologia Centrali-Americana: Neuroptera, Odonata 50: 17–420. Porter and Dulau, London.

———. 1923. *Leucorrhinia proxima* at a high altitude in Colorado. Entomol. News 34: 88.

COCKERELL, T. D. A. 1913. The dragon-fly *Agrion* (*Calopteryx*) in Colorado. Psyche 20: 173–175.

———. 1927. Zoology of Colorado. University of Colorado, Boulder. 262 pp.

GARRISON, R. W. 1984. Revision of the genus *Enallagma* of the United States west of the Rocky Mountains and identification of certain larvae by discriminant analysis (Odonata: Coenagrionidae). Univ. California Publ. Entomol. 105: 1–129.

GLOYD, L. K. 1958. The dragonfly fauna of the Big Bend Region of Trans-Pecos Texas. Occ. Pap. Mus. Zool. Univ. Michigan 593: 1–23.

HAGEN, H. A. 1874. Odonata. Pages 583–598 *in* Annual report, U.S. geol. and geographical survey of the territories embracing Colorado. Government Printing Office, Washington, D.C.

_____. 1875. Report on the collections of Neuroptera and pseudo-neuroptera made in portions of Colorado, New Mexico and Arizona, during the years 1872, 1873 and 1874. Pages 911–922 *in* Rept. Geog. Expl. Surv. West 100th Merid. Engineer Dept. U.S. Army.

HESS, A. D. 1940. The altitudinal range of dragonflies in the Pikes Peak region (Odonata). Entomol. News 51: 31–32.

HUGGINS, D. G. 1978. Additional records of Kansas Odonata. Tech. Publs. Biol. Survey Kansas 6: 1–35.

KENNEDY, C. H. 1918a. New species of Odonata from the southwestern U.S. Canadian Entomol. 50: 256–261.

_____. 1918b. The varieties of the dragonfly, *Agrion aequabile* (Say). Canadian Entomol. 50: 406–410.

KORMONDY, E. J. 1960. New North American records of Anisopterous Odonata. Entomol. News 71: 121–130.

KUMAR, R., R. J. LAVIGNE, J. E. LLOYD, AND R. E. PFADT. 1976. Insects of the central plains experimental range, Pawnee National Grasslands. Agric. Expt. Sta., Univ. Wyoming, Science Monograph 32: 1–74.

MONTGOMERY, B. E. 1968. The distribution of western Odonata. Proc. North Carolina Branch, Entomol. Soc. Amer. 23: 126–136.

MUTTKOWSKI, R. A. 1910. Catalogue of the Odonata of North America. Bull. Public Mus. Milw. 1: 1–207.

NEEDHAM, J. G., AND M. J. WESTFALL, JR. 1955. A manual of the dragonflies of North America (Anisoptera). University of California Press, Berkeley and Los Angeles. 615 pp.

TAI, L. 1967. Biosystematic study of *Sympetrum* (Odonata: Libellulidae). Unpublished dissertation, Purdue University, Lafayette, Indiana (Univ. Microfilms, Ann Arbor, 67–10, 260).

TUCKER, E. S. 1907. Odonata. Pages 78–79 *in* Some results of desultory collections of insects of Colorado and Kansas. Univ. Kansas Sci. Bull. 4: 51–112.

WALKER, E. M. 1912. The North American dragonflies of the genus *Aeshna*. Univ. Toronto Studies, Biol. Series. 213 pp.

_____. 1925. The North American dragonflies of the genus *Somatochlora*. Univ. Toronto Studies, Biol. Series. 202 pp.

_____. 1951. *Sympetrum semicinctum* (Say) and its nearest allies (Odonata). Entomol. News 62: 153–163.

_____. 1952. The *Lestes disjunctus* and *forcipatus* complex (Odonata: Lestidae). Trans. Amer. Entomol. Soc. 78: 59–74.

_____. 1953. The Odonata of Canada and Alaska. Vol. 1. Zygoptera. University of Toronto Press. 292 pp.

WILLIAMSON, E. B. 1906. *Plathemis subornata* (Odonata). Entomol. News 17: 351.

_____. 1907. Two new North American dragonflies (Odonata). Entomol. News 18: 1–7.

_____. 1913. Some Colorado dragonfly records (Odonata). Entomol. News 24: 372.

A CHECKLIST OF THE VASCULAR PLANTS OF THE HOUSE RANGE, UTAH

Ronald J. Kass[1]

ABSTRACT.—A checklist of the vascular plants of the House Range, Juab and Millard counties, Utah, is presented. A flora of 373 species and infraspecific taxa in 231 genera and 60 families are reported. The geology, physiography, climate, and plant communities are briefly discussed. Several endemics occur in the study area and a new taxon has been described.

Plant checklists are useful to natural resource managers, amateur and professional botanists, and plant ecologists. In the absence of completed floristic treatments, localized checklists are often the main source of information available on a local flora. They reduce the number of possible choices when comparing numerous choices available from regional floras (Goodrich 1984). Local checklists are also a source of information for ecological studies ranging from pollination ecology to phytogeography.

The primary objective of this study was to provide a checklist of the vascular plants found in the House Range, Utah. This information has been included in the Utah Flora by Welsh et al. (1987). The secondary objective was to provide specimens for future taxonomic and phytogeographic works.

Approximately 600 collections were made and deposited as voucher specimens in the Brigham Young University Herbarium (BRY), the New York Botanical Garden (NY), and the Garrett Herbarium, University of Utah (UT).

METHODS AND MATERIALS

A statewide herbaria search was conducted prior to the 1981 field season. Collecting stations were established throughout the study area and visited several times during the field seasons (April-September) of 1981 and 1982. Additional areas were also searched that were topographically, geologically, or floristically interesting. Frequency of collected species is based on the following scale from Thorne (1967): rare, 1–2 stations; infrequent, 3–5 stations; frequent, 6–8 stations; and common, more than 8 stations.

A collection number is cited for each species. Taxa with no collection number were observed and not collected. All collections are by the author unless otherwise indicated.

STUDY AREA

The House Range, situated in western Millard and Juab counties, Utah, is located between 39° 37′ and 38° 50′ N latitude and 113° 25′ and 113° 16′ W longitude. The House Range is bounded on the west by Tule Valley, on the east by Whirlwind Valley and Sevier Dry Lake, on the north by Sand Pass and the Fish Springs Range, and on the south by U.S. Highway 6–50 at Skull Rock Pass. An additional area called the Black Hills was included in the study area (Fig. 1).

The House Range is 90 km (56 mi) long and averages 10 km (6 mi) wide; it occupies an area of 900 square km (336 square mi). The elevation ranges from 1,312 m (4,305 ft) on the valley floor to 2,948 m (9,669 ft) at the summit of Swasey Peak, the highest point in the range.

The House Range is a narrow, steep, fault-block range. Drainages plunge steeply on the western flanks, while gentle relief is characteristic on the eastern flanks. The west face of the range is an eroded fault scarp visible as one views Notch Peak while driving east on U.S. Highway 6–50.

The House Range is composed mostly of Cambrian and Ordovician limestone. The Wheeler Shale and Marjum Formations in the area yield the most continuous Cambrian fossil succession in Utah (Hintze 1973). Igneous activity during the Tertiary caused doming and fracturing of the strata, thus producing a

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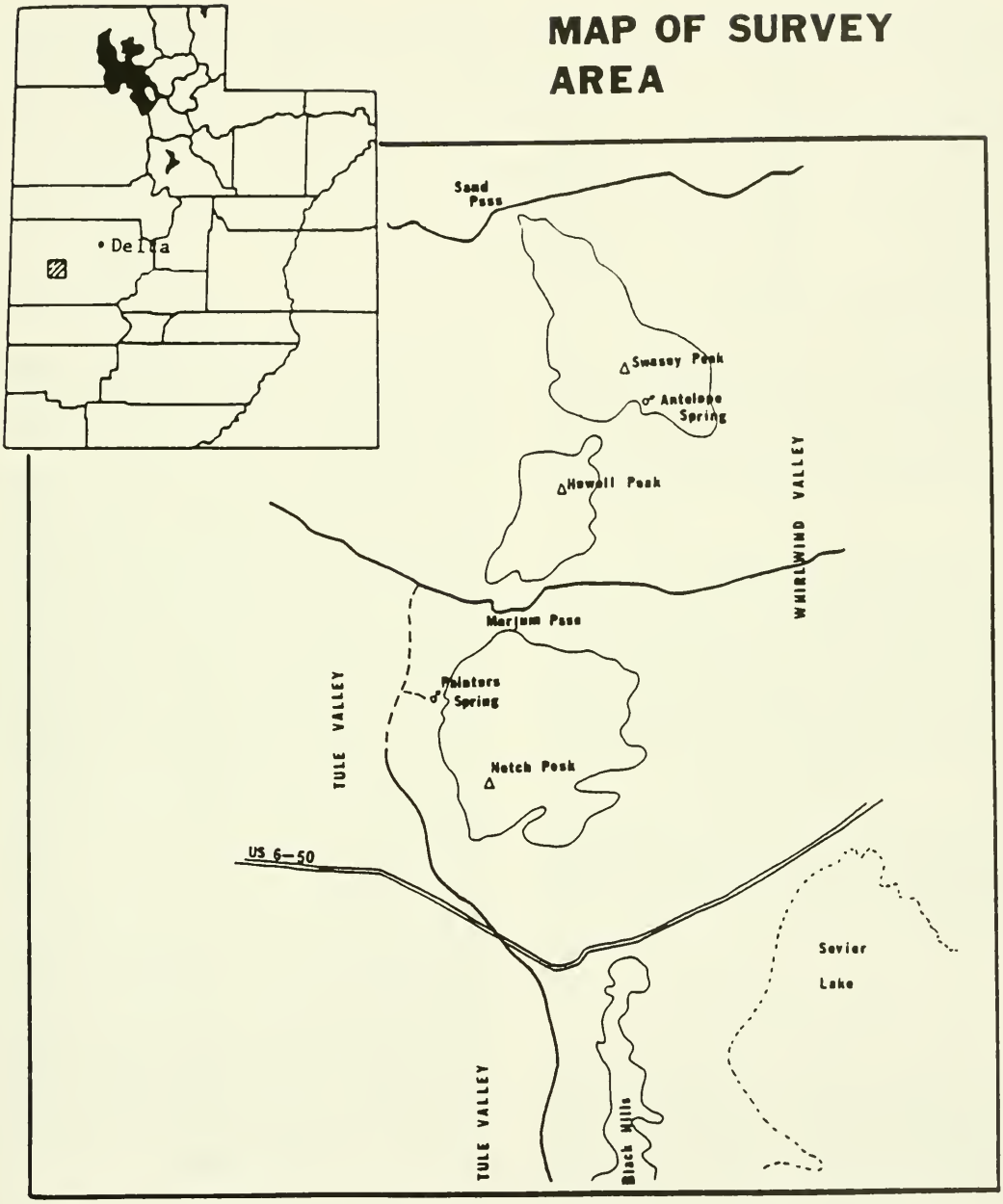

Fig. 1. Map of the survey area, with study areas indicated.

series of steep, shaded canyons that are visible at Painter Spring (Fig. 1). Quaternary sediments, deposited as alluvial fans and valley fill, have been reworked and covered during the existence of Lake Bonneville (Hanks 1962).

The climate is typical of the Great Basin with cold, moist winters and warm, dry summers. The city of Delta, located 80 km (50 mi) to the east of the House Range, has average January temperatures of −4.4 C (24 F) and average July air temperatures of 22 C (72 F). During winter, when high atmospheric pressure exists, low-level temperature inversions develop, causing the lower valleys to become colder than slopes at higher elevations.

TABLE 1. Precipitation data from the Desert Experiment Station[a].

Station	Elev. (m)	Habitat type	Years	Average/year
DER Hq.	1604	winterfat-shadscale	10	15.2 cm
Pine Plot	1616	winterfat-grass	10	15.4 cm
Advance	1787	big sagebrush	6	21.9 cm
Budsage	1891	winterfat-budsage	10	17.3 cm
James	1937	blacksage-grass	8	18.0 cm
Pine Grove	1891	lower juniper	9	26.1 cm
Upper Shady	1952	blacksage	8	23.0 cm
Wagon	1967	lower juniper	9	25.3 cm
Cottonwood	2135	pinyon-juniper	10	35.6 cm
Needletop	2745	upper sagebrush	10	44.4 cm

[a]Courtesy of Ralph Holmgren, USFS Shrub Lab.

Houghton et al. (1975) report valley bottom temperatures in Nevada as much as 16.6 C (30 F) colder than higher-elevation slopes. Summers are characterized by warm days and cool nights. July is the hottest month, with air temperatures on most days exceeding 32 C (90 F).

Precipitation data recorded at two weather stations (Delta and Deseret) show 10-year annual averages (1970–1980) of 16.8 cm (6.6 in) at Delta and 15.9 cm (6.3 in) at Deseret (U.S. Dept. of Commerce 1980). Table 1 compares annual average precipitation with habitat type at the Desert Experiment Station (DER) located 18 km (29 mi) southwest of the House Range. Convectional rain storms occur during the summer months and are often preceded by strong winds. These storms are often unpredictable, and rainfall amounts are highly variable both spatially and temporally (Holmgren 1983).

PLANT COMMUNITIES

Desert Shrub

This community is dominated by low, widely spaced shrubs principally of the Chenopodiaceae and Asteraceae. Its elevation ranges between 1,320 m (4,330 ft) and 1,690 m (5,545 ft). Plant cover is estimated at 5–15%, and annual precipitation is approximately 15.2 cm (6 in) (Holmgren 1983).

Shadscale (*Atriplex confertifolia*) is the dominant shrub in this community. It covers vast areas on the valley floors and occupies the upper benches created by Pleistocene Lake Bonneville. Stutz (1983) states that differences in ploidy level may be responsible for this observed distribution pattern of shadscale in the Great Basin. Principal shrubby species in this community include budsage (*Artemisia spinescens*), Mormon tea (*Ephedra nevadensis*), green holly (*Kochia americana*), spiny hopsage (*Grayia spinosa*), and winterfat (*Ceratoides lanata*).

Major changes in plant composition are apparently associated with edaphic factors. Winterfat often occurs in pure stands on silty loam and sandy soils. On overgrazed areas, winterfat is often replaced by rabbitbrush (*Chrysothamnus greenei*) and horsebrush (*Tetradymia glabrata*). Principal grass species include galleta (*Hilaria jamesii*), Indian ricegrass (*Oryzopsis hymenoides*), sandberg bluegrass (*Poa secunda*), needle and thread (*Stipa comata*), and squirreltail (*Sitanion hystrix*).

Playas often develop in basins where evaporation exceeds inflow. Commonly, a system of plant species develop with more deeply rooted and less-salt-tolerant species developing in the outer margins and species with greater salt tolerance and shallower roots developing nearer the playa (Holmgren 1983). Species such as seepweed (*Suaeda torreyana*) and saltbush (*Atriplex gardneri* var. *tridentata*) are found on the outer margins and pickleweed (*Allenrolfea occidentalis*) is found near the playa. Greasewood (*Sarcobatus vermiculatus*) is widespread in the valley bottoms and around playa margins.

Sagebrush

Sagebrush is widely distributed both vertically and horizontally throughout the House Range. Its elevation ranges from 1,690 m (5,545 ft) to nearly 2,940 m (9,646 ft). Annual precipitation is estimated at 17.8 cm (7 in) in the lower elevations and 46.0 cm (18 in) in the higher elevations (Holmgren, personal communication 1983).

Five specialized taxa of sagebrush were recognized in the study area. Black sage

(*Artemisia nova*) is characteristic of the upland desert shrub community. It is codominant with shadscale and occurs in pure stands within and above the pinyon-juniper community. Low sagebrush (*Artemisia arbuscula*) occurs on shallow, rocky, alkaline soils. It is found on limestone gravels and cobbles, often growing in pure stands and forming associations with xeric grasses and forbs on windswept ridges in and above the pinyon-juniper community.

Basin big sagebrush (*Artemisia tridentata* ssp. *tridentata*) occurs on dry, deep alluvial soils in valleys and washes at middle elevations. Its elevational limits are approximately 2,135 m (7,000 ft). Above this elevation, mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) occurs in well-drained soils where concave topography exists. Species richness is greater here than in other sagebrush communities. Species commonly associated with mountain big sagebrush include serviceberry (*Amelanchier utahensis*), lupine (*Lupinus caudatus*), snowberry (*Symphoricarpos oreophilus*), arrowleaf balsamroot (*Balsamorrhiza sagittata*), curlleaf mountain mahogany (*Cercocarpus ledifolius*), slender wheatgrass (*Agropyron trachycaulum*), and letterman needlegrass (*Stipa lettermanii*). Vasey sagebrush is limited to small areas within and above the pinyon-juniper community.

Occasionally, Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) occurs in the higher valleys at elevations above 2,134 m (7,000 ft) but is usually found on gentle slopes of alluvial fans and valley bottoms. Soils characteristic of these communities are often associated with a calcic layer 20–50 cm (8–20 in) below the surface.

Pinyon-Juniper

Single-leaf pinyon (*Pinus monophylla*) and juniper (*Juniperus osteosperma*) are codominant in the intermediate elevations ranging from 1,983 to 2,288 m (6,500–7,500 ft). The composition of this woodland changes altitudinally, with juniper dominating in the lower elevations 1,690 m (5,545 ft) and pinyon dominating at higher elevations 2,438 m (8,000 ft). Pinyon can often be found at 2,590 m (8,498 ft) on south exposures, and juniper is occasionally found below 1,690 m in drainages. West et al. (1978) report the wide variation in Basin-wide elevational limits of this community. This woodland develops in areas where annual precipitation is usually in excess of 30 cm (12 in) (Cronquist et al. 1972).

Stands of curlleaf mountain mahogany are common within this community where cobbles and boulders are at or near the soil surface. Needleleaf mountain mahogany (*Cercocarpus intricatus*) is also common within this community and often found on steeper slopes where soils are shallower. Herbaceous species commonly occurring in the community include dwarf lousewart (*Pedicularis centranthera*), low phlox (*Phlox austromontana*), ball gilia (*Gilia congesta*), rock goldenrod (*Petradoria pumila*), heartleaf twistflower (*Streptanthus cordatus*), bladderpod (*Physaria chambersii*), and penstemon (*Penstemon confusus*).

Two major riparian areas (Painter Spring and Swasey Spring) occur in this pinyon-juniper zone and are characterized by the following species: narrowleaf cottonwood (*Populus angustifolia*), sandbar willow (*Salix exigua*), Wood rose (*Rosa woodsii*), chokecherry (*Prunus virginiana* var. *melanocarpa*), and Great Basin wildrye (*Elymus cinereus*).

Mountain Brush

The mountain brush community is not well defined in the House Range. It generally borders the upper edge of the pinyon-juniper community and extends into portions of the subalpine community on steep, rocky exposures. It also follows canyons and drainages well down into the pinyon-juniper zone. Average annual precipitation is estimated at 38 cm (15 in) (Holmgren, personal communication 1983). Curlleaf mountain mahogany and needleleaf mountain mahogany are the dominant shrubs and often form pure stands on shallow, rocky soils. Black sagebrush, low sagebrush, Mormon tea, and pinyon are also common within this community.

Aspen (*Populus tremuloides*), white fir (*Abies concolor*), and Douglas-fir (*Pseudotsuga menziesii*) are limited in the House Range and are confined to moist depressions, canyons, and cool exposures on north- and east-facing slopes.

Rocky Mountain juniper (*Juniperus scopulorum*) is limited to shaded canyons and along higher-elevation drainages. Apparently, it is less drought tolerant than Utah juniper and is

less abundant (Cronquist et al. 1972).

Subalpine

Cronquist et al. (1972) describes this community as the limber-bristlecone pine zone. It is the open subalpine forest of the Basin ranges and is best developed between 2,865 m (9,400 ft) and 3,200 m (10,500 ft). Precipitation in this community is estimated at 46 cm (18 in) a year (Holmgren, personal communication 1983).

The highest point on the House Range is 2,947 m (9,669 ft); this elevation represents only the lower limits of subalpine habitat. As a consequence of this elevation and other limiting factors such as steep, rocky exposures, lack of persistent snowdrifts, and poor soil development, well-developed subalpine forest communities are not present in the House Range.

Mixed stands of needleleaf mountain mahogany, black sagebrush, low sagebrush, and Mormon tea occupy the steep, exposed slopes of Notch Peak. Occasionally, small, scattered clumps of bristlecone pine are found growing below the summit. Swasey Peak located 24 km (15 mi) north of Notch Peak, supports more well-developed bristlecone pine forests because of its gentle relief, better soil development, and a more northern exposure.

Limber pine (*Pinus flexilis*) is apparently absent from the House Range but occurs in the Deep Creek Mountains, located 48 km (30 mi) northwest of the range (McMillian 1948). Critchfield and Allenbaugh (1969) describe the sporadic distribution of the Pinaceae in the Great Basin. These observed patterns seem explainable in terms of random colonization and/or Pleistocene extinction (Harper et al. 1978).

Understory species commonly occurring in this community include buckbrush (*Ceanothus martinii*), fleabane (*Erigeron tener*), rock mat (*Petrophytum caespitosum*), goldenweed (*Haplopappus acaulis*), goldenweed (*Haplopappus cervinus*), *Sphaeromeria diversifolia*, buckwheat (*Eriogonum ovalifoium* var. *nivale*), and desert parsley (*Lomatium scabrum*).

PLANTS OF SPECIALIZED HABITATS

There are a variety of specialized habitats in the House Range resulting from certain climatological and geological processes. These processes modify the substrate and create a unique set of environmental conditions for plant growth and development. These specialized habitats are often occupied by species with distinctive life forms and life history characteristics.

Aeolian Sands

Sand is transported by the prevailing westerly winds and deposited as sand dunes in Whirlwind Valley and at Sand Pass (Fig. 1). Most species growing on the dunes are spring annuals, and their abundance and composition vary on a yearly basis. The following plants are restricted to or common to wind-deposited sands: *Abronia elliptica*, *Ambrosia acanthicarpa*, *Astragalus callithrix*, *Chrysothamnus nauseosus* ssp. *turbinatus*, *Crypthantha circumscissa*, *Cryptantha confertiflora*, *Cryptantha kelseyana*, *Cymopterus fendleri*, *Cymopterus newberryi*, *Eriogonum kearney*, *Eriogonum nummulare* var. *ammophilum*, *Gilia polycladon*, *Lupinus pusillus*, *Lygodesmia dianthopsis*, *Malacothrix sonchioides*, *Mentzelia albicaulis*, *Nama demissum*, *Oenothera pallida*, *Phacelia ivesiana*, *Polygala acanthoclada*, *Rhus trilobata*, *Sporobolus flexuosus*, and *Stipa comata*.

Rocky Substrates

Much of the middle and upper elevations of the House Range is composed of massive limestone and dolomite outcrops and steep cliff faces. These geomorphic structures provide habitat for several specialized plant species that include *Cystoperis fragilis*, *Cryptantha compacta*, *Echinocereus triglochidatus*, *Erigeron nauseosus*, *Haplopappus cervinus*, *Haplopappus nanus*, *Heuchera rubescens*, *Holodiscus dumosus*, *Leptodactylon caespitosa*, *Lewisia redivia*, *Perityle stansburyii*, *Petrophytum caespitosum*, *Primula domensis*, *Sedum lanceolatum*, and *Sphaeromeria diversifolia*.

RANGE EXTENSIONS

The following species reach their distributional limits in the House Range.

Allium parvum: previously known from Tooele County and northward into Idaho.

Astragalus platytropis: a Nevada species known in Utah from the Deep Creek Mountains and the Mountain Home Range.

Castilleja scabrida* ssp. *barneyana: a Nevada species reaching its easternmost distribution in the House Range.

Cymopterus fendleri: reaches its northern distribution on the sand dunes in the Black Hills.

Cymopterus newberryi: reaches its southern distribution on the sand dunes in the Black Hills.

Penstemon leonardii: a range extension of approximately 112 km (67 mi) east from the Canyon Mountains.

Penstemon patricus: previously known from the Deep Creek Mountains and Kern Mountains of White Pine County, Nevada.

NEW AND RARE TAXA

Primula domensis has been described as a new taxon from collections taken in the House Range (Kass and Welsh 1985). This dwarf primrose prefers cool, shady exposures and moist substrates particularly where long-standing snows persist.

Astragalus callithrix, an obscure and rare species in Utah, and *Eriogonum nummulare* var. *ammophilum* occur on sandy soils in Tule Valley.

Cryptantha compacta inhabits rock outcrops and ridges near Notch Peak.

Eriogonum spathulatum var. ***natum*** grows on ancient marly playa remnants on the Tule Valley floor.

THE FLORA

A total of 60 families, 231 genera, and 373 species and infraspecific taxa are reported for the House Range. The most abundant families are represented by Asteraceae 19%, Poaceae 13%, Brassicaceae 8%, Fabaceae 5%, Chenopodiaceae 4%, Scrophulariaceae 4%, Boraginaceae 3.5%, and Polygonaceae 3% of the taxa. Onagraceae, Polemoniaceae, and Rosaceae combined contain 8% of the taxa. The largest genera are represented by *Astragalus*, *Eriogonum*, *Artemisia*, and *Cryptantha*, containing 12, 10, 9, and 7 species and infraspecific taxa, respectively.

The House Range occupies 0.41% of Utah's 212,939 sq km (82,100 sq mi) of land area. It contains 12.4% (320) of the state's 2,575 native species. A total of 47 species are adventive, representing 12.6% of the House Range flora.

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LITERATURE CITED

CRITCHFIELD, W. B., AND G. L. ALLENBAUGH. 1969. The distribution of the Pinaceae in northern Nevada. Madroño 20: 12–26.

CRONQUIST, A., A. H. HOLMGREN, N. H. HOLMGREN, AND J. R. REVEAL. 1972. Intermountain flora. Vol. I. Hafner Publishing Co., Inc., New York, New York.

GOODRICH, S. 1984. Checklist of the vascular plants of the Canyon and Church mountains. Great Basin Nat. 44: 277–295.

HANKS, K. L. 1962. Geology of the central House Range area. Millard County, Utah. Brigham Young University Geology Studies 9: 115–137.

HARPER, K. T., D. C. FREEMAN, W. K. OSTLER, AND L. G. KLIGOFF. 1978. The Flora of the Great Basin mountain ranges: diversity, sources and dispersal ecology. Intermountain Biogeography: A Symposium. Great Basin Nat. Mem. 2: 81–103.

HINTZE, L. F. 1973. Geologic history of Utah. Brigham Young University Geology Studies 20: 1–181.

HOLMGREN, R. C. 1983a. The Great Basin cold desert: some physical geography. *In*: A. R. Tiedemann, E. B. McArthur, H. C. Stutz, R. Stevens, and K. L. Johnson, Proceedings—symposium on the biology of *Atriplex* and related chenopods. Provo, Utah. Gen. Tech. Rept. IN–172, Ogden, Utah, USFS, Intermountain Forest and Range Experiment Station. 309 pp.

_____. 1983b. Personal communication.

HOUGHTON, J. B., C. M. SAKAMATO, AND R. O. GIFFORD. 1975. Nevada's weather and climate. Special Publication 2. Mackay School of Mines, University of Nevada at Reno. 150 pp.

KASS, R. J., AND S. L. WELSH. 1985. New species of *Primula* (Primulaceae) from Utah. Great Basin Nat. 45: 48–50.

MCMILLIAN, C. 1948. A taxonomic and ecological study of the flora of the Deep Creek Mountains of central western Utah. Unpublished thesis, University of Utah, Salt Lake City.

STUTZ, H. C. 1983. A tour of chenopods in western Utah. *In:* A. R. Tiedemann, E. D. McArthur, H. C. Stutz, R. Stevens, and K. L. Johnson, Proceedings—symposium on the biology of *Atriplex* and related chenopods. Provo, Utah. Gen. Tech. Rept. IN–172. Ogden, Utah, USFS, Intermountain Forest and Range Experiment Station. 309 pp.

THORNE, R. F. 1967. A flora of Santa Catalina Islands, California. Aliso 6: 1–77.

U.S. DEPARTMENT OF COMMERCE. 1980. Climatological data, annual summary of Utah. National Oceanic and Atmospheric Administration, Asheville, North Carolina.

WELSH, S. L., N. B. ATWOOD, L. C. HIGGINS, AND S. GOODRICH. 1987. A Utah flora. Great Basin Nat. Mem. 9: 1–894.

WEST, N. W., F. J. TAUSCH, K. M. REA, AND P. T. TUELLER. 1978. Phytogeographical variation within the pinyon-juniper woodland of the Great Basin. Great Basin Nat. Mem. 2: 119–136.

THE CHECKLIST

The checklist is arranged alphabetically by family, genus, and species without regard for phylogenetic order. Nomenclature generally follows that of Welsh et al. (1987).

Aceraceae

Acer glabrum **Torr.** Tree in shaded canyons and along streams at medium elevations. Sawtooth Canyon, 483.

Anacardiaceae

Rhus trilobata **Nutt. in T. & G.** Frequent in shaded canyons and locally abundant in sandy areas in and below the pinyon-juniper zone. Marjum Canyon, 540.

Apiaceae

Berula erecta **(Huds.) Colville.** Collected only once submerged in water at Antelope Spring Reservoir, 1074.

Cicuta maculata **L. var. *angustifolia* Hook.** Rare but locally common in cattle ponds. Antelope Spring Reservoir, 560.

Cymopterus fendleri **Gray.** Reported by Sherel Goodrich in the Black Hills on sandy soil, desert shrub zone.

Cymopterus globosus **S. Wats.** Rare, desert shrub zone. 725.

Cymopterus newberryi **(S. Wats.) Jones.** Rare but locally common in sandy areas, desert shrub zone. Black Hills, 701.

Cymopterus purpurascens **(Gray) Jones.** Infrequent at medium elevations. Wildhorse Canyon, 176; Sawtooth Canyon, 886.

Lomatium grayii **Coult. & Rose.** Common on limestone cliffs from low to high elevations. Swasey Mountain, 173.

Lomatium kingii **(Wats.) Cronq. var. *alpina* S. Wats.** Rare, pinyon-juniper zone. Swasey Peak, 570.

Lomatium scabrum **(Coult. & Rose) Mathias.** Common on limestone slopes, pinyon-juniper zone. Antelope Spring, 186, 188; Swasey Spring, 257: Notch Peak, 292; Water Canyon, 497; Miller Canyon, 791.

Asclepiadaceae

Asclepias asperula **(Dene.) Woodson.** Rare in washes, desert shrub zone. Marjum Canyon, 546.

Asclepias speciosa **Torr.** Infrequent in washes, desert shrub zone. Whirlwind Valley, 525.

Asteraceae

Achillea millefolium **L.** Infrequent in canyons and grassy slopes in and above the pinyon-juniper zone. Sawtooth Canyon, 559.

Agoseris glauca **(Pursh) Raf. var. *lanciniata*.** Infrequent in the pinyon-juniper zone and vasey sagebrush zone. Water Canyon, 364; Swasey Peak, 571.

Ambrosia acanthicarpa **Hook.** Common in sandy areas and on disturbed sites, desert shrub zone. Skull Rock Pass, 629.

Antennaria microphylla **Rydb.** Infrequent at medium elevations. Water Canyon, 362; Notch Peak, 476.

Arctium minus **(Hill) Bernh.** Infrequent on moist, disturbed sites, desert shrub zone. Painter Spring, 547.

Artemisia arbuscula **Nutt.** Dominant on rocky, shallow and sometimes alkaline soils from medium to high elevations. Sand Pass, 1062.

Artemisia biennis **Willd.** Rare but locally common at Sinbad and Antelope Spring, 591.

Artemisia dracunculus **L.** Rare but locally common in gravelly soil, pinyon-juniper zone. Miller Canyon, 1075.

Artemisia ludoviciana **Nutt. var. *ludoviciana*.** Frequent, pinyon-juniper zone. Swasey Spring, 511; Painter Spring, 1021.

Artemisia nova **A. Nels.** Dominant in the desert shrub zone and in and above the pinyon-juniper zone. Occasionally in the higher elevations. Swasey Peak, 1066, 1068, 1069.

Artemisia spinescens **D.C. Eaton.** Frequent in the desert shrub zone. Whirlwind Valley, 174.

Artemisia tridentata **Nutt. ssp. *vaseyana* (Rydb.) Beetle.** Infrequent but locally common on deep, well-drained soils at medium to high elevations. Swasey Peak, 1067.

Artemisia tridentata **Nutt. ssp. *wyomingensis* Beetle & Young.** Frequent on alluvial soils in and below the pinyon-juniper zone. Antelope Spring, 1071–1073.

Aster chilensis **Nees.** Infrequent along springs and disturbed sites at low to medium elevations. Painter Spring, 584.

Brickellia californica **(T. & G.) Gray.** Infrequent in shaded canyons in the pinyon-juniper zone. Painter Spring, 622.

Brickellia microphylla **(Nutt.) Gray var. *watsonii* (Robins) Welsh.** Frequent on gravelly soils and in washes in the desert shrub zone. Painter Spring, 623.

Brickellia oblongifolia **Nutt.** Infrequent on gravelly soils and in washes in the desert shrub zone. Sawtooth Canyon, 487; Skull Rock Pass, 878.

Centaurea repens **L.** Found only on gravelly roadside at Skull Rock Pass, 987.

Chaenactis douglasii **(Hook.) H. & A.** Frequent in the desert shrub zone. Swasey Bottom. 271.

Chaenactis macrantha **D.C. Eaton.** Common in the desert shrub zone. Black Hills, 303; Whirlwind Valley, 716.

Chaenactis stevioides **H. & A.** Infrequent in the desert shrub zone. Whirlwind Valley, 812.

Chrysothamnus greenei **(Gray) Greene.** Common in pure stands in the desert shrub zone. Painter Spring, 623, 1024; Miller Canyon, 1084.

Chrysothamnus nauseosus **(Pallas) Britt. ssp.** ***hololeucus*** **(Gray) H. & A.** Frequent in the pinyon-juniper zone and around drainages and washes. Antelope Spring, 620, 1065.

Chrysothamnus nauseosus **(Pallas) Britt. ssp.** ***graveolens*** **(Nutt.) Piper.** Frequent in washes from low to medium elevations. Antelope Spring, 619, 1072: Skull Rock Pass, 992, 1082.

Chrysothamnus viscidiflorus **(Hook.) Nutt. ssp.** ***viscidiflorus.*** Frequent on gravelly soils in overgrazed or disturbed areas in and below the pinyon-juniper zone. Swasey Peak, 588; Antelope Spring, 621; Miller Canyon, 1077; Painter Spring, 1022.

Cirsium neomexicanum **Gray.** Infrequent in sagebrush and the pinyon-juniper zone. Peabody et al. 372.

Cirsium **c.f.** ***ownbeyi*** **Welsh.** Collected at Painter Spring; more material is needed to positively identify this taxon. 1019.

Cirsium undulatum **(Nutt.) Spreng.** Frequent on dry, open slopes at low to medium elevations, 442a; Marjum Canyon, 539.

Conyza canadensis **(L.) Cronq.** Infrequent along streams at medium elevations. Painter Spring, 552.

Crepis intermedia **Gray.** Infrequent but locally common in the vasey sage zone. Swasey Spring, 265; Swasey Peak, 572; Water Canyon, 983.

Enceliopsis nudicaulis **(Gray) A. Nels.** Infrequent on limestone in the pinyon-juniper zone. Swasey Mountain, 224.

Erigeron argentatus **Greene.** Infrequent on limestone and clay soils at low to medium elevation. North Canyon, 320.

Erigeron nauseosus **(Jones) Cronq.** Rare but locally common on granite in the pinyon-juniper zone. Water Canyon, 356, 973.

Erigeron pumilus **(Hook.) ssp.** ***concinnoides*** **Cronq.** Common on gravelly slopes and alluvial flats at medium elevations. Sawtooth Canyon, 298; Skull Rock Pass, 794, 877.

Erigeron tener **Gray.** Common in the subalpine zone. Notch Peak, 474, 616.

Grindelia squarrosa **(Pursh) Dunal.** Locally common along main roads in the desert shrub zone. 526.

Happlopapus acaulis **(Nutt.) Gray.** Locally common on open, rocky slopes from low to medium elevations. Swasey Mountain, 225; Skull Rock Pass, 882, 892; Water Canyon, 982.

Haplopappus cervinus **Wats.** Frequent on limestone cliffs in the pinyon-juniper zone and subalpine zone. Swasey Peak, 592, 615.

Haplopappus nanus **(Nutt.) D.C. Eaton.** Rare on limestone outcrops in the desert shrub zone. Sand Pass, 1061.

Helianthus annus **L.** Common in washes and along roadsides in the desert shrub zone. Marjum Canyon, 545.

Heterotheca villosa **(Pursh) Shinners.** Locally common on granite substrates in dry, open areas in the pinyon-juniper zone. Painter Spring, 554, 625.

Hymenopappus filifolius **Hook.** Infrequent on open slopes in the pinyon-juniper zone. Swasey Mountain, 227.

Hymenoxys acaulis **(Pursh) Parker.** Frequent on open slopes at medium to high elevations. Miller Canyon, 786.

Iva axillaris **Pursh.** Infrequent near springs and disturbed areas in the desert shrub zone. Antelope Spring, 400; Swasey Spring, 447.

Lactuca serriola **L.** Infrequent in washes and disturbed areas within the desert shrub zone. Marjum Canyon, 543.

Leucelene ericoides **(Torr.) Greene.** Collected only at Swasey Spring on gravelly soils in the pinyon-juniper zone. 437.

Lygodesmia grandiflora **var.** ***dianthopsis*** **(D.C. Eaton) Welsh.** Infrequent but locally common on sandy soils in the desert shrub zone. Sand Pass, 418.

Machaeranthera canescens **(Pursh) Gray.** Common at all elevations. Notch Peak, 494; Swasey Mountain, 508; Skull Rock Pass, 800.

Machaeranthera grindelioides **(Nutt.) Shinners var.** ***grindelioides.*** Collected only on gravelly alluvium at Skull Rock Pass, 876.

Malacothrix sonchoides **(Nutt.) T. & G.** Rare but locally common in sandy areas in the desert shrub zone. Black Hills, 709.

Malacothrix torreyi **Gray.** Infrequent in sandy area in the desert shrub zone. Black Hills, 799.

Onopardum acanthium **L.** Seen on U.S. Hwy. 6–50 outside the study area. No collection.

Perityle stansburyii **(Gray) Macbr.** Frequent on cliff faces and rock outcrops in the pinyon-juniper zone. Swasey Mountain, 384.

Petradoria pumila **(Nutt.) Greene.** Frequent in the pinyon-juniper zone. 561.

Prenanthella exigua **(Gray) Rydb.** Infrequent on gravelly and sandy soils in the desert shrub zone. Tule Valley, 994.

Psathyrotes annua **(Nutt.) Gray.** Frequent on alluvial soils and washes in the desert shrub zone. Whirlwind Valley, 520; U.S. Hwy. 6–50, 557, 599.

Ratibida columnifera **(Nutt.) Woot. & Standl.** Collected on roadside at Skull Rock Pass, 991.

Senecio multilobatus **T. & G. ex Gray.** Common in washes and slopes at low to medium elevations. Swasey Mountain, 226.

Solidago sparsiflora **Gray.** Infrequent on open, rocky slopes in the pinyon-juniper zone. Painter Spring, 582; Sinbad Spring, 590.

Sphaeromeria diversifolia **(D.C. Eaton) Rydb.** Frequent on rock outcrops at medium to high elevations. Swasey Peak, 614; Miller Canyon, 1012.

Stephanomeria pauciflora **(Torr.) A. Nels.** Common along roadsides in the desert shrub zone. 552.

Taraxacum officinale **Weber in Wiggers.** Infrequent around springs at medium elevations. Swasey Spring, 264.

Tetradymia canescens **D.C.** Infrequent in chained and seeded areas in the pinyon-juniper zone. Stove Spring, 507.

Tetradymia glabrata **Gray.** Common in the desert shrub zone. Often the dominant shrub in overgrazed areas. Whirlwind Valley, 328.

Tetradymia nuttallii **T. & G.** Infrequent in the desert shrub zone. No collection.

Tetradymia spinosa **H. & A.** Rare in the desert shrub zone. No collection.

Townsendia florifer **(Hook.) Gray.** Common in the desert shrub zone. Swasey Bottom, 274.

Tragopogon dubius **Scop.** Rare in disturbed areas in the pinyon-juniper zone. Water Canyon, 978.

Xanthium strumarium **L.** Infrequent near cattle troughs and developed springs in the desert shrub zone. 584.

Xanthocephalum microcephala **(D.C.)** Gray. Collected only in chained pinyon-juniper area below Swasey Peak, 589.

Xanthocephalum sarothrae **(Pursh) Shinners.** Common on dry, open slopes at low to medium elevations. No collection.

Berberidaceae

Mahonia repens **(Lindl.) G. Don.** Infrequent but locally common understory shrub in shaded canyons at medium elevations. Antelope Spring, 192.

Boraginaceae

Cryptantha circumscissa **(H. & A.) Johnston.** Collected on sandy soils in the desert shrub zone. Maguire and Becraft, 2768 (UTC).

Cryptantha compacta **Higgins.** Rare on limestone slopes and rock outcrops at medium to high elevations. C. Fullmer, 11, Notch Peak.

Cryptantha confertiflora **(Greene) Payson.** Frequent in sandy areas in the desert shrub zone. Black Hills, 707, 708, 796; Whirlwind Valley, 315.

Cryptantha flavoculata **(A. Nels.) Payson.** Frequent on open slopes in the pinyon-juniper zone. Water Canyon, 360; Sawtooth Canyon, 489; Miller Canyon, 784.

Cryptantha humilis **(Gray) Payson var.** *commixta* **(Maebr.) Higgins.** Infrequent on open slopes from low to medium elevations. No collection.

Cryptantha humilis **(Gray) Payson var.** *orina* **(Payson) Higgins.** Common on open slopes in the desert shrub and pinyon-juniper zones. Swasey Mountain, 230, 231, 389; Black Hills, 715, 792, 793; Miller Canyon, 783; Notch Peak, 468.

Cryptantha kelseyana **Greene.** Collected only from sandy area in the Black Hills, 702.

Cynoglossum officinale **L.** Infrequent in disturbed areas in the pinyon-juniper zone. Water Canyon, 381.

Hackelia patens **(Nutt.) Johnst.** Frequent on dry, open slopes at medium elevations. Swasey Spring, 263.

Heliotropium curassavicum **L. var.** *oboratum* **D.C.** Rare in the desert shrub zone on heavy clay soils. 600.

Lappula occidentalis **(Wats) Greene.** Common in the desert shrub and pinyon-juniper zones. Antelope Spring, 190; Whirlwind Valley, 304.

Lithospermum incisum **Lehm.** Infrequent on open slopes in the pinyon-juniper zone. Swasey Spring, 255; Antelope Spring, 182.

Tequilia nuttallii **(Benth.) Richardson.** Rare but locally common in sandy areas in the Black Hills. 989.

Brassicaceae

Alyssum desertorum **Stapf.** Infrequent on dry, open slopes in the pinyon-juniper zone.

Arabis hirsuta **var.** *pycnocarpa* **(Hopkins) Rollins.** Rare in the pinyon-juniper zone. Water Canyon, 373.

Arabis holboellii **Hornem var.** *secunda* **(Howell) Jepson.** Infrequent on dry, open slopes in the desert shrub and pinyon-juniper zones.

Arabis pendulina **Greene.** Rare on limestone slopes in the subalpine zone. Swasey Peak, 564.

Arabis perennans **Wats.** Infrequent in shaded canyons in the pinyon-juniper zone. Water Canyon, 370.

Camelina microcarpa **Andrz.** Infrequent in the pinyon-juniper zone. No collection.

Cardaria draba **(L.) Desv.** Collected from an exclosure in the pinyon-juniper zone. Swasey Spring, 446.

Caspella bursa-pastoris **(L.) Medic.** Infrequent in the pinyon-juniper zone. No collection.

Caulanthus crassicaulis **(Torr.) Wats.** Infrequent on open limestone slopes in the pinyon-juniper zone. No collection.

Caulanthus pilosus **Wats.** Common spring annual in the desert shrub zone. Whirlwind Valley, 303.

Chorispora tenella **(Pallas) D.C.** Infrequent in disturbed areas in the desert shrub zone. No collection.

Descurainia pinnata **(Walt.) Britt.** Frequent in the pinyon-juniper zone. North Canyon, 307.

Descurainia sophia **(L.) Webb. in Engler & Prantl.** Frequent on disturbed areas within the desert shrub zone. Sand Pass, 416; Whirlwind Valley, 808.

Draba cuneifolia **Nutt. ex T. & G.** Infrequent on open, dry slopes in the pinyon-juniper zone. Miller Canyon, 378.

Erysimum asperum **(Nutt.) D.C.** Frequent on clay soils in the desert shrub zone. 193.

Euclidium syriacum **(L). R. Br.** Rare around springs in the desert shrub zone. Whirlwind Valley, 456.

Halimolobos virgata **Nutt.** Rare in the vasey sagebrush zone. Water Canyon, 974.

Isatis tinctoria **L.** Rare along the roadside into Swasey Spring. 273.

Lepidium lasiocarpum **Nutt. in T. & G. var.** *lasiocarpum*. Infrequent on sands and gravels in the desert shrub zone. Black Hills, 702.

Lepidium montanum **Nutt. var.** *montanum*. Common in the desert shrub zone. Swasey Bottom, 270.

Lepidium perfoliatum **L.** Frequent on U.S. Hwy. 6–50 and disturbed areas in the desert shrub zone. 194.

Lesquerella kingii **Wats.** Infrequent on limestone in the higher elevations. Notch Peak, 493.

Lesquerella occidentalis **Wats.** Rare on open, rocky, limestone slopes in the subalpine zone. Sawtooth Canyon, 887.

Malcomia africana **R. Br. in Ait.** Infrequent but locally common in disturbed areas in the desert shrub zone. Wildhorse Canyon, 178; Swasey Bottom, 276.

Nasturtium officinale **R. Br.** Infrequent in ponds and springs in the desert shrub zone. Antelope Spring Reservoir, 391.

Physaria chambersii **Rollins.** Common on dry slopes in the pinyon-juniper zone. Antelope Spring, 192.

Sisymbrium altissimum **L.** Infrequent along roadsides and in disturbed areas in the desert shrub zone. Antelope Mountains, 576; Black Hills, 874.

Stanleya pinnata **(Pursh) Britt.** Infrequent on heavy clay soils in the desert shrub zone. Sand Pass, 417.

Streptanthella longirostris **(Wats.) Rydb.** Common in sandy areas in the desert shrub zone. Sand Pass, 238; Black Hills, 724.

Streptanthus cordatus **Nutt. ex. T. & G.** Common on dry slopes in the pinyon-juniper zone. Swasey Spring, 281.

Thelypodium sagittatum **(Nutt.) Endl. var.** ***vermicularis*** **Welsh & Reveal.** Rare but locally common in heavy clay soils in the desert shrub zone. Swasey Bottom, 195–275.

Cactaceae

Coryphantha vivipara **(Nutt.) Britt & Rose.** Rare on gravelly alluvium in the desert shrub zone. Skull Rock Pass, 883.

Echinocereus engelmannii **(Parry) Rumpler.** Infrequent on rocky, exposed slopes in the desert shrub zone. Swasey Mountain, 414.

Echinocereus trighlochidatus **Engelm.** Infrequent but locally common on granite boulders in the pinyon-juniper zone. Contact Canyon, 412.

Opuntia polycantha **Haw.** Common from the valley floor to the pinyon-juniper zone on dry, open slopes. Miller Canyon, 305.

Pediocactus simpsonii **(Engelm.) Britt & Rose.** Rare on dry, gravelly slopes in the pinyon-juniper zone. Water Canyon, 383a.

Sclerocactus pubispinus **(Engelm.) Benson.** Rare on Quaternary alluvium in the desert shrub zone. Whirlwind Valley, 349.

Capparaceae

Cleome serrulata **Pursh var.** ***serrulata.*** Frequent on disturbed areas in the desert shrub zone. Marjum Canyon, 539.

Caprifoliaceae

Sambucus caerulea **Raf.** Infrequent on dry, open slopes in the vasey sagebrush zone. Swasey Spring, 438.

Symphoricarpos longiflorus **Gray.** Rare on limestone slopes in the pinyon-juniper zone. Sawtooth Canyon, 488.

Symphoricarpos oreophilus **Gray.** Rare in the vasey sagebrush zone. Water Canyon, 186.

Caryophyllaceae

Arenaria kingii **(Wats.) Jones.** Frequent on open, gravelly slopes in the desert shrub and pinyon-juniper zones. Water Canyon, 383.

Stellaria jamesiana **Torr.** Frequent as an understory species in the subalpine zone. Swasey Peak, 568; Water Canyon, 986.

Celastraceae

Forsellesia nevadensis **(Gray) Greene.** Frequent on open slopes in the desert shrub and pinyon-juniper zones. Wildhorse Canyon, 180.

Pachystima myrsinites **(Pursh) Raf.** Infrequent in conifer understory and in shaded canyons in the pinyon-juniper and subalpine zones. Water Canyon, 968.

Chenopodiaceae

Allenrolfea occidentalis **(Wats.) Kuntze.** Infrequent on heavy clay and saline soils in the desert shrub zone. No collection.

Atriplex canescens **(Pursh) Nutt.** Frequent on sandy soils and on open slopes in the desert shrub zone. 499.

Atriplex confertifolia **(Torr. & Frem.) Wats.** Common dominant in the desert shrub zone. 505.

Atriplex rosea **L.** Frequent around springs in the desert shrub and pinyon-juniper zones. Antelope Spring, 514, 596, 1057.

Atriplex gardneri **var.** ***falcata*** **(Jones) Welsh.** Infrequent but locally common on alluvial deposits in the desert shrub zone. No collection.

Atriplex gardneri **var.** ***tridentata*** **(Kuntze) Macbr.** Infrequent but locally common on playas. Swasey Bottom, 316, 1063, 1064.

Chenopodium album **L.** Infrequent around springs in the desert shrub and pinyon-juniper zone. Painter Spring, 1025.

Chenopodium fremontii **Wats.** Rare on open slopes in the pinyon-juniper zone. Antelope Spring, 1074a.

Grayia spinosa **(Hook.) Moq. in D. & C.** Infrequent on sands in the desert shrub zone. Sand Pass, 236.

Halogeton glomeratus **Meyer.** Common annual on disturbed sites within the desert shrub zone. Antelope Spring, 458.

Kochia americana **Wats.** Frequent on saline and clay soils in the desert shrub zone. Swasey Mountain, 384a.

Salsola iberica **Sennen & Pay.** Locally common on disturbed areas in the desert shrub zone. Sand Pass, 519.

Sarcobatus vermiculatus **(Hook.) Torr.** Infrequent but locally common on saline soils in the desert shrub zone. No collection.

Suadea torreyana **Wats.** Infrequent on playas and clay soils in the desert shrub zone. 521.

Convolvulaceae

Convolulus arvensis **L.** Infrequent but locally common in disturbed areas in the desert shrub and pinyon-juniper zones. Miller Canyon, 377.

Crassulaceae

Sedum debile **Wats.** Infrequent on open slopes in the pinyon-juniper zone. Notch Peak, 495; Water Canyon, 969.

Sedum lanceolatum **Torr.** Infrequent on rocky areas in the pinyon-juniper and subalpine zones. Water Canyon, 363.

Cupressaceae

Juniperus communis **L.** Infrequent in the subalpine zone. Notch Peak, 491.

Juniperus osteosperma **(Torr.) Little.** Common dominant in the pinyon-juniper zone. No collection.

Juniperus scopulorum **Sarg.** Infrequent in shaded canyons and in drainages in the pinyon-juniper and subalpine zones. Swasey Peak, 569.

Cyperaceae

Carex aurea **Nutt.** Infrequent around springs in the desert shrub zone. Swasey Spring, 261.

Carex douglasii **F. Boott. in Hook.** Rare around springs in the pinyon-juniper zone. Swasey Spring, 283.

Carex microptera **Mack.** Rare around springs at medium elevations. Water Canyon, 369.

Carex nebrascensis **Dewey.** Rare around springs in the upper pinyon-juniper zone. Sinbad Spring, 409.

Carex praegracilis **W. Boott.** Rare around springs within the pinyon-juniper zone. Painter Spring, 1015.

Eleocharis palustris **(L.) R. & S.** Infrequent around springs in the desert shrub zone. Antelope Spring Reservoir, 460.

Eleocharis parishii **Britt.** Rare around springs in the pinyon-juniper zone. Antelope Spring, 597.

Eleocharis pauciflora **(Lightf.) Link.** Rare around springs in the pinyon-juniper zone. Sinbad Spring, 407.

Scirpus acutus **Munl.** Rare around springs in the pinyon-juniper zone. Painter Spring, 1016.

Elaeagnaceae

Elaeagnus angustifolia **L.** Rare in the desert shrub zone. Painter Spring, 1020.

Ephedraceae

Ephedra nevadensis **Wats.** Common in the desert shrub zone. No collection.

Ephedra viridis **Colville.** Common shrub in the pinyon-juniper and subalpine zones. Notch Peak, 480; Swasey Mountain, 386.)

Equisetaceae

Equisetum laevigatum **A. Br.** Infrequent along streams at low elevations. Antelope Spring, 398; Painter Spring, 1023.

Euphorbiaceae

Euphorbia glyptosperma **Engelm.** Infrequent in gravelly washes and open slopes in the desert shrub and pinyon-juniper zones. Painter Spring, 626.

Fabaceae

Astragalus argophyllus **Nutt. var.** *martinii* **Jones.** Frequent on dry, open slopes in the pinyon-juniper zone. Water Canyon, 358, 382; Swasey Spring, 269.

Astragalus beckwithii **T. & G. var.** *purpureus* **Jones.** Infrequent on gravelly soils in the pinyon-juniper zone. North Canyon, 805.

Astragalus callithrix **Barneby.** Rare on sandy areas and alluvial deposits in the desert shrub zone. Black Hills, 710, 718.

Astragalus calycosus **Torr.** Frequent and locally common on dry, gravelly slopes in the desert shrub zone. Sand Pass, 240.

Astragalus cibarius **Sheldon.** Rare on open slopes in the pinyon-juniper zone. Swasey Spring, 268.

Astragalus lentiginosus **Doug. var.** *araneosus* **(Sheldon) Barneby.** Infrequent but locally common on gravelly soils in the desert shrub and pinyon-juniper zone. Swasey Mountain, 277.

Astragalus lentiginosus **Doug. var.** *scorpionis* **Jones.** Rare on limestone gravels in the lower edge of the pinyon-juniper zone. Miller Canyon, 788.

Astragalus marianus **(Rydb.) Barneby.** Rare in the pinyon-juniper zone. Sawtooth Canyon, 888.

Astragalus newberryi **Gray.** Common on dry, open slopes in sagebrush and in the pinyon-juniper zone. Notch Peak, 480a, 482; Miller Canyon, 787, 803.

Astragalus platytropis **Gray.** Rare on open, rocky slopes in the subalpine zone. Notch Peak, 466.

Astragalus uncialis **Barneby.** Collected approximately 25 km outside the study area on saline sands and limestone gravels in the desert shrub zone. Long's Ridge, 801.

Astragalus utahensis **(Torr.) T. & G.** Infrequent in the pinyon-juniper zone. Antelope Spring, B.F. Harrison, 6321; J. Guidinger, 225.

Lathyrus brachycalyx **Rydb. var.** *brachycalyx.* Frequent on open slopes and in washes in the pinyon-juniper zone. Wildhorse Canyon, 177.

Lupinus caudatus **Kellog.** Infrequent but locally common in the vasey sagebrush zone. Water Canyon, 357, 975.

Lupinus pusillus **Pursh.** Rare but locally common on sands in the desert shrub zone. Black Hills, 699, 873.

Medicago sativa **L.** Infrequent on disturbed areas in the desert shrub zone. Sawtooth Canyon, 490.

Melilotus alba **Medicus.** Frequent around springs and occasionally on roadsides in the desert shrub and pinyon-juniper zone. Painter Spring, 550.

Melilotus officinalis **(L.) Lam.** Frequent around springs and disturbed areas in the desert shrub and pinyon-juniper zones. Swasey Spring, 509.

Trifolium gymnocarpon **Nutt.** Rare on limestone in the upper pinyon-juniper zone. Sawtooth Canyon, 492.

Geraniaceae

Erodium cicutarium **(L.) L'Her.** Common annual in disturbed areas. No collection.

Grossulariaceae

Ribes cereum **Dougl.** Infrequent in shaded canyons in the pinyon-juniper zone. Sawtooth Canyon, 485, 891.

Ribes velutinum **Greene.** Infrequent in canyons in the pinyon-juniper zone. No collection.

Hydrophyllaceae

Nama demissum **Gray.** Infrequent in sandy areas in the desert shrub zone. Black Hills, 722.

Phacelia iresiana **Torr.** Infrequent but locally common in sand in the desert shrub zone. Black Hills, 705.

Phacelia crenulata **var.** *corrugata* **A. Nels.** Frequent and locally common on disturbed and sandy areas in the desert shrub zone. 301.

Juncaceae

Juncus articus **Willd.** Rare around springs at medium elevations. Water Canyon, 371.

Juncus bufonius **L.** Infrequent around springs and moist alkaline areas in the desert shrub zone. 454.

Juncus ensifolius **Willd.** Locally common around springs in the desert shrub and pinyon-juniper zones. Antelope Spring, 395, 598; Swasey Spring, 445; Sinbad Spring, 501.

Juncus longistylis **Torr.** Rare along springs in the pinyon-juniper zone. Painter Spring, 1015a.

Lamiaceae

Hedeoma drummondii **Benth.** Rare in dry, open places

at lower to middle elevations. No collection.

Marrubium vulgare **L.** Infrequent in disturbed areas in the desert shrub zone. 455.

Mentha arvensis **L.** Infrequent around springs in the pinyon-juniper zone. Antelope Spring, 595.

Salvia dorrii **(Kellogg) Abrams.** Infrequent on dry, open slopes at medium elevations. Sawtooth Canyon, 299a.

Liliaceae

Allium acuminatum **Hook.** Infrequent in mesic, shaded canyons in the pinyon-juniper zone. Water Canyon, 971.

Allium nevadense **Wats.** Common in the desert shrub zone. Sinbad Spring, 405; Black Hills, 700.

Allium parvum **Kellogg.** Rare but locally frequent on open, rocky slopes where moisture accumulates in the subalpine zone. Notch Peak, 291; Sawtooth Canyon, 886.

Calochortus aureus **Wats.** Infrequent but locally common in the vasey sagebrush zone. Water Canyon, 972.

Fritillaria atropurpurea **Nutt.** Infrequent in moist, shaded areas in the pinyon-juniper zone. Wildhorse Canyon, 181; Sawtooth Canyon, 889; Sinbad Spring, 402.

Smilacina stellata **(L.) Desf.** Rare in aspen understory in upper Water Canyon, 977.

Yucca harrimaniae **Trel.** Infrequent on dry, open slopes in the desert shrub zone. No collection.

Zigadenus paniculatus **(Nutt.) Wats.** Infrequent in sagebrush and pinyon-juniper. Swasey Spring, 255.

Linaceae

Linum perenne **L.** Infrequent but locally common in the vasey sagebrush zone. Swasey Spring, 253.

Linum subteres **(Trelease) Engelm.** Rare on conglomerate in the desert shrub zone. Skull Rock Pass, 990.

Loasaceae

Mentzelia albicaulis **Dougl.** Infrequent in sandy areas in the desert shrub zone. Sand Pass, 235.

Mentzelia laevicaulis **(Dougl.) T. & G.** Infrequent in gravelly washes in the desert shrub zone. Whirlwind Valley, 528a.

Malvaceae

Malvella leprosa **(Dougl.) Torr.** Common along roadsides, especially U.S. Hwy 6–50. 556.

Sphaeralcea grossulariifolia **(H. & A.) Rydb.** Common in the desert shrub zone. Swasey Bottom, 272.

Nyctaginaceae

Abronia elliptica **A. Nels.** Frequent in sandy areas in the desert shrub zone. Black Hills, 697.

Mirabilis linearis **(Pursh) Heimerl.** Rare in the desert shrub zone. Painter Spring, 577.

Onagraceae

Calylophus lavandulifolius **(T. & G.) Raven.** Infrequent on dry, open slopes in the pinyon-juniper zone. Swasey Bottom, 321.

Camissonia boothii **(Dougl.) Raven ssp.** ***alyssoides*** **(H. & A.) Raven.** Infrequent in gravelly washes in the desert shrub zone. Whirlwind Valley, 524.

Camissonia scapoidea **(T. & G.) Raven.** Frequent in gravelly washes in the desert shrub zone. Antelope Spring, 394; Whirlwind Valley, 524.

Epilobium ciliatum **Raf.** Infrequent around springs in the desert shrub and pinyon-juniper zones. Painter Spring, 581.

Gaura parviflora **Dougl.** Infrequent but locally common on gravels near roadsides and in washes in the desert shrub zone.

Gayophytum racemosum **T. & G.** Infrequent on moist soils and on disturbed areas in various communities. Water Canyon, 976a.

Gayophytum ramosissimum **Nutt.** Rare in and around aspen communities. Water Canyon, 976.

Oenothera brachycarpa **(Gray) Britt.** Rare on open slopes in the pinyon-juniper zone. Swasey Spring, 512.

Oenothera caespitosa **Nutt.** Frequent in gravelly washes in the desert shrub zone. Antelope Spring, 394; Whirlwind Valley, 524.

Oenothera pallida **Lindl.** Locally common on sandy soils in the desert shrub zone. Sand Pass, 237.

Orchidaceae

Epipactis gigantea **Dougl.** Rare around Painter Spring on shaded, moist soils. 1017.

Orobanchaceae

Orobanche multiflora **Nutt.** Parasitic on *Tetradymia* and a variety of host plants. Black Hills, 706.

Orobanche fasciculata **Nutt.** Parasitic on *Artemisia* in the desert shrub zone. Water Canyon, 354a.

Paperveraceae

Argemone munita **Dur. & Hilg.** Infrequent in disturbed areas in the pinyon-juniper zone. Miller Canyon, 380.

Pinaceae

Abies concolor **(Gord. & Glend.) Lindl.** Rare along streams and mesic slopes at medium elevations. Water Canyon, 966.

Pinus longaeva **D.K. Bailey.** Dominant species in the subalpine zone and infrequent in the drainages in the pinyon-juniper zone. Antelope Spring, 187.

Pinus monophylla **Torr. & Frem.** Common species of the pinyon-juniper zone. No collection.

Pinus ponderosa **Laws.** Rare and restricted to several individuals at Sinbad Spring. Probably planted near springs. 502.

Pseudotsuga menziesii **(Mirb.) Franco.** Frequent in the subalpine zone and on north-facing slopes in the pinyon-juniper zone. Sinbad Spring, 401.

Poaceae

Agropyron cristatum **(L.) Gaertn.** Locally common in range improved areas within the pinyon-juniper zone. Swasey Peak, 330.

Agropyron intermedium **(Host) Beauv.** Infrequent along roadsides in sagebrush and pinyon-juniper zones. Sand Pass, 420.

Agropyron smithii **Rydb.** Infrequent in range improved areas within the pinyon-juniper zone. Sinbad Spring, 558, 587.

Agropyron spicatum (Pursh) Scribn. & Smith. Frequent on open slopes and often in pure stands in the desert shrub and pinyon-juniper zones. Marjum Pass, 462; North Canyon, 806.

Agropyron trachycaulum (Link) Malte var. *trachycaulum*. Frequent in the pinyon-juniper zone on mesic slopes. Marjum Pass, 461; Water Canyon, 970; Stove Spring, 504.

Agrostis stolonifera L. var. *stolonifera*. Common around springs and other moist places at low to medium elevations. Painter Spring, 549, 580.

Artistida purpurea Nutt. Common along roadsides in the desert shrub zone. Swasey Mountain, 386.

Blepharidachne kingii (Wats.) Hack. Infrequent but locally common in the desert shrub zone. Skull Rock Pass, 789, 880.

Bromus inermis Leyss. Infrequent in the vasey sagebrush zone. No collection.

Bromus rubens L. Collected at north end of study area. E. M. Christensen, 115.

Bromus tectorum L. Common in overgrazed areas and in sandy areas in the desert shrub and pinyon-juniper zones. Sand Pass, 234.

Dactylis glomerata L. Rare along roadside to North Canyon in the desert shrub zone. 811.

Deschampsia caespitosa (L.) Beauv. Infrequent in moist areas in the upper pinyon-juniper zone. Antelope Spring, 396.

Distichlis spicata (L.) Greene var. *stricta* (Torr.) Scribn. Common in alkaline soils in the desert shrub zone. Painter Spring, 612.

Echinochola crus-galli (L.) Beauv. Collected near cattle trough in the desert shrub zone. Whirlwind Valley, 1058.

Elymus ambiguus Vasey & Scribn. Locally common on open slopes and often occurring in pure stands at low to medium elevations. Black Hills, 711; Miller Canyon, 789.

Elymus canadensis L. Infrequent around springs and occasionally scattered along roadsides in the desert shrub and pinyon-juniper zones. 556.

Elymus cinereus Scribn. & Merr. Infrequent but locally common around springs and occasionally occurring in the pinyon-juniper zone. Sinbad Spring, 573.

Elymus junceus Fisch. Rare on roadsides in the desert shrub zone. Whirlwind Valley, 809.

Erioneuron pilosus (Buckley) Nash. Infrequent but locally common on clay soils in the desert shrub zone. Skull Rock Pass, 795, 875.

Erioneuron pulchellum (H.B.K.) Tateoka. Collected only once on clay soil in the desert shrub zone at the south end of study area. 602.

Glyceria elata (Nash) Jones. Rare around springs in the upper pinyon-juniper zone. Sinbad Spring, 410.

Glyceria striata (Lam.) A.S. Hitchc. Locally common around springs and other moist places in the pinyon-juniper zone. Swasey Spring, 282; Sinbad Spring, 500.

Hilaria jamesii (Torr.) Benth. Common in the desert shrub zone. Swasey Mountain, 280.

Hordeum jubatum L. Locally common around springs and moist, disturbed places within the desert shrub zone. 457.

Hordeum pusillum Nutt. Rare near springs and disturbed areas in the desert shrub zone. Whirlwind Valley, 399; Antelope Spring, 1059.

Muhlenbergia asperifolia (Nees & Meyen) Parodi. Infrequent but locally common in and around springs at low to medium elevations. Painter Spring, 579.

Oryzopsis hymenoides (Roem. & Schult.) Ricker. Common on sandy soils in the desert shrub zone. 464.

Oryzopsis micrantha (Trin. & Rupr.) Thurb. Infrequent on rocky areas in the pinyon-juniper zone. Water Canyon, 370; Sawtooth Canyon, 478.

Phragmites australis (Cav.) Trin. Collected only at Painter Spring, 625.

Poa fendleriana (Steud.) Vasey. Common in the vasey sagebrush and pinyon-juniper zones. Sinbad Spring, 403; Sawtooth Canyon, 479.

Poa pratensis L. Infrequent but locally common in moist areas and around springs. Antelope Spring, 399; Sinbad Spring, 408; Water Canyon, 980.

Poa secunda Presl. Common on a variety of soils at low to medium elevations. Swasey Mountain, 174; Swasey Bottom, 324; Sawtooth Canyon, 496; Skull Rock Pass, 804.

Polypogon monspeliensis (L.) Desf. Infrequent around springs and other moist alkaline areas at low to medium elevations. Whirlwind Valley, 451.

Puccinellia distans (L.) Parl. Infrequent in moist alkaline areas in the desert shrub zone. Whirlwind Valley, 452.

Puccinellia nuttalliana (J.A. Schultes) Hitchc. Infrequent in moist alkaline areas in the desert shrub zone. Sinbad Spring, 406.

Secale cereale L. Collected only once on a roadside in the desert shrub zone. Whirlwind Valley, 450.

Sphenopholis obtusata (Michx.) Scribn. Rare around springs in the desert shrub zone. Painter Spring, 578.

Sporobolus airoides Torr. Frequent in alkaline soils in the desert shrub zone. 574.

Sporobolus contractus A.S. Hitchc. Collected only once in the Antelope Mountains on dry, open slopes. 575.

Sporobolus cyrptandrus Torr. Frequent in the desert shrub zone. Antelope Spring Reservoir, 393; Whirlwind Valley, 449.

Sporobolus flexuosus (Thurber) Rydb. Rare on sandy areas in the desert shrub zone. Black Hills, 996.

Stipa arida M.E. Jones. Infrequent on dry, open slopes in the desert shrub zone. Swasey Mountain, 388.

Stipa comata Trin. & Rupr. Common on various soils, especially on sands in the desert shrub zone. Swasey Spring, 280.

Stipa lettermanii Vasey. Infrequent in the vasey sagebrush zone. Water Canyon, 967.

Stipa coronata (Thurb.) var. *depauperata* (Jones) Hitchc. Frequent on open, rocky slopes at low to medium elevations. Swasey Mountain, 387; Notch Peak, 469, 474; Whirlwind Valley, 810.

Trisetum spicatum (L) Richt. Rare in shaded areas in the subalpine zone. 615a.

Vulpia octoflora (Walter) Rydb. Infrequent annual on dry, open slopes in the desert shrub zone. Black Hills, 712.

Polemoniaceae

Gilia aggregata (Pursh) Spreng. Infrequent on dry to mesic slopes at medium elevations. Water Canyon, 359.

Gilia congesta Hook. Common on dry, open slopes in the desert shrub and pinyon-juniper zones. Antelope Spring, 185; Swasey Bottom, 318; Sand Pass, 239.

Gilia inconspicua (Smith) Sweet. Frequent on gravelly soils in washes and on dry slopes in the desert shrub and

pinyon-juniper zones. Water Canyon, 361; Black Hills, 704; Miller Canyon, 790.

***Gilia hutchinsifolia* Rydb.** Frequent on gravelly soils in washes in the desert shrub zone. Tule Valley Road, 515–993.

***Gilia polycladon* Torr.** Infrequent but locally common in sandy areas in the desert shrub zone. Black Hills, 714, 797.

***Leptodactylon caespitosum* Nutt.** Rare on limestone cliffs in the pinyon-juniper zone. Swasey Mountain, 229.

***Leptodactylon pungens* (Torr.) Nutt.** Frequent on sandy soils within the desert shrub zone. No collection.

***Phlox austromontana* Colville.** Common on open, dry slopes in the pinyon-juniper zone. Swasey Mountain, 230; Notch Peak, 295; Skull Rock Pass, 802; Sawtooth Canyon, 890.

***Phlox longifolia* Nutt.** Common in sagebrush and in the pinyon-juniper zone. Sawtooth Canyon, 299.

Polygalaceae

***Polygala acanthoclada* Gray.** Infrequent on sandy areas in the desert shrub zone. Sand Pass, 415.

Polygonaceae

***Eriogonum cernuum* Nutt. var. *cernuum*.** Infrequent on gravelly soils in the desert shrub zone. Black Hills, 995.

***Eriogonum hookeri* Wats.** Frequent on roadsides and in gravelly washes in the desert shrub zone, 527; Painter Spring, 630.

***Eriogonum howellianum* Reveal.** Rare in gravelly soils and washes in the desert shrub zone. Whirlwind Valley, 523.

***Eriogonum kearneyi* Tidestr.** Locally common in sandy areas in the desert shrub zone. Sand Pass, 518.

***Eriogonum microthecum* Nutt. var. *laxiflorum* Hook.** Frequent on dry, rocky areas at low to medium elevations. Swasey Peak, 463, 594.

***Eriogonum nummulare* var. *ammophilum* (Reveal) Welsh.** Rare on sands in the desert shrub zone. Black Hills, 997.

***Eriogonum ovalifolium* Nutt. var. *nivale* (Canby) Jones.** Infrequent on open slopes in the subalpine zone. Notch Peak, 470; Miller Canyon, 1014.

***Eriogonum ovalifolium* Nutt. var. *ovalifolium*.** Frequent on a variety of soils in the desert shrub zone. Swasey Mountain, 278; Sawtooth Canyon, 498.

***Eriogonum shockleyi* Wats. var. *shockleyi*.** Common on a variety of soils in the desert shrub zone. Sand Pass, 419.

***Eriogonum spathulatum* var. *natum* (Reveal) Welsh.** Rare on marly playa remnant in the desert shrub zone. J. Reveal, 3999, 4000; S. L. Welsh, 18,200, 18,202.

***Polygonum aviculare* L.** Infrequent around moist, disturbed areas in the desert shrub zone. Whirlwind Valley, 452.

***Polygonum sawatchense* Small.** Infrequent on disturbed areas in various zones. No collection.

***Rumex crispus* L.** Infrequent around springs and moist disturbed areas in the desert shrub zone. No collection.

Polypodiaceae

***Cystoperis fragilis* (L.) Bernh. in Schrader.** Rare under shaded rock outcrops. S. Flowers; Swasey Gulch, 3034.

***Woodsia oregana* D.C. Eaton.** Rare in shaded canyons and mesic substrates at medium elevations. Water Canyon, 306.

Portulaceae

***Lewisia rediviva* Pursh.** Rare on exposed, rocky ridges in the pinyon-juniper zone. Sinbad Spring, 404.

Primulaceae

***Dodecatheon pulchellum* (Raf.) Merr.** Infrequent around springs and mesic areas in the pinyon-juniper zone. Water Canyon, 374.

***Primula domensis* Kass & Welsh.** Rare on shaded limestone cliff faces in the pinyon-juniper and subalpine zone. Notch Peak, 473; Sawtooth Canyon, 884.

Ranunculaceae

***Aquilegia formosa* Fisch.** Infrequent around springs and in wet areas at medium elevations. Water Canyon, 367.

***Clematis ligustisifolia* Nutt.** Rare but locally common in mesic, shaded canyons in the pinyon-juniper zone. Painter Spring, 550.

***Delphinium andersonii* Gray.** Common on dry, open slopes in the desert shrub zone. Swasey Mountain, 172; Swasey Spring, 254; Swasey Bottom, 325, 326.

***Ranunculus cymbalaria* Pursh.** Common around springs in the desert shrub and pinyon-juniper zones. Swasey Spring, 259.

***Ranunculus juniperinus* Jones.** Frequent in early spring on open slopes in the pinyon-juniper zone. Wildhorse Canyon, 175.

***Ranunculus testiculatus* Crantz.** Infrequent in the pinyon-juniper zone. No collection.

Rhamnaceae

***Ceanothus martinii* Jones.** Infrequent on open slopes in the subalpine zone. Swasey Spring, 443; Swasey Peak, 567.

Rosaceae

***Amelanchier utahensis* Koehn.** Infrequent in the vasey sagebrush zone and on open slopes at medium elevations. Swasey Spring, 513.

***Cercocarpus intricatus* Wats.** Common dominant on rocky slopes at medium to high elevations. Wildhorse Canyon, 179.

***Cercocarpus ledifolius* Nutt.** Frequent on dry, open slopes and often in pure stands at medium elevations. Swasey Spring, 444.

***Chamaebatiaria millefolium* (Torr.) Maxim.** Infrequent in shaded canyons in the pinyon-juniper zone. Sinbad Spring, 503, 627.

***Cowania mexicana* D. Don. var. *stansburiana* (Torr.) Jepson.** Frequent on dry, gravelly slopes in the desert shrub and pinyon-juniper zones. Swasey Bottom, 317.

***Holodiscus dumosus* (Nutt.) Heller.** Infrequent in crevices of limestone cliffs in the pinyon-juniper zone. Sawtooth Canyon, 486.

***Petrophytum caespitosum* (Nutt.) Rydb.** Common on limestone cliff faces at all elevations. 593.

***Potentilla biennis* Greene.** Rare around springs in the pinyon-juniper zone. Miller Canyon, 797.

Rosa woodsii **Lindl.** Infrequent in shaded canyons and around springs at medium elevations. Water Canyon, 351, 357, 984.

Prunus virginiania **L.** var. *melanocarpa* **(Nels.) Sarg.** Infrequent but locally common in shaded canyons and around springs at medium elevations. Water Canyon, 309a.

Rubiaceae

Galium multiflorum **Kell.** Infrequent on dry, rocky slopes at low to medium elevations. Swasey Spring, 448.

Salicaceae

Populus angustifolia **James** x *Populus trichocarpa* **T. & G.** Rare in Water Canyon, 1018.

Populus angustifolia **James.** Dominant tree at Painter Spring. No collection.

Populus tremuloides **Michx.** Infrequent in moist depressions and around springs in the upper pinyon-juniper zone. No collection.

Salix exigua **Nutt.** Infrequent around springs in the pinyon-juniper zone. Water Canyon, 353; Painter Spring, 584.

Santalaceae

Comandra umbellata **(L.).** Infrequent on sandy areas in the desert shrub zone. No collection.

Saxifragaceae

Fendlerella utahensis **(S. Wats.) Heller.** Rare in shaded canyons at medium elevations. Sawtooth Canyon, 475.

Heuchera parvifolia **Nutt.** Rare on moist, shaded cliff faces at medium to high elevations. Water Canyon, 368.

Heuchera rubescens **Torr.** Infrequent on moist, shaded cliff faces at medium to high elevations. Swasey Peak, 613.

Jamesia americana **T. & G.** Rare in shaded canyons at medium elevations. Sawtooth Canyon, 484.

Philadelphus microphyllus **Gray.** Rare in shaded canyons and on rocky substrates at medium elevations. Miller Canyon, 1013.

Scrophulariaceae

Castilleja angustifolia **Nutt. (G. Don.)** var. *flavescens* **(Pennell ex Edwin) N. Holmgren.** Rare in sagebrush at medium elevations. F. Peabody et al., 361.

Castilleja scabrida var. *barneybyana* **(Eastw.) N. Holmgren.** Infrequent on limestone ledges and outcrops in the pinyon-juniper zone. Notch Peak, 290; Miller Canyon, 785.

Castilleja chromosa **A. Nels.** Common in sagebrush at low to medium elevations. Antelope Spring, 183; Black Hills, 719.

Castilleja exilis **Gray.** Infrequent around springs at low to medium elevations. Painter Spring, 548.

Castilleja linariifolia **Benth. in D.C.** Rare on open slopes in the pinyon-juniper zone. Swasey Spring, 442.

Collinsia parviflora **Dougl. ex Lindl.** Frequent and locally common around springs in the desert shrub and pinyon-juniper zone. Water Canyon, 354; Antelope Spring, 392.

Mimulus guttatus **Fisch.** Infrequent but locally common in springs and moist soils in the pinyon-juniper zone. Water Canyon, 354.

Pedicularis centranthera **Gray.** Common in the pinyon-juniper zone. Antelope Spring, 184; Swasey Spring, 262.

Penstemon confusus **Jones.** Common on dry, open slopes in the pinyon-juniper zone. Swasey Mountain, 228; Swasey Bottom, 327.

Penstemon eatonii **Gray.** Frequent in shaded canyons in the pinyon-juniper zone. Swasey Spring, 441; Water Canyon, 352.

Penstemon humilis **Nutt.** Common on dry, open slopes in the pinyon-juniper zone. Swasey Bottom, 267, 323; Water Canyon, 355; Notch Peak, 294, 467; Skull Rock Pass, 881.

Penstemon leonardii **Rydb.** Infrequent in the vasey sagebrush zone and on gravelly soils in the pinyon-juniper zone. Swasey Spring, 439.

Penstemon patricus **N. Holmgren.** Rare on open limestone slopes in the pinyon-juniper zone. Sawtooth Canyon, 479.

Verbascum thapsus **L.** Locally common on gravelly soils and disturbed areas in the desert shrub zone. 517.

Solanaceae

Lycium andersonii **Gray.** Infrequent on open, dry slopes in the desert shrub zone. Black Hills, 721.

Nicotiana attenuata **Torr. ex Wats.** Frequent on disturbed sites in the pinyon-juniper zone. Stove Spring, 505.

Solanum triflorum **Nutt.** Infrequent on disturbed sites in the pinyon-juniper zone. Miller Canyon, 1076.

Tamaricaceae

Tamarix ramosissima **Ledeb.** Collected only from Painter Spring, 554.

Ulmaceae

Celtis reticulata **Torr.** Rare in the desert shrub zone. Black Hills, 988.

Urticaceae

Urtica dioica **L. ssp.** *gracilis* **(Ait.) Seland.** Collected from Water Canyon, 981.

Verbenaceae

Verbena bracteata **Lag. & Rodr.** Common in disturbed areas in the desert shrub and pinyon-juniper zones. Antelope Spring Reservoir, 390, 459.

Violaceae

Viola nephrophylla **Greene.** Rare on moist soils and around shaded springs. Swasey Spring, 258.

Viscaceae

Arceuthobium campylopodium **Engelm.** Parasitic on pinyon pine. No collection.

POTENTIAL SOIL COMPACTION FORTY YEARS AFTER LOGGING IN NORTHEASTERN CALIFORNIA

Robin S. Vora[1]

ABSTRACT.—Surface-bearing pressure in newer logging skid trails compared to the 40+-year-old trails was approximately 60% greater as measured by a cone penetrometer. Surface soil compaction from tractor skidding may last 40 years or more, as evidenced by the fact that skid trails of that age were 20% more resistant to the penetrometer than areas adjacent to trails. No relationship was found between dry-bulk density (measured with a balloon apparatus) and surface-bearing pressure.

The resistance of the soil surface to root penetration will affect the ability of a newly germinated seedling to survive. Root-penetration resistance is a function of soil density. Soil-bearing pressure can be correlated to root-penetration resistance because bearing pressure is also a function of soil density, as well as other factors, including moisture content, soil type, and strength parameters of friction and cohesion (Ayers and Perumpral 1981).

Alexander (1985) stated that soil compaction is an increase in the density of a soil as the result of applied loads or pressure. A potential consequence of soil compaction could be reduced site productivity. Increases in soil bulk density can result in physical barriers to root penetration, reduced gaseous transfer (soil aeration), and reduced availability of water and nutrients to the roots. Soil compaction can also produce hydrologic impacts such as reduced infiltration capacity, decreased hydraulic conductivity (subsurface permeability), and reduced soil moisture retention. Peak surface water flows can increase, thus increasing surface erosion and topsoil loss.

In a study on the Tahoe National Forest (200 km S of Blacks Mountain), Froehlich et al. (1980) found that soil densities increased rapidly during the first few passes of any loaded logging equipment, with 60% of the compaction occurring after 6 trips. The increase in soil density after 20 trips was accompanied by a 43% reduction in soil macroporosity, an 80% reduction in saturated hydraulic conductivity, and a 67–78% reduction in water infiltration capacity. Air permeability of the surface soil decreased rapidly during the first few passes of the machines. Soil compaction, or change in bulk density, in that experiment was described by a regression equation that included an exponential expression for number of trips and a second term for soil-penetration resistance; these two variables defined 54% of the variance in the density data.

There is a negative correlation between seedling height growth and soil density for several conifer species (Froehlich and McNabb 1984). In a later study also on the Tahoe National Forest, Helms and Hipkin (1986) found that soil bulk density increased by 43, 30, and 18% on a landing, a skid trail, and areas adjacent to skid trails, and mean tree volume and initial survival volume per unit area were reduced by 69, 55, and 13%, respectively. Trees in areas of highest bulk density grew 43% less at age 1 and 13% less at age 15 than those in areas of lowest bulk density.

The eastside pine type of northeastern California contains numerous stands of timber that have been logged over the past 40 years. Skid trails are prominent in both the older and the more recent cuts; often relatively few conifers are growing in the skid trails. Reasons for this may include soil compaction from logging activity, seed periodicity and timing in relation to ground disturbance associated with that activity, climatic factors, biotic factors (seed-eating rodents), ground cover, and competition by other vegetation. An exploratory study was conducted to see if soil

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compaction could be a reason for slow recovery of logging skid trails in the eastside pine type of northeastern California.

STUDY AREA

The Blacks Mountain Experimental Forest, located in the eastside pine type of northeastern California (Fig. 1), contains experimental units harvested under various cutting methods. Some units were cut about 40 years ago (Hallin 1959), and others were cut and thinned during the past 5–10 years. Four of these units were studied, and these are hereafter designated by year of cutting and an identifying number. Timber harvest on two of them was undertaken in 1939 and 1942, with 80% of all trees larger than 30 cm diameter-breast-height (dbh) removed; there has been no use of the skid trails in those units since that time. In the other two units, all trees larger than 46 cm dbh were removed in 1979–80. Elevations ranged between 1,750 and 1,875 m. Slopes were 0–15%, with northwest aspects. Mean annual precipitation varied from 23 to 74 cm and averaged 46 cm during the period 1935–53 (Hallin 1959). Soils in the four units were similar. Storie et al. (1940) described the soils as being a reddish brown loam with a granular surface structure and neutral in reaction. The subsoil was clay loam. The texture was stony loam, with most of the soils being shallow—15–45 cm to lava bedrock, and possibly up to 90 cm deep in parts of one unit (39-6).

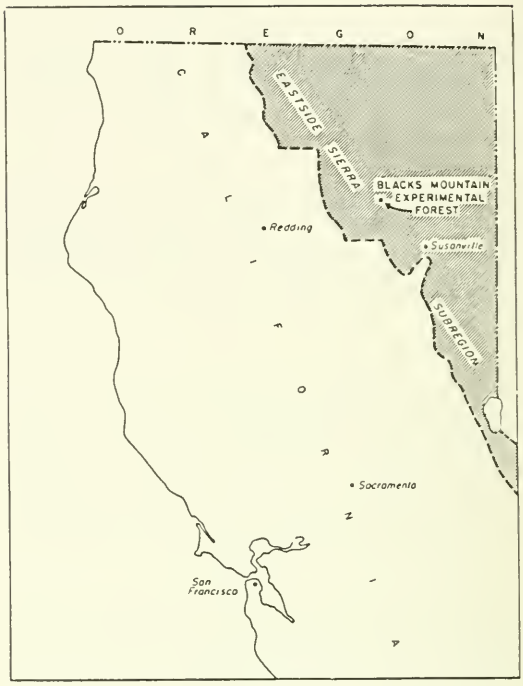

Fig. 1. Location of Blacks Mountain Experimental Forest and the eastside Sierra subregion in northern California (Hallin 1959). Copied with permission of the U.S. Forest Service.

METHODS

A 30° cone penetrometer was used to estimate bearing pressure. The cone had a diameter of 2.715 cm and a height of 5.067 cm. The penetrometer was pushed into the ground to the base of the cone and pressure on the scale was recorded. The scale reading was correlated with known weights on a cement floor in a laboratory and the following equation was developed:

Bearing pressure (kg/cm^2) = −0.14 + 1.29 × (scale reading) (R^2 = .997, MSE = 2.03, n = 16).

In-place soil bulk density was measured with a rubber-balloon apparatus (AASHTO 1978 Test Method T-205—density of soil in-place by rubber-balloon method). Soil was scooped out of a hole 12–16 cm deep and weighed. It was later dried in the lab at 105 C for 24 hrs. The difference in weights was divided by the dry weight to calculate moisture content. The volume of the hole was estimated using a balloon filled with water. The volume of water needed to fill the balloon was recorded. Wet and dry in-place densities of the soil were calculated.

Cone penetrometer readings were taken on and off the skid trails in each of the four units by random wandering throughout the units. Between 30 and 53 points were measured in each unit on skid trails, and the same number were taken in undisturbed areas.

Bulk density and soil moisture were measured at sample points in two of the old units and in the 1980 logging site (39-6, 42-2, and 80T-1). Three points were located in skid trails and three in adjacent, undisturbed areas in each unit. These plots were located 120–150 m from the landing (about one-third of the average maximum skidding distance). Moisture content was estimated at these 18

points and in a similar manner at 6 additional points in the fourth unit (79T-1). Penetrometer readings were taken at each of these bulk density points. Average soil moisture content was 20% (range 11–26%) in August 1984 when the field work was done. Correlations between penetrometer readings and bulk density estimates were analyzed with regression analysis. Potential impacts of tractor skidding and time since skidding on bearing pressure, bulk density, and soil moisture content were examined by an exploratory two-way Analysis of Variance (ANOVA) (SAS 1982). The independent variables were bearing pressure, bulk density, and soil moisture; and the dependent variables were tractor skidding (on and off skid trail), time since skidding activity (40 or 5 yrs), and interaction between these two variables. The residuals were tested for the null hypothesis that they were a random sample from a normal population, using the Shapiro-Wilk statistic, W. The probability < W ranged between 0.62 and 1.0 for the dependent variables (i.e., they were normally distributed). The interaction between tractor skidding and time since skidding was insignificant for the three variables (P = .07–.82).

RESULTS AND DISCUSSION

No relationship was found between dry-bulk density (measured with a balloon apparatus) and surface-bearing pressure (measured with a cone penetrometer); the coefficient of determination (R^2) was calculated at 0.015 (P = .63). The sample size of 17 was too small to make any definite conclusions. The penetrometer was not measuring bulk density to the same depth as the balloon apparatus; thus it is likely that surface compaction, measured by the penetrometer, may differ from that measured when a portion of the subsurface is included (balloon apparatus).

Mean bulk density on skid trails was 0.98 g/cm^3 (0.88–1.20 g/cm^3), and 0.81 g/cm^3 (0.77–0.85 g/cm^3) off skid trails. ANOVA did not show these differences to be significant (P = .25) for this small sample.

Froehlich et al. (1980) suggest that compaction should be measured as the average change in density in the surface 20 cm when the concern is for planted seedlings. That volume of soil serves as their root environment for several years and provides the principal nutrient stores for feeder roots of older trees as well. The balloon apparatus is better than the penetrometer for estimating bulk density to 20 cm depth, and it is actually measuring in-place bulk density. The penetrometer gives an approximate measure of soil-bearing pressure, which is only partially a function of soil density. Measurement of penetrometer resistance to a depth of 15–20 cm may have provided a basis for comparing bearing pressure (soil strength) with bulk density (H. A. Froehlich, Oregon State University, personal communication 21 November 1985).

TABLE 1. Effect of tractor skidding on bearing pressure.

Analysis of variance (SAS 1982)			
Source	df	F value	P>F
Skid trail	1	7.35	0.04 (significant)
Age of cut	1	3.02	0.14

There was no planting done in the experimental units. Surface compaction would impact natural establishment of plants from seed, and this is perhaps better measured with the penetrometer. Penetrometer resistance in the newer trails compared to the 40+-year-old trails was approximately 60% greater (5.01 vs. 3.06 kg/cm^2). However, an ANOVA test did not show this difference (age of cut) to be significant (P = .14), a result of having performed only two replications of each main effect (Table 1).

ANOVA test results were significant only for the effect of tractor skidding on bearing pressure (P = .04, Table 1). Again, sample sizes were not large enough for this to be a confirmatory test. The 95% confidence limits for bearing pressure (kg/cm^2) overlapped (Table 2):

On skid trail: 4.03 kg/cm^2 ± 2.04 kg/cm^2 (1.99–6.07)

Off skid trail: 2.52 kg/cm^2 ± 0.22 kg/cm^2 (2.30–2.74)

It also remains to be shown whether an increase in surface-bearing pressure from 2.5 kg/cm^2 to 4.0 kg/cm^2 is significant from the standpoint of natural plant establishment. Even after 40 years the older trails were approximately 20% more resistant to the penetrometer than areas adjacent to trails (Table 2, units 39-6 and 42-2).

TABLE 2. Bearing pressures based on penetrometer readings.

Experimental unit	Off skid trail n	Off skid trail Mean (kg/cm^2)	Off skid trail Std. dev.	On skid trail n	On skid trail Mean (kg/cm^2)	On skid trail Std. dev.
39-6	30	2.64	0.96	30	2.56	0.69
42-2	51	2.41	0.96	51	3.56	1.72
80T-1	49	2.38	1.14	49	4.44	1.73
79T-1	53	2.65	0.91	53	5.58	2.02
Mean of units	4	2.52	0.14	4	4.03	1.28

ACKNOWLEDGMENTS

I am very grateful to Earl Alexander, Gordon Keller, and Robert Powers of the U.S. Forest Service, Henry Froehlich of Oregon State University, and John Helms of the University of California at Berkeley for their assistance.

LITERATURE CITED

AASHTO 1978. Standard method of test for density of soil in-place by the rubber-balloon method. AASHTO: T205-64(1974).

ALEXANDER, E. B. 1985. Principles and review. Pages 1–74 *in* Soil disturbance and compaction in wildland management. USDA For. Serv., Region 5, Earth Res. Monogr. 8.

AYERS, P. D., AND J. V. PERUMPRAL. 1981. Moisture and density effects on cone index. Amer. Soc. Agric. Engineers summer meeting. Paper No. 81-1047. St. Joseph, Michigan. 15 pp.

FROEHLICH, H. A., J. AZEVADA, P. CAFFERATA, AND D. LYSNE. 1980. Predicting soil compaction of forested land. Final Project Rept. under Coop. Agreement 228, USDA U.S. For. Serv. PNW and Missoula Equipment Development Center. 120 pp.

FROEHLICH, H. A., AND D. H. MCNABB. 1984. Minimizing soil compaction in Pacific Northwest forests. Pages 159–192 *in* E. L. Stone, ed., Forest soils and treatment impacts. Dept. For., Wildl., and Fish., University of Tennessee, Knoxville.

HALLIN, W. E. 1959. The application of unit area control in the management of ponderosa-Jeffrey pine at Blacks Mountain Experimental Forest. USDA For. Serv., Washington, D.C. Tech. Bull. 1191. 96 pp.

HELMS, J. A., C. HIPKIN, AND E. B. ALEXANDER. 1986. Effects of soil compaction on height growth of a California ponderosa pine plantation. Western J. Appl. For. 1(4): 104–108.

HELMS, J. A., AND C. HIPKINS. 1986. Effects of soil compaction on tree volume in a California ponderosa pine plantation. Western J. Appl. For. 1(4): 121–124.

MCDONALD, P. M. 1983. Climate, history, and vegetation of the eastside pine type in California. Pages 1–16 *in* T. F. Robson and R. B. Standiford, eds., Management of the eastside pine type in northeastern California, proceedings of a symposium. N. California Soc. Amer. For. SAF 83-06. Arcata, California.

ROY, D. F. 1983. Natural regeneration. Pages 87–102 *in* T. F. Robson and R. B. Standiford, eds., Management of the eastside pine type in northeastern California, proceedings of a symposium. N. California Soc. Amer. For., SAF 83-06. Arcata, California.

STATISTICAL ANALYSIS SYSTEM (SAS). 1982. SAS user's guide: statistics, 1982. 3d edition. SAS Institute Inc., Cary, North Carolina. 548 pp.

STORIE, R. E., W. W. WEIR, AND R. C. COLE. 1940. Soil survey of Blacks Mountain Experimental Forest. Div. of Soils, University of California at Berkeley. On file at USDA For. Serv., PSW Expt. Sta., Redding, California.

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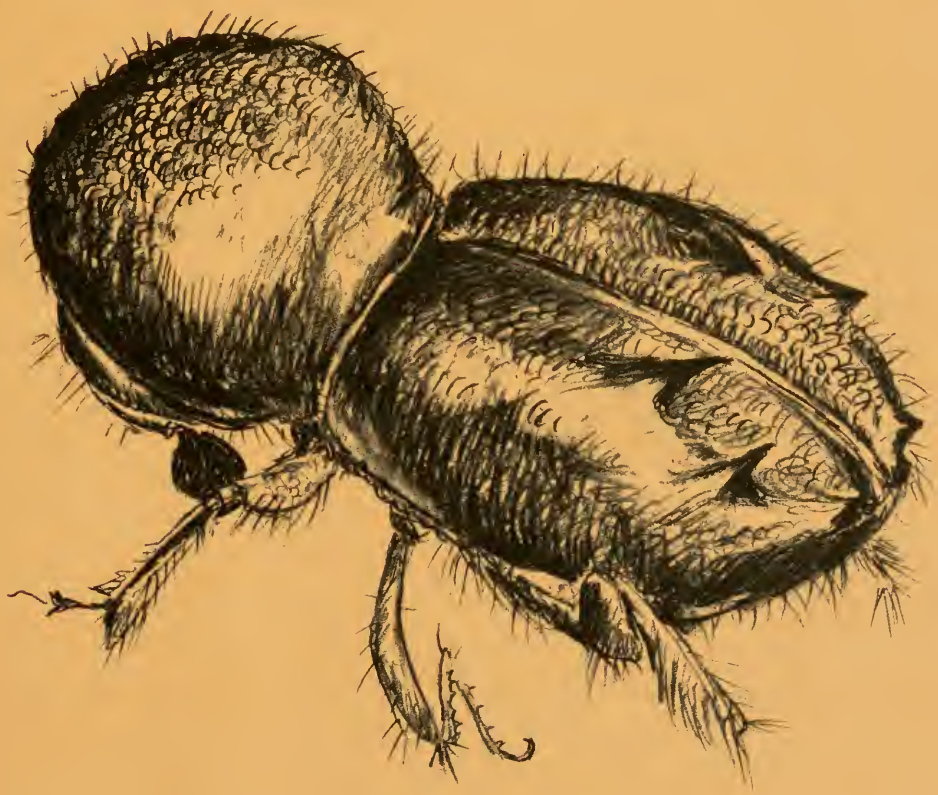

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A FOURTH NEW SAUROPOD DINOSAUR FROM THE UPPER JURASSIC OF THE COLORADO PLATEAU AND SAUROPOD BIPEDALISM

James A. Jensen[1]

ABSTRACT.—The new sauropod, *Cathetosaurus lewisi*, is named and assigned to the Camarasauridae; it was collected from the Upper Jurassic Morrison Formation in western Colorado in 1967. Novel structural features of the skeleton in this genus, particularly in the axial skeleton, enabled it to assume and function to an unknown degree in a bipedal posture. Comparisons are made between *C. lewisi* and previously described sauropods. The following problems of sauropod locomotion are discussed: (1) sauropods lack two elements, sesamoids and patella, present in titanotheres; (2) sauropod limb and foot musculature, lacking leverage, is very inferior to that of titanotheres; (3) no previously described sauropod displays adequate structural specializations for voluntary bipedalism comparable to that of the new genus *Cathetosaurus;* (4) great weight and cartilaginous limb and foot joint structure restricted sauropods to a slow tempo of locomotion, suggesting a moderate to low rate of catabolic metabolism. Mammal and sauropod foot bones and their function are compared, and comparisons are made between the weight and structure of modern mobile machines and the locomotion and movement of large sauropods. Occurrence and taphonomy of *C. lewisi* are discussed.

Three sauropod dinosaurs, *Ultrasaurus macintoshi*, a brachiosaurid, *Supersaurus vivianae*, a (?)diplodocid, and *Dystylosaurus edwini*, family indeterminate, were recently described (Jensen 1985) from the Uncompahgre fauna (Jensen 1985) of the Jurassic Morrison Formation on the Southwestern Colorado Plateau in western Colorado. Diagnostic elements of these sauropods were collected from Dry Mesa Quarry, above the mouth of Middle Fork of Escalante Creek, on the eastern Uncompahgre monocline. The articulated skeleton of a fourth new, North American Jurassic sauropod, also from the Uncompahgre fauna, is described here as *Cathetosaurus lewisi*, new genus, new species. It was collected in 1967 from Dominguez/Jones Quarry on the eastern monocline of the Uncompahgre Upwarp, near the confluence of Big and Little Dominguez creeks.

The basic novelty of this fourth new sauropod is seen in the structural specializations of its skeleton, which enabled it to elevate its preacetabular body and maintain a bipedal posture. No sauropod genus has been previously described with comparable structural features. I do not suggest that this new sauropod was capable of significant bipedal locomotion, as if reverting to the supposedly bipedal behavior of an ancestral prosauropod, but only that it could stand bipedally and possibly engage in limited activities, one of which may have been arboreal foraging.

SYSTEMATIC PALEONTOLOGY

Order Saurischia
Suborder Sauropodomorpha
Infraorder Sauropoda
Family Camarasauridae
Cathetosaurus lewisi n. gen., n. sp.

ETYMOLOGY.—Greek: *kathetos*, perpendicular, referring to an ability to stand erect on its rear legs; *sauros*, lizard. Specific name *lewisi*, honoring Mr. Arnold D. Lewis, stout

[1]Earth Sciences Museum, Brigham Young University. Present address: 2821 N. 700 E., Provo, Utah 84604.

companion of the trail, who patiently trained me in laboratory and field work.

HOLOTYPE.—BYU 9740, an articulated sauropod skeleton including: atlas/axis plus 12 cervical vertebrae with ribs; right humerus, radius, ulna, and partial manus; 12 dorsal vertebrae, 1 dorsosacral vertebra; 20 dorsal ribs; 4 sacral vertebrae, and ribs co-ossified with 1 ilium; 1 pubis; both ischia; 43 anterior caudal vertebrae with many articulated chevrons.

TYPE LOCALITY.—Dominguez-Jones Quarry, Pit 1, above confluence of Big and Little Dominguez creeks; T14S, R98W, New Mexico Principal Meridian, Mesa County, Colorado.

HORIZON.—Approximately 10 m above the base of the Brushy Basin Member, Morrison Formation, Upper Jurassic Period.

COLLECTOR.—James A. Jensen, 1967.

DIAGNOSIS.—All cervical neural spines bifid except atlas/axis; prominent pre-epipophyseal ridges, not reported in any other sauropod, present on superior surfaces of all cervical postzygapophyses; suprapostzygapophyseal laminae on cervical vertebrae not aligned nor confluent with epipophyses, as in all other sauropods; all dorsal spines bifid except last dorsal; pelvis with anterior iliac processes rotated ventrally around transverse acetabular axis, lowering anterior point of iliac blade 18 to 20 degrees below axis of vertebral column, in contrast to 4 degrees in *Diplodocus*, a bifid-spined genus, and 7 degrees in the single-spined genus, *Haplocanthosaurus;* metapophyseal spurs directed lateroventrally on all dorsal and sacral neural spines; prediapophyseal spurs projecting from anterior face of diapophyses on dorsal transverse processes; diagonal bone-struts connecting metapophyseal spurs on second and third sacral neural spines with subhorizontal supracostal plates on dorsal edge of third and fourth sacral ribs. All other North American Jurassic sauropods, including *Apatosaurus*, *Diplodocus*, *Camarasaurus*, and the single-spined *Haplocanthosaurus*, lack such plates, spurs, and bone-struts; chevrons on anterior third of tail one-third longer than those of *Camarasaurus supremus* Cope, as arbitrarily arranged by Osborn and Mook (1921).

DESCRIPTION.—*Cathetosaurus* is assigned to Camarasauridae Cope (1877) on the basis of its general structural affinities to that family, particularly in its axial and appendicular skeletons, including: bifid cervical and thoracic neural spines; strongly opisthocoelous presacral vertebrae; heavy thoracic ribs; ischium with long, slender shaft not distally expanded as in the Apatosauridae and Diplodocidae; pubis thick and massively constructed, distally flattened but not rounded as in the Apatosauridae, Diplodocidae, and *Haplocanthosaurus*.

At least seven specialized skeletal structures in *C. lewisi*, not seen in any other camarasaurid genus nor in any other sauropod family, qualify the specimen as a new genus and species. These unique features include, but are not restricted to: (1) neural spine bifurcation (Fig. 6B) beginning directly behind the atlas/axis on spine number three, instead of at the fifth or sixth spine, as in almost all other sauropods. Bifurcation continues from the third cervical spine to the last dorsal, or first presacral, spine, in which the apex of the spinal crest is compressed anteroposteriorly and slightly indented but not bifid. The depth of bifurcation is greatest through the cervicodorsal transition, diminishing to the indented crest in the first presacral spine. The cervicodorsal transition was well preserved in the skeleton as found, but badly damaged during collection, obscuring the precise vertebrae involved.

(2) Pre-epipophyseal ridges (Fig. 8a [per]) extending anteriorly from the epipophyses, lateral to the suprapostzygapophyseal laminae, on the superior surface of the cervical postzygapophyses. These ridges pass the base of the neural spine laterally (Fig. 8A) and extend to, or near, the anterior margin of the transverse process and are functionally coequal with prediapophyseal spurs on the dorsal transverse processes, inserting spinal ligaments originating on the metapophyses of the preceding neural spine.

(3) Prediapophyseal spurs (Figs. 3B, $5B_1$–B_2) project from the anterior diapophyseal faces of the transverse processes on all dorsal vertebrae (Fig. 9A–B).

(4) Metapophyseal spurs (Figs. 3B–C, $4B_1$, 5A–C, 6B, 9A–B) on lateral borders of the spinal metapophyses. Apparently strong ligature originated on these spurs, passing diagonally, posteroventrally, to insert on the prediapophyseal spurs located anteriorly on the diapophyses of the transverse process of the succeeding vertebrae (Fig. 9A).

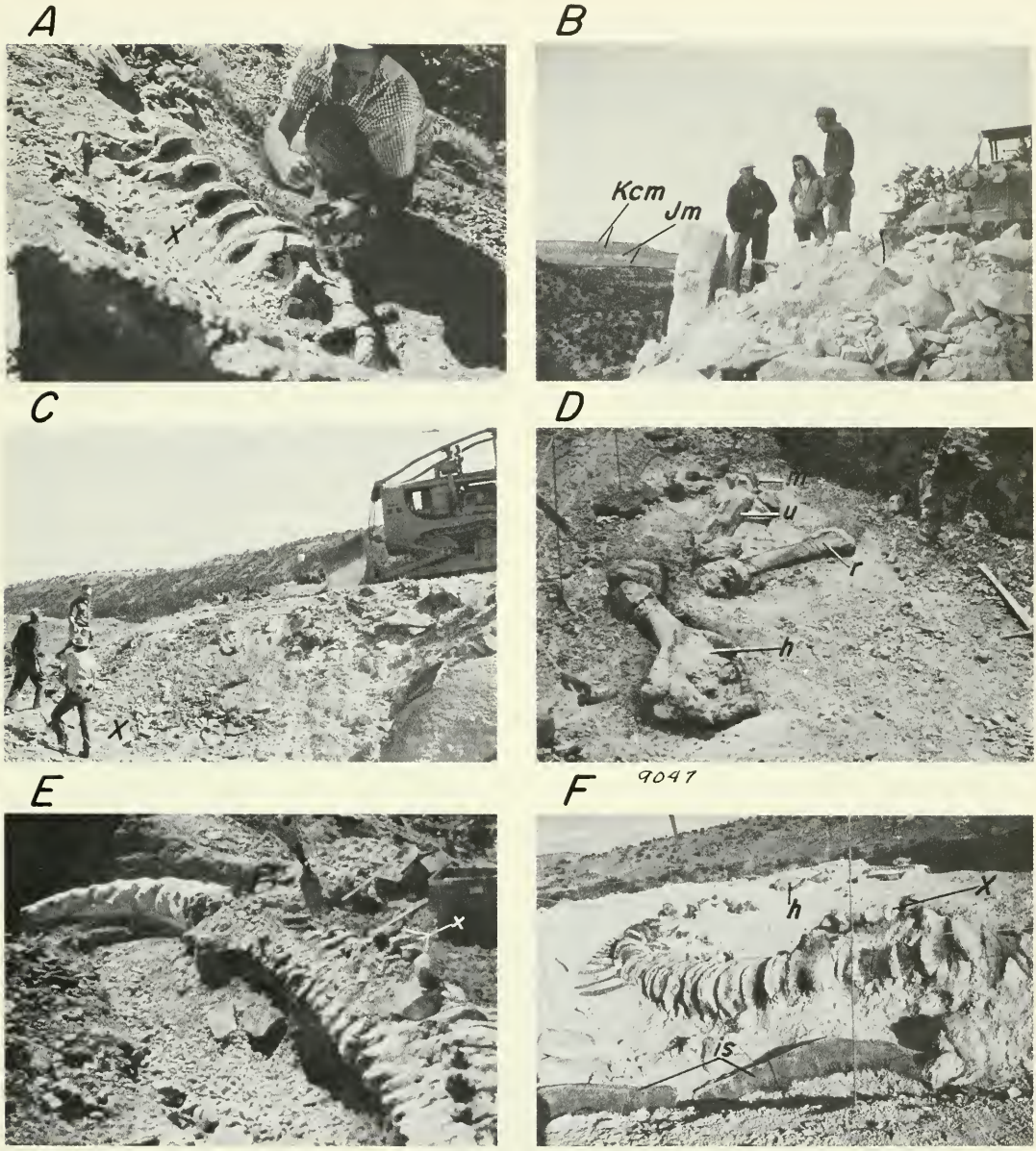

Fig. 1. Discovery and working at Dominguez/Jones Quarry: A, exposed right side of sacral vertebrae at discovery point; B, road building from top of Dakota Sandstone down to Morrison Formation; figures left to right, D. E. and Vivian Jones, discoverers of locality, Mike Heinz, excavator; C, beginning of excavations; D, forelimb and partial manus of *Cathetosaurus lewisi*; E, skeleton of *C. lewisi*; F, ischia and caudal section of *C. lewisi* partially excavated. Abbreviations: h–humerus; is–ischia; Jm–Jurassic Morrison Formation; Kcm–Cretaceous Cedar Mountain Formation; m–manus; r–radius; u–ulna; X–discovery point.

(5) Subcircular supracostal plates, disposed in a near-horizontal plane on the dorsal edge of the sacral ribs (Fig 4C [sp]) with ligature and bone-struts from metapophyseal spurs (Figs. $4B_1$, C_1) inserting their anterior borders. These plates originated sacrocaudal musculature passing caudad to insert serially on caudal neural arches.

(6) Sacral bone-struts connecting metapophyseal spurs with supracostal plates. These struts may have ossified from diagonal ligaments between sacral metapophyseal spurs

and supracostal plates (Fig. $4C_1$ [ds, sp]).

(7) Ilia rotated around a transverse acetabular axis, lowering the anterior iliac processes approximately 0–20 degrees, ventrally, below the axis of the vertebral column (see definition of 0 in Fig. 2A), compared to 4 degrees in *Diplodocus* sp. (Fig. 2B), and 7 degrees in *Haplocanthosaurus* sp. (Fig. 2C). Orientation of the ilia to the sacral vertebrae in the composite pelvis of *Camarasaurus*, restored by Osborn and Mook (1921, Fig. 2D) may be incorrect, being modeled with its anterior iliac points located above instead of below the sacral vertebral axis.

DISCUSSION.—Discussed below are some of the most significant structural features identifying *C. lewisi* as novel and the only North American Jurassic sauropod identified to date capable of voluntary bipedalism. *C. lewisi* possessed an interspinal channel carrying the ligamentum nuchae–ligamentum apicum dorsalis complex from skull to pelvis. This channel is formed of bifid neural spines, involving the majority of neural arches between the skull and pelvis. The length of this channel contrasts with much shorter intraspinal channels in all other sauropods, such as *Apatosaurus* (Gilmore 1936), in which bifurcation begins in the fifth to sixth cervical neural arch and ends in the fifth to sixth dorsal neural arch. Being shorter than the interspinal channel in *C. lewisi*, the same channel in bifid-spined sauropods provided a ligamentaceous, long-muscle group of limited length, restricting its effectiveness to elevating the neck, whereas extension of the interspinal channel from skull to pelvis in *C. lewisi* provided an elongate muscle complex capable of elevating the entire preacetabular body from skull to pelvis. This previously undescribed interspinal channel length is here deemed prima facie evidence of an ability to assume and sustain a bipedal posture. The continuum of massive soft-tissue flexors filling an intraspinous channel from skull to pelvis demonstrates a complete involvement of the preacetabular body, including the skull, neck, forelimbs, and thorax, as the anterior body rotated around a transverse acetabular axis allowing the genus to attain a balanced, bipedal stance. Supporting this claim, the long chevrons (Fig. 7D), compared with other genera in the Camarasauridae, increased the anterior sagittal plane and, consequently, weight of the tail, providing a more effective counterbalance to preacetabular weight.

A remarkably strong diagonal intervertebral reinforcement system of ligaments between neural spines and transverse processes in all presacral neural arches is demonstrated in *C. lewisi* by the presence of pre-epipophyseal ridges on cervical neural arches (described below); matching intervertebral, prediapophyseal, and metapophyseal spurs on dorsal neural arches; and by diagonal intervertebral bone-struts or ligaments in the sacrum, the four or five sacral spines being thus diagonally connected to supracostal plates on the dorsal edge of the sacral ribs. The principal function of prediapophyseal spurs is adduced to be the insertion of strong muscles and ligature from metapophyseal spurs on neural spines (Figs. 9A–B) of the preceding vertebra. This method of intervertebral cross-, or diagonal, bracing and reinforcement may have been present to some degree in all sauropods, but the importance of such a system in *C. lewisi* is evident by the prominence of the rugose, spurlike processes at the points of origin and insertion of the diagonal ligaments (Figs. 5B–C). The pre-epipophyseal ridges extending forward from the cervical epipophyses (Fig. 8A [per]) were independent from, and parallel to, the suprapostzygapophyseal laminae (Fig. 8A [spozl]), providing for intervertebral cross-bracing in the cervical series of *C. lewisi*. These epipophyseal ridges originate on the superior surface of the postzygapophyses, bypassing the base of the neural spine to reach the anterior margin of the transverse processes. Epipophyseal ridges and metapophyseal and prediapophyseal spurs (Figs. $3B–B_1$) are evidence of a stronger ligamental connection between dorsal neural spines and transverse processes than is claimed or inferred in the analysis of any previously described sauropod. For clarity, interspinal cross-bracing in *C. lewisi* is further described as strong tendons attaching each neural spine to the distal end of the diapophysis on the succeeding transverse process. This diagonal reinforcement was effected by ligaments in cervical and dorsal vertebrae, and with ligaments on three sacral neural arches and bone-struts on two others (Figs. 9A–B). These bone-struts connect the second sacral metapophyses to subhorizontal supracostal plates (Fig. 3C) on the dorsal

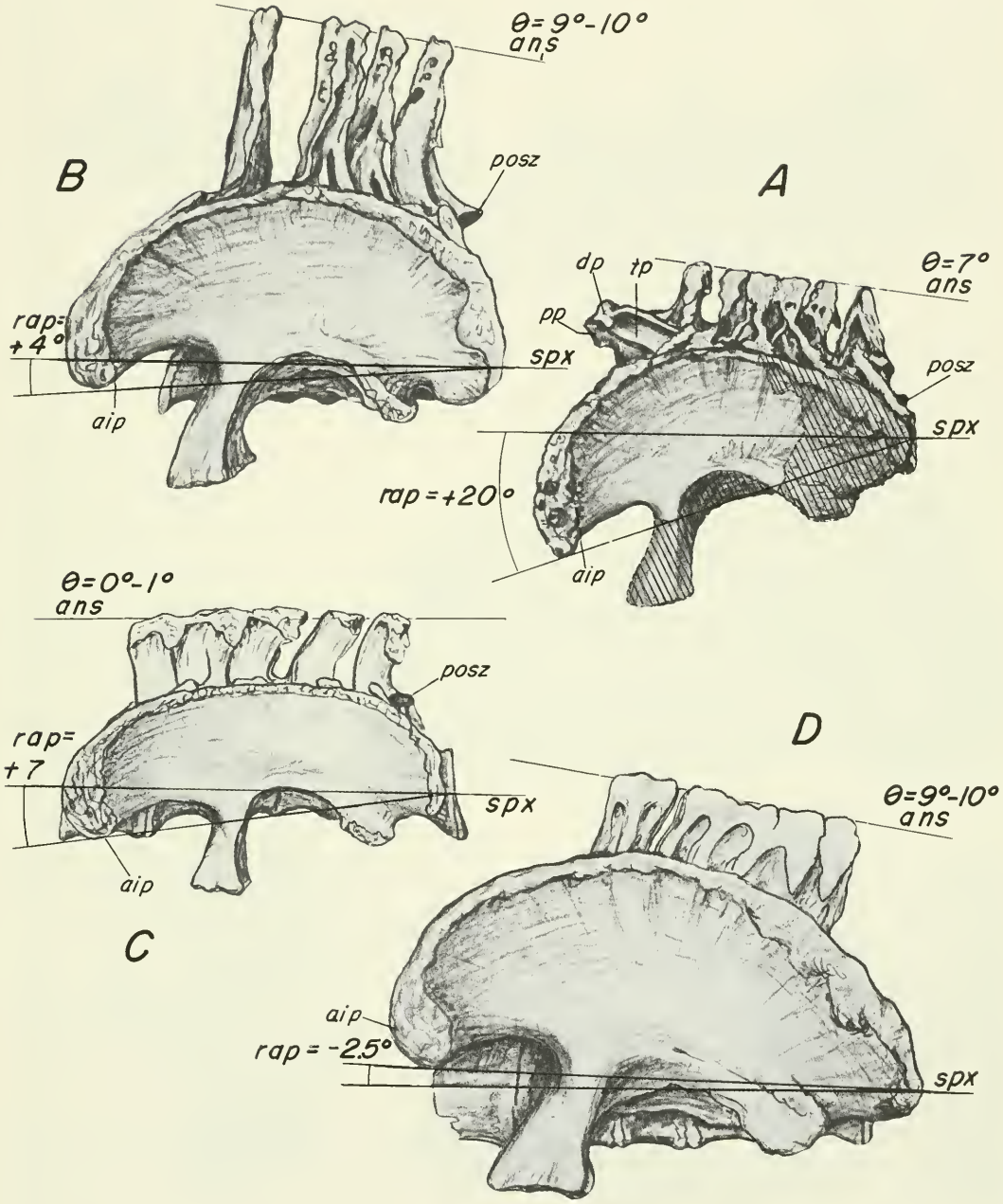

Fig. 2. Four sauropod pelves: A, *Cathetosaurus lewisi*; B, *Diplodocus carnegie*; C, *Haplocanthosaurus priscus*; D, *Camarasaurus supremus*. Abbreviations: aip–anterior iliac process; θ–angle between vertebral axis (spx) and apices of neural spines (ans); rap–degrees of rotation of anterior iliac process counterclockwise below vertebral axis. Drawings not to scale.

edges of the third sacral ribs; bone-struts connect the third sacral metapophyses to supracostal plates on the dorsal edges of the fourth sacral ribs (Fig. $4C_1$). The presence of such a well-developed system of intervertebral diagonal bracing is seen here as an advantage in elevating the preacetabular body to a bipedal stance by providing highly integrated,

relatively inelastic, connective tissue between skull and pelvis, and once in a bipedal-tripodal position a reinforced vertebral column may have been an advantage in successful bipedal activities. Rudimentary metapophyseal spurs occur on the sacral neural spines of other mature sauropods, including *Diplodocus* (Holland 1901), *Camarasaurus* (Osborn and Mook 1921), and *Haplocanthosaurus* (Hatcher 1903), but in those genera no diagonal bone-struts are present connecting their rudimentary spurs to sacral ribs. These three genera also lack prominent prediapophyseal and dorsal metapophyseal spurs and independent cervical epipophyseal ridges. Hatcher (1901) notes that in *Diplodocus*

> the inferior blades of the diapophyseal laminae are broadly expanded in the anterior caudals and terminate externally and superiorly in broad rugosities, providing great surface for the attachment of the powerful dorsocaudal musculature, which in life may have aided in the alteration of anterior body position from the usual horizontal or quadrupedal position to a more erect bipedal or tripodal position . . . [which] was perhaps less frequently assumed during the life of the individual.

Diplodocus lacked the more basic structural reinforcements and morphological adaptations supporting bipedalism, which are present in the skeleton of *C. lewisi* (this paper).

Subcircular supracostal plates provided an anchoring junction for ligaments and bone-struts extending from the sacral spines to stabilize the supracostal plates against the posterior pull generated by contraction of strong sacrocaudal musculature. These supracostal plates (Figs. 3C, 4C–C_1), with their distal borders depressed 10 to 15 degrees, rest subhorizontally on the dorsal edge of the sacral ribs. The superior surfaces of the plates are striated, with the striae overriding anterior and posterior margins of the plate, parallel to the axis of the vertebral column and to the anteroposterior line of stress generated by powerful sacrocaudal musculature during bipedal activities.

Ventral rotation of the anterior end of the ilium to a comparatively extreme degree around the acetabular axes maintained a center of gravity, or locus of force, within the strongest cross-section of the acetabulum when the anterior body was elevated to a bipedal posture. This 20-degree rotation of the ilia, relative to the sacral vertebrae, in *C. lewisi* (Fig. 2A), verified by co-ossification of all pelvic elements, is interpreted here as strong evidence for persistent, voluntary bipedalism. When the anterior body was elevated to a bipedal stance, the most heavily buttressed sections of the acetabulae were rotated to an optimum weight-bearing position above the femoral axes, whereas in other sauropods, except the brachiosaurs (discussed later), elevation of the anterior body with the concomitant rotation of the pelvis around a transverse acetabular axis would have positioned a major portion of body weight on the weakest midshaft, unbuttressed cross-section of the pubic peduncle. An additional advantage achieved by the 20-degree ventral rotation of the anterior iliac processes in *C. lewisi* may have been that of increased support to the ventral surface of the visceral mass during bipedal posture. This support could have been provided in a manner similar to, but to a lesser degree than, that seen in the large edentates such as *Megatherium americanum* Cuvier and *Megalonyx jeffersoni*, which were habitual bipedal arboreal feeders (Scott 1937). The anterior iliac processes of these edentates flare out on a subhorizontal plane, adding support to their visceral mass during bipedal activity. Compared with *C. lewisi*, the position of the anterior iliac processes in most other sauropods could have offered little support to the ventral surface of the visceral mass, were those sauropods capable of raising their anterior body to an erect, bipedal stance.

Orientation of the ilia to the axis of the sacral vertebrae in apparently obligate quadrupeds, such as the Diplodocidae and Titanosauridae, when verified by co-ossification of all pelvic elements, was generally less than 10 degrees (Fig. 2). However, the brachiosaurs with single neural spines throughout their spinal column—and for which, as far as I am able to learn, no well-preserved pelvis exists to be measured—may have evolved anteroventrally rotated ilia similar to the ilio-sacral relationship seen in *C. lewisi*.

The thorax in the Brachiosauridae was significantly elevated by front limbs equal to, or longer than, rear (Riggs 1921, Janensch 1936). Because of their great size (80 tons calculated, Colbert 1983), members of this family were probably obligate quadrupeds. Elevation of their thorax on long front limbs would have

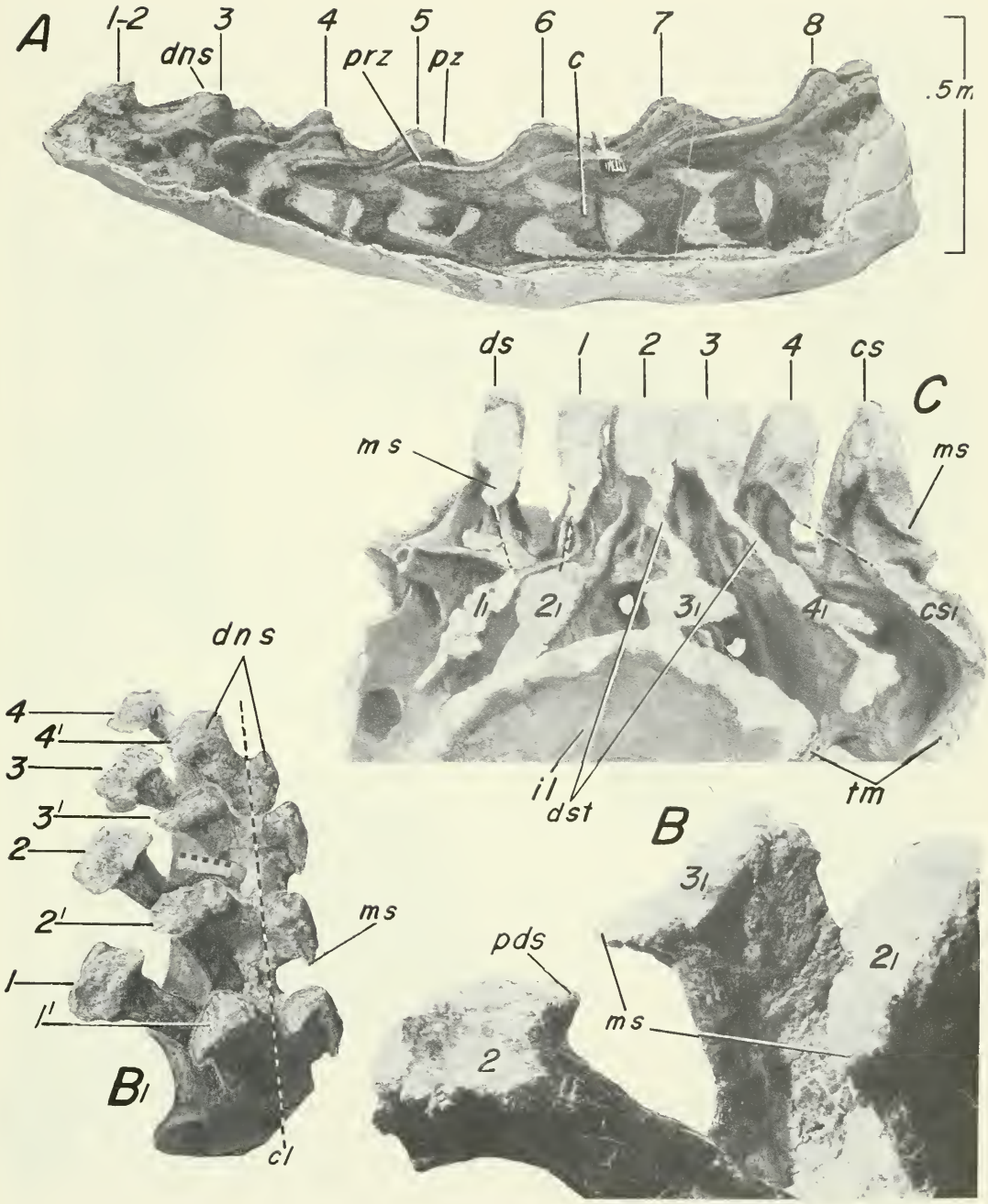

Fig. 3. Cervical, sacral, and dorsal vertebrae of *Cathetosaurus lewisi:* A, 1–8, cervical series from atlas/axis to number eight (partially prepared). B–B_1, metapophyseal (lts) and prediapophyseal (pds) spurs on *C. lewisi* presacral vertebrae. B, two metapophyseal spurs (lts), one prediapophyseal spur (pds). B_1, four transverse processes (1–4), four metapophyses (1_1–4_1): 1, 1_1 are on same neural arch, posterodorsal view. C, *C. lewisi* sacrum with supracostal plates (1_1-csi), neural spines (ds-cs), left lateral view. Abbreviations: c–centrum; cl–center line; cs–caudosacral; csi–caudosacral supracostal plate; dns–bifid neural spines; ds–dorsosacral spine; dst–diagonal metapophyseal bone struts to supracostal plates (3_1, 4_1); il–ilium; prz–prezygapophysis; lts–metapophyseal spurs; pds–prediapophyseal spur; pz–postzygapophysis; tm–teeth marks.

rotated their ilia around a transverse acetabular axis, locating the weakest, unbuttressed cross-section of the pubic peduncular shaft above the femoral axis—if the anterior ilium was in fact ventrally rotated less than 10 degrees below the spinal axis, as it is in other sauropod families including the Apatosauridae and Diplodocidae. I collected a *Brachiosaurus* ilium (described elsewhere) from the Uncompahgre fauna in 1975 and verify the shaft of the pubic peduncle as being thin and fragile, suggesting the anterior ilium was rotated ventrally, below the spinal axis, in a manner similar to the 20-degree ventral rotation of the anterior iliac processes of *C. lewisi* (Fig. 2A). The only complete brachiosaur pelvis I am aware of is mounted as part of a restored display skeleton standing in the Museum für Naturkunde, Berlin (Janensch 1936). In this mount the anterior iliac processes appear to be ventrally rotated approximately 15 degrees below the spinal axis; however, I have been unable to find a report on the accuracy of the restoration.

The pubic and ischiadic peduncles of *C. lewisi* are missing from the only ilium present with the skeleton (Figs, 4C–C_1), and so their relative strength and morphology are incompletely known except that, as previously noted, the 20-degree ventral rotation of the anterior end of the ilium, relative to the spinal axis, is verified by co-ossification of all pelvic elements present (Fig. 2A).

Jurassic sauropods such as *Barosaurus*, *Diplodocus*, and *Apatosaurus*, none of which had anterior iliac processes ventrally rotated more than a few degrees below the spinal axis, nor which displayed significant evidence of structural reinforcement of the spine and pelvis, were recently illustrated (Bakker 1986) as habitual, bipedal, arboreal feeders, although no convincing structural evidence to support such a claim is provided, except to note the possible value of tall sacral spines. The incompletely known sauropod *Barosaurus* was also illustrated by Bakker (1986) in an erect, bipedal pose, foraging high in trees, despite a considerable lack of important information on its skeleton. Lull (1919) illustrates *Barosaurus*, known from only one partial, badly eroded skeleton. This material consists of 4 incomplete posterior cervical vertebrae, 10 dorsal and 19 caudal vertebrae, a massive chunk of sacrum, and fragments of a badly eroded appendicular skeleton. Lull's restoration (1919: Pl. VII), overlaid on a partial skeleton of *Diplodocus* for comparison, interprets the basal cervical and anterior dorsal vertebrae of *Barosaurus* as indicating a distinct upward flexure at the base of the neck, a feature not reported in other Jurassic sauropods. This upturn flexure at the base of an apparently long neck would have allowed *Barosaurus* to feed arboreally as a quadruped, providing a convincing alternative to Bakker's (1986) representation. Marsh (1890) placed *Barosaurus* in the Atlantosauridae, together with *Atlantosaurus* and *Apatosaurus*, while describing it as "being very much like *Diplodocus*."

In addition to Bakker (1986), other authors (McLoughlin 1979), ignoring the empirical demands of biomechanics, have painted fanciful scenarios depicting various sauropods as being capable of voluntary bipedalism. McLoughlin (1979:60) even suggests a prehensile tail on *Diplodocus*, wrapped around a tree "to steady itself on its hind legs." None of these imaginative claims is supported by verifiable evidence from structural morphology published in legitimate scientific descriptions. The present paper is the first to definitively describe a sauropod capable of sustained, voluntary bipedalism, with incontrovertible evidence recovered from existing skeletal elements.

The hypothetical postural transition from a bipedal prosauropod to a heavy quadrupedal sauropod (Romer 1956) may have occurred as an evolutionary response to environmental and other factors; but, prior to this paper, the notion that after becoming heavily quadrupedal, optional bipedalism was still possible, was without any substantiating physical evidence. Some sauropods may have been able to rise up momentarily to a semibipedal, or tripodal posture, but none, prior to the discovery of *C. lewisi*, display any convincing structural, or morphological, evidence of a capability for a sustained, bipedal posture.

Various relevant factors apply to this paper's claim that bipedalism in sauropods is presently restricted to one species, and these factors need further discussion.

SAUROPOD BIPEDALISM

The relevant laws of physics cannot be ignored in calculating the probable stresses

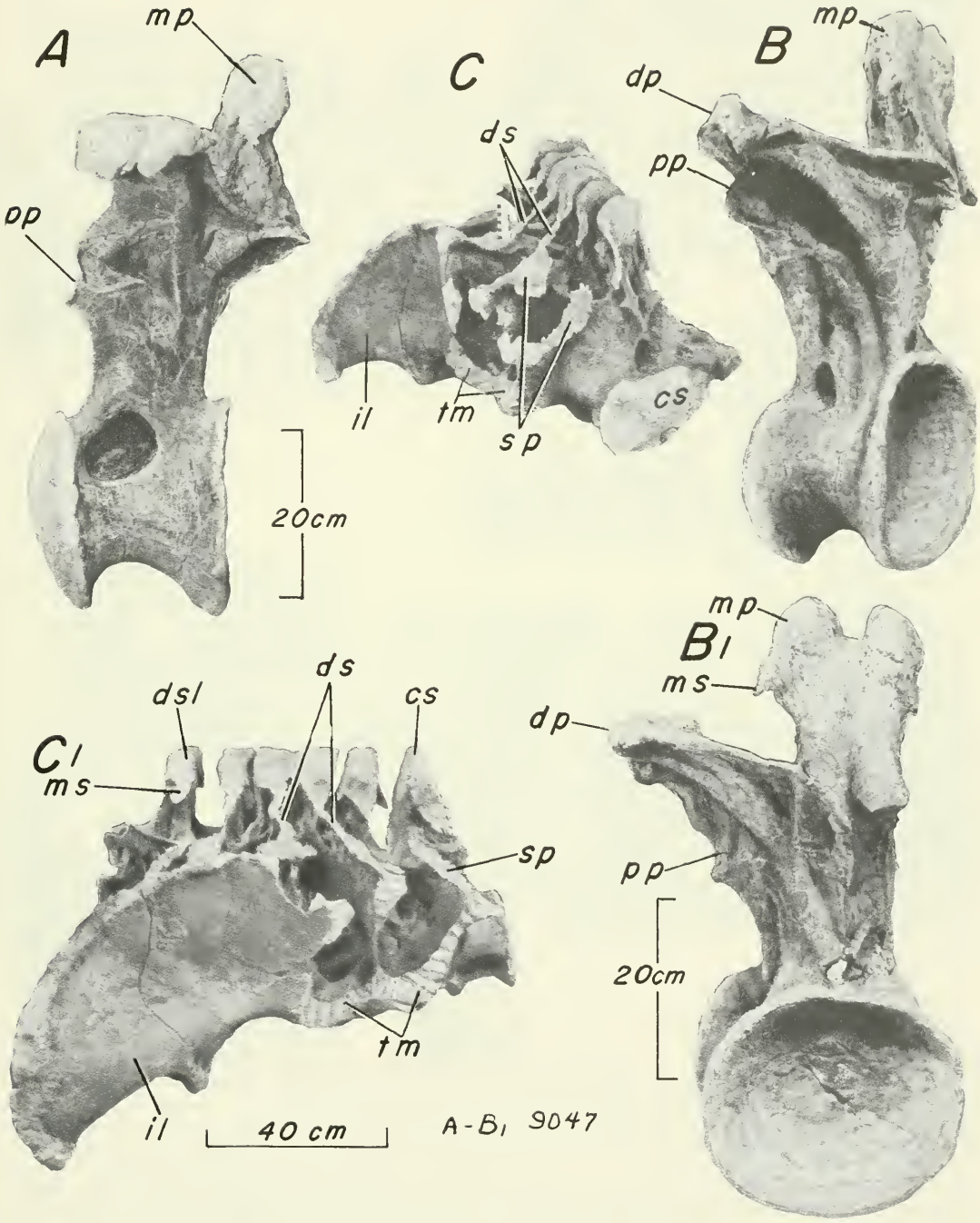

Fig. 4. *Cathetosaurus lewisi* presacral vertebrae and sacrum: A, second presacral vertebra, left lateral view; B, second presacral vertebra, posterolateral view; B_1, second presacral vertebra, posterior view; C, sacrum, oblique posterior view; C_1, sacrum, left lateral view. Abbreviations: cs–caudosacral vertebra; dp–diapophysis; dsl–dorsosacral vertebra; ds–diagonal bone strut; il–ilium; ms–metapophyseal spur; mp–metapophysis; pp–parapophysis; sp–supracostal plate; tm–teeth marks.

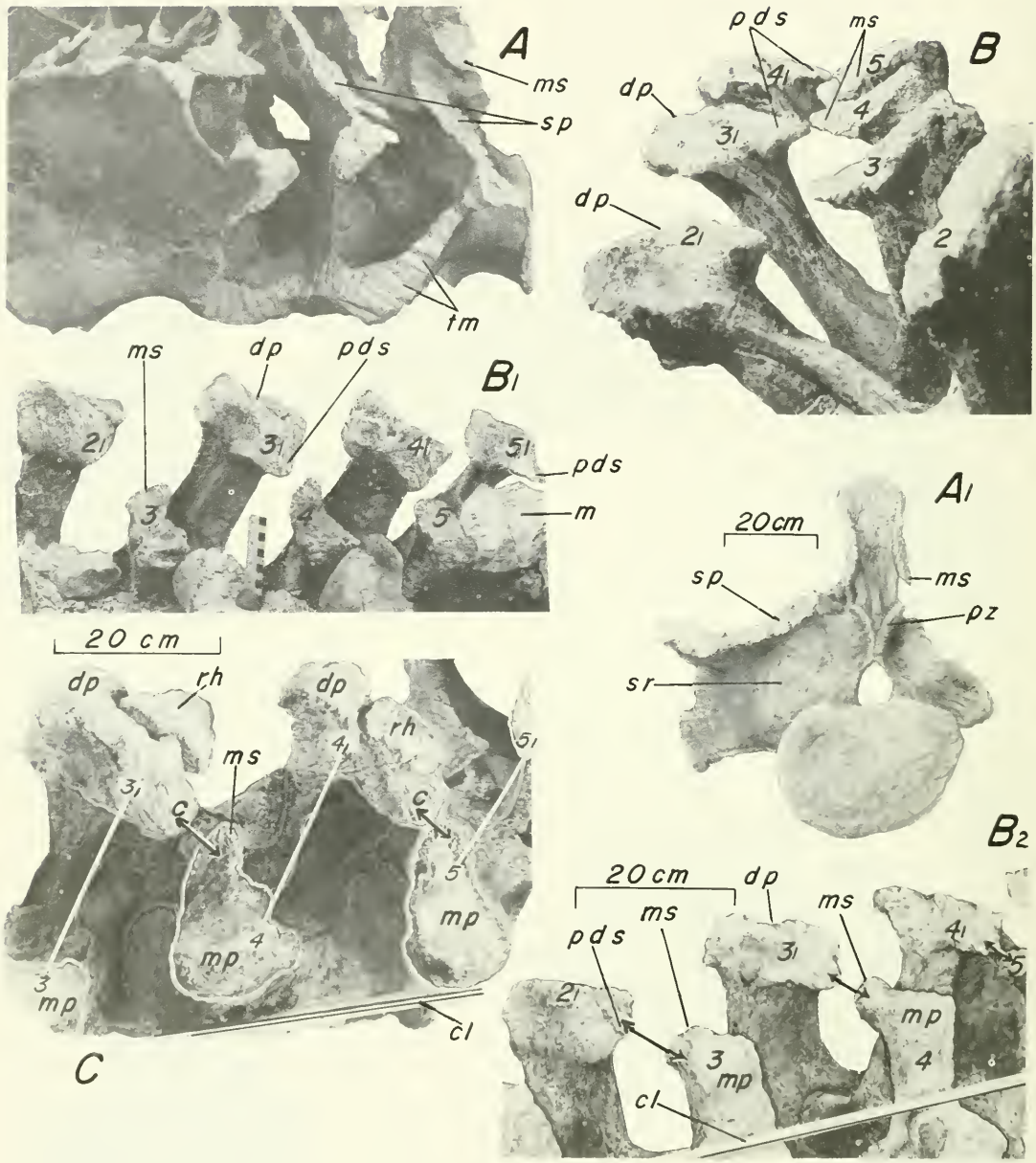

Fig. 5. *Cathetosaurus lewisi* sacrum and details of presacral spines and transverse processes: A, left lateral view of sacrum with teeth marks (tm); A_1, posterior view of sacrocaudal vertebra; B, posterolateral view of presacral metapophyses (2–5) and transverse processes (2_1–4_1); B_1, prediapophyseal spurs (pds) and metapophyseal spurs (ms); B_2, dorsomedial view of left diapophyses (dp, 2_1, 3_1, 4_1) and metapophyses (3–5) (arrows indicate ligamental connection between prediapophyseal spurs [pds] and metapophyses [mp]); C, detail of diapophyses and metapophyses (white lines indicate same neural arch; black arrows [c] indicate ligamental connection between adjacent neural arches by spurs). Abbreviations: cl–center line; dp–diapophysis; lts–metapophyseal spur; m–matrix; mp–metapophyseal spur; pds–prediapophyseal spur; pz–postzygapophysis; sp–supracostal plate; rh–rib head; sr–sacral rib.

developing in a large sauropod's skeleton if, as an obligate quadruped, it made an attempt to rise to a bipedal posture and its many tons of weight, calculated from 80 to 100 tons (Colbert 1983, Halsted and Halsted 1981), were transferred from four legs to two. Not only

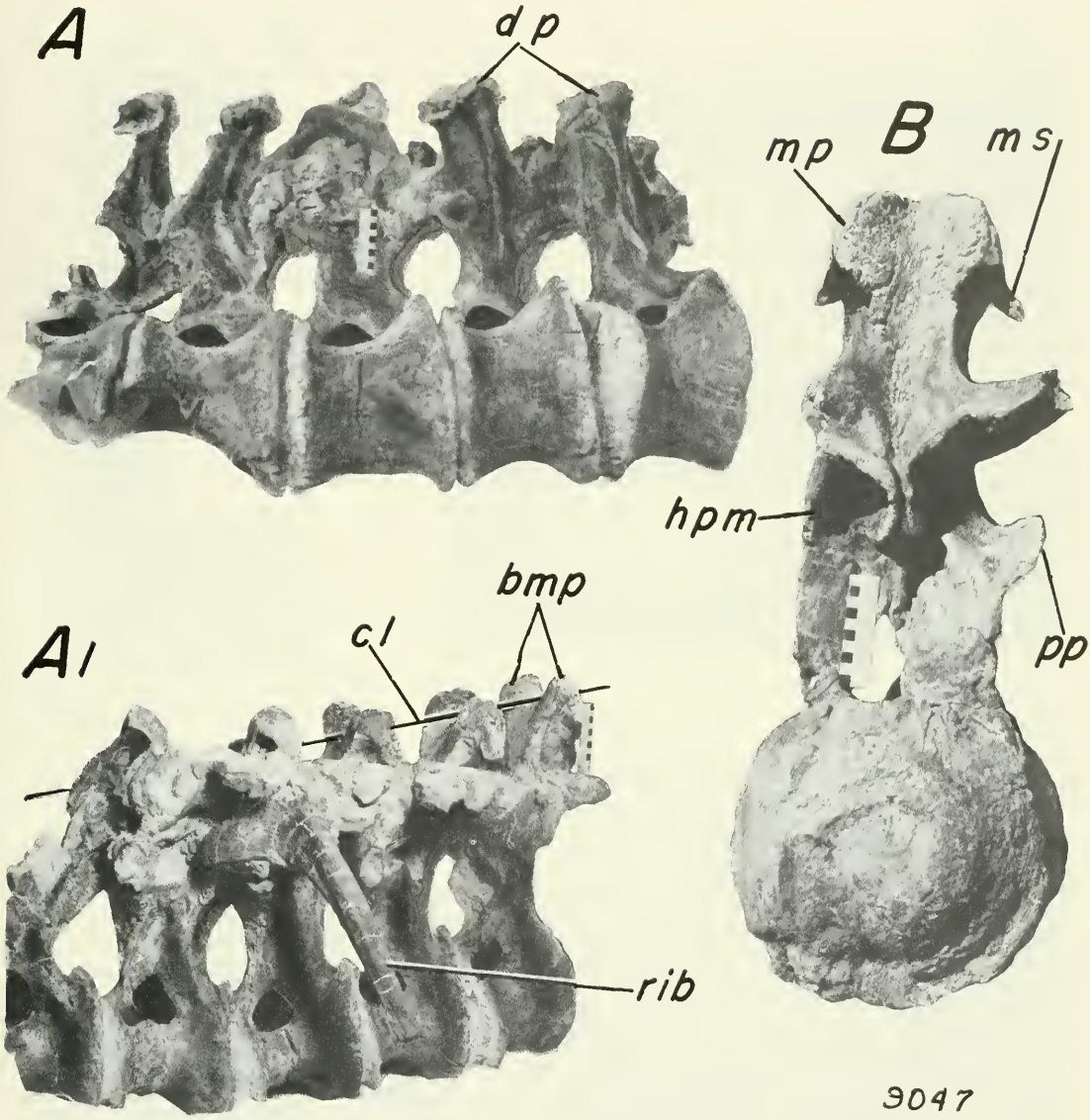

Fig. 6. Six *Cathetosaurus lewisi* presacral vertebrae: A, ventral view (centrum width equal to length); A_1, lateral view (centrum length greater than height); B, dorsosacral, or first presacral, vertebra, anterior view. Abbreviations: bmp–bifid metapophyses; cl–center line; dp–diapophyses; hpm–hypantrum (closed by crushing); mp–metapophyseal spur; ms–metapophyseal spur; pp–parapophysis.

would its skeletal structure be inadequate for such a massive weight shift, but its musculature would lack the necessary adaptation and strength to support the surge of such an overload.

Physical laws pertaining to the design and operation of heavy, modern, self-propelled machines, such as cranes and caterpillar tractors, would no doubt have applied equally to the behavior of 80-ton animals in the Mesozoic Era. One modern bipedal, earth-moving machine with a weight comparable to that of a medium-sized sauropod is the D–8 Caterpillar tractor. With a blade it weighs approximately 34 tons, or considerably less than half the 80 tons estimated for a large sauropod

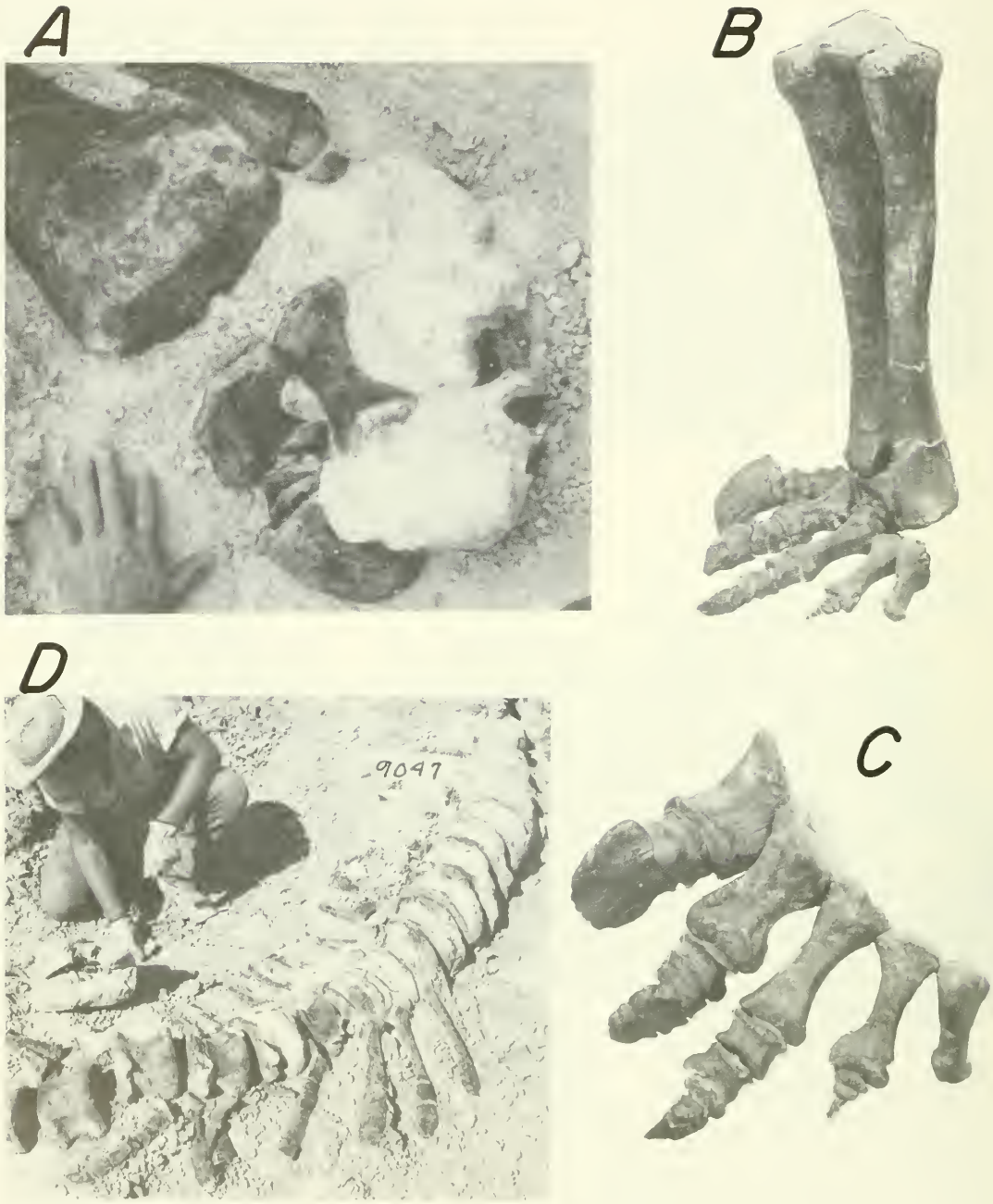

Fig. 7. A, *Camarasaurus* sp. left rear foot in concretion; B, same as A, prepared; C, detail of pes with four ungals; D, anterior section of *C. lewisi* caudal vertebrae with first seven chevrons (much longer than neural spines).

(Colbert 1983:45). Bipedal supports distribute the tractor's weight over an area of more than 50 square feet by means of two endless jointed tracks, while the weight of a large sauropod, standing on its rear legs, would have been supported on a total footpad area of approximately 12 square feet, if that footpad area is generously calculated as six square feet for each rear foot, based on Gilmore's (1936) calculations of 27 × 31 inches

as the approximate size of the *Apatosaurus louisae* pes. This is approximately one-fourth the area supporting the much smaller 34-ton tractor.

A vertebrate skeleton is like a machine: a structural arrangement of rigid parts and the functional range of motion in both systems is governed by the mechanical design of those rigid parts. The capability for motion and acceleration in both systems is strongly affected by interacting factors: inertia and balance; the influence of gravity over mass during motion and acceleration; mechanical sophistication in the weight-support and locomotion systems, and the requirement of a suitable substrate on which to function; an energy supply, and the unit's efficiency in transforming that energy into motion. Most of these factors would affect a sauropod's mobility and speed, but the primary concern here is simply the matter of the structural and muscular adaptations necessary to elevate and support a large quadruped, particularly a sauropod dinosaur, in an upright posture with its rear legs and tail in tripodal contact with the ground.

In raising a heavy beam to a vertical position the greatest structural stress and the maximum energy demand are imposed by gravity at the beginning of elevation, when the mass is horizontal and furthest from a vertical line above the fulcrum, and the angle between the rising structure and the horizon is smallest, such as the angle of applied stress occurring when a construction crane begins elevating a long boom from the ground.

Physical laws affecting the successful elevation and operation of modern crane booms no doubt applied as well to a sauropod attempting to elevate its anterior body and function bipedally. The acetabulum is the basic pivotal point in all bipedal and quadrupedal vertebrates. Thus, in any sauropod adapted to bipedalism, pelvic design surrounding that pivot could be expected to display some recognizable structural specializations, such as bony reinforcements and processes, to accommodate the additional weight shift from front legs to rear. *Cathetosaurus lewisi* displays bony strengthening and novel processes (Fig. 3C) to a degree significantly greater than that seen in any other described North American Jurassic sauropod.

The prime force elevating the anterior body of *C. lewisi* was generated by several long-muscle groups combined in an extended series with the M. ligamentum nuchae–M. ligamenta apicum dorsalis complex, supported in an interspinal channel of bifid neural spines (Figs. $6A_1$, 9B) from skull to pelvis. These muscles, anterior to the acetabular fulcrum, were counterbalanced and augmented by caudal long-muscle groups originating in the sacrum and inserting serially on caudal vertebrae. The contraction of these presacral and postsacral muscle groups involved most of the spinal column in shifting body weight back toward the rear limbs and tail as the neck and thorax were elevated toward a vertical line above the fulcrum. Tail weight, acting as a counterbalance, aided the shift. Very long chevrons (Fig. 7D), nearly twice the length of those in *Camarasaurus* (Osborn and Mook 1921), increased the area in the sagittal plane of the tail, with a concomitant increase in weight, providing greater postsacral muscularity and improving the strength of the tail for use in bipedal activities.

An equitable distribution of weight in a 50-ton sauropod standing with tail raised, as depicted in various modern illustrations (McLoughlin 1979, Bakker 1986), would have placed a load of 25,000 lbs on the joints of each limb and foot. If the thorax were elevated to a bipedal position, lowering the tail and shifting body weight caudally, 100,000 lbs would be imposed on the pelvis, minus a generous 10 tons for postacetabular weight to be supported by the tail. The remainder would be transmitted through the acetabular area to the rear legs, requiring each rear ankle to support a static load of probably more than 20 tons. Each time the sauropod shifted body position, a temporary surge of increased pressure, and resultant stress, would be imposed on the limb and foot nearest the center of gravity.

A degree of structural sophistication similar to that seen in the feet of proboscidians was present (Figs. 12A–B) in the extinct, graviportal, long-limbed digitigrade feet of the titanotheres (Osborn 1929). In both, the manual pisiform, and radial processes on other carpal bones, provided muscular leverage to the front foot, whereas no pisiform or other comparable bones were present in the sauropod locomotor apparatus. Sauropods also lacked the pedal calcaneum, which in mammals (Figs. 12B–C_1) is an important lever providing increased mechanical advantage to the

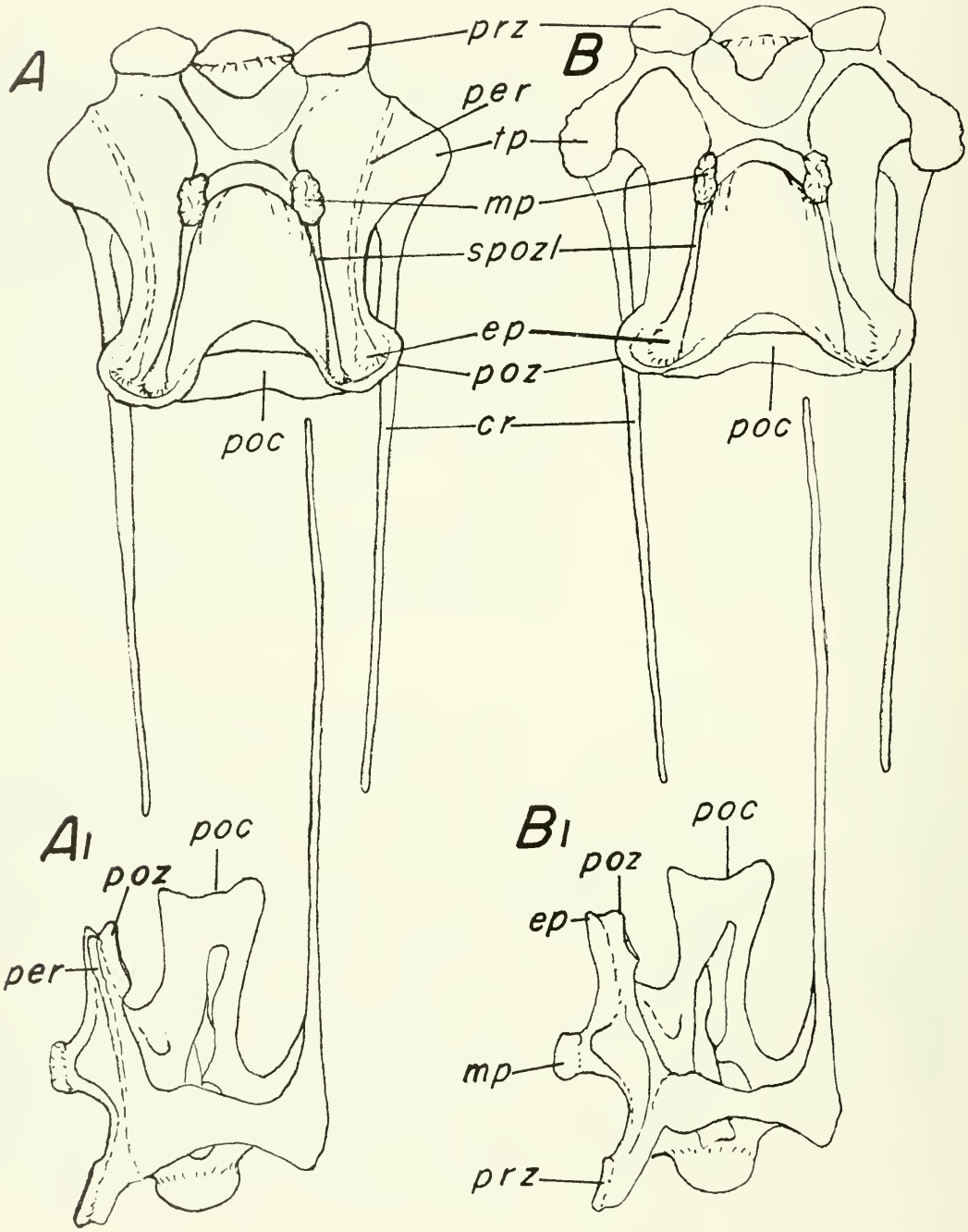

Fig. 8. Line drawing of two sauropod cervical vertebrae with very long cervical ribs: A, A_1, *Cathetosaurus lewisi*; B, B_1, *Uintasaurus (Camarasaurus) douglassi*. Abbreviations: cr–cervical rib; ep–epipophyses; mp–metapophyses; per–precipophyseal ridge; poc–posterior concavity; poz–postzygapophyses; prz–prezygapophyses; spozl–suprapostzygapophyseal laminae; tp–transverse process.

various muscles, including the M. gastrocnemius–M. plantaris–M. soleus complex, extending the pes.

Pedal extensors in sauropods (if there were muscles large enough to be identified as such) functioned without a calcaneum and

consequently with very little leverage to extend the pes, basically because the area of insertion on the proximoventral borders of the metatarsals was too near the fulcral area on the ventral surface of the astragalus (Figs. 7B, 13A). It cannot be demonstrated, therefore, that sauropods had any significant muscle-leverage system for extending or otherwise manipulating the pes. It probably served in locomotion with little more flexure than the rubber extension on the distal end of a crutch.

The lower front limb extensor in the large mammal *Palaeosyops* (Osborn 1929), the M. caput laterale (Fig. 13C [c. la]), enjoys a favorable ratio of leverage to ulnar length of approximately 1 to 2.5, with the olecranon process rising approximately 40 degrees above the center of the humeral joint radius (Fig. 13 [ejr]). The M. caput laterale inserts the olecranon process and rocks the ulna across a fulcral surface on the distal end of the humerus to extend the lower limb. No olecranon process is present on the sauropod ulna (Figs. 13A–B) to provide equivalent, advantageous leverage.

I mounted a large, free-standing mammoth skeleton from the LaBrea Tar Pits in the Page Museum in Los Angeles, California (1977), for the opportunity to study and compare limb and foot joint structure in a heavy mammal with the design and function of similar joints in sauropods. The study confirmed that limb and foot joints in the most agile dinosaur, large or small, are structurally and functionally inferior to those of probosidians and, in large measure, to all mammals.

When the elephant does a single, front-limb "handstand" (Asian elephant, Circus of the Stars, CBS-TV, December 1986), the weight of its entire body is transferred to one foreleg. The joints in its scapula, elbow, and wrist withstand the abnormally high pressure in this radical posture because of compact, bone-to-bone joint geometry that includes ball-and-socket joints and curvilinear flanged joints mating perfectly with matching incurvate forms (Figs. 10B–B_4, 11B–E_1) in an articulated system of solid bone, glazed with a thin layer of dense cartilage and encapsulated with lubricating fluid. No equivalent bone-to-bone joint structure is present in sauropods.

FOOT STRUCTURE.—Sauropod feet were of simple construction (Fig. 12E) in contrast to the number of bones and geometric complexity of those in heavy mammals such as titanotheres (Figs. 12A–B). A significant feature of titanothere limb and foot construction is the very close articulation and almost complete communication of apposing surfaces in the multifaceted bones of the carpus and tarsus (Figs. 12A–B). Another important feature is bones with processes, radial to limb axes, functioning as levers, such as in the pisiform, cuboid, calcaneum, and the ulnar olecranon process. Sauropod limb and foot bones have no equivalent comparable "levers," or compact joint structure, and, therefore, have less comparative potential for strength and agility. This leaves them mechanically inferior to mammals—empirical evidence that various present-day speculators (Bakker 1986, McLoughlin 1979) on sauropod locomotion and physical behavior ignore.

Sauropod foot bones are reduced and simply arranged (Figs. 7C, 12E), lacking the structural sophistication of "lever" bones and large areas of articulating communication present in the compact mass of subrectangular bones in the mammalian carpus and tarsus, in which the bones are conformably shaped and lubricated to move together, pushing as they do so against each other, as the entire group responds to a flow of energy originating in limb muscles during locomotion. By contrast, the number of bones in the sauropod carpus and tarsus was extremely reduced (Fig. 12E), being reported as one bone in the carpus of *Apatosaurus louisae* Holland (Gilmore 1936), which Hatcher (1902) described as the scapho-lunar, and one bone in the tarsus of *Diplodocus* and *Apatosaurus*, reported as the astragalus (Gilmore 1936). Sauropod carpi and tarsi are very poorly known because of the small number of sauropod feet described. However, mobile wrists and ankles were obviously of small importance in sauropod locomotion; otherwise they would have been more sophisticated. In any three-dimensional arrangement of mechanical joints, complex-motion capability decreases in direct proportion to a decrease in the number of participating elements. The result was that sauropod feet had very little circular mobility in their distad spheres on the lower limbs; simply put, sauropods had little wrist and ankle movement.

My study of the LaBrea Tar Pit mammoth revealed that rotary motion of the pes can

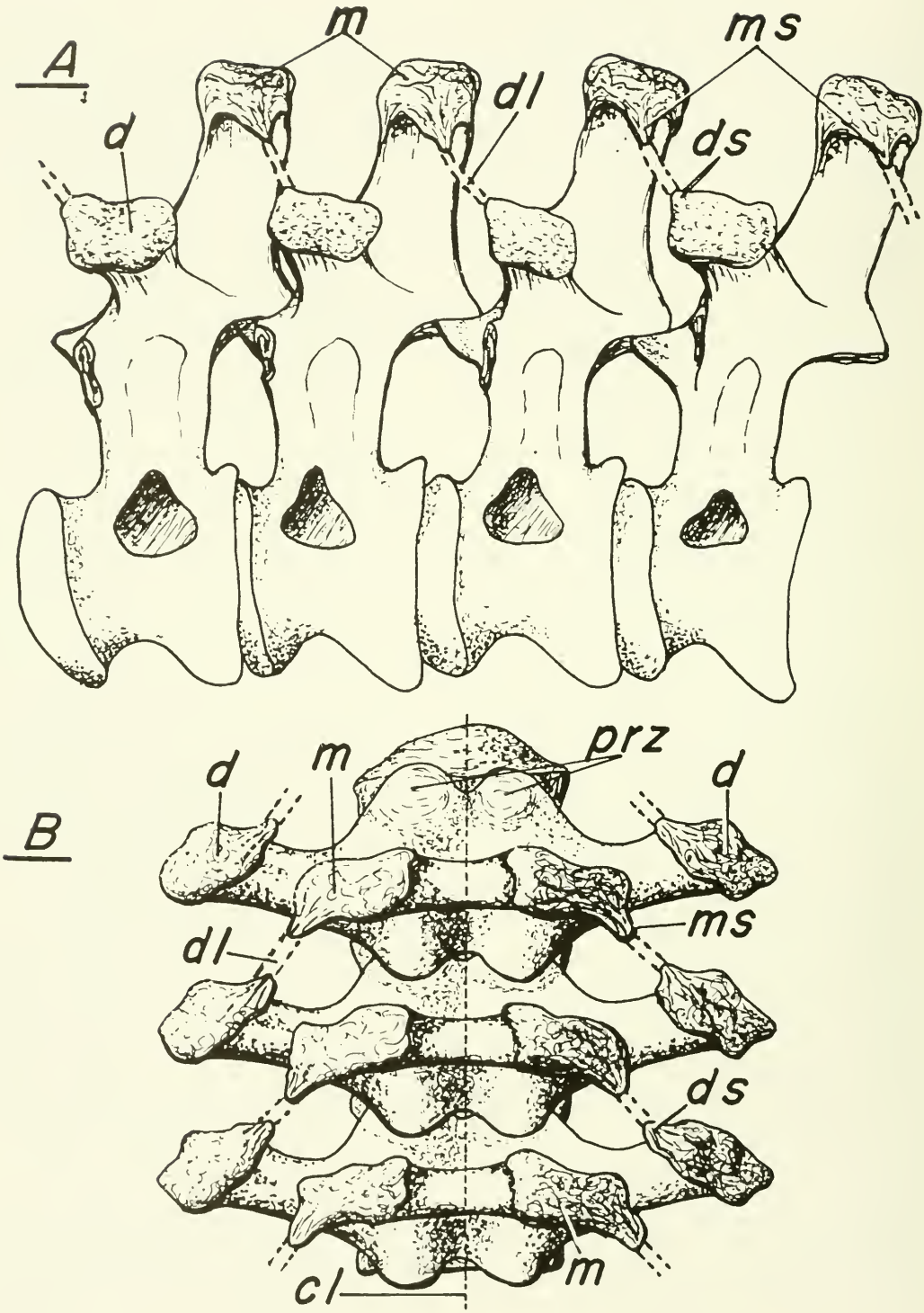

Fig. 9. A, lateral and B, superior views. Scheme of diagonal ligament (dl) bracing in dorsal vertebrae of *Cathetosaurus lewisi*: diagonal ligaments from metapophyses (m) to diapophyses (d) connect all adjacent vertebrae throughout the series. Abbreviations: cl–center line; d–diapophysis; dl–diagonal ligament; ds–diapophyseal spur; m–metapophyses; ms–metapophyseal spurs; prz–prezygapophyses.

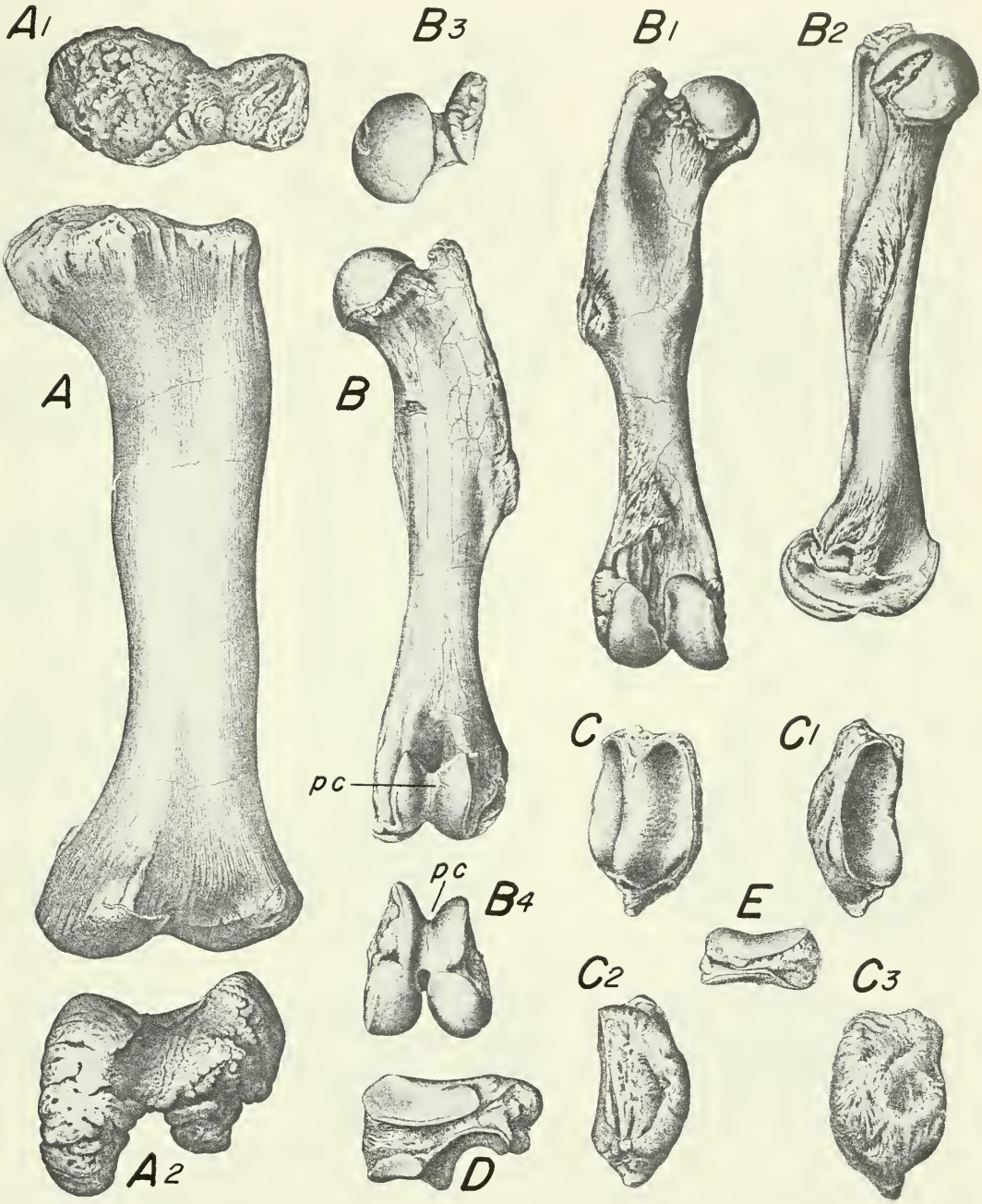

Fig. 10. A–A_1, sauropod dinosaur, Camarasauridae; B–E, mammal, Brontotheridae. *Camarasaurus:* A, left femur, anterior view; A_1, proximal view; A_2, distal view. *Brontops:* A, left femur, anterior view; B_1, posterior view; B_2, medial view; B_3, proximal view; B_4, distal view; C, left patella, posterior view; C_1, lateral view; C_2, medial view; C_3, anterior view; D, left scaphoid, ulnar view; E, trapezoid, medial view. Abbreviations: pc–patellar channel. Not to scale.

occur as a blend of simultaneous movement in separate carpal joint planes, similar to the arrangement seen in titanotheres (Fig. 12A). In this system the manus can swing in a mediolateral arc on the proximal joint plane at the articulation of the radius-ulna and scaphoid-lunar-cuneiform and then through a second arc, at a right angle to the first,

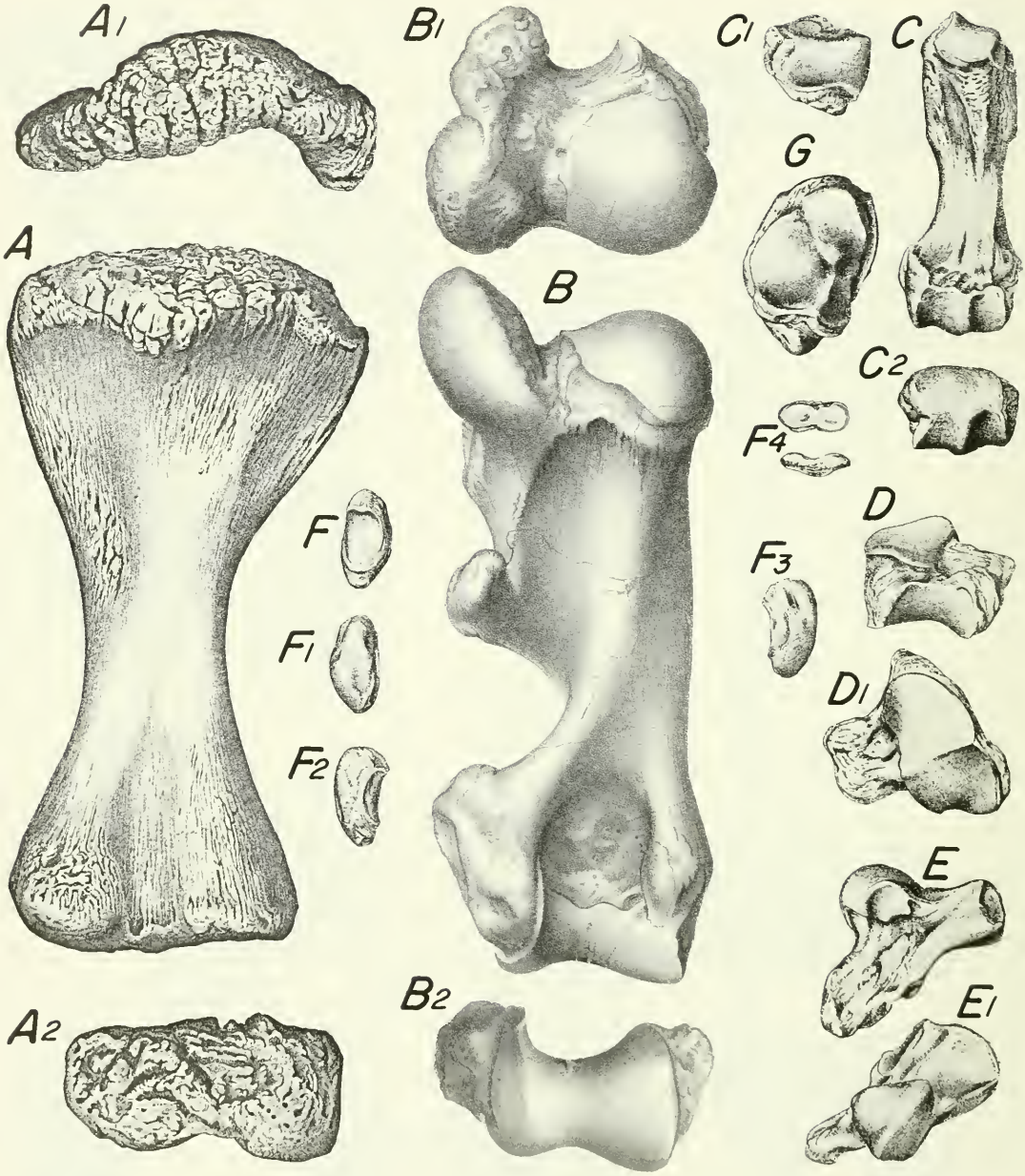

Fig. 11. Sauropod dinosaur, Camarasauridae, A–A_2; mammal, Brontotheridae, B–F_4. *Camarasaurus:* A, left humerus, anterior view; A_1, proximal view; A_2, distal view. *Brontops:* A, left humerus; B_1, proximal view; B_2, distal view; C, fifth, left metacarpal, posterior view; C_1, proximal view; C_2, distal view; D, left, unciform, lateral view; D_1, proximal view; E, left magnum, medial view; E_1, proximal view; F–F_4, left manual sesamoids; G, left scaphoid, distal view. Not to scale.

through the joint plane of the scaphoid-lunar-cuneiform and trapezoid-magnum-unciform/pisiform articulation. Rotary motion of the manus does not depend strictly on a division of movement into these two right-angle planes. It may be attained by a blending of the two and may occur as the manus rotates one way or the other around the lower-limb axis.

The sauropod carpus and its function are poorly known, but the number of bones

involved is a small fraction of the number found in titanothere and elephant carpi, supporting a long-held conviction (Hatcher 1901) that sauropod locomotion was little more than slow and ponderous and cannot realistically be modeled on the physical activities of modern, large mammals.

JOINT SURFACES.—Bone ends forming sauropod limb and foot joints are of simple geometric form, compared with the geometrically sophisticated joint design in mammals, in which all apposing spherical and curvate surfaces are precisely matched as male and female systems (Figs. 10B–C, 11B–F_4, 12B–D). The irregular, spongy, rugose surfaces (Figs. $10A_1$, A_2) forming sauropod joint areas attached cartilaginous articulating structures of unknown form, none of which have been found as ossified elements. These thick, cartilaginous pads (Hatcher 1901) were probably composed of varying tissue densities and certainly lacked the rigidity and structural resistance to deformation of the close-fitting, compact joints seen in the integrated geometrical shapes of mammalian joints (Figs. 10–12). This inherent joint weakness in sauropods was a limiting factor and is a reality that must be included in all qualitative comparisons of sauropod and mammal locomotion and other physical behaviors. Such studies will reveal the comparative ineffectiveness of the sauropod joint system, and all speculations regarding the comparative physical abilities of mammals and sauropods must be tempered by this biomechanical reality. Furthermore, because of the high-energy demands of running, speculations about sauropod metabolic tempo and the vulgar term "hot-bloodedness" might also be examined from a strictly mechanical point of view inasmuch as the sauropod skeleton, being a mechanical arrangement, was not designed to move rapidly; its great weight, simple limb and foot joint structure, and particularly the nonrigid, cartilaginous composition of the joints in its appendicular skeleton all argue strongly against its being able to run, or move about bipedally, even if it possessed a high metabolic rate.

The geometric shape of any joint controls its mechanical function, and, though the force of gravity is mitigated when a body floats in water, a joint's movement and excursional limits are constant despite the presence or absence of gravity. Although sauropod limb joints were constructed of nonossified cartilaginous tissue, they were nevertheless restricted by their form to certain limits of excursion, while being required to support far greater weight per unit area of joint surface than that carried by equivalent joints in the elephant and titanothere. A sauropod's cartilaginous joint structure was obviously adequate for walking gaits, during which there was an alternate shifting of many tons of body weight from the joints of one leg to those of another. But if the gait were to be accelerated from walking to running, the joints would probably be subjected to a disproportionate increase in impact stress, creating a danger of joint failure and pathological bone fracture.

Ten years of work experience as a longshoreman on the waterfront, operating cranes and lifts handling more than 50-ton loads, has convinced me that the notion of a single, cartilaginous sauropod ankle joint capable of momentarily carrying a 40-ton, or even supporting a 20-ton, static load is structurally impossible. However, *C. lewisi* appears to have successfully functioned bipedally because of its various structural specializations; but, judging from its body size and the mature condition of fused epiphyseal unions present in the articulated skeleton of the type-specimen, it was a small sauropod of probably no more than 10 to 15 tons.

An elephant's weight is but a fraction of that of a large sauropod, and yet, despite its ball-and-socket acetabular joints, the elephant moves ponderously in bipedal activity. Any departure from quadrupedal locomotion by sauropods weighing more than 10 times as much as an elephant would have been very difficult and vastly more ponderous, if not impossible. No sauropod could raise its multiton body to a vertical position without the mechanical and muscular adaptations necessary to pay the weight tax imposed by gravity. The stresses of weight, friction, pressure, and inertia, imposed by gravity today, applied equally to Jurassic animals on a planet of essentially the same diameter and density.

TRIAD BONES.—Two different elements, sesamoids (Fig. 10F) and patellae (Fig. 10C), are present in the locomotor apparatus of mammals, and each type functioned in a triad joint. These two elements were absent from sauropod limbs and feet, which had no triad joints.

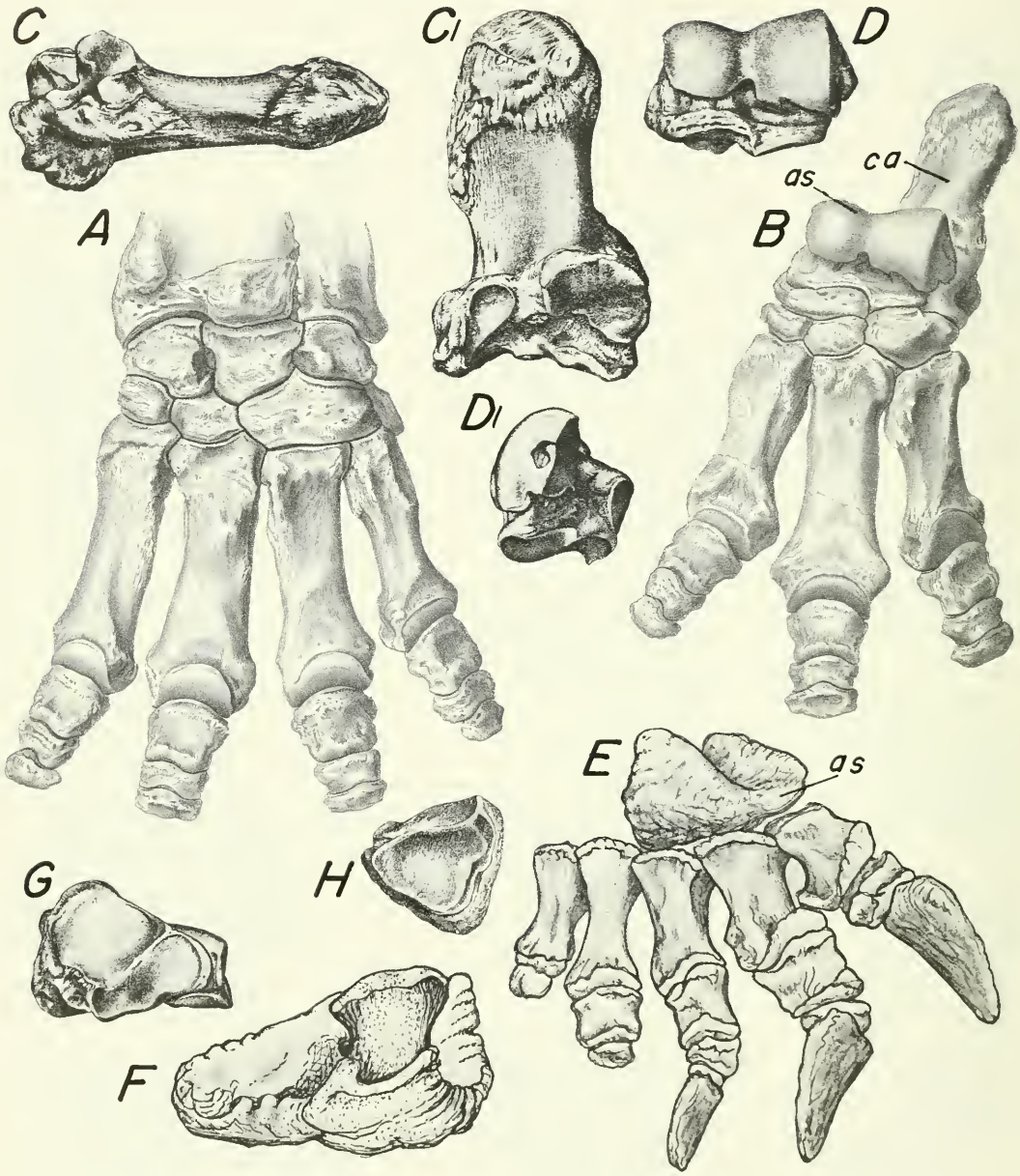

Fig. 12. Mammal, Brontotheridae, A–D_1, G; sauropod dinosaurs, Camarasauridae, E–F. Mammal, *Brontops:* A, left manus; B, left pes; C, left calcaneum, external view; C_1, anterosuperior view; D, left astragalus, anterior view; D_1, lateral view. Dinosaurs: *Apatosaurus*, E, right pes and astragalus; *Camarasaurus*, F, left astragalus. Abbreviations: as–astragalus; ca–calcaneum. Not to scale.

I submit that the function and importance of these two bone types in the mammalian locomotor apparatus indicate a significant difference between the mammalian physiological system and that of a sauropod by implying a discrepancy between two levels of physical activity, and that a discussion of the nature and importance of that difference is relevant to a consideration of the well-known proposition that *sauropods were capable of little more than slow, ponderous locomotion* (Colbert 1961).

SESAMOID BONES.—Sesamoid bones are imbedded in the plantar surface of all four feet

in mammals, each sesamoid forming a triadal union with two apposing phalangeal elements by articulating with the ventral surface of their joints. The distal, ventral surfaces of the metatarsal and metacarpal bones, and the ventral surface of the digital joints move in conjunction with the superior articular surfaces of the sesamoids, the entire triad joint system being encapsulated with lubricating fluid. Sauropod feet lacked sesamoid bones and triadal joints.

Sesamoid articular surface area was no doubt greatly enlarged by dense cartilage formed around the bone, similar to the cartilaginous enlargement of the articular surface in the avian patella (Numididae, Meleagrididae, personal experience). This cartilaginous enlargement of sesamoid bone would have increased ventral support from the sesamoid bone to the triad joint, probably by 100%. The majority of phalangeal joints in mammalian feet are triadal.

Variable pressure from body weight, fluctuating according to the intensity of foot activity, is exerted on the phalanges by various muscles, such as the M. flexor profundus digitorum and surrounding adductive tissues. This pressure is transmitted through the lubricated triadal joint and into the substrate by the inferior position of the sesamoid bone, mitigating (to an unknown degree) the effects of friction from flexure within the massive footpad tissues. Sesamoid bones also protect the ventral surfaces of phalangeal joints from damage during the radical flexure of vigorous activity. If the footpad were peeled away from the plantar, or ventral surface of the phalanges, the superior surface of the footpad would display the lubricated joint surfaces of the sesamoid bones remaining imbedded in footpad tissue. Sauropod metatarsi and metacarpi had no such intermediate bony structures supporting their ventral surfaces and transmitting weight to the substrate on which the foot rested.

It has been suggested, based on an incomplete, partially disarticulated sauropod pes (Gilmore 1923), that sesamoid bones may occur in sauropod feet; however, in more recent years I collected an articulated lower leg and complete pes of a Jurassic camarasaurid (Figs. 7A–C) that clearly revealed the few small "sesamoid" bones of Gilmore to be very compressed distal phalanges, which, with greatly shortened axes, resemble mammalian sesamoid bones.

Sesamoid bones in mammalian feet aid in the distribution of weight and pressure and the reduction of intraphalangeal friction, by presenting a lubricated surface, imbedded in plantar cartilage, over which the ventral surfaces of the phalanges move, enabling large mammals to engage in accelerated activities and lighter ones, such as the cheetah, to move at high speeds.

PATELLA.—In the titanothere *Palaeosyops* (Osborn 1929) the patella is involved in both flexing and extending the rear limb. The M. rectus femoris, one of the major femoral flexors, inserts the proximal end of the patella. The principal extensor muscles, the M. biceps 3 complex, insert in serial fashion down along the broad aponeurosis of insertion, anchoring the patella to the proximal end of the tibia. This complex, together with the M. semi tendinosis–1 and M. semi membranosus, constitutes a powerful muscular force at the knee, extending the titanothere rear limb (Osborn 1929). During fast locomotion the patella, as a muscular junction across the knee joint, provides a continuously effective distribution of muscular force against both ends of the apposing limb bones involved, the femur and tibia. No evidence exists for equivalent muscular energy, applied simultaneously to femur and tibia, to extend the sauropod rear limb. Muscles extending its rear limbs were comparatively weak, having a much smaller ratio of muscular leverage to total limb length than the ratio seen in titanotheres. Sauropod femoral extensors inserted on the fourth trochanter, generally located scarcely halfway down the femoral shaft, whereas in titanotheres (Osborn 1929) rear limb extensors originated high on the neural spines and pelvis and insert at, and below, the total length of the femur.

The patella remains near the head of the tibia during locomotion, being attached there by the broad aponeurosis of insertion carrying various rear limb extensors. These muscles, including the M. biceps 3 complex, contact the aponeurosis of insertion in an extended dorsoventral area spanning the femorotibial joint. When the knee is flexed, the posteroproximal surface of the patella moves in a radial path over the anterodistal joint surface of the femur, regardless of the varying

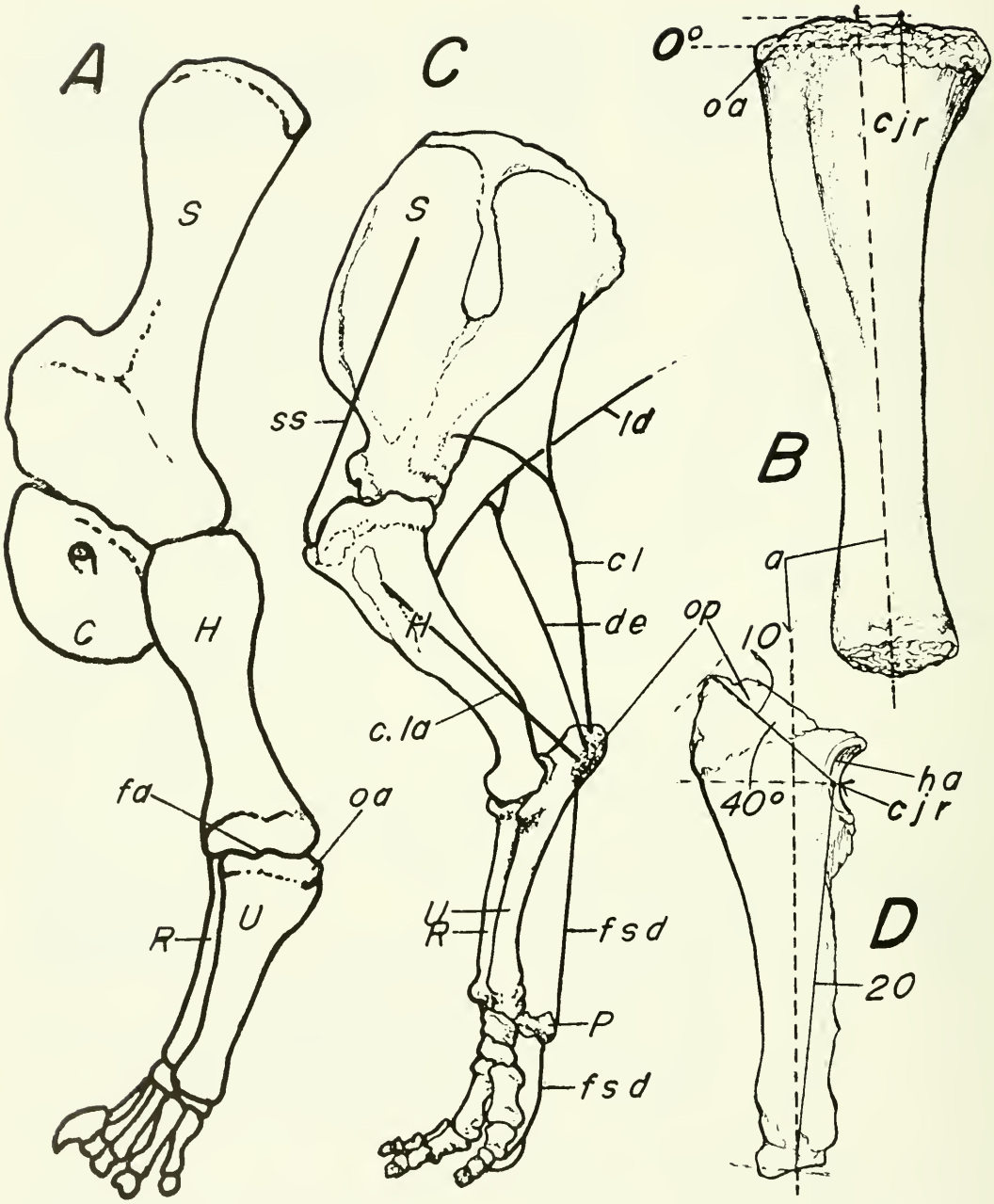

Fig. 13. Dinosaur and mammal forelimbs: A, the sauropod *Camarasaurus* forelimb; B, camarasaur ulna; C, titanothere forelimb; D, titanothere ulna. Abbreviations: C–coracoid; H–humerus; P–pisiform; R–radius; S–scapula; U–ulna; a–axes; cjr–center of joint radius; c.la–M. caput laterale; cl–M. caput longum; de–M. dorso-epitrochlearis; fsd–M. flexor sublimis digitorum; ha–humeral articulation; ld–M. latissimus dorsi; oa–olecranon area; op–olecranon process; ss–M. supra spinatus; 40 degrees = height of olecranon process above center of joint radius; 10 = leverage factor of olecranon process on humeral articulation and against ulnar shaft length; 20 = ratio of 2:1. Not to scale.

angularity developed between the axes of femur and tibia, transmitting rectilinear force across the working joint.

The superiority of titanothere rear limb function and power over that of sauropods is demonstrated by the length of the M. biceps 3

group and the participating M. gluteus maximus, M. semi membranosus, and M. semi tendinosus–1, all of which extend from elevated origins on the sacral spines, caudal vertebrae, and posterior pelvis to the aponeurosis of insertion attaching the patella to the tibia. As noted, these muscles exert a powerful extending force at the *middle* of the rear limb, whereas sauropod rear limb extensors have comparatively weak muscular leverage, inserting as they do on the fourth trochanter approximately halfway down the femoral shaft. This comparison demonstrates the superior ability for fast locomotion in mammals. Patellar function appears to be essentially the same in all mammals. The posterior surface of the patella, with a rounded dorsoventral, median ridge (Fig. 10C), is almost entirely occupied with knee joint function in a lubricated environment.

Judging from rear limb attitudes seen on various mounted sauropod skeletons in North American museums (some mounts appearing more realistic than others), the femorotibial angle of flexure in a sauropod's lower leg was small, with the angle rarely exceeding 45 degrees.

Because of their great weight and unsophisticated limb and foot joint structure (Figs. 7B–C), I am convinced that sauropods were slow-moving creatures with a moderate to low rate of catabolic metabolism; that is, they were homeothermic but not endothermic. As slow-moving animals, the sauropods were able to function without the complex joint geometry of mammals; but their great weight and cartilaginous joint structure, lacking patellae and sesamoid bones, made it difficult, if not impossible, for them to run, which would have required an accelerated metabolic rate.

I believe, in view of its structural and apparent soft-tissue development, that *C. lewisi* habitually assumed a bipedal posture and did so without patellae and sesamoids but, except for localized shifts in feeding positions, that its general locomotion probably remained a quadrupedal event.

OCCURRENCE AND TAPHONOMY

Dominguez/Jones Quarry is located on the eastern monocline of the Uncompahgre Upwarp in Mesa County, Colorado, and consists of two pits 300 m apart on approximately the same horizon, 10 m above the base of the Brushy Basin Member of the Morrison Formation. Each pit produced remains of a single sauropod, the nearly complete skeleton of *C. lewisi* coming from Pit 1 and the pelvis, some rear limb material, and most of the caudal vertebrae of a second unknown sauropod (to be described elsewhere) being collected from Pit 2. Both occurrences were autochthonous. The skeletons were buried near their death site in well-graded (now), pale green sediments in a relatively quiet depositional environment an unknown distance from intermittent levee overwash during burial.

When *C. lewisi* was discovered, the axis of its vertebral column was crescentically distorted (Fig. 1E), with the tail and neck dorsally curved toward each other, the two curves oriented downstream toward each other, confluent with an apparent NE stream flow. This direction of hydraulic pressure was later verified by the position of disarticulated front limb elements (Figs. 1D, F) transported beyond the carcass before final burial.

No lenticular sandstones or other high-energy structures were present adjacent to the skeleton, or nearby on the same horizon, although some postmortem disturbance was evident in the displacement of front limb elements several meters downstream from the carcass (Figs. 1D–F). Deep teeth marks in the left ilium (Figs. 3C, 4C–C_1) and the final disposition of the skeleton (Figs. 1D–F) suggest that a large carnivore, equal in size to *Torvosaurus tanneri* Galton & Jensen (1979), killed and fed on the sauropod. Apparently the body was turned over later and dismembered during a second feeding by the killer or another predator of equal size, providing one explanation for the absence of rear limb and foot elements. The neck and rib cage were preserved intact, indicating predator preference for the more heavily muscled pelvic-rear limb area as the best food source. Between the large carnosaur(s) feeding periods, small scavenging carnosaurs intruded and fed, imposing their teeth marks across the much larger tooth marks in the ilium.

An unknown period of time after the kill and initial feeding invasion, during which the killer fed only in the rear limb and pelvic area, an overbank flood may have floated the bloated carcass an unknown distance from the

death site and initial feeding episode, further explaining the absence of rear limb elements near the skeleton. Small, eroded, organic detritus, common in allochthonous deposits, was entirely absent from matrix surrounding the skeleton.

When the skeleton of *C. lewisi* was collected in 1967, the existence in the Uncompahgre fauna (Jensen 1985) of a sauropod killer more powerful than *Allosaurus* was deduced from the size and spacing of teeth marks in the ilium (Fig. 5A), but the first elements of such a carnosaur, later described as *Torvosaurus tanneri*, were not discovered until five years later in Dry Mesa Quarry. The many elements known from this new carnosaurian genus (Jensen 1985) indicate an animal large enough to easily catch, kill, and dismember a sauropod the size of the *C. lewisi* skeleton; however, various elements of an unusually large allosaurid (to be described elsewhere) were subsequently found in Dry Mesa Quarry and represent an individual also capable of easily killing medium-sized sauropods.

ACKNOWLEDGMENTS

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MEMORIAL

A tribute is paid to the late Daniel E. "Eddie" Jones, of Delta, Colorado, on behalf of the discipline of Vertebrate Paleontology and in particular all workers and students interested in dinosaurs. All will be forever indebted to his many years of successful efforts to find dinosaurs in Colorado.

"Eddie," with his wife, Vivian, as his constant companion, over a period of more than 20 years made the greatest single contribution to the renewal of dinosaur studies occurring in the last half century. Because of the productive localities they discovered and revealed to science, an important new group of fossil vertebrates was uncovered, including the "world's largest" dinosaurs and a new flying reptile. These discoveries received wide international media exposure, catapulting many eager, young minds into the beginning flush of a great "dinosaur renaissance." Elementary school children, excited over new dinosaurs from the Jones's discoveries in the 60s, are now professional vertebrate paleontologists, judging from my 25-year accumulation of thousands of letters.

"Eddie" and Vivian's persistent toil over many rough mountain ridges and exhausting, hot, dry badlands will continue to pay scientific dividends for many years of dinosaur research in the future, while thousands of bones in localities they discovered still remain to be collected and studied. In 1985 two new sauropod dinosaurs were named in their honor: *Dystylosaurus edwini*, and *Supersaurus vivianae*. Thank you, "Eddie."

LITERATURE CITED

COLBERT, E. H. 1983. Dinosaurs, an illustrated history. Hammond Inc., New Jersey. 220 pp.

GALTON, P. M. AND J. A. JENSEN. 1979. A new large theropod dinosaur from the Upper Jurassic of Colorado. Brigham Young Univ. Geol. Studies 26(2): 1–12.

GILMORE, C. W. 1936. Osteology of *Apatosaurus*, with special reference to specimens in the Carnegie Museum. Memoirs Carnegie Museum 11(4): 177–269.

HALSTED, L. B. AND J. HALSTED. 1981. Dinosaurs. Blanford Press, Poole Dorset, England. 170 pp.

JANENSCH, W. 1935. Die Schadel der Sauropoden *Brachiosaurus*, *Barosaurus*, und *Dicraeosaurus* aus den Tendaguru schichten Deutsch-Ostafrikas. Paleontographica, Suppl. VII, Erste Reihe, Teil II, 16 pl. in text, 138 figs., pl. IX-XIII, 145–298.

HOLLAND, W. J. 1924. Description of the type of *Uintasaurus douglassi* Holland. Annals of the Carnegie Museum 15(2–3): 119–138.

JENSEN, J. A. 1985. Three new sauropod dinosaurs from the Upper Jurassic of Colorado. Great Basin Nat. 45(4): 697–709.

LULL, R. S., AND N. E. WRIGHT. 1942. Hadrosaurian dinosaurs of North America. Geol. Soc. Amer., Spec. Paper 40: 1–242.

MCLOUGHLIN, J. C. 1979. Archosauria: a new look at the old dinosaur. Viking Press.

OSBORN, H. F. 1929. The titanotheres of ancient Wyoming, Dakota, and Nebraska. U.S. Geol. Survey, Monogr. 55, Vol. 2.

OSBORN, H. F., AND C. C. MOOK 1921. *Camarasaurus*, *Amphicoelous*, and other sauropods of Cope. Mem. Amer. Mus. Nat. Hist. 3(3): 247–387.

OSTROM, J. H. 1969. Osteology of *Deinonychus antirrhopus*, an unusual theropod from the Lower Cretaceous of Montana. Peabody Mus. Nat. Hist., Bull. 30: 1–165.

RIGGS, E. S. 1904. Structure and relationships of opisthocoelian dinosaurs. Part II. The Brachiosauridae. Field Columbian Mus., Geol. Ser., Pub. 94, 2(6): 229–247.

SCOTT, W. B. 1937. A history of land mammals in the western hemisphere. Macmillan Company, New York. Pages 665–670.

EFFECTS OF LIVESTOCK GRAZING EXCLOSURE ON AQUATIC MACROINVERTEBRATES IN A MONTANE STREAM, NEW MEXICO

John N. Rinne[1]

ABSTRACT.—Aquatic macroinvertebrate populations inhabiting reaches of a stream within areas excluded from livestock grazing for a decade were markedly different from those in grazed areas when density, biomass, biotic condition indices, and mean chi square indices of the two populations were compared. Increased densities and biomasses of more tolerant forms of macroinvertebrates were observed in grazed reaches. Because pretreatment data were not available, differences in macroinvertebrate populations and relative tolerances of taxa in grazed and ungrazed areas could be as easily attributed to linear changes in stream habitat as to removal of domestic livestock. Results of this study have implications for the design of future research on the effects of livestock grazing on stream environments and biota: (1) baseline/pretreatment information is prerequisite, and (2) the study should take a watershed (ecosystem) approach.

National forests, in their multiple-use role, are managed to serve and meet the needs of water, timber, wildlife, recreation, and grazing interests. The potential for conflict between respective uses is ever present. In recent years grazing has been implicated in having contributed significantly to widespread deterioration of habitat and decline of biota inhabiting riparian-stream areas (Platts 1982, Kauffman and Krueger 1984, Skovlin 1984). Thus, both managers and researchers recognize the need to better understand the impact of grazing on riparian ecosystems.

The Rio de las Vacas in northwestern New Mexico provides excellent trout sport fishing (Rinne 1988), and its valley provides camping opportunities and high-quality forage for livestock grazing. Because of concern over conflicts of use, this montane stream was partially fenced by the USDA Forest Service to exclude domestic livestock and thereby improve in-stream and near-stream habitat. Effects of grazing on in-stream and near-stream habitat and extant biota were examined a decade later. Results of several years of study indicated that apparent changes in habitat and biota had occurred (Rinne 1985, Rinne 1988, Szaro et al. 1985, Szaro and Rinne 1988).

Studies on how grazing impacts aquatic macroinvertebrates are nonexistent in the literature. This is largely attributable to the inherent difficulty of devising reliable sampling techniques required to adequately define temporal and spatial variability in stream macroinvertebrate populations (Resh 1979). Nevertheless, Buikema and Cairns (1980) and Munther (1985) have suggested that insects are very sensitive to environmental perturbations and therefore valuable in early detection of habitat changes resulting from particular management activities. A study was initiated in 1982 on the effects of grazing removal on stream habitat and biota (Rinne 1985, Rinne, in press). This paper reports the effects of exclusion of livestock grazing on aquatic macroinvertebrates in this particular montane stream.

STUDY AREA

The Rio de las Vacas (hereafter called the Vacas) is a third-order (Hynes 1975) montane stream draining the San Pedro Parks Wilderness Area, Santa Fe National Forest. The study area is at an elevation of 2,600 m, MSL, about 17 km southeast of the town of Cuba, Sandoval County, New Mexico. Two exclosures, each about 1 km in length and 50 m in width (ca 10 hectares), were established in 1972 and 1975 (Fig. 1). These exclosures were separated by private land holdings from a downstream grazed area (Fig. 1). The exclosures are within the Cuba Community Grazing Allotment, which comprises about 11,000 ha. Almost half of this allotment is classified as "no-allowable capacity" for grazing because of

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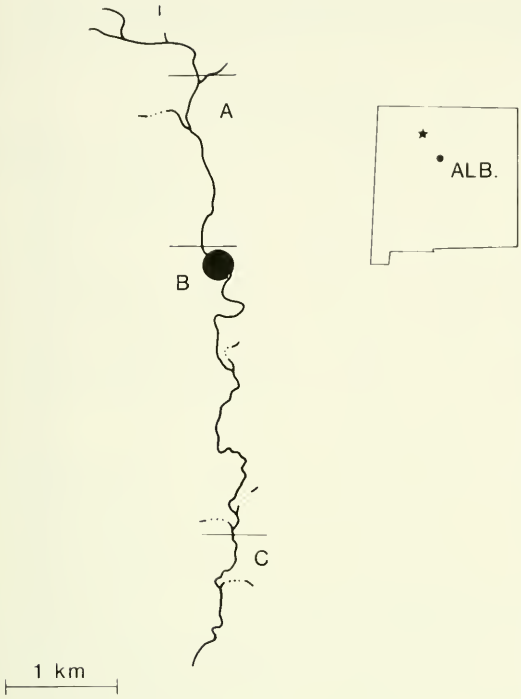

Fig. 1. Location and detailed map of study area indicating upstream ungrazed (A), grazed (B), and lower grazed (C) reaches. Sample site on private lands in 1984 is indicated by solid circle.

terrain and lack of forage. Near-equal percentages of lands (10% each of total allotment) are private holdings and riparian. Historically (1949–1980), the grazing strategy has been season-long (1 June to 31 October), at the average annual rate of 2,688 animal unit months (AUM). For further description and photos of the area, see Rinne (1985) and Szaro et al. (1985).

METHODS

Aquatic macroinvertebrates were sampled with a standard Surber sampler (1024-micron mesh size) during summer low flow conditions in reaches of stream in ungrazed (fenced) and grazed areas. Samples were preserved with 10% formalin in 1982 and with a glycerin-formalin-ethyl alcohol solution in 1983 and 1984. In 1982, samples were randomly taken in riffle habitats of the stream (Table 1) within the upstream exclosures and the downstream grazed area (Fig. 1). Because of variability in 1982 data (see RESULTS), which has been suggested to be the norm (Resh 1979), an attempt was made on ensuing (1983–84) samples to stratify within substrate composition categories to aid in reducing variability among samples (Table 1). In addition to sampling more for pebble-cobble substrate (17–256 mm), uniformity of water depth and velocity were likewise selected (Table 1). In 1984, because of suspected linear change in stream habitat, samples also were taken at stream sites within an upstream, contiguous area of private, grazed lands (Fig. 1).

In the laboratory invertebrate samples were sorted in gridded petri dishes with the aid of a compound dissecting microscope and identified to the lowest practicable taxon; taxonomic keys in Usinger (1956) and Merritt and Cummins (1984) were primary sources to aid in organism identification. Biomass of samples was estimated in 1982 and 1983 by using the length–dry weight equations of Smock (1980). Length was separated into seven size classes (0–6 mm); the largest individuals in the last class were measured directly because of the lack of an upper limit for this class. Because biomass values were not significant once stratified sampling was initiated in 1983, values were not estimated in 1984.

Tolerance quotients (TQ) were used to calculate biotic condition indices (BCI) following methods outlined in Winget and Mangum (1979) and discussed in Platts et al. (1983). The use of TQ reflects the tolerance of an invertebrate to alkalinity and sulfate content of the water in addition to its selectivity for or against fine substrate materials and stream gradient. Winget and Mangum (1979) have calculated TQ for a number of families and genera based on field data. Basically, if lower alkalinity and sulfate and greater gradients and larger substrate particle size are selected by an organism, its TQ will be lower. In turn, the BCI incorporates stream habitat, water quality, and TQ. The index is a function of a predicted community (TQ_p) divided by an actual community (TQ_a).

Chi-square indices (CSI) (Parrish and Wagner 1983) also were utilized to aid in comparing and quantifying community composition of stream macroinvertebrate populations in the grazed and ungrazed areas. Nonparametric Kolmogorov-Smirnov (KS) tests and standard t-tests (Statgraphics) were employed

TABLE 1. Characteristics of stream sample sites in grazed and ungrazed areas in the Rio de las Vacas, New Mexico, 1982–84. Ranges are in parentheses. Substrate classes are modified from Hynes (1975): (1) sand (< 2 mm); (2) gravel (3–16 mm); (3) pebble (17–64 mm); and (4) cobble (65–256 mm).

Year	Area	Velocity (cm/sec)	Depth (cm)	Substrate class 1	2	3	4	n
1982	Grazed	41.1 (13–60)	23.4 (10–35)	0	40	0	60	10
	Ungrazed	30.3 (10–75)	19.1 (8–40)	35	18	5	42	20
1983	Grazed	20.9 (13–25)	22.0 (21–25)	20	10	35	35	10
	Ungrazed	33.9 (10–40)	23.3 (19–30)	15	19	25	49	10
1984	Grazed	36.6 (27–40)	17.0 (15–22)	0	0	50	50	10
	Ungrazed	34.6 (23–40)	14.4 (10–17)	0	0	50	50	5

to determine distribution patterns and significance of density, biomass, TQ, and BCI in reaches of the stream in the two differently managed areas.

RESULTS

Eight orders, 39 families, and 71 genera of aquatic macroinvertebrates were collected and identified during the study (Table 2). As is common in streams, dipterans, trichopterans, ephemeropterans, odonatans, and coleopterans dominated the macroinvertebrate fauna in the Vacas in 1982 and 1983, comprising 88–97% of the total biomass (Table 3).

KS tests demonstrated uniform distribution of organism densities and biomasses in reaches of the stream within grazed and within ungrazed areas. Densities of macroinvertebrates were significantly greater in stream reaches within the grazed areas in 1982 and 1983, but not in 1984 (Table 4, Fig. 2). Samples from the upper and lower reaches of the stream taken within grazed areas in 1984 (B and C, Figs. 1 and 2) were separated and densities compared to densities in the ungrazed area (A). In 1984 differences were significant ($P < .02$) between samples from within the livestock grazing exclosures (A) and samples taken in the lower, grazed reaches (C) of the stream (Table 4, Fig. 2). In comparison, differences between densities from the ungrazed area (A) and those of the upper grazed area (B, Fig. 1), both taken in 1984, were not significantly different at the .05 confidence level (Table 4, Fig. 2).

Differences in macroinvertebrate biomass estimates in stream reaches within grazed areas were significantly higher than in ungrazed areas only in 1982 (Table 4, Fig. 3). There were no significant differences in biomass of macroinvertebrates between years (1982–83) in grazed or in ungrazed areas. Estimated biomass was consistently greater and more variable in the reaches of the stream within the grazed area in 1982 and 1983 (Fig. 3).

Average TQ was significantly higher in the ungrazed than in the grazed area in 1982, but the reverse was true in 1983 once stratified sampling was initiated. TQ was significantly higher in the lower grazed compared to the upper ungrazed area in 1984 (Table 4). BCI was significantly greater in the ungrazed reaches than in the grazed reaches of the stream in both 1983 and 1984.

Densities and BCI of four of the most common taxa in 1983 (i.e., those occurring in 10 or more samples) were compared to further illustrate that the overall tolerance of aquatic macroinvertebrates in the Vacas, as indicated by relative BCI, was greater in reaches of the stream in the grazed area. Two low-tolerance taxa, *Helicopsyche* sp. (TQ = 18) and *Ephemerella inermis* (TQ = 48), averaged 95 and 37 individuals/m^2, respectively, at stream sites in the grazed area. By comparison, these same taxa averaged 137 and 77 individuals/m^2 in the ungrazed area. Conversely, two

TABLE 2. Taxonomic listing and densities of aquatic macroinvertebrates per Surber sample collected in grazed (G) and ungrazed (U) reaches of the Rio de las Vacas, 1983–84. Chironomids were combined in 1984 because taxa were identified only to generic level in 1983.

	1983		1984	
Taxa	U	G	U	G
Ephemeroptera				
Ephemerella inermis	85	55	84	116
Paraleptophlebia sp.	32	29	11	34
Ameletus sp.	14	47	30	67
Baetis sp.	68	86	172	553
Cinygmula sp.	0	0	32	258
Tricorythodes minutus	40	396	4	45
Epeorus longimanus	19	11	256	85
Siphlonurus sp.	0	0	0	1
Ephemerella drunella grandis	0	0	0	2
Rhithrogena sp.	0	0	0	1
Diptera				
Culicoides sp.	11	11	0	0
Palpomyia sp.	22	38	0	0
Hydrophorus sp.	0	11	0	0
Hemerodromia sp.	11	0	0	8
Prosimulium sp.	22	0		
Simulium sp.	17	11	69	134
Tabanus sp.	14	11	2	1
Calopsectra sp.	19	87		
Cardiocladius sp.	14	32		
Corynoneura sp.	57	119		
Cryptochironomus sp.	0	22		
Hydrobaenus sp.	38	32		
Microtendipes sp.	36	18		
Paratendipes sp.	0	95		
Pentaneura sp.	11	11		
Polypedilum sp.	0	22		
Prodiamesa sp.	0	11		
Tanytarsus sp.	0	11		
Tendipes sp.	0	28		
Hexatoma sp.	11	33		
Ormosia sp.	16	0		
Tipula sp.	0	22		
Chironomidae			252	711
Hexatoma sp.			2	10
Maruina lanceolata			2	1
Picranota sp.			4	0
Ceratopogenidae			11	22
Deuterophebia sp.			2	0
Molophilus sp.			6	1
Ulomorpha sp.			0	1
Trichoptera				
Brachycentrus sp.	11	0	6	3
Agapetus sp.	11	0	30	15
Glossosoma sp.	15	0	54	61
Helicopsyche sp.	200	109	65	183
Hydropsyche sp.	47	78	265	318
Stactobiella sp.	11	0		
Lepidostoma sp.	46	0	0	6
Nectopsyche sp.	0	18		
Oecetis sp.	11	11	2	6
Asynarchus sp.	11	11		
Grammotaulis sp.	11	0		
Hesperophylax sp.	15	0	0	8
Polycentropus sp.	0	22	0	2
Amphicosmoecus sp.	2	9		

Table 2 continued.

Taxa	1983 U	1983 G	1984 U	1984 G
Plecoptera				
Alloperla (super genus)	0	11	0	0
Hastaperla sp.	0	27	0	0
Amphinemura sp.	19	11	26	16
Isoperla sp.	0	11	4	20
Unidentified genus	6	22		
Pteronarcella badia	0	11	6	1
Chloroperla sp.			17	10
Claasenia sp.			17	2
Nemoura (super genus)			0	1
Hemiptera				
Ambrysus sp.	22	18	2	24
Odonata				
Ophiogomphus sp.	22	19	2	2
Lepidoptera				
Parargyractis sp.	22	11	0	5
Coleoptera				
Helichus sp.	11	11		
Cleptelmis sp.	11	0		
Dubiraphia sp.	22	30		
Heterelmis sp.	11	0		
Optioservus sp.	25	11		
Stenelmis sp.	11	0		
Elmidae			136	168
Stenopelmus sp.			2	0
Dryopidae			0	2
Terrestrials	88	24	15	10

tolerant taxa (TQ = 108), *Calopsectra* sp. and *Tricorythodes minutus*, averaged 396 and 95/m^2 in the grazed compared to only 2.4 and 16 individuals/m^2, respectively, at sites in the ungrazed area.

Calculated mean chi square indices for the Vacas were 1.23 for 1983 and 2.3 for 1984. These high values indicate a marked difference in the structure of macroinvertebrate communities between the grazed and ungrazed areas (Parrish and Wagner 1983).

DISCUSSION

Use of the BCI and CSI on this group of macroinvertebrates in the Vacas suggests these organisms, indeed, may be a more suitable group than fishes to detect grazing effects on aquatic ecosystems. Although macroinvertebrate densities were variable in the Vacas, data (Table 4) serve to point out, as do selected water quality and fish data (Rinne 1988, Rinne, in press), that linear changes in physical stream habitat may have affected water quality and biota in this stream. To illustrate, during 1984 densities of aquatic macroinvertebrates estimated from samples collected in the ungrazed areas were not significantly ($P > .05$) different from pooled, downstream, disjunct, grazed (C, Fig. 1; $n = 5$) and contiguous, upstream, grazed (B, Fig. 1; $n = 5$) areas. However, separation of the 1984 samples into upper (contiguous) grazed and lower (disjunct) grazed sampling localities (Fig. 1) emphasized the greater densities of higher tolerance organisms in the downstream, disjunct, grazed area (Table 4, Fig. 2).

Significantly greater total alkalinity ($\bar{x}$ = 127 vs. 98 mg/l $CaCO_3$; $n = 15$) in summer combined with the slightly (ca 3 C) elevated water temperatures (Rinne, in press) in the downstream reach of the stream may have contributed to the greater macroinvertebrate and fish populations, as has been demonstrated elsewhere by Krueger and Waters (1983) and Egglishaw (1968). The lack of riparian vegetation in the lower grazed area of the Vacas (Rinne 1985, Rinne, in press) permitted

TABLE 3. Biomass (mg/m^2 wet weight) of the major groups of aquatic macroinvertebrates in ungrazed and grazed reaches of the Rio de las Vacas, 1982–83.

	1982		1983	
Order	Ungrazed	Grazed	Ungrazed	Grazed
Coleoptera	82.90	173.95	31.02	16.11
Diptera	127.90	174.23	39.47	191.83
Ephemeroptera	333.04	196.82	164.84	274.70
Hemiptera	2.09	111.37	1.03	13.17
Lepidoptera	0.00	9.57	8.80	5.79
Odonata	128.90	550.74	166.94	396.57
Plecoptera	10.53	3.48	0.20	6.68
Tricoptera	38.02	728.34	274.48	194.60
Totals	790.21	1960.34	764.70	1110.76

TABLE 4. Average number, biomass, tolerance quotients (TQ), and Biotic Condition Indices (BCI) for aquatic macroinvertebrates in grazed and ungrazed areas of the Rio de las Vacas, 1982–84. The number of samples is designated by n and significant ($P \leqq .05$) (single asterisk), and highly significant ($P \leqq .01$) (double asterisk) differences as determined by unpaired t-tests are indicated. Ranges are in parentheses.

Year	Treatment	Number/m^2	Biomass (g/m^2)	TQ	BCI	n
1982						
	Grazed	1897** (786–5216)	2.03* (.41–3.71)	64* (45–93)	88** (57–132)	10
	Ungrazed	787** (43–1691)	0.57* (.001–2.5)	78* (57–103)	71** (58–89)	20
1983						
	Grazed	1035* (701–2451)	1.01 (.31–3.04)	88* (68–101)	61** (52–78)	10
	Ungrazed	550* (108–1412)	0.69 (.02–2.61)	67* (44–89)	82** (60–121)	10
1984						
	Grazed					
	Upper	1509 (905–2058)	No	71 (60–85)	76 (62–87)	5
	Lower	4375* (2522–6283)	Data	78* (69–82)	68* (64–76)	5
	Ungrazed	1541* (765–2974)		65* (51–77)	84* (69–103)	5

increased solar radiation to the stream and that, in turn, may have facilitated greater populations of macroinvertebrates, as reported in the Pacific Northwest by Murphy and Hall (1981), Murphy et al. (1981), and Hawkins et al. (1982). Also, significantly greater mean stream conductivity in summer in the grazed area than in the ungrazed area (216 umhos/cm vs. 164 umhos/cm, respectively) suggests that an increase in dissolved solids in stream water in the lower grazed area actually may be beneficial to aquatic macroinvertebrate communities. Winget and Mangum (1979) pointed out that high-elevation, "distilled water," first-order streams actually benefit from an increase in dissolved solids. Similarly, Egglishaw (1968) suggested that a more rapid turnover of organic matter resulted in more food availability for invertebrates in hard water (or high alkalinity) streams.

Mean TQs of aquatic macroinvertebrates were significantly less in 1982 in the grazed areas. Values, nevertheless, were significantly greater in both 1983 and 1984 when stratified sampling was initiated and when samples within the grazed area in 1984 were separated into upper and lower subsets. The combination of significant TQ and BCI suggests that although insect densities and biomasses were always greater in grazed

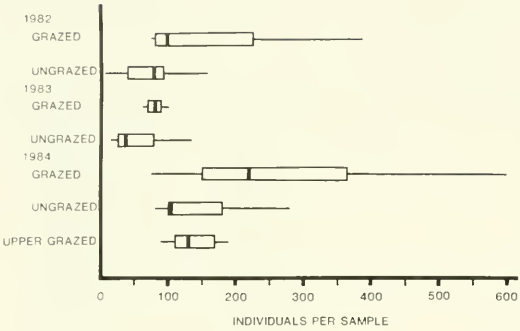

Fig. 2. Estimated number of aquatic macroinvertebrates per surber in grazed and ungrazed areas. Estimates for the upper (B, Fig. 1) and lower (C, Fig. 1) grazed samples taken in 1984 are also provided. Medians (large verticals), upper and lower quartiles (small verticals), ranges (single horizontals), and outlying values (dots) are indicated in plots.

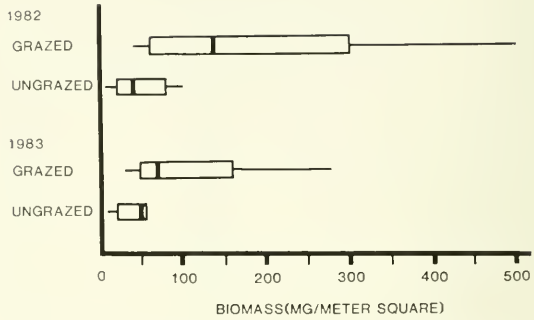

Fig. 3. Estimated biomass (mg/m^2) of aquatic macroinvertebrates in the Rio de las Vacas in grazed and ungrazed areas, 1982–83. Plots contain the same statistics as described for Fig. 2.

stream reaches (Table 4, Figs. 2, 3), these communities were comprised of the more-tolerant taxa. There was greater silt content in the substrate of the downstream reaches of the stream than in the upstream ungrazed area (Rinne 1988), which might, in part, explain the absence of some less-tolerant taxa. Further, the extremely high CSIs strongly suggest a difference in the structure of the aquatic macroinvertebrate community in the grazed compared to the ungrazed area of the Vacas. This difference, however, might as easily be attributed to naturally greater alkalinities, temperatures, and dissolved solids in the water column in the lower, disjunct grazed reaches of the stream, as to the effects of cattle grazing. Ward (1976) similarly reported that warmer water temperature and higher dissolved solid content of water paralleled increased macroinvertebrate populations in a Colorado mountain river.

In light of the stream continuum concept (Vannote et al. 1980) and watershed principles (Hynes 1975, Likens 1984) operating as discussed by Rinne (1988), it is perhaps surprising that there was any detectable difference between aquatic macroinvertebrate populations in stream reaches in the grazed and ungrazed areas of the Vacas. It is possible that the areas sampled were naturally different both in structure and in macroinvertebrate fauna prior to fencing. There was definitely a marked difference in streambank stability and vegetation between the two areas (Rinne 1985). Lack of any baseline, pretreatment data, however, precludes unequivocably stating that exclusion of grazing enhanced aquatic macroinvertebrate populations in the Vacas.

Based on limited literature and this study, we can state that aquatic macroinvertebrates are useful biological indicators of grazing impacts on stream ecosystems. However, case history studies of grazing effects on this group, on stream habitat, and on fishes (Rinne 1988) emphasize the importance of baseline, pretreatment definition of variability of factors within study areas prior to implementing treatments and ensuing research (Szaro and Rinne 1988).

CONCLUSIONS

Both qualitative and quantitative differences in habitat and biota were found in the Vacas, but lack of pretreatment (prefencing) data precludes making unequivocable statements regarding livestock grazing effects on the habitat and biota of this stream. Many factors create difficulties in a study of this problem (Rinne 1985). Future research on grazing effects on stream habitat and biota must be carefully designed (Rinne 1988) if viable, defendable information is to result.

LITERATURE CITED

BUIKEMA, A. L., AND J. CAIRNS, JR. 1980. Aquatic invertebrates bioassays. American Society Testing Material, Philadelphia. 208 pp.

EGGLISHAW, H. J. 1968. The quantitative relationship between bottom fauna and plant detritus in streams of different calcium concentration. J. Appl. Ecol. 5: 731–740.

HAWKINS, C. P., M. C. MURPHY, AND N. H. ANDERSON. 1982. Effects of canopy, substrate composition, and gradient on the structure of macroinvertebrate communities in Cascade streams of Oregon. Ecology 63: 1840–1856.

HYNES, H. B. N. 1975. The stream and its valley. Verhandlungen Internal. Vereihigung Limnol. 19: 1–15.

KAUFFMAN, J. B., AND W. C. KRUEGER. 1984. Livestock impacts on riparian ecosystems and streamside management implications. A review. J. Range Manage. 37: 430–437.

KRUEGER, C. C., AND T. F. WATERS. 1983. Annual production of macroinvertebrates in three streams of different water quality. Ecology 64: 840–850.

LIKENS, G. E. 1984. Beyond the shoreline: a watershed-ecosystem approach. Intnat. Verein. Theor. Angewan. Limnol. 22: 1–22.

MERRITT, R. W., AND K. W. CUMMINS, EDS. 1984. An introduction to the aquatic insects of North America. 2d ed. Kendall/Hunt, Dubuque, Iowa. 722 pp.

MUNTHER, G. L. 1985. Use of macroinvertebrates to monitor forest management activities. West. Wildl. 11: 8–11.

MURPHY, M. L., AND J. O. HALL. 1981. Varied effects of clearcut logging on predators and their habitat in small streams of the Cascade Mountains, Oregon. Canadian J. Fish. Aquat. SW 38: 137–145.

MURPHY, M. L., C. P. HAWKINS, AND N. H. ANDERSON. 1981. Effects of canopy modification and accumulated sediment on stream communities. Trans. Am. Fish. Soc. 110: 468–478.

PARRISH, F. R., AND J. A. WAGNER. 1983. An index of community structure sensitive to water pollution. J. Freshwater Ecol. 2: 103–107.

PLATTS, W. S. 1982. Livestock and riparian fishery interactions: What are the facts? Pages 507–515 *in* Trans. Forty-seventh N. Am. Wildlife and Nat. Res. Conf., March 26–31, Portland, Oregon.

PLATTS, W. S., W. F. MEGAHAN, AND G. W. MINSHALL. 1983. Methods for evaluating stream, riparian and biotic conditions. USDA Forest Service Gen. Tech. Rept. INT–138. Ogden, Utah. 70 pp.

RESH, V. H. 1979. Sampling variability and life history features: basic considerations in the design of aquatic insect studies. J. Fish. Res. Board Can. 36: 290–311.

RINNE, J. N. 1985. Livestock grazing effects on southwestern streams: a complex research problem. USDA Forest Service Gen. Tech. Rept. RM–120: 295–299.

———. 1988. Grazing effects on stream habitat and fishes: research design considerations. N. Amer. J. Fish Manage. 8(2).

———. In press. Livestock grazing effects on riparian-stream ecosystems: research complexity and design. *In* R. R. Johnson et al., eds., Riparian ecosystems: ecology, conservation and management. University of Arizona Press, Tucson, Arizona.

SKOVLIN, J. M. 1984. Impacts of grazing on wetlands and riparian habitat: a review of our knowledge. Pages 1001–1103 *in* Developing strategies for rangeland management. Nat. Research Council/Nat. Acad. Sci., Westview Press, Boulder, Colorado.

SMOCK, L. A. 1980. Relationships between body size and biomass of aquatic insects. Freshwater Biol. 10: 375-383.

SZARO, R. C., S. C. BELFIT, J. K. AITKIN, AND J. N. RINNE. 1985. A preliminary study on the impact of grazing on a riparian garter snake. USDA Forest Service Gen. Tech. Rept. RM–120: 359–363. Fort Collins, Colorado.

SZARO, R. C., AND J. N. RINNE. 1988. Ecosystem approach to management of southwestern riparian communities. Trans. N. Amer. Wildl. and Nat. Resources Conf. 52.

USINGER, R. L., ED. 1956. Aquatic insects of California. University of California Press, Berkeley. 508 pp.

VANNOTE, R. L., G. W. MINSHALL, K. W. CUMMINS, J. R. SEDELL, AND C. E. CUSHING. 1980. The river continuum concept. Canadian J. Fish. Aquat. Sci. 37: 130–137.

WARD, J. O. 1976. Comparative limnology of differentially regulated sections of a Colorado mountain river. Arch. Hydrobiol. 78: 319–342.

WINGET, R. N., AND F. A. MANGUM. 1979. Biotic condition index: integrated biological, physical and chemical stream parameters for management. USDA Forest Service, Intermountain Region, Ogden, Utah. 51 pp.

COMPREHENSIVE LIST BY HABITAT OF THE ALGAE OF UTAH, USA

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ABSTRACT.—A list of the algal species that have been reported from the state of Utah is presented. Also listed are the habitats from which these algae were collected. A total of nearly 1,900 taxa have been identified to the species level or below. Diatoms comprise the largest group, with nearly 1,000 taxa, followed by the green algae with over 550 taxa.

The state of Utah encompasses a large geographical region with diverse geology and habitats. Elevational and habitat variabilities range between hot desert environments at about 750 m and high mountain tundra as high as 3,600 m. A wide range of specific habitat types are present. Salt marshes and lakes are common, as are freshwater lakes and reservoirs. Streams of a wide variety, from relatively warm, intermittent desert streams to high mountain, cold water rivers, are common. Marshes, acidic and basic bogs, wet meadows, wet walls, and thermal and cold springs are all present in Utah, some in abundance.

We have examined the algal floras of many of these habitats in western North America over the past several years, and during the process of our work, we began to keep a list of the algal taxa recorded from the state of Utah. We searched several hundred articles dealing with the algae of Utah and recorded the taxa listed by those authors who had done floristic, taxonomic, or ecological work. This amounted to 125 papers of primary importance in developing the Utah algal species list. These papers are listed in the bibliography at the end of this paper. Although our search of nearly all the papers dealing with the algae of Utah contributed to our understanding of select taxa or groups, we found that many papers did not add to the total floristic list (see Christensen 1956, 1962 for a list of most of the papers published on Utah algae prior to 1962).

It is of interest to note when these works were published. Only three papers we are aware of dealing with the algal taxa of the state were published during the nineteenth century. During the 30-year period from the turn of the century to the end of the 1920s, a total of 6 additional papers were published. The decade of the 1930s saw 10 papers published, while only 3 papers were published during the 1940s. Around 30 papers in each of the decades of the 1960s, 1970s, and to date in the 1980s have been published.

The algal flora of Utah is large and diverse. Nearly 1,900 algal taxa with complete specific, varietal, or forma epithets have been reported in the literature as having been collected in the state. Many additional taxa are reported as unknown species. We have not been able to verify most of these taxa since specimens are not available, and this is somewhat beyond the scope of this introductory list. Many of the diatoms are available for further study, and we hope to examine these algae in more detail in the future.

There also exist many problems with taxonomy and nomenclature. We have not made nomenclatural changes except in instances where authors themselves have made or mentioned such changes. However, it is clear that many of the names used by authors dealing with Utah algae are invalid and should be placed in synonymy. Unraveling these problems awaits the writing of a comprehensive algal flora for the state. In the present paper it is merely our intent to present a list of the algal taxa reported as occurring in the state. It has been difficult to determine the authors of all taxa listed in the Utah algal flora. In many cases, the original researchers did not record species authors, and we have attempted to add them. We have also made changes in authorships where it was clear that a mistake was made. In a few cases, we were not able to determine the author of a taxon, and these will

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be evident in the species list (Table 1).

It should also be mentioned that we have followed a very traditional scheme of classification above the generic level. The reassessment of orders, classes, and divisions of algae (particularly in the Chlorophyta) is currently receiving a good deal of attention from many researchers. We have been conservative in this matter since it is not particularly important to the aim of this paper, and it is certain that further changes are ahead in the near future. We felt that most algologists would be familiar with the traditional scheme we have followed.

The largest group of Utah algae is the diatoms, which contains 977 taxa in 63 genera. The Chlorophyta is represented by a total of 568 taxa in 119 genera. Cyanophyta are represented in Utah by a total of 254 taxa in 53 genera. The Chrysophyceae is represented by 15 taxa in 7 genera, and the Xanthophyceae by 28 taxa in 7 genera. Euglenophyta in the state are represented by 26 taxa in 6 genera. Dinoflagellates (Pyrrhophyta) have been reported in Utah as 7 species in 5 genera. Two genera of Cryptophyta containing 2 species have been reported, as have 2 genera of Rhodophyta containing 2 species.

TABLE 1. List of algal taxa reported from the state of Utah from the earliest recorded collections to the present. The taxa are listed alphabetically according to taxonomic category (except for Bacillariophyceae, which are listed strictly alphabetically). An attempt has been made to categorize all taxa according to the habitat of their occurrence. The letter at the end of the species name refers to the specific habitat type from which the alga was collected: Habitat A is lakes and reservoirs, B is rivers and streams, C is the Great Salt Lake, D is soils, E is wet walls, F is wet meadows, G is thermal springs, H is salt marshes, I is fossils, J is cold springs, and K is undesignated or miscellaneous.

DIVISION CYANOPHYTA	
Class Cyanophyceae	
Order Chroococcales	
Anacystis cyanea (Kütz.) Dro. & Dai.	A
Anacystis marginata Meneg.	B
Anacystis rupestris (Lyngb.) Dro. & Dai.	A
Anacystis sp.	A
Aphanocapsa elachista West & West	A,B
Aphanocapsa elachista var. *conferta* West & West	A
Aphanocapsa endophytica G.M.Sm.	B
Aphanocapsa grevillei (Hass.) Rabh.	A,B,K
Aphanocapsa halophytica Fremy	C
Aphanocapsa pulchra (Kütz.) Rabh.	A,B,J
Aphanocapsa rivularis (Carm.) Rabh.	A,B,J
Aphanocapsa virescens (Hass.) Rabh.	A,F,J
Aphanocapsa sp.	A
Aphanothece castagnei (Bréb.) Rabh.	D
Aphanothece clathrata G.S.West	A,B,H,J
Aphanothece gelatinosa (Henn.) Lemm.	A,E
Aphanothece nidulans Rich	A,B,H
Aphanothece packardii (Farl.) Setch. (see *Coccochloris elabens*)	
Aphanothece prasina A.Br.	B,E,K
Aphanothece saxicola Naeg.	A,B,K
Aphanothece stagnina (Spreng.) A.Br.	A,B,J,K
Aphanothece utahensis Tild. (see *Coccochloris elabens*)	
Aphanothece sp.	A
Chroococcus cohaerens (Bréb.) Naeg.	A,B,G,K
Chroococcus hansgiri Schmidle	D
Chroococcus limneticus Lemm.	A,B,K
Chroococcus limneticus var. *distans* G.M.Sm.	A
Chroococcus macrococcus Rabh.	B
Chroococcus minor (Kütz.) Naeg.	D
Chroococcus minutus (Kütz.) Naeg.	A,B,E
Chroococcus multicoloratus Wood	B,J,K
Chroococcus pallidus Naeg.	D,E
Chroococcus prescottii Dro. & Dai.	A
Chroococcus rufescens (Kütz.) Naeg.	D
Chroococcus schizodermaticus West	A
Chroococcus turgidus (Kütz.) Naeg.	A,B,D,E,F,G,J
Chroococcus varius A.Br.	E
Chroococcus sp.	A,C,D
Chroothece cryptarum Farl.	A
Coccochloris elabens (Bréb.) Dro. & Dai. (= *Polycystis packardii* Farl.) (= *Microcystis packardii* [Farl.] Setch.) (= *Aphanothece utahensis* Tild.) (= *Aphanothece packardii*)	C
Coelosphaeriopsis halophila Lemm. (see *Coelosphaerium halophilum*)	
Coelosphaerium dubium Grun.	A,B
Coelosphaerium halophilum (Lemm.) Geitl. (= *Coelosphaeriopsis halophila*)	A
Coelosphaerium kuetzingianum Naeg.	A,B,J
Coelosphaerium naegelianum Unger	A
Coelosphaerium sp.	A
Dactylococcopsis acicularis Lemm.	A
Dactylococcopsis raphidiodes Hansg.	J,K
Dactylococcopsis rupestris Hansg.	A
Dactylococcopsis sp.	A
Eucapsis alpina Clem. & Shantz.	A
Gloeocapsa aeruginosa (Carm.) Kütz.	B,D,E
Gloeocapsa arenaria (Hass.) Rabh.	B,E,K
Gloeocapsa calcarea Tild.	A,B
Gloeocapsa decorticans (A.Br.) P.Richt.	A
Gloeocapsa nigrescens Naeg.	E

Table 1 continued.

Gloeocapsa punctata Naeg.	A,D
Gloeocapsa rupestris Kütz.	B,D,E
Gloeocapsa violacea (Corda) Rabh.	B,K
Gloeocapsa sp.	A,B,C
Gloeothece confluens Naeg.	A
Gloeothece fuscolutea Naeg.	A,B
Gloeothece linearis Naeg.	A
Gloeothece linearis var. *composita* G. M.Sm.	D
Gloeothece palea (Kütz.) Rabh.	E
Gloeothece rupestris (Lyngb.) Born.	E
Gloeothece sp.	C
Gomphospheria aponina Kütz.	A,B,E
Gomphospheria aponina var. *delicatula* Vir.	A
Gomphospheria lacustris Chod.	A
Gomphospheria sp.	A
Heterohormogonium schizodicholomum J.Cope.	A
Holopedium irregulare Lager.	A
Marssoniella elegans Lemm.	A
Merismopedia aeruginosa Bréb.	A,B
Merismopedia brebisson Lemm.	A,B
Merismopedia elegans A.Br.	A,B
Merismopedia glauca (Ehr.) Naeg.	A,B,F
Merismopedia nova Wood	A
Merismopedia punctata Meyen.	D,J
Merismopedia tenuissima Lemm.	A,B,E
Merismopedia sp.	A,B
Microcystis aeruginosa Kütz. em. Elenk.	A,J,K
Microcystis aeruginosa var. *major* Witt.	A
Microcystis aeruginosa f. *minor* Elenk.	J
Microcystis flos-aquae (Wittr.) Kirch.	A,B,J
Microcystis incerta Lemm.	A
Microcystis packardii (Farl.) Setch. (see *Coccochloris elabens*)	
Microcystis protocystis Crow	A
Microcystis pulverea (Wood) Migula	A,B
Microcystis sp.	A,G
Polycystis packardii Farl. (see *Coccochloris elabens*)	
Rhabdoderma irregulare (Naum.) Geit.	A
Rhabdoderma lineare Schm. & Laut.	A
Synechococcus aeruginosa Naeg.	A,D,G,K
Synechococcus sp.	A,G
Synechocystis aquatilis Sauv.	J
Synechocystis sp.	A
Order Chamaesiphonales	
Chamaesiphon incrustans Grun.	A,B,E,K
Chamaesiphon sp.	B
Entophysalis lemaniae (Ag.) Dro. & Dai.	B
Entophysalis rivularis (Kütz.) Dro.	B,C
Entophysalis rivularis f. *papillosa* (Kütz.) Dro. & Dai.	B
Pleurocapsa cf. *entophysaloides* Setch. & Gard.	C

Table 1 continued.

Xenococcus schousboei Thur.	A,J
Xenococcus sp.	A
Order Oscillatoriales	
Amphithrix janthina (Mont.) Bourn. & Flah.	B
Anabaena affinis Lemm.	B
Anabaena azollae Stras.	A,B,K
Anabaena catenula (Kütz.) Bourn.	B
Anabaena circinalis Rabh.	B,K
Anabaena cylindrica Lemm.	A,K
Anabaena flos-aquae (Lyngb.) Bréb.	A,B
Anabaena inaequalis (Kütz.) Bourn. & Fla.	A,B,K
Anabaena oscillarioides Bory	A,B,G
Anabaena sphaerica Bourn. & Flah.	A,B
Anabaena spiroides Kleb.	A
Anabaena spiroides var. *crassa* Lemm.	A
Anabaena torulosa (Carm.) Lager.	A,K
Anabaena variabilis Kütz.	A,B,D,K
Anabaena sp.	A,B,D,H,K
Anabaenopsis sp.	A
Aphanizomenon flos-aquae (Lemm.) Ralfs	A,B
Arthrospira gomontiana Setch.	B,G,K
Aulosira sp.	A
Calothrix clavata West	E
Calothrix parietina (Naeg.) Thur.	B,D,E,J,K
Calothrix stagnalis Gom.	B
Calothrix stellaris Bourn. & Fla.	B
Calothrix sp.	A,B,D
Cylindrospermum catenatum Ralfs	K
Cylindrospermum catenatum var. *ellipticum* Flow.	B
Cylindrospermum catenatum var. *elongatum* Flow.	K
Cylindrospermum catenatum var. *ovatum* Flow.	A,E
Cylindrospermum comatum Wood	K
Cylindrospermum licheniforme (Bory) Kütz.	K
Cylindrospermum muscicola Kütz.	A,K
Cylindrospermum sp.	J,K
Dasygloea amorpha Berkeley	B,K
Desmonema pachyderma Flow.	B
Desmonema sp.	A
Dichothrix meneghiniana Kütz.	B
Dichothrix orsiniana (Kütz.) Bourn. & Flah.	B,K
Dichothrix utahensis	C
Dichothrix sp.	K
Hapalosiphon sp.	A
Lyngbya aeruginco-caerulea (Kütz.) Gom.	A,B,G,H,K
Lyngbya aestuarii (Mert.) Leibm.	A,B,D,G
Lyngbya birgei G.M.Sm.	A
Lyngbya circumcreta G.S.West	A
Lyngbya contorta Lemm.	A

Table 1 continued.

Lyngbya diguetii Gom.	A
Lyngbya epiphytica Hier. ex Eng. & Prant.	A
Lyngbya kuetzingii Schmidle	G,J
Lyngbya limnetica Lemm.	D,E
Lyngbya major Meneg.	A,B,J,K
Lyngbya majusculla (Dill.) Harv.	A,K
Lyngbya martensiana Meneg.	A,B,D,G,H
Lyngbya martensiana var. *calcarea* Tild.	B
Lyngbya martensiana var. *capitata* Flow.	K
Lyngbya martensiana var. *tenuivaginata* Gom.	G
Lyngbya nana Tild.	A,B,K
Lyngbya nordgaardii Wille	E
Lyngbya ochracea (Kütz.) Thuret.	K
Lyngbya sordida (Zanard.) Gom.	A,K
Lyngbya versicolor (Wart.) Gom.	B
Lyngbya sp.	A,B,G,K
Microchaete robusta Setch. & Gard.	B
Microcoleus lyngbyaceus (Kütz.) Crouan	C
Microcoleus paludosus (Kütz.) Gom.	A,B
Microcoleus vaginatus (Vauch.) Gom.	B,D,K
Microcoleus sp.	A
Nodularia amorica Thuret	A,J
Nodularia harveyana (Thw.) Thuret	A,B,K
Nodularia paludosa Wolle	K
Nodularia sphaerocarpa Bourn.	A,K
Nodularia spumigena Mert.	A,C,J
Nodularia sp.	A
Nostoc caeruleum Lyngb.	A
Nostoc commune Vauch.	A,D,E,K
Nostoc ellipsosporum (Desmaz.) Rabh.	E,K
Nostoc linckia (Roth) Bourn. & Thur.	A,B
Nostoc microscopicum Carm.	E
Nostoc muscorum C.A.Ag.	A,D,E,K
Nostoc paludosum Kütz.	A,B,D,E
Nostoc parmelioides Kütz.	B
Nostoc piscinale Kütz.	A,B,K
Nostoc pruniforme (L.) C.A.Ag.	A,H,K
Nostoc punctiforme (Kuetz.) Hariot	B,D
Nostoc sphaericum (L.) Vauch.	B,C,K
Nostoc sphaeroides Kütz.	B,F,K
Nostoc spongiaeforme C.A.Ag.	A,B
Nostoc verrucosum Vauch.	A,B
Nostoc sp.	A,B,D,H
Nostochopsis sp.	A
Oscillatoria agardhii Gom.	A,B,E,J,K
Oscillatoria amoena (Kütz.) Gom.	A,B,G,H,K
Oscillatoria amphibia C.A.Ag.	A,B,D,G,H,K
Oscillatoria anguina (Bory) Gom.	B
Oscillatoria angusta Koppe	A,B,D,E,J
Oscillatoria angustissima West & West	A,B,D,G,H,K
Oscillatoria animalis Ag.	A,B,D,G,H,K
Oscillatoria articulata Gard.	A
Oscillatoria boryana Bory.	D
Oscillatoria brevis Kütz.	B,G,H,K
Oscillatoria brevis var. *neopolitana* (Kütz.) Gom.	G
Oscillatoria chalybea Mert.	B,G,H,K

Table 1 continued.

Oscillatoria chalybea var. *genuina* (Coll.) Hold. & Setch.	A
Oscillatoria chlorina Kütz.	J
Oscillatoria cortiana Menegh.	G,J,K
Oscillatoria cruenta Grun.	A,B,D,E,F, G,J
Oscillatoria curviceps C.A.Ag.	B
Oscillatoria formosa Bory	A,B,F,G,K
Oscillatoria geminata Meneg.	A,B,D,E,G,K
Oscillatoria janthophora Gom.	G,H
Oscillatoria laetevirens Crouan	G,K
Oscillatoria lemmermanni Kütz.	A,B,F,G,K
Oscillatoria limnetica Lemm.	A,E
Oscillatoria limosa (Roth) Ag.	A,B,D,G,J,K
Oscillatoria lutea Ag.	B,D
Oscillatoria minnesotensis Tild.	B,G,K
Oscillatoria nigro-viridis Thw.	A,B,G,H,K
Oscillatoria okeni Ag.	G
Oscillatoria princeps Vauch.	A,B,C,G,K
Oscillatoria prolifica (Grev.) Gom.	A,K
Oscillatoria rubscens DeCand.	B,E
Oscillatoria sancta (Kütz.) Gom.	A,B,D,G,K
Oscillatoria sancta var. *aequinoctialis* Gom.	A,J
Oscillatoria simplicissima Gom.	K
Oscillatoria splendida Grev.	B,J,K
Oscillatoria subbrevis Schmidle	A,E
Oscillatoria subbrevis f. *minor* Desik.	E
Oscillatoria subtillissima Kütz.	A,G,H,K
Oscillatoria tenuis C.A.Ag.	A,B,D,G,K
Oscillatoria tenuis var. *natans* (Kütz.) Rab.	C,H,K
Oscillatoria tennis var. *turgestina* (Kütz.) Rab.	C,G,H,K
Oscillatoria terebriformis C.A.Ag.	G
Oscillatoria sp.	A,B,C,H,K
Phormidium ambiguum Gom.	A,B
Phormidium angustissimum West & West	A,G,H,K
Phormidium autumnale (Ag.) Gom.	A,B,G,K
Phormidium favosum (Bory) Gom.	B,J,K
Phormidium foveolarum (Mont.) Gom.	B,G,H,K
Phormidium fragilis Menegh.	H,K
Phormidium incrustatum (Naeg.) Gom.	A,B
Phormidium inundatum Kütz.	A,G,J,K
Phormidium minnesotense (Tild.) Druet	D
Phormidium ramosum Boye	G,H,K
Phormidium subfuscum Kütz.	A,B,G
Phormidium subfuscum var. *joannianum* (Kütz.) Gom.	B
Phormidium tenue (Meneg.) Gom.	A,B,D,G
Phormidium uncinatum (C.A.Ag.) Gom.	B,J,K
Phormidium sp.	A,B,K
Plectonema boryanum Gom.	A
Plectonema nostocorum Bornet	K
Plectonema tenue Thuret	K
Plectonema tomasinianum (Kütz.) Bornet	J
Rivularia echinulata	K
Rivularia sp.	A,J
Sacconema rupestre Borzi	B

Table 1 continued.

Schizothrix calcicola (Ag.) Gom.	D
Schizothrix fasiculata (Naeg.) Gom.	B
Schizothrix fragilis (Kütz.) Gom.	B,E
Schizothrix lacustris A.Br. ex Kütz.	A,E
Schizothrix sp.	A
Scytonema alatum (Carm.) Borzi	E
Scytonema hofmannii Ag.	D
Scytonema myochrous (Dillw.) C.A.Ag.	D,E,K
Scytonema tolypothricoides Kütz.	A,B,E
Scytonema sp.	K
Spirulina calderia Tild.	B,G,K
Spirulina laxa G.M.Sm.	A,E
Spirulina major Kütz.	A,B,C,G,K
Spirulina nordstedtii Gom.	B
Spirulina princeps (West & West) G.W.West	A,B
Spirulina subsalsa Oersted	E,J,K
Spirulina subtilissima Kütz.	G
Spirulina sp.	A,B
Stigonema hormoides (Kütz.) Bourn. & Fla.	D
Stigonema mamillosum (Lyngb.) C.A.Ag.	E
Stigonema turfaceum (Berk.) Cooke	A,B
Stigonema sp.	A,B
Tolypothrix bouteillei (Bréb. & Desm.) Forti	D
Tolypothrix distorta Kütz.	A
Tolypothrix lanata Wartm.	A,B,E
Tolypothrix limbata Thuret	A,F
Tolypothrix penicillata Ag.	A,B,K
Tolypothrix tenuis Kütz.	A,D,E,G,H, J,K
Tolypothrix sp.	A,D,K
Trichodesmium erythraeum Ehr.	A,B
Trichodesmium sp.	A
Class Chlorobacteriaceae	
Pelogloea bacillifera Lauterb.	A
DIVISION CHLOROPHYTA	
Class Chlorophyceae	
Order Volvocales	
Carteria cordiformis (Cart.) Dill.	A
Carteria klebsii (Dang.) France em. Troitz.	A,B
Carteria stellifera Nyg.	A
Carteria sp.	A,C,H
Chlamydomonas altera Skuja	A
Chlamydomonas angulosa Dill.	B
Chlamydomonas globosa Snow	A
Chlamydomonas gloeocystiformis Dillw.	K
Chlamydomonas nivalis (Bau.) Wille	K
Chlamydomonas polypyrenoideum Pres.	A
Chlamydomonas sp.	A,B,C,D,H
Chloromonas brevispina (Fritz.) Hoh., Roem. & Müll.	K

Table 1 continued.

Chloromonas nivalis (Chod.) Hoh. & Müll	K
Cryocystis granulosa Kol.	K
Dunaliella salina Teod.	C,H
Dunaliella viridis Teod.	C
Dunaliella sp.	A
Eudorina elegans Ehr.	A,B
Eudorina sp.	A
Gonium pectorale Müll.	A
Gonium sp.	A
Pandorina morum (Müll.) Bory	A,B,K
Pandorina sp.	A
Pedinomonas sp.	A
Platymonas elliptica G.M.Sm.	A
Pleodorina illinoiseusis Kofoid	A
Pleodorina sp.	A,B
Pteromonas cordiformis Lemm. em Fott	A
Pteromonas cruciata Playf.	A
Pteromonas sp.	A
Spermatozopsis exultans Korsch	C
Sphaerellopsis aulata (Pasch.) Gerl.	A
Sphaerellopsis gloeocystiformis (Korsch) Gerloff	C
Volvox aureus Ehr.	K
Volvox globator L.	A,K
Volvox tertius A.Meyer	B
Volvox sp.	A,B
Wislouchiella planktonica Skv.	A
Order Tetrasporales	
Asterococcus limneticus G.M.Sm.	A,B,J
Asterococcus sp.	A
Chlorosarcina brevispinosa Chant. & Bold	D
Elakatothrix gelatinosa Wille	A
Elakatothrix viridis Printz.	A
Gloeocystis ampla (Kütz.) Lager.	A
Gloeocystis gigas (Kütz.) Lager.	A,B
Gloeocystis major Gerneck	A
Gloeocystis planctonica (West & West) Lemm.	B
Gloeocystis vesiculosa Naeg.	A,B
Gloeocystis sp.	A,B,C
Palmella miniata Leibl.	D,E
Palmella mucosa Kütz.	A,B,F
Palmella sp.	A,J
Sphaerocystis schroeteri Chod.	A,B,D,E
Sphaerocystis sp.	A
Tetraspora cylindrica (Wahl.) Ag.	A
Tetraspora gelatinosa (Vauch.) Desvaux	A,B
Tetraspora lacustris Lemm.	A
Tetraspora lubrica (Roth) Ag.	A,B,F
Tetraspora lubrica var. *lacunosa* Chauv.	C
Tetraspora sp.	A,B

Table 1 continued.

Order Ulotrichales	
Binuclearia tatrana Wittr.	A
Binuclearia sp.	A
Chlorotylium cataractum Kütz.	B
Cylindrocapsa conferta W. West	A,B
Cylindrocapsa geminella Wolle	A,B,K
Geminella interrupta Turpin	B
Geminella minor Naeg.	B
Geminella scalariformis G.S. West	A,K
Hormidium sp.	A
Microspora amoena (Kütz.) Rabh.	G
Microspora crassior (Hansg.) Haz.	A,G
Microspora floccosa (Vauch.) Thur.	A
Microspora loefgrenii (Nordst.) Lager.	A,B
Microspora quadrata Haz.	B
Microspora stagnorum (Kütz.) Lager.	A
Microspora tumidula Haz.	A,K
Microspora willeana Lager.	A,B
Microspora wittrockii (Wille) Lager.	K
Microspora sp.	A
Microthamnion sp.	A
Palmodictyon varians (Naeg.) Lemm.	A,B
Stichococcus bacillaris Naeg.	A,K
Stichococcus scopulinus Haz.	K
Stichococcus subtilis (Kütz.) Klercker	B,K
Stichococcus sp.	A
Ulothrix aequalis Kütz.	A,B
Ulothrix calderia (Kütz.) Collins	G
Ulothrix cylindricum Pres.	A,E
Ulothrix oscillarina Kütz.	J
Ulothrix scalariformis G.S. West	A
Ulothrix subtillissima Rabh.	B
Ulothrix tenerrima Kütz.	A,B,D,K
Ulothrix tenuissima Kütz.	A,B
Ulothrix variabilis Kütz.	A
Ulothrix zonata (Web. & Mohr.) Kütz	A,B,E,F,H,K
Ulothrix sp.	A,B,H
Order Sphaeropleales	
Sphaeroplea annulina (Roth) Ag.	K
Sphaeroplea sp.	K
Order Chaetophorales	
Aphanochaete repens A. Br.	A,B,K
Chaetophora elegans (Roth) Ag.	A,B,G,K
Chaetophora incrassata (Hds.) Haz.	A,B
Chaetophora sp.	A,B,F,G,K
Chaetosphoeridium sp.	A
Coleochaete irregularis Pringsheim	B
Dicranochaete reniformis Hiero.	A
Draparnaldia acuta (C.A.Ag.) Kütz.	F
Draparnaldia glomerata (Vauch.) C.A.Ag.	A,B
Draparnaldia plumosa (Vauch.) Ag.	A,B
Draparnaldia sp.	A,B
Gongrosira sp.	A

Table 1 continued.

Microthamnion kuetzingianum Naeg.	J
Myxonema protensum Dill.	A
Myxonema stagnatile Haz. (see *Stigeoclonium stagnatile*)	
Myxonema sp. (see *Stigeoclonium* sp.)	
Protococcus viridis Ag.	A,D,K
Protoderma viride Kütz.	B
Stigeoclonium aestivale Haz.	A
Stigeoclonium attenuatum (Haz.) Collins	A,B
Stigeoclonium lubricum (Dillw.) Kütz.	B,K
Stigeoclonium stagnatile (Haz.) Coll. (=*Myxonema stagnatile*)	A,B,J
Stigeoclonium subsecundum Kütz.	A
Stigeoclonium subuligerum Kütz.	J
Stigeoclonium tenue (Ag.) Kütz.	A,K
Stigeoclonium sp. (=*Myxonema* sp.)	A,B,E
Order Trentepohliales	
Trentepohlia aurea (L.) Martius	E
Order Schizogoniales	
Prasiola mexicana J.G.Ag.	A
Order Oedogoniales	
Bulbochaete sp.	A
Oedogonium capilliforme Kütz.	A,K
Oedogonium capilliforme var. *debaryanum* (Chm.) Hirn.	A,K
Oedogonium fonticola Wolle	B
Oedogonium grande Kütz.	J
Oedogonium vaucherii LeClere	B
Oedogonium sp.	A,B,D,E,F H,K
Order Ulvales	
Enteromorpha aconthophora Kütz.	A,B,K
Enteromorpha crinita (Roth) C.A.Ag.	A,K
Enteromorpha intestinalis (L.) Grev.	A,B,C,H,K
Enteromorpha marginata J.G.Ag.	C
Enteromorpha micrococca Kütz.	A,B,K
Enteromorpha plumosa Kütz.	B,H
Enteromorpha prolifera (Dan.) J.G.Ag.	A,B,H
Enteromorpha salina	A,B,K
Enteromorpha tubulosa	C
Enteromorpha sp.	A,B,F,H
Monostroma quaternarium Kütz.	C
Monostroma sp.	A
Ulva marginata Ag.	C
Order Cladophorales	
Cladophora callicoma Kütz.	A,B
Cladophora canalicularis Roth	B
Cladophora crispata (Roth) Kütz.	A,B
Cladophora fracta (Dillw.) Kütz.	A,B,C,H,K
Cladophora glomerata (Lemm.) Kütz.	A,B,E,H,J
Cladophora insignis (Ag.) Kütz.	A,K

Table 1 continued.

Cladophora kuetzingiana Grun.	A,B
Cladophora sp.	A,B,F,H,K
Rhizoclonium crassipellitum West & West	H
Rhizoclonium crispum Kütz.	A,C,H
Rhizoclonium giganteum Silva	G
Rhizoclonium hieroglyphicum (Ag.) Kütz.	A,B,C,H,K
Rhizoclonium pachydermum Kjell	B
Rhizoclonium salinum	C
Rhizoclonium sp.	A,B
Order Schizogoniales	
Prasiola mexicana J.G.Ag.	B
Schizogonium sp.	B
Order Chlorococcales	
Actinastrum gracilimum G.M.Sm.	A
Actinastrum hantzschii Lager.	A
Actinastrum hantzschii var. *elongatum* G.M.Sm.	A
Actinastrum hantzschii var. *fluviatile* Schr.	A
Ankistrodesmus convolutus Corda	A
Ankistrodesmus falcatus (Corda) Ralfs	A,B
Ankistrodesmus falcatus var. *mirabilis* (West & West) G.S.West	A
Ankistrodesmus falcatus var. *spirilliformis* West	A
Ankistrodesmus falcatus var. *stipitatus* (Chod.) Lemm.	A
Ankistrodesmus spiralis (Turn.) Lemm.	A
Ankistrodesmus sp.	A,B
Ankyra judayi (G.M.Sm.) Fott.	A
Botryococcus braunii Kütz.	A,B,E
Botryococcus sudeticus Lemm.	A,B,J
Characium acuta	K
Characium ambiguum Hermann	A,B
Characium ellipsoidea	B
Characium longipes A.Br.	K
Characium naegelii (A.Br.) Lemm.	B
Characium obtusum A.Br.	B
Characium pringsheimii	A,K
Characium sp.	A
Chlorella vulgaris Beijer.	A,K
Chlorella sp.	A
Chlorococcum humicola (Naeg.) Rab.	A,D,K
Chlorococcum infusionum (Schr.) Meneg.	A
Chlorococcum sp.	A,D
Closteriopsis longissima var. *tropica* West & West	A,B
Closteriopsis sp.	A
Coelastrum microporum Naeg.	A
Coelastrum reticulatum Dang.	J
Coelastrum sp.	A,B
Crucigenia quadrata Morr.	A
Crucigenia rectangularis (A.Br.) Gay	A

Table 1 continued.

Crucigenia tetrapedia (Kirch.) West & West	A
Dictyosphaerium ehrenbergianum Naeg.	A
Dictyosphaerium pulchellum Wood	A
Dictyosphaerium sp.	A
Eremosphaera viridis DeBary	A
Franceia droescheri (Lemm.) G.M.Sm.	A
Gloeocystopsis limneticus G.M.Sm. (see *Nephrocytium limneticum*)	
Gloeotaenium loitelsbergerianum Hans.	B
Golenkinia paucispina West & West	A
Hydrodictyon reticulatum (L.) Lager.	A,K
Hydrodictyon sp.	K
Kirchneriella contorta Schm.	J
Kirchneriella elongata Sm.	B,J
Kirchneriella lunaris (Kirch.) Moeb.	A,J
Kirchneriella obesa West	A,B
Kirchneriella obesa var. *major* (Bernard) G.M.Sm.	B
Kirchneriella westii	K
Kirchneriella sp.	A
Lagerheimia ciciliata (Lag.) Chod.	K
Lagerheimia ciciliata var. *minor* G.M.Sm.	A
Lagerheimia longiseta var. *major* G.M.Sm.	A
Lagerheimia subsalsa Lemm.	A
Lagerheimia wratislawiensis Schr.	A
Lagerheimia sp.	A
Micractinium pusillum Fres.	A
Nephrocytium agardhianum Naeg.	A,H,J
Nephrocytium limneticum (G.M.Sm.) G.M.Sm. (=*Gloeocystopsis limneticus*)	B,H
Nephrocytium lunata W.West	B
Nephrocytium obesum W.West	A
Nephrocytium sp.	A
Oocystis borgei Snow	A,E
Oocystis crasse Wittr.	A
Oocystis elliptica W.West	A,B
Oocystis eremosphaeria Sm.	B
Oocystis gigas Arch.	A,B
Oocystis gloeocystiformis Borge	A
Oocystis lacustris Chod.	A
Oocystis marssonii Lemm.	A
Oocystis nagelli A.Br.	B
Oocystis novae-semliae Wille	A
Oocystis parva West & West	A,C,J
Oocystis pusilla Hans.	A
Oocystis rotunda Schm.	B
Oocystis solitaria Wittr.	A,B
Oocystis submarina Lager.	A
Oocystis sp.	A,B,D,E
Palmellococcus sp.	B,D,K
Pediastrum angulosum	B
Pediastrum bidentulum A.Br.	A

Table 1 continued.

Pediastrum biradiatum Meyen	B
Pediastrum boryanum (Turp.) Meneg.	A,B
Pediastrum boryanum var. *rugolosum* West	A
Pediastrum duplex Meyen	A
Pediastrum duplex var. *brachylobum* A.Br.	A
Pediastrum duplex var. *cornutum* Racib.	A
Pediastrum duplex var. *clathratum* (A.Br.) Lager.	A
Pediastrum duplex var. *gracilimum* West & West	A
Pediastrum granulatum Kütz.	B
Pediastrum integrum Naeg.	B
Pediastrum integrum var. *scutum* Racib.	B
Pediastrum integrum f. *glabra* Racib.	B
Pediastrum muticum var. *brevicorne* Racib.	A
Pediastrum pertusum Kütz.	A
Pediastrum sculptatum Sm.	A
Pediastrum simplex (Meyen) Lemm.	A
Pediastrum simplex var. *duodenarium* (Bail.) Rabh.	A
Pediastrum tetras (Ehr.) Ralfs.	A,B,D
Pediastrum tetras var. *tetraodon* (Chorda) Rabh.	A
Pediastrum sp.	A,B
Planktosphaeria gelatinosa G.M.Sm.	A
Planktosphaeria sp.	A
Quadrigula chodatii (Tanner-Full.) Sm.	A
Quadrigula closteriodes (Bohlin) Printz	A
Quadrigula lacustria (Chod.) G.M.Sm.	A
Scenedesmus abundans var. *brevicauda* G.M.Sm.	A
Scenedesmus acuminatus (Lager.) Chod.	A
Scenedesmus arcuatus var. *platydisca* G.M.Sm.	A
Scenedesmus armatus (Chod.) G.M.Sm.	A
Scenedesmus bijuga (Turp.) Lager.	A,B,J
Scenedesmus bijuga var. *alterans* (Rein.) Hansg.	A
Scenedesmus bijuga var. *flexuosus* Lemm.	A
Scenedesmus denticulatus Lager.	A,B,J
Scenedesmus denticulatus var. *linearis* Hansg.	J
Scenedesmus dimorphus (Turp.) Kütz.	A
Scenedesmus ecornis	A
Scenedesmus longus var. *naegelii* (Bréb.) G.M.Sm.	A
Scenedesmus obliquus (Turp.) Kütz.	A
Scenedesmus opoliensis P.Richter	A
Scenedesmus perforatus Lemm.	A
Scenedesmus quadricauda (Turp.) Bréb.	A,B,J
Scenedesmus quadricauda var. *longispina* (Chod.) G.M.Sm.	A
Scenedesmus quadricauda var. *parvus* G.M.Sm.	A
Scenedesmus quadricauda var. *maximus* West & West	A
Scenedesmus quadricauda var. *quadrispina* (Chod.) G.M.Sm.	A

Table 1 continued.

Scenedesmus quadricauda var. *westii* G.M.Sm.	A
Scenedesmus quadrispina (Chod.) Sm.	A,B,F
Scenedesmus sp.	A
Schroederia setigera (Schr.) Lemm.	A
Schroederia sp.	A
Selenastrum bibraianum Reinsch	A
Selenastrum gracile Reinsch	A
Selenastrum minutum (Naeg.) Collins	A
Selenastrum westii G.M.Sm.	A,F,J
Selenastrum sp.	A
Sorastrum americanum (Bohlin) Schmidle	A
Tetraedron caudatum (Corda) Hansg.	A
Tetraedron minimum (A.Br.) Hansg.	A
Tetraedron pentaedricum West & West	A
Tetraedron sp.	A
Treubaria setigerum (Archer) G.M.Sm.	A
Treubaria triappendiculata Bern.	A,C
Trochiscia granulata (Reinsch) Hansg.	K
Trochiscia reticularis (Reinsch) Hansg.	G,J
Westella botryoides (West) deWild.	A
Westella linearis Sm.	A,J
Order Zygnematales	
Arthrodesmus bulnheimii var. *subincus* W. West	A
Arthrodesmus convergens Ehr.	A
Arthrodesmus fragilis Wolle	A
Arthrodesmus incus (Bréb.) Hass.	A
Arthrodesmus phimus Turn.	A
Arthrodesmus ralfsii W.West	A
Arthrodesmus subulatus Kütz.	A
Arthrodesmus subulatus var. *subaequalis* West & West	A
Arthrodesmus triangularis Lager.	A
Arthrodesmus triangularis var. *inflatus* West & West	A
Calacylindrus minutus (Ralfs) Kirch.	B
Closterium abruptum W.West	A,B,F
Closterium acerosum (Schr.) Ehr.	A,B
Closterium aerolatum Wood	J
Closterium angustatum Kütz.	A
Closterium archeranianum Cl.	A
Closterium calosporum Wittr.	A
Closterium costatum Corda	A
Closterium cynthia DeNot.	A
Closterium decussatum Kütz.	B
Closterium delpontei Klebs.	F
Closterium dianae Ehr.	A,B,F,J
Closterium dianae var. *acutum*	A,B
Closterium didymotocum Corda	A
Closterium ehrenbergii Meneg.	A,B
Closterium ensis Delp.	B
Closterium intermedium Ralfs	A
Closterium juncidum Ralfs	A,B,F
Closterium juncidum var. *elongatum* Roy & Biss.	A

Table 1 continued.

Closterium kuetzingii Bréb.	A,F
Closterium lanceolatum Kütz.	A,B
Closterium laterale Nords.	A
Closterium lineatum Ehr.	A,B
Closterium litorale Gay	B
Closterium lunula Reinsch	A
Closterium macilentum Bréb.	A,B
Closterium moniliferum (Bory) Ehr.	A,B
Closterium parvulum Naeg.	A,F
Closterium prelongum (Bréb.) Delph.	J
Closterium pseudodiane Roy	A
Closterium pusillum Hantz.	A
Closterium ralfsii var. *hybridum* Rabh.	A
Closterium rostratum Ehr.	A,B,F
Closterium striolatum Ehr.	A,B,F
Closterium venus Kütz.	A
Closterium sp.	A,B,F
Cosmarium amoenum Bréb.	A
Cosmarium angulosum Bréb.	A
Cosmarium angulosum var. *concinnum* West & West	A
Cosmarium bioculatum Bréb.	A
Cosmarium boeckii Wille	A
Cosmarium botrytis Menegh.	A,B
Cosmarium broomii Thw.	A
Cosmarium cambricum Arch.	B
Cosmarium circulare Reinsch	A
Cosmarium connatum Bréb.	A
Cosmarium constrictum Delponte	B,E
Cosmarium contractum f. *jacobsenii* Roy	A
Cosmarium costatum Nords.	A
Cosmarium crenatum Ralfs	A,F
Cosmarium cucumis (Corda) Ralfs	A
Cosmarium denticulatum f. *borgei*	A
Cosmarium depressum (Bréb.) Ralfs	A
Cosmarium difficile Lutkem	A
Cosmarium elegantissimum f. *minor* West	A
Cosmarium eloisianum var. *depressum* West & West	A
Cosmarium excavatum Ralfs	A
Cosmarium furcatospermum West & West	A
Cosmarium hammeri var. *protuberance* West & West	A
Cosmarium intermedium Delp.	B
Cosmarium isthmochondrum Nordst.	A
Cosmarium margaritatum (Lund) Roy & Biss.	A,B
Cosmarium margaritiferum Meneg.	A,B
Cosmarium melanosporum Arch.	A
Cosmarium meneghinii Bréb.	A,B
Cosmarium meneghinii var. *concinnum* Rabh.	E
Cosmarium moniliforme (Bory) Ehr.	A,B
Cosmarium moniliforme f. *punctata* Lager.	A
Cosmarium nitidulum DeNot.	A
Cosmarium norvegicum Strom.	A
Cosmarium obtusatum Schmidle	A
Cosmarium ochthodes Nord.	B
Cosmarium oculiferum Lagh.	A,K

Table 1 continued.

Cosmarium orbiculatum Ralfs	A
Cosmarium ornatum Ralfs	A
Cosmarium orthostichum Lund	A
Cosmarium orthostichum var. *pumilum* Lund	A
Cosmarium ovale Ralfs	A,B
Cosmarium phaseolus Bréb.	A
Cosmarium phaseolus var. *elevatum* Nords.	A
Cosmarium portianum Arch.	A
Cosmarium protactum (Naeg.) D.By.	A
Cosmarium pseudamoenum Wille	A
Cosmarium pseudamoenum var. *basilare* Nords.	A
Cosmarium pseudoconnatum Nords.	A
Cosmarium pseudopyramidatum Lund	A
Cosmarium punctulatum Bréb.	A
Cosmarium punctulatum var. *subpunctulatum* (Nords.) Borg.	A
Cosmarium pycnochondrum Nord.	A
Cosmarium pyramidatum Bréb.	A
Cosmarium quadratulum (Gay) DeT.	A
Cosmarium quadrifarium f. *hexasticha* (Lund) Nords.	A
Cosmarium quinarium Lund	B
Cosmarium quinarium f. *irregularis* Nords.	A
Cosmarium ralfsii Bréb.	A,K
Cosmarium refringens var. *minor*	A
Cosmarium reniforme (Ralfs) Arch.	A
Cosmarium retusum (Perty) Rabh.	A,B
Cosmarium speciosum Lund	A
Cosmarium sportella Bréb.	B
Cosmarium subcrenatum Hantz.	A
Cosmarium subcrenatum var. *isthmochondrum*	A
Cosmarium subcucumis Schmidle	A
Cosmarium subexcavatum var. *ordinatum* West & West	A
Cosmarium subspeciosum var. *validius* Nords.	A
Cosmarium supraspeciosum Wolle	A
Cosmarium tetraophthalmum (Kütz.) Bréb.	A,B,F,K
Cosmarium tinctum Ralfs	A,B
Cosmarium trachypleurum var. *minus* Racib.	A
Cosmarium tumidum Lund	A
Cosmarium turpinii Bréb.	A
Cosmarium turpinii var. *exmium* West & West	A
Cosmarium undulatum Corda	A,B
Cosmarium undulatum var. *crenulatum*	E
Cosmarium venustum (Bréb.) Arch.	A
Cosmarium viride (Corda) Josh.	A
Cosmarium viride var. *glabra* (Josh.) West & West	A
Cosmarium sp.	A,B,E,F,K
Desmidium coarctatum Nords.	A
Desmidium coarctatum var. *cambricum* West	A
Desmidium cylindricum Grev.	A
Desmidium quadratum Nords.	A

Table 1 continued.

Desmidium swartzii Ag.	A,B
Desmidium swartzii var. *amblyodon* (Itz.) Rabh.	A
Desmidium sp.	A,B
Docidium nobile Rich.	B
Docidium sp.	A
Euastrum aboense Elfv.	A
Euastrum affine Ralfs	A
Euastrum americanum Ehr.	A
Euastrum ansatum Ralfs	A,B
Euastrum bidentatum Naeg.	A
Euastrum binale (Turp.) Ralfs	A
Euastrum binale f. *gutwinskii* Schmidle	A
Euastrum crassum (Bréb.) Kütz.	A,B
Euastrum denticulatum (Kirch.) Gay	A
Euastrum didelta (Turp.) Ralfs	A,B
Euastrum elegans (Bréb.) Kütz.	A,B
Euastrum elegans var. *novae semliae* Wille	A
Euastrum everettense Wolle	A,B,F
Euastrum gemmatum Bréb.	A
Euastrum humerosum Ralfs	A
Euastrum insulare (Wittr.) Roy	A
Euastrum obesum Josh.	A
Euastrum pinnatum Ralfs	A,B
Euastrum pulchellum Bréb.	A,B
Euastrum spinosum Ralfs	A
Euastrum verrucossum Ehr.	A
Euastrum verrucossum var. *rhombideum* Lund	A
Euastrum sp.	A,B
Genicularia sp.	A
Gonatozygon brebissonii DeBary	A
Gonatozygon sp.	A
Gymnozyga brebissonii	A,B,F
Gymnozyga moniliformis Ehr.	A
Gymnozyga sp.	A
Hyalotheca dissiliens (Sm.) Bréb.	A,B,F
Hyalotheca mucosa (Dillw.) Ehr.	A,B
Hyalotheca undulata Nords.	A
Hyalotheca sp.	B
Mesotaenium sp.	A
Micrasterias americana (Ehr.) Ralfs	A
Micrasterias apiculata (Ehr.) Menegh.	A
Micrasterias apiculata var. *brachyptera* (Lund) Nob.	A
Micrasterias conferta Lund	A,B,F
Micrasterias denticulata Bréb.	A
Micrasterias depauperata var. *wollei* Cush.	A
Micrasterias fimbriata Ralfs	A
Micrasterias furcata (Ag.) Ralfs	A,B
Micrasterias muricata (Bail.) Ralfs	A
Micrasterias oscitans Ralfs	A
Micrasterias papillifera Bréb.	A
Micrasterias papillifera f. *major*	A
Micrasterias pinnatifida (Kütz.) Ralfs	A
Micrasterias radiata Hass.	A
Micrasterias rotata (Grev.) Ralfs	A,B,F
Micrasterias sol (Ehr.) Kütz.	A

Table 1 continued.

Micrasterias sol var. *ornata* Nords.	A
Micrasterias truncata (Corda) Bréb.	A
Micrasterias sp.	A,B
Mougeotia capucina (Bory) Ag.	A,B,F
Mougeotia crass Wolle	A
Mougeotia genuflexa (Dellw.) Ag.	A,B
Mougeotia genuflexa var. *gracilis* Reinsch	A
Mougeotia laetevirens (Br.) Wittr.	B
Mougeotia parvula Hass.	A,B,F
Mougeotia sp.	A,B,E,F,H,K
Netrium digitus (Ehr.) Itz. & Rothe	A
Netrium digitus var. *constrictum* West	A
Netrium interruptum (Bréb.) Luetk.	A
Netrium nagelli (Bréb.) Nob.	A
Netrium oblongum (DeBary) Lutkem.	A
Netrium sp.	A
Onychoneum filiforme (Ehr.) Roy & Biss.	A
Penium closterioides Ralfs	A,B
Penium interruptum Bréb.	B
Penium margaritacem (Ehr.) Bréb.	A
Penium navicula Bréb.	A
Penium spirostriolarum Barker	A
Penium sp.	A
Pleurotaenium coronatum (Bréb.) Rabh.	A
Pleurotaenium coronatum var. *nodilosum* (Bréb.) West	A
Pleurotaenium ehrenbergii Ralfs	A,B
Pleurotaenium ehrenbergii var. *undulatum* Schaarschm.	A
Pleurotaenium maximum (Reinsch) Lund	A
Pleurotaenium nodosum (Bail.) Lund	A,B
Pleurotaenium trabecula (Ehr.) Naeg.	A
Pleurotaenium trabecula var. *rectum* Delp.	A
Pleurotaenium truncatum (Bréb.) Naeg.	A,B
Pleurotaenium sp.	A,B
Sirogonium sticticum Kütz.	B
Sphaerozosma filiforme (Ehr.) Ralfs	A,B
Sphaerozosma granulatum Roy & Biss.	A
Sphaerozosma pulchrum Bail.	A
Sphaerozosma wallichii var. *anglicum* West & West	A
Sphaerozosma sp.	A
Spirogyra bellis (Hassal) Cl.	B
Spirogyra catenoformis Hass.	B
Spirogyra communis (Hass.) Kütz.	A,B,F
Spirogyra crassa Kütz.	A,B
Spirogyra decimina (Müll.) Kütz.	A,B
Spirogyra dubia Kütz.	A,B,G,K
Spirogyra ellipsospora Trans.	J
Spirogyra fluviatilis Hilse ex Rabh.	E,G
Spirogyra formosa (Trans.) Czur.	A
Spirogyra grevilleana (Hass.) Kütz.	A,B,J
Spirogyra inflata (Vauch.) Kütz.	A,B,F
Spirogyra insignis (Hass.) Kütz.	B
Spirogyra jugalis (Fl. Dan.) Kütz.	A

Table 1 continued.

Spirogyra lutetiana Petit	A,B
Spirogyra neglecta (Hass.) Kütz.	A,B
Spirogyra parvula (Trans.) Czurda	A
Spirogyra porticalis (Müll.) Cl.	A,B
Spirogyra varians (Hass.) Kütz.	A,B,J
Spirogyra varians var. *minor* Teodor.	J
Spirogyra weberi Kütz.	A,B,F,J,K
Spirogyra sp.	A,B,E,H,J,K
Spiroteanium sp.	A
Staurastrum aculeatum (Ehr.) Meneg.	A
Staurastrum alternans Bréb.	A
Staurastrum anatinum Cooke & Wills	A
Staurastrum anatinum var. *lagerheimii* (Schm.) West & West	A
Staurastrum anatinum var. *truncatum* West	A
Staurastrum arctiscon (Ehr.) Lund	A,B
Staurastrum brasiliense var. *lundellii* West & West	A
Staurastrum cerastes Lund	A
Staurastrum concinnum	A
Staurastrum cornutum Arch.	A
Staurastrum coronulatum Wolle	A
Staurastrum crenulatum (Naeg.) Delp.	A
Staurastrum cuspidatum Bréb.	A
Staurastrum cuspidatum var. *divergens* Nords.	A
Staurastrum dilatatum Ehr.	A
Staurastrum echinatum Bréb.	A
Staurastrum eustephanum (Ehr.) Ralfs	B
Staurastrum furcatum (Ehr.) Bréb.	A
Staurastrum gladiosum Turn.	A
Staurastrum gracile Ralfs	A,B
Staurastrum gracile var. *coronulatum* Boldt	A
Staurastrum grallatorium Nord.	A,B
Staurastrum grande Bulnh.	A
Staurastrum hexacerum (Ehr.) Wittr.	A
Staurastrum limneticum var. *cornutum* G.M.Sm.	A
Staurastrum macrocerum Wolle	A,B
Staurastrum margaritaceum (Ehr.) Meneg.	A
Staurastrum muticum Bréb.	A,B,F
Staurastrum natator West	A
Staurastrum natator var. *crassum* West & West	A
Staurastrum ophiura Lund	A,B
Staurastrum orbiculare Ralfs	B
Staurastrum orbiculare var. *ralfsii* West & West	A
Staurastrum paradoxum Meyen	A
Staurastrum polymorphum Bréb.	A
Staurastrum polymorphum var. *pusillum* West	A
Staurastrum polytrichum Perty	A
Staurastrum pseudofurcigerum Reinsch	A
Staurastrum punctulatum Bréb.	A
Staurastrum pygmaeum Bréb.	A,B
Staurastrum quaternium Wolle	A
Staurastrum rotula Nords.	B
Staurastrum sebaldi Reinsch	B
Staurastrum setigerum Cl.	A

Table 1 continued.

Staurastrum spongiosum Bréb.	A
Staurastrum tetracerum Ralfs	A
Staurastrum vestitum	A
Staurastrum sp.	A,B
Triploceras gracile Bail.	A,B
Triploceras verticillatum Bail.	A,B
Triploceras sp.	A
Xanthidium antilopaeum (Bréb.) Kütz.	A
Xanthidium antilopaeum var. *hebridarum* West & West	A
Xanthidium antilopaeum var. *laeve* Schmidle	A
Xanthidium antilopaeum var. *polymazum* Nords.	A
Xanthidium armatum var. *fissum* Nords.	A
Xanthidium columbianum Wolle	A
Xanthidium cristatum (Bréb.) Ralfs	A,F
Xanthidium cristatum var. *uncinatum* Bréb.	A
Xanthidium subhastiferum West	A
Zygnema chalybeospermum Hansg.	J
Zygnema cruciatum Vauch.	A,B
Zygnema ericetorum Kütz.	A
Zygnema insigne (Hass.) Kütz.	A,B,F,J
Zygnema lactevirens Klebs.	A
Zygnema pectinatum (Vauch.) Ag.	A,B
Zygnema sterile Trans.	E
Zygnema sp.	A,B,E,H,J
Zygogonium sp.	A
Class Charophyceae	
Chara contraria A.Br.	C
Chara foetida L.	H
Chara cf. *fragilis* Desvaux	H
Chara vulgaris L.	B
Chara sp.	A,B,F,J,K
Nitella subglomerata	A
DIVISION CHRYSOPHYTA	
Class Chrysophyceae	
Order Chromulinales	
Chromulina chionophila Stein	K
Hydrurus foetidus (Vill.) Trev.	A,B
Order Ochromonadales	
Chrysosphaerella longispina Lauter.	A
Dinobryon bavaricum Imhof	A
Dinobryon cylindricum Imhof	B
Dinobryon divergens Imhof	A
Dinobryon sertularia Ehr.	A,B
Dinobryon sociale Ehr.	A
Dinobryon sociale var. *americanum* (Brunn.) Bach.	A
Dinobryon sp.	A,B,K
Mallomonas acaroides Perty	A
Mallomonas caudata Iwan.	A

Table 1 continued.

Mallomonas pseudocoronata Pres.	A
Mallomonas tonsurata Teil.	A
Synura uvella Ehr.	A
Synura sp.	A
Uroglenopsis american (Calkins) Lemm.	A
Class Xanthophyceae	
Order Mischococcales	
Characiopsis acuta (A.Br.) Borzi	B
Characiopsis cylindrica (Lamb.) Lemm.	A
Characiopsis longipes (Rabh.) Borzi	B
Charciopsis nageli A.Br.	A
Chlorobotrys regularis (W.West) Bohl.	A
Chlorocloster sp.	A
Gloeobotrys sp.	A
Ophiocytium capitatum Wolle	A,B
Ophiocytium cochleare (Eich.) A.Br.	A,B,F,K
Ophiocytium cuspidatum (Bail.) Rabh.	A,K
Ophiocytium gracilipes (Br.) Rabh.	A
Ophiocytium majus Naeg.	A,K
Ophiocytium parvulum (Perty) A.Br.	A,K
Ophiocytium sp.	B
Order Tribonematales	
Tribonema bombycinum (Ag.) Derb. & Sol.	A,B,F,J,K
Tribonema bombycinum var. *tenue* Haz.	A,B,G,J
Tribonema minor (Wille) Haz.	A,J
Tribonema minus Haz.	A,B,K
Tribonema utriculosum Haz.	A,B,J,K
Tribonema sp.	A,B,F
Order Vaucheriales	
Vaucheria borealis Hirn.	A,B
Vaucheria geminata (Vauch.) DeCand.	A,B,D,J,K
Vaucheria geminata var. *racemosa*	K
Vaucheria hamata Vauch.	A,B
Vaucheria orthocarpa Reinsch	G
Vaucheria sessilis Vauch.	A,B,K
Vaucheria sessilis var. *clavata* (Vauch.) DeCand.	A,B,K
Vaucheria terrestris Lyngb.	B
Vaucheria uncinata Kütz.	B
Vaucheria woroniniana Hur.	B
Vaucheria sp.	A,B,F,J
Class Bacillariophyceae	
Achnanthes affinis Grun.	A,E
Achnanthes cf. *atomus* var. *congolensis* Hust.	C
Achnanthes austriaca Hust.	B
Achnanthes austriaca var. *helvetica* Hust.	A
Achnanthes biasolettiana (Kütz.) Grun.	A
Achnanthes bottnica (Cl.) Cl.	F,G
Achnanthes chilensis var. *subaequalis* Reim.	A,E

Table 1 continued.

Achnanthes clevei Grun.	A,E
Achnanthes clevei var. *rostrata* Hust.	A,B
Achnanthes coarctata (Bréb.) Grun.	E,J,K
Achnanthes conspicua A.May.	A,H
Achnanthes cottoriensis Foged	G
Achnanthes crenulata Grun.	H
Achnanthes deflexa Reim.	A,B,E
Achnanthes delicatula (Kütz.) Grun.	A
Achnanthes didyma Hust.	A
Achnanthes exigua Grun.	A,B,C,D,E,F,G,H
Achnanthes exigua var. *heterovalvata* Krass.	A,F,G
Achnanthes flexella (Kütz.) Brun.	B,E
Achnanthes gibberula Grun.	A,G
Achnanthes hauckiana Grun.	A,B,G
Achnanthes hauckiana var. *rostrata* Schultz	A
Achnanthes hungarica (Grun.) Grun.	A,E,H
Achnanthes kryophila Peters.	A
Achnanthes lanceolata (Bréb.) Grun.	A,B,C,D,E,F,G,H,J,K
Achnanthes lanceolata var. *dubia* Grun.	A,B,E,F,G,J,K
Achnanthes lanceolata var. *hynaldii* (Sch.) Cl.	B
Achnanthes lanceolata var. *omissa* Reim.	B
Achnanthes laterostrata Hust.	A
Achnanthes levanderi Hust.	A
Achnanthes lewisiana Patr.	A,E
Achnanthes linearis (W.Sm.) Grun.	A,B,D,E,G,H,K
Achnanthes linearis f. *curta* H.Sm.	A,B,H
Achnanthes linearis var. *pusilla* Grun.	A
Achnanthes marginulata Grun.	A,B
Achnanthes microcephala (Kütz.) Grun.	A,E
Achnanthes minutissima Kütz.	A,B,D,E,F,G,H,J,K
Achnanthes minutissima var. *cryptocephala* Grun.	A
Achnanthes cf. *nodosa* A.Cl.	A
Achnanthes orientalis Petit	A
Achnanthes peragalli Brun. & Herib.	B
Achnanthes peragalli var. *fossilis* Temp. & Perag.	A
Achnanthes pinnata Hust.	A
Achnanthes saxonica Krass.	A
Achnanthes similis Hust.	G
Achnanthes simplex Hust.	G
Achnanthes cf. *subhudsonis* Hust.	G
Achnanthes sublaevis Hust.	A
Achnanthes sublaevis var. *crassa* Reim.	A,B
Achnanthes cf. *submarina* Hust.	G
Achnanthes suchlandti Hust.	A
Achnanthes tropica Hust.	G
Achnanthes sp.	A,B,D
Actinocyclus cf. *ingens* Rattray	A
Amphicampa hemicyclus (Ehr.) Karsten	B
Amphicampa sp.	A
Amphipleura pellucida Kütz.	A,B,F,G,K
Amphipleura rutilans (Trent.) Cl.	A

Table 1 continued.

Amphiprora alata (Ehr.) Kütz.	A,B,F,G
Amphiprora sp.	A
Amphora acutiuscula Kütz.	G,H
Amphora arcus var. *sulcata* (A.Schm.) Cl.	G
Amphora coffeaeformis (Ag.) Kütz.	A,B,C,E,F,G, H,I,K
Amphora coffeaeformis var. *fossilis* (Pant.) Cl.	G
Amphora coffeaeformis var. *perpusilla* Grun.	G
Amphora cognata Choln.	B
Amphora commutata Grun.	G
Amphora crassa Greg.	I
Amphora cymbifera Greg.	I
Amphora delicatissima Krass.	C
Amphora hyalina Kütz.	G,I
Amphora libyca Ehr.	C
Amphora macilenta Greg.	G
Amphora marina (W.Sm.) V.H.	A
Amphora normani Rabh.	A,B,D
Amphora ovalis (Kütz.) Kütz.	A,B,C,D,E,F, G,H,I,K
Amphora ovalis var. *affinis* (Kütz.) V.H. ex DeT.	A,B,D,G,K
Amphora ovalis var. *pediculus* (Kütz.) V.H.	A,B,E,F,G
Amphora pellucida Greg.	I
Amphora perpusilla Grun.	A,B,D,E,G, H,K
Amphora proteus Greg.	G,I
Amphora proteus var. *oculata* Perag.	G
Amphora tenuissima Hust.	G
Amphora veneta Kütz.	A,B,E,F,G,H
Amphora sp.	A,H
Anomoeoneis costata (Kütz.) Hust.	A,B,E
Anomoeoneis exilis var. *lanceolata* A.May.	A
Anomoeoneis follis (Ehr.) Cl.	G
Anomoeoneis polygramma (Ehr.) Cl.	K
Anomoeoneis sculpta (Ehr.) Pfitz.	K
Anomoeoneis serians (Bréb.) Cl.	A
Anomoeoneis serians var. *acuta* Hust.	A
Anomoeoneis serians var. *brachysira* (Bréb.) Cl.	A,B
Anomoeoneis sphaerophora (Kütz.) Pfitz.	A,B,C,F,G, H,J,K
Anomoeneis sphaerophora var. *guentheri* O.Müll.	A
Anomoeoneis sphaerophora f. *costata* (Kütz.) A.Schmid	G
Anomoeoneis vitrea (Grun.) Ross	A,B,E,F,G
Anomoeoneis zellensis (Grun.) Cl.	A,E
Anomoeoneis zellensis f. *difficilis* (Grun.) Hust.	A
Anomoeoneis sp.	A,D
Asterionella formosa Hass.	A,B,K
Asterionella sp.	A,K
Bacillaria paradoxa Gmel. (see *Bacillaria paxillifer*)	

Table 1 continued.

Bacillaria paxillifer (O.Müll.) Hend. (= *Bacillaria paradoxa*)	A,F,G,H
Biddulphia laevis Ehr.	A,C,H
Brachysira aponina Kütz.	G
Brachysira exilis (Kütz.) Round & Mann	G
Brachysira exilis f. *undulata* Kisselev	G
Brebissonia boechii (Ehr.) Grun.	A
Caloneis alpestris (Grun.) Cl.	E
Caloneis amphisbaena (Bory) Cl.	A,B,C,E,G, H,I,K
Caloneis bacillaris (Greg.) Cl.	G
Caloneis bacillaris var. *thermalis* (Grun.) A.Cl.	A,F,G
Caloneis bacillum (Grun.) Cl.	A,B,D,E,F, G,K
Caloneis fenzlii (Grun.) Patr.	A
Caloneis fenzlioides Cl.-Eul.	A
Caloneis formosa (Greg.) Cl.	K
Caloneis hyalina Hust.	A
Caloneis lamella Zakr.	A
Caloneis lewisii Patr.	A,B
Caloneis lewisii var. *inflata* (Schultze) Patr.	A
Caloneis limosa (Kütz.) Patr.	A
Caloneis oregonica (Ehr.) Patr.	A
Caloneis permagna (J.W.Bail.) Cl.	A
Caloneis schumanniana (Grun.) Cl.	A
Caloneis schumanniana var. *fasciata* Hust.	A
Caloneis schumanniana var. *linearis* Hust.	A
Caloneis silicula (Ehr.) Cl.	A
Caloneis silicula var. *limosa* (Kütz.) V.Land.	A
Caloneis silicula var. *minuta* (Grun.) Cl.	K
Caloneis ventricosa (Ehr.) Meist.	A,B,E,G
Caloneis ventricosa var. *alpina* (Cl.) Patr.	B,E
Caloneis ventricosa var. *subundulata* (Grun.) Patr.	A
Caloneis ventricosa var. *truncatula* (Grun.) Meist.	A,B,H,K
Caloneis westii (W.Sm.) Hend.	G
Caloneis sp.	A,F
Campylodiscus alactus Setty	I
Campylodiscus bicostata W.Sm.	I
Campylodiscus clypeus Ehr.	A,C,G
Campylodiscus ehrenbergii Ralfs	I
Campylodiscus hibernicus Ehr.	A,I
Campylodiscus noricus Ehr.	I
Campylodiscus sp.	A
Ceratoneis arcus (Ehr.) Kütz.	B
Chaetoceros amanita Cl.-Eul.	G
Chaetoceros elmorei Boyer	A
Chaetoceros muelleri Lemm.	C,K
Chaetoceros sp.	A
Cocconema (= *Cymbella*) sp.	A,C
Cocconeis diminuta Pant.	A,B,F,G
Cocconeis disculus (Schum.) Cl.	A,B,D
Cocconeis finnica Ehr.	C

Table 1 continued.

Cocconeis fluviatilis Wall.	A
Cocconeis lineata Ehr.	I,K
Cocconeis mormonorum Ehr.	C
Cocconeis pediculus Ehr.	A,B,C,D,E,F, G,J,K
Cocconeis placentula Ehr.	A,B,C,G,H, I,K
Cocconeis placentula var. *euglypta* (Ehr.) Grun.	A,B,C,D,E, G,K
Cocconeis placentula var. *lineata* (Ehr.) V.H.	A,B,D,E,F, G,K
Cocconeis rugosa Sov.	B
Cocconeis scutellum Ehr.	I
Cocconeis sp.	A,B
Coscinodiscus apiculatus Ehr.	K
Coscinodiscus argus Ehr.	A
Coscinodiscus disciformis Setty	I
Coscinodiscus elegans Grev.	I
Coscinodiscus lacustris Grun.	A
Coscinodiscus marginulatus var. *campeachiana* Grun.	I
Coscinodiscus nitidulus Grun.	I
Coscinodiscus occuliformis Setty	I
Coscinodiscus odontodiscus Grun.	A
Coscinodiscus porcelaineous (Stod.) Setty	I
Coscinodiscus rothii (Ehr.) Grun.	A
Coscinodiscus subtilis Ehr.	C
Coscinodiscus velatus Ehr.	I
Coscinodiscus sp.	A
Cosmiolithus discus Ehr.	C
Cyclotella antiqua W.Sm.	A,I
Cyclotella bodanica Eulen.	A,B,D
Cyclotella caspia Grun.	A,E
Cyclotella catenata (Brun.) Bach.	A
Cyclotella comensis Grun.	A
Cyclotella comta (Ehr.) Kütz.	A,B,D,I
Cyclotella glomerata Bachmann	B,K
Cyclotella kuetzingiana Thw.	A,D
Cyclotella kuetzingiana var. *planetophora* Fricke	A,D
Cyclotella meneghiniana Kütz.	A,B,C,D,F, G,H,I,J,K
Cyclotella meneghiniana var. *pumila* (Grun. ex V.H.) Hust.	A,G
Cyclotella meneghiniana f. *plana* (Fricke) Hust.	G
Cyclotella michiganiana Skvor.	A
Cyclotella ocellata Pant.	A,D
Cyclotella operculata (Ag.) Kütz.	K
Cyclotella rotula Kütz.	I
Cyclotella stelligera (Cl.&Grun.) V.H.	A
Cyclotella striata (Kütz.) Grun.	A,I,K
Cyclotella striata var. *ambigua* (Grun.) Grun.	A
Cyclotella striata var. *bipunctata* Fricke	B
Cyclotella sp.	A,B,D
Cylindrotheca gracilis (Bréb.) Grun.	A,K
Cymatopleura angulata Grev.	A

Table 1 continued.

Cymatopleura elliptica (Bréb.) W.Sm.	A,B
Cymatopleura elliptica var. *constricta* Grun.	A
Cymatopleura solea (Bréb.) W.Sm.	A,B,C,D,H, I,K
Cymatopleura solea var. *palffyi* (Pant.) Cl.-Eul.	A
Cymatopleura solea var. *regula* (Ehr.) Grun.	A,H
Cymbella affinis Kütz.	A,B,D,E,F, G,H,I
Cymbella amphicephala Naeg. ex Kütz.	A,B,E,F,G
Cymbella amphioxys (Kütz.) Cl.	A
Cymbella angustata (W.Sm.) Cl.	A,B,F,G
Cymbella aspera (Ehr.) Cl.	A,B,E,I,K
Cymbella bonnevillensis Setty	I
Cymbella brehmii Hust.	A,J
Cymbella cesatii (Rabh.) Grun.	A
Cymbella cistula (Hemp.) Kirch.	A,B,D,E,F, G,K
Cymbella cistula var. *maculata* (Kütz.) V.H.	B,G
Cymbella cuspidata Kütz.	A,B
Cymbella cymbiformis Ag.	A,B,I
Cymbella cymbiformis var. *nonpunctata* Fontell	E,G
Cymbella delicatula Kütz.	A,E,F,G
Cymbella ehrenbergii Kütz.	A,B
Cymbella fonticola Hust.	G
Cymbella gasteroides (Kütz.) Kütz.	A,B,I
Cymbella gracilis (Ehr.) Kütz.	A,B
Cymbella hebredica (Grun.) Cl.	A
Cymbella heteropleura (Ehr.) Kütz.	A,B
Cymbella heteropleura var. *subrostrata* Cl.	A
Cymbella hustedtii Krass.	H
Cymbella inaequalis (Ehr.) Rabh.	A
Cymbella incerta (Grun.) Cl.	E,F,G
Cymbella incerta var. *naviculacea* (Grun.) Cl.	E
Cymbella laevis Nag.	A,F,G,H
Cymbella lanceolata (Ehr.) V.H.	A,B,I
Cymbella leptoceros (Ehr.) Kütz.	F,G
Cymbella lunata W.Sm.	A
Cymbella mexicana (Ehr.) Cl.	A,B,E,H
Cymbella microcephala Grun.	A,B,E,F,G
Cymbella microcephala var. *crassa* Reim.	E
Cymbella minuta Hilse ex Rabh.	A,B,C
Cymbella minuta f. *latens* (Krass.) Reim.	A,B,E
Cymbella minuta var. *pseudogracilis* (Choln.) Reim.	A
Cymbella minuta var. *silesiaca* (Bleisch ex Rabh.) Reim.	A,B,E,K
Cymbella muelleri Hust.	A
Cymbella muelleri f. *ventricosa* (Temp. et Perag.) Reim.	A
Cymbella naviculiformis Auers.	A,B,D,H,K
Cymbella norvegica Grun.	A,E
Cymbella parva (W.Sm.) Wolle	B,I
Cymbella perpusilla A.Cl.	A,E
Cymbella prostrata (Berk.) Grun.	A,B,K
Cymbella prostrata var. *aeurswaldii* (Rabh.) Reim.	A

Table 1 continued.

Cymbella protracta Ost.	A
Cymbella proxima Reim.	A
Cymbella pusilla Grun.	A,B,G,H
Cymbella rupicola Grun.	A
Cymbella sinuata Greg.	A,B,F,G,J,K
Cymbella subaequalis f. *Krasseki* (Foged) Reim.	K
Cymbella subturgida Hust.	A
Cymbella tumida (Bréb. ex Kütz.) V.H.	A,B,I
Cymbella tumidula Grun. ex A.Schmidt	A,B
Cymbella turgida Greg.	A,B,E,I
Cymbella turgidula Grun.	A
Cymbella uncinata (Ehr.) Perag.	C
Cymbella ventricosa Ag.	A,B,D,E,F,G,I
Cymbella sp.	A,B,E,F,G,H,J
Denticula elegans Kütz.	A,B,E,F,G,H,I,K
Denticula elegans var. *kittoniana* (Grun.) DeT.	A,G
Denticula elegans f. *valida* Pedic.	A,D,E
Denticula lauta J.W. Bail.	I
Denticula cf. *parva* Hust.	G
Denticula subtilis Grun.	A
Denticula tenuis Kütz.	A,B,K
Denticula tenuis var. *crassula* (Naeg.) Hust.	A
Denticula thermalis Kütz.	I,K
Denticula valida (Pedicino) Grun.	I
Denticula sp.	A
Diatoma anceps (Ehr.) Kirchn.	A,B
Diatoma anceps var. *linearis* M.Perag.	B
Diatoma elongatum (Lyngb.) Ag.	A,B
Diatoma hiemale (Lyngb.) Heib.	A,B
Diatoma hiemale var. *mesodon* (Ehr.) Fricke	A,B,C,D,E,G,J,K
Diatoma tenue Ag.	A,B,H
Diatoma tenue var. *elongatum* Lyngb.	A,B,C,D,H
Diatoma vulgare Bory	A,B,C,D,E,G,K
Diatoma vulgare var. *breve* Grun.	A,B,H
Diatoma vulgare var. *grande* (W.Sm.) Grun.	A
Diatoma sp.	A,B
Diatomella balfouriana (W.Sm.) Grev.	A,I
Diploneis didyma (Ehr.) Ehr.	C
Diploneis elliptica (Kütz.) Cl.	A,B,F,G,I,K
Diploneis interrupta (Kütz.) Cl.	A,E,G,I,K
Diploneis marginestriata Hust.	A,G
Diploneis oblongella (Naeg. ex Kütz.) Ross	A,B,D,E,G,K
Diploneis oculata (Bréb.) Cl.	A,K
Diploneis ovalis (Hilse.) Cl.	E,K
Diploneis pseudovalis Hust.	A,B
Diploneis puella (Schum.) Cl.	A
Diploneis smithii (Bréb.ex W.Sm.) Cl.	A,D
Diploneis smithii var. *dilatata* (M.Perag.) Terry	A
Diploneis smithii var. *pumila* (Grun.) Hust.	A

Table 1 continued.

Diploneis smithii f. *rhombica* (Meresch.) Hust.	G
Diploneis suborvalis Cl.	A,G
Diploneis sp.	A,D
Entomoneis alata (Ehr.) Ehr.	A,E,G
Entomoneis ornata (Bail.) Reim.	A
Entomoneis paludosa (W.Sm.) Reim.	A,B,G,H
Entomoneis paludosa var. *duplex* (Donk.) Cl.	G
Entomoneis pulchra (Bail.) Reim.	C
Epithemia adnata (Kütz.) Ross	A,B
Epithemia adnata var. *minor* (Perag. et Herib.) Patr.	A,D
Epithemia adnata var. *porcellus* (Kütz.) Patr.	A
Epithemia adnata var. *proboscidea* (Kütz.) Hend.	A
Epithemia adnata var. *saxonica* (Kütz.) Patr.	H
Epithemia argus (Ehr.) Kütz.	A,B,C,E,F,I,K
Epithemia argus var. *alpestris* (W.Sm.) Grun.	A,I,K
Epithemia argus var. *longicornus* (Ehr.) Grun.	A,E
Epithemia argus var. *protracta* A.May.	A,E
Epithemia hyndmanii W.Sm.	A,I
Ephithemia intermedia Fricke	A,K
Epithemia ocellata (Ehr.) Kütz.	A
Epithemia smithii Carr.	A
Epithemia sorex Kütz.	A,B,I,K
Epithemia sorex var. *gracilis* Hust.	K
Epithemia turgida (Ehr.) Kütz.	A,B,C,D,E,I,K
Epithemia turgida var. *granulata* (Ehr.) Brun.	A,B,K
Epithemia turgida var. *westermannii* (Ehr.) Grun.	A,B
Epithemia ventricosa Kütz.	I
Epithemia zebra (Ehr.) Kütz.	A,D,F,G,I,K
Epithemia zebra var. *porcellus* (Kütz.) Grun.	B
Epithemia zebra var. *saxonica* (Kütz.) Grun.	A,B,E,K
Epithemia sp.	A
Eunotia cf. *alpina* (Naeg.) Hust.	A
Eunotia arcus Ehr.	A,B,G
Eunotia arcus var. *bidens* Grun.	A,B,E
Eunotia arcus var. *uncinata* (Ehr.) Grun.	A
Eunotia bigibba Kütz.	B
Eunotia curvata (Kütz.) Lagerst.	A,B,E,F,G
Eunotia curvata var. *capitata* (Grun.) Patr.	A,F,G
Eunotia diodon Ehr.	A,B
Eunotia exigua (Bréb.) Rabh.	A
Eunotia cf. *faba* var. *densestriata* Öst.	A
Eunotia gracilis (Ehr.) Rabh.	K
Eunotia hexaglyphis Ehr.	A
Eunotia incisa Greg.	A,B,C
Eunotia lapponica Grun.	A
Eunotia lunaris (Ehr.) Bréb.	B
Eunotia lunaris var. *subarcuata* (Naeg.) Grun.	B

Table 1 continued.

Eunotia major (W.Sm.) Rabh.	A,I,K
Eunotia meisteri Hust.	A
Eunotia minor (Kütz.) Grun.	K
Eunotia mira var. *ovata* A.Berg.	A
Eunotia monodon Ehr.	A,C
Eunotia mosis Ehr.	C
Eunotia naegelii Migula	A
Eunotia nymanniana Grun.	A
Eunotia pectinalis (Dillw.) Rabh.	A,B
Eunotia pectinalis var. *minor* (Kütz.) Rabh.	A,B
Eunotia pectinalis var. *recta* A.May.	A
Eunotia perpusilla Grun.	B
Eunotia praerupta var. *bidens* (Ehr.) Grun.	A,B
Eunotia praerupta var. *inflata* Grun.	A,B
Eunotia quaternaria Ehr.	B
Eunotia septentrionalis Öst.	A,B
Eunotia serra Ehr.	B
Eunotia serra var. *diadema* (Ehr.) Patr.	A
Eunotia sudetica O.Müll.	B
Eunotia suecica A.Cl.	A
Eunotia tenella (Grun.) Hust.	A,B
Eunotia tridentula Ehr.	A
Eunotia valida Hust.	A,F,G
Eunotia vanheurckii Patr.	A
Eunotia vanheurckii var. *intermedia* (Krass.) Patr.	A
Eunotia veneris (Kütz.) DeT.	A
Eunotia sp.	A
Fragilaria bicapitata A.May.	A
Fragilaria brevistriata Grun.	A,B,C,D,G,K
Fragilaria brevistriata var. *capitata* Herib.	A
Fragilaria brevistriata var. *inflata* (Pant.) Hust.	A,E,F,G
Fragilaria capucina Desmaz.	A,B,H,I,K
Fragilaria capucina var. *mesolepta* (Rabh.) Rabh.	A,B,F,G
Fragilaria constricta Ehr.	A
Fragilaria constricta f. *stricta* (A.Cl.) Hust.	A
Fragilaria construens (Ehr.) Grun.	A,B,C,E,F, G,I,K
Fragilaria construens var. *binodis* (Ehr.) Grun.	A,B,G,K
Fragilaria construens var. *pumila* Grun.	A
Fragilaria construens var. *subsalina* Hust.	G
Fragilaria construens var. *venter* (Ehr.) Grun.	A,B,C,D,F,G, H
Fragilaria crotonensis Kitton	A,B,F,G
Fragilaria crotonensis var. *oregonica* Sover.	A
Fragilaria fremontii Ehr.	C
Fragilaria harrissonii (W.Sm.) Grun.	B,I,K
Fragilaria inflata (Heid.) Hust.	G
Fragilaria intermedia (Grun.) Grun.	A
Fragilaria lapponica Grun.	A,G
Fragilaria lapponica var. *minuta* A.Cl.	G
Fragilaria leptostauron (Ehr.) Hust.	A,B,D,K
Fragilaria leptostauron var. *dubia* (Grun.) Hust.	A

Table 1 continued.

Fragilaria mutabilis (W.Sm.) Grun.	K
Fragilaria pacifica Grun.	I
Fragilaria pinnata Ehr.	A,B,C,D,E, G,K
Fragilaria pinnata var. *intercedens* (Grun.) Hust.	A,B
Fragilaria pinnata var. *lancettula* (Schum.) Hust.	A,B
Fragilaria pulchella Kütz.	A,B
Fragilaria rhabdosoma Ehr.	C
Fragilaria similis Krass.	A,G
Fragilaria striolata Ehr.	C
Fragilaria turgens Ehr.	C
Fragilaria vaucheriae (Kütz.) Peters.	A,B,C,D,E,F, G,H,K
Fragilaria vaucheriae var. *capitellata* (Grun.) Ross	A
Fragilaria virescens Ralfs	A,B,F,H,K
Fragilaria sp.	A,B
Frustulia rhomboides (Ehr.) DeT.	A,B
Frustulia rhomboides var. *amphipleuroides* (Grun.) Cl.	A
Frustulia rhomboides var. *capitata* (A.May.) Patr.	A
Frustulia rhomboides var. *crassinervia* (Bréb.) Ross	A
Frustulia rhomboides var. *saxonica* (Rabh.) DeT.	A
Frustulia rhomboides f. *undulata* Hust.	A
Frustulia vulgaris (Thw.) DeT.	A,B,G,K
Gomphoneis herculeana (Ehr.) Cl.	A,B
Gomphonema acuminatum Ehr.	A,B,E
Gomphonema acuminatum var. *coronatum* (Ehr.) W.Sm.	B
Gomphonema acuminatum var. *turris* (Ehr.) Wolle	B
Gomphonema affine Kütz.	A,G
Gomphonema affine var. *insigne* (Greg.) Andrews	A,H
Gomphonema angustatum (Kütz.) Rabh.	A,B,C,E,F, G,H
Gomphonema angustatum var. *intermedia* Grun.	A
Gomphonema angustatum var. *producta* Grun.	B,H,K
Gomphonema angustatum var. *sarcophagus* (Greg.) Grun.	B
Gomphonema apicatum Ehr.	A
Gomphonema elevei Fricke	A
Gomphonema constrictum Ehr.	A,B,E,G
Gomphonema constrictum var. *capitata* (Ehr.) Grun.	B
Gomphonema dichotomum Kütz.	A,E,G
Gomphonema elegans Grun.	B
Gomphonema geminatum (Lyngb.) Ag.	A,B
Gomphonema gracile Ehr.	A,B,F,G,J
Gomphonema gracile var. *intricatiforme* A.May.	A
Gomphonema gracile f. *turris* Hust.	F,G
Gomphonema grunowii Patr.	A
Gomphonema instabilis Hohn & Hellerman	A,G

Table 1 continued.

Gomphonema intricatum Kütz.	A,B,D,E,F,G
Gomphonema intricatum cf. var. *fossilis* Pant.	G
Gomphonema intricatum var. *pumila* Grun.	A
Gomphonema intricatum var. *vibrio* (Ehr.) Cl.	A
Gomphonema lalithaea Setty	I
Gomphonema lanceolatum Ag.	A,B
Gomphonema lanceolatum var. *insignis* (Greg.) Cl.	F,G
Gomphonema cf. *longiceps* Ehr.	A
Gomphonema longiceps var. *subclavata* Grun.	K
Gomphonema longiceps var. *subclavata* f. *gracilis* Hust.	F,G
Gomphonema montanum Schum.	B
Gomphonema navicularis Setty	I
Gomphonema olivaceum (Lyngb.) Des.	A,B,C,D,E,F,G,H,K
Gomphonema olivaceum var. *calcarea* (Cl.) V.H.	A,B
Gomphonema parvulum (Kütz.) Kütz.	A,B,D,E,F,G,H
Gomphonema parvulum var. *micropus* (Kütz.) Cl.	A,B,E,G
Gomphonema rhombicum Fricke	B
Gomphonema septum Mogh.	A
Gomphonema sphaerophorum Ehr.	A,E,F,G
Gomphonema subclavatum (Grun.) Grun.	A
Gomphonema subclavatum var. *commutatum* (Grun.) A.May.	A,H
Gomphonema subclavatum var. *mexicanum* (Grun.) Patr.	A
Gomphonema subtile Ehr.	A
Gomphonema tenellum Kütz.	A
Gomphonema truncatum Ehr.	A,B,K
Gomphonema truncatum var. *capitatum* (Ehr.) Patr.	A
Gomphonema truncatum var. *turgidum* (Ehr.) Patr.	A
Gomphonema ventricosum Greg.	A
Gomphonema sp.	A,B,E
Grammatophora stricta Ehr.	C
Gyrosigma acuminatum (Kütz.) Rabh.	A,B,H,K
Gyrosigma attenuatum (Kütz.) Cl.	A
Gyrosigma fasciola (Ehr.) Griff. & Henfr.	A
Gyrosigma obscurum (W.Sm.) Griff. & Henfr.	G
Gyrosigma obtusatum (Sull. & Worml.) Boyer	A,B
Gyrosigma spencerii (W.Sm.) Griff. & Henfr.	A,B,F
Gyrosigma spencerii var. *curvula* (Grun.) Reim.	A,G,H
Gyrosigma strigilis (W.Sm.) Griff. & Henfr.	A
Gyrosigma sp.	A,B,C,G
Hannaea arcus (Ehr.) Patr.	A,B,E,K
Hannaea arcus var. *amphioxys* (Rabh.) Patr.	A,B,K

Table 1 continued.

Hantzschia amphioxys (Ehr.) Grun.	A,B,D,E,F,G,I,K
Hantzschia amphioxys var. *linearis* (O.Müll.) Cl.-Eul.	E
Hantzschia amphioxys var. *maior* Grun.	J
Hantzschia amphioxys var. *vivax* Grun.	B
Hantzschia amphioxys f. *capitata* O.Müll.	A,B,D
Hantzschia distincte-punctata (Hust.) Hust.	A
Hantzschia virgata (Roper) Grun.	A
Hantzschia sp.	A
Hyalodiscus valens A.Schmidt	I
Hyalodiscus whitneyi Ehr.	C,G,H
Licmophora gracilis (Ehr.) Grun.	J
Mastogloia aquilegiae Grun.	G
Mastogloia braunii Grun.	A,G
Mastogloia elliptica (Ag.) Cl.	A,C
Mastogloia elliptica var. *danseii* (Thw.) Cl.	A,F,G,H,I
Mastogloia grevillei W.Sm.	E
Mastogloia pumila (Cl.) Grun.	A,C
Mastogloia smithii Thw. ex W.Sm.	A,B,E
Mastogloia smithii var. *lacustris* Grun.	A,E,F,G
Melosira arenaria Moore	K
Melosira crenulata (Ehr.) Kütz.	A,B,K
Melosira dendroteres (Ehr.) Ross	D
Melosira dickiei (Thw.) Kütz.	A,B
Melosira distans (Ehr.) Kütz.	A,B,I,K
Melosira distans var. *alpigena* Grun.	A
Melosira distans var. *pfaffiana* (Reinsch) Grun.	A
Melosira granulata (Ehr.) Ralfs	A,B,D,I,K
Melosira granulata var. *angustissima* O.Müll.	A,C,G
Melosira islandica O.Müll.	A
Melosira islandica var. *helvetica* (O.Müll.) Meist.	A
Melosira italica (Ehr.) Kütz.	A,B,D,E,H,K
Melosira italica var. *subarctica* O.Müll.	A
Melosira italica var. *tenuissima* (Grun.) O.Müll.	A
Melosira italica var. *valida* (Grun.) Hust.	A
Melosira laevis (Ehr.) Ralfs	C
Melosira nummuloides (Dillw.) Ag.	C
Melosira roseana Rabh.	A,B,E,K
Melosira scalaris (Grun.)	I
Melosira solida (Eulen.) F.W.Mills	I
Melosira sulcata (Ehr.) Kütz.	C
Melosira undulata (Ehr.) Kütz.	I
Melosira varians Ag.	A,B,D,G,I,K
Melosira sp.	A,B,D,F
Meridion circulare (Grev.) Ag.	A,B,E,G,H
Meridion circulare var. *constrictum* (Ralfs) V.H.	A,B,E
Meridion sp.	A,B
Navicula abiskoensis Hust.	A
Navicula accepta Hust.	A
Navicula accomoda Hust.	A
Navicula acrospheria (Bréb.) Kütz.	I

Table 1 continued.

Navicula affinis Ehr.	I
Navicula aikenensis Patr.	A
Navicula amphibola Cl.	A
Navicula amphigomphus Ehr.	A
Navicula anglica Ralfs	A,B
Navicula anglica var. *subsalsa* (Grun.) Cl.	A
Navicula angusta Grun.	A,B
Navicula appendiculata (Ag.) Kütz.	A
Navicula arenaria Donk.	A
Navicula arvensis Hust.	A,B,E,J
Navicula asellus Weigold	D
Navicula atomus (Kütz.) Grun.	A,K
Navicula auriculata Hust.	A
Navicula aurora Sov.	A
Navicula bacilliformis Grun.	A
Navicula bacillum Ehr.	A,B,K
Navicula bacillum var. *lepida* (Greg.) Cl.	K
Navicula bicapitellata Hust.	B
Navicula bicephala Hust.	A,B
Navicula biconica Patr.	H,K
Navicula bohemica Ehr.	C,I
Navicula bombus (Ehr.) Kütz.	I
Navicula bottnica Grun.	A
Navicula brebissonii Kütz. (see *Pinnularia brebissonii*)	
Navicula brekkaensis Peters.	A,E
Navicula bryophila J.B.Peters.	A
Navicula capitata Ehr.	A,B
Navicula capitata var. *hungarica* (Grun.) Ross.	A,B,G,H,K
Navicula capitata var. *luneburgensis* (Grun.) Patr.	A
Navicula cari Ehr.	B
Navicula cincta (Ehr.) Ralfs	A,E,G,H,K
Navicula circumtexta Meist.	A,H,K
Navicula clementioides Hust.	A
Navicula clementis Grun.	A,B
Navicula coarctata A.Schmidt	I
Navicula cocconeiformis (Greg.) Grev.	A,B
Navicula contenta f. *biceps* (Arnott) Grun.	A,K
Navicula contenta f. *parallela* (Peters.) Hust.	D
Navicula convergens Patr.	H,K
Navicula crabro (Ehr.) Kütz.	I
Navicula crucicula (W.Sm.) Donk.	A
Navicula cryptocephala Kütz.	A,B,C,E,J,K
Navicula cryptocephala var. *exilis* Grun.	A,B,D
Navicula cryptocephala var. *veneta* (Kütz.) Rabh.	A,B,D,E,F,G, H,J,K
Navicula cryptocephaloides Hust.	D,G
Navicula cuspidata (Kütz.) Kütz.	A,B,D,E,F,G, H,J,K
Navicula cuspidata var. *ambigua* (Ehr.) Cl.	B
Navicula cuspidata var. *heribaudi* Perag.	A
Navicula cuspidata var. *major* Meist.	A,B,E
Navicula dactylus (Ehr.) Kütz.	I
Navicula decussis Öst.	A,B
Navicula detenta Hust.	A

Table 1 continued.

Navicula dicephala Ehr.	A,B,F,G
Navicula difficillimoides Hust.	A
Navicula digitoradiata (Greg.) Ralfs	G
Navicula digitulus Hust.	A
Navicula disjuncta Hust.	A
Navicula disputans Patr.	B
Navicula dulcis Patr.	A
Navicula elginensis (Greg.) Ralfs	A,B,D
Navicula elginensis var. *rostrata* (A.May.) Patr.	A,B,D,F
Navicula ellipsis Setty	I
Navicula exigua (Greg.) Grun.	A,B
Navicula exigua var. *capitata* (Greg.) Grun.	A,B
Navicula exselsa Krass.	D,E
Navicula festiva Krass.	A
Navicula feuerborni Hust.	G
Navicula firma var. *subundulata* Grun.	I
Navicula fischeri A.Schmidt	I
Navicula formosa Greg.	I
Navicula fragilarioides Krass.	A,E
Navicula frugalis Hust.	A
Navicula gallica (W.Sm.) Lagerst.	E
Navicula gastrum (Ehr.) Kütz.	A
Navicula gibba Cl.	A
Navicula gottlandica Grun.	A
Navicula gracilis Ehr.	A,J,K
Navicula graciloides A.May.	A,C,H
Navicula gregaria Donk.	A,B,C,F,G
Navicula grimmei Krass.	A
Navicula gysingensis Foged	A,B
Navicula halophila (Grun.) Cl.	A,B,E,F,G
Navicula halophila f. *tenuirostris* Hust.	A
Navicula heufleri Grun.	A
Navicula heufleri var. *leptocephala* (Bréb.) Perag.	A,E
Navicula hoefleri Choln.	A
Navicula impressa Grun.	I
Navicula indifferens Hust.	A
Navicula inflexa (Greg.) Ralfs	A
Navicula insociabilis Krass.	A
Navicula insociabilis var. *dissipatoides* Hust.	A
Navicula integra (W.Sm.) Ralfs	A,H
Navicula jaernfeltii Hust.	A
Navicula lacustris Greg.	A
Navicula laevissima Kütz.	A,B,E,H,K
Navicula lanceolata (Ag.) Kütz.	A,B,C,D,E,F, G,H
Navicula lapidosa Krass.	A
Navicula laterostrata Hust.	A
Navicula levanderi Hust.	A
Navicula longa (Greg.) Ralfs	I
Navicula longirostris Hust.	A,G
Navicula luzonensis Hust.	A,B,H,K
Navicula lyra Ehr.	A
Navicula maculata (J.W.Bail.) Edwards	I
Navicula mediocovexa Hust.	A
Navicula mediocris Krass.	A
Navicula menisculus var. *upsaliensis* (Grun.) Grun.	A,H,K
Navicula minima Grun.	A,B,D,E,H,K
Navicula minima var. *atomoides* (Grun.) Cl.	B

Table I continued.

Navicula minuscula Grun.	A
Navicula molestiformis Hust.	A
Navicula mormonorum Grun.	I
Navicula muralis Grun.	A,G
Navicula murrayi West & West	F,G,K
Navicula mutica Kütz.	A,B,D,E,F,G, K
Navicula mutica var. *binodis* Hust.	K
Navicula mutica var. *cohnii* (Hilse) Grun.	A,D
Navicula mutica var. *nivalis* (Ehr.) Hust.	B
Navicula mutica var. *undulata* (Hilse) Grun.	A,D,F,K
Navicula nivalis Ehr.	A,B,D,H
Navicula nummularia Grev.	I
Navicula oblonga (Kütz.) Kütz.	A,B,F,G,I,K
Navicula odiosa Wall.	A,B
Navicula omissa Hust.	A
Navicula paramutica Bock	D
Navicula paramutica var. *binodis* Bock	B
Navicula parva (Menegh.) Cl.-Eul.	G
Navicula pelliculosa Hilse	A,B,F,G
Navicula peregrina (Ehr.) Kütz.	A,B,D,E,F,G, H,K
Navicula permitis Hust.	A,H,K
Navicula perpusilla Grun.	G
Navicula placentula (Ehr.) Kütz.	A
Navicula placentula f. *rostrata* (A.May.) Hust.	A
Navicula cf. *poconoensis* Patr.	A
Navicula praetexta Ehr.	I
Navicula protomonttana Cl.	A
Navicula protracta (Grun.) Cl.	A
Navicula protracta f. *subcapitata* (Wisl. et Por.) Hust.	A
Navicula pseudocrassirostris Hust.	G
Navicula pseudoreinhardtii Patr.	A,B
Navicula pseudoscutiformis Hust.	A,B
Navicula pseudosilicula Hust.	A
Navicula pseudotuscula Hust.	A
Navicula pupula Kütz.	A,B,E,G,H,K
Navicula pupula var. *capitata* Skv. & Meyer	A
Navicula pupula var. *elliptica* Hust.	A,B
Navicula pupula var. *mutata* (Krass.) Hust.	A
Navicula pupula var. *rectangularis* (Greg.) Cl. & Grun.	A,B,E,F,G
Navicula pygmaea Kütz.	A,C,E,G,H,K
Navicula radiosa Kütz.	A,B,E,F,G,K
Navicula radiosa var. *parva* Wall.	A
Navicula radiosa var. *tenella* (Bréb.) Cl.	A,B,E,K
Navicula reinhardtii Grun.	A,B
Navicula reinhardtii var. *elliptica* Herib.	A,B
Navicula rhynchocephala Kütz.	A,B,C,E,F,G, K
Navicula rhyncocephala var. *amphiceros* (Kütz.) Grun.	A,K
Navicula rhyncocephala var. *germainii* (Wall.) Patr.	A,B
Navicula rostrata Ehr.	I
Navicula rotaeana (Rabh.) Grun.	B
Navicula salinarum Grun.	A,E,F,G,H,K

Table I continued.

Navicula salinarum var. *capitata* Schulz	G
Navicula salinarum var. *intermedia* (Grun.) Cl.	A,B,K
Navicula schroeteri var. *escambia* Patr.	A
Navicula scutelloides W.Sm. ex Greg.	A,B
Navicula scutum Schum.	A
Navicula secreta Pant.	A
Navicula secreta var. *apiculata* Patr.	A,B,H
Navicula secura Patr.	A
Navicula seminuloides Hust.	A
Navicula seminulum Grun.	A
Navicula seminulum var. *hustedtii* Patr.	B
Navicula septata Hust.	A
Navicula smithii Bréb.	I
Navicula sohrensis Krass.	A
Navicula strenzkei Hust.	A
Navicula subadnata Hust.	A,B
Navicula subbacillum Hust.	A,E
Navicula subhamulata Grun.	A
Navicula subinflatoides Hust.	G,H
Navicula submolesta Hust.	A
Navicula submuralis Hust.	G
Navicula subsulcatoides Hust.	G
Navicula subtillissima Cl.	A,B
Navicula symmetrica Patr.	A,B,K
Navicula tantula Hust.	G
Navicula tenelloides Hust.	A,D,G
Navicula tenera Hust.	A
Navicula tripunctata (O.Müll.) Bory	A,B,C,D,E, G,H,K
Navicula tripunctata var. *schizonemoides* (V.H.) Patr.	A,B,C,F,G,H, K
Navicula tulugakii Carter	F
Navicula tuscula Ehr.	A
Navicula vanheurckii Patr.	A,B
Navicula variostriata Krass.	A,B
Navicula ventricosa Ehr.	B,I
Navicula viridula (Kütz.) Ehr.	A,B,C
Navicula viridula var. *avenacea* (Bréb.ex Grun.) V.H.	A,B,H,K
Navicula viridula var. *linearis* Hust.	A
Navicula viridula var. *rostellata* (Kütz.) Cl.	A,H
Navicula vulpina Kütz.	B
Navicula wardii Patr.	A
Navicula wittrockii (Lagerst.) Temp. et Perag.	A,E,G
Navicula zanoni Hust.	G
Navicula sp.	A,B,C,D,E,F, G,H,K
Neidium affine (Ehr.) Pfitz.	A,B
Neidium affine var. *amphirhyncus* (Ehr.) Cl.	A
Neidium affine var. *longiceps* (Greg.) Cl.	A,B
Neidium bisulcatum (Lagerst.) Cl.	A,B
Neidium bisulcatum f. *lineare* (Oestr.) Cl.-Eul.	A
Neidium bisulcatum f. *undulata* (O.Müll.) Hust.	A
Neidium bisulcatum var. *baicalense* (Skv. & Meyer) Reim.	A
Neidium binode (Ehr.) Hust.	B,K
Neidium dubium (Ehr.) Cl.	A,B

Table 1 continued.

Neidium dubium f. *constricta* Hust.	B
Neidium iridis (Ehr.) Cl.	A,B,C,F,G
Neidium iridis var. *amphigomphus* (Ehr.) Temp. & Perag.	A
Neidium iridis var. *ampliatum* (Ehr.) Cl.	A
Neidium temperi Reim.	B
Neidium sp.	A
Nitzschia acicularis (Kütz.) W.Sm.	A,B,C,H,I
Nitzschia acicularoides Hust.	A
Nitzschia acuminata (W.Sm.) Grun.	B
Nitzschia acuta Hantz.	A
Nitzschia amphibia Grun.	A,B,D,E,F,G, H,K
Nitzschia angularis var. *affinis* (Grun.) Grun.	B
Nitzschia angustata Grun.	A,B,E,H
Nitzschia angustata var. *acuta* Grun.	A,K
Nitzschia apiculata (Greg.) Grun.	A,B,E,H,K
Nitzschia capitellata Hust.	A
Nitzschia circumsuta (J.W.Bail.) Grun.	A,I
Nitzschia clausii Hantz.	A,I,J
Nitzschia communis Rabh.	A,B,D,E,G, H,J
Nitzschia commutata Grun.	A,I
Nitzschia denticula Grun.	A,B,E,G,H,J
Nitzschia dissipata (Kütz.) Grun.	A,B,D,G,K
Nitzschia distans Greg.	I
Nitzschia dubia W.Sm.	A
Nitzschia epithemioides Grun.	A,C,E,H,K
Nitzschia filiformis (W.Sm.) Hust.	A,B
Nitzschia fonticola Grun.	A,B,C,D,H
Nitzschia frustulum (Kütz.) Grun.	A,B,E,G,H,J, K
Nitzschia frustulum var. *perminuta* Grun.	B,G,H
Nitzschia frustulum var. *perpusilla* (Rabh.) Grun.	B,G
Nitzschia frustulum var. *subsalina* Hust.	A,F,G,H
Nitzschia gandersheimiensis Krass.	A
Nitzschia gracilis Hantz.	A
Nitzschia granulata Grun.	A
Nitzschia hantzschiana Rabh.	A,B,D,E,H,J, K
Nitzschia heufleriana Grun.	B
Nitzschia holsatica Hust.	A
Nitzschia hungarica Grun.	A,B,C,F,G,H, K
Nitzschia inconspicua Grun.	A,B,D,E,H,J, K
Nitzschia intermedia Hantz.	A,H
Nitzschia kuetzingiana Hilse	C
Nitzschia lacunarum Hust.	A
Nitzschia lanceolata W.Sm.	A
Nitzschia linearis (Ag.) W.Sm.	A,B,C,D,E,F, G,K
Nitzschia longissima var. *closterium* (Ehr.) V.H.	A
Nitzschia lorenziana Grun.	B,K
Nitzschia microcephala Grun.	A,E,F,G
Nitzschia minuta Bleisch	A
Nitzschia minutula Grun.	A
Nitzschia obtusa W.Sm.	A,B,D,F,G
Nitzschia obtusifida Setty	I

Table 1 continued.

Nitzschia ovalis Arnott	A,B,H,K
Nitzschia palea (Kütz.) W.Sm.	A,B,C,D,E,F, G,H,I,J,K
Nitzschia palea var. *debilis* (Kütz.) Grun.	A
Nitzschia paleacea Grun.	A,D,E,H,K
Nitzschia panduriformis Greg.	I
Nitzschia parvula W.Sm.	K
Nitzschia perminuta (Grun.) M.Perag.	A
Nitzschia pseudostagnorum Hust.	G
Nitzschia punctata (Grun.) Grun.	A,I,K
Nitzschia punctata var. *elongata* Grun.	K
Nitzschia pusilla (Kütz.) Grun. em. Lange-Bert.	A
Nitzschia recta Hantz.	A
Nitzschia reversa W.Sm.	A
Nitzschia romana Grun.	A,E,H
Nitzschia scalaris (Ehr.) W.Sm.	I
Nitzschia sigma (Kütz.) W.Sm.	A,B,C,H,K
Nitzschia sigma var. *sigmatella* Grun.	A
Nitzschia sigmatella Greg.	A
Nitzschia sigmoidea (Nitz.) W.Sm.	A,B,I,K
Nitzschia sinuata (Thwaites) Grun.	A
Nitzschia sinuata var. *tabellaria* (Grun.) Grun.	A,B,E
Nitzschia sociabilis Hust.	A
Nitzschia socialis Greg.	K
Nitzschia spectabilis (Ehr.) Ralfs	A
Nitzschia stagnorum (Rabh.) Grun.	A
Nitzschia subacicularis Hust.	A
Nitzschia sublinearis Hust.	B
Nitzschia subtilis (Kütz.) Grun.	A,G,H
Nitzschia subtilis var. *paleacea* Grun.	K
Nitzschia thermalis (Ehr.) Auers.	A,I,K
Nitzschia thermalis var. *minor* Hilse	A
Nitzschia tryblionella Hantz.	A,B,H
Nitzschia tryblionella var. *debilis* (Arnott) Hust.	A,E
Nitzschia tryblionella var. *levidensis* (W.Sm.) Grun.	A,K
Nitzschia tryblionella var. *victoriae* (Grun.) Grun.	A
Nitzschia valdestriata Aleem et Hust.	A
Nitzschia valida (Grun.) Pelletan	I
Nitzschia vermicularis (Kütz.) Hantz.	B,C
Nitzschia vitrea cf. var. *scaphiformis* Wisl. & Poretz.	G,H
Nitzschia vivax W.Sm.	G
Nitzschia sp.	A,B,E,F,G,H, K
Opephora martyi Herib.	A
Pinnularia abaujensis (Pant.) Ross	B
Pinnularia abaujensis var. *linearis* (Hust.) Patr.	A
Pinnularia abaujensis var. *rostrata* (Patr.) Patr.	A,B
Pinnularia abaujensis var. *subundulata* (A.May. ex Hust.) Patr.	A
Pinnularia acrosphaeria (Bréb.) W.Sm.	A
Pinnularia acuminatum W.Sm.	A,B
Pinnularia aestuarii var. *interrupta* (Hust.) Cl.-Eul.	A
Pinnularia amphistylus Ehr.	C

Table 1 continued.

Pinnularia appendiculata (Ag.) Cl.	A,D,E,F,G
Pinnularia biceps Greg.	A,B
Pinnularia biceps var. *minor* (Peters.) Cl.-Eul.	E
Pinnularia bogotensis (Grun.) Cl.	A
Pinnularia bogotensis var. *undulata* (M.Perag.) Boyer	A,G
Pinnularia borealis Ehr.	A,B,D,K
Pinnularia borealis var. *rectangularis* Carlson	A
Pinnularia braunii (Grun.) Cl.	A,B
Pinnularia braunii var. *amphicephala* (A.May.) Hust.	A
Pinnularia brebissonii (Kütz.) Rabh. (= *Navicula brebissonii*)	A,B,D,E,H,I,K
Pinnularia brebissonii var. *diminuta* (Grun.) Cl.	A,D,G
Pinnularia brebissonii f. *biundulata* O.Müll.	B
Pinnularia burkii Patr.	A
Pinnularia cardinalis (Ehr.) W.Sm.	K
Pinnularia dactylus Ehr.	A,B
Pinnularia divergens W.Sm.	A
Pinnularia divergens var. *elliptica* (Grun.) Cl.	A
Pinnularia divergentissima (Grun.) Cl.	A,B
Pinnularia episcopalis var. *subelliptica* Cl.-Eul.	B
Pinnularia gentilis (Donk.) Cl.	D
Pinnularia gibba Ehr.	A
Pinnularia intermedia (Lagerst.) Cl.	A,B,E,K
Pinnularia lata (Bréb.) Rabh.	A,B
Pinnularia maior (Kütz.) Rabh.	A,B,I,K
Pinnularia maior var. *transversa* (A.Schmidt) Cl.	B
Pinnularia mesolepta (Ehr.) W.Sm.	A,B
Pinnularia mesolepta f. *angusta* (Cl.) Hust.	A
Pinnularia microstauron (Ehr.) Cl.	A,B,C,F,G
Pinnularia microstauron var. *biundulata* O.Müll.	C
Pinnularia molaris (Grun.) Cl.	A
Pinnularia nobilis (Ehr.) Ehr.	A,I
Pinnularia obscura Krass.	A
Pinnularia platycephala (Ehr.) Cl.	A
Pinnularia rupestris Hantz.	B
Pinnularia ruttneri Hust.	A
Pinnularia stauroneis Ehr.	C
Pinnularia subcapitata Greg.	A
Pinnularia sublinearis (Grun.) Cl.	A
Pinnularia subsolaris (Grun.) Cl.	A
Pinnularia substomatophora Hust.	A
Pinnularia termitina (Ehr.) Fricke	A,C
Pinnularia undulata Greg.	A
Pinnularia viridis (Nitz.) Ehr.	A,B,D,E,F,G,H,K
Pinnularia viridis var. *commutata* (Grun.) Cl.	A
Pinnularia viridis var. *minor* Cl.	A,B,F,G
Pinnularia sp.	A,D,E,F,G
Plagiotropis (see *Tropidoneis*)	
Pleurosigma australe Grun.	A

Table 1 continued.

Pleurosigma decorum W.Sm.	I
Pleurosigma delicatulum W.Sm.	A,B,G,H,K
Pleurosigma eximium (Thw.) Grun.	K
Pleurosigma sp.	A,I
Rhizosolenia minima Levan.	A
Rhoicosphenia curvata (Kütz.) Grun.	A,B,C,D,E,F,G,H,I,K
Rhopalodia gibba (Ehr.) O.Müll.	A,B,D,E,F,G,K
Rhopalodia gibba var. *ventricosa* (Kütz.) Perag. & Perag.	A,H,K
Rhopalodia gibberula (Ehr.) O.Müll.	A,B,D,E,F,G,J,K
Rhopalodia gibberula var. *protracta* (Grun.) O.Müll.	A,E
Rhopalodia gibberula var. *vanheurckii* O.Müll.	A,D
Rhopalodia musculus (Kütz.) O.Müll.	A,C,H,K
Rhopalodia musculus var. *constricta* (Bréb.) Perag. et Perag.	K
Rhopalodia sp.	A
Scoliopleura peisonis Grun.	A,I,K
Semiorbis hemicyclus (Ehr.) Patr.	F,G
Stauroneis agrestis Peters.	A
Stauroneis anceps Ehr.	A,B,E
Stauroneis anceps f. *gracilis* Rabh.	A,B,E
Stauroneis anceps f. *linearis* Rabh.	A,B
Stauroneis anceps var. *siberica* Grun.	A
Stauroneis cf. *dubitabilis* Hust.	A
Stauroneis fluminea Patr. & Freese	B
Stauroneis ignorata Hust.	B
Stauroneis inclinatus Setty	I
Stauroneis kriegeri Patr.	A,B,D
Stauroneis legleri Hust.	G,H
Stauroneis muriella f. *linearis* Lund	A
Stauroneis nana Hust.	A
Stauroneis phoenicenteron (Nitz.) Ehr.	A,B
Stauroneis phoenicenteron var. *brunii* (M.Perag. & Herib.) F.W.Mills	A
Stauroneis phoenicenteron f. *gracilis* (Dippel) Hust.	A,B
Stauroneis salina W.Sm.	F
Stauroneis smithii Grun.	A,B
Stauroneis smithii var. *incisa* Pant.	A
Stauroneis wislouchii Poretz. & Anis.	A,G
Stauroneis sp.	A
Stenopterobia intermedia (Lewis) V.H.	A
Stephanodiscus astraea (Ehr.) Grun.	A,I,K
Stephanodiscus astraea var. *minutula* (Kütz.) Grun.	A,B,D,G,H,J,K
Stephanodiscus carconensis (Eul.) Grun.	D,E
Stephanodiscus carconensis var. *pusilla* Grun.	A,D
Stephanodiscus dubius (Fricke) Hust.	A
Stephanodiscus hantzschii Grun.	A,D
Stephanodiscus invisitatus Hohn & Heller.	A
Stephanodiscus minutus Cl. & Moell.	A
Stephanodiscus niagarae Ehr.	A,B,D,K

Table I continued.

Stephanodiscus subtilis (V.Goor) Cl.-Eul.	A
Stephanodiscus sp.	A,B,D,H
Surirella angusta Kütz.	A,B,H,K
Surirella baileyi Lewis	B
Surirella biseriata Bréb.	A,B,I
Surirella craticula Ehr.	K
Surirella crumena Bréb.	I
Surirella delicatissima Lewis	A,B
Surirella elegans Ehr.	I
Surirella laevigata Ehr.	I
Surirella linearis W.Sm.	A,B
Surirella linearis var. *constricta* Grun.	A
Surirella ovalis Bréb.	A,B,D,E,H,I,K
Surirella ovalis var. *baltica* (Schum.) Cl.-Eul.	B
Surirella ovalis var. *brightwellii* (W.Sm.) Perag. & Perag.	A
Surirella ovata Kütz.	A,B,C,F,G,H,K
Surirella ovata var. *pinnata* (W.Sm.) Brun.	A,B
Surirella ovata var. *utahensis* Grun.	K
Surirella patella Ehr.	A
Surirella pseudovalis Hust.	A
Surirella regina Janisch	I
Surirella rhombus Setty	I
Surirella roburii Setty	I
Surirella robusta Ehr.	A
Surirella robusta var. *splendida* (Ehr.) V.H.	A,C
Surirella robusta var. *splendida* f. *hustedtiana* (A.May.) Hust.	A
Surirella rostrata Setty	K
Surirella spiralis Kütz.	A
Surirella splendida (Ehr.) Kütz.	I
Surirella striatula Turp.	A,C,F,G,I,K
Surirella testudo Ehr.	C
Surirella utahensis (Grun.) Hanna & Grant	I
Surirella sp.	A,B
Synedra acus Kütz.	A,B,C,F,G,H,K
Synedra affinis Kütz.	B
Synedra affinis var. *acuminata* Grun.	K
Synedra affinis var. *lancettula* Grun.	K
Synedra amphicephala Kütz.	A
Synedra amphicephala var. *austriaca* (Grun.) Hust.	A
Synedra capitata Ehr.	A,B,F,G
Synedra cyclopum Bruts.	A
Synedra cyclopum var. *robustum* Schultz	A
Synedra delicatissima W.Sm.	A,B,G
Synedra delicatissima var. *angustissima* Grun.	A
Synedra famelica Kütz.	A
Synedra fasciculata Kütz.	A,B,G,H
Synedra fasciculata var. *truncata* (Grev.) Patr.	A,B,D,F,G,H,J,K
Synedra filiformis var. *exilis* Cl.-Eul.	A
Synedra incisa Boyer	E,G

Table I continued.

Synedra lanceolata Kütz.	I
Synedra mazamensis Sov.	A
Synedra minuscula Grun.	A,B
Synedra parasitica (W.Sm.) Hust.	A,B,D,E
Synedra parasitica var. *subconstricta* (Grun.) Hust.	A,B
Synedra pulchella (Ralfs) Kütz.	A,B,E,H,I,K
Synedra pulchella var. *lanceolata* O'Meara	A,B,F,G,K
Synedra radians Kütz.	A,B,F,G,H
Synedra rumpens Kütz.	A,B,D
Synedra rumpens var. *familiaris* (Kütz.) Grun.	A
Synedra rumpens var. *fragilarioides* Grun.	A
Synedra rumpens var. *meneghiniana* Grun.	A
Synedra rumpens var. *scotica* Grun.	A,G
Synedra socia Wall.	A
Synedra spectabilis Ehr.	C
Synedra splendens Kütz.	A
Synedra subaequalis Grun.	A
Synedra tabulata (Ag.) Kütz.	A,F,G
Synedra tabulata var. *obtusa* (Arn.) Hust.	A,F,G
Synedra tenera W.Sm.	A,E,F
Synedra tenuissima Kütz.	I
Synedra ulna (Nitz.) Ehr.	A,B,C,D,E,F,G,H,K
Synedra ulna var. *amphirhynchus* (Ehr.) Grun.	B
Synedra ulna var. *biceps* (Kütz.) Schoenfeld	I
Synedra ulna var. *constricta* Venkataraman	B
Synedra ulna var. *contracta* Oestr.	A,B,G,K
Synedra ulna var. *danica* (Kütz.) Grun.	A
Synedra ulna var. *longissima* (W.Sm.) Brun.	A,G
Synedra ulna var. *oxyrhynchus* (Kütz.) V.H.	A,B
Synedra ulna var. *oxyrhynchus* f. *mediocontracta* (Forti) Hust.	A
Synedra ulna var. *ramesi* (Herib.) Hust.	A,B
Synedra ulna var. *spathulifera* Grun.	A
Synedra ulna var. *subaequalis* Grun.	A,B
Synedra sp.	A,B,C,F
Tabellaria fenestrata (Lyngb.) Kütz.	A,B,D
Tabellaria flocculosa (Roth) Kütz.	A,B
Tabellaria sp.	A,B,F
Terpsinoe intermedia Grun.	C
Terpsinoe musica Ehr.	F,G
Tetracyclus lacustris Ralfs	A,B
Tetracyclus sp.	A
Thalassiosira fluviatilis Hust.	A,C
Thalassiosira sp.	A
Tropidoneis arizonica Czar. & Blinn	A,G
Tropidoneis lepidoptera (Greg.) Cl.	G
Tropidoneis vitrea (W.Sm.) Cl.	A
Tropidoneis vitrea var. *scaligera* (Grun.) Cl.	A

Table 1 continued.

DIVISION EUGLENOPHYTA	
Class Euglenophyceae	
Order Euglenales	
Euglena acus Ehr.	A,B
Euglena adhaerens Matv.	B
Euglena deses Ehr.	A,B
Euglena ehrenbergii Klebs	A
Euglena elastic Prescott	A
Euglena gracilis Klebs	A,B,D
Euglena minuta Prescott	B
Euglena oxyuris Schmar.	A
Euglena pisciformis Ehr.	A,B
Euglena proxima Dang.	A,B
Euglena sanguinea Ehr.	B
Euglena tripteris (Duj.) Klebs	A
Euglena viridis Ehr.	A
Euglena sp.	A,B,D
Eutreptia sp.	B
Lepocinclis salina Fritsch	A
Lepocinclis sp.	A
Phacus acuminatus Stokes	A,B
Phacus chloroplastes Pres.	A
Phacus pyrum (Ehr.) Stein	B
Phacus spiralis All. et Jahn	A
Phacus tortus (Lemm.) Skv.	A
Phacus sp.	A,B
Strombomonas fluviatilis (Lemm.) Defl.	A
Trachelomonas abrupta (Swir.) Defl.	A
Trachelomonas crebea (Kill.) Defl.	A
Trachelomonas dybowskii Dreze.	A
Trachelomonas robusta Swir.	B
Trachelomonas sp.	A
DIVISION PYRRHOPHYTA	
Class Dinophyceae	
Order Peridiniales	
Ceratium hirundinella (O. Müll.) Dujard.	A,B,C
Ceratium sp.	A
Peridinium cinctum (O. Müll.) Ehr.	B
Peridinium wille Huitfeld	A
Order Glenodiniales	
Glenodinium dinobryonis (Wol.) Lind.	A
Glenodinium penardiforme (Lind.) Schill.	A
Glenodinium pulvisculus (Ehr.) Stein	A
Glenodinium sp.	A,C
Order Gymnodiniales	
Gymnodinium sp.	A
DIVISION CRYPTOPHYTA	
Class Cryptophyceae	
Order Cryptomonadales	
Chroomonas sp.	A

Table 1 continued.

Cryptomonas erosa Ehr.	A
Cryptomonas sp.	A
DIVISION RHODOPHYTA	
Class Rhodophyceae	
Order Nemalionales	
Audouinella violacea (Kütz.) Hamel	B,J
Batrachospermum moniliforme Roth	B,J
Batrachospermum sp.	A

Column letters in the above table refer to the following habitat categories:

A Lakes and reservoirs
B Rivers and streams
C Great Salt Lake
D Soils
E Wet walls
F Wet meadows
G Thermal springs
H Salt marshes
I Fossils
J Cold springs
K Undesignated

REFERENCES

ANDERSON, D. C., AND S. R. RUSHFORTH. 1976. The cryptogam flora of desert soil crusts in southern Utah, USA. Nova Hedwigia 28(4): 691–729.

ASHLEY, J., AND S. R. RUSHFORTH. 1984. Growth of soil algae on top soil and processed oil shale from the Uintah Basin, Utah, USA. Reclam. Reveg. Res. 3: 49–63.

ASHLEY, J., S. R. RUSHFORTH, AND J. R. JOHANSEN. 1985. Soil algae of cryptogamic crusts from the Uintah Basin, Utah, USA. Great Basin Nat. 45(3): 432–442.

BATEMAN, L., AND S. R. RUSHFORTH. 1984. Diatom floras of selected Uinta mountain lakes, Utah, USA. Bibliotheca Diatomologica 4: 1–99.

BENSON, C. E., AND S. R. RUSHFORTH. 1975. The algal flora of Huntington Canyon, Utah, USA. Bibliotheca Phycologica 18: 1–177.

BESSEY, G. E. 1960. Aquatic plants of central Utah and their distribution. Unpublished thesis, Brigham Young University, Provo, Utah.

BOLKE, E. L. 1979. Dissolved-oxygen depletion and other effects of storing water in Flaming Gorge Reservoir, Wyoming and Utah. U.S. Geol. Surv. Water-Supply Pap. N. 2058.

BOLLAND, R. F. 1974. Paleoecological interpretations of the diatom succession in recent sediments of Utah Lake. Unpublished dissertation, University of Utah, Salt Lake City.

BROCK, T. D. 1976. Halophilic blue-green algae. Arch. Microbiol. 107: 109–111.

CHANTANACHAT, S., AND H. C. BOLD. 1962. Phycological studies II. Some algae from arid soils. Pub. No. 6218, University of Texas, Austin.

CHATWIN, S. L. 1956. The vertical distribution of phytoplankton of Deer Creek Reservoir, Wasatch County, Utah. Unpublished thesis, University of Utah, Salt Lake City.

CHENG, M. S. 1973. A taxonomic investigation of the algae of the Brigham Young University Campus, Provo, Utah. Unpublished thesis, Brigham Young University, Provo, Utah.

CHENG, M. S., AND S. R. RUSHFORTH. 1977. The algal flora of the campus of Brigham Young University, Provo, Utah. Great Basin Nat. 37(3): 402–406.

CHRISTENSEN, E. M. 1956. Bibliography of Utah aquatic biology. Proc. Utah Acad. Sci., Arts, and Letters 33: 91–100.

_____. 1962. Bibliography of Utah aquatic biology. No. II. Great Basin Nat. 22(1–3): 32–53.

CLARK, W. J. 1956. An evaluation of methods of concentrating and counting phytoplankton of Bear Lake, Utah-Idaho. Unpublished thesis, Utah State University, Logan.

_____. 1958. The phytoplankton of the Logan River, Utah, a mountain stream. Unpublished dissertation, Utah State University, Logan.

CLARK, W. J., AND W. F. SIGLER. 1961. Preliminary investigation of the phytoplankton of Bear Lake, Utah-Idaho. Trans. Amer. Micro. Soc. 80(1): 28–32.

COOMBS, R. J. 1964. A floristic and ecological survey of the algal flora of the western Uinta Mountains and adjacent areas. Unpublished thesis, University of Utah, Salt Lake City.

CORDNER, S. H. 1982. A contribution to the salt marsh diatom flora of the Great Salt Lake, Utah, USA. Unpublished thesis, Brigham Young University, Provo, Utah.

DAINES, L. L. 1910. Physiological experiments on some algae of Great Salt Lake. Unpublished thesis, University of Utah, Salt Lake City.

_____. 1917. On the flora of Great Salt Lake. Amer. Nat. 51: 499–506.

EARDLEY, A. J. 1938. Sediments of Great Salt Lake, Utah. Bull. Amer. Assoc. Petro. Geol. 22(10): 1305–1411.

EHRENBERG, C. G. 1871. Über die waehsende Kenntniss des unsichtbaren Lebens als felsbildende Bacillarien in Californien. Abh. Königl. Akad. Wiss. Berlin 1870: 1–74.

EVENSON, W. E., S. R. RUSHFORTH, J. D. BROTHERSON, AND N. FUNGLADDA. 1981. The effects of selected physical and chemical factors on attached diatom populations in the Uintah Basin of Utah, USA. Hydrobiologia 83: 325–330.

FELIX, E. A., AND S. R. RUSHFORTH. 1977. The algal flora of the Great Salt Lake, Utah: a preliminary report. Pages 385–392 *in* D. Greer, ed., Desertic terminal lakes. Utah Water Res. Lab. Pub.

_____. 1979. The algal flora of the Great Salt Lake, Utah, USA. Nova Hedwigia 31(1–2): 163–195.

_____. 1980. Biology of the south arm of the Great Salt Lake, Utah. Utah Geol. Miner. Surv. Bull. 116: 305–312.

FLOWERS, S. 1934. Vegetation of the Great Salt Lake region. Bot. Gaz. 95(3): 353–418.

_____. 1939. Common algae of Utah. University of Utah, Salt Lake City. 70 pp. (mimeo).

_____. n.d. The bluegreen algae of Utah. University of Utah, Salt Lake City. 69 pp. (mimeo).

FLOWERS, S., AND F. R. EVANS. 1966. The flora and fauna of the Great Salt Lake region, Utah. Pages 367–393 *in* H. Boyko, ed., Salinity and aridity: new approaches to old problems. W. Junk Pub., The Hague.

FLOWERS, S., H. H. HALL, AND C. T. GROVES. 1960. An annotated list of the plants found in Flaming Reservoir Basin. Pages 49–98 *in* C. E. Dibble, ed., Ecological studies of the flora and fauna of Flaming Gorge Reservoir Basin, Utah and Wyoming. Univ. Utah Anthro. Pap. 48.

FOSTER, H. N. 1960. An ecological study of a warm sulphur spring in Salt Lake Valley, Utah. Unpublished thesis, University of Utah, Salt Lake City.

FUNGLADDA, N. 1978. The effects of dissolved heavy metals on diatom populations: a study in the Uintah Basin of Utah, USA. Unpublished thesis, Brigham Young University, Provo, Utah.

FUNK, W. H. 1963. Growth and control of algae in Deer Creek Reservoir. Unpublished thesis, University of Utah, Salt Lake City.

_____. 1966. Phytoplankton productivity of a newly developed reservoir. Unpublished dissertation, University of Utah, Salt Lake City.

FUNK, W. H., AND A. R. GAUFIN. 1965. Control of taste and odor producing algae in Deer Creek Reservoir. Trans. Amer. Micro. Soc. 84: 263–269.

GAUFIN, A. R., AND D. B. MCDONALD. 1965. Factors influencing algal productivity in Deer Creek Reservoir, Utah. Trans. Amer. Micro. Soc. 84: 269–279.

GOEDE, R. W. 1961. Some effects of sodium fluoride on the benthic algae of a lotic environment. Unpublished thesis, Utah State University, Logan.

GRIFFIN, G. D. 1956. An investigation of *Anabaena unispora* Gardner and other bluegreen algae as a possible mosquito control factor in Salt Lake County of Utah. Unpublished thesis, University of Utah, Salt Lake City.

GRIMES, J. A. 1980. Taxonomy and ecology of diatoms of surface sediments of Utah Lake, Utah, USA. Unpublished dissertation, Brigham Young University, Provo, Utah.

GRIMES, J. A., AND S. R. RUSHFORTH. 1982. Diatoms of recent bottom sediments of Utah Lake, Utah, USA. Bibliotheca Phycologica 55: 1–179.

_____. 1983. Diatoms of surface sediments of Utah Lake, Utah, USA. Hydrobiologia 99: 161–174.

GRIMES, J. A., S. R. RUSHFORTH, J. D. BROTHERSON, AND W. E. EVENSON. 1984. Diatoms in recent bottom sediments and trophic status of eight lakes and reservoirs in northeastern Utah. Great Basin Nat. 44: 36–48.

GRIMES, J. A., L. L. ST. CLAIR, AND S. R. RUSHFORTH. 1980. A comparison of epiphytic diatom assemblages on living and dead stems of the common grass *Phragmites australis*. Great Basin Nat. 40(3): 223–228.

HARDING, W. J. 1970. A preliminary report on the algal species presently found in Utah Lake. Great Basin Nat. 30(2): 99–105.

_____. 1971. The algae of Utah Lake. Part II. Great Basin Nat. 31(3): 125–134.

HARRISON, W. J. 1926. A preliminary study of the freshwater algae of Washington County, Utah. Unpublished thesis, Brigham Young University, Provo, Utah.

HASLER, J. W., AND A. L. CRAWFORD. 1938. Diatomaceous marl of Bonneville age. Proc. Utah Acad. Sci., Arts, and Letters 15: 25–26.

HEVLY, R. H. 1961. Notes on aquatic non-flowering plants of northern Arizona and adjoining regions. Plateau 33(3): 88–92.

HICKS, C. E. 1964. The effects of a synthetic detergent, alkyl benzene sodium sulfonate, on the productivity of stream algal communities. Unpublished thesis, Utah State University, Logan.

HOHAM, R. W. AND D. W. BLINN. 1979. Distribution of cryophilic algae in an arid region, the American Southwest. Phycologia 18: 133–145.

IVORY, T. M. 1967. The growth of phytoplankton in Mountain Dell Reservoir. Unpublished thesis, University of Utah, Salt Lake City.

JATKAR, S. A., S. R. RUSHFORTH, AND J. D. BROTHERSON. 1979. Diatom floristics and succession in a peat bog near Lily Lake, Summit County, Utah. Great Basin Nat. 39: 15–43.

JAVAKUL, A. J., A. GRIMES, AND S. R. RUSHFORTH. 1983. Diatoms in sediment cores in Utah Lake, Utah, USA. Hydrobiologia 98: 159–170.

JOHANSEN, J. R. 1984. Response of soil algae to a hundred year storm in the Great Basin Desert, USA. Phykos 23(1–2): 51–54.

JOHANSEN, J. R., AND S. R. RUSHFORTH. 1981. Diatoms of surface waters and soils of selected oil shale lease areas of eastern Utah. Nova Hedwigia 34: 333–390.

———. 1985. Cryptogamic soil crusts: seasonal variation in algal populations in the Tintic Mountains, Juab County, Utah. Great Basin Nat. 45(1): 14–21.

JOHANSEN, J. R., AND L. L. ST. CLAIR. 1986. Cryptogamic soil crusts: recovery from grazing near Camp Floyd State Park, Utah, USA. Great Basin Nat. 46(4): 632–640.

JOHANSEN, J. R., L. L. ST. CLAIR, B. L. WEBB, AND G. T. NEBEKER. 1984. Recovery patterns of cryptogamic soil crusts in desert rangelands following fire disturbance. Bryologist 87(3): 238–243.

JOHANSEN, J. R., A. JAVAKUL, AND S. R. RUSHFORTH. 1982. Effects of burning on the algal communities of a high desert soil near Wallsburg, Utah. J. Range Management 35(5): 598–600.

JOHANSEN, J. R., S. R. RUSHFORTH, AND I. KACZMARSKA. 1982. Algal populations in Bottle Hollow Reservoir, Duchesne County, Utah. Great Basin Nat. 42(2): 205–218.

JOHANSEN, J. R., S. R. RUSHFORTH, R. ORBENDORFER, N. FUNGLADDA, AND J. A. GRIMES. 1983. The algal flora of selected wet walls in Zion National Park, Utah, USA. Nova Hedwigia 38: 765–808.

KACZMARSKA, I., AND S. R. RUSHFORTH. 1983a. Notes on a rare inland *Hyalodiscus*. Bacillaria 6: 157–164.

———. 1983b. The diatom flora of Blue Lake, Tooele County, Utah. Bibliotheca Diatomologica 2(1): 1–123.

———. 1984. Diatom associations in Blue Lake Warm Spring, Tooele County, Utah, USA. Proc. 7th Internat. Diat. Sym., Philadelphia, 22–27 August 1982.

KACZMARSKA, I., S. R. RUSHFORTH, AND J. R. JOHANSEN. 1985. *Chaetoceros amanita* Cleve-Euler (Bacillariophyceae) from Blue Lake Warm Spring, Utah, USA. Phycologia 24(1): 103–109.

KIRKPATRICK, R. 1934. The life of the Great Salt Lake with special reference to the algae. Unpublished thesis, University of Utah, Salt Lake City.

LAWSON, L. L. 1974. The diatom flora of the Provo River, Utah. Unpublished thesis, Brigham Young University, Provo, Utah.

LAWSON, L. L., AND S. R. RUSHFORTH. 1975. The diatom flora of the Provo River, Utah. Bibliotheca Phycologica 17: 1–149.

LONGLEY, G., JR. 1966. The seasonal variation of periphyton in Trout Creek, Wasatch County, Utah. Unpublished thesis, University of Utah, Salt Lake City.

———. 1969. Plankton associations in the Antelope Flat area, Flaming Gorge Reservoir. Unpublished dissertation, University of Utah, Salt lake City.

MCCOARD, D. L. 1967. An ecological study of the algae and mosses of Cascade Springs, Wasatch County, Utah. Unpublished thesis, Brigham Young University, Provo, Utah.

MCDONALD, D. B. 1962. The productivity of Deer Creek Reservoir with special reference to phytoplankton. Unpublished dissertation, University of Utah, Salt Lake City.

MERKLEY, W. B. 1966. Evaluation of three methods of concentrating plankton of Deer Creek Reservoir. Unpublished thesis, University of Utah, Salt Lake City.

MILLER, G. L. 1959. An investigation of pollution in the Price River, Carbon County, Utah. Unpublished thesis, University of Utah, Salt Lake City.

MURRAY, R. B. 1972. Nutrients and phytoplankton in Hyrum Lake. Unpublished thesis, Utah State University, Logan.

NAVE, R. H. 1960. A limnological study of Clover Creek, Tooele County, Utah. Unpublished thesis, University of Utah, Salt Lake City.

NORRINGTON, A. 1925. Phycological study of some of the mountain lakes and streams of the Wasatch and Uinta ranges in Utah. Unpublished dissertation, University of Chicago, Chicago, Illinois.

———. 1927. Phycological study of some of the mountain lakes and streams of the Wasatch and Uinta ranges in Utah. Chicago Univ. Abst. Thesis Sci. Ser. 3: 287–292.

PACKARD, A. S., JR. 1897. The sea-weeds of Salt Lake. Amer. Nat. 13: 701–703.

PALMER, A. C. 1968. A taxonomic and ecological study of the algae of Lily Lake. Unpublished thesis, Brigham Young University, Provo, Utah.

PATRICK, R. 1936. Some diatoms of Great Salt Lake. Bull. Torrey Bot. Club 63(3): 157–166.

PEDERSON, J. L. 1969. A taxonomic and ecological study of the desmids of Lily Lake. Unpublished thesis, Brigham Young University, Provo, Utah.

POST, F. J. 1975. Life in the Great Salt Lake. Utah Sci. 36: 43–47.

PRATT, G. A. 1957. Studies on the periodicity of certain plankton species of Salem Lake. Unpublished thesis, Brigham Young University, Provo, Utah.

QUINN, B. G. 1958. The effects of sugar beet wastes upon the Periphyton of the Jordan River, Salt Lake County, Utah. Unpublished thesis, University of Utah, Salt Lake City.

RABE, F. W., AND A. R. GAUFIN. 1964. Some limnological effects of fertilizing three cirque lakes in the Uinta Mountains. Proc. Utah Acad. Sci., Arts, and Letters 41: 255–260.

ROSS, L., AND S. R. RUSHFORTH. 1980. The effects of a new reservoir on the attached diatom communities in Huntington Creek, Utah, USA. Hydrobiologia 68(2): 157–165.

RUSHFORTH, S. R., J. D. BROTHERSON, N. FUNGLADDA, AND W. E. EVENSON. 1981. The effects of dissolved heavy metals on attached diatoms in the Uinta Basin of Utah, USA. Hydrobiologia 83: 313–323.

RUSHFORTH, S. R., AND E. A. FELIX. 1982. Biotic adjustments to changing salinities in the Great Salt Lake, Utah, USA. Micro. Ecol. 8: 157–161.

RUSHFORTH, S. R., AND I. KACZAMARSKA. 1984. New records of diatoms from Blue Lake warm spring, Tooele County, Utah. Great Basin Nat. 44(1): 120–124.

RUSHFORTH, S. R., L. L. ST. CLAIR, J. A. GRIMES, AND M. C. WHITING. 1981. Phytoplankton of Utah Lake. Great Basin Nat. Mem. 5: 85–100.

RUSHFORTH, S. R., L. L. ST. CLAIR, T. A. LESLIE, K. H. THORNE, AND D. C. ANDERSON. 1976. The algae of two hanging gardens from southeastern Utah. Nova Hedwigia 27: 231–323.

RUSHFORTH, S. R., AND L. E. SQUIRES. 1985. New records and comprehensive list of the algal taxa of Utah Lake, Utah, USA. Great Basin Nat. 45(2): 237–254.

ST. CLAIR, L. L., AND S. R. RUSHFORTH. 1976. The diatoms of Timpanogos Cave National Monument, Utah. Amer. J. Bot. 63(1): 49–59.

———. 1977. The diatom flora of the Goshen warm spring ponds and wet meadows, Goshen, Utah, USA. Nova Hedwigia 28(2): 353–425.

———. 1978. The diatom flora of the Goshen playa and wet meadow. Nova Hedwigia 29(1–2): 191–230.

ST. CLAIR, L. L., L. E. SQUIRES, AND S. R. RUSHFORTH. 1978. A comparative analysis of the diatom flora on the snail *Ampullaria cuprina* from the Goshen Ponds, Utah. Great Basin Nat. 38(2): 211–214.

SETTY, M. G. A. P. 1963a. Paleontology and paleoecology of diatoms of Lake Bonneville, Utah. Unpublished dissertation, University of Utah, Salt Lake City.

———. 1963b. Pliocene diatoms from the Bryce Canyon area, Utah. Proc. Utah Acad. Sci., Arts, and Letters 40: 247.

SMITH, G. R. 1959. Effects of pollution on the Weber River, Utah. Unpublished thesis, University of Utah, Salt Lake City.

SNOW, E. 1931. A preliminary study of the algae of Utah Lake. Unpublished thesis, Brigham Young University, Provo, Utah.

———. 1932. A preliminary report on the algae of Utah Lake. Proc. Utah Acad. Sci., Arts, and Letters 9: 21–28.

———. 1940. Desmids of Mirror Lake, Utah. Bot. Gaz. 102(2): 410–411.

SNOW, E., AND G. STEWART. 1939. A preliminary report of the algae of Mirror Lake. Proc. Utah Acad. Sci., Arts, and Letters 16: 113–115.

SQUIRES, L. E. 1972. A quantitative and ecological survey of the algae of Huntington Canyon, Utah. Unpublished thesis, Brigham Young University, Provo, Utah.

SQUIRES, L. E., AND S. R. RUSHFORTH. 1986. Winter phytoplankton communities of Utah Lake, Utah, USA. Hydrobiologia 131: 235–248.

SQUIRES, L. E., S. R. RUSHFORTH, AND J. D. BROTHERSON. 1979. Algal response to a thermal effluent: a study of a power station on the Provo River, Utah, USA. Hydrobiologia 63: 17–32.

SQUIRES, L. E., S. R. RUSHFORTH, AND C. J. ENDSLEY. 1973. An ecological survey of the algae of Huntington Canyon, Utah. Brigham Young Univ. Sci. Bull., Biol. Series 18(2): 1–87.

SQUIRES, L. E., M. C. WHITING, J. D. BROTHERSON, AND S. R. RUSHFORTH. 1979. Competitive displacement as a factor influencing phytoplankton distribution in Utah Lake, Utah. Great Basin Nat. 39(3): 245–252.

STEWART, A. J., AND D. W. BLINN. 1974. Phytoplankton population dynamics in Warm Creek Bay, Lake Powell. J. Phycol. 10(suppl.): 11.

———. 1976. Studies on Lake Powell, USA: environmental factors influencing phytoplankton success in a high desert warm monomictic lake. Arch. Hydrobiol. 78: 139–164.

SWALLOW, O. T. 1932. A preliminary limnological study of Utah Lake. Unpublished thesis, Brigham Young University, Provo, Utah.

TILDEN, J. E. 1898. Observations on some west American thermal algae. Bot. Gaz. 3:89–107.

VARLEY, J. D. 1976. Plankton periodicity as related to the chemical, physical, and biological environment of Flaming Gorge Reservoir, Utah-Wyoming. Unpublished thesis, University of Utah, Salt Lake City.

VORHIES, C. T. 1917. Notes on the fauna of the Great Salt Lake. Amer. Nat. 51: 494–499.

WHITING, M. C., T. LESLIE, AND L. L. ST. CLAIR. 1974. The non-diatom algae of Utah Lake. Proc. Utah Acad. Sci., Arts, and Letters 51: 73–74.

WHITING, M. C., S. R. RUSHFORTH, AND J. D. BROTHERSON. 1978. Environmental interaction in summer algal communities of Utah Lake. Great Basin Nat. 38(1): 31–41.

WIRICK, C. D. 1972. *Dunaliella-Artemia* plankton community of the Great Salt Lake, Utah. Unpublished thesis, University of Utah, Salt Lake City.

WORKMAN, G. W., AND W. F. SIGLER. 1965. Net-plankton of the Bear Lake littoral zone, Utah-Idaho. Proc. Utah Acad. Sci., Arts, and Letters 42: 74–84.

YOUNG, O. W. 1947. Notes on periphyton of Ogden River, Utah. Proc. Utah Acad. Sci., Arts, and Letters 24: 137.

———. 1948. Observations on periphyton of Ogden River. Proc. Utah Acad. Sci., Arts, and Letters 25: 171–172.

ZAHL, P. A. 1967. Life in a "dead" sea—Great Salt Lake. Nat. Geogr. 132: 252–265.

ROZELLA PEARL BEVERLY BLOOD SMITH, 1911–1987

Hobart M. Smith[1]

ABSTRACT —The life, activities, and contributions of an energetic, catholic woman scholar, Rozella B. Smith, are reviewed. Her pioneer innovations in bibliographic data retrieval and mapping by use of the computer, creating a permanent niche for her in the annals of herpetology, are emphasized. A list of her publications is included.

On 15 December 1987 herpetology lost one of its most energetic, catholic women scholars of all time. Her name in herpetology was known largely from seven books and 69 articles shared with her husband, two popular ones of which she was sole author, and one booklet shared with a colleague at the University of Colorado. Numerous other publications and cataloged manuscripts that were never published brought her list of formal writings to 95.

Those writings, however seminal in part, were not her only qualifications as a scholar. Her interests were extremely broad, including medieval history, Shakespeare, Heinrich Boll, Hanseatic League, Upton Sinclair, the history of printing, European and English history, Russian icons, English literature, James Michener, Kenneth Roberts, Hervey Allen, Benedict Arnold, anatomy, neurology, histology, entomology, chemistry, languages, Richard III, Sherlock Holmes, Nero Wolfe, correlation indexing, computer graphics, fixed-field data retrieval, needlework (of prize-winning caliber), photography (professional quality), sewing, stamps, Indian jewelry, teaching, beadwork, music and art history, music itself (piano, recorder), art itself (considerable scientific illustration was done during undergraduate and graduate days), classical literature, bibliographic methods, cataloging techniques, Hieronymus Brunschweig, gardening, flower culture, mathematics, classical movies, Irish history, cooking, and no doubt other fields. Each was tackled with total commitment and exhaustive accumulation of reference works and materials (the extent of her stockpiling for future work almost surpasses belief) until its potential for stimulating discovery and learning diminished, whereupon some other topic was pursued with equal zeal. However, she often returned after a time to a subject previously abandoned, carrying it still further. She pursued her interests like one possessed—a perfect example of Aeschylus' proverb that "when a man is willing and eager, the gods join in." Perhaps they did, for she exhibited not only animated enthusiasm but often also an astonishing extrasensory perception and psychic/psychokinetic abilities.

An expert in so many areas and extremely articulate, she was a captivating and insuppressibly animated conversationalist and raconteur. With her extrovert personality, she would neither hesitate to speak to strangers nor shrink from extemporaneous public speaking. Not being a conventional thinker, but revealing an exuberant originality, she was the despair of conservatives, the joy of innovators.

Certainly she exercised diplomacy to a degree, but her normal way was to say what she thought, be it bluntly offensive or not. She could needle with the best but tended to shun irritating topics or people, in part because they tended to raise her always high blood pressure. A very calculating pragmatist, she was always conscious of where the power lay in her environment, what course would best serve her interests, and therefore what facade would be expedient. Highly intolerant of incompetence, she was very astute in choosing her friends and developing beneficial contacts, zeroing in on not only the seat of power but also of competence, meticulously avoiding those she regarded as "losers" and concentrating on "winners." She rarely made a

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Fig. 1. Rozella B. Smith, 1982.

mistake in that context. An insight into her modus operandi is provided by her detestation of Thomas Becket as an utter ass. However strongly negative she was in some contexts, she nevertheless could be a persuasive team-builder, lauding and promoting good will and cooperation, often in the face of contrary evidence and pressures.

These are attributes of indeed a complex person. She disliked multiple interactions because she saw herself as a different person with each friend or group. Indeed, she regarded herself as a multiple personality, and although no psychological extreme existed, her appraisal was probably correct. Too many antithetical facets of behavior were revealed to think otherwise. One would assume, for example, that her exuberant, articulate facade left no room for self-doubt; yet in reality she was intensely insecure, like Queen Elizabeth I, strongly dependent upon continual reassurance of the merit and excellence of her accomplishments. Lacking sufficient encouragement in one endeavor, she would seek another outlet for her energies that might be more rewarding of praise. To a considerable degree her peripatetic career and catholic interests were due to unfulfilled expectations of unceasing enlivenment. Yet she was always a commanding presence and exemplified the liberated woman when models were rare indeed.

But her claim to fame in herpetology and, more importantly, in general scientific endeavors came from her captivation with the intricacies and potentials of computer applications to fixed-field data manipulation and graphics. Her interest in that field began over 25 years ago, as computers were coming into being as a research tool in universities. She took related courses at the University of Illinois and helped with application of computer methods in cataloging materials as head cataloger in the library of the National Center for Atmospheric Research in Boulder, Colorado, in 1966. That work built upon the master's degree in library science she had obtained at the University of Illinois in 1963 and upon her work from 1963 to 1965 as bibliographer, Acquisitions Sections, Slavic Department, University of Illinois Library, Urbana. Several more months of experience in library automation were obtained in 1967 as acquisitions librarian in the Clendening Medical Library at the University of Kansas Medical Center in Kansas City.

Moving permanently to Boulder in 1968, she turned her creative originality to computerization of the enormous quantity of data accumulated over a period of nearly 30 years by her husband on the literature pertinent to Mexican herpetology. It was not an easy undertaking because most programmers consulted at that time were "number-crunchers" who had little experience or patience with the simplified (fixed-field) method of data retrieval and manipulation that she wanted. Attempts while at the University of Illinois got nowhere, but shortly after arriving at the University of Colorado she successfully ferreted out a brilliant programmer who could see her goal and, while grumbling some at first, provided her with the necessary techniques and programs. He eventually was enthusiastically converted to her philosophy and aims, for they were achieved with great success. She,

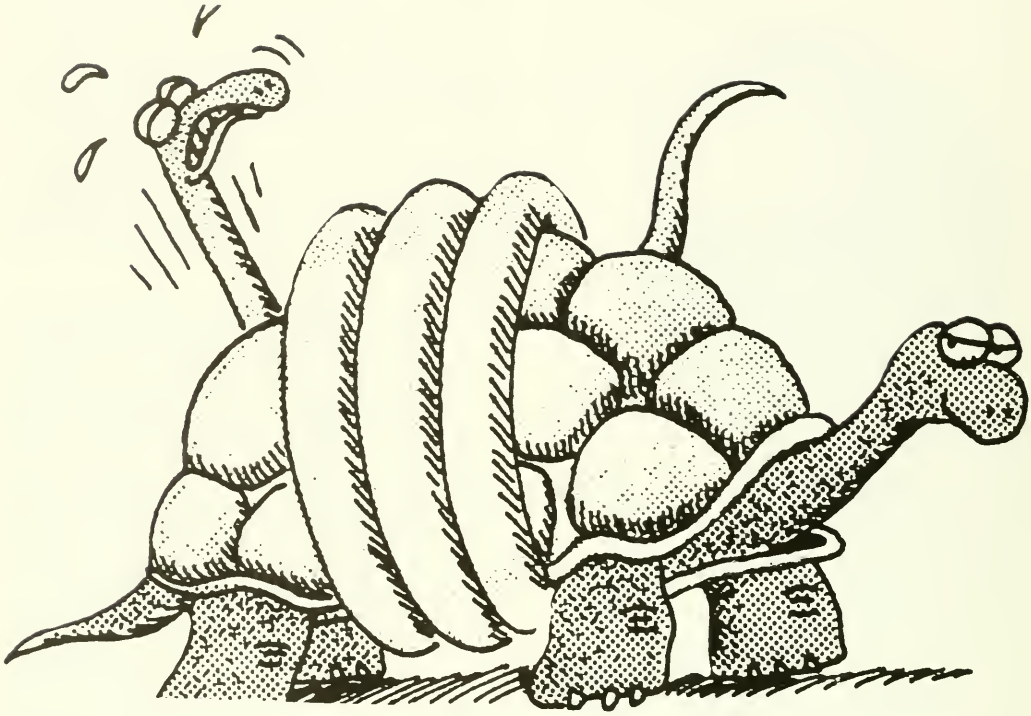

Fig. 2. An inspired representation adopted by Rozella Smith as her semi-heraldic symbol, portraying the exasperatingly Sisyphean struggle she (the snake) encountered in attempting to get anything out of some of her more important, seemingly smugly reluctant associates (the turtle). (Courtesy of the artist, Gary Larson, and the copyright owner, Frank Slavens.)

likewise, felt vindicated and took fully justified pride in having done it "my way," making Frank Sinatra's song by the same title her theme.

The skills she then developed in a wide variety of data manipulations were responsible for the plethora of indices and analyses in volumes one and two, both of which she typed, of the series she started, entitled "Synopsis of the Herpetofauna of Mexico." The same sort of data manipulation was involved in volumes three and four of that series, although both of those volumes were produced from computer output. Volumes five and six were produced with the help of a word processor. No other herpetological works have been so thoroughly analyzed and indexed as the volumes she prepared of the Mexican synopsis. The last volume, number six, contained probably her crowning achievement: numerous distribution maps prepared completely by computer. No other major work in herpetology has exploited the potential of computer-drawn, spot-distribution maps.

Throughout this time Rozella expanded her capabilities tremendously, supported continuously from 1971 to 1985 by grants from the National Library of Medicine and various divisions of the National Science Foundation. Numerous unpublished projects she completed demonstrated her versatility in data retrieval in English literature as well as biology. Indeed, her output capacity far exceeded assimilability. Several analyses of data on the herpetofaunal literature of Mexico were prepared but never published, and in her spare time she produced a complete concordance of all of the Sherlock Holmes corpus, plus several other concordances, none ever published under her name.

In the field of computerized data retrieval and graphics, she was an innovator considerably ahead of her time, initiating applications that established precedents yet to be approached by others. Her basic contribution

was to make accessible to innocent, inexperienced tyros some of the benefits of computer usage otherwise limited to experts.

She was clearly a workaholic. Approximately one million IBM cards were punched, 35 programs for recording and retrieving data were developed, and numerous others utilized. Much of her work that was never published should have been, including not only computer techniques and results of their application, but also highly original research papers written for graduate literature courses at the University of Illinois. Had she been blessed with better health in her final years she would no doubt have continued in her innovative ways and published more examples of her creativity.

As it was, she had unknowingly possessed an aneurysm on the left middle cerebral artery most of her life. It began leaking periodically in 1977, causing small strokes, from each of which she soon recovered. A CAT-scan taken in 1977 did not reveal the aneurysm, unfortunately, which continued occasionally to release blood through the brain tissue into the ventricles, partially occluding the aqueduct and producing a chronic condition of hydrocephalus. From that point on her health slowly but steadily deteriorated as the hydrocephalus became more pronounced and, in late summer of 1987, acute. Two operations, 30 September and 7 November, were followed by successful recovery until 11 December, when the first evidence, in the form of a nearly fatal pulmonary embolus, appeared of disseminated intravascular coagulation, a fatal complication of unknown origin. Although its effects were temporarily stemmed, on 14 December the condition became totally systemic and death followed the next day.

Born 18 May 1911 in Wichita, Kansas, to Charles Gillman Blood and Sarah Dorothy ("Dollie") Sherman (Shearman) Blood, half English and half Irish (the Kansas Blood family is famed in Irish circles), Rozella was the only child in her family. Little is known of the Blood side of the family, although one ancestor is known to have captained a river boat on the Mississippi. The Sherman side, however, included five sisters and one brother, who settled in various parts of Kansas and Colorado. Rozella's parents traveled widely in western United States during World War I, with stays in California, Oregon, Washington, Idaho, Utah, and Colorado, imprinting an affinity for the West that persisted throughout their daughter's life.

She graduated from Wichita High School in 1929, from the University of Wichita (Bachelor of Arts) in 1932 and (Master of Science, entomology) 1933, and from the University of Illinois (Master of Science, library science) in 1963. In addition, she attended the University of Kansas Medical School as a graduate student and assistant instructor in anatomy, neurology, and histology, serving also as staff artist, from 1933 to 1937. At the University of Illinois she was an unattached graduate student from 1953 to 1961. Numerous unrelated courses were audited or enrolled in throughout much of her postgraduate life. German was her favorite foreign language, in which she took enough courses for a degree; other languages studied, some intensively, were French, Spanish, Latin, Gothic, Arabic, Polish, and Czechoslovakian. She was awarded a teaching certificate in Kansas (teaching science and mathematics in Altoona High School, 1937–1938) and in Illinois (teaching ancient history in University High School, Urbana, 1965–1966). In conjunction with the latter she served also as a research associate, editing several experimental teaching manuals.

Thus, upon leaving Wichita for the University of Kansas in 1933, she moved to Altoona in 1937–1938; returned to Wichita to teach in the Department of Zoology in the summer of 1938; married Hobart M. Smith in Chicago, Illinois (Karl P. Schmidt and Howard K. Gloyd witnesses in a private ceremony), August 26, 1938; collected amphibians and reptiles throughout much of Mexico (over 20,000 specimens) under a Walter Rathbone Bacon Scholarship (1938–1940) awarded to her husband by the U.S. National Museum of Natural History; spent a year (1940–41) in Washington, D.C., while the collections of the preceding two years were being studied; lived in Rochester, New York, 1941–1945, while her husband was employed at the University of Rochester; in Lawrence, Kansas, for one semester, 1945; in Bryan, Texas, for one year (1946), incidental to her husband's stint at Texas A & M University; in Urbana and St. Joseph, Illinois, in connection with the University of Illinois, 1947–1968; and in Boulder,

Colorado, 1968–1987, with the University of Colorado.

At the University of Colorado her services included guidance to undergraduates, graduates, and faculty members in her own and other departments, and to affiliates of the Center for Computer Research in the Humanities, in techniques of her special forte of fixed-field data processing and retrieval, and of correlation indexing.

In August 1982 she received an honorary Doctor of Science degree from the University of Colorado in recognition of her seemingly infinite talents and creativity. The "Inventory of Live Reptiles and Amphibians in Captivity Current January 1, 1983," published in July 1983, was dedicated to her by the author, Frank Slavens. A month later the Society for the Study of Amphibians and Reptiles dedicated to her and her husband a symposium on Mexican biogeography held during a joint meeting with the Herpetologist's League. A forthcoming book on middle American herpetology by Drs. Jaime Villa R., Larry David Wilson, and Jerry D. Johnson is likewise so dedicated.

The memory of Rozella Smith will be perpetuated in the minds of the hundreds who knew or were influenced by her, including her small family: husband, Hobart M. Smith, Boulder, Colorado; son, Bruce Dyfrig (born 1943 in Rochester, New York), living with his family in Lakewood, Colorado; daughter-in-law, Dorothy Lee Tanner Smith; granddaughters Rebecca Rozella June and Elizabeth McKenzie Smith; daughter, Sally Frances Nadvornik (born 1946 in Bryan, Texas) living with her family in Lawrence, Kansas; son-in-law, Ronald Joe Nadvornik; and grandsons Patrick Joseph, Charles Ronald, and Gregory Lee Nadvornik. Also in her memory the Rozella Smith Research Fund has been established in her department (Environmental, Population and Organismic Biology) at the University of Colorado, supporting graduate student research of all types—a most fitting memorial to this most versatile scholar the department and herpetology have ever known. A personal memorial in her name has also been established at Boulder Memorial Hospital, where she spent the last ten weeks of her life among doctors, nurses, and technicians who became truly treasured friends and shared with her and her family the most poignant memories of her life.

At least four nominal species-group taxa bear the name *rozellae* in perpetuity: *Thamnophis rozellae* Smith, 1940 (= *T. marcianus praeocularis* [Bocourt, 1892]); *Celestus rozellae* Smith, 1942; *Hyla rozellae* Taylor, 1942 (= *Ptychohyla e. euthysanota* [Kellogg, 1923]); and *Tantillita lintoni rozellae* Pérez-Higareda, 1985.

FORMAL WRITINGS

Publications usually constitute the primary achievements of scholars. Although Rozella Smith's publications are collectively an impressive monument, they are a mere shadow of her enormously diverse productivities. That they are still of major significance is remarkable in itself. Yet she was quite cynical about the significance of publications per se, inasmuch as she pointed out that data retrieval methods could produce quantities of articles on varied facets of a limited subject, without contributing much. She was well aware that quantity has nothing to do with quality in publication and scorned those who sought quantity. In her disdain of quantity she unfortunately was not adequately motivated to make available numerous high-quality writings of her own.

A. Published

1. 1935. The anatomy of *Pyrota melabrina* (Chev.). J. N.Y. Ent. Soc. 43: 1–17, pls. 1–3. Rozella Blood.
2. 1937. (Abstract) Defective development of the cerebellum in the dog. Proc. Amer. Physiol. Soc. 49:18. Rozella Blood.
3. 1937. (Abstract) Chronic effects of nearly total ablation of the cerebellum. Proc. Amer. Physiol. Soc. 49: 154. O. O. Stoland, Richard Greer, and Rozella Blood.
4. 1941. Collecting Mexican amphibians and reptiles. Expl. Field Work Smithsonian Inst. 1940: 35–38, Figs. 38–41. Dr. and Mrs. Hobart M. Smith.
5. 1947. Herpetologist's holiday. Fauna 9(1): 18–22, ill. Rozella B. Smith.
6. 1947. Tropical mountain. Fauna 9(2): 53–57, ill. Rozella B. Smith.
7. 1959. A tribute to Margaret Scott. African Violet Leaves 5(2): 4–6, 1 fig. Rozella B. Smith.
8. 1965. First herpetological conference of the U.S.S.R. BioScience 15: 801–802 (reprinted 1966, Bull. Philadelphia Herpetological Soc. 14[1]: 1–3). Rozella B. Smith, Tom Lewis, and Hobart M. Smith.
9. 1967. Titles and selected abstracts of papers presented at the First Herpetological Conference of the U.S.S.R. Herp. Rev. (1): 3–8. Rozella B. Smith, Tom Lewis, and Hobart M. Smith.

10. 1969. The history of the herpetological section of the Senckenberg Natural History Museum and Research Institute in Frankfurt a. M. (including a list of types in the Museum). Bull. Maryland Herp. Soc. 5(1): 1–48, Figs. 1–12. Robert Mertens, Rozella B. Smith, and Hobart M. Smith.
11. 1969. Early foundations of Mexican herpetology: an annotated and indexed bibliography of the herpetological publications of Alfredo Dugès, 1826–1910. Urbana, Univ. Illinois Press. x, 85 pp., 3 figs. Hobart M. Smith and Rozella B. Smith.
12. 1970. Xolotl, twins and monsters. Bull. Philadelphia Herp. Soc. 17: 2–3. Frances M. Kranz, Hobart M. Smith, and Rozella B. Smith.
13. 1970. Polish contributions to the study of the axolotl. Bull. Philadelphia Herp. Soc. 17: 4–16, Fig. 1. Henryk Szarski, H. M. Smith, and R. B. Smith.
14. 1970. A review of the literature on osteology of the axolotl. Bull. Philadelphia Herp. Soc. 17: 17–28, Fig. 1. Rozella B. Smith and Hobart M. Smith.
15. 1970. Sources for axolotl myology. Bull. Philadelphia Herp. Soc. 17: 29–35, Fig. 1. Rozella B. Smith and Hobart M. Smith.
16. 1970. An analysis of the literature on the viscera and lymphatic system of the Mexican axolotl. Bull. Philadelphia Herp. Soc. 17: 36–46, Fig. 1. Rozella B. Smith and Hobart M. Smith.
17. 1970. Literature on the blood vascular system of the axolotl. Bull. Philadelphia Herp. Soc. 17: 47–52, Fig. 1. Rozella B. Smith and Hobart M. Smith.
18. 1970. J. G. Wood and the Mexican axolotl. J. Soc. Biblphy. Nat. Hist. 5: 362–365. H. M. Smith, G. E. Fawcett, J. D. Fawcett, and R. B. Smith.
19. 1971. Foundations of early modern Mexican herpetology: an indexed bibliography of the herpetological works of Walter Mosauer, 1905–1937. Trans. Kansas Acad. Sci. 73: 302–318, Figs. 1–2. Hobart M. Smith and Rozella B. Smith
20. 1971. An analytical survey of the literature on the endocrinology of the axolotl (Amphibia: Caudata). Trans. Kansas Acad. Sci. 73: 319–347, Fig. 1. Rozella B. Smith, David O. Norris, and Hobart M. Smith.
21. 1971. Interpretive essay on the eleventh book of the history of Sahagun. Bull. Philadelphia Herp. Soc. 18: 11–24, Figs. 1–11. Frances M. Kranz, Hobart M. Smith, and Rozella B. Smith.
22. 1971. Amphibians and reptiles of the codices and narrations of the ancient Mexicans. Bull. Philadelphia Herp. Soc. 18: 25–43, Figs. 1–18. F. M. Kranz, H. M. Smith, and R. B. Smith.
23. 1971. Synopsis of the herpetofauna of Mexico. Vol. I. Analysis of the literature on the Mexican axolotl. Augusta, W. Va., Eric Lundberg. xxviii, 245 pp., 6 figs. H. M. Smith and R. B. Smith.
24. 1972. The principles of distributional correlation and distributional specificity. Biologist 54: 8–10. H. M. Smith, R. B. Smith, and G. C. Bryce.
25. 1971. An analysis of Colorado Christmas counts. Amer. Birds 25: 945–947. Carl E. Bock and Rozella B. Smith.
26. 1972. (Abstract) Cultural influences upon herpetological research. J. Colo. Wyo. Acad. Sci. 7: 73–74. H. M. Smith and R. B. Smith.
27. 1973. Chresonymy ex synonymy. Syst. Zool. 21: 445. H. M. Smith and R. B. Smith.
28. 1973. Nominal taxa of recent amphibians and reptiles. I. Gymnophiona. Trans. Kansas Acad. Sci. 75: 52–99, Fig. 1. R. B. Smith and H. M. Smith.
29. 1973. Synopsis of the herpetofauna of Mexico. Vol. II. Analysis of the literature exclusive of the Mexican axolotl. Augusta, W. Va., Eric Lundberg. xxxiii, 367 pp., 6 figs. H. M. Smith and R. B. Smith.
30. 1973. (Abstract) Nominal taxa of recent amphibians and reptiles: a pilot project on caecilians. J. Colo. Wyo. Acad. Sci. 7: 45. R. B. Smith and H. M. Smith.
31. 1973. (Abstract) Perspectives of research as revealed by analysis of the literature on Mexican herpetology. J. Colo. Wyo. Acad. Sci. 7: 45. H. M. Smith and R. B. Smith.
32. 1973. (Review) Revision der Geckonidengattung *Phelsuma* Gray, 1825. Copeia 1973(3): 631–633. Hobart M. Smith and Rozella B. Smith.
33. 1974. (Abstract) The chresonymy of Mexican snakes and crocodilians. J. Colo. Wyo. Acad. Sci. 7(5): 79. Rozella B. Smith, Samuel S. Coleman, Hobart M. Smith, and H. Lewis Sawin.
34. 1975. (Abstract) Resurrection of a *nomen dubium* for an Asiatic skink, formerly thought to be American. J. Colo. Wyo. Acad. Sci. 7(6): 46. Hobart M. Smith, Rozella B. Smith, and Jean Guibe.
35. 1975. (Abstract) Resurrection of *Callopsis* Gray for American turtles formerly designated as *Geoemyda* or *Rhinoclemys*. J. Colo. Wyo. Acad. Sci. 7(6): 47. Hobart M. Smith, Rozella B. Smith, and H. Lewis Sawin.
36. 1975. The authorship and date of publication of *Siren intermedia* (Amphibia: Caudata). Great Basin Nat. 35(1): 100–102. Hobart M. Smith, Rozella B. Smith, and H. Lewis Sawin.
37. 1975. The identity of Bocourt's *Eumeces capito* 1879. Great Basin Nat. 35(1); 109–112, Figs. 1–4. Hobart M. Smith, Rozella B. Smith, and Jean Guibe.
38. 1975. An analysis of the knowledge of the turtle fauna of Mexico. Chelonia 2(3): 3–8. Hobart M. Smith and Rozella B. Smith.
39. 1975. Submerged-subject photography for preserved material. Bull. Chicago Herp. Soc. 10(1–2): 10–13, Figs. 1–4. Hobart M. Smith and Rozella B. Smith.
40. 1976. The generic name of the neotropical semiterrestrial emydine turtles. Trans. Kansas Acad. Sci. 77(4): 211–217. Hobart M. Smith, Rozella B. Smith, and H. Lewis Sawin.
41. 1976. Synopsis of the herpetofauna of Mexico. Vol. III. Source analysis and index for Mexican reptiles. North Bennington, Vt., John Johnson. 997 pp. Hobart M. Smith and Rozella B. Smith.
42. 1976. (Abstract) The higher categories in snake classification. J. Colo. Wyo. Acad. Sci. 8(1): 74. Hobart M. Smith, Rozella B. Smith, and H. Lewis Sawin.
43. 1976. The herpetological names of Herrera, 1899, and their status. Trans. Kansas Acad. Sci. 78(1–2): 85–87. Hobart M. Smith and Rozella B. Smith.
44. 1976. Synopsis of the herpetofauna of Mexico. Vol. IV. Source analysis and index for Mexican amphibians. North Bennington, Vt., John Johnson. 254 pp. Hobart M. Smith and Rozella B. Smith.
45. 1976. Request for suppression and validation of names related to the Elapidae. (Reptilia: Serpentes). Bull. Zool. Nomencl. 33(2): 73–84. Hobart M. Smith and Rozella B. Smith.

46. 1976. Another perspective on the Adventure of the Mazarin Stone. Baker St. J. (n.s.) 26(4): 213–216. David Chiszar, Rozella B. Smith, and Lorna Simonsen.
47. 1977. [Computer graphics design.] Community Free School Catalog of Courses 9(4): 31. Rozella B. Smith.
48. 1977. (Abstract) The two-legged amphisbaenid of the upper Balsas River Basin, Guerrero, Mexico. J. Colo. Wyo. Acad. Sci. 9(1): 44–45. Hobart M. Smith and Rozella B. Smith.
49. 1977. (Abstract) A bionumeric coding system for extant taxa. J. Colo. Wyo. Acad. Sci. 9: 46. Ronald D. Hochnadel, Hobart M. Smith, and Rozella B. Smith.
50. 1977. Synopsis of the herpetofauna of Mexico. Vol. V. Guide to Mexican amphisbaenians and crocodilians. Bibliographic addendum II. North Bennington, Vt., John Johnson. 191 pp., ill. Hobart M. Smith and Rozella B. Smith.
51. 1977. A summary of snake classification. J. Herpet. 11(2): 115–121. H. M. Smith, Rozella B. Smith, and H. Lewis Sawin.
52. 1977. An overlooked synonym of the giant toad *Bufo marinus* (Linnaeus) (Amphibia, Anura, Bufonidae). J. Herpet. 11(4): 423–425. H. M. Smith, Thomas Schneider, and Rozella B. Smith.
53. 1977. [Computer graphics designs.] Digit 12(5): 11, Figs. 1–2.
54. 1978. Bionumeric codes for amphibians and reptiles of the world. I. Salamanders. Trans. Kansas Acad. Sci. 81(1): 43–56. Arden H. Brame, Jr., Ronald Hochnadel, H. M. Smith, and Rozella B. Smith.
55. 1978. Rate of acceretion of taxonomic nomenclatural errors in the postlinnaean literature on Mexican amphibians. J. Herpet. 12(3): 337–341. H. M. Smith, David Chiszar, and Rozella B. Smith.
56. 1979. *Coluber chiametla* Shaw, 1802 (Reptilia, Serpentes): revived proposal for suppression under the plenary powers. Bull. Zool. Nomencl. 35(3): 184–185. Hobart M. Smith and Rozella B. Smith.
57. 1979. Depicting the geographic range of various species of flora and fauna using computer graphics. Digit (Univ. Colorado Computing Center) 14(3): 4–5, Figs. 1–4. Rozella B. Smith and Hobart M. Smith.
58. 1979. (Abstract) Current resources for the study of turtles of Mexico. J. Colo. Wyo. Acad. Sci. 10(1): 45. H. M. Smith and Rozella B. Smith.
59. 1979. (Abstract) The status of an overlooked work by Rafinesque (1822) on turtles of the United States. J. Colo. Wyo. Acad. Sci. 11(1): 83–84. H. M. Smith, David Chiszar, and Rozella B. Smith.
60. 1980. Synopsis of the herpetofauna of Mexico. Vol. VI. Guide to Mexican turtles, bibliographic addendum III. North Bennington, Vt., John Johnson. xviii, 1,044 pp., 46 maps, 64 figs. (1979). H. M. Smith and Rozella B. Smith.
61. 1980. Comment on application for suppression and validation of elapid snake names. Bull. Zool. Nomencl. 36(4): 199–200. H. M. Smith and Rozella B. Smith.
62. 1980. Herrera's formulae are not names. Proposed Direction supplementary to Direction 32. Bull. Zool. Nomencl. 36(4): 246–248. Hobart M. Smith and Rozella B. Smith.
63. 1980. Rafinesque, 1822, "On the turtles of the United States" (Reptilia, Testudines): proposed suppression by use of the plenary powers. Bull. Zool. Nomencl. 37(1): 53–56. Hobart M. Smith, David Chiszar, and Rozella B. Smith.
64. 1980. *Sternotherus* Gray, 1825, correct spelling; and *Pelusios* Wagler, 1830, proposed conservation (Reptilia, Testudines). Bull. Zool. Nomencl. 37(2): 124–128. Hobart M. Smith, Rozella B. Smith, and David Chiszar.
65. 1981. *Geocmyda* Gray, 1834, and *Rhinoclemmys* Fitzinger, 1835 (Reptilia, Testudines): proposed conservation. Bull. Zool. Nomencl. 37(4): 233–239. Hobart M. Smith, Carl H. Ernst, and Rozella B. Smith.
66. 1981. *Testudo scripta* Schoepff, 1792: *Emys cataspila* Günther, 1885: Proposed conservation (Reptilia, Testudines). Bull. Zool. Nomencl. 37(4): 240–246. John M. Legler, Hobart M. Smith, and Rozella B. Smith.
67. 1981. Another epiphytic alligator lizard (*Abronia*) from Mexico. Bull. Maryland Herpet. Soc. 17(2): 51–60, Figs. 1–3. Hobart M. Smith and Rozella B. Smith.
68. 1982. (Review) Axolotls. Peter W. Scott. Bull. Philadelphia Herp. Soc. 28: 24–27. Hobart M. Smith and Rozella B. Smith.
69. 1982. Support for the proposed conservation of Teiidae Gray, 1827. Bull. Zool. Nomencl. 39(3): 157–178. Hobart M. Smith and Rozella B. Smith.
70. 1982. Nero Wolfe: herpetologist. Gazette (J. of the Wolfe Pack) 1(3): 1–7, Fig. 1. Hobart M. Smith and Rozella B. Smith.
71. 1982. [Letter to the Editor.] Kansan questions. Gazette (J. of the Wolfe Pack) 1(3): 69. Rozella B. Smith.
72. 1982. Fifty years of herpetology: publications of Hobart M. Smith. North Bennington, Vt., John Johnson. v, 78 pp., frontis. David Chiszar and Rozella B. Smith.
73. 1983. (Abstract) National responsibility for maturation of Mexican herpetology. Abstr. SSAR-HL Mtg., Salt Lake City, Utah: 91. Hobart M. Smith and Rozella B. Smith.
74. Comparison of regional taxonomic densities. Bull. Philadelphia Herp. Soc. 29: 9–13, Fig. 1. Hobart M. Smith, David Chiszar, and Rozella B. Smith.
75. 1983. The history of the concept of viviparity in the alligator lizard genus *Barisia*. Herp. Rev. 14(2): 34–35. Hobart M. Smith, Michael J. Preston, and Rozella B. Smith.
76. 1984. The specific name of the ground skink of North America. Bull. Maryland Herp. Soc. 19(4): 100–104. Hobart M. Smith, Michael J. Preston, and Rozella B. Smith.
77. 1984. The herpetological works of Jacob Klein, with emphasis on their pertinence to Mexican herpetology. Bull. Maryland Herp. Soc. 20(4): 174–189, Figs. 1–2. John Johnson, Malvin L. Skaroff, Hobart M. Smith, and Rozella B. Smith.
78. 1984. The herpetology of Herman Melville's Moby Dick. Bull. Philadelphia Herp. Soc. 30: 9–14. Hobart M. Smith and Rozella B. Smith.
79. 1984. *Chelydra osceola* Stejneger, 1918 (Reptilia, Testudines): proposed conservation by use of the plenary powers. Bull. Zool. Nomencl. 40(4): 225-227. Hobart M. Smith, Rozella B. Smith, and David Chiszar.
80. 1985. A brief review of the career and writings of T. Paul Maslin, 1909–1984. Bull. Maryland Herp.

Soc. 21(1): 45–56, Fig. 1. Hobart M. Smith and Rozella B. Smith.

81. 1985. A new species of *Tantilla* from Veracruz, Mexico. J. Herp. 19(2): 290–292, Figs. 1–2. Gonzalo Pérez-Higareda, Hobart M. Smith, and Rozella B. Smith.
82. 1986. The growth of primate field studies. Pages 73–91, Figs. 1–10, *in* G. Mitchell and J. Erwin, eds., Comparative primate biology. Vol. 2A. Behavior, conservation and ecology. New York, Alan R. Liss. Charles H. Southwick and Rozella B. Smith.
83. 1987. Concording turtle names: an illustration of computer-assisted analysis of scientific names. Bull. Philadelphia Herp. Soc. 31: 2–19. Michael J. Preston, Rozella B. Smith, and Hobart M. Smith.

B. Unpublished

(All in multiple copy form, available from the sponsoring organization.)

1. 1965. An annotated bibliography for students. Geography. Soc. Sci. Curr. Study Center, Univ. High School, Urbana, Ill. 5 pp.
2. 1965. Annotations. Soc. Sci. Curr. Study Center, Univ. High School, Urbana, Ill. 5 pp.
3. 1965. A brief survey of the history of Russian icons. Soc. Sci. Curr. Study Center, Univ. High School, Urbana, Ill. 5 pp.
4. 1965. A brief list of journal articles on Peru and the Incas. Soc. Sci. Curr. Study Center, Univ. High School, Urbana, Ill. 5 pp.
5. 1965. A selected list of books in the University of Illinois Library on Peru and the Incas. Soc. Sci. Curr. Study Center, Univ. High School, Urbana, Ill. 5 pp.
6. 1965. Greece. Emergence. Soc. Sci. Curr. Study Center, Univ. High School, Urbana, Ill. 8 pp.
7. 1965. The history of Greece. Soc. Sci. Curr. Study Center, Univ. High School, Urbana, Ill. 127 pp.
8. 1965. Organization of the materials presently being collected for the Social Sciences Curriculum Study Center, Univ. High School, University of Illinois. Soc. Sci. Curr. Study Center, Univ. High School, Urbana, Ill. 11 pp.
9. 1965. Selected events leading to the rise of Moscow. Soc. Sci. Curr. Study Center, Univ. High School, Urbana, Ill. 15 pp.
10. 1966. A sorting program for processing bibliographic data. NCAR unpubl. mss. (225): 1–4.
11. 1966. Analysis of Dewey, LC and UDC numbers in a sample of 500 books in the NCAR Library. NCAR unpubl. mss. (227): 1–2.
12. 1966. A graphic representation of the content of the NCAR Library book collection. NCAR unpubl. mss. (231): 1, graph.
13. 1966. A flowchart of procedures in relabeling the books in the NCAR Library. NCAR unpubl. mss. (232): 1–5.

C. In Preparation

(Several manuscripts on the Sherlock Holmes corpus are to be completed under joint authorship with David Chiszar but are not now sufficiently near finalization to list titles.)

1. Stimulus representations and imagery processes in animals. David Chiszar and Rozella B. Smith.

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Hundreds of people have contributed importantly to the career of Rozella Smith and its brief review here. Preeminent professionally in recent years are Jane Bock, William Briggs, David Chiszar, Sam Coleman, Jerolyn and Richard Holland, Betty and John Johnson, William Lewis, Milton Lipetz, Sally Nadvornik, Michael Preston, Lewis Sawin, and Bruce Smith. To all I am very grateful.

NOMENCLATURAL CHANGES AND NEW SPECIES OF SCOLYTIDAE (COLEOPTERA), PART II

Stephen L. Wood[1]

ABSTRACT.—The following new synonymy is proposed: *Halystus* Schedl (= *Phlocographus* Wood), *Hylesinopsis* Eggers (= *Aridiamerus* Schedl), *Halystus namibiae* Schedl (= *Phlocographus namibiae* Wood), *Ips stebbingi* Strohmeyer (= *Tomicus blandfordi* Stebbing), *Olonthogaster (Hylurgus) concinnulus* (Walker) (= *Olonthogaster nitidifrons* Motschulsky), *Olonthogaster nitidicollis* Motschulsky (= *Hyledius asper* Sampson), *Polygraphus longifolia* Stebbing (= *Polygraphus himalayensis* Stebbing), *Pseudochramesus harringtoni* Blackman (= *Pseudochramesus multiseriatus* Schedl), *Pseudodiamerus obscurus* Eggers (= *Phloeoditica obscura* Schedl, 1962, and *Phloeoditica obscura* Schedl, 1963), *Xylechinosomus brasiliensis* (Schedl) (= *Xylechinosomus araucariae* Schedl), *Xylechinus (Pseudochramesus) imperialis* (Schedl), new combination (= *Xylechinus calvus* Schedl). The following species are named as new to science: *Aphanarthrum indicum* (India), *Aphanarthrum reticulatum* (India), *Aphanarthrum royaleanum* (India), *Bothinodroctonus indicus* (India), *Bothinodroctonus setosus* (Andaman Islands), *Carphoborus lautus* (India), *Liparthrum artocarpus* (India), *Liparthrum tinianesis* (Tinian Island), *Polygraphus anogeissi* (India and Burma), *Polygraphus difficilis* (India and Pakistan), *Polygraphus querci* (Burma).

On the following pages are presented 2 cases of new generic synonymy, 9 cases of new specific synonymy, 1 new combination, and 11 species new to science. These items are necessary nomenclatural housekeeping discovered during the preparation of a new world catalog of Scolytidae and are published here to facilitate citation for the catalog. The new synonymy affects species from Africa, southeastern Asia, and South America. The species new to science represent the genera *Aphanarthrum* (3), *Bothinodroctonus* (2), *Carphoborus* (1), *Liparthrum* (2), and *Polygraphus* (3). They are from the following countries or areas: India (8), Burma (2), Pakistan (1), Tinian Island (1), Andaman Islands (1).

NEW SYNONYMY

Halystus Schedl

Halystus Schedl, 1982, Ann. Transv. Mus. 33(15):283 (Type-species: *Halystus namibiae* Schedl, monobasic)

Phlocographus Wood, 1984, Great Basin Nat. 44(2):229 (Type-species: *Phlocographus namibiae* Wood = *Halystus namibiae* Schedl, original designation. *New synonymy of genus and species*

Schedl had the habit of placing manuscript names on undescribed species in his collection and then describing them at a subsequent date. On several occasions such names appeared repeatedly in the literature but were never validated. When the holotype of *Halystus namibiae* Schedl was found in his collections in 1981, two years after his death, it was assumed that this was another nomen nudum. When no record of its publication had been found by 1984, either by myself or by the Wien Museum staff, it was decided to publish the genus and species in order to make it available for my generic study (Wood 1986). The validation of Schedl's name was found within days after the generic study was printed. Both *Halystus namibiae* Schedl and *Phlocographus namibiae* Wood were based on the same female specimen in the Schedl Collection at the Wien Museum; consequently, they are objective synonyms of one another.

Hylesinopsis Eggers

Hylesinopsis Eggers, 1920, Ent. Blätt. 16(1–3):40 (Type-species: *Hylesinopsis dubius* Eggers, monobasic)

Aridiamerus Schedl, 1982, Ann. Transv. Mus. 33(15):284 (Type-species: *Aridiamerus angolensis* Schedl, monobasic). *New synonymy*

The holotype of *Aridiamerus angolensis* Schedl was examined and found to represent a species of *Hylesinopsis*. For this reason,

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Schedl's genus is placed in synonymy as indicated above.

Ips stebbingi Strohmeyer

Ips stebbingi Strohmeyer, 1908, Ent. Rundschau 25:69 (Syntypes, male; Kulu, Himalaya occidentalis, *Cedrus deodara;* Strohmeyer Collection)

Tomicus blandfordi Stebbing, 1909, Indian For. Mem. 1(2):27 (Syntypes, 3, female; Shinghar Chilgaza forests, North Zhob, Baluchistan, Pakistan; Forest Research Institute, Dehra Dun). *New synonymy*

At the Forest Research Institute, Dehra Dun, I found three female syntypes of *Tomicus blandfordi* Stebbing and one syntype of *Ips stebbingi* Strohmeyer. The comparison of these specimens to one another and to a long series of this species clearly indicates that only one species is represented. For this reason, Stebbing's name must be placed in synonymy as indicated above.

This species should not be confused with *Ips longifolia* Stebbing, which is quite distinct.

Olonthogaster concinnulus (Walker)

Hylurgus concinnulus Walker, 1859, Ann. Mag. Nat. Hist. (3)3:261 (Holotype, male; Ceylon; British Museum, Natural History)

Olonthogaster nitidifrons Motschulsky, 1866, Bull. Soc. Imp. Nat. Moscow 39:402 (Holotype, male; Ceylon; Institute of Zoology, Academy of Science, Moscow). *New synonymy*

The male holotypes of *Hylurgus concinnulus* Walker and *Olonthogaster nitidifrons* Motschulsky were examined and compared to a series I collected in Ceylon. There is no doubt whatever that these specimens all represent the same species that is common in *Myristica dactyloides*. The Motschulsky name is here placed in synonymy as indicated above.

Olonthogaster nitidicollis Motschulsky

Olonthogaster nitidicollis Motschulsky, 1866, Bull. Soc. Imp. Nat. Moscow 39:401 (Holotype, male; Ceylon; Institute of Zoology, Academy of Science, Moscow)

Hyledius asper Sampson, 1921, Ann. Mag. Nat. Hist. (9) 7:35 (Holotype, male; Luang Prebang, Houei Ko; British Museum, Natural History). *New synonymy*

The male holotypes of *Olonthogaster nitidicollis* Motschulsky and *Hyledius asper* were examined and compared to several examples from southeastern Asia, New Guinea, and Ceylon. Although minor variation is present, all are considered to represent the same species. For this reason, Sampson's species is here placed in synonymy as indicated above.

Polygraphus longifolia Stebbing

Polygraphus longifolia Stebbing, 1902, Departmental notes on insects that affect forestry, Supt. Doc., Gov. Printing, Calcutta, p. 255 (Holotype, female; labeled as Tons Valley, Tehri Garhwal, U.P., India, published as NW Himalayas, Beshahr. St.; Taklesh; Gaunsar Div.; Tehri-Garhwal; Forest Research Institute, Dehra Dun)

Polygraphus himalayensis Stebbing, 1908, Indian For. Mem. 1(1):8 (Holotype, male; labeled as Ringali, Chakrata, U.P., India, published as North-Western Himalayan Forests; Forest Research Institute, Dehra Dun). *New synonymy*

The female holotype of *Polygraphus longifolia* Stebbing, the male holotype of *P. himalayensis* Stebbing, and more than 300 other examples of this species were examined at the Forest Research Institute. From this material it is evident that the two holotypes represent the two sexes of this common species.

Pseudochramesus harringtoni Blackman

Pseudochramesus harringtoni Blackman, 1939, Rev. de Ent. 10(1):93 (Holotype, male; Aguio, Bolivia; U.S. National Museum)

Pseudochramesus multiseriatus Schedl, 1978, Entomol. Abh. Mus. Tierk. Dresden 41(8):296 (Holotype, female; Argentinien, Tablillas Salta; Schedl Collection in Wien Museum). *New synonymy*

The type series, including the male holotype, of *Pseudochramesus harringtoni* Blackman were compared to my series of this species and were found to be identical. These specimens were then compared to the female holotype of *Pseudochramesus multiseriatus* Schedl. Because only one species is represented by these specimens, Schedl's name is here placed in synonymy as indicated above.

Pseudodiamerus obscurus Eggers

Pseudodiamerus obscurus Eggers, 1943, Entomologische Blätt. 39:72 (Syntypes, sex?; Mozambique [La Pery; Chimoio]; Paris Museum and 2 in Eggers Collection, Eggers' 2 syntypes on loan to Schedl)

Phloeoditica obscura Schedl, 1962, Verhandl. Naturf. Ges. Basel 73(1):189 (Holotype, sex?; Basutoland; Schedl Collection, preoccupied). *New synonymy*

Phloeoditica obscura Schedl, 1963, Entom. Abh. Ber. Mus. Tierk. Dresden 28(6):261 (Holotype, sex?;

Basutoland; Schedl Collection, preoccupied). *New synonymy*

For reasons not at all apparent, Schedl (1962:189) described a preoccupied genus, *Phloeoditica*, and then assigned the species *obscura* to it. A year later Schedl (1963:261) again named the same specimens *Phloeoditica obscura*. These were placed in his collection immediately behind the two Eggers cotypes with the note that they were the same. The genus *Phloeoditica* of Eggers, from southeastern Asia, is entirely unrelated. Both of Schedl's names must be transferred to *Pseudodiamerus* and must receive a masculine spelling. This makes them both junior homonyms as well as junior synonyms of the Eggers species as indicated above.

Xylechinosomus brasiliensis (Schedl)

Pseudohylesinus brasiliensis Schedl, 1951, Dusenia 2:95 (Syntypes, sex?; Brasilien, Santa Catarina, Nova Teutonia; Schedl and Plaumann collections)
Xylechinosomus araucariae Schedl, 1963, Reichenbachia 1:210 (Holotype, male; Brasilien: Santa Catarina, Nova Teutonia). *New synonymy*

The Schedl syntypes of *Pseudohylesinus brasiliensis* Schedl were compared directly to the male holotype *Xylechinosomus araucariae* Schedl and were found to represent only one species. The junior name is here placed in synonymy as indicated above.

Xylechinus imperialis (Schedl), n. comb.

Pseudochramesus imperialis Schedl, 1958, Acta Zool. Lilloana 16:39 (Lectotype, male; Argentinien: Buenos Aires: Tigre; Wien Museum, designated by Wood 1986:268)
Xylechinus calvus Schedl, 1978, Acta Zool. Lilloana 33:60 (Holotype, male; publication not seen; Schedl Collection in Wien Museum). *New synonymy*

The Schedl syntypes of *Pseudochramesus imperialis* Schedl were examined and found to represent the genus *Xylechinus*. They were compared directly to the male holotype of *Xylechinus calvus* Schedl and found to be identical. It is, therefore, necessary to transfer *imperialis* to *Xylechinus* and to place *calvus* in synonymy under the senior name as indicated above.

NEW TAXA

Aphanarthrum indicum, n. sp.

The three species of *Aphanarthrum* named here are the first species of this genus known from this far east in Asia. The species *indicum* is distinguished from the other two by the impressed elytral declivity, by the larger, deeper strial and interstrial punctures, and by the more strongly, broadly elevated costa on the anterior margin of the pronotum.

MALE.—Length 2.0 mm (paratypes 1.5–2.1 mm), 2.4 times as long as wide; color light brown with variable, yellowish brown markings on elytra, vestiture pale.

Frons transversely convex, longitudinally almost flat from epistoma to upper level of eyes; surface apparently smooth, shining, and closely, rather coarsely punctured; vestiture of fine, rather short, inconspicuous hair.

Pronotum 1.2 times as long as wide; widest behind middle, sides rather weakly arcuate on posterior half, strongly converging to narrowly rounded anterior margin; median part of anterior margin acutely costate; summit indefinite, behind middle; surface on posterior four-fifths smooth, shining, uniformly very closely, rather coarsely punctured, interspaces equal to less than diameter of a puncture, anterior fifth reticulate and with punctures replaced by very small granules; vestiture of fine, short, abundant hair.

Elytra 1.3 times as long as wide, 1.2 times as long as pronotum; sides almost straight and parallel on more than basal half, very broadly rounded behind; striae not impressed, punctures distinct, rather small, not deep, in definite rows; interstriae smooth, shining, punctures in rows, only slightly smaller and spaced similar to those of striae. Declivity steep, subconcavely impressed between interstriae 3; sculpture similar to that on disc. Vestiture of rather abundant, moderately short, fine, strial and interstrial hair uniformly distributed, except reduced on lower declivity.

FEMALE.—Similar to male except costa on anterior margin of pronotum reduced and largely replaced by a single, median serration; impression on declivity greatly reduced, very weak.

TYPE MATERIAL.—The male holotype, female allotype, and 13 paratypes were taken at Chikalda, Melghat, C.P., India, 9-XI–1936, R.R.D. 106, B.C.R. 181, Cage 660, ex *Euphorbia* sp., by N. C. Chatterjee. The holotype (uppermost), allotype (lowermost), and 1 paratype (middle) are all mounted on the same pin that is in the Forest Research

Institute, Dehra Dun. The remaining 12 paratypes are in my collection. About 200 additional specimens are at the FRI.

Aphanarthrum reticulatum, n. sp.

This species is distinguished from *royaleanum* by the dull, pseudoreticulate pronotal and elytral surfaces, by the smaller, confused elytral punctures, and by the subangulate anterior margin of the pronotum.

MALE.—Length 1.7 mm (paratypes 1.6–1.9 mm), 2.4 times as long as wide; color pale yellowish brown, darker brown spots at middle of pronotum, at humeral angles (2), at middle of elytra (4), and on lower declivity (2), vestiture pale.

Frons about as in *royaleanum*.

Pronotum as in *royaleanum* except anteromedian costa obsolete, replaced by one median, strong serration; surface reticulate throughout; color primarily yellowish brown with a dark, transverse mark near middle.

Elytra similar to *royaleanum* except surface uniformly reticulate, punctures confused, not in rows.

FEMALE.—Similar to male except anterior margin of pronotum more narrowly produced into a slightly larger median denticle.

TYPE MATERIAL.—The male holotype, female allotype, and 4 paratypes are from Hunsur, Mysore, India, 10-VII–1930, ex *Euphorbia* sp., by C.F.C. Beeson; 3 paratypes are labeled near Hunsur, Mysore, Madras, 28-VII–1930, R.R.D. 149, B.C.R. 203, Cage 804, ex *Euphorbia* sp., C.F.C. Beeson; 3 paratypes are labeled 4,000′, Mussoorie, U.P., India, 7-IV–1934, ex *Euphorbia royaleana*, G. D. Bhasin. The holotype (lowermost), allotype (middle), and 1 paratype (uppermost) are all mounted on the same pin that is in the Forest Research Institute, Dehra Dun. The remaining 9 paratypes are in my collection. About 70 additional specimens are at the FRI.

Aphanarthrum royaleanum, n. sp.

The species is distinguished from *reticulatum* by the shining pronotal and elytral surfaces, by the strial and interstrial rows of punctures, and by the more broadly rounded anterior margin of the pronotum.

MALE.—Length 1.7 mm (paratypes 1.5–1.7 mm), 2.4 times as long as wide; color light brown except elytra pale yellowish brown with darker markings on costal margin, declivity, and near middle of disc, vestiture pale.

Frons resembling *indicum* except surface subreticulate, punctures small to obsolete, vestiture inconspicuous.

Pronotum 1.2 times as long as wide; as in *indicum* except granules on anterior slope larger, more numerous; punctures on posterior half very small, each with a rounded granule on its lateral or posterior margin; reticulate in anterior and lateral areas.

Elytra 1.3 times as long as wide; as in *indicum* except outline more narrowly rounded behind, elytral punctures slightly smaller, in more definite rows, declivity convex (without any impression).

FEMALE.—As in male except sexual differences on pronotum as in *indicum*.

TYPE MATERIAL.—The male holotype, female allotype, and 1 paratype are from Chikalda, Malghat, C.P., India. 14-XI–1936, R.R.D. 106, B.C.R. 181, Cage 660, ex *Euphorbia* sp., by N. C. Chatterjee; 9 paratypes are labeled Sulphur Spring, Dehra Dun, U.P., India, 11-VIII–1930 or 6-VIII–1930, R.R.D. 147, B.C.R. 202, *Euphorbia royaleana*, B. M. Bhatia. The holotype (lowermost), allotype (middle), and 1 paratype (uppermost) are all mounted on the same pin in the Forest Research Institute, Dehra Dun. The remaining 9 paratypes are in my collection. About 150 additional specimens are at the FRI.

Bothinodroctonus indicus, n. sp.

This species is distinguished from *bicinctus* Schedl by the much shorter frontal vestiture on the female, by the absence of pronotal granules, by the more distinctly punctured striae, by the absence of granules on discal interstriae, and by the much stronger declivital impression, elytral scales much less abundant to obsolete, erect setae more slender.

MALE.—Length 2.1 mm (paratypes 1.8–2.4 mm), 2.1 times as long as wide; color almost black, vestiture pale.

Frons profoundly excavated and armed as in *bicinctus* except almost glabrous.

Pronotum similar to *bicinctus* except surface smooth, shining, closely, rather coarsely punctured, granules reduced to about 4 to 6 near middle; vestiture very sparse, slender.

Elytra resembling *bicinctus* except strial

punctures distinctly impressed, punctures small, shallow, close; interstriae about four times as wide as striae, smooth, shining, punctures only slightly smaller than those of striae, confused. Declivity moderately steep, broadly impressed, almost flat between interstriae 3 (1 not elevated as in *bicinctus*); striae not evident, punctures confused; interstriae 3 each armed by three or four small granules; lateral margin from interstriae 7 to sutural apex strongly, acutely elevated (explanate somewhat as in *Ips*), crest armed by about five obtuse tubercles (elevation much stronger than in *bicinctus*). Ground vestiture obsolete; interstriae on and near declivity each with a sparse row of erect, rather stout setae.

FEMALE.—Similar to male except frons moderately concave, vertex not modified, surface apparently closely punctured, covered by a dense tuft of long, yellow hair, hair much longer on lateral and upper margins; pronotum with sparse, slender hair; elytral declivity steeper, much less strongly impressed, ventrolateral margin less strongly elevated, sparse granules also on interstriae 1 and 2, vestiture in interstrial rows attains base, longer, much more slender.

TYPE MATERIAL.—The male holotype, female allotype, and six paratypes are labeled Tavargati, Belgaum Div., Bombay, 28-X–29, *Odina wodier*, B. M. Bhatia, except two paratypes bear the date 27-X–29. Specimens from Bengal (India) and Sri Lanka have been seen, but were not at hand.

The holotype and allotype are in the Forest Research Institute; the paratypes are in my collection.

Bothinodroctonus setosus, n. sp.

This unique species is distinguished by the reddish brown color, by the more abundant, shorter female frontal vestiture, by the more narrowly impressed elytral declivity, and by the larger spines on the posterolateral area of the declivity.

FEMALE.—Length 1.7 mm, 2.2 times as long as wide; color reddish brown, vestiture pale.

Frons shallowly concave on central half; surface closely, rather finely punctured; vestiture of dense, erect, rather stout setae of uniform length, about half as long as in *indicus*.

Pronotum 1.3 times as long as wide; widest on basal third, sides weakly arcuate, converging slightly to very broadly rounded anterior margin; vestiture of erect scales, each about twice as long as wide, and fine hair.

Elytra 1.6 times as long as wide; sides almost straight and parallel on slightly more than basal two-thirds, rather broadly rounded behind, posterolateral profile interrupted by tubercles; striae not impressed, punctures rather coarse, moderately deep, very close; interstriae less than twice as wide as striae, shining, each armed by a uniseriate row of very closely set, low, rounded nodules (almost as wide as an interstriae) except on 2, these nodules confused on posterior half of disc. Declivity steep, impressed between striae 2; interstriae 1 and 2 with tubercles suppressed, 1 feebly elevated, 3 much more strongly elevated on lower half, this crest continuing with 7 to suture; tubercles becoming pointed on 3 to 9, those along 7 to suture moderately large. Vestiture of rather sparse, short, strial and interstrial hair, and rows of longer, erect scales, each scale about four times as long as wide and about two-thirds as long as distance between rows.

TYPE MATERIAL.—The female holotype is labeled North Andaman, 30-III–30, *Canarium euphyllum*, C.F.C. Beeson. It is in my collection.

Carphoborus lautus, n. sp.

This species is distinguished from *boswelliae* (Stebbing) by the much stouter body form, by the small, shallow, distinct, strial punctures, by the presence of small tubercles on declivital interstriae 1 and 3, and by the less strongly impressed female frons that is armed by a conspicuous, subcarinate, median tubercle, with setae on lateral and upper margins shorter. All published citations to *boswelliae* except those by Stebbing are to this species. The name *lautus* was used by Beeson as a nomen nudum for this species.

FEMALE.—Length 1.8 mm (paratypes 1.6–2.0 mm), 2.0 times as long as wide (2.2 times in *boswelliae*); color rather pale brown, vestiture pale.

Frons broadly, shallowly impressed on lower two-thirds, armed on upper third by a conspicuous, subcarinate, median tubercle; surface smooth, shining, punctures very abundant, small; vestiture shorter in central area, longer on lateral and upper margins, distance from eye to lateral fringe equal to

three times diameter of a facet of eye (in *boswelliae* frons shallowly concave, tubercle absent, eye separated from lateral fringe by six diameters of a facet).

Pronotum 0.74 times as long as wide; outline somewhat semicircular; surface subreticulate, punctures fine, small, close; vestiture of small, erect scales.

Elytra 1.3 times as long as wide; sides almost straight and parallel on basal half, broadly rounded behind; striae 1 feebly others not impressed, punctures small, shallow, distinct (largely obsolete in *boswelliae*); interstriae about six times as wide as striae, smooth, shining, a few impressed lines, punctures small, close, confused. Declivity steep, convex; sculpture about as on disc except interstriae 1 and 3 each with a row of small, pointed tubercles, a few similar tubercles on 5, 7, and 9. Vestiture of minute, strial hair and erect, small, interstrial scales.

MALE.—Similar to female except frons more nearly convex, median tubercle higher, more sharply pointed, frontal vestiture inconspicuous.

TYPE MATERIAL.—The female holotype, male allotype, and two paratypes were taken at Baihar, Balaghat, C.P., G.D., 7-VIII–1927, ex bark *Boswellia serrata*; 3 paratypes are labeled India (M.P.), Sillari Forest, Nagpur-Wardah Div., 24-V–1953, *Boswellia serrata*, M. L. Roonwal; 3 paratypes are labeled India, M.P., 14 mi. S. Kanker, 450 m, 31-1–1962, E. S. Ross, D. Q. Cavegnaro. The holotype and allotype are in the Forest Research Institute, and the paratypes are in my collection.

Liparthrum artocarpus, n. sp.

This species is distinguished from *longifoliae* (Stebbing) by the much more coarsely punctured striae and by the fine, regular, rather closely spaced interstrial granules. This is *L. artocarpus*, nomen nudum, of Beeson 1941:290.

MALE.—Length 0.8 mm (paratypes 0.8–0.9 mm), 2.0 times as long as wide; color brown, vestiture pale.

Frons weakly convex from epistoma to well above eyes, epistomal margin weakly elevated; surface finely rugose-reticulate except smooth and shining near epistoma and on median line on lower half; vestiture of fine, inconspicuous hair.

Pronotum 0.90 times as long as wide, widest just behind middle, sides strongly arcuate; surface shining, obscurely reticulate, median third armed by fine, rather abundant tubercles of uniformly small size from anterior margin to near base; anterior margin unarmed; vestiture of rather abundant, stout, recumbent hair and less numerous, erect scales, each scale rather short, wider than long.

Elytra 1.75 times as long as wide; outline as for most members of genus; basal margin of each elytron armed by five crenulations; striae not impressed, punctures rather coarse, impressed; interstriae slightly narrower than striae, smooth, shining, each armed by a row of small, rounded, rather closely set tubercles. Declivity convex, steep; sculpture as on disc except striae more distinctly impressed. Vestiture of semirecumbent, stout hair and rows of erect scales, both of equal length; widest scales almost as wide as long.

FEMALE.—Specimens considered to be females are as in male except frons more strongly convex and pronotum with a few (two to four) asperities on anterior half distinctly larger.

TYPE MATERIAL.—The male holotype, female allotype, and 4 paratypes were taken at Hattikeri, S. Kanara Div., Bombay, 18-XI–29, ex *Artocarpus integrifolia*, B. M. Bhatia. The holotype and allotype are in the forest Research Institute, Dehra Dun; the paratypes are in my collection. There are 15 other specimens in the FRI.

Liparthrum tinianensis, n. sp.

This unique species is distinguished by the stout body form, by the concave female frons, by the total absence of hairlike setae on the elytra, and by the rather slender, interstrial scales.

FEMALE.—Length 1.0 mm, 2.1 times as long as wide; color brown, vestiture pale.

Frons shallowly concave on a triangular area extending from epistoma to upper level of eyes; surface in impressed area finely rugose-reticulate, subreticulate in dorsal and lateral areas; vestiture of fine, rather sparse, inconspicuous hair.

Pronotum 0.83 times as long as wide; widest on basal third, sides strongly arcuate, converging to rather broadly rounded anterior margin; surface shining, obscurely

reticulate, median fourth with small, rounded granules except near anterior and posterior margins; vestiture abraded, apparently restricted to a few erect, rather slender scales in median area.

Elytra 1.3 times as long as wide; outline about as for genus; striae not impressed, punctures impressed, rather coarse; interstriae slightly narrower than striae, smooth, unarmed, punctures small, in rows. Declivity convex, steep; sculpture similar to disc except striae slightly impressed, interstriae with low, rounded granules. Ground vestiture not represented; each interstriae with a row of erect, spatulate scales, each about twice as long as wide, spaced in a row by distances slightly longer than a scale.

TYPE MATERIAL.—The female holotype is from south end of Tinian Isl., 11-VI–46, No. 628, H. K. Townes. The holotype is in my collection.

Polygraphus anogeissi, n. sp.

This species is unique in having the female frons transversely impressed and armed above by a pair of transverse tubercles as in the males of many species of this genus. Its comparatively small size and slender body form also help to distinguish it. Beeson used the manuscript names *anogeissi* and *bassiae* for this species. The label on the latter series had been turned over by him and replaced by the former name.

FEMALE.—Length 1.7 mm (paratypes 1.5–1.7 mm), 2.5 times as long as wide; color dark brown, vestiture pale.

Frons as in male, strongly, transversely impressed on lower half, convex above and armed just below upper level of eyes by a pair of transversely arranged tubercles; surface closely, deeply, rather coarsely punctured, lower area between punctures smooth, shining, upper area subreticulate; vestiture below tubercles of rather sparse, fine, long hair. Eye large, coarsely faceted, divided. Antennal funicle 5-segmented; club small, ovate.

Pronotum 0.90 times as long as wide; sides almost straight and parallel on basal half, moderately constricted before broadly rounded anterior margin; surface smooth and shining except reticulate on anterior third, punctures rather small, shallow, moderately abundant, spaced by about two diameters of a puncture; vestiture an almost equal mixture of fine hair and slender scales.

Elytra 1.8 times as long as wide, 2.1 times as long as pronotum; sides almost straight and parallel on basal three-fourths, broadly rounded behind; surface finely rugose, punctures small, obscure, confused; most interstriae marked by a row of fine granules at least near declivity. Declivity steep, convex; sculpture as on disc, fine granules on at least interstriae 1–3. Vestiture of a ground cover of small, suberect, short, interstrial scales, each scale about two to three times as long as wide, and rows of erect, interstrial scales, each scale about twice as long as ground cover and four times as long as wide.

MALE.—Similar to female except rows of interstrial setae usually extend to base, granules slightly larger.

TYPE MATERIAL.—The female holotype is labeled Kirwatti, E. Kanara, Bombay, India, 19-I–1930, R.R.D. 42, R.C.R. 178, Cage 654, ex *Bassia latifolia*, B. M. Bhatia; the male allotype bears the same data except it was taken on 27-VI–1930; 3 paratypes bear the same data except the date was 18-XII–1929 and the host was *Odina wodier*; 1 paratype is labeled Okkan Res., Insein, Burma, 11-II–1927, *Anogeissus acuminata*. The holotype and allotype are in the Forest Research Institute, Dehra Dun; the paratypes are in my collection. More than 90 additional specimens are in the FRI collection.

Polygraphus difficilis, n. sp.

This species is allied to *querci* Wood in having the eye emarginate, but it differs in having the protibia as in other members of the genus. The elytral scales are also smaller and less abundant than in other members of the genus. This name was used as a nomen nudum by Beeson.

FEMALE.—Length 2.0 mm (paratypes 2.0–2.2 mm), 2.2 times as long as wide; color reddish brown, vestiture pale.

Frons moderately concave on central half from epistoma to above upper level of eyes; surface smooth, shining, rather coarsely, very closely punctured; vestiture of rather abundant hair of moderate length in concave area, much longer on upper and lateral margins, longest setae on vertex could extend two-thirds of distance to epistoma; eye rather large, two-thirds divided by deep

emargination. Antennal funicle 6-segmented; club rather small, ovate, with apex acutely acuminate.

Pronotum about as in *querci*, punctures very slightly larger, vestiture very short, sparse, fine hair (scales not evident).

Elytra 1.55 times as long as wide, outline as in *querci*; striae not impressed, punctures in obscure rows; interstriae four times as wide as striae, punctures slightly smaller than those of striae, close, confused. Declivity steep, convex except shallowly sulcate on interstriae 2; striae not indicated; interstriae 1 weakly elevated, 1 and 3 each armed by a row of small tubercles. Vestiture of small, rather sparse, interstrial scales, each scale about three to four times as long as wide.

MALE.—Similar to female except frons transversely impressed on lower third, convex above, armed by a transverse pair of rather widely spaced tubercles at upper level of eyes, vestiture on frons inconspicuous.

TYPE MATERIAL.—The female holotype and male allotype are labeled Sitoli, C. Almora [India], VIII–1919, H. G. Champion, in plantation [of *Pinus roxburghii*] trees killed by *Peridermium*. Two paratypes are from Pakistan, N. W. Himalayas, Muiree Hills, 11-1951, M.A.H. Qadri, Com. Inst. Ent. Coll. No. 16222. The holotype is in the Forest Research Institute, Dehra Dun; the allotype and paratypes are in my collection.

Polygraphus querci, n. sp.

This species is unique among northern hemisphere members of the genus. The eye is about half divided by an emargination (as in *difficilis*), and the protibia is armed by only one unsocketed spine as in *thitsi* (Beeson). It is obviously very primitive in all characters.

FEMALE.—Length 3.3 mm (paratypes 2.4–3.6 mm), 2.4 times as long as wide; color reddish brown, vestiture pale.

Frons moderately convex, narrow, eyes separated by width of an eye; surface smooth, shining, punctures rather small, moderately abundant; vestiture of fine, short, inconspicuous hair; eye large, about half divided by a broad emargination. Antennal funicle 6-segmented; club ovate, rather small.

Pronotum 0.60 times as long as wide; widest on basal third, strongly arcuate on basal half, a strong constriction just in front of very broadly rounded anterior margin; surface smooth, shining, punctures very small, moderately abundant, interspaces equal in width to one to four diameters of a puncture; vestiture uniformly short, erect, of hair and slender scales, each scale at least six times as long as wide.

Elytra 1.8 times as long as wide, 2.5 times as long as pronotum; sides almost straight and parallel on basal three-fourths, broadly rounded behind; striae feebly impressed, punctures small, shallow, close; interstriae three to four times as wide as striae, minute punctures confused and each interstriae with a uniseriate row of minute tubercles. Declivity convex, steep; sculpture about as on disc except striae slightly more strongly impressed. Vestiture of minute strial hair and small, suberect, interstrial scales, scales arising from tubercles slightly longer, almost twice as long as declivity.

Protibia slender, armed on outer apical angle by one unsocketed denticle, a smaller denticle on apical margin.

TYPE MATERIAL.—The female holotype and eight female paratypes were taken at Mehalkhali (Burma?) from *Quercus incana*. The holotype (uppermost) and four paratypes on one pin are in the Forest Research Institute, Dehra Dun. The four other paratypes are in my collection.

NOMENCLATURAL CHANGES AND NEW SPECIES OF SCOLYTIDAE (COLEOPTERA), PART III

Stephen L. Wood[1]

ABSTRACT —New synonymy is proposed for *Phloeosinus (Hylesinus) machilus* (Schedl) (*Phloeosinus cinnamomi* Tsai & Yin). New replacement names are proposed for junior homonyms as follows: *Cyrtogenius africus* for *Cyrtogenius (Metahylastes) africanus* (Eggers), *Cyrtogenius elongatissimus* for *Cyrtogenius (Ozodendron) elongatus* (Schedl), *Cyrtogenius elongatulus* for *Cyrtogenius (Eidophelus) elongatus* (Schedl), *Cyrtogenius gracillimus* for *Cyrtogenius gracilis* Browne, *Cyrtogenius papuae* for *Cyrtogenius (Pelicerus) papuanus* (Eggers), *Cyrtogenius papuensis* for *Cyrtogenius (Eidophelus) papuanus* (Schedl), *Cyrtogenius ruginosus* for *Cyrtogenius (Mimidendrulus) rugicollis* (Browne). The following species are named as new to science: *Indocryphalus machili* (India), *Olonthogaster jiri* (India), *Olonthogaster regalis* (Sri Lanka), *Phloeosinus phoebe* (India), *Scolytomimus andamanensis* (Andaman Islands), *Scolytomimus mimusopis* (Sri Lanka), *Scolytomimus quadridens* (New Guinea), and *Scolytomimus rectus* (Sri Lanka).

On the following pages are presented one case of new specific synonymy, seven cases of new homonymy, and eight species named as new to science. These items are necessary nomenclatural housekeeping discovered during preparation of a new world catalog of Scolytidae and are published to facilitate citation for the catalog. The new synonymy affects a species from India and China. The new homonymy and new replacement names affect species of *Cyrtogenius* from Africa (2), Borneo (1), and New Guinea (4). The new species represent the genera *Indocryphalus* (1), *Olonthogaster* (2), *Phloeosinus* (1), and *Scolytomimus* (4) from the Andaman Islands (1), India (3), New Guinea (1), and Sri Lanka (3).

NEW SYNONYMY

Phloeosinus machilus (Schedl)

Hylesinus machilus Schedl, 1959, Indian For. Rec. 9:173 (Holotype, sex?; Uttar Pradesh: Chacrata, Chachpur; supposedly returned by Schedl to Forest Research Institute, Dehra Dun, but lost if it ever existed)

Phloeosinus cinnamomi Tsai & Yin, 1964, Acta Zootaxon. Sin. 1:94, 96 (Holotype, male; Fukien, China; Institute of Zoology, Academia Sinica, Beijing). *New synonymy*

The "paratype" of *Hylesinus machilus* Schedl and a long series of this species from which the "type" specimen came at the Forest Research Institute were examined and compared to a series collected by me. These specimens agree in all details with several paratypes of *Phloeosinus cinnamomi* Tsai & Yin in my collection, except that the size varies in Indian material while those from China are uniformly near the small end of the size spectrum. It is apparent that only one species is represented and synonymy is proposed as indicated above.

NEW NAMES

Cyrtogenius africus, n. n.

Metahylastes africanus Eggers, 1922, Ent. Blätt. 18(4):165 (Holotype, sex?; Flüssgebiet des oberen Mewena und Ramissi, British Ostafrika; Methner Collection). *Preoccupied*

The holotype of *Dryocoetes africanus* Schreiner (1882:246) was examined and was found to be a member of the genus *Cyrtogenius* to which it is here transferred. This action creates a junior homonym of *Metahylastes africanus* Eggers (1922:165) that was previously transferred to *Cyrtogenius* (Wood 1986:74). The new name *africus* is proposed as a replacement name for the Eggers species as indicated above.

Cyrtogenius elongatissimus, n. n.

Ozodentron elongatus Schedl, 1964, Reichenbachia 4(27):244 (Holotype, sex?; Borneo; Schedl Collection. *Preoccupied*

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The type and cotypes of *Pelicerus elongatus* Eggers (1927:85) clearly belong to the genus *Cyrtogenius* to which this species was transferred long ago. The recent transfer of *Ozodendron elongatus* Schedl (1964:244) to *Cyrtogenius* by Wood (1986:74) created a junior homonym. The new name *elongatissimus* is proposed as a replacement for the Schedl name as indicated above.

Cyrtogenius elongatulus, n. n.

Eidophelus elongatus Schedl, 1979, Faun. Abh. St. Mus. Tierk. Dresden 7(12):101 (Holotype, female; Papua New Guinea; Schedl Collection in Wien Museum). *Preoccupied*

The holotype of *Eidophelus elongatus* Schedl (1979:101) was examined and found to belong to the genus *Cyrtogenius* to which it is here transferred. This transfer makes this species a junior homonym of *Pelicerus elongatus* Eggers (1927:85), cited above, that was previously transferred to *Cyrtogenius*. The new name *elongatulus* is proposed as a replacement for the Schedl name as indicated above.

Cyrtogenius gracillimus, n. n.

Cyrtogenius gracilis Browne, 1984, South Pacific J. Nat. Sci. 6:95 (Holotype, sex?; Papua New Guinea; British Museum, Natural History). *Preoccupied*

When the genus *Ozodendron* Schedl was made a synonym of *Cyrtogenius* (Wood 1986: 74), the species *O. gracilis* Schedl (1974:462) was transferred to *Cyrtogenius*. Consequently, the name *Cyrtogenius gracilis* Browne (1984:95) was preoccupied. Because Mr. Browne died a few months after the homonymy was created, he could not act upon it. The new name *gracillimus* is proposed as a replacement for the Browne name as indicated above.

Cyrtogenius papuae, n. n.

Pelicerus papuanus Eggers, 1923, Zool. Meded. R. Mus. Nat. Hist. Leiden 7:217 (Lectotype, male; Deutsch New Guinea [Kaiserin Augustafluss]; U.S. National Museum, designated by Anderson and Anderson 1971:23). *Preoccupied*

Pelicerus papuanus Eggers (1923:217) was transferred to *Cyrtogenius* long ago. Recently, a syntype of *Dryocoetes papuanus* Eggers (1923:162) was examined and found to belong to *Cyrtogenius*. Due to page priority, the later name (on p. 217) thereby became a junior homonym. The new name *papuae* is proposed as a replacement as indicated above.

Cyrtogenius papuensis, n. n.

Eidophelus papuanus Schedl, 1973, Papua New Guinea Agric. J. 24(2):71 (Holotype, sex?; Mt. Dayman, Maneau Range, N slope, M. Bay Distr., 700 m; Amer. Mus. Nat. Hist.). *Preoccupied*

Paratypes of *Eidophelus papuanus* Schedl (1973:71) in the Wien Museum were examined and found to belong to the genus *Cyrtogenius*. For this reason the species must be transferred to that genus. This transfer caused this species to become a junior homonym of *Cyrtogenius papuanus* Eggers (1923:162), cited above. The new name *papuensis* is proposed as a replacement for the Schedl name as indicated above.

Cyrtogenius ruginosus, n. n.

Mimidendrulus rugicollis Browne, 1965, Zool. Meded. 40:194 (Holotype, male; Ivory Coast; Adiopodoume; Leiden Museum). *Preoccupied*

When the genus *Mimidendrulus* became a synonym of *Cyrtogenius* (Wood 1986:74), *Mimidendrulus rugicollis* Browne (1965:194) became a junior homonym of *Orosiotes rugicollis* Eggers (1940:132) that had previously been transferred to *Cyrtogenius*. The new name *ruginosus* is proposed as a replacement for the Browne name as indicated above.

NEW TAXA

Indocryphalus machili, n. sp.

This species is distinguished from *pubipennis* (Blandford) by the larger, less strongly confused elytral punctures, by the much steeper, impressed elytral declivity, by the declivital granules, and by other characters described below.

FEMALE.—Length 3.0 mm (paratypes: females 2.7–3.0 mm, males 2.5–2.7 mm), 2.4 times as long as wide; color dark brown, base of pronotum and elytral disc usually pale.

Frons weakly convex; surface dull, finely rugose-reticulate, a few isolated, shining granules on upper half; vestiture of fine, rather sparse, long hair; eye and antenna as in *pubipennis*.

Pronotum about as in *pubipennis;* mycetangium longitudinal, occupying most of middle third.

Elytra similar to *pubipennis* except more abruptly, more broadly rounded behind; punctures small, distinctly impressed, those on striae in obscure rows, scarcely distinguishable from confused interstrial punctures. Declivity very steep, rather broadly impressed; striae on upper two-thirds more distinctly marked, interstriae in this area each armed by several small, rounded tubercles. Vestiture mostly on and near declivity, consisting of rather abundant, fine, erect hair of variable length.

MALE.—Similar to female except frons slightly impressed, dorsolateral margin rather abrupt; pronotal mycetangium absent; elytral punctures apparently more strongly impressed.

TYPE MATERIAL.—The female holotype, male allotype, and three male paratypes bear the labels Ramgarh, Naini Tal, U.P. [India], 7,000 [ft], 24-V–1930 (type) or 23-V–1930, R.R.D. 114, B.C.R. 84, ex *Machilus odoratissima*, C.F.C. Beeson; three paratypes are labeled Senchal Range, Darjeeling, Bengal, 2-IV–1930, R.R.D. 29, B.C.R. 458, Cage 630, *Cinnamomum impressinervium;* one paratype is labeled Debrepani, Darjeeling, Bengal, 18-IX–1929, 6,000 ft, ex *Machilus odoratissima*, J.C.M. Gardner; one paratype is labeled Rangirum, Darjeeling, Bengal, 6-IX–1929, 6,000 ft, *Cinnamomum impressinervium*, J.C.M. Gardner. The holotype, allotype, and one paratype are in the Forest Research Institute, Dehra Dun; the remaining paratypes are in my collection.

Olonthogaster jiri, n. sp.

This species is distinguished from the remotely related *nitidicollis* Motschulsky by the very different frons and elytra as described below. This is *Phloeosinus jiri* Beeson, nomen nudum.

FEMALE.—Length 1.7 mm (paratypes 1.5–1.8 mm), 1.8 times as long as wide; color reddish brown when mature, vestiture pale.

Frons moderately, uniformly concave from eye to eye from epistoma to vertex, a fine, median carina on lower half; surface finely, rather closely punctured, largely obscured by a brush of long, yellow hair, longer and more abundant above, longest setae equal in length to half distance between eyes; eye divided by emargination into two parts.

Pronotum 0.85 times as long as wide; about as in *nitidicollis* except more closely punctured, constriction slightly stronger.

Elytra 1.2 times as long as wide, 1.5 times as long as pronotum; sides almost straight and parallel on basal half, broadly rounded behind; striae rather deeply, narrowly impressed, punctures small, distinctly impressed; interstriae two to three times as wide as striae, smooth, shining, crenulations on basal fourth of disc rounded, becoming tuberculate toward declivity, somewhat confused on 2 and 3, uniseriate elsewhere. Declivity convex, steep; sculpture about as on posterior disc except interstriae 2 and 4 feebly impressed, often with one or more tubercles obsolete. Vestiture with ground cover of small, pale scales restricted to posterior half of disc and declivity, with sparse, confused, short, hairlike setae on basal half.

MALE.—Similar to female except frontal impression weak, narrowed, restricted to lower half, median carina on lower half strong and of uniform height and on upper half a stronger, median carina, its lower extremity near upper level of eyes somewhat subdentate, frontal vestiture sparse, inconspicuous; rounded crenulations on disc always uniseriate, extending to near declivity; declivital tubercles distinctly larger except obsolete on declivital interstriae 2, 4, and most of 6.

TYPE MATERIAL.—The female holotype, male allotype, and six paratypes were taken at Jiri Forest, Cachar, Assam [India], 11-IV–1924 (type, allotype, two paratypes) or 19-V–1924 (four paratypes), ex *Myristica longifolia*, R.R.D. 226, B.C.R. 165, G.E. Jar. 11, by S. N. Chatterjee. The holotype, allotype, and several other specimens are in the Forest Research Institute, Dehra Dun; the paratypes are in my collection.

Olonthogaster regalis, n. sp.

This unique species is distinguished by the large body size, by the elaborate declivital armature, and by characters of the frons that are described below.

FEMALE.—Length 5.0 mm (paratypes 4.7–5.5 mm), 1.8 times as long as wide; color reddish brown.

Frons rather deeply concave from eye to eye from epistoma to vertex, epistomal

process with a pair of calluses laterally on median half; surface smooth, shining, densely, finely, uniformly punctured; impressed area with a brush of moderately long, erect hair of uniform length, not longer on margins; a small tubercle on carina extending into occular emargination. Eye half divided by an emargination.

Pronotum similar to *nitidicollis* Motschulsky except punctures very small, not close; glabrous.

Elytra 1.15 times as long as wide; sides almost straight and parallel on basal half, posterior profile interrupted by declivital spines; striae deeply, narrowly impressed, punctures minute, distinct; interstriae slightly convex, four to five times as wide as striae, punctures obscure, minute, confused, 2 and 3 with low, obscure, rounded elevations (derived from nearly obsolete crenulations). Declivity steep, subimpressed between interstriae 3; sutural interstriae distinctly elevated, with one or two small tubercles at base, 2 impressed on median side, sloping upward laterally, armed at base by one moderate and about two small tubercles; interstriae 3 forming lateral summit (rather low), armed on upper margin by about three small tubercles and on lower two-thirds by three very large spines, upper spine as high as basal width, its apex sharply pointed, middle spine similar but half again longer (curved slightly mesad), lower spine with double base, blunt, as wide as high; interstriae 4 to 8 each with a row of rather small tubercles, 9 low, almost subcarinate. Glabrous.

MALE.—Similar to female except frons subglabrous, impression slightly deeper, its upper margin armed by a pair of calluses in lateral areas.

TYPE MATERIAL.—The female holotype, male allotype, and 25 paratypes were taken at Weddagala, Rat. Distr., Sri Lanka, 19 May 1975, from bark of a *Myristica dactyloides* log, by me. The holotype, allotype, and some paratypes are in the U.S. National Museum, and the remaining paratypes are in my collection.

Phloeosinus phoebe, n. sp.

This species is distinguished from the distantly related *machilus* (Schedl) by the closely, rather deeply punctured pronotum, by the larger, uniseriate interstrial tubercles, and by other characters described below. This is *Phloeosinus phoebe* Beeson (1941:291), nomen nudum.

MALE.—Length 3.0 mm (paratypes 2.9–3.4 mm), 1.8 times as long as wide; color brown, vestiture rather pale.

Frons similar to *machilus* except less strongly impressed, median carina reduced to a small tubercle just above epistoma, tubercles in lateral areas smaller, usually with punctures distinct, vestiture finer, slightly more abundant.

Pronotum 0.74 times as long as wide; outline similar to *machilus;* surface smooth, dull, densely, deeply, rather finely, uniformly punctured, interspaces mostly less than half as wide as diameter of a puncture, without any granules; vestiture of fine, rather short, semirecumbent hair.

Elytra 1.3 times as long as wide, 2.1 times as long as pronotum; humeral angles slightly produced anteriorly in lateral areas; outline as in *machilus;* striae moderately, not abruptly impressed, punctures small, distinctly impressed; interstriae about twice as wide as striae, convex, each armed to base by a uniseriate row of moderately coarse tubercles, those on 1, 2, and 4 obsolete by base of declivity. Declivity convex, rather steep, interstriae 2, 4, and sometimes 6 constricted to half their basal width and unarmed; 1 and 3 weakly elevated. Vestiture of ground cover of interstrial scales, longer and slender at base, shorter on declivity, and longer, similar bristlelike setae arising from posterior base of interstrial tubercles, each about two to three times as long as ground cover.

FEMALE.—Similar to male except frons convex and with a low, median carina on lower half.

TYPE MATERIAL.—The male holotype, female allotype (both callow), and four paratypes were taken at Nauri, Landowne [Uttar Pradesh, India], IV–1926 (type), 19-III–1926 (allotype and two paratypes), 31-III–1926 (one paratype), or 4-IV–1926, 2,500 ft, R.R.D. 544, B.C.R. 44, Cage 579, ex *Phoebe lanceolate*, by B. M. Bhatia. The holotype, allotype, and 16 other specimens are in the Forest Research Institute, Dehra Dun; the paratypes are in my collection.

Scolytomimus andamanensis, n. sp.

This species is distinguished from *philip-*

pinensis Eggers by the much more coarsely punctured, more rugose frons, the epistomal area much less strongly impressed, by the more broadly rounded apical half of the antennal club, and by the more confused organization of tubercles on the posterior face of the protibia.

MALE.—Length 1.9 mm (paratypes 1.9–2.1 mm), 1.9 times as long as wide; color yellowish brown.

Frons rather strongly convex, without a transverse impression above epistoma; surface densely, deeply, rather coarsely punctured, some of those on lower half of median half with their margin subcrenulate, spaces between punctures less than diameter of a puncture; vestiture minute and hairlike except longer near epistoma. Antennal club wider than *philippinensis*, its apex more broadly rounded.

Pronotum and elytra essentially as in *philippinensis* except punctures on sides and base of pronotum coarser, deeper, and rugosities behind summit larger.

Protibia with tubercles confused (a submarginal row occurs in *philippinensis*).

FEMALE.—Similar to male except frons more broadly convex, and a distinct, transverse impression present just above epistoma; anterior margin of pronotum armed by two denticles (these submarginal in male).

TYPE MATERIAL.—The male holotype (middle), female allotype (top), and one paratype (bottom) are mounted on the same pin and labeled Andaman Islands, 19-III–1930, R.R.D. 88, B.C.R. 37, Cage 716, *Sideroxylon longepetiolatum*, C.F.C. Beeson; 12 paratypes bear identical labels except that the dates are 22- or 23-III–1930. The holotype, allotype, and one paratype are in the Forest Research Institute, Dehra Dun, and the remaining paratypes are in my collection.

Scolytomimus mimusopis, n. sp.

This species is distinguished from *assamensis* Schedl by the smaller size, by the circular strial punctures, by the normal spaces between strial punctures within a row, and by the different details of interstrial carinae as described below. The name was used as a nomen nudum by Beeson (1941:310).

FEMALE.—Length 1.8 mm (paratypes 1.7–2.1 mm), 1.9 times as long as wide; yellowish brown (callow?) to brown (mature?).

Frons similar to *assamensis* except more rugose, reticulation less evident, slightly more strongly convex. Specimens with median line modified on vertex could be males.

Pronotum similar to *assamensis* except low crenulations extend almost to base.

Elytra similar to *assanensis* except interstrial carinae less acutely elevated on basal half; strial punctures almost circular (in *assamensis* quadrate, twice as wide as long), spaced within a row by less than half diameter of a puncture, these partitions never tuberculate or nodulate (as in *assamensis*); interstrial carinae 7 and 9 unite in line with 7 and continue almost to 3 where they unite with costal margin before joining 3 (in *assamensis* 7 and 9 unite before level of 6 and then continue almost to 2 and unite with 3 before uniting with costal margin); 2 to suture usually slightly enlarged and/or produced caudad. Glabrous except for a few minute hairlike setae in basal area.

TYPE MATERIAL.—The female holotype and 10 female paratypes are labeled Palugama, Anuradhapura, Ceylon, N.C.P., 250, F.R.I. coll. Gauri Dutt., 27-XI–1934 (type), or 29-XI–1934 (some paratypes), *Mimusops elengi*; one female paratype is labeled Baihar, Balaghat, C.P., G.D., 27-VII–1927, ex *Bassia latifolia*. The holotype and 21 other specimens are in the Forest Research Institute, Dehra Dun; the paratypes are in my collection.

Scolytomimus quadridens, n. sp.

This species is distinguished from all others in the genus by the four large serrations near the anterior margin of the pronotum. From *baloghii* it is also distinguished by the smaller size, by the strongly reticulate elytral surface, by the small strial punctures, by the less strongly convex interstriae, and by other characters.

MALE.—Length 1.6 mm, 2.0 times as long as wide; color yellowish brown.

Frons shallowly impressed (shrinkage of a convex frons in a callow specimen?); surface reticulate, punctures sparse, shallow, rather coarse.

Pronotum 0.85 times as long as wide; outline typical of genus; anterior margin armed by four serrations, middle pair conspicuously larger; asperities large, low, anterior to summit; strongly reticulate, posterior and lateral

areas shallowly, coarsely punctured, without crenulation. Glabrous.

Elytral outline typical of genus; surface strongly reticulate; striae feebly if at all impressed, punctures small, shallow, close; interstriae four to five times as wide as striae, feebly convex on disc, punctures very small, confused. Declivity weak, convex; costal margin weakly, subacutely elevated from elytral base to apex, interstriae 9 weakly, obtusely elevated from base of declivity to junction with interstriae 3 and continuing to costal margin, 3 and 5 feebly elevated but not joining 9. Glabrous.

TYPE MATERIAL.—The male holotype is labeled New Guinea (NE), Huon Peninsula, Finschhafen, 180 m, 16-IV–1963, M.V. light, J. Sedlacek. The holotype is in my collection.

Scolytominus rectus, n. sp.

This species is distinguished from *mimusopis* Wood by the strongly convex but noncostate elytral interstriae, and by a different alignment of the declivital interstriae.

MALE.—Length 1.8 mm (paratypes 1.7–2.0 mm), 2.0 times as long as wide; color grayish brown.

Frons similar to *mimusopis* except smoother, punctures smaller, margins much less rugose; vertex with a conspicuous median band of nonrugose-reticulate sculpture extending to base.

Pronotum similar to *mimusopis* except a bit more coarsely sculptured.

Elytra similar to *mimusopis* except interstriae usually less acutely costate; interstriae 2 to 8 end before reaching 9, some of 3 to 8 occasionally unite or nearly so just before ending; 9 and costa unite just before level of 3 and continue to suture, this costa from junction to suture not enlarged or abnormally protruding as in most *mimusopis*. Glabrous or nearly so.

FEMALE.—Similar to male except median line on vertex unmodified, uniformly rugose-reticulate; protibiae with a submarginal row of tubercles.

TYPE MATERIAL.—The male holotype, female allotype, and 16 paratypes were taken 40 km NE Polonnaruwa, Pol. Distr., Sri Lanka, 12 June 1975, No. 168, *Osbeckia aspera*, by S. L. Wood; 11 paratypes are labeled 5 km SE or 48 km N Naula, Mate. Distr., Sri Lanka, 14 June 1975, No. 212, *Manikara hexandra*, S. L. Wood, 6 paratypes bear the same labels except No. 208 from a liana; 5 paratypes are from 30 km NE Puttalam, Put. Distr., 18 June 1975, No. 215, *Manikara hexandra*, S. L. Wood. The holotype, allotype, and half of the paratypes are in the U.S. National Museum; the remaining paratypes are in my collection.

GRAY PARTRIDGE FORAGING ECOLOGY IN EASTERN SOUTH DAKOTA[1]

Jerry W. Hupp[2], John T. Ratti[3], and Loren M. Smith[4]

ABSTRACT.—We examined crop contents of 217 Gray Partridge (*Perdix perdix*) collected during a two-year period in eastern South Dakota. Row crop grains (corn, sunflowers) dominated late fall, winter, and spring diets. Small grains (oats, barley, wheat, rye) were rarely consumed although fields of small grains were widely available. During a severe winter when waste row crop grains were buried by snow, partridge consumed more leafy vegetation. Insects dominated the early summer diet, while foxtail (*Setaria* spp.) seeds were a major late summer and early fall food.

Previous North American studies of Gray Partridge foraging ecology have demonstrated the importance of agricultural crops. Most studies have been conducted in areas where small grains were the predominant agricultural crop (Yocom 1943, Westerskov 1966, Hunt 1974, Kobriger 1977, 1981). Not surprisingly, small grains comprised the majority of foods consumed. There has been little evaluation of Gray Partridge foraging ecology in areas with both row crop and small grain production. Therefore, opportunities to evaluate relative forage preference between these two types of domestic grains have been limited. Only Yeatter (1934) and Bishop et al. (1977) presented food habits data from areas where row crops were produced. Their studies were based on small samples (53 and 33 respectively) and data for all seasons were limited.

We studied Gray Partridge foraging ecology during a two-year period in an agriculturally diverse region of South Dakota. Our objective was to assess variation in partridge diets in response to seasonal changes in agricultural treatments and weather. Because both small grains and row crops were available on our study area, we were able to evaluate dietary proportions of these domestic grains relative to the available acres of crops.

METHODS

We conducted the study in Brookings County in eastern South Dakota. Row crops comprised 33–42% and small grains 22–29% of agricultural acreage in the county in 1978–80. Both types of domestic grains were highly interspersed with each other and widely available throughout the region (Smith et al. 1982, Ratti et al. 1983). Pastures, alfalfa/grass hayfields, and idle grass cover were also available and comprised approximately 30% of the region.

Partridge were collected from July 1978 to June 1980. We collected most individuals along section roads within the study area. Hunter cooperators provided additional samples from birds shot during the fall hunting season. Crop contents of collected Gray Partridge were removed and oven-dried at 80 C. Food items were identified, segregated, and volumetrically measured ($\pm$ 0.1 ml). Volumes $<$ 0.1 ml were considered trace levels. Only crops with $>$ 0.1 ml of food were used in the analysis. Data were summarized into two-month periods to evaluate seasonal variation. Data are presented using aggregate percent and percent occurrence methods (Martin et al. 1946, Swanson et al. 1974). Individual items were classified as either row crop grains, small grains, wild seeds, leafy vegetation, or invertebrate food. We used Krsukal-Wallis tests to evaluate differences in consumption of each food category among two-month periods (Conover 1980:229). Complete lists of food items consumed by Gray Partridge are in Hupp (1980) and Smith (1980).

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TABLE 1. Composition of Gray Partridge diets in Brookings County, South Dakota, 1978–80.

	22 Jun–21 Aug (n = 13)		22 Aug–21 Oct (n = 53)		22 Oct–21 Dec (n = 54)		22 Dec–21 Feb (n = 34)		22 Feb–21 Apr (n = 18)		22 Apr–21 Jun (n = 22)	
	Agg %[a]	% Occ[b]	Agg %	% Occ	Agg %	% Occ	Agg %	% Occ	Agg %	% Occ	Agg %	% Occ
Row crop grains[c,d]	18.7	30.8	28.2	35.8	34.7	66.7	52.1	82.3	48.8	88.9	47.3	81.8
Small grains	3.1	53.8	10.8	35.8	9.1	25.9	5.3	20.6	4.3	16.7	4.8	31.8
Wild seeds[c]	15.4	46.2	40.4	92.4	34.9	87.0	15.3	85.3	7.2	55.6	12.3	72.7
Leafy vegetation[c,d]	7.7	15.4	14.2	86.8	17.1	85.5	26.5	73.5	39.6	88.9	29.6	86.4
Animal[c]	49.7	69.2	6.0	35.8	0.3	12.7	0	0	0	0	5.4	50.0

[a]Aggregate percent
[b]Percent occurrence
[c]Consumption differed ($P < .05$) among two-month periods.
[d]Consumption differed ($P < .05$) between years during some two-month periods (see Table 2).

TABLE 2. Yearly differences in late fall through winter consumption of row crop grains and leafy vegetation by Gray Partridge in Brookings County, South Dakota, 1978–80.

	22 Aug–21 Oct			22 Oct–21 Dec			22 Dec–21 Feb		
	n	Agg %[a]	% Occ[b]	n	Agg %	% Occ	n	Agg %	% Occ
Row crop grain									
1978–79	34	14.1	20.1	26	19.5	61.5	25	42.4	76.0
1979–80	19	53.5	63.2	28	48.9	71.4	9	78.8	100.0
Leafy vegetation									
1978–79	34	21.8	94.1	26	26.6	92.3	25	34.9	76.0
1979–80	19	0.7	73.7	28	8.3	82.1	9	3.6	66.7

[a]Aggregate percent
[b]Percent occurrence

RESULTS

We examined crops of 217 Gray Partridge; 194 contained > 0.1 ml of food and were included in the analysis. Seasonal differences in consumption of row crop grains were apparent (Table 1). The proportion of row crop grains in the diet increased from late summer (22 Aug–21 Oct) through winter (22 Dec–21 Feb), and remained high during early (22 Feb–21 Apr) and late (22 Apr–21 Jun) spring. From winter through late spring, row crop grains comprised approximately 50% of the foods consumed by Gray Partridge. During that period, corn was a much larger proportion (33–49%) of the diet than sunflowers (0–14%). Late summer through winter consumption of row crop grains was lower in 1978–79 than in 1979–80 (Table 2).

Small grains comprised a minor proportion (< 10%) of the diet during all collection periods (Table 1). Seasonal variation in small grains consumption was not apparent ($P = .31$). Barley and oats were the small grains usually consumed by Gray Partridge.

Consumption of leafy vegetation was highest during early and late spring (Table 1). Leafy vegetation included leaves of alfalfa and cool season grasses available in pastures and hayfields. During late summer through winter, Gray Partridge consumed more leafy vegetation in 1978–79 than in 1979–80 (Table 2).

Wild seeds were a major proportion (35–40%) of the late summer and fall (22 Oct–21 Dec) diet but comprised a smaller proportion (7–15%) of foods consumed during other periods (Table 1). Foxtail (*Setaria* spp.) dominated the wild seed portion of the diet (Hupp 1980). Other wild seeds that frequently appeared in crops included wild buckwheat (*Polygonum* spp.) and ragweed (*Ambrosia* spp.).

Invertebrate foods were primarily consumed during early summer (22 Jun–21 Aug) (Table 1). Early summer data were primarily based on juvenile Gray Partridge; only three

adults were collected during that period. Insects of the orders Lepidoptera and Orthoptera were the major early summer invertebrate foods. Invertebrate foods were rarely consumed between fall and early spring. Consumption of insects increased slightly in late spring.

DISCUSSION

In agricultural regions domestic grains are primarily available to ground-foraging birds following harvest of crops but before field tillage in preparation for planting (Balldassare et al. 1983, Warner et al. 1985). Small grain fields in Brookings County were usually harvested in early August. Therefore, during late summer waste small grains were available in unplowed stubble. In spite of the wide distribution of small grain fields and availability of waste seeds following harvest, small grains were a minor proportion of the late summer diet. Gray Partridge primarily fed on wild seeds during that period. Concurrent evaluation of Gray Partridge habitat use in Brookings County indicated that coveys primarily remained in unharvested row crops during late summer (Smith et al. 1982). Partridge apparently preferred to forage in the more protective cover of standing row crops rather than the shorter, more exposed small grain stubble. Wild seed-producing plants were available between rows and along borders of corn and sunflower fields. Foxtail was the source of wild seeds usually consumed by Gray Partridge and was the most common wild plant in agricultural fields in eastern South Dakota (South Dakota Cooperative Extension Service 1975:57).

Small grains remained a minor component of the diet throughout the fall and winter periods. Consumption of row crop grains increased in October and November. Increased consumption of row crop grains likely reflected greater availability of waste corn and sunflowers following harvest. Gray Partridge coveys were more frequently observed in row crop rather than small grain stubble in late fall and winter (Smith et al. 1982). Row crop grains may have been preferred fall and winter forage because they were energetically superior to small grains (McDonald et al. 1971:376).

Gray Partridge consumed more leafy vegetation and less row crop grain in 1978–79 than in 1979–80. Annual differences in late summer consumption of row crop grains were likely due to variation in timing of collections relative to harvest of corn and sunflowers. During late summer in 1978–79 most birds were collected before harvest of row crops was initiated. In 1979–80 a higher proportion of Gray Partridge was collected after harvest of row crops started, and when waste grain was more available. Differences in winter severity likely caused late fall and winter consumption of row crop grain and leafy vegetation to differ between years. Conditions during late fall and winter 1978–79 were severe, with maximum snow depths of 54 cm. Waste grain was buried by drifted snow during the 1978–79 winter, and Smith et al. (1982) observed that Gray Partridge coveys used pasture habitats more frequently during that period. Pastures were often blown free of snow, and birds were able to forage on available leafy vegetation. Also, forage resources in pastures are likely uniformly distributed, and the energetic investment in digging through snow may be less "risky" than in row crop stubble where resource distribution is likely more patchy (Krebs 1978). The 1979–80 winter was mild, with maximum snow depths of 4 cm. During that period waste grains were not covered by snow, and Gray Partridge primarily foraged on corn and sunflower seeds available in row crop stubble.

Juvenile Gray Partridge were primarily collected in early summer when the proportion of invertebrate foods in the diet was high. Juvenile birds often require a high percentage of invertebrates in the diet to meet nutritional demands of growth (Scott 1972). Survival of Gray Partridge chicks may be affected by the availability of insect foods (Potts 1970, 1980). Invertebrate consumption declined in late summer and fall as wild seeds and domestic grains became more available, insect abundance decreased, and chicks matured.

Forage exploitation by Gray Partridge in eastern South Dakota varied seasonally. Our results demonstrate the importance of year-round analysis of avian foraging ecology (Gullion 1966). Agricultural treatments and winter snow depth affected food resource availability and influenced foraging behavior of Gray Partridge. Gray Partridge apparently prefer to forage on row crops rather than small grains in

an area where both types of domestic crops are produced.

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LITERATURE CITED

BALLDASSARE, G. A., R. J. WHYTE, E. E. QUINLAN, AND E. G. BOLAN. 1983. Dynamics and quality of waste corn available to breeding waterfowl in Texas. Wildl. Soc. Bull. 11: 25–31.

BISHOP, R. A., R. C. NOMSEN, AND R. D. ANDREWS. 1977. A look at Iowa's Hungarian Partridge. Pages 10–13 *in* G. D. Kobriger, ed., *Perdix* I: Hungarian Partridge workshop. Central Mountains and Plains Section and the North Dakota Chapter of The Wildlife Society, Dickinson, North Dakota.

CONOVER, W. J. 1980. Practical nonparametric statistics. John Wiley and Sons, New York, N.Y. 493 pp.

GULLION, G. W. 1966. A viewpoint concerning the significance of studies of game bird food habits. Condor 68: 372–376.

HUNT, H. M. 1974. Habitat relations and reproductive ecology of Hungarian Partridge in a hedgerow complex in Saskatchewan. Sask. Dept. of Tourism and Renewable Resour., Wildl. Rept. 3. 51 pp.

HUPP, J. W. 1980. Summer and fall ecology of Gray Partridge in eastern South Dakota. Unpublished thesis, South Dakota State University, Brookings. 69 pp.

KOBRIGER, G. D. 1977. Foods of the Hungarian Partridge in North Dakota. Pages 66–88 *in* G. D. Kobriger, ed., *Perdix* I: Hungarian Partridge workshop. Central Mountains and Plains Section and North Dakota Chapter of The Wildlife Society, Dickinson, North Dakota.

———. 1981. Foods, food availability, nutrition, and body weights of Gray Partridge in North Dakota. Pages 70–86 *in* S. R. Peterson and L. Nelson, Jr., eds., *Perdix* II: Gray Partridge workshop. For. Wildl. and Range Expt. Sta., University of Idaho, Moscow.

KREBS, J. R. 1978. Optimal foraging: decision rules for predators. Pages 23–63 *in* J. R. Krebs and N. B. Davies, eds., Behavioral ecology: an evolutionary approach. Sinauer Associates, Inc., Sunderland, Massachusetts.

MARTIN, A. C., R. H. GENSCH, AND C. P. BROWN. 1946. Alternative methods in upland game bird food analysis. J. Wildl. Manage. 10: 8–12.

MCDONALD, P., R. A. EDWARDS, AND J. F. D. GREENHALGH. 1971. Animal nutrition. Oliver and Boyd, Edinburgh. 407 pp.

POTTS, G. R. 1970. Recent changes in the farmland fauna with special reference to the decline of Gray Partridge. Bird Study 17: 145–166.

———. 1980. The effects of modern agriculture, nest predation, and game management on population ecology of partridges (*Perdix perdix* and *Alectoris rufa*). Adv. Ecol. Res. 11: 1–79.

RATTI, J. T., L. M. SMITH, J. W. HUPP, AND J. L. LAAKE. 1983. Line transect estimates of density and the winter mortality of Gray Partridge. J. Wildl. Manage. 47: 1088–1096.

SCOTT, M. L. 1972. Nutrition in reproduction—direct effects and predictive functions. Pages 46–77 *in* D. S. Farner, ed., Breeding biology of birds. Natl. Acad. Sci., Washington, D.C.

SMITH, L. M. 1980. Winter and spring ecology of Gray Partridge in east central South Dakota. Unpublished thesis, South Dakota State University, Brookings. 67 pp.

SMITH, L. M., J. W. HUPP, AND J. T. RATTI. 1982. Habitat use and home range of Gray Partridge in eastern South Dakota. J. Wildl. Manage. 46: 580–587.

SOUTH DAKOTA COOPERATIVE EXTENSION SERVICE. 1975. South Dakota weeds. South Dakota State Weed Control Comm., Pierre. 228 pp.

SWANSON, G. A., G. L. KRAPU, J. C. BARTONEK, J. R. SERIE, AND D. H. JOHNSON. 1974. Advantages in mathematically weighting waterfowl food habits data. J. Wildl. Manage. 38: 302–307.

WARNER, R. E., S. P. HAVERA, AND L. M. DAVID. 1985. Effects of autumn tillage systems on corn and soybean harvest residues in Illinois. J. Wildl. Manage. 49: 185–190.

WESTERSKOV, K. E. 1966. Winter food and feeding habits of partridge (*Perdix perdix*) in the Canadian prairie. Canadian J. Zool. 44: 303–322.

YEATTER, R. E. 1934. The Hungarian Partridge in the Great Lakes region. Univ. of Michigan, School of For. and Conserv. Bull. 5. 92 pp.

YOCOM, C. F. 1943. The Hungarian Partridge (*Perdix perdix* Linn.) in the Palouse region, Washington. Ecol. Monogr. 13: 167–202.

MORPHOLOGICAL CHARACTERISTICS OF *DENTOSTOMELLA TRANSLUCIDA*, A NEMATODE (OXYUROIDEA) FOUND IN MONGOLIAN GERBILS

Jea Kim Yi[1] and Richard A. Heckmann[1]

ABSTRACT —*Dentostomella translucida* Schulz & Krepkorgorskaja (1932) was found in the small intestine of the Mongolian gerbil, *Meriones unguiculatus* Milne-Edwards, housed at the small animal center at Brigham Young University, Provo, Utah. Pertinent taxonomical characteristics were studied to differentiate *D. translucida* from *D. kuntzi* (Myers 1961) *D. grundmanni* (Chitwood 1963), *D. legerae* (Quentin 1975), and *D. karachiensis* (Bilqees 1978). *Dentostomella translucida* is distinguished by a large, evenly proportioned body, the presence of five unequal teeth per esophageal sector, and a spicule tip bifid in ventral view in males. This project included the analysis of the structure and histochemistry of the adult nematode cuticle layers and egg-shell layers through the use of light and electron microscopy. Embryonation of *D. translucida* eggs was attempted to recover various larval stages. Additional information on *D. translucida* includes the presence of six cuticle layers, one exogenous with three endogenous egg-shell layers, and an egg operculum similar to that of *D. kuntzi*.

Dentostomella translucida Schulz & Krepkorgorskaja (1932) is a parasitic nematode found in the intestine of wild rodents including *Meriones unguiculatus* Milne-Edwards (Wightman et al. 1978, Pilitt and Wightman 1979), *Meriones meridanus* (Danzan 1978), *Rhombomys opimus* (Schulz and Krepkorgorskaja 1932, Shleikher and Samsonova 1954, Danzan 1978), *Dipus sagitta* (Danzan 1978), *Mastomys fumatus* (Chitwood 1963), and *Mesocricetus auratus* (Greve 1985). Even though the genus *Dentostomella* has not been shown to be detrimental to the hosts, it is highly infectious and continues to appear in parasite surveys for rodents. *Dentostomella* was established by Schulz and Krepkorgorskaja in 1932 while describing *D. translucida* in *Rhombomys opimus* Lichtenstein in Kazakhstan, USSR. The genus was later placed in the suborder Oxyurata due to the presence of male caudal alae, genital papillae surrounding the cloaca, spicule weakly chitinized, absence of gubernaculum, and the position of vulva in the anterior half of female worm. Skrjabin et al. (1960) established the new family Heteroxynematidae (superfamily Oxyuroidea), and Petter and Quentin (1976) established the subfamily Heteroxynematinae, which included *Dentostomella* as one of the five known genera. The characteristics of Heteroxynematinae include: the absence of a cuticular shield at the cephalic end, and a cuticular ornamentation before the male cloaca consisting of curry combs and plates with suckerlike membranes. There are four other known species in the genus, *D. kuntzi*, *D. grundmanni*, *D. legerae*, and *D. karachiensis* described by Myers (1961), Chitwood (1963), Quentin (1975), and Bilqees (1978), respectively. Compared to other pinworms in the same genus, *D. translucida* is distinguished by a large, evenly proportioned body, the presence of five teeth per esophageal sector, and a spicule tip bifid in ventral view for the male.

Mongolian gerbils, *Meriones unguiculatus*, housed at the small animal center at Brigham Young University, were hosts for *D. translucida*. The source or route of infection to the host is probably via infective eggs in the bedding and food. The probable life cycle of the worm would be similar to that of other pinworms, namely: eggs are released in large numbers from a mature, gravid female nematode at death and subsequently appear sporadically in the fecal mass of the host. The eggs embryonate within 1–4 days into an infective stage and, following ingestion, develop into larvae in the stomach of the host because of the favorable low pH and digestive enzymes.

The objective of this study is to incorporate different levels of microscopy (from light to electron optics) and histochemistry to provide

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pertinent morphological and anatomical features whereby *D. translucida* can be further described and taxonomically delineated from other species of the same genus. These techniques provide the first information on the structure of the egg-shell layers and the cuticle layers of the adult *D. translucida*.

MATERIALS AND METHODS

Live *Dentostomella translucida* were obtained from the small intestine of 50 necropsied *Meriones unguiculatus*. The nematodes were washed in tap water and were further prepared for various microscopic analyses as follows.

Fecal Examination and Embryonation

Fecal samples were collected and thoroughly mixed with Sheather's solution, strained through a wire sieve to remove coarse elements, transferred to test tubes, and allowed to stand undisturbed for 1 hr. The tubes were filled so that a clean slide placed over the mouth closed the tube without trapping air between the suspension and the slide. Each slide was then examined with bright field, as well as Nomarski interference, light microscopy to determine the presence of helminth eggs. Gravid female nematodes, teased from the small intestine, were put in petri dishes with warm water and cut into pieces to expel the eggs. The petri dishes were kept in the dark at 37 C for 4–7 days and observed daily; digestive enzymes were added to attempt in vitro hatching following embryonation.

Histochemistry

Specimens of *D. translucida* were placed in 10% buffered formalin and Bouins fixatives. After dehydration with ethanol and embedding in paraffin, the specimens were sectioned at 4–6 μm with a rotary microtome. Sections were mounted on slides and stained with haematoxylin and eosin (H & E), Masson trichrome, pentachrome, orcein, Sudan IV, periodic acid schiff (PAS), and azure with toluidine-blue stains in order to identify the presence and the locations of various types of tissues.

Scanning Electron Microscopy (SEM)

Male and female specimens of *D. translucida* were fixed in 3% glutaraldehyde in a 0.1 M phosphate buffer (pH 7.3). They were rinsed in the buffer and dehydrated through a graded series of ethanol, followed by changes in absolute acetone, and critical-point dried with liquid CO_2 as the transitional fluid. The specimens were mounted on aluminum stubs, coated with gold utilizing a Polaron sputter coater, and examined in an Amray 1000A at 20 KV.

Transmission Electron Microscopy (TEM)

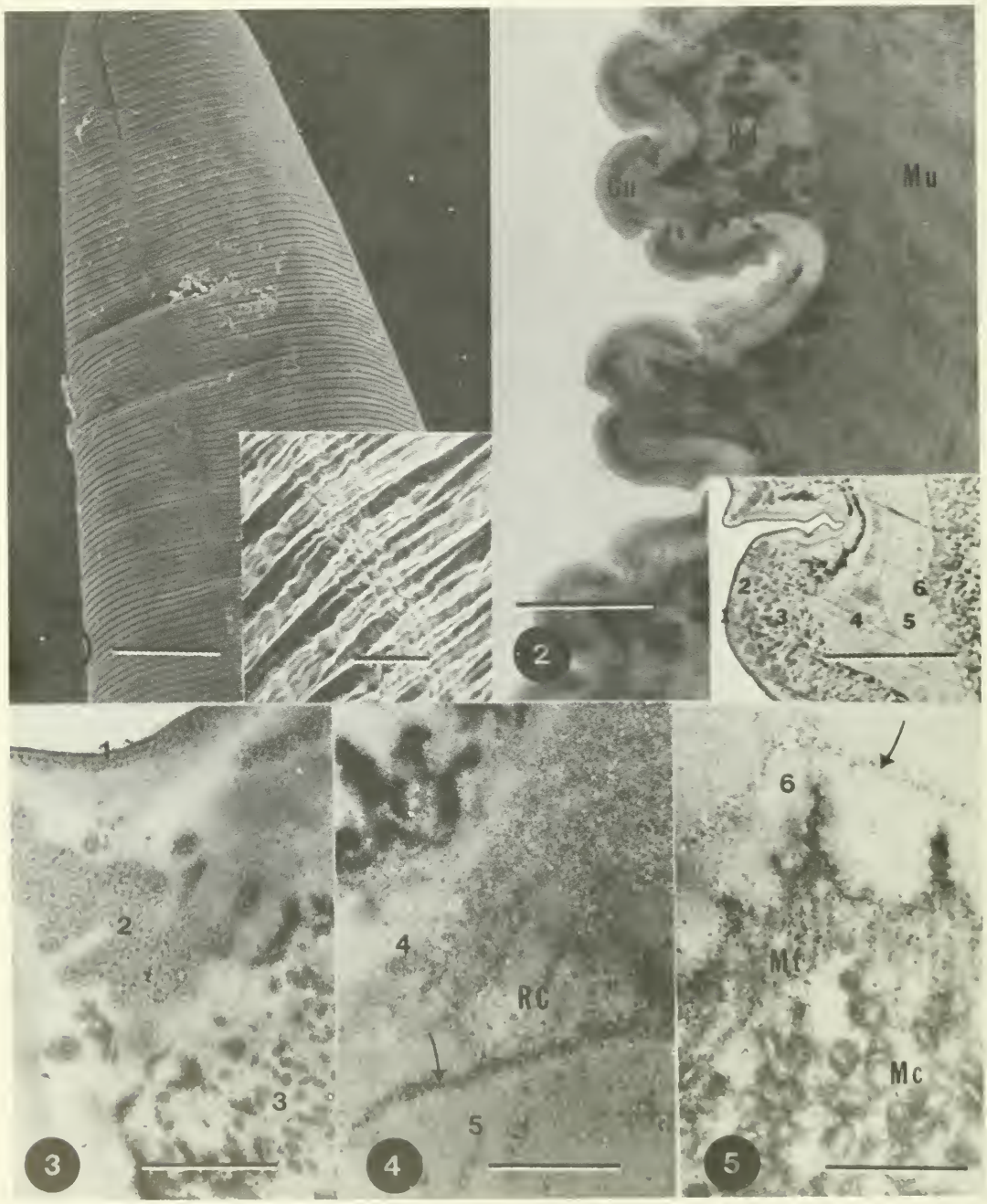
Specimens of *D. translucida* were rapidly removed from the gerbils. Whole nematodes were cut into 3–4 parts to allow fixation of internal viscera. Sections were fixed for 2 hr in 2% glutaraldehyde–3% acrolein in 0.1 M sodium cacodylate buffer (pH 7.3), then rinsed with several changes in 0.1 M sodium cacodylate washing buffer. The specimens were post-fixed in 1% osmium tetroxide for 2 hr, washed several times in 0.1 M sodium cacodylate buffer, and left in 0.5% uranyl acetate overnight. Following dehydration with a graded series of ethanol, the specimens were embedded in 100% Spurr resin (Spurr 1969). The tissue was sectioned with glass knives on a Sorvall MT–2 microtome and placed on formvar-coated grids (200 mesh). Prior to viewing, sections were stained with lead citrate and 1% uranyl acetate. The grids were examined in a Philips high-resolution EM 400 transmission electron microscope.

RESULTS

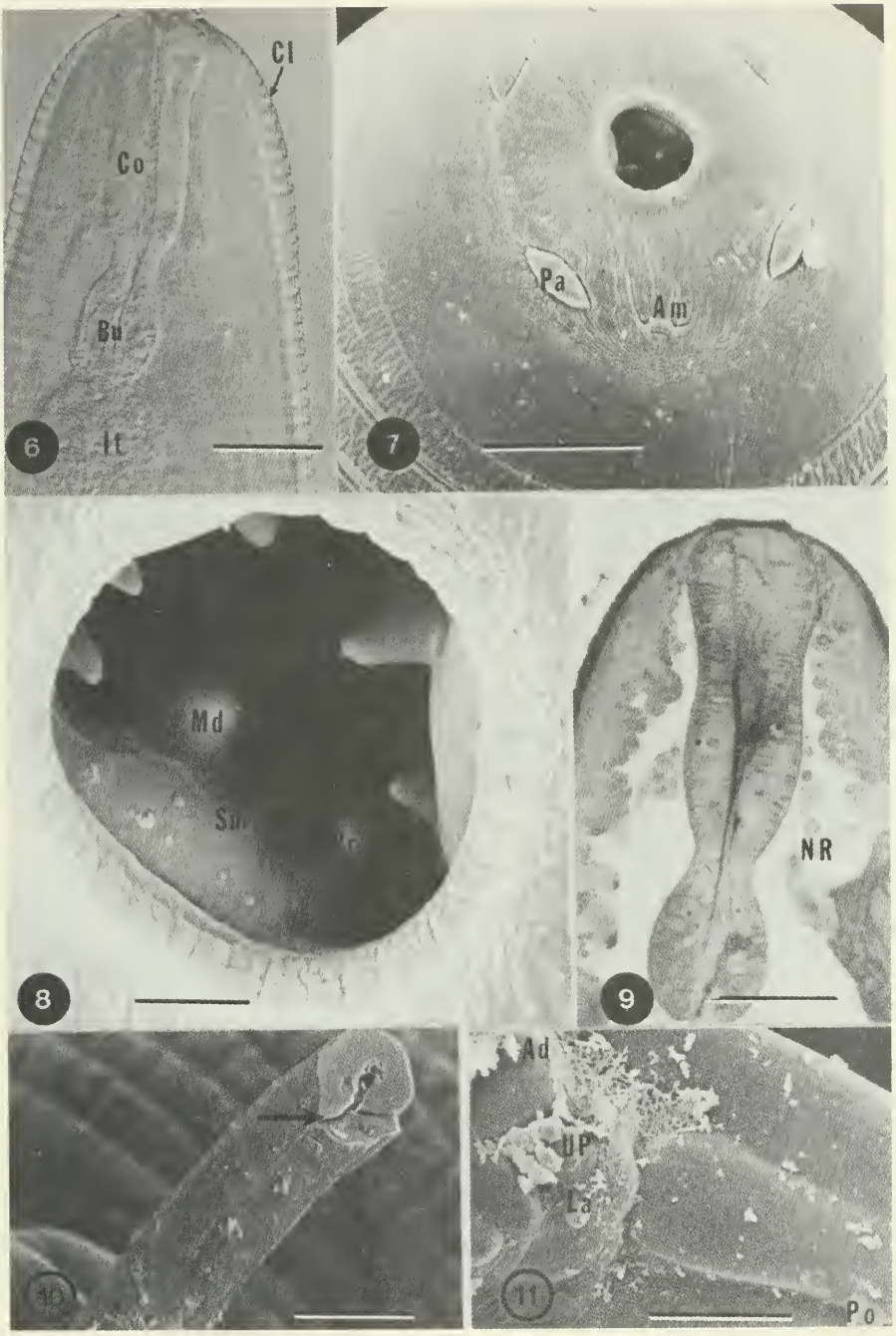
Description

The following features, determined with light and electron optics, characterize *D. translucida* specimens.

ADULT.—The body is cylindrical and elongated with a transparent cuticle possessing transverse striations. There are ventral and dorsal annulations interrupted by two lateral longitudinal ridges extending the full length of the body (Fig. 1). The cuticle is divisible into the following six rudimentary layers (Figs. 2–5): (1) layer one is 30 nm thick and consists of a highly electron-dense, double membranelike structure; (2) layer two is 950 nm thick, separated by a fine granular band from layer one, and consists of an electron-lucent matrix with granular patches; (3) layer three is 1.3 μm thick and is composed of two



Figs. 1–5. *Dentostomella translucida*. 1. Scanning electron micrograph showing the cylindrical body with annulations and longitudinal ridge (bar = 100 μm). Inset showing the interruption of annulae by the ridge (bar = 5 μm). 2. Azure with toluidine-blue stained photomicrograph showing a rugose pattern of the cuticle layers (Cu), hypodermis layer (Hd), and muscle band (Mu) (bar = 50 μm). Inset showing six distinct cuticle layers (TEM) (bar = 4 μm). 3–5. Transition electron micrographs of six cuticle layers and hypodermocyte. 3. Layer 1, electron-dense double bands; layer 2, electron-lucent granular patches, layer 3, electron-dense and electron-median globules (bar = 670 nm). 4, 5. Layers 4–6, homogenous matrix with radial channels (RC), and the layers separated by electron-dense bands (arrows). Note hypodermocyte (Hd) bounded with microtubules (Mt) and mitochondria (Mc) (bars = 670 nm).



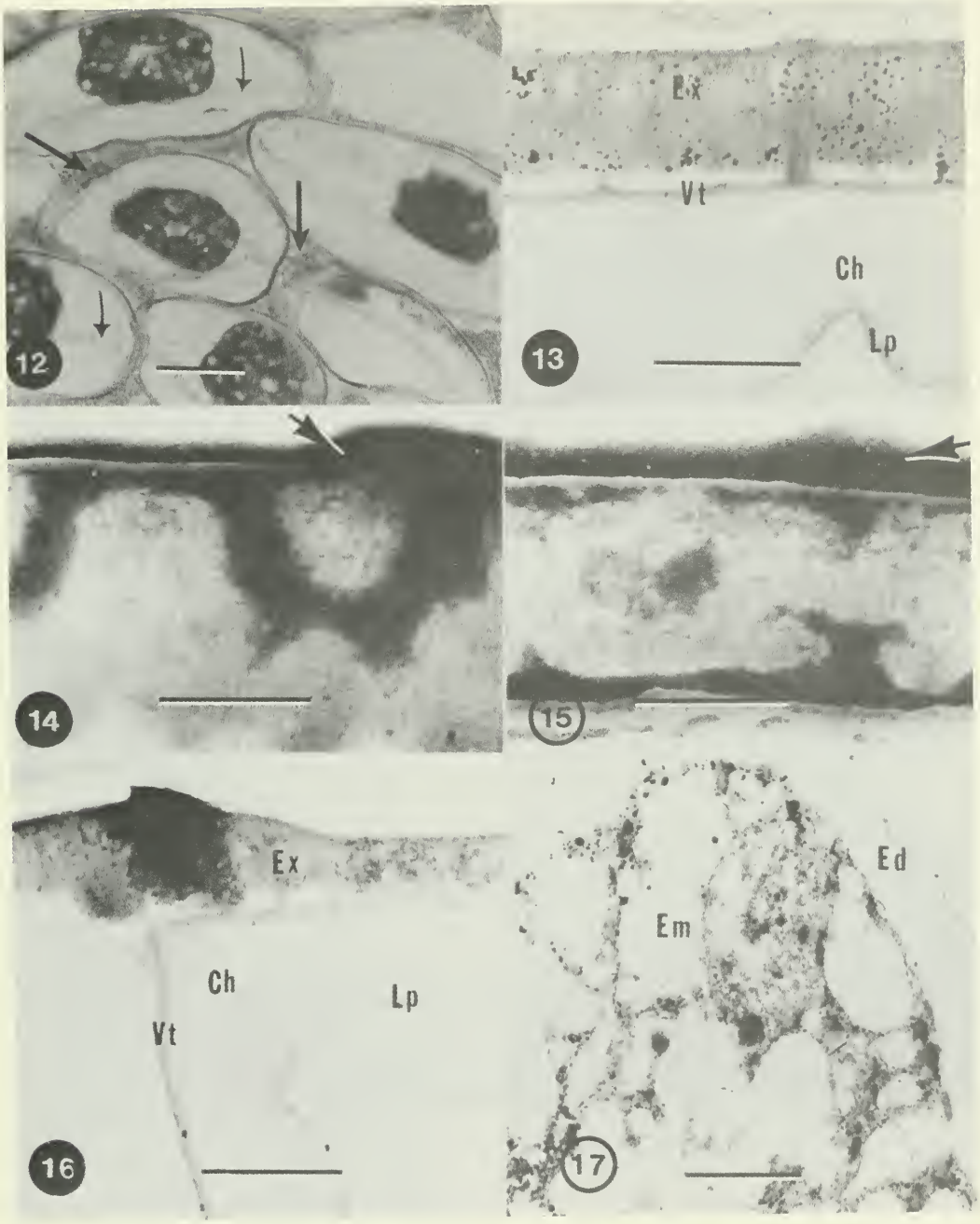
Figs. 6–11. Cephalic end of *D. translucida*. 6. Nomarski interference micrograph showing small cephalic inflation (Cl), esophageal corpus (Co), bulb (Bu), and enlarged intestine (It) (bar = 180 μm). 7. Presence of four cephalic papillae (Pa) and two amphids (Am) on the outer circle (bar = 18 μm) (SEM). 8. Mouth opening showing three esophageal sectors, each sector with one median tooth (Md), two perimeter teeth (Pr), and two small teeth (Sm) (bar 2.8 μm) (SEM). 9. Toluidine-blue with azure-stained photomicrograph showing neurons that form a nerve ring (NR) (bar = 140 μm). 10, 11. Male *D. translucida* caudal end. 10. Male spicule tip bifid in ventral view (arrow) (bar = 10 μm). 11. Male caudal papillae on the bursa; one adanal pair (AD), one unpaired (UP), one lateral pair (La), and one postanal (Po) pair (bar = 50 μm).

types of globular patches—an electron-dense and an electron-median; and (4) layers four, five, and six are composed of a similar homogenous matrix and measure 2.1, 1.0, and 0.4 μm, respectively. The latter three layers are separated by electron-dense granular bands. Electron-dense radial channels running perpendicular to the surface extend through layers four, five, and six. With staining for LM, the cuticle layers had an affinity for orcein, aniline blue, and pentachrome (yellow coloration), but no affinity for PAS and acid fuchsin. Toluidine-blue showed a strong affinity with layers two and three, but weaker affinity with four and five. The clarity of pattern and thickness of the cuticle layers varied among specimens and probably depends on the maturity of *D. translucida*. Due to the constriction at the annulation of the cuticle, a rugose pattern is expressed for this cuticular region (Fig. 2). The measurements for the six layers are taken at the thickest portions of the annulae. Below the cuticle layers, hypodermal cells are bound with numerous infolding microtubules (Fig. 5). A slight lateral cervical inflation (Fig. 6) is present, while the pharyngeal cavity, cephalic vesicle, lips, and alae are absent. One pair of subventral papillae, one pair of subdorsal papillae, and two lateral amphids are present at the external circle of the cephalic end (Fig. 7). The buccal cavity is characterized by a row of teeth arranged symmetrically on the margin of the triradiating esophagus sectors, one dorsal and two subventral. One sector of the esophagus includes a conical-shaped median tooth, which is the largest, and projects outward. Two perimeter teeth are situated on either side of the median tooth. The two smallest teeth connect to the perimeter teeth at the base located at the outer edge of the buccal cavity (Fig. 8). The esophagus is short (1/45 of body) and thick, with a constriction at the posterior end at the position of the esophago-sympathetic nerve ring that divides the spherical bulbous part from the cylindrical part (Fig. 9). The triradiating lumen of the esophagus is continuous with a fibrous esophago-intestinal valve. The esophagus is covered externally by a semicuticular membrane but without internal chitinized armament.

MALES.—The average length of the male nematode is 10.25 mm; the width at the level of the esophagus bulb, midbody, and anus measures up to 0.24, 0.47, and 0.23 mm, respectively. The esophagus is 0.29 mm long, 0.07 mm wide at the level of the esophagus bulb, and the cylindrical esophageal corpus is 0.21 mm long. The nerve ring, which measures 0.07 mm wide, encircles the base of the corpus (Fig. 9). There is an excretory pore 2.29 mm from the cephalic end. A cuticular swelling (bursa) at the ventral surface of the tail forms caudal cords on both sides, which range from 0.5 mm to 0.95 mm (situated 0.11 mm from the tail tip). The bursa is without supporting rays but has transverse annulation with cuticular platelets situated on the anterior surface of the cloaca. A single spicule, weakly chitinized, is 0.35 mm long, cylindrical, with a blunt distal end rounded in lateral view and bifid in ventral view (Fig. 10). The ventral caudal papillae on the fleshy bursa are present (Fig. 11). There is a pair of large adanal papillae 0.32 mm from the tail tip, an unpaired papilla between the adanal pair, and a pair of small lateral papillae slightly posterior to the protuberance. One pair of asymmetrically arranged postanal papillae is found 0.174 mm from the tail tip.

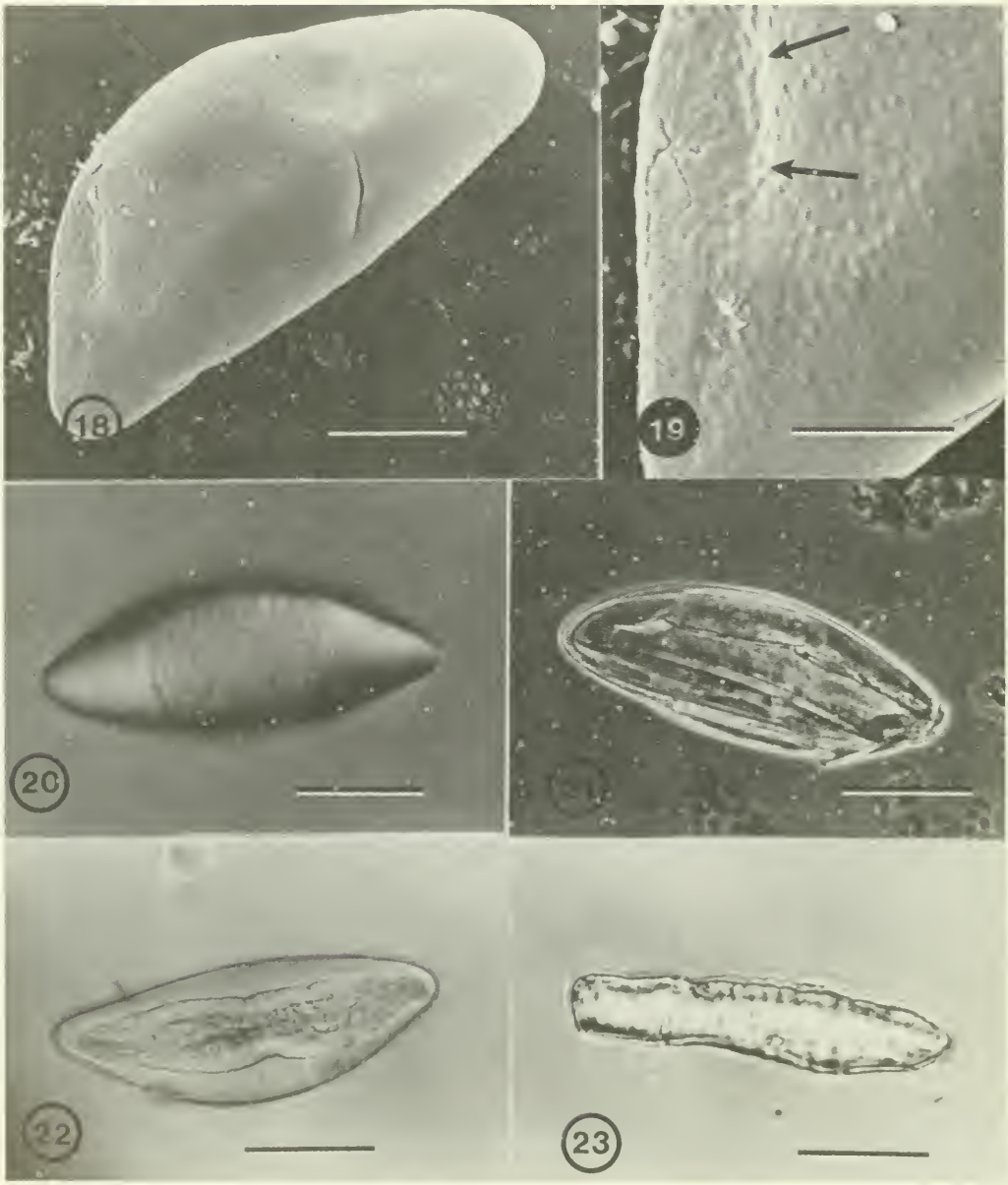
FEMALES.—The average length of the female nematode is 29 mm, and the width at the level of the esophagus bulb, midbody, and anus is 0.52 mm, 1.15 mm, and 0.35 mm, respectively. The esophagus is 0.4 mm long and 0.2 mm wide at the bulb, with a cylindrical corpus part 0.25 mm long terminating at the encircling nerve ring. An excretory pore situated behind the esophagus is 3.9 mm from the cephalic end. Two bulbous seminal receptacles are present, one above and one below the vulva. The vulva is characterized by a transverse slit 12 mm from the cephalic end. The vagina is 1.1 mm long by 0.23 mm thick, directed cephalad and connected to a muscular, walled vagina vera. The vagina vera is directed caudad after a reflex to an unpaired uterine tube and widens into a common egg chamber. The egg chamber, 1 mm long, divides into two uteri situated posterior to the vulva and terminates at 0.64–1.4 mm from the tail (Fig. 15) tip.

OVA.—*Dentostomella translucida* eggs are elongated, asymmetrical, flattened on one side, and measure 130 μm long by 44 μm wide (Fig. 12). The thickness of the shell is uneven, and the egg-shell consists of: (1) an exogenous uterine layer, (2) a vitelline layer, (3) a



Figs. 12–17. *Dentostomella translucida* eggs. 12. Azure with toluidine-blue-stained photomicrograph. Note the position of endogenous egg-shell layers (small arrows) on the flattened side of the egg. Large arrows show dense granules secreted by uterine cells (bar = 30 μm). 13. Four egg-shell layers: exogenous (Ex), vitelline (Vt), chitinous (Ch), and lipid (Lp) layers (bar = 530 μm). 14, 15. Exogenous egg-shell layers showing electron-dense plugs and columnous materials. Note the fringe materials on the surface (arrows) (bar = 300 nm). 16. Four egg-shell layers (abbreviations same as 13) showing the endogenous layers being separated from the exogenous layer (bar = 640 nm). 17. Flattened side of the egg showing the embryo (Em) adjacent to the endogenous layers (Ed) (bar = 4 μm).

chitinous layer, and (4) a lipid layer (Figs. 13–17). This nomenclature for the egg is based on Wharton's description of oxyurid eggs (Wharton 1979a, 1979b, 1979c). The



Figs. 18–23. 18, 19. Scanning electron micrographs of *D. translucida* egg with bumps on the surface. Note the opercular groove (arrows) with sutures (18, bar = 20 μm; 19, bar = 10 μm). 20–23. Larval stages of *D. translucida* (bar = 43 μm). 20. A single-celled embryo. 21. A coiled (a ring and a half) larva. 22. A vermiform larva. 23. A hatched larva.

exogenous uterine layer is 560 nm thick, continuous, and highly variable in morphology. This layer consists of electron-dense plugs or columnous materials embedded between coarse fibrils that are perpendicular to the outer surface. Histochemically, the exogenous uterine layer shows an intense red coloration with pentachrome, Masson trichrome, and Sudan IV. The exogenous uterine layer has an affinity for azure with toluidine-blue, but has no affinity for orcein and PAS. At the outer surface of the egg-shell, there are irregular fringes of electron-dense materials that are tightly adhered (Figs. 14, 15). The vitelline layer is membranelike, 30 nm thick, and situated adjacent to the curved side of the egg, but this layer is separated from the exogenous layer on the flattened side of

TABLE 1. Comparative measurements (in mm) and structures of five *Dentostomella* spp.

Species:	*D. grundmanni*		*D. legerae*		*D. karachiensis*		*D. kuntzi*		*D. translucida*	
Source of data:	Chitwood (1963)		Quentin (1975)		Bilqees (1978)		Ashour and Lewis (1982)		Present study	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Body: length	4.8	15.6	7.5	21.0	9.1		10.1	19.9	10.25	29.0
width	0.26	0.7	0.3	0.8	0.8		0.22	0.33	0.47	1.15
Esophagus: length	0.23	0.34	0.27	0.31	1.17		0.29	0.34	0.29	0.4
Excretory pore	3.9*		2.32	3.60			2.64	2.88	2.29	3.9
Spicule: length	0.26		0.24		0.2		0.16		0.35	
distal end	bidentate		rounded		brushlike		rounded		bifid	
Vulva from anterior end		8.3		10.0				7.43		12.0
egg: length	0.13		0.15				0.13		0.13	
width	0.04		0.04				0.06		0.04	
Host	*Eutamias quadrivittatus*		*Gerbillus campestris*		*Axis* spp.		*Acomys cahirinus*		*Meriones unguiculatus*	
Cephalic inflation	small		narrow, long		large, long		large		small	
Cephalic papillae	10		4				4		4	
No. of teeth	3		9		8		9		15	
Caudal papillae	8		6		0		7		7	
adanal	1 pair		0				1 pair		1 pair	
postanal	3 pairs		3 pairs				2½ pairs		2½ pairs	

*Sex not available

the egg (Figs. 16, 17). The chitinous layer is 650 nm thick, electron-lucent, and demarcated on its inner face by the innermost lipid layer, which is 16 nm thick. Endogenous layers, which include the vitelline, chitin, and lipid layers, were not found in the histological sections presumably because of their fragile nature. However, research has confirmed that the chitinous layer contains chitin secreted by the embryo (Bird and McClure 1976, Pearse 1968). The lipid layer is characterized by positive reactions with lipid and phospholipid stains (Wharton 1979a). For the scanning electron micrographs, the surface of the shell was covered with numerous bumps, but no pores or ridges were present (Fig. 18). Although we were unable to detect a marked opercular spot using LM and TEM, SEM showed sutures on an operculum near one pole of the curved side of the egg (Figs. 18, 19). This observation is consistent with another report for operculated *D. kuntzi* ova (Ashour and Lewis 1982).

Embryonation

Most *D. translucida* eggs recovered from the host's feces contain a single-celled embryo (Fig. 20). The eggs from the feces or directly from the uterus of a fertilized female worm can develop into a coiled (a ring and a half) larva within a few hours (Fig. 21). The next stage is a vermiform larva, which appears within 48 hours when incubated in water at 37 C (Fig. 22). The vermiform larva is stout, 130 μm long, and possesses a well-formed anterior portion of the digestive system, but the sex cannot be identified at this stage of development. Chitwood and Chitwood (1950) indicated that oxyurid larvae may have an inactive stage between the first and second vermiform stages, but *D. translucida* larvae did not exemplify these stages. However, the active larvae seemed to enter an inactive phase and seldom hatched out of the egg-shell. After 6 days of incubation, some larvae emerged from the egg via the operculum, and one larva without the egg-shell was recovered on another occasion (Fig. 23). Further attempts to incubate and hatch the larvae beyond 6 days were not successful.

DISCUSSION

Comparisons of *Dentostomella* Species

Dentostomella translucida is distinguished from the other four *Dentostomella* species primarily by a large body size with a minute cephalic inflation, the presence of five teeth per esophageal sector, and, in the male, the presence of seven caudal papillae and a bifid spicule tip. Table 1 shows the body measurements and other pertinent characteristics of

D. translucida, *D. grundmanni* (Chitwood 1963), *D. kuntzi* (Ashour and Lewis 1982), *D. legerae* (Quentin 1975), and *D. karachiensis* (Bilqees 1978). Measurements for five *Dentostomella* species given in Table 1 were obtained from both full-grown and juvenile nematodes. The juvenile nematodes tend to have different body proportions than adult nematodes. Thus, some of the measurements, such as the length of the esophagus, the position of the excretory pore and vulva from the anterior end, and the size of the spicule in the male, are unreliable sources for differentiating species based on current data. Pertinent characteristics listed in Table 1 will be emphasized in this discussion.

Scanning electron micrographs on *D. kuntzi* published by Ashour and Lewis (1982) show structures similar to *D. translucida*, such as four submedian papillae and two amphids on the external circle (Fig. 7), and the number and arrangement of caudal papillae for males; they also show differences in the number of teeth when the two species are compared. *Dentostomella kuntzi* has a more conspicuous cephalic inner circle than *D. translucida*, which may be why Myers' (1961) LM studies indicated that *D. kuntzi* has six papillae in the inner circle. Chitwood (1963) indicated that *D. grundmanni* has four cephalic papillae on the outer circle and six more papillae on the inner circle that are not found in other *Dentostomella* species. With additional SEM work, the presence of papillae on the inner circle can be confirmed. *Dentostomella legerae* does not possess structures that are strikingly diverse from or similar to *D. translucida*. However, *D. legerae* shows greater similarities with *D. Kuntzi* in body measurements and conformation for female nematodes. Chitwood (1963) previously distinguished *D. grundmanni*, *D. translucida*, and *D. kuntzi* by the body conformation of adult females as follows: *Dentostomella grundmanni* is very stout, especially in the post-vulvar region, *D. translucida* is long and evenly proportioned, and *D. kuntzi* is very slender. *Dentostomella karachiensis* appears most different from the other species in morphology; the male caudal papillae do not exist, and eight teeth are present on three esophageal sectors that result in an uneven distribution of teeth. Also, the presence of modified cuticle squares near the cloaca and a brushlike spicule tip are distinct characteristics of *D. karachiensis*. Characters of the female *D. karachiensis* cannot be reviewed since it has not been recovered from host animals.

The cuticle of *D. translucida* has morphological characters that may be used to differentiate it from other oxyurids. The TEM study indicated that cuticle layers are highly complex, with many layers of different chemical composition that aid in worm survival when subjected to digestive enzymes from the host. The histochemical study shows the presence of reticular, elastin, and collagenous-type proteins that maintain the texture and structure of the nematode.

Dentostomella translucida Ova

The egg-shell of *D. translucida* exemplifies the basic pattern for most oxyurids as described by Wharton (1979a, 1979b, 1979c) for *Aspiculuris tetraptera*, *Syphacia obvelata*, and *Hammerschmidtiella diesingi*. However, the exogenous uterine layer is considerably different in morphology for *D. translucida* as compared to the other three oxyurids listed above. The structures of the vitelline, chitin, and lipid layers are similar. Wharton (1979b, 1979c) indicated that exogenous layers are formed by secretions from the uterine cells; thus, such differences between the oxyurids he studied and *D. translucida* may reflect the structural and physiological differences of the female reproductive tract, wherein the variability of egg-shell structure for different species can be a pertinent taxonomic feature. The exogenous layer, being nonporous, indicates that the embryo and the endogenous layers are not under direct influence from the uterine cells. The histochemical reactions of the exogenous layers show the presence of lipids and fibrinoid and reticular proteins. The dense granules (Fig. 12) secreted by the uterine cells that surround the egg have a similar histochemical reaction to that of the exogenous layers, thus indicating a common origin for these layers. Figures 14 and 15 show the egg surface being laced by electron-dense fringe materials that seem to provide stickiness to the oxyurid ovum. The *D. translucida* egg has an adhesive nature, as do most other oxyurids, which aids in spreading infections to other hosts. The endogenous layers, the vitelline, chitin, and lipid layers, run parallel

to the exogenous layer on the curved side of the egg, but peel at a 90-degree angle on the flattened side of the egg (Fig. 16). It appears that the exogenous layer is not directly associated with nor bonded to any of the three endogenous layers. Although Wharton (1979a), in TEM studies, found that the composition of the operculum is different from the remainder of the egg-shell, only SEM showed the existence of an operculum for *D. translucida* eggs. The presence of an operculum is in contrast to previous reports that the eggs of Heteroxnematidae do not have an operculum (Petter and Quentin 1976).

A limited number of larval stages were recovered from our attempts to cause embryonation. As indicated by the experimental passages of Wightman et al. (1978), the eggs released with the fecal mass of the host are infectious within 1–4 days. Thus, according to the embryonation studies, eggs with a coiled larva and a vermiform larva are the infective stages. It should be noticed that the size of the larva hatched from the egg is approximately the same as the larva inside the egg. Also, the presence of a rather stout and large esophagus for the larva indicates the abilities to receive a better type of nourishment and to attach to the mucous membranes of gastrointestinal tissues.

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LITERATURE CITED

ASHOUR, A. A., AND J. W. LEWIS. 1982. The morphology of *Dentostomella kuntzi* (Nematoda: Oxyuroidea) from Egyptian rodents. Journal of Helminthology 56: 159–168.

BILQEES, F. M. 1978. *Dentostomella karachiensis*, new species (Nematoda: Oxyuridae) from *Axis* sp. Pakistan Journal of Zoology 10: 279–281.

BIRD, A. F., AND M. A. MCCLURE. 1976. The tylenchid (Nematoda) egg-shell: structure, composition and permeability. Parasitology 72: 19–28.

CHITWOOD, B. G., AND M. B. CHITWOOD. 1950. Introduction to nematology. University Park Press, Baltimore. 334 pp.

CHITWOOD, M. B. 1963. *Dentostomella grundmanni* n. sp. (Nematoda: Oxyuridae) from *Eutamias quadrivittatus* (Say 1823). Proceedings of the Helminthological Society of Washington 30: 70–72.

DANZAN, G. 1978. On the nematode fauna of lagomorphs and rodents of the Mongolian People's Republic. Trudy Gel'mintologii Lab Akademii Nauk S.S.S.R. 28: 9–16.

GREVE, J. H. 1985. *Dentostomella translucida*, a nematode from the golden hamster. Laboratory Animal Science 35: 497–498.

MYERS, B. J. 1961. Helminth parasites of reptiles, birds, and mammals in Egypt. VI. *Dentostomella kuntzi* n. sp., a new oxyurid nematode from *Acomys* sp. Canadian Journal of Zoology 39: 55–57.

PEARSE, A. G. E. 1968. Histochemistry: theoretical and applied. Churchill, London.

PETTER, A. J., AND J. C. QUENTIN. 1976. Keys to genera of the Oxyuroidea. *In:* CIH keys to nematode vertebrates. No. 4. Commonwealth Agricultural Bureaux, England. 30 pp.

PILITT, P. A., AND S. R. WIGHTMAN. 1979. A redescription of *Dentostomella translucida* Schulz and Krepkorgorskaja, 1932 (Nematode: Heteroxynematidae) parasite of domestic Mongolian gerbils, *Meriones unguiculatus* Milne-Edwards. Proceedings of the Helminthological Society of Washington 46: 36–42.

QUENTIN, J. C. 1975. Oxyures de rongeurs. Deuxieme partie. Essai de classification of oxyures Heteroxynematidae. Memoires du Museum National D'Histoire Naturelle. Nouvelle Serie A, Zoologie 94: 51–61.

SCHULZ, R. E., AND T. A. KREPKORGORSKAJA. 1932. *Dentostomella translucida* n. gen., n. sp. (Nematoda, Oxyurinae) aus einem Nagetier (*Rhombomys opimus* Licht.). Zoologischer Anzeiger 97: 330–334.

SCHLEIKHER, E. I., AND A. V. SAMSONOVA. 1954. Helminthfauna of the great gerbil (*Rhombomys opimus*) of Uzbekistan. Contributions to Helminthology. Published to commemorate 75th birthday of K. I. Skrjabin. Akademii Nauk S.S.S.R., Moscow. English translation, 1966. U.S. Department of Commerce, Washington, D.C. 804 pp.

SKRJABIN, K. I., N. P. SHIKHOBALOVA, AND E. A. LAGODOVSKAYA. 1960. Oxyurata of animals and man. Part I. Oxyuroidea. Osnovy Nematodologii. Akademii Nauk S.S.S.R., Moscow. English translation, 1974. U.S. Department of Commerce, Washington, D. C. 526 pp.

SPURR, A. R. 1969. A low-viscosity epoxy resin embedding medium for electron microscopy. Journal of Ultrastructural Research 26: 31–43.

WHARTON, D. A. 1979a. The structure of the egg-shell of *Aspiculuris tetraptera* Schulz (Nematoda, Oxyuroidea). Parasitology 78: 145–154.

———. 1979b. The structure and formation of the egg-shell of *Hammerschmidtiella diesingi* Hammerschmidt (Nematoda: Oxyuroidea). Parasitology 79: 1–12.

———. 1979c. The structure and formation of the egg-shell of *Syphacia obvelata* Rudolphi (Nematoda: Oxyurida). Parasitology 79: 13–28.

WIGHTMAN, S. R., P. A. PILITT, AND J. E. WAGNER. 1978. *Dentostomella translucida* in Mongolian gerbils (*Meriones unguiculatus*). Laboratory Animal Science 28: 290–296.

SELECTION OF MICROHABITAT BY THE RED-BACKED VOLE, *CLETHRIONOMYS GAPPERI*

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ABSTRACT.—*Clethrionomys gapperi* were captured in microhabitats with greater densities of overall cover than at noncapture or random sites within the study area. Variables describing cover density and distance from free water were selected in a discriminant function analysis to differentiate between vole capture and noncapture sites. Vole capture sites had greater amounts of cover within 4 dm above ground surface and were further from standing water than noncapture sites. The preferential use by *C. gapperi* of microhabitats with greater densities of cover is in agreement with laboratory and field assessments of habitat use reported in the literature.

Gapper's red-backed vole occurs in forests of the Hudsonian and Canadian life zones. It occurs chiefly in coniferous, deciduous, and mixed forests but sometimes occurs in cutover areas or blowdowns. Its presence appears to be associated with abundant litter of stumps, rotting logs, exposed roots, and a dense leaf litter. Its diet consists of hypogeous fungi, vegetation, seeds, insects, and other invertebrates (Merritt 1981). The abundance of red-backed voles has frequently been reported to be related to moist habitats (Gunderson 1959, Getz 1969, Kirkland and Griffin 1974, Miller and Getz 1977, Merritt and Merritt 1978, Mihok 1981, Vickery 1981) and dense cover (Lovejoy 1975, Kirkland 1977, Miller and Getz 1972, 1973, Gunther et al. 1983). The relationship between cover density and vole occurrence, however, has not been well quantified.

We made a statistical analysis of the relationship between the abundance of red-backed voles and characteristics of the habitat as part of a study to investigate the relationship between habitat structure and predation in red-backed voles and deer mice, *Peromyscus maniculatus* (Wywialowski 1987). To assess the importance of habitat attributes to red-backed vole abundance, we compared capture sites with noncapture and random sites (Williams 1983). Habitat variables reported as important to *C. gapperi* by other studies (Johnson 1981) were selected a priori for this study.

STUDY AREA

The study site was south of the South Sink on the Cache National Forest in northern Utah. The site ranged from 2,370 to 2,380 m elevation and had a prevailing northerly aspect. The trapping area was dissected by numerous small streams and seeps. A mixture of habitats occurred on the site ranging from a small, open meadow to mature forest. The site was dominated by subalpine fir, *Abies lasiocarpa*, with Engelmann spruce, *Picea engelmannii*, Douglas-fir, *Pseudotsuga menziesii*, lodgepole pine, *Pinus contorta*, and quaking aspen, *Populus tremuloides*, also present. The dominant "shrub" was subalpine fir seedlings, and a variety of forbs were present. See Schimpf et al. (1980) for a detailed description of the area.

METHODS

Livetraps were placed in a grid pattern on 10 July 1983. The trapping grid was located in an area where *C. gapperi* had been successfully captured the previous fall. Traps were spaced approximately 15 m apart and were set in what was judged to be the best potential vole capture microsite within a 9-m^2 area centered on each grid node. The traps were baited with a mixture of oatmeal and peanut butter and set on 13 July 1983. Traps were checked the following morning, evening, and the next morning, at which time they were closed. All voles were removed from the site

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for use in a laboratory experiment (Wywialowski 1987), while other rodent species were released. The same procedures were followed starting on 11 August and on 5 October 1983, except that during the second session both deer mice and voles were removed.

To determine the range of the habitat attributes available to voles, we selected 70 random points within the trapping area. These points were chosen by randomly locating a point in the northeast quadrant of the study area and systematically spacing the remaining 69 points across the study area.

Habitat structure, including composition of horizontal cover, plant species composition, and physical attributes, were recorded at each of the 101 trap sites and 70 random points within the trapping area (Table 1). Measures of habitat structure were taken within a 1-m radius of each trap site or random point. Cover density was estimated at 10-cm intervals up to 1 m by visually aggregating the cover and estimating the percent of the total area, similar to the methods used in habitat typing (Steele et al. 1981). The amount of cover was recorded as: none, trace to 5%, 5–15%, 15–25%, through 85–100%. Percent of horizontal cover was measured by line-intercept on two 2-m transects centered on the trap to estimate the amount of standing tree, downed wood, rock, evergreen or deciduous shrub, and herbaceous cover. Tree overstory was measured by summing five ocular sightings of the canopy (recorded as 0 = sky or 1 = blocked by trees, with a sighting over the trap and at both ends of the two transects). Nearest tree, shrub, and herbaceous species were recorded. Physical factors measured included distance to, diameter of, and age class of the nearest downed wood; depth of duff (to mineral soil); and distance to nearest free water.

Analysis of the data was done using SPSSx, the Statistical Package for the Social Sciences (SPSS Inc. 1983). Sites where a single juvenile male was captured (n = 7) were not included in the analysis because this group of voles ranks at the bottom of the dominance hierarchy of sex and age classes (Mihok 1981), and the animals were most likely to occupy suboptimal microhabitats. Therefore only 94 trapping sites were used in the analysis.

Differences between random, noncapture, and capture sites were tested using t-tests for differences between trap and random sites, Kendall's Tau for comparisons of habitat attributes between capture and noncapture sites, and Chi-square for determining whether plant species presence was related to vole capture and noncapture sites (Hollander and Wolfe 1973).

Discriminant function analysis (DFA) was used to assess the ability to predict vole capture or noncapture sites based on the habitat structure at the trap sites. Prior probabilities were set at size of the groups to minimize any sample-size bias (Titus et al. 1984).

TABLE 1. Habitat variable names and their descriptions.

Name	Description
CD1-CD10	Percent of cover density within a meter radius of the site at 0–10 to 90–100 cm above ground, respectively.
CLOW	Mean of the values from CD1 through CD3.
CMID	Mean of the values from CD4 through CD7.
CHIGH	Mean of the values from CD8 through CD10.
CSUM	Mean of the values from CD1-CD10.
SHRUB	Percent of cover composed of shrubs within a 1-m radius of the site.
FORB	Percent of cover composed of forbs within a 1-m radius of the site.
GREEN	Sum of SHRUB and FORB.
WOODY	Percent of cover composed of downed woody material within a 1-m radius of the site.
TREE	Percent of area composed of standing tree trunks within a 1-m radius of the site.
CANOPY	Percent of five measurements at the site and 1 m from the site in the four cardinal points.
DUFF	Depth of organic material to mineral soil in cm.
WATER	Distance to nearest open water in m.
LOG-DIST	Distance to nearest log greater than 1 dm in cm.
LOG-SIZE	Size of nearest log greater than 1 dm in diameter in cm.
LOG-CLASS	Age of downed logs rated on a scale of 1 = freshly fallen to 5 = mostly decayed after Thomas (1979).

TABLE 2. Means and standard errors of cover and habitat variables for random, vole capture, and vole noncapture sites.

	Sites					
	Random n = 70		Vole noncapture n = 41		Vole capture n = 53	
Variables	x	SE	x	SE	x	SE
CD1	27.2	3.0	56.0	4.1	60.5	6.1
CD2	16.5	2.5	43.9	3.7	50.7	3.9
CD3	11.8	2.2	33.1	3.2	40.8	3.2
CD4	8.9	1.9	24.9	2.8	32.5	2.9
CD5	7.2	1.7	19.5	2.4	25.2	2.5
CD6	5.9	1.6	15.7	2.1	19.1	1.9
CD7	5.0	1.4	13.9	2.1	16.3	1.5
CD8	3.8	1.2	11.9	1.8	14.6	1.5
CD9	3.6	1.2	11.6	1.8	12.4	1.2
CD10	3.4	1.2	11.4	1.8	10.9	1.1
CLOW	14.0	2.1	44.3	4.3	50.7	3.4
CMID	7.0	1.6	18.5	2.2	23.3	2.0
CHIGH	4.0	1.3	11.6	1.8	12.7	1.2
CSUM	9.0	1.6	24.8	2.2	28.9	1.9
SHRUB	13.2	3.0	34.0	5.0	41.1	4.8
FORB	27.1	4.1	10.9	2.7	13.1	2.9
GREEN	40.2	4.3	45.0	5.5	54.1	4.7
WOODY	8.4	2.0	12.0	2.1	11.5	1.9
TREE	0.7	0.3	3.8	0.9	2.1	0.6
CANOPY	45.0	4.1	74.0	4.2	57.0	9.0
DUFF	6.3	0.8	12.2	1.3	12.1	1.7
WATER	12.0	1.5	15.2	2.8	20.9	2.2
LOG-DIST	141.8	16.6	49.4	13.6	54.5	11.2
LOG-SIZE	18.3	2.0	24.1	3.5	21.3	2.3
LOG-CLASS	2.3	0.1	3.0	0.2	2.5	0.2

TABLE 3. Tests for ordered relationships between vole capture (n = 53) and noncapture (n = 41) sites with respect to the habitat variables at the trapsites. * = P ≤ .05, ** = P < .01.

Variable	Tau c value	Significance level
CD1	0.107	0.169
CD2	0.167	0.063
CD3	0.185	0.057
CD4*	0.189	0.052
CD5	0.149	0.099
CD6	0.152	0.092
CD7	0.162	0.079
CD8*	0.201	0.040
CD9	0.150	0.092
CD10	0.096	0.197
CLOW	0.125	0.138
CMID*	0.201	0.029
CHIGH	0.058	0.243
CSUM	0.088	0.216
SHRUB	0.106	0.172
FORB	0.035	0.373
GREEN	0.103	0.220
WOODY	−0.016	0.445
TREE**	−0.252	0.004
CANOPY	−0.099	0.193
DUFF	−0.061	0.296
WATER**	0.278	0.009
LOG-DIST	0.151	0.094
LOG-SIZE	−0.071	0.268
LOG-CLASS	−0.145	0.089

RESULTS

Over the three trapping sessions 119 red-backed voles were captured during 593 trapnights. Capture success averaged 20 voles per 100 trapnights.

Microhabitat differed among vole capture, noncapture, and random sites. The mean percentage of cover for all trap sites (capture and noncapture) was greater than the mean percentage of cover for the trapping area, as sampled by random points within the trapping grid ($t = 7.95$, $P < .001$, Table 2). Voles were captured at sites that had more cover than noncapture sites for the mean cover density from 30 through 70 cm (CMID, Tau c = 0.201, P = .029, Table 3). Eight of the 10 cover density variables (all except the bottom and top 1 dm) were significantly positively related at $P < .10$. Vole capture sites were less likely to be near trees (Tau c = −0.252, P = .004) and were farther from water than noncapture sites (Tau c = 0.278, P = .009, Table 3).

TABLE 4. Nearest tree to sites. Actual number and percent of the total for the study area given for random and trap sites. Observed and expected numbers are given for vole capture and noncapture sites.

	Tree species				
Site	*Abies lasiocarpa*	*Picea engelmannii*	*Pinus contorta*	*Populus tremuloides*	Total
Random (n)	20	28	6	14	70
(Percent)	28.6	40.0	8.6	20.0	97.1[a]
Trap (n)	42	30	7	15	94
(Percent)	44.7	31.9	7.4	16.0	100.0
Noncapture (n)	16	15	5	5	41
(Expected n)	18.3	13.1	3.1	6.5	
Capture (n)	26	15	2	10	53
(Expected n)	23.7	16.9	3.9	8.5	

[a]Two (2.9%) random sites had no tree within 5 m.

TABLE 5. Nearest shrub to sites. Actual number and percent of the total for the study area given for random and trap sites. Observed and expected numbers are given for vole capture and noncapture sites.

	Shrub species				
Site	*Abies lasiocarpa*	*Picea engelmannii*	*Pinus contorta*	*Populus tremuloides*	Total
Random (n)	32	0	9	15	70
(Percent)	45.7	0.0	12.9	21.4	79.3[a]
Trap (n)	66	4	8	16	94
(Percent)	70.2	4.3	8.5	17.0	100.0
Noncapture (n)	29	2	4	6	41
(Expected n)	28.8	1.7	3.5	7.0	
Capture (n)	37	2	4	10	53
(Expected n)	37.2	2.3	4.5	9.0	

[a]Fourteen (20.7%) random sites had no shrub within 5 m.

Capture sites were not associated with the species of the nearest tree ($X^2 = 3.86$, 3 d.f., $P = .28$, Table 4), the nearest shrub ($X^2 = 0.45$, 3 d.f., $P = .93$, Table 5), nor the nearest forb ($X^2 = 0.92$, 4 d.f., $P = .92$, Table 6).

The discriminant function analysis selected cover density from 3 to 4 dm above ground, distance from water, and number of trees within 1 m of the trap as the variables to distinguish between vole capture and noncapture sites (Table 7). Using these three variables, we correctly classified 65% of the sites as capture or noncapture sites. More errors in classification occurred for the noncapture sites (54% were classified as capture sites), whereas 78% of the capture sites were correctly classified. If only vole captures from the first nights of trapping were included in the discriminant analysis, 80% of the sites were correctly classified (76% of the capture sites and 95% of the noncapture sites).

DISCUSSION

The density of cover and the structure of the vegetation were important (Table 3) in determining probable capture sites of red-backed voles. Vole capture sites had high values of cover density through the 1-m height (Table 3). The cover density from 3 to 4 dm above the ground was the most important variable distinguishing between vole capture and noncapture sites (Table 7). Voles used areas of dense, and appeared to avoid areas with sparse, ground cover. Miller and Getz (1973) found *C. gapperi* to be more abundant in areas with shrub cover greater than 50%, herb cover greater than 25%, and debris cover greater than 25%. Similarly, California red-backed voles, *Clethrionomys californicus*, were negatively associated with the amount of light reaching the forest floor and the amount of ground vegetation (Maser et al. 1981) and

TABLE 6. Nearest forb to sites. Actual number and percent of the total for the study area given for random and trap sites. Observed and expected numbers are given for vole capture and noncapture sites.

	Forb species					
Site	*Arnica* spp.	*Ranunculus* spp.	*Osmorhiza* spp.	*Thalictrum* spp.	Other	Total
Random (n)	12	5	16	0	37	70
(Percent)	17.1	7.1	22.9	0.0	52.9	100.0
Trap (n)	27	11	17	7	32	94
(Percent)	28.7	11.7	18.1	7.5	34.0	100.0
Noncapture (n)	13	5	8	2	14	42
(Expected n)	12.1	4.9	7.6	3.1	14.3	
Capture (n)	14	6	9	5	18	52
(Expected n)	14.9	6.1	9.4	3.9	17.7	

TABLE 7. Classification function and discriminant coefficients for vole capture and noncapture sites.

	Classification function		
Variables	Group 1 (Capture)	Group 2 (Noncapture)	Discriminant function
CD4	0.101	0.076	0.025
WATER	0.101	0.076	0.025
TREE	0.089	0.146	−0.058
Constant	−2.641	−3.368	6.009

thus, presumably, positively associated with canopy. In contrast with *C. californicus*, green vegetation and canopy coverage were not associated with the presence of *C. gapperi* in this study (Table 3), nor was the close association found by Maser et al. (1981) of California red-backed voles with rotting and punky logs (class 3 or more; see Table 1 for definition of classes) true for *C. gapperi* in our study. In fact, *C. gapperi* capture sites were positively associated with more recently fallen class 2 logs (Table 3). While releasing voles in the field, we observed that they frequently ran along or under class 2 logs. Because class 2 logs are still above the ground surface in some places, they provide a secure travel lane for voles. Class 3 or older logs usually cannot function the same way. Fewer class 2 logs may have been present on Maser et al.'s (1981) plots than in this study. Olszewski (1968) reported that the bank vole, *Clethrionomys glareolus*, traveled under fallen timber, a behavior that appears similar to that which we observed for red-backed voles.

Distance from water was significantly different between vole capture and noncapture sites (Tables 3 and 7). Voles were captured farther from water, on a relative scale within the study site (Table 2). Voles in captivity are dependent on free water (Odum 1944, Getz 1968), unless their food is very succulent (personal observation). In Connecticut, the southern portion of the geographic range in the northeastern USA, *C. gapperi* were restricted to swampy areas, but in Vermont, farther north, voles acquire adequate water from their food (Miller and Getz 1972).

Voles in this study were captured relatively far from water; if they were too close, their burrows could have been flooded by the frequently fluctuating water levels in the study area. For example, Merritt and Merritt (1978) found that the spring snowmelt was the period of greatest mortality for a Colorado subalpine population of *C. gapperi*. The greatest density of voles was close to a creek within their study plot.

Although distance from water is not equivalent to distance above water level, given the topography of the study area, a strong positive relationship is likely. Voles should not have occurred within our study area immediately near water. Only distances from 0 to 45 m from water were sampled in this study, resulting in the positive relationship observed. If sites further from water had been sampled, fewer voles would likely have been captured. Prior investigations of vole densities on drier sites within close proximity of the study site captured few (Anderson et al. 1980) or no voles (personal observation). Additionally, voles within our moist study site may not have been dependent upon free water, as the site may have provided sufficient moisture through the vegetation to meet vole requirements.

The number of trees in the area was the

third variable chosen (Table 7). Voles were more likely to be captured within the study area at sites with fewer trees present. This is consistent with vole selection of microhabitat sites with greater amounts of cover. Many of the trees within the study area were mature trees with large bole diameter. These trees had little cover 0 to 4 dm above ground in the areas immediately surrounding their bases.

The relationship of red-backed voles to the presence of free water illustrates a problem that exists with all studies, similar to ours, that use correlation analysis to investigate relationships of habitat and animal abundance. As demonstrated by Price and Kramer (1984), the location selected by researchers for their traps can influence the conclusions drawn about habitat affinities of a species. In our case, (1) locating the trapping grid in an area with a wider moisture gradient would have resulted in a different statistical relationship between vole density and distance to free water, and (2) placing the traps in random locations on the trapping grid would have increased the significance between vole abundance and habitat attributes. In order to meet objectives other than those reported here, however, we located traps at sites we believed most likely to catch voles. As a result, trapping sites did not encompass the full range of values for most of the habitat attributes (Table 2). Random or stratified random placement of traps would have resulted in relationships that were statistically more significant for all variables (Table 3), but use of a random design would not have changed our conclusions as to the importance of the currently significant cover variables. It would have made the relationships between variables more significant and perhaps would have resulted in less significant ($P > .05$) variables becoming significant. The variables most likely to have changed would be other density (CD2-CD9) and the log-class variables.

Floristic composition was not important in determining whether or not a vole was captured at a site (Tables 4, 5, 6). Similar analyses have not been reported for *Clethrionomys* but have been reported for other rodent species (e.g., *Peromyscus leucopus*, M'Closkey and Lajoie 1975).

Researchers studying small mammals and their habitats usually assume that capture location is indicative of preferred or most used habitats (Dueser and Shugart 1979). The correlation of *C. gapperi* with cover density described here agrees with the laboratory preference of the species for more cover (Wywialowski 1987) and use of microhabitats with greater cover as assessed by radiotelemetry in a forest enclosure (Nams 1981).

The habitat in which an individual occurs in a field situation is always confounded by the presence of other animals. Dispersers and subordinate animals are more likely to be in suboptimal habitats. Density may be a poor indicator of habitat quality (Van Horne 1983). Van Horne (1982) found that dominant adult deer mice occupied forest habitats with greater cover and had higher overwinter survival, while subordinate subadults occupied habitats with less cover where densities were higher but overwinter survival was less. A similar pattern of use between adult and juvenile *C. gapperi* in a forest and tornado blowdown, respectively, was observed by Powell (1972), although he did not have any measure of fitness of individuals within each habitat. Mihok (1981) found that mature females were dominant and occupied preferred habitats. In this study, 8 of the 14 voles captured the first night of the first trapping period were females, whereas only 2 of the 10 captured the second night were female. The sex-biased captures concur with the female-dominated social organization of the genus *Clethrionomys* (Mihok 1981, Bujalska 1985, Vitala and Hoffmeyer 1985, Bondrup-Nielson 1986a, 1986b). Many territorial females were likely removed the first night of trapping. The pattern of capture of mostly adult female voles during the first night of trapping was not as prevalent during the second and third trapping periods, when mostly young-of-the-year voles were captured and territories and social order were likely disrupted by the previous removal of voles. The effect of social organization on our conclusions is not completely clear. It did, however, affect our ability to correctly classify the habitat use of voles. When only the first trapnights were used in the analysis and trapped voles consisted mostly of adults, 80% of the sites were correctly classified. When the second trapnight consisting of mostly juvenile voles was added, only 65% of the sites were correctly classified. The major difference between the

two analyses appears to be in the importance of cover below the 4-dm height. We conclude that optimal vole habitat has high values of cover below 4 dm.

Population size may also affect habitat use by a species. Bock (1972) found that *C. glareolus* occupied a wider range of habitats when populations were larger. This may not be true for *C. gapperi*, as they have been reported not to have exhibited significant opportunistic niche expansion in one study on an island situation (Crowell 1983). However, microhabitats that were preferentially used in this study are in agreement with the laboratory research of Wywialowski (1987) and the field observations of Nams (1981). Capture rates of red-backed voles in other studies have averaged 0.7–8.7 captures per 100 trapnights (Gunderson 1959, Martell 1981, Gunther et al. 1983, Fuller 1985), except for Martell's (1983) study where snap-trap capture rates as great as 37.8 per 100 trapnights were obtained. The capture rate of 20.1 captures per 100 trapnights observed during our study, excluding Martell (1983), is about an order of magnitude greater than the average capture rate reported elsewhere for red-backed voles. Vole captures in this study probably occurred in suboptimal as well as optimal habitats, and, as a result, our ability to identify what constitutes optimal vole habitat is more difficult than it would have been if vole populations had been lower.

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LITERATURE CITED

ANDERSON, D. C., J. A. MACMAHON, M. L. WOLFE. 1980. Herbivorous mammals along a montane sere: community structure and energetics. J. Mammal. 63: 500–519.

BOCK, E. 1972. Use of forest associations by bank vole populations. Acta Theriol. 17: 203–219.

BONDRUP-NIELSEN, S. 1986a. Analysis of spacing behaviour of females from a live-trapping study of *Clethrionomys gapperi*. Ann. Zool. Fennici 23: 261–267.

———. 1986b. Investigations of spacing behaviour of *Clethrionomys gapperi* by experimentation. J. Animal Ecology 55: 269–279.

BUJALSKA, G. 1985. Regulation of female maturation in *Clethrionomys* species, with special reference to an island population of *C. glareolus*. Ann. Zool. Fennici 22: 331–342.

CROWELL, K. L. 1983. Islands—insight or artifact? Population dynamics and habitat utilization in insular rodents. Oikos 41: 442–454.

DUESER, R. D., AND H. H. SUGART, JR. 1979. Niche pattern in a forest-floor small-mammal fauna. Ecology 60: 108–118.

FULLER, W. A. 1985. Demography of *Clethrionomys gapperi*, parapatric *C. rutilus*, and sympatric *Peromyscus maniculatus* in northern Canada. Ann. Zool. Fennici 22: 229–241.

GETZ, L. L. 1968. Influence of water balance and microclimate on the local distribution of the redback vole and white-footed mouse. Ecology 49: 276–286.

———. 1969. Laboratory studies of interactions between the white-footed mouse and redback vole. Canadian Field-Natur. 83: 141–146.

GUNDERSON, H. L. 1959. Red-backed vole habitat studies in central Minnesota. J. Mammal. 40: 405–412.

GUNTHER, P. M., B. S. HORN, AND G. D. BABB. 1983. Small mammal populations and food selection in relation to timber harvest practices in the western Cascade Mountains. Northwest Sci. 57: 32–44.

HOLLANDER, M., AND D. A. WOLFE. 1973. Nonparametric statistical methods. John Wiley and Sons, Inc., New York. 503 pp.

JOHNSON, D. H. 1981. The use and misuse of statistics in wildlife habitat studies. Pages 11–19 *in* D. E. Capen, ed., The use of multivariate statistics in studies of wildlife habitat. USDA For. Serv. Gen. Tech. Rept. RM–87. 249 pp.

KIRKLAND, G. L., JR. 1977. Responses of small mammals to the clearcutting of northern Appalachian forest. J. Mammal. 58: 600–609.

KIRKLAND, G. L., JR., AND R. J. GRIFFIN. 1974. Microdistribution of small mammals at the coniferous-deciduous forest ecotone in northern New York. J. Mammal. 55: 417–427.

LOVEJOY, D. A. 1975. The effects of logging on small mammal populations in New England northern hardwoods. Occas. Pap. Univ. Connecticut Biol. Sci. Ser. 2: 269–271.

MARTELL, A. M. 1981. Food habits of southern red-backed voles (*Clethrionomys gapperi*) in northern Ontario. Canadian Field-Natur. 95: 325–328.

———. 1983. Changes in small mammal communities after logging in north-central Ontario. Canadian J. Zool. 61: 970–980.

MASER, C., B. R. MATE, J. F. FRANKLIN, AND C. T. DYRNESS. 1981. Natural history of Oregon coast mammals. USDA For. Serv. Gen. Tech. Rept. PNW–133. 496 pp.

MCCLOSKEY, R. T., AND D. T. LAJOIE. 1975. Determinants of local distribution and abundance in white-footed mice. Ecology 56: 467–472.

MERRITT, J. F. 1981. *Clethrionomys gapperi*. Mamm. Species 146: 1–9.

MERRITT, J. F., AND J. M. MERRITT. 1978. Population ecology and energy relationships of *Clethrionomys gapperi* in a Colorado subalpine forest. J. Mammal. 59: 576–598.

MIHOK, S. 1981. Chitty's hypothesis and behavior of subarctic red-backed voles, *Clethrionomys gapperi*. Oikos 36: 281–295.

MILLER, D. H., AND L. L. GETZ. 1972. Factors influencing the local distribution of the red-backed vole, *Clethrionomys gapperi*, in New England. Occas. Pap. Univ. Connecticut Biol. Sci. Ser. 2: 115–138.

_____. 1973. Factors influencing the local distribution of the redback vole, *Clethrionomys gapperi*, in New England. II. Vegetation cover, soil moisture, and debris cover. Occas. Pap. Univ. Connecticut Biol. Sci. Ser. 2: 159–180.

_____. 1977. Factors influencing local distribution and species diversity of forest small mammals in New England. Canadian J. Zool. 55: 806–814.

NAMS, V. 1981. Prey selection mechanisms of the ermine (*Mustela ermina*). Pages 861–882 *in* J. A. Chapman and D. Pursley, eds., The worldwide furbearer conference proceedings. Vol. II. Frostburg, Maryland. 1,552 pp.

ODUM, E. P. 1944. Water consumption of certain mice in relation to habitat selection. J. Mammal. 25: 404–405.

OLSZEWSKI, J. 1968. Role of uprooted trees in movements of rodents in forests. Oikos 19: 99–104.

POWELL, R. A. 1972. A comparison of populations of boreal red-backed vole (*Clethrionomys gapperi*) in tornado blowdown and standing forest. Canadian Field-Natur. 86: 377–379.

PRICE, M. V., AND K. A. KRAMER. 1984. On measuring microhabitat affinities with special reference to small mammals. Oikos 42: 349–354.

SCHIMPF, D. J., J. A. HENDERSON, AND J. A. MACMAHON. 1980. Some aspects of succession in the spruce-fir forest zone of northern Utah. Great Basin Nat. 40: 1–26.

SPSS INC. 1983. Users Guide SPSSx. McGraw-Hill Book Co., New York. 806 pp.

STEELE, R., R. D. PFISTER, R. A. RYKER, AND J. A. KITTAMS. 1981. Forest habitat types of central Idaho. USDA For. Serv. Gen. Tech. Rept. INT–114. 138 pp.

THOMAS, J. W., ED. 1979. Wildlife habitats in managed forests. The Blue Mountains of Oregon and Washington. USDA For. Serv. Agric. Handbook 553. 512 pp.

TITUS, K., J. A. MOSHER, AND B. K. WILLIAMS. 1984. Chance-corrected classification for use in discriminant function analysis: ecological applications. Amer. Midl. Nat. 111: 1–7.

VAN HORNE, B. 1982. Niches of adult and juvenile deer mice (*Peromyscus maniculatus*) in seral stages of coniferous forest. Ecology 63: 992–1003.

_____. 1983. Density as a misleading indicator of habitat quality. J. Wildl. Manage. 47: 898–901.

VICKERY, W. L. 1981. Habitat use by northeastern forest rodents. Amer. Midl. Nat. 106: 111–118.

VITALA, J., AND I. HOFFMEYER. 1985. Social organization in *Clethrionomys* compared with *Microtus* and *Apodemus:* social odours, chemistry and biological effects. Ann. Zool. Fennici 22: 359–371.

WILLIAMS, B. K. 1983. Some observations on the use of discriminant analysis in ecology. Ecology 64: 1283–1291.

WYWIALOWSKI, A. P. 1987. Habitat structure and predators: choices and consequences for rodent habitat specialists and generalists. Oecologia 72: 39–45.

A COMPARISON OF THE SPHERICAL DENSIOMETER AND OCULAR METHODS OF ESTIMATING CANOPY COVER

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ABSTRACT —Percent tree canopy cover in a ponderosa pine (*Pinus ponderosa*) forest of northeastern California was estimated by the point intercept spherical densiometer and ocular methods. Estimates derived by the two methods were similar ($P > .05$). The ocular method is recommended when understory vegetation is tall or clumped instead of randomly distributed, or if available field time limits sample size.

Canopy cover, or percent canopy cover, refers to the proportion of an area covered by the vertical projection of plant crowns to the ground surface (Gysel and Lyon 1980). The measurement of cover provides information on the structure of vegetation. Several instruments and methods have been used to measure canopy cover, including photometers, light meters, photographic methods, densiometers and ceptometers, vertical crown projection methods, ocular estimations, point intercept, line intercept, and the Bitterlich method (Lemmon 1956, Mueller-Dombois and Ellenberg 1974, Hays et al. 1981).

Robinson (1947, cited in Lemmon 1956) was one of the first researchers to use a densiometer; he used a flat mirror to estimate relative area of crown coverage. This method required use of both a large mirror and a large number of samples. Lemmon (1956) improved the method by using a spherical densiometer and reported that at probability levels of 70, 95, and 99%, average measurements of the same overstory area could be expected to be within ±1.3, ±2.4, and ±3.1%, respectively. Strickler (1959) recommended limiting use to 17 points in a wedge-shaped area on the densiometer to avoid multiple counting of intercepts. Dealy (1960) used a densiometer in conjunction with the line intercept method to measure canopy cover in tall shrub–small tree vegetation types.

Densiometer measurements were found to be highly correlated with measurements taken by a canopy camera (Hoffer 1962, cited in Hays et al. 1981). The amount of open canopy in the east, south, and west directions, as measured with the spherical densiometer, accounted for the largest proportion of the variance in light penetration in an Arizona ponderosa pine forest (McLaughlin 1978). Total understory, shrub, and forb production was correlated with canopy cover measured with a spherical densiometer, but not with tree basal area, stand height, or number of trees/ha in the grand fir (*Abies grandis*)/myrtle boxwood (*Pachistima myrsinites*) habitat type of north central Idaho (Pyke and Zamora 1982).

The ocular method estimates cover "by eyeball" over a sample area that is laid out on the ground. Proponents of its use include Braun-Blanquet (1932) and Daubenmire (1959). These scientists used cover classes (e.g., 0–5%, 5–25%, etc.). Steele et al. (1981) used the ocular method to estimate canopy coverage of all vascular plant species by classes and recommend it from the standpoint of efficiency. Hays et al. (1981) stated that the ocular method can be "moderately accurate." They recommended use of the line intercept or point intercept techniques when greater accuracy is desired.

I compared estimates of tree canopy cover obtained by the ocular method to estimates obtained by the point intercept spherical densiometer on the same study plots to determine if the ocular method could be used as a reliable estimate of percent overstory canopy in a ponderosa pine forest in northeastern California.

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STUDY SITE

Tree canopy cover was estimated on plots in the Blacks Mountain Experimental Forest in northeastern California (Lassen County). Approximately half of the study area was in a gently rolling basin; the rest extended up moderate slopes to the north and east. Elevations ranged from 1,700 to 2,100 m.

The forest vegetation was characteristic of the Interior Ponderosa Pine type (Eyre 1980). Dominant were ponderosa pine and Jeffrey pine (*Pinus jeffreyi*), as well as white fir (*Abies concolor*) and incense cedar (*Calocedrus decurrens*) at higher elevations. The understory was often open, with scattered shrubs, forbs, and grasses, along with clumps of sapling and pole-sized conifer thickets. Bitterbrush (*Purshia tridentata*) and big sagebrush (*Artemisia tridentata*) were abundant in the understory at lower elevations. Typical understory species at higher sites were snowberry (*Symphoricarpos oreophilus*) and pennyroyal (*Monardella odoratissima*).

METHODS

Conifers greater than 1.5-m height were considered to be trees. Ocular estimates of tree canopy cover were made for 25-m^2 circular microplots (2.82-m radius) in June 1983. An initial training exercise was conducted in which canopy cover was also estimated using 40 points located within the plot in the four cardinal directions for the first 10 microplots. Later, with two-thirds of the sampling completed, an estimate on another 10 microplots was used as a check. Results were compared with paired t-tests. A total of 330 sample points were located along 33 transects. Each of the transects was about 400 m long and contained 10 randomly located microplots. Twenty-six transects were located in experimental units that were logged approximately 40 years ago, and the remaining 7 were located in units cut within the past 10 years.

Tree canopy cover was remeasured with a spherical densiometer on all 330 plots in June 1984 without the data sheets from the previous year in hand. The densiometer measurements served as a standard to which the ocular estimates could be compared. Paired t-tests were used to compare the ocular estimates to those derived using a spherical densiometer. Normality of distribution was tested using the Kolomogorov D statistic (SAS 1982).

Hallin (1959) stated that these 40-year-old experimental units were cut using a randomized block design to study the effects of six harvest treatments on tree growth. The treatments ranged from no harvest (control) to removal of all trees larger than 29.5 cm dbh. Analysis of variance (ANOVA) was used to test for treatment effects on mean canopy cover estimated by the ocular method and by the spherical densiometer for the 26 transects in the older cuts (SAS 1982). Normality of distribution was tested using the Shapiro-Wilk statistic, W (SAS 1982).

RESULTS

The difference in canopy cover between paired observations was less than 41% for 90% of the observations, less than 28% for 80% of the observations, and less than 12% for 50% of the 330 observations.

The t value was -1.60 ($P = .11$). The data (paired differences) were not distributed normally (Kolomogorov $D < 0.01$). The data were not further analyzed using the nonparametric Wilcoxon's signed-rank test because of large sample size, robust nature of the t-test, and nonsignificance of the results using the parametric test.

The data were further sorted into three categories to examine for differences due to plant community and length of time after timber harvest (limited to recent cuts or 40-year-old cuts). The paired t-test results for the differences between the two methods of estimating canopy cover were not significant for any of these categories (Table 1). Both methods of estimating cover provided similar ANOVA results (Table 2). The six timber harvest treatments did not have significant effects on total tree canopy cover 40 years after harvest as measured by the two methods. This was due to the natural heterogeneity in forest structure. The forest was composed of a variety of small, even-aged groups of trees of various ages. The overstory was broken by groups of smaller-sized trees or scattered, older residuals in younger stands. The age classes were not evenly distributed spatially, but instead formed a mosaic of small, homogeneous units that varied in size from a fraction of a hectare to 4 ha (Hallin 1959).

TABLE 1. Differences between ocular and densiometer estimates of tree canopy cover by age of cut and plant community.

Category	t value	P	Number of samples
Recent cuts (4–10 yrs)	−1.95	0.06	70
Older cuts (40 yrs)	−0.81	0.42	260
Lower-elevation community (ponderosa pine and bitterbrush)	1.18	0.24	100
Higher-elevation community (ponderosa pine, white fir, incense cedar, and snowberry)	−0.02	0.80	160

TABLE 2. Analyses of variance of effect of treatment and block on tree canopy cover as measured by densiometer and ocular methods.

		Ocular[a]				Densiometer[b]	
Source	df	F value	P	Source	df	F value	P
Treatment	5	0.91	0.51	Treatment	5	0.94	0.48
Block	4	1.58	0.23	Block	4	1.77	0.18

[a]Macroplot means were distributed normally (Pr<W = 0.47).
[b]Macroplot means were distributed normally (Pr<W = 0.43).

The two checks on the ocular method showed that this method did not deviate significantly from cover estimated from the 40 points within the plot ($t = -1.40$, $P = .18$; normality test, $P = .34$).

DISCUSSION

The results of the paired t-tests and ANOVA do not indicate significant differences between estimates of canopy cover obtained from a spherical densiometer and from the ocular method. The choice of methods is dependent upon time available in the field, needed accuracy, range of tree sizes, nature of understory, and species of trees.

The ocular method is quicker and is fairly accurate with a trained observer. The densiometer takes several more minutes at each plot and is subject to error in counting of intercept points by the observer. The ocular method works well in all size classes of vegetation and probably does a better job of estimating canopy cover as defined by drip lines of trees rather than canopy cover in terms of light penetration, although the latter is probably of greater biological significance. Light penetration through loose ponderosa pine foliage is difficult to estimate either visually or with a spherical densiometer.

The spherical densiometer is most effective in stands of medium to large trees (> 10 m tall) where there is little understory greater than 1 m in height. In some cases the plot center was located under a tall seedling or sapling. In these instances densiometer estimates of cover were too high for the 25-m^2 plot. Also, it was sometimes difficult to get readings in four directions with the densiometer in low, dense vegetation. Estimates of cover obtained by a densiometer at the plot center did not include cover provided by small trees at the edge of the plot; the lesser the tree height, the smaller the portion of the canopy reflected in the mirror. In these cases, the ocular estimate of cover was superior to that obtained using a spherical densiometer at the plot center. The densiometer uses the point intercept method; hence measurements at the plot center cannot be extrapolated to a large plot without additional measurements within the plot.

The paired t-test for recently cut areas was almost significant ($P = .06$, Table 1). The vegetation in these areas was dominated by sapling and pole-sized trees, and densiometer estimates taken at plot center were probably less accurate for coverage estimates of the 25-m^2 plot. Differences between the ocular and densiometer methods were least significant ($P = .80$) in older harvest areas at higher elevations where there were large trees with dense foliage, such as white fir and incense cedar. The degree of nonsignificance drops ($P = .24$) in the more open ponderosa pine

and bitterbrush community. Here, densiometer estimates may be more accurate where large trees dominate over a low understory. The method suggested by Dealy (1960) for low shrubs and small trees may work better where a tall understory is present, but it requires use of the more time consuming line intercept method.

Weather conditions may also impact the accuracy of densiometer readings. Looking into the mirror can be blinding when the sun is overhead. Wind movement of foliage can make determination of point intercept in the mirror difficult.

CONCLUSIONS

Ocular estimates provided an estimate of tree canopy coverage that was not statistically different from that estimated using a spherical densiometer. Use of the spherical densiometer and line intercept methods is probably more accurate under certain conditions but may yield erroneous results if understory vegetation is tall, if vegetation is clumped instead of randomly distributed, or if available field time limits sample size. In the latter case, the lower accuracy of the ocular method may be more than compensated by the larger sample sizes. Observers using the ocular estimating method should be initially trained with and periodically checked against a reliable mechanical cover estimation method.

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LITERATURE CITED

BRAUN-BLANQUET, J. 1932. Plant sociology. English translation. McGraw-Hill, New York. 438 pp.

CLARY, W. P., AND P. F. FFOLLIOT. 1966. Differences in herbage-timber relationships between thinned and unthinned ponderosa pine stands. USDA Forest Service Research Note RM-74. 4 pp.

DAUBENMIRE, R. 1959. A canopy-coverage method of vegetation analysis. Northw. Sci. 33: 43–64.

DEALY, E. J. 1960. The densiometer for measurement of crown intercept above a line transect. USDA, Forest Service PNW 199. 5 pp.

EYRE, F. H. 1980. Forest cover types of the United States and Canada. Soc. of Amer. For., Washington, D.C. 148 pp.

GYSEL, L. W., AND L. J. LYON. 1980. Habitat analysis and evaluation. Pages 305–327 *in* S. D. Schemnitz, ed., Wildlife management techniques manual. The Wildlife Soc., Washington, D.C.

HALLIN, W. E. 1959. The application of unit area control in the management of ponderosa-Jeffrey pine at Blacks Mountain Experimental Forest. USDA, Forest Service Technical Bulletin 1191, Washington, D.C. 96 pp.

HAYS, R. L., C. SUMMERS, AND W. SEITZ. 1981. Estimating wildlife habitat variables. USDI, Fish and Wildlife Service FWS/OBS-81/47. 111 pp.

LEMMON, P. E. 1956. A spherical densiometer for estimating forest overstory density. For. Sci. 2: 314–320.

MCLAUGHLIN, S. P. 1978. Overstory attributes, light throughfall, and the interpretation of overstory relationships. For. Sci. 24: 550–553.

MUELLER-DOMBOIS, D., AND H. E. ELLENSBURG. 1974. Aims and methods of vegetation ecology. John Wiley and Sons, New York. 547 pp.

PYKE, D. A., AND B. A. ZAMORA. 1982. Relationships between overstory structure and understory production in the grand fir/myrtle boxwood habitat type of northcentral Idaho. J. Range Manage. 35: 769–773.

SAS INSTITUTE. 1982. SAS (Statistical Analysis System) user's guide: statistics, 1982. 3d ed. Cary, North Carolina. 548 pp.

STEELE, R., R. D. PFISTER, R. A. RYKER, AND J. A. KITTAMS. 1981. Forest habitat types of central Idaho. USDA Forest Service, General Technical Report INT-114. 138 pp.

STRICKLER, G. S. 1959. Use of the densiometer to estimate density of forest canopy on permanent sample plots. USDA, Forest Service PNW 180. 5 pp.

MONOTERPENE CONCENTRATIONS IN LITTER AND SOIL OF SINGLELEAF PINYON WOODLANDS OF THE WESTERN GREAT BASIN

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ABSTRACT.—Mean monoterpene content of singleleaf pinyon (*Pinus monophylla* [Torr.] Frem.) litter from stands growing on two soil series was 340 ± 310 ug/g air dry weight (adw). Individual monoterpene hydrocarbons suggested as potential allelopathic compounds occur in extremely small amounts, 0.5–110 ug/g adw. Mineral soils contained 50 times less total terpene, 6.6 ug/g ± 4.8 adw, than the litter immediately above. Results suggest that allelopathic effects would more likely occur in litter than mineral soil. These findings are substantiated by previous reports of decreased emergence and growth of herbaceous species in pinyon litter but not mineral soil.

Terpene hydrocarbons are potentially involved in the inhibition of germination and growth of herbaceous plant species under the pinyon-juniper canopy (Everett 1981, Jameson 1980). Terpenes have long been suspected as allelopathic substances causing germination inhibition or growth regulation (Rice 1974, 1984, Muller 1966, 1968, 1971). The possibility of such interactions has also been suggested by various field and laboratory observations (Rice 1974, 1984, Elmore 1985, Groves and Anderson 1981, Putnam 1985).

The terpene content of wood and gum turpentines from living pinyon has been established. Zavarin and Snajberk (1980) reported the presence of monoterpenes α-pinene, β-pinene, sabinene, camphene, 3-carene, myrcene, limonene, γ-terpinene, terpinolene, p-cymene, and β-phellandrene in 11 species of pinyon (Fig. 1). Also reported was the inconsistent occurrence of cis-ocimene, tricylene, α-phellandrene, α-thujene, and α-terpinene. These compounds are characteristic of the three conifer families Cupressaceae, Pinaceae, and Taxodiaceae (Zavarin 1971) and have been suggested as having allelopathic properties (Rice 1984, Mandava 1985).

Data are not available on the transport and fate of these compounds in litter and soils. It has been suggested that soils act as a repository for the sorption of volatile terpene hydrocarbons (Muller 1971), but studies have not specifically revealed where or at what concentrations terpene compounds accumulate on the forest floor.

The purpose of this study was to document the presence and amounts of monoterpenes found in singleleaf pinyon litter and the surface mineral soils immediately below. Monoterpene levels contained in mineral soil or pinyon litter suggest probable concentrations at which allelopathic effects are naturally exhibited. Defined in situ monoterpene concentrations will be used to test for allelopathic effects on herbaceous species in future research.

FIELD AND LABORATORY METHODS

Samples of singleleaf pinyon litter and surface mineral soils below the litter were taken from two sites 113 km apart on the western edge of the Great Basin. Site 1 was located on an east slope of the Virginia Range on the Duco soil series (Lithic Argixeroll; Soil Survey Staff 1975). Site 2 was on an east slope of the Wellington Hills on the Roloc soil series (Aridic Argixeroll). Litter samples taken 50 cm from the tree trunk were comprised of decomposing needle, twig, cone, and bark tissue. Mineral soil samples were taken from the upper 2.5 cm of soils immediately below the litter layer.

Paired litter and soil samples were collected adjacent to 13 randomly chosen trees at each site. Samples were analyzed for monoterpenes α-pinene, β-pinene, sabinene, camphene, 3-carene, myrcene, limonene, p-cymene, and γ-terpinene.

Samples of pinyon tree litter and mineral

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TABLE 1. Monoterpene concentrations in tree litter.

	Terpene ug/g sample air dry weight					
	Site 1			Site 2		
Compound	Mean	SD	Range	Mean	SD	Range
α-pinene	14.0	25.0	0.6–110	5.4	7.3	0.5–23
sabinene	7.1	4.1	2.4–15	3.5	1.6	0.9–7.3
β-pinene/ myrcene	3.0	3.6	0.7–15	7.6	7.8	0.8–23
camphene	5.3	1.2	4.1–6.5	ND	ND	ND
3-carene	2.1	1.4	0.5–9	1.2	0.6	0.7–2.7
p-cymene	3.1	3.1	0.7–9	1.0	0.6	0.5–2.4
limonene	4.0	7.4	0.6–3.1	4.0	7.6	0.6–2.5
γ-terpinene	3.1	3.2	0.8–1.5	1.6	1.3	0.6–4.3
	Total terpene ug/g sample air dry weight					
	Litter			Soil		
	Mean	SD	Range	Mean	SD	Range
Site 1	340	300	130–1400	7.3	4.5	2.3–15.4
Site 2	340	320	23–960	5.8	5.0	0.5–19.9

ND not detected.
SD standard deviation.

soil were prepared for analysis by pulverizing the material with mortar and pestle. Ten-gram aliquots of either soil or litter were placed in 25-ml test tubes and extracted with 10 ml of petroleum ether. Samples were subjected to 60 seconds of vigorous shaking on a Pulser Vortex Test Tube Mixer (Kraft Apparatus, Inc., Mineola, N.Y.), and then solvent and sample were allowed to equilibrate for 48 hours at room temperature. The extracts were then filtered through Whatman #1 and washed with 100 ml pet ether. The resulting extracts were concentrated to 0.5 ml under nitrogen in calibrated centrifuge tubes. Each sample was then analyzed by injection of 2 ul aliquots onto a Varian Aerograph series 1700 gas chromatograph using a 0.75 mm i.d. × 60 m Supelco methylsilicone widebore glass capillary column. The oven was temperature programmed from 70 to 270 C at a rate of 10 C/min. Individual compounds were integrated using a Hewlett-Packard 18850A GC terminal.

Quantitation of monoterpenes present in the extracts was accomplished using external standards. Standards of monoterpenes were prepared at a concentration of 1 ug/ul. β-phellandrene and terpinolene were not available as standards at the time of analysis. Monoterpenes in the extracts were identified by cochromatography and GC-MS (gas chromatograph–mass spectrometer) analysis. The quantity of individual monoterpenes identified in the extracts was determined from the integrated values obtained from each

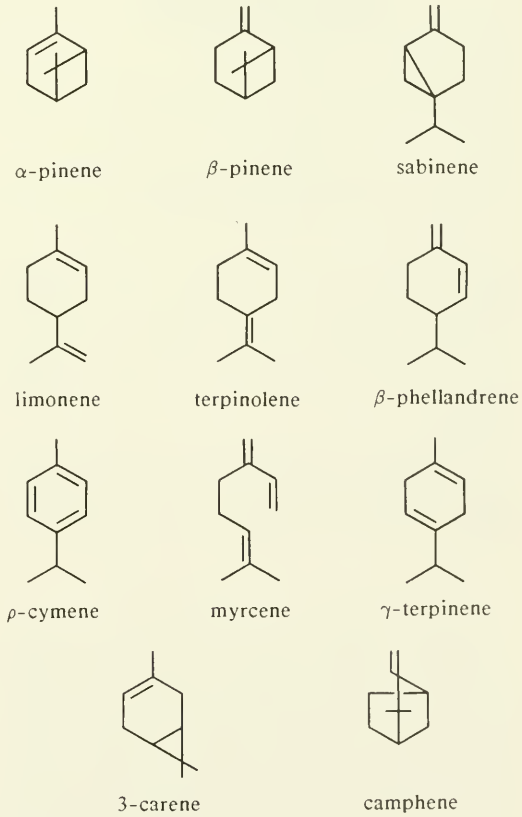


Fig. 1. Monoterpenes from Coniferales.

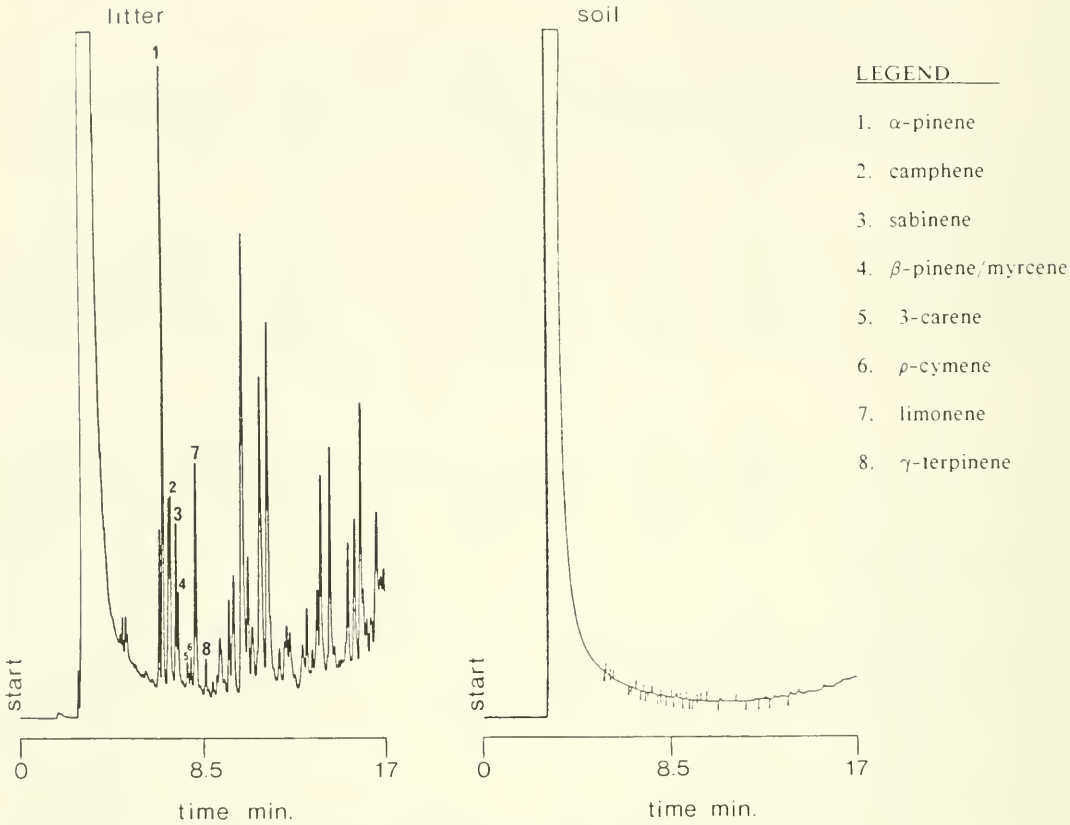


Fig. 2. Gas chromatograms of litter and soil extracts of sample number 4 from Site 1.

sample and expressed as mg/g air dry weight. Total monoterpene content was estimated by summing integrated areas of each compound from 6 minutes retention time to 17 minutes and is also expressed as an air dry weight basis.

Compounds eluting after 17 minutes were not included in the estimation of the monoterpene content since they were presumably higher molecular weight hydrocarbons.

RESULTS AND DISCUSSION

The monoterpenes present in litter extracts (Table 1) were consistent with those reported for oleoresins of pinyon (Zavarin and Snajberk 1980, Fig. 1). Several other 10-carbon compounds were present at comparable concentrations but were not identified. Other constituents were evident in the extracts and probably included higher carbon number terpenes. A large variety of sesquiterpenes (C–15) and oxygenated monoterpenes were found present by Zavarin and Snajberk (1980) in both wood and gum turpentines. Gum and wood rosins were reported to be mainly composed of pimaric with smaller amounts of abietic acids. Low amounts of free fatty acids were found mainly in sapwood, along with trace amounts of unidentified ether-soluble compounds in wood. Our analysis of pinyon litter extracts by GC-MS confirmed the presence of higher molecular weight constituents, although they were not identified.

No attempt was made to identify individual monoterpenes from the mineral soil extracts because of their very low levels of occurrence. These soils have not previously been reported as allelopathic (Everett 1987). However, any integrated areas for the mineral soil samples were assumed to be terpene hydrocarbons. β-pinene coeluted with myrcene; therefore, these monoterpene concentrations are expressed as combinations. Camphene was detected in only two samples, both from Site 1.

The concentration of monoterpenes in the litter samples exhibited substantial variation, probably corresponding with the actual

amount of woody material in the samples and the degree of weathering of the litter. The total terpene content of some individual Site 2 samples was much lower than those of Site 1, although the average values for both sites were equal.

Soil samples at both sites showed very low levels of monoterpene, which, on the average, were 50 times less than in the litter samples (Fig. 2). Litter results indicate a range of concentrations appropriate for testing allelopathic effects on understory species. Further study is suggested to identify and quantify the remaining components of these litter extracts and evaluate their involvement in seed germination inhibition and/or growth regulation.

LITERATURE CITED

ELMORE, C. D. 1985. Assessment of the allelopathic effects of weeds on field crops in the humid Midsouth. Pages 21–32 *in* A. C. Thompson, ed., The chemistry of allelopathy. American Chemical Society.

EVERETT, R. L. 1987. Allelopathic effects of pinyon and juniper litter on emergence and growth of herbaceous species. *In:* Proc., Symposium on Seed and Seedbed Ecology of Rangeland Plants. USDA-ARS, Tucson, Arizona, 21–23 April 1987.

GROVES, C. R., AND J. E. ANDERSON. 1981. Allelopathic effects of *Artemisia tridentata* leaves on germination and growth of two grass species. Amer. Midl. Nat. 106: 73–79.

JAMESON, D. A. 1966. Pinyon-juniper litter reduces growth of blue grama. J. Range Manage. 19: 214–217.

MANDAVA, N. B. 1985. Chemistry and biology of allelopathic agents. Pages 33–54 *in* A. C. Thompson, ed., The chemistry of allelopathy. American Chemical Society.

MULLER, C. H. 1966. The role of chemical inhibition (allelopathy) in vegetational composition. Bull. Torrey Bot. Club 93: 332–351.

———. 1968. Allelopathic control of herb growth in the fire cycle of California chaparral. Bull. Torrey Bot. Club 95: 225-231.

———. 1971. Phytotoxins as plant variables. Pages 64–72 *in* Biochemical interactions among plants. National Academy of Sciences, Washington, D.C.

PUTNAM, A. R. 1985. Allelopathic research in agriculture: past highlights and potential. Pages 1–8 *in* A. C. Thompson, ed., The chemistry of allelopathy. American Chemical Society.

RICE, E. L. 1974. Allelopathy. 1st ed. Academic Press, New York. 353 pp.

———. 1984. Allelopathy. 2d ed. Academic Press, New York. 400 pp.

SOIL SURVEY STAFF. 1975. Soil taxonomy: a basic system of soil classification for making and interpreting soil surveys. USDA-SCS Agric. Handb. 436. U.S. Government Printing Office, Washington, D.C.

ZAVARIN, E. 1971. Monoterpenoids of Coniferales. Pages 57–63 *in* Biochemical interactions among plants. National Academy of Sciences, Washington, D.C. Also in Bulletin of IAWA, 1968.

ZAVARIN, E., AND K. SNAJBERK. 1980. Oleoresins of pinyons. J. Agric. Food Chem. 28: 829–834.

NEW GENERA AND NEW SPECIES OF NEOTROPICAL COELIDIINI (HOMOPTERA: CICADELLIDAE: COELIDIINAE)

M. W. Nielson[1]

ABSTRACT.—Three new genera and 14 new species in 9 genera in the tribe Coelidiini are described and illustrated. Revised keys to males of species in several genera are also given. New genera include: *Pygmaelidia*, type-species *Pygmaelidia bullata*, n. sp.; *Gracilidia*, type-species *Gracilidia gracilis*, n. sp.; *Fistulidia*, type-species *Fistulidia simplex*, n. sp. Additional new species include the following: *Boliviela bispinosa*, *Boliviela paraortha*, *Tinocripus huggerti*, *Lodia parapectinata*, *Calodicia circulata*, *Dicolecia serrata*, *Evansolidia massa*, *Evansolidia bifurcata*, *Evansolidia digitula*, *Spinolidia sarmenta*, *Spinolidia magna*.

The tribe Coelidiini is very rich in the Neotropical region. Collections during the latter part of the current century have brought to light an additional number of new taxa that are described in this paper. The majority of genera in the region is small in number of species, but those taxa described here and in other papers (Nielson 1983, 1986) flesh out several genera and thus add to our knowledge of the variety and complexity of the group.

Three new genera and 14 new species in these and 7 other genera in the tribe are described and illustrated in this paper. Revised keys to males of species in several genera are also presented to update the classification and provide ready access to more complete keys.

The three genera described below are each represented by a single species and all are from Brasil. The number of monobasic genera is fairly large for the group, and they represent about half the known genera in the Neotropical region.

Pygmaelidia, n. gen.

TYPE-SPECIES.—*Pygmaelidia bullata*, n. sp.

Medium-sized, very broad, robust species.

LENGTH.—Male 7.80–8.00 mm, female 8.90–12.50 mm.

General habitus unlike any other known genus in the tribe owing to its robust size. Similar to *Crinolidia* Nielson in some male genital characters.

Head slightly narrower than pronotum, very broad and short; crown broad; pronotum and scutellum short, only slightly longer than median length of crown; forewings macropterus in male, micropterous in female, veins and some cells rugulose, 5 apical cells and 3 anteapical cells present, outer one closed; clypeus long and broad, sometimes with a very faint median, longitudinal carina that does not reach basal origin; femoral setal arrangement 2:2:1.

Male genitalia symmetrical; pygofer without processes; segment 10 long and rather broad; dorsal apodeme typical; aedeagus simple, long, tubular; gonopore subapical; connective Y-shaped with short stem; style very long, narrow; plate long and somewhat broad before apex.

The genus is known only from Brasil and is represented by a single species described below. It is distinguished from other genera by its robust size, very broad, short head with rugulose markings on the forewings, and symmetrical aedeagus.

Pygmaelidia bullata, n. sp.

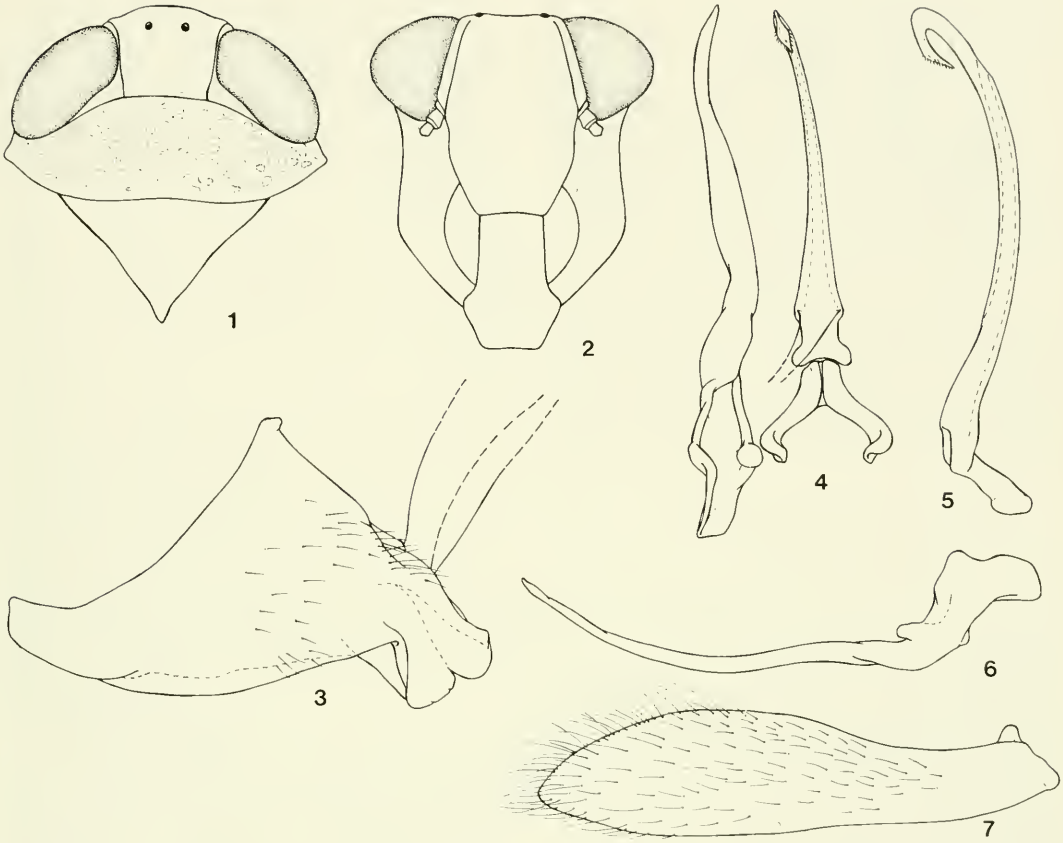
Figs. 1–7

LENGTH.—Male 7.80 mm, female 8.90–12.50 mm.

General color light to deep tannish with pale, corrugated bullae on pronotum and veins of forewings.

Head short and very broad, slightly narrower than pronotum, broadly rounded anteriorly; crown broad, about as wide as eyes, surface finely sculptured; eyes large, elongate; pronotum rather short, median length about as long as median length of crown, surface with irregular, corrugated bullae;

[1]Monte L. Bean Life Science Museum, Brigham Young University, Provo, Utah 84602.



Figs. 1–7. *Pygmaelidia bullata*, n. sp. 1. Head, pronotum, and scutellum, dorsal view. 2. Face, ventral view. 3. Pygofer, lateral view. 4. Connective, aedeagus, and right style, dorsal view. 5. Aedeagus, lateral view. 6. Right style, lateral view. 7. Plate, ventral view.

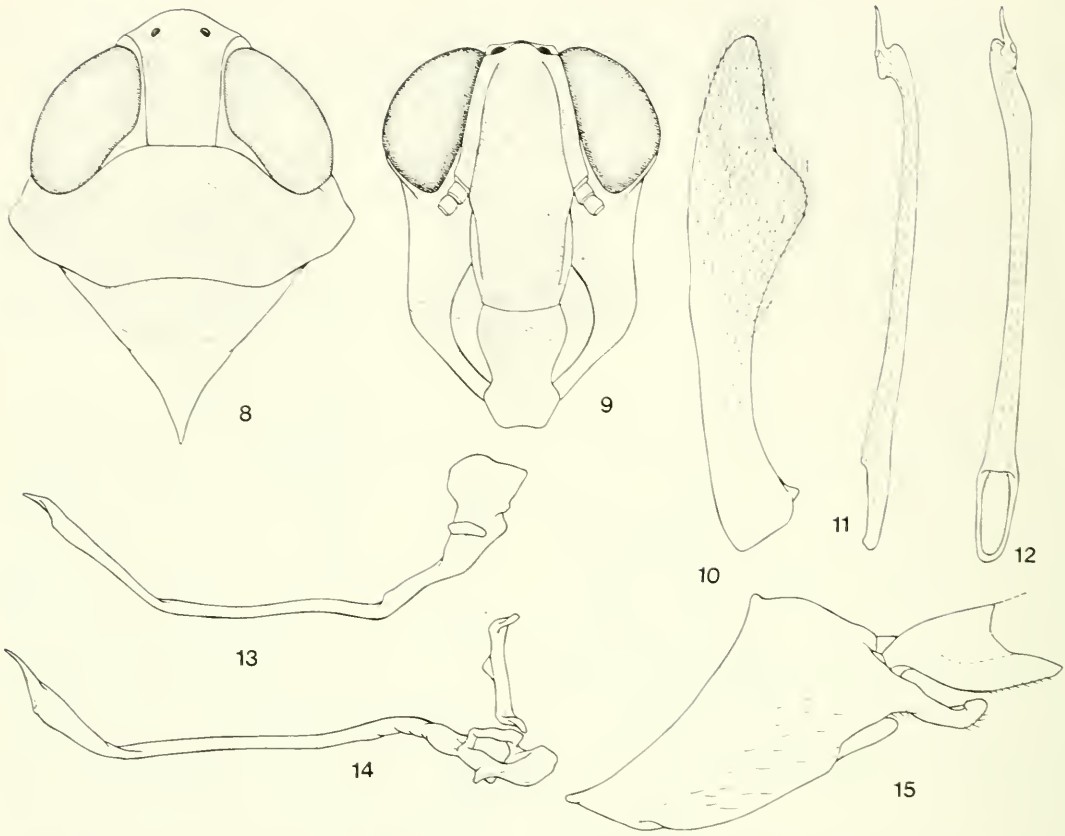
scutellum short, median length slightly longer than median length of crown, surface finely sculptured except for median, transverse indentation; forewings with normal venation in male, micropterus in female exposing distal portion of segment 9 and ovipositor, veins and some cells with corrugated bullae, appendix poorly developed, especially in female; clypeus long and broad, sometimes with a very faint, median, longitudinal carina that does not reach basal origin; clypellus long with distal third expanded laterally.

MALE.—Pygofer in lateral view with caudodorsal margin bilobed (Fig. 3); aedeagus symmetrical, long, tubular, and broadly curved in lateral view, strongly recurved distally with minute spines apically, apex sometimes sharply pointed (Fig. 5), somewhat compressed laterally toward apex in dorsal view, gonopore subapical on ventral margin; style very long, sinuate, tapered apically (Fig. 6); plate long and narrow, enlarged toward apex (Fig. 7).

FEMALE.—Seventh sternum with caudal margin produced medially and broadly convex.

HOLOTYPE (male).—BRASIL: Minas Gerais, Santa Barbara, Caraca, __.I.1970, F. M. Oliveira, B. M. 1971-165 (BMNH). Allotype (female), same data as holotype (BMNH). Paratypes: BRASIL: one female, same data as holotype (BMNH), one male and one female, same data as holotype (author's collection), one female, BRASIL: no locality, __.__.1895, J. Fallou (MNHN).

REMARKS.—This is the only known species in the genus. Its broad, robust appearance and simple aedeagus will distinguish the species from other genera in the tribe Coelidiini.



Figs. 8–15. *Gracilidia gracilis*, n. sp. 8. Head, pronotum, and scutellum, dorsal view. 9. Face, ventral view. 10. Plate, ventral view. 11. Aedeagus, lateral view. 12. Aedeagus, dorsal view. 13. Right style, lateral view. 14. Connective and right style, dorsal view. 15. Pygofer, lateral view.

Gracilidia, n. gen.

TYPE-SPECIES.—*Gracilidia gracilis*, n. sp.

Medium-sized, slender species.

LENGTH.—Male 7.00–7.50 mm.

General habitus dark brown to black with markings on forewings. Similar to *Boliviela* DeLong but with distinctive male genitalia.

Head distinctly narrower than pronotum; crown produced beyond anterior margin of eyes, much narrower than width of eyes; eyes large, semiglobular; pronotum and scutellum moderately large, each with median length greater than median length of crown; forewings with 5 apical cells and 3 anteapical cells, outer one closed; clypeus long and narrow, without a median, longitudinal carina; clypellus swollen basally; femoral setal arrangement 2:2:1.

Male genitalia slightly asymmetrical; pygofer with moderately long caudodorsal; lobe; dorsal apodeme typical; aedeagus simple, long, tubular, with terminal spine, gonopore subapical; connective Y-shaped, stem short; style very long and slender; plate long, heavily setose.

The genus is known only from Ecuador and is represented by a single species. It can be distinguished from *Boliviela* by the simple aedeagus without secondary processes.

Gracilidia gracilis, n. sp.

Figs. 8–15

LENGTH.—Male 7.00–7.50 mm.

General color dark brown to blackish with broad markings on forewings; crown and pronotum dark brown to black with tannish markings or spots; scutellum dark brown to purplish black, sometimes with tan spots;

forewings with broad areas of smokey brown to black in distal half, brownish translucent basally, large, tannish spot near middle of costa, veins with tan spots; face black with numerous tannish spots on clypeus.

Head much narrower than pronotum; crown produced beyond anterior margin of eyes, much narrower than width of eyes, slightly carinate on lateral margins; eyes large, semiglobular; pronotum and scutellum as in description of genus; forewings and venation typical; clypeus long and narrow, without a median, longitudinal carina; clypellus swollen basally.

MALE.—Pygofer in lateral view with moderately long caudodorsal lobe, lobe curved dorsally at apex (Fig. 15); aedeagus long, narrow, tubular throughout, slightly asymmetrical, shaft abruptly curved dorsad before apex, terminating in caudally directed, sharp spine, gonopore subapical on dorsal margin (Fig. 11); style very long and slender, slightly enlarged distally (Fig. 13); plate long and narrow, enlarged subapically on outer margin, profusely setose (Fig. 10).

FEMALE.—Unknown.

HOLOTYPE (male).—ECUADOR: Napo, past road from Baeza to Papallacta, km 186, 13.IV.1977, Elaine R. Hodges (USNM). Paratype: one male, ECUADOR: Napo, Baeza, 12–22.II.1983, L. Huggert (UL).

REMARKS.—This species can be separated from other species of related genera by the simple, elongate, tubular aedeagus with a terminal spine. The aedeagus is remarkably similar to the aedeagus of *Licolidia angusta* Nielson, a member of the tribe Teruliini. However, tribal and other generic characters distinguish *gracilis* from that species.

Fistulidia, n. gen.

TYPE-SPECIES.—*Fistulidia simplex*, n. sp.

Medium-sized, slender species.

LENGTH.—Male 7.50 mm, female 8.40 mm.

General color light to dark brown with tannish markings on forewings. Similar in general habitus to *Crassinolanus* Nielson but with distinctive male genitalia.

Head distinctly narrower than pronotum, subconically produced as in *Crassinolanus;* crown narrow, narrower than width of eyes; eyes large, semiglobular; pronotum and scutellum large, each with median length greater than median length of crown; forewings with 5 apical cells, 3 anteapical cells, outer one closed, appendix well developed; clypeus long and narrow, without a median, longitudinal carina; femoral setal arrangement 2:2:1.

Male genitalia asymmetrical; pygofer with small lobe on caudal margin; aedeagus asymmetrical, simple, very long, tubular; dorsal apodeme attached laterally to base of aedeagus; connective with short stem; style very short; plate long and narrow.

This genus is known only from Brasil and is represented by a single species. It is distinguished from *Crassinolanus* by the tubular aedeagus, short style, and lateral attachment of the dorsal apodeme to the base of the aedeagus.

Fistulidia simplex, n. sp.

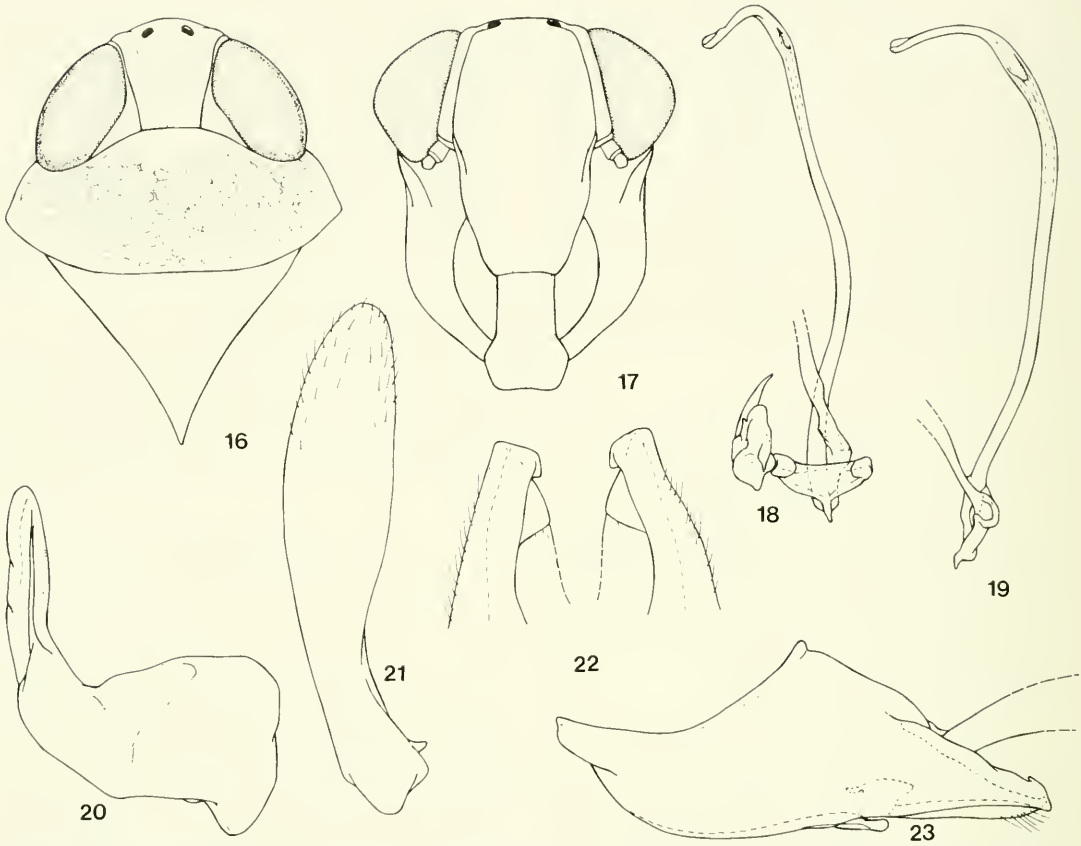
Figs. 16–23

LENGTH.—Male 7.50 mm, female 8.40 mm.

General color light to dark brown with tannish spots and markings on pronotum and forewings; crown tannish; pronotum dark brown with tannish spots on anterior half; forewings dark brown with small to large, tannish spots on costa and broken, tannish transverse band medially; face tan with reddish, longitudinal stripe bordering lateral margins of clypeus.

Head much narrower than pronotum, subconical on anterior margin; crown narrow, lateral margins converging basally, narrower than width of eyes; eyes large, semiglobular; pronotum large, median length greater than median length of crown; scutellum large, median length greater than median length of pronotum; forewings as in description of genus; clypeus long and narrow, flat, without a median, longitudinal carina; clypellus narrow with lateral margins expanded apically.

MALE.—Pygofer in lateral view with small lobe on middle of caudal margin (Fig. 23); aedeagus asymmetrical, long, tubular in lateral and dorsal views (Figs. 18, 19), curved dorsally at apex in lateral view (Fig. 19), slightly curved laterally in dorsal view (slightly exaggerated in Fig. 18), gonopore subapical on lateral margin before curvature; dorsal apodeme arising laterally from base of aedeagus; style very short, broad in lateral view becoming tapered in distal half (Fig. 20);



Figs. 16–23. *Fistulidia simplex*, n. sp. 16. Head, pronotum, and scutellum, dorsal view. 17. Face, ventral view. 18. Connective, right style, and aedeagus, dorsal view. 19. Aedeagus, lateral view. 20. Right style, lateral view. 21. Plate, ventral view. 22. Terminus of pygofer, dorsal view. 23. Pygofer, lateral view.

plate long and narrow, constricted subbasally (Fig. 21).

FEMALE.—Seventh sternum large, about twice as long as preceding segment, caudal margin truncate.

HOLOTYPE (male).—BRASIL: Reserva Ducke Mn. Am., 5.XII.1968, #2829, E. V. Silva and A. Faustino (INPA). Allotype (female), same data as holotype (INPA). Paratypes: one male, BRASIL: Manaus, Amazonas, 7–19.XII.1977, B. C. Ratcliffe (author's collection).

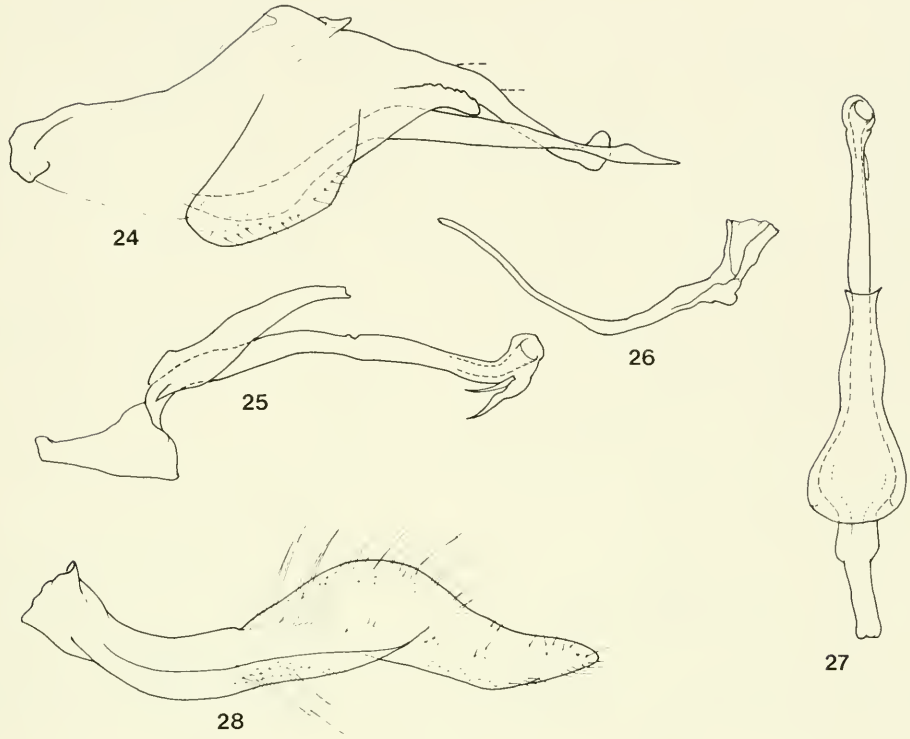
REMARKS.—This species can be separated from *Crassinolanus dementius* Nielson by the long, tubular aedeagus, short style, and position of the basal attachment of the dorsal apodeme.

Boliviela DeLong

Six species of *Boliviela* are treated in my paper on the tribe Coelidiini (Nielson 1982). Two new species are added here with a revised key to the species. The group is apparently restricted to northwestern South America, from Bolivia north to Colombia.

Key to males of *Boliviela*

1. Aedeagus with retrorse distal process(es) 2
— Aedeagus with apex curved, process directed distally 3
2(1). Aedeagus with single retrorse distal process (Nielson 1982, Fig. 683) ..... *retrorsa* Nielson
— Aedeagus with two retrorse distal processes (Fig. 25) ..... *bispinosa*, n. sp.
3(1). Aedeagus with lateral processes or flanges on shaft 4
— Aedeagus not as above 6
4(3). Aedeagus with triangular lateral flanges 5
— Aedeagus with long, bladelike lateral flanges (Nielson 1982, Fig. 688) .... *angustiformis* (Linnavuori)



Figs. 24–28. *Boliviela bispinosa*, n. sp. 24. Pygofer, lateral view. 25. Aedeagus and dorsal apodeme, lateral view. 26. Style, lateral view. 27. Aedeagus and dorsal apodeme, dorsal view. 28. Plate, ventral view.

5(4). Aedeagus with symmetrical lateral flanges (Nielson 1982, Fig. 698) ..... *delongi* Nielson

— Aedeagus with asymmetrical lateral flanges (Nielson 1982, Fig. 704) ..... *inflata* Nielson

6(3). Aedeagus with paired basal paraphyses 7

— Aedeagus without paraphyses (Nielson 1982, Fig. 715) ..... *linnavuori* Nielson

7(6). Aedeagus with basal paraphyses long and acuminate (Nielson 1982, Fig. 709) ..... *ortha* Nielson

— Aedeagus with basal paraphyses long and semisaggitate (Figs. 35, 36) ..... *paraortha*, n. sp.

Boliviela bispinosa, n. sp.

Figs. 24–28

LENGTH.—Male 8.40 mm.

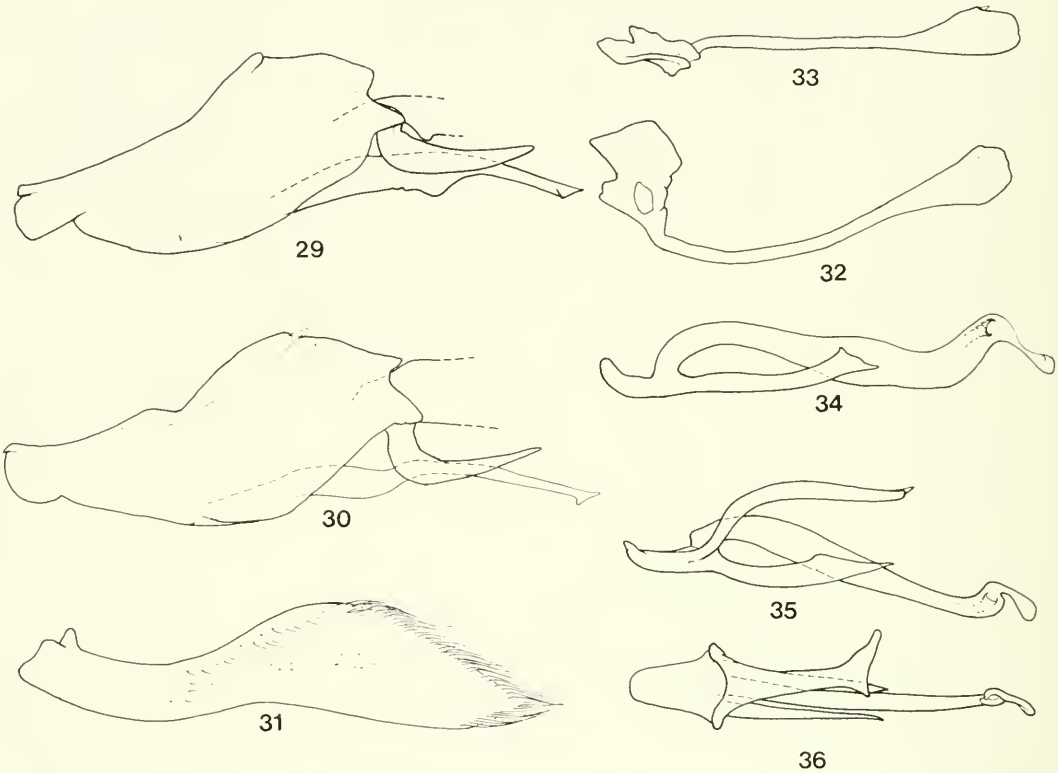
General color deep tan with dark brown markings. Crown, pronotum, and scutellum deep tan with black markings; forewings deep tan with black markings on apical half and veins marked with orange spots, large, translucent spot about middle of clavus; face tan with brown markings.

Head much narrower than pronotum, anterior margin narrowly rounded; crown broad, about as wide as width of eyes; eyes large, elongate-ovoid; pronotum and scutellum large, each with median length greater than median length of crown; forewings and venation typical; clypeus long and broad, without a median, longitudinal carina; clypellus swollen basally.

MALE.—Pygofer in lateral view with very long caudoventral process and moderately long caudodorsal process (Fig. 24), process extending beyond caudodorsal process; aedeagus in lateral view with large base, narrowed and tubular distally with two ventral spines apically, distal spine larger than basal spine, gonopore apical (Fig. 25); dorsal apodeme forked basally and attached near base of shaft before socle; style very long and slender at distal 3/4 (Fig. 26); plate long, sinuate, and profusely pilose at distal half (Fig. 28).

FEMALE.—Unknown.

HOLOTYPE (male).—PERU: Tingo Maria, roadside veg., Los Cuevos Road, SW of town,



Figs. 29–36. *Boliviela paraortha*, n. sp. 29. Pygofer, lateral view. 30. Pygofer, lateral view (showing variation). 31. Plate, ventral view. 32. Right style, lateral view. 33. Right style, dorsal view. 34. Aedeagus and paraphysis, lateral view. 35. Aedeagus, dorsal apodeme, and paraphysis, lateral view (showing variation). 36. Aedeagus, dorsal apodeme, and paraphysis, dorsal view.

forested eastern foothills of Andes, 2,000 ft, 13.VIII.1971, P. S. and H. L. Broomfield, B. M. 1971-486 (BMNH).

REMARKS.—From *B. retrorsa* Nielson, *bispinosa* can be separated by the pair of distal spines on the aedeagus and by the very long caudoventral pygofer process, which extends beyond a moderately long caudodorsal process.

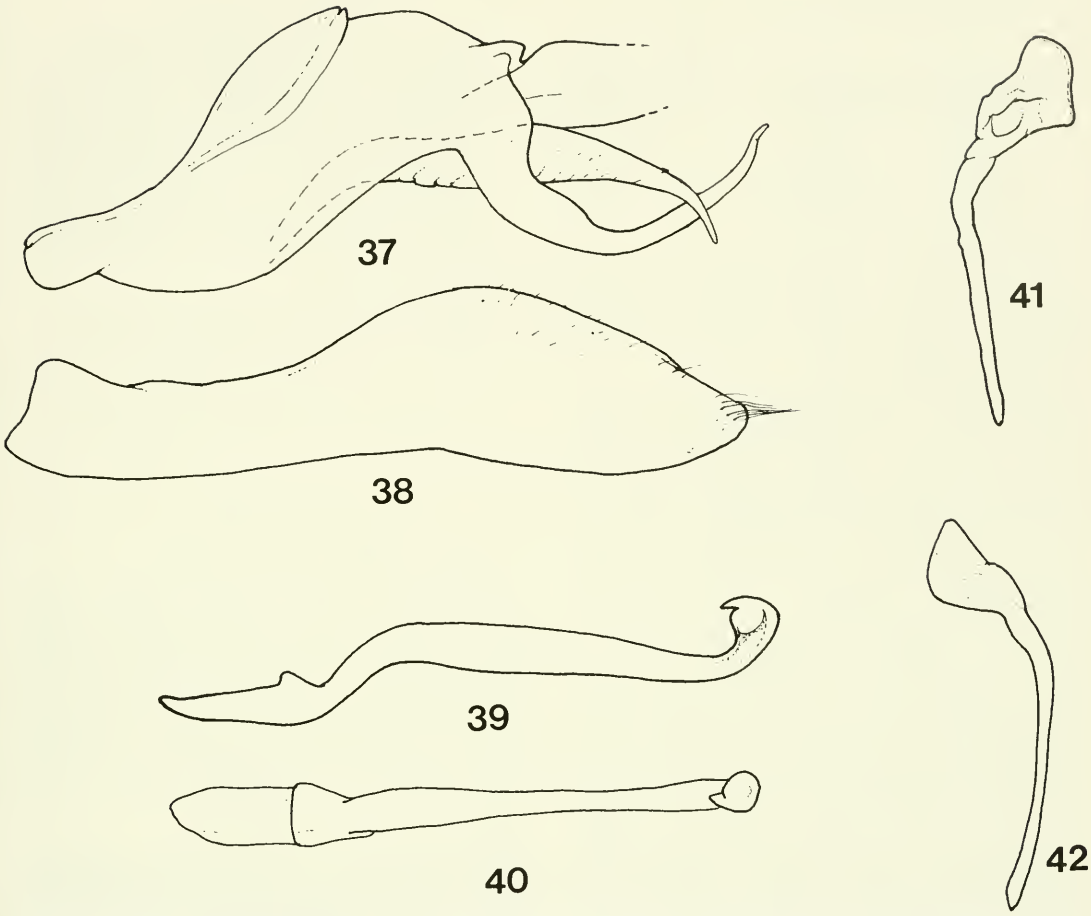
Boliviela paraortha, n. sp.
Figs. 29–36

LENGTH.—Male 8.20–8.90 mm.

General color dark brown to blackish with pale, translucent markings on forewings. Crown dark brown to black; pronotum dark brown to black, sometimes with tan markings or spots; scutellum purplish black except for dark brown triangle distally; forewings dark brown to blackish in distal half, translucent basally and with translucent spot on about middle of costa, veins with small tan spots; face reddish brown with very small, tannish spots.

Head distinctly narrower than pronotum; crown narrow, lateral margins carinate, produced distally beyond anterior margin of eyes, narrower than width of eyes; eyes large, elongate-ovoid; pronotum and scutellum large, each with median length greater than median length of crown; forewings and venation typical; clypeus long and narrow, without a median, longitudinal carina; clypellus swollen basally.

MALE.—Pygofer in lateral view with two long processes on caudal margin, caudoventral process very long, extending beyond apex of caudodorsal process (Figs. 29, 30), sinuate, with small, triangular lobe distally on ventral margin, caudodorsal process short, sickle-shaped; aedeagus in lateral view long, sinuate, constricted subapically, paired ventral



Figs. 37–42. *Tinocripus huggerti*, n. sp. 37. Pygofer, lateral view. 38. Plate, ventral view. 39. Aedeagus, lateral view. 40. Aedeagus, dorsal view. 41. Left style, dorsal view. 42. Left style, lateral view.

paraphyses subbasal which extend to about midlength of aedeagal shaft, paraphyses sword-shaped with triangle lobe subapically (Figs. 35, 36); gonopore subapical on lateral margin; dorsal apodeme bifurcate basally, straddling base of aedeagus; style very long, narrow except basally and distal 1/4 (Fig. 32); plate long, sinuate, broad near middle, and profusely setose (Fig. 31).

FEMALE.—Unknown.

HOLOTYPE (male).—ECUADOR: Napo, Baeza, 12–22.II.1983, L. Huggert (UL). Paratypes: ECUADOR: 4 males, same data as holotype (UL, author's collection).

REMARKS.—This species is very near *B. ortha* Nielson but can be distinguished by the configuration of the ventral paraphysis of the aedeagus and the more tapered plate.

Tinocripus Nielson

Three species of this genus are discussed in my revision of the tribe Coelidiini (Nielson 1982). A fourth species is described herein with a revised key to the species. Ecuador is added to the distribution of the genus, which was previously known only in Peru.

Key to the males of *Tinocripus*

1. Pygofer with caudoventral process bladelike . . . 2
— Pygofer with caudoventral process not as above . 3
2(1). Pygofer with caudoventral process attenuated distally, caudodorsal process long, broad in basal half (Fig. 37) . . . . . *huggerti*, n. sp.
— Pygofer with caudoventral process narrowed abruptly near apex, caudodorsal process short, lateral margins nearly equal throughout length (Nielson 1982, Fig. 722) . . . . . *gladius* Nielson

3(1). Pygofer with caudoventral process transversely corrugated in distal 1/4 (Nielson 1982, Fig. 717) ..... *spinosus* Nielson

— Pygofer with caudoventral process enlarged distally (Nielson 1982, Fig. 730) .. *schlingeri* Nielson

Tinocripus huggerti, n. sp.
Figs. 37–42

LENGTH.—Male 7.40 mm.

General color deep brown to blackish; crown, pronotum, and scutellum black; forewings smoky black on clavus and basal half; face tannish brown.

Head distinctly narrower than pronotum; crown narrow, produced distally beyond anterior margin of head, narrower than width of eyes; eyes large, semiglobular; crown and pronotum moderately large, each with median length slightly longer than median length of crown; forewings and venation typical; clypeus long and narrow, narrower distally than basally; clypellus swollen basally.

MALE.—Pygofer in lateral view with two long caudal processes, caudoventral process broad at basal 3/4, attenuated distally and curved ventrad, caudodorsal process broad in basal half and abruptly narrowed and curved caudodorsad in distal half (Fig. 37); aedeagus in lateral view narrow, tubular, sinuate, curved dorsad at apex, with subapical constriction and small, blunt spine distally, gonopore subapical (Fig. 39); style long, narrow at distal 3/4 (Fig. 41); plate long, narrow, enlarged near middle on outer margin (Fig. 38).

FEMALE.—Unknown.

HOLOTYPE (male).—ECUADOR: Napo, Baeza, 12–22.II.1983, L. Huggert (UL).

REMARKS.—From *T. gladius* Nielson, to which it is most closely related, *huggerti* can be separated by configuration of the caudal processes of the pygofer and the longer style. This species is named for Dr. L. Huggert, who has collected much new material on the subfamily Coelidiinae in the Neotropics.

Lodia Nielson

This genus was established with four species and placed in the tribe Coelidiini by Nielson (1982). A new species is added here from Ecuador, and a revised key to the species is also given. *Lodia* is restricted to Ecuador and Peru.

Key to males of *Lodia*

1. Aedeagus with a single subapical spine on shaft . 2

— Aedeagus with 2 subapical spines on shaft 3

2(1). Aedeagus with subapical spine glabrous (Nielson 1982, Fig. 759) ..... *glabrosa* Nielson

— Aedeagus with subapical spine enlarged distally and toothed (Fig. 46) ..... *parapectinata*, n. sp.

3(1). Style with distinct lateral lobe in lateral view (Nielson 1982, Fig. 763) ..... *pectinata* Nielson

— Style without such lobe 4

4(3). Aedeagus with distal spine glabrous, nearly reaching to apex of shaft (Nielson 1982, Fig. 772) ..... *proxima* Nielson

— Aedeagus with distal spine toothed, not reaching to apex of shaft (Nielson 1982, Fig. 779) ... . *negans* Nielson

Lodia parapectinata, n. sp.
Figs. 43–49

LENGTH.—Male 7.40–8.10 mm.

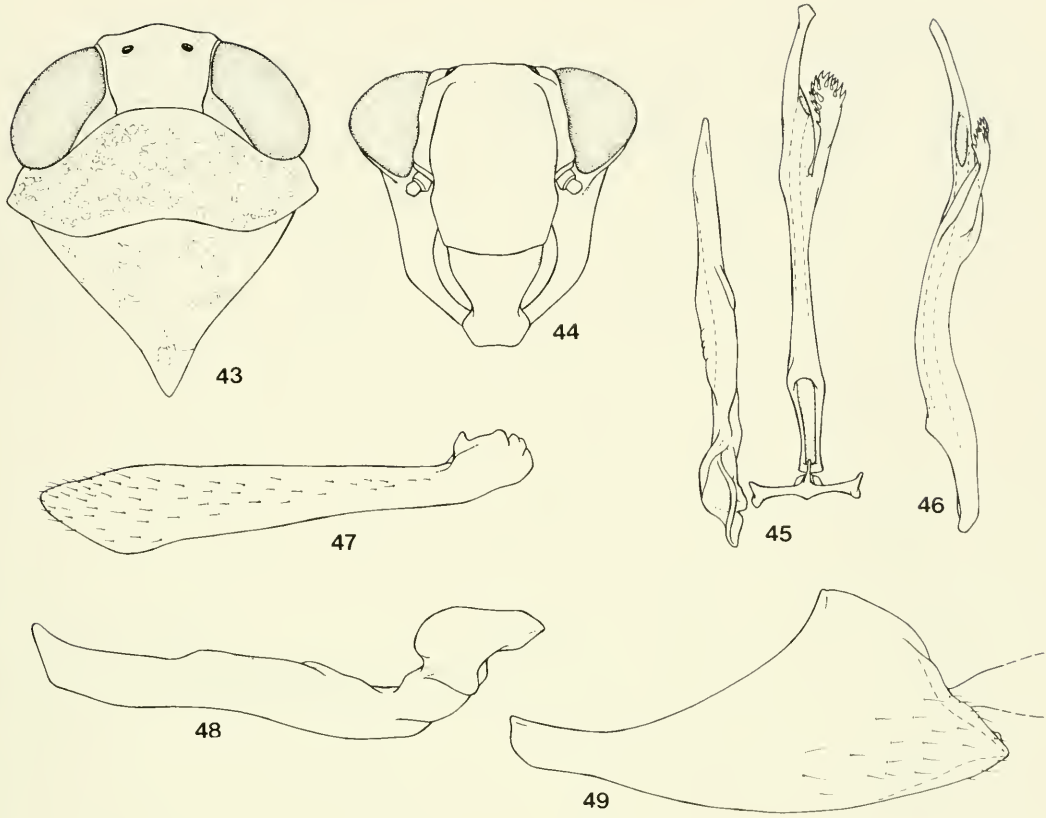
General color dark brown to black, usually with very faint, narrow, pale, sordid yellow, transverse band on about middle of forewings; crown deep tan, sometimes with dark markings basally on disc; pronotum and scutellum black with small, deep tan spots or markings; forewings black with deep orange spots on veins; face black except for deep tan in ocellocular area.

Head narrower than pronotum, anterior margin rounded; eyes large, semiglobular; crown broad, width greater than width of eyes; pronotum and scutellum large, each with median length greater than median length of crown; forewings and venation typical; clypeus broad, without a median, longitudinal carina; clypellus swollen basally.

MALE.—Pygofer in lateral aspect without processes or lobes (Fig. 49); aedeagus asymmetrical, in lateral view long, somewhat tubular, sinuate, with prominent, apically dentate spine on lateral margin near middle of shaft (Fig. 46), enlarged at distal half in dorsal view (Fig. 45), gonopore subapical on lateral margin; style long and moderately broad, somewhat compressed laterally (Fig. 48); plate long and narrow (Fig. 47).

FEMALE.—Unknown.

HOLOTYPE (male).—ECUADOR: Napo, Puerto Montufar, 28.IV.1976, Malaise trap, Jeffrey Cohen (USNM). Paratypes: 81 males, same data as holotype (USNM), 8 males, same data as holotype (CAS, BMNH, author's collection).



Figs. 43–49. *Lodia parapectinata*, n. sp. 43. Head, pronotum, and scutellum, dorsal view. 44. Face, ventral view. 45. Connective, right style, and aedeagus, dorsal view. 46. Aedeagus, lateral view. 47. Plate, ventral view. 48. Right style, lateral view. 49. Pygofer, lateral view.

REMARKS.—This species is similar to *pectinata* Nielson in certain male genitalia characters but is distinguished by the lack of the medial, glabrous spine on the aedeagus, by the lack of the preapical lobe on the inner lateral margin of the style, and by the much less prominent, transverse band on the forewings.

The large series of male specimens collected of this species is unusual for members of the subfamily Coelidiinae, particularly in the Neotropical region where only a few specimens of each sex of most species are taken by sweep-net or by black-light techniques. The use of a Malaise trap, however, may provide a great amount of material on this large and rarely accessible subfamily of leafhoppers.

Calodicia Nielson

Two species are known in the genus (Nielson 1982). A third species is described, and a revised key to males of all known species is given. *Calodicia* was previously known from Panama and Colombia. The new species from Paraguay suggests disjunctive distribution for the group, but further collecting may bring to light additional species to bridge the gap between the widely separate species.

Key to male of *Calodicia*

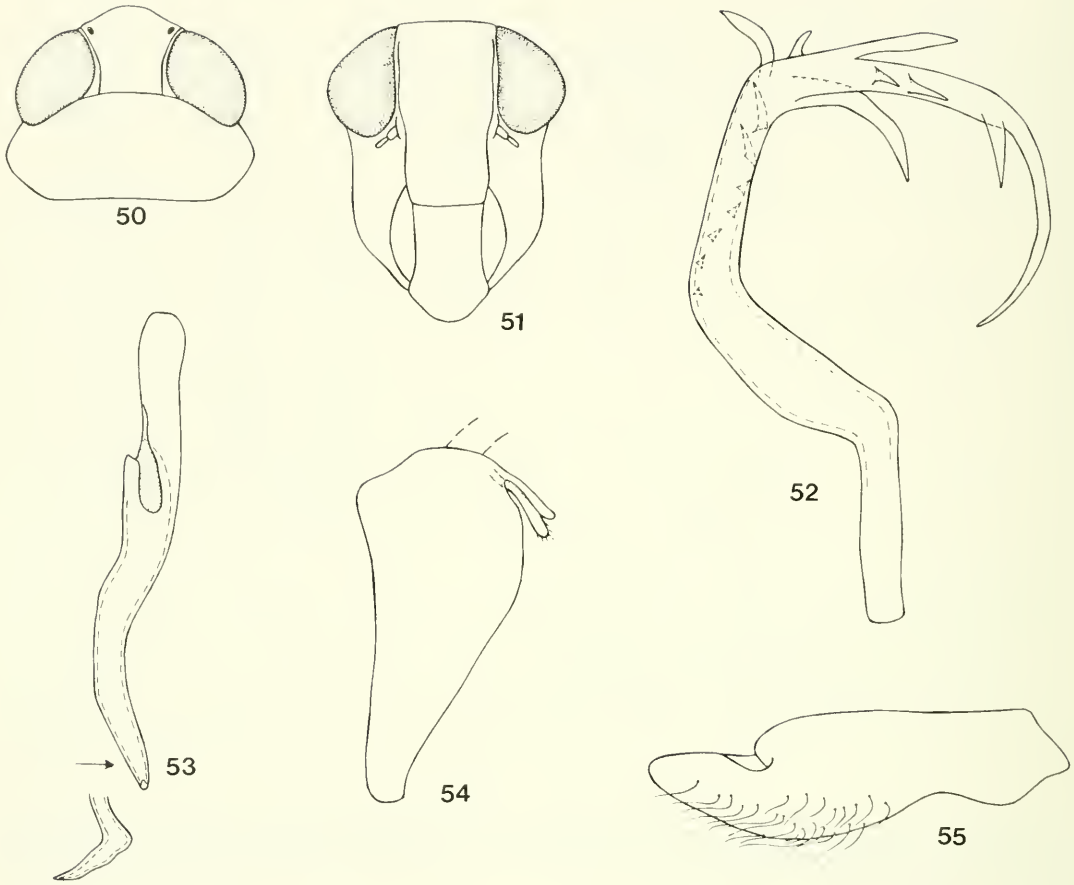
1. Style heavily setose 2
— Style glabrous (Fig. 53) . . . . . *circulata*, n. sp.
2(1). Aedeagus very long, strongly recurved at distal 1/3 (Nielson 1982, Fig. 925) . . . . . *maculipennis* (Spangberg)
— Aedeagus short, broadly curved throughout shaft (Nielson 1982, Fig. 934) . . . . *abrupta* Nielson

Calodicia circulata, n. sp.

Figs. 50–55

LENGTH.—Male 7.00 mm.

General color brown; crown tannish with



Figs. 50–55. *Calodicia circulata*, n. sp. 50. Head and pronotum, dorsal view. 51. Face, ventral view. 52. Aedeagus, dorsal view. 53. Right style, dorsal view. 54. Pygofer, lateral view. 55. Plate, ventral view.

dark brown markings basally; eyes light reddish brown; pronotum and scutellum black; forewings light reddish brown except for large, suffused, tannish spot at apex of clavus; face black.

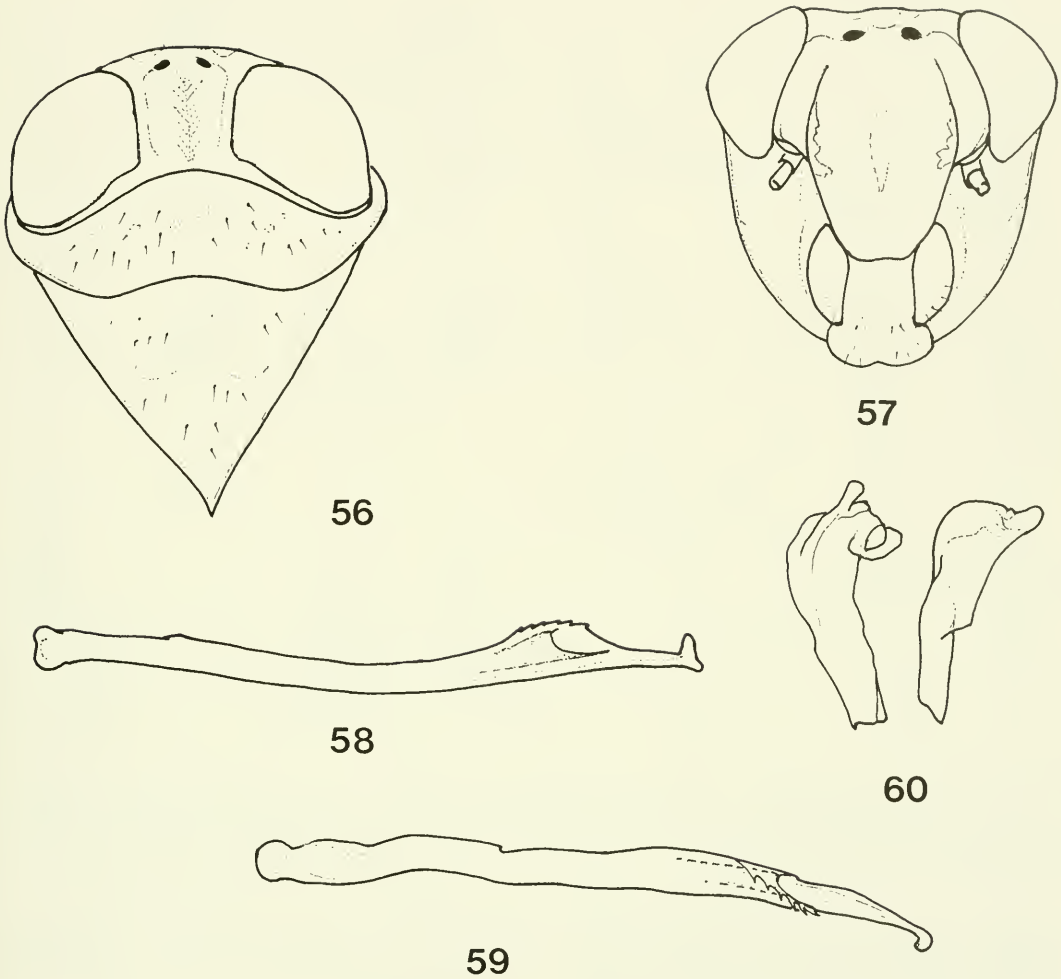
Head narrower than pronotum (Fig. 50), anterior margin slightly produced, nearly rounded anteriorly; eyes large, semiglobular; ocelli near anterior margin of crown; forewings with 5 apical cells, 3 anteapical cells, outer one closed, appendix well developed; clypeus broad throughout length (Fig. 51), without a median, longitudinal carina; clypellus slightly constricted medially and elevated along median line; hind femoral setal arrangement 2:2:1.

MALE.—Pygofer narrow with pair of narrow caudodorsal lobes directed anteriodorsally (Fig. 54); aedeagus very long, forming near circle in dorsal view (Fig. 52), shaft with many stout, short to long spines, spines originating near middle of shaft and generally becoming longer toward distal portion of shaft, shaft attenuated distally at apical 1/5; gonopore not apparent; style very long, narrow, tapered toward apex in dorsal view (Fig. 53), apex foot-shaped in lateral view; plate broad, incised on inner lateral margin near apex (Fig. 55).

FEMALE.—Unknown.

HOLOTYPE (male).—PARAGUAY: St. Antonio, no date, no collector, in the Melichar collection (MMB).

REMARKS.—*Calodicia circulata* is similar to *C. maculipennis* (Spangberg) in the general shape of the aedeagus but differs in having



Figs. 56–60. *Dicolecia serrata*, n. sp. 56. Head, pronotum, and scutellum, dorsal view. 57. Face, ventral view. 58. Aedeagus, dorsal view. 59. Aedeagus, lateral view. 60. Base of right style, dorsal and lateral views.

larger and greater number of spines on the shaft, a lack of setae on the style, and an additional, narrow lobe on the caudodorsal margin of the pygofer.

Dicolecia Nielson

One species was described and treated in my revision of the tribe Coelidiini (Nielson 1982). A new species is added with a key to the species. The genus is thus far restricted to Colombia and Peru.

Key to males of *Dicolecia*

1. Aedeagus with 2 lateral processes subapically, basal process dentate (Nielson 1982, Fig. 961) . . . . . *bifurcata* Nielson

— Aedeagus with lateral serrate flange (Fig. 59) . . . . . *serrata*, n. sp.

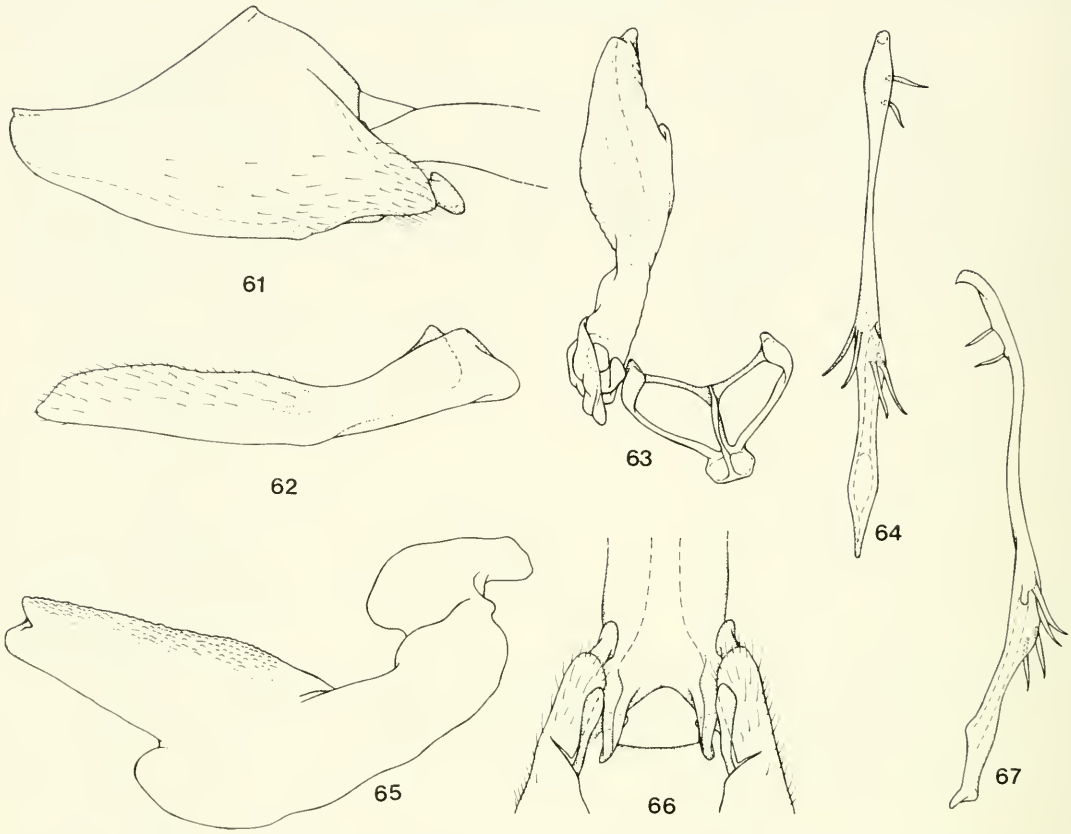
Dicolecia serrata, n. sp.

Figs. 56–60

LENGTH.—Male 6.90 mm.

General color reddish brown to black with distinctive, very broad, yellow, transverse band on forewings. Crown pale orange; pronotum purplish black; scutellum reddish brown; forewings reddish brown except for purplish black clavus basally and broad, yellow, transverse band from costa crossing middle of clavus; face pale orange. A beautifully marked species.

Head large, narrower than pronotum,



Figs. 61–67. *Evansolidia massa*, n. sp. 61. Pygofer, lateral view. 62. Plate, ventral view. 63. Connective and right style, dorsal view. 64. Aedeagus, dorsal view. 65. Right style, lateral view. 66. Terminus of pygofer and segment 10, ventral view. 67. Aedeagus, lateral view.

rounded anteriorly; eyes large, semiglobular; crown broad but narrower than width of eyes; pronotum short, median length less than median length of crown; scutellum large, median length greater than median length of crown; forewings and venation typical; clypeus broad, without a median, longitudinal carina; clypellus with lateral margins expanded distally.

MALE.—Pygofer with caudal margin damaged on holotype specimen; aedeagus asymmetrical, in ventral view long, tubular, with lateral serrate flange subapically, apex with small lobe laterally (Fig. 59), gonopore subapical on dorsal margin in expanded portion; style damaged in holotype specimen; plate long and narrow, heavily setose apically.

FEMALE.—Unknown.

HOLOTYPE (male).—COLOMBIA: Bolivar Batatal, 1938–1939, M. Althen-Dahl (UL).

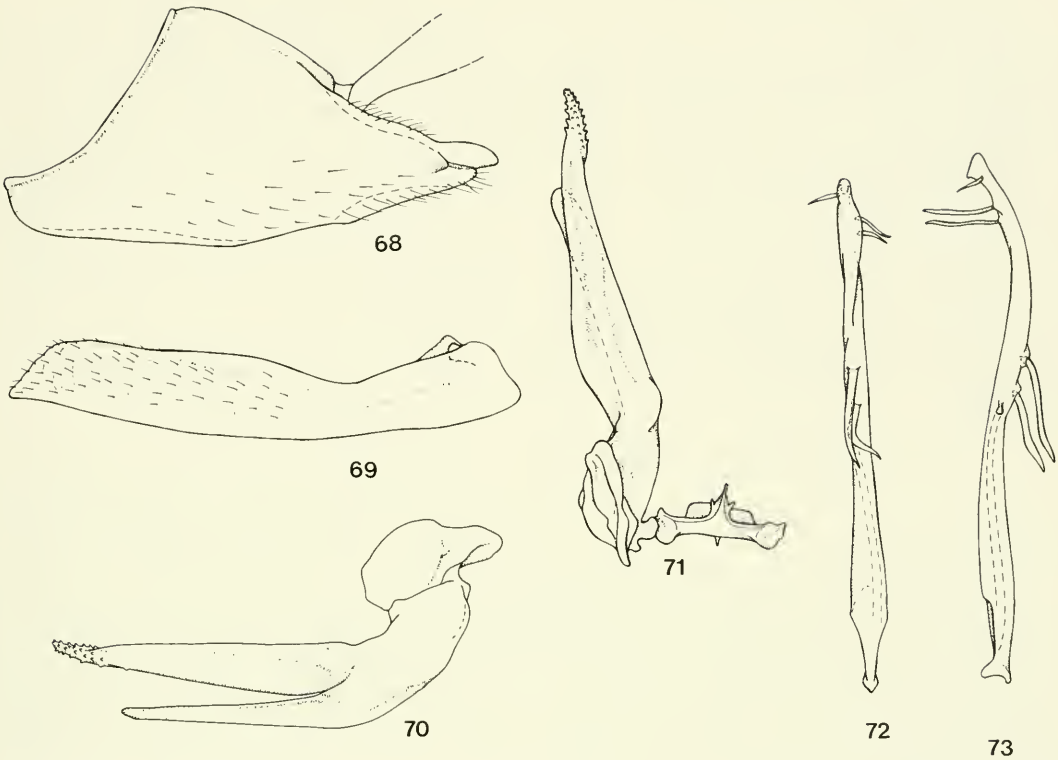
REMARKS.—This species can be easily distinguished from *D. bifurcata* by the distinctive, broad, yellow, transverse band on the forewings and subapical serrate expanded portion of the aedeagus.

Evansolidia Nielson

Three species of the genus were treated in my revision of Coelidiini (Nielson 1982). Three additional new species are described here, and a revised key to the species is provided. The genus occurs in Brasil, Guyana, and more recently in Peru.

Key to males of *Evansolidia*

1. Style in lateral view with distal 2/3 broadly expanded or bilobed 2
— Style in lateral view with distal 2/3 not so or slightly expanded laterally 4
2(1). Aedeagus with distal and medial setae on shaft . 3
— Aedeagus with basal setae only on shaft (Nielson 1982, Fig. 989) . . . . . *libera* (Walker)
3(2). Style with large, lateral lobe medially in lateral view (Fig. 65) . . . . . *massa*, n. sp.



Figs. 68–73. *Evansolidia bifurcata*, n. sp. 68. Pygofer, lateral view. 69. Plate, ventral view. 70. Right style, lateral view. 71. Connective and right style, dorsal view. 72. Aedeagus, dorsal view. 73. Aedeagus, lateral view.

— Style with distal half asymmetrically bifurcate in lateral view (Fig. 70) ..... *bifurcata*, n. sp.

4(1). Aedeagus with numerous setae or spines on shaft 5

— Aedeagus with basal setae only on shaft (Nielson 1982, Fig. 982) ..... *bispinosa* Nielson

5(4). Aedeagus with setal arrangement subbasal and subapical, shaft constricted medially in dorsal view, gonopore medial (Nielson 1982, Fig. 974) ..... *evansi* Nielson

— Aedeagus with setal arrangement on middle third of shaft, shaft with sides nearly parallel, gonopore subbasal (Fig. 78) ..... *digitula*, n. sp.

Evansolidia massa, n. sp.

Figs. 61–67

LENGTH.—Male 8.00 mm, female 8.40–8.90 mm.

General color fuscous to black with sordid yellow markings; crown sordid yellow with two longitudinal, black bands extending along lateral borders of clypeus; pronotum and scutellum sordid yellow with black markings; forewings dark brown to black with yellow claval veins medially, broad, interrupted, transverse, sordid yellow band from costa and crossing apex of clavus.

Head narrower than pronotum, anterior margin broadly rounded; crown narrow, width distally narrower than width of eyes, eyes elongate ovoid; pronotum and scutellum large, median length of each greater than median length of crown; forewings and venation typical; clypeus long and narrow, without a median, longitudinal carina.

MALE.—Pygofer with small caudodorsal lobe (Fig. 61); aedeagus asymmetrical, in lateral view long, narrow, tubelike, sinuate with 2 long lateral setae subapically and 4 long ventral setae basad of middle of shaft (Fig. 67), shaft constricted between subbasal and subapical setae, expanded subapically in dorsal view (Fig. 64), gonopore basad of middle of shaft on lateral margin near subbasal setae; style large, ornate, somewhat compressed laterally along ventral half, with large, ventral, preapical lobe and small cleft apically (Fig. 65); plate long and narrow (Fig. 62).

FEMALE.—Seventh sternum with truncate caudal margin.

HOLOTYPE (male).—BRASIL: Amazon, Fonteboa, no date, no collector (NR). Allotype (female), same data as holotype (NR). Paratypes: three females, same data as holotype (NR), one female, same data as holotype (author's collection); PERU: Ucayule, one female, no date, no collector (NR).

REMARKS.—This species is most nearly related to *E. libera* (Walker) but is distinguished by the presence of an additional subbasal setae and two subapical setae on the aedeagal shaft and by the distinctive configuration of the style.

Evansolidia bifurcata, n. sp.
Figs. 68–73

LENGTH.—Male 8.60–9.00 mm, female 9.20 mm.

General color dark brown to blackish with yellow and ivory markings on pronotum, scutellum, and forewings; crown yellow with two black, longitudinal bands extending to face and bordering lateral margins of clypeus; forewings with large, yellow, subquadrate spot on middle of clavus and pale yellow to ivory markings near middle of costa and apex of clavus, veins with small, yellow spots.

Head narrower than pronotum, rounded along anterior margin; crown broad, narrower than width of eyes; eyes large, semiglobular; pronotum large, median length greater than median length of crown; scutellum large; forewing and venation typical; clypeus long and narrow, without a median, longitudinal carina.

MALE.—Pygofer in lateral view with small caudodorsal lobe (Fig. 68); aedeagus asymmetrical, in lateral view long, tubular, slightly sinuate, with 2–3 long ventral setae near middle of shaft and 3 long dorsal setae subapically (Fig. 73), narrow groove on distal 1/4 of dorsal margin in dorsal view (Fig. 72), gonopore small, near middle of shaft on lateral margin; style ornate, asymmetrically bifurcate, distal arm dentate apically (Fig. 70); plate long and narrow, constricted at basal 1/4, obliquely truncate distally (Fig. 69).

FEMALE.—Seventh sternum with caudal margin produced somewhat distally along middle and slightly sinuate.

HOLOTYPE (male).—BRASIL: Amazon, Fonteboa, no date, no collector (NR). Allotype (female), BRASIL: Amazon, Manaus, no date, Roman (NR). Paratypes: one male and one female, same data as holotype and allotype, respectively (author's collection); BRASIL: Obidos, one female. 19.VII.no year (OSU); BRASIL: Amazon, sup., one male, no date, Olivenca (NR); PERU: Huanuco, Tingo Maria, one male, 27.I.1974, L. Huggert (UL).

REMARKS.—This species can be distinguished from all other known species of *Evansolidia* by its unique, asymmetrically bifurcate style.

Evansolidia digitula, n. sp.
Figs. 74–79

LENGTH.—Male 7.80 mm.

General color dark brown to black with ivory or yellow markings. Crown sordid ivory with two broad, black, longitudinal bands extending along lateral borders of clypeus; pronotum and scutellum black with sordid ivory markings; forewings dark brown to black with veins ivory on middle of clavus and cells translucent medially, large, translucent spot above and below apex of clavus, cells basad of apical series partially translucent, veins blackish.

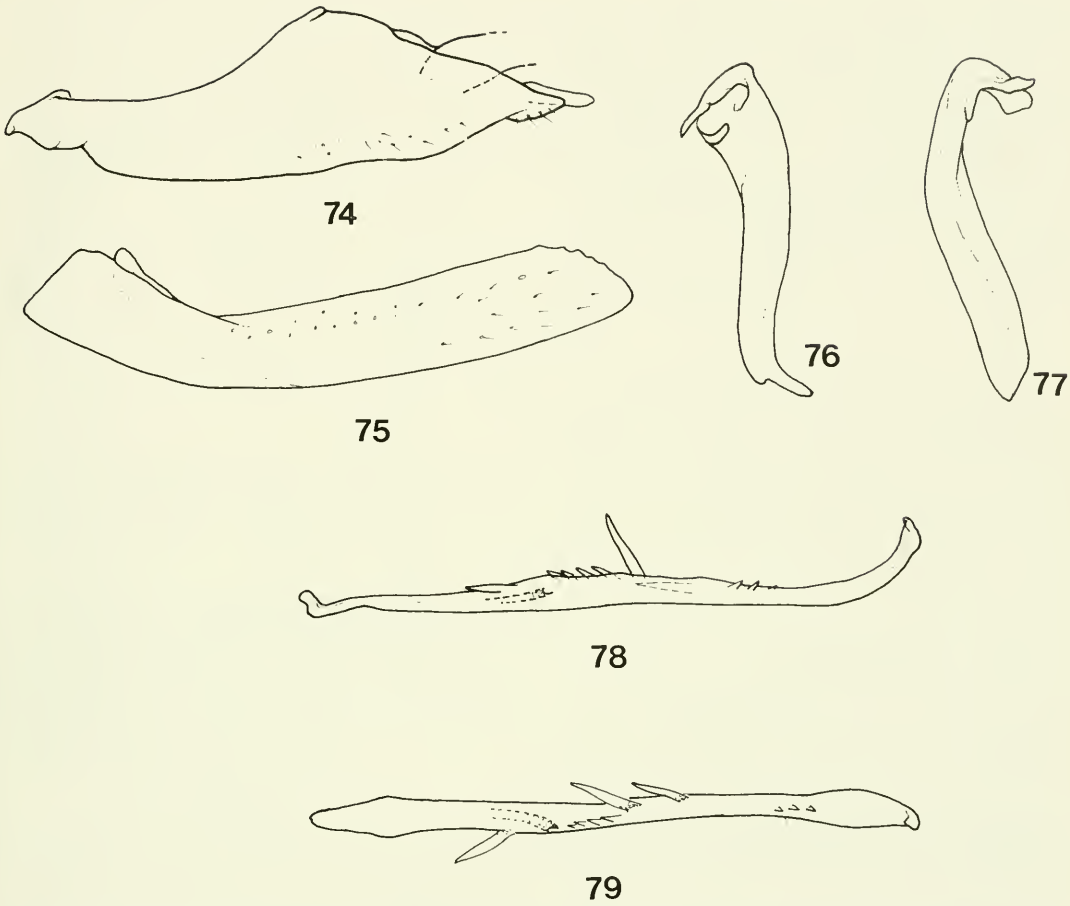
Head large, slightly narrower than pronotum; crown broad but narrower than width of eyes; eyes large, semiglobular; pronotum and scutellum large, each with median length greater than median length of crown; forewings and venation typical; clypeus long and narrow, without a median, longitudinal carina.

MALE.—Pygofer in lateral view with small caudodorsal lobe (Fig. 74); aedeagus asymmetrical, in lateral view long, narrow, somewhat tubular, slightly curved laterally at apical 1/4 (Fig. 78), in dorsal view with 3 stout setae on middle third of shaft on dorsal margin, one basad of gonopore and 2 distad, row of 4 short setae between and 3 very small, spinelike setae about middle of distal third (Fig. 79), gonopore small, basad of middle of shaft on lateral margin; style long, slender with digitate, subapical, lateral process on inner margin (Fig. 76); plate long and narrow (Fig. 75).

FEMALE.—Unknown.

HOLOTYPE (male).—PERU: Huanuco, Tingo Maria, 27.I.1974, L. Huggert (UL).

REMARKS.—From *E. bispinosa*, to which it is similar in some male genital characters,



Figs. 74–79. *Evansolidia digitula*, n. sp. 74. Pygofer, lateral view. 75. Plate, ventral view. 76. Right style, dorsal view. 77. Right style, lateral view. 78. Aedeagus, lateral view. 79. Aedeagus, dorsal view.

digitula can be separated by the presence of additional setae, large and small, on the shaft of the aedeagus and by the subapical, digitate process on the style.

Spinolidia Nielson

Four species of the genus were treated in my revision of *Coelidiini* (Nielson 1982). Two new species are described here with a revised key to the species. The genus occurs primarily in northwestern South America; only a single record is known in Brasil.

Key to the males of *Spinolidia*

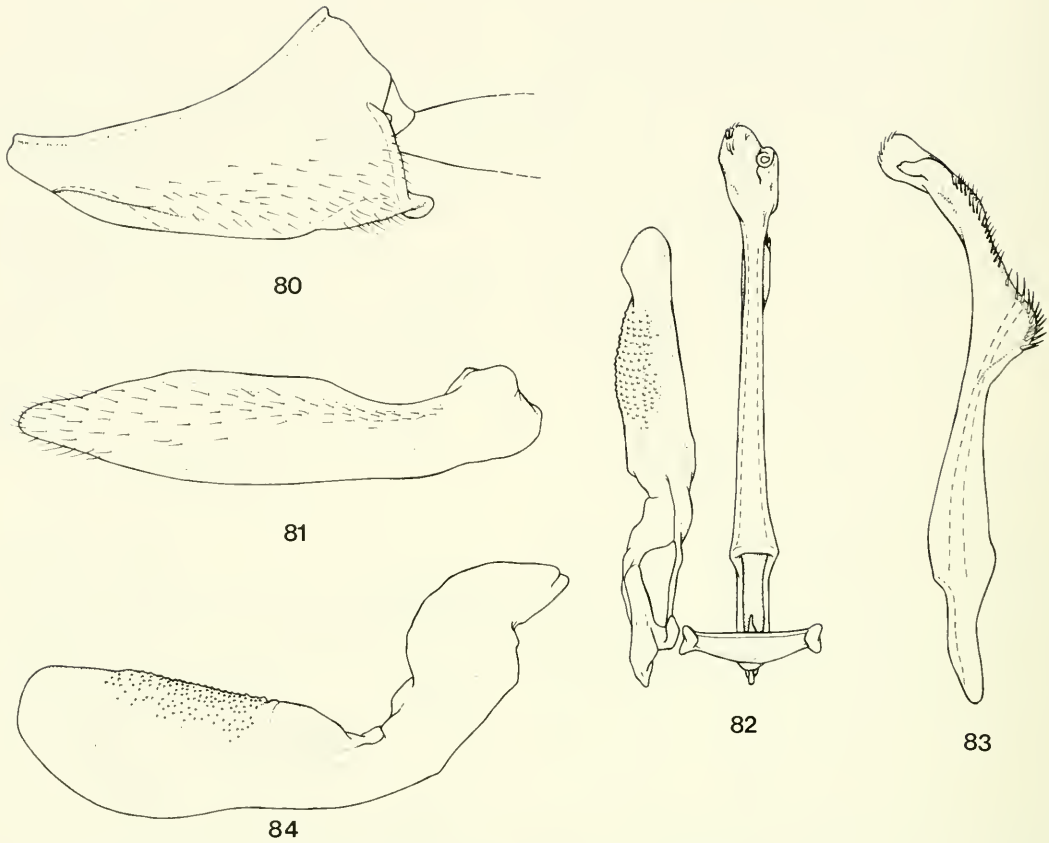
1. Aedeagus with numerous setae on distal third of shaft. 2
— Aedeagus with fewer setae, spicules or spines on middle of shaft 3

2(1). Aedeagus with an oblique row of dense setae subapically on lateral side of shaft and a few setae distally (Nielson 1982, Fig. 1012) . *osborni* Nielson
— Aedeagus with a row of sparse setae ventrally on about distal third of shaft and several setae distally (Fig. 83) . . . . . *sarmenta*, n. sp.

3(1). Style in lateral view narrow with obvious medial constriction, narrow toward apex 4
— Style in lateral view constricted subbasally, very broad at distal third (Fig. 85) . . . . . *magna*, n. sp.

4(4). Plate with subbasal constriction and expanded before apex; aedeagus with large gonopore 5
— Plate not subbasally constricted, margins gradually tapered toward apex (Nielson 1982, Fig. 1031); aedeagus with small, cryptic gonopore . . . . . *spinolai* Nielson

5(5). Aedeagus with numerous spicules and serrations medially on shaft (Nielson 1982, Fig. 1020) . . . . . *spiculata* Nielson



Figs. 80–84. *Spinolidia sarmenta*, n. sp. 80. Pygofer, lateral view. 81. Plate, ventral view. 82. Connective, right style, and aedeagus, dorsal view. 83. Aedeagus, lateral view. 84. Right style, lateral view.

— Aedeagus with a small tuft of setae medially on shaft (Nielson 1982, Fig. 1026) .... *flavifrons* (Osborn)

Spinolidia sarmenta, n. sp.

Figs. 80–84

LENGTH.—Male 7.50 mm.

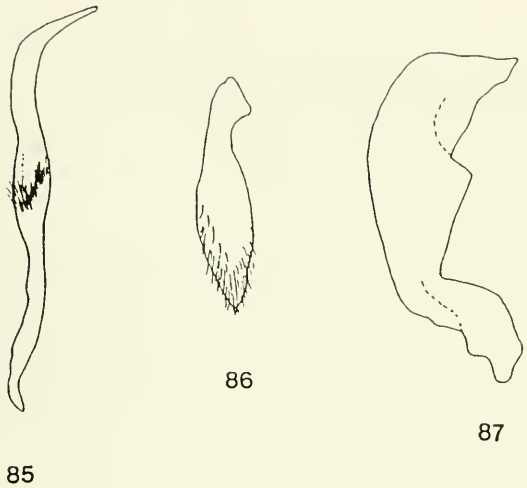
General color dark brown; crown tannish with blackish markings on disc; pronotum black except for small, tannish spots on dorsal surface; scutellum tannish with black markings anteriorly; forewings translucent, veins black; clypeus tan with broad, longitudinal, black bands on either side of middle.

Head narrower than pronotum, broadly rounded anteriorly; crown broad, slightly narrower than width of eyes; eyes large, semiglobular; pronotum large, median length greater than median length of crown; scutellum large; forewing and venation typical; clypeus without a median, longitudinal carina.

MALE.—Pygofer in lateral view with small caudodorsal lobe (Fig. 80); aedeagus asymmetrical, in lateral view long, curved laterally at distal 1/3, with enlarged flange on ventral margin just below middle, small subapical lobe laterally, numerous setae on ventral margin at distal 1/3 from near medial flange to near apex, few setae at apex (Fig. 83), gonopore large on ventral margin near base of submedial flange; style very large, somewhat compressed laterally, in lateral view greatly enlarged at distal 2/3, rounded distally, spiculated on portion of dorsal surface (Fig. 84); plate elongate, constricted subbasally, tapered distally (Fig. 81).

FEMALE.—Unknown.

HOLOTYPE (male).—BOLIVIA: Cochabamba, Chipare Mts., 5,000 ft, Cochabamba to Villa Tunari, 30.III.1976, C. R. Ward (USNM). Paratype: one male, BOLIVIA: El Limbo, 2,000 m, Dept. Cochabamba, __.XI.1962, F. H. Walz (MSU).



Figs. 85–87. *Spinolidia magna*, n. sp. 85. Aedeagus, lateral view. 86. Plate, ventral view. 87. Right style, lateral view.

REMARKS.—This species is similar to *S. osborni* Nielson in male genital characters but can be distinguished by the broader style, by the position and configuration of the ventral flange, and by more numerous setae on the ventral margin of the aedeagus.

Spinolidia magna, n. sp.
Figs. 85–87

LENGTH.—Male 7.20 mm.

General color brown; crown tannish with deep brown markings on disc and suffused with light brown on anterior margin; eyes reddish; pronotum black with numerous small, tannish spots on surface; forewings translucent, veins deeply marked; clypeus and clypellus light tannish, with broad, longitudinal, black band on either side of middle.

Head narrower than pronotum; crown broad, width equal to width of eyes, anterior margin rounded; pronotum large, median length greater than median length of crown; forewing and face similar to other species of *Spinolidia;* clypeus without a median, longitudinal carina.

MALE.—Pygofer similar to *flavifrons* (Osborn); aedeagus long, narrow, without preapical lobe, small tuft of fine setae medially on shaft near gonopore (Fig. 85); style very large in lateral view, broad at distal 2/3 with apex curved laterally and bluntly pointed (Fig. 87); plate similar to *flavifrons* (Fig. 86).

FEMALE.—Unknown.

HOLOTYPE (male).—BOLIVIA: Coroico, no date, no collector, in the Melichar collection (MMB). Paratypes: one male, PERU: Callanga, no date, no collector (NR); one male, BOLIVIA: __.__.1898, Noualhier (MNHN); one male, PERU: Dept. Huanuco, Vic. San Domingo, Andes, 3,000 m, 11–23.XI.1937, F. Woytkowski, No. 3812 (author's collection).

REMARKS.—From *flavifrons*, to which it is similar in general habitus and certain male genital characters, *magna* can be separated by the very broad style.

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LITERATURE CITED

NIELSON, M. W. 1982. A revision of the subfamily Coelidiinae (Homoptera: Cicadellidae)). IV. Tribe Coelidiini. Pacific Insects Monograph 38. 318 pp.

_____. 1983. New leafhopper species of *Coelidia* with a revised key and notes on homonymy and distribution (Homoptera: Cicadellidae: Coelidiinae). Great Basin Nat. 43(4): 669–675.

_____. 1986. Genus *Paralidia* with descriptions of new species (Homoptera: Cicadellidae: Coelidiinae). Great Basin Nat. 46(2): 329–335.

RELATIONSHIPS OF ASPEN (*POPULUS TREMULOIDES*) TO FORAGING PATTERNS OF BEAVER (*CASTOR CANADENSIS*) IN THE STRAWBERRY VALLEY OF CENTRAL UTAH

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ABSTRACT.—Eight study sites were examined in Strawberry Valley, Utah, to assess the response of aspen (*Populus tremuloides* Michx.) to cutting activities of beaver (*Castor canadensis* Warren & Hall) and to determine patterns by which the animals utilize aspen stands. Sites utilized by beaver, along with adjacent control plots in mature, uncut aspen stands, were sampled. Age-class profiles of control plots were composed of a broad age distribution with trees ranging from 3 to 108 years old. Age-class profiles for aspen sprouts in areas previously used by beavers were composed of trees averaging seven years of age with a range of 1 to 24 years. Age distribution of sprouts in areas used by beaver show a tendency to be skewed toward younger age classes. Average density of aspen in areas used by beaver was 15,800 stems per hectare compared to 2,980 stems per hectare in controls. Stump densities in use areas ranged from 900 to 5,066 stems per hectare. Densities of stumps in the 0–5-cm size class were greater in areas used by beavers than in the corresponding size class in the mature forests. A regression equation describing age versus diameter relationships was calculated using data from 312 aspen trees.

Total phenolics and mineral nutrients in the twigs and bark of mature aspen trees and aspen sprouts were also examined to determine if variations could explain foraging patterns of beaver in the valley. Total phenolics were highly variable between sampling groups, and differences were not significant. Twigs from mature aspen and aspen sprouts were significantly higher in nitrogen, phosphorus, and iron. Zinc was significantly higher in the bark of mature aspen trees and twigs of aspen sprouts. Calcium concentrations were significantly higher in mature aspen bark, and magnesium was significantly higher in mature aspen twigs.

Aspen (*Populus tremuloides* Michx.) is the most widespread forest type in Utah, occupying approximately 1,425,000 acres (Choate 1965). Aspen is a prolific root sprouter and is considered to be important in erosion control, wildlife habitat, and wildlife and livestock forage (Barton et al. 1983, Crouch 1983, Reynolds 1969). Commercially it is used for pulpwood, furniture core stock, excelsior, fuelwood, and building material (Keays 1972).

Beaver (*Castor canadensis* Warren & Hall) rely heavily on aspen for food and building material. Aldous (1938) found that aspen is the most important food species for beaver, with birch, alder, and willow next in rank. Some authors suggest that the distribution of beaver is largely governed by the distribution of aspen (Stegeman 1954, Hall 1960). Several workers have studied the compatibility of aspen and beaver (Hall 1960, Hiner 1938, Shadle and Austin 1939) and have questioned whether aspen can survive under cutting pressure from beaver. Hall (1960) suggested that any combination of aspen and beaver eventually leads to the complete loss of aspen. In contrast, Yeager and Hill (1950) suggested that a colony of beavers can maintain itself for many years or even permanently because aspen sprouts will grow to usable size as the cutting of older stems progresses. They also contend that livestock utilization of young sprouts is the main reason for loss of aspen during the time that beavers are utilizing a stand.

Aspen is an important species in the ecology of beaver; where they coexist, beaver rely heavily upon it (Aldous 1938). Some authors suggest that the distribution of beaver in North America is largely influenced by aspen distribution (Stegeman 1956, Hall 1960). Several studies of beaver ecology have focused on patterns by which they utilize aspen. For example, Aldous (1938) studied the importance of aspen stem size as related to the cutting activities of beaver. Although relative availability of aspen was not documented in his study, the greatest numbers of trees cut were in size classes 10–15 cm in diameter. Once the trees were cut, the percentage of biomass utilization of downed trees was

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greatest in the 2- and 5-cm-diameter classes, with increasing wastage as stem diameter increased. In diameter classes greater than 8 cm, a large percentage of trees had only the tops utilized.

In a study comparing relative availability of aspen and observed cutting by beaver, Hall (1960) concluded that size preference by beaver was very slight. He also found increased preference for 5-cm trees while dam building was occurring within a colony. As building declined, differential preference for the smaller trees diminished. Jenkins (1978, 1979) suggested that beaver exhibit spatial and temporal preference in food items. Seasonal variation in the concentrations of stored nutrients in the bark of various tree genera was thought to explain switches in preference. Pine was favored during spring months when carbohydrate reserves were greater than in the bark of neighboring deciduous trees. Jenkins (1980) also studied food selection by beaver with respect to an optimal foraging model of size-distance relations. His data suggest that beavers are more selective in cutting behavior as the distance from shore increases. A smaller range of sizes was cut far from shore, with greater numbers of small trees cut and fewer large ones.

Studies addressing the relationship between beaver and aspen have focused mainly on patterns by which the animals utilize the trees. For instance, do size-class preferences exist? Little documentation is available quantifying the effects on aspen of utilization by beaver.

The objectives of the present study were to determine the pattern of aspen utilization by beaver near Strawberry Reservoir, Wasatch Co., Utah, and to quantify the sprouting response of aspen in areas where beaver have utilized stands over long periods of time. Also, we wish to present ideas concerning the foraging patterns of beaver on aspen in central Utah and to discuss the relative value of aspen as a forage species for beaver.

STUDY SITE

This study was conducted in the Strawberry Valley, Wasatch Co., Utah, on the east slopes of the Wasatch Mountains (lat. 40°11′15″N, long. 111°11′30″W) at an elevation of approximately 2,325 m. The study site was characterized by broad valleys and low, rolling hills. Several valleys accommodate perennial streams and are wide and flat in their lower reaches. The valleys head at elevations of approximately 2,743 m along the Strawberry Ridge, range in length from 6 to 10 km, and drain into Strawberry Reservoir.

The climate of the area is characterized by cool summers and cold winters with heavy snow cover. Average annual precipitation taken at the east portal of the Strawberry Reservoir is 610 mm of which 60% falls as snow. The area lies within the Heber Ranger District of the Uinta National Forest and has been grazed by cattle since the 1860s.

Vegetation on the study area is a combination of montane sagebrush (*Artemisia* spp.) steppe in the valleys and aspen-conifer (*Abies*, *Picea*, *Pseudotsuga*) forests higher on the slopes (Walker and Brotherson 1982). The riparian areas along stream banks in their lower reaches are dominated by willow (*Salix* spp.).

METHODS

Eight study sites were selected based on a high degree of past utilization by beaver. Slope and aspect were recorded for each site. The size of the area affected by beavers was estimated by pacing. A plot measuring 20 × 20 m (0.04 ha) was established in the center of the cutting area. Corners were permanently staked and a line was strung to mark the plot. A second control plot with equal dimensions was also established at each study site. It was located in the aspen forest as close as possible to the study site but beyond any evident beaver activity and on areas with similar slope and aspect.

The quarter-method (Cottam and Curtis 1956) was used to determine density of trees or stumps in the study plots. Ten sampling points were randomly located within each plot, yielding data on 40 trees per plot. In each quarter, the following measurements were recorded: distance to nearest aspen stem; height of stem or stump (measured up to 6 m with a retractable tape), stem diameter at 0.3-m height; and stem age. Diameters were taken at 0.3 m above the ground so that the stem diameter of living trees could be compared to that of the stumps (which rarely reached breast height).

TABLE 1. Site factor data from areas used by beavers and adjacent control areas in Strawberry Valley, Wasatch Co., Utah.

Site factor	Site 1	2	3	4	5	6	7	8
Size of cutting (ha)	0.61	0.18	0.20	0.18	0.51	0.30	0.30	0.40
Distance from stream to stand (m)	39.7	33.6	24.4	36.6	25.9	30.0	21.4	18.3
Beaver use area								
Aspect (degrees)	90	315	204	124	202	17	20	130
Slope	28%	13%	14%	18%	23%	6%	8%	50%
Control plot								
Aspect (degrees)	40	314	204	160	204	21	20	128
Slope	22%	15%	12%	20%	16%	10%	10%	28%

Age of sprouts (individuals with stem diameters less than 5 cm) was determined in the field using an ax, sharp knife, hand lens, and a solution of 15% hydrochloric acid saturated with phloroglucin as a stain to increase visibility of annual rings (Alder 1970). Aging trees greater than 5 cm in diameter was done by taking a core sample with an increment bore at 0.3 m above the ground. Cores were stored in labeled drinking straws.

Core samples were permanently mounted with wood glue into grooves cut lengthwise in 90 × 30 × 3-cm boards. Portions of the core that were exposed above the surface of the board were sanded to facilitate counting. Sanded cores were stained with 15% hydrochloric acid/phloroglucin solution. Counting was done by hand using a 10X hand lens or dissecting microscope when necessary. Each ring was marked by punching a small hole in the core where needed. Annual rings were identified by the shadow created as the gradient from large to small xylem elements abruptly changed to earlywood (Maini and Coupland 1964). The few false rings encountered did not display this shading effect and were not counted. All cores were subjected to two independent counts.

Counts of all aspen stems or stumps found within each plot were conducted. Diameter was measured and each stump was placed into one of six diameter-size classes: 0–5 cm, 5–10 cm, 10–15 cm, 15–20 cm, 20–25 cm, and greater than 25 cm. Selection of size classes was partially based on studies by DeByle (1976) and Hittenrauch (1976) where two inches of dbh was used as the size class, delineating sprouts from mature trees. We considered all stems or stumps in the 0–5-cm size class to be sprouts. All counted stems or stumps were marked with red paint to avoid counting twice.

Mean ages and standard deviations were calculated for aspen stems or stumps sampled on each of the eight study areas or their adjacent controls. Chi-square analyses were then used to determine if the age-class structure of stands used by beaver was the same as aspen stands on control areas.

Three of the eight study sites that were in the Clyde Creek drainage of Strawberry Valley, Wasatch Co., Utah, were selected and sampled in December 1983 for vegetative materials of aspen to use in determining forage quality. Even though the sampling period was later in the season than the peak period during which beaver cut aspen for dam construction and food supplies, research by Gifford et al. (1983) indicates that transpiration in aspen ceases near the end of September and does not begin again until late May. Also, Dietz (1972) found that vitamins, mineral nutrients, and crude protein in aspen did not change significantly from fall to winter.

Each of the three sites had been utilized by beaver for several years and had been cut during the late summer and fall prior to sampling. Sites were characterized by a dense growth of aspen sprouts near the stream. The area most recently utilized by the beaver was upslope and at greater distances from the dam and beyond the sprouts.

Mature, uncut aspen stands continued up the slopes beyond the cutting zone. Five sprouts ranging in diameter from 3 to 5 cm were selected at random within the sprouting area and cut down. All twigs from the top 30 cm of the sprout were trimmed and placed

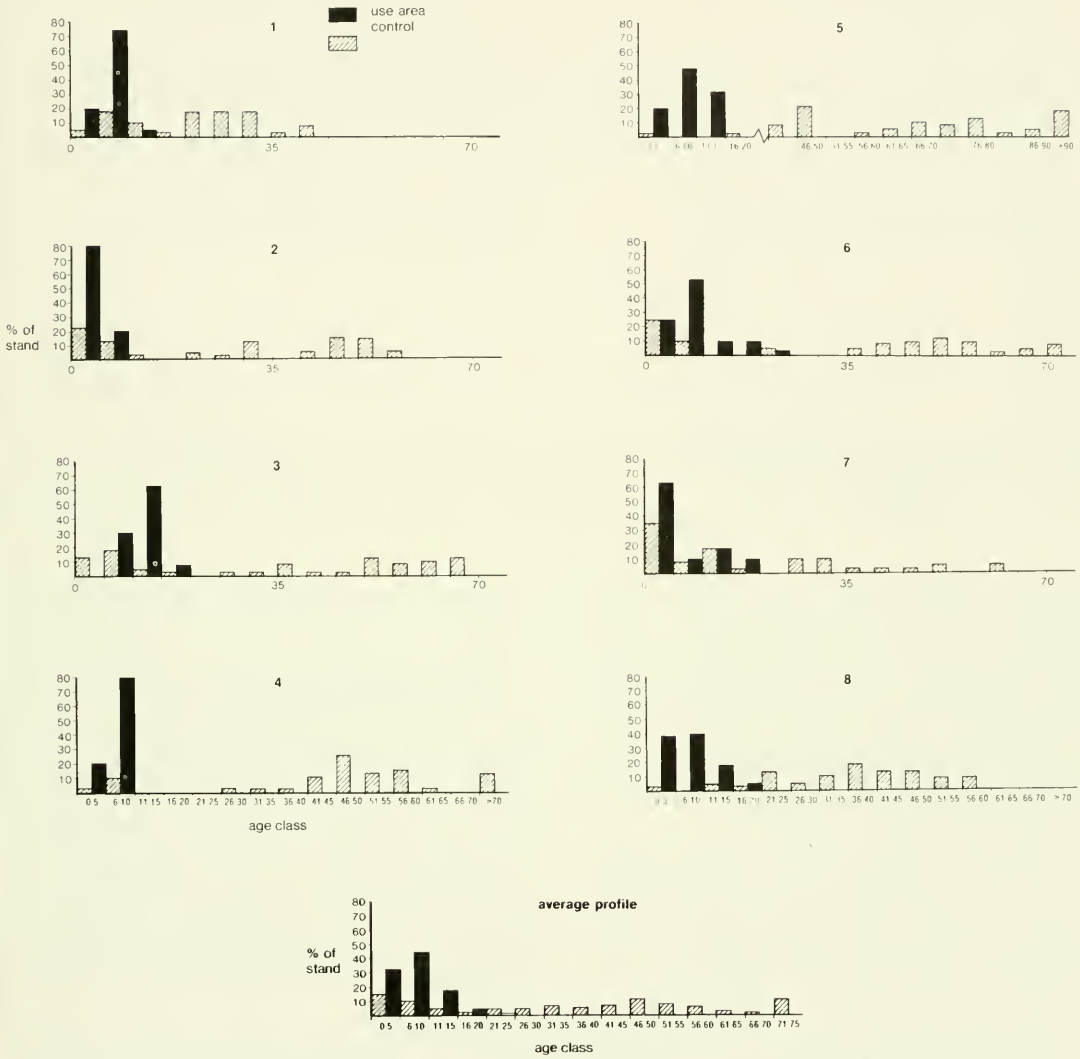

Fig. 1. Stand-age profiles of eight study sites and eight control plots in Strawberry Valley, Wasatch Co., Utah.

into sealed plastic packages. Sprout bark was also removed using a draw knife and sealed into packages. Smaller-size sprouts were not selected because of inadequate amounts of material for analysis.

In the mature aspen stands, five mature trees of various diameters greater than 5 cm were randomly selected and cut down. Twigs from the tree top and bark from the bole at breast height were removed as described above and placed into sealed packages. Samples were kept at −5 C (ambient air temperature during sampling) in the field and were later frozen at −30 C until processed. Frozen samples were cut into smaller pieces in the laboratory and then frozen in liquid nitrogen before being ground into powder with an electric mortar and pestle. Prepared samples were sealed in bottles and kept at −30 C until laboratory analysis.

Twig and bark samples were analyzed for calcium, magnesium, sodium, potassium, phosphorus, manganese, iron, zinc, and copper using the nitric and pyloric acid digestion process (Johnson and Ulrich 1959). Percent nitrogen was determined by the Kjeldahl method (Horwitz 1983). Total phenols were determined by analyzing a 50% methanol/50% distilled-water extract with a Coleman Model 440 spectrophotometer. The standard

TABLE 2. Age-class breakdown for aspen trees sampled in study plots and control plots in Strawberry Valley, Wasatch Co., Utah.

Age class	Site 1	Ctrl	Site 2	Ctrl	Site 3	Ctrl	Site 4	Ctrl	Site 5	Ctrl	Site 6	Ctrl	Site 7	Ctrl	Site 8	Ctrl
0–5	10	2	32	9	0	5	9	1	8	1	10	10	25	14	15	1
6–10	30	7	8	5	12	7	31	4	19	0	21	4	4	3	16	0
11–15	0	4	0	1	26	2	0	0	13	0	4	0	7	7	7	2
16–20	0	1	0	0	2	1	0	0	0	1	4	0	4	1	2	1
21–25	0	7	0	2	0	0	0	0	0	0	1	2	0	0	0	5
26–30	0	7	0	1	0	1	0	1	0	0	0	0	0	4	0	2
31–35	0	7	0	5	0	1	0	1	0	0	0	0	0	4	0	4
36–40	0	1	0	0	0	3	0	1	0	0	0	2	0	1	0	7
41–45	0	3	0	2	0	1	0	4	0	3	0	3	0	1	0	5
46–50	0	0	0	6	0	1	0	10	0	9	0	4	0	1	0	5
51–55	0	0	0	6	0	5	0	5	0	0	0	5	0	2	0	3
56–60	0	0	0	2	0	3	0	6	0	1	0	4	0	0	0	4
61–65	0	0	0	0	0	4	0	1	0	2	0	1	0	2	0	0
66–70	0	0	0	0	0	5	0	0	0	4	0	2	0	0	0	0
>70	0	0	0	0	0	0	0	5	0	18	0	3	0	1	0	0
$\bar{x}$ age	7.3	22.5	4.3	29.0	11.2	37.9	6.3	48.5	8.7	67.4	7.7	35.9	6.9	20.2	7.4	37.4
s age	2.9	11.6	1.6	20.5	2.6	27.0	1.2	22.6	3.8	22.7	4.8	25.5	5.6	20.6	4.6	13.5

curve was constructed using a buffered quebracho solution, and data were expressed as % quebracho equivalents. Tannin capacity of the extract was determined using a modification of the hemoglobin-astringency method (Bate-Smith 1973). Quebracho tannin was used in formulating the standard curve. Terpenes were analyzed with gas chromatography using a fused silica capillary column.

Means and standard deviations were calculated for the total phenolics, calcium to phosphorus ratios, and all nutrients. Two-way analysis of variance was used to test differences between sites and sampling groups (Snedecor and Cochran 1967). Means were separated using Fisher's least significant difference method (Ott 1984).

RESULTS AND DISCUSSION

Aspen stands occur continuously along one or both sides of all drainages studied. Distance between stands and the edge of the stream varied from 18 to 40 m (Table 1). Within this area, the flat ground adjacent to the stream was occupied by willow while the slopes above the floodplain were dominated by sagebrush steppe. Slope of areas with aspen stands utilized by beaver ranged from 6 to 50%. Aspect of study sites varied widely, with general aspects either to the north or south.

Beavers were active in all areas studied. Most aspen cutting occurred in September and October of the years the study took place. Cutting was concentrated in localized areas of mature aspen stands within 100 m of the stream.

Stand-age profiles provide a visual comparison between trees sampled in areas used by beavers and trees in adjacent mature forests (Fig. 1). Each graph represents approximately 80 trees, 40 from the beaver-use area and 40 from the control plot. Eight trees out of the 640 sampled could not be accurately aged because of heart rot. All aspen stems were assigned to five-year age classes to facilitate graphing. A bar in the histogram represents percentage of sampled trees that fall within each age class.

Age-class profiles of control plots show that aspen stands in the study area are composed of a broad age distribution. These data are consistent with other studies done on aspen in the intermountain area (Alder 1970). Noteworthy similarities between stands are a short period of unfavorable growth 16 to 25 years ago and a favorable growth period between 40 and 60 years ago. Variation between stands may reflect differences in site potential, genetic differences in clones, and/or local history of disturbance. The age of aspen stems sampled from the mature forest (control areas) ranged from 3 years to 108 years, with an average of 70 (Table 2).

Age-class profiles of areas used by beavers were composed of trees averaging seven years of age, with a range of 1 to 24 years. Differences between the age profiles of mature

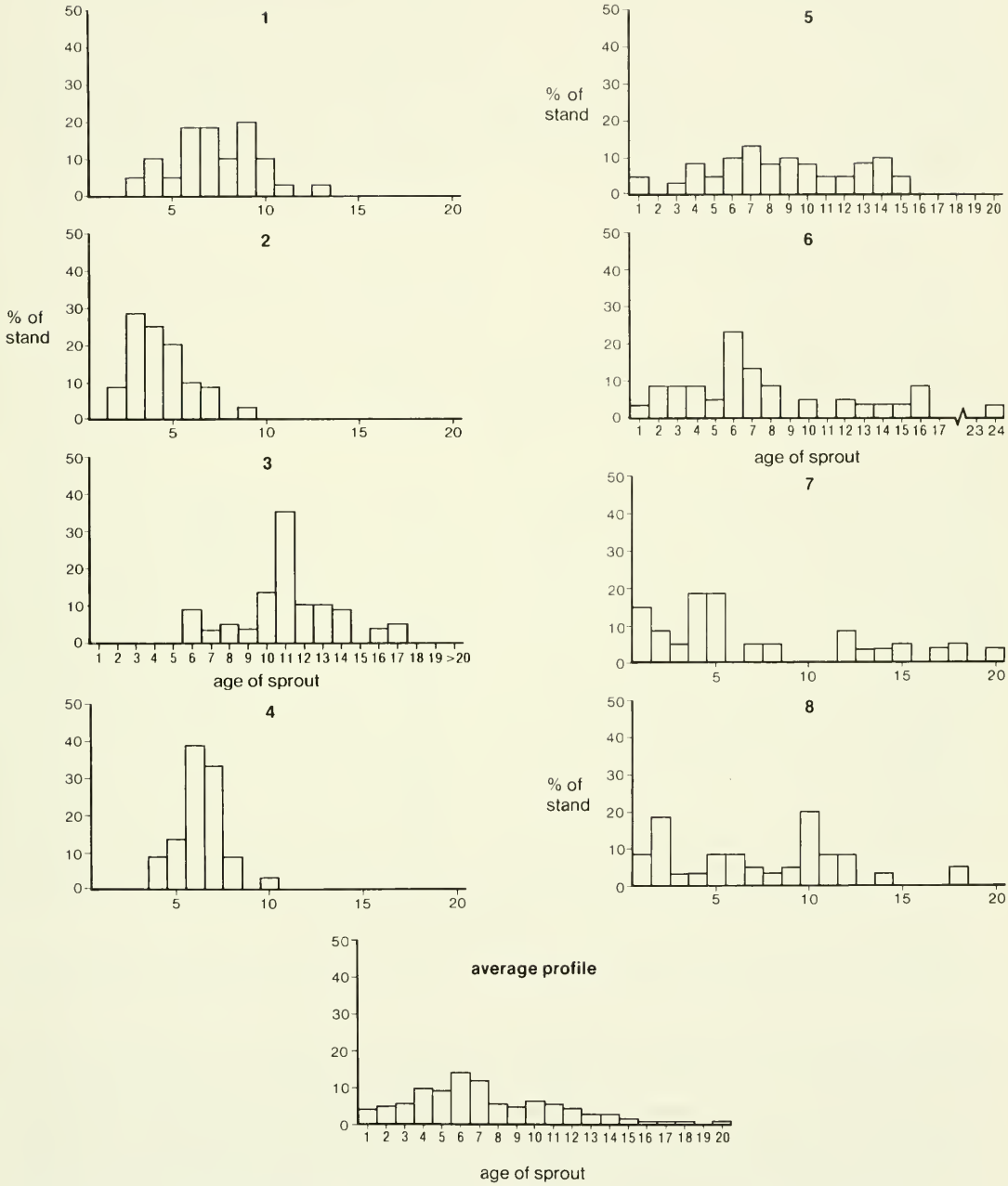

Fig. 2. Age-class profiles of sprouts in areas used by beavers in Strawberry Valley, Wasatch Co., Utah.

aspen forests and areas cut by beavers are clearly illustrated in each graph. Differences are due to a combination of the following factors: (1) patterns by which the beaver cut aspen while procuring food and building materials, (2) root sprouting by aspen in response to cutting activities of beaver, (3) differential grazing pressure between sprout areas and mature forests, and (4) differences in growth potential due to site differences and genetic variation among clones of aspen.

The leftward skew in the average age profile of the use areas suggests that beavers utilize sprouts that are approaching 20 years old.

TABLE 3. Density of aspen sprouts and aspen stumps in areas used by beaver and density of aspen trees in control areas. Strawberry Valley, Wasatch Co., Utah.

Sampling group	Site 1	2	3	4	5	6	7	8	$\bar{x} \pm s$
Sprouts (use area)	30,300	18,180	5,620	9,350	5,350	13,300	34,500	9,803	15,800 ± 11,095
Control (mature forest)	2,700	4,290	1,450	2,440	2,190	4,149	3,330	3,290	2,980 ± 974
Stumps (use area)	900	2,170	2,080	1,900	2,640	2,350	2,400	5,060	2,440 ± 1,183

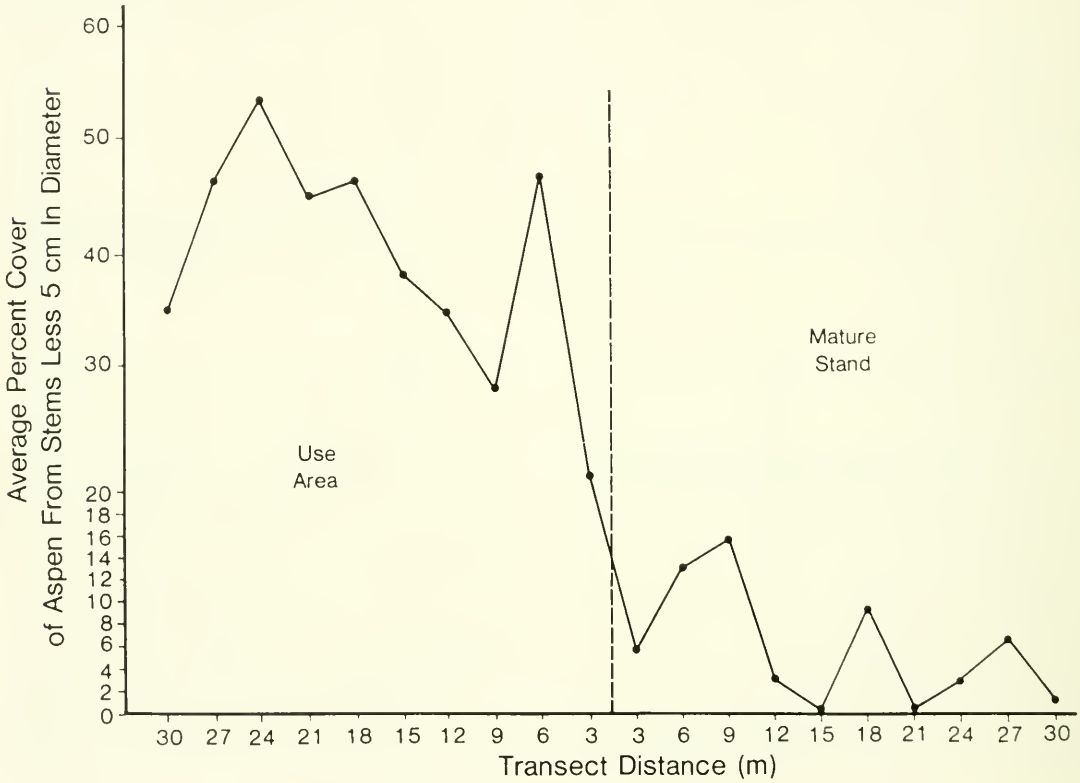

Fig. 3. Cover values for aspen sprouts taken along a transect passing through beaver use areas and adjacent control areas.

More precise histograms of the age-class profiles on the sprout areas are presented in Figure 2. Each histogram represents 40 trees sampled in areas used by beaver. Age classes are in one-year increments. Bars in the graphs represent the percentage of sampled trees in each age class. The tendency for a skewed age distribution toward younger trees is seen clearly in the average profile for the eight sites.

A comparison of densities of cut and uncut aspen trees in use plots with aspen trees in control plots is summarized in Table 3. Densities of aspen stems in areas used by beaver ranged from a low of 5,617 stems per hectare to a high of 34,482 stems per hectare, with an average of 15,801. These densities exceed those found on the control areas by five times. Figure 3 represents a graph of cover values for aspen sprouts taken along a transect passing through areas used by beaver and into adjacent stands not yet utilized. Cover of sprouts in areas cut by beavers averaged 39.5%, while in mature, unutilized stands sprout cover averaged only 5.9%.

The density and cover values found on the beaver use areas approach those found in silvicultural studies on the response of aspen to clearcutting (DeByle 1976, Hittenrauch 1976, Jones 1975). The high values for aspen sprouts

found on areas cut by beaver, along with the absence of mature trees, indicate that the pattern of year-to-year utilization of mature aspen forests by beavers as they gradually cut farther up the slope effectively simulates silvicultural clearcutting practices.

Clearcutting aspen, as opposed to selective cutting, provides the optimum conditions necessary for sprouting (DeByle 1976, Jones 1975, 1976). Sprout numbers between 24,710 and 98,840 per hectare are not uncommon after clearcutting (DeByle 1976, Hittenrauch 1976). Average density of aspen on our control areas was only 2,980 stems per hectare, with a low of 1,449 and a high of 4,298. Differences in average stem densities between the control and use areas were significant (Chi square = 12.54, $p < .05$).

High sprout densities in areas used by beavers might also be attributed to differential grazing pressure by livestock over long periods of time between aspen stands in the control areas and areas used by beaver. Research has demonstrated that heavy grazing pressure by livestock, deer, and elk can effectively suppress regeneration of aspen stands by sprouting (Crouch 1983, DeByle 1976, Hittenrauch 1976, Jones 1975). The unutilized boles of larger aspen trees lying on the ground in areas cut over by beaver may produce an effective barrier to grazing animals by preventing their access into the area. Silvicultural studies by Hittenrauch (1976) demonstrated that unmerchantable timber left lying on the ground in clearcuts completely eliminated grazing of sprouts by cattle. Reynolds (1969) also concluded that fallen timber was an effective barrier for deer, elk, and cattle, allowing aspen sprouts to develop.

Stump densities in use areas ranged from 900 to 5,066 stems per hectare. Size-class distribution of stumps showed a similar pattern to size classes of trees in a mature forest, although densities were different (Fig. 4). In size classes greater than 5 cm, densities of stumps on the use areas were consistently lower than those of corresponding size classes in the mature forest. In the 0–5-cm size class, densities of stumps on the use areas were greater than densities of the same size class in the mature forest. Several factors may explain the disparity between stump densities on study plots versus densities of aspen trees in control plots. A proportion of the stumps on

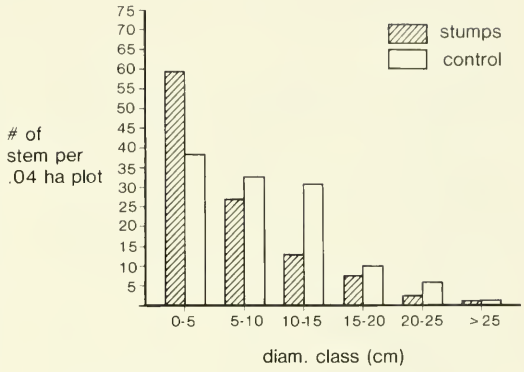

Fig. 4. Comparison between densities of aspen stumps found in study areas and densities of aspen trees in control areas based on size-class distribution. Strawberry Valley, Wasatch Co., Utah.

the study plots may have been lost to decay or may have been overlooked because of dense growth of aspen sprouts and associated species (which on some plots was almost impenetrable). The fact that beavers were still active in all the study areas also complicated comparisons.

Values for diameter versus values for age were plotted to develop a regression equation (Fig. 5). With this equation to predict the age of aspen tree stumps on the study area, several relationships become clear. When the upper size limit of the 0–5-cm size class is used for the diameter variable in the equation, the predicted value for maximum age oftrees in that size class was approximately 23 years. Twenty-three years of age roughly corresponds to the highest age found for sprouts in areas used by beaver. These data indicate that beaver are returning to previously cutover areas to utilize aspen sprouts as they approach 5 cm in diameter or an age of around 20 years.

The results clearly show that vegetative reproduction of aspen is enhanced by the cutting activities of beaver. However, when considering management of aspen forests and long-term impacts of continuous utilization by beavers, other factors must be considered. For example, factors controlling resources such as willow need to be better understood. Range management practices such as aerial spraying of 2,4-D (2,4-dichlorophenoxy acetic acid) to eliminate willows and improve forage for livestock may divert increased foraging pressures to aspen. It would also be valuable

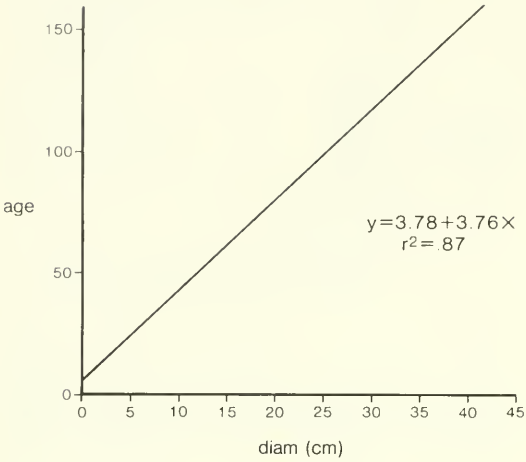

Fig. 5. Regression line derived by plotting age and diameter data from 312 aspen trees in control plots in Strawberry Valley, Wasatch Co., Utah.

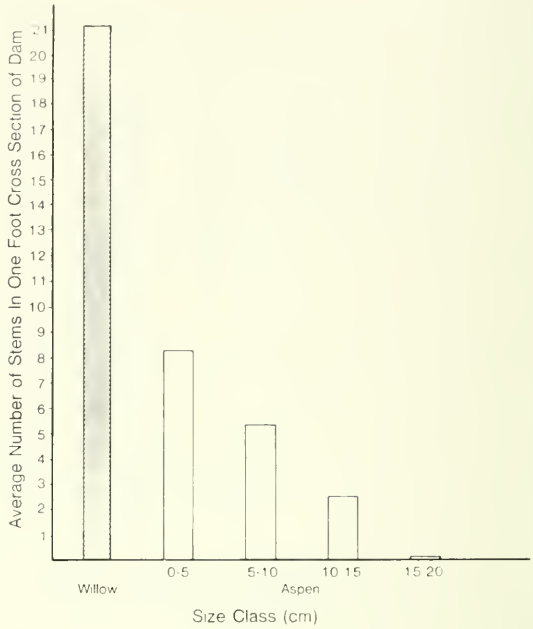

Fig. 6. Proportions of different size classes of stems used by beaver for construction of their dams. Willows were all placed together in the size class 0–5 cm.

to determine optimum beaver densities for specific sites and to manage populations at levels that allow aspen stands to perpetuate themselves. In areas where utilization of aspen sprouts by cattle is preventing establishment of smaller size classes, beaver activity may be beneficial by creating physical barriers that protect suckers from heavy utilization by livestock.

Proportions of the different size classes of stems used by beaver for construction of their dams on our study sites are shown in Figure 6. Even though all size classes of aspen were cut, only stems in the smaller size classes were incorporated into the dams. Some of the smaller size class material found in the dam probably represents stems taken from the tops of larger trees. Willow accounted for 57% of all stems counted in the dams (Fig. 6). The importance of willow as an alternate food source and building material has been discussed by several researchers. Hall (1960) concluded that willow is the second woody staple of a beaver's diet and can sustain the animals in the absence of aspen. Rasmussen and West (1943) feel that willow, not aspen, is the key plant in beaver habitat.

Data on mineral nutrient content of aspen twigs and bark showed several differences between sampling groups. For example, phosphorus and iron were significantly higher ($p < .05$) in the twigs of both mature aspen and aspen sprouts than in the stem bark (Table 4). In contrast, zinc was highest ($p < .05$) in the bark of trees and sprouts while calcium concentrations were greatest in the mature bark. Magnesium was significantly higher ($p < .05$) in the twigs of mature aspen trees. Copper showed no significant differences in concentrations among the four sampling groups. Levels of nitrogen, potassium, and manganese varied significantly among sites ($p < .01$). Twigs from mature aspen trees had the highest values in six out of the nine minerals (N, P, K, Fe, Mn, and Mg) and second highest in two others (Cu and Ca). If the bark and twigs of mature aspen are considered together, mature trees have the highest concentrations of all the nutrients with the exception of copper.

The relative proportions of calcium and phosphorus within and between the sampling groups are also of interest. Dietary calcium to phosphorus ratios ranging from 1:1 to 2:1 are considered best for proper absorption and metabolism in most herbivores (Robbins 1983). Abnormally high ratios (greater than 7:1) have been shown to interfere with the absorption of phosphorus and other mineral nutrients, particularly magnesium, zinc, and manganese (Underwood 1966). Calcium to

TABLE 4. Total phenolic and nutrient content from samples of twigs and bark of mature aspen and aspen sprouts collected at Strawberry Valley, Wasatch Co., Utah.

	% quebracho equivalents	%N	%P	%K	PPM/Zn	PPM/Fe	PPM/Mn	PPM/Cu	%Ca	%Mg	Ca/P ratio
Tree twigs											
$\bar{x}$	2.16a	.96a	.14a	.29a	53.5c	23.8a	27.6a	6.4a	1.50b	.16a	11.6a
s	±.61	.23	.04	.07	10.8	7.5	9.4	2.8	.31	.02	3.9
Tree bark											
$\bar{x}$	1.78a	.41c	.07b	.15c	98.2c	14.3a	23.0ab	5.4ab	1.86a	.12c	37.2c
s	.74	.07	.06	.07	15.5	8.5	7.5	5.1	.34	.03	14.1
Sapling twigs											
$\bar{x}$	2.14a	.90a	.13a	.24ab	52.1c	20.9a	19.2b	6.5a	1.18c	.14b	10.4a
s	.86	.17	.04	.08	12.0	8.2	10.1	2.8	.25	.02	4.2
Sapling bark											
$\bar{x}$	2.5a	.68b	.08b	.20bc	82.1b	14.4a	18.7b	3.4b	1.48b	.13c	24.6b
s	1.2	.29	.04	.11	19.2	7.7	13.6	1.1	.18	.02	13.4

[1]Means, within a column, with the same lowercase letter are not significantly different at $p < .05$.

phosphorus ratios found in the four sampling groups range from 10:1 in the sprout twigs to 37:1 in the mature aspen bark (Table 4). High Ca/P ratios have also been reported by Stricklan (1987) for oak (*Quercus gambelii*) utilized by porcupine. He suggests that the porcupines dealt with the high levels of calcium by concentrating it in their urine (i.e., the Ca/P ratios in the porcupine urine were approximately 221:1). Differences in the Ca to P ratios are significant between sapling twigs and mature aspen bark ($p < .05$). Foraging on twigs from either aspen sprouts or mature aspen would provide Ca to P ratios closer to those considered optimal for herbivores.

Phenolic concentrations in the aspen samples were highly variable and ranged from a low of 0.72 to a high of 4.57% quebracho equivalents. The individual samples were lumped into 10 equal-width concentration units and then plotted by sample group (Fig. 7A-E). Trends were observed in the tree twig and tree bark categories. For example, 75% of the individual samples in the tree twig category were contained in the concentration groups above 1.89% quebracho equivalents, while 69% of the individual samples in the tree bark category fell below the 1.89% concentration level (Fig. 7A, B). However, because of the high variability within the individual subsamples (Fig. 7E) as well as small sample sizes, the differences in the total phenolics between the sampling groups (twigs and bark of mature trees versus twigs and bark of sprouts) were not significant (Table 4). Further, we found no terpenes or tannins as measured by astringency (protein-complexing capacity of the extract) in the samples analyzed. Although the absence of terpenes is not unusual, the absence of tannins in the samples is noteworthy. Data summarized by Rhoades and Cates (1976) illustrated that 79% of deciduous woody perennials (211 species) tested positive for tanniferous compounds.

Bryant (1981) studied the phytochemical deterrence of snowshoe hare browsing in four species of deciduous trees (including aspen) in Alaska. His data indicated that adventitious shoots of all species contained significantly higher concentrations of phenolic resins and terpenes than twigs from mature growth of the same species. The resins were experimentally shown to repel snowshoe hares and appeared to explain the avoidance of adventitious shoots by hares.

In a more recent study on green alder (*Alnus crispa* [Ait.] Pursh.) and snowshoe hare (*Lepus americanus* Erxleben), Bryant et al. (1983, Carbon/nutrient) found that total phenols had no relationship with preferential foraging of alder parts by hares. Instead, a single phenol, pinosylvin methyl ether (PME), accounted for the low palatability in foliar buds and catkins, while internode parts (older growth) did not have high concentrations of PME and were utilized heavily by hares. More specific assays of individual chemicals and individual plant parts will be required before conclusions can be made on the influence of phenolic compounds on the foraging patterns of beaver in our study area. An important class of compounds that should be

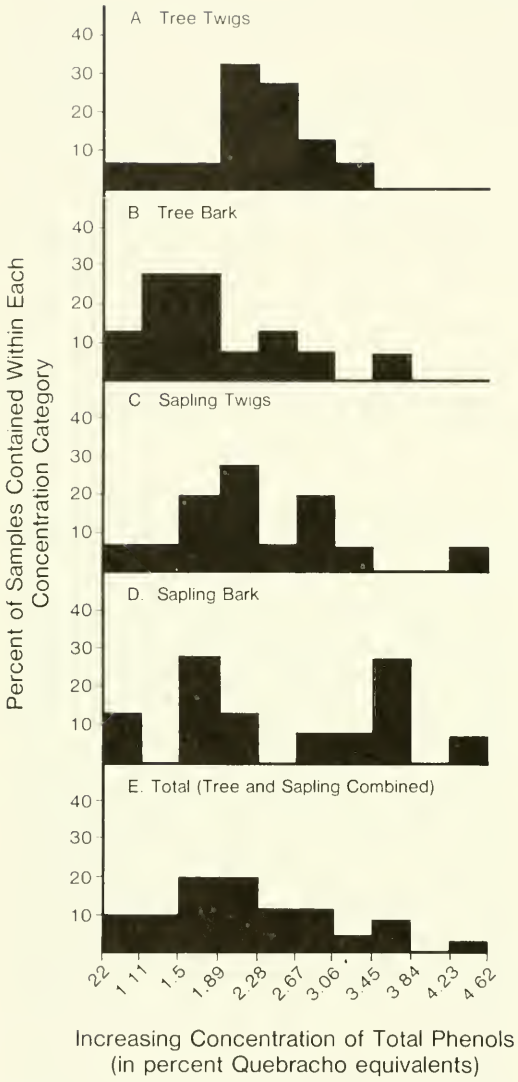

Fig. 7. Percent of aspen phenolic samples contained within each concentration category plotted against increasing concentrations of total phenols. Concentration of total phenols is expressed in percent quebracho equivalents.

included is the phenolic glycosides, which are known to occur in aspen, willow, and other potential host plants.

Bryant et al. (1983, Pinosylvin methyl ether) discussed strategies of disturbance-adapted trees relative to defense against vertebrate herbivory. Many species that invade recently disturbed sites, including aspen, have resistance to browsing because their rapid growth rate enables them to grow out of the reach of browsing animals. Root storage also allows the plant to survive after being heavily browsed. Still, heavy utilization during the few years when plants are within reach of browsing mammals can cause extensive growth retardation and/or mortality. Bryant et al. (1983, Carbon nutrient) suggested that early successional trees have responded to browsing pressure by evolving toxic chemical defenses (Rhoades and Cates 1976) during the juvenile state that are not present in the mature life stages. These ideas are consistent with foraging patterns observed on our study area.

Understanding foraging patterns of beaver on aspen is a complex problem that will require consideration of additional factors pertaining to beaver ecology. First, beavers utilize plant materials for dam building as well as food supplies. If a range of size classes of materials is available, then selection of certain size classes for dam building may be independent of food selection. Certain sizes of materials may be more efficient in dam construction.

Second, we found that beaver on our study sites passed through young stands of sprouting aspen and exhibited a preference for larger trees further from their dams. Beaver traveled distances greater than 100 m from the stream to forage on mature aspen trees even though abundant aspen sprouts (5 cm or less in diameter) were highly available near the stream. The beaver mainly utilized smaller branches on the mature trees, those in the same diameter classes as the more accessible sprouts. Since the beavers must exert a certain amount of energy on foraging excursions, it may be that the animals are trying to maximize energy return. It is possible that by traveling greater distances and cutting trees in the larger size classes they make the trips more energetically efficient. Cutting trees in larger size classes would make available greater amounts of biomass, while cutting the smallest size classes near the stream may not provide sufficient plant material to make a trip energetically profitable.

Third, beavers are generalist herbivores and utilize many species of plants for food. It may be possible that they are foraging on certain plants to avoid specific secondary metabolites and on others to meet specific needs. Such trade-offs may not be evident unless complete studies of food habits are undertaken. Also, the fact that beavers store

food in caches for use during the winter poses a unique situation for food habit studies. Since the animals are subject to being icebound for periods sometimes exceeding 100 days, the nutritional value and potential changes in secondary metabolites of forage stored in winter caches could be very important.

Data on mineral nutrients from the aspen on our study area suggest that differences exist between the nutritional value of mature aspen trees and aspen sprouts. The idea that beaver can differentiate between forages of various nutritional value may help explain patterns of preferential foraging on mature aspen trees in Strawberry Valley. The influence of specific monomer phenolic and phenolic glycoside compounds on size-class selection by beavers may also be important but requires further study.

LITERATURE CITED

ALDOUS, S. E. 1938. Beaver food utilization studies. J. Wildl. Manage. 2: 215–222.

ALDER, M. G. 1970. Age-profiles of aspen forests in Utah and northern Arizona. Unpublished thesis, Brigham Young University, Provo, Utah. 31 pp.

BARTON, D. L., F. R. WARD, AND G. S. INNIS. 1983. Aspen succession in the Intermountain West: a deterministic model. USDA Forest Serv. Gen. Tech. Rept. INT–153. Intermountain Forest and Range Expt. Sta., Ogden, Utah. 60 pp.

BATE-SMITH, E. 1973. Haemanalysis of tannins: the concept of relative astringency. Phytochemistry 12: 907–912.

BRYANT, J. P. 1981. Phytochemical deterrence of snowshoe hare browsing by adventitious shoots of four Alaskan trees. Science 213: 889–890.

BRYANT, J. P., G. D. WIELAND, P. B. REICHARDT, V. E. LEWIS, AND M. C. MCCARTHY. 1983. Pinosylvin methyl ether deters snowshoe hare feeding on green alder. Science 222: 1023–1025.

BRYANT, J. P., F. S. CHAPIN III, AND D. R. KLINE. 1983. Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. Oikos 40: 357–368.

CHOATE, G. A. 1965. Forests in Utah. USDA Forest Serv. Resource Bull. INT–5. Intermountain Forest and Range Expt. Sta., Ogden, Utah. 58 pp.

COTTAM, G., AND J. T. CURTIS. 1956. The use of distance measures in phytosociological sampling. Ecology 37: 451–460.

CROUCH, G. L. 1983. Aspen regeneration after commercial clearcutting in southwestern Colorado. J. For. 83: 316–319.

DEBYLE, N. V. 1976. The aspen forest after harvest. *In:* Utilization and marketing as tools for aspen management in the Rocky Mountains: proceedings of the symposium, 8–9 September 1976, Fort Collins, Colorado. Panel II. Aspen ecology and harvesting responses. USDA Forest Serv. Gen. Tech. Rept. RM–29. Rocky Mtn. Forest and Range Expt. Sta., Fort Collins, Colorado.

DIETZ, D. R. 1972. Nutritional value of shrubs. Pages 289–302 *in* Wildland shrubs—their biology and utilization. USDA Forest Serv. Gen. Tech. Rept. INT–1. Intermountain Forest and Range Expt. Sta., Ogden, Utah.

GIFFORD, G. F., W. HUMPHRIES, AND R. A. JAYNERS. 1983. A preliminary quantification of the impacts of aspen to conifer succession on water yield within the Colorado River Basin (a process aggravating the salt pollution problem). Utah Water Research Laboratory, Utah State University, Logan, Utah. 67 pp.

HALL, J. G. 1960. Willow and aspen in the ecology of beaver on Sagehen Creek, California. Ecology 41: 484–494.

HINER, L. 1938. Observations on the foraging habits of beavers. J. Mammal. 19: 317–319.

HITTENRAUCH, H. R. 1976. Response of aspen to various techniques. *In:* Utilization and marketing as tools for aspen management in the Rocky Mountains: proceedings of the symposium, 8–9 September 1976, Fort Collins, Colorado. Panel II. Aspen ecology and harvesting responses. USDA Forest Serv. Gen. Tech. Rept. RM–29. Rocky Mtn. Forest and Range Expt. Sta., Fort Collins, Colorado.

HORWITZ, W., ED. 1983. Improved Kjeldahl methods for nitrate free samples, procedure 2.057. *In:* Official methods of analysis of the Association of Official Analytical chemists. Association of Official Analytical Chemists, Washington, D.C. 1,018 pp.

JENKINS, S. H. 1978. Food selection by beavers: sampling behavior. Breviora 447: 1–6.

———. 1979. Seasonal and year-to-year differences in food selection by beavers. Oecologia 44: 112–116.

———. 1980. A size-distance relation in food selection by beavers. Ecology 61: 740–746.

JOHNSON, C. M., AND A. ULRICH. 1959. Analytical methods for use in plant analysis. Pages 32–33 *in* California Agric. Expt. Sta. Bull. 766.

JONES, J. R. 1975. Regeneration on an aspen clearcut in Arizona. USDA Forest Res. Note RM–285. Rocky Mtn. Forest and Range Expt. Sta., Fort Collins, Colorado. 8 pp.

———. 1976. Aspen harvesting and reproduction. *In:* Utilization and marketing as tools for aspen management in the Rocky Mountains: proceedings of the symposium, 8–9 September 1976, Fort Collins, Colorado. Panel II. Aspen ecology and harvesting responses. USDA Forest Serv. Gen. Tech. Rept. RM–29. Rocky Mtn. Forest and Range Expt. Sta., Fort Collins, Colorado.

KEAYS, J. L. 1972. The resource and its potential in North America. Pages 59–67 *in* U.S. Dept. Agric. Gen. Tech. Rept. NC–1. North Central Forest and Range Expt. Sta.

MAINI, J. S., AND R. T. COUPLAND. 1964. A simple technique for age determination in trembling aspen. Forest. Chron. 40: 219–226.

OTT, L. 1984. An introduction to statistical methods and data analysis. Duxbury Press, Boston, Massachusetts. 775 pp.

RASMUSSEN, D. I., AND N. WEST. 1943. Experimental beaver transplantation in Utah. Trans. N. Amer. Wildl. Conf. 8: 311–318.

REYNOLDS, H. G. 1969. Aspen grove use by deer, elk, and cattle in the southwestern coniferous forests. USDA Forest Serv. Res. Note RM–138. Rocky Mtn. Forest and Range Expt. Sta., Fort Collins, Colorado. 4 pp.

RHOADES, D., AND R. G. CATES. 1976. Toward a general theory of plant antiherbivore chemistry. *In*: J. W. Wallace and R. L. Mansell, eds., Biochemical interaction between plants and insects. Recent Advances in Phytochem. 10: 168–213.

ROBBINS, C. T. 1983. Wildlife feeding and nutrition. Academic Press, New York. 343 pp.

SHADLE, A. R., AND T. AUSTIN. 1939. Fifteen months of beaver work at Allegany State Park, N.Y. J. Mammal. 20: 299–303.

SNEDECOR, G. W., AND W. G. COCHRAN. 1967. Statistical methods. Iowa State University Press, Ames. 593 pp.

STEGEMAN, L. C. 1954. The production of aspen and its utilization by beaver on the Huntington Forest. J. Wildl. Manage. 18: 348–358.

STRICKLAN, D. 1987. Factors affecting dietary selection and movements of porcupines in Utah. Unpublished thesis, Brigham Young University, Provo, Utah. 39 pp.

UNDERWOOD, E. J. 1966. The mineral nutrition of livestock. Central Press Ltd., Aberdeen, Great Britain. 237 pp.

WALKER, G. R., AND J. D. BROTHERSON. 1982. Habitat relationships of basin wildrye in high mountain valleys of central Utah. J. Range Manage. 35: 628–633.

YEAGER, L. E., AND R. R. HILL. 1950. Beaver management problems on western public lands. Trans. N. Amer. Wildl. Conf. 19: 462–479.

COURTSHIP BEHAVIOR IN *RHINOCLEMMYS AREOLATA* FROM WESTERN TABASCO, MEXICO (TESTUDINES: EMYDIDAE)

Gonzalo Pérez-Higareda[1] and Hobart M. Smith[2]

ABSTRACT.—Observations in nature and captivity reveal that members of the population of *Rhinoclemmys areolata* of western Tabasco, México, exhibit underwater courtship and mating and appear to lay one egg per nest.

Reports on the habits of turtles of the genus *Rhinoclemmys* are few. Courtship behavior has been noted in *R. annulata* (Mittermeier 1971), *R. funerea* (Iverson 1975), and *R. pulcherrima incisa* (Hidalgo 1982). Curiously, data on courtship in *R. areolata* are little known, although the species is not rare, having an extensive distribution from Guatemala and northern Honduras northward on Atlantic slopes to central Veracruz, México; it is most abundant on Isla Cozumel, Quintana Roo (Smith and Smith 1979). The species inhabits savannas for the most part and has terrestrial or semiaquatic habits (Smith and Smith 1979, Pritchard 1979). Its activity has been observed principally during summer rains in northern Chiapas (Alvarez del Toro 1982) and in Cozumel Island (R. C. Vogt, personal communication).

Distinctive characteristics of two different populations of *Rhinoclemmys areolata* are pointed out by Pérez-Higareda and Smith (1988). One of these populations, essentially aquatic, is found in the swamps and rivers of western Tabasco from the north central part of the state to the border of southern Veracruz (Río Tonalá). Its courtship and mating behaviors are different from those of the populations of the Yucatán peninsula, northern Chiapas, eastern Tabasco, and central western Veracruz, all with terrestrial or semiaquatic habits (Mittermeier 1971, Iverson 1975, Hidalgo 1982, Pritchard 1979, Smith and Smith 1979, and personal observations by GPH).

The observations reported here were made in the field and in captivity. One pair (male and female) was observed in April 1983 (GPH) in the Río Tonalá on the border of Veracruz and Tabasco, near the municipality of Agua Dulce, Veracruz, as courtship and mating took place underwater at a depth of approximately 25 cm. Similar behavior was observed (GPH) in another pair at the same place in May 1984 in water approximately 0.5 m deep. Both pairs were collected and kept alive in a garden provided with a pond. Subsequent aquatic courtships and matings were observed there in March, April, and May 1985; all were carried out underwater (40 cm in depth), none on land.

COURTSHIP (Fig. 1).—Males had no difficulty recognizing females underwater. They approached and began to sniff around the cloaca of the female. If the female accepted the courtship, she walked on the bottom of the stream or pond, and the male walked behind her (Fig. 1a). Sometimes the female repelled the courtship, vigorously biting the head of the male. In such instances the male then retreated and began swimming around the female (Fig. 1b). The female meanwhile remained stationary on the bottom, her head almost hidden. The male again sniffed around the cloaca (Fig. 1c). If the female accepted his second approach, she stretched her neck and opened her mouth, while the male swam speedily above her, staying some distance in front of her and hiding his head (Fig. 1d). The female approached him, stretched her neck, and searched the nose of the male with her mouth open (Fig. 1e). The female hid her head, and then the male stretched his neck and rubbed her nose with his for a short period, not exceeding 15 minutes (Fig. 1f).

MATING (Fig. 2).—The male moved quickly to position himself above the female,

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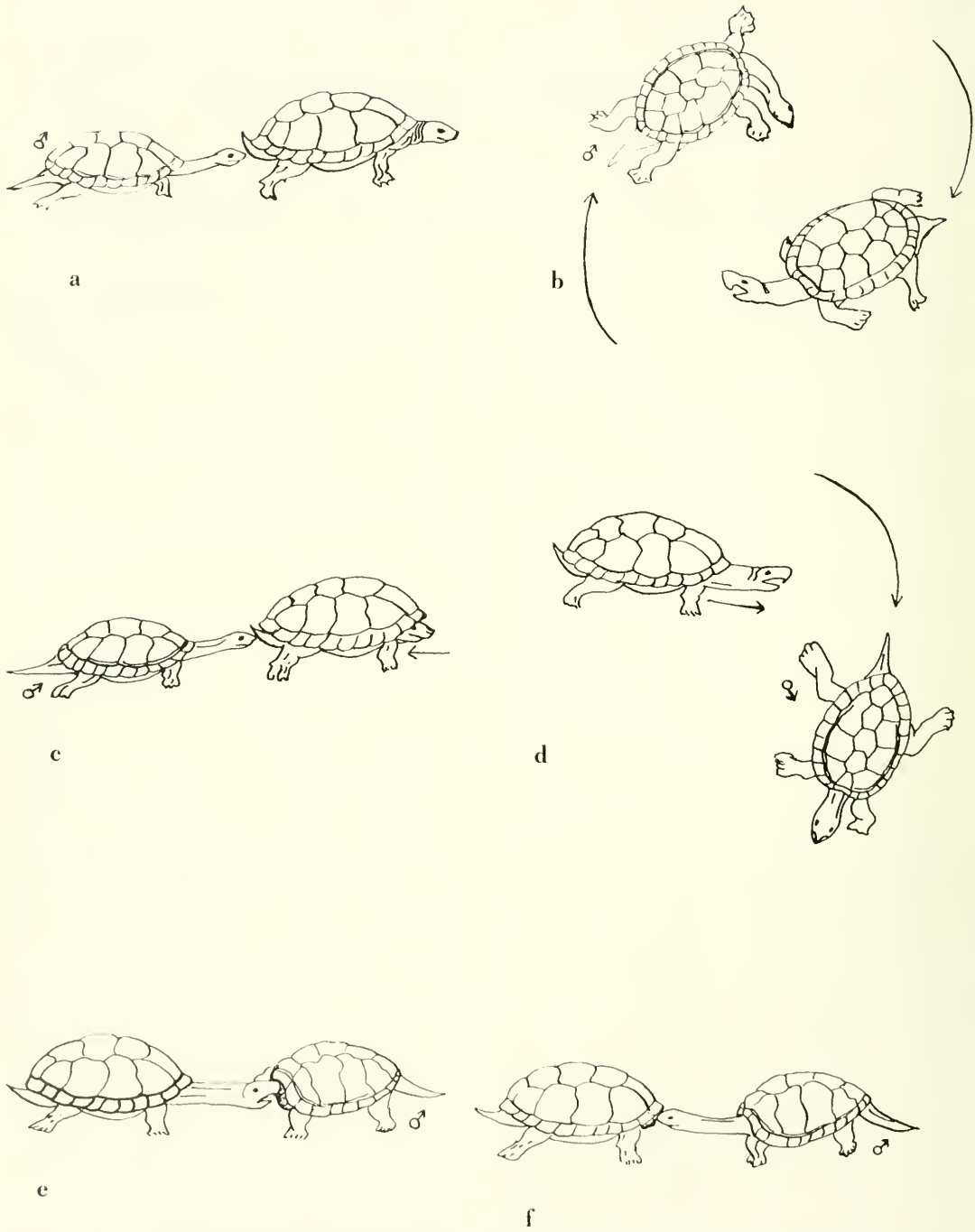

Fig. 1. Phases in the observed courtship behavior of the aquatic subspecies of *Rhinoclemmys areolata*.

stretching his neck to rub nose to nose; this action was sometimes repeated once or twice more (Fig. 2a). Afterwards, the male slipped backward, curling his tail around the tail of the female. The female stretched and retracted her neck once or twice (Fig. 2b). When the penis was inserted in the cloaca of the female, the male released his grip on the female, his body essentially free although still united to her by the tail (Fig. 2c). The female, her hind

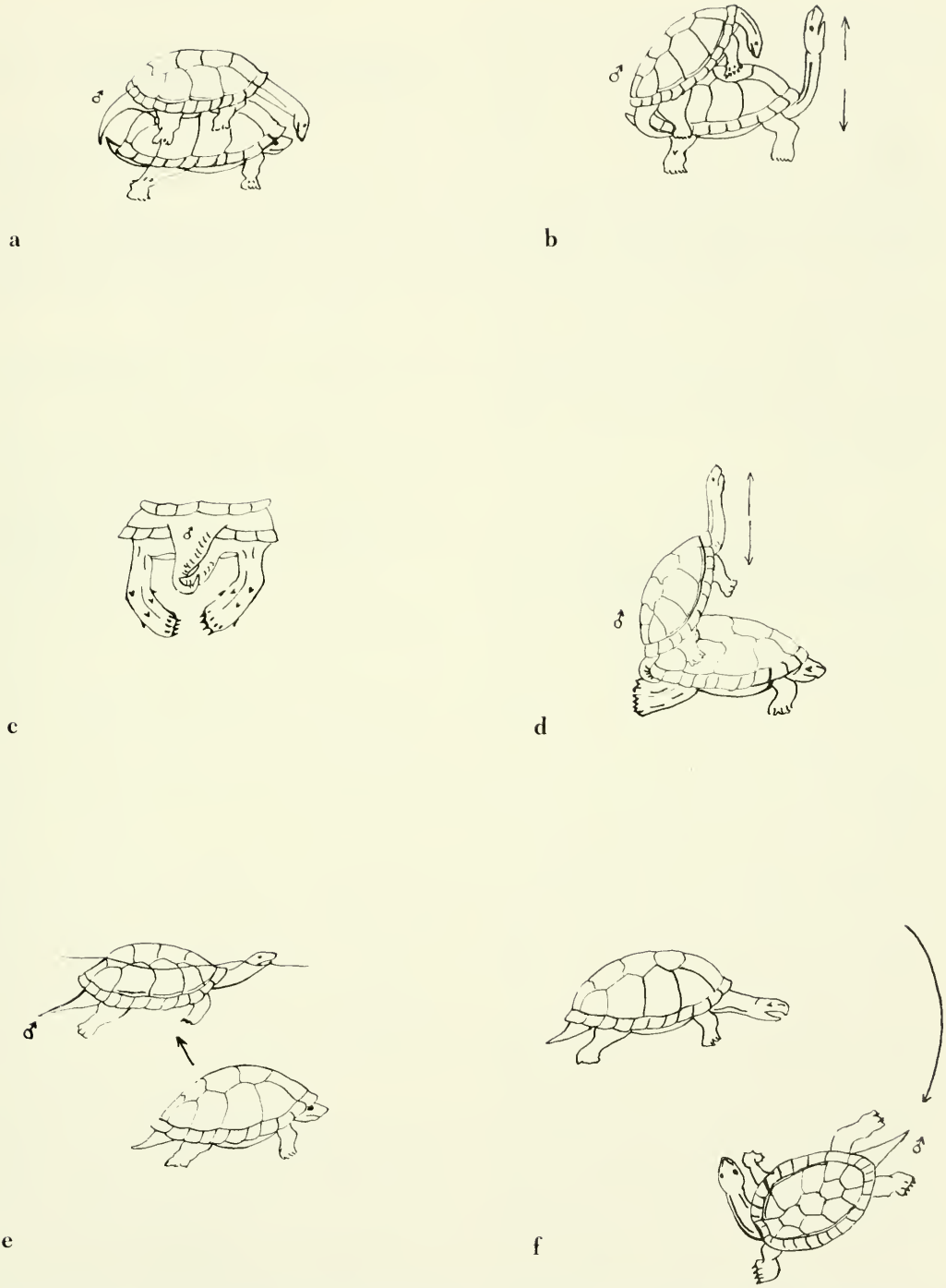

Fig. 2. Phases of the observed mating and postmating behavior of the aquatic subspecies of *Rhinoclemmys areolata*.

limbs outstretched, remained motionless while the male rhythmically protracted and retracted his neck for 25–40 minutes (Fig. 2d). When coitus ended, the male separated and floated; the female remained on the bottom (Fig. 2e). Sometimes the male tried to free himself, but the female stayed attached by the tail, trailing him. Usually after mating

the female was aggressive toward the male; in such cases, he retreated a long distance from her (Fig. 2f). The maximum observed duration of mating was 45 minutes.

NESTING DATA.—We do not have complete information about the nesting customs of *R. areolata* in a natural environment, but one of us (GPH) observed a specimen ovipositing at the edge of a swamp near Villahermosa, Tabasco, in July 1985. The female was laying one egg and covering the hole on land near a swamp. The specimen was captured when it abandoned the nest and was walking to water; she was kept alive in a small garden. After a week she laid a second egg in a depression she dug, and at five-day intervals laid one more egg in each of two different nests. None of the eggs hatched.

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LITERATURE CITED

ALVAREZ DEL TORO, M. 1982. Los reptiles de Chiapas. Tuxtla Gutiérrez, Chiapas, México, Inst. Hist. Nat. 247 pp., 168 figs. (color).

HIDALGO, H. 1982. Courtship and mating behavior in *Rhinoclemmys pulcherrima incisa* (Testudines: Emydidae: Batagurinae). Trans. Kansas Acad. Sci. 85(2): 82–95.

IVERSON, J. B. 1975. Notes on courtship in *Rhinoclemmys funerea*. J. Herp. 9(2): 249–250.

MITTERMEIER, R. A. 1971. Notes on the behavior and ecology of *Rhinoclemmys annulata* Gray. Herpetologica 27(4): 485–488.

PÉREZ-HIGAREDA, G., AND H. M. SMITH. 1988. Comments on geographic variation in *Rhinoclemmys areolata* (Testudines). Bull. Maryland Herp. Soc. (in press).

PRITCHARD, P. C. H. 1979. Encyclopedia of turtles. T.F.H. Publ., Neptune, New Jersey. 895 pp.

SMITH, H. M., AND R. B. SMITH. 1979. Synopsis of the herpetofauna of Mexico. Vol. VI. Guide to Mexican turtles. Bibliographic addendum III. John Johnson, North Bennington, Vermont. 1,044 pp.

SHREW AND HETEROMYID RECORDS FROM THE GREAT BASIN OF OREGON AND UTAH

Harold J. Egoscue[1]

ABSTRACT.—Oregon records from Harney County establish a minimum altitudinal occurrence for the water shrew (*Sorex palustris*), identify an isolated population of the montane shrew (*Sorex monticola obscurus*), and provide an additional specimen of Merriam's shrew (*Sorex merriami*). Utah records extending the ranges in the southeastern part of the Bonneville Basin for the little pocket mouse (*Perognathus longimembris*), long-tailed pocket mouse (*Perognathus formosus*), and dark kangaroo mouse (*Microdipodops megacephalus*) are also given.

Studies in progress designed to determine the ecology of *Peromyscus* fleas in the Great Basin have resulted in the capture of many kinds of small mammals in addition to mice. Among them were three species of shrews from parts of southeastern Oregon, where few soricids have been reported, and three heteromyids, whose capture extends their ranges in western Utah.

Specimens mentioned, including examples of the associated small mammals identified to subspecies, were deposited in collections at the University of Utah, Salt Lake City.

***Sorex monticolus obscurus* Merriam.**—Two montane shrews of this subspecies were collected in the Trout Creek Mountains, an isolated range, most of which lies just north of the Nevada boundary in southeastern Harney County, Oregon.

An adult female (lactating, no embryos) was trapped 20 June 1970 on a dry, densely vegetated hillside at the head of a small tributary canyon of Big Trout Creek (elev. 2,022 m). The principal plants in order of abundance were big sagebrush (*Artemisia tridentata*), bitterbrush (*Purshia tridentata*), and snowberry (*Symphoricarpos* sp.), with a heavy understory of herbaceous plants.

The second specimen, an adult male, was caught 10 September 1982 near the headwaters of Big Trout Creek about 2.4 km north of the Nevada line (elev. 2,135 m). The traps were set streamside, where the dominant vegetation included willow, river birch, and other riparian plants. Besides deer mice, other small mammals caught here were the long-tailed vole (*Microtus longicaudus*) and least chipmunk (*Eutamias minimus*).

These records identify a previously unknown, apparently isolated population of *S. m. obscurus* located between Steen Mountains, Harney County, Oregon, and the Santa Rosa Mountains, Humboldt County, Nevada (see map by Hennings and Hoffman 1977).

***Sorex palustris navigator* (Baird).**—An adult female (no embryos) was collected 10 October 1983 at the mouth of Cottonwood Creek, a tiny stream flowing out of the east side of the Pueblo Mountains 11.3 km south of Fields, Harney County, Oregon (elev. 1,281 m). Almost the entire trapline was set streamside, but the only other mammals captured were *Peromyscus maniculatus*. Altitudinally, this is the lowest place on record where *S. palustris* has been taken in the Great Basin. The conditions here resemble those described by Hall (1946) for a place in Esmeralda County, Nevada, where water shrews were found at a much lower than normal elevation.

***Sorex merriami merriami* Dobson.**—An adult female (no embryos, molt to winter pelage in progress) was collected 25 October 1984 about 16 km south of Crane (elev. 1,318 m). My trapline was set on a steep, dry, talus and boulder-strewn hillside with numerous small ledges and several prominent basalt outcrops. The dominant plant was spiny hopsage (*Grayia spinosa*), with scattered horsebrush (*Tetradymia* sp.) and big sagebrush. Other small mammals trapped here were deer mice (*Peromyscus maniculatus* ssp.), canyon mice (*P. crinitus crinitus*), western harvest mice

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(*Reithrodontomys megalotis megalotis*), desert woodrats (*Neotoma lepida nevadensis*), bushy-tailed woodrats (*N. cinerea alticola*), sagebrush voles (*Lagurus curtatus pauperrimus*), and Great Basin pocket mice (*Perognathus parvus parvus*), all caught within 75 m of where the Merriam's shrew was trapped. With the possible exception of the bushy-tailed woodrat, the biota was typically Upper Sonoran. Lindsay and Perry (1977) reviewed what little was known about this shrew in Oregon when they reported the fourth record for the state.

***Perognathus longimembris gulosus* Hall.**—An adult male provisionally referred to this subspecies was obtained 29 March 1986 in Escalante Valley, 24 km west-southwest of Minersville, Beaver County, Utah, and about 100 m north of the Iron County line. This extends the range about 72 km southeast from localities in extreme southwestern Millard County as mapped by Hall (1981). See account of *Microdipodops megacephalus paululus* for other details about the area.

***Perognathus formosus incolatus* Hall.**—An adult male referrable to *P. f. incolatus* was collected 28 March 1986 about .2 km north of Black Rock, Millard County, Utah (elev. 1,418 m), a range extension well into the eastern part of the southern Bonneville Basin from the nearest localities in southwestern Millard County reported by Hall (1981). Traps were set among the boulders and extensive basalt ledges of an ancient lava flow. Dominant plants were horsebrush and rabbitbrush (*Chrysothamnus* sp.). Associated small mammals were the desert woodrat and deer mouse.

***Microdipodops megacephalus paululus* Hall & Durrant.**—Two adult males fitting the description of this subspecies (Hall and Durrant 1941) were caught 29 March 1986 in the northern end of Escalante Valley, 24 km west-southwest of Minersville, Beaver County, Utah, and about 100 m north of the Iron County line (elev. 1,550 m). This is a range extension southeastward of about 75 km from places in southwestern Millard County mapped by Hall (1981).

The mice were caught in low, semistabilized, vegetated dunes of fine, light-colored sand, where the dominant plants were rabbitbrush and four-winged saltbush (*Atriplex canescens*). Other small mammals caught here were the little pocket mouse, Ord kangaroo rat (*Dipodomys ordii cinderensis*), and deer mouse.

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LITERATURE CITED

HALL, E. R. 1946. The mammals of Nevada. University of California Press, Berkeley and Los Angeles. 710 pp.

———. 1981. Pages 601–1181 *in* The mammals of North America. Vol. 2. John Wiley and Sons, New York.

HALL, E. R., AND S. D. DURRANT. 1941. Two new kangaroo mice from Utah. The Murrelet 22: 5–7.

HENNINGS, D., AND R. S. HOFFMANN. 1977. A review of the taxonomy of the *Sorex vagrans* species complex from western North America. Occas. Papers Mus. Nat. Hist., Univ. Kansas 68: 1–35.

LINDSAY, S. L., AND A. E. PERRY. 1977. An additional Merriam's shrew (*Sorex m. merriami*) from Oregon. The Murrelet 58: 17.

MYCOPHAGY OF RED-BACKED VOLES, *CLETHRIONOMYS CALIFORNICUS* AND *C. GAPPERI*

Chris Maser[1] and Zane Maser[2]

ABSTRACT.—We examined stomach contents of 426 *Clethrionomys*, 217 *C. californicus* from western Oregon and 209 *C. gapperi* from widely scattered areas across North America. *Clethrionomys californicus* consumed fungi of 28 genera. *Clethrionomys gapperi* from the Rocky Mountains westward consumed fungi of 23 genera, whereas *C. gapperi* east of the Rocky Mountains consumed fungi of 7 genera. This study supports the conclusions of an earlier study, limited to Oregon and Washington, that food habits of *C. californicus* and *C. gapperi* are more closely related to habitat than to species or subspecies of vole.

Red-backed voles (*Clethrionomys californicus* and *C. gapperi*) in the Pacific Northwest are primary mycophagists in the coniferous forest (Hayes et al. 1986, Ure and Maser 1982); they disperse viable spores of mycorrhizal fungi (obligatory mycosymbionts of coniferous trees) and nitrogen-fixing bacteria (Li et al. 1986, Ure and Maser 1982).

Maser et al. (1978) examined stomach contents of red-backed voles and identified the mycorrhizal fungi to order. More recently, Hayes et al. (1986) also identified the mycorrhizal fungi to order but based their study on fecal analysis. Fecal analysis is biased for two reasons: fungal spores can be stored in the cecum and expelled days after a vole's last meal on a particular fungus (Maser and Maser, unpublished data), and fungal spores can be overrepresented in the feces because of differential digestion; the spores remain in good condition when many other foods have been digested.

Our purpose is twofold: (1) to compare the fungal diet of *C. californicus* from Oregon with *C. gapperi* from the West Coast to the East Coast of North America, based only on stomach analysis, and (2) to test the notion of Ure and Maser (1982) that food habits of *C. californicus* and *C. gapperi* are more closely related to habitat than to species or subspecies of vole.

METHODS AND MATERIALS

All specimens were dead-trapped to avoid contamination of stomach contents with bait. A total of 426 *Clethrionomys* was examined over 15 years, 217 *C. californicus* from western Oregon and 209 *C. gapperi* from widely scattered areas across North America. Most specimens were quick-frozen in the field for later analysis. Stomach contents were preserved in vials of 10% formalin.

Stomach contents were microscopically examined at 100, 400, and 1,000X magnification. A small amount of material was equally mixed and randomly removed from each vial with narrow, parallel-sided forceps, placed on a microscope slide, mixed with a drop of Melzer's reagent (I, KI, and chloral hydrate), and enclosed under a 22 × 40-mm coverslip. The slide was systematically examined for fungal spores. Fungal taxa were identified with the aid of a spore key (Trappe et al., in press). The percentage by volume of fungal spores for each genus was visually estimated and recorded.

RESULTS AND DISCUSSION

Clethrionomys californicus occurs from the Columbia River south through western Oregon into northwestern California. Although three subspecies are listed (Hall 1981), C. Maser has recognized only two in over 20 years of work in Oregon: *C. c. californicus* in the Coast Range and *C. c. mazama* in the Cascade Range.

Clethrionomys californicus has a specialized diet predominantly composed of

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TABLE 1. Percent volume of stomach contents and percent frequency, in parentheses, of fungal taxa from 217 California red-backed voles (*Clethrionomys californicus*).

Fungal genera	*Clethrionomys californicus*	
	californicus 37[1]	*mazama* 180
Basidiomycetes		
Rhizopogon	33.00 (70)	31.00 (88)
Alpova	5.00 (11)	
Gautieria	1.20 (16)	7.00 (58)
Thaxterogaster		0.20 (2)
Hymenogaster	2.00 (14)	1.00 (16)
Melanogaster	0.40 (8)	1.00 (13)
Octavianina	1.10 (8)	0.20 (1)
Martellia	0.30 (5)	0.40 (2)
Radiigera		0.40 (2)
Hysterangium	5.00 (30)	5.00 (46)
Leucogaster	0.20 (8)	1.00 (23)
Leucophleps		0.40 (8)
Hydnangium		0.01 (1)
Hydnangiales	1.10 (8)	1.00 (14)
Ascomycetes		
Cenococcum	0.02 (3)	0.01 (2)
Elaphomyces	2.40 (35)	1.00 (15)
Balsamia	0.02 (3)	0.01 (1)
Geopora	0.02 (3)	0.02 (3)
Picoa		0.02 (3)
Genabea		0.01 (1)
Genea	0.20 (5)	0.10 (7)
Hydnotrya	1.00 (8)	1.00 (6)
Barssia	0.30 (5)	
Peziza		0.10 (7)
Choiromyces		0.20 (9)
Tuber	2.30 (30)	0.40 (6)
Zygomycetes		
Endogone	1.00 (14)	0.10 (2)
Glomus	1.00 (14)	0.40 (12)
Sclerocystis	0.10 (8)	0.02 (1)
Epigeous	5.00 (19)	1.00 (10)
Undetermined	12.00 (54)	0.40 (12)
Lichens	6.00 (19)	4.00 (18)

[1]Number of animals sampled

sporocarps of hypogeous fungi and lichens (Hayes et al. 1986, Ure and Maser 1982). *Clethrionomys c. californicus* is more strictly a mycophagist than is *C. c. mazama*. Although *C. c. californicus* eats more lichens than does *C. c. mazama* (Ure and Maser 1982) (Table 1), *C. c. mazama* eats more vascular plant material than does *C. c. californicus* (Ure and Maser 1982). As shown in Table 1, *C. c. californicus* may be more selective in the fungi it eats (seven genera with a stomach volume of 2% or more) than is *C. c. mazama* (three genera with a stomach volume of 2% or more). Both subspecies are closely associated with large, fallen trees because the wood, under closed forest canopies, remains wet throughout the year and is a site of prolonged fruiting of hypogeous fungi—the vole's specialized food (Hayes 1983, Maser and Trappe 1984, Ure and Maser 1982).

Clethrionomys gapperi is widely distributed across the northern United States and all but the northernmost reaches of Canada, extending south along the Rocky Mountains in the West and the Appalachians in the East. A correspondingly greater number of subspecies, 29, is recognized (Hall 1981).

The food habits of *C. gapperi* subspecies in western Washington (*C. g. nivarius* on the Olympic Peninsula and *C. g. cascadensis* in the Cascades) generally parallel those of *C. c. californicus* and *C. c. mazama*, respectively (Ure and Maser 1982) (Table 2).

Clethrionomys gapperi (subspecies *idahoensis* and *galei* in Table 2) consumed less hypogeous fungi in the Rocky Mountains (Merritt and Merritt 1978) than was consumed by *C. gapperi nivarius* and *cascadensis* along the West Coast (Table 2). Williams and Finney (1964) found that Endogonaceae comprised from 5% to 100% of the volume in individual stomachs of *C. gapperi* from northwestern Wyoming and north central Colorado. The voles are closely associated with moist habitats (Campbell and Clark 1980) that may foster and prolong fungal fruiting. Clark (1973) found that vascular plant material formed 59% of the stomach contents by volume of 25 *C. gapperi* from Grand Teton National Park, Wyoming; seed fragments 9%, hair 6%, and unidentified 26%.

Consumption of hypogeous fungal sporocarps by *C. gapperi* (subspecies *gapperi* and *carolinensis* in Table 2) decreases in percentage of volume and frequency on the East Coast. Martell (1981) studied the diet of 258 *C. gapperi* in northern Ontario. Lichens were dominant in early May and remained important throughout early summer. Fresh green plants were important from mid-May to mid-July. Seeds were important in June and early July, followed by berries in late July. Mushrooms were important in early summer and became the primary food in August and September. A similar pattern was found by Dyke (1971) in coniferous forests of the Northwest Territories and by Perrin (1979) in Manitoba. Hamilton (1941) noted no fungi in the

TABLE 2. Percent volume of stomach contents and percent frequency, in parentheses, of fungal taxa from 209 southern red-backed voles (*Clethrionomys gapperi*).

Fungal genera	*Clethrionomys gapperi*					
	nivarius 13[1]	*cascadensis* 98	*idahoensis* 27	*galei* 16	*gapperi* 25	*carolinensis* 30
Basidiomycetes						
Rhizopogon	13.00 (39)	31.00 (66)	18.00 (33)	1.00 (38)		
Gautieria		1.00 (12)	1.00 (7)	1.00 (50)		
Thaxterogaster	0.10 (8)	1.00 (18)	0.04 (7)			
Hymenogaster		0.01 (1)	0.04 (7)	6.00 (30)		0.10 (10)
Melanogaster		1.00 (3)	0.10 (4)			0.10 (7)
Octavianina		1.00 (5)				
Martellia		1.00 (1)				
Hysterangium		3.00 (18)	0.04 (4)	2.00 (19)		
Leucogaster	7.00 (23)	2.00 (11)		0.30 (6)		
Leucophleps				0.20 (30)		
Mycolevis			0.04 (7)			
Ascomycetes						
Elaphomyces		0.04 (7)				1.00 (10)
Balsamia	0.10 (31)	0.40 (4)	0.04 (4)		1.00 (4)	
Geopora		0.01 (2)		7.00 (30)		
Picoa	0.20 (31)	0.01 (1)				
Genabea		0.03 (1)				
Genea		1.00 (6)				
Hydnotrya		3.00 (22)				
Peziza			0.04 (4)			
Tuber	6.00 (23)	0.03 (4)				0.10 (10)
Zygomycetes						
Endogone	0.10 (8)	1.00 (3)		0.10 (6)		
Glomus	1.00 (31)	1.20 (17)		1.00 (19)	40.00 (44)	3.00 (63)
Sclerocystis		2.00 (12)				0.03 (7)
Epigeous	22.00 (62)	3.00 (13)	15.00 (82)	24.00 (69)	1.00 (8)	11.00 (47)
Undetermined	8.00 (31)	2.00 (6)	4.00 (15)	3.00 (30)	0.04 (4)	2.00 (10)
Lichens		20.00 (56)	8.00 (52)		0.04 (4)	

[1]Number of animals sampled

stomachs of 100 *C. gapperi* collected from March to December in New York. He found 75% of the stomach contents to be vascular vegetation with various amounts of fruits and insects. Whitaker (1962) reported Endogonaceae formed 20.2% of the volume in stomachs of 162 *C. gapperi* in New York, however. Butsch (1954) considered *C. gapperi* to be a generalist. Linzey and Linzey (1973) found Endogonaceae constituted only 0.02% of the volume of 19 stomachs of *C. gapperi* from the Great Smoky Mountains National Park on the Tennessee–North Carolina border. They stated that 64.8% of the stomach contents by volume was vascular vegetation, 12% seeds, and 4.4% insects. And Schloyer (1977) found chlamydospores, zygospores, and hyphae of *Endogone* composed 19% by volume of stomach contents from 139 *C. gapperi* in West Virginia. Invertebrates made up 1% by volume of the stomach contents. Vascular plant material was the major food and accounted for a mean of 76% of the diet by stomach volume.

Clethrionomys californicus, in particular, has a specialized diet predominantly composed of sporocarps of hypogeous fungi and lichens. The diet is so specialized that *C. californicus* is strictly tied to the coniferous forest habitat producing its food (Gashwiler 1970, Ure and Maser 1982).

Clethrionomys gapperi inhabits tremendously different habitats that include deciduous, mixed deciduous-coniferous, and coniferous forests (Gunderson 1959, Lovejoy 1975, Merritt 1981, Miller and Getz 1972, 1973, Schloyer 1977, Wharton and White 1967). In the lowlands of the Olympic Peninsula, Washington, it has a fungal diet similar to *C. californicus* (Ure and Maser 1982), but its diet becomes much more varied as its range extends northward, higher in elevation, and eastward toward the Atlantic Coast (Abbott

1961, Hamilton and Whitaker 1979, Martell 1981, Merritt 1981, Merritt and Merritt 1978, Schloyer 1977).

The West Coast forests are composed primarily of conifers with hardwoods during early succession (Franklin and Dyrness 1973, Hall et al. 1985). Eastern forests are primarily hardwoods with intermixed conifers. The western coniferous forests have a tremendous belowground biomass of hypogeous fungal sporocarps (see, for example, Fogel 1976, Fogel and Hunt 1979, Hunt and Trappe, in press). The eastern hardwood forests lack the diversity of species, and presumably biomass, of belowground fungal sporocarps (Miller 1986), but they have a tremendous aboveground crop of mast-producing trees (Braun 1950). This study supports the conclusion by Ure and Maser (1982) that food habits of *C. californicus* and *C. gapperi* are more closely related to habitat than to species or subspecies of vole.

LITERATURE CITED

ABBOTT, H. G. 1961. White pine seed consumption by small mammals. J. For. 59: 197–201.

BRAUN, E. L. 1950. Deciduous forest of eastern North America. The Blakison Co., Philadelphia, Pennsylvania. 594 pp.

BUTSCH, R. S. 1954. The life history and ecology of the red-backed vole, *Clethrionomys gapperi gapperi* Vigors, in Minnesota. Unpublished dissertation, University of Michigan, Ann Arbor. 148 pp.

CAMPBELL, T. M., III, AND T. W. CLARK. 1980. Short-term effects of logging on red-backed voles and deer mice. Great Basin Nat. 40: 183–189.

CLARK, T. W. 1973. Local distribution and interspecies interactions in microtines, Grand Teton National Park, Wyoming. Great Basin Nat. 33: 205–217.

DYKE, G. R. 1971. Food and cover of fluctuating populations of northern cricetids. Unpublished dissertation, University of Alberta, Edmonton, Canada. 245 pp.

FOGEL, R. D. 1976. Ecological studies of hypogeous fungi. II. Sporocarp phenology in a western Oregon Douglas-fir stand. Canadian J. Bot. 54: 1152–1162.

FOGEL, R., AND G. HUNT. 1979. Fungal and arboreal biomass in a western Oregon Douglas-fir ecosystem: distribution patterns and turnover. Canadian J. For. Res. 9: 245–256.

FRANKLIN, J. F., AND C. T. DYRNESS. 1973. Natural vegetation of Oregon and Washington. U.S. Dept. Agric., For. Serv. Gen. Tech. Rept. PNW-8. Pacific Northwest For. and Range Expt. Sta., Portland, Oregon. 417 pp.

GASHWILER, J. S. 1970. Plant and mammal changes on a clearcut in central Oregon. Ecology 51: 1018–1026.

GUNDERSON, H. L. 1959. Red-backed vole habitat studies in central Minnesota. J. Mammal. 40: 405–412.

HALL, E. R. 1981. The mammals of North America. Vol. II. 2d ed. John Wiley & Sons, New York.

HALL, F. C., L. W. BREWER, J. F. FRANKLIN, AND R. L. WERNER. 1985. Plant communities and stand conditions. Pages 17–31 *in* E. R. Brown, tech. ed., Management of wildlife and fish habitats in forests of western Oregon and Washington. USDA For. Serv. R6-F and WL-192-1985. Portland, Oregon.

HAMILTON, W. J., JR. 1941. The food of small forest mammals in eastern United States. J. Mammal. 22: 250–263.

HAMILTON, W. J., JR., AND J. O. WHITAKER, JR. 1979. Mammals of the eastern United States. Comstock Publ. Assoc., Ithaca, New York. 346 pp.

HAYES, J. P. 1983. Forestry related aspects of the ecology of *Clethrionomys californicus*. Unpublished thesis, Southern Oregon State College, Ashland. 103 pp.

HAYES, J. P., S. P. CROSS, AND P. W. MCINTIRE. 1986. Seasonal variation in mycophagy by the western red-backed vole, *Clethrionomys californicus*, in southwestern Oregon. Northw. Sci. 60: 250–257.

HUNT, G., AND J. M. TRAPPE. In press. Seasonal hypogeous sporocarp production in a western Oregon Douglas-fir stand. Canadian J. Bot.

LI, C. Y., C. MASER, Z. MASER, AND B. A. CALDWELL. 1986. Role of three rodents in forest nitrogen fixation in western Oregon: another aspect of mammal-mycorrhizal fungus-tree mutualism. Great Basin Nat. 46: 411–414.

LINZEY, D. W., AND V. A. LINZEY. 1973. Notes on food of small mammals from Great Smoky Mountains National Park, Tennessee–North Carolina. J. Elisha Mitchell Sci. Soc. 89: 6–14.

LOVEJOY, D. A. 1975. The effect of logging on small mammal populations in New England northern hardwoods. Univ. Conn. Occas. Pap. (Biol. Sci. Ser.) 17: 269–291.

MARTELL, A. M. 1981. Food habits of southern red-backed voles (*Clethrionomys gapperi*) in northern Ontario. Canadian Field-Nat. 95: 325–328.

MASER, C., AND J. M. TRAPPE, TECH. EDS. 1984. The seen and unseen world of the fallen tree. USDA For. Serv., Gen. Tech. Rept. PNW-164. Pacific Northwest For. and Range Expt. Sta., Portland Oregon, in cooperation with U.S. Department of the Interior, Bureau of Land Management. 56 pp.

MASER, C., J. M. TRAPPE, AND R. A. NUSSBAUM. 1978. Fungal–small mammal interrelationships with emphasis on Oregon coniferous forests. Ecology 59: 799–809.

MERRITT, J. F. 1981. *Clethrionomys gapperi*. Mamm. Species 146: 1–9.

MERRITT, J. F., AND J. M. MERRITT. 1978. Population ecology and energy relationships of *Clethrionomys gapperi* in a Colorado subalpine forest. J. Mammal. 59: 576–598.

MILLER, D. H., AND L. L. GETZ. 1972. Factors influencing the local distribution of the redback vole, *Clethrionomys gapperi*, in New England. Univ. Conn. Occas. Pap. (Biol. Sci. Ser.) 2: 115–138.

———. 1973. Factors influencing the local distribution of the redback vole, *Clethrionomys gapperi*, in New England. II. Vegetation cover, soil moisture, and

debris cover. Univ. Conn. Occas. Pap. (Biol. Sci. Ser.) 2: 159–180.

MILLER, S. L. 1986. Hypogeous fungi from the southeastern United States. I. The genus *Rhizopogon*. Mycotaxon 27: 193–218.

PERRIN, M. R. 1979. Seasonal variation in growth, body composition, and diet of *Clethrionomys gapperi* in spruce forest. Acta Theriol. 24: 299–318.

SCHLOYER, C. R. 1977. Food habits of *Clethrionomys gapperi* on clearcuts in West Virginia. J. Mammal. 58: 677–679.

TRAPPE, J. M., M. A. CASTELLANO, Z. MASER, AND C. MASER. In press. Synoptic key to genera of hypogeous fungi of northern temperate forests with special reference to animal mycophagy. Mad River Press, Inc., Eureka, California.

URE, D. C., AND C. MASER. 1982. Mycophagy of red-backed voles in Oregon and Washington. Canadian J. Zool. 60: 3307–3315.

WHARTON, C. H., AND J. J. WHITE. 1967. The red-backed vole, *Clethrionomys gapperi*, in north Georgia. J. Mammal. 48: 670–672.

WHITAKER, J. O., JR. 1962. *Endogone*, *Hymenogaster*, and *Melanogaster* as small mammal foods. Amer. Midl. Nat. 67: 152–156.

WILLIAMS, O., AND B. A. FINNEY. 1964. *Endogone*—food for mice. J. Mammal. 45: 265–271.

SELECTION OF BIG SAGEBRUSH BY SAGE GROUSE

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ABSTRACT.—Feeding sites of wintering sage grouse (*Centrocercus urophasianus*) were located, one each in stands of three subspecies of big sagebrush (*Artemisia tridentata*: ssp. *tridentata*, basin; ssp. *vaseyana*, mountain; and ssp. *wyomingensis*, Wyoming). Evidences of differential use of plants within subspecies were observed. Whole leaves from fed-on and nonfed-on big sagebrush plants were examined for intrasubspecies chemical comparisons of crude protein, phosphorus, in vitro digestibility, and monoterpenoids. No significant differences were detected except for in vitro digestibility of Wyoming fed-on and nonfed-on big sagebrush and monoterpenoid content of basin big sagebrush. Nutritive content of all three subspecies was high, which may in part help to explain wintering sage grouse weight gains.

Smith (1950) was the first to report differential preference of a wintering animal, mule deer (*Odocoileus hemionus hemionus*), for individual plants of big sagebrush (*Artemisia tridentata*). Since then, other workers have reported differential preference of mule deer not only for individual plants but for subspecies of big sagebrush and accessions within subspecies (Plummer et al. 1968, Scholl et al. 1977, Willms et al. 1979, Sheehy and Winward 1981, Welch and McArthur 1986, Personius et al. 1987). Other animal species also express differential preference for individual plants, subspecies, and accessions within subspecies of big sagebrush. These include domestic sheep (*Ovis aries*, Sheehy and Winward 1981, Welch et al. 1987), pygmy rabbit (*Brachylagus idahoensis*, White et al. 1982), and sage grouse (*Centrocercus urophasianus*, Remington and Braun 1985). The last species, sage grouse, is the subject of this investigation.

Wintering sage grouse have a near-obligate relationship with sagebrush, particularly big sagebrush (Braun et al. 1977, Autenrieth 1981, Roberson 1986). Leaves of sagebrush are the primary winter food for sage grouse (Patterson 1952, Wallestad et al. 1974). The Remington and Braun (1985) report is the first evidence that sage grouse may[3] express differential preference for subspecies of big sagebrush and for individual plants within subspecies. The purpose of our study was to locate wintering sage grouse fed-on and nonfed-on big sagebrush plants in stands of three subspecies of big sagebrush (*A. t.* ssp. *tridentata*, basin; *A. t.* ssp. *vaseyana*, mountain; *A. t.* ssp. *wyomingensis*, Wyoming) and to watch for evidence that might support the report of Remington and Braun (1985) that sage grouse show preferential use among subspecies and individuals within subspecies. Also, the nutritive value was determined for leaves from fed-on and nonfed-on plants.

STUDY SITE

The study area, on the Awapa Plateau near Loa, Utah, in western Wayne County, supports a population of sage grouse. Specific study sites were Jake's Knoll on sections 22 and 23 (R1E, T29S), Vance Reservoir on sections 10 and 11 (R1E, T29S), Elsie's Nipple on section 33 (R2E, T28S), and a Wyoming big sagebrush flat south of State Highway 24 about 12.9 km west of Loa, on sections 2 and 7 (R1E, T27S).

Elevations range from the Jake's Knoll site at about 2,650 m to the Elsie's Nipple site at about 2,500 m. Black sagebrush (*A. nova*) and mountain big sagebrush were the dominant shrubs at the Jake's Knoll and Vance Reservoir

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[3]We do not fully accept the interpretation of the data presented in the Remington and Braun (1985) report concerning the preferential use of Wyoming big sagebrush over mountain big sagebrush by wintering sage grouse. Data in their Table 1 suggest two to one that the use of Wyoming and mountain big sagebrush is a function of occurrence and not palatability differences between the two kinds of big sagebrush. We believe their random sample method is biased because portions of mountain big sagebrush grow at the bottom of draws where sage grouse seldom feed. Consequently, part of their perceived preferential use could be due to feeding habit and not to palatability differences.

sites. Mountain big sagebrush on these two sites was limited to the bottom of drainages, northern exposures, and swells where water tends to concentrate. Black sagebrush was distributed on the flats and on southern exposures. In the Elsie's Nipple site, basin big sagebrush and Utah juniper (*Juniperus osteosperma*) were the dominant shrubs. On the site south of State Highway 24, Wyoming big sagebrush was the dominant shrub.

MATERIALS AND METHODS

Feeding sites, one each for three subspecies of big sagebrush, were located with the aid of radio-collared sage grouse (Hulet et al. 1986). At each feeding site, fed-on and nonfed-on plants were tagged and mapped. A plant had to meet certain criteria to be selected as a nonfed-on plant and to remain as such for this study. The criteria were: (1) no signs of being fed on by sage grouse or any other animal, (2) presence of fresh sage grouse tracks or droppings around or through the plant, (3) within 1.5 m of a fed-on plant, and (4) remained a nonfed-on plant while sage grouse were feeding on the sites for at least two weeks. These four criteria increased the probability that the selected nonfed-on plants were really plants that the sage grouse were discriminating against. Careful and close—on hands and knees—inspection was required to identify nonfed-on plants.

In early February 1984, vegetative samples of current year's growth were removed from five fed-on and five nonfed-on plants on three sites supporting stands of one of three subspecies of big sagebrush. Samples were placed in individual plastic bags, packed in snow inside a cooler, and transported to a laboratory freezer. Frozen whole leaves were separated from stems with a pair of small surgical scissors and were then kept frozen by placing them inside a 1-L, stainless steel, wide-mouth vacuum bottle containing 500 ml of liquid nitrogen. Later all leaves were poured out of the vacuum bottle into a strainer. After the liquid nitrogen evaporated, the leaves were placed in a plastic bag, sealed, and stored in a freezer until needed for grinding. Grinding was done inside the mortar of a steel, motorized mortar and pestle that had been precooled twice with liquid nitrogen. Liquid nitrogen was then poured over the leaves and the leaves ground to a fine powder. The leaf material was placed in a plastic bottle with airtight cap after grinding and stored in a freezer until needed for chemical analysis.

Chemical determinations made on the samples were dry matter, monoterpenoids, in vitro digestibility, crude protein, and phosphorus. Dry matter was determined by oven drying at 100 C until constant weight was achieved, usually after 48 hours. Monoterpenoids were extracted and analyzed by the method outlined by Welch and McArthur (1981). This method is based on Soxhlet extraction with absolute ether and gas chromatographic analysis. Concentration of monoterpenoids was expressed on a dry-matter basis. Pearson's (1970) method was used to determine in vitro digestibility of ground leaves. Rumen inoculum was obtained from a slaughterhouse steer (Welch et al. 1983, Striby et al. 1987). Digestibility data were expressed as a percentage of dry matter digested. Crude protein was determined by the Kjeldahl method (Association of Official Analytical Chemists 1980); and the data were expressed as a percentage of dry matter. Phosphorus was determined by wet digestion-spectrophotometric method (Association of Official Analytical Chemists 1980); and the data were expressed as a percentage of dry matter. Unpaired t-tests ($P = .05$) were used to compare fed-on and nonfed-on plants within subspecies for the various chemical determinations.

RESULTS AND DISCUSSION

This study supports and extends the field observations of Remington and Braun (1985) concerning sage grouse preferential use of individual plants within subspecies of big sagebrush. Because the stands of subspecies in our study area were disjunct, we were unable to make any judgments concerning selection at the subspecies level.

On four occasions we observed the feeding behavior of sage grouse for 2 hours. We saw a general wandering by the birds among the sagebrush plants, as if they were inspecting the plants. Then, for no apparent reason, one bird would start eating the leaves of a plant. Often (60% or more of the time) a feeding bird would be joined by others. In these groups there appeared to be no particular

TABLE 1. Nutritive comparison between leaf tissue of fed-on and nonfed-on plants of big sagebrush for wintering sage grouse. Each subspecies of big sagebrush is represented by five fed-on and five nonfed-on plants. Data expressed as a percentage of dry matter. Data statistically analyzed by unpaired t-test comparison between fed-on and nonfed-on plants within subspecies.

Subspecies	Crude protein %	Phosphorus %	In vitro digestibility %
A. t. ssp. *vaseyana*			
fed-on	9.5	0.18	56.4
nonfed-on	9.2	0.18	55.8
A. t. ssp. *tridentata*			
fed-on	14.9	0.21	60.0
nonfed-on	15.4	0.22	57.8
A. t. ssp. *wyomingensis*			
fed-on	12.3	0.20	58.4[a]
nonfed-on	12.6	0.19	54.1

[a]T-test detected significant difference between the two means for in vitro digestibility for *A. t.* ssp. *wyomingensis* at the 5% probability level.

TABLE 2. Comparisons between the monoterpenoid levels of wintering sage grouse fed-on and nonfed-on plants of mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*, leaf tissue). Data expressed on a dry-matter basis. Unpaired t-tests used to compare treatment means.

Plant type	Plant no.	Percentage of monoterpenoid								
		α-pinene	Camphene	1,8 Cineol	8.50[a]	β-thujone	Camphor	13.06[a]	Terpineol	Total
Nonfed-on	1	0.00	0.00	0.07	0.00	1.48	0.05	0.04	0.56	2.20
	2	0.00	0.00	0.00	0.00	2.74	0.00	0.08	0.67	3.49
	3	0.00	0.06	0.00	0.00	2.57	0.36	0.00	0.62	3.61
	4	0.03	0.20	0.68	0.01	1.52	0.98	0.00	0.47	3.89
	5	0.00	0.00	0.11	0.00	2.84	0.00	0.04	0.65	3.64
Means		0.01	0.05	0.17	0.00	2.23	0.28	0.03	0.59	3.37
Fed-on										
	1	0.00	0.00	0.00	0.33	2.33	0.00	0.07	0.71	3.44
	2	0.00	0.00	0.00	0.00	2.76	0.00	0.08	0.78	3.62
	3	0.00	0.00	0.28	0.23	1.91	0.09	0.03	0.45	2.99
	4	0.00	0.00	0.19	0.00	3.05	0.00	0.00	0.13	3.37
	5	0.00	0.00	0.11	0.00	3.70	0.00	0.00	0.52	4.33
Means		0.00	0.00	0.12	0.11	2.75	0.02	0.04	0.52	3.55
t-test		NS[b]	NS	NS	NS	NS	NS	NS	NS	NS

[a]Unknown monoterpenoid, number represents retention time.
[b]NS means not significantly different at the 5% probability level.

relationship of birds to one another (hen-chick relationship). Birds seemed to mingle freely together. Once feeding on a plant started, it lasted from 5 to 15 min. Then the birds would start their wandering again. We did observe feeding on the same plants over 3 to 5 weeks; and, equally important, there was no feeding on plants selected as nonfed-on plants. These field observations strongly indicate preferential use of individual plants within subspecies. Consequently, we felt that the nonfed-on plants selected for this study had a high probability of being plants the birds were discriminating against.

Table 1 lists the nutritive comparisons between fed-on and nonfed-on plants of three subspecies of big sagebrush. The only significant ($P = .05$) comparison as detected by t-tests was for in vitro digestibility in Wyoming big sagebrush. Here, fed-on plants were more highly digestible. Remington and Braun (1985) reported that browsed Wyoming big sagebrush contained higher levels of crude protein than unbrowsed plants. They also observed that the most preferred subspecies, Wyoming big sagebrush, contained higher levels of crude protein than mountain big sagebrush (15.4 to 17.8% vs. 10.2 to 13.4%). They concluded that crude protein levels were important in sage grouse selection of big sagebrush plants. Our results do not support their observation. However, it is quite

TABLE 3. Comparisons between the monoterpenoid levels of wintering sage grouse fed-on and nonfed-on plants of Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*, leaf tissue). Data expressed on a dry-matter basis. Unpaired t-tests used to compare treatment means.

		Percentage of monoterpenoids											
Plant type	Plant no.	1.07[a]	Camphene	4.84[a]	1,8 Cineol	8.50[a]	β-thujone	10.87[a]	Camphor	12.09[a]	12.45[a]	13.06[a]	Total
Nonfed-on													
	1	0.03	0.00	0.00	0.00	2.70	0.00	0.04	0.00	0.19	0.13	0.00	3.09
	2	0.03	0.00	0.00	0.00	1.96	0.03	0.26	0.30	0.05	0.00	0.00	2.63
	3	0.04	0.00	0.00	0.00	2.49	0.10	0.31	0.22	0.15	0.07	0.00	3.38
	4	0.06	0.00	0.44	0.08	0.12	0.28	0.00	0.48	0.00	0.00	0.12	1.58
	5	0.03	0.14	0.06	0.39	0.00	0.14	0.07	1.06	0.00	0.00	0.01	1.90
Means		0.04	0.03	0.10	0.09	1.45	0.11	0.14	0.41	0.08	0.04	0.03	2.52
Fed-on													
	1	0.05	0.00	0.00	0.00	2.67	0.07	0.27	0.19	0.08	0.00	0.04	3.37
	2	0.04	0.00	0.00	0.08	1.79	0.15	0.28	0.15	0.04	0.04	0.03	2.60
	3	0.03	0.00	0.00	0.00	2.03	0.06	0.34	0.00	0.07	0.00	0.00	2.53
	4	0.10	0.00	0.00	0.18	0.00	0.32	0.00	1.04	0.00	0.00	0.16	1.80
	5	0.03	0.00	0.00	0.00	1.37	0.00	0.41	0.00	0.00	0.00	0.00	1.81
Means		0.05	0.00	0.00	0.05	1.57	0.12	0.26	0.28	0.04	0.01	0.05	2.42
t-test		NS[b]	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

[a]Unknown monoterpenoid, number represents retention time.
[b]NS means not significantly different at the 5% probability level.

TABLE 4. Comparisons between the monoterpenoid levels of wintering sage grouse fed-on and nonfed-on plants of basin big sagebrush (*Artemisia tridentata* ssp. *tridentata*, leaf tissue). Data expressed on a dry-matter basis. Unpaired t-tests used to compare treatment means.

		Percentage of monoterpenoids												
Plant type	Plant no.	1.07[a]	1.89[a]	α-pinene	Camphene	4.84[a]	1,8 Cineol	8.50[a]	β-thujone	10.87[a]	Camphor	12.09[a]	12.45[a]	Total
Nonfed-on														
	1	0.04	0.46	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.36	1.04	1.94
	2	0.04	0.54	0.00	0.00	0.00	0.00	0.00	0.10	0.08	0.00	0.44	0.90	2.10
	3	0.04	0.40	0.00	0.00	0.00	0.00	0.00	0.06	0.12	0.00	0.44	1.02	2.08
	4	0.04	0.46	0.00	0.00	0.00	0.00	0.00	0.14	0.12	0.00	0.58	1.40	2.74
	5	0.04	0.50	0.00	0.00	0.00	0.00	0.00	0.06	0.02	0.00	0.32	0.84	1.78
Means		0.04	0.47	0.00	0.00	0.00	0.00	0.00	0.07	0.08	0.00	0.43	1.04	2.13
Fed-on														
	1	0.12	0.00	0.14	0.08	0.90	0.00	0.00	0.38	0.00	1.58	0.00	0.00	3.20
	2	0.08	0.00	0.00	0.40	0.56	0.42	0.00	0.24	0.00	1.47	0.00	0.00	3.17
	3	0.08	0.00	0.02	0.00	0.46	0.20	0.50	0.36	0.32	0.44	0.00	0.10	2.48
	4	0.12	0.00	0.00	0.30	0.84	0.22	0.00	0.36	0.00	0.96	0.00	0.06	2.86
	5	0.08	0.00	0.00	0.28	0.20	1.20	0.00	0.16	0.06	1.16	0.00	0.00	3.14
Means		0.10	0.00	0.03	0.21	0.59	0.41	0.10	0.30	0.08	1.12	0.00	0.03	2.97
t-test		S[b]	S	NS	S	S	S	NS	S	NS	S	S	S	S

[a]Unknown monoterpenoid; number represents retention time.
[b]NS means not significantly different at the 5% probability level
S means are significantly different at the 5% probability level.

obvious from Table 1 that the birds in our study did not have much of an intrasubspecies choice. Based on results of t-tests, fed-on and nonfed-on plants did not differ in crude protein levels. There were probable differences among subspecies, but, because the subspecies were disjunct, the birds did not have an opportunity at each feeding site to choose one over the other. The pattern of nutrient levels among the subspecies follows that of previous reports: basin big sagebrush was the most nutritious, followed by Wyoming and mountain big sagebrush (Welch 1983). Big sagebrush leaves are as nutritious as any winter forage found on Great Basin ranges (Behan and Welch 1986, Bunderson et al. 1986, Davis and Welch 1986). This may help explain in part why Beck and Braun (1978) reported weight gains in wintering sage grouse.

Tables 2, 3, and 4 list the comparisons between the monoterpenoid levels of the fed-on and nonfed-on plants. T-tests detected no significant differences (P = .05) between fed-on and nonfed-on plants for mountain and Wyoming big sagebrush for individual or total monoterpenoids. Significant differences may exist between the two subspecies (means of 3.55 and 3.37% vs. 2.42 and 2.52%). Welch and McArthur (1981) reported differences in monoterpenoid content of leaves and stems for these two subspecies. Remington and Braun (1985) noted differences in monoterpene content between Wyoming and mountain big sagebrush but not among browsed, unbrowsed, and random plants of the same subspecies.

The basin big sagebrush comparison is quite a different story. Table 4 shows that we are dealing with two distinct populations of basin big sagebrush. A criterion for a plant to be selected as a nonfed-on plant was to be within 1.5 m of a fed-on plant, meaning that the two populations were thoroughly mixed. All five nonfed-on plants contained two unknown monoterpenoids (1.89 and 12.09) not found in the fed-on plants. All five fed-on plants contained one unknown monoterpenoid (4.84) and camphor not found in the nonfed-on plants. Four fed-on plants contained camphene and 1,8 cineol. None of the five nonfed-on plants contained these two monoterpenoids. These differences are direct evidence that the study area supports two populations of basin big sagebrush. 'Hobble Creek,' a highly preferred big sagebrush by wintering mule deer (Welch and McArthur 1986) and by wintering domestic sheep (Welch et al. 1987), also contains high camphor levels, as do the fed-on plants listed in Table 4.

One might be tempted to claim that the birds and perhaps deer and sheep are selecting plants high in camphor. But a check of the camphor content in mountain and Wyoming big sagebrush listed in Tables 2 and 3 tempers such temptation. The differences in monoterpenoid content between fed-on and nonfed-on plants for basin big sagebrush are interesting, but behavioral data are lacking regarding preferences among subspecies.

We will be using the results of this study and that of Remington and Braun (1985) to justify a more definitive study. The heart of such a study will be the use of a uniform garden, placing birds in the garden to test their preference for subspecies, accessions, and individual plants of big sagebrush. This technique is similar to studies used for determining wintering mule deer and domestic sheep preferences for big sagebrush (Welch and McArthur 1986, Welch et al. 1981).

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LITERATURE CITED

ASSOCIATION OF OFFICIAL ANALYTICAL CHEMISTS. 1980. Official methods of analysis. 13th ed. Washington, D.C. 1,018 pp.

AUTENRIETH, R. E. 1981. Sage grouse management in Idaho. Fish and Game Bull. 9. Idaho State Fish and Game Commission, Boise, Idaho. 238 pp.

BECK, T. D., AND C. E. BRAUN. 1978. Weights of Colorado sage grouse. Condor 80: 241–243.

BEHAN, B., AND B. L. WELCH. 1986. Winter nutritive content of black sagebrush (*Artemisia nova*) grown in a uniform garden. Great Basin Nat. 46: 161–165.

BRAUN, C. E., T. BRITT, AND R. O. WALLESTAD. 1977. Guidelines for maintenance of sage grouse habitats. Wildl. Soc. Bull. 5: 99–106.

BUNDERSON, E. D., B. L. WELCH, AND D. J. WEBER. 1986. In vitro digestibility of *Juniperus osteosperma* (Torr.) Little from 17 Utah sites. For. Sci. 32: 834–840.

DAVIS, J. N., AND B. L. WELCH. 1986. Winter preference, nutritive value, and other range use characteristics of *Kochia prostrata* (L.) Schrad. Great Basin Nat. 45: 778–783.

HULET, B. Y., J. T. FLINDERS, J. S. GREEN, AND R. B. MURRAY. 1986. Seasonal movements and habitat selection of sage grouse in southern Idaho. Pages 168–175 *in* E. D. McArthur and B. L. Welch, compilers, Proceedings, symposium on the biology of *Artemisia* and *Chrysothamnus*. U.S. Department of Agriculture, Forest Service Gen. Tech. Rep. INT–200. Intermountain Research Station, Ogden, Utah.

PATTERSON, R. L. 1952. The sage grouse in Wyoming. Sage Books, Denver, Colorado.

PEARSON, H. A. 1970. Digestibility trials: in vitro techniques. Pages 85–92 *in* H. A. Paulson, Jr., E. H. Reid, and K. W. Parker, eds., Range and wildlife

habitat evaluation, a research symposium. U.S. Department of Agriculture, Forest Service Misc. Publ. 1147. Washington, D.C.

PERSONIUS, T. L., C. L. WAMBOLT, J. R. STEPHENS, AND R. G. KELSEY. 1987. Crude terpenoid influence on mule deer preference for sagebrush. J. Range Manage. 40: 84–88.

PLUMMER, A. P., D. R. CHRISTENSEN, AND S. B. MONSEN. 1968. Restoring big game range in Utah. Utah Division of Wildlife Resources Publ. 68-3. Salt Lake City, Utah. 183 pp.

REMINGTON, T. E., AND C. E. BRAUN. 1985. Sage grouse food selection in winter, North Park, Colorado. J. Wildl. Manage. 49: 1055–1061.

ROBERSON, J. A. 1986. Sage grouse–sagebrush relationships: a review. Pages 157–161 *in* E. D. McArthur and B. L. Welch, compilers, Proceedings, symposium on the biology of *Artemisia* and *Chrysothamnus*. U.S. Department of Agriculture, Forest Service Gen. Tech. Rep. INT–200. Intermountain Research Station, Ogden, Utah.

SCHOLL, J. P., R. G. KELSEY, AND F. SHAFIZADEH. 1977. Involvement of volatile compounds of *Artemisia* in browse preference by mule deer. Biochem. Sys. and Ecol. 5: 291–295.

SHEEHY, D. P., AND A. H. WINWARD. 1981. Relative palatability of seven *Artemisia* taxa to mule deer and sheep. J. Range Manage. 34: 397–399.

SMITH, A. D. 1950. Sagebrush as winter food for mule deer. J. Wildl. Manage. 14: 285–289.

STRIBY, K. D., C. L. WAMBOLT, R. G. KELSEY, AND K. M. HAUSTAD. 1987. Crude terpenoid influence on in vitro digestibility of sagebrush. J. Range Manage. 40: 244–248.

WALLESTAD, R. O., J. G. PETERSON, AND R. L. ENG. 1974. Foods of adult sage grouse in central Montana. J. Wildl. Manage. 38: 630–633.

WELCH, B. L. 1983. Big sagebrush: nutrition, selection, and controversy. Pages 21–33 *in* K. L. Johnson, ed., Proceedings of the first Utah shrub ecology workshop. College of Natural Resources, Utah State University, Logan.

WELCH, B. L., AND E. D. MCARTHUR. 1981. Variation of monoterpenoid content among subspecies and accessions of *Artemisia tridentata* grown in a uniform garden. J. Range Manage. 34: 380–384.

———. 1986. Wintering mule deer preference for 21 accessions of big sagebrush. Great Basin Nat. 46: 281–286.

WELCH, B. L., E. D. MCARTHUR, AND J. N. DAVIS. 1981. Differential preference of wintering mule deer for accessions of big sagebrush and for black sagebrush. J. Range Manage. 34: 409–411.

WELCH, B. L., E. D. MCARTHUR, AND R. L. RODRIGUEZ. 1987. Variation in utilization of big sagebrush accessions by wintering sheep. J. Range Manage. 40: 113–115.

WELCH, B. L., J. C. PEDERSON, AND W. P. CLARY. 1983. Ability of different rumen inocula to digest range forages. J. Wildl. Manage. 47: 873–878.

WHITE, S. M., J. T. FLINDERS, AND B. L. WELCH. 1982. Preference of pygmy rabbits (*Brachylagus idahoensis*) for various populations of big sagebrush (*Artemisia tridentata*). J. Range Manage. 35: 724–726.

WILLMS, W., A. MCLEAN, R. TUCKER, AND R. RITCEY. 1979. Interactions between mule deer and cattle on big sagebrush range in British Columbia. J. Range Manage. 32: 299–304.

TIME-ACTIVITY BUDGETS OF DRAKE GADWALL AND NORTHERN SHOVELERS ON INDUSTRIAL COOLING PONDS DURING LATE WINTER AND EARLY SPRING IN CENTRAL UTAH

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ABSTRACT.—Time-activity budgets of drake Gadwall and Northern Shoveler ducks were studied in the winter of 1985. Total duck numbers peaked in mid-March. Gadwall numbers increased from late January to mid-March and then declined, while Northern Shoveler numbers declined from late January to mid-February and then increased to mid-March before declining. Behavior categories considered in the time-activity budgets were flying, preening, swimming, courtship, feeding, and resting. Time allocated to these different activities varied for both duck species, with feeding being the only behavior pattern wherein differences were significant. Gadwalls spent 58% of their time feeding, Northern Shovelers only 26%. Possible reasons for these differences are suggested.

The Gadwall (*Anas strepera*) and Northern Shoveler (*Anas clypeata*), like other Holarctic surface-feeding ducks, occupy a broad geographical range across much of North America (Bellrose 1976). Survey data indicate that the largest winter concentrations of Gadwall occur in the Mississippi Flyway, while the largest concentrations of Northern Shoveler occur equally distributed in the Pacific and Mississippi flyways (Johnsgard 1975). Wintering information indicates that in inland areas they are found on natural ponds and marsh impoundments with the Northern Shovelers preferring artificial impoundments along drainage systems (Stewart 1962). Information from Utah indicates that low numbers of both species remain in the state throughout the winter where there is open water (Hayward et al. 1976).

Behavioral studies of the two species have included aspects of their biology including flocking patterns (Bezzel 1959, Frith 1967, Poysa 1984), pair-forming and copulation (McKinney 1970, Duebbert 1966, Johnsgard 1965), nesting and brooding activities (Girard 1939, Gates 1962, Duebbert et al. 1986, Lokemoen et al. 1984), interspecific relationships (Eddleman et al. 1985, Amat and Soriguer 1984), feeding patterns (Hepp 1985, Nudds and Bowlby 1984), and postbreeding activities (McKinney 1967, Oring 1969, Dubowy 1985). Few studies have involved the daily behavioral patterns or activity budgets of the two birds. This paper is concerned with the daily behavior patterns of Gadwall and Northern Shoveler drakes in central Utah during late January, February, and March.

STUDY AREA

The study area (approximately 86 ha) is on the southeast corner of the large (771-ha) settling pond at U.S. Steel's Geneva plant (Fig. 1). Because the pond is ice-free during winter and access to the pond is restricted, timed observations on selected birds could be accomplished free of public disturbance. The pond depth averages 6 m and is enclosed by earth-filled and slag-filled dikes to the north and west. Water volume changes daily as water is pumped (253 million liters) from the pond to the plant. In the plant the water is used in cooling operations at the various steel-making furnaces. Following use, the water is returned to the billion-liter reservoir for cooling, storage, and reuse. The average temperature of the return flow is 26 C. Ambient air temperatures during the study averaged 6 C.

Vegetation around the study site included peachleaf willow (*Salix amygdaloides*), Russian olive (*Elaeagnus angustifolia*), narrowleaf cottonwood (*Populus angustifolia*), saltcedar (*Tamarix ramosissima*), Pacific aster (*Aster chilensis*), dogbane (*Apocynum cannabinum*), showy milkweed (*Asclepias speciosa*), motherwort (*Leonurus cardiaca*),

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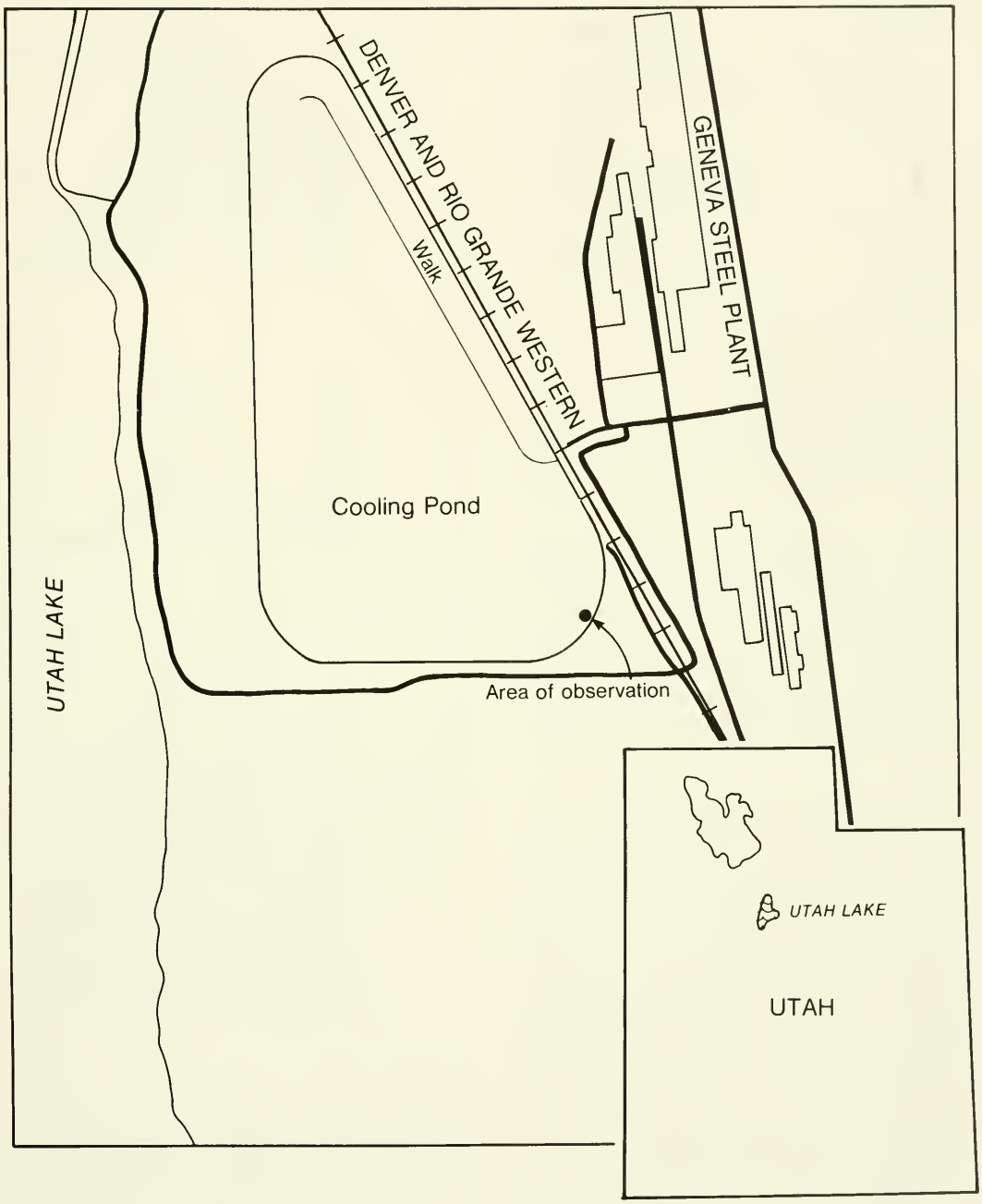

Fig. 1. Map showing location of Geneva Steel cooling pond and observation area on south dike.

rubber rabbitbrush (*Chrysothamnus nauseosus*), sunflower (*Helianthus annuus*), thistle (*Cirsium* sp.), and yellow clover (*Melilotus officinalis*).

METHODS

Thirteen days, 28 January to 31 March 1984, were spent observing Gadwall and Northern Shoveler drakes. Early morning mists, caused by the warm water of the pond coming into contact with the much colder ambient air, precluded observations prior to 10:30 A.M. Therefore, observation periods were selected from 30-minute blocks of time

beginning at 10:30 A.M. and ending at 4:30 P.M. Observations were made with the aid of 7 × 35 binoculars and a spotting scope with a zoom lens. One individual (the focal animal) was selected randomly by looking through a transparent numbered grid and selecting the drake closest to the number selected from the random numbers table for that day. Each bird was observed for 15 minutes and classified as to behavior; then the length of time spent in each behavioral bout was recorded. A stopwatch was used to time each bout.

Six behavior classes were considered: (1) preening—grooming, smoothing, or cleaning the feathers with the beak, (2) swimming—actively moving across the surface of the water, (3) courtship—behavior consisting of conspicuous displays associated with actual pair formation or pair-bond maintenance, (4) resting—not engaged in any of the other behaviors, or a period of inactivity, (5) flight—flying, and (6) foraging—searching for or ingesting food. Before actual observations commenced, total numbers for all species of waterfowl on the 86-ha pond were recorded.

Behavioral patterns were statistically compared using the Mann-Whitney test (Weiss and Hassett 1982).

RESULTS AND DISCUSSION

The numbers of waterfowl on the pond fluctuated from a beginning total of 282 birds on 28 January to an ending total of 208 birds on 31 March. The greatest number of birds (428) was observed on 10 March during the middle of the spring migration. As the weather ameliorated and the season for migration moved forward, the numbers of ducks using the pond dwindled, especially dabbling ducks such as the Mallard, Pintail, and Widgeon. Totals for coots always exceeded 100 birds and were, therefore, generally estimated.

Differences between the occurrence of Gadwalls and Shovelers during the sampling period are shown in Figure 2. As shown, Gadwall numbers remained fairly stable during February, jumped in early March, and then declined to very low levels by 31 March. Shovelers, on the other hand, underwent a major dip in numbers during mid-February, jumped to their highest levels in mid-March, and then showed declines similar to the Gadwalls by 31 March. Other duck species began with 87 birds on 28 January, peaked at 184 birds on 28 February, and then leveled off at 125 birds in the latter part of March.

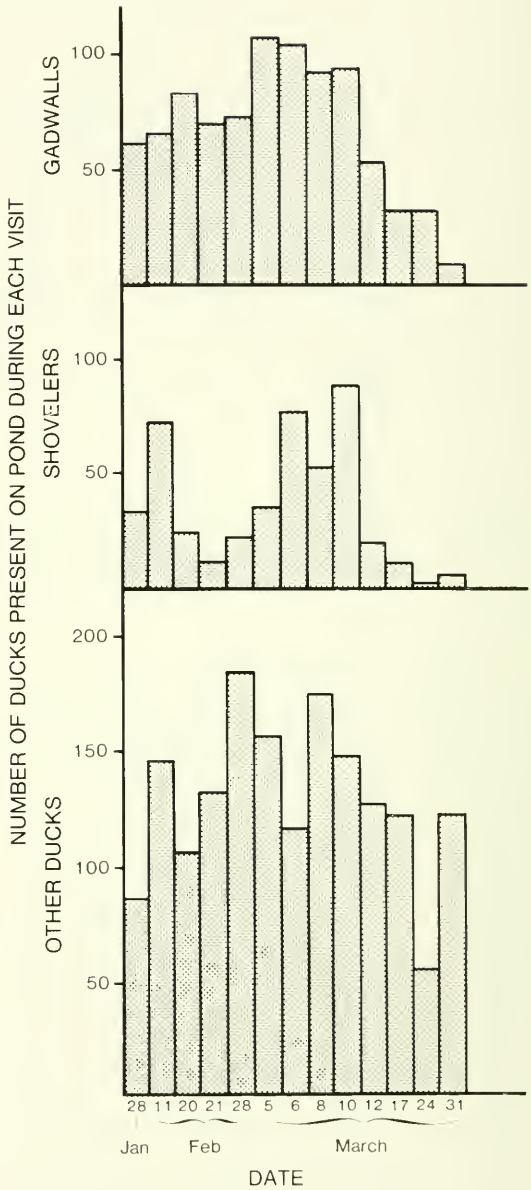

Fig. 2. Histogram showing the number of ducks present on the cooling pond during each of the observation visits. Gadwalls and Northern Shovelers are shown separately, while all other ducks are lumped together.

One reason for the abundance of waterfowl on the pond during the cold winter months may be that it is a way for the ducks to conserve energy through thermoregulation. Not only is the pond ice-free but the water is

TABLE 1. The time-activity budgets (means and standard deviations) for drake Gadwall and drake Shoveler ducks in minutes per observation period (15-minute units) on USX's Geneva Steel cooling pond.

	Gadwall		Shoveler	
	% of time	Mean	% of time	Mean
Flight	.50	.07 ±.13	2.56	.38 ±1.22
Preening	2.50	.37 ±.93	16.93	2.54 ±4.87
Swimming	28.58	4.29 ±6.05	28.06	4.21 ±6.23
Courtship	6.03	.90 ±3.53	6.31	.95 ±3.54
Feeding	57.68	8.65 ±7.03	24.28	3.64 ±6.20
Resting	4.32	.65 ±2.75	21.86	3.28 ±5.54

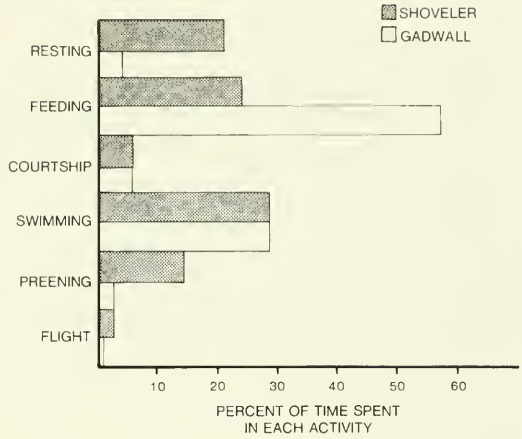

Fig. 3. Time-activity budgets for the Gadwall and Northern Shoveler drakes during the observation visits. The histogram bars represent the percentage of time (15-minute intervals) the ducks spent in each activity.

warm; therefore, the ducks should undergo less stress from the cold. When the weather warmed, the numbers of ducks on the pond declined. This decrease may be attributed to two factors. First, by the end of March hundreds of California Gulls (*Larus californicus*) began to move in and compete for nesting places on the dikes, gradually displacing the ducks from their resting areas. And, second, as the season warmed, resulting in snow and/or ice melt on agricultural fields and other ponds, food availability on foraging areas outside the confines of the study area increased.

Behavior categories were compared within and between drakes of Gadwall and Northern Shoveler ducks on the pond (Table 1, Fig. 3). As shown, time allocated to the different behavior categories by both duck species varied greatly. Both species spent little time in flight during the observation hours and much time in feeding and swimming. Differences between the behavior patterns of the two species were observed for time spent in resting, preening, and feeding, with feeding being the only behavior pattern in which differences were significant ($p \leq 0.05$). The large percentage of their daily activity budgets (58%) spent by the Gadwalls in feeding corresponds well to a study made in Louisiana (Paulus 1984) wherein nonbreeding Gadwalls spent 64% of their time feeding. Time spent in courtship activity was low for both species and averaged about 6% of the observation hours.

We suggest several possible reasons the Gadwall spends so much more time feeding than the Northern Shoveler. First, in a deep, open-water pond such as the Geneva holding pond, Gadwalls may be less-efficient feeders in relationship to bill size and lamellae number. The bill of the Gadwall is narrower in proportion to its length and has fewer lamellae than those of other dabbling ducks (Bellrose 1976, Nudds and Bowlby 1985), while the Northern Shoveler has an extraordinarily large bill and a great number of lamellae. In fact, the bill's breadth and spoon-shaped tip make it unique in size among waterfowl (Johnsgard 1975). Its width near the tip, about twice as wide as at the base, has several rows of comblike lamellae. This makes the Northern Shoveler highly efficient as a surface-feeder with respect to straining out small organisms in the water column (Dubowy 1985). Second, the feeding behavior of the Northern Shoveler is such that it tends to enhance its feeding efficiency (Kortright 1967). The birds feed in small groups, each bird rotating in a "pinwheel" motion that stirs up the suspended material in the water column (Bellrose 1976). Third, in studies done on food types, the Gadwall has consistently shown a granivorous diet low in animal material and high in vegetable material. Conversely, the Northern Shoveler is zoophagous, consuming large amounts of small aquatic animal life (Johnsgard 1975, Pirot et al. 1984). This consumption of animal material should be energetically more efficient for the Northern

Shoveler. Fourth, drake body weight for the Gadwall generally exceeds that of the Northern Shoveler by nearly 30%, or about 295 g (0.65 lbs) (Johnsgard 1975). Assuming that the two species show equivalent abilities to metabolize food (Miller 1984), the greater Gadwall body weight and higher activity level relative to foraging would require more energy for maintenance under the winter conditions observed during this study. Needing less time for foraging, the Northern Shoveler should allocate a greater percentage of its time to other activities. This was observed in our study; the Northern Shoveler spent nearly 37% of the time resting or preening while the Gadwall spent an average of only 7% of the time in such activities.

LITERATURE CITED

AMAT, J. A., AND R. C. SORIGUER. 1984. Kleptoparasitism of coots by Gadwalls. Ornis. Scand. 15: 188–194.

BELLROSE, F. C. 1976. Ducks, geese and swans of North America. The Stackpole Books Co., Harrisburg, Pennsylvania. 543 pp.

BEZZEL, E. 1959. Beitrage zur biologie der geschlecter bei entenvogeln. Anzeiger der Ornithologischen Gesellschaft in Bayern 5: 269–355.

DUBOWY, P. J. 1985. Feeding ecology and behavior of postbreeding male Blue-winged Teal (*Anas discors*) and Northern Shovelers (*Anas clypeata*). Canadian J. Zool. 63: 1292–1297.

DUEBBERT, H. F. 1966. Island nesting of the Gadwall in North Dakota. Wilson Bull. 78: 12–25.

DUEBBERT, H. F., J. T. LOKEMOEN, AND D. E. SHARP. 1986. Nest sites of ducks in grazed mixed-grass prairie in North Dakota. Prairie Nat. 18: 99–108.

EDDLEMAN, W. R., C. T. PATTERSON, AND F. L. KNOPF. 1985. Interspecific relationships between American Coots (*Fulica americana*) and waterfowl during fall migration. Wilson Bull. 97: 463–472.

FRITH, H. C. 1967. Waterfowl in Australia. East-West Center Press, Honolulu, Hawaii.

GATES, J. M. 1962. Breeding biology of the Gadwall in northern Utah. Wilson Bull. 74: 43–67.

GIRARD, G. L. 1939. Notes on life history of the Shoveler. North Amer. Wildl. Conf. Trans. 4: 364–371.

HAYWARD, C. L., C. COTTAM, A. M. WOODBURY, AND H. H. FROST. 1976. Birds of Utah. Great Basin Nat. Mem. No. 1. 229 pp.

HEPP, G. R. 1985. Effects of environmental parameters on the foraging behavior of 3 species of wintering dabbling ducks. Canadian J. Zool. 63: 289–294.

JOHNSGARD, P. A. 1965. Handbook of waterfowl behavior. Cornell Univ. Press, Ithaca, N.Y. 378 pp.

———. 1975. Waterfowl of North America. Indiana Univ. Press, Bloomington. 575 pp.

KORTRIGHT, F. H. 1967. The ducks, geese and swans of North America. The Stackpole Books Co., Harrisburg, Pennsylvania. 476 pp.

LOKEMOEN, J. T., T. F. DUEBBERT, AND D. E. SHARP. 1984. Nest spacing, habitat selection and behavior of waterfowl on Miller Lake Island, North Dakota. J. Wildl. Manage. 48: 309–321.

MCKINNEY, F. 1967. Breeding behavior of captive shovelers. Wildlife Trust Annual Rept. 18(1965–1966): 108–121.

———. 1970. Displays of four species of blue-winged ducks. Living Bird 9: 29–64.

MILLER, M. R. 1984. Comparative ability of Northern Pintails (*Anas acuta*), Gadwalls (*Anas strepera*) and Northern Shoveler (*Anas clypeata*) to metabolize food. J. Wildl. Manage. 48: 362–370.

NUDDS, T. D., AND J. N. BOWLBY. 1984. Predator-prey size relationships in North American dabbling ducks. Canadian J. Zool. 62: 2002–2008.

ORING, L. D. 1969. Summer biology of the Gadwall at Delta, Manitoba. Wilson Bull. 81: 44–54.

PAULUS, S. L. 1984. Activity budgets of non-breeding Gadwalls (*Anas strepera*) in Louisiana. J. Wildl. Manage. 48: 371–380.

PIROT, J. Y., D. CHESSEL, AND A. TAMISIER. 1984. The preferred feeding habitats of 5 species of wintering and migrating dabbling ducks (*Anas* spp.) in the Camargue wetlands (France): a spatio-temporal model. Rev. Ecol. Terre. Vie 39: 167–192.

POYSA, H. 1984. Species assembly in the dabbling ducks (*Anas* spp.) guield in Finland. Ann. Zool. Fenn. 21: 451–464.

STEWART, R. E. 1962. Waterfowl populations in the upper Chesapeake region. U.S. Fish and Wildlife Serv. Spec. Sci. Rept. 65. 208 pp.

WEISS, N., AND M. HASSETT. 1982. Introductory statistics. Addison-Wesley Publishing Co., Reading, Massachusetts. 651 pp.

STATUS AND DISTRIBUTION OF AMERICAN WHITE PELICAN NESTING COLONIES IN WYOMING: AN UPDATE

Scott L. Findholt[1] and Kenneth L. Diem[2]

ABSTRACT.—Historically, one American White Pelican nesting area was known in Wyoming. In 1986 White Pelicans nested at four locations consisting of four different colonies and approximately 949 active nests. Nesting success was probably adequate for population stability at Pathfinder Reservoir from 1984 through 1986 and at Yellowstone Lake in 1984 and 1985, but insufficient there in 1986. White Pelican colonies at Bamforth and Cooper lakes most likely failed because of predation. With the exception of the Yellowstone Lake colony, the future of White Pelican nesting colonies in Wyoming is uncertain. Current threats are human disturbance of nesting birds, predation, and loss of habitat, including breeding areas and foraging sites.

Historically, only one nesting colony of American White Pelicans (*Pelecanus erythrorhynchos*) was reported for Wyoming (Knight 1902, McCreary 1939). This colony is located on the Molly Islands, Yellowstone Lake, Yellowstone National Park (Schaller 1964, Diem and Condon 1967, Diem 1979). In 1984 a new White Pelican nesting colony was discovered in the state at Pathfinder Reservoir (Findholt 1986). Our objective is to provide recent information on the status of the Yellowstone Lake and Pathfinder Reservoir colonies and report on two additional but unsuccessful nesting attempts by White Pelicans in Wyoming during 1986.

METHODS

Since 1981 and more intensively in 1984 and 1986, we have conducted a comprehensive survey in Wyoming for breeding locations of colonially nesting waterbirds, including American White Pelicans. Fifteen aerial surveys in fixed-wing aircraft were made for new nesting sites of all colonial waterbirds for a total of 67.1 hours of flight time in 1984 and 1986. Reservoirs, lakes, marshes, and other potential breeding areas not observed during aerial searches were checked from the ground with binoculars or a 20-45X spotting scope. Other sources of information on potential locations of White Pelican nesting colonies included a literature review, an examination of the files of the Wyoming Game and Fish Department, and correspondence with biologists, naturalists, bird-watchers, and others considered knowledgeable of White Pelican breeding areas in the state. In all colonies an attempt was made to count active nests when the majority of pelicans were in late incubation–early hatching stages. Active nests were counted using aerial photography or ground counts from within colonies except at Yellowstone Lake where censuses were made from a boat 31–61 m from shore.

In 1984 juvenile White Pelicans present on the nesting island at Pathfinder Reservoir were counted before fledging when they were banded with U.S. Fish and Wildlife Service numbered aluminum bands. Numbers of ready-to-fledge young were determined at Pathfinder Reservoir using ground or aerial photography in 1985 and 1986, respectively. Each year a thorough search was made of the nesting island to locate juvenile pelicans that died before fledging. The number of dead young found was then subtracted from previous counts of prefledged young to calculate nesting success.

At Yellowstone Lake juvenile White Pelicans were censused from a boat 31–61 m from the nesting islands. Because no attempt was made to determine prefledgling mortality, nesting success is probably overestimated each year at Yellowstone Lake. Nest and fledgling censuses were made by the authors except as otherwise noted.

As discussed by Buckley and Buckley

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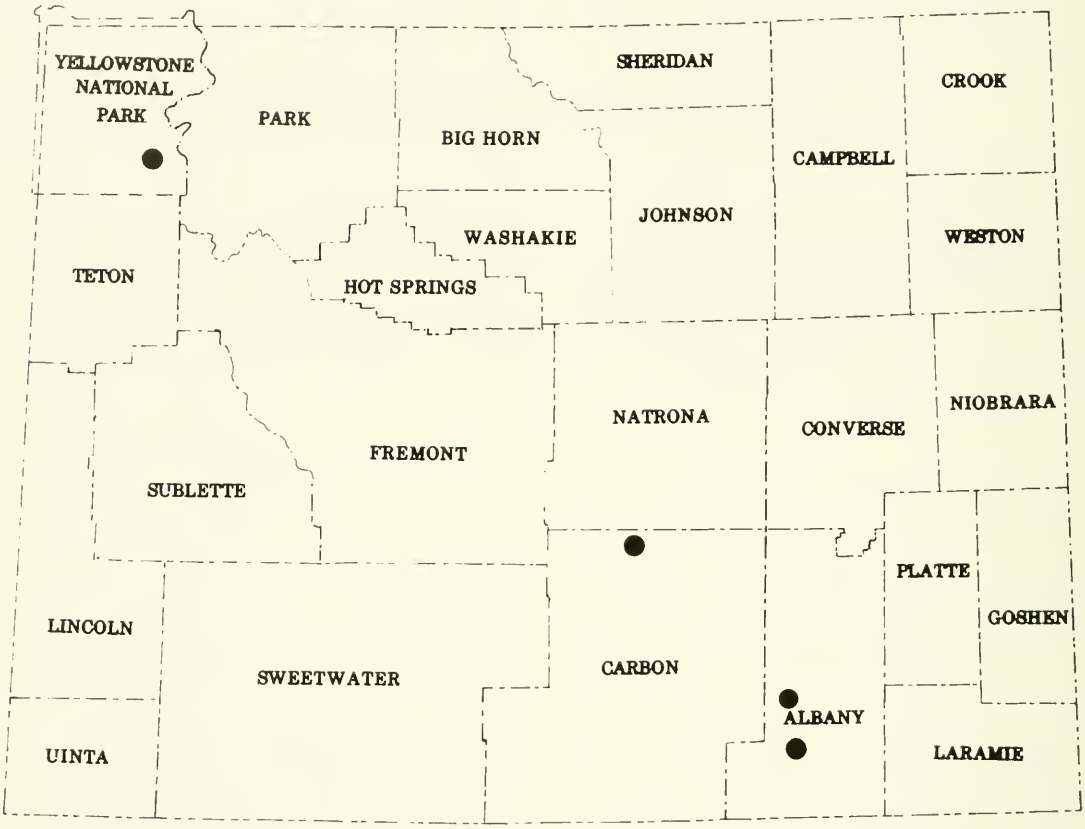

Fig. 1. Distribution of American White Pelican nesting areas in Wyoming, 1986.

(1979), a waterbird colony is difficult to define. For the purposes of this report we defined a colony as an assemblage of nesting birds (Kushlan 1986). One exception was at Yellowstone Lake where the two adjacent Molly Islands White Pelican colonies were treated as one colony.

RESULTS

American White Pelicans nested at four known locations in Wyoming during the 1984–1986 period (Fig. 1). Based on the 1986 colony censuses, we estimated the number of active nests in the state to be 949 (Table 1). Breeding colonies ranged in size from 41 to 624 active nests. At Pathfinder Reservoir, compared to the counts of the previous year, the number of active White Pelican nests increased by 57% and 63% in 1985 and 1986, respectively. In contrast, the number of active pelican nests at Yellowstone Lake remained relatively stable in 1984 and 1985 but declined by approximately 86% in 1986. Population trends are unknown for the Bamforth and Cooper lake colonies.

Nesting success at each colony is presented in Table 2. Between 1984 and 1986, from 0.78 to 0.93 juvenile White Pelicans fledged per nesting attempt at Pathfinder Reservoir. At Yellowstone Lake maximum estimated production varied from 0.32 to 2.25 young per nest during this period. No young were produced at the Bamforth and Cooper lake colonies in 1986.

DISCUSSION

In the most recent survey of American White Pelican nesting colonies, Sidle et al. (1985) concluded that breeding populations were currently stable or increasing in most areas of North America. Information gathered on White Pelican nesting colonies from 1984 through 1986 suggests that White Pelicans are increasing in Wyoming. However, population

TABLE 1. Location, number of active nests, and habitat of American White Pelican colonies in Wyoming, 1984–1986.

Colony site	Location	Number of active nests 1984	1985	1986	Habitat
Albany County					
Bamforth Lake (Peninsula Island)	41°24′N, 105°44′W	0	0	63[1]	Lake
Cooper Lake[2]	41°38′N, 105°51′W	—	—	221	Lake
Carbon County					
Pathfinder Reservoir (Bird Island)	42°23′N, 106°56′W	245	384	624	Reservoir
Yellowstone National Park					
Yellowstone Lake (Molly Islands)	44°19′N, 110°16′W	317	284	41	Lake

[1]Data from B. H. Pugesek (personal communication).
[2]Not surveyed for nesting pelicans in 1984 and 1985.

TABLE 2. Nesting success of American White Pelican breeding colonies in Wyoming, 1984–1986.

Colony site	Number of young fledged 1984	1985	1986
Albany County			
Bamforth Lake (Peninsula Island)	0	0	0
Cooper Lake	—	—	0
Carbon County			
Pathfinder Reservoir (Bird Island)	203 (0.83)[1]	300 (0.78)	583 (0.93)
Yellowstone National Park[2]			
Yellowstone Lake (Molly Islands)	482 (1.52)	650 (2.25)	13 (0.32)

[1]Number of juvenile White Pelicans fledged per nesting attempt.
[2]Reproductive success is probably overestimated each year.

growth may be partially attributed to more extensive surveys in recent years. Before 1981 only limited effort was made in Wyoming to locate White Pelican or other colonially nesting waterbird breeding sites.

Strait and Sloan (1974) determined from band-recovery data and reproductive success studies that a fledging rate of slightly less than one young per nest was probably required for population stability in White Pelicans. Although White Pelican reproductive success at Pathfinder Reservoir from 1984 through 1986 appeared to be sufficient for population maintenance, long-term population stability needs to be determined over a period of several years.

At Yellowstone Lake the number of juvenile White Pelicans fledged in 1984 and 1985 exceeded the number required for population maintenance but was inadequate in 1986. Poor nesting success in 1986 was attributed to an extremely high snowmelt runoff in northwestern Wyoming, which caused high water levels in Yellowstone Lake. As a result, the Molly Islands nesting area was almost completely inundated during much of the nesting season.

All White Pelican nests at Cooper Lake were destroyed by coyotes (*Canis latrans*) and possibly other predators in 1986. White Pelicans were nesting on the mainland, which made their nests extremely vulnerable to mammalian predators, including coyotes (Bunnell et al. 1981). Although it is not known when the Cooper Lake colony was initiated, White Pelicans may have started nesting there a few years before the colony's discovery in 1986. In the early 1980s high water levels existed at Cooper Lake, and the nesting site used in 1986 was probably an island.

Golden Eagles (*Aquila chrysaetos*), observed harassing White Pelicans nesting at

Bamforth Lake, were thought to be responsible for the nesting failure in 1986 (B. H. Pugesek, personal communication). On three occasions one Golden Eagle was observed in the colony, causing pelicans to flush from their nests. Eggs in unguarded nests were then robbed by California Gulls (*Larus californicus*) nesting among the pelicans; eventually all nests were destroyed or abandoned. Other than the pelican nesting attempt reported at Bamforth Lake in 1986, we have found no evidence of White Pelicans breeding there during surveys conducted since the 1950s.

Although White Pelicans have nested at four locations in Wyoming since 1984, only the Yellowstone Lake colony is reasonably secure and effectively protected. The Yellowstone Lake nesting area has existed since at least 1890 (Linton 1891, Diem and Condon 1967). In Yellowstone National Park, the National Park Service has closed a portion of the Southeast Arm of Yellowstone Lake to all motorboat traffic, thus reducing human disturbance of nesting White Pelicans. Other measures implemented by the Park Service to protect pelicans have included restrictions on scientific investigations and the establishment of a 400-m buffer zone around the nesting islands. Currently one possible threat to the White Pelican breeding population on the Molly Islands may be loss of nesting habitat. Periodic substrate uplifts occurring along the north shore of Yellowstone Lake have significantly raised and lowered the stable water level of the Southeast Arm of the lake where the Molly Islands are located.

We are encouraged by the establishment of the Pathfinder colony and population growth of White Pelicans documented there, but we view these findings with guarded optimism. The White Pelican breeding population at Pathfinder Reservoir is currently threatened by human disturbance, intentional and accidental, of nesting birds. Other serious threats include erosion of the nesting island, formation of a land bridge between the nesting island and mainland during low reservoir water levels, and loss of foraging habitat (Findholt 1987).

Breeding populations of American White Pelicans have declined dramatically in North America. Historically, at least 24 pelican colonies existed west of the Rocky Mountains; now there are only 8 (Anonymous 1983). Current surveys indicate that fewer than 20 breeding locations may be present in the entire United States (Sidle et al. 1985). Due to the limited number of breeding localities, the White Pelican (western population) has been identified as a "sensitive species" by the U.S. Fish and Wildlife Service (Anonymous 1985). Sensitive species are defined as

> vulnerable or declining species, subspecies, or distinct populations that could become Federally listed as endangered or threatened in the foreseeable future, throughout all or in a significant portion of their ranges, without active management or removal of threats.

In Wyoming there is no official state list of threatened and endangered species. The Wyoming Game and Fish Department currently classifies the American White Pelican as a "Priority I" species, which means that it needs immediate attention and active management to insure that extirpation or a significant decline in the breeding population in Wyoming does not occur (Anonymous 1987). We hope that natural resource management agencies in Wyoming will take the appropriate measures necessary to ensure the protection and long-term maintenance of White Pelican nesting colonies in the state.

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LITERATURE CITED

ANONYMOUS. 1983. Guidelines for the management of the White Pelican, western population. U.S. Fish and Wildlife Service, Portland, Oregon.

———. 1985. Sensitive bird species. U.S. Fish and Wildlife Service, Portland, Oregon.

———. 1987. Nongame bird and mammal strategic plan. Wyoming Game and Fish Dept., Cheyenne.

BUCKLEY, P. A., AND F. G. BUCKLEY. 1979. What constitutes a waterbird colony? Reflections from the northeastern U.S. Colonial Waterbirds 3: 1–15.

BUNNELL, F. L., D. DUNBAR, L. KOZA, AND G. RYDER. 1981. Effects of disturbance on the productivity and numbers of White Pelicans in British Columbia—observations and models. Colonial Waterbirds 4: 2–11.

DIEM, K. L. 1979. White Pelican reproductive failures in the Molly Islands breeding colony in Yellowstone National Park. Proc. Research in National Parks Symposium. U.S. National Park Service Transactions and Proceedings. Sec. No. 5: 489–496.

DIEM, K. L., AND D. D. CONDON. 1967. Banding studies of waterbirds on the Molly Islands, Yellowstone Lake, Wyoming. Yellowstone Library and Museum Assoc., Yellowstone National Park, Wyoming.

FINDHOLT, S. L. 1986. New American White Pelican nesting colony in Wyoming. Western Birds 17: 136–138.

_____. 1987. Population status, reproductive success, food habits, foraging areas, prey availability, movements, and some management considerations of American White Pelicans nesting at Pathfinder Reservoir, Wyoming. Nongame Special Report. Wyoming Game and Fish Dept., Cheyenne.

KNIGHT, W. C. 1902. The birds of Wyoming. Univ. Wyoming Agric. Expt. Sta. Bull. No. 55.

KUSHLAN, J. A. 1986. Colonies, sites, and surveys: the terminology of colonial waterbird studies. Colonial Waterbirds 9: 119–120.

LINTON, E. 1891. A contribution to the life history of *Dibothrium cordiceps* Leidy, a parasite infesting the trout of Yellowstone Lake. Bull. U.S. Fish Comm. 9(1889): 337–358.

MCCREARY, O. 1939. Wyoming bird life. Burgess Publ. Co., Minneapolis.

SCHALLER, G. B. 1964. Breeding behavior of the White Pelican at Yellowstone Lake, Wyoming. Condor 66: 3–23.

SIDLE, J. G., W. H. KOONZ, AND K. RONEY. 1985. Status of the American White Pelican: an update. Amer. Birds 39: 859–864.

STRAIT, L. E., AND N. F. SLOAN. 1974. Life table analysis for the White Pelican. Inland Bird Banding News 46: 20–28.

CURRENT STATUS AND DISTRIBUTION OF THE CICONIIFORMS NESTING IN WYOMING

Scott L. Findholt[1,2] and Kevin L. Berner[1,3]

ABSTRACT —Five species of Ciconiiforms breed in Wyoming: the American Bittern (*Botaurus lentiginosus*), Great Blue Heron (*Ardea herodias*), Snowy Egret (*Egretta thula*), Black-crowned Night-Heron (*Nycticorax nycticorax*), and White-faced Ibis (*Plegadis chihi*). Field surveys conducted from 1984 through 1986 indicate that at least 151 Great Blue Heron colony sites exist in Wyoming, making it the most abundant and widespread Ciconiiform in the state. Only small breeding populations have been discovered for the remaining species. Except for the Snowy Egret, where numbers of active nests have remained relatively stable, population trends are unknown for the other species. We believe most colonies have been found in Wyoming, but additional inventories may result in the discovery of other nesting areas, especially for the Great Blue Heron.

From 1981 through 1983 the first comprehensive statewide survey for breeding locations of Ciconiiforms in Wyoming was conducted by Findholt (1984), mostly by a review of historical and recent published and unpublished reports; through correspondence with professional biologists, amateur bird-watchers, and others considered knowledgeable of colony sites; and through a request in a newspaper article for information on Great Blue Heron (*Ardea herodias*) colonies. This survey was based on limited field inventories. Since 1983, however, intensive field surveys have been made for breeding sites of colonially nesting waterbirds. Our purpose is to provide information on the distribution and population status of the Ciconiiforms known to nest in Wyoming.

METHODS

Surveys were conducted in Wyoming from 1984 through 1986 to locate new breeding sites of colonially nesting waterbirds, including the Ciconiiforms. From 4 April to 31 May 1984 and from 28 March to 5 June 1986, 15 aerial searches in fixed-wing aircraft totaling 67.1 hrs of flight time were made to locate new nesting areas. Reservoirs, lakes, marshes, and other potential breeding locations not observed during aerial surveys were checked from the ground with binoculars or a 20-45X spotting scope.

In most colonies active nests were counted when birds were in late incubation or early hatching stages. The majority of colonies were censused by making ground counts of nests during a single visit to each colony. Where ground counts were not feasible, we estimated the number of nests (ground estimates) or used counts of nests made during aerial surveys.

In some Great Blue Heron colonies we marked the position of all nests on a rough map to determine how many nests were active. Also, estimates of active nests in a few very large Great Blue Heron colonies were made by noting the status (active or inactive) of at least 75% of the nests there. From these sampling results, estimates of the total nesting population were extrapolated by entering the colony and counting all nests present.

As discussed by Buckley and Buckley (1979), a waterbird colony is difficult to define. For this study we defined a colony as an assemblage of nesting birds (Kushlan 1986). In addition, Great Blue Heron nests were not considered as separate colonies unless they were at least 200 m from the main breeding group. Nests were classified as active if birds were sitting or standing on nest platforms, if incubation was observed, or if eggs or young were present (McCrimmon 1982).

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TABLE 1. Location, number of nests, and habitat of Snowy Egret colonies in Wyoming, 1984–1986.[a]

Colony name	Location	Number of active nests 1984	1985	1986	Habitat
Albany County					
Bamforth Lake	41°24′N, 105°44′W				Lake
(Bamforth Island)		0	0	16	
(Peninsula Island)		7	0	0	
Carroll Lake	41°25′N, 105°44′W	NC[b]	15	0	Lake
Fremont County					
Sand Mesa WHMU	43°19′N, 108°20′W	1	0	0	Reservoir
Natrona County					
Soda Lake					Reservoir
(East Island)	42°54′N, 106°18′W	0	2	0	
(West Island)	42°54′N, 106°19′W	2	3	0	
(Man-made Island)	42°54′N, 106°18′W	1	1	3	
Sweetwater County					
Old Eden Reservoir	42°13′N, 109°23′W	NC	0	1–2[c]	Reservoir

[a]All colonies were censused by making total ground counts of nests except as otherwise noted.
[b]NC not censused.
[c]Nests not actually located but suspected of being present.

RESULTS AND DISCUSSION

American Bittern

Other than the apparently large breeding population of American Bitterns (*Botaurus lentiginosus*) in marshes adjacent to the Bear River in Lincoln and Uinta counties, this species has been documented as nesting at few locations in Wyoming (Findholt 1984). Since 1983 one additional breeding area has been found. On 19 June 1986 we located one nest containing four eggs at Caldwell Lake, about 23 km southwest of Laramie, Albany County. Because accurate counts of American Bitterns nesting in Wyoming have not been made, population trends are unknown. Most available habitat for American Bitterns has been surveyed; therefore, probably few new nesting areas will be located.

Great Blue Heron

The Great Blue Heron (*Ardea herodias*) was the most widespread and abundant Ciconiiform in Wyoming (Appendix). During 1984 and 1986 we documented 151 heronries, which is a 148% increase in known heronries since 1983 when Findholt (1984) reported 61 colony sites. Assuming that heronries censused in 1984 contained the same number of active nests in 1986, at least 1,929 nesting pairs of Great Blue Herons occur in Wyoming. Although widespread in the state, most colonies occurred in the Bighorn, Green, North Platte, Powder, and Wind river drainages. Twenty-five (17%) heronries occur in the North Platte River drainage, which is the greatest concentration of colonies in the state. Of 147 (97%) known heronries censused in 1984 or 1986, the mean number of active nests was 13.1 ± 1.9 (SE, extreme values 0–150). Excluding 34 (23%) heronries that were inactive, the mean number of active nests for 113 heronries was 17.1 ± 2.4 (SE, extreme values 1–150). Of these, 3 (3%) contained 89 or more occupied nests, 23 (20%) contained from 22 to 70 occupied nests, and the remaining 87 (77%) contained 20 or fewer occupied nests.

Of 34 heronries inactive during recent surveys, at least 4 were probably abandoned due to human disturbance, namely: Glendo Reservoir, Converse County, (human recreational activity); Boulder, Sublette County, and Crazy Woman Creek, Johnson County, (trailer houses placed too close to colonies); Afton, Lincoln County, 15 adults were shot, but nesting resumed in 1985). We are uncertain why the remaining 30 colonies were inactive in 1984 or 1986.

Population trends cannot be assessed because most heronries have been censused only once. Although the majority of Great Blue Heron colonies in Wyoming have undoubtedly been located, a few additional colonies may be discovered through future surveys.

TABLE 2. Location, number of nests, and habitat of Black-crowned Night-Heron colonies in Wyoming, 1984–1986.[a]

Colony name	Location	Number of active nests 1984	1985	1986	Habitat
Albany County					
Bamforth Lake	41°24′N, 105°44′W				Lake
(Bamforth Island)		1	0	23	
Caldwell Lake	41°09′N, 105°48′W	NC[b]	NC	48	Lake
Carroll Lake	41°25′N, 105°44′W	NC	125	41	Lake
Hutton Lake NWR	41°11′N, 105°44′W	0	0	0	Marsh
Kay Ranch	41°15′N, 105°42′W	16	19	4	Marsh
Pilger Lake	41°23′N, 105°50′W	NC	NC	9	Lake
Webb Lake	41°21′N, 105°59′W	NC	NC	28	Lake
Carbon County					
Rouse Reservoir	41°13′N, 106°39′W	NC	NC	5–7[c]	Reservoir
Lincoln County					
Bear River	42°01′N, 110°58′W	0	0	2	Marsh
Natrona County					
Soda Lake					Reservoir
(East Island)	42°54′N, 106°18′W	1	1	2	
(West Island)	42°54′N, 106°19′W	3	2	1	
(Man-made Island)	42°54′N, 106°18′W	0	0	5	
Sweetwater County					
Old Eden Rerservoir	42°13′N, 109°23′W	NC	40–50[c]	54	Reservoir

[a]All colonies were censused by making total ground counts of nests except as otherwise noted.
[b]NC = not censused.
[c]Estimate (ground) of active nests present.

Snowy Egret

Seven active Snowy Egret (*Egretta thula*) colonies were present at four locations in Wyoming during the 1984–1986 period (Table 1). However, not all colonies were active each year. The Carroll Lake colony was the only new nesting area discovered during our recent surveys. Based on the 1986 censuses, we estimated that the number of active nests in the state was 19. Although nests were not discovered at Old Eden Reservoir, one or two pairs were suspected of breeding there. Snowy Egrets have not been found nesting at Sand Mesa Wildlife Habitat Management Unit (WHMU) since 1984, when the colony was destroyed by humans. Small numbers of Snowy Egrets continued to nest at Soda Lake. Man-made Island was not used for nesting until 1984 because it was developed after the 1983 breeding season. In 1986 all Snowy Egrets nested on Man-made Island probably because nesting habitat had deteriorated on East and West islands. In 1985, 15 active nests existed at Carroll Lake, but none were present in 1986 probably because of low water levels. However, in 1986, 16 active nests were present at Bamforth Lake, only 2 km away. It appears that this species breeds at either Bamforth Lake or Carroll Lake, depending on existing nesting conditions.

In 1983 Snowy Egrets in Wyoming nested at three locations consisting of three colonies and 22 active nests (Findholt 1984). Since 1983, except for a possible decline in active nests in 1984, the Snowy Egret breeding population has remained relatively stable. Although it is possible that very small colonies or solitary nesting pairs may have been overlooked during recent surveys, it seems unlikely that any large colonies were missed.

Black-crowned Night-Heron

Twelve colonies of the Black-crowned Night-Heron (*Nycticorax nycticorax*) existed in Wyoming at 10 locations in 1986 (Table 2). Based on the 1986 censuses, we have calculated that approximately 222–224 active nests were present. This compares to 20 active nests in five colonies at four locations in 1983 (Findholt 1984). The increase in the breeding population was primarily a consequence of locating seven additional nesting areas during recent surveys. Although one new colony each was discovered in the Bear, Green, and North Platte river drainages, most were found

TABLE 3. Location, number of nests, and habitat of White-faced Ibis colonies in Wyoming, 1984–1986.[a]

Colony name	Location	Number of active nests			Habitat
		1984	1985	1986	
Albany County					
Caldwell Lake	41°09′N, 105°48′W	NC[b]	NC	19	Lake
Hutton Lake NWR	41°11′N, 105°44′W	0	0	0	Marsh
Lincoln County					
Bear River	42°01′N, 110°58′W	0	0	1	Marsh
Bear River	42°01′N, 110°58′W	0	0	32	Marsh
Sweetwater County					
Old Eden Reservoir	42°13′N, 109°23′W	NC	0	14(15–20)[c]	Reservoir

[a]All colonies were censused by making total ground counts of nests except as otherwise noted.
[b]NC not censused.
[c]Estimate (ground) of active nests present.

in the Laramie River drainage near Laramie, Albany County.

Night-herons failed to breed at Hutton Lake National Wildlife Refuge (NWR) during the 1984–1986 period, most likely because of poor nesting conditions resulting from excessively high or low water levels. In 1986 low water levels appeared to contribute to a decline in active nests at both Carroll Lake and the Kay Ranch. Compared to previous years, Bamforth Lake supported an unusually large nesting population in 1986. It appears that Bamforth Lake is an alternate nesting site utilized by night-herons when nesting conditions are unsuitable at nearby Carroll Lake. Four to eight pairs nested at Soda Lake from 1984 through 1986. Night-herons initiated nesting on Man-made Island in 1986, two years after the island was developed. Most night-herons at Soda Lake will probably nest on Man-made Island in the future as nesting substrate disappears on East and West islands. Rouse Reservoir probably will not be used by night-herons in the future because the reservoir drained in 1986 after the dam collapsed.

Population trends of Black-crowned Night-Herons are difficult to assess because of the large number of new colonies discovered since 1984. Although most potential night-heron nesting habitat has been surveyed in Wyoming, small breeding populations may have been overlooked.

White-faced Ibis

In 1986 White-faced Ibis (*Plegadis chihi*) nested in Wyoming at three locations consisting of four different colonies (Table 3). This was the first year since 1982 that ibis have been documented as breeding in the state. In 1982 two White-faced Ibis nests existed at Hutton Lake NWR, and 40 nests were in the marshes adjacent to the Bear River, south of Cokeville, Lincoln County (Findholt 1984). During our recent surveys White-faced Ibis were not discovered nesting at Hutton Lake NWR. However, two colonies were located in marshes associated with the Bear River in the vicinity of the site where they nested in 1982. This species may not have nested along the Bear River in 1984 and 1985 and at Hutton Lake NWR during the 1984–1986 period because of poor nesting conditions brought on by excessively high or low water levels. In 1986 previously unknown colonies were found at Caldwell Lake and Old Eden Reservoir. Old Eden Reservoir did not contain nesting ibis in 1985. It is unknown whether colonies were present here before 1985 or at Caldwell Lake before 1986 because these areas were not surveyed.

Population trends are unknown for White-faced Ibis in Wyoming because of the new colonies located in 1986. It seems doubtful that any White-faced Ibis colonies were overlooked during our recent surveys.

CONCLUSIONS

Much interest and concern exist with the conservation and management of the Ciconiiforms in the United States and elsewhere. These species occupy high trophic levels on aquatic food chains and are probably sensitive to disturbance of aquatic ecosystems, especially loss of wetland habitat and contamination by chemical pollutants. In addition, because most of these species nest in colonies,

they are vulnerable to human intervention. We hope that natural resource management agencies will develop long-term monitoring programs to determine population trends and implement appropriate management strategies to ensure that current breeding populations of the Ciconiiforms are maintained in Wyoming.

ACKNOWLEDGMENTS

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LITERATURE CITED

BUCKLEY, P. A. AND F. G. BUCKLEY. 1979. What constitutes a waterbird colony? Reflections from the northeastern U.S. Colonial Waterbirds 3: 1–15.

FINDHOLT, S. L. 1984. Status and distribution of herons, egrets, ibises, and related species in Wyoming. Colonial Waterbirds 7: 55–62.

KUSHLAN, J. A. 1986. Commentary. Colonies, sites, and surveys: the terminology of colonial waterbird studies. Colonial Waterbirds 9: 119–120.

MCCRIMMON, D. A., JR. 1982. Populations of the Great Blue Heron (*Ardea herodias*) in New York State from 1964 to 1981. Colonial Waterbirds 5: 87–95.

APPENDIX. Location, number of nests, and habitat of Great Blue Heron colonies in Wyoming, 1984–1986.[a]

Colony name	Location	Number of nests: Active	Number of nests: Inactive	Date censused	Habitat
Albany County					
Lake Hattie	41°14′N, 105°58′W	8[b]	0	5 June 1986	Reservoir
Laramie River (east)	41°09′N, 105°51′W	20–25[b]		22 April 1986	Riparian woodland
Laramie River (west)	41°10′N, 105°49′W	8–12[b]		22 April 1986	Riparian woodland
Pioneer Canal (north)	41°14′N, 105°51′W	11	4	23 May 1984	Riparian woodland
Pioneer Canal (south)	41°13′N, 105°51′W	9	1	23 May 1984	Riparian woodland
Twin Buttes Lake	41°14′N, 105°51′W	5	1	3 May 1984	Reservoir
Big Horn County					
Big Horn Lake	44°52′N, 108°13′W	7	0	5 July 1984	Riparian woodland
Big Horn River (north)	44°47′N, 108°10′W	0	70	30 April 1984	Riparian woodland
Byron	44°48′N, 108°27′W	70	11	13 April 1984	Riparian woodland
Manderson (north)	44°19′N, 108°01′W	5	0	30 April 1984	Riparian woodland
Manderson (south)	44°18′N, 108°00′W	0	5	12 April 1984	Riparian woodland
Nowood Creek (north)	44°11′N, 107°42′W	14	4	12 April 1984	Riparian woodland
Nowood Creek (south)	44°11′N, 107°42′W	0	11	12 April 1984	Riparian woodland
Nowood Creek	44°11′N, 107°42′W	0	6	12 April 1984	Riparian woodland
Shell Creek (lower)	44°32′N, 107°57′W	1[b]	0	28 March 1986	Riparian woodland
Shell Creek (upper)	44°33′N, 107°51′W	3[b]	0	28 March 1986	Riparian woodland
Wardel Reservoir	44°21′N, 108°19′W	4	8	30 April 1984	Reservoir
Yellowtail WHMU	44°52′N, 108°16′W	8	35	30 April 1984	Riparian woodland
Campbell County					
Avery Ranch	44°48′N, 105°23′W	6	0	15 April 1986	Riparian woodland
Bow and Arrow Ranch	44°58′N, 105°56′W	0	9	24 April 1984	Riparian woodland
Little Powder River (reservoir)	44°27′N, 105°29′W	5[b]	0	8 April 1986	Reservoir
Little Powder River (south)	44°51′N, 105°21′W	0	3	16 April 1986	Riparian woodland
Piney	44°05′N, 105°14′W	1	1	17 April 1984	Riparian woodland
Trail Creek	44°58′N, 105°20′W	5	3	16 April 1986	Riparian woodland
Weston (north)	44°45′N, 105°22′W	0	3	15 April 1986	Riparian woodland
Weston	44°38′N, 105°18′W	4	8	16 April 1986	Riparian woodland
Carbon County					
Beaver Creek (north)	41°11′N, 106°37′W	1	3	2 May 1984	Riparian woodland
Beaver Creek (south)	41°11′N, 106°37′W	0	3	2 May 1984	Riparian woodland
Bennett Peak	41°16′N, 106°40′W	2	4	23 May 1984	Riparian woodland
Little Snake River	41°01′N, 107°25′W	6	0	31 May 1984	Riparian woodland
Mill Iron Ranches	41°25′N, 106°46′W	68	26	2 May 1984	Riparian woodland
Pathfinder Reservoir	42°23′N, 106°56′W	38	5	15 June 1984	Reservoir
Rattlesnake Butte	41°48′N, 107°00′W	0	12	24 May 1984	Riparian woodland
Rouse Reservoir	41°13′N, 106°39′W	30	8	11 June 1986	Reservoir
Savery Creek	41°04′N, 107°24′W	5	9	31 May 1984	Riparian woodland
Sheep Mountain	41°30′N, 106°50′W	0	20	24 May 1984	Riparian woodland

Appendix continued.

Colony name	Location	Number of nests Active	Inactive	Date censused	Habitat
Converse County					
Ferris Ranch	42°38′N, 105°07′W	150[c]	25	19 April 1984	Riparian woodland
Fetterman	42°51′N, 105°33′W	6	4	19 April 1984	Riparian woodland
Glendo Reservoir	42°37′N, 105°06′W	0	16	19 April 1984	Riparian woodland
Morton	42°49′N, 105°26′W	28	1	19 April 1984	Riparian woodland
Upper Glendo Reservoir	42°35′N, 105°02′W	45–50[b]		6 May 1986	Upland coniferous forest
Valentine Ranch	42°51′N, 106°00′W	35	42	19 April 1984	Riparian woodland
Crook County					
Alzada	44°59′N, 104°28′W	3[b]	0	8 April 1986	Reservoir
Bush Creek Reservoir	44°52′N, 104°48′W	32	6	7 June 1984	Reservoir
Crow Creek Reservoir	44°53′N, 104°07′W	6	8	18 June 1986	Reservoir
Hulett	44°38′N, 104°39′W	3–4[b]		8 April 1986	Riparian woodland
Keyhole Reservoir Dam	44°24′N, 104°46′W	10–15[b]		8 April 1986	Riparian woodland
Little Missouri River (north)	44°53′N, 104°48′W	8	8	7 June 1984	Reservoir
Moorcroft (north)	44°20′N, 104°56′W	14	5	24 April 1984	Riparian woodland
Moorcroft (south)	44°19′N, 104°57′W	5	0	17 April 1984	Riparian woodland
Oak Creek Reservoir (east)	44°45′N, 104°06′W	8	3	18 June 1986	Reservoir
Oak Creek Reservoir (west)	44°45′N, 104°06′W	5	1	18 June 1986	Reservoir
Spring Creek	44°22′N, 104°34′W	NC[d]			Upland coniferous forest
Fremont County					
Arapaho	42°58′N, 108°27′W	14	15	6 May 1984	Riparian woodland
Ethete	43°02′N, 108°49′W	23	3	13 May 1984	Riparian woodland
Givens Ranch (east)	43°00′N, 108°39′W	9	2	13 May 1984	Riparian woodland
Givens Ranch	43°00′N, 108°39′W	8	4	13 May 1984	Riparian woodland
Lander	42°52′N, 108°38′W	37	22	10 April 1984	Riparian woodland
Lenore	43°20′N, 109°10′W	9	2	19 May 1984	Riparian woodland
Morton	43°10′N, 108°45′W	7	1	14 May 1984	Riparian woodland
Muddy Creek (east)	43°17′N, 108°19′W	2	0	19 May 1986	Riparian woodland
Muddy Creek (west)	43°18′N, 108°22′W	0	4	19 May 1986	Riparian woodland
Muddy Creek	43°18′N, 108°22′W	12	7	12 May 1984	Riparian woodland
Neble Hill	43°07′N, 108°15′W	4	2	13 May 1984	Riparian woodland
Riverton	43°08′N, 108°12′W	2	1	13 May 1984	Riparian woodland
Shotgun Butte	43°26′N, 108°44′W	3	0	19 May 1986	Riparian woodland
Wind River	43°06′N, 108°39′W	0	5	14 May 1984	Riparian woodland
Yellowstone Ranch	42°40′N, 108°19′W	13	2	20 June 1984	Riparian woodland
Goshen County					
Hawk Springs Reservoir	41°42′N, 104°11′W	NC		19 June 1986	Reservoir
Rawhide	42°06′N, 104°20′W	45	6	3 May 1984	Riparian woodland
Whalen Diversion Dam	42°15′N, 104°38′W	89	17	3 May 1984	Riparian woodland
Hot Springs County					
Kirby	43°47′N, 108°10′W	0	13	30 April 1984	Riparian woodland
Owl Creek (north)	43°44′N, 108°33′W	12	2	19 April 1986	Riparian woodland
Owl Creek (south)	43°43′N, 108°40′W	0	4	19 April 1986	Riparian woodland
Johnson County					
Clear Creek	44°32′N, 106°32′W	0		15 April 1986	Riparian woodland
Crazy Woman Creek (old)	44°06′N, 106°31′W	0	8	4 June 1984	Riparian woodland
Crazy Woman Creek (new)	44°04′N, 106°36′W	7	8	15 April 1986	Riparian woodland
Kaycee I	43°40′N, 106°45′W	4	1	1 May 1984	Riparian woodland
Kaycee II	43°40′N, 106°46′W	7	0	1 May 1984	Riparian woodland
Linch	43°42′N, 106°20′W	4	5	4 June 1984	Riparian woodland
Powder River (North Fork)	43°47′N, 106°45′W	0	2	1 May 1984	Reservoir
Shell Creek	44°30′N, 106°47′W	12	2	5 June 1984	Riparian woodland
Lincoln County					
Afton	42°44′N, 110°58′W	0	18	16 May 1984	Upland deciduous forest
Border	42°11′N, 111°02′W	39	7	16 May 1984	Riparian woodland
Cokeville	42°06′N, 110°57′W	8	5	16 May 1984	Riparian woodland
Diamondville	41°45′N, 110°29′W	11	2	15 May 1986	Riparian woodland
Kemmerer Reservoir	41°53′N, 110°37′W	14	4	23 May 1986	Riparian woodland
Marse	42°09′N, 111°00′W	0	21	16 May 1984	Riparian woodland
Names Hill	42°10′N, 110°11′W	36	15	9 May 1984	Riparian woodland
Opal	41°46′N, 110°18′W	0	14	16 May 1984	Riparian woodland

Appendix continued.

Colony name	Location	Number of nests Active	Inactive	Date censused	Habitat
Natrona County					
Bates Creek (lower)	42°40′N, 106°34′W	0	7	16 April 1984	Riparian woodland
Bates Creek (upper)	42°34′N, 106°23′W	37	6	18 April 1984	Riparian woodland
Bates Creek	42°39′N, 106°27′W	1	0	18 April 1984	Riparian woodland
Strand Ranch	42°52′N, 106°07′W	5	6	19 April 1984	Riparian woodland
Niobrara County					
Manville	42°54′N, 104°44′W	7	0	14 June 1984	Reservoir
Park County					
Bobcat Ranch	44°16′N, 109°30′W	2	9	19 July 1984	Riparian woodland
T E Ranch	44°16′N, 109°29′W	0	7	19 July 1984	Riparian woodland
Valley	44°11′N, 109°35′W	NC			Riparian woodland
Platte County					
Guernsey Reservoir	42°20′N, 104°50′W	5	3	13 June 1984	Reservoir
Uva	42°08′N, 104°54′W	70[a]	20	13 June 1984	Riparian woodland
Wendover	42°24′N, 104°56′W	15	20	19 April 1984	Riparian woodland
Sheridan County					
Arvada I	44°37′N, 106°05′W	2	0	4 July 1984	Riparian woodland
Arvada II	44°37′N, 106°05′W	3[b]	0	15 April 1986	Riparian woodland
Clear Creek	44°51′N, 106°06′W	6	7	6 June 1984	Upland deciduous forest
Clearmont	44°42′N, 106°19′W	0	3	15 April 1986	Riparian woodland
Goose Creek	44°51′N, 106°58′W	22	4	1 May 1984	Riparian woodland
Leiter	44°44′N, 106°16′W	1	1	15 April 1986	Riparian woodland
Parkman	44°57′N, 107°17′W	0	15	5 June 1984	Reservoir
Powder River (south)	44°47′N, 106°05′W	0	3	6 June 1984	Riparian woodland
Powder River	44°50′N, 106°04′W	0	7	6 June 1984	Riparian woodland
Ranchester	44°57′N, 107°16′W	0	1	23 April 1984	Reservoir
Story	44°34′N, 106°54′W	1	0	2 July 1986	Upland coniferous forest
Tongue River	44°54′N, 107°07′W	42	11	23 April 1984	Riparian woodland
Ucross	44°34′N, 106°35′W	69	12	23 April 1984	Upland deciduous forest
Sublette County					
Boulder	42°46′N, 109°45′W	0	15	7 May 1984	Riparian woodland
Circle Cattle Company	42°37′N, 109°57′W	43	28	8 May 1984	Riparian woodland
Cottonwood Creek	42°41′N, 109°59′W	6	31	8 May 1984	Riparian woodland
Daniel (east)	42°54′N, 110°08′W	7	32	9 May 1984	Riparian woodland
Daniel (west)	42°57′N, 110°08′W	5	17	9 May 1984	Riparian shrub
Daniel	42°53′N, 110°02′W	3	56	7 May 1984	Riparian woodland
Fear Ranch	42°26′N, 110°06′W	0	18	8 May 1984	Riparian woodland
Five-mile Bridge	42°30′N, 110°04′W	0	11	15 April 1986	Riparian woodland
Hoback River	43°14′N, 110°27′W	11	3	27 May 1984	Upland coniferous forest
Horse Creek	42°56′N, 110°14′W	4	0	15 May 1984	Riparian shrub
New Fork River	42°40′N, 109°48′W	0	28	8 May 1984	Riparian woodland
North Piney Creek	42°37′N, 110°13′W	14	1	9 May 1984	Riparian woodland
South Piney Creek	42°30′N, 110°13′W	7	7	9 May 1984	Riparian shrub
Sweetwater County					
Henrys Fork (east)	41°01′N, 109°42′W	8	45	13 May 1986	Riparian woodland
Henrys Fork (west)	41°03′N, 109°47′W	35	4	13 May 1986	Riparian woodland
Pal Heronry (north)	41°52′N, 109°48′W	50	17	10 May 1984	Riparian woodland
Pal Heronry	41°51′N, 109°47′W	44	15	10 May 1984	Riparian woodland
Teal Island	41°58′N, 110°00′W	16	3	10 May 1984	Riparian woodland
Teton County					
Blacktail Ponds	43°41′N, 110°42′W	24	7	26 May 1984	Riparian woodland
Goosewing Creek	43°34′N, 110°18′W	6	4	28 June 1984	Riparian shrub
Moran	43°50′N, 110°31′W	11	0	29 June 1984	Riparian woodland
Oxbow (north)	43°52′N, 110°33′W	10	5	26 May 1984	Riparian woodland
Oxbow (south)	43°52′N, 110°33′W	14	1	26 May 1984	Riparian woodland
Prichard Pond	43°17′N, 110°48′W	7	1	27 May 1984	Riparian woodland
South Park	43°28′N, 110°51′W	150[c]	37	17 May 1984	Riparian woodland
Uinta County					
Evanston I	41°12′N, 110°53′W	2	9	14 May 1986	Riparian woodland
Evanston II	41°12′N, 110°53′W	0	4	14 May 1986	Riparian woodland
Evanston (Substation I)	41°18′N, 111°01′W	2	0	14 May 1986	Riparian woodland

Appendix continued.

Colony name	Location	Number of nests Active	Inactive	Date censused	Habitat
Evanston (Substation II)	41°18′N, 111°00′W	1	1	14 May 1986	Riparian woodland
Millburne	41°13′N, 110°27′W	1	0	13 May 1986	Riparian woodland
Mountain View (east)	41°14′N, 110°26′W	6	1	13 May 1986	Riparian woodland
Mountain View (west)	41°14′N, 110°26′W	4	2	13 May 1986	Riparian woodland
Woodruff Narrows	41°24′N, 111°01′W	0	7	14 May 1986	Riparian woodland
Washakie County					
Kirby II	43°52′N, 108°08′W	5–6[b]		28 March 1986	Riparian woodland
Worland (south)	44°04′N, 107°57′W	11	1	12 April 1984	Riparian woodland
Worland (north)	44°04′N, 107°56′W	1	8	12 April 1984	Riparian woodland
Yellowstone National Park					
Yellowstone Lake					Lake
(Frank Island)	44°25′N, 110°22′W	NC			

[a]All colonies were censused by making total ground counts of nests except as otherwise noted
[b]Estimate (fixed-wing airplane) of active nests present
[c]Estimate (ground) of active nests present.
[d]NC not censused.

FIRST RECORDS OF THE GLAUCOUS-WINGED GULL IN UTAH

David L. Fischer[1]

ABSTRACT.—First occurrences of the Glaucous-winged Gull (*Larus glaucescens*), and hybrids between it and the Western (*L. occidentalis*) and Herring Gull (*L. argentatus*), in Utah are documented. Sightings of 14 individuals over two winters (1984–86) may represent an inland expansion of the winter range of this species.

The Glaucous-winged Gull (*Larus glaucescens*) is a coastal species of western North America that breeds from the southern Bering Sea and southeastern Alaska to northwestern Oregon (A.O.U. 1983). In the southern portion of the breeding range, it hybridizes frequently with the Western Gull (*L. occidentalis*, Hoffman et al. 1978). Hybridization with the Herring Gull (*L. argentatus*) occurs infrequently in south-coastal and southeastern Alaska (Williamson and Peyton 1963, Patten and Weisbrod 1974). In migration and winter, it occurs as far south as Baja California and casually inland in Alberta, Idaho, and western Arizona. Extreme inland records are known from Manitoba and Oklahoma (A.O.U. 1983). In the Mountain West Region as defined by *American Birds* (Colorado, Wyoming, Utah, and Nevada), the species has previously been reported only from southern Nevada (Lake Mead), but it occurs there regularly (H. Kingery, personal communication). This note documents the first occurrences of the Glaucous-winged Gull, and probable hybrids of it and the Western Gull and the Herring Gull, in Utah.

On 20 November 1984, I encountered the Glaucous-winged Gull, a first-winter individual, at a small pond near the Provo City Dump, Utah County, Utah. The bird was perched on a narrow mud bar along with several first-winter Herring Gulls, one first-winter Thayer's Gull (*L. thayeri*), and many of the California (*L. californicus*) and Ring-billed gulls (*L. delawarensis*). It was noticeably paler than the other first-winter gulls, and its wing tips (folded primaries) differed from them in being no darker (essentially the same pale gray color) than the remainder of the wing. The tips of the folded primaries were edged with white (as in first-winter Thayer's), and the upperparts were a very uniform grayish tan. The wing coverts lacked the "marbling" or "scaley" pattern typical of *thayeri* or *argentatus*. It was the largest gull present, and its completely black bill was noticeably thicker and more bulbous toward the tip than that of any of the Herring Gulls. In flight its greater size and stockier build relative to the Herring Gull were even more apparent. The underside of the primaries was immaculate white, while the dorsal surfaces of the primaries and tail were pale gray, concolorous with the remainder of the upperparts. When perched, the folded wings did not extend much beyond the tail, giving the bird a "stubby" look toward its posterior when viewed from the side. I was able to show the bird to two other experienced birders, Merrill Webb on 21 November and Michael Tove on 15 December, both of whom corroborated the identification. Efforts to locate the bird between these dates and after 19 December were unsuccessful. I obtained several good photographs during the initial sighting that have been reviewed and verified by the Utah Field Ornithologist's Records Committee, the regional and Christmas bird count editors of *American Birds*, and the authors of a newly revised checklist of Utah birds (Behle et al. 1985).

On 7 December 1984, I found a second immature Glaucous-wing 12 km NW of the initial sighting at the Orem City Dump, Utah County. This bird was even heavier-billed and paler than the first, but was smaller, appearing no different in length (though stockier in build) than the Herring Gulls with which it

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associated. The color of the wings and tail was similar to the Provo bird.

On 19 January 1985, Michael Tove and I observed two Glaucous-winged Gulls and one Glaucous-winged x Western hybrid at the Salt Lake City Landfill, Salt Lake County. One of the Glaucous-wings appeared to be the same individual seen earlier in Orem. The other was a first-year bird about as large as the Provo bird, but browner, with a more scaley pattern on the upper wing coverts. The Glaucous-wing x Western hybird, also a first-year bird, was basically similar to the latter Glaucous-wing, but differed in that: (1) the upper surface of the outer primaries was noticeably darker than the remainder of the wing, (2) the tail was bicolored with an obvious dark band toward the tip, (3) the general body color was a shade darker, and (4) the gonyeal bulge of the bill was even more pronounced. The general effect was that of a large Thayer's Gull with an oversized bill. We observed a second Glaucous-winged x Western hybrid, in the company of the first, at the same location on 2 February.

I observed two more first-year Glaucous-winged Gulls late that season, one on 26 February at the Bountiful Area Refuse Dump on the south shore of Farmington Bay of the Great Salt Lake, Davis County, and one on 30 March at a flooded area 0.5 km SE of the Provo Dump. Both birds exhibited worn plumage and appeared extremely pale. Based on body size, bill size, and plumage, each was thought to be a different individual from earlier sightings.

During the winter of 1985–86, I observed four additional Glaucous-winged, two Glaucous-winged x Western, and one Glaucous-winged x Herring gulls during monthly surveys of gulls present at the Provo, Orem, Salt Lake City, and Bountiful landfills. One of the Glaucous-wings was a second-year bird; the remainder were first-year birds. The Glaucous-winged x Western hybrids were an adult at Salt Lake on 19 December and a second-winter immature at the same place on 1 February. The Glaucous-winged x Herring was a first-winter bird observed at the Bountiful Landfill from 7 December to 25 March. Its wing and tail pattern appeared very similar to a pale Thayer's Gull. Identification as Glaucous-wing x Herring rather than Glaucous-wing x Western was based on the following criteria: (1) body size was the same as a Herring Gull, (2) the bill was just slightly thicker than a Herring Gull's, and (3) during late winter, the bird molted in adultlike back feathers that were, in a side-by-side comparison, no darker than those of adult Herring Gulls.

To summarize, over two seasons (1984–86), I observed a minimum of 9 Glaucous-winged Gulls, 4 Glaucous-winged x Western hybrids, and 1 Glaucous-winged x Herring hybrid. Eleven of these birds were first-year immatures; 2 were second-year immatures, 1 was an adult. Sightings were made at each of four landfills along the Wasatch front from Provo to Bountiful.

Although the Glaucous-winged Gull has not previously been recorded in Utah, based on the number of sightings reported here, it appears now to be a regular migrant and winter visitant to the state. To what extent it has occurred but gone undetected in the past is unknown, but there is reason to believe the current proliferation of sightings represents a real change in status. Gull populations in the western United States have increased dramatically in recent years, possibly as a result of increased food in the form of edible human garbage and the creation of new nesting habitat in the form of large reservoirs (Conover 1983). The Glaucous-winged Gull, formerly thought to be strictly a coastal species, now breeds up to 412 km inland in Oregon and Washington (Conover and Thompson 1984). The recent sightings in Utah may represent the beginning of expansion of the winter range into the eastern Great Basin.

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LITERATURE CITED

AMERICAN ORNITHOLOGISTS UNION 1983. Check-list of North American birds. 6th ed. Allen Press, Inc., Lawrence, Kansas. 877 pp.

BEHLE, W. H., E. D SORENSEN, AND C. M WHITE. 1985. Utah birds: a revised checklist. Occasional Publication No. 4, Utah Museum of Natural History, University of Utah, Salt Lake City, Utah. 108 pp.

CONOVER, M. R. 1983. Recent changes in Ring-billed and California gull populations in the western United States. Wilson Bull. 95: 362–383.

CONOVER, M. R., AND B. C. THOMPSON. 1984. Inland breeding by the Glaucous-winged Gull. J. Field Ornith. 55: 380–382.

HOFFMAN, W., J. A. WIENS, AND J. M. SCOTT. 1978. Hybridization between gulls (*Larus glaucescens* and *L. occidentalis*) in the Pacific Northwest. Auk 95: 441–458.

PATTEN, S., AND A. R. WEISBROD. 1974. Sympatry and interbreeding of Herring and Glaucous-winged gulls in southeastern Alaska. Condor 76: 343–344.

WILLIAMSON, S. L., AND L. J. PEYTON. 1963. Interbreeding of Glaucous-winged and Herring gulls in the Cook Inlet region, Alaska. Condor 65: 24–28.

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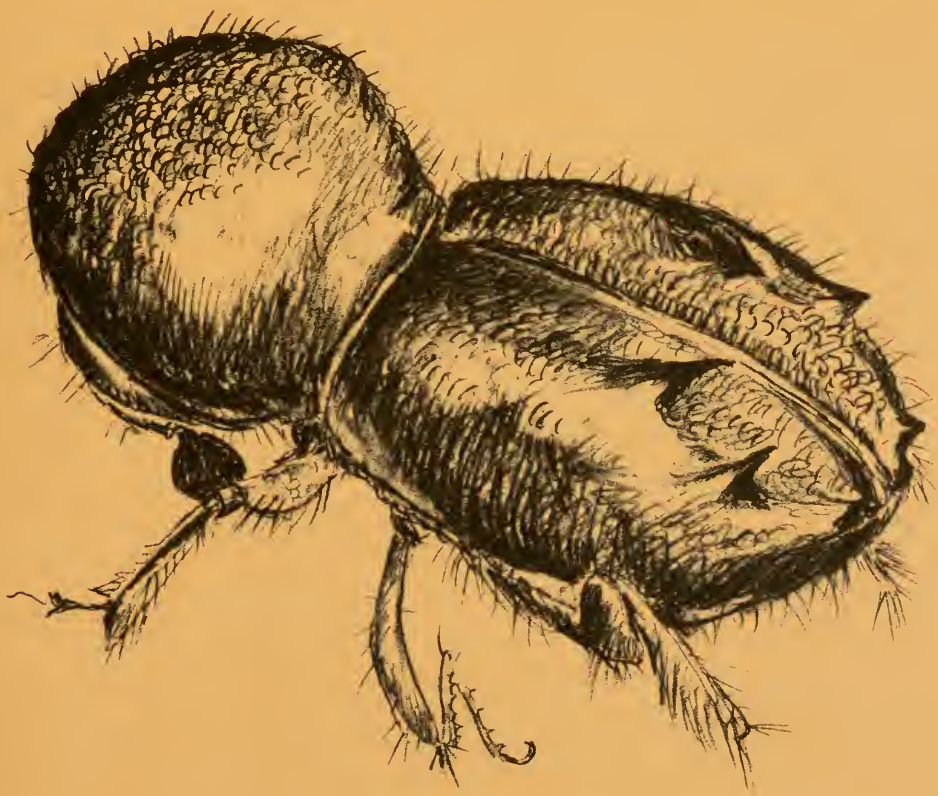

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BIBLIOGRAPHY OF MONTANA VEGETATION DESCRIPTION[1]

P. S. Bourgeron[2], A. M. Kratz[3],
T. Weaver[4], and N. Weidman[2]

ABSTRACT.—Listed in alphabetical order by author are 549 references to literature that describes the native vegetation of Montana. This updates the 1965 list of Habeck and Hartley. A keyword subject index is included.

This bibliography includes published and unpublished references to studies of Montana's native vegetation 1870–1987. Vegetation is broadly defined as the sum of the plant communities that are found in a given area. This work updates and expands Habeck and Hartley's (1965) bibliography of the vegetation of Montana. However, papers cited in Habeck and Hartley (1965), but irrelevant to our objective, were not included here.

Systematically included are references to the natural groupings of plants, the structural and synthetic characters of the groupings, and the techniques leading to recognizing the groupings. Also included are references dealing with the relationships of the vegetation to soils and climate, and with the successional relationships among plant communities. References dealing with the flora of the region were usually omitted on the grounds that, although the flora provides the historical background from which plant communities are differentiated on the basis of floristic composition, knowledge provided by the flora alone does not tell us much about the assemblages of species and their relationships to the habitats and to each other.

The subjects covered exhaustively are vegetation zones, description, classification, physiognomy, structure, and function, as well as grazing, fire history, succession, soil-plant relationships, and habitat studies. Selected references to autecology, population biology, competition, phenology, management, and species range are included. Coverage of these tangential topics is not comprehensive. Most studies included herein were conducted in the field. The exceptions are included only when they explain Montana's native vegetation patterns. References are included if at least part of the study area is in Montana. Many references to work relevant to Montana but done in adjoining states or Canada are excluded. Readers are therefore referred to bibliographies from adjoining areas for these references.

References are listed alphabetically by author. Following the reference list is an index of keywords. When applicable, they include a broad definition of the vegetation type and geographical coverage. Broad vegetation types defined include, but are not limited to, alpine meadow, conifer forest, shrubland, grassland, wetland, and riparian vegetation.

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[2]The Nature Conservancy, 134 Union Blvd., Suite 125, Lakewood, Colorado 80228.
[3]Montana Natural Heritage Program, 1515 E. 6th Ave., Helena, Montana 59620.
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These keywords describe only major kinds of vegetation defined both by physiognomy and environment. Geographical coverage follows Arno's (1978) Montana forest regions. This use of broadly defined keywords pertaining to general vegetation type and geographical coverage does not substitute either for a formal classification of communities or precise location of the study sites. They are provided solely for easy information retrieval.

The choice of the other keywords reflects our interest in vegetation patterns and not necessarily the authors' emphasis. These keywords were subject to two constraints: (1) the consistent use of the same term for the same concept/object of study throughout the bibliography, and (2) respect for the author's original wording. Species names and some other words appear as keywords when they are the central subject of the paper. However, additional information on the topic may be found under a more general keyword (e.g., *Abies lasiocarpa* under conifer forest; competition under community structure; etc.)

Readers seeking complete information on a particular topic should check for reference numbers in the keyword index.

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BIBLIOGRAPHY OF MONTANA VEGETATION

1. AASE, J. K. AND J. R. WIGHT. 1973. Prairie sandreed (*Calamovilfa longifolia*): water infiltration and use. J. Range Mgt. 26: 212–214.
2. ADAMS, L. 1949. The effects of deer on conifer reproduction in northwestern Montana. J. For. 47: 909–913.
3. ADDOR, E. E. 1958. The wind-pollinated plants of the Missoula Valley, Montana. Unpublished thesis, University of Montana, Missoula. 174 pp.
4. ALEXANDER, R. R. 1985. Major habitat types, community types, and plant communities in the Rocky Mountains. USDA For. Serv. Gen. Tech. Rept. RM-123. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado. 105 pp.
5. ALLEN, E. O. 1965. Food and range use habits of white-tail deer on Missouri River bottomlands in north-central Montana. Unpublished thesis, Montana State University, Bozeman. 41 pp.
6. ALLEN, E. O. 1968. Range use, foods, condition, and productivity of white-tailed deer in Montana. J. Wildl. Mgt. 32: 130–141.
7. ALLEN, H. L. 1980. Floodplain plant communities of the North Fork, Flathead River, Montana. Unpublished Research/Management Rept. Serv. No. 1. USDI, National Park Service, Glacier National Park, West Glacier, Montana. 71 pp.
8. ALLER, A. R. 1960. The composition of the Lake McDonald forest, Glacier National Park. Ecology 41: 29–33.
9. ALLRED, B. W. 1941. Grasshoppers and their effect on sagebrush on the Little Powder River in Wyoming and Montana. Ecology 22: 387–392.
10. ANDERSON, F. W. 1889. The pastoral resources of Montana. Pages 311–324 *in*: Report of the Commission of Agriculture, 1888. Government Printing Office, Washington, D.C.
11. ANDERSON, N. L. 1962. Grasshopper-vegetation relationships on Montana grasslands. Unpublished dissertation, Montana State University, Bozeman. 73 pp.
12. ANDERSON, N. L. 1964. Some relationships between grasshoppers and vegetation. Ann. Entomol. Soc. Amer. 57: 736–742.
13. ANDERSON, N. L. 1973. The vegetation of rangeland sites associated with some grasshopper studies in Montana. Montana Agricultural Experiment Station Bull. No. 668. Montana State University, Bozeman.
14. ANTOS, J. A. 1977. Grand fir (*Abies grandis*) forests of the Swan Valley, Montana. Unpublished thesis, University of Montana, Missoula. 220 pp.
15. ANTOS, J. A., AND J. R. HABECK. 1981. Successional development in *Abies grandis* (Dougl.) Forbes forests in the Swan Valley, western Montana. Northwest Sci. 55: 26–39.
16. ANTOS, J. A., AND R. C. SHEARER. 1980. Vegetation development on disturbed grand fir sites, Swan Valley, northwestern Montana. USDA For. Serv. Res. Pap. INT-251. Intermountain Forest and Range Experiment Station, Ogden, Utah. 26 pp.
17. ANTOS, J. A., B. MCCUNE, AND C. BARA. 1983. The effect of fire on an ungrazed western Montana grassland. Amer. Midl. Nat. 110: 354–364.
18. ARNO, S. F. 1966a. Alpine larch (*Larix lyallii* Parl.) and its natural occurrence. Unpublished paper, School of Forestry, University of Montana, Missoula. 52 pp.
19. ARNO, S. F. 1966b. Interpreting the timberline: an aid to help park naturalists to acquaint visitors with the subalpine-alpine ecotone of western North America. Unpublished thesis, University of Montana, Missoula. 206 pp.
20. ARNO, S. F. 1970. Ecology of alpine larch (*Larix lyallii* Parl.) in the Pacific Northwest. Unpublished dissertation, University of Montana, Missoula. 264 pp.

21. ARNO, S. F. 1976. The historical role of fire on the Bitterroot National Forest. USDA For. Serv. Res. Pap. INT-187. Intermountain Forest and Range Experiment Station, Ogden, Utah. 29 pp.
22. ARNO, S. F. 1977. Forest succession in Montana: a selected annotated bibliography. Unpublished report on file at the USFS Northern Fire Laboratory, Missoula, Montana.
23. ARNO, S. F. 1978. Preliminary classification of successional stages in the *Pseudotsuga/Physocarpus* habitat type. Progress Report, Study INT-1205-587. Intermountain Forest and Range Experiment Station, Ogden, Utah. 31 pp.
24. ARNO, S. F. 1979. Forest regions of Montana. USDA For. Serv. Res. Pap. INT-218. Intermountain Forest and Range Experiment Station, Ogden, Utah.
25. ARNO, S. F. 1980. Forest fire history in the northern Rockies. J. For. 78: 460–465.
26. ARNO, S. F. 1982. Classifying forest succession on four habitat types in western Montana. Pages 54–62 *in*: J. Means, ed., Forest succession and stand development research in the Northwest. Proc. Symp., 26 March 1981, Oregon State University, Corvallis. 170 pp.
27. ARNO, S. F., AND G. E. GRUELL. 1983. Fire history at the forest-grassland ecotone in southwestern Montana. J. Range Mgt. 36: 332–336.
28. ARNO, S. F., AND G. E. GRUELL. 1986. Douglas-fir encroachment into mountain grasslands in southwestern Montana. J. Range Mgt. 39(3): 272–276.
29. ARNO, S. F., AND J. R. HABECK. 1972. Ecology of alpine larch (*Larix lyallii* Parl.) in the Pacific Northwest. Ecol. Monogr. 42: 417–450.
30. ARNO, S. F., AND R. P. HAMMERLY. 1984. Timberline-mountain and arctic forest frontiers. Published by the Mountaineers, Seattle, Washington. 304 pp.
31. ARNO, S. F., AND T. D. PETERSEN. 1983. Variation in estimates of fire intervals: a closer look at fire history on the Bitterroot National Forest. Res. Pap. INT-301. Intermountain Forest and Range Experiment Station, Ogden, Utah. 8 pp.
32. ARNO, S. F., AND R. D. PFISTER. 1977. Habitat types: an improved system for classifying Montana's forests. West. Wildlands 3(4): 6–11.
33. ARNO, S. F., D. G. SIMMERMAN, AND R. E. KEANE. 1985. Forest succession on four habitat types in western Montana. USDA For. Serv. Gen. Tech. Rept. INT-177. Intermountain Forest and Range Experiment Station, Ogden, Utah. 74 pp.
34. ARNO, S. F., AND K. M. SNECK. 1977. A method for determining fire history in coniferous forests in the mountain west. USDA For. Serv. Gen. Tech. Rept. INT-42. Intermountain Forest and Range Experiment Station, Ogden, Utah. 28 pp.
35. AUSTIN, R. R. 1972. Habitat diversity as related to pheasant use on a game management area in northwestern Montana. Montana Department of Fish and Game, Project No. W-120-12-2,3. 63 pp.
36. AYRES, H. B. 1900a. The Flathead Forest Reserve. 20th Annual Report, U.S. Geological Survey (1898–99), Part V: 245–316.
37. AYRES, H. B. 1900b. Lewis and Clark Forest Reserve, Montana. 21st Annual Report, U.S. Geological Survey, Part V: 27–80.
38. B. C. RESEARCH, AND SOMERS LAND CO. (Helena, Montana). 1973. Environmental analysis: Sarpy Creek coal development. Prepared for Westmoreland Resources, Hardin, Montana. 57 pp.
39. BAILEY, V. 1918. Wild animals of Glacier National Park: the mammals, with notes on physiography and life zones. USDI, National Park Service. 210 pp.
40. BALLARD, W. G. 1973. The relationship among precipitation, range vegetation and range cattle production in the plains region of Montana. Unpublished thesis, Montana State University, Bozeman. 71 pp.
41. BAMBERG, S. A. 1961. Plant ecology of alpine tundra areas in Montana and adjacent Wyoming. Unpublished thesis, University of Colorado, Boulder. 163 pp.
42. BAMBERG, S. A. 1964. Ecology of the vegetation and soils associated with calcareous parent material in the alpine region of Montana. Unpublished dissertation, University of California, Davis. 106 pp. (Diss. Abstr. 25: 4370).
43. BAMBERG, S. A., AND J. MAJOR. 1968. Ecology of the vegetation and soils associated with calcareous parent materials in three alpine regions of Montana. Ecol. Monogr. 38: 127–167.
44. BARRETT, S. W. 1980. Indian fires in the presettlement forests of western Montana. Pages 35–41 *in* Proceedings of the Fire History Workshop. USDA For. Serv. Gen. Tech. Rept. RM-81. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.
45. BARRETT, S. W. 1981. Relationship of Indian-caused fires to the ecology of western Montana forests. Unpublished thesis, University of Montana, Missoula. 198 pp.
46. BARRETT, S. W., AND S. F. ARNO. 1982. Indian fires as an ecological influence in the northern Rockies. J. For. 80: 647–651.
47. BATCHELOR, R., M. ERWIN, R. MARTINKA, D. MCINTOSH, R. PFISTER, E. SCHNEEGAS, J. TAYLOR, AND K. WALTHER. 1982. A taxonomic classification system for Montana riparian vegetation types. Montana State Rural Areas Development Commission. 16 pp.
48. BATSON, F. T., AND J. C. ELLIOTT. 1975. Surface resource inventory of eastern Montana rangelands utilizing high altitude color infrared aerial photography. Proc. Fort Union Coal Field Symp. 5: 651–662.
49. BAUER, P. J. 1983. Bumblebee pollination relationships on the Beartooth Plateau tundra of southern Montana. Amer. J. Bot. 70: 134–144.
50. BAYLESS, S. R. 1967. Food habits, range use, and home range of pronghorn antelope in central Montana during winter. Unpublished thesis, Montana State University, Bozeman. 65 pp.
51. BAYLESS, S. R. 1969. Winter food habits, range use, and home range of antelope in Montana. J. Wildl. Mgt. 33: 538–551.
52. BIRKBY, J. L. 1983. Interaction of western harvester ants with southeastern Montana soils and vegetation. Unpublished thesis, Montana State University, Bozeman. 35 pp.
53. BLACK, A. L. 1968. Nitrogen and phosphorus fertilization for production of crested wheatgrass and

native grass in northeastern Montana. Agron. J. 60: 213–216.

54. BLANKENSHIP, J. W. 1905. A century of botanical exploration in Montana, 1805–1905: collectors, herbaria and bibliography. Montana Agric. Coll. Sci. Studies 1: 1–31.
55. BLINN, D. W. 1966. Analysis of the vegetation on the glacial moraines in the upper Blackfoot Valley, Montana. Unpublished thesis, University of Montana, Missoula. 90 pp.
56. BLINN, D. W., AND J. R. HABECK. 1967. An analysis of morainal vegetation in the upper Blackfoot Valley, Montana. Northwest Sci. 41: 126–140.
57. BOE, K. N. 1948. Is Douglas-fir replacing ponderosa pine in the cutover stands in western Montana? Proc. Mont. Acad. Sci. 8: 42–49.
58. BOE, K. N. 1954. Periodicity of cone crops for five Montana conifers. Proc. Mont. Acad. Sci. 14: 5–9.
59. BOGGS, K. W. 1984. Succession in riparian communities of the lower Yellowstone River, Montana. Unpublished thesis, Montana State University, Bozeman. 107 pp.
60. BOOTH, W. E. 1947. The effect of grass competition on the growth and reproduction of big sagebrush, *Artemisia tridentata*. Proc. Mont. Acad. Sci. 7: 23–25.
61. BRADLEY, A. F. 1984. Rhizome morphology, soil distribution, and the potential fire survival of eight woody understory species in western Montana. Unpublished thesis, University of Montana, Missoula. 184 pp.
62. BRANSON, F. A. 1956. Range forage production changes on a water spreader in southeastern Montana. J. Range Mgt. 9: 187–191.
63. BRANSON, F. A., AND T. LOMMASSON. 1957. Quantitative effects of twenty-three years of controlled use on mountain range. J. Range Mgt. 11: 67.
64. BRANSON, F. A., AND R. F. MILLER. 1981. Effects of increased precipitation and grazing management on northeastern Montana rangelands. J. Range Mgt. 36: 3–10.
65. BRANSON, F. A., R. F. MILLER, AND I. S. MCQUEEN. 1970. Plant communities and associated soil and water factors on shale-derived soils in northeastern Montana. Ecology 51: 391–407.
66. BRANSON, F. A., AND G. F. PAYNE. 1957. Effects of sheep, gophers, and protection on the meadows of the Bridger Mountains. Proc. Mont. Acad. Sci. 17: 47.
67. BRANSON, F. A., AND G. F. PAYNE. 1958. Effects of sheep and gophers on meadows of the Bridger Mountains of Montana. J. Range Mgt. 11: 165–169.
68. BRANT, L. A. 1980. A palynological investigation of post-glacial sediments at two locations along the continental divide near Helena, Montana. Unpublished dissertation, Pennsylvania State University, College Park. 163 pp.
69. BRINK, D., AND L. M. MAYER. 1978. A floristic survey of eight coal sites in the Decker, Montana–Sheridan, Wyoming area. Phytologia 38: 483–497.
70. BRITTON, M. P. 1955. An ecological study of a relict grassland and an adjacent grazed pasture in Beaverhead Valley, Montana. Unpublished thesis, Montana State University, Bozeman. 23 pp.
71. BROWN, R. W. 1965. The distribution of plant communities in the badlands of southeastern Montana. Unpublished thesis, University of Montana, Missoula. 145 pp.
72. BROWN, R. W. 1971. Distribution of plant communities in southeastern Montana badlands. Amer. Midl. Nat. 85: 458–477.
73. BUCHANAN, B. 1972. Ecological effects of weather modification, Bridger Range area, Montana: relationship of soil, vegetation, and microclimate. Unpublished dissertation, Montana State University, Bozeman. 135 pp.
74. BUCSIS, R. A. 1974. Ecological characteristics of the Armstrong mule deer winter range, Bridger Mountains, Montana. Unpublished thesis, Montana State University, Bozeman. 104 pp.
75. BUREAU OF INDIAN AFFAIRS. 1971. Soil and range resources inventory: east of the Little Bighorn River, Crow Indian Reservation, Montana. Report No. 186, Missouri River Basin investigations. USDI.
76. BUREAU OF LAND MANAGEMENT. 1979. Historical comparison photography: Missouri Breaks, Montana. USDI, BLM Montana State Office, Billings, Montana. 109 pp.
77. BUREAU OF LAND MANAGEMENT. 1980. Historical comparison photography: mountain foothills, Dillon Resource Area, Montana. USDI, BLM Montana State Office, Billings, Montana. 120 pp.
78. BUREAU OF LAND MANAGEMENT. 1984. Historical comparison photography: Headwaters Resource Area, Butte District. BLM-MT-GI-85-004-4322. USDI, BLM Montana State Office, Billings, Montana.
79. BUTLER, D. R. 1979. Snow avalanche path terrain and vegetation, Glacier National Park, Montana. Arctic and Alpine Res. 11: 17–32.
80. BUTLER, D. R. 1985. Vegetation and geomorphic change on snow avalanche paths, Glacier National Park, Montana, USA. Great Basin Nat. 45: 313–317.
81. CADA, J. D. 1968. Populations of small mammals in central Montana with special reference to tentative sagebrush control sites. Unpublished thesis, Montana State University, Bozeman. 52 pp.
82. CAMPBELL, R. B. 1970. Pronghorn, sheep, and cattle range relationships in Carter County, Montana. Project No. W-98-R-9,10,11. Montana Department of Fish and Game. 87 pp.
83. CARTER, R. L. 1951. An environmental analysis of winter game range in western Montana. Unpublished thesis, University of Montana, Missoula. 103 pp.
84. CASEBEER, R. L. 1948. A study of the food habits of the mountain goat (*Oreamnus americanus missoulae*) in western Montana. Unpublished thesis, University of Montana, Missoula. 99 pp.
85. CHADWICK, D. H. 1974. Mountain goat ecology—logging relationships in the Bunker Creek drainage of western Montana. Unpublished thesis, University of Montana, Missoula. 262 pp.
86. CHAFFEE, G. B. 1981. Vegetation report, Limestone Hills quarry area. Report prepared for Continental Lime, Inc. by Econ, Inc., Helena, Montana. 41 pp. + app.

87. CHAFFEE, G. B. 1982. Response of subalpine needlegrass, *Stipa occidentalis* var. *minor* (Vasey) C.L. Hitchc. to grazing disturbance in western Montana. Proc. Montana Acad. Sci. 41: 71–78.

88. CHOATE, C. M. 1963. Ordination of the alpine plant communities of Logan Pass, Glacier National Park, Montana. Unpublished thesis, University of Montana, Missoula. 106 pp.

89. CHOATE, C. M., AND J. R. HABECK. 1967. Alpine plant communities at Logan Pass, Glacier National Park. Proc. Mont. Acad. Sci. 27: 36–54.

90. CHOATE, T. N., AND C. M. CHOATE. 1963. Life above timberline. Naturalist 14(2): 26–32.

91. CLARKE, J. W. 1982. Analysis of direct seeding methods for establishment of native shrub and forb species on mine soils in southeastern Montana. Unpublished thesis, Montana State University, Bozeman. 204 pp.

92. COENENBERG, J. G., AND E. J. DEPUIT. 1979. Baseline wildlife studies, Crow coal lease, southeastern Montana, 1975–1978. Mountain Agricultural Experiment Station, Reclamation Research Unit, Bozeman, Montana. 133 pp.

93. COLE, G. F. 1956. The pronghorn antelope—its range use and food habits in central Montana with special reference to alfalfa. Montana State College Agricultural Experiment Station. Bull. No. 516. 63 pp.

94. COLLINS, D., AND T. WEAVER. 1978. Effects of summer weather modification (irrigation) in *Festuca idahoensis—Agropyron spicatum* grasslands. J. Range Mgt. 31: 264–269.

95. CONWAY, T. M. 1982. Response of understory vegetation to varied lodgepole pine (*Pinus contorta*) spacing intervals in western Montana. Unpublished thesis, Montana State University, Bozeman. 76 pp.

96. COOPER, J. G. 1870. The sylva of Montana. Amer. Nat. 3: 405–422.

97. COOPER, S. V. 1975. Forest habitat types of northwestern Wyoming and contiguous portions of Montana and Idaho. Unpublished dissertation, Washington State University, Pullman. 190 pp.

98. COOPER, S. V., AND R. D. PFISTER. 1981. Forest habitat types of the Blackfeet Indian Reservation. Review draft, 5/21/81, for Bureau of Indian Affairs, Wind River Agency, Fort Washakie, Wyoming. 87 pp.

99. COOPER, S. V., AND R. D. PFISTER. 1985. Forest habitat types of the Crow and Northern Cheyenne Indian Reservations. Termination report to Bureau of Indian Affairs, Billings Area Office (draft). USDA For. Serv., Intermountain Forest and Range Experiment Station, Ogden, Utah.

100. COOPERRIDER, A. Y. 1969. Competition for food between mule deer and bighorn sheep on Rock Creek winter range, Montana. Unpublished thesis, University of Montana, Missoula. 92 pp.

101. COTTER, J. F. 1963. Causation and plant succession in disturbed areas of southwestern Montana. Unpublished thesis, University of Montana, Missoula. 88 pp.

102. COUPLAND, R. T. 1958. The effects of fluctuations in weather upon the grasslands of the Great Plains. Bot. Rev. 24: 273–317.

103. CRAIGHEAD, J. J., J. S. SUMNER, AND G. B. SCAGGS. 1982. A definitive system for analysis of grizzly bear habitat and other wilderness resources. Wildlife–Wildlands Institute Monogr. No. 1. University of Montana Foundation, Missoula, Montana. 279 pp.

104. CRANE, M. F., J. R. HABECK, AND W. C. FISHER. 1983. Early forest fire revegetation in a western Montana Douglas-fir forest. USDA For. Serv. Res. Pap. INT-319, Intermountain Forest and Range Experiment Station, Ogden, Utah. 29 pp.

105. CULWELL, L. D. 1977a. Vegetation analysis of Pearl area, Montana. Unpublished report. Westech, Helena, Montana.

106. CULWELL, L. D. 1977b. Preliminary vegetation analysis of a proposed copper mine disturbance area (00041A), Silver Bow County, Montana. Unpublished report for Anaconda Co. Westech, Helena, Montana. 17 pp.

107. CULWELL, L. D. 1977c. Vegetation analysis, Youngs Creek area, Montana. Unpublished final report for Shell Oil Co. Westech, Helena, Montana. 50 pp.

108. CULWELL, L. D. 1977d. Vegetation analysis. Divide Coal Mine, Musselshell County, Montana. Unpublished report. Westech, Helena, Montana. 22 pp.

109. CULWELL, L. D. 1977e. Vegetation analysis. P M Coal Mine, Musselshell County, Montana. Unpublished report. Westech, Helena, Montana. 18 pp.

110. CULWELL, L. D. 1979a. Vegetation communities of the Coal Creek study area, Powder River County, Montana, 1978. Unpublished report. Westech, Helena, Montana. 45 pp. + app.

111. CULWELL, L. D. 1979b. Vegetation analysis—1979. Pearl Exclosure (reference area), Big Horn County, Montana. Unpublished report for Shell Oil Co. Westech, Helena, Montana. 36 pp.

112. CULWELL, L. D. 1979c. Vegetation communities of the Coal Creek study area (T.35S, R.45E, SEC.3), Powder River County, Montana, 1978–1979. Unpublished report. Westech, Helena, Montana. 126 pp.

113. CULWELL, L. D., AND D. J. RAMSDEN. 1978. Vegetation inventory of the Zortman and Landusky areas, Little Rocky Mountains, Montana. Unpublished report for Zortman and Landusky Mining Co., Inc. Westech, Helena, Montana. 69 pp.

114. CULWELL, L. D., AND K. L. SCOW. 1981. Vegetation inventory of the Youngs Creek study area, Big Horn County, Montana, 1980. Unpublished report for Shell Oil Co. Westech, Helena, Montana. 57 pp. + app.

115. CULWELL, L. D., AND K. L. SCOW. 1982a. Terrestrial vegetation inventory: Dominy project area, Custer County, Montana, 1979–1980. Unpublished report for Western Energy Co. Westech, Helena, Montana. 144 pp. + app.

116. CULWELL, L. D., AND K. L. SCOW. 1982b. Vegetation monitoring and reference area evaluation, North King mining unit, Rosebud County, Montana, 1981. Unpublished report for Montco. Westech, Helena, Montana. 45 pp. + app.

117. CULWELL, L. D., AND K. L. SCOW. 1982c. Vegetation inventory of the Jardine project area, Park

County, Montana, 1981. Unpublished report for Homestake Mining Co. Westech, Helena, Montana. 138 pp.

118. CULWELL, L. D., K. L. SCOW, AND L. A. LARSEN. 1982. Vegetation reference area monitoring. North King unit, Rosebud County, Montana (draft). Unpublished report for Montco. Westech, Helena, Montana. 35 pp.

119. CULWELL, L. D., K. L. SCOW, AND L. A. LARSEN. 1984. Vegetation inventory of the Montana Tunnels study area, Jefferson County, Montana, 1984. Unpublished tech. report for Centennial Minerals, Inc. Westech, Helena, Montana. 87 pp. + app.

120. CULWELL, L. D., K. L. SCOW, AND L. A. LARSEN. 1985. Vegetation baseline inventory, Peabody Coal Co., Big Sky Mine area B, Rosebud County, Montana. Unpublished report. Westech, Helena, Montana.

121. CULWELL, L. D., K. L. SCOW, AND L. A. LARSEN. 1986a. A preliminary evaluation of the vegetation of the Makoshika State Park area, Dawson County, Montana (draft). Unpublished report for Montana Department of Fish, Wildlife and Parks. Westech, Helena, Montana. 77 pp. + app.

122. CULWELL, L. D., K. L. SCOW, AND L. A. LARSEN. 1986b. Reference area and reclamation monitoring, Peabody Coal Co., Big Sky Mine area A, Rosebud County, Montana, 1985. Unpublished report for Peabody Coal Co. Westech, Helena, Montana. 65 pp. + app.

123. CUSKER, H. J. 1958. History of development and migration of Douglas-fir (*Pseudotsuga menziesii*). Proc. Mont. Acad. Sci. 18: 9.

124. CUTRIGHT, P. R. 1969. Lewis and Clark: pioneering naturalists. University of Illinois Press, Chicago. 279 pp.

125. DALE, D. 1973. Effects of trail use under forests in the Madison Range, Montana. Unpublished thesis, Montana State University, Bozeman. 96 pp.

126. DALE, D., AND T. WEAVER. 1974. Trampling effects on vegetation of the trail corridors of northern Rocky Mountain forests. J. Appl. Ecology 11: 767–772.

127. DARLING, A. P. 1983. The effects of native hay mulch on stabilization and revegetation of strip mined lands in southeastern Montana. Unpublished thesis, Montana State University, Bozeman. 102 pp.

128. DAUBENMIRE, R. 1943. Vegetational zonation in the Rocky Mountains. Bot. Rev. 9: 325–393.

129. DAUBENMIRE, R. 1946. The life zone problem in the northern intermountain region. Northwest Sci. 20: 28–38.

130. DAUBENMIRE, R. 1969a. Ecologic plant geography of the Pacific Northwest. Madroño 20: 111–128.

131. DAUBENMIRE, R. 1969b. Structure and ecology of coniferous forests of the Rocky Mountains. Pages 25–40 *in:* R. D. Taber, ed., Coniferous forests of the northern Rocky Mountains. Proc. of the 1968 Symp. University of Montana, Missoula.

132. DAVIS, C. 1975. A guide for determining potential herbage productivity of central Montana range areas and potential range area. Unpublished rept. Gallatin National Forest. 55 pp.

133. DAVIS, K. M., B. D. CLAYTON, AND W. C. FISCHER. 1980. Fire ecology of Lolo National Forest habitat types. USDA For. Serv. Gen. Tech. Rept. INT-79. Intermountain Forest and Range Experiment Station, Ogden, Utah. 75 pp.

134. DEBYLE, N. V. 1981. Clearcutting and fire in the larch/Douglas-fir forests of western Montana: a multifaceted research summary. USDA For. Serv. Gen. Tech. Rept. INT-99. Intermountain Forest and Range Experiment Station, Ogden, Utah.

135. DEPUIT, E. J. 1975. Preliminary range resource analysis: Tanner Creek study area. Montana Agricultural Experimental Station Res. Rept. 73. Montana State University, Bozeman. 34 pp.

136. DEPUIT, E. J., W. H. WILLMUTH, AND J. G. COENENBERG. 1975. Preliminary range resource analysis: Wolf Mountain mining area. Prepared for Mining Ventures Department, Shell Oil. Montana Agricultural Experiment Station, Bozeman, Montana. 23 pp. + maps.

137. DEPUIT, E. J., W. H. WILLMUTH, AND J. G. COENENBERG. 1976. Vegetation and watershed analysis, Tanner Creek study area. Project final report, Reclamation Research Unit, Montana Agricultural Experiment Station, Bozeman, Montana. 74 pp.

138. DEPUIT, E. J., W. H. WILLMUTH, AND J. G. COENENBERG. 1978. Vegetation and watershed analysis, Squirrel Creek study area. Prepared for Mining Ventures Department, Shell Oil Reclamation Research Unit, Montana Agricultural Experiment Station, Bozeman, Montana.

139. DESATO, T. S. 1971. Subalpine larch of Glacier National Park. Unpublished report prepared for Glacier National Park.

140. DICE, L. R. 1923. Mammal associations and habitats of the Flathead Lake region, Montana. Ecology 4: 247–260.

141. DORN, R. D. 1969. Relations of moose, cattle and willows in southwestern Montana. Unpublished thesis, Montana State University, Bozeman. 79 pp.

142. DORN, R. D. 1970. Moose and cattle food habits in southwest Montana. J. Wildlife Mgt. 34: 559–564.

143. DUBOIS, K. L. 1979. An inventory of the avifauna in the Long Pines of southeastern Montana. Unpublished thesis, Montana State University, Bozeman. 113 pp.

144. DUNCAN, E. A. 1975. The ecology of curl-leaf mountain mahogany (*Cercocarpus ledifolius* Nutt.) in southwestern Montana with special reference to use by mule deer. Unpublished thesis, Montana State University, Bozeman. 87 pp.

145. DUSEK, G. L. 1971. Range relationships of mule deer in the prairie habitat, northcentral Montana. Unpublished thesis, Montana State University, Bozeman. 63 pp.

146. DUSEK, G. L. 1978. Bull Mountains coal field study Final report. Montana Department of Fish and Game. 120 pp.

147. DUSEK, G. L. 1980. An inventory of vegetation, wildlife, and recreational resources of the Long Pines, Montana. Final report. Montana Department of Fish, Wildlife and Parks, Ecological Services Division. 158 pp.

148. ECON. INC. 1973. Annual report to Montana Power Co. and Western Energy Co. Wildlife investigations. Project No. 9-01-A. Colstrip, Montana. 103 pp.

149. ECON, INC. 1975a. Mining permit requirements for wildlife and vegetation areas A1 and E2. August 15, 1974. Project No. 82-23-A. Report to Western Energy Co.

150. ECON, INC. 1975b. Vegetation, production, condition, and community typing. Mining areas A, B and E. Western Energy Project No. 107-23-A. 39 pp.

151. ECON, INC. 1976. Annual vegetation description, condition, and production report. Western Energy Co. mining areas A, B, and E. Western Energy Co. Project No. E07-23-A. 38 pp.

152. ECON, INC. 1978. Vegetation report for mining area C, 1978. Western Energy Co. Project No. 194-83-A. Final report. 49 pp.

153. ECON, INC. 1979. Vegetation report for mining area D, 1977–1978. Western Energy Co. Project 206-83-A. 56 pp.

154. ELLISON, L. 1960. Influence of grazing on plant succession of rangelands. Bot. Rev. 26: 1–78.

155. ELLISON, L., AND E. J. WOOLFOLK. 1937. Effects of drought on vegetation near Miles City, Montana. Ecology 18: 329–336.

156. ELROD, M. J. 1902a. A biological reconnaissance in the vicinity of Flathead Lake. University of Montana. Bull. No. 10, Biol. Series No. 3: 91–182 + 46 plates.

157. ELROD, M. J. 1902b. *Daphnia* pond, a study in environment. University of Montana. Bull. No. 16, Biol. Series No. 5: 230–233.

158. ERICKSON, A. W., M. B. HANSON, AND C. A. CLAMPITT. 1985. An assessment of the impact of the Rock Creek mining project on the grizzly bear population in the Cabinet Mountains, Montana. Report prepared for Asarco, Inc., Wallace, Idaho. 217 pp. + app.

159. ERICKSON, G. L. 1972. The ecology of Rocky Mountain bighorn sheep in the Sun River area of Montana with special reference to summer food habits and range movements. Unpublished thesis, Montana State University, Bozeman. 50 pp.

160. EUSTACE, C. D. 1967. Food habits, range use and relationships between elk and livestock in the Gravelly Mountains, Montana. Unpublished thesis, Montana State University, Bozeman. 55 pp.

161. EVANKO, A. B., AND R. A. PETERSON. 1955. Comparisons of protected and grazed mountain rangelands in southwestern Montana. Ecology 36: 71–82.

162. EVERSMAN, S. T. 1968. A comparison of plant communities and substrates of avalanche and nonavalanche areas in southcentral Montana. Unpublished thesis, Montana State University, Bozeman. 39 pp.

163. FINK, T. 1985. Montana's vegetation (with roadside guide). Manuscript.

164. FIREBAUGH, J. E. 1969. Relationship of mule deer to livestock on summer range in the Pryor Mountains, Montana. Unpublished thesis, Montana State University, Bozeman. 55 pp.

165. FISCHER, W. C. 1981. Photo guide for appraising natural fuels in Montana forests: interior ponderosa pine, ponderosa pine–larch–Douglas-fir, larch–Douglas-fir, and interior Douglas-fir cover types. USDA For. Serv. Gen. Tech. Rept. INT-97. Intermountain Forest and Range Experiment Station, Ogden, Utah. 130 pp.

166. FISHER, W. C., AND B. D. CLAYTON. 1983. Fire ecology of Montana forest habitat types east of the continental divide. USDA For. Serv. Gen. Tech. Rept. INT-141. Intermountain Forest and Range Experiment Station, Ogden, Utah.

167. FISSER, H. G. 1961. A comparison of line intercept, inferred point contact, and weight measurement methods on foothill grassland vegetation. Unpublished thesis, Montana State College, Bozeman. 141 pp.

168. FOOTE, G. G. 1965. Phytosociology of the bottomland hardwood forests in western Montana. Unpublished thesis, University of Montana, Missoula. 140 pp.

169. FORCELLA, F. 1977. Flora, chorology, biomass and productivity of the *Pinus albicaulis–Vaccinium scoparium* association. Unpublished thesis, Montana State University, Bozeman. 99 pp.

170. FORCELLA, F. 1978. Flora and chorology of the *Pinus albicaulis–Vaccinium scoparium* association. Madroño 25: 139–150.

171. FORCELLA, F., AND T. WEAVER. 1977. Biomass and productivity of the subalpine *Pinus albicaulis–Vaccinium scoparium* association in Montana, USA. Vegetatio 35: 95–105.

172. FORCELLA, F., AND T. WEAVER. 1980. Food production in the *Pinus albicaulis–Vaccinium scoparium* association. Proc. Mont. Acad. Sci. 39: 73–80.

173. FOSTER, J. W. 1977. Impact of off-road vehicle traffic on soils and vegetation on rangeland in southeastern Montana and photographic monitoring of the effects. Unpublished dissertation, Montana State University, Bozeman.

174. GABRIEL, H. W. 1976. Wilderness ecology: the Danaher Creek drainage, Bob Marshall Wilderness, Montana. Unpublished dissertation, University of Montana, Missoula. 224 pp.

175. GOLDAN, D. S. 1982. Baseline data on vegetation, breeding bird populations, and small mammals in relation to proposed contour furrowing in southeastern Montana. Unpublished thesis, Montana State University, Bozeman. 29 pp.

176. GOLDIN, A. 1976. Effects of limestone on plant distribution in the Garnet Mountains, Montana. Unpublished thesis, University of Montana, Missoula. 115 pp.

177. GORDON, C., K. LACKSCHEWITZ, W. MOLINA, K. BIXBY, W. TOMLINSON, AND T. DONOHOE. 1977. Baseline evaluation of the aquatic and terrestrial ecosystems potentially impacted by mining in the vicinity of the Flathead Silver Mine, Hog Heaven mining district, Montana. Unpublished report to Congdon and Carey Co.

178. GORDON, F. A. 1968. Range relationships of elk and cattle on elk winter range, Crow Creek, Montana. Unpublished thesis, Montana State University, Bozeman. 52 pp.

179. GRAY, A., AND J. D. HOOKER. 1880. The vegetation of the Rocky Mountain region and a comparison with that of other parts of the world. Bull. U.S. Geological and Geographical Survey of the Territories 6: 1–77.

180. GRIGGS, R. F. 1938. Timberlines in the northern Rocky Mountains. Ecology 19: 548–564.

181. GRUELL, G. E. 1983. Indian fires in the interior west—a widespread influence. Pages 68–74 *in*

Proceedings of symposium and workshop on wilderness fire, Missoula, Montana, 15–18 November 1983. USFS Gen. Tech. Rept. INT-182. Intermountain Forest and Range Experiment Station, Ogden, Utah.

182. GRUELL, G. E. 1985. Fire on the early western landscape: an annotated record of wildland fires, 1776–1900. Northwest Sci. 59: 97–107.

183. GRUELL, G. E., W. C. SCHMIDT, S. F. ARNO, AND W. J REICH. 1982. Seventy years of vegetative change in a managed ponderosa pine forest in western Montana—implications for resource management. USDA, For. Serv. Gen. Tech. Rept. INT-130. Intermountain Forest and Range Experiment Station, Ogden, Utah. 42 pp.

184. HABECK, J. R. 1963a. Lichen distribution in the Lake McDonald forest communities. Proc. Mont. Acad. Sci. 23: 34–36.

185. HABECK, J. R. 1963b. The composition of several climax forest communities in the Lake McDonald area of Glacier National Park. Proc. Mont. Acad. Sci. 23: 37–44.

186. HABECK, J. R. 1967a. The vegetation of northwestern Montana: a preliminary report. Department of Botany, University of Montana, Missoula. 57 pp.

187. HABECK, J. R. 1967b. Mountain hemlock communities in western Montana. Northwest Sci. 41: 169–177.

188. HABECK, J. R. 1968. Forest succession in the Glacier Park cedar-hemlock forests. Ecology 49: 872–880.

189. HABECK, J. R. 1969. A gradient analysis of a timberline zone at Logan Pass, Glacier National Park, Montana. Northwest Sci. 43: 65–73.

190. HABECK, J. R. 1970a. Fire ecology investigations in Glacier National Park: historic considerations and current observations, 1970. Botany Department, University of Montana, Missoula. 80 pp.

191. HABECK, J. R. 1970b. The vegetation of Glacier National Park, Montana. Department of Botany, University of Montana, Missoula. 132 pp.

192. HABECK, J. R., AND C. M. CHOATE. 1963. An analysis of krummholz communities at Logan Pass, Glacier National Park. Northwest Sci. 37: 165–166.

193. HABECK, J. R., AND E. HARTLEY 1965. The vegetation of Montana: a bibliography. Northwest Sci. 39: 60–72.

194. HABECK, J. R., AND R. W. MUTCH. 1973. Fire-dependent forests in the northern Rocky Mountains. Quat. Res. 3: 408–424.

195. HABECK, J. R., AND T. WEAVER. 1969. A chemosystematic analysis of some hybrid spruce (*Picea*) populations in Montana. Canadian J. Bot. 47: 1565–1570.

196. HADDEN, D. A., W. J HANN, AND C. J JONKEL. 1985. An ecological taxonomy for evaluation of grizzly bear habitat in the Whitefish Range of Montana. Proc. Grizzly Bear Habitat Symp., 2–3 May 1985. Interagency Grizzly Bear Committee.

197. HAGLUND, B. M. 1972. Ecological effects of weather modification, Bangtail Ridge, Bridger Range, Montana: relationships of pocket gophers (*Thomomys talpoides*) to time of snow melt. Unpublished thesis, Montana State University, Bozeman. 26 pp.

198. HAKIM, S. E. A. 1975. Range condition on the Threemile Game Range in western Montana. Unpublished thesis, University of Montana, Missoula. 62 pp.

199. HAMLIN, K. L. 1974. Ecological relationships of mule deer in the Bridger Mountains, Montana, with special reference to daily and seasonal movements. Manuscript. Montana State University, Bozeman. 65 pp.

200. HANN, W. J. 1982. A taxonomy for classification of seral vegetation of selected habitat types in western Montana. Unpublished dissertation, University of Idaho, Moscow. 235 pp.

201. HANSEN, H. P. 1948. Postglacial forests of the Glacier National Park region. Ecology 29: 146–152.

202. HANSEN, P. L. 1985. An ecological study of the vegetation of the Grand River/Cedar River, Sioux, and Ashland districts of the Custer National Forest. Unpublished dissertation, South Dakota State University, Brookings. 257 pp.

203. HANSEN, P. L. 1986. Riparian dominance types. *In:* Riparian vegetation work session, 3–4 June 1986, Helena, Montana. Unpublished proceedings. 8 pp.

204. HANSEN, P. L., S. W. CHADDE, AND R. D. PFISTER. 1987. Riparian dominance types of Montana. Review draft, August 14. Montana Riparian Association, School of Forestry, University of Montana, Missoula. 358 pp.

205. HANSEN, P. L., AND G. R. HOFFMAN. 1985. An ecological study of the vegetation of the Grand River/Cedar River, Sioux, and Ashland districts of the Custer National Forest: a habitat type classification. USFS Coop Agreement No. RM-80-131-CA. University of South Dakota, Vermillion. 249 pp.

206. HANSEN, P. L., G. HOFFMAN, AND G. STECHANER. 1985. Upland forest and woodland habitat types of the Missouri Plateau, Great Plains province. *In:* Proceedings, Wooded draws: characteristics and values for the northern High Plains Symposium, Rapid City, South Dakota. Great Plains Agr. Counc. 12 pp.

207. HARTLEY, E. A. 1976. Man's effects on the stability of alpine and subalpine vegetation in Glacier National Park, Montana. Unpublished dissertation, Duke University, Durham, North Carolina. 277 pp. (Diss. Abstr. 37: 2642 B).

208. HARVEY, S. J. 1980. The potential and current vegetation of the Sun River Game Range. Montana Department of Fish, Wildlife and Parks. Helena, Montana. 85 pp.

209. HARVEY, S. J 1981. Life history and reproductive strategies in *Artemisia*. Unpublished thesis, Montana State University, Bozeman. 132 pp.

210. HARVEY, S. J. 1982. Vegetation of Musselshell and Petroleum counties, Montana. Unpublished report to the Soil Conservation Service, Roundup, Montana. 27 pp.

211. HARVEY, S. J., AND T. WEAVER. 1979. Vegetative reproduction in twenty-one native shrubs in Montana. Proc. Mont. Acad. Sci. 38: 73–77.

212. HAVARD, V. 1878. Botanical outlines of the country marched over by the Seventh United States Cavalry during the summer of 1877. Pages 1681–1687 *in* U.S. House of Rep. 45th Cong., 3rd Sess., (H. Ex. Doc. 1). U.S. Government Printing Office, Washington, D.C.

213. HEADY, H. F. 1950. Studies on bluebunch wheatgrass in Montana and height-weight relationships of certain range grasses. Ecol. Monogr. 20: 56–81.

214. HEINSELMAN, M. L. 1981. Fire intensity and frequency as factors in the distribution and structure of northern ecosystems. *In:* H. Mooney, et al., The role of past and present fire frequency and intensity on ecosystem development and management.

215. HEMMER, D. M. 1975. Serviceberry: ecology, distribution, and relationships to big game. Unpublished thesis, University of Montana, Missoula. 76 pp.

216. HEMPHILL, M. L. 1983. Fire, vegetation and people —charcoal and pollen analysis of Sheep Mountain Bog, Montana: the last 2800 years. Unpublished thesis, Washington State University, Pullman. 70 pp.

217. HEUSSER, C. J. 1969. Late-pleistocene coniferous forests of the northern Rocky Mountains. Pages 1–21 *in* R. D. Taber, ed., Coniferous forests of the northern Rocky Mountains. Proc. 1968 Symp., University of Montana, Missoula.

218. HEYWARD, P., R. WRIGHT, AND E. KRUMPE. 1984a. Glacier National Park Biosphere Reserve: a history of scientific study. Vol. I. A narrative description of scientific studies. U.S. Man and the Biosphere Progress Report #9. University of Idaho, Moscow. 137 pp.

219. HEYWARD, P., R. WRIGHT, AND E. KRUMPE. 1984b. Glacier National Park Biosphere Reserve: a history of scientific study. Vol. II: Biblio., subject annotat., tabular data summ., and app. U.S. Man and the Biosphere Report #9. University of Idaho, Moscow. 198 pp.

220. HOFFMAN, G. R., AND P. L. HANSEN. 1981. Habitat types of the Custer National Forest. USFS contract RM-RFP-80-131-CA. Rocky Mountain Forest and Range Experiment Station, Forest Research Lab, South Dakota School of Powder River Co. Mines and Technology, Rapid City, South Dakota.

221. HOUSTON, D. B. 1973. Wildfires in northern Yellowstone National Park. Ecology 54: 1111–1117.

222. HOUSTON, W. R. 1961. Some interrelations of sagebrush, soils and grazing intensity in the northern Great Plains. Ecology 42: 31–38.

223. HUMES, H. R. 1960. The ecological effects of fire on natural grasslands in western Montana. Unpublished thesis, University of Montana, Missoula. 85 pp.

224. HUSBY, P. 1982. Effects of grazing on vegetation in the *Artemisia tridentata–Festuca idahoensis* habitat type. Unpublished thesis, Montana State University, Bozeman. 76 pp.

225. HUSBY, P., AND J. ANTOS. 1978. Vegetation inventory and analysis of the proposed Nance Mine site. Interim report by Olson-Elliot and Assoc. to Montana Department of State Lands. 67 pp.

226. HUSBY, P., J. ANTOS, J. ELLIOT, AND T. OLSON. 1979. Vegetation inventory and analysis of the Montco project area. Interim report. Olson-Elliot and Assoc., Helena, Montana.

227. HUSTED, W. M. 1974. Prehistoric occupation of the alpine zone in the Rocky Mountains. Pages 857–872 *in* J. D. Ives and R. G. Barry, eds., Arctic and alpine environments. Methuen, London.

228. ILLGNER, J. L. 1977. Squaw Rock, a proposed Montana State Natural Area. Unpublished thesis, University of Montana, Missoula. 132 pp.

229. INTERMOUNTAIN FIRE RESEARCH COUNCIL. 1970. The role of fire in the Intermountain West. Proceedings of a symposium held at Missoula, Montana, 27–29 October 1970. Intermountain Fire Research Council and School of Forestry, University of Montana, Missoula. 229 pp.

230. JAMESON, D. A. 1952. The chemical composition and utilization of greasewood and other browse species as related to some aspects of cattle nutrition on winter ranges in southeastern Montana. Unpublished thesis, Montana State University, Bozeman. 77 pp.

231. JANSSON, J. R. 1949. A survey of old growth Douglas-fir stands in the Big Belt Mountains of Montana. Unpublished thesis, University of Montana, Missoula. 60 pp.

232. JANSSON, J. R. 1951. Some effects of fire upon Douglas-fir soils in the Big Belt Mountains. Proc. Mont. Acad. Sci. 9: 17–21.

233. JOHNSON, J. L., AND R. D. PFISTER. 1981. A survey of potential ecological natural landmarks of the northern Rocky Mountains. Intermountain Forest and Range Experiment Station, Ogden, Utah. 416 pp.

234. JOHNSON, J. L., AND R. D. PFISTER. 1982. A survey of potential ecological natural landmarks of the middle Rocky Mountains. Intermountain Forest and Range Experiment Station, Ogden, Utah. 197 pp.

235. JOHNSON, J. R. 1966. The effects of some environmental influences on big sagebrush, *Artemisia tridentata* Nutt. reinvasion. Unpublished thesis, Montana State University, Bozeman. 100 pp.

236. JOHNSON, P., AND C. YOUMANS. 1983. Western Energy Co. vegetation report for mining area C. 1982. Project No. 295-83-A. Econ, Inc. 75 pp. + app.

237. JOHNSON, P. L. 1961. The alpine vegetation of the Beartooth Plateau in relation to cryopedogenic processes and patterns. Unpublished dissertation, Duke University, Durham, North Carolina. 203 pp. (Diss. Abstr. 23: 41).

238. JOHNSON, P. L., AND W. D. BILLINGS. 1962. The alpine vegetation of the Beartooth Plateau in relation to cryopedogenic patterns and processes. Ecol. Monogr. 32: 105–135.

239. JOHNSON, T. W. 1982. An analysis of pack and saddle stock grazing areas in the Bob Marshall Wilderness, Montana. Unpublished thesis, Montana State University, Bozeman. 105 pp.

240. JONAS, R. 1966. Merriam's turkey in southeastern Montana. Montana Department of Fish and Game, Tech. Bull. No. 3: 1–36.

241. JONES, M. E. 1910. Life zones. Contrib. to West. Bot. 13: 52–58.

242. JONKEL, C. 1977. Border grizzly project. Annual Report No. 2. School of Forestry, University of Montana, Missoula. 134 pp.

243. JORGENSEN, H. E. 1970. Ecological aspects of the life history of *Agropyron smithii* Rydb. in central Montana with related effects of selective herbicide treatments of rangeland. Unpublished dissertation, Montana State University, Bozeman.

244. JORGENSEN, H. E. 1976. Development of a habitat type classification system for the vegetation of

eastern Montana. Project #W120R7. Study #H-3.1. Job #1. Montana Department of Fish and Game. 7 pp.

245. JORGENSEN, H. E. 1979. Vegetation of the Yellow Water Triangle, Montana. Montana Department of Fish and Game, in cooperation with the Bureau of Land Management. Helena, Montana. 57 pp.

246. JOY, J., AND J. COLE. 1975. Deerlodge National Forest vegetative habitat types. 41 pp.

247. KAMPS, G. F. 1969. Whitetail and mule deer relationships in the Snowy Mountains of central Montana. Montana Department of Fish and Game. Project W-98-R-8,9 and W-74-R-13,14. Unpublished thesis, Montana State University, Bozeman. 59 pp.

248. KEELEY, J. E. 1981. Reproductive cycles and fire regimes. Pages 231–277 *in* H. Mooney, et al., The role of past and present fire frequency and intensity on ecosystem development and management. USDA For. Serv. Gen. Tech. Rept. WO-26.

249. KELLER, M. C. 1980. Postfire recovery within ravine forest communities of Pattee Canyon, Missoula, Montana. Unpublished thesis, University of Montana, Missoula. 136 pp.

250. KELLY, M. F. 1941. Effect of *Fomes igniarius* on *Populus tremuloides* in the Gallatin National Forest of Montana. Proc. Mont. Acad. Sci. 2: 49.

251. KEOWN, L. D. 1977. Blacktail Hills prescribed fire project implementation and results. Unpublished interim report, 28 February 1977. Lewis and Clark National Forest, Great Falls, Montana. 8 pp.

252. KEOWN, L. D. 1982. An evaluation of qualitative plant responses to prescribed burning on a central Montana ecosystem. Unpublished draft manuscript, December 1982. Lewis and Clark National Forest, Great Falls, Montana.

253. KESSELL, S. R. 1976. Wildland inventories and fire modeling by gradient analysis in Glacier National Park. Tall Timbers Fire Ecology Conference 14: 115–162.

254. KESSELL, S. R. 1979. Gradient modeling: resource and fire management. Springer-Verlag, New York. 432 pp.

255. KESSELL, S. R., AND W. C. FISCHER. 1981. Predicting postfire plant succession for fire management planning. USDA For. Serv. Gen. Tech. Rept. INT-94. Intermountain Forest and Range Experiment Station, Ogden, Utah.

256. KILGORE, B. M. 1981. Fire in ecosystem distribution and structure: western forests and scrublands. *In:* H. Mooney, et al., The role of past and present fire frequency and intensity on ecosystem development and management. USDA For. Serv. Gen. Tech. Rept. WO-26.

257. KIRKWOOD, J. E. 1922. Forest distribution in the northern Rocky Mountains. Bull. No. 247, State University Studies Series No. 2. University of Montana, Missoula. 180 pp.

258. KIRKWOOD, J. E. 1926. Botany of the Montana Rockies. Torreya. 26: 105–109.

259. KIRKWOOD, J. E. 1927a. Botanical explorations in the Rocky Mountains. Scientific Monthly 24: 236–250.

260. KIRKWOOD, J. E. 1927b. Botanical explorations in the Rocky Mountains—Selway River. Scientific Monthly 25: 515–528.

261. KIRKWOOD, J. E. 1927c. The pacific element in the Rocky Mountain flora. Northwest Sci. 1: 14.

262. KIRKWOOD, J. E. 1928. Botanical explorations in the Rocky Mountains—the Lolo Trail. Scientific Monthly 26: 315–328.

263. KLEBENOW, D. A. 1962. Ecology and productivity of a montane forest winter deer range, western Montana. Unpublished thesis, University of Montana, Missoula. 93 pp.

264. KLEBENOW, D. A. 1965. A montane forest winter deer habitat in western Montana. J. Wildl. Mgt. 29: 27–33.

265. KNAPP, S. J. 1972. Range use of mule deer prior to initiation of rest rotation grazing for cattle on the Fort Howes Ranger District, Custer National Forest, Montana. Unpublished thesis, Montana State University, Bozeman. 50 pp.

266. KNIGHT, R. R. 1960. Vegetative characteristics of two water areas in Teton County, Montana, in relation to waterfowl usage. Unpublished thesis, Montana State University, Bozeman. 38 pp.

267. KNIGHT, R. R. 1965. Vegetative characteristics and waterfowl usage of a Montana water area. J. Wildl. Mgt. 29: 782–788.

268. KNIGHT, R. R. 1970. The Sun River elk herd. Wildlife Soc. Publ. 23: 1–66.

269. KNOWLTON, F. F. 1960. Food habits, movements, and populations of moose in the Gravelly Mountains, Montana. J. Wildl. Mgt. 24: 162–170.

270. KNUDSEN, G. M., S. F. ARNO, J. R. HABECK, AND G. M. BLAKE. 1968. Natural distribution of western larch (*Larix occidentalis*) and subalpine larch (*Larix lyallii*). Montana Forest and Conservation Experiment Station, Res. Note 7. Missoula, Montana. 5 pp.

271. KOCH, E. 1942. History of the 1910 forest fires in Idaho and western Montana. 25 pp. Mimeographed report prepared in 1942, reproduced by Coeur d'Alene N.F. in 1976 under title "When the mountains roared, stories of the 1910 forest fire." 39 pp.

272. KOTERBA, W. D. 1968. An analysis of the North Fork Valley grasslands in Glacier National Park, Montana. Unpublished thesis, University of Montana, Missoula. 81 pp.

273. KOTERBA, W. D., AND J. R. HABECK. 1971. Grasslands of the North Fork Valley, Glacier National Park, Montana. Canadian J. Bot. 49: 1627–1636.

274. KUCERA, C. L. 1981. Grassland and fire. Pages 90–111 *in* H. Mooney, et al., The role of past and present fire frequency on ecosystem development and management. USDA For. Serv. Gen. Tech. Rept. WO-26.

275. LACKSCHEWITZ, K. H. 1970. Alpine and timberline flora in the Bitterroot Mountains, Montana. Proc. Mont. Acad. Sci. 30: 1–30.

276. LARSEN, J. A. 1930. Forest types of the northern Rocky Mountains and their climatic controls. Ecology 11: 631–672.

277. LARSEN, J. A., AND C. C. DELAVEN. 1922. Climate and forest fires in Montana and northern Idaho, 1909 to 1919. Montana Weather Rev. 49: 55–68.

278. LAUENROTH, W. K., J. L. DODD, R. HEITSCHMIDT, AND R. G. WOODMANSEE. 1975. Biomass dynamics and primary production in mixed prairie grasslands in southeastern Montana. Pages 559–578 *in*

Proc. Fort Union Coal Field Symp., Mont. Acad. Sci., Billings, Montana.

279. LAUFF, G. H. 1953. A contribution to the water chemistry and phytoplankton relationships of Rogers Lake, Flathead County, Montana. Proc. Mont. Acad. Sci. 13: 5–19.

280. LEBARRON, R. K., AND G. M. JEMISON. 1953. Ecology and silviculture of the Engelmann spruce–alpine fir type. J. For. 51: 349–355.

281. LEE, L. C. 1979. A study of plant associations in upland riparian habitats in western Montana. Unpublished thesis, University of Montana, Missoula. 250 pp.

282. LEE, L. C. 1983. Floodplain and wetland vegetation of two Pacific Northwest river ecosystems. Unpublished dissertation, University of Washington, Seattle. 284 pp. (Diss. Abstr. 44: 966-B).

283. LEE, L. C., AND C. J. JONKEL. 1980. The vegetation structure and ecology of grizzly bear habitat in the Pine and Antelope Butte wetlands, Montana. Border Grizzly Project Special Rept. No. 36. University of Montana, Missoula. 63 pp.

284. LEE, L. C., AND C. J. JONKEL. 1981. Grizzlies and wetlands. West. Wildlands 7(4): 26–30.

285. LEE, L. C., AND R. D. PFISTER. 1978. A training manual for Montana forest habitat types. Montana Forest and Conservation Experiment Station, University of Montana, Missoula.

286. LEIBERG, J. B. 1900. Bitterroot Forest Reserve. 20th Annual Report, U.S. Geological Survey (1898–99), Part V: 317–410.

287. LEIBERG, J. B. 1904a. Forest conditions in the Absaroka Division of the Yellowstone Forest Reserve, Montana, and the Livingston and Big Timber Quadrangles. U.S. Geological Survey, Prof. Pap. No. 29. 148 pp.

288. LEIBERG, J. B. 1904b. Forest conditions in the Little Belt Mountains Forest Reserve, Montana, and the Little Belt Mountains Quadrangle. U.S. Geological Survey, Prof. Pap. No. 30. 75 pp.

289. LESICA, P. 1982. Vegetation of the wetland and riparian areas of Pine Butte Preserve, Teton County, Montana. Report to The Nature Conservancy, Helena, Montana. 50 pp.

290. LESICA, P. 1986. Vegetation and flora of Pine Butte fen, Teton County, Montana. Great Basin Nat. 46: 22–32.

291. LEWIS, B. P. 1967. Forage production and utilization in western Montana clearcuts. Unpublished thesis, University of Montana, Missoula. 101 pp.

292. LOMMASSON, T. 1946. Transition of sagebrush, *Artemisia tridentata*, on high mountain rangeland in southwestern Montana, 1915–1945. Developments in Range Mgt. No. 4: 1–7, U.S. For. Serv. Region 1, Missoula, Montana.

293. LOMMASSON, T. 1947. Transition of sagebrush, *Artemisia tridentata*, on the semi-arid foothills of the upper Missouri River Valley following burning. Developments in Range Management No. 6: 1–2. U.S. For. Serv. Region 1, Missoula, Montana.

294. LOMMASSON, T. 1948. Succession in sagebrush. J. Range Mgt. 1: 19–21.

295. LONNER, T. N. 1972. Age distributions and some relationships of key browse plants on big game ranges in Montana. Wildlife Res. Final Report, Montana Fish and Game Department, Helena, Montana. 79 pp.

296. LONNER, T. N. 1973. Age distributions and some relationships of key browse plants on big game ranges in Montana. Unpublished thesis, Montana State University, Bozeman. 79 pp.

297. LOVAAS, A. L. 1958. Mule deer food habits and range use, Little Belt Mountains, Montana. J. Wildl. Mgt. 22: 275–282.

298. LUNAN, J. S. 1972. Phytosociology and fuel description of *Pinus ponderosa* communities in Glacier National Park. Unpublished thesis, University of Montana, Missoula. 79 pp.

299. LUNAN, J. S., AND J. R. HABECK. 1973. The effects of fire exclusion on ponderosa pine communities in Glacier National Park, Montana. Canadian J. For. Res. 3: 574–579.

300. LYNCH, D. 1955. Ecology of the aspen groveland in Glacier County, Montana. Ecol. Monogr. 25: 321–344.

301. LYON, J. L. 1976. Vegetal development on the Sleeping Child burn in western Montana, 1961 to 1973. USDA For. Serv. Res. Pap. INT-184. Intermountain Forest and Range Experiment Station, Ogden, Utah. 24 pp.

302. LYON, J. L., AND P. F. STICKNEY. 1976. Early vegetal succession following large northern Rocky Mountain wildfires. Proc. Tall Timbers Fire Ecology Conference 14: 355–375.

303. MACCRACKEN, J. G., L. E. ALEXANDER, AND D. W. URESK. 1983. An important lichen of southeastern Montana rangelands. J. Range Mgt. 36(1): 35–37.

304. MACCRACKEN, J. G., AND D. W. URESK. 1984. Big game habitat use in southeastern Montana. The Prairie Nat. 16(3): 135–139.

305. MACCRACKEN, J. G., D. W. URESK, AND R. M. HANSEN. 1983. Plant community variability on a small area in southeastern Montana. Great Basin Nat. 43: 660–668.

306. MACE, D. R. 1984. Identification and evaluation of grizzly bear habitat in the Bob Marshall Wilderness Area, Montana. Unpublished thesis, University of Montana, Missoula. 176 pp.

307. MACKIE, R. J. 1965. Range ecology and relationships of mule deer, elk, and cattle in the Missouri River breaks, Montana. Unpublished dissertation, Montana State University, Bozeman. 229 pp.

308. MACKIE, R. J. 1970. Range ecology and relations of mule deer, elk, and cattle in the Missouri River breaks, Montana. Wildl. Monogr. 20: 1–79.

309. MAGADDINO, R. 1978. Browse condition and trend survey on the National Bison Range, Moise, Montana. 8 pp.

310. MAJERUS, M. E., AND K. PROCTOR. 1974. Timber resource analysis, Young's Creek study area. Prepared for Special Projects Group, Shell Oil Co., Montana Agricultural Experiment Station, Bozeman, Montana.

311. MAJERUS, M. E., AND B. W. SINDELAR. 1974. Range resource analysis, Young's Creek study area. Prepared for Special Projects Group, Shell Oil Co., Montana Agricultural Experiment Station, Bozeman, Montana. 32 pp.

312. MALANSON, G. P., AND D. R. BUTLER. 1984. Transverse pattern of vegetation on avalanche paths in the northern Rocky Mountains, Montana. Great Basin Nat. 44: 453–458.

313. MALOUF, C. 1969. The coniferous forests and their use in the northern Rocky Mountains through 9000 years of prehistory. Pages 271–290 *in* Coniferous forests of the northern Rocky Mountains. Proc. Center for Natural Resources, University of Montana, Missoula.

314. MARCUM, C. L. 1971. Vegetal development on montane fir clearcuts in western Montana. Unpublished thesis, University of Montana, Missoula. 122 pp.

315. MARCUM, C. L. 1975. Summer-fall habitat selection and use by a western Montana elk herd. Unpublished dissertation, University of Montana, Missoula. 188 pp.

316. MARTIN, P. R. 1972. Ecology of skunkbrush sumac (*Rhus trilobata* Nutt.) in Montana with special reference to use by mule deer. Unpublished thesis, Montana State University, Bozeman. 97 pp.

317. MARTINKA, C. J. 1968. Habitat relationships of white-tailed deer in northern Montana. J. Wildl. Mgt. 32: 558–565.

318. MASTROGUISEPPE, R. R., M. E. ALEXANDER, AND W. H. ROMME. 1983. Forest and rangeland fire history bibliography. USDA For. Serv., Intermountain Forest and Range Experiment Station, Northern Forest Fire Lab, Missoula, Montana. 49 pp.

319. MATTOX, J. E. 1955. A study of percent of plants grazed method of utilization determination and its application. Montana State College Agricultural Experiment Station. Mimeo Cir. No. 88. 140 pp.

320. MATTSON, D. J., AND D. G. DESPAIN. 1985. Grizzly bear habitat component mapping handbook for the Yellowstone ecosystem. Interagency Grizzly Bear Study Team: National Park Service and U.S. Forest Service, May 1985. 37 pp.

321. MCALLISTER, D. C. 1981. CX ranch project: vegetation inventory. Unpublished report prepared by Olson-Elliot and Assoc., Helena, Montana. 283 pp.

322. MCALLISTER, D. C. 1983a. Forest habitat types on the Pine Butte Swamp Preserve. Report to The Nature Conservancy, Helena, Montana.

323. MCALLISTER, D. C. 1983b. A study of nonforested plant communities on the Pine Butte Swamp Preserve. Report to The Nature Conservancy, Helena, Montana.

324. MCARTHUR, K. L. 1979. Apgar terrestrial resources inventory. USDI, National Park Service, Glacier National Park, West Glacier, Montana. 57 pp.

325. MCCLELLAND, J. D. 1983. Growth response of *Agropyron smithii* and *Bouteloua gracilis* to simulated grazing and water treatments. Unpublished thesis, Montana State University, Bozeman. 55 pp.

326. MCCULLOUGH, Y. B. 1980. Niche separation of seven North American ungulates on the National Bison Range, Montana. Unpublished dissertation, University of Michigan, Ann Arbor. 226 pp.

327. MCCUNE, B. 1979. Comparative ecology of structural groups: compositional patterns in the Swan Valley forests, Montana. Unpublished thesis, University of Montana, Missoula. 94 pp.

328. MCCUNE, B. 1982. Fire frequency reduced two orders of magnitude in the Bitterroot canyons, Montana. Canadian J. For. Res. 13: 212–218.

329. MCCUNE, B., AND T. F. H. ALLEN. 1984. Will similar forests develop on similar sites? Canadian J. Bot. 53: 367–376.

330. MCCUNE, B., AND T. F. H. ALLEN. 1985. Forest dynamics in the Bitterroot canyons, Montana. Canadian J. Bot. 63: 377-383.

331. MCCUNE, B., AND J. A. ANTOS. 1981a. Correlations between forest layers in the Swan Valley, Montana. Ecology 62: 1196–1204.

332. MCCUNE, B., AND J. A. ANTOS. 1981b. Diversity relationships of forest layers in the Swan Valley, Montana. Bull. Torr. Bot. Club 108: 354–361.

333. MCCUNE, B., AND J. A. ANTOS. 1982. Epiphyte communities of the Swan Valley, Montana. The Bryologist 85: 1–12.

334. MCMULLIN, R. R. 1953. A study of variation in a *Dodecatheon* (Primulaceae) colony in western Montana. Unpublished thesis, University of Montana, Missoula. 48 pp.

335. MCNEAL, A. F. 1984. Site characteristics and effect on elk and mule deer use of the Gardiner Winter Range, Montana. Unpublished thesis, Montana State University, Bozeman. 133 pp.

336. MCNEAL, A. F., AND T. WEAVER. 1982. Soil compaction as a determinant of subalpine snowdrift vegetation. Proc. Mont. Acad. Sci. 41: 46–50.

337. MCWILLIAMS, J. L., AND P. E. VAN CLEAVE. 1960. A comparison of crested wheatgrass and native grass mixtures seeded on rangeland in eastern Montana. J. Range Mgt. 13: 91–94.

338. MEHRINGER, P. J., S. F. ARNO, AND K. L. PETERSEN. 1977. Postglacial history of Lost Trail Pass bog, Bitterroot Mountains, Montana. Arctic and Alpine Res. 9: 345–368.

339. MILLER, J. G. 1978. An ecological study of creeping juniper (*Juniperus horizontalis* Moench) in Montana. Montana Fish and Wildlife Management manuscript, Montana State University, Bozeman. 129 pp.

340. MILLER, M. 1976. Shrub sprouting response to fires in a Douglas-fir/western larch ecosystem. Unpublished thesis, University of Montana, Missoula. 124 pp.

341. MILLER, M. 1977. Response of blue huckleberry to prescribed fires in a western Montana larch-fir forest. USDA For. Serv. Res. Pap. INT-188. Intermountain Forest and Range Experiment Station, Ogden, Utah.

342. MITCHELL, M. D. 1983. Westmoreland data set. Exhibit H–12. Vegetation. Westmoreland Resources, Inc. Unpublished report.

343. MITCHELL, W. W. 1957. An ecological study of the grasslands in the region of Missoula, Montana. Unpublished thesis, University of Montana, Missoula. 111 pp.

344. MONTANA DEPARTMENT OF NATURAL RESOURCES AND CONSERVATION. 1979a. Circle West vegetation monitoring study: first annual report. Report No. 3. Montana Department of Natural Resources and Conservation, Helena, Montana.

345. MONTANA DEPARTMENT OF NATURAL RESOURCES AND CONSERVATION. 1979b. Circle West vegetation monitoring study: second annual report. Report No. 5. Montana Department of Natural Resources and Conservation, Helena, Montana.

346. MOORE, C. T. 1972. Man and fire in the central North American grassland 1535–1890: a documentary historical geography. Unpublished dissertation, University of California at Los Angeles. 155 pp.

347. MOORE, G. L., AND L. D. CULWELL. 1981. Baseline vegetation analysis of the Bull Mountain study area, Musselshell County, Montana. Prepared for Bull Mountain Coal Co., Roundup, Montana. 21 pp.

348. MORRIS, M. S. 1945. An ecological basis for the classification of the Montana grasslands. Proc. Mont. Acad. Sci. 5: 41–44.

349. MORRIS, M. S. 1947. The grazing use of forest lands in the northern Rocky Mountain region. Pages 303–311 *in* Proc. Soc. Amer. For.

350. MORRIS, M. S. 1970. Comprehensive network site description: bison grassland biome. U.S. International Biological Program Tech. Rept. No. 37, Colorado State University, Fort Collins.

351. MORRIS, M. S., AND J. D. BRUNNER. 1971. Primary productivity of the fescue grassland in western Montana. Grassland Biome, U.S. International Biological Program Tech. Rept. No. 113, Colorado State University, Fort Collins. 74 pp.

352. MORRIS, M. S., R. KELSEY, AND D. GRIGGS. 1976. The geographic and ecological distribution of big sagebrush and other woody *Artemisias* in Montana. Proc. Mont. Acad. Sci. 36: 56–79.

353. MORRIS, M. S., AND R. E. LOVEGROVE. 1975. The topographic and edaphic distribution of several plant communities of warm and cool season species in southeastern Montana. Proc. Fort Union Coal Field Symp. 5: 684–702. Mont. Acad. of Sci., Billings, Montana.

354. MORRIS, M. S., AND J. E. SCHWARTZ. 1957. Mule deer and elk food habits on the National Bison Range. J. Wildl. Mgt. 21: 189–193.

355. MOSELEY, ROBERT. 1987. Synecological relationships of alpine spike-fescue (*Leucopoa kingii* [Wats.] Weber) grasslands in east-central Idaho, USA. Unpublished report in preparation for Arctic and Alpine Res. 33 pp.

356. MUEGGLER, W. F. 1967. Response of mountain grassland vegetation to clipping in southwestern Montana. Ecology 48: 942–949.

357. MUEGGLER, W. F. 1971. Weather variations on a mountain grassland in southwestern Montana. USDA For. Serv. Res. Pap. INT-99. Intermountain Forest and Range Experiment Station, Ogden, Utah. 25 pp.

358. MUEGGLER, W. F. 1972. Plant development and yield on mountain grasslands in southwestern Montana. USDA For. Serv. Res. Pap. INT-124. Intermountain Forest and Range Experiment Station, Ogden, Utah. 20 pp.

359. MUEGGLER, W. F., AND W. P. HANDL. 1974. Mountain grassland and shrubland habitat types of western Montana (Interim Rept., 1974.) USDA For. Serv., Intermountain Forest and Range Experiment Station, and Region 1. 89 pp.

360. MUEGGLER, W. F., AND W. L. STEWART. 1980. Grassland and shrubland habitat types of western Montana. USDA For. Serv. Gen. Tech. Rept. INT-66. Intermountain Forest and Range Experiment Station, Ogden, Utah. 154 pp.

361. MUIR, P. S., AND J. E. LOTAN. 1985. Serotiny and life history of *Pinus contorta* var. *latifolia*. Canadian J. Bot. 63: 938–945.

362. MULTITECH. Undated. Salem plant licensing information. Vol. VIII. Unpublished report prepared for Montana Power Co. 171 pp. + maps.

363. MUNN, L. 1977. Relationships of soils to mountain and foothill range habitat types and production in western Montana. Unpublished dissertation, Montana State University, Bozeman.

364. MUNSHOWER, F. E., AND E. J. DEPUIT. 1976. The effects of stack emissions on the range resource in the vicinity of Colstrip, Montana: progress report, 1975. Montana Agricultural Experiment Station Report No. 98. Montana State University, Bozeman. 112 pp.

365. MUNSHOWER, F. E., B. W. SINDELAR, AND D. R. NEUMAN. 1975. The effect of stack emissions on the range resource in the vicinity of Colstrip, Montana. Progress Report 1972–1974. Montana Agricultural Experiment Station Res. Rept. No. 71. 73 pp.

366. MURRAY, E. P. 1974. Species composition of a near-pristine grassland community: Montana. Proc. Mont. Acad. Sci. 34: 1–4.

367. MURRAY, R. B. 1961. A study of range condition in a fescue grassland in western Montana. Unpublished thesis, University of Montana, Missoula. 111 pp.

368. NELSON, E. W. 1936. Some phases of the land use problem in Montana. The Forestry Kaimin, School of Forestry, University of Montana, Missoula.

369. NERCO, INC. 1979. Spring Creek Coal Co. vegetation community descriptions. Prepared for Montana Department of State Lands. Northern Energy Resources Co., Portland, Oregon.

370. NIMIR, B. M. 1974. The effect of spring burning of big sagebrush-grassland (*Artemisia tridentata* Nutt. grassland) on the soil and vegetation. Unpublished thesis, Montana State University, Bozeman. 139 pp.

371. NOREM, W. L. 1940. Contrasting density changes of *Poa secunda* and *Bouteloua gracilis* in eastern Montana through seven years, including the extreme droughts of 1934 and 1936. Northwest Sci. 14: 92.

372. OEA RESEARCH. 1982. Beal Mining Co., German Gulch, environmental studies. Vegetation analysis. 87 pp.

373. OLSON, G. R. 1973. Range conditions on abandoned croplands in north central Montana. Unpublished thesis, University of Montana, Missoula. 96 pp.

374. OLSON, K. C. 1982. Effect of precipitation on mixed grass plant communities of southeastern Montana and its implications for grazing intensity. Unpublished thesis, Montana State University, Bozeman. 205 pp.

375. OLSON-ELLIOTT AND ASSOCIATES. 1975. Powerline effects on vegetation with special reference to southwest Montana: a literature review and rationale for evaluating impact of transmission line and access road construction and maintenance on vegetative communities. Report for Montana Department of Natural Resources.

376. OLSON-ELLIOTT AND ASSOCIATES. 1980. Vegetation inventory and analysis of the Montco vegetation study area. Final report for Montco, Billings, Montana. 181 pp.

377. PAC, D. F. 1976. Distribution, movements, and habitat use during spring, summer, and fall by mule deer associated with Armstrong Winter Range, Bridger Mountains, Montana. Unpublished thesis, Montana State University, Bozeman. 120 pp.

378. PARKER, A. J. 1982. Comparative structural/functional features in conifer forests of Yosemite and Glacier National Parks, USA. Amer. Midl. Nat. 107: 55–68.

379. PARKER, K. G. 1956. Range vegetational types, range condition and range sites in relation to the incidence of urolithiasis in range cattle. Unpublished thesis, Montana State University, Bozeman. 128 pp.

380. PARKER, T. 1986. Ecology of western red cedar groves. Unpublished dissertation, University of Idaho, Moscow. 187 pp.

381. PASE, C. P. 1958. An ecological study of sagebrush, *Artemisia tridentata* Nutt., in western Montana. Unpublished thesis, University of Montana, Missoula. 65 pp.

382. PATTEN, D. T. 1959. An ecological study of the "parks" of the Rocky Mountains in the Gallatin area of Montana. Unpublished thesis, University of Massachusetts, Amherst. 45 pp.

383. PATTEN, D. T. 1962. The vegetational pattern in relation to environments in the Madison Range, Montana. Unpublished dissertation, Duke University, Durham, North Carolina. 201 pp.

384. PATTEN, D. T. 1963. Vegetational pattern in relation to environments in the Madison Range, Montana. Ecol. Monogr. 33: 375-406.

385. PATTEN, D. T. 1968. Dynamics of the shrub continuum along the Gallatin River in Yellowstone National Park. Ecology 49: 1107–1112.

386. PATTEN, D. T. 1969. Succession from sagebrush to mixed conifer forest in the northern Rocky Mountains. Amer. Midl. Nat. 82: 229–240.

387. PAULLIN, D. G. 1971. The ecology of submerged aquatic macrophytes of Red Rock Lakes National Wildlife Refuge, Montana. Unpublished thesis, University of Montana, Missoula. 171 pp.

388. PAYNE, G. F. 1973. Vegetative rangeland types in Montana. Montana Agricultural Experiment Station. Bull. No. 671. Montana State University, Bozeman.

389. PAYNE, G. F. 1983. Southwestern Montana mountain vegetation and its reaction to 2,4-D. Montana Agricultural Experiment Station Res. Rept. No. 210. Montana State University, Bozeman.

390. PEMBLE, R. H. 1965. A survey of distribution patterns in the Montana alpine flora. Unpublished thesis, University of Montana, Missoula. 146 pp.

391. PETERSON, R. A. 1953. Cliff Lake Natural Area. Proc. Mont. Acad. Sci. 13: 29–33.

392. PFISTER, R. D. 1976. Land capability assessment by habitat types. Pages 312–325 *in* America's renewable resource potential—1975: the turning point. Proc. 1975 National Convention Soc. Amer. For.

393. PFISTER, R. D. 1977. Ecological classification of forest land in Idaho and Montana. Pages 329–358 *in* 1977 Proc. Ecol. Class. of For. Land in Canada and Northwest USA. University of British Columbia, Vancouver.

394. PFISTER, R. D. 1981. Status of forest successional studies in the northern Rocky Mountains. Pages 80–90 *in* Proc. 2nd U.S.-USSR Symp. on Biosphere Reserves, 10–15 March 1980. U.S. National Commission for Man and the Biosphere, Washington, D.C.

395. PFISTER, R. D. 1984. Forest habitat type classification in the western U.S. Pages 149–162 *in* Proc. Symp. on Site Productivity of Fast Growing Plantations. Vol. 1. International Union of Forestry Research Organizations. Pretoria, South Africa.

396. PFISTER, R. D., AND S. F. ARNO. 1980. Classifying forest habitat types based on potential climax vegetation. For. Sci. 26: 52–70.

397. PFISTER, R. D., AND R. F. BATCHELOR. 1984. Montana riparian vegetation types. West. Wildlands 9: 19–23.

398. PFISTER, R. D., AND R. DAUBENMIRE. 1975. Ecology of lodgepole pine, *Pinus contorta* Dougl. *In:* D. M. Baumgartner, ed., Management of lodgepole pine ecosystems, Symp. Proc. Washington State University Cooperative Extension Service, Vol. 1: 27–46.

399. PFISTER, R. D., B. L. KOVALCHIK, S. F. ARNO, AND R. C. PRESBY. 1977. Forest habitat types of Montana. USDA For. Serv. Gen. Tech. Rept. INT-34. Intermountain Forest and Range Experiment Station, Ogden, Utah. 174 pp.

400. PHILLIPS, W. S. 1963. Vegetational changes in the northern Great Plains. Agricultural Experiment Station Rept. No. 214. University of Arizona, Tucson. 185 pp.

401. PICTON, H. D. 1960. Migration patterns of the Sun River elk herd, Montana. J. Wildl. Mgt. 24: 279–290.

402. PIERCE, J. R. 1982. A floristic study of the Big Hole National Battlefield. Unpublished thesis, University of Montana, Missoula. 265 pp.

403. PIERCE, J. R. 1986. Wetland community types of west-central Montana. Unpublished draft report to U.S. Forest Service, Region 1, Missoula, Montana. 57 pp.

404. PLANTENBERG, P. L. 1983. Factors affecting vegetation development on mined land at Colstrip, Montana. Unpublished thesis, Montana State University, Bozeman. 121 pp.

405. POLK, R. B., AND K. N. BOE. 1950. Succession of trees in cut-over larch–Douglas-fir stock in western Montana. Proc. Mont. Acad. Sci. 10: 31–38.

406. PRODGERS, R. 1978. Circle West vegetation baseline study: final report. Circle West Tech. Rept. No. 1. Energy Division, Montana Department of Natural Resources and Conservation, Helena, Montana. 115 pp.

407. PRODGERS, R. 1981. Circle West vegetation monitoring study: third annual report. Circle West Tech. Rept. No. 7. Facility Siting Division, Montana Department of Natural Resources and Conservation, Helena, Montana. 48 pp.

408. PRODGERS, R. 1982. Circle West vegetation monitoring study: fourth annual report. Circle West Tech. Rept. No. 9. Energy Division, Montana Department of Natural Resources and Conservation, Helena, Montana. 38 pp.

409. PYRAH, D. B., AND H. E. JORGENSEN. 1974. Ecology of sagebrush control. Montana Department of Fish and Game, Project No. W-105-R-9. 129 pp.

410. PYRAH, D. B., H. E. JORGENSEN, AND R. O. WALLESTAD. 1972. Ecology of sagebrush control: vegetation, soils, precipitation, and soil moisture studies. Montana Department of Fish and Game, Project No. W-05-R-6. Job V-1.1. 79 pp.

411. QUINNILD, C., L. D. CULWELL, AND D. JORDAN. 1978. Vegetation study, Savage Mine control area. Unpublished technical report for Knife River Coal Co., Savage Mine, Richland County, Montana.

412. REHFELDT, G. E. 1978. Genetic differentiation of Douglas-fir populations from the northern Rocky Mountains. Ecology 59: 1264–1270.

413. REITZ, L. P. 1937. Crop regions in Montana as related to environmental factors. Montana State College Agricultural Experiment Station. Bull. No. 340. 84 pp.

414. RENNICK, R. B. 1981. Effects of prescribed burning on mixed prairie vegetation in southeastern Montana. Unpublished thesis, Montana State University, Bozeman. 144 pp.

415. ROATH, L. R. 1974. Evaluation of nitrogen fertilization and grazing effects on a porcupine grass (*Stipa spartaea* var. *curtiseta*) community. Unpublished thesis, Montana State University, Bozeman. 114 pp.

416. ROBERTS, D. W. 1980. Forest habitat types of the Bear's Paw Mountains and Little Rocky Mountains, Montana. Unpublished thesis, University of Montana, Missoula. 116 pp.

417. ROBERTS, D. W., J. I. SIBBERNSEN, AND R. D. PFISTER. 1979a. Forest habitat types of the Bear's Paw Mountains. Final report to the Bureau of Indian Affairs, Rocky Boy Agency, Montana. #6C59-0100032, Ammendment #1 (Contract No. YA-512-CT6-84) 60 pp.

418. ROBERTS, D. W., J. I. SIBBERNSEN, AND R. D. PFISTER. 1979b. Forest and woodland habitat types of northcentral Montana. Vol. 2: The Missouri River breaks. School of Forestry, University of Montana. IFRES for Bureau of Land Management, State Office, Res. Div., Billings, Montana. YA-512-CT6-84. 24 pp.

419. ROBERTS, D. W., J. I. SIBBERNSEN, AND R. D. PFISTER. 1979c. Forest habitat types of the Little Rocky Mountains. School of Forestry, University of Montana. IFRES for Bureau of Indian Affairs, Fort Belknap Agency Branch of Natural Resources, Harlem, Montana. Order #6C55-0100-130.

420. ROBINSON, D. H. 1956. Trees and forests of Glacier National Park. USDI, National Park Service Special Bulletin No. 4. 50 pp. (Reprinted in 1968 by the Glacier Natural History Association, Inc., West Glacier, Montana.)

421. ROE, A. L. 1956. The effect of competition in old growth western larch–Douglas-fir stands. Proc. Mont. Acad. Sci. 16: 41–45.

422. ROOT, R. A. 1968. Analysis of subalpine grasslands in western Montana. Unpublished thesis, University of Montana, Missoula. 72 pp.

423. ROSS, R. L., AND H. E. HUNTER. 1976. Climax vegetation of Montana based on soils and climate. USDA Soil Conservation Service, Bozeman, Montana. 64 pp.

424. ROSS, R. L., E. P. MURRAY, AND J. G. HAIGH. 1973. Soil and vegetation inventory of near-pristine sites, Montana. USDA Soil Conservation Service, Bozeman, Montana. 55 pp.

425. ROUSE, R. A. 1957. Elk food habits, range use and movements, Gravelly Mountains, Montana. Unpublished thesis, Montana State University, Bozeman. 29 pp.

426. RYDBERG, P. A. 1900. Phytogeography of Montana. Bull. Torr. Bot. Club 27: 292–294.

427. RYDBERG, P. A. 1914a. Phytogeographical notes on the Rocky Mountain region. II. Origin of the alpine flora. Bull. Torr. Bot. Club 41: 89–103.

428. RYDBERG, P. A. 1914b. Phytogeographical notes on the Rocky Mountain region. III. Formations in the alpine zone. Bull. Torr. Bot. Club 41: 459–474.

429. RYDBERG, P. A. 1915a. Phytogeographical notes on the Rocky Mountain region. IV. Forests of the subalpine and montane zones. Bull. Torr. Bot. Club 42: 11–15.

430. RYDBERG, P. A. 1915b. Phytogeographical notes on the Rocky Mountain region. V. Grasslands of the subalpine and montane zones. Bull. Torr. Bot. Club 42: 629–642.

431. RYDBERG, P. A. 1916a. Phytogeographical notes on the Rocky Mountain region. VI. Distribution of the subalpine plants. Bull. Torr. Bot. Club 43: 343–364.

432. RYDBERG, P. A. 1916b. Vegetative life zones of the Rocky Mountains. Mem. N.Y. Bot. Garden 6: 477–499.

433. RYDBERG, P. A. 1917. Phytogeographical notes on the Rocky Mountain region. VII. Formations in the subalpine zone. Bull. Torr. Bot. Club 44: 431–454.

434. RYDBERG, P. A. 1922. Phytogeographical notes on the Rocky Mountain region. X. Grasslands and other open formations of the montane zone of the southern Rockies. Bull. Torr. Bot. Club 48: 315–326.

435. RYKER, R. A. 1975. A survey of factors affecting regeneration of Rocky Mountain Douglas-fir. USDA For. Serv. Res. Pap. INT-174. Intermountain Forest and Range Experiment Station, Ogden, Utah. 19 pp.

436. SAMMONS, I. 1959. Flora of Logan Pass, Glacier National Park, Montana. Unpublished report, Department of Botany, University of Montana, Missoula. 16 pp.

437. SANDVIG, E. D. 1941. The wild land requirements for domestic livestock. Proc. Mont. Acad. Sci. 2: 50–57.

438. SAUNDERS, J. K. 1955. Food habits and range use of the Rocky Mountain goat in the Crazy Mountains, Montana. J. Wildl. Mgt. 19: 429–437.

439. SCHAEFFER, J. 1978. Forest habitat types of the Gallatin National Forest. Final draft. 62 pp.

440. SCHMIDT, W. C., R. C. SHEARER, AND A. L. ROE. 1976. Ecology and silviculture of western larch forests. USDA For. Serv. Tech. Bull. No. 1520. Washington, D.C. 96 pp.

441. SCHULER, J. H. 1968. The composition and distribution of Douglas-fir forest communities in the Pattee Canyon area, Missoula, Montana. Unpublished thesis, University of Montana, Missoula. 84 pp.

442. SCHWARZKOPH, W. F. 1973. Range use and relationships of mule deer on the west slope of the Bridger Mountains, Montana. Manuscript, Montana Department of Fish and Game, Project No. W-120-R-4. Job No. BG-4.04. Montana State University, Bozeman. 65 pp.

443. SCHWARZKOPH, W. F., AND D. SELL. 1978. Peabody Coal Co. Big Sky Mine annual small mammal and vegetation report for 1978. Unpublished.

444. SCOW, K. L. 1983. Appendix II. Vegetation inventory of the Landusky extension areas, Little Rocky Mountains, Montana. Unpublished report. Westech, Helena, Montana. 58 pp.

445. SCOW, K. L., AND L. D. CULWELL. 1986. Vegetation inventory of the Mill Gulch Extension area, Little Rocky Mountains, Montana. Unpublished report for Hydrometrics, Inc. Westech, Helena, Montana. 26 pp. + app.

446. SCOW, K. L., L. D. CULWELL, AND L. A. LARSEN. 1986. Vegetation inventory of the Chartam project area, Broadwater County, Montana. Unpublished report for Western Energy Co. Westech, Helena, Montana. 91 pp.

447. SCOW, K. L., L. D. CULWELL, AND L. A. LARSEN. 1987. Vegetation inventory of the Rock Creek study area, Sanders County, Montana. Unpublished report for Asarco, Inc. Westech, Helena, Montana.

448. SERVHEEN, C., AND L. C. LEE. 1979. Mission Mountain grizzly bear studies, an interim report, 1976–1978. Border Grizzly Project, Montana Forest and Conservation Experiment Station. University of Montana, School of Forestry, Missoula, Montana. 299 pp.

449. SHAW, C. 1967. The Flathead story. USDA For. Serv., Flathead National Forest, Kalispell, Montana. 145 pp.

450. SHEARER, R. C. 1959. Western larch seed dispersal over clear-cut blocks in northwest Montana. Proc. Mont. Acad. Sci. 19: 130–134.

451. SHEARER, R. C. 1960. First-year mortality of coniferous seedlings in the western larch–Douglas-fir type. Proc. Mont. Acad. Sci. 20: 18–19.

452. SHEARER, R. C. 1981. Silviculture. Pages 27–31 *in* N. V. DeByle, Clear cutting and fire in the larch/Douglas-fir forests of western Montana. USDA For. Serv. Gen. Tech. Rept. INT-99. Intermountain Forest and Range Experiment Station Ogden, Utah.

453. SHEARER, R. C., AND W. C. SCHMIDT. 1970. Natural regeneration in ponderosa pine forests of western Montana. USDA For. Serv. Res. Pap. INT-86. Intermountain Forest and Range Experiment Station, Ogden, Utah. 19 pp.

454. SIEG, C. H., D. W. URESK, AND R. M. HANSEN. 1983. Plant-soil relationships on bentonite mine spoils and sagebrush-grassland in the northern high plains. J. Range Mgt. 36: 289–294.

455. SIMMONS, C. A. 1974. Seasonal range use and migration patterns of elk using various portions of the Lower South Fork winter range. Montana Department of Fish and Game, Project No. W-120-R-5,6. Study No. 31.01, Job No. BG-3.14. 99 pp.

456. SIMS, P. L., AND J. S. SINGH. 1978. The structure and function of ten western North American grasslands. III. Net primary production, turnover and efficiencies of energy capture and water use. J. Ecology 66: 573–597.

457. SIMS, P. L., J. S. SINGH, AND W. K. LAUENROTH. 1978. The structure and function of ten western North American grasslands. I. Abiotic and vegetational characteristics. J. Ecology 66: 251–285.

458. SINDELAR, B. W. 1971. Douglas-fir invasion of western Montana grasslands, Missoula, Montana. Unpublished dissertation, University of Montana, Missoula. 131 pp.

459. SINDELAR, B. W. 1973a. A report of natural revegetation on abandoned coal spoils in the Colstrip, Montana, vicinity. Technical report prepared for Westinghouse Electric Corp.

460. SINDELAR, B. W. 1973b. Certain ecological analyses and information for study areas A, B, C, D, and E in the vicinity of Colstrip, Montana. Technical report prepared for Westinghouse Electric Corp.

461. SINDELAR, B. W. 1973c. Factors influencing plant species distribution in the Colstrip, Montana study area. Technical report prepared for Westinghouse Electric Corp.

462. SINGH, J. S., W. K. LAUENROTH, R. K. HEITSCHMIDT, AND J. L. DODD. 1983. Structural and functional attributes of the vegetation of northern mixed prairie of North America. Bot. Rev. 49: 117–149.

463. SKILBRED, C. L. 1979. Plant succession on five naturally revegetated strip-mined deposits at Colstrip, Montana. Unpublished thesis, Montana State University, Bozeman. 128 pp.

464. SMITH, B. L. 1976. Ecology of the Rocky Mountain goats in the Bitterroot Mountains, Montana. Unpublished thesis, University of Montana, Missoula. 203 pp.

465. SMITH, D. W. 1969. A preliminary classification and characterization of big sagebrush, *Artemisia tridentata* Nutt., communities in central Montana. Unpublished thesis, Montana State University, Bozeman. 68 pp.

466. SNECK, K. M. 1977. The fire history of Coram Experimental Forest. Unpublished thesis, University of Montana, Missoula. 134 pp.

467. SNYDER, R. O. 1969. Forage competition between cattle and elk in the Gird Creek drainage of western Montana. Unpublished thesis, University of Montana, Missoula. 76 pp.

468. SOUTH, P. R. 1957. Food habits and range use of the mule deer in the Scudder Creek area, Beaverhead County, Montana. Unpublished thesis, Montana State University, Bozeman. 34 pp.

469. SOUTH, P. R. 1974 (revised 1980). Pryor Mountain ecosystems, Custer National Forest, Billings, Montana. Unpublished report. 55 pp.

470. SPRAGG, F. A. 1902. Forage conditions of central Montana. Montana State College Agricultural Experiment Station Bull. No. 36. 40 pp.

471. STANDLEY, P. C. 1921. Flora of Glacier National Park, Montana. Contrib. U.S. Nat. Herb. 22: 235–438.

472. STARK, N. M. 1977. Fire and nutrient cycling in a Douglas-fir/larch forest. Ecology 58: 16–30.

473. STARK, N. M., AND R. STEELE. 1977. Nutrient content of forest shrubs following burning. Amer. J. Bot. 64: 1218–1224.

474. STAUFFER, J. M. 1976. Ecology and floristics of Ohio Slide and other avalanche tracks in Lost Horse

Canyon, Bitterroot Mountains, Montana. Unpublished thesis, University of Montana, Missoula. 146 pp.

475. STEENEY, W. F. 1979. Distribution, range use, and population characteristics of mule deer associated with the Schafer Creek Winter Range, Bridger Mountains, Montana. Montana Department of Fish and Game, Project No. W-120-R-8,9. Study No. BG-1.00.

476. STEFFEN, ROBERTSON, KIRSTEN, INC., AND MULTITECH. 1984. Mine permit application for Montana talc project. Prepared for Montana Talc Co., Ennis, Montana. 228 pp.

477. STERMITZ, J. E., M. G. KLAGES, AND J. E. LOTAN. 1974. Soil characteristics influencing lodgepole pine regeneration near West Yellowstone, Montana. USDA For. Serv. Res. Pap. INT-163. Intermountain Forest and Range Experiment Station, Ogden, Utah.

478. STEVENS, D. R. 1966. Range relationships of elk and livestock, Crow Creek drainage, Montana. J. Wildl. Mgt. 30: 349–363.

479. STEVENS, D. R. 1970. Winter ecology of moose in the Gallatin Mountains, Montana. J. Wildl. Mgt. 34: 37–46.

480. STEWART, R. E., AND H. A. KANTRUD. 1971. Classification of natural ponds and lakes in the glaciated prairie region. USDI, Fish and Wildlife Service, Resource Publication No. 92, Washington, D.C. 55 pp.

481. STEWART, S. T. 1975. Seasonal ecology of bighorn sheep in the Beartooth Mountains. Manuscript, Montana Department of Fish and Game, Project No. 1-120-R-6,7. Montana State University, Bozeman. 130 pp.

482. STEWART, W. L. 1976. Mountain grassland and shrubland habitat types of western Montana. Progress report FY-1976. USDA For. Serv. Region 1/Intermountain Forest and Range Experiment Station, Ogden, Utah.

483. STICKNEY, P. F. 1980. Data base for post-fire succession, first 6 to 9 years, in Montana larch-fir forests. USDA For. Serv. Gen. Tech. Rept. INT-62. Intermountain Forest and Range Experiment Station, Ogden, Utah. 133 pp.

484. STICKNEY, P. F. 1981. Vegetative recovery and development. Pages 32–40 *in* N.V. DeByle, Clear cutting and fire in the larch/Douglas-fir forests of western Montana. USDA For. Serv. Gen. Tech. Rept. INT-99. Intermountain Forest and Range Experiment Station, Ogden, Utah.

485. STURM, J. J. 1954. A study of a relic area in northern Montana. Wyoming Range Mgt. 72: 1–2.

486. SWENSON, J. E. 1981. The hardwood draws of southeastern Montana: their importance to wildlife and vulnerability to man's activities. Management of riparian ecosystems, Proc. Annual Meeting Montana Chapter, The Wildlife Society.

487. TACKLE, D. 1964. Regenerating lodgepole pine in central Montana following clear cutting. USDA For. Serv. Res. Note INT-17. Intermountain Forest and Range Experiment Station, Ogden, Utah.

488. TAHA, F. K. 1972. The role of some environmental and man-made factors on big sagebrush (*Artemisia tridentata* Nutt.) reinvasion. Unpublished thesis, Montana State University, Bozeman.

489. TAYLOR, D. L. 1974. Forest fires in Yellowstone National Park. J. For. History. 18: 68–77.

490. TAYLOR, J. E., AND T. L. HOLST. 1976. Grass and shrub plant community classification. Final report, USFS Contract Research Project 26-3494, Ashland District, Custer National Forest.

491. TAYLOR, J. E., W. C. LEININGER, AND R. J. FUCHS. 1975. Baseline vegetational studies near Colstrip. Proc. Fort Union Coal Field Symp. 5: 537–551.

492. TESCH, S. D. 1975. The composition and dynamics of the tree strata within an old growth Douglas-fir forest in western Montana. Unpublished thesis, University of Montana, Missoula. 141 pp.

493. THILENIUS, J. F. 1975. Alpine range management in the western United States—principles, practices, and problems. USDA For. Serv. Res. Pap. RM-157. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado. 32 pp.

494. THOMPSON, L. S. 1983. Shoreline vegetation in relation to water level at Toston Reservoir, Broadwater County, Montana. Proc. Mont. Acad. Sci. 42: 7–16.

495. THOMPSON, L. S. 1984. Biogeography of Montana: preliminary observations on major floristic and faunal distribution patterns. Proc. Mont. Acad. Sci. 43: 40–41.

496. THOMPSON, L. S., AND J. KUIJT. 1976. Montane and subalpine plants of the Sweetgrass Hills, Montana, and their relation to early postglacial environments of the northern Great Plains. Canadian Field-Nat. 90: 432–448.

497. TIRMENSTEIN, D. A. 1983. Grizzly bear habitat and management in the Rattlesnake National Recreation Area and Wilderness. Unpublished thesis, University of Montana, Missoula. 213 pp.

498. TISCH, E. L. 1961. Seasonal food habits of the black bear in the Whitefish Range of northwestern Montana. Unpublished thesis, University of Montana, Missoula. 108 pp.

499. TREE, W. E. 1971. Spruce-fir forests in the vicinity of Missoula, Montana. Unpublished thesis, University of Montana, Missoula. 84 pp.

500. TSCHACHE, O. P. 1970. Ecological effects of chemical and mechanical sagebrush control. Montana Department of Fish and Game, Project No. W-105-R-4,5. Job No. V.8.1. 51 pp.

501. TUINSTRA, K. E. 1967. Vegetation of the floodplains and first terraces of Rock Creek near Red Lodge, Montana. Unpublished dissertation, Montana State University, Bozeman. 110 pp.

502. VOGEL, W. G. 1960. Comparison of three range measurement techniques and a study of the response of native vegetation to protection from sheep grazing. Unpublished thesis, Montana State University, Bozeman. 168 pp.

503. VOGEL, W. G., AND G. M. VAN DYNE. 1966. Vegetation responses to grazing management on a foothill sheep range. J. Range Mgt. 19: 80–85.

504. VOGL, R. L., AND C. RYDER. 1969. Effects of slash burning on conifer reproduction in Montana's Mission Range. Northwest Sci. 43: 135–147.

505. VTN ENVIRONMENTAL CONSULTANTS. 1977. Vegetation: Spring Creek project. Unpublished technical report prepared for Northern Energy Resources Co. 47 pp. + app.

506. WALTON, T. P. 1984. Reproductive mechanisms of plains silver sagebrush, *Artemisia cana cana*, in

southeastern Montana. Unpublished thesis, Montana State University, Bozeman.

507. WARNER, R. A. 1970. Some aspects of browse production in relation to timber harvest methods and succession in western Montana. Unpublished thesis, University of Montana, Missoula.

508. WEAVER, T. 1974. Ecological effects of weather modification: effect of late snow melt on *Festuca idahoensis* meadows. Amer. Midl. Nat. 92: 346–356.

509. WEAVER, T. 1977a. Area-mass relationships for common Montana shrubs. Proc. Mont. Acad. Sci. 37: 54–58.

510. WEAVER, T. 1977b. Root distribution and soil water regimes in nine habitat types of the northern Rocky Mountains. Pages 239–244 *in* J. Marshall, The belowground ecosystem. Range Sci. Dept. Sci. Series 26, Colorado State University, Fort Collins.

511. WEAVER, T. 1979a. Changes in soils along a vegetational-altitudinal gradient of the northern Rocky Mountains. Pages 14–29 *in* C. Youngberg, ed., Proc. 5th North American Forest Soils Conference, Soil Sci. Soc. Amer., Madison, Wisconsin.

512. WEAVER, T. 1979b. Vegetation series associated with fourteen soil great groups in Montana. Proc. Mont. Acad. Sci. 38: 68–72.

513. WEAVER, T. 1980. Climates of vegetation types of the northern Rocky Mountains and adjacent plains. Amer. Midl. Nat. 103: 392–398.

514. WEAVER, T. 1987. Yield response of high plains grasslands to water enrichment, three phases. Manuscript. Biology Department, Montana State University, Bozeman.

515. WEAVER, T., AND K. BLANCHET. 1973. A bibliography of the literature on Idaho fescue, *Festuca idahoensis* Elmer. Proc. Mont. Acad. Sci. 33: 42–45.

516. WEAVER, T., AND D. COLLINS. 1977. Possible effects of weather modification (increased snow pack) on *Festuca idahoensis* meadows. J. Range Mgt. 30: 451–456.

517. WEAVER, T., AND D. DALE. 1974. *Pinus albicaulis* in central Montana: environment, vegetation and production. Amer. Midl. Nat. 92: 222–230.

518. WEAVER, T., AND D. DALE. 1978. Trampling effects of hikers, motorcycles and horses in meadows and forests. J. Appl. Ecology. 15: 451–457.

519. WEAVER, T., AND F. FORCELLA. 1977. Biomass of fifty conifer forests and nutrient exports associated with their harvest. Great Basin Nat. 37: 395–401.

520. WEAVER, T., AND F. FORCELLA. 1979. Seasonal variation in soil nutrients under six Rocky Mountain vegetation types. Soil Sci. Soc. Amer. 43: 589–593.

521. WEAVER, T., AND F. FORCELLA. 1986. Cone production in *Pinus albicaulis* forests. Pages 68–76 *in* R. Shearer, ed., Conifer tree seed in the inland mountain west—symposium proceedings. USDA For. Serv. Gen. Tech. Rept. INT-203. Intermountain Forest and Range Experiment Station, Ogden, Utah.

522. WEAVER, T., AND S. HARVEY. 1980. Soil water availability along a grassland topographic gradient, southwestern Montana. Proc. Mont. Acad. Sci. 39: 51–57.

523. WEAVER, T., AND C. JOHNSON. 1987. Plant response to single showers in the dry summer season, *Agropyron smithii*. Manuscript. Biology Department, Montana State University, Bozeman.

524. WEAVER, T., AND D. KLARICH. 1977. Allelopathic effects of volatile substances from *Artemisia tridentata*. Amer. Midl. Nat. 97: 508–512.

525. WEAVER, T., AND R. LUND. 1982. Diameter-weight relationships for juniper from wet and dry sites. Great Basin Nat. 42: 72–76.

526. WEAVER, T., AND D. PERRY. 1978. Relation of cover type to altitude, aspect and substrate in the Bridger Range, Montana. Northwest Sci. 52: 212–219.

527. WEAVER, T., AND A. B. SUPER. 1973. Ecological consequences of winter cloud seeding. J. Irrigation and Drainage Division, Amer. Soc. Civil Eng. 99: 387–399.

528. WELLNER, C. A. 1965. The history and role of fire in Inland Empire forests. Unpublished paper presented 9 September 1965, at the meeting of the Inland Reforestation Council, University of Montana, Missoula. 10 pp.

529. WELLNER, C. A. 1970. Fire history in the northern Rocky Mountains. Pages 42–64 *in* The role of fire in the intermountain west, symp. proc., School of Forestry, University of Montana, Missoula.

530. WENTLAND, H. J. 1968. Summer range habits of the pronghorn antelope in central Montana with special reference to proposed sagebrush control study plots. Montana Department of Fish and Game, Project No. W-105-R-2.

531. WESTECH 1981. Vegetation, Anaconda-Stillwater project. 12-month Environmental Baseline Report, 30 July 1981. Westech, Helena, Montana.

532. WESTECH, AND P. LESICA 1985. Conservation easement documentation report. Loon Lake. Prepared for The Nature Conservancy, Helena, Montana.

533. WHITE, K. L. 1958. Summer range ecology of Rattlesnake Creek mule deer in the spruce-fir zone. Unpublished thesis, University of Montana, Missoula. 95 pp.

534. WHITE, L. M., J. J. NEWBAUER III, AND R. WIGHT. 1978. Vegetational differences on native range during 38 years in eastern Montana. Pages 260–262 *in* D. N. Hyder, ed., Proc. First International Rangeland Congress. Society for Range Management, Denver, Colorado.

535. WHITFORD, H. N. 1902a. The forest and the prairie. University of Montana. Bull. No. 16, Biol. Series No. 5: 249–254.

536. WHITFORD, H. N. 1902b. The plant associations. University of Montana Bull. No. 16., Biol. Series No. 5: 271–274.

537. WHITFORD, H. N. 1905. Forests of the Flathead Valley, Montana. Bot. Gaz. 39: 99–122, 194–218, 276–296.

538. WILKINS, B. T. 1957. Range use, food habits, and agricultural relationships of the mule deer, Bridger Mountains, Montana. J. Wildl. Mgt. 21: 159–169.

539. WILLIAMS, C. A. 1977. Changes in a Douglas-fir (*Pseudotsuga menziesii* [Mirbel] Franco) forest as a result of floride fumigation. Unpublished thesis, University of Montana, Missoula. 81 pp.

540. WILLIAMS, R. S. 1892. The flora of a Montana pond. Bull. Torr. Bot. Club 19: 192–194.

541. WOOD, M. 1982. Natural communities of Montana. Unpublished report on file with The Nature Conservancy, Helena, Montana. 20 pp.
542. WRIGHT, H. A. 1978. The effect of fire on vegetation in ponderosa pine forests: a state-of-the-art review. Texas Tech University Range and Wildlife Information Service. No. 2. Coll. Agr. Sci. Pub. No. T-9-199. Texas Tech University, Lubbock.
543. WRIGHT, H. A., AND A. W. BAILEY. 1980. Fire ecology and prescribed burning in the Great Plains—a research note. USDA For. Serv. Gen. Tech. Rept. INT-77. Intermountain Forest and Range Experiment Station, Ogden, Utah. 61 pp.
544. WRIGHT, H. A., L. NEUENSCHWANDER, AND C. BRITTON. 1979. The role and use of fire in sagebrush-grass and pinyon-juniper plant communities—a state of the art review. USDA For. Serv. Gen. Tech. Rept. INT-58. Intermountain Forest and Range Experiment Station, Ogden, Utah. 48 pp.
545. WRIGHT, J. C., AND E. A. WRIGHT. 1948. Grassland types of southcentral Montana. Ecology 29: 449–460.
546. YOUMANS, C., AND P. JOHNSON. 1980. Vegetation report for mining area C. Project No. 248-83-A. Unpublished report prepared by Econ, Inc., Helena, Montana.
547. YOUMANS, C., AND P. JOHNSON. 1982. Vegetation survey 1981. Peabody Coal Co., Big Sky mine, Rosebud County, Montana. Project 257-83-A. Econ, Inc., Helena, Montana.
548. YOUNG, R. T. 1935. The life of Flathead Lake, Montana. Ecol. Monogr. 5: 91–163.
549. ZAGER, P. E. 1980. The influence of logging and wildfire on grizzly bear habitat in northwestern Montana. Unpublished dissertation, University of Montana, Missoula.

KEYWORD-CITATION INDEX

OCCURRENCE OF *PHAEDACTYLUM TRICORNUTUM* IN THE GREAT SALT LAKE, UTAH, USA

Samuel R. Rushforth[1], Jeffrey R. Johansen[2], and Darwin L. Sorensen[3]

ABSTRACT.—The diatom *Phaedactylum tricornutum* Bohlin forms blooms in the south arm of the Great Salt Lake, Utah, during cool months. This represents the first report of this taxon from Utah and the first from nonmarine waters in the United States.

Phaedactylum tricornutum Bohlin was first described from coastal waters of Runmarö near Stockholm, Sweden, in 1897. Bohlin (1897) described this organism as being triradiate with each arm being 10–12 um long. Bohlin was not certain of the taxonomic position of this taxon but suggested it was closely related to the diatoms.

In 1907 Allen isolated a diatom culture from Plymouth, England, which he designated but did not describe as *Nitzschia closterium* W.Sm. f. *minutissima* (Allen and Nelson 1910). This diatom was used extensively as food for various marine invertebrate larvae. It was kept for many years at Plymouth and widely distributed to other laboratories in Europe and America. In 1935 Barker noted the occurrence of triradiate and oval cells in his subculture of the organism. Wilson and Lucas (1942) noted that the diatom was polyphasic, producing fusiform, triradiate, and oval cells; and Wilson (1946) later presented considerable detail on the life cycle of the Plymouth strain. Though Wilson drew attention to the fact that the Plymouth culture resembled *P. tricornutum*, he did not recognize *N. closterium* f. *minutissima* as a synonym.

Hendey (1954) reviewed the taxonomic history of *P. tricornutum* and indicated that it was the same organism as *N. closterium* f. *minutissima*. Hendey presented electron micrographs of both triradiate and fusiform cells from the Plymouth culture and noted that he could not determine if the cell was frustular and therefore questioned whether or not it was a diatom. Bourrelly and Dragesco (1955) also were unable to find evidence of valve structure.

Lewin et al. (1958) finally demonstrated that *P. tricornutum* was indeed a diatom by finding siliceous valves associated with the oval cells. Lewin and co-workers discussed the fact that the fusiform and oval cells of *P. tricornutum* dominated their laboratory cultures but triradiate cells were commonly recognized in littoral water samples. Lewin (1958) concluded that *P. tricornutum* was allied with *Cymbella* Ag., a conclusion with which Hendey (1964) concurred.

This diatom was collected from the Great Salt Lake by Felix and Rushforth in 1979, but it was incorrectly identified as *Treubaria triappendiculata* Bernard. We have since observed this taxon frequently in samples collected from the Great Salt Lake.

METHODS

Detailed studies of the Great Salt Lake east of Antelope Island have been conducted during the past two years. These studies were designed to provide data on the biota, nutrients, heavy metals, organics, pathogenic bacteria, and sediments of the lake. As a part of these studies, we established 34 collecting localities for algal studies in the lake east of Antelope and Fremont islands, ranging from Farmington Bay on the south to the Southern Pacific Causeway on the north (Fig. 1).

Collections for algal identification and enumeration started on 25 July 1986 and continued at least monthly (except for November)

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Fig. 1. Map of the Great Salt Lake showing the position of the three collecting localities for *Phaedactylum tricornutum*.

through 22 December 1986. Plankton samples were collected from surface waters by submerging wide-mouthed plastic bottles directly into the lake.

Samples were returned to our laboratory at Brigham Young University where they were suction filtered using 1.2 μm pore membrane filters. The filters were cleaned in 10 ml distilled water, and the algae were immediately counted using Palmer counting chambers (Palmer and Maloney 1954). Algal numbers were then multiplied by known factors to project numbers of organisms per liter of lake water.

Independent of this project, two Great Salt Lake water samples containing *P. tricornutum* were collected by Johansen from Farmington Bay on 23 October 1986 and 6 March 1987. Two clonal cultures of the triradiate form of this taxon were isolated from enrichment cultures and designated PHAEO3 and PHAEO4. The clones are available from Microalgae Culture Collection at the Solar Energy Research Institute.

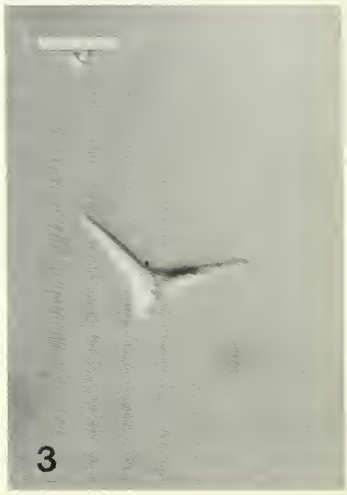
RESULTS AND DISCUSSION

Phaedactylum tricornutum is abundant in the Great Salt Lake during months of cool temperature and low light. We collected it from October through March. During December it forms rather large blooms, ranging up to 2×10^7 cells per liter (Table 1). It occurs with the diatoms *Chaetoceros muelleri* var. *subsalsum* Johansen & Rushforth, *Nitzschia acicularis* (Kütz.) Wm.Sm., *Thalassiosira weisflogii* (Grun.) Fryxell & Hasle, the green alga *Oocystis* species, and the cyanophytes *Nodularia spumigena* Mertens and *Oscillatoria* species. *Phaedactylum tricornutum* codominates the winter diatom flora with *N. acicularis* and *C. muelleri* var. *subsalsum*.

Phaedactylum tricornutum has previously been found in coastal brackish waters in both Europe and North America. It has been observed both in small bodies of water, such as fishery tanks and rock pools, as well as open waters. It commonly occurs in waters of elevated nutrient content (Wilson 1946, Barclay, personal communication). The south arm of the Great Salt Lake is also of elevated nutrient

TABLE 1. Abundance of *Phaedactylum tricornutum* and descriptive water data in the Great Salt Lake during the fall of 1986.

Date	Site	Cells per liter	Surface temp.	Dissolved oxygen	pH
10/23/86	Farmington Bay	4.5×10^6	13.4	13.4	9.2
10/23/86	Antelope Island	3.1×10^6	13.7	10.7	9.0
10/23/86	Fremont Island	4.9×10^5	14.3	9.4	9.0
	Mean density of *P. tricornutum*, 10/23/86, = 1.6×10^6 cells/liter.				
12/22/86	Farmington Bay	2.0×10^7	0.3	13.6	8.4
12/22/86	Antelope Island	1.7×10^7	1.3	13.3	8.3
	Mean density of *P. tricornutum*, 12/22/86, = 1.8×10^7 cells/liter.				



Figs. 2–3. Cells of *Phaedactylum tricornutum*: 2, several cells illustrating characteristic triradiate cell shape; 3, cell with two long arms and one shortened arm.

content due to the influence of sewage and industrial effluents from several Wasatch Front cities. *Phaedactylum tricornutum* is most abundant in Farmington Bay (including the inner bay and Antelope Island sites) possibly because these waters are more enriched than other parts of the lake.

Phaedactylum tricornutum seems to occur within the Great Salt Lake when surface water temperatures fall below 15 C. Barker (1935) found the photosynthetic optimum of this species to be between 25 and 30 C. We have noted that a number of species we isolated from cold, inland, saline waters have growth optima at 25–30 C, even though they are abundant in nature only during cool seasons. There are apparently other factors, such as light intensity, that contribute to the abundance of these diatoms during the winter. It is also likely that decreased competition and/or decreased invertebrate grazing pressure modify community structure. Wilson (1946) noted that the triradiate form of *P. tricornutum* could not be ingested easily by marine invertebrate larvae.

Our specimens are primarily triradiate (Fig. 2), although fusiform and oval cells have been observed. Triradiate cells dominate field collections. However, we have observed oval and fusiform cells in culture. This agrees with the observations of Lewin et al. (1958).

To our knowledge, this report is the first for *P. tricornutum* from inland waters. However, it is possible that it does occur in other inland saline waters but has been overlooked. It is easily destroyed and will not survive a typical acid clearing procedure for preparation of diatom-strewn mounts.

LITERATURE CITED

ALLEN, E. J., AND E. W. NELSON. 1910. On the artificial culture of marine plankton organisms. J. Mar. Biol. Assoc., U.K. 8:421–474.

BARKER, H. A. 1935. Photosynthesis in diatoms. Archiv f. Mikrobiol. 6: 141–156.

BOHLIN, K. 1897. Zur Morphologie und Biologie einzelliger Algen. Öfvers. Kongl. Vetens.-Akad. Förh. 9: 507–529.

BOURRELLY, P., AND J. DRAGESCO. 1955. Contribution à la connaissance d'une algue rarissme "*Phaedactylum tricornutum*" Bohlin. Bull. Micr. Appl. (2)5: 41–44.

HENDEY, N. I. 1954. Note on the Plymouth "*Nitzschia*" culture. J. Mar. Biol. Assoc., U.K. 33: 335–339.

———. 1964. An introductory account of the smaller algae of British coastal waters. Part V: Bacillariophyceae. H. M. Stationery Office, London. 317 pp., 45 pl.

LEWIN, J. 1958. The taxonomic position of *Phaedactylum tricornutum*. J. Gen. Microbiol. 18: 427–432.

LEWIN, J. C., R. A. LEWIN, AND D. E. PHILPOTT. 1958. Observations on *Phaedactylum tricornutum*. J. Gen. Microbiol. 18: 418–426.

PALMER, C. M., AND T. E. MALONEY. 1954. A new counting slide for nannoplankton. Amer. Soc. Limnol. Ocean. Spec. Publ. 21. 6 pp.

WILSON, D. P. 1946. The triradiate and other forms of *Nitzschia closterium* (Ehrenberg) Wm. Smith, forma *minutissima* of Allen and Nelson. J. Mar. Biol. Assoc., U.K. 26: 235–270.

WILSON, D. P., AND C. E. LUCAS. 1942. *Nitzschia* cultures at Hull and at Plymouth. Nature 149: 331.

ARBOREAL ARTHROPOD COMMUNITY STRUCTURE IN AN EARLY SUCCESSIONAL CONIFEROUS FOREST ECOSYSTEM IN WESTERN OREGON

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ABSTRACT.—This study was designed to characterize arboreal arthropod community structure in an early successional coniferous ecosystem. We sampled six-year-old snowbrush (*Ceanothus velutinus* Dougl. ex Hook) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) at the H. J. Andrews Experimental Forest in western Oregon during 1982. The arthropod fauna was dominated in terms of densities by psyllids and aphids on snowbrush and by adelgids and cecidomyiids on Douglas-fir. Significant associations among taxa, e.g., positive correlation between aphids and ants, indicated trophic interactions or similar responses to host conditions. Significant seasonality was observed for individual taxa and for the community, reflecting the integration of individual life-history patterns. Significant spatial pattern (patchiness) in the arthropod community may reflect the influence of faunas on individual plants within neighborhoods and/or the influence of ant foraging patterns.

Patterns in terrestrial arthropod community structure remain poorly understood, largely because of their taxonomic complexity. Most community-level studies have reduced this complexity to indices of diversity or have examined only subsets (guilds) of the community (Price 1984). Unfortunately, such restriction likely masks patterns that could be useful in identifying community responses to changes in environmental conditions (e.g., Lawton 1984, Thompson 1985). Changes in community structure may promote or limit pest population growth (Dixon 1985, Schowalter 1986, Strong et al. 1984, Tilman 1978) and may control temporal and spatial patterns in ecosystem nutrient cycling and succession (e.g., Mattson and Addy 1975, Schowalter 1985, Seastedt and Crossley 1984). At the same time, community structure reflects the integration of population responses to environmental conditions (Lawton 1983, 1984, Schowalter 1985, Schowalter and Crossley 1987, Strong et al. 1984).

Our purpose in this study was to describe the pattern(s) of arboreal arthropod community structure in an early successional coniferous ecosystem in western Oregon. We tested the hypothesis that the integration of patterns at the species level results in distinct temporal and spatial patterns, rather than unintelligible overlap, at the community level (Lawton 1984, Thompson 1985). Multivariate statistical techniques were used to examine the effect of seasonality and spatial position of host plants on arthropod community patterns as well as on individual arthropod taxa.

MATERIALS AND METHODS

The study was conducted during 1982 on Watershed (WS) 6 at the H. J. Andrews Experimental Forest Long Term Ecological Research (LTER) Site in the western Cascades, 65 km east of Eugene, Oregon. The Andrews Forest is administered jointly by the Pacific Northwest Forest and Range Experiment Station, the Willamette National Forest, and Oregon State University.

The climate of Andrews Forest is maritime with wet, relatively mild winters and dry, cool summers. Mean annual temperature is 8.5 C, and mean annual precipitation is 2,300 mm, with more than 75% falling as rain between October and March. The Andrews Forest is dominated by old-growth (>200-yr-old) Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), western hemlock (*Tsuga heterophylla* [Raf.] Sarg.), and western redcedar (*Thuja plicata* Donn) (Grier and Logan 1977).

WS 6 is a south-facing, 13-ha watershed at 1,000–1,100 m elevation, with an average slope of 35%. The watershed was clearcut in 1974, broadcast burned and planted to Douglas-fir at 3 × 3-m spacing in 1975. The six-yr-old vegetation in 1982 was dominated by

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evergreen snowbrush (*Ceanothus velutinus* Dougl. ex. Hook) and Douglas-fir with a canopy height of 1–2 m.

A belt transect 50 × 4 m was established strategically across the middle of the watershed to represent vegetation diversity and spatial heterogeneity. Because other community studies have indicated that the various arthropod taxa are distributed largely independently (Schowalter et al. 1981, Strong et al. 1984), we considered our sampling of a plot designed to maximize intersection of habitat patches to sufficiently represent the arthropod community in this relatively simple system. This design maximized sampling efficiency and safety on the steep, debris-strewn slope. Furthermore, unlike random sampling across the watershed, this design permitted evaluation of potentially important effects of plant position on insect demographics (Schowalter 1986, Thompson 1985, Tilman 1978).

The 40 snowbrush and 20 Douglas-fir within this transect were mapped to explore spatial patterns and were sampled eight times at 3–4 week intervals, between 19 May (Julian date 139) and 10 November (Julian date 314) 1982 to address temporal patterns. Sampling consisted of quickly enclosing a single, randomly selected branch, bearing 2–5 g dry wt. foliage (or 1–3% of the foliage mass), from each plant in a large plastic bag, clipping the sample, and sealing the bag for return to the laboratory. Samples were chilled at 5 C until processed. This sampling procedure was designed to represent arthropod intensity (#/g foliage) through time on a spatially discrete set of host plants. Chemical or other changes in host quality brought about by periodic removal of small foliage samples (Schultz and Baldwin 1982) were assumed to have a negligible effect on successive samples. Sample bias may exist due to selection of healthy, foliage-bearing plant parts and to the underrepresentation or absence of active species that leap, fly, or drop when motion or contact in their vicinity occurred during sample collection. (Note: Care was taken to minimize disturbance during sampling.)

Samples were sorted into foliage and arthropod components. Foliage material was dried at 45 C to constant weight. Arthropods were tabulated by taxon.

Trends in arthropod intensities (#/g foliage) and community structure were analyzed statistically using the SAS statistical software package (SAS Institute, Inc. 1982). The square-root transformation was used to normalize the intensity data in the analyses. Degrees of freedom were adjusted to account for autocorrelation arising from the sampling procedure (Milliken and Johnson 1984) in the analysis of variance for each of 18 taxa. Correlation analysis, principal component analysis, cluster analysis, stepwise discriminant analysis, and Spearman's rank correlation (Lawton 1984, Steel and Torrie 1960) were used to explore interactions and temporal and spatial patterns among the 18 taxa.

RESULTS

Mean intensities of arthropods on WS 6 during 1982 are summarized in Table 1. Principal component analysis using the covariance matrix verified the obvious importance of the sap-sucking Homoptera, especially woolly aphids (*Adelges cooleyi* [Gillette]) and psyllids (*Arytaina robusta* Crawford, some *Craspedolepta* sp.). Overall, these two principal components explained 95% of the total variance.

Correlation analysis revealed significant ($P < .05$) interactions that we believe indicate trophic relationships or similar responses to host conditions. As expected (Dixon 1985, Fritz 1983, Schowalter et al. 1981, Strong et al. 1984), aphids and ants were positively correlated ($r = 0.31$, $df = 480$, $P < .0001$), reflecting ant (*Camponotus modoc* Wheeler) tending of *Aphis ceanothi* Clark on snowbrush and *Cinara pseudotaxifoliae* Palmer on Douglas-fir. Positive correlation between psyllids and leaf-mining gelechiid larvae ($r = 0.31$, $df = 480$, $P < .0001$) suggested similar responses to host conditions. Surprisingly, significant negative correlations ($P < .05$) were found only between taxa restricted in occurrence to different hosts.

Statistically significant ($P < .05$) temporal trends were found for aphids, psyllids, aleyrodids, pollen-feeding thrips, defoliating tortricid larvae, gelechiid larvae, and ants on snowbrush (ANOVA, $F > 4$; $df = 7, 44$; $P < .01$) (Fig. 1) and for adelgids on Douglas-fir (ANOVA, $F = 12$; $df = 7, 21$; $P < .01$; (Fig. 2). Aphids, aleyrodids, thrips, and tortricid larvae were most abundant May–August. Psyllids and gelechiid larvae were most abundant September–November. Woolly aphids showed peaks in spring and fall on Douglas-fir.

TABLE 1. Mean (± SEM) arthropod intensities (number/kg foliage) and percent of total arboreal arthropods on six-yr-old snowbrush (*Ceanothus velutinus*, N = 40) and Douglas-fir (*Pseudotsuga menziesii*, N = 20) on WS 6 at the H. J. Andrews Experimental Forest, Oregon, during 1982.

	Snowbrush		Douglas-fir	
Taxon	Number/kg	Percent of total	Number/kg	Percent of total
Sap-sucking phytophages				
Wooly aphid (*Adelges cooleyi*)	0	0	17,000 (1700)	99
Aphids				
Aphis ceanothi	388 (220)	4.8	0	0
Cinara pseudotaxifoliae	0	0	34 (19)	0.2
Cicadellids (3–4 spp.)	48 (7)	0.6	16 (8)	0.1
Aleyrodid (1 sp.)	40 (6)	0.5	0	0
Psyllids (*Arytaina robusta* and *Craspedolepta* sp.)	7,300 (520)	91	2 (2)	0
Mirid (*Psallus* sp.)	5 (2)	0	0	0
Thrips (2 spp.)	64 (10)	0.8	8 (4)	0
Chewing phytophages				
Geometrid (1 sp.)	15 (14)	0.2	0	0
Tortricid (1 sp.)	17 (4)	0.2	0	0
Gelechiid (1 sp.)	37 (7)	0.5	0	0
Chrysomelid (*Scelolyperus varipes*)	6 (2)	0.1	8 (8)	0
Gall-formers				
Cecidomyiid (*Contarinia* sp.)	1 (1)	0	0	0
Omnivores				
Formicid (*Camponotus modoc*)	9 (3)	0.1	13 (10)	0.1
Predators				
Parasitic Hymenoptera (5–6 spp.)	5 (2)	0.1	14 (6)	0.1
Spiders (2 spp.)	29 (5)	0.4	62 (15)	0.4
Miscellaneous arthropods[a]	43 (7)	0.5	71 (23)	0.4

[a]Primarily nonfeeding adult midges.

The temporal dynamics of the various taxa produced a distinct seasonality in community structure. Cluster analysis on faunal similarity among plants separated 93% of snowbrush samples collected May–August (season 1) from 97% of snowbrush samples collected September–November (season 2) but failed to separate samples by time for the Douglas-fir fauna.

Cluster analysis was used to explore spatial patterns in community organization. We derived four geometric clusters (patches) of plants from coordinate geometry of nearest neighbors within the plot. Spearman's rank correlation was used to compare these clusters to four faunal clusters derived from faunal similarity among these plants. Each plant species was analyzed for each of the two seasons. Significant ($P < .05$) patch effects on arthropod community structure were found during both seasons for Douglas-fir (Spearman's r_s for season 1 and 2 = 0.48 and 0.71, $t = 2.3$ and 4.3, $df = 18$, respectively). The snowbrush fauna was relatively homogenous during season 1, with 36 plants supporting a common fauna; the remaining four plants, distributed in three vegetation patches, supported three distinct faunas. The four patches became faunally distinct during season 2 (Spearman's $r_s = 0.91$, $t = 13$, $df = 38$), suggesting that the four plants distinguished during season 1 constituted centers for subsequent development of arthropod communities at the patch level.

Stepwise discriminant analysis was used to identify taxa constituting the groups identified by cluster analysis. Mirid adults, thrips ($P < .05$), cicadellids ($P = .07$), and ants ($P = .13$) contributed to the spatial pattern for snowbrush during season 1, and psyllids and cicadellids ($P < .05$) for snowbrush during season 2. Woolly aphids ($P = .06$), chrysomelid adults ($P = .08$), and cicadellids ($P = .13$) contributed to the spatial pattern for Douglas-fir during season 1, and aphids ($P = .15$) for Douglas-fir during season 2.

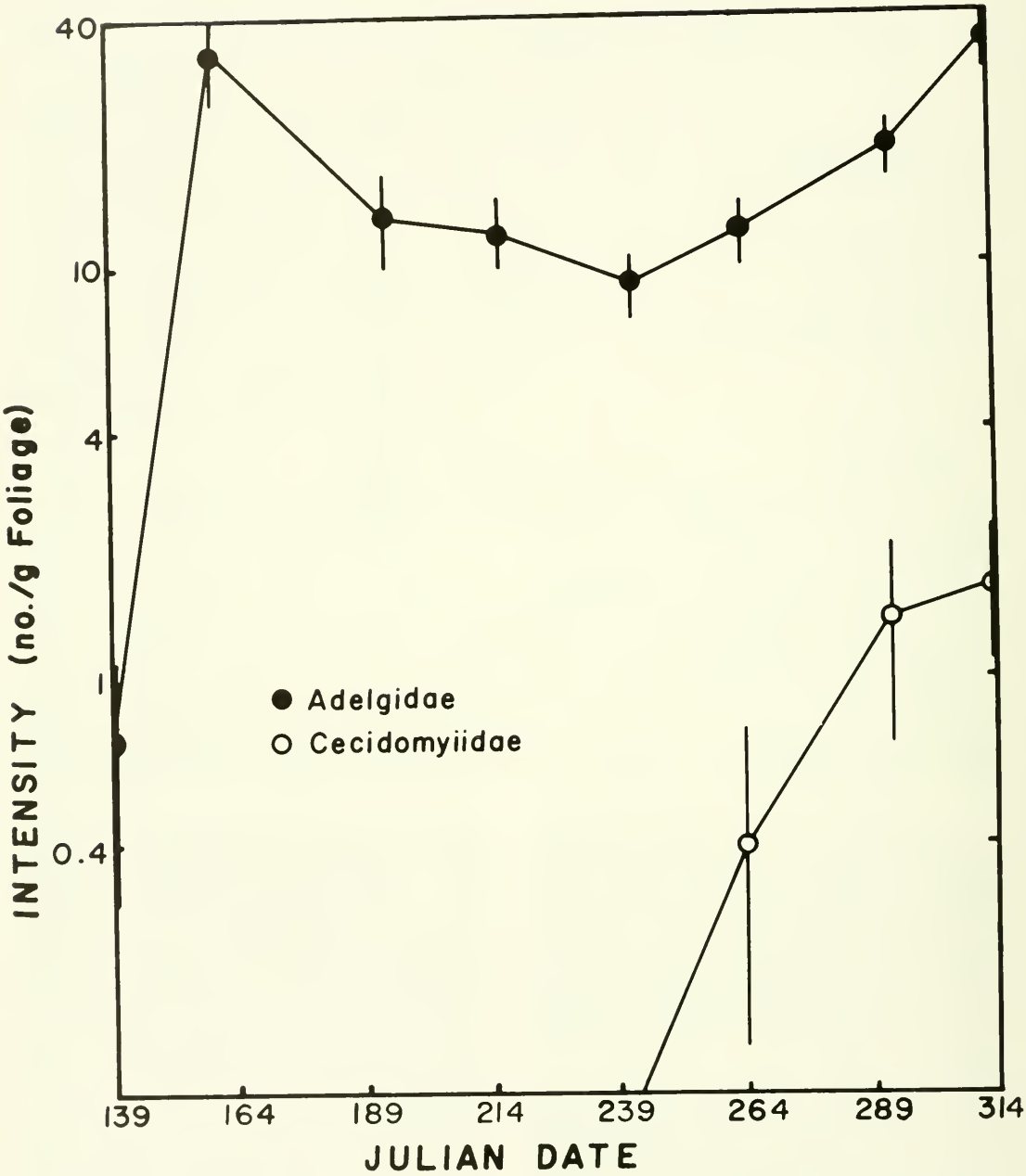

Fig. 1. Mean (± 1 SEM) intensities of arthropods showing significant ($P < .05$) temporal trends on young snowbrush (*Ceanothus velutinus*) from May 19 (Julian date 139) to November 10 (Julian date 314) 1982.

DISCUSSION

Four species of Homoptera (one woolly aphid, one aphid, and two psyllids), all small phloem-sucking insects, characterized the arthropod community in this early successional ecosystem. Other species occurred at low population levels but showed some evidence of interaction with the dominating Homoptera.

This arthropod community structure is functionally similar to the aphid-dominated community of an early successional hardwood forest at Coweeta (Schowalter and Crossley 1987), but distinct from the

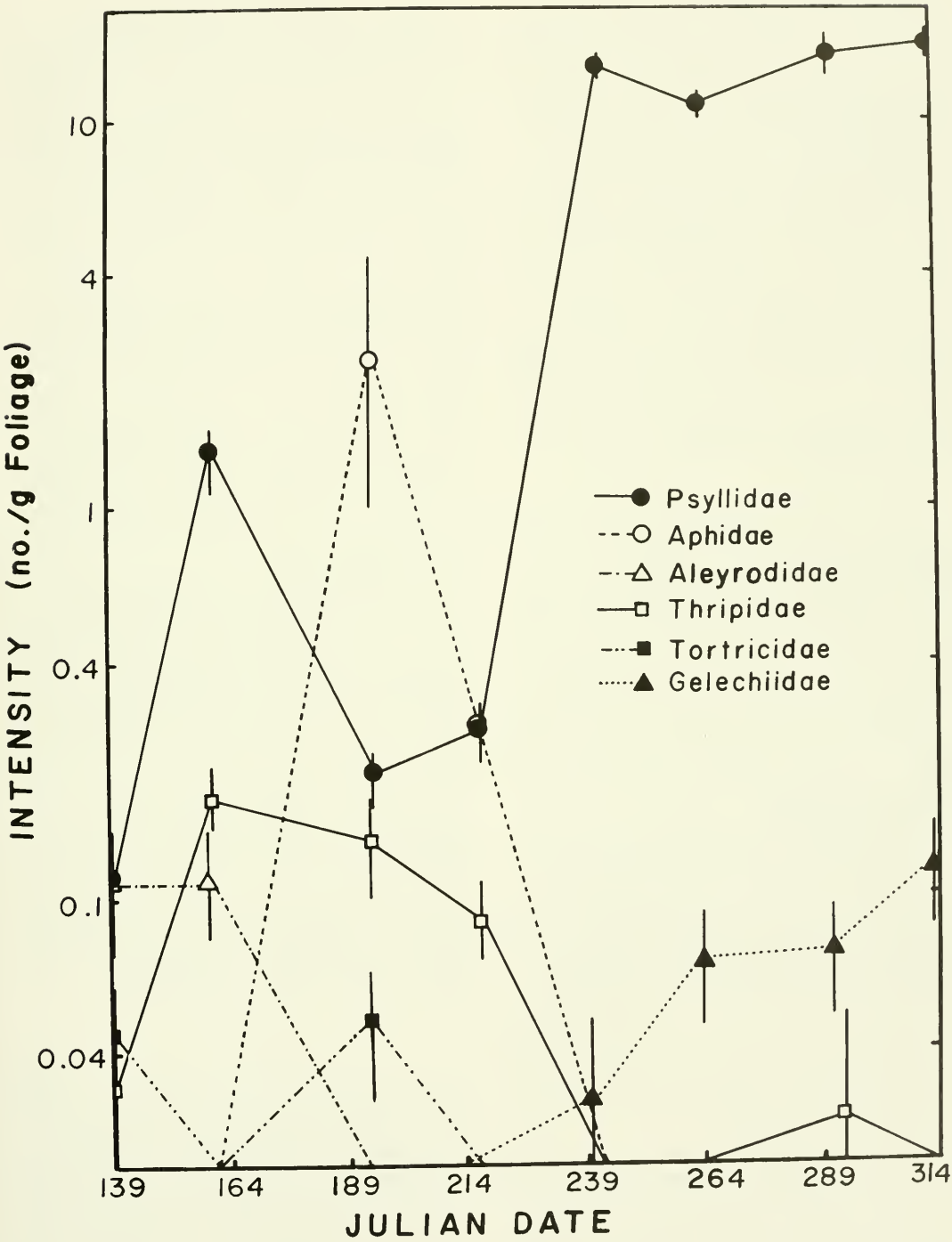

Fig. 2. Mean (± 1 SEM) intensities of woolly aphids (*Adelges cooleyi*) on young Douglas-fir (*Pseudotsuga menziesii*) from May 19 (Julian date 139) to November 10 (Julian date 314) 1982.

defoliator-dominated communities characterizing mature forests at both sites (Schowalter and Crossley 1987, Schowalter, unpublished data). In particular, the faunal association on snowbrush, a symbiotic N-fixer, is functionally identical to that on the ecologically equivalent black locust, *Robinia pseudoacacia* L., a symbiotic N-fixer at Coweeta that was dominated by aphids, *Aphis craccivora* Koch, and ants, *Formica* sp. (Schowalter and Crossley 1987). Thus, although these forest communities were taxonomically distinct, they were functionally similar in the dominance of phloem-sucking Homoptera at similar stages of forest development. These data support the hypothesis that arthropod communities are not randomly organized but rather reflect functional interactions (Lawton 1984, Schowalter 1986).

The faunal structure on Douglas-fir also was similar to the faunal structure on 20-year-old Douglas-fir studied by Mispagel and Rose (1978). *Adelges cooleyi* constituted a much higher proportion of arthropods on Douglas-fir in our study (96% vs. 58%). This may reflect a successional trend or may be due to our inclusion of immatures. Species richness on Douglas-fir was much lower in our study (11 vs. 75 taxa of equivalent rank) as expected if species richness increases with increasing habitat complexity (Schowalter et al. 1986, Strong et al. 1984).

Temporal trends in community structure observed in this study reflected the life history patterns of the constituent species. For example, the appearance of adult psyllids on nonhost Douglas-fir in August was the result of dispersal of winged adults; subsequent reproduction on snowbrush was evident in the rapid increase in intensity (of nymphs) during late summer and fall. The seasonal structure of the community suggests a greater suitability of environmental conditions in spring and fall, relative to summer.

Spatial heterogeneity on a scale of meters in arboreal arthropod community structure has not been reported previously. Our data are consistent with the scale of heterogeneity reported for terrestrial plant (Pickett and White 1985), litter arthropod (Santos et al. 1978, Seastedt and Crossley 1981), stream arthropod (Reice 1985), and marine intertidal communities (Sousa 1985). Such patch patterns underlie the demography of outbreaks and patterns of herbivory (Schowalter 1985) but would be masked by random sampling.

Our data suggest that individual plants supporting distinct arthropod communities early in the growing season could have constituted centers for the development of faunal patches later in the growing season. The patch pattern in arthropod community structure could have reflected the effect of environmental gradients or of foraging patterns of keystone species such as ants, as suggested by our stepwise discriminant analysis. Ants are attracted to particular plants by floral or extrafloral nectary production and by honeydew-producing Homoptera (Dixon 1985, Fritz 1983, Schowalter and Crossley 1987, Tilman 1978). Ants patrolling these plants remove nonmyrmecophilous herbivores and predators, thereby promoting homopteran-dominated communities. The spatial distribution of ant foraging could produce a patch pattern of homopteran- and nonhomopteran-dominated communities (e.g., Tilman 1978).

In conclusion, the results of this study indicate that arthropod community structure in this early successional coniferous forest ecosystem was dominated by Homoptera. This dominance may reflect the influence of plant architecture interacting with ant foraging pattern in young forests. Spatial and temporal trends in these factors may contribute to patchiness in arthropod community structure. The similarity of canopy arthropod community structure between this western coniferous ecosystem and an eastern deciduous ecosystem suggests that arthropod communities are not organized randomly but rather are based on functional interactions common to taxonomically distinct ecosystems.

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LITERATURE CITED

DIXON, A. F. G. 1985. Aphid ecology. Blackie, London. 157 pp.

FRITZ, R. S. 1983. Ant protection of a host plant's defoliator: consequence of an ant-membracid mutualism. Ecology 64: 789–797.

GRIER, C. C., AND R. S. LOGAN. 1977. Old-growth *Pseudotsuga menziesii* communities of a western Oregon watershed: biomass distribution and production budgets. Ecol. Monogr. 47: 373–400.

LAWTON, J. H. 1983. Plant architecture and the diversity of phytophagous insects. Ann. Rev. Entomol. 28: 23–39.

———. 1984. Herbivore community organization: general models and specific tests with phytophagous insects. Pages 329–352 *in* P. W. Price, C. N. Slobodchikoff, and W. S. Gaud, eds., A new ecology. Wiley, New York.

MATTSON, W. J., AND N. D. ADDY. 1975. Phytophagous insects as regulators of forest primary production. Science 190: 515–522.

MILLIKEN, G. A., AND D. E. JOHNSON. 1984. Analysis of messy data. Vol. 1: Designed experiments. Lifetime Learning Publications, Belmont, California. 473 pp.

MISPAGEL, M. E., AND S. D. ROSE. 1978. Arthropods associated with various age stands of Douglas-fir from foliar, ground, and aerial strata. US/IBP Coniferous Forest Biome Bulletin 13, University of Washington, Seattle. 55 pp.

PICKETT, S. T. A., AND P. S. WHITE. 1985. The ecology of natural disturbance and patch dynamics. Academic Press, New York. 472 pp.

PRICE, P. W. 1984. Insect ecology. 2d ed. John Wiley & Sons, New York. 607 pp.

REICE, S. R. 1985. Experimental disturbance and the maintenance of species diversity in a stream community. Oecologia 67: 90–97.

SANTOS, P. F., E. DEPREE, AND W. G. WHITFORD. 1978. Spatial distribution of litter and microarthropods in a Chihuahuan desert system. J. Arid Environ. 1: 41–48.

SAS INSTITUTE, INC. 1982. SAS user's guide: statistics, 1982 edition. SAS Institute, Inc., Cary, North Carolina. 584 pp.

SCHOWALTER, T. D. 1985. Adaptations of insects to disturbance. Pages 235–252 *in* S. T. A. Pickett and P. S. White, eds., The ecology of natural disturbance and patch dynamics. Academic Press, New York.

———. 1986. Ecological strategies of forest insects: the need for a community-level approach to reforestation. New Forests 1: 57–66.

SCHOWALTER, T. D., AND D. A. CROSSLEY, JR. 1987. Canopy arthropods and their response to forest disturbance. Pages 207–218 *in* W. T. Swank and D. A. Crossley, Jr., eds., Forest hydrology and ecology at Coweeta. Springer-Verlag, New York.

SCHOWALTER, T. D., W. W. HARGROVE, AND D. A. CROSSLEY, JR. 1986. Herbivory in forested ecosystems. Ann. Rev. Entomol. 31: 177–196.

SCHOWALTER, T. D., J. W. WEBB, AND D. A. CROSSLEY, JR. 1981. Community structure and nutrient content of canopy arthropods in clearcut and uncut forest ecosystems. Ecology 62: 1010–1019.

SCHULTZ, J. C., AND I. T. BALDWIN. 1983. Oak leaf quality declines in response to defoliation by gypsy moth larvae. Science 217: 149–151.

SEASTEDT, T. R., AND D. A. CROSSLEY, JR. 1981. Microarthropod response following cable logging and clear-cutting in the southern Appalachians. Ecology 62: 126–135.

———. 1984. The influence of arthropods on ecosystems. BioScience 34: 157–161.

SOUSA, W. P. 1985. Disturbance and patch dynamics on rocky intertidal shores. Pages 101–124 *in* S. T. A. Pickett and P. S. White, eds., The ecology of natural disturbance and patch dynamics. Academic Press, New York.

STEEL, R. G. D., AND J. H. TORRIE. 1960. Principles and procedures of statistics. McGraw-Hill, New York. 481 pp.

STRONG, D. R., J. H. LAWTON, AND T. R. E. SOUTHWOOD. 1984. Insects on plants: community patterns and mechanisms. Harvard University Press, Cambridge, Massachusetts. 313 pp.

THOMPSON, J. N. 1985. Within-patch dynamics of life histories, populations, and interactions: selection over time in small spaces. Pages 253–264 *in* S. T. A. Pickett and P. S. White, eds., The ecology of natural disturbance and patch dynamics. Academic Press, New York.

TILMAN, D. 1978. Cherries, ants and tent caterpillars: timing of nectar production in relation to susceptibility of caterpillars to ant predation. Ecology 59: 686–692.

COMPUTER ANALYSIS OF CROSS SECTIONS OF LEAVES OF *CHRYSOTHAMNUS* TAXA AND THEIR RELATION TO ENVIRONMENTAL CONDITIONS

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ABSTRACT.—Thirty-eight accessions of 20 taxa (species and subspecies) of *Chrysothamnus* from a range of environments were grown in a uniform garden. During mid-June, terminal and lateral leaves were removed, fixed, and processed for light-microscopy studies. Area and perimeter measurements of ink tracings of midleaf vein cross sections were measured using computer-scan techniques. Leaf area and perimeter were compared with vein perimeter and area measurements. Area and perimeter of these *Chrysothamnus* leaves varied in response to the environment at the collection location. Plants native to hot, dry conditions had small, thick leaves, whereas plants native to cooler, more mesic conditions had relatively large, thin leaves. Similarly, leaves with round veins were adapted to hot, dry environments and leaves with elliptical veins were adapted to cooler, more mesic environments. Both terminal (young) and lateral (older) leaves were sampled. Terminal leaves showed significant ($p < .05$) correlational responses to environmental parameters, whereas the lateral leaves, while fronding in the predicted morphological directions, did not generally show significant responses. The different responses of terminal and lateral leaves may have been due to canopy position and uniform environmental conditions of the garden. Leaves with large cross sections characteristically had large veins, and leaves with small cross sections characteristically had small veins. Large leaf cross sections were normally flat. Small leaf cross sections were normally round. Decreasing leaf size and increasing leaf thickness were correlated with aridity.

Plants in any given environment tend to adjust to that environment through adaptations in physiological processes, morphologic structure, and/or life cycle modifications (Futuyma 1986). Leaf morphology reflects the adaptive ability of plants and may be expressed by leaf shape, size, and thickness. Since plant life history traits are often viewed as fixed, phenotypic plasticity in response to changing conditions is not expected. Few ecologists and morphologists have examined how environmental conditions affect leaf size, shape, and thickness of individual plants. In an early study with *Encelia farinosa*, Shreve (1924) reported that during hot, dry periods of the year no leaves, or only a few very small leaves, were present. However, during periods of high precipitation the shrubs had numerous large leaves. Cunningham and Strain (1969) studied the function of seasonal leaf variability in adapting *E. farinosa* to a desert environment and demonstrated that leaf quantity and structure are controlled by the moisture status of the environmental conditions.

The effects of climate upon variation of leaf size and thickness as a result of evolutionary convergence were reported by Theophrastus as discussed by Hort (1948) and have been discussed by others (Bailey and Sinnott 1916, Gentry 1969). The ecological significance of leaf shape and size and some implications of these morphological variations in natural habitats were studied by Lightbody (1985), who predicted that leaf shape could vary in response to microhabitat within a species. Mooney et al. (1974) stated that leaves of the desert shrub *Atriplex hymenelytra* grown in the cool Bodega head environment were twice the size of leaves grown in Death Valley. These authors indicated that there was a similar but temporal relationship in this species growing in Death Valley. The new spring leaves, which were produced when temperatures were cool, were the largest. As the temperatures increased in late spring, the last leaves formed were smaller. Concerning leaf thickness, Mooney et al. (1974) stated that Bodega head leaves were thinner, but averaged twice the surface area of the Death

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Valley leaves. Parkhurst and Loucks (1972) reported that plants in any given environment would tend to become adapted to that environment. Furthermore, Yun and Taylor (1986) reported that increased leaf thickness would result in a higher photosynthetic rate with little influence on transpiration and water-use efficiency. The effects were greater for thick leaves than for thin leaves under sunny conditions. Yun and Taylor (1986) concluded that increased productivity without increased water use is of adaptive significance in thickened, sun-grown leaves. Also, the expression of the genotype for leaf form may be influenced by the environment during ontogeny (Akimoto 1979). As an example, Jackson (1967) reported that sun leaves are often thicker than shade leaves.

Chrysothamnus is ideally suited for studying the relationship between leaf traits and environmental conditions, because *Chrysothamnus* is able to survive and grow vigorously over a wide range of environmental conditions. This genus ranges in distribution from northern Mexico to Canada and from near sea level to 10,000 feet (Weber et al. 1985). Furthermore, Anderson (1986a, 1986b, 1986c) indicated that within specific and subspecific taxa, i.e., the subspecies of rubber rabbitbrush, there are few morphological differences.

Chrysothamnus is a member of the Asteraceae and is a dominant shrub in the western United States (McArthur 1984, Weber et al. 1985). There are 16 species in the genus *Chrysothamnus* (Anderson 1986a, 1986b, 1986c), three of which form large species complexes consisting of a number of subspecies (*C. nauseosus*, rubber rabbitbrush; *C. parryi*, Parry's rabbitbrush; *C. viscidiflorus*, low rabbitbrush). *Chrysothamnus* has many uses and potential uses such as revegetation, livestock and wildlife forage, landscaping, and resin and rubber production. It has the unusual physiological characteristic of a high rate of net photosynthesis for a woody C-3 plant that does not become light saturated at full sun (Weber et al. 1985). *Chrysothamnus* is a potential source of natural insecticides and fungicides (Weber et al. 1985). Recently, interest in this shrub as a possible rubber source has increased, and researchers have begun to look at different populations of *C. nauseosus* for potential use as a producer of natural rubber (Ostler et al. 1986, Hegerhorst et al. 1987). Environmental factors play an important role in both resin and rubber production (Weber et al. 1985, Ostler et al. 1986, Hegerhorst et al. 1988). A better understanding of leaf characteristics as related to an array of environmental conditions may help in the interpretation of factors that contribute to the production of natural products.

The objectives of this paper were to (1) determine the relationship between leaf size and thickness for species and subspecies of *Chrysothamnus* and (2) attempt to correlate these factors with environmental parameters.

MATERIALS AND METHODS

Sampling and Microtechnique

Leaf material from 38 accessions representing 20 taxa (species and subspecies) of *Chrysothamnus* was collected for study in June 1986. This leaf material was mostly from two-year-old plants growing in a uniform garden at the Snow Field Station, Ephraim, Utah, but additional material was collected from naturally occurring populations and from greenhouse-grown plants (Table 1).

For each accession, a terminal (young) and a lateral (older) leaf were compared. Leaves were processed using procedures described by Nawaz and Hess (1987). Middle portions of leaves were fixed after cutting leaves into sections. Leaves were fixed in 2% glutaraldehyde and 3% acrolein in 0.1 M of sodium cacodylate buffer (pH 7.2–7.4) for 2 hr at room temperature. Aerosol OT wetting agent was used to reduce surface tension. After fixation, samples were washed six times with 1:1 water:buffer solution, and post-fixed and stained with buffered 1% osmium tetroxide for 2 hr at 0–4 C. The fixed tissues were washed six times with 1:1 water:buffer and stained overnight with aqueous 0.5% uranyl acetate followed by dehydration in a graded series of ethanol and embedment in Spurr (1969) resin. Leaf sections were cut with a Sorvall JB-4 rotary microtome at 2–3 micron thickness and stained with Toluidine Blue, Azure II, and sodium carbonate. Coverslips were sealed with permount.

Quantitative Determination Using Microcomputer System

A Leitz Wetzlar Prado Universal Projection was used to project leaf cross sections

TABLE 1. Location and identification of accessions of *Chrysothamnus*.*

ID no.	*Chrysothamnus* taxon	Code		Native site
1.	*C. nauseosus* ssp. *albicaulis*	chna-a-24	24BT	Walker River, CA
2.	*C. nauseosus* ssp. *albicaulis*	chna-a-36	36BT	Kamas Junction, UT
3.	*C. nauseosus* ssp. *arenarius*	chna-a-37	37BT	Coral Pink Sand Dunes, UT
4.	*C. nauseosus* ssp. *consimilis*	chna-c-3	3BT	Knolls, UT
5.	*C. nauseosus* ssp. *consimilis*	chna-c-4	4BT	Black Rock Desert, NV
6.	*C. nauseosus* ssp. *consimilis*	chna-c-11	11BT	Big Rock Candy Mountain, UT
7.	*C. nauseosus* ssp. *consimilis*	chna-c-20	20BT	Chester, UT
8.	*C. nauseosus* ssp. *consimilis*	chna-c-21	21BT	Trout Creek, NV
9.	*C. nauseosus* ssp. *consimilis*	chna-c-31	31BT	Fountain Green, UT
10.	*C. nauseosus* ssp. *hololeucus*	chna-h-2	2BT	Hilltop Near Milburn, UT
11.	*C. nauseosus* ssp. *hololeucus*	chna-h-33	33BT	Goshen Dam, UT
12.	*C. nauseosus* ssp. *hololeucus*	chna-h-8	8BT	New Cuyama, CA
13.	*C. nauseosus* ssp. *hololeucus*	chna-h-16	16BT	Nephi (Salt Creek) Canyon, UT
14.	*C. nauseosus* ssp. *graveolens*	chna-g-7	7BT	Salina Canyon, UT
15.	*C. nauseosus* ssp. *graveolens*	chna-g-14	14BT	Paragonah, UT
16.	*C. nauseosus* ssp. *graveolens*	chna-g-15	15BT	Point of Rocks, AZ
17.	*C. nauseosus* ssp. *graveolens*	chna-g-23	23BT	Near Colorado City, AZ
18.	*C. nauseosus* ssp. *junceus*	chna-j-35	35BT	Mokee Dugway, UT, near Natural Bridges Nat. Mon.
19.	*C. nauseosus* ssp. *mohavensis*	chna-m-25	25BT	Lancaster, CA
20.	*C. nauseosus* ssp. *nitidus*	chna-n-39	39BT	Big Water, AZ
21.	*C. nauseosus* ssp. *nauseosus*	chna-n-19	19BT	Terry, MT
22.	*C. nauseosus* ssp. *salicifolius*	chna-s-26	26BT	Ephraim Canyon, UT
23.	*C. nauseosus* ssp. *turbinatus*	chna-t-9	9BT	Lund, UT
24.	*C. nauseosus* ssp. *turbinatus*	chna-t-32	32BT	Goshen Dam, UT
25.	*C. nauseosus* ssp. *leiospermus*	chna-l-40	40BT	Mokee Dugway, UT, near Natural Bridges Nat. Mon.
26.	*C. nauseosus* ssp. *viridulus*	chna-v-5	5BT	Victorville, CA
27.	*C. nauseosus* ssp. *viridulus*	chna-v-6	6BT	Lee Vining, CA
28.	*C. nauseosus* ssp. *viridulus*	chna-v-12	12BT	Barstow, CA
29.	*C. nauseosus* ssp. *viridulus*	chna-v-13	13BT	Benton, CA
30.	*C. nauseosus* ssp. *viridulus*	chna-v-22	22BT	Palmetto, NV
31.	*C. parryi* ssp. *attenuatus*	chpa-a-1	1BT	Hilltop Near Milburn, UT
32.	*C. viscidiflorus* ssp. *viscidiflorus*	chvi-v-38	38BT	Salina Canyon, UT
33.	*C. viscidiflorus* ssp. *viscidiflorus*	chvi-v-18	18BT	Benton, CA
34.	*C. viscidiflorus* ssp. *viscidiflorus*	chvi-v-10	10BT	Piute Reservoir, UT
35.	*C. greenei*	chgr-17	17BT	Black Rock, UT
36.	*C. teretifolius*	chte-34	34BT	Death Valley, CA
37.	*C. linifolius*	chli-28	28BT	South of Price, UT
38.	*C. viscidiflorus* ssp. *lanceolatus*	chvi-l-27	27BT	NE of Ephraim, UT

*At the time leaf samples were taken, all the *Chrysothamnus* accessions were growing in the uniform garden for the second season, except 9, 10, 11, 24, and 31, which were collected from the native site; 37, which had been grown adjacent to the uniform garden for several years; and 3, 18, 20, 25, and 32, which were growing in a glasshouse in containers.

onto drawing paper mounted on a wall. A stage micrometer was used to calibrate enlargement at 250 times. Outlines of individual leaves were traced, inked, and scanned with an image analyzer (Apple II computer equipped with a digitizer board connected to a television camera [Russ and Stewart 1983]). The procedure made it possible to quantify the perimeter and area of leaf and vein cross sections. The image analyzer detected 63 shades of grey; the darker shades, those between 50 and 63, were selected for analysis.

Climate Data

Mean July maximum temperature and mean annual precipitation were estimated for the native site for each accession. These estimates of climatic conditions under which the 38 sampled populations (species and subspecies) had survived were interpolated from isohyetal and isotherm maps (Water Information Center 1974). Data were also examined from weather stations at comparable elevations near collection sites for corroboration of interpolated values. In addition, the moisture availability index, which was based on the ratio of yearly precipitation and July maximum temperature, was used to measure the aridity at each site. The lower the value of this

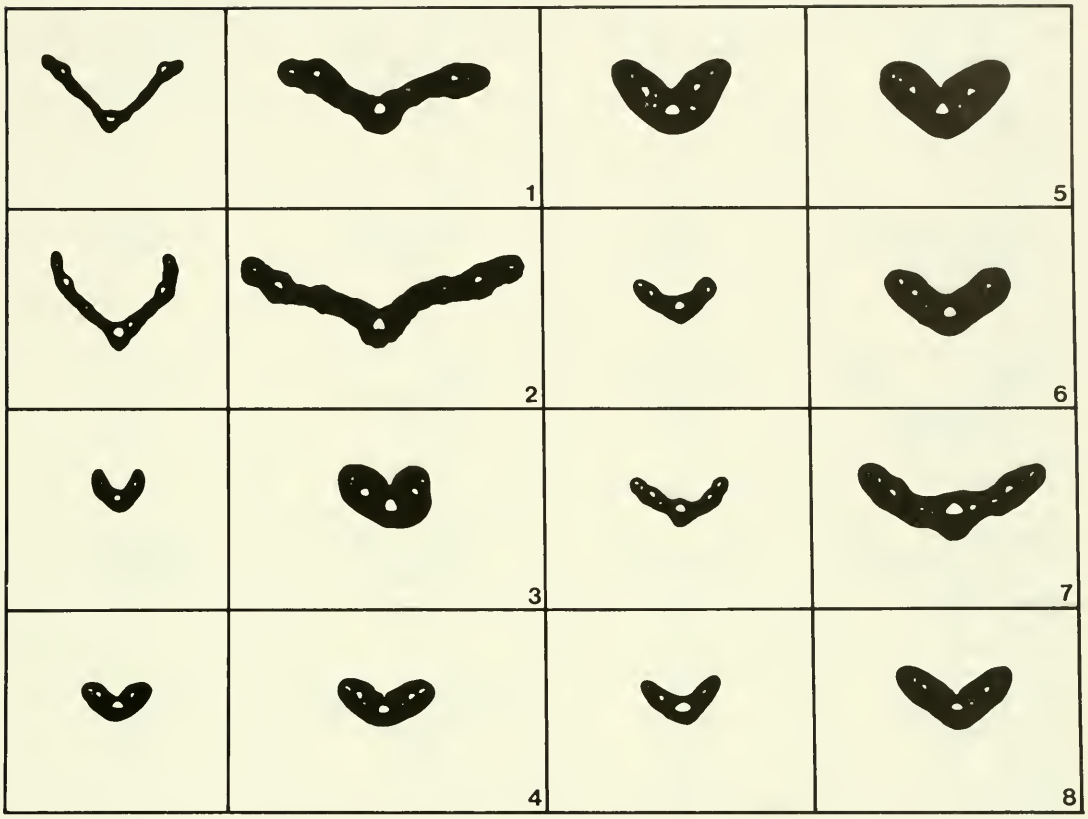

Fig. 1. Leaf cross sections of drawings of accessions of *Chrysothamnus*. Left = terminal leaf, right = lateral leaf; drawings 14.5X (see Table 1). 1–2, *C. nauseosus* ssp. *albicaulis*; 3, *C. nauseosus* ssp. *arenarius*; 4–8, *C. nauseosus* ssp. *consimilis*.

ratio, the greater the aridity of the native site. Higher values of the ratio indicate less arid sites.

Statistical Analysis

Statview 512+ (1986) was used for regression analysis. Statistical work was done using climatic and image analysis data from the various sites and image analysis of leaf cross sections of plants that originated at the various sites. A probability of $p < .05$ was the level at which null hypotheses were rejected.

RESULTS

Drawings of terminal and lateral leaves of 38 species and subspecies of *Chrysothamnus* are shown in Figures 1–4. Table 1 shows original collection sites and identification of species and subspecies of *Chrysothamnus*. Tables 2–6 show terminal and lateral leaf and vein cross-section characteristics and climatic data from native sites. Table 7 shows probability and correlation coefficients of areas and perimeters of *Chrysothamnus* leaf cross sections.

Terminal Leaf Cross-section Characteristics and Their Relation to the Environment

The leaves of the accessions examined (Table 1) displayed a broad range in form. Leaves varied from relatively thin and large to relatively thick and small (Figs. 1–4 upper). Leaf cross-section areas ranged in size from 0.13 mm^2 to 0.67 mm^2, and the leaf cross-section thickness ratio (perimeter of leaf cross section in mm/area of leaf cross section in sq mm) ranged from 5.16 to 18.48 (Table 2). There was a positive correlation between the leaf cross-section perimeter and the leaf cross-section thickness ratio ($r^2 = 0.219$; Table 7). As

TABLE 2. Terminal leaf cross-section characteristics of 38 accessions of *Chrysothamnus*.

ID no.	*Chrysothamnus*	Perimeter of leaf x-section (mm)	Area of leaf x-section (mm^2)	Leaf thickness ratio (perimeter/area of leaf x-section - mm/mm^2)
1.	chna-a-24	4.14	0.31	13.42
2.	chna-a-36	7.47	0.40	18.48
3.	chna-a-37	1.79	0.17	10.60
4.	chna-c-3	3.47	0.67	5.16
5.	chna-c-4	2.31	0.25	9.40
6.	chna-c-11	2.73	0.25	10.79
7.	chna-c-20	2.23	0.25	8.98
8.	chna-c-21	2.21	0.19	11.40
9.	chna-c-31	1.95	0.22	8.80
10.	chna-h-2	3.84	0.66	5.86
11.	chna-h-33	3.41	0.30	11.24
12.	chna-h-8	3.03	0.41	7.43
13.	chna-h-16	3.41	0.31	11.00
14.	chna-g-7	3.31	0.27	12.24
15.	chna-g-14	2.59	0.26	9.87
16.	chna-g-15	3.23	0.32	10.10
17.	chna-g-23	4.58	0.37	12.38
18.	chna-j-35	1.87	0.29	6.51
19.	chna-m-25	1.79	0.21	8.64
20.	chna-n-39	2.71	0.31	8.68
21.	chna-n-19	2.89	0.37	7.83
22.	chna-s-26	4.03	0.29	13.95
23.	chna-t-9	2.25	0.24	9.44
24.	chna-t-32	2.79	0.37	7.45
25.	chna-l-40	1.85	0.21	8.78
26.	chna-v-5	3.49	0.27	12.97
27.	chna-v-6	5.08	0.76	6.68
28.	chna-v-12	2.33	0.24	9.75
29.	chna-v-13	2.61	0.31	8.44
30.	chna-v-22	1.75	0.18	9.62
31.	chpa-a-1	1.81	0.13	13.53
32.	chvi-v-38	4.30	0.38	11.40
33.	chvi-v-18	5.44	0.52	10.44
34.	chvi-v-10	1.93	0.21	9.02
35.	chgr-17	2.41	0.25	9.65
36.	chte-34	1.95	0.31	6.30
37.	chli-28	7.89	0.59	13.36
38.	chvi-l-27	2.29	0.23	10.17

leaf cross-section perimeter increased, leaf cross-section thickness also increased.

The effects of environmental conditions at the native sites on the size and thickness of *Chrysothamnus* leaves were studied. As moisture availability index increased, the leaf cross-section perimeter also increased (Table 7). For example, as yearly precipitation increased from 45.7 mm (1.8 inches) (*C. teretifolius* at Death Valley) to 457.2 mm (18 inches) (*C. nauseosus* ssp. *graveolens* at Salina Canyon) and moisture availability index increased from 0.02 to 0.21 (Table 6), the leaf cross-section perimeter increased proportionally. Therefore, leaf cross-section perimeter is positively correlated to moisture availability index. Correlation coefficient for perimeter of leaf cross section vs. yearly precipitation/July mean maximum temperature (moisture availability) was 0.157 (Table 7), which was significant. This suggests that plants with small leaves tend to grow in hot, dry environments and plants with large leaves grow in cool, wet environments.

Positive correlations were found between leaf cross-section thickness ratio and environmental factor. The thickness ratio of leaf cross section positively correlated to moisture availability (Table 7). Correlation coefficient for thickness ratio of leaf cross section vs. yearly precipitation/July mean maximum temperature was 0.14 (Table 7). This suggests that plants with round cross sections were adapted to hot, dry environments. Plants

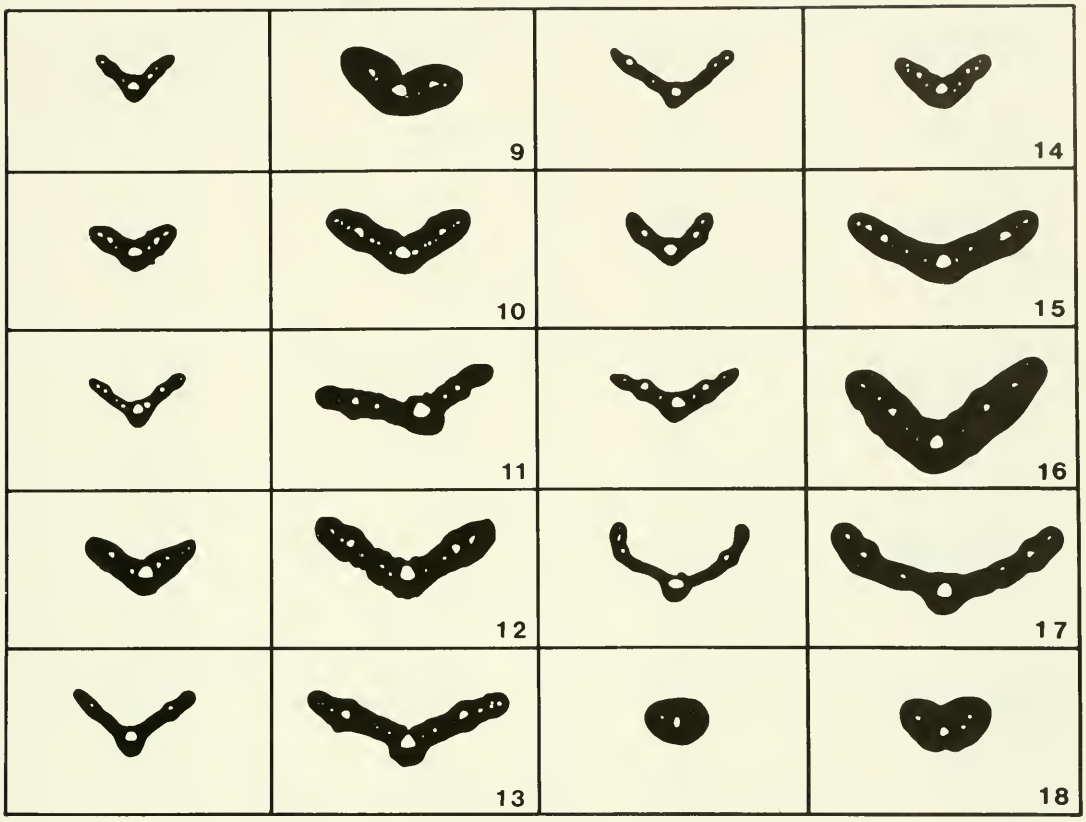

Fig. 2. Leaf cross sections of drawings of accessions of *Chrysothamnus*. Left = terminal leaf, right = lateral leaf; drawings 14.5X (see Table 1). 9, *C. nauseosus* ssp. *consimilis;* 10–13, *C. nauseosus* ssp. *hololeucus;* 14–17, *C. nauseosus* ssp. *graveolens;* 18, *C. nauseosus* ssp. *junceus*.

with thin leaves and flat cross sections were adapted to cooler, more mesic environments.

Terminal Leaf Vein Cross-section Characteristics and Their Relation to Leaf Cross Section and Environments

Vein cross section ranged in area from 2.1×10^{-2} mm^2 to 1.19 mm^2 and vein cross-section thickness ratio (perimeter of leaf vein cross section in mm/area of leaf vein cross section in sq mm) ranged from 19.40 to 45.00 (Table 3).

There was a positive correlation between the size of vein cross section and leaf cross section. Vein perimeter increased with increasing leaf cross-section perimeter (Table 7). Vein area also increased with increasing leaf cross-section area (Table 7). Thus leaves with large cross sections had large veins, whereas leaves with small cross sections had small veins.

However, there was not a positive correlation between leaf cross-section thickness ratio vs. vein cross-section thickness ratio (Table 7). If leaves were elliptical in cross section, their veins were not necessarily elliptical in cross section; whereas, if leaves were round in cross section, their veins were not round.

The effects of environmental conditions at the native site on the thickness of veins were compared to the area of leaf section. Significant correlations were also found between vein cross-section thickness ratio and environmental parameters (Table 7). The thickness ratio of vein cross section was positively correlated with moisture availability index. Leaves with round veins in cross section were adapted to hot, dry environments. Leaves with flat veins were adapted to cooler, more mesic environments.

Lateral Leaf Cross-section Characteristics and Their Relation to Environmental Parameters

The variation in size and thickness of lateral

TABLE 3. Terminal vein cross-section characteristics of 38 accessions of *Chrysothamnus*.

ID no. *Chrysothamnus*	Perimeter of vein x-section (mm)	Area of vein x-section (mm^2)	Vein thickness ratio (perimeter/area of vein x-section - mm/mm^2)
1. chna-a-24	2.70	0.06	45.00
2. chna-a-36	3.91	0.13	30.08
3. chna-a-37	1.61	0.05	32.20
4. chna-c-3	4.28	0.18	23.78
5. chna-c-4	2.33	0.08	29.13
6. chna-c-11	2.92	0.10	29.20
7. chna-c-20	1.94	0.10	19.40
8. chna-c-21	2.63	0.09	29.22
9. chna-c-31	2.27	0.08	28.38
10. chna-h-2	3.42	0.15	22.80
11. chna-h-33	3.03	0.13	23.31
12. chna-h-8	3.42	0.15	22.80
13. chna-h-16	2.85	0.10	28.50
14. chna-g-7	3.29	0.12	27.42
15. chna-g-14	3.34	0.16	20.88
16. chna-g-15	4.64	0.19	24.42
17. chna-g-23	4.94	0.19	26.00
18. chna-j-35	2.04	0.07	29.14
19. chna-m-25	2.80	0.11	25.45
20. chna-n-39	3.94	0.13	30.31
21. chna-n-19	4.24	0.13	32.61
22. chna-s-26	0.81	0.02	38.57
23. chna-t-9	2.36	0.08	29.50
24. chna-t-32	2.55	0.11	23.18
25. chna-l-40	2.75	0.10	27.50
26. chna-v-5	4.26	0.19	22.42
27. chna-v-6	4.52	0.13	34.77
28. chna-v-12	2.99	0.11	27.18
29. chna-v-13	3.69	0.13	28.38
30. chna-v-22	2.39	0.08	29.88
31. chpa-a-1	1.38	0.04	34.50
32. chvi-v-38	3.92	0.11	35.64
33. chvi-v-18	5.58	0.17	32.82
34. chvi-v-10	3.37	0.10	33.70
35. chgr-17	2.88	0.09	32.00
36. chtc-34	1.59	0.08	19.88
37. chli-28	3.53	0.16	30.30
38. chvi-l-27	1.97	0.05	39.40

leaf cross sections is shown in Table 4. The variation of the size and thickness of vein cross sections is shown in Table 5. The relationships of leaf cross-section characteristics and vein cross-section characteristics and their relation to environmental conditions are summarized in Table 7. There were similar relationships between leaf cross section and vein cross section. That is, leaf cross-section size was positively correlated to vein cross-section size and leaf thickness was not correlated to vein thickness (Table 7). However, leaf cross-section size and thickness ratio were not correlated (Table 7). None of the leaf cross-section characteristics and vein cross-section characteristics were related to environmental parameters of native sites (Table 7). In other words, the size and thickness of lateral leaves and the thickness of lateral leaf veins had no relationship with environmental conditions of the native sites.

DISCUSSION

Leaves are the principal sites of light interaction, gas exchange, and transpiration in plants. It is expected that a broad range of leaf structures is closely related to the specific microclimatic conditions of the growing sites (Catarino and Kummerow 1981). Our study shows that variable leaf cross-section area and thickness tend to reflect changes in environmental conditions. Leaf cross-section area and

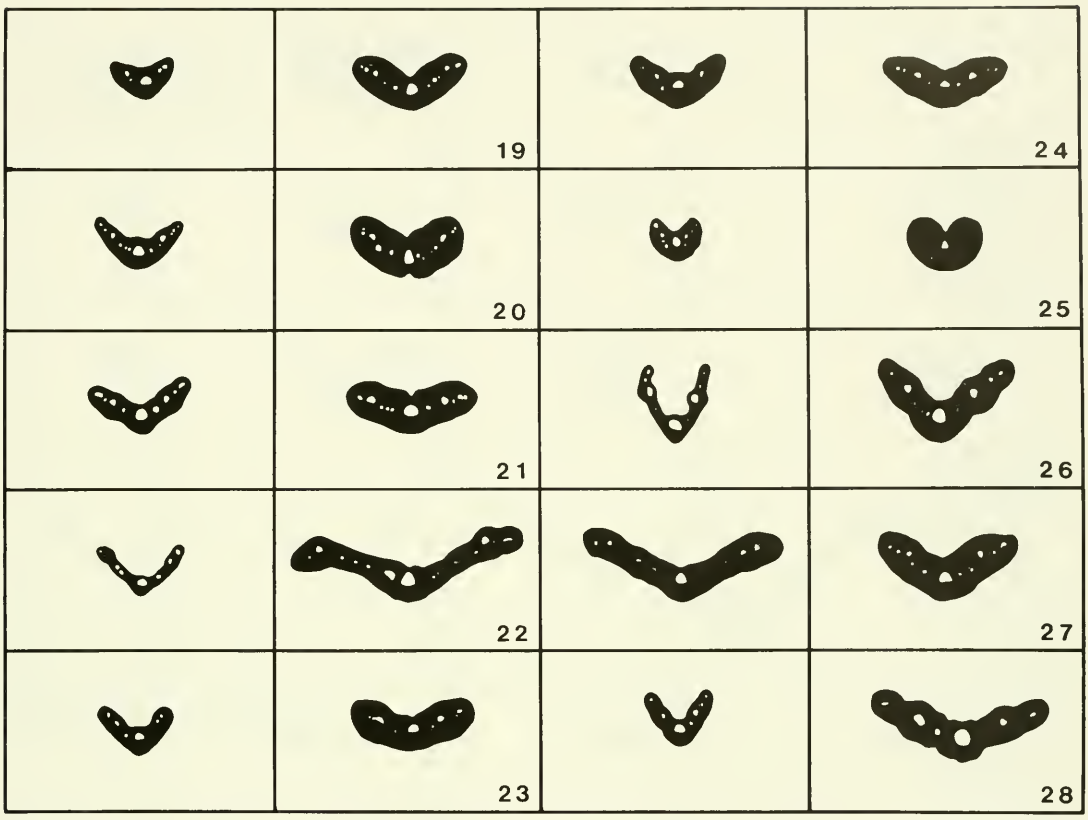

Fig. 3. Leaf cross sections of drawings of accessions of *Chrysothamnus*. Left = terminal leaf, right = lateral leaf; drawings 14.5X (see Table 1). 19, *C. nauseosus* ssp. *mohavensis;* 20, *C. nauseosus* ssp. *nitidus;* 21, *C. nauseosus* ssp. *nauseosus;* 22, *C. nauseosus* ssp. *salicifolius;* 23–24, *C. nauseosus* ssp. *turbinatus;* 25, *C. nauseosus* ssp. *leiospermus;* 26–28, *C. nauseosus* ssp. *viridulus*.

thickness ratio of different species and subspecies of *Chrysothamnus* were correlated with natural habitat at the original collection site. In hot, dry environments, plants had small leaf cross-sectional areas. In response to cooler, more mesic environments, plants had large leaf cross-sectional areas (Table 7). This relationship between leaf cross-sectional size and environmental parameters suggests that the size of leaf cross section may represent a significant plant adaptation. Givnish (1976) indicated that leaf area affects gas exchange indirectly through its effects on the thickness of the leaf boundary layer. Generally, the larger and broader a leaf is, the more it interferes with the free flow of air around the photosynthetic surface. The boundary layer of a sunlit leaf impedes convective heat loss. Large leaves with deep boundary layers tend to impede heat loss more than small leaves, and so they heat up more in sunlight (Gates and Papian 1971). Small leaves exchange heat rapidly and in this way remain close to ambient temperature. In his studies with leaf size and leaf temperature of tropical vines, Givnish (1976, 1978, 1979) found that temperatures of large leaves were significantly higher than the temperatures of smaller leaves. Parkhurst and Loucks (1972) and Gates (1980) suggested that narrow leaves were more efficient heat exchangers and were less likely to overheat when exposed to drought and high irradiance.

As relative humidity increases, there is a tendency for transpiration and evaporative cooling to decline. This causes leaf temperature to rise more rapidly, which tends to favor larger leaves in more humid environments (Givnish 1979, Givnish and Vermeij 1976).

Givnish (1976) also indicated that leaf size has evolved in part as a response to leaf temperature. Selection should favor leaf sizes that

TABLE 4. Lateral leaf cross-section characteristics of 38 accessions of *Chrysothamnus*.

ID no.	*Chrysothamnus*	Perimeter of leaf x-section (mm)	Area of leaf x-section (mm^2)	Leaf thickness ratio (perimeter/area of leaf x-section - mm/mm^2)
1.	chna-a-24	5.32	0.79	6.76
2.	chna-a-36	4.56	1.04	4.39
3.	chna-a-37	2.98	0.57	5.19
4.	chna-c-3	3.57	0.79	4.53
5.	chna-c-4	3.39	0.61	5.53
6.	chna-c-11	4.95	0.81	6.13
7.	chna-c-20	3.20	0.51	6.32
8.	chna-c-21	3.41	0.68	4.99
9.	chna-c-31	2.55	0.38	6.69
10.	chna-h-2	2.36	0.29	8.06
11.	chna-h-33	5.55	0.89	6.24
12.	chna-h-8	4.85	0.84	5.57
13.	chna-h-16	5.18	0.43	12.03
14.	chna-g-7	2.61	0.34	7.63
15.	chna-g-14	4.81	0.83	5.77
16.	chna-g-15	5.42	1.21	4.46
17.	chna-g-23	6.57	0.89	7.33
18.	chna-j-35	2.59	0.49	5.30
19.	chna-m-25	2.94	0.51	5.75
20.	chna-n-39	3.25	0.63	5.20
21.	chna-n-19	3.31	0.61	5.47
22.	chna-s-26	7.01	0.96	7.29
23.	chna-t-9	3.31	0.57	5.84
24.	chna-t-32	3.23	0.55	5.89
25.	chna-l-40	2.26	0.37	6.05
26.	chna-v-5	4.11	0.69	5.96
27.	chna-v-6	3.70	0.71	5.20
28.	chna-v-12	4.48	0.75	5.97
29.	chna-v-13	4.07	0.93	4.39
30.	chna-v-22	2.49	0.39	6.40
31.	chpa-a-1	3.25	0.51	6.40
32.	chvi-v-38	4.09	0.49	8.40
33.	chvi-v-18	5.16	0.71	7.28
34.	chvi-v-10	2.07	0.30	6.96
35.	chgr-17	2.26	0.31	7.37
36.	chte-34	2.38	0.40	5.96
37.	chli-28	8.63	0.91	9.52
38.	chvi-l-27	3.74	0.46	8.08

keep leaf temperatures near the optimum temperature for photosynthesis, while preventing thermal damage or death of leaves. Therefore, *Chrysothamnus* leaves with small cross sections may have an adaptive advantage for survival under hot, dry environmental conditions, whereas, large leaves on plants in wetter, cooler, more mesic environments do not become so hot that there is a decline in photosynthetic rate. In fact, under such conditions large leaves may absorb more light and CO_2 than smaller leaves and thus accrue some selective advantage.

The relationship of the leaf cross-section thickness ratio to environmental parameters of native sites provides the evidence for leaf thickness as an adaptive characteristic. In their studies with potentially adaptive effects of leaf thickness on photosynthesis and transpiration in leaves of *Abutilon theophrasti*, Yun and Taylor (1986) found that there was little difference in transpiration rate between thick and thin leaves. Thick leaves of *A. theophrasti* grown under high light had greater water-use efficiency without decreasing net photosynthesis in moderately sunny environments. This was not observed for thin leaves. These authors concluded that increased productivity without increased water use is potentially of adaptive significance in plants where sun-grown leaves thicken. Horn (1971) hypothesized that thin leaves would

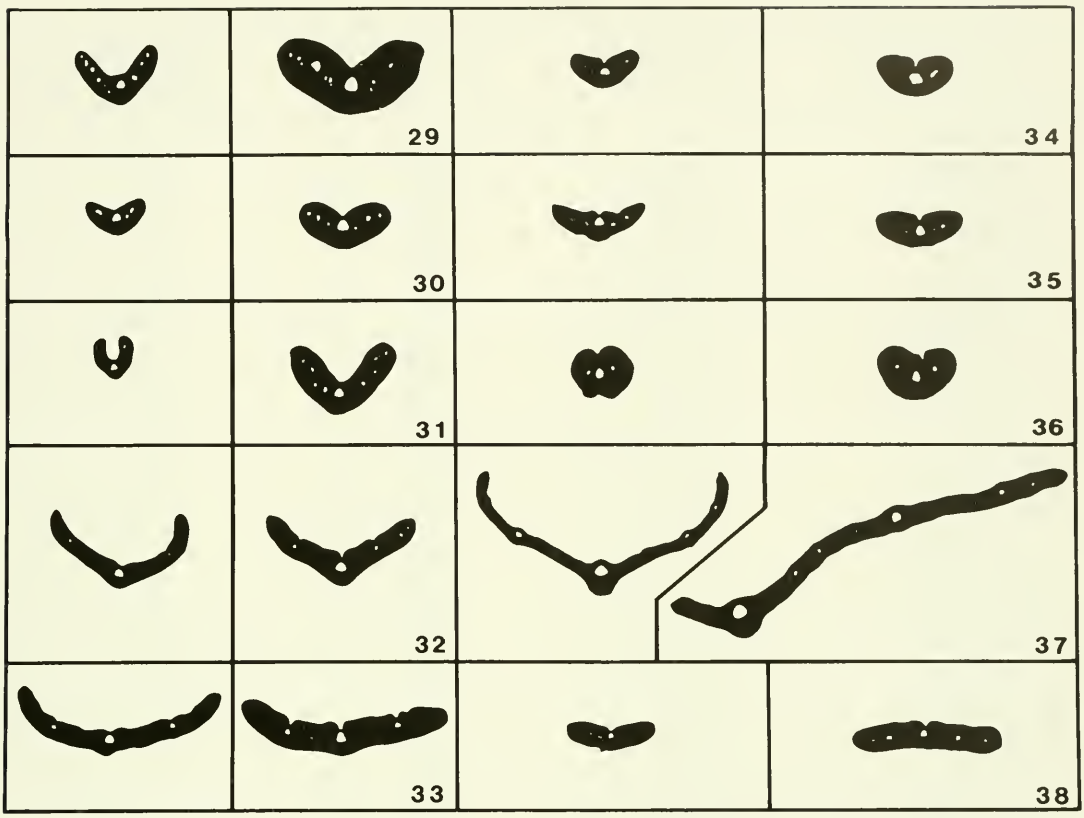

Fig. 4. Leaf cross sections of drawings of accessions of *Chrysothamnus*. Left = terminal leaf, right = lateral leaf; drawings 14.5X (see Table 1). 29–30, *C. nauseosus* ssp. *viridulus;* 31, *C. parryi* ssp. *attenuatus;* 32–34, *C. viscidiflorus* ssp. *viscidiflorus;* 35, *C. greenei;* 36, *C. teretifolius;* 37, *C. linifolius;* 38, *C. viscidiflorus* ssp. *lanceolatus.*

be more productive than thick leaves at light near the compensation point, while thick leaves would have substantially higher rates of photosynthesis at high light levels.

Leaf cross-sectional size and leaf cross-sectional thickness ratio were related. The relative leaf thickness ratio increased as leaf cross-section area decreased. Leaves with small cross-sectional area were relatively thicker, and leaves with large cross-sectional area were thinner. As leaf thickness ratio increases in *Chrysothamnus*, there is a concomitant reduction in leaf size. Therefore, both leaf cross-sectional area and leaf thickness ratios were related to moisture availability index. Changes in leaf cross-sectional area and thickness appear to correspond with changes in environmental conditions.

Environmental conditions affect the selection of leaf sizes and the efficiency of water utilization. The optimal leaf size in a given environment is the size yielding maximum water-use efficiency (Parkhurst and Loucks 1972). According to Yun and Taylor (1986), the water-use efficiency for thick leaves is greater than for thin leaves under sunny conditions. Rosen (1967) stated that natural selection should produce a combination of form and function optimal for growth and reproduction in the environment in which an organism lives. In an environment with high precipitation and high temperature, the combination of relatively thick and small leaf cross-section form will have a high water-use efficiency and will be more adapted to hot, dry conditions. The leaf cross-sectional areas and relative thickness characteristics of *Chrysothamnus* are consistent with this principle.

The strength of these data is that, notwithstanding the diverse phylogenetic lines in *Chrysothamnus*, leaf shape and size are significantly correlated with a moisture gradient.

TABLE 5. Lateral vein cross-section characteristics of 38 accessions of *Chrysothamnus*.

ID no.	*Chrysothamnus*	Perimeter of vein x-section (mm)	Area of vein x-section (mm^2)	Vein thickness ratio (perimeter/area of vein x-section - mm/mm^2)
1.	chna-a-24	4.31	0.16	26.39
2.	chna-a-36	3.82	0.16	24.67
3.	chna-a-37	2.74	0.12	22.04
4.	chna-c-3	3.69	0.17	23.73
5.	chna-c-4	3.57	0.14	26.32
6.	chna-c-11	5.12	0.21	24.24
7.	chna-c-20	3.04	0.09	32.19
8.	chna-c-21	3.59	0.16	21.83
9.	chna-c-31	3.29	0.12	27.71
10.	chna-h-2	5.61	0.19	29.75
11.	chna-h-33	4.98	0.31	16.28
12.	chna-h-8	5.61	0.19	29.75
13.	chna-h-16	5.05	0.21	24.07
14.	chna-g-7	3.77	0.13	28.42
15.	chna-g-14	5.76	0.27	21.61
16.	chna-g-15	6.49	0.31	20.93
17.	chna-g-23	6.11	0.11	57.12
18.	chna-j-35	3.13	0.12	25.54
19.	chna-m-25	2.75	0.11	24.53
20.	chna-n-39	4.53	0.17	27.01
21.	chna-n-19	4.59	0.19	23.94
22.	chna-s-26	5.02	0.02	23.30
23.	chna-t-9	3.16	0.13	24.15
24.	chna-t-32	3.37	0.11	29.88
25.	chna-l-40	2.35	0.07	32.54
26.	chna-v-5	4.98	0.25	19.67
27.	chna-v-6	5.18	0.18	28.46
28.	chna-v-12	4.98	0.29	17.01
29.	chna-v-13	4.81	0.21	22.77
30.	chna-v-22	3.01	0.12	24.75
31.	chpa-a-1	4.01	0.15	26.76
32.	chvi-v-38	4.05	0.13	30.64
33.	chvi-v-18	5.13	0.16	31.42
34.	chvi-v-10	2.42	0.07	32.50
35.	chgr-17	2.45	0.08	29.99
36.	chte-34	2.32	0.10	23.50
37.	chli-28	4.94	0.25	19.68
38.	chvi-l-27	2.85	0.09	32.45

Anderson (1975) pointed out that the structural basis for adaptation to drought differs among species. Even so, our data show that leaf adaptation to a moisture gradient has apparently occurred. The species *C. teretifolius*, for example, is from the driest habitat and it had very small leaves in cross section (Fig. 4). This subspecies was from the highest temperature zone (46 C in July) and the lowest annual precipitation (45.7 mm). In contrast, *C. nauseosus* ssp. *salicifolius* ordinarily grows in the most mesic habitats occupied by *Chrysothamnus* species, near montane aspen (*Populus tremuloidies*) groves (McArthur et al. 1979). Our representative *C. nauseosus* ssp. *salicifolius* population sample had among the largest leaves (Fig. 3) and grew in a zone of relatively high annual precipitation and low July temperature (Table 6). Some plants do not fit this pattern, e.g., *C. parryi* ssp. *attenuatus* (Fig. 4, Table 6), possibly because of different developmental pathways (Anderson 1975).

The vascular elements affect the mechanical strength of the leaf and distribution of water, minerals, metabolites, and hormones within it (Parkhurst and Loucks 1972). These functions of veins are influenced by vein and leaf shape and appear to be significantly affected by environment. In our study, vein cross sections tended to be round as moisture availability index decreased (July mean

TABLE 6. Climate data at native sites for 38 accessions of *Chrysothamnus*.

ID *Chrysothamnus* no.	Yearly precip. (inches)	(cm)	July mean max. temp. (F)	(C)	Yearly precip./July mean max. temp (inches/F)
1. chna-a-24	16.00	44.64	82.00	28.00	0.19
2. chna-a-36	17.70	44.96	85.00	29.44	0.21
3. chna-a-37	14.60	37.08	91.00	33.00	0.16
4. chna-c-3	5.00	12.70	92.00	33.33	0.05
5. chna-c-4	7.90	20.07	94.00	34.44	0.08
6. chna-c-11	9.30	23.62	89.00	32.00	0.10
7. chna-c-20	10.70	27.18	89.00	32.00	0.12
8. chna-c-21	7.00	17.78	92.00	33.33	0.08
9. chna-c-31	9.30	23.62	90.00	32.22	0.10
10. chna-h-2	16.00	40.64	86.00	30.00	0.19
11. chna-h-33	10.50	26.70	92.00	33.33	0.11
12. chna-h-8	12.50	31.75	96.00	36.00	0.13
13. chna-h-16	13.50	34.30	94.00	34.44	0.14
14. chna-g-7	18.00	45.72	84.00	29.00	0.21
15. chna-g-14	12.20	40.00	88.00	31.11	0.14
16. chna-g-15	12.00	30.50	93.00	34.00	0.13
17. chna-g-23	10.60	26.92	98.00	37.00	0.11
18. chna-j-35	13.20	33.53	91.00	33.00	0.15
19. chna-m-25	7.90	20.06	98.00	37.00	0.08
20. chna-n-39	8.00	20.32	100.00	38.00	0.08
21. chna-n-19	11.40	29.00	91.00	33.00	0.13
22. chna-s-26	15.50	39.37	83.00	28.33	0.19
23. chna-t-9	8.60	21.84	93.00	34.00	0.09
24. chna-t-32	10.50	26.70	92.00	33.33	0.11
25. chna-l-40	13.20	33.53	91.00	33.00	0.15
26. chna-v-5	5.20	13.21	98.00	37.00	0.05
27. chna-v-6	16.00	40.64	74.00	23.33	0.22
28. chna-v-12	3.90	9.91	104.00	40.00	0.04
29. chna-v-13	7.90	20.07	94.00	34.44	0.08
30. chna-v-22	8.00	20.32	88.00	31.11	0.09
31. chpa-a-1	16.00	40.64	86.00	30.00	0.19
32. chvi-v-38	18.00	45.72	84.00	29.00	0.21
33. chvi-v-18	14.00	35.60	82.00	28.00	0.17
34. chvi-v-10	9.30	23.62	89.00	32.00	0.10
35. chgr-17	8.60	21.84	93.00	34.00	0.09
36. chte-34	1.80	4.57	114.00	46.00	0.02
37. chli-28	9.70	24.64	91.00	33.00	0.11
38. chvi-l-27	10.70	27.18	89.00	32.00	0.12

maximum temperature increased or yearly precipitation decreased). Therefore, the difference in size and thickness of both leaf and vein between cool, mesic and hot, dry environments can perhaps be assumed to be one of the adaptive mechanisms of leaves. Leaf morphology may be molded by selection operating through efficiency of the photosynthetic process.

Chrysothamnus leaves display significant variation in leaf and vein cross-sectional areas. As viewed in cross section, larger leaves have veins that are larger. However, the thickness of leaves and veins was not correlated. Leaves with round leaf cross section do not necessarily have round veins. These observations have not been reported previously for *Chrysothamnus*. Similar studies need to be conducted with *Chrysothamnus* plants grown in their native habitats rather than in a uniform garden.

For the lateral leaves of *Chrysothamnus*, leaf cross-sectional size was correlated with vein cross-sectional size (Table 7), which suggests that as plants are grown in a uniform garden, environmental influences may modify morphology although leaf and vein cross-section morphology remain constant.

However, leaf cross-sectional area, leaf cross-sectional thickness, and vein thickness

TABLE 7. Probability and correlation coefficients of areas and perimeters of *Chrysothamnus* leaf cross sections.

Correlation	r^2 of coefficient[a] Terminal	Lateral
Perimeter of leaf x-section vs. perimeter/area of leaf x-section	.219*	.09
Perimeter of leaf x-section vs. yearly precip./July mean max. temp.	.157*	.027
Perimeter/area of leaf x-section vs. yearly precip./July mean max. temp.	.14*	.054
Perimeter of leaf x-section vs. perimeter of vein x-section	.275*	.475*
Area of leaf x-section vs. area of vein x-section	.308*	.298*
Perimeter/area of leaf x-section vs. perimeter/area of vein x-section	.082	.018
Perimeter/area of vein x-section vs. yearly precip./July mean max. temp.	.209*	.053

[a]Significant ($p < .05$) correlations at this 5% level are shown by an asterisk.

were not correlated with environmental conditions at the sites of origin (Table 7). Perhaps this is because the 38 accessions sampled were grown in a uniform garden instead of their original locations. Although it is not known why, there are more positive correlations with terminal leaves of *Chrysothamnus* than with lateral leaves. This may be because young leaves reflect genotype more directly. It may also reflect the more exposed canopy position of terminal versus lateral leaves. Possibly the modifying effects of environment at the common garden, which tend to cause morphology to be more similar, have not yet influenced these leaves as much as the older lateral leaves. Further studies of plants in their native habitats could help elucidate the differential response of these two types of leaves.

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LITERATURE CITED

AKIMOTO, Y. 1979. Final leaf shape of tobacco in relation to temperature during the young leaf stage: 1. Effects of high temperature during the young leaf stage of tobacco leaf on its leaf shape. Japanese J. Crop Sci. 47: 483–490.

ANDERSON, L. C. 1975. Modes of adaptation to desert conditions in *Chrysothamnus*. Page 141 *in* H. C. Stutz, Proceedings Symposium and Workshop, wildland shrubs, on the occasion of the dedication of the U.S. Forest Service Shrub Sciences Laboratory. Brigham Young University Print Services, Provo, Utah.

———. 1986a. An overview of the genus *Chrysothamnus* (Asteraceae) Pages 29–45 *in* E.D. McArthur and B. L. Welch, Proceedings—Symposium on the biology of *Artemisia* and *Chrysothamnus*. USDA Forest Service, General Technical Report INT-200. Intermountain Research Station, Ogden, Utah.

———. 1986b. Cytogeography of *Chrysothamnus viscidiflorus*. Pages 93–97 *in* E. D. McArthur and B. L. Welch, Proceedings—Symposium on the biology of *Artemisia* and *Chrysothamnus*. USDA Forest Service General Technical Report INT-200. Intermountain Research Station, Ogden, Utah.

———. 1986c. Sympatric subspecies in *Chrysothamnus nauseosus*. Pages 98–103 *in* E. D. McArthur and B. L. Welch, Proceedings—Symposium on the biology of *Artemisia* and *Chrysothamnus*. USDA Forest Service, General Technical Report INT-200. Intermountain Research Station, Ogden, Utah.

BAILEY, I. W., AND E. W. SINNOTT. 1916. The climatic distribution of certain types of angiosperm leaves. Amer. J. Bot. 3: 24–39.

CATARINO, F., AND J. KUMMEROW. 1981. Leaf morphology (evolutionary adaptation to environment) tasks for vegetation science. V. 4, 1981. I.C. 3. The Hague: W. Junk Publishers.

CUNNINGHAM, G. L., AND B. R. STRAIN. 1969. An ecological significance of seasonal leaf variability in a desert shrub. Ecology 50: 400–408.

FUTUYMA, D. J. 1986. Evolutionary biology. Sinauer Associates, Inc., Sunderland, Massachusetts. 600 pp.

GATES, D. M. 1980. Biophysical ecology. Springer Verlag, New York. 611 pp.

GATES, D. M., AND L. E. PAPIAN. 1971. Atlas of energy budgets of plant leaves. Plenum Press, New York. 277 pp.

GENTRY, A. H. 1969. A comparison of some leaf characteristics of tropical dry forest and tropical wet forest in Costa Rica. Turrialba 19: 419–428.

GIVNISH, T. J. 1976. Leaf form in relation to environment: a theoretical study. Unpublished dissertation, Princeton University. 467 pp.

_____. 1978. On the adaptive significance of compound leaves, with particular reference to tropical trees. Pages 351–380 *in* P. B. Tomlinson and M. H. Zimmerman, Tropical trees as living systems. Cambridge University Press, Cambridge.

_____. 1979. On the adaptive significance of leaf form. Pages 375–707 *in* O. T. Solbrig, P. H. Raven, S. Jain, and G. B. Johnson, Tropics in plant population biology. Columbia University Press, New York.

GIVNISH, T. J., AND G. J. VERMEIJ. 1976. Sizes and shapes of liana leaves. Amer. Nat. 110: 743–778.

HEGERHORST, D. F., R. B. BHAT, D. J. WEBER, AND E. D. MCARTHUR. 1988. Seasonal changes of selected secondary plant products in *Chrysothamnus nauseosus* ssp. *turbinatus*. Great Basin Nat. 48: 1–8.

HEGERHORST, D. F., D. J. WEBER, AND E. D. MCARTHUR. 1987. Resin and rubber contents in *Chrysothamnus*. Southw. Nat. 32: 475–482.

HORT, A. (trans.). 1948. Enquiry into plants (Vol. I), by Theophrastus. Harvard University Press, Cambridge, Mass.

HORN, H. S. 1971. The adaptive geometry of trees. Princeton University Press, Princeton, New Jersey. 144 pp.

JACKSON, L. W. R. 1967. Effects of shade on leaf structure of deciduous tree species. Ecology 48: 498–499.

LIGHTBODY, J. P. 1985. Distribution of leaf shapes of *Piper* sp. in a tropical cloud forest: evidence for the role of drip-tips. Biotropica 17: 339–342.

MCARTHUR, E. D. 1984. Natural diversity of western range shrubs. Pages 193–209 *in* J. L. Cooley and J. H. Cooley, Natural diversity in forest ecosystems. Proceeding of the workshop. Institute of Ecology, University of Georgia. 294 pp.

MCARTHUR, E. D., A. C. BLAUER, A. P. PLUMMER, AND R. STEVENS. 1979. Characteristics and hybridization in important intermountain shrubs. III. Sunflower family. Research Paper INT-220. USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, Utah. 82 pp.

MOONEY, J., O. BJORKMAN, AND J. TROUGHTON. 1974. Seasonal changes in the desert shrub *Atriplex hymenlytra*. Ann. Rept. Dept. Plant Biol. Carnegie Inst. 1974: 846–852.

NAWAZ, M. S., AND W. M. HESS. 1987. Ultrastructure of *Neovossia horrida* teliospores. Mycologia 79: 173–179.

OSTLER, W. K., C. M. MCKELL, AND S. WHITE. 1986. *Chrysothamnus nauseosus*, a potential source of natural rubber. Pages 389–394 *in* E. D. McArthur and B. L. Welch, Proceedings—Symposium on the biology of *Artemisia* and *Chrysothamnus*. USDA Forest Service General Technical Report INT-200. Ogden, Utah, 398 pp.

PARKHURST, D. F., AND O. L. LOUCKS. 1972. Optimal leaf size in relation to environment. J. Ecol. 60: 505–537.

ROSEN, R. 1967. Optimality principles in biology. Plenum Press, New York. 198 pp.

RUSS, J. C., AND W. D. STEWART. 1983. Quantitative image measurement using a microcomputer system. Amer. Lab. 12: 71–75.

SHREVE, E. B. 1924. Factors governing seasonal changes of the Sonoran Desert. Stanford University Press, Stanford, California. 289 pp.

SPURR, A. R. 1969. A low viscosity epoxy resin embedding medium for electron microscopy. J. Ultrastruct. Res. 26: 31–43.

STATVIEW 512+. 1986. Statistics Software, Brain Power Co., Calabass, California. 35 pp.

WATER INFORMATION CENTER. 1974. Climates of the states II. Western states. Water Information Center, Inc., Port Washington, New York. 975 pp.

WEBER, D. J., T. D. DAVIS, D. MCARTHUR, AND N. SANKHLA. 1985. *Chrysothamnus nauseosus* (rabbitbrush), multi-use shrub of the desert. Desert Plants 7: 172–180, 208–210.

YUN, J. I., AND S. E. TAYLOR. 1986. Adaptive implications of leaf thickness for sun- and shade-grown *Abutilon theophrasti*. Ecology 67: 1314–1318.

DOUGLAS-FIR BEETLE (*DENDROCTONUS PSEUDOTSUGAE* HOPKINS, COLEOPTERA: SCOLYTIDAE) BROOD PRODUCTION ON DOUGLAS-FIR DEFOLIATED BY WESTERN SPRUCE BUDWORM (*CHORISTONEURA OCCIDENTALIS* FREEMAN, LEPIDOPTERA: TORTRICIDAE) IN LOGAN CANYON, UTAH

S. E. Fredericks[1] and M. J. Jenkins[1]

ABSTRACT.—Douglas-fir beetle brood production was studied on Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) trees defoliated by the western spruce budworm between 1983 and 1985. Tallies were made of the number of attacks, total length and number of egg galleries, number of eggs deposited, number of larval tunnels, number of pupal chambers, and number of emerging beetles (per female and per unit area). Data analysis showed no significant differences among the three years studied. The number of emerging beetles per female parent was 0.59, and emergence per 90 cm^2 was 2.32 beetles. Egg, larval, and pupal survivals were 47.5%, 30.0%, and 15.5%, respectively.

The Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins, Coleoptera: Scolytidae) attacks Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) trees throughout its range in western North America. The beetle is normally considered a secondary pest, attacking trees that are windthrown, diseased, or stressed by other environmental factors. Damage from logging operations, drought, wildfire, and snow breakage is commonly associated with Douglas-fir beetle epidemics (Bedard 1950, Furniss and Carolin 1977, Coulson and Witter 1984). Stress created by tree defoliation can also contribute to increased beetle populations (Wright et al. 1984) and may be a factor in the current beetle outbreak in Logan Canyon, Utah. Endemic levels of Douglas-fir beetles are commonly found in felled and damaged trees (Bedard 1950, Furniss et al. 1979), and studies on host selection indicate the beetle prefers freshly felled trees (McMullen and Atkins 1962). When such host material is abundant, populations can build to epidemic levels so the beetle may be able to successfully attack relatively healthy trees (Bedard 1950, Furniss et al. 1979). For a discussion on the mechanisms of beetle host colonization and the role of semio-chemicals see Wood (1982).

Douglas-fir beetle outbreaks decline due to lack of suitable host material, greater host resistance (Furniss et al. 1979), and increased intraspecific competition (McMullen and Atkins 1961, Berryman et al. 1973, Wright et al. 1984). Other biotic agents, such as predators, parasites, and pathogens, are important in population collapse (Furniss et al. 1979). Periodic Douglas-fir beetle outbreaks in the Intermountain West and the northern Rocky Mountain areas generally last from three to six years (Furniss and McGregor 1979, Wright et al. 1984).

The western spruce budworm (*Choristoneura occidentalis* Freeman, Lepidoptera: Tortricidae) defoliates current year's growth and may feed on previous years' needles as well. Western spruce budworm outbreaks in western North America generally lack a typical pattern and occur at irregular intervals, thus making it difficult to predict future outbreaks (Brookes et al. 1985). Stand conditions favorable to the western spruce budworm result, in part, from past fire suppression and selective cutting practices that have produced multistoried stands with an abundance of shade-tolerant species favored by the western spruce budworm (Coulson and Witter 1984, Brookes et al. 1985).

This study was undertaken to obtain a better understanding of Douglas-fir beetle outbreaks in northeastern Utah. This paper describes brood production during the peak of Douglas-fir beetle activity to determine maximum attack density, optimum brood production, and beetle emergence (per unit area and per female) at peak production levels. Results

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TABLE 1. Douglas-fir beetle densities and brood development over a three-year period of defoliation by western spruce budworm. Values based on 90-cm^2 sample.

	1983	1984	1985	$\bar{X}$
Mean number of attacks	4.50	3.58	3.80	3.97
Mean gallery length (cm)	2.89	3.01	2.90	2.93
Mean number of egg niches	123.69	99.88	104.12	109.23
% egg survival[1]	45.00	49.06	48.51	47.52
% larval survival[2]	32.90	35.20	22.00	30.03
% pupal survival[3]	12.70	14.00	19.89	15.53
% emergence beetles	51.85	67.44	57.89	59.06
Emergence per female[4]	0.52	0.67	0.58	0.59
Emergence per 90 cm^2 [5]	2.33	2.42	2.22	2.32

[1]% Egg survival = number of larval tunnels/number of egg niches × 100
[2]% Larval survival = number of pupal chambers/number of larval tunnels × 100
[3]% Pupal survival = number of emerging beetles/number of pupal chambers × 100
[4]Emergence per female = number of emerging beetles/number of attacks
[5]Emergence per 90 cm^2 = number of emergence holes/bark sample

may contribute to a better understanding of Douglas-fir beetle population dynamics in the Intermountain West.

METHODS AND MATERIALS

Study Area

The two outbreak centers were 4.1 and 8.1 hectares and were located in Logan Canyon in the Wasatch-Cache National Forest, near Logan, Utah. The stand was multistoried with Douglas-fir as the predominant species. Elevation ranged from 2,340 to 2,377 m, with an average slope of 34% and a west-southwest aspect.

A western spruce budworm epidemic in Logan Canyon, Utah, began in 1981, with a light amount of defoliation on 6,880 hectares. In 1982 there were pockets of heavy defoliation, but by 1983 the area of infestation was reduced to 5,900 hectares with 4,112 hectares sustaining light defoliation and 1,789 hectares with moderate defoliation (Anhold and Holland 1983).

Tree mortality of 15% is predicted for the next 10–15 years in Logan Canyon as a result of budworm defoliation (Anhold and Holland 1983). On the two plots studied in this report, little budworm activity was observed after 1985.

In the Logan Canyon study area, fire-damaged trees created a center for an endemic population of beetles. Subsequent defoliation by the spruce budworm weakened trees adjacent to this center, thus providing additional host material suitable for the Douglas-fir beetle that resulted in an outbreak in 1983.

Sampling

Three trees of similar diameter and height in each of the two outbreak centers attacked by the Douglas-fir beetle were randomly selected during each year of attack from 1983 to 1985. Mean diameter of sample trees was 56.8 cm. One bark sample from the north side and one sample from the south side at a height of three meters were extracted using a 90-cm^2 bark punch and the procedure described by Furniss (1962). Samples were returned to the lab and analyzed to determine number and length of egg galleries, and number of egg niches, larval tunnels, pupal chambers, and exit holes.

The number of attacking females per sample was estimated by counting the number of galleries on each bark sample. Successful attacks were those that resulted in oviposition. The number of eggs deposited is a function of gallery length and was found by using the regression equation $Y = -10.64 + 10.32X$, where Y = number of eggs deposited and X = gallery length (Furniss 1962).

RESULTS AND DISCUSSION

There were no significant differences in the beetle parameters measured during the three years of the study using a t-test at the .05 level (Table 1). At peak production levels expected emergence per female parent was 0.59 beetles, with total emergence per 90 cm^2 calculated to be 2.32 beetles. The mean attack density observed during this study was 3.97 attacks per 90 cm^2, with an estimated 58.5% of attacking females producing emerging beetles.

McMullen and Atkins (1961) suggested that brood production and survival of the Douglas-fir beetle are related to attack density. They also found that egg gallery length and eggs per unit gallery length may be influenced by attack density, and there was an inverse relationship between average gallery length and attack density. However, Schmitz and Rudinsky (1968) in similar studies did not find a correlation between average gallery length and attack density.

In our study there were 3.97 attacks per 90 cm^2, population levels typical of an outbreak (McMullen and Atkins 1961, Berryman 1974). Our results make it possible to define a Douglas-fir beetle outbreak based on attack density. A low beetle population will have a mean attack density of 0–2 attacks per 90 cm^2, a moderate population (optimum for brood production) will have 3–5 attacks per 90 cm^2, and a high beetle population will have more than 5 attacks per 90 cm^2. Studies also suggest that heavily defoliated trees may not be the most optimal host for beetle brood production due to loss of nutrients (Wright et al. 1979). Others have found that optimum bark beetle survival occurs at medium attack densities and that survival at high attack densities is limited by intraspecific competition and host availability/resistance (McMullen and Atkins 1961, Berryman and Pienaar 1973, Berryman 1974, Furniss et al. 1979). In our study the beetle population reached a peak and was stable at that level for the three years sampled. Optimum attack density occurred at 3–5 attacks per 90 cm^2 in this study. Given the fact that the beetle epidemic was in its fourth year and that Douglas-fir beetle epidemics generally last from three to six years, the beetle outbreak in Logan Canyon probably will not be sustained much longer. Population levels will most likely decrease markedly within the next year as a result of a combination of greater host resistance/lack of host material and resultant intraspecific competition.

According to Wright et al. (1984), emergence per female is more indicative of intraspecific competition, while emergence per unit area generally indicates the degree of host suitability. In the present study emerging beetles per female and per unit area have peaked during the same period. These results differ from those of Wright et al. (1984), who found that Douglas-fir beetle emergence per female was highest in years of Douglas-fir tussock moth (*Orgyia pseudotsugata* McDunnough, Lepidoptera: Lymantriidae) defoliation, while emergence per unit area peaked three years after defoliation ceased.

In the study by Wright et al. (1984) the beetles generally attacked trees that were defoliated 90% or greater by the tussock moth. Heavy defoliation lasted only one year, with many trees recovering within two years after defoliation ceased. They also found that beetle attacks were less strongly associated with defoliation intensity in later years. In the present study defoliation intensity by the budworm was classified as light to moderate (Anhold and Holland 1983) over a period of two to three years. Thus, the type and amount of defoliation can be a major factor in beetle brood production. Wright et al. (1984) suggested that heavily defoliated trees may not be optimal for beetle brood production due to loss of nutrients.

Furniss (1962) divided the infested portion of standing trees into three zones. The basal zone extends 2.7–4.6 m from the base of the tree. The middle zone, which has the greatest survival potential for beetles, extends to within 1.0–3.0 m of the uppermost infestation. The top zone is above this, but successful attacks are rare in this zone. The uppermost area of infestation in this study did not exceed a height of 12.2 m.

Sampling in the basal zone involved use of a standard 90-cm^2 bark punch. Population sampling by this method avoids the need to fell or climb trees and provides a quick method of evaluating a beetle outbreak.

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LITERATURE CITED

ANHOLD, J. A., AND D. H. HOLLAND. 1983. Biological evaluation of western spruce budworm on the Logan Ranger District Wasatch-Cache National Forest, Utah. USDA Forest Service Pest Management, Publ. R4-83-18, Intermountain Region, Ogden, Utah. 7 pp.

BEDARD, W. D. 1950. The Douglas-fir beetle. USDA Circ. 817. Washington, D.C. 10 pp.

BERRYMAN, A. A. 1973. Population dynamics of the fir engraver, *Scolytus ventralis* (Coleoptera: Scolytidae). Analysis of population behavior and survival from 1964–1971. Canadian Entomol. 105: 1465–1488.

BERRYMAN, A. A., AND L. PIENAAR. 1973. Simulation of intraspecific competition and survival of *Scolytus ventralis* broods (Coleoptera: Scolytidae). Environ. Entomol. 2(1): 447–459.

_____. 1974. Dynamics of bark beetle populations: toward a general productivity model. Environ. Entomol. 3(4): 579–585.

BROOKES, M. H., J. J. COLBERT, R. G. MITCHELL, AND R. W. STARK. 1985. Managing trees and stands susceptible to western spruce budworm. USDA Forest Service Cooperative State Research Service, Tech. Bull. 1695. Washington, D.C.

COULSON, R. N., AND J. A. WITTER. 1984. Forest entomology: ecology and management. John Wiley and Sons, Inc., New York. 669 pp.

FURNISS, M. M. 1962a. Infestation patterns of the Douglas-fir beetle in standing and windthrown trees in southern Idaho. J. Econ. Entomol. 55(4): 486–491.

_____. 1962b. A circular punch for cutting samples of bark infested with beetles. Canadian Entomol. 94: 959–963.

_____. 1964. A method to determine progressive mortality during seasonal development of the Douglas-fir beetle brood. J. Econ. Entomol. 57(1): 178–181.

FURNISS, M. M., M. D. MCGREGOR, M. W. FOILES, AND A. D. PARTRIDGE. 1979. Chronology and characteristics of a Douglas-fir beetle outbreak in northern Idaho. USDA Forest Service Gen. Tech. Rept. INT-59. Intermountain Forest and Range Expt. Sta., Ogden, Utah.

FURNISS, M. M., AND P. W. ORR. 1978. Douglas-fir beetle. USDA Forest Insect and Disease Leaflet. Washington, D.C. 4 pp.

FURNISS, R. L., AND V. M. CAROLIN. 1977. Western forest insects. USDA Forest Service Misc. Publ. 1339.

MCMULLEN, L. H., AND M. D. ATKINS. 1961. Intraspecific competition as a factor in the natural control of the Douglas-fir beetle. For. Sci. 7: 197–203.

_____. 1962. On the flight and host selection of the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins (Coleoptera: Scolytidae). Canadian Entomol. 94: 1309–1325.

SCHMITZ, R. F., AND J. A. RUDINSKY. 1968. Effects of competition on survival in western Oregon of the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins (Coleoptera: Scolytidae). School of Forestry, Oregon State University, Corvallis. Research Paper 8. 42 pp.

WICKMAN, B. E. 1978. Tree mortality and top-kill related to defoliation by the Douglas-fir tussock moth in the Blue Mountains outbreak. USDA Forest Service Res. Pap. PNW-233. 47 pp.

WOOD, D. L. 1982. The role of pheromones, kairomones and allomones in host selection and colonization behavior of the bark beetle. Ann. Rev. Entomol. 27: 411–446.

WRIGHT, L. C., A. A. BERRYMAN, AND B. E. WICKMAN. 1984. Abundance of the fir engraver, *Scolytus ventralis*, and the Douglas-fir beetle, *Dendroctonus pseudotsugae*, following tree defoliation by the Douglas-fir tussock moth, *Orgyia pseudotsugata*. Canadian Entomol. 116: 293–305.

ADDITIONS TO THE VASCULAR FLORA OF BRYCE CANYON NATIONAL PARK, UTAH

Gregory P. Hallsten[1] and David W. Roberts[2]

ABSTRACT.—Twenty-seven plant taxa previously unreported from Bryce Canyon National Park are listed.

Buchanan and Graybosch (1981) published a checklist of 446 vascular plant taxa known to occur in Bryce Canyon National Park. During vegetation sampling in 1986 and 1987 Linda Gottschalk and Gregory P. Hallsten collected an additional 27 taxa listed here. Nomenclature follows Welsh et al. (1987). Specimens are deposited in the Bryce Canyon National Park Herbarium and the Intermountain Herbarium (UTC).

SPECIES LIST

APIACEAE
Berula erecta (Hudson) Cov. var. *incisa* (Torr.) Cronq.

ASCLEPIADACEAE
Asclepias speciosa Torr.

ASTERACEAE
Artemisia campestris L.
A. tridentata Nutt. var. *tridentata*
Cirsium neomexicanum Gray
C. vulgare (Savi) Ten.
Conyza canadensis (L.) Cronq.
Haplopappus scopulorum (Jones) Blake
H. zionis L. C. Anderson
Senecio hartianus Heller
S. hydrophilus Nutt.

CACTACEAE
Echinocereus triglochidiatus Engelm. var. *melanacanthus* (Engelm.) L. Benson
Sclerocactus whipplei (Engelm.) Britt. & Rose var. *roseus* (Clover) L. Benson

CHENOPODIACEAE
Atriplex confertifolia (Torr. & Frem.) Wats.
Sarcobatus vermiculatus (Hook.) Torr. in Emory

CYPERACEAE
Eleocharis palustris (L.) R. & S.

FUMARIACEAE
Corydalis aurea Willd.

GENTIANACEAE
Gentianella tortuosa (Jones) J. M. Gillett

ONAGRACEAE
Oenothera longissima Rydb.

ORCHIDACEAE
Habenaria dilitata (Pursh) Hook.

POACEAE
Elymus glaucus Buckley
Festuca octoflora Walter
Sporobolus cryptandrus (Torr.) Gray
Stipa pinetorum Jones

POLEMONIACEAE
Phlox tumulosa Wherry

SCROPHULARIACEAE
Cordylanthus parviflorus (Ferris) Wiggins
Penstemon strictus Benth.

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LITERATURE CITED

BUCHANAN, H., AND R. GRAYBOSCH. 1981. Revised checklist of the vascular plants of Bryce Canyon National Park, Utah. Great Basin Nat. 41: 109–120.

WELSH, S. L., N. D. ATWOOD, L. C. HIGGINS, AND S. GOODRICH. 1987. A Utah flora. Great Basin Nat. Mem. 9: 1–894.

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WATERFOWL AND SHOREBIRD USE OF SURFACE-MINED AND LIVESTOCK WATER IMPOUNDMENTS ON THE NORTHERN GREAT PLAINS

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ABSTRACT.—Cluster analysis and stepwise discriminant analysis were used to group waterfowl and shorebird use on water impoundments (bentonite, coal, livestock) on the Northern High Plains. Three bird-use categories—high, medium, and low—were delineated by these analytical procedures. Eleven physical, chemical, and biological parameters of impoundments were related to bird use; water area, nitrogen, and low basin slopes were found to be important parameters in estimating bird use on impoundments. Spring and summer were the best seasons for surveying waterfowl and shorebird water impoundment use.

Water impoundments created by mining activity provide habitat for waterfowl and shorebirds on the Northern Great Plains. An assessment of waterfowl use on natural wetlands and stock ponds was made by Ruwaldt et al. (1979). No such study has been done on strip-mine impoundments, although water quality and morphometry of strip-mine water areas examined in conjunction with this study on the same impoundments have been reported by Hawkes (1978), Bjugstad et al. (1983), Rumble et al. (1985), and Rumble (1985). These parameters have not been previously related to waterfowl and shorebird use of impoundments, nor have management recommendations relating waterfowl and shorebird production to surface-mine impoundments been suggested.

Early studies on waterfowl production on the Northern Great Plains were conducted only on livestock impoundments (Bue et al. 1952, Smith 1953). Other studies have related waterfowl and shorebird use to habitat conditions (surface water available, submergent and emergent vegetation, amount of shoreline and shallow water) of lakes, and livestock, dugout, ephemeral, temporary seasonal, semipermanent, and permanent water impoundments (Beard 1953, Uhlig 1963, Patterson 1976, Kantrud and Stewart 1977, Ruwaldt et al. 1979, Mack and Flake 1980, Kaminski and Prince 1981, Rumble et al. 1985). The importance and value of these impoundments to waterfowl and shorebird production on the Northern Great Plains has been emphasized by Lokemoen (1973), Evans and Kerbs (1977), Flake et al. (1977), Mack and Flake (1980), and Rumble and Flake (1983).

The purpose of this study was to determine waterfowl and shorebird use as related to bentonite clay, coal surface mine, and livestock watering impoundments; to identify impoundments characteristics that could increase waterfowl and shorebird use; and to recommend management strategies.

STUDY AREA AND METHODS

The study areas were located in northeastern Wyoming, western South Dakota, and western North Dakota. Four general areas were studied: (1) Colony, Wyoming; (2) Gascoyne, North Dakota; (3) Beulah, North Dakota; and (4) Firesteel, South Dakota. Seventeen coal surface-mine impoundments, 13 bentonite surface-mine impoundments, and 7 livestock ponds were selected for study. Impoundments were selected to represent a range of waterfowl and shorebirds in assigned use categories of low, medium, and high. Approximately one-half of the mine impoundments were distributed in low- and medium-use categories based on observations of waterfowl and shorebirds, with seven livestock ponds in the high-use category.

Livestock impoundments were the oldest, averaging 41 years, with well-developed aquatic vegetation. They were designed with minimal disturbance to provide water for livestock and were constructed in rolling topography with dams across natural drainages. Coal mine impoundments averaged 25 years in age

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TABLE 1. Selected physical, chemical, and vegetative characteristics of ponds in each analysis group. Means and standard errors calculated from data included in Anderson et al. (1979) and Olson (1979).

	Use class		
	Low	Medium	High
Number of ponds	17	3	1
Age (yr)	29.7 ± 3.9	43.3 ± 17.5	42
Impoundment area (ha)	2.4 ± 0.2	6.8 ± 4.0	14.9
Pond volume (m^3)	13546 ± 1733	28295 ± 12441	85350
Water depth—max (m)	5.0 ± 0.1	5.0 ± 0.5	2.0
$\bar{X}$ (m)	0.8 ± 0.0	0.8 ± 0.0	0.7
Shoreline development[1]	1.74 ± 0.09	2.21 ± 0.32	2.82
Percent shallow[2]	20.0 ± 1.2	36.7 ± 6.2	59.0
Percent slope (+1 m elev. to shoreline)	38.9 ± 6.01	26.3 ± 13.4	11.0
Plant density (stems/m^2/yr)	500 ± 104	1428 ± 380	1928 ± 216
Plant standing crop (kg/ha/yr)	30864 ± 6166	37578 ± 7375	41691 ± 3661
Nitrogen (mg/l)	0.37 ± 0.01	0.56 ± 0.16	1.31
Phosphorus (mg/l)	0.02 ± 0.00	0.07 ± 0.06	0.28

and resulted from open-pit mining where soil overburden and coal were removed. These impoundments had steep banks below and above the water surface with minimal aquatic vegetation. Bentonite impoundments averaged approximately 12 years in age. These impoundments were generally steep on three sides, but where scrapers removed the bentonite, gradual slopes occurred on at least one side of the impoundment allowing for growth of aquatic vegetation. A detailed description of impoundments is provided by Anderson et al. (1979), Olson (1979), and Rumble et al. (1985).

Waterfowl and shorebirds were sampled by species 25 times over seven seasons from 1976 to 1978 (two spring, two summer, three fall) on the 37 water impoundments. Within each season, three to seven successive surveys were conducted. All birds were observed, identified, and counted with the aid of spotting scopes and binoculars. Approximately 15 to 60 minutes was spent observing birds on each impoundment. In addition, measurements of 12 parameters were collected during the same period of bird observations and were compiled for 21 of the impoundments (Anderson et al. 1979, Olson 1979, Rumble et al. 1985, Rumble 1985): age of impoundment, basin area, impoundment volume, water depth, shoreline development, percent shallow (Lind 1974), percent slope (between the water line and +1 m elevation), percent shallow water slope (between the waterline and the −1 m elevation), plant density, plant standing crop, and nitrogen and phosphorus content of water (Table 1).

Waterfowl and shorebird data were averaged by impoundment types (mean birds/impoundment/observation) for cluster analysis (ISODATA) (Ball and Hall 1969). Cluster analysis was used to separate mean birds for spring, summer, and fall, with years combined. Stepwise discriminant analysis (Dixon 1983) was next used to estimate reliability of separations of cluster analysis (F to enter 4; F to remove 3.996). Kulzaynski's similarity index (Oosting 1956) and Spearman's rank order correlation (r_s) (Siegel 1956) compared species of birds among the three impoundment groups. All statistical inferences were made at $\alpha = 0.05$.

RESULTS

Waterfowl and shorebirds were separated into three significantly different use groups (Table 2): high bird use (158 birds/impoundment/observation, n = 1), medium bird use (30 birds/impoundment/observation, n = 3), and low bird use (3 birds/impoundment/observation, n = 33). Numbers on impoundments during spring were greatest for high- and moderate-use impoundments, while low-use impoundments had greatest numbers during fall. All bentonite and all coal impoundments, except one, were in the low-use group. Livestock impoundments were in all three groups.

Mallards (*Anas platyrhynchos*), American Widgeons (*A. americana*), Pintails (*A. acuta*), and Blue-winged Teals (*A. discors*) were the most abundant of the 32 species observed on impoundments in the low-use class (Table 2).

TABLE 2. Average (± SE) number of birds per impoundment observed by species at a given time in three use classes[1] during spring, summer, and fall.

	Low use			Medium use			High use		
	Spring	Summer	Fall	Spring	Summer	Fall	Spring	Summer	Fall
American Coot	0.06 ± 0.03	0.06 ± 0.03	0.05 ± 0.03	2.44 ± 1.80	2.39 ± 1.89	0.33 ± 0.26	28.83	31.67	80.23
American Widgeon	0.40 ± 0.22	0.21 ± 0.09	0.39 ± 0.19	3.94 ± 2.95	1.56 ± 1.39	1.23 ± 0.55	9.50	6.67	15.31
Bufflehead	0.07 ± 0.07	0	0.01 + 0.01	0.39 ± 0.24	0	0.05 ± 0.05	2.67	0	0
Blue-winged Teal	0.15 ± 0.06	0.49 ± 0.22	0.05 ± 0.03	1.22 ± 1.22	7.89 ± 5.40	1.23 ± 0.69	8.83	30.17	0.38
Canada Goose	0	0	0	0	0	0	12.00	0	0
Canvasback	0.02 ± 0.01	0	0.01 ± 0.01	3.61 ± 1.30	0	0	33.83	0.67	0.69
Common Goldeneye	0.01 ± 0.01	0	0.01 ± 0.01	0	0	0.13 ± 0.13	0	0	0.31
Common Loon	0	0	0	0	0	0.03 ± 0.03	0	0	0
Common Merganser	0.07 ± 0.04	0.02 ± 0.02	0	0.33 ± 0.33	0	0.05 ± 0.05	0	0	0
Common Snipe	0.01 ± 0.01	0	0	0	0	0	0	0	0
Double-crested Cormorant	0.02 ± 0.01	0	0.01 ± 0.01	0.61 ± 0.61	0	0.05 ± 0.05	0	0	0.38
Eared Grebe	0	0.01 ± 0.01	0	0.78 ± 0.78	0.28 ± 0.28	0.03 ± 0.03	0.67	4.17	0.08
Gadwall	0.08 ± 0.05	0.10 ± 0.09	0.13 ± 0.08	0.89 ± 0.89	0.94 ± 0.78	1.59 ± 0.86	12.83	0.50	12.92
Great Blue Heron	0.01 ± 0.01	0.04 ± 0.02	0.01 ± 0.01	0.11 ± 0.11	0.11 ± 0.11	0.03 ± 0.03	0	0.17	0.23
Green-winged Teal	0.18 ± 0.08	0.03 ± 0.03	0.11 ± 0.05	2.50 ± 1.25	0	2.31 ± 0.47	5.83	0.17	2.69
Horned Grebe	0.01 ± 0.01	0	0	0	0	0	0	0	0
Hooded Merganser	0	0	0	0	0	0	0.33	0	0
Killdeer	0.03 ± 0.03	0.08 ± 0.03	0.07 ± 0.07	0	0	0.10 ± 0.07	0	0	0
Long-billed Dowitcher	0	0	0	0	0	0	3.00	0	0
Lesser Scaup	0.19 ± 0.13	0	0.14 ± 0.06	15.89 ± 6.31	0	1.59 ± 1.55	30.67	0.17	0.31
Lesser Yellowlegs	0	0	0	0	0.06 ± 0.06	0	0	0	0
Marbled Godwit	0	0.10 ± 0.10	0	0	0	0	0	0	0
Mallard	1.04 ± 0.23	0.77 ± 0.35	1.32 ± 0.45	4.56 ± 0.53	7.67 ± 7.12	5.9 ± 2.51	34.83	21.50	19.23
Pied-billed Grebe	0	0.02 ± 0.02	0.02 ± 0.01	0.11 ± 0.11	0.17 ± 0.17	1.21 ± 0.65	0	2.33	1.08
Pectoral Sandpiper	0	0.01 ± 0.01	0	0	0	0	0	0	0
Pintail	0.27 ± 0.10	0.13 ± 0.07	0.22 ± 0.13	1.17 ± 0.23	0.94 ± 0.78	1.64 ± 1.41	20.17	3.0	1.85
Ring-billed Gull	0	0	0.01 ± 0.01	0	0	0.33 ± 0.29	0	0	0
Redhead	0.01 ± 0.01	0	0.06 ± 0.06	12.67 ± 9.82	0.06 ± 0.06	0.82 ± 0.47	6.33	0.50	3.31
Ring-necked Duck	0.16 ± 0.07	0	0.07 ± 0.07	4.67 ± 2.38	0	0.05 ± 0.05	8.00	0	0
Ruddy Duck	0.01 ± 0.01	0	0	1.44 ± 1.20	0	0	9.00	1.00	1.31
Sandhill Crane	0	0	0.01 ± 0.01	0	0	0	0	0	0
Shoveler	0.07 ± 0.04	0.14 ± 0.11	0.09 ± 0.05	0.50 ± 0.29	0.61 ± 0.61	0.23 ± 0.23	4.00	1.50	1.31
Snow Goose	0	0	0	0.06 ± 0.06	0	0	0	0	0
Spotted Sandpiper	0	0.01 ± 0.01	0	0	0	0	0	0	0
Unknown dabblers	0.03 ± 0.03	0.04 ± 0.02	0.16 ± 0.09	0	0.22 ± 0.22	0.82 ± 0.42	5.50	2.50	4.23
Western Grebe	0	0.02 ± 0.02	0.01 ± 0.01	0.06 ± 0.04	0	0	0	0.17	0.08
Whistling Swan	0	0	0.01 ± 0.01	0	0	0.05 ± 0.05	0	0	0
Willet	0	0	0.01 ± 0.01	0	0	0.05 ± 0.05	0.17	0	0.23
Wood Duck	0	0	0	0.06 ± 0.06	0	0	0	0	0

[1]Low n = 33 ponds; medium n = 3 ponds; high n = 1 pond.

Mallards, Lesser Scaup (*Aythya affinis*), and Redheads (*Aythya americana*) were the most abundant of the 30 species observed in medium-use impoundments. In high-use impoundments, American Coot (*Fulica americana*), Mallard, American Widgeon, Gadwall (*A. strepera*), and Blue-winged Teal were the most abundant species. Fewer species were observed on the high-use impoundment (25), but greater densities were reported.

Similarities were all low, ranging from 4% to 24%, when bird species were compared among the three classes. This indicates that the number of species did not occur in similar proportions among impoundments. Rank order correlations of bird species were significant ($P \leq .05$) among the three use classes. Correlations were: low vs. medium (.70), low vs. high (.51), and medium vs. high (.78). Bird abundance by species among classes was in the same relative rankings, indicating that the same population was available for all classes of ponds. Therefore, factors other than bird density influenced selection for certain impoundments.

Trends across use classes relative to the physical, chemical, and biological parameters given in Table 1 indicate that old, large, shallow impoundments with low basin slopes, irregular shorelines, and significant vegetation were favored by waterfowl. Nitrogen and phosphorus content of water was also greater in the high-use impoundments.

The three seasons were subjected to discriminant analysis on the medium and low groups, which showed spring and summer seasons as the most important in evaluating waterfowl and shorebird use on impoundments. These two seasons accounted for 93% of the variation. Discriminant analysis of low- and medium-use impoundments showed that impoundment area, nitrogen in water, and percent slope (+1 m elevation to shoreline) were important for bird use and accounted for 95% of the variation.

DISCUSSION

Thirty-seven impoundments (coal, bentonite, and livestock) were analyzed with multivariate techniques (ISODATA, discriminant analysis) as related to waterfowl and shorebird use. These analyses resulted in grouping 33 impoundments in low-, 3 in medium-, and 1 in high-use categories. ISODATA (cluster analysis) examines response patterns of all variables in waterfowl and shorebird data and separates the data into groups that are more meaningful for interpretation because of group homogeneity with minimum variances. Discriminant analysis examines groupings for significant separation and also includes variables which best separate groups. As a result of these multivariate techniques, the original classification and number of impoundments for low, medium, and high use by birds was different. Field observations, even with preliminary data, are often too complex, and/or highly variable, to determine adequate sample size of impoundments in low- to high-use categories. Thus, when the complete data set with 25 sample periods over seven seasons was analyzed, a small number of impoundments resulted in medium- and high-use categories with multivariate techniques.

Species richness (number of species), which was higher on the low-use impoundments, primarily bentonite and coal, was 32, followed by medium- (30), and high- (25) use impoundments. However, total numbers (densities) of waterfowl and shorebirds showed opposite trends by impoundment grouping. Therefore, many researchers advocate that waterfowl and shorebird use of impoundments should be managed by criteria developed for high-use livestock impoundments (Smith 1953, Evans and Kerbs 1977, Flake et al. 1977, Lokemoen 1973, Mack and Flake 1980, Rumble and Flake 1983).

Average percent similarities were low when bird species were compared among the three classes of impoundments, indicating that selection for certain ponds occurred. Rank order correlations indicated that species and densities of waterfowl and shorebirds had a similar ranking in abundance among the three impoundment classes, which means that all ponds had the same opportunity of being selected for use.

Surface area of impoundments was an important criterion to consider for waterfowl and shorebirds in this study. Impoundments in our study ranged in size from 0.3 to 15 ha. Other studies (on impoundments that ranged in size from 0.4 to 9.5 ha) also reported that surface area was an important variable to consider for waterfowl (Smith 1953, Lokemoen 1973, Flake et al. 1977, Evans and Kerbs 1977, Rumble and Flake 1983). Lokemoen (1973) recommended that minimum pond size be 0.6 ha and largest be dictated only by topography and economics of construction. The percent of the total impoundment area between the waterline and −1 m elevation (percent shallow), and the submerged vegetation have been important for predicting waterfowl and shorebird use on impoundments (Rumble and Flake 1983). However, in our study the percent slope (+1 m elevation to shoreline) was our important variable for estimating bird use on impoundments. Impoundments with gently sloping shorelines and abundant vegetation in shallow water have greater densities of birds (Evans and Kerbs 1977).

Water nutrients are associated with increased plant production. Lokemoen (1973) found that as nutrients increased, plant abundance increased, and so did waterfowl use. In this study nitrogen was an important variable. Aquatic vegetation and grassy shorelines are extremely important for waterfowl use and do influence waterfowl densities (Rumble and Flake 1983, Lokemoen 1973, Flake et al. 1977, Mack and Flake 1980). Generally, aquatic vegetation will develop in newly constructed impoundments within a short period of time, provided adequate shallow areas no deeper than 1 m are available. In some strip-mine impoundments (coal and bentonite) aquatic productivity could possibly be increased with addition of nitrogen and phosphate fertilizers.

Although all impoundments that were highly or moderately used by waterfowl and shorebirds in this study were livestock ponds, characteristics of such ponds may still be used to design impoundments resulting from bentonite and coal strip mining. In some cases parent spoil materials may adversely affect waterfowl use of strip-mine impoundments, because of chemical or soil texture problems, regardless of structural design. However, such cases may be mitigated by time or other management techniques such as fertilization or recovering with topsoil materials. Results obtained on livestock impoundments from this and other studies indicate that newly developed impoundments should have as minimum parameters 0.6 ha in surface area, 2.2 in shoreline development (index), 40% in shallow water (−1 m depth), 1500 stems/m^2 density in shallow areas, N content of 0.6 mg/l, and P content of 0.07 mg/l.

LITERATURE CITED

ANDERSON, M. T., A. J. BJUGSTAD, C. L. HAWKES, AND D. W. URESK. 1979. Design and management requirements for water impoundments in Northern Great Plain's strip mined areas. Final report. Rocky Mt. For. and Range Expt. Sta., South Dakota School of Mines and Technology, Rapid City, South Dakota. 146 pp.

BALL, G. H., AND D. J. HALL. 1969. A clustering technique for summarizing multivariate data. Behavioral Sci. 12: 153–155.

BEARD, E. B. 1953. The importance of beaver in waterfowl management at the Seney National Wildlife Refuge. J. Wildl. Manage. 17: 398–436.

BJUGSTAD, A. J., M. A. RUMBLE, R. A. OLSON, AND W. T. BARKER. 1983. Prairie pond morphometry and aquatic plant zonation—Northern High Plains. Pages 101–112 *in* Proceedings of the Third Biennial Plains Aquatic Research Conference, Bozeman, Montana.

BUE, I. B., L. H. BLANKENSHIP, AND W. H. MARSHALL. 1952. The relationship of grazing practices to waterfowl breeding populations and production on stock ponds in western South Dakota. Transactions of the North American Wildlife Conference 17: 396–414.

DIXON, W. J. 1983. BMDP statistical software. University of California Press, Berkeley.

EVANS, K. E., AND R. R. KERBS. 1977. Avian use of livestock watering ponds in western South Dakota. U.S. Dept. of Agric., Rocky Mt. For. and Range Expt. Sta., Gen. Tech. Rept. RM–35, Fort Collins, Colorado.

FLAKE, L. D., G. L. PETERSON, AND W. L. TUCKER. 1977. Habitat relationships of breeding waterfowl on stock ponds in northwestern South Dakota. Proceedings of the South Dakota Academy of Science 56: 135–151.

HAWKES, C. L. 1978. Aquatic habitat of coal and bentonite clay strip mine ponds in the northern Great Plains. Pages 609–614 *in* M. K. Wali, ed., Ecology and resource development. Vol. 2. Pergamon Press, New York.

KAMINSKI, R. M., AND H. H. PRINCE. 1981. Dabbling duck and aquatic macroinvertebrate response to manipulated wetland habitat. J. Wildl. Manage. 45: 1–15.

KANTRUD, H. A., AND R. E. STEWART. 1977. Use of natural basin–wetlands by breeding waterfowl in North Dakota. J. Wildl. Manage. 41: 243–253.

LIND, O. T. 1974. Handbook of common methods in limnology. C. V. Mosby Co., St. Louis, Missouri.

LOKEMOEN, J. T. 1973. Waterfowl production on stock-watering ponds in the northern plains. J. Range Manage. 26: 179–184.

MACK, G. D., AND L. D. FLAKE. 1980. Habitat relationships of waterfowl broods on South Dakota stock ponds. J. Wildl. Manage. 44: 695–700.

OLSON, R. A. 1979. Ecology of wetland vegetation on selected strip mine ponds and stockdams in the northern Great Plains. Unpublished dissertation, North Dakota State University, Fargo. 476 pp.

OOSTING, H. J. 1956. The study of plant communities. W. H. Freeman and Co., San Francisco, California. 440 pp.

PATTERSON, J. H. 1976. The role of environmental heterogeneity in the regulation of duck populations. J. Wildl. Manage. 40: 22–32.

RUMBLE, M. A. 1985. Quality of water for livestock in man-made impoundments in the Northern High Plains. J. Range Manage. 38: 74–77.

RUMBLE, M. A., M. T. ANDERSON, AND C. L. HAWKES. 1985. Morphometry of coal and bentonite surface mine and livestock impoundments in the Northern High Plains. Reclamation and Revegetation Research 3: 293–300.

RUMBLE, M. A., AND L. D. FLAKE. 1983. Management considerations to enhance use of stock ponds by waterfowl broods. J. Range Manage. 36: 691–694.

RUWALDT, J. J., JR., L. D. FLAKE, AND J. M. GATES. 1979. Waterfowl pair use of natural and man-made wetlands in South Dakota. J. Wildl. Manage. 43: 375-383.

SIEGEL, S. 1956. Non-parametric statistics for behavioral sciences. McGraw-Hill Book Co., Inc., New York. 312 pp.

SMITH, R. H. 1953. A study of waterfowl production on artificial reservoirs in eastern Montana. J. Wildl. Manage. 17: 276–291.

UHLIG, H. G. 1963. Use of Minnesota pond and pits by waterfowl. The Wilson Bulletin 75: 28–82.

INTERACTIONS AMONG SQUIRRELS, MYCORRHIZAL FUNGI, AND CONIFEROUS FORESTS IN OREGON

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ABSTRACT.—We examined the mycophagy (ingestion of fungi) of squirrels of five genera and eight species in the coniferous forests of Oregon. Data from 644 dietary samples demonstrated that squirrels of all eight species are mycophagous and eat the belowground fruiting bodies of at least 26 genera of mycorrhizal fungi. Four species are primarily arboreal and active throughout the year; the other four are primarily terrestrial and hibernate during winter. Of the squirrels examined, only the northern flying squirrel (*Glaucomys sabrinus* [Shaw]) is nocturnal and almost exclusively a fungivore. The flying squirrel is used to illustrate the dynamics of all the squirrels in association with hypogeous mycorrhizal fungi, nitrogen-fixing bacteria, yeast, and coniferous trees in Oregon forests because we have studied it the most. Squirrels may prove to be vital links among different processes within temperate coniferous forests.

Although early studies of small-mammal food habits included a few papers dealing with mycorrhizal fungi (e.g., Bakerspigel 1956, 1958, Dowding 1955, Hamilton 1941, Tevis 1952, 1953, Whitaker 1962, Williams and Finney 1964), the first interdisciplinary studies to examine the role of small mammals as dispersal agents for spores of mycorrhizal fungi are recent (Kotter and Farentinos 1984a, 1984b, Maser, Trappe, and Nussbaum 1978, Maser, Trappe, and Ure 1978, Trappe and Maser 1976, 1977, Ure and Maser 1982). The first extensive literature review of small-mammal mycophagy was published in 1978 (Fogel and Trappe 1978). Symbioses between small-mammal and mycorrhizal fungus have also been documented recently in Europe (Blaschke and Bäumler 1986, Durrieu et al. 1984, Froidevaux 1981). Only now are researchers beginning to understand the importance of nitrogen-fixing bacteria in the symbiotic relation of small-mammal, mycorrhizal fungus, coniferous tree mutualism (Li et al. 1986).

In this paper we present data on the fungal diet of squirrels of four genera and six species from the coniferous forests of Oregon, and we examine potential interactions among five genera of eight species of mycophagous squirrels and the coniferous forests of Oregon.

In addition to giving new data on the 118 squirrels, this paper is intended as a synthesis of the potential ecological roles squirrels play in coniferous forests of the Pacific Northwest. Other studies of the northern flying squirrel (Maser et al. 1985, 1986), the yellow-pine chipmunk (*Eutamias amoenus* [J.A. Allen]) (Maser and Maser 1987), and the Siskiyou chipmunk (*Eutamias siskiyou* A.H. Howell) (McIntire 1980) are based on 524 samples. So, for all practical purposes, this paper is based on data from 644 squirrels in Oregon forests.

STUDY AREA

Squirrels from five physiographic provinces were studied: Coast Range, Klamath Mountains, Western Cascades, High Cascades, and Blue Mountains (Fig. 1). They were taken from five forest types within these areas: (1) western hemlock (*Tsuga heterophylla* [Raf.] Sarg.) zone, which encompasses most of the Coast Range and Western Cascades provinces of western Oregon; (2) mixed-conifer and mixed-evergreen zone of the Klamath Mountains province of extreme southwestern Oregon; (3) subalpine forest—Pacific silver fir (*Abies amabilis* [Dougl.] Forbes), subalpine fir (*A. lasiocarpa* [Hook.] Nutt.), and mountain hemlock (*T. mertensiana* [Bong.] Carr.) zone—along the crest of the High Cascades; (4) ponderosa pine (*Pinus ponderosa* Dougl. ex Loud.) zone on the east slope of the High Cascades; and (5) grand fir (*A. grandis* [Dougl.] Lindl.) and Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) zone of the Blue Mountains province in extreme northeastern Oregon (Franklin and Dyrness 1973).

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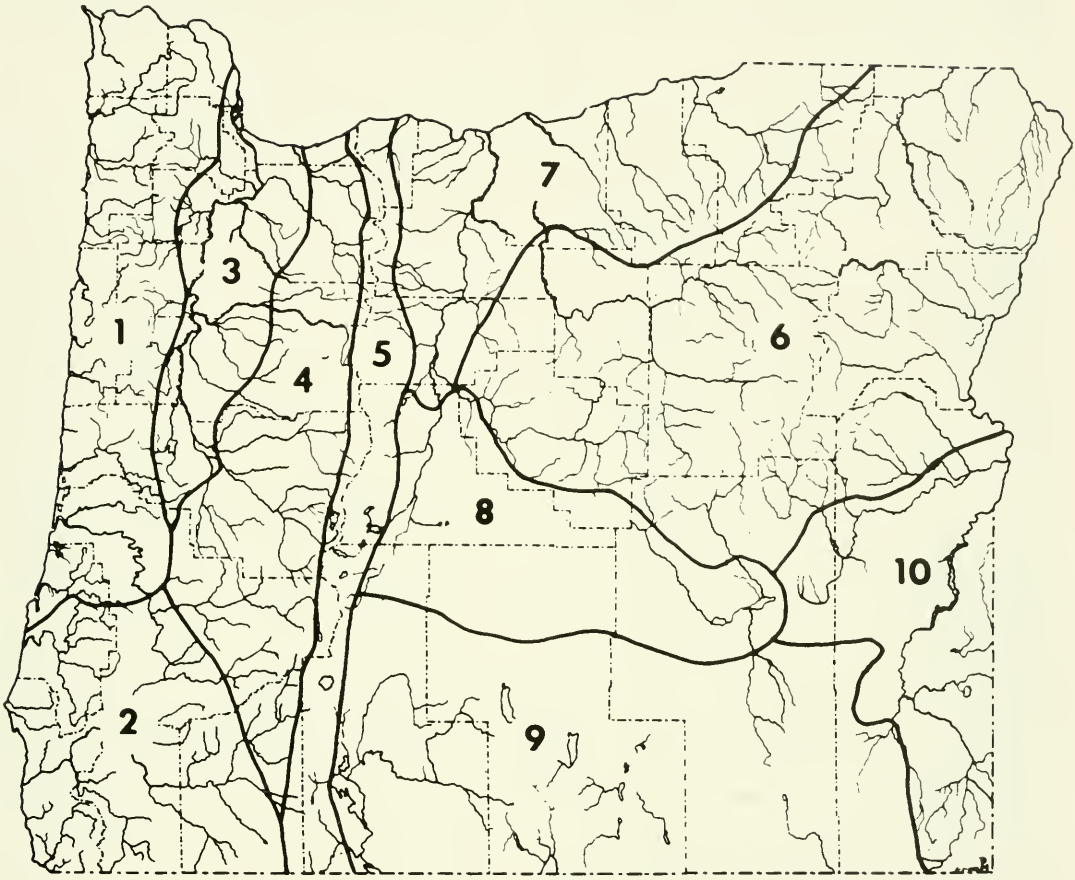

Fig. 1. Physiographic and geological provinces of Oregon (after Franklin and Dyrness 1973): 1 = Coast Range, 2 = Klamath Mountains, 3 = Willamette Valley, 4 = Western Cascades, 5 = High Cascades, 6 = Blue Mountains, 7 = Columbia Basin, 8 = High Lava Plains, 9 = Basin and Range, and 10 = Owyhee Upland.

METHODS AND MATERIALS

One hundred and two squirrels of four genera and six species were either dead-trapped or shot and quick-frozen in the field for later analysis. Stomachs were excised in the laboratory and preserved in vials of 10% formalin.

Stomach contents were examined microscopically at 100, 400, and 1000X magnification. For fungal analysis, each vial was shaken vigorously and opened. Narrow, parallel-sided forceps were plunged to the bottom, closed, and withdrawn. The captured material was placed on a microscope slide, mixed with a drop of Melzer's reagent, and enclosed under a 22 × 40-mm cover slip. (See Trappe et al., in press, for details of methods.) The slide was systematically moved over the entire area of the cover slip to examine fungal spores. Fungal taxa were identified by use of a spore key (Trappe et al., in press). Percentage of volume of each fungal taxon in each stomach was estimated visually and recorded for each slide.

RESULTS

Twenty-six genera of hypogeous (belowground fruiting) mycorrhizal fungi were identified from the stomachs of the 118 squirrels (Table 1). *Rhizopogon* was the dominant genus in all squirrel diets, followed by *Gautieria*. These two genera were the only ones eaten by all eight species of squirrels. *Hymenogaster* was third, although it was consumed by only three species of squirrels. *Hysterangium*, not eaten in great abundance, was found in four of the eight species of squirrels.

TABLE 1. The occurrence of spores of 26 fungal taxa in the stomachs of 118 squirrels (Sciuridae) from a range of forest types in Oregon. Percent volume by stomach contents and percent frequency (in parentheses) of fungal taxa; n = number of individuals sampled.

Fungal genera	Taxa of squirrels						Total
	Eutamias amoenus n = 17	*E. townsendi* n = 39	*Spermophilus lateralis* n = 16	*Tamiasciurus douglasi* n = 15	*T. hudsonicus* n = 15	*Sciurus griseus* n = 16	
ASCOMYCETES							
Balsamia		0.30 (8)					0.30 (8)
Cenococcum		0.02 (3)					0.02 (3)
Choiromyces			0.40 (13)				0.40 (13)
Elaphomyces		0.02 (3)				0.30 (6)	0.06 (2)
Genabea				0.06 (7)			0.06 (7)
Genea		2.00 (18)				0.06 (6)	0.90 (9)
Geopora	0.30 (6)	0.02 (3)	6.00 (31)		0.40 (13)	0.80 (13)	1.20 (13)
Peziza		0.02 (3)			0.06 (7)		0.001 (2)
Picoa		1.20 (13)					1.20 (13)
Tuber		0.70 (15)		0.20 (7)		0.80 (25)	0.40 (11)
BASIDIOMYCETES							
Gautieria	5.00 (12)	0.05 (8)	3.00 (25)	6.00 (27)	2.00 (27)	5.00 (19)	3.30 (20)
Hydnangiales		1.40 (15)	0.06 (6)				0.60 (6)
Hydnangium		0.30 (5)					0.30 (5)
Hymenogaster		0.60 (8)		12.00 (13)	5.00 (7)		2.70 (6)
Hysterangium		1.00 (8)	0.40 (13)	2.10 (20)	0.06 (7)	0.06 (6)	0.90 (10)
Leucogaster		0.50 (13)		4.00 (33)		2.00 (6)	1.00 (11)
Leucophleps				7.00 (27)		0.10 (13)	1.00 (6)
Melanogaster		0.40 (8)		6.00 (20)			1.00 (6)
Octavianina			0.50 (6)		0.06 (7)	0.06 (6)	0.09 (3)
Rhizopogon	34.00 (59)	35.00 (67)	44.00 (94)	51.00 (80)	75.00 (100)	12.00 (63)	46.00 (34)
Radiigera			0.06 (6)	0.06 (7)			0.02 (2)
Scleroderma			0.60 (13)				0.60 (13)
Thaxtergaster		0.05 (3)					0.05 (3)
ZYGOMYCETES							
Endogone		0.10 (5)		0.06 (7)			0.05 (3)
Glomus	0.60 (12)	0.50 (15)					0.30 (8)
Sclerocystis		0.10 (3)					0.10 (3)
UNIDENTIFIED SPORES							
Epigeous	2.00 (6)			0.06 (7)	0.40 (13)	3.00 (19)	0.80 (7)
Other	0.30 (6)	2.00 (23)	6.00 (31)	0.30 (20)	8.00 (60)	0.30 (13)	3.00 (29)
UNIDENTIFIED LICHENS							
					0.70 (7)		0.60 (7)

Percentage by volume of *Rhizopogon* in the stomachs of yellow-pine chipmunks ranged from 0 to 100%, *Gautieria* ranged from 0 to 80%, and *Glomus* from 0 to 10%. The most fungal genera from one yellow-pine chipmunk stomach was three. Although *Rhizopogon* also ranged from 0 to 100% of the stomach volume of Townsend chipmunks (*E. townsendi* [Bachman]), *Gautieria* was found only in trace amounts. Other genera of hypogeous fungi found to comprise 10% or more of an individual Townsend chipmunk's stomach contents included *Genea*, *Picoa*, *Tuber*, *Hydnangiales*, *Hydnangium*, *Hymenogaster*, *Hysterangium*, *Melanogaster*, and *Glomus*. The most fungal genera from one Townsend chipmunk stomach was six.

Rhizopogon ranged from 0 to 90% by volume in stomachs of the mantled ground squirrel (*Spermophilus lateralis* [Say]); *Gautieria* ranged from 0 to 45%. *Geopora* was the only other genus of hypogeous fungus that comprised 10% or more of an individual mantled ground squirrel's stomach contents. The most fungal genera from one stomach was seven.

Rhizopogon ranged from 0 to 100% in stomachs of the Douglas squirrel (*Tamiasciurus douglasi* [Bachman]), and *Gautieria* ranged from 0 to 40%. Other genera of fungi that comprised 10% or more of stomach contents

in a single Douglas squirrel included *Leucogaster*, *Leucophelps*, *Hymenogaster*, *Hysterangium*, and *Melanogaster*. The most fungal genera from one Douglas squirrel stomach was seven. Although *Rhizopogon* ranged from 0 to 100% of the stomach contents of the red squirrel (*T. hudsonicus* [Erxleben]), *Gautieria* ranged from 0 to 20%. The only other hypogeous fungus that accounted for more than 10% of stomach contents was *Hymenogaster;* it accounted for 80% in one stomach. The most fungal genera from one red squirrel stomach was four.

Rhizopogon ranged from 0 to 71% of the stomach contents from western gray squirrels (*Sciurus griseus* Ord), and *Gautieria* ranged from 0 to 70%. The only other hypogeous fungi that accounted for 10% or more of a western gray squirrel's stomach contents were *Tuber* and *Leucogaster*. The most fungal genera from one stomach was five.

DISCUSSION

The following is a synthesis of how we think some of the forest puzzle fits together. The whole is far greater than the sum of its parts; this view may help in understanding that simplification of forest diversity may have negative effects that go beyond our expectations or knowledge.

The Hypogeous Fungi

The term mycorrhiza, literally meaning "fungus-root," denotes the symbiotic relation between certain fungi and plant roots. Fungi that produce hypogeous sporocarps (belowground fruiting bodies) are probably all mycorrhizal (Miller 1983, Trappe and Maser 1977). Woody plants in the Pinaceae (pine, *Pinus;* fir, *Abies;* spruce, *Picea;* larch, *Larix;* Douglas-fir, *Pseudotsuga;* hemlock, *Tsuga*), Fagaceae (oak, *Quercus*), and Betulaceae (birch, *Betula;* alder, *Alnus*) especially depend on mycorrhiza-forming fungi for nutrient uptake, a phenomenon traceable back some 400 million years to the earliest known fossils of plant rooting structures (Harley and Smith 1983, Marks and Kozlowski 1973, Pirozynski and Malloch 1975).

Mycorrhizal fungi absorb nutrients and water from soil and translocate them to a host plant. The host provides sugars through photosynthesis to the mycorrhizal fungi. Fungal hyphae extend into the soil and serve as extensions of the root systems of the hosts and are both physiologically and geometrically more effective for nutrient absorption than are the roots themselves (Maser, Trappe, and Nussbaum 1978, Trappe 1981, Trappe and Fogel 1977, Trappe and Maser 1977). Both ectomycorrhizal and endomycorrhizal fungi serve similar purposes, but the fungi usually occur on different host plants.

When ectomycorrhizal fungi are predominant in the fungal diet of small mammals, they are also predominant in the habitat, such as coniferous forests. There, they are mostly Ascomycetes and Basidiomycetes associated with Pinaceae, Fagaceae, Salicaceae, Betulaceae, and a few other plant families (Fogel and Trappe 1978, Maser, Trappe, and Nussbaum 1978, Trappe and Maser 1977).

The Endogonaceae (Zygomycetes) include saprophytic, ectomycorrhizal, and vesicular-arbuscular (VA) endomycorrhizal species. Vesicular-arbuscular mycorrhizae are formed by Endogonaceae with most higher plants that are not ectomycorrhizal, including the Cupressaceae, Taxodiaceae, Aceraceae, and most herbaceous plants. Most plants on stream banks, meadows, and prairies, and in early stages of forest succession, in forest understories, or in forests containing VA-mycorrhizal tree species have VA-mycorrhizal Endogonaceae associated with their roots (Maser, Trappe, and Nussbaum 1978, Miller 1979, Reece and Bonham 1978, Trappe 1981, Williams and Aldon 1976).

Fungal-Forest Relations

Sporocarps of hypogeous fungi may be available year-round, in the Oregon Coast Range for example, although their abundance varies seasonally and always decreases in winter (Hunt and Trappe, in press) (Fig. 2). Numbers of species and biomass of hypogeous fungi differ among stands that have the same species of trees. For example, 30 species of Basidiomycetes and Ascomycetes, with monthly biomass averaging 2.09 kg/ha, were recorded for a north-facing stand of Douglas-fir in the central Oregon Coast Range. Fifteen species, with monthly biomass averaging 1.20 kg/ha, were present on a nearby south-facing slope (Fogel and Hunt 1979, Hunt and Trappe, in press).

Production of sporocarps fluctuates widely

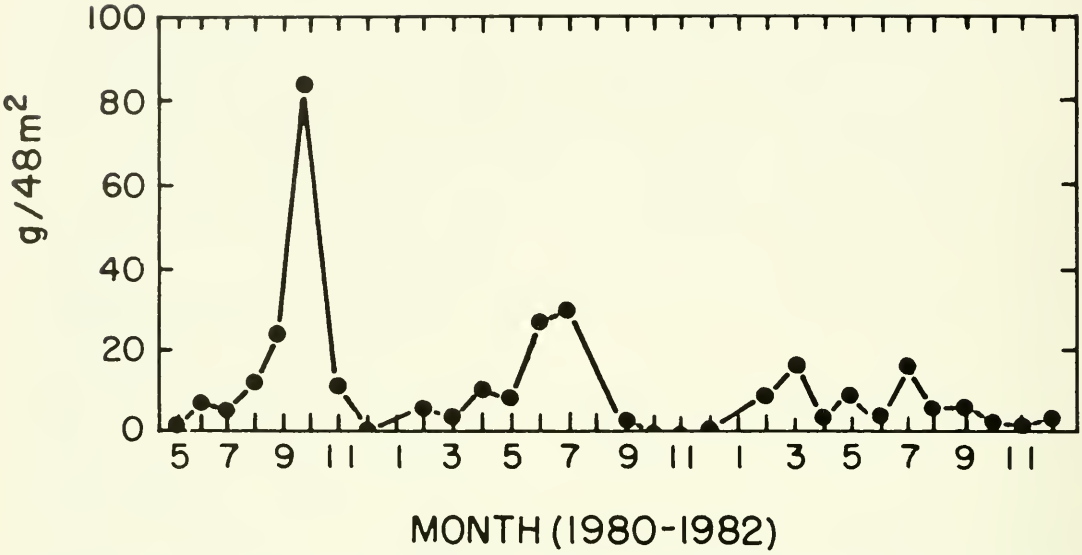

Fig. 2. Monthly production of hypogeous sporocarps in an Oregon Coast Range Douglas-fir stand (after Hunt and Trappe, in press).

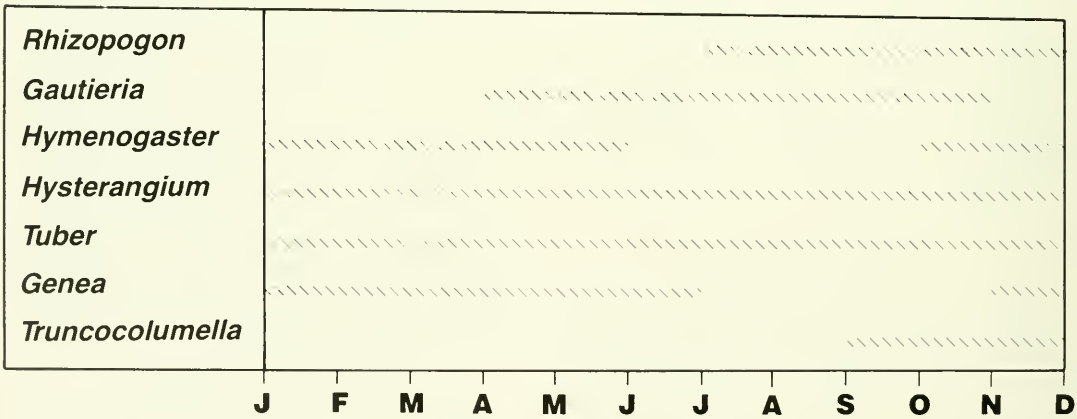

Fig. 3. Seasonal occurrence of selected genera of hypogeous fungi in the Oregon Coast Range (adapted from Hunt and Trappe, in press).

over short periods in a given stand. Peaks in biomass frequently result from "blooms" of one species, such as a large crop of *Gautieria monticola* Harkn. that comprised 89% of the total sporocarp biomass in October 1980 (Hunt and Trappe, in press). Most genera of hypogeous fungi fruit seasonally and can predictably be found during certain months (Fig. 3).

Fruiting patterns are relatively consistent, although length of the annual fruiting period for a given genus or species varies with year, stand structure, and weather conditions. Many hypogeous Ascomycetes (true truffles, such as *Geopora* sp. and *Genea* sp.) fruit more abundantly in winter and spring than in summer and fall. Of the hypogeous Basidiomycetes (false truffles), the genus *Rhizopogon* fruits primarily in summer and fall, but a few species, such as *R. vinicolor* A.H. Smith, fruit throughout the year. Fruiting of *Truncocolumella citrina* Zeller is invariably restricted to

TABLE 2. General distribution of mycophagous squirrels in Oregon by physiographic province and forest type.

Physiographic province Forest type	Taxa of squirrels							
	Northern flying squirrel	Douglas squirrel	Red squirrel	Western gray squirrel	Yellow-pine chipmunk	Townsend chipmunk	Siskiyou chipmunk	Mantled ground squirrel
COAST RANGE								
Western hemlock zone	x	x				x		
KLAMATH MOUNTAINS								
Mixed-conifer and mixed-evergreen zone	x	x		x		x[a]	x[a]	x
WESTERN CASCADES								
Western hemlock zone	x	x				x		
HIGH-CASCADES (crest)								
Pacific silver fir, subalpine fir, and mountain hemlock zone	x	x			x[b]	x[b]		x
HIGH CASCADES (east flank)	x	x		x	x			x
Ponderosa pine zone								
BLUE MOUNTAINS								
Grand fir and Douglas-fir zone	x	x[c]	x[c]		x			x

[a]The Townsend chipmunk and the Siskiyou chipmunk are separated in the Klamath Mountains Province by habitat. The Townsend chipmunk is associated primarily with the mixed-conifer forest type; the Siskiyou chipmunk is associated primarily with the mixed-evergreen forest type.

[b]The yellow-pine chipmunk and the Townsend chipmunk are separated along the crest of the High Cascades Province by habitat. The yellow-pine chipmunk is largely confined to the lodgepole pine (*Pinus contorta*) forest type that extends down the east flank of the High Cascades Province into the Ponderosa Pine Zone. The Townsend chipmunk occurs primarily in the Pacific silver fir–subalpine fir–mountain hemlock forest that extends down the west flank of the High Cascades Province to the Western hemlock zone of the Western Cascades Province.

[c]The Douglas squirrel and the red squirrel both occur in the Blue Mountains Province. Their separation, in the extreme northeastern part of the province, is apparently the result of dominant tree species. The red squirrel is closely associated with lodgepole pine, which dominates much of the northeastern Blue Mountains Province. The Douglas squirrel occurs throughout the rest of the forested areas in Oregon, which are dominated by conifers other than lodgepole pine (Hatton and Hoffmann 1979).

September through December in the Pacific Northwest. In contrast, the two most abundant species of *Hysterangium* in the Coast Range (*H. coriaceum* Hesse and *H. crassum* [Tul. & Tul.] Knapp) commonly fruit throughout the year (Hunt and Trappe, in press). Seasonal abundance of hypogeous fungi generally follows changes in temperature and precipitation (Fogel 1976).

Several species of hypogeous fungi, including *Rhizopogon vinicolor*, *R. truncatus* Linder, and *Gautieria monticola*, are known to fruit in or adjacent to large, well-decomposed, woody debris. Thus, stands that have substantial amounts of large, rotting wood may enhance the fruiting of some species. Further, the seasonal fruiting period may be extended by proximity of fungi to large, fallen, rotting trees because of the high water content such trees retain through dry periods (Maser and Trappe 1984). Production of hypogeous sporocarps throughout the year provides a remarkably reliable nutrient base for small mammals, even though most species of hypogeous fungi fruit only part of the year and total annual abundance differs substantially from year to year.

The Squirrels

Five genera and eight species of squirrels were collected in the study area: (1) northern flying squirrel, (2) Douglas squirrel, (3) red squirrel, (4) western gray squirrel, (5) yellow-pine chipmunk, (6) Townsend chipmunk, (7) Siskiyou chipmunk, and (8) mantled ground squirrel. These squirrels do not occur simultaneously in either a given physiographic province or a given forest type (Table 2).

The squirrels are separated in habitat use in three basic ways. First, if habitat use is very similar, the squirrels occur in different forest types, such as the Townsend chipmunk in mixed conifer and the Siskiyou chipmunk in mixed evergreen (Table 2). Second, if habitat use is very similar in one site, the squirrels are separated by time of activity, such as nocturnal for the northern flying squirrel and diurnal for the Douglas squirrel (Table 3). Third, if squirrels are in the same area and are active at the same time, they use the habitat differently, such as the yellow-pine chipmunk that climbs into shrubs and trees and the mantled ground squirrel that does not (Table 3). Some species, such as the Siskiyou chipmunk,

TABLE 3. General behavior patterns of mycophagous squirrels in Oregon.

Behavior	Taxa of squirrel								Source
	Northern flying squirrel	Douglas squirrel	Red squirrel	Western gray squirrel	Yellow-pine chipmunk	Townsend chipmunk	Siskiyou chipmunk	Mantled ground squirrel	
REPRODUCTION AND NESTING									
In canopy	x	x	x	x					Brand 1974, Broadbooks 1974, 1958, Huestis 1951, Maser et al. 1981, Shaw 1944
Occasionally above ground and low in trees					x	x			
On or below ground					x	x	x	x	
DIET									
Mycorrhizal fungi	x	x	x	x	x	x	x	x	Bailey 1936, Broadbooks 1958, Gordon 1943, Maser and Maser 1987, Maser et al. 1978, 1981, 1985, 1986, McIntire 1980, 1984, Stienecker and Browning 1970, Tevis 1952, 1953
Lichens	x								
Nonfungal foods		x	x	x	x	x	x	x	
TIME OF ACTIVITY									
Nocturnal	x								Bailey 1936, Maser et al. 1981
Diurnal		x	x	x	x	x	x	x	
CLIMBS									
Into trees	x	x	x	x					Bailey 1936, Maser et al. 1981, McIntire 1980, 1984
Shrubs and trees					x	x	x		
Neither shrubs nor trees								x	
HIBERNATES									
No	x	x	x	x					Bailey 1936, Maser et al. 1981
Yes					x	x	x	x	

further divide the habitat by sex; females of this species are more closely associated with trees and large, fallen woody material (logs) than are males because females keep their young in and around such protective cover. Such differences in habitat use carry over to food habits (McIntire 1980).

Behavior among Squirrels

The northern flying squirrel occurs throughout coniferous forests of Oregon (Table 2). Where the flying squirrel and either the Douglas squirrel or red squirrel occupy the same area, they are separated by activity period; the flying squirrel is nocturnal, and the Douglas squirrel and red squirrel are diurnal (Table 3). The diurnal squirrels, however, do not overlap in habitat use (Table 2). These squirrels are primarily inhabitants of coniferous forests. The western gray squirrel, on the other hand, may be associated with the flying squirrel and the Douglas squirrel, but usually in mixed forests, such as the ecotone between oak woodlands and coniferous forest. The western gray squirrel, although diurnal, is largely separated from the Douglas squirrel by habitat and food habits other than mycophagy.

The above squirrels are primarily arboreal. The chipmunks and mantled ground squirrel are mainly terrestrial, and both are diurnal (Table 3). Where the yellow-pine chipmunk and Townsend chipmunk come together, they are separated by habitat (Maser, unpublished data) (Table 2) or by the use of vegetative cover, or both (Meredith 1972). The Townsend chipmunk and Siskiyou chipmunk also use different habitats where they occur together (Table 2). The mantled ground squirrel may overlap in habitat use with all species of chipmunks but is different enough in temperament that serious overt aggression does not appear to be a problem (Broadbooks 1958, Gordon 1943).

Of all the squirrels we studied, only the northern flying squirrel is nocturnal and a strict fungivore (Table 3). The other seven species are diurnal and opportunistic fungivores. Where they are sympatric, their diets—other than fungi—differ.

The squirrels that are primarily arboreal are active all year, but those that are primarily terrestrial hibernate (Table 3). The chipmunks apparently store food, such as seeds, in their nests for winter sustenance (Broadbooks 1958, Stebbins and Orich 1977); whereas the mantled ground squirrel accumulates much body fat in preparation for hibernation (Blake 1972, Yousef and Bradley 1971).

Squirrel-Forest Relations

We will use the northern flying squirrel to illustrate the squirrels we studied because we know the most about the flying squirrel and because the other squirrels serve similar ecological functions in the forest.

The most obvious northern flying squirrel–forest relations are those that occur on the surface of the ground, such as foraging. Even their nesting and reproductive behavior remains relatively obscure because of nocturnal habits. As we probe the secrets of the flying squirrel, however, at least four interconnected cycles emerge that unite the aboveground and belowground parts of the forest.

The Fungal Connection

Fungal hyphae penetrate the tiny, nonwoody rootlets of the host plant to form a balanced, harmless mycorrhizal symbiosis with the roots. The host plant provides simple sugars and other metabolites to the chlorophyll-lacking mycorrhizal fungi, which generally are not competent saprophytes. The fungus absorbs minerals, other nutrients, and water from the soil and translocates them into the host. Further, nitrogen-fixing bacteria (*Azospirillum* sp.) that occur inside the mycorrhiza use a fungal "extract" as food and in turn fix atmospheric nitrogen (Li and Castellano 1985). The available nitrogen may be used by both the fungus and the host tree. In effect, mycorrhiza-forming fungi serve as highly efficient extensions of the host root system. Many of the fungi also produce growth regulators that induce production of new root tips and increase the useful life span of the host roots. At the same time, host plants prevent mycorrhizal fungi from damaging the roots. Mycorrhizal colonization enhances resistance to attack by pathogens. Some mycorrhizal fungi produce compounds that prevent pathogens from contacting the root system (Harley and Smith 1983, Marks and Kozlowski 1973, Trappe and Maser 1977). Basidiomycetes and Ascomycetes that produce hypogeous sporocarps are all presumed to be mycorrhizal (Miller 1983, Trappe and Maser 1977).

The Sporocarp Connection

Sporocarps are the initial link between hypogeous mycorrhizal fungi and the flying squirrel. Flying squirrels nest and reproduce in the tree canopy and come to the ground where they dig and eat hypogeous sporocarps. As a sporocarp matures, it produces a strong odor that attracts the foraging squirrel (Maser, Trappe, and Nussbaum 1978, Trappe and Maser 1977). (The odors are strong enough that we can detect many of them.) Evidence of a squirrel's foraging remains in the form of shallow pits in the forest soil and occasional partially eaten sporocarps.

Sporocarps of hypogeous fungi contain nutrients necessary for small mycophagists (Fogel and Trappe 1978, Gronwall and Pehrson 1984, Sanders 1984). In addition to having nutritional value, sporocarps contain water, fungal spores, nitrogen-fixing bacteria, and yeast (Li and Castellano 1985, Li et al. 1986, Maser, Trappe, and Nussbaum 1978, Maser et al. 1985).

The Squirrel Connection

Most nutrients required by vascular plants are absorbed from soil via mycorrhizal fungi.

These fungi therefore clearly play a vital role in nutrient cycling, productivity, and plant succession. As forest succession advances, mycophagous squirrels have different fungi available as food in differing relative abundances, and the squirrels' defecation of viable spores may help pace successional advancement. Spore dispersal is thus an integral part of the fungal cycle.

When flying squirrels eat sporocarps, they consume fungal tissue containing nutrients, water, viable fungal spores, nitrogen-fixing bacteria, and yeast. Pieces of sporocarp move to the stomach where fungal tissue is digested, then through the small intestine where absorption takes place, then to the cecum. The cecum is like an eddy along a swift stream; it concentrates, mixes, and retains fungal spores, nitrogen-fixing bacteria, and yeast (Li et al. 1986, Maser and Maser, unpublished data). Captive deer mice (*Peromyscus maniculatus* [Wagner]) retained fungal spores in the cecum for more than a month after ingestion (Maser and Maser, unpublished data). In the colon, undigested materials, including cecal contents, are formed into excretory pellets containing viable fungal spores, nitrogen-fixing bacteria, and yeast (Li et al. 1986). The fecal pellet therefore reconnects the squirrel to the fungus.

The Pellet Connection

A fecal pellet is more than a package of waste products; it is a "pill" of symbionts dispensed into the forest. Each fecal pellet contains four components of potential importance to the forest: (1) spores of hypogeous mycorrhizal fungi, (2) yeast, (3) nitrogen-fixing bacteria, and (4) the complete nutrient component for nitrogen-fixing bacteria.

The spores of the mycorrhizal fungi are viable (Kotter and Farentinos 1984b, Trappe and Maser 1976). Spores of some mycorrhizal-forming fungi are stimulated in germination by extractives from other fungi, such as yeast (Fries 1966, Oort 1974).

Each fecal pellet also contains the entire nutrient requirement for *Azospirillum* sp. The yeast, as a part of the nutrient base, has some ability to stimulate both growth and nitrogen-fixation in *Azospirillum* sp. (Li et al. 1986). Abundant yeast propagules may also stimulate spore germination.

The fate of fecal pellets varies, depending on where they fall. In the forest canopy, the pellets might remain and disintegrate in the tree tops. Or a pellet could drop to a fallen, rotting tree and inoculate the wood (Maser and Trappe 1984). On the ground, a squirrel might defecate on a disturbed area of the forest floor where a pellet could land near a conifer feeder rootlet that may become inoculated with the mycorrhizal fungus when spores germinate (Fries 1982). If environmental conditions are suitable and root tips are available for colonization, a new fungal colony may be established. Otherwise, hyphae of germinated spores may fuse with an existing fungal thallus and thereby contribute new genetic material (Trappe and Molina 1986).

The northern flying squirrel exerts a dynamic, functionally diverse influence within the forest. The complex of effects ranges through the crown of the tree, down to the soil surface, and into the soil mantle where, through mycorrhizal fungi, nutrients are conducted through the roots and into the trunk and crown of the tree (Fig. 4).

CONCLUSIONS

The world is losing both species and habitats because people are not sensitive to how and why they are functionally interconnected. For maximum information to be derived from the remaining, intact systems, well-planned interdisciplinary studies are needed. As emphasized by Rausch (1985), we must understand the organism and habitat in context with each other if we are to understand the organism, or its function within its habitat. If we do not understand the organism and its function within its habitat, how can we understand the results of unexpected changes in the habitat when the organism is removed? For example, forest rodents, such as the squirrels in our study, eat hypogeous mycorrhizal fungi that are obligatory symbionts with coniferous trees. This seems to be a widespread phenomenon in temperate forests. If the potential importance of such interconnected ecological processes is not appreciated, what might the effects be of forest simplification through loss of organisms and habitats that may severely impair ecological processes?

The focus of biological research has recently shifted from the autecology of species to community ecology, but neither approach captures the functional dynamics of a species in

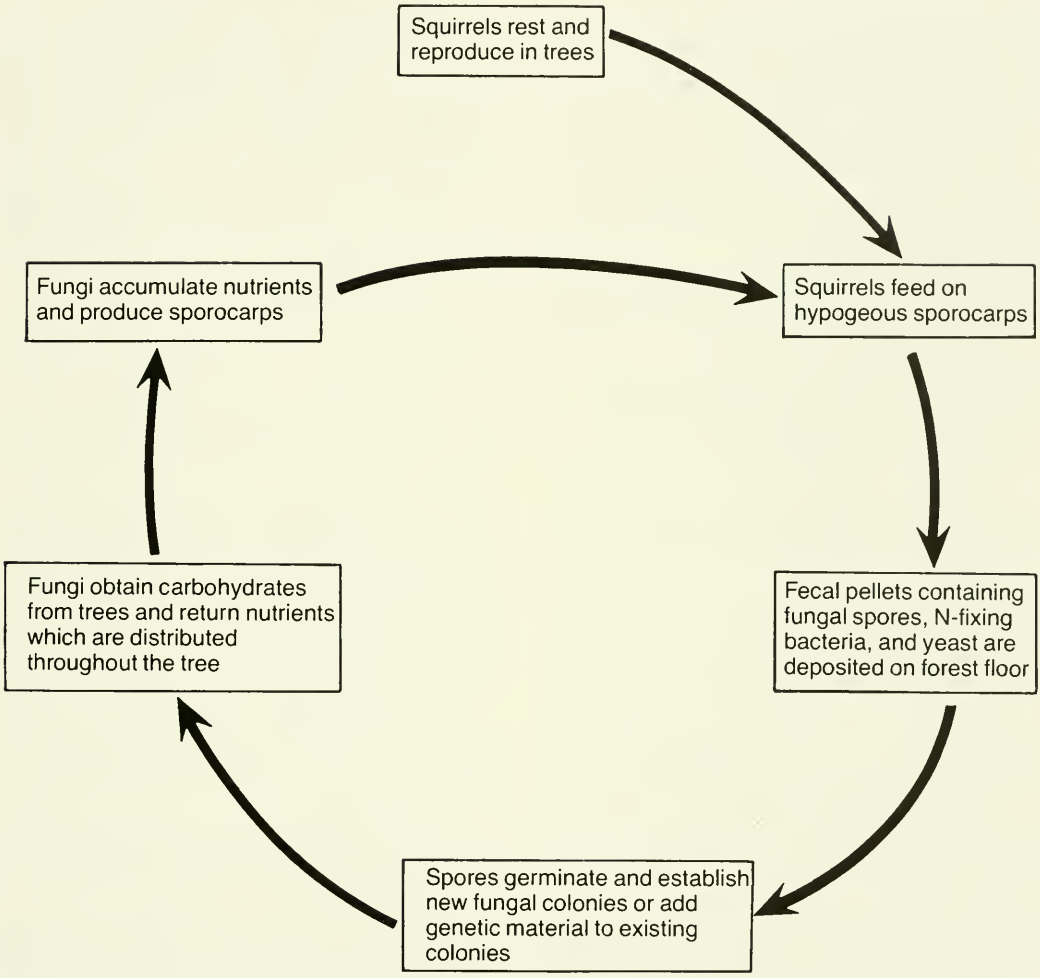

Fig. 4. Major components of flying squirrel-fungus-tree mutualism.

concert with the ecosystem. Data for this paper, for example, have been derived through cooperative efforts of biologists, mycologists, and microbiologists. Such a team approach is essential to understanding the vast array of interactions that are part of ecosystem processes.

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LITERATURE CITED

BAILEY, V. 1936. The mammals and life zones of Oregon. N. Amer. Fauna 55: 1–416.

BAKERSPIGEL, A. 1956. *Endogone* in Saskatchewan rodents. Amer. J. Bot. 43: 471–475.

_____. 1958. The spores of *Endogone* and *Melanogaster* in the digestive tracts of rodents. Mycologia 50: 440–442.

BLAKE, B. H. 1972. The annual cycle and fat storage in two populations of golden-mantled ground squirrels. J. Mammal. 53: 157–167.

BLASCHKE, H., AND W. BÄUMLER. 1986. Uber die Rolle der Biogeozonose in Wurzelbereich von Waldbaumen. Forstwissenschaftliches Centralblatt 105: 122–130.

BRAND, L. R. 1974. Tree nests of California chipmunks (*Eutamias*). Amer. Midl. Nat. 91: 489–491.

BROADBOOKS, H. E. 1958. Life history and ecology of the chipmunk, *Eutamias amoenus*, in eastern Washington. Mus. Zool., University of Michigan, Ann Arbor. Miscellaneous Publ. No. 103: 2–42.

_____. 1974. Tree nests of chipmunks with comments on associated behavior and ecology. J. Mammal. 55: 630–639.

DOWDING, E. S. 1955. *Endogone* in Canadian rodents. Mycologia 47: 51–57.

DURRIEU, G., M. GENARD, AND F. LESCOURRET. 1984. Les micromammiferes et la symbiose mycorhizienne dan une forêt de montagne. Bull. Ecol. 15: 253–263.

FOGEL, R., AND G. HUNT. 1979. Fungal and arboreal biomass in a western Oregon Douglas-fir ecosystem: distribution patterns and turnover. Canadian J. For. Res. 9: 245–256.

FOGEL, R., AND J. M. TRAPPE. 1978. Fungus consumption (mycophagy) by small animals. Northw. Sci. 52: 1–31.

FOGEL, R. D. 1976. Ecological studies of hypogeous fungi. II. Sporocarp phenology in a western Oregon Douglas-fir stand. Canadian J. Bot. 54: 1152–1162.

FRANKLIN, J. F., AND C. T. DYRNESS. 1973. Natural vegetation of Oregon and Washington. Gen. Tech. Rept. PNW–8, USDA Forest Service, Portland, Oregon. 417 pp.

FRIES, N. 1966. Chemical factors in the germination of spores of basidiomycetes. Pages 189–199 *in* M. F. Madelin, ed., The fungus spore. Butterworths, London.

_____. 1982. Effects of plant roots and growing mycelia on basidiospore germination in mycorrhiza-forming fungi. Pages 493–508 *in* G. A. Laursen and J. F. Ammirati, eds., Arctic and alpine mycology. University of Washington Press, Seattle.

FROIDEVAUX, L. 1981. Les ectomycorrhizes micro-usines productrices de bois et de champignons comestibles. Pecheur romand 38: 18–20.

GORDON, K. 1943. The natural history and behavior of the western chipmunk and the mantled ground squirrel. Oregon State Monogr., Studies in Zool., No. 5: 1–104.

GRÖNWALL, O., AND A. PEHRSON. 1984. Nutrient content in fungi as a primary food of the red-squirrel *Sciurus vulgaris* L. Oecologia 64: 230–231.

HAMILTON, W. J., JR. 1941. The food of small forest mammals in eastern United States. J. Mammal. 22: 250–263.

HARLEY, J. L., AND S. E. SMITH. 1983. Mycorrhizal symbiosis. Academic Press, New York. 483 pp.

HATTON, L. E., AND R. S. HOFFMAN. 1979. The distribution of red squirrels (*Tamiasciurus*) in eastern Oregon. Murrelet 60: 23–25.

HUESTIS, R. R. 1951. The golden mantled ground squirrel. Crater Lake Nature Notes, Special Number. Crater Lake Nat. Hist. Assoc., Crater Lake Natl. Park. 22 pp.

HUNT, G., AND J. M. TRAPPE. In press. Seasonal hypogeous sporocarp production in a western Oregon Douglas-fir stand. Canadian J. Bot.

KOTTER, M. M., AND R. C. FARENTINOS. 1984a. Formation of ponderosa pine ectomycorrhizae after inoculation with feces of tassel-eared squirrels. Mycologia 76: 758–760.

_____. 1984b. Tassel-eared squirrels as spore dispersal agents of hypogeous mycorrhizal fungi. J. Mammal. 65: 684–687.

LI, C. Y., AND M. A. CASTELLANO. 1985. Nitrogen-fixing bacteria isolated from within sporocarps of three ectomycorrhizal fungi. Page 164 *in* R. Molina, ed., Proceedings of 6th North American Conference on Mycorrhiza. Forest Research Laboratory, Corvallis, Oregon.

LI, C. Y., C. MASER, Z. MASER, AND B. CALDWELL. 1986. Role of three rodents in forest nitrogen fixation in western Oregon: another aspect of mammal-mycorrhizal fungus-tree mutualism. Great Basin Nat. 46: 411–414.

MARKS, G. C., AND T. T. KOZLOWSKI. 1973. Ectomycorrhizae—their ecology and physiology. Academic Press, New York.

MASER, C., Z. MASER, J. W. WITT, AND G. HUNT. 1986. The northern flying squirrel: a mycophagist in southwestern Oregon. Canadian J. Zool. 64: 2086–2089.

MASER, C., B. R. MATE, J. F. FRANKLIN, AND C. T. DYRNESS. 1981. Natural history of Oregon Coast mammals. USDA For. Serv. Gen. Tech. Rept. PNW-133, USDA Forest Service, Portland, Oregon. 496 pp.

MASER, C., AND J. M. TRAPPE, TECH. EDS. 1984. The seen and unseen world of the fallen tree. Gen. Tech. Rept. PNW-164, USDA Forest Service, Portland, Oregon. 56 pp.

MASER, C., J. M. TRAPPE, AND R. A. NUSSBAUM. 1978. Fungal–small mammal interrelationships with emphasis on Oregon coniferous forests. Ecology 59: 799–809.

MASER, C., J. M. TRAPPE, AND D. C. URE. 1978. Implications of small mammal mycophagy to the management of western coniferous forests. Trans. N. Amer. Wildl. and Nat. Resour. Conf. 43: 78–88.

MASER, Z., AND C. MASER. 1987. Notes on mycophagy of the yellow-pine chipmunk (*Eutamias amoenus*) in northeastern Oregon. Murrelet 68: 24–27.

MASER, Z., C. MASER, AND J. M. TRAPPE. 1985. Food habits of the northern flying squirrel (*Glaucomys sabrinus*) in Oregon. Canadian J. Zool. 63: 1084–1088.

MCINTIRE, P. W. 1980. Population structure and microhabitat utilization of *Eutamias siskiyou* within a variously treated shelterwood cut. Unpublished thesis, Southern Oregon State College, Ashland. 113 pp.

_____. 1984. Fungus consumption by the Siskiyou chipmunk within a variously treated forest. Ecology 65: 137–146.

MEREDITH, D. H. 1972. Subalpine cover associations of *Eutamias amoenus* and *Eutamias townsendii* in the Washington Cascades. Amer. Midl. Nat. 88: 348–357.

MILLER, O. K., JR. 1983. Ectomycorrhizae in the Agaricales and Gastromycetes. Canadian J. Bot. 61: 909–916.

MILLER, R. M. 1979. Some occurrences of vesicular-arbuscular mycorrhiza in natural and disturbed ecosystems of the Red Desert. Canadian J. Bot. 57: 619–623.

OORT, A. J. P. 1974. Activation of spore germination in *Lactarius* species by volatile compounds of *Ceratocystis fagacearum*. Konikl. Ned. Akad. Wetensch. ser. C, 77: 301–307.

PIROZYNSKI, K. A., AND D. W. MALLOCH. 1975. The origin of land plants: a matter of mycotrophism. BioSystems 6: 153–164.

RAUSCH, R. L. 1985. Presidential address. Parasitology: retrospect and prospect. J. Parasitol. 71: 139–151.

REECE, P. E., AND C. D. BONHAM. 1978. Frequency of endomycorrhizal infection in grazed and ungrazed blue grama plants. J. Range Manage. 31: 149–151.

SANDERS, S. D. 1984. Foraging by Douglas tree squirrels (*Tamiasciurus douglasii:* Rodentia) for conifer seeds and fungi. Unpublished dissertation, University of California, Davis. 95 pp.

SHAW, W. T. 1944. Brood nests and young of two western chipmunks in the Olympic Mountains of Washington. J. Mammal. 25: 274–284.

STEBBINS, L. L., AND R. ORICH. 1977. Some aspects of overwintering in the chipmunk, *Eutamias amoenus*. Canadian J. Zool. 55: 1139–1146.

STIENECKER, W., AND B. M. BROWNING. 1970. Food habits of the western grey squirrel. California Fish and Game 56: 36–48.

TEVIS, L., JR. 1952. Autumn foods of chipmunks and golden-mantled ground squirrels in the northern Sierra Nevada. J. Mammal. 33: 198–205.

_____. 1953. Stomach contents of chipmunks and mantled squirrels in northeastern California. J. Mammal. 34: 316–324.

TRAPPE, J. M. 1981. Mycorrhizae and productivity of arid and semiarid rangelands. Pages 581–599 *in* Advances in food producing systems for arid and semiarid lands. Academic Press, Inc., New York.

TRAPPE, J. M., AND R. D. FOGEL. 1977. Ecosystematic functions of mycorrhizae. Pages 205–214 *in* J. K. Marshal, ed., The belowground ecosystem: a synthesis of plant-associated processes. Range Sci. Dept. Sci. Ser. 26, Colorado State University, Fort Collins.

TRAPPE, J. M., AND C. MASER. 1976. Germination of spores of *Glomus macrocarpus* (Endogonaceae) after passage through a rodent digestive tract. Mycologia 68: 433–436.

_____. 1977. Ectomycorrhizal fungi: interactions of mushrooms and truffles with beasts and trees. Pages 165–178 *in* T. Walters, ed., Mushrooms and man: an interdisciplinary approach to mycology. Linn Benton Community College, Albany, Oregon.

TRAPPE, J. M., Z. MASER, C. MASER, AND M. A. CASTELLANO. In press. Synoptic spore key to genera of hypogeous fungi of northern temperate forests with special reference to animal mycophagy. Mad River Press, Inc., Eureka, California.

TRAPPE, J. M., AND R. MOLINA. 1986. Taxonomy and genetics of mycorrhizal fungi: their interaction and relevance. Pages 133–146 *in* V. Gianinazzi-Pearson and S. Gianinazzi, Proceedings of 1st European symposium on mycorrhizae. Institut National Researche Agronomique.

URE, D. C., AND C. MASER. 1982. Mycophagy of red-backed voles in Oregon and Washington. Canadian J. Zool. 60: 3307–3315.

WHITAKER, J. O., JR. 1962. *Endogone*, *Hymenogaster*, and *Melanogaster* as small mammal foods. Amer. Midl. Nat. 67: 152–156.

WILLIAMS, O., AND B. A. FINNEY. 1964. *Endogone*—food for mice. J. Mammal. 45: 265–271.

WILLIAMS, S. E., AND E. F. ALDON. 1976. Endomycorrhizal (vesicular-arbuscular) association of some arid zone shrubs. Southw. Nat. 20: 437–444.

YOUSEF, M. K., AND W. G. BRADLEY. 1971. Physiological and ecological studies on *Citellus lateralis*. Comp. Biochem. Physiol. 39A: 671–682.

SURVEY OF WYOMING CRAYFISHES

Wayne A. Hubert[1]

ABSTRACT.—Collections of crayfish by Wyoming Game and Fish Department biologists and University of Wyoming staff in 1985–1987 included five species: *Pacifastacus gambelii*, the only species found in the Snake River and Bear River drainages of western Wyoming; *Orconectes neglectus neglectus*, collected from one reservoir in the South Platte River drainage in southeastern Wyoming (its first reported occurrence in the state); *O. immunis* and *O. virilis*, widespread east of the Continental Divide and in the Green River drainage of southwestern Wyoming; and *Cambarus diogenes diogenes*, collected from a tributary of the North Platte River in eastern Wyoming.

The introduction of *Orconectus rusticus* into Wisconsin and the subsequent ecological and fisheries management problems have heightened awareness of the potential adverse impacts of exotic crayfish (Lodge et al. 1985). In Wyoming, crayfish are considered valuable fish forage in most waters where they occur, but several potential problems with introduced crayfish are of concern to fisheries managers. They include possible impacts on native species (Schwartz et al. 1963, Bouchard 1976), possible forage imbalance in some trout fisheries (Hepworth and Duffield 1987), and the loss of aquatic macrophytes in aquatic systems where plants are ecologically important (Dean 1969, Lodge et al. 1985). Since no inventory of the crayfish species in Wyoming had been conducted, the Wyoming Game and Fish Department (WGFD) began one in 1985. I describe the information obtained on occurrence and distribution of crayfish species in Wyoming.

METHODS

Fishery biologists with WGFD were asked to collect and preserve crayfish found by them in 1985, 1986, and 1987. Collections were generally made during the performance of other assigned tasks on particular waters. Written instructions were provided to each biologist for preservation, labeling of specimens, and site identification. Diagrams of first-forms males were also provided, with instructions for identifying males and instructions to collect only males. Specimen jars, alcohol, and labels were provided to the biologists.

Collections were transferred to the University of Wyoming Department of Zoology and Physiology for storage and identification. Identifications follow Hobbs (1976).

RESULTS AND DISCUSSION

Occurrence

Five species of crayfish were found: *Pacifastacus gambelii*, *Orconectes neglectus neglectus*, *O. immunis*, *O. virilis*, and *Cambarus diogenes diogenes* (Table 1). This was the first record of *O. neglectus neglectus* in Wyoming (Williams 1954, Hobbs 1976).

Distributions

The only species collected in both the Snake River and the Bear River drainages was *Pacifastacus gambelii*. It is probably endemic to these drainages in Wyoming (Hobbs 1976, Johnson 1986).

Two species, *Orconectes immunis* and *O. virilis*, were collected in the Green River drainage in southeastern Wyoming. *Orconectes virilis* was reported to occur in Flaming Gorge Reservoir by Johnson (1986), but this was the first report of *O. immunis* in the watershed. Both species were in collections from Flaming Gorge Reservoir in Wyoming; however, *O. immunis* was collected only at the upstream end of the reservoir and was the only species found in the drainage upstream from the reservoir. Both species were introduced into the Colorado River drainage,

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TABLE 1. Crayfish collection sites and species of the genera *Cambarus*, *Orconectes*, and *Pacifastacus* found in Wyoming, 1985–1987.

Drainage	County	Site	Species
Snake River	Teton	Teton Valley Ranch spring	*P. gambelii*
		Polecat Creek	*P. gambelii*
Bear River	Uinta	Woodruff Reservoir	*P. gambelii*
		Bear River	*P. gambelii*
		Sulphur Creek	*P. gambelii*
Green River	Sublette	Big Sandy Reservoir	*O. immunis*
	Sweetwater	Flaming Gorge Reservoir	*O. immunis*
			O. virilis
		Green River	*O. immunis*
North Platte River	Albany	Lake Hattie	*O. immunis*
		Alsop Lake	*O. immunis*
		Lezenbee Lake	*O. immunis*
		Huck Finn Pond	*O. immunis*
		Rock Creek	*O. immunis*
	Carbon	Seminoe Reservoir	*O. immunis*
		North Platte River	*O. immunis*
	Goshen	Hawk Springs Reservoir	*O. immunis*
		Horse Creek	*O. immunis*
			O. virilis
			C. diogenes
	Natrona	Alcova Reservoir	*O. immunis*
			O. virilis
		Barbe Pond	*O. immunis*
		Kendrick Canal	*O. virilis*
	Platte	Festo Lake	*O. immunis*
		Joe Johnson Reservoir	*O. immunis*
South Platte River	Laramie	Sloans Lake	*O. immunis*
			O. virilis
		Wyoming Travel Commission Pond	*O. immunis*
		Crystal Lake Reservoir	*O. neglectus*
Belle Fourche River	Campbell	Gillette Fishing Lake	*O. immunis*
	Crook	Keyhole Reservoir	*O. immunis*
		Sundance Pond	*O. immunis*
Powder River	Johnson	Todd Reservoir	*O. virilis*
		Sandstone Draw Reservoir	*O. immunis*
		Sand Creek	*O. immunis*
		Shell Creek	*O. immunis*
Big Horn River	Freemont	Boysen Reservoir	*O. immunis*
		Maverick Pond	*O. immunis*
		Wind River	*O. immunis*
		Popo Agie River	*O. immunis*
			O. virilis
	Park	Lily Lake	*O. immunis*

where no native crayfish were known (Johnson 1976).

East of the Continental Divide in the North Platte River drainage, *O. immunis* was the most commonly collected species. *Orconectes virilis* was also collected at scattered locations. *Cambarus diogenes diogenes* was found in one stream, Horse Creek, a tributary to the North Platte River in eastern Wyoming. All three species are probably endemic to Wyoming east of the Continental Divide (Crocker and Barr 1968).

In the South Platte River drainage in southeastern Wyoming, *Orconectes neglectus neglectus* was collected from Crystal Lake Reservoir at the headwaters of the Crow

Creek drainage, Laramie County. This species has been previously reported in the South Platte River drainage in Sedgwick County, Colorado (Williams 1954). Both *O. immunis* and *O. virilis* were also collected from impoundments in the South Platte River drainage.

In the river drainages that flow to the Missouri River—Belle Fourche, Powder, and Big Horn—both *O. immunis* and *O. virilis* were collected, but *O. immunis* was the more common.

Management Considerations

Pacifastacus gambelii was the only species found in the Snake River and Bear River drainages. Because the introduction of exotic species could lead to displacement of this native crayfish, the transplanting or transporting of crayfish from other drainages into these two drainages should be discouraged.

Orconectes neglectus neglectus was found in a single coldwater reservoir at the headwater of the Crow Creek drainage, Laramie County. It has been reported in streams cold enough to support trout (Williams 1954). Only three other sites in the South Platte River drainage were sampled during this survey. Possibly *O. neglectus neglectus* is more widespread in Wyoming and is endemic to clear, rocky streams in the South Platte River drainage in Wyoming (Williams 1954).

Cambarus diogenes diogenes was collected from one stream in eastern Wyoming. It is likely to be more widespread in the state, but few samples were collected from small streams in eastern Wyoming.

Both *Orconectes immunis* and *O. virilis* were native to all drainages east of the Continental Divide and have been introduced into the Green River drainage west of the Continental Divide. Johnson (1986) described introduction of *O. virilis* into the Green River drainage with a shipment of largemouth bass (*Micropterus salmoides*) from a pond in Johnson County, Wyoming, to Flaming Gorge Reservoir.

Orconectes virilis has been known to adversely affect rainbow trout (*Salmo gairdneri*) in reservoirs (Hepworth and Duffield 1987), to displace native crayfish (Schwartz et al. 1963, Bouchard 1976), and to consume aquatic macrophytes (Dean 1969, Johnson 1976); consequently, transplanting of this species to enhance fish forage should be done with caution. Since no similar problems have been identified with *O. immunis*, it may be a more desirable forage species; however, its ecological impacts on waters where it is an introduced species are not known.

ACKNOWLEDGMENTS

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LITERATURE CITED

BOUCHARD, R. W. 1976. Geography and ecology of crayfishes of the Cumberland Plateau and Cumberland Mountains, Kentucky, Virginia, Tennessee, Georgia, and Alabama. Part I. The genera of *Procambarus* and *Orconectes*. Freshwater Crayfish 2: 563–584.

CROCKER, D. W., AND D. W. BARR. 1968. Handbook of the crayfishes of Ontario. Life Sciences Miscellaneous Publications, Royal Ontario Museum, University of Toronto. 158 pp.

DEAN, J. L. 1969. Biology of the crayfish *Orconectes causeyi* and its use for control of aquatic weeds in trout lakes. U.S. Bureau of Sport Fisheries and Wildlife, Technical Paper 24. 15 pp.

HEPWORTH, D., AND D. DUFFIELD. 1987. Impact of an exotic crayfish on stocked rainbow trout in Newcastle Reservoir. North American Journal of Fisheries Management 7: 554–561.

HOBBS, H. H., JR. 1976. Crayfishes (Astacidae) of North and Middle America. U.S. Environmental Protection Agency Water Pollution Control Research Series, 18050 ELD05/72. Cincinnati, Ohio. 173 pp.

JOHNSON, J. E. 1986. Inventory of Utah crayfish with notes on current distribution. Great Basin Naturalist 46: 625–631.

LODGE, D. M., A. L. BECKEL, AND J. J. MAGNUSON. 1985. Lake-bottom tyrant. Natural History 8/85: 33–35.

SCHWARTZ, F. J., R. RUBELMANN, AND J. ALLISON. 1963. Ecological population expansion of the introduced crayfish, *Orconectes virilis*. Ohio Journal of Science 63: 266–273.

WILLIAMS, A. B. 1954. An explanation for the distribution of a North American crayfish. Ecology 35: 573–575.

STREAM CHANNEL AND VEGETATION CHANGES IN SECTIONS OF MCKNIGHT CREEK, NEW MEXICO

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ABSTRACT.—Measurements taken at three-year intervals between 1977 and 1985 of channel morphology and vegetation cover between sections inside and outside a cattle exclosure showed that channels increased in depth and width on all plots. Tree canopy cover decreased significantly between 1977 and 1985, but changes in density of trees and shrubs and herbaceous cover were small. Exclusion of cattle use did not prevent channel erosion or deterioration of vegetation; rather, changes were attributed to a wildfire in the headwaters and subsequent storm events that temporarily upset the dynamic equilibrium of the stream.

Riparian ecosystems provide many benefits, such as recreation, fisheries, grazing, and water. However, these ecosystems are fragile, and many consider cattle grazing not compatible with the more aesthetic uses. Various studies (Johnson and McCormick 1978, Kauffman and Krueger 1984) have demonstrated adverse effects resulting from improper land uses. Others report adverse effects caused by natural phenomena, such as floods (Hayes 1978, Buckhouse et al. 1981). Although floods are known to adversely affect riparian habitats (Leopold and Wolman 1957, Lane 1957), the interrelationships between riparian vegetation and stream hydraulics are also poorly understood (Heede 1980).

This study was done to evaluate changes over a nine-year period in channel morphology and riparian vegetation in lightly grazed and essentially ungrazed sections of McKnight Creek on the Gila National Forest.

STUDY AREA

McKnight Creek is a headwater tributary of the Mimbres River in southwestern New Mexico. A 438-ha (0.8 × 4.3-km) cattle exclosure plus adjacent grazed portions of the Little McKnight unit of the Powderhorn grazing allotment (75,832 ha) were used as the study area. McKnight Canyon is a steep-sided, narrow-bottomed drainage with a stream gradient of between 0.5% and 2% in most reaches. Channel substrates were estimated in 1982 to be about 80% cobble, 9% gravels, 6% sands, 3% organic materials (i.e., fallen logs), and 2% boulders. Stream bank soils are principally shallow to deep silty-clay loams with recent sandy-loam deposits. Common streamside trees include *Populus angustifolia* (narrowleaf cottonwood), *Quercus gambelii* (Gambel oak), *Pinus ponderosa* (ponderosa pine), and *Juglans major* (Arizona walnut). Major shrub species were *Robinia neomexicana* (New Mexico locust), *Prunus serotina* (Gila chokecherry), *Symphoricarpos oreophilus* (mountain snowberry), and *Sambucus neomexicana* (New Mexican elder). Herbaceous vegetation is largely dominated by *Poa pratensis* (Kentucky bluegrass) and *Bromus anomalus* (nodding brome).

Prior to 1968 Forest Service records show the allotment had a history of heavy cattle use, with an average stocking rate of 2,340 and as high as 3,369 animal-unit-months (aum) yearlong. From 1968 to 1975 the allotment was grazed May through September only in alternate summers, with a seasonal stocking rate of about 1,145 aum's. During this period (1968–1975), the allotment was rested four years out of seven. Cattle grazing in the exclosure since it was built in 1975 has been limited to occasional strays. Meanwhile, during the period of study, the adjacent range was not stocked from 1977 to 1981. Since 1982 it has been stocked very lightly (< 228 aum's) in summer only. Grazing during the study period has been negligible.

Average annual precipitation at the Mimbres Ranger Station, located about 6–7 miles from the study site, is about 48 cm, with yearly variation between 25 and 71 cm

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(n = 48). Precipitation is bimodal, with 55% of average rainfall occurring from July through September, 36% during the fall-winter months, and 9% during spring months. Stream flows are highly variable, with modal flows between 0.3 and 3.5 m^3/minute (Rinne 1978). In severe drought, surface water may be reduced to intermittent pools. Peak flows occur in April, July, or August, and occasionally in December. Flood flows may exceed 150 m^3/minute but are of short duration (1–2 days) (Rinne 1980). McKnight Creek has served as restoration area for the endangered Gila trout, and because of this, use of the riparian area is limited to hiking.

METHODS

Seven study plots (6 × 30.5 m) were randomly established within straight reaches and adjacent to the channel in May 1977. Plot 1 was located about .5 km below the exclosure, plots 2–6 were located about .5 km apart within the exclosure, and plot 7 was .5 km above. The longitudinal center line of each plot was marked with stakes at either end. A tape along this center line was used to determine frequency of rooted herbaceous species by the 3/4-inch-loop method (100 loops/transect) (Parker 1951) to define the boundaries of eight 3 × 7.6-m plots on which the density, diameter at breast height, total height of trees, and density of shrubs were measured, and to estimate tree canopy cover at 7.6-m intervals using a modified densiometer. Data for herbaceous species in 1985, however, are for canopy cover (Daubenmire 1952) rather than basal cover and are based on 60 0.1-m^2 quadrats rather than 100 1.9-cm (3/4-inch) circles. At each plot three stream cross-sectional transects were established perpendicular to the stream channel 15.25 m apart to determine the approximate shape of stream cross sections. Surface elevations were obtained at 0.6-m intervals by measuring the perpendicular distance to ground level from a line stretched between stakes on either side of the channel. Photographs were taken to visually document vegetation and stream morphological conditions. Measurements were taken in May 1977, 1979, 1982, and 1985. Plant nomenclature follows Martin and Hutchins (1980).

Changes in channel cross sections for each transect and plot were depicted as cross-sectional graphs. Quantitative assessments of stream cross sections were made by comparing differences in mean cross-sectional depths, width-depth ratios, and channel-shape factors (Heede 1980) for individual transects within a plot for given years. Mean cross-sectional depth was defined as the mean of depth observations for a given transect and year. The width-depth ratio is the top width of the channel divided by the mean depth and is a quantitative expression of channel shape (Heede 1975). Shape factor is the quotient of the maximum depth divided by mean depth. These attributes are useful in quantifying geomorphological changes. They are also related to the efficiency of water flow through a channel.

DATA ANALYSIS

Analysis of variance using a repeated measure approach was used to assess temporal and plot differences for both morphology and vegetation data. Individual degree of freedom contrasts were used to assess pairwise differences among years and among plots. Where evident, variation in time for individual plots was also analyzed with individual repeated measure analyses. Multiyear comparisons of individual transects were subjectively made through graphs of cross-sectional areas and indices of change, i.e., shape factors, width-depth ratios. Discussion of these parameters is qualitative since each requires simultaneous interpretation of more than one variable. For example, width-depth ratios may remain the same, even though both width and depth change.

RESULTS

Stream Morphology

Significant ($p < .01$) changes over time occurred on all plots (Fig. 1). However, differences over time within individual transects yield better estimates of changes in channel morphology because each transect is unique with respect to space and time. Significant differences ($p < .05$) were observed for all years on all plots except plot 5.

The strong interaction observed between plots and time was attributed primarily to

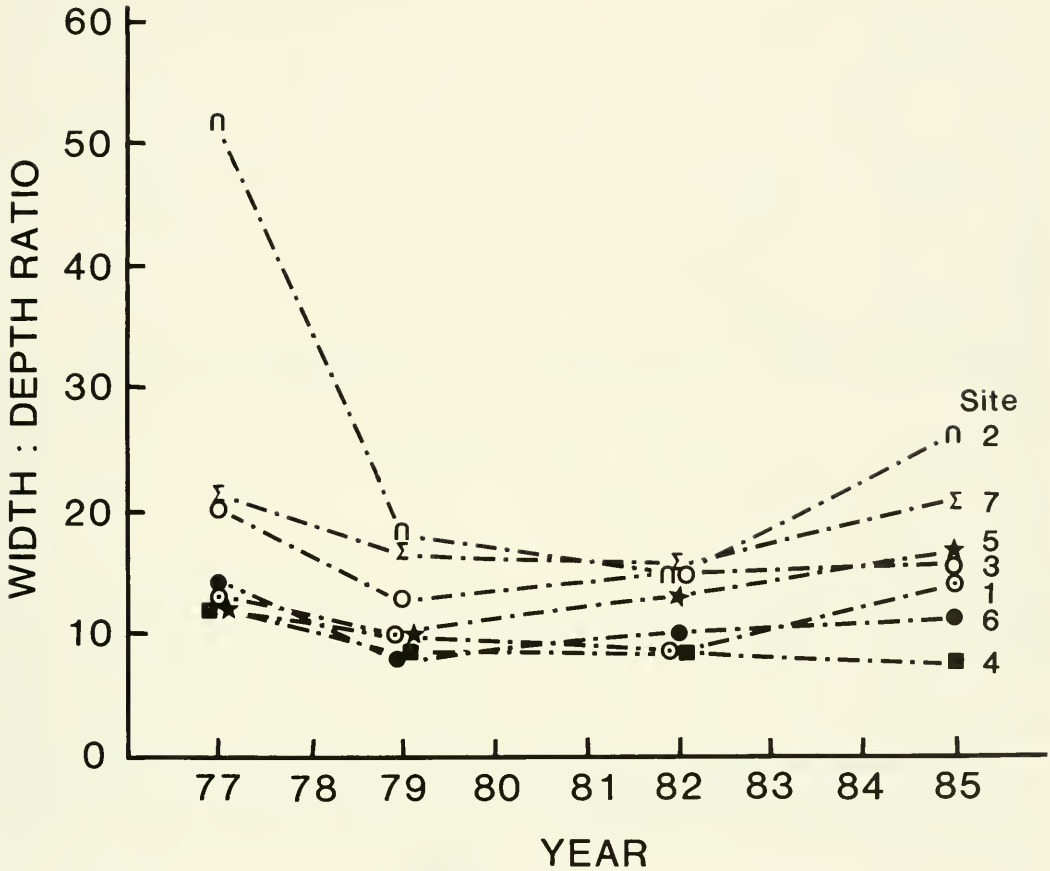

Fig. 1. Width-depth ratios of individual plots for years 1977, 1978, 1979, 1982, and 1985.

TABLE 1. Mean width-depth ratios (W:D), mean shape factors (SF), and mean channel depth (D) (in meters) by years of stream sections for all plots. Plots 1 and 7 were located outside the exclosure.

	1977			1979			1982			1985		
Plot	W:D	SF	D	W:D	SF	D	W:D	SF	D	W:D	SF	D
1	13.1	1.5	0.41	9.9	1.9	0.74	8.6	1.8	0.85	13.9	1.8	0.83
2	51.7	2.0	0.16	18.1	1.9	0.52	14.9	1.6	0.73	26.1	2.0	0.75
3	20.3	1.5	0.57	12.7	1.6	0.87	15.0	1.9	0.62	15.8	1.4	1.32
4	12.1	1.6	0.82	8.4	1.2	1.19	8.3	1.6	1.03	7.6	1.5	1.49
5	12.1	1.7	0.85	10.0	1.5	1.04	13.1	1.8	0.82	16.8	1.8	0.88
6	14.1	1.7	0.92	7.9	1.4	1.12	10.1	2.0	0.91	11.1	1.4	1.24
7	21.4	1.7	0.52	16.6	1.9	0.69	15.4	2.0	0.65	20.8	1.7	0.71

major changes in width and depth in most plots from year to year. However, variation among transects within plots was often as high as or higher than variation among plots. Channel substrate conditions are dynamic, constantly changing over time.

Plots 1 and 7 outside the exclosure and available for cattle use exhibited changes in channel morphology similar to some plots (four of five) within the exclosure (Table 1). In plot 1 below the exclosure, major differences ($p < .05$) in mean cross-sectional depth occurred between 1977 and all subsequent years. The stream section changed from a shallow, parabolic profile in 1977 to a deeper, triangular profile in 1979. Depth increased in

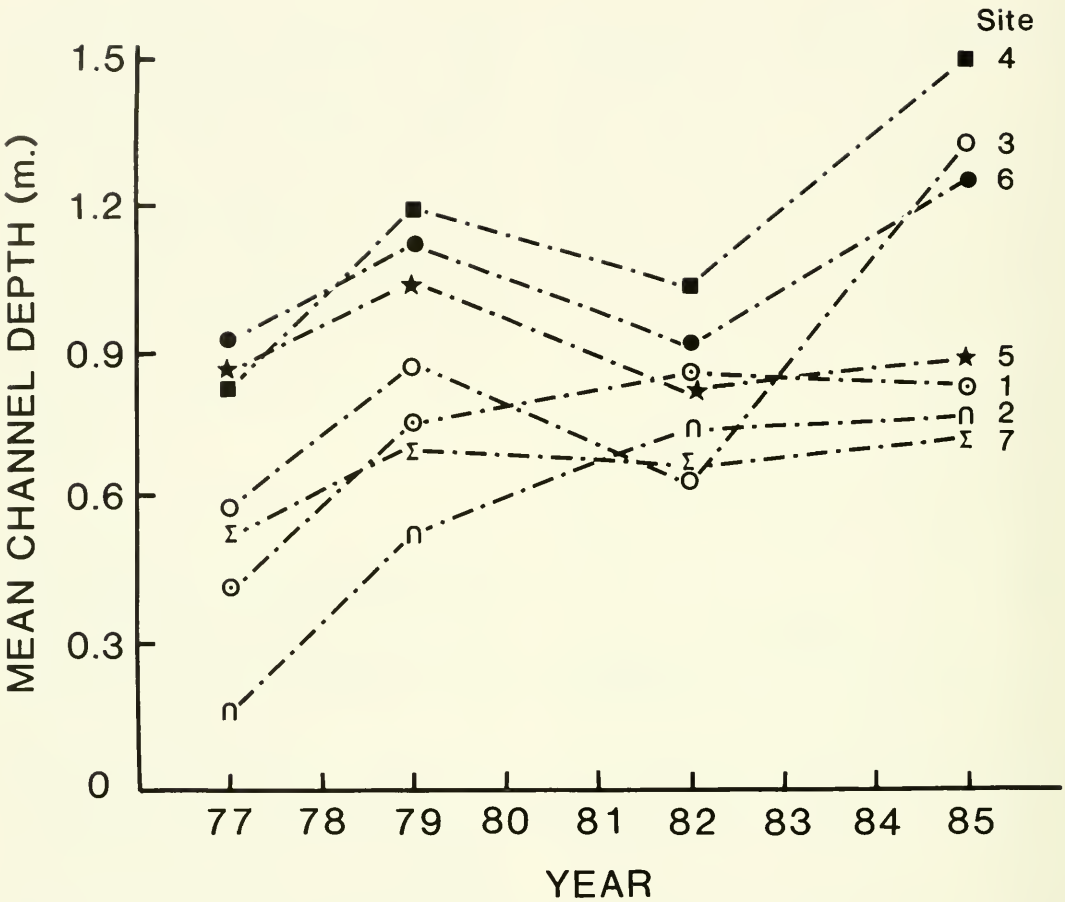

Fig. 2. Mean channel depths of individual plots for years 1977, 1978, 1979, 1982, and 1985.

1982, and the stream exhibited a decreased average shape factor; it maintained similar characteristics in 1985. Width-depth ratios were nearly the same in 1977 and 1985, but decreased in 1979 and 1982 (Fig. 1). This suggests a channel deepening, as graphically indicated in Figure 3.

Channel deepening and widening were also observed for plot 7 above the exclosure. Shape factors increased in 1979 and 1982 and decreased in 1985. Mean depths increased each year, going from 0.52 m in 1977 to 0.71 m in 1985. Width-depth ratios were about the same in 1977 and 1985, with a decrease noted in 1979 and 1982 just as on plot 1. Extensive changes of stream banks were noted, along with a general loss of bank material, particularly between 1979 and 1985 (Fig. 2).

Changes in channel morphology between years on plots within the exclosure were mixed. An overall increase in channel widths and depths occurred between 1977 and 1985 on all plots except plot 5. No major change in mean cross-sectional depth between all years for transects 2 and 3 of plot 5 were observed. In general, greater stability, as evidenced by small changes in depth and width, was observed on plots inside the exclosure. A slight decrease in channel width and depth was observed in 1982 on most plots, suggesting that depositional activity might have occurred. However, the severe winter flood of 1984–85 caused extensive changes in channel depth and width on most plots.

Qualitative examination of width-depth ratios and shape factors for plots inside the exclosure (Table 1) supports previous observations. Width-depth ratios changed relatively little from 1979 to 1982 because of simultaneous increases in widths and depths. The

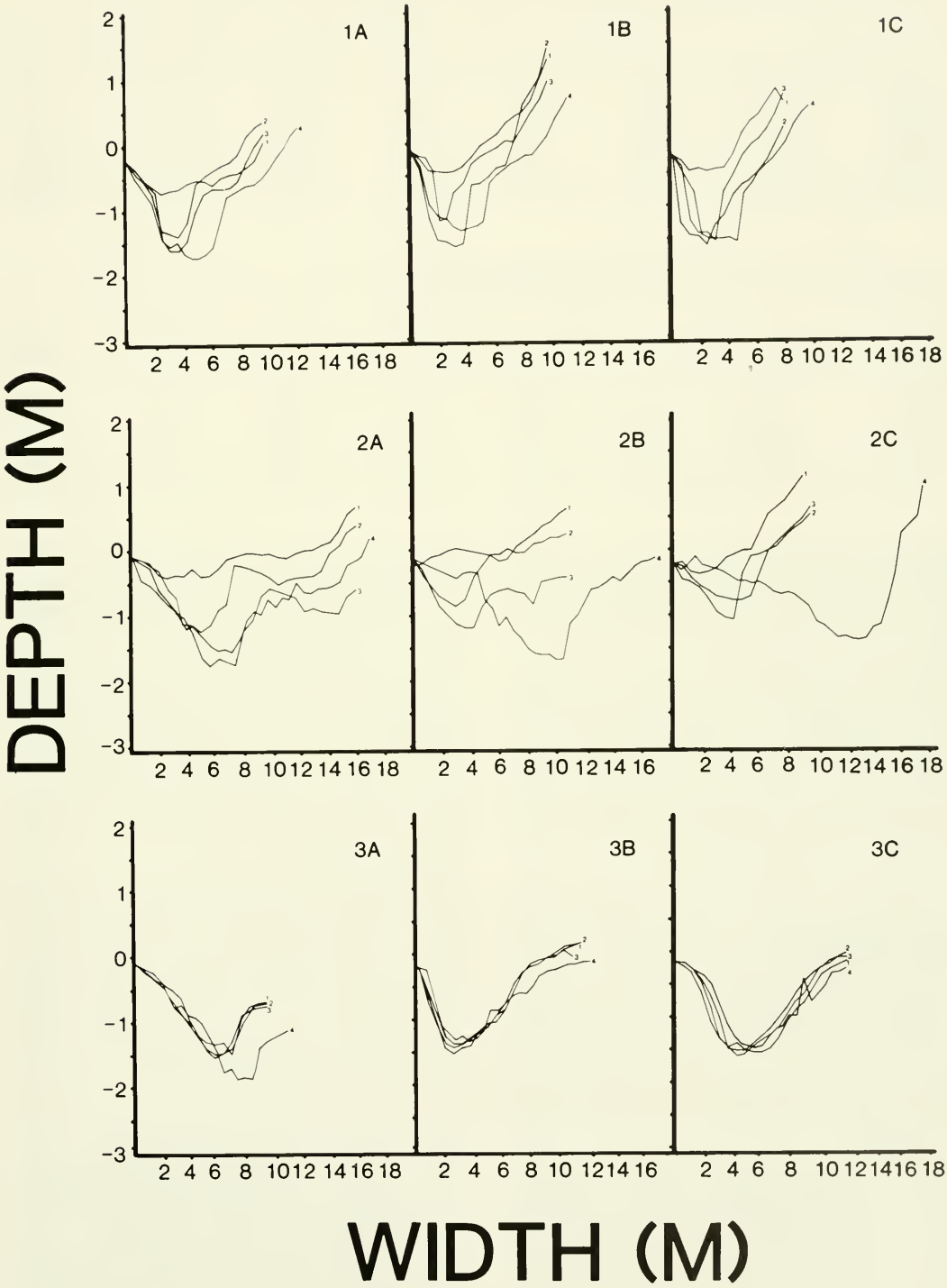

Fig. 3. Cross-sectional profiles of individual transects of plot 1 (la–lc), plot 2 (2a–2c), and plot 5 (3a–3c). Plot 1 represents the typical response of the two plots located outside, and plot 2 represents the typical response of four plots located inside the exclosure. Plot 5 was the main exception with no major changes over time.

TABLE 2. Total tree density (trees > 5 cm dbh) per hectare for all plots by year.

Year	Plot 1	2	3	4	5	6	7
1977	270	162	324	432	486	162	108
1978	270	162	324	378	270	162	270
1979	270	108	324	432	432	162	378
1982	216	108	378	324	486	162	324
1985	432	216	432	378	486	54	594

TABLE 3. Total shrub density per hectare for all plots by year.

Year	Plot 1	2	3	4	5	6	7
1977	3888	324	702	1782	24300	0	54
1978	4914	270	540	324	15876	54	54
1979	3996	486	270	432	8910	54	0
1982	4212	2592	864	648	9288	918	108
1985	3886	650	217	915	4480	0	54

higher width-depth ratios noted for 1985, relative to 1979 and 1982, were a result of channel widening. Mean width-depth ratios ranged from 7.6 to 51.7, with an average of 15.9.

Based on visual examination of profile graphs and Table 1, plots 1 and 7 outside the exclosure did not respond to changes in channel morphology differently than plots within the exclosure. All plots exhibited similar trends in changes in width and depth during the nine-year observation period.

Vegetation

No major changes in tree density were noted between years except for increases, noted on plots 1, 2, and 3, which were a result of maturation of young trees that were saplings in 1977 (Table 2). Decreased density was from natural mortality of mature trees in most cases (plots 4 and 7), except on plot 6 where flooding removed immature and mature trees.

Fluctuations in shrub density were greater than fluctuations of tree density (Table 3). Significant ($p < .05$) increases in density of Gambel oak were observed on plot 2 between 1977 and 1978 and between 1979 and 1982 and of *Salix* spp. on plots 3 and 6 between previous years and 1982. Although Gambel oak accounted for decreased density on plots 3 through 6, density of other shrubs (Gila chokecherry, mountain snowberry, New Mexico locust, and *Rosa* spp.) remained essentially unchanged.

A negative trend in mean herbaceous cover was noted for all plots, except plot 1, between 1977 and 1985 (Table 4). However, no significant ($p < .16$) differences over time were detected between plots. Differences within plots were generally small. Graminoids comprised between 80% and 100% of herbaceous cover, with Kentucky bluegrass as the dominant species. Species composition remained nearly unchanged.

Significant ($p < .03$) differences in percent tree canopy cover (Table 5) over time were observed between plots. Differences ($p < .05$) within plots over time were observed for years 1977, 1982, and 1985. Fluctuations in canopy cover ranged from 0 to 67% among years. A trend toward decreasing tree cover can be observed for all plots in Table 5.

DISCUSSION

The dynamic equilibrium of the stream was upset in 1951 as a result of a large wildfire in the headwater section of the stream. This event triggered a series of hydrological processes similar to those described by Heede (1986b). Headwater sections became filled with vast amounts of sediment (aggradation), raising the channel bottom. From the early 1970s through 1976, channel aggradation continued, with sediments being transported

TABLE 4. Mean frequency (1977–82) and mean percent herbaceous cover (1985) by year and plot.

Year	Plot 1	2	3	4	5	6	7
1977	0.20	2.35	2.30	1.30	1.45	1.35	0.75
1978	0.35	1.15	2.70	0.85	0.25	0.70	0.60
1979	0.55	1.00	2.70	0.75	0.50	1.05	0.25
1982	0.20	0.55	0.70	0.30	0.25	0.70	0.20
1985	1.20	1.70	0.90	0.83	0.67	0.87	0.36

TABLE 5. Percent tree canopy cover by year for plots on McKnight Creek.

Year	Plot 1	2	3	4	5	6	7
1977	94	95	98	96	96	97	96
1978	93	93	95	94	92	97	95
1979	93	92	95	94	92	96	93
1982	77	73	52	72	79	41	58
1985	68	50	55	75	71	32	61

downstream. Deposition of sediment above plot 2 was speeded up by the construction of a fish barrier in 1970. The barrier acted as a gradient-control structure, reducing bed erosion above it (Heede 1986b). Hence, the shallow, parabolic cross sections evidenced in 1975–1977 resulted. With sediment transport reduced, flow velocities increased, resulting in channel erosion as was evidenced from cross-sectional data since 1977. Channel erosion (downcutting) will continue until a sufficiently flatter gradient is reached and a new balance is attained (Heede 1986b). The increases in depth and width that were observed on most plots were hydrologic adjustments being made relative to each storm event. Removal of bank slough deposits enhances steepening of stream banks (Grissinger and Bowie 1984) and further contributes to channel widening and deepening (Heede 1975). In addition, a general tendency toward linearity and convexity in longitudinal bed profiles, coupled with numerous occurrences of channel nickpoints, provides additional evidence of a loss in equilibrium.

The principal factors causing channel changes were probably not changes in vegetation density but instead hydrologic adjustment processes (e.g., aggradation, downcutting) within the stream. Weather records show that major rainfall and stream-discharge events occurred before each sampling period (Figs. 4, 5). Hence, it is reasonable to expect sufficient stream discharge in McKnight Creek to significantly alter channel cross sections. Changes in channel morphology within the sections examined were a product of adjustments being made both above and below the study reaches. Also, the exclusion of cattle grazing did not prevent damage to stream banks and channel bottom. Grazing intensity was probably too light to show an effect, and nine years might have been too short a period to detect major changes in vegetation.

The overall increase in channel depth and width of plots 1 through 7 may have negative effects on streamside herbaceous and shrubby vegetation in later years. Heede (1986a) reported that one of the most influential channel changes is change in local base levels. Loss of base level may lead to degradation of stream banks and lowering of streamside water tables. This action may result in loss of vegetation density or mortality that, in turn, may lead to accelerated bank erosion if root systems die. The riparian plant community, as it existed in 1977, may be replaced by younger stands of obligate riparian vegetation as the stream proceeds toward equilibrium.

Vegetational changes were generally small and were attributed largely to flooding events that scoured stream banks and also deposited alluvium. Increases in mature tree density were simply a process of saplings growing to greater diameter, while decreases were from floods or natural mortality. Examination of

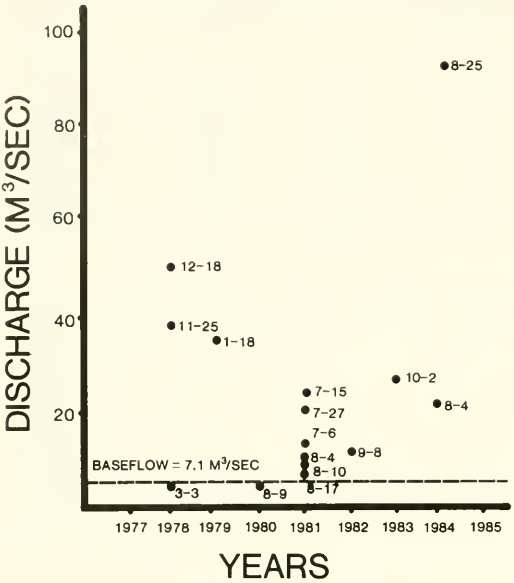

Fig. 4. Total annual rainfall recorded at nearest weather station, Mimbres Ranger Station, during the nine years of study.

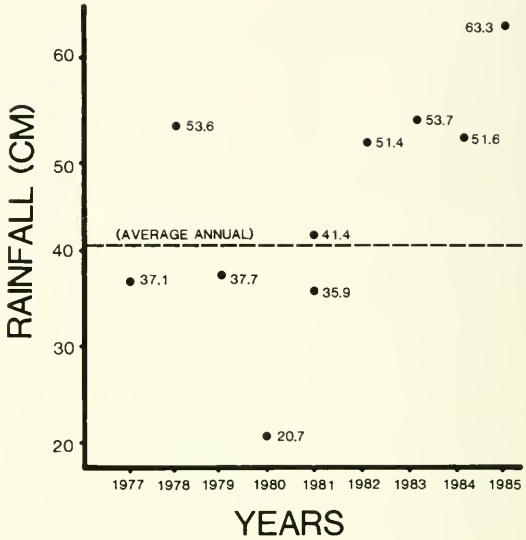

Fig. 5. Recorded discharge events above and near base flow at Mimbres Basin recording station, Mimbres, New Mexico. Numbers indicate month and day of event.

subplots within each plot revealed no gain in tree recruitment between 1977 and 1985. Similar results were noted for most shrubs. Establishment of *Salix* spp. was most notable during years of greatest change in channel morphology, due primarily to deposition of fine alluvial gravels. Hence, the disturbed or unstable condition of stream banks was more conducive to establishment than were other riparian soils. Increased herbaceous cover is attributed to increased sunlight to the soil surface. Significant changes in tree canopy cover were noted between 1977 and 1985 on all plots. This decrease is attributed to natural pruning of older cottonwood trees. Broken limbs were common both on and off the study plots. This decrease in canopy cover could have positive and negative effects on the system. Additional sunlight could benefit young broadleaf trees and increase herbaceous production, but it could also elevate water temperatures and negatively affect aquatic biota.

In summary, changes in stream morphology were attributable to a large fire in the headwaters and subsequent floods that caused a high degree of sedimentation in the upper channel, resulting in a "dam effect" (Williams and Wolman 1984) with the lower reaches being scoured out. This was also evidenced in lower reaches where the fish barrier was located. Vegetational changes were attributed to flood events as well as natural processes of mortality and recruitment. Vegetation density and cover changed very little over the nine-year period, both on protected and unprotected plots. In addition, major changes in stream geometry occurred in both protected and unprotected plots. We attribute said differences to hydrologic processes of stream equilibrium, because there was no evidence that plots available for cattle use responded differently from protected plots to channel and vegetation changes.

LITERATURE CITED

BUCKHOUSE, J. C., J. M. SKOVLIN, AND R. W. KNIGHT. 1981. Streambank erosion and ungulate grazing relationships. J. Range Manage. 34: 339–340.

DAUBENMIRE, R. 1952. Forest vegetation of northern Idaho and adjacent Washington, and its bearing on concepts of vegetation classification. Ecol. Monogr. 22: 301–329.

GRISSINGER, E. H., AND A. J. BOWIE. 1984. Material and site controls of stream bank vegetation. Trans. of the ASAE 27: 1829–1835.

HAYES, F. A. 1978. Streambank stability and meadow condition in relation to livestock grazing in mountain meadows of central Idaho. Unpublished master's thesis, University of Idaho, Moscow. 91 pp.

HEEDE, B. H. 1975. Mountain watersheds and dynamic

equilibrium. Pages 407–420 *in* Watershed Management Symposium. ASCE Irrigation and Drainage Division, Logan, Utah.

_____. 1980. Stream dynamics: an overview for land managers. USDA For. Serv. Gen. Tech. Rept. RM-72, Rocky Mt. For. & Range Expt. Sta., Fort Collins, Colorado. 26 pp.

_____. 1986a. Designing for dynamic equilibrium in streams. Water Resour. Bull. 22: 351–357.

_____. 1986b. Balance and adjustment processes in stream and riparian systems. Pages 3–7 *in* Proc. Wyoming Water 1986 and Streamside Zone Conference. University of Wyoming Agric. Ext. Serv., Laramie. 181 pp.

JOHNSON, R. R., AND J. F. MCCORMICK, TECH. COORD. 1978. Strategies for protection and management of floodplain wetlands and other riparian ecosystems. Proc. Symp. Dec. 11–13, 1978, Callaway Gardens, Georgia. USDA For. Serv. Gen Tech. Rept. WO-12, Washington, D. C. 410 pp.

KAUFFMAN, J. B., AND W. C. KRUEGER. 1984. Livestock impacts on riparian ecosystems and streamside management implications . . . a review. J. Range Manage. 37: 430–438.

LANE, E. W. 1957. A study of the shape of channels formed by natural streams flowing in erodible material. U.S. Corps of Eng. Rept. No. 9, Omaha, Nebraska. 109 pp.

LEOPOLD, L. B., AND M. G. WOLMAN. 1957. River channel patterns; braided, meandering, and straight. U.S. Geol. Surv. Prof. Pap. 282-B. 84 pp.

MARTIN, W. C., AND C. R. HUTCHINS. 1980. A flora of New Mexico. A. R. Ganter Verlag K. G., Hirschberg, Germany. 2,591 pp.

PARKER, K. W. 1951. A method of measuring trend in range condition on national forest ranges. USDA Forest Service, Washington, D.C. (mimeo).

RINNE, J. N. 1978. Development of methods of population estimation and habitat evaluation for management of the Arizona and Gila trouts. Pages 113–115 *in* J. R. Moring, ed., Proceedings of the wild trout—catchable trout symposium. Oregon Dept. of Fish and Wildlife, Eugene.

_____. 1980. Spawning habitat and behavior of Gila trout, a rare salmonid of the southwestern United States. Trans. Amer. Fish. Soc. 109: 83–91.

WILLIAMS, G. P., AND M. G. WOLMAN. 1984. Downstream effects of dams on alluvial rivers. U.S. Geol. Surv. Prof. Pap. 1286. 84 pp.

CICUTA BULBIFERA L. (UMBELLIFERAE) IN ALASKA

Stephen L. Talbot[1], Sandra J. Looman[1], and Stanley L. Welsh[2]

ABSTRACT.—Cited are distribution records for Alaska of *Cicuta bulbifera* L. It was discovered growing in the Nowitna National Wildlife Refuge in north central Alaska in 1984 and again in 1987. An earlier record is also known from near Fairbanks.

Populations of *Cicuta bulbifera* L. were discovered during aquatic plant inventories of Nowitna National Wildlife Refuge in north central Alaska at 64°50′N, 154°15′W and at 65°07′N, 153°08′W. An earlier record from Alaska, taken near Fairbanks, is acknowledged by Dr. David Murray (personal communication). The nearest previously reported location for this species is from the central Yukon Territory, Canada (A. E. Porsild and W. J. Cody, Vascular plants of the continental Northwest Territories, Canada, p. 476. 1980). It is a transcontinental species known also in western Canada from British Columbia and Alberta (H. J. Scoggan, Flora of Canada, part 4: 1162. 1969). W. J. Cody (Canadian Field-Nat. 74(2): 92. 1960) reported the northernmost site at 65°17′N in the central District of Mackenzie, which the Nowitna record approaches in latitude. The collection from Nowitna National Wildlife Refuge is a considerable extension of the known range.

The population in Nowitna National Wildlife Refuge (Talbot and Looman #022101B-6, 19 August) sampled in 1987 was growing on the shore of an alluvial lake along the Yukon River between Lange Island and Brant Island in the Melozitna (A1) Quadrangle at an elevation of 46 m. It occurred in a *Carex-lasiocarpa* Ehrh.–*Potentilla palustris* L. floating shore mire. Companion species in the community included *Equisetum fluviatile* L., *Cicuta mackenzieana* Raup, *Menyanthes trifoliata* L., *Lycopus uniflorus* Michx., *Chamaedaphne calyculata* (L.) Moench, *Andromeda polifolia* L., *Drosera rotundifolia* L., *Pedicularis parviflora* Smith ex Rees, *Eriophorum polystachion* L., *Sphagnum* spp., and *Drepanocladus* spp. Contiguous plant communities were an aquatic forb association dominated by *Potamogeton robbinsii* Oakes and *P. natans* L., and a raised ombotrophic peatland dominated by *Picea mariana* (Mill.) Britt., Sterns & Pogg and *Ledum decumbens* (Ait.) Lodd. ex Steud. The 1984 collection (Talbot #C23-12, August) is from a graminoid bog.

Voucher specimens are deposited at herbaria of Brigham Young University, Provo, Utah; University of Alaska, Fairbanks; and the Nowitna National Wildlife Refuge, Galena, Alaska.

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TRAPPING METHODS FOR RANGELAND INSECTS IN BURNED AND UNBURNED SITES: A COMPARISON

James D. Hansen[1]

ABSTRACT.—Different insect trapping methods were compared weekly on recently burned and nearby unburned rangeland in the Great Basin of western Utah. Flight traps (or wing traps) collected the most specimens (total = 4,916 at burned site, 4,384 at unburned site) but represented the fewest species (no more than 11 spp./wk at either site); this method was not recommended because of difficulty in removing specimens from adhesive. Water traps amassed the next largest number of specimens ($\bar{x} \pm$ SE/wk = 150.9 ± 75.3 at burned site, 158.0 ± 66.4 at unburned site) and the most species ($\bar{x} \pm$ SE/wk = 21.6 ± 6.4 at burned site, 35.1 ± 4.5 at unburned site). The weekly collections from pitfall traps between the sites were significantly different ($P < .05$) in number of specimens ($\bar{x} \pm$ SE/wk = 8.1 ± 1.5 at burned site, 19.7 ± 4.8 at unburned site) and species ($\bar{x} \pm$ SE/wk = 4.7 ± 0.6 at burned site, 9.5 ± 2.0 at unburned site). Malaise traps were the most convenient. Black Malaise traps collected more specimens ($\bar{x} \pm$ SE/wk = 99.8 ± 19.4 at burned site, 90.6 ± 16.4 at unburned site) and species ($\bar{x} \pm$ SE/wk = 22.9 ± 3.9 at burned site, 19.4 ± 6.5 at unburned site) than white malaise traps (specimens: $\bar{x} \pm$ SE/wk = 72.1 ± 22.4 at burned site, 87.1 ± 31.2 at unburned site; species: $\bar{x} \pm$ SE/ wk = 19.7 ± 6.6 at burned site, 16.4 ± 5.4 at unburned site), although this difference was not significant.

Insect trapping methods vary in their ability to collect insects (Peterson 1953, Southwood 1978). Unfortunately, few studies have compared different insect collecting methods in the same habitat. Recently, Canaday (1987) evaluated differences in sampling insects with sweep nets and with window, sticky, light, suspended cone, and two kinds of yellow pan traps in a Douglas-fir forest in California. Likewise, Norment (1987) compared sticky board and pitfall traps with sweep netting in alpine tundra of the Beartooth Mountains in Wyoming.

Although range fires historically have been common on western rangeland in the United States (Gruell 1985), insects are not often sampled from burned areas. Arthropod responses to grassland fires have been generally examined with prescribed burns (Warren et al. 1987). Most collections (e.g., Nagel 1973, Evans 1984, Forde et al. 1984) used net-sweeping techniques, which implied that substantial post-burn vegetative cover remained.

However, net sweeping is not practical after a severe fire. To collect flying insects following a spring burn on a prairie in Missouri, Cancelado and Yonke (1970) used lightly colored Malaise traps. On recently burned rangeland in the Great Basin, Hansen (1986) used pitfall traps in addition to white Malaise traps.

Insect trapping in burned areas presents unique challenges. Naturally occurring range fires, such as those started by lightning, are unique, uncontrollable events. Insect sampling is difficult to study because the fires are unpredictable in time, location, land ownership, and size of burn. Intensely hot fires destroy the vegetative canopy, thus preventing traditional net sweeping. Burned areas are so severely disrupted that insects are collected during a period of transition and recovery. Changes in plant species composition and vegetative cover vary due to localized environmental factors. Finally, it is unknown whether Malaise traps become attractive because of their structural prominence or the contrast between the white fabric and the dark background.

The objectives of this study were to sample range insects immediately after a natural range fire, to compare previous collection techniques with other methods not traditionally used on burned rangeland, and to ascertain which trapping procedures are feasible under these field conditions.

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MATERIALS AND METHODS

The study area was on a hill ca 10 km north of Kelton in Box Elder Co., Utah. Dominant plant species were cheatgrass, *Bromus tectorum* L.; big sagebrush, *Artemisia tridentata* Nutt.; and Utah juniper, *Juniperus osteosperma* (Torr.) Little. In early July 1985 a fire started by lightning burned an irregularly defined area (5–12 km^2), including the northeastern portion of the hill, which served as the burned study site. A comparison study site was established in an unburned area on the same hill ca 1 km from the fire boundary and 2 km from the burn site. On July 11 the first traps were installed while the burned area was still smoldering.

Different trapping methods were used: (1) An earlier method (Hansen 1986) was repeated using a white Malaise trap made of cream-colored polyester marquisetta; the square trap had four central vanes and was topped with a clear acrylic collecting tube. (2) A similar Malaise trap sprayed black was located 25 m away. The Malaise traps were obtained from BioQuip Products[2] (Box 61, Santa Monica, CA 90406). (3) Evenly spaced in a line between the Malaise traps were 10 pitfall traps. Each trap, which resembled that described by Morrill (1975), was made of a 4-oz plastic collecting cup housed in a 16-oz plastic cup and topped with a 7-oz tapered plastic cup in which the bottom had been removed to serve as a funnel. (4) Placed on the ground in the same vicinity, a water trap was made from a yellow plastic bowl (21.5 w × 22.0 l × 10.0 h cm) and filled with water and antifreeze. (5) A flight trap was constructed from four 31 × 31–cm plywood squares arranged at right angles and mounted on a pole 113 cm above the ground; the traps were painted flat black and covered with insect trapping adhesive. (6) Nesting traps, comprised of 10 wooden blocks and 100 elderberry (*Sambucus* sp.) stems, were located at each site on 17 July. Every block contained a total of 50 holes; 10 holes of each size were of five diameters (2, 4, 6, 8, and 10 mm). Half of the stems had 3-mm-diameter holes in one end, while the remaining stems had 6-mm-diameter holes. The blocks were placed 50 m apart and the stems in the ground 3 m apart, both along SE transects. The traps were recovered in late September.

The same types of traps were arranged identically at the other site. From 17 July to 25 September weekly collections were made at both sites. Specimens were sorted to "species" by using the morphospecies classification technique (Janzen and Schoener 1968, Allan et al. 1975).

For each trapping procedure, weekly collection data between the sites were analyzed by using paired Student's t-test. Linear correlation tests (Zar 1974) were conducted between time of sampling and the collection data.

RESULTS AND DISCUSSION

NUMBER OF SPECIMENS.—An analysis of the data of all the traps indicated that more specimens were collected at the burned site ($n = 8,447$) than from the unburned area ($n = 7,602$), a tendency observed in an earlier study involving burned rangeland in the Great Basin (Hansen 1986). Perhaps flying insects in burned areas are attracted to the traps that may replace normal landmarks of the destroyed shrubs and other sheltering plants.

Among the trapping methods (Fig. 1), the flight traps collected the most specimens (burned site, $n = 4,916$; unburned site, $n = 4,384$). There were significant differences in weekly number of specimens only with the pitfall traps ($t = 2.715$, $df = 9$, $P < .05$). Pitfall traps from the unburned site consistently had more specimens than those from the burned site. No insects were found in the nest traps at either site.

Among weekly collections, the black Malaise trap obtained more specimens than the white Malaise trap at the burned site (black Malaise trap, $\bar{x} \pm SE = 99.8 \pm 19.4$; white Malaise trap, $\bar{x} \pm SE = 72.1 \pm 22.4$) and the unburned site (black Malaise trap, $\bar{x} \pm SE = 90.6 \pm 16.4$; white Malaise trap, $\bar{x} \pm SE = 87.1 \pm 31.2$). This occurred even though the white Malaise traps were more conspicuous and, presumably, more attractive to insects. Although differences were not significant, this trend suggested that the color of Malaise traps may affect insect collectability.

[2]Mention of trade names is for identification only and does not imply an endorsement to the exclusion of other products that may be suitable.

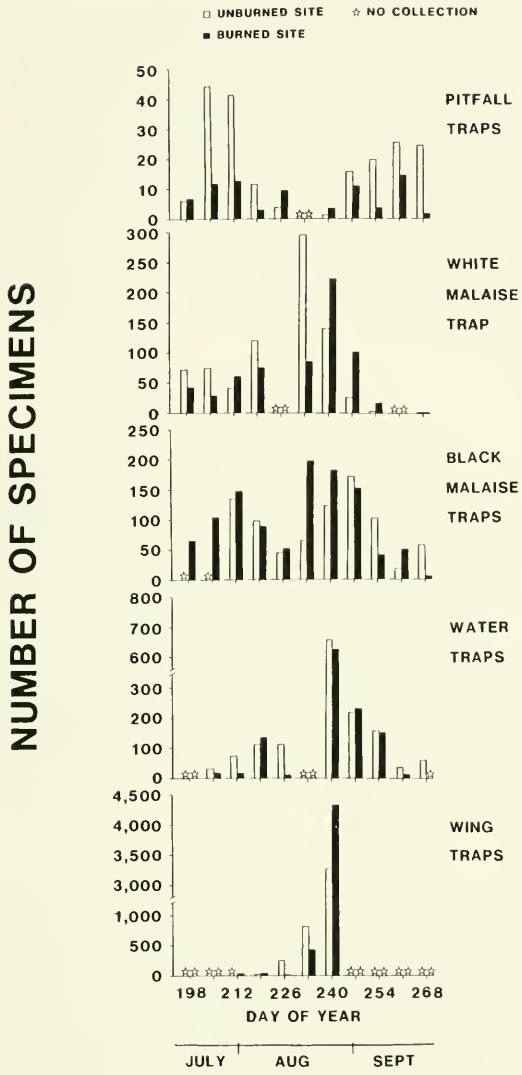

Fig. 1. Summary of weekly collections of specimens from 17 July to 25 September 1985, obtained from five trapping methods on burned and unburned study sites near Kelton, Utah.

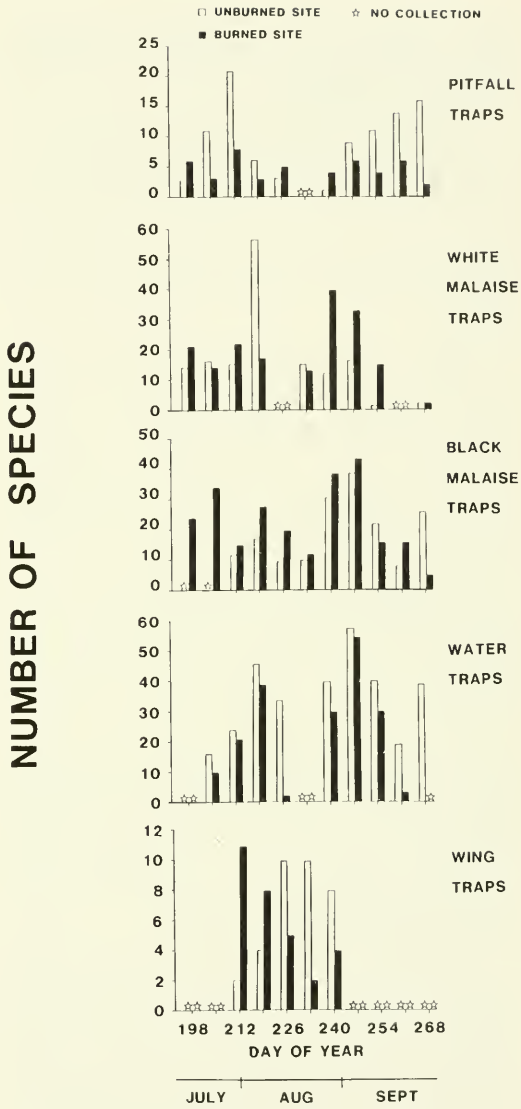

Fig. 2. Summary of weekly collections of species from 17 July to 25 September 1985, obtained from five trapping methods on burned and unburned study sites near Kelton, Utah.

No significant linear correlations with the number of specimens and time of collection were found for any of the trapping methods.

NUMBER OF SPECIES.—Diptera was the most dominant group obtained from all the traps. The flight traps had the fewest number of species of the different traps (Fig. 2). Water traps amassed the most species in the weekly collections (burned site, $\bar{x} \pm SE = 21.6 \pm 6.4$; unburned site $\bar{x} \pm SE = 35.1 \pm 4.5$), and paired Student's t-tests showed that this difference was significant ($t = 3.027$, $df = 7$, $P < .05$). The number of species caught per week by the pitfall traps was significantly different between the sites ($t = 2.428$, $df = 9$, $P < .05$), with consistently more species in the unburned area. More species were obtained each week by the black Malaise traps (burned site, $\bar{x} \pm SE = 22.9 \pm 3.6$; unburned site, $\bar{x} \pm SE = 19.4 \pm 6.5$) than by the white Malaise traps (burned site, $\bar{x} \pm SE = 19.7 \pm 6.6$; unburned site, $\bar{x} \pm SE = 16.4 \pm 5.4$),

although these differences were not significant. There were no significant correlations among trapping data, time of trapping, and collection methods.

OTHER COMPARISONS.—When trapping efficiency was estimated by the number of specimens collected divided by the number of species, there were no significant differences among the trapping methods except for the flight traps. Hence, other aspects must be considered when selecting trapping procedures.

Flight traps collected large numbers of a few species but required various solvents (e.g., kerosene, gasoline, hexane) to remove specimens from the adhesive. Once extracted, the specimens were often damaged, thus rendering them useless for identification. Also, the traps were unstable and were often blown over by high winds.

The pitfall traps in the burned site were often filled with ash and other debris, thus lowering their efficiency. This problem would have been solved by using covers over the traps.

The greatest diversity of species accumulated in the water traps, which were also easy to use. However, collections were strongly influenced by weather extremes. Flooding during intensive rains, evaporation under drought conditions, and animals drinking the water disturbed the specimens.

The Malaise traps were the most convenient of the traps tested but were unstable in wind. If the traps are too noticeable, they may attract vandals. Painting the fabric black helped conceal the traps and also seemed to increase their collecting efficiency. However, the use of different colors, patterns, and shapes should be further explored.

No bees or wasps nested in wood traps at either site. The time of placement may have been a factor since most shrubs and forbs bloom from April to early July at such sites. At the unburned site the only dominant plant to bloom after the nearby burn was rabbitbrush, *Chrysothamnus* sp. Apparently, xylophilous nesting Hymenoptera associated with this fall-blooming perennial were uncommon at those locations.

CONCLUSIONS

The selection of trapping method depends on the needs of the researcher. To easily collect ground-inhabiting insects, use pitfall traps; for flying insects, use Malaise traps. To survey for taxa diversity, use either Malaise traps or water traps. To obtain the largest number of specimens of flying insects, flight traps are recommended. To meet the replication requirements for statistical analysis, use smaller versions of water traps or, if the species are easily recognizable, flight traps. Pitfall traps provide much data but caution is advised in interpreting results (Southwood 1978).

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LITERATURE CITED

ALLAN, J. D., H. J. ALEXANDER, AND R. GREENBERG. 1975. Foliage arthropod communities of crop and fallow fields. Oecologia (Berl.) 22: 49–56.

CANADAY, C. L. 1987. Comparison of insect fauna captured in six different trap types in a Douglas-fir forest. Canadian Entomol. 119: 1101–1108.

CANCELADO, R., AND T. R. YONKE. 1970. Effect of prairie burning on insect populations. J. Kansas Entomol. Soc. 43: 274–281.

EVANS, E. W. 1984. Fire as a natural disturbance to grasshopper assemblages of tallgrass prairie. Oikos 43: 9–16.

FORDE, J. D., N. F. SLOAN, AND D. A. SHOWN. 1984. Grassland habitat management using prescribed burning in Wind Cave National Park, South Dakota. Prairie Nat. 16: 97–110.

GRUELL, G. E. 1985. Fire on the early western landscape: an annotated record of wildland fires 1776–1900. Northw. Sci. 59: 97–107.

HANSEN, J. D. 1986. Comparison of insects from burned and unburned areas after a range fire. Great Basin Nat. 46: 721–727.

JANZEN, D. H., AND T. W. SCHOENER. 1968. Differences in insect abundance and diversity between wetter and drier sites during a tropical dry season. Ecology 49: 96–110.

MORRILL, W. L. 1975. Plastic pitfall trap. Environ. Entomol. 4: 596.

NAGEL, H. G. 1973. Effect of spring prairie burning on herbivorous and non-herbivorous arthropod populations. J. Kansas Entomol. Soc. 46: 485–496.

NORMENT, C. J. 1987. A comparison of three methods for measuring arthropod abundance in tundra habitats and its implications in avian ecology. Northw. Sci. 61: 191–197.

PETERSON, A 1953. A manual of entomological techniques. W. Edwards, Publ., Inc., Ann Arbor, Michigan. 367 pp.

SOUTHWOOD, T. R. E. 1978. Ecological methods. Chapman and Hall, New York. 524 pp.

WARREN, S. D., C. J. SCIFRES, AND P. D. TEEL. 1987. Response of grassland arthropods to burning: a review. Agric. Ecosys. Environ. 19: 105–130.

ZAR, J. 1974. Biostatistical analysis. Prentice-Hall, Inc., Englewood Cliffs, N. J. 620 pp.

STUDIES OF A UNIPARENTAL FORM OF *APHYTIS VANDENBOSCHI* (HYMENOPTERA: APHELINIDAE), A PARASITE OF THE SAN JOSE SCALE IN NORTHERN UTAH[1]

Manas Titayavan[2,3] and Donald W. Davis[2]

ABSTRACT.—The only San Jose scale parasite found at two sites in northern Utah was a uniparental form of *Aphytis vandenboschi* DeBach & Rosen. Parasites overwintered as pupae and were attracted to San Jose scale pheromone traps. Mature female scales were most heavily parasitized, although some prepupal males and instar II female scales were attacked. Only partial development occurred between 11.7 and 18.3 C, and fecundity was reduced between 28 and 31 C. Based on 11.7 C, 460 degree days were required in the field and 410 degree days at 26 C in the laboratory per generation. By the end of the season during 1981 at Brigham City, 30.9% of the adult scales on twigs and 79.2% on leaves were parasitized. During 1982, parasitism was 21.1% on twigs and 70.9% on leaves. A mite, *Pyemotes herfsi* (Oudemans), was a major predator of *Aphytis* in both laboratory cultures and field populations.

Field studies of the San Jose scale and its natural enemies were conducted at Brigham City and Hyde Park (near Logan), Utah, during 1981 and 1982. Laboratory studies were done at Utah State University, Logan.

The more common San Jose scale parasites, such as *Prospatella* (=*Encarsia*) *perniciosi* Tower (DeBach 1964) and *Aphytis aonidiae* (Mercet) (Gulmahamad and DeBach 1978), were not encountered. Only one species of parasite occurred. Specimens for identification were sent to the University of California, Riverside, where they were examined by Paul DeBach, David Rosen, and Mike Rose. The initial identification given was *Aphytis* nr. *vandenboschi* (Hymenoptera: Aphelinidae), but they stated that it was probably a new species. Later correspondence indicated an inability to compare the material to specimens from the type location of *A. vandenboschi;* therefore, the best taxonomic designation was as uniparental forms of *A. vandenboschi.*

METHODS

Both San Jose scales and *Aphytis* parasites were reared using banana squash (DeBach and White 1960) at 26.7 ± 1.5 C, 47 ± 3% RH, and using a 16-hr light: 8-hr dark cycle. The scale culture was on the squash. Adult *Aphytis* were caged with the scale-infested squash. Life history studies were conducted in growth chambers at selected temperatures between 10 and 31 C. Photoperiods and relative humidities were not manipulated. All studies were replicated, although the number of replicates varied with the different experiments. Honey was supplied as adult food during all laboratory work with *Aphytis* adults. Experiments extending over the life span of the adult parasites began less than 12 hr after eclosion. Short-term studies were started when parasites were 2 ± .5 days old so that comparative data could be obtained near the peak oviposition period.

The field studies involved time-series sampling on apple trees. This information was then correlated with temperature records within the orchards and with results of pheromone trapping. Both adult parasites and San Jose scale males were collected readily on pheromone traps (Pherocon® San Jose scale traps, Zoecon Corp.). The Brigham City orchard was an unsprayed, but cared for, backyard area of mixed fruit types. The Hyde Park orchard was an old, abandoned apple orchard of about four acres.

Part of the information for life tables was obtained by lifting scales to observe the *Aphytis* eggs and larvae. The substrate next to the scales was marked to identify scales for sequential observations.

The population curves, shown in several figures, used third-order polynomials.

[1]This research was part of the Ph.D. requirements at Utah State University, Logan, Utah.
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TABLE 1. Field parasitism of San Jose scales on apple trees by *Aphytis vandenboschi* at Brigham City, Utah.

Dates	Percentage of scales on twigs that were adult females		Percentage of parasitized adult female scales on twigs	
	1981	1982	1981	1982
23–30 April	7.5	—	0	—
21–30 May	17.7	2.9	4.3	0
20–29 June	36.2	18.1	13.1	5.4
2–11 August	87.5	88.4	8.8	3.3
20–29 August	80.3	81.3	17.9	4.0
15–25 September	12.7	15.4	30.9	21.2
	Percentage of adult females on leaves[1]		Percentage parasitized on leaves	
15–25 September	100.00	100.0	79.2	70.9

[1]Scales on leaves did not mature before September.

RESULTS

Of several thousand adult parasites collected or reared, all were females. Eggs were deposited on the surface of the scale body, under the scale cover, and then the larvae developed as ectoparasites. Adult *Aphytis* appeared to be weak fliers but walked actively. When disturbed, they flew short distances only. When undisturbed, they flew infrequently.

Parasite eggs were yellowish white, ovate with a short stalk projecting from the narrower end of the egg. Newly hatched instars I lacked obvious segmentation and had minute, spinelike mandibles. Instars II and III had visible segmentation and showed reddish brown food in the gut. Prepupae had distinctly pointed cauda and were always accompanied by 12–17 dark fecal pellets or meconia. Each parasite larva completely consumed a host scale. Pupae were initially whitish, then darkened gradually until they were nearly black. Adult *Aphytis* emerged by cutting a hole through the scale cover.

More San Jose scales and parasites occurred at Brigham City than at Hyde Park. This difference was due partially to the fact that the Hyde Park orchard was unmanaged and dusty, but primarily because it was warmer in Brigham City. By 30 September 1981, Brigham City had accumulated 1,533 degree days above 11.7 C, while Hyde Park had only 1,082. Three *Aphytis* generations occurred at Brigham City during 1981, but only two at Hyde Park. The 1982 season was cooler than 1981, resulting in only a partial third generation at Brigham City. By the end of the growing season, during both years and at both locations, *Aphytis* were present in all stages. At the beginning of the following seasons only pupae were found, strongly indicating that parasites overwintered in northern Utah only as pupae.

San Jose scales were examined sequentially for maturity and percent parasitism. The results from Brigham City are summarized in Table 1. A similar pattern occurred at Hyde Park, but populations were lower. As the seasons progressed, parasitism of scales on the twigs increased. By the end of the 1981 season 30.9% of the adult females on twigs were parasitized, while in 1982 the percentage was 21.2. Scales on leaves were more heavily parasitized, but mature scales were not present before September.

A predatory mite, *Pyemotes herfsi* (Oudemans), fed on San Jose scales and immature *Aphytis* at both Brigham City and Hyde Park. These mites showed a distinct preference for the parasites in the laboratory studies and became a major factor in parasite mortality. The mites fed on both parasite larvae and pupae, but the destruction of pupae had more impact on the parasites (Table 2). During 1982 these mites were accidentally introduced into laboratory cultures and nearly destroyed parasite cultures if allowed to multiply. The mites fed gregariously under the scales, but detailed biological data were not obtained.

At Brigham City we marked 240 adult female San Jose scales containing *Aphytis* eggs. A partial life table (Table 2) was prepared. Note the important role of *P. herfsi*. During these field studies the effects of other predators were clearly visible, but the identity of the predator was not always apparent.

TABLE 2. Partial field life table for *Aphytis vandenboschi* at the Brigham City apple orchard, July through August 1982.

Stage of development	Cause of mortality	Survivors based on 1,000	k value
Eggs (n = 240)			
	Desiccation[1]	654.17	$0.18 = k_1$
	Misc. predators[2]	587.50	$0.05 = k_2$
Larvae			
	Desiccation[1]	391.67	$0.18 = k_3$
	Pyemotes herfsi	333.33	$0.07 = k_4$
	Misc. predators[2]	291.67	$0.05 = k_5$
Pupae			
	Pyemotes herfsi	33.33	$0.95 = k_6$
	Desiccation[1]	20.83	$0.20 = k_7$
Adults (n = 5)			
			K = 1.63

[1]Desiccation by heat, wind, and low relative humidity. Lifting San Jose scales to examine for parasitism apparently increased desiccation.
[2]Thrips were common at the parasite egg stage, while coccinellid adults tended to become important later. European earwigs were involved but, being nocturnal, were difficult to observe.

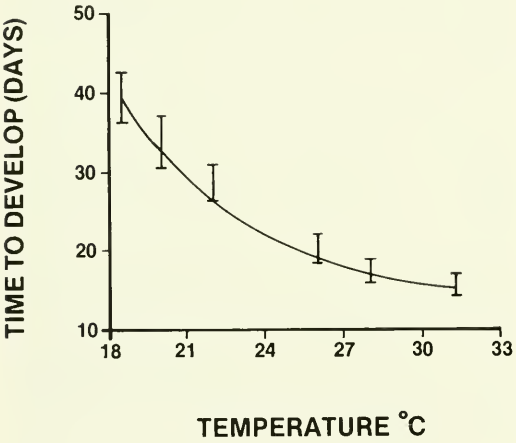

Fig. 1. Duration of development from egg to adult for *Aphytis vandenboschi* at six constant temperatures. The vertical lines show the standard error of the mean.

Unidentified thrips were often associated with dead *Aphytis* eggs. Adult coccinellids commonly fed on both parasitized and nonparasitized scales. European earwigs consumed the entire scale, including the cover, leaving little evidence of the scales having been present.

The time required for *Aphytis* to complete development in the laboratory is shown in Figure 1 and Table 3. At 10 C a few eggs were laid, but no embryonic development was detected. At 12.8 and 15.6 C there was egg hatch and some larval development. The lowest temperature showing any development was 11.7 C. The lowest temperature having complete parasite development was 18.3 C, where the cycle required an average of 38.6 days. A precise upper threshold was not determined, but 31 C was clearly above the optimum. Total eggs laid and adult longevity (Table 4) declined between 28 and 31 C. Maximum fecundity was calculated at about 26 C. The curve illustrated in Figure 1 shows the developmental rates obtained in laboratory experiments. At 31 C an average of 16.2 days was required for the full developmental cycle. Adult longevity was extremely short at higher temperatures (Table 4).

The parasite had three larval instars. Measurements and time spent in each stage are shown in Table 5. These data are similar to data obtained in other studies of the genus *Aphytis* (DeBach et al. 1978, Rosen and Eliraz 1978).

Aphytis vandenboschi showed a strong preference for adult female San Jose scales (Table 6) but apparently did not distinguish between gravid and nongravid hosts. A few prepupal males and instar II females were parasitized in the laboratory, but parasite development was incomplete. No instar I nymphs, instar II males, or pupal males were parasitized.

The oviposition pattern at 23.8 C is shown in Figure 2. Oviposition peaked on day 2 with a subsequent rapid decline on days 4 and 5. At higher temperatures the decline following day 2 was even more rapid. At 25.6 C little oviposition took place on day 5 and none on day 6.

Figures 2 and 3 are similar, demonstrating consistency of searching ability. The percentage of scales parasitized daily (Fig. 3),

TABLE 3. Progeny produced by 100 *Aphytis vandenboschi* when placed with ca 6,400 adult female San Jose scales for 24 hr, and the developmental time from egg to adult.[1]

Temperature (C)	Adults developing (Mean ± S.E.)	Days to develop (Mean ± S.E.)
10.0	0	eggs laid, no hatch
12.8	0	hatch, no maturity
15.6	0	hatch, no maturity
18.3	2.5 ± 0.9	38.6 ± 3.5
20.0	9.8 ± 1.1	33.2 ± 2.5
22.0	22.3 ± 5.2	27.6 ± 1.3
26.0	60.3 ± 4.7	19.9 ± 1.1
28.0	71.0 ± 4.6	17.0 ± 1.0
31.0	52.0 ± 11.0	16.2 ± 0.4

[1]Replicated four times.

TABLE 4. Comparative longevity of adult *Aphytis vandenboschi* under various constant temperatures at 47% RH and 16-hr photophase.

Temperature (C)	Adult longevity in days[1]	
	Mean ± S.E.[2]	Range
10	45.65 ± 2.98 a	32.33–52.87
20	17.62 ± 2.70 b	14.25–25.80
23	10.35 ± 2.10 c	6.60–17.85
28	3.57 ± 0.70 d	1.00– 6.20
31	1.35 ± 0.10 d	0.90– 1.60

[1]Six replicates of 10 adult females at each temperature. Adults were fed honey.
[2]Data were analyzed by analysis of variance and Duncan's multiple range. Treatment means followed by the same letter are not significantly different (5%).

TABLE 5. Developmental time and measurements of *Aphytis vandenboschi* immature stages, reared at 26.7C, 47% RH, and 16-hr photophase.

Stage	Length[1] (mm)	Width[1] (mm)	Developmental time[1] (days)
Egg	0.18 ± 0.05	0.07 ± 0.01	3.17 ± 0.01
Instar I	0.19 ± 0.05	0.08 ± 0.01	2.35 ± 0.03
Instar II	0.25 ± 0.02	0.21 ± 0.02	2.19 ± 0.02
Instar III	0.75 ± 0.07	0.57 ± 0.07	3.32 ± 0.03
Pupa	0.86 ± 0.08	0.40 ± 0.06	6.38 ± 0.03

[1]Means and S.E. of 40 individuals selected at random in each stage.

TABLE 6. Percent parasitism of the various San Jose scale stages when exposed separately to five *Aphytis vandenboschi* for 24 hr at 23.8C.

Stages	Number of replicates	Percent parasitism (Mean ± S.E.)
Instar I (both sexes)	70	0
Instar II males	60	0
Prepupal males	70	4.78 ± 1.45[1]
Pupal males	60	0
Instar II females	60	6.03 ± 1.37[1]
Adult females (nongravid)	60	35.25 ± 2.17
Adult females (gravid)	60	34.64 ± 1.92

[1]The parasites did not mature.

according to parasite age, reflects eggs deposited per parasite (Fig. 2). On day 2, 15 *Aphytis* parasitized 51% of the available 105 female scales. The number and percentage of scales receiving more than one parasite egg were determined. As many as four eggs were found on one scale. Superparasitism was high on days 2 and 3 (Fig. 4). On day 2, out of 105 female San Jose scales per replicate, an average of 35 contained single eggs, while 22 had more than one egg. Under laboratory conditions the *Aphytis* adults seemed unable to recognize previously parasitized scales. In both laboratory and field work whenever the ratio of parasites to hosts was high, superparasitism was high. However, in no instance did more than one parasite per host complete its development. It was not determined whether the presence of parasite larvae deterred additional oviposition.

Experiments using low numbers of host scales with varying numbers of parasites showed that both searching efficiency and numbers of scales parasitized by each *Aphytis* decreased as the number of parasites increased (Table 7). The searching efficiency was calculated according to Varley et al. (1973). Superparasitism was not determined in this experiment.

Various numbers of scales were exposed to 24 parasites for 24-hr intervals (Fig. 5). The numbers of scales above 1,000 per replicate were estimated. When 117 scales were present, parasitism was 58.1% or 2.83 parasitized scales per *Aphytis*. When 2,125 scales were present, the parasitism was 4.5% or 2.98 per parasite. The tendency for the numbers of scales attacked per parasite to increase as the

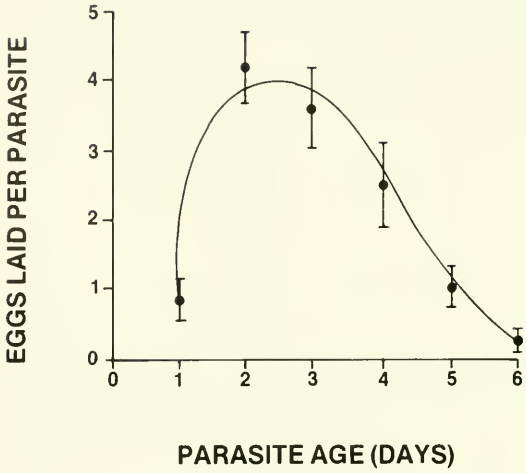

Fig. 2. Influence of *Aphytis vandenboschi* age on number of eggs laid per female at 23.8 C. Vertical lines show the standard error of the mean.

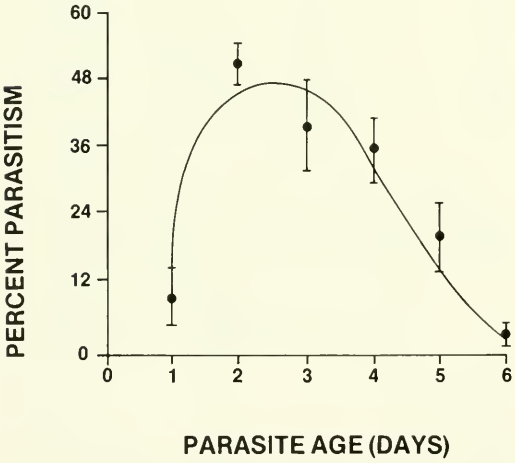

Fig. 3. Influence of *Aphytis vandenboschi* age on percent parasitism at 23.8 C using 15 parasites to a fresh supply of ca 105 female scales daily. Vertical lines show the standard error of the mean.

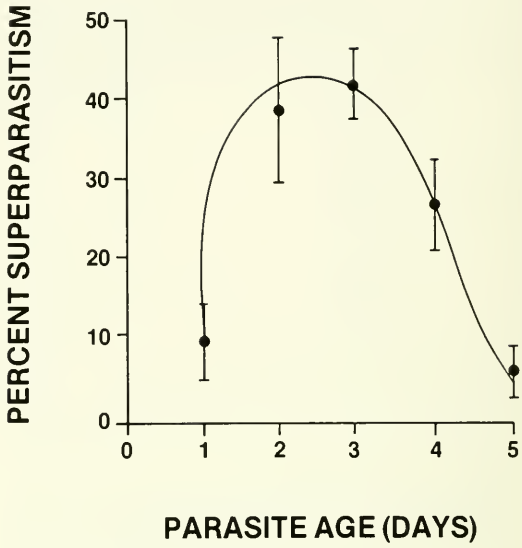

Fig. 4. Influence of *Aphytis vandenboschi* age on percent of parasitized scales that were superparasitized at 23.8 C using 15 parasites to ca 105 scales with a fresh supply daily. Vertical lines show the standard error of the mean.

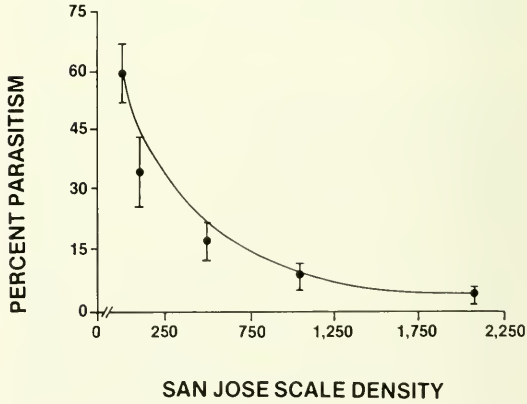

Fig. 5. Relationship between adult female San Jose scale density and percent parasitism by 24 *Aphytis vandenboschi* with 24-hr exposures at 23.8 C. Vertical lines indicate the standard error of the mean.

numbers of scales increased was due in part to reduced superparasitism.

DISCUSSION AND SUMMARY

At two orchard sites in northern Utah a uniparental form of *Aphytis vandenboschi* was the only San Jose scale parasite present. It was an ectoparasite primarily of adult female scales but occasionally of prepupal males and instar II females. In the laboratory *Aphytis* completed development in the adult females only. A mite, *Pyemotes herfsi*, was an important predator of *Aphytis* in both laboratory and field populations. The mite also attacked the scales but preferred parasite larvae.

Winter parasite survival was as pupae. By the end of the 1981 season 30% of the adult female scales on twigs at Brigham City were parasitized and 21.2% were parasitized during 1982. Scales on the foliage were more

TABLE 7. Number and percent of female San Jose scales parasitized by varied numbers of *Aphytis vandenboschi*, and their searching efficiency, in six hours at 23.8C.[1]

Number of parasites	Parasitism rate per *Aphytis* (Mean ± S.E.)[2]	Percent parasitism (Mean ± S.E.)[2]	Searching efficiency
3	3.67 ± 0.31 a	22.00 ± 1.83 a	0.0831 a
6	3.04 ± 0.14 b	36.50 ± 1.71 b	0.0756 b
9	2.70 ± 0.14 b	48.50 ± 2.50 c	0.0760 b
12	1.94 ± 0.09 c	46.50 ± 2.22 c	0.0523 c
15	1.98 ± 0.13 c	59.50 ± 3.86 d	0.0597 c

[1]Four replicates of 50 scales each.
[2]Data were analyzed by analysis of variance and Duncan's multiple range. Means followed by the same letter are not significantly different (5%).

heavily parasitized and averaged about 75% during September 1981.

The parasites in the laboratory showed partial development starting at 11.7 C, but complete life cycles were not observed below 18.3 C. The upper developmental threshold was not determined, but fecundity was reduced starting near 28 C. Using 11.7 C as the lower threshold, field data indicated an average of about 460 degree days per generation. Under laboratory conditions, at constant temperatures, a full life cycle including a preoviposition period required an average of 410 degree days.

There are no records of *A. vandenboschi* being introduced into Utah. The introductions of this species have been reported as biparental; the adults have weak flight habits, the adult longevity is short, and rather few eggs are laid when reared on San Jose scales. This raises several questions: Why was this parasite of San Jose scales present while the more commonly encountered species were not? Is *A. vandenboschi*, an introduced species, the correct identity of the Utah form? Could the parasite actually be native to the region on some other scale species and then became adapted to San Jose scales?

While *A. vandenboschi* were clearly significant biological control agents of the San Jose scale in northern Utah, they failed to achieve the level of control needed. The San Jose scale is still a major pest of Utah orchards, commonly requiring insecticidal control.

ACKNOWLEDGMENTS

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LITERATURE CITED

DEBACH, P. 1964. Biological control of insect pests and weeds. Reinhold Publ. Co., New York. 844 pp.

DEBACH, P., M. ROSE, AND D. ROSEN. 1978. Biological and systematic studies of developmental stages in *Aphytis* (Hymenoptera: Aphelinidae). III. Meconia as a possible systematic tool in *Aphytis*. Hilgardia 46(3): 96–101.

DEBACH, P., AND E. B. WHITE. 1960. Commercial mass culture of the California red scale parasite, *Aphytis lingnanensis*. University of California Agric. Expt. Sta. Bull. 770. 58 pp.

GULMAHAMAD, H., AND P. DEBACH. 1978. Biological studies on *Aphytis aonidiae* (Mercet) (Hymenoptera: Aphelinidae), an important parasite of the San Jose scale. Hilgardia 46(7): 239–255.

ROSEN, D., AND A. ELIRAZ. 1978. Biological and systematic studies of the developmental stages in *Aphytis* (Hymenoptera: Aphelinidae). I. Developmental history of *Aphytis chilensis* Howard. Hilgardia 46(3): 77–95.

VARLEY, C. G., G. R. GRADWELL, AND M. P. HASSELL. 1973. Insect population ecology, an analytical approach. University of California Press, Berkeley. 212 pp.

CHECKLIST OF THE MOSSES OF THE INTERMOUNTAIN WEST, USA

John R. Spence[1]

ABSTRACT.—A revised list of the mosses of the Intermountain West, including all of Utah and Nevada and parts of surrounding states, is presented. Recorded are 342 species in 122 genera and 39 families in this region. Nomenclatural and taxonomic changes as well as floristic additions since the publication of Seville Flowers's book are included.

In a recent survey of the floristic literature of North America, Schofield and Miller (1982) indicated the following regions as being the least known bryologically: the Southwest, Rocky Mountains, Great Plains, and Arctic and boreal North America. Although not specifically indicated, the Intermountain Region of the western United States, consisting primarily of Utah and Nevada, is part of both the Southwest and the Rocky Mountain regions.

This paper begins a series on the bryophyte flora of the Intermountain West (sensu Cronquist et al. 1972), which includes the states of Utah and Nevada as well as portions of Oregon, Idaho, Wyoming, and Arizona. The boundaries are similar to those used in the Intermountain Flora Project (Cronquist et al. 1972 and subsequent volumes) and largely for the same reasons. The main difference is that I have included all of Nevada and the Colorado Plateau portion of northern Arizona (Fig. 1). This region is almost identical to the Great Basin Province of Gleason and Cronquist (1964). Western Colorado is floristically similar to eastern Utah (Weber 1973), with the floristic change to the southern Rocky Mountains almost impossible to delimit. Hence an indefinite fringe of eastern Colorado and adjacent New Mexico is included.

The Intermountain West is highly diverse in landforms, geology, climate, and vegetation. In the south is found the hot and arid Mojave Desert, while northward stretch semiarid shrub steppe, pygmy conifer woodlands, montane forests, and alpine tundra. Four natural physiographic provinces comprise the Intermountain West: Snake River Plain, Great Basin, Colorado Plateau, and Wasatch Plateau. Recent work on the vascular flora provides support for the integrity of this region (McLaughlin 1986). Two small, disparate elements are included: Uinta Mountains and a small portion of the Mojave Desert in southwestern Utah and southern Nevada. The inclusion of the Mojave Desert portions of Utah and Nevada provides essentially complete floras for these states, and adds only a few Mojavean taxa, e.g., *Entostodon bolanderi*, *Jaffueliobryum wrightii*, *Pleurochaete squarrosa*, and *Splachnobryum obtusum*.

The bryophyte flora of the region has been summarized by Lawton (1958, 1971), Clark (1957), Haring (1961), and Flowers (1961, 1973). A wide variety of shorter reports (see below) also exists, while Behle (1984) lists Flowers's many papers. As yet no attempt has been made to compile a bryophyte flora for the Intermountain West, as is being done for the vascular plants (Cronquist et al. 1972 and subsequent volumes).

Although state checklists that include portions of the Intermountain West (e.g., McCleary and Green 1971) exist, this paper is the first to bring together information on the mosses of the entire area as a checklist. Future work will include the hepatics. The main aims of this paper are to provide a list and to update classification and nomenclature of species. Major sources for the list include: Utah (Flowers 1973), Nevada (Lawton 1958, 1971, Lavin 1981, 1982), and Arizona (Haring 1961, Johnson and Vitt 1971, Vitt et al. 1971). Included in these papers are many additional references. Many additional species probably remain to be discovered, especially in the Pottiaceae (cf. Spence 1987). Some areas, especially southeastern Oregon, the Colorado

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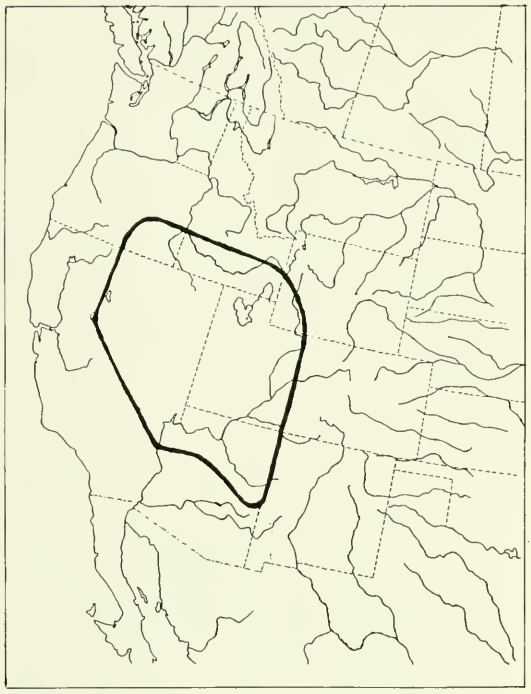

Fig. 1. The approximate boundaries of the study area are outlined in black. Included are all of Utah and Nevada, northern Arizona to the Mogollon Rim, and parts of Oregon, Idaho, and Wyoming.

Plateau, and the Uinta Mountains, are still poorly known.

Recent monographs have drastically changed the taxonomy and nomenclature of many groups. I have followed the opinions of workers who have specialized in particular groups: *Aloina* (Delgadillo 1975), *Amblystegium* (Crum and Anderson 1981), *Barbula* (Zander 1979), *Bryum* (Spence 1988), *Crossidium* (Delgadillo 1975), *Dicranum* (Peterson 1979), *Didymodon* (Zander 1978), *Encalypta* (Horton 1983), *Hygrohypnum* (Jamieson 1976), *Leskeella* and *Pseudoleskeella* (Lewinsky 1974), *Orthodicranum* (Peterson 1979), *Orthotrichum* (Vitt 1973), *Pohlia* (Shaw 1982), *Pseudocrossidium* (Zander 1979), *Schistidium* (Bremer 1980a, 1980b, 1981), and *Weissia* (Stoneburner 1985).

At the family level I have used the classification of Vitt (1984) and Buck and Vitt (1986), except for the Leskeaceae and Thuidiaceae, where I have used the traditional generic concepts (Spence unpublished manuscript). For other families the following are used: Ambystegiaceae in part (Kanda 1975, 1976), Grimmiaceae (Churchill 1981), Mniaceae (Koponen 1968, 1973), Polytrichaceae (Smith 1971), Plagiotheciaceae (Buck and Ireland 1985), and Scouleriaceae (Churchill 1985).

Genera are arranged alphabetically, with family position given in parentheses. Taxonomic categories below the rank of species are not listed. The bibliographic sources are designated by numbers after each name. For some species of *Bryum*, specimens from UBC are used for documentation. More details on *Bryum* can be found in Spence (1988).

Abietinella C. Muell. (Thuidiaceae)
  A. *abietina* (Hedw.) Fleisch., 15, 17.
Aloina Kindb. (Pottiaceae)
  A. *bifrons* (De Not.) Delg., 13, 15.
Amblystegium B.S.G. (Amblystegiaceae)
  A. *fluviatile* (Hedw.) B.S.G., 15, 17.
  A. *riparium* (Hedw.) B.S.G., 15, 17.
  A. *serpens* (Hedw.) B.S.G., 15, 17, 29.
  A. *tenax* (Hedw.) C. Jens., 15, 17, 29.
  A. *trichopodium* (Schultz) Hartm. (Corley et al. 1981 suggest that the correct name is A. *humile*), 15, 17, 29.
  A. *varium* (Hedw.) Lindb., 15, 17.
Amphidium Schimp. (Rhabdoweisiaceae)
  A. *lapponicum* (Hedw.) Schimp., 15, 29.
Anacolia Schimp. (Bartramiaceae)
  A. *menziesii* (Turn.) Par., 15, 27.
Andreaea Hedw. (Andreaeaceae)
  A. *rupestris* Hedw., 17.
Anomodon Hook. & Tayl. (Anomodontaceae)
  A. *attenuatus* (Hedw.) Hueb., 17.
  A. *rostratus* (Hedw.) Schimp., 17.
Antitrichia Brid. (Leucodontaceae)
  A. *californica* Sull. ex Lesq., 29.
Atrichum P. Beauv. (Polytrichaceae)
  A. *selwynii* Aust., 15.
  A. *undulatum* (Hedw.) P. Beauv., 17.
Aulacomnium Schwaegr. (Aulacomniaceae)
  A. *androgynum* (Hedw.) Schwaegr., 15, 29.
  A. *palustre* (Hedw.) Schwaegr., 15, 17, 29.
Barbula Hedw. (Pottiaceae)
  B. *convoluta* Hedw., 15.
  B. *ehrenbergii* (Lor.) Fleisch., 15, 17.
  B. *eustegia* Card. & Ther., 15.
  B. *indica* (Hook.) Spreng., 15, 49.
  B. *unguiculata* Hedw., 15, 17.
Bartramia Hedw. (Bartramiaceae)
  B. *ithyphylla* Brid., 15, 27.
Brachythecium B.S.G. (Brachytheciaceae)
  B. *acuminatum* (Hedw.) Aust., 17.
  B. *albicans* (Hedw.) B.S.G., 15.
  B. *asperrimum* (Mitt.) Sull., 15, 17.
  B. *campestre* (C. Muell.) B.S.G., 15.
  B. *collinum* (Schleich. ex C. Muell.) B.S.G., 15, 17, 29.
  B. *delicatulum* Flow., 15.
  B. *digastrum* C. Muell. & Kindb. ex Macoun & Kindb., 15.
  B. *erythrorrhizon* B.S.G., 15, 17.
  B. *fendleri* (Sull.) Jaeg. & Sauerb., 15, 29.

B. frigidum (C. Muell.) Besch., 15, 17, 29.
B. leibergii Grout, 29.
B. nelsonii Grout, 15, 17, 29.
B. oxycladon (Brid.) Jaeg. & Sauerb., 15.
B. plumosum (Hedw.) B.S.G., 17.
B. rivulare B.S.G., 15, 17, 29.
B. rutabulum (Hedw.) B.S.G., 29.
B. salebrosum (Web. & Mohr) B.S.G., 15, 17.
B. starkei (Brid.) B.S.G., 15.
B. velutinum (Hedw.) B.S.G., 17.
Bryoerythrophyllum Chen (Pottiaceae)
B. recurvirostrum (Hedw.) Chen, 15, 17, 29.
Bryohaplocladium Wats. & Iwat. (Thuidiaceae)
B. microphyllum (Hedw.) Wats. & Iwat., 17.
Bryoxiphium Mitt. (Bryoxiphiaceae)
B. norvegicum (Brid.) Mitt., 35.
Bryum Hedw. (Bryaceae)
B. algovicum Sendtn. ex C. Muell., 15, 29.
B. amblyodon C. Muell., 15, 29.
B. arcticum (R. Brown) B.S.G., 15.
B. argenteum Hedw., 15, 17, 29.
B. caespiticium Hedw., 15, 17, 29.
B. capillare Hedw., 15, 17, 29.
B. cyclophyllum (Schwaegr.) B. & S., 15, 17.
B. dichotomum Dicks., 15.
B. flaccidum Brid., 41, UBC!
B. gemmiparum De Not., 15, 17.
B. lanatum P. Beauv., 41, UBC!
B. lisae De Not., 15, 17.
B. miniatum Lesq., 15.
B. muhlenbeckii B.S.G., 17, 29.
B. pallescens Schleich. ex Schwaegr., 15, 17.
B. pallens Sw., 15, 17, 29.
B. pseudotriquetrum (Hedw.) Gaertn., Meyer & Scherb., 15, 17, 29.
B. stirtonii Schimp., 41, UBC!
B. torquescens B. & S., 41, UBC!
B. turbinatum (Hedw.) Turn., 15, 17, 29.
B. uliginosum (Brid.) B. & S., 15.
B. weigelii Spreng., 15, 17.
Callicladium Crum (Sematophyllaceae)
C. haldanianum (Grev.) Crum, 15.
Calliergon (Sull.) Kindb. (Amblystegiaceae)
C. cordifolium (Hedw.) Kindb., 15.
C. stramineum (Brid.) Kindb., 15.
Campyliadelphus (Kindb.) Chopra (Amblystegiaceae)
C. chrysophyllus (Brid.) Kanda, 15, 17.
C. polygamus (B.S.G.) Kanda, 15.
C. stellatus (Hedw.) Kanda, 15, 27.
Campylium (Sull.) Mitt. (Amblystegiaceae)
C. hispidulum (Brid.) Mitt., 15.
Ceratodon Brid. (Ditrichaceae)
C. conicus (Hampe) Lindb., 15.
C. purpureus (Hedw.) Brid., 15, 17, 29.
C. stenocarpus B.S.G., 17.
Claopodium (Lesq. & James) Ren. & Card. (Thuidiaceae)
C. whippleanum (Sull.) Ren. & Card., 17.
Climacium Web. & Mohr (Climaceaceae)
C. americanum Brid., 17.
C. dendroides (Hedw.) Web. & Mohr, 15, 17.
Conardia Robins. (Brachytheciaceae)
C. compacta (C. Muell.) Robins., 15, 17, 29.
Coscinodon Spreng. (Grimmiaceae)
C. calyptratus (Hook.) C. Jens., 15, 17.
Cratoneuron (Sull.) Spruce (Amblystegiaceae)
C. commutatum (Hedw.) Roth, 15, 29.
C. decipiens (De Not.) Loeske, 15.
C. filicinum (Hedw.) Spruce, 15, 17, 29.
Crossidium Jur. (Pottiaceae)
C. aberrans Holz. & Bartr., 13, 15, 17, 27.
C. crassinerve (De Not.) Jur., 13, 15, 17.
C. squamiferum (Vir.) Jur., 13, 15.
Crumia Schof. (Pottiaceae)
C. latifolia (Kindb.) Schof., 15, 29.
Desmatodon Brid. (Pottiaceae)
D. cernuus (Hueb.) B. & S., 15, 17, 29.
D. convolutus (Brid.) Grout, 15, 17.
D. glacialis Funck ex Brid., 15, 29.
D. latifolius (Hedw.) Brid., 15, 29.
D. laureri (K.F. Schultz) B. & S., 15.
D. obtusifolius (Schwaegr.) Schimp., 15, 17.
D. plinthobius Sull. & Lesq. ex Sull., 15.
Dichelyma Myr. (Fontinalaceae)
D. falcatum (Hedw.) Myr., 15.
Dichodontium Schimp. (Dicranaceae)
D. pellucidum (Hedw.) Schimp., 15.
Dicranella (C. Muell.) Schimp. (Dicranaceae)
D. schreberiana (Hedw.) Dix., 15.
Dicranodontium B.S.G. (Dicranaceae)
D. denudatum (Britt.) Britt., 17.
Dicranoweisia Lindb. ex Milde (Dicranaceae)
D. cirrhata (Hedw.) Lindb. ex Milde, 17.
D. crispula (Hedw.) Lindb. ex Milde, 15, 17, 29.
Dicranum Hedw. (Dicranaceae)
D. muehlenbeckii B.S.G., 17, 34.
D. rhabdocarpum Sull., 17, 34.
D. scoparium Hedw., 15, 17.
D. spadiceum Zett., 15.
Didymodon Hedw. (Pottiaceae)
D. fallax (Hedw.) Zand., 15.
D. rigidicaulis (C. Muell.) K. Saito, 17, 48.
D. rigidulus Hedw., 15, 17.
D. tophaceus (Brid.) Lisa, 15, 17, 29.
D. vinealis (Brid.) Zand., 15, 17, 29.
Distichium B.S.G. (Ditrichaceae)
D. capillaceum (Hedw.) B.S.G., 15, 17.
D. inclinatum (Hedw.) B.S.G., 15, 29.
Ditrichum Hampe (Ditrichaceae)
D. flexicaule (Schwaegr.) Hampe, 15, 47.
Drepanocladus (C. Muell.) G. Roth (Amblystegiaceae)
D. aduncus (Hedw.) Warnst., 15, 17, 29.
D. exannulatus (B.S.G.) Warnst., 15.
D. fluitans (Hedw.) Warnst., 15, 17.
Encalypta Hedw. (Encalyptaceae)
E. ciliata Hedw., 15.
E. intermedia Jur., 18.
E. rhaptocarpa Schwaegr., 15, 29.
E. vulgaris Hedw., 15, 29.
Entosthodon Schwaegr. (Funariaceae)
E. bolanderi Lesq., 17.
E. planiconvexus (Bartr.) Grout, 15.
E. rubrisetus (Bartr.) Grout, 17.
E. wigginsii Steere, 15.
Eucladium B.S.G. (Pottiaceae)
E. verticillatum (Brid.) B.S.G., 15.
Eurhynchium B.S.G. (Brachytheciaceae)
E. hians (Hedw.) Sande Lac., 17.
E. pulchellum (Hedw.) Jenn., 15, 17, 29.
Fabronia Raddi (Fabroniaceae)
F. pusilla Raddi, 27.
Fissidens Hedw. (Fissidentaceae)
F. bryoides Hedw., 15.

F. cristatus Wils. ex Mitt., 17.
F. grandifrons Brid., 15, 17, 29.
F. obtusifolius Wils., 15.
F. viridulus (Sw.) Wahlenb., 17.
Fontinalis Hedw. (Fontinalaceae)
F. antipyretica Hedw., 15, 17, 29.
F. hypnoides Hartm., 15.
F. neomexicana Sull. & Lesq., 15.
Funaria Hedw. (Funariaceae)
F. hygrometrica Hedw., 15, 17, 29.
F. muhlenbergii Turn., 15, 17.
Grimmia Hedw. (Grimmiaceae)
G. affinis Hoppe & Hornsch., 15, 29.
G. alpestris (Web. & Mohr) Schleich., 15, 17, 29.
G. anodon B. & S., 15, 17, 29.
G. anomala Hampe ex Schimp., 15.
G. arizonae Ren. & Card., 17.
G. donniana Sm., 15.
G. laevigata (Brid.) Brid., 15, 17, 29.
G. orbicularis Bruch ex Wils., 15, 29.
G. ovalis (Hedw.) Lindb., 15, 17, 29.
G. plagiopoda Hedw., 15.
G. poecilostoma Card. & Seb. ex Seb., 28.
G. pulvinata (Hedw.) Sm., 15, 17, 29.
G. torquata Hornsch. ex Grev., 28, 29.
G. trichophylla Grev., 17, 28, 29.
Gymnostomum Nees. & Hornsch. (Pottiaceae)
G. aeruginosum Sm., 15, 17, 29.
Hedwigia P. Beauv. (Hedwigiaceae)
H. ciliata (Hedw.) P. Beauv., 17.
Helodium Warnst. (Thuidiaceae)
H. blandowii (Web. & Mohr) Warnst., 15, 17, 29.
Homalothecium B.S.G. (Brachytheciaceae)
H. nevadense (Lesq.) Ren. & Card., 15, 29.
Homomallium (Schimp.) Loeske (Hypnaceae)
H. adnatum (Hedw.) Broth., 17.
H. mexicanum Card., 17.
Hygrohypnum Lindb. (Amblystegiaceae)
H. bestii (Ren. & Bryhn ex Ren.) Holz. ex Broth., 15.
H. duriusculum (De Not.) Jamieson, 20.
H. luridum (Hedw.) Jenn., 15, 17.
H. molle (Hedw.) Loeske, 15, 29.
H. ochraceum (Turn. ex Wils.) Loeske, 15, 17, 29.
H. smithii (Sw.) Broth., 15, 27.
H. styriacum (Limpr.) Broth., 20.
Hymenostylium Brid. (Pottiaceae)
H. recurvirostrum (Hedw.) Dix., 15, 29.
Hyophila Brid. (Pottiaceae)
H. involuta (Hook.) Jaeg. & Sauerb., 15.
Hypnum Hedw. (Hypnaceae)
H. cupressiforme Hedw., 17.
H. lindbergii Mitt., 15, 17.
H. imponens Hedw., 17.
H. hamulosum B.S.G., 15.
H. pratense (Rabenh.) W. Koch ex Hartm., 15.
H. revolutum (Mitt.) Lindb., 15, 17, 29.
H. vaucheri Lesq., 15, 29.
Isopterygium Mitt. (Hypnaceae)
I. pulchellum (Hedw.) Jaeg. & Sauerb., 15.
I. muellerianum (Schimp.) Jaeg., 15.
Jaffueliobryum Thér. (Grimmiaceae)
J. raui (Aust.) Thér., 15.
J. wrightii (Sull.) Thér, 17, 28, 29.
Kindbergia Ochyra (Brachytheciaceae)
K. praelonga (Hedw.) Ochyra, 29.
Leptobryum (B.S.G.) Wils. (Bryaceae)
L. pyriforme (Hedw.) Wils., 15, 17, 29.
Lescuraea B.S.G. (Leskeaceae)
L. saxicola (B.S.G.) Mol. ex Lor., 15.
Leskea Hedw. (Leskeaceae)
L. gracilescens Hedw., 17.
Leskeella (Limpr.) Loeske (Leskeaceae)
L. arizonae (Williams) Flow., 15.
L. nervosa (Brid.) Loeske, 17.
Leucodon Schwaegr. (Leucodontaceae)
L. brachypus Brid., 17.
Meesia Hedw. (Meesiaceae)
M. triquetra (Richt.) Angstr., 29.
M. uliginosa Hedw., 29.
Metaneckera Steere (Neckeraceae)
M. menziesii (Hook. ex Drumm.) Steere, 15.
Mielichhoferia Nees. & Hornsch. (Bryaceae)
M. macrocarpa (Hook. ex Drumm.) Bruch & Schimp., 15.
Mnium Hedw. (Mniaceae)
M. ambiguum H. Muell., 17.
M. arizonicum Amann, 15, 17, 29.
M. blyttii B.S.G., 15.
M. marginatum (With.) P. Beauv., 15, 17, 29.
M. spinulosum B.S.G., 17.
M. thomsonii Schimp., 15.
Myurella B.S.G. (Anomodontaceae)
M. tenerrima (Brid.) Lindb., 17.
Neckera Hedw. (Neckeraceae)
N. pennata Hedw., 15.
Oncophorus (Brid.) Brid. (Dicranaceae)
O. virens (Hedw.) Brid., 15, 17, 29.
Orthodicranum (B.S.G.) Loeske (Dicranaceae)
O. montanum (Hedw.) Loeske, 15.
O. strictum Culman. (reported as *O. tauricum* in 15; see 20).
Orthothecium B.S.G. (Hypnaceae)
O. diminutivum (Grout) Crum, Steere & Anderson, 15.
Orthotrichum Hedw. (Orthotrichaceae)
O. affine Brid., 15.
O. alpestre Hornsch. ex B.S.G., 15, 17, 29.
O. anomalum Hedw., 15, 17.
O. bartramii Williams, 44.
O. cupulatum Brid., 44.
O. diaphanum Brid., 44.
O. flowersii Vitt, 43.
O. hallii Sull. & Lesq. ex Sull., 15, 17, 29.
O. laevigatum Zett., 15, 29.
O. obtusifolium Brid., 44.
O. pallens Bruch ex Brid., 15.
O. pellucidum Lindb., 17, 29, 44.
O. praemorsum Vent. ex Roell, 29, 44.
O. pumilum Sw., 15.
O. pylaisii Brid., 44.
O. rivulare Turn., 27, 29.
O. rupestre Schleich. ex Schwaegr., 15, 17, 29.
O. speciosum Nees, 44.
Oxystegus (Limpr.) Hilp. (Pottiaceae)
O. tenuirostre (Hook. & Tayl.) A.J.E. Smith, 15.
Paraleucobryum (Limpr.) Loeske (Dicranaceae)
P. enerve (Thed. ex C.J. Hartm.) Loeske, 15, 17.
P. sauteri (B.S.G.) Loeske, 17.
Phascum Hedw. (Pottiaceae)
P. cuspidatum Hedw., 15, 27.
Philonotis Brid. (Bartramiaceae)
P. fontana (Hedw.) Brid., 15, 17, 29.
P. marchica (Hedw.) Brid., 15, 17.

P. tomentella Mol., 15.
Physcomitrium (Brid.) Brid. (Funariaceae)
P. californicum Britt., 15, 29.
P. hookeri Hampe, 15.
P. megalocarpum Kindb. ex Macoun, 29.
P. pygmaeum James, 15, 29.
P. pyriforme (Hedw.) Brid., 15.
Plagiomnium T. Kop. (Mniaceae)
P. affine (Bland.) T. Kop., 15, 17, 29.
P. cuspidatum (Hedw.) T. Kop., 15, 17.
P. medium (B. & S.) T. Kop., 15, 29.
Plagiothecium B.S.G. (Plagiotheciaceae)
P. denticulatum (Hedw.) B.S.G., 15, 17, 29.
Platydictya Berk. (Hypnaceae)
P. jungermanniodes (Brid.) Crum, 15.
P. minutissimum (Sull. & Lesq. ex Sull.) Crum, 15.
Platygyrium B.S.G. (Hypnaceae)
P. fuscoluteum Card., 17.
Pleurochaete Lindb. (Pottiaceae)
P. squarrosa (Brid.) Lindb., 17.
Pohlia Hedw. (Bryaceae)
P. andalusica (Hoehn.) Broth., 38.
P. annotina (Hedw.) Lindb., 15.
P. bolanderi (Lesq.) Broth., 38.
P. cruda (Hedw.) Lindb., 15, 17, 29.
P. drummondii (C. Muell.) Andr., 15, 29.
P. elongata Hedw., 15.
P. longicolla (Hedw.) Lindb., 15.
P. nutans (Hedw.) Lindb., 15, 17, 29.
P. obtusifolia (Brid.) L. Koch, 38.
P. proligera (Kindb. ex Breidl.) Lindb. ex H. Arn., 15.
P. tundrae Shaw, 17, 37.
P. wahlenbergii (Web. & Mohr) Andr., 15, 17, 29.
Polytrichastrum G.L. Smith (Polytrichaceae)
P. alpinum (Hedw.) G.L. Smith, 15, 17.
P. longisetum (Sw. ex Brid.) G.L. Smith, 15, 27.
P. lyallii (Mitt.) G.L. Smith, 15, 17, 29.
Polytrichum Hedw. (Polytrichaceae)
P. commune Hedw., 15.
P. juniperinum Hedw., 15, 17, 29.
P. piliferum Hedw., 15, 17.
Pottia (Reichenb.) Fuernr. (Pottiaceae)
P. arizonica Wareh., 15.
P. heimii (Hedw.) Hampe, 15, 29.
P. nevadensis Card. & Thér., 15, 29.
Pseudocrossidium Williams (Pottiaceae)
P. aureum (Bartr.) Zand., 17, 29, 40.
P. replicatum (Tayl.) Zand., 17, 49.
P. revolutum (Brid.) Zand., 40, UBC!
Pseudoleskea B.S.G. (Leskeaceae)
P. incurvata (Hedw.) Loeske, 15, 17, 29.
P. patens (Lindb.) Kindb., 15, 17, 29.
P. radicosa (Mitt.) Macoun & Kindb., 15, 17, 29.
Pseudoleskeella Kindb. (Leskeaceae)
P. catenulata (Brid. ex Schrad.) Kindb., 17, 29.
P. tectorum (Funck ex Brid.) Kindb. ex Broth., 15, 17, 29.
Pterigynandrum Hedw. (Pterigynandraceae)
P. filiforme Hedw., 17.
Pterygoneurum Jur. (Pottiaceae)
P. lamellatum (Lindb.) Jur., 15, 27.
P. ovatum (Hedw.) Dix., 15, 17, 29.
P. subsessile (Brid.) Jur., 15, 17.
Pylaisiella Kindb. ex Grout (Hypnaceae)
P. polyantha (Hedw.) Grout, 17.
P. selwynii (Kindb.) Crum, Steere & Anderson, 17.
Rhacomitrium Brid. (Grimmiaceae)
R. canescens (Hedw.) Brid., 15.
R. ericoides (Brid.) Brid., 15.
R. heterostichum (Hedw.) Brid., 28.
R. sudeticum (Funck) B. & S., 17.
Rhizomnium (Broth.) T. Kop. (Mniaceae)
R. punctatum (Hedw.) T. Kop., 15.
Rhodobryum (Schimp.) Hampe (Bryaceae)
R. ontariense (Kindb.) Kindb., 17, 19.
Rhynchostegium B.S.G. (Brachytheciaceae)
R. riparioides (Hedw.) Card., 17.
R. serrulatum (Hedw.) Jaeg. & Sauerb., 17.
Rhytidiadelphus (Limpr.) Warnst. (Hylocomiaceae)
R. squarrosus (Hedw.) Warnst., 29.
R. triquetrus (Hedw.) Warnst., 17.
Roellia Kindb. (Bryaceae)
R. roellii (Broth.) Andr. ex Crum, 15.
Saelania Lindb. (Ditrichaceae)
S. glaucescens (Hedw.) Bonmanss. & Broth., 17.
Sanionia Loeske (Amblystegiaceae)
S. uncinata (Hedw.) Loeske, 15, 17, 29.
Schistidium Brid. (Grimmiaceae)
S. agassizii Sull. & Lesq., 15, 28.
S. apocarpum (Hedw.) B. & S., 15, 17, 29.
S. atrichum (C. Muell. & Kindb. ex Macoun & Kindb.) W.A. Weber, 28.
S. dupretii (Ther.) W.A. Weber, 15, 17.
S. occidentale (Lawt.) W. A. Weber, 28.
S. pacificum in ed., 28.
S. platyphyllum (Mitt.) Kindb., 15, 28.
S. pulvinatum (Hedw.) Brid., 28.
S. rivulare (Brid.) Podp., 15, 17.
S. strictum (Turn.) Loeske, 17, 28, 29.
Scleropodium B.S.G. (Brachytheciaceae)
S. obtusifolium (Hook.) Kindb., 15, 29.
S. touretii (Brid.) L. Koch, 15, 29.
Scorpidium (Schimp.) Limpr. (Amblystegiaceae)
S. turgescens (T. Jens.) Loeske, 15.
Scouleria Hook. in Drumm. (Scouleriaceae)
S. aquatica Hook., 8, 15.
Seligeria B.S.G. (Seligeriaceae)
S. campylopoda Kindb. ex Macoun & Kindb., 15.
Sphagnum L. (Sphagnaceae)
S. fuscum (Schimp.) Klinggr., 15.
S. nemoreum Scop., 15.
S. recurvum P. Beauv., 15.
S. squarrosum Crome, 15.
S. warnstorfii Russ., 15.
Splachnobryum C. Muell. (Splachnaceae)
S. obtusum (Brid.) C. Muell., 12.
Stegonia Vent. (Pottiaceae)
S. latifolia (Schwaegr. ex Schultes) Vent. ex Broth., 15.
Taxiphyllum Fleisch. (Hypnaceae)
T. deplanatum (Bruch & Schimp. ex Sull.) Fleisch., 17.
Tayloria Hook. (Splachnaceae)
T. acuminata Hornsch., 15, 29.
T. froelichiana (Hedw.) Mitt. ex Broth., 26.
T. serrata (Hedw.) B. & S., 29.
Tetraphis Hedw. (Tetraphidaceae)
T. pellucida Hedw., 21.
Timmia Hedw. (Timmiaceae)
T. austriaca Hedw., 15, 17, 29.
T. megapolitana Hedw., 15, 17, 29.
Tomenthypnum Loeske (Brachytheciaceae)
T. nitens (Hedw.) Loeske, 15.
Tortella (Lindb.) Limpr. (Pottiaceae)

T. fragilis (Drumm.) Limpr., 29.
T. tortuosa (Hedw.) Limpr., 15.
Tortula Hedw. (Pottiaceae)
T. brevipes (Lesq.) Broth., 15.
T. caninervis (Mitt.) Broth., 15, 17, 29.
T. fragilis Tayl., 17.
T. inermis (Brid.) Mont., 15, 17, 27.
T. intermedia (Brid.) De Not., 15, 17.
T. mucronifolia Schwaegr., 15, 17.
T. muralis Hedw., 15.
T. norvegica (Web.) Wahlenb. ex Lindb., 15, 29.
T. obtusissima (C. Muell.) Mitt., 17, 29.
T. pagorum (Milde) De Not., 12.
T. papillosa Wils., 17.
T. papillosissima (Copp.) Broth., 15, 29.
T. princeps De Not., 15, 29.
T. ruraliformis (Besch.) Dix., 15.
T. ruralis (Hedw.) Gaertn., Meyer & Scherb., 15, 17, 29.
Trichostomum Bruch (Pottiaceae)
T. crispulum Bruch, 42.
Weissia Hedw. (Pottiaceae)
W. condensa (Voit.) Lindb., 15, 17, 42.
W. controversa Hedw., 15, 17, 29.
W. ligulaefolia (Bartr.) Grout, 15, 42.
W. occidentalis (Flow.) Stoneb., 15, 42.
Zygodon Hook. & Tayl. (orthotrichaceae)
Z. viridissimus (Dicks.) Brid., 21.

Below is a list of species in the Intermountain West that Zander (1979) considers to be varieties of the polymorphic *Didymodon rigidulus* and *D. vinealis*. Many other bryologists consider them to be species.

D. brachyphyllus (Sull.) Zander (= *D. vinealis*)
D. acutus (Brid.) K. Saito (= *D. rigidulus*)
D. insulanus (De Not) M. Hill (= *D. vinealis*)
D. luridus Hornsch. ex Spreng. (= *D. vinealis*)
D. mexicanus var. *subulatus* Thér. & Bartr. ex Bartr. (= *D. rigidulus*)

List of Synonyms

The following list indicates name changes that have occurred between the publication of Lawton (1958), Haring (1961), and Flowers (1973) and the present. In each case the synonym is on the left and the presently accepted name is on the right.

Aloina pilifera = *A. bifrons*
Amblystegium americanum = *Conardia compacta*
Amblystegium compactum = *Conardia compacta*
A. juratzkanum = *A. serpens*
A. kochii = *A. trichopodium*
Astomum occidentale = *Weissia occidentalis*
Barbula acuta = *Didymodon rigidulus*
B. bescherellei = *Didymodon rigidicaulis*
B. cruegeri = *B. indica*
B. cylindrica = *Didymodon vinealis*
B. fallax = *Didymodon fallax*
B. reflexa = *Didymodon fallax*
B. spiralis = *Pseudocrossidium replicatum*
B. vinealis = *Didymodon vinealis*
Brachythecium flagellare = *B. plumosum*
B. lamprochryseum = *B. frigidum*
B. petrophilum = *B. velutinum*
B. suberythrorrhizon = *B. velutinum*
B. utahense = *B. fendleri*
Bryum angustirete = *B. algovicum*
B. bicolor = *B. dichotomum*
B. cirrhatum = *B. pallescens*
B. creberrimum = *B. lisae*
B. cuspidatum = *B. lisae*
B. inclinatum = *B. amblyodon*
B. lonchocaulon = *B. lisae*
B. pendulum = *B. algovicum*
B. sandbergii = *Roellia roellii*
B. stenotrichum = *B. amblyodon*
B. tortifolium = *B. cyclophyllum*
Calliergon turgescens = *Scorpidium t.*
Campylium chrysophyllum = *Campyliadelphus c.*
C. polygamum = *Campyliadelphus p.*
C. stellatum = *Campyliadelphus s.*
Chamberlainia acuminata = *Brachythecium a.*
Cratoneuron falcatum = *C. commutatum*
Crossidium desertorum = *C. crassinerve*
C. griseum = *C. squamiferum*
Dicranum montanum = *Orthodicranum m.*
Didymodon mexicanus = *D. rigidulus*
D. recurvirostris = *Bryoerythrophyllum r.*
D. trifarius = excluded
Drepanocladus uncinatus = *Sanionia u.*
Eurhynchium diversifolium = *E. pulchellum*
E. stokesii = *Kindbergia praelonga*
E. substrigosum = *E. pulchellum*
Fissedens limbatus = *F. bryoides*
Grimmia agassizii = *Schistidium a.*
G. alpicola = *Schistidium rivulare*
G. a. var. *latifolia* = *Schistidium platyphyllum*
G. apocarpa = *Schistidium apocarpum*
G. a. var. *ambigua* = *Schistidium apocarpum*
G. a. var. *atrofusca* = *Schistidium apocarpum*
G. a. var. *conferta* = *Schistidium apocarpum*
G. a. var. *gracilis* = *Schistidium strictum*
G. atricha = *Schistidium atrichum*
G. calyptratus = *Coscinodon c.*
G. commutata = *G. ovalis*
G. decipiens = excluded
G. dupretii = *Schistidium d.*
G. flaccida = *Schistidium pulvinatum*
G. montana = *G. alpestris*
G. raui = *Jaffueliobryum r.*
G. tenerrima = *G. alpestris*
G. wrightii = *Jaffueliobryum w.*
Gymnostomum recurvirostrum = *Hymenostylium r.*
Husnotiella pringlei = *Didymodon tophaceus*
Hygroamblystegium fluviatile = *Amblystegium f.*
H. irriguum = *Amblystegium tenax*
H. orthocladon = *Amblystegium tenax*
Hypnum haldanianum = *Callicladium h.*
Leptodictyon riparium = *Amblystegium r.*
L. trichpodium = *Amblystegium t.*
Lescuraea incurvata = *Pseudoleskea i.*
L. patens = *Pseudoleskea p.*
L. radicosa = *Pseudoleskea r.*
Leskea cyrtophylla = *Pseudoleskeella tectorum*
L. nervosa = *Leskeella n.*
L. tectorum = *Pseudoleskeella t.*
Leskea williamsii = *Pseudoleskeella tectorum*

Leskeella tectorum = *Pseudoleskeella t.*
Merceya latifolia = *Crumia l.*
Mnium affine = *Plagiomnium a.*
M. cuspidatum = *Plagiomnium c.*
M. lycopodioides = *M. ambiguum*
M. medium = *Plagiomnium m.*
M. orthorhynchum = *Mnium thomsonii*
M. punctatum = *Rhizomnium p.*
M. serratum = *M. marginatum*
Neckera menziesii = *Metaneckera m.*
N. neomexicana = *Metaneckera menziesii*
Oncophorus gracilescens = excluded
Orthotrichum garrettii = *O. diaphanum*
O. jamesianum = *O. pellucidum*
O. lescurii = *O. strangulatum* (excluded)
O. macounii = *O. laevigatum*
O. strangulatum = excluded
O. texanum = *O. rupestre*
Plagiothecium deplanatum = *Taxiphyllum d.*
P. muellerianum = *Isopterygium m.*
P. pulchellum = *Isopterygium p.*
Pogonatum alpinum = *Polytrichastrum alpin-um*
Pohlia annotina var. *decipiens* = *P. tundrae*
Pohlia rothii = *P. filum*
Polytrichadelphus lyallii = *Polytrichastrum lyallii*
Polytrichum gracile = *Polytrichastrum longisetum*
Porotrichum neomexicanum = *Metaneckera menziesii*
Pottia latifolia = *Stegonia l.*
Pseudoleskea arizonae = *Leskeella a.*
P. atrovirens = *P. patens*
P. oligoclada = *P. incurvata*
Rhodobryum roseum = *R. ontariense*
Scleropodium illecebrum = *S. tourettii*
Scopelophila latifolia = *Crumia l.*
Sphagnum capillaceum = *S. nemoreum*
Thuidium abietinum = *Abietinella a.*
T. microphyllum = *Bryohaplocladium m.*
Timmia bavarica = *T. megapolitana* var. *b.*
Tortella nitida = excluded
Tortula aurea = *Pseudocrossidium a.*
Tortula bistratosa = *T. caninervis*
Trichostomum tenuirostre = *Oxystegus t.*
Weissia andrewsii = *W. controversa*
W. glauca = *W. andersoniana* (excluded)
W. perligulata = *Trichostomum crispulum*
W. sweetii = *Trichostomum crispulum*
W. tortilis = *W. condensa*

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LITERATURE CITED

1. BEHLE, W. H. 1984. In memoriam: Seville Flowers (1900–1968). Great Basin Naturalist 44: 210–222.
2. BREMER, B. 1980a. A taxonomic revision of *Schistidium* (Grimmiaceae, Bryophyta) 1. Lindbergia 5: 99–104.
3. ———. 1980b. A taxonomic revision of *Schistidium* (Grimmiaceae, Bryophyta) 2. Lindbergia 6: 89–117.
4. ———. 1981. A taxonomic revision of *Schistidium* (Grimmiaceae, Bryophyta) 3. Lindbergia 7: 73–90.
5. BUCK, W. R., AND R. R. IRELAND. 1985. A reclassification of the Plagiotheciaceae. Nova Hedwigia 41: 89–125.
6. BUCK, W. R., AND D. H. VITT. 1986. Suggestions for a new familial classification of pleurocarpous mosses. Taxon 35: 21–60.
7. CHURCHILL, S. P. 1981. A phylogenetic analysis, classification and synopsis of the genera of the Grimmiaceae (Musci). Pages 127–144 *in* V. Funk and D. R. Brooks, ed., Advances in cladistics. New York Botanical Gardens, New York.
8. ———. 1985. The systematics and biogeography of *Scouleria* Hook. (Musci: Scouleriaceae). Lindbergia 11: 59–71.
9. CLARK, L. 1957. Hepaticae collected in Nevada by Elva Lawton in 1955. Bryologist 60: 32–35.
10. CORLEY, M. F. V., A. C. CRUNDWELL, R. DULL, M. O. HILL, AND A. J. E. SMITH. 1981. Mosses of Europe and the Azores: an annotated list of species, with synonyms from the recent literature. J. Bryology 11: 609–689.
11. CRONQUIST, A., A. H. HOLMGREN, N. H. HOLMGREN, AND J. L. REVEAL. 1972. Intermountain flora. Vol. 1. Hafner Press, New York.
12. CRUM, H. A., AND L. E. ANDERSON. 1981. Mosses of eastern North America. 2 vols. Columbia University Press, New York.
13. DELGADILLO, C. M. 1975. Taxonomic revision of *Aloina*, *Aloinella* and *Crossidium* (Musci). Bryologist 78: 245–303.
14. FLOWERS, S. 1961. The Hepaticae of Utah. Univ. Utah Biol. Ser. 12(2): 1–89.
15. ———. 1973. Mosses: Utah and the West. Brigham Young University Press, Provo.
16. GLEASON, H. A., AND A. CRONQUIST. 1964. The natural geography of plants. Columbia University Press, New York.
17. HARING, I. M. 1961. A checklist of the mosses of the state of Arizona. Bryologist 64: 222–240.
18. HORTON, D. G. 1983. A revision of the Encalyptaceae (Musci), with particular reference to the North American taxa. Part II. J. Hattori Bot. Lab. 54: 353–532.
19. IWATSUKI, Z., AND T. KOPONEN. 1972. On the taxonomy and distribution of *Rhodobryum roseum* and its related species (Bryophyta). Acta Bot. Fennica 96: 1–22.
20. JAMIESON, D. W. 1976. A monograph of the genus *Hygrohypnum* Lindb. (Musci). Unpublished dissertation, University of British Columbia, Vancouver.
21. JOHNSON, A. B., AND D. H. VITT. 1971. Bryophytes new to Arizona from the White Mountains. Bryologist 74: 39–40.
22. KANDA, H. 1975. A revision of the family Amblystegiaceae of Japan. Part 1. J. Science Hiroshima Univ., Ser. B 15: 201–276.
23. ———. 1976. A revision of the family Amblystegiaceae of Japan. Part 2. J. Science Hiroshima Univ., Ser. B. 16: 47–119.
24. KOPONEN, T. 1968. Generic revision of the Mniaceae Mitt. (Bryophyta). Ann. Bot. Fenn. 5: 117–151.
25. ———. 1973. A guide to the Mniaceae in Canada. Lindbergia 2: 160–184.

26. LAFARGE-ENGLAND, C., AND D. H. VITT. 1985. A taxonomic study of *Tayloria hornschuchii* and *T. froelichiana* in North America. Bryologist 88: 82–93.
27. LAVIN, M. 1981. New records for the moss flora of Nevada. Bryologist 84: 93–94.
28. ——. 1982. Distribution of the moss family Grimmiaceae in Nevada. Great Basin Naturalist 42: 583–588.
29. LAWTON, E. 1958. Mosses of Nevada. Bryologist 61: 314–334.
30. ——. 1971. Moss flora of the Pacific Northwest. Nichinan, Japan.
31. LEWINSKY, J. 1974. The genera *Leskeella* and *Pseudoleskeella* in Greenland. Bryologist 77: 601–611.
32. MCCLEARY, J. A., AND V. V. GREEN. 1971. A checklist of Idaho mosses. Bryologist 74: 175–180.
33. MCLAUGHLIN, S. P. 1986. Floristic analysis of the southwestern United States. Great Basin Naturalist 46: 46–65.
34. PETERSON, W. 1979. A revision of the genera *Dicranum* and *Orthodicranum* (Musci) in North America north of Mexico. Unpublished dissertation, University of Alberta, Edmonton.
35. REESE, W. D. 1974. *Bryoxiphium norvegicum* in Arizona. Bryologist 77: 252–253.
36. SCHOFIELD, W. B., AND N. G. MILLER. 1982. The status of floristic bryology in North America. Pages 399–429 *in* P. Geissler and S. W. Greene, eds., Bryophyte taxonomy. Beihefte zur Nova Hedwigia.
37. SHAW, A. J. 1981. *Pohlia tundrae* spec. nov. and *P. andrewsii* spec. nov., two new arctic-alpine species from North America. Bryologist 84: 65–74.
38. ——. 1982. *Pohlia* Hedw. in North and Central America and the West Indies. Contr. Univ. Mich. Herb. 15: 219–295.
39. SMITH, G. L. 1971. Conspectus of the genera of Polytrichaceae. Mem. New York Bot. Gard. 21: 1–83.
40. SPENCE, J. R. 1987. *Pseudocrossidium aureum* (Bartr.) Zand. (Pottiaceae, Musci) new to Utah. Great Basin Naturalist 47: 347–348.
41. ——. 1988. *Bryum* Hedw. (Bryaceae) in western North America. Bryologist 91: 73–85.
42. STONEBURNER, A. 1985. Variation and taxonomy of *Weissia* in the southwestern United States. II. Taxonomic treatment. Bryologist 88: 293–314.
43. VITT, D. H. 1971. New taxa of *Orthotrichum* from western North America. Bryologist 74: 159–164.
44. ——. 1973. A revision of the genus *Orthotrichum* in North America, north of Mexico. Bryophyt. Bibliotheca 1: 1–208.
45. ——. 1984. Classification of the Bryopsida. Pages 696–759 *in* R. M. Schuster, ed., New manual of bryology. Vol. 2. Nichinan, Japan.
46. VITT, D. H., N. G. MILLER, AND A. B. JOHNSON. 1971. Bryophytes new to Arizona. Bryologist 74: 499–501.
47. WEBER, W. A. 1973. Guide to the mosses of Colorado. INSTAAR, Univ. Colo. Occ. Pap. No. 6: 1–48.
48. ZANDER, R. H. 1978. New combinations in *Didymodon* (Musci) and a key to the taxa in North America north of Mexico. Phytologia 41: 11–32.
49. ——. 1979. Notes on *Barbula* and *Pseudocrossidium* (Bryopsida) in North America and an annotated key to the taxa. Phytologia 44: 177–214.

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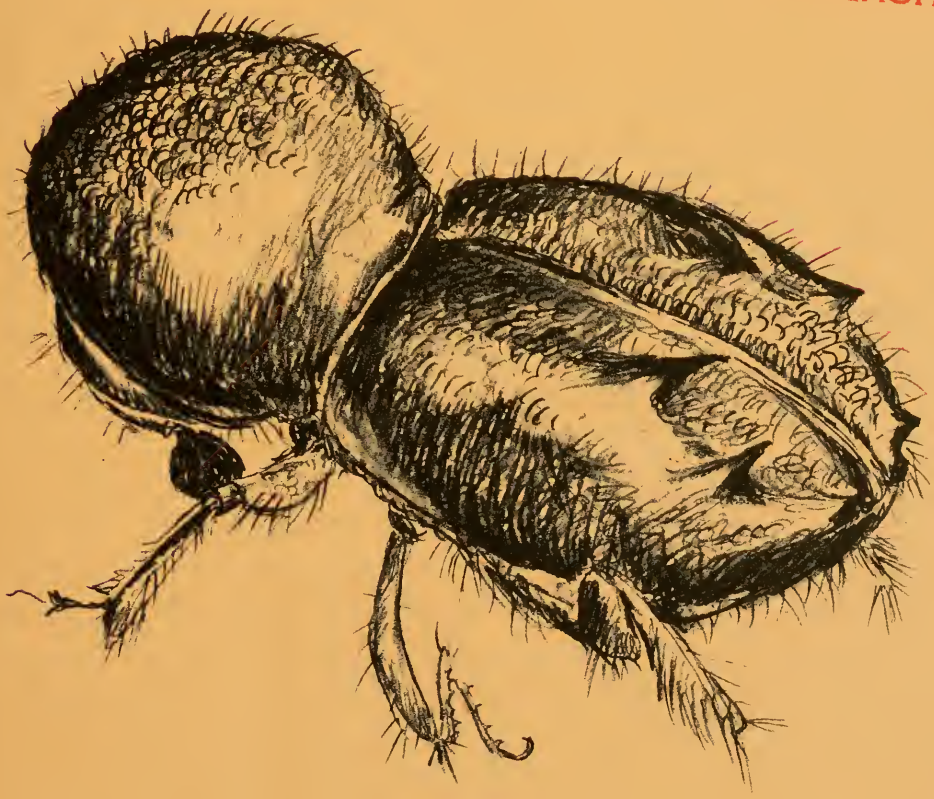

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VEGETATION CHARACTERISTICS OF MOUNTAINOUS NORTHEASTERN NEVADA SAGEBRUSH COMMUNITY TYPES

M. E. Jensen[1], L. S. Peck[2], and M. V. Wilson[3]

ABSTRACT.—Vegetation characteristics of 15 sagebrush community types identified on the Humboldt National Forest, northeastern Nevada, are described. A total of 218 plant species were found over the 372 relatively undisturbed rangeland communities sampled. The dominant plant families encountered were the Asteraceae (45 taxa), Poaceae (32 taxa), Scrophulariaceae (14 taxa), and the Fabaceae (12 taxa). Average annual dry weight production of the community types ranged from about 400 kg/ha/yr on types with *Artemisia nova* as the dominant sagebrush species to 1,200 kg/ha/yr on some *A. tridentata* ssp. *vaseyana* community types. A general increase in species richness and vegetation plus litter ground cover was observed within community types as the dominant sagebrush species changed from *A. nova* to *A. arbuscula* to *A. longiloba* to *A. tridentata* spp. *tridentata* to *A. tridentata* ssp. *vaseyana*. Major differences in plant species production and constancy exist between the sagebrush community types studied.

Sagebrush-dominated plant communities are ubiquitous throughout Nevada. The mountainous areas of the state characteristically support various shrub species of the genus *Artemisia* and subgenus Tridentatae. These species are commonly used to differentiate vegetation groupings in rangeland classification because of their environmental indicator values (Winward 1983). Habitat types, which utilize *Artemisia* species in the naming of classification groups, have been developed for a variety of western rangelands (Hironaka et al. 1983, Mueggler and Stewart 1980, Zamora and Tueller 1973). Limited data exist, however, for the higher-elevation, sagebrush (*Artemisia* spp.)–dominated rangelands of Nevada.

A study of rangeland communities of the Humboldt National Forest, northeastern Nevada, produced a needed sagebrush community type classification of these Great Basin plant communities (Jensen et al. 1988). The objective of this paper is to provide vegetation characterizations for those community types. Such information is required if knowledgeable management of Nevada's rangeland resources is to be made.

STUDY AREA AND METHODS

The Humboldt National Forest comprises approximately 1 million ha within eight mountain ranges of northeastern Nevada (Fig. 1). The forest is characteristic of higher-elevation rangelands of the Great Basin in the semiarid climatic zone. Elevation ranges from 1,800 to 3,100 m, and average annual precipitation is about 33 cm. General plant association zones of the forest range from saltbush (*Atriplex* spp.) at the lowest elevations to Utah juniper (*Juniperus osteosperma*), pinyon pine (*Pinus monophylla*), mountain mahogany (*Cerocarpus ledifolius*), quaking aspen (*Populus tremuloides*), white fir (*Abies concolor*) to

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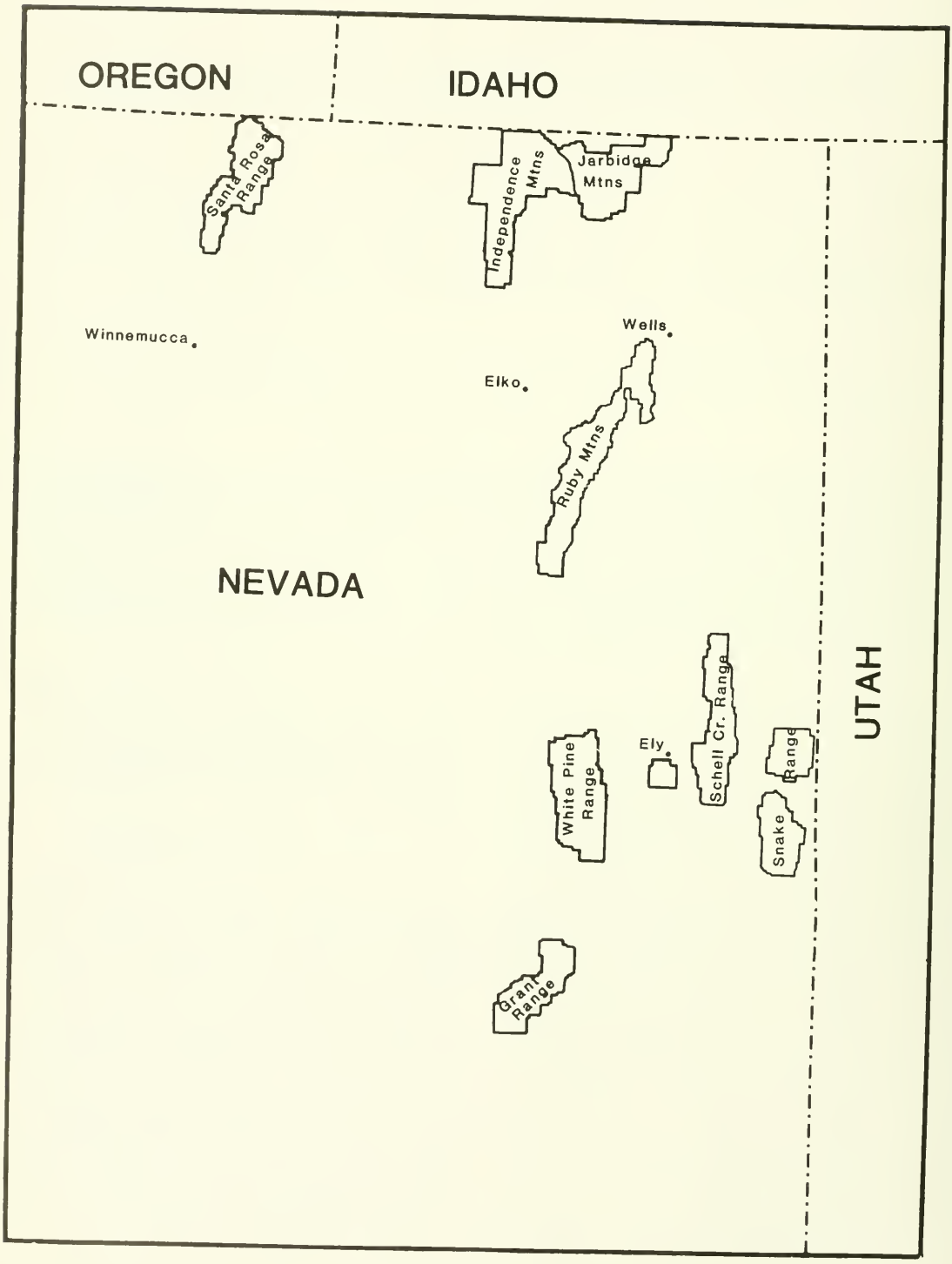

Fig. 1. The Humboldt National Forest of northeastern Nevada.

TABLE 1. List of sagebrush community types and abbreviated codes referred to in the text.

Abbreviated code	Community type
ARNO/ATCO/SIHY	*Artemisia nova/Atriplex confertifolia/Sitanion hystrix*
ARNO/ORHY	*A. nova/Oryzopsis hymenoides*
ARNO/AGSP	*A. nova/Agropyron spicatum*
ARAR/AGSP	*A. arbuscula/Agropyron spicatum*
ARAR/FEID/POSA	*A. arbuscula/Festuca idahoensis/Poa sandbergii*
ARAR/FEID	*A. arbuscula/Festuca idahoensis*
ARLO/FEID	*A. longiloba/Festuca idahoensis*
ARWYO/SIHY	*A. tridentata* ssp. *wyomingensis/Sitanion hystrix*
ARWYO/POSA	*A. tridentata* ssp. *wyomingensis/Poa sandbergii*
ARWYO/AGSP	*A. tridentata* ssp. *wyomingensis/Agropyron spicatum*
ARTR/AGSP	*A. tridentata* ssp. *tridentata/Agropyron spicatum*
ARTR/FEID	*A. tridentata* ssp. *tridentata/Festuca idahoensis*
ARVA/AGSP	*A. tridentata* ssp. *vaseyana/Agropyron spicatum*
ARVA/FEID	*A. tridentata* ssp. *vaseyana/Festuca idahoensis*
ARVA/ELCI	*A. tridentata* ssp. *vaseyana/Elymus cinereus*
ARVA/SYOR/AGSP	*A. t.* ssp. *vaseyana/Symphoricarpos oreophilus/Agropyron spicatum*
ARVA/SYOR/BRCA	*A. t.* ssp. *vaseyana/Symphoricarpos oreophilus/Bromus carinatus*

bristlecone pine (*Pinus aristata*) with increasing elevation. Various sagebrush (*Artemisia* spp.)–dominated communities also occur along this elevation gradient. They comprise approximately 70% of the forest.

A total of 372 sagebrush communities were sampled throughout the forest between 1983 and 1986. Site selection was based on "subjective sampling without preconceived bias" as described by Mueller-Dombois and Ellenberg (1974), with relatively undisturbed sites sampled to document the late seral or climax community expressions present. Sampling was performed on modal soil polypedons that supported a representative plant community for an area. Most of the communities sampled meet the criteria of a potential natural community for an ecological site as defined by the RISC committee (RISC 1983).

The vegetation and soil sampling methods employed have been described previously (Jensen et al. 1988). Sampling was conducted within a 232-m^2 macroplot located to represent average vegetation and soil conditions present. The following parameters (Cook and Stubbendieck 1986) were measured to characterize the vegetation at a site: annual production by plant species was recorded within ten 2.9-m^2 circular microplots (weight estimate method), rooted frequency and ocular canopy cover by plant species were recorded within twenty-five 25 × 50-cm quadrats, shrub species canopy cover was recorded beneath five 15.2-m line transects (line intercept method), and shrub species density by age class was recorded within five 15.2 × 0.9-m belts. Cover estimates were obtained for important soil surface parameters (e.g., bare soil, rock, litter) by a point cover method.

Soil descriptions were made within all macroplots utilizing standard pedon description methods (USDA 1975). Soils were described to a depth of 1.5 m or to a shallower depth if a restrictive layer was present. This facilitated classification of soils to the family level of soil taxonomy. Statistical analyses utilized programs contained in the Statistical Package for the Social Sciences (Norusis 1985).

RESULTS AND DISCUSSION

A total of 218 plant species were found within the 372 rangeland sites sampled. The graminoids were represented by 35 species belonging to 4 families, the shrubs by 39 species belonging to 13 families, and the forbs by 140 species belonging to 31 families. Tree species were present in minor amounts on some sites with 4 species described. The dominant plant families encountered were the Asteraceae (45 taxa), Poaceae (32 taxa), Scrophulariaceae (14 taxa), and Fabaceae (12 taxa).

A total of 17 sagebrush community types (Table 1) were identified through TWINSPAN analysis of production data (Jensen et al. 1988). Abbreviations used to designate these communities hereafter are explained in Table 1. Generalized site characteristics for 15 of the community types are presented in Table 2. The ARWYO/POSA and ARWYO/AGSP community types presented in Table 1

TABLE 2. Listing of the major sagebrush community types of the Humboldt National Forest with general site characterizations provided.

Community type	Sample size	Principal soil great group	Elevation range (m)	Average slope (%)	Average soil depth (cm)	Average thickness mollic epipedon (cm)	Total number of plant species observed within type
ARNO/ATCO/SIHY	12	Haplargids	1,829–2,225	23	90	0	50
ARNO/ORHY	16	Paleorthids	1,859–3,048	15	77	0	46
ARNO/AGSP	44	Calciorthids	1,829–3,048	20	81	16	58
ARAR/AGSP	27	Argixerolls	1,981–2,926	24	73	26	74
ARLO/FEID/POSA	19	Argixerolls	1,524–3,109	13	71	22	67
ARAR/FEID	19	Cryoborolls	1,768–2,438	13	74	28	56
ARLO/FEID	4	Argixerolls	1,829–1,981	6	81	29	27
ARWYO/SIHY	4	Haploxerolls	1,829–2,134	4	99	27	45
ARTR/AGSP	6	Haploxerolls	1,707–1,920	20	118	43	25
ARTR/FEID	8	Haploxerolls	1,615–2,103	16	132	48	45
ARVA/AGSP	63	Cryoborolls	1,829–3,048	24	104	37	124
ARVA/FEID	67	Cryoborolls	1,707–2,743	17	111	45	93
ARVA/ELCI	9	Cryoborolls	1,859–2,316	33	117	37	49
ARVA/SYOR/AGSP	23	Cryoborolls	2,012–2,743	26	117	43	88
ARVA/SYOR/BRCA	47	Cryoborolls	1,768–2,499	28	136	53	95

are not discussed in this paper because of limited sampling of these sites (i.e., two samples in each). Data from five climatological stations located adjacent to the forest indicate that annual precipitation during the study period ranged from 21% below to 150% above the 20-year long-term average of a station (NOAA 1986). The vegetation characterizations provided in this study reflect plant community response to a wide range of climatic conditions.

The total number of plant species comprising a given community type increases as the dominant sagebrush species change from *Artemisia nova* to *A. arbuscula* to *A. tridentata* ssp. *vaseyana* (Table 2). Ordination of samples by DECORANA indicated that a gradient in increasing soil moisture also follows this transition in sagebrush species (Jensen et al. 1988). Species richness of these community types is assumed to be related to available soil moisture, which in turn is a function of the climate and soil properties of a site.

The average production composition and constancy of plant species within each community type were calculated for graminoid (Table 3), shrub (Table 4), and forb (Table 5) growth forms. These tables present both the dominant (high production composition and constancy) and rare (low production composition and constancy) plant species that characterize sagebrush community types in the study area. They are considered representative of floristic composition within similar community types in adjacent areas of Idaho, Oregon, and Utah. In general, the number of graminoid and forb species observed within the community types increases with higher available soil moisture, as suggested in the transition from ARNO/ATCO/SIHY to ARVA/SYOR/BRCA community types (Tables 3, 5). The number of rare plant species tends to be greatest within more mesic community types (e.g., ARVA/SYOR/BRCA).

Total herbaceous production of community types also follows an available soil moisture gradient (Table 6). Sagebrush community types occupying the xeric end of this gradient (e.g., ARNO/ORHY, ARAR/AGSP) display lower average annual production rates than do mesic types (e.g., ARVA/ELCI, ARVA/SYOR/BRCA). Variability in average annual production follows a similar trend, with mesic community types displaying the largest variation in total production. The mesic communities occupy a large diversity of soil types in this study (Jensen 1988), which undoubtedly contributes to the high production variability observed.

The community types vary in the relative percentage of annual production contributed by various growth forms (Fig. 2). Relative shrub production (i.e., composition) tends to be highest on the more xeric community types within a given sagebrush community series. On the *A. nova*–dominated community types, the shrub component increases from about 60% to 80% of the total production

TABLE 3. Average production composition and percent constancy of graminoid species within various sagebrush community types. The production composition values represent the average percentage of the total biomass that a species represents when it occurs within a community type.

Family	Taxa	ARNO ATCO SIHY	ARNO ORHY	ARNO AGSP	ARAR AGSP	ARAR FEID POSA	ARAR FEID	ARLO FEID	ARWYO SIHY
Cyperaceae									
	Carex spp.	2(8)				2(5)			
Equisetaceae									
	Equisetum spp.								
Juncaceae									
	Juncus spp.								
Poaceae									
	Agropyron cristatum			1(2)					
	A. intermedium		5(6)	T(2)	8(4)				2(25)
	A. smithii			1(7)					30(25)
	A. spicatum		2(19)	12(93)	9(90)	4(53)	13(89)	19(50)	3(25)
	A. trachycaulum								
	Bromus carinatus								
	B. inermis								
	B. tectorum	1(75)	5(25)	3(23)	1(15)	8(10)	T(5)		1(25)
	Danthonia unispicata								
	Elymus cinereus						1(10)	5(25)	5(50)
	Festuca idahoensis				9(15)	39(68)	49(100)	27(100)	20(25)
	Hesperochloa kingii			2(2)		3(20)			
	Hilaria jamesii		T(6)	2(2)		3(20)	1(5)		
	Koelaria cristata						T(5)		
	Lucopa kingii								
	Melica bulbosa				3(1)				
	Muhlenbergia spp.								
	Oryzopsis hymenoides	6(33)	5(100)	2(20)	T(1)				2(25)
	Poa ampla								
	P. bulbosa								
	P. fendleriana		19(12)	6(32)	11(66)	4(20)	T(5)		5(25)
	P. nevadensis	6(50)		3(11)	2(4)	1(15)	23(15)		2(25)
	P. pratensis								1(25)
	P. sandbergii	4(67)	1(6)	10(80)	9(70)	9(89)	10(20)	14(100)	4(100)
	Sitanion hystrix	6(100)	4(69)	3(40)	6(48)	4(52)	2(35)	4(100)	10(100)
	Stipa columbiana				1(4)				
	S. comata	3(8)	2(12)	1(9)					4(25)
	S. lettermanii			5(9)	2(4)	1(5)	5(5)	17(25)	
	S. occidentalis								
	S. thurberiana	T(8)	2(6)		1(8)				
	S. williamsii								
	Vulpia octoflora					8(10)			

present at a site as *Agropyron spicatum* is replaced by *Sitanion hystrix* and *Oryzopsis hymenoides* as the dominant grass species. This same trend is also observed in the *A. arbuscula* and *A. tridentata* spp. *vaseyana* community types where shrub composition increases from 19% to 56% and 38% to 63%, respectively, as *Festuca idahoensis* is replaced by *Agropyron spicatum* as the dominant grass species. The enhanced competitive ability of sagebrush species under moisture-limiting conditions (Sturges 1977) probably accounts for these changes in shrub composition.

Production variability is greatest in the forb component of a community type (Table 6). Grass and shrub growth forms display similar magnitudes of production variability within community types and are usually half as variable as forb production. The coefficients of variation in total production show a general increase as community types become more mesic, with the ARVA/SYOR/BRCA type displaying the highest total production variability. Absolute grass and forb production also tends to increase as community types become more mesic, while shrub production remains relatively unaffected by changes in community moisture status.

TABLE 3. Continued.

Family	Taxa	ARTR AGSP	ARTR FEID	ARVA AGSP	ARVA FEID	ARVA ELCI	ARVA SYOR AGSP	ARVA SYOR BRCA
Cyperaceae								
	Carex spp.			T(2)	2(18)	1(20)	2(4)	3(18)
Equisetaceae								
	Equisetum spp.	T(17)						
Juncaceae								
	Juncus spp.	T(17)						
Poaceae								
	Agropyron cristatum			8(4)				
	A. intermedium			4(10)			1(4)	T(4)
	A. smithii			4(18)	T(1)		2(43)	2(2)
	A. spicatum	9(100)	5(60)	11(95)	10(76)	8(60)	9(91)	8(62)
	A. trachycaulum	T(17)	9(25)	2(10)	3(9)	3(10)	9(8)	8(44)
	Bromus carinatus			3(4)	2(22)	4(60)	4(39)	10(80)
	B. inermis							
	B. tectorum	22(83)		4(30)	2(9)	5(40)	1(8)	1(8)
	Danthonia unispicata							
	Elymus cinereus	6(66)	6(75)	4(20)	3(22)	12(90)	2(4)	9(46)
	Festuca idahoensis		22(100)	5(16)	26(100)	T(10)	10(26)	8(44)
	Hesperochloa kingii			3(10)	20(3)			5(16)
	Hilaria jamesii							
	Koelaria cristata							
	Lucopa kingii							T(4)
	Melica bulbosa				1(3)	1(30)	1(8)	1(20)
	Muhlenbergia spp.							T(2)
	Oryzopsis hymenoides			2(12)	5(1)			
	Poa ampla							T(2)
	P. bulbosa							T(2)
	P. fendleriana		4(12)	7(12)	5(13)		3(78)	1(6)
	P. nevadensis	1(33)		3(35)	8(18)		1(17)	3(12)
	P. pratensis	13(17)	12(12)	2(6)			1(4)	T(8)
	P. sandbergii	5(100)	11(25)	3(57)	5(24)	2(20)	2(17)	2(18)
	Sitanion hystrix	8(33)	2(38)	2(40)	4(39)	1(40)	1(13)	5(22)
	Stipa columbiana	T(17)	3(12)		6(13)		5(4)	4(12)
	S. comata			4(2)	1(1)		1(4)	
	S. lettermanii			2(24)	20(9)	1(10)	7(22)	4(18)
	S. occidentalis		7(12)		11(12)			9(12)
	S. thurberiana			4(8)	5(1)		1(8)	
	S. williamsii					T(10)		
	Vulpia octoflora							

Percent canopy cover of shrub species shows no apparent trend with community moisture status (Table 7). Density of shrub species, however, responds to a moisture gradient with the greatest number of shrubs per ha occurring on xeric community types (Table 8). The low-growing sagebrush species studied (i.e., *A. nova*, *A. arbuscula*, and *A. longiloba*) display much greater density levels within a community than do larger sagebrush species such as *A. tridentata* ssp. *vaseyana*. The drier sites, which the low-growing sagebrush species occupy, are probably more favorable than mesic sites for sagebrush establishment since they tend to support fewer grass and forb species that often compete with sagebrush.

Age-class distributions of shrub species tend to be similar across the community types (Fig. 3). Most community types have about 70% of the shrub species present in a mature age class. The percentage of shrubs within the seedling and young age classes is much lower than the percentage within the decadent and dead age classes for most community types. This suggests that the grass and forb components of such types may exert greater dominance with time as the mature shrub species senesce. Exceptions to this relationship are present within the ARAR/FEID/POSA and ARLO/FEID community types, which have a much higher percentage of shrub species within seedling and young age classes. It is likely that more recent disturbances within

TABLE 4. Average production composition and percent constancy of shrub species within various sagebrush community types. The production composition values represent the average percentage of the total biomass that a species represents when it occurs within a community type.

Family	Taxa	ARNO ATCO SIHY	ARNO ORHY	ARNO AGSP	ARAR AGSP	ARAR FEID POSA	ARAR FEID	ARLO FEID	ARWYO SIHY
Asteraceae									
	Artemisia arbuscula	18(25)		30(5)	50(100)	39(100)	17(100)	20(25)	
	A. cana								
	A. frigida								
	A. longiloba							37(100)	
	A. ludoviciana								
	A. nova	64(100)	73(100)	57(100)	28(14)				
	A. tridentata ssp. *tridentata*						8(5)		
	A. tridentata ssp. *vaseyana*	4(8)		1(10)	14(4)	1(5)	4(30)	12(50)	
	A. tridentata ssp. *wyomingensis*	4(8)	30(6)	2(2)					34(100)
	Chrysothamnus nauseosus					8(5)			
	C. viscidiflorus	7(58)	7(37)	5(64)	5(28)	2(30)	4(70)	1(25)	4(100)
	Tetradymia canescens			2(8)	3(12)	1(10)			
	T. glabrata								
Caprifoliaceae									
	Sambucus cerulea								
	Symphoricarpos oreophilus			1(2)	1(4)	2(5)	2(5)		
Celastraceae									
	Forsellesia nevadensis						T(5)		
Chenopodiaceae									
	Atriplex canescens	1(8)							
	A. confertifolia	17(50)							
	Ceratoides lanata		10(6)						
	Grayia spinosa	3(8)	1(6)						
	Sarcobatus vermiculatus								
Ephedraceae									
	Ephedra nevadensis	10(42)	3(19)						
	E. viridis	1(8)		6(2)					
Pinaceae									
	Pinus monophylla			1(8)					
Rhamnaceae									
	Ceanothus velutinus								
Rosaceae									
	Amelanchier alnifolia			T(2)					
	A. utahensis								
	Cerocarpus ledifolius			T(2)	1(4)				
	Cowania mexicana	9(8)	6(25)						
	Peraphyllum ramosissimum			T(2)					
	Prunus virginiana								
	Purshia tridentata			11(2)	1(8)	1(5)	4(5)	9(25)	T(25)
	Rosa woodsii								
Saxifragaceae									
	Ribes aureum								
	R. cereum								

TABLE 4. Continued.

Family	Taxa	ARTR AGSP	ARTR FEID	ARVA AGSP	ARVA FEID	ARVA ELCI	ARVA SYOR AGSP	ARVA SYOR BRCA
Asteraceae								
	Artemisia arbuscula		1(12)	6(8)	7(7)			
	A. cana				T(1)			
	A. frigida				T(1)			
	A. longiloba			10(4)	4(1)			
	A. ludoviciana			13(2)				17(2)
	A. nova			2(4)			7(4)	
	A. tridentata ssp. *tridentata*	28(100)	20(100)		7(9)			
	A. tridentata ssp. *vaseyana*			49(100)	27(100)	17(100)	36(100)	22(90)
	A. tridentata ssp. *wyomingensis*			8(2)				
	Chrysothamnus nauseosus	5(17)	1(12)	5(12)		6(4)	4(8)	
	C. viscidiflorus	2(17)	7(75)	6(60)	4(70)	5(43)	4(72)	
	Tetradymia canescens	1(17)		2(20)		2(10)	1(4)	
	T. glabrata			1(4)				
Caprifoliaceae								
	Sambucus cerulea						6(4)	
	Symphoricarpos oreophilus			3(30)	2(31)		12(86)	9(90)
Celastraceae								
	Forsellesia nevadensis							
Chenopodiaceae								
	Atriplex canescens							
	A. confertifolia							
	Ceratoides lanata							
	Grayia spinosa							
	Sarcobatus vermiculatus					T(10)		
Ephedraceae								
	Ephedra nevadensis							
	E. viridis			3(1)				
Pinaceae								
	Pinus monophylla							
Rhamnaceae								
	Ceanothus velutinus				1(1)			
Rosaceae								
	Amelanchier alnifolia		2(12)	1(6)	10(1)		2(8)	5(20)
	A. utahensis			1(2)				
	Cerocarpus ledifolius							
	Cowania mexicana			T(2)	4(1)			
	Peraphyllum ramosissimum							
	Prunus virginiana							3(12)
	Purshia tridentata	2(33)	7(12)	15(50)	10(13)	7(30)	5(22)	5(20)
	Rosa woodsii		2(25)	3(2)	1(4)		1(4)	T(12)
Saxifragaceae								
	Ribes aureum					T(10)		4(2)
	R. cereum		5(12)	1(2)	1(1)			3(16)

TABLE 5. Average production composition and percent constancy of forb species within various sagebrush community types. The production composition values represent the average percentage of the total biomass that a species represents when it occurs within a community type.

Family	Taxa	ARNO ATCO SIHY	ARNO ORHY	ARNO AGSP	ARAR AGSP	ARAR FEID POSA	ARAR FEID	ARLO FEID	ARWYO SIHY
Apiaceae									
	Cymopterus ibapensis								
	Lomatium dissectum								
	L. nudicaule				3(8)	2(10)			
	L. sp.	T(8)		T(14)	T(24)	T(15)	T(5)	1(25)	T(25)
	Osmorhiza depauperata								
	O. occidentalis								
	Perideridia bolanderi								
Asteraceae									
	Achillea millefolium					1(5)	1(20)		1(25)
	Agoseris glauca	T(16)		T(10)	1(12)	1(10)	1(10)	T(75)	
	Antennaria microphylla	T(8)		3(4)	1(16)	4(15)	7(25)	T(25)	
	Aster scopulorum				1(16)				
	A. sp.	T(50)	1(19)	2(83)	2(8)	1(20)	1(5)	3(25)	T(25)
	Balsamorhiza hookeri			5(2)	5(4)	1(15)			
	B. sagittata			5(2)	5(4)		7(5)		
	Chaenactis douglasii			T(4)	T(8)	T(15)			T(25)
	Circium utahense					6(5)			
	Crepis acuminata	1(16)	T(6)	2(10)	1(32)	1(15)	T(15)	3(80)	
	C. modocensis								
	C. occidentalis			1(7)	2(12)	1(15)	2(5)		
	Erigeron argenteus	2(16)		1(10)	1(4)				
	E. pumilus	1(16)	1(31)	3(33)	2(44)	1(30)	2(5)		
	E. sp.		1(6)	1(7)	1(4)	1(20)	T(5)		
	Haplopappus acaulis		8(6)	2(43)	4(24)	3(15)			
	Helianthella uniflora			4(2)			T(5)	T(25)	
	Helianthus sp.								
	Heliomeris multiflora	1(8)	1(6)						
	Iva axillaris								
	Lygodesmia spinosa		1(6)	5(8)	1(36)	1(10)			
	Machaeranthera canescens			1(14)		T(5)			T(25)
	Madia glomerata								
	Pentradoria pumilus			3(2)					
	Senecio integerrimus	3(8)		T(2)	T(8)		1(25)	8(50)	
	S. multilobatus	T(8)	T(6)	3(50)	2(32)	T(15)			1(25)
	S. serra								
	Solidago occidentalis								
	Taraxacum officinale				T(8)				
	Tragopogon dubius			T(2)	T(4)		T(15)		
	Wyethia amplexicaulis						8(20)	4(25)	
	W. mollis							8(25)	
Berberidaceae									
	Mahonia repens								
Boraginaceae									
	Cryptantha gracilis	T(24)	1(8)	1(25)	T(12)	T(5)			2(25)
	C. sp.								
	Hackelia floribunda								
	H. micrantha						3(5)		
	H. patens	T(8)			T(4)				
	Lithospermum ruderale								
	Mertensia ciliata								
	M. oblongifolia			1(2)			T(5)		
Brassicaceae									
	Arabis confinus	8(8)							
	A. drummondi				T(4)				

TABLE 5. Continued.

Family	Taxa	ARTR AGSP	ARTR FEID	ARVA AGSP	ARVA FEID	ARVA ELCI	ARVA SYOR AGSP	ARVA SYOR BRCA
Apiaceae								
	Cymopterus ibapensis				T(1)			
	Lomatium dissectum	T(17)			T(1)	6(20)	10(4)	5(14)
	L. nudicaule						T(4)	
	L. species			1(18)	10(3)			4(4)
	Osmorhiza depauperata							
	O. occidentalis						T(4)	
	Perideridia bolanderi						T(4)	
Asteraceae								
	Achillea millefolium		4(50)	1(2)	3(45)		1(13)	1(32)
	Agoseris glauca		1(12)	T(50)	1(10)	1(20)	1(48)	T(10)
	Antennaria microphylla		2(25)	1(12)	3(24)		1(8)	1(10)
	Aster scopulorum			1(8)				
	A. sp.		T(12)	3(28)	5(3)		T(35)	T(10)
	Balsamorhiza hookeri							
	B. sagittata			12(22)	10(21)	24(40)	10(63)	15(57)
	Chaenactis douglasii			T(16)	T(3)		1(8)	
	Circium utahense		1(12)	T(8)				1(6)
	Crepis acuminata			1(54)	3(21)	3(20)	2(60)	1(20)
	C. modocensis			T(8)				
	C. occidentalis			1(22)	1(3)		1(4)	T(10)
	Erigeron argenteus			1(6)				
	E. pumilus			T(20)	1(4)	9(10)	1(4)	7(4)
	E. sp.				1(1)			
	Haplopappus acaulis			4(12)	3(1)			
	Helianthella uniflora		3(12)	3(4)	3(8)	7(20)	3(4)	5(32)
	Helianthus sp.				1(1)			5(4)
	Heliomeris multiflora			T(2)				
	Iva axillaris			T(2)				
	Lygodesmia spinosa			1(6)				
	Machaeranthera canescens	1(33)	T(12)	T(28)	1(3)			T(2)
	Madia glomerata			T(2)				
	Pentradoria pumilus			2(4)				
	Senecio integerrimus		1(25)	T(4)	T(21)		T(43)	T(16)
	S. multilobatus			1(40)	T(1)		1(17)	
	S. serra				1(1)			T(2)
	Solidago occidentalis				T(1)			
	Taraxacum officinale		T(25)	T(4)	1(3)		T(4)	T(4)
	Tragopogon dubius	4(17)		1(8)		2(30)		1(8)
	Wyethia amplexicaulis				6(9)	16(30)	11(8)	T(12)
	W. mollis							
Berberidaceae								
	Mahonia repens						T(4)	
Boraginaceae								
	Cryptantha gracilis	T(17)		T(12)				T(2)
	C. sp.			T(10)				
	Hackelia floribunda	5(17)	T(25)			T(10)		4(46)
	H. micrantha							
	H. patens			T(20)	3(1)	8(10)	1(48)	4(22)
	Lithospermum ruderale	4(17)	T(25)	6(10)	1(10)	6(20)		3(24)
	Mertensia ciliata				1(6)		3(4)	1(10)
	M. oblongifolia			T(6)	3(4)		1(8)	7(2)
Brassicaceae								
	Arabis confinus				1(3)			T(4)
	A. drummondi							

TABLE 5. Continued.

Family	Taxa	ARNO ATCO SIHY	ARNO ORHY	ARNO AGSP	ARAR AGSP	ARAR FEID POSA	ARAR FEID	ARLO FEID	ARWYO SIHY
Brassicaceae									
	A. glabra				T(4)				
	A. holboellii	1(24)	1(19)	2(11)	1(16)	T(5)	11(5)		T(25)
	A. sparsiflora	T(8)	T(19)	T(50)	1(36)	T(40)	T(25)	1(100)	1(25)
	Caulanthus crassicaulis								
	Draba sp.						2(5)		
	Erysimum capitatum	4(16)							
	Lesquerella kingii		1(6)	1(10)					
	Physaria chambersii			5(8)			T(5)		
	Streptanthus cordatus			T(2)					
Cactaceae									
	Echinocactus sp.								
	Mammalaria sp.								
	Opuntia polyacantha		T(6)	1(8)					
Caryophyllaceae									
	Arenaria kingii		4(6)	2(25)	4(16)				
	Silene douglasii								
	Stellaria jamesiana								
Chenopodiaceae									
	Halogeton glomeratus		T(6)						
Crassulaceae									
	Sedum stenopetalum			2(8)	1(12)	1(5)			
Euphorbiaceae									
	Euphorbia albomarginata			1(2)					
Fabaceae									
	Astragalus calycosus			1(23)					T(25)
	A. lentiginosus			2(4)	T(4)				
	A. newberryi	T(8)	T(6)	1(14)					
	A. oophorus				1(32)	2(10)	11(10)		T(25)
	A. purshii	1(8)	T(30)	1(39)	1(20)	7(15)	T(5)	1(25)	
	A. sp.		T(6)	1(10)	T(4)	8(10)	1(15)	1(25)	1(25)
	A. utahensis			T(2)		T(5)			T(25)
	Lathyrus sp.			3(4)					
	Lupinus argenteus	9(16)	3(6)	1(8)	14(8)	5(10)	3(60)		14(50)
	L. caudatus			8(4)	2(8)	3(10)	6(15)	8(50)	5(50)
	L. sercieus								
	Trifolium andersonii		T(6)	2(10)	5(16)	1(5)			
Gentianaceae									
	Frasera speciosa			1(4)					
	F. albomarginata								
Geraniaceae									
	Geranium fremontii								
	G. viscosissimum	T(1)							
Hydrophyllaceae									
	Hydrophyllum capitatum				T(4)				
	Phacelia hastata								
Lamiaceae									
	Agastache urticifolia								
	Monordella odoratissima								
	Scuttelaria antirrhinoides								
Linaceae									
	Linum perenne			1(18)	2(20)	2(15)			

TABLE 5. Continued.

Family	Taxa	ARTR AGSP	ARTR FEID	ARVA AGSP	ARVA FEID	ARVA ELCI	ARVA SYOR AGSP	ARVA SYOR BRCA
Brassicaceae								
	A. glabra							
	A. holboellii	T(17)		T(8)	T(6)		T(8)	
	A. sparsiflora	T(17)	T(25)	T(45)	T(37)		T(21)	1(20)
	Caulanthus crassicaulis			T(4)				
	Draba sp.			T(4)				
	Erysimum capitatum							
	Lesquerella kingii			1(4)				
	Physaria chambersii						T(4)	
	Streptanthus cordatus							
Cactaceae								
	Echinocactus sp.			T(2)				
	Mammalaria sp.			2(2)				
	Opuntia polyacantha			1(2)				
Caryophyllaceae								
	Arenaria kingii			1(12)	5(1)			
	Silene douglasii			1(4)				
	Stellaria jamesiana			3(4)				
Chenopodiaceae								
	Halogeton glomeratus							
Crassulaceae								
	Sedum stenopetalum			1(2)				
Euphorbiaceae								
	Euphorbia albomarginata			T(2)				
Fabaceae								
	Astragalus calycosus							
	A. lentiginosus			T(8)				
	A. newberryi			T(10)				
	A. oophorus			1(18)	T(9)	7(10)	T(30)	1(6)
	A. purshii			1(25)	T(3)			
	A. sp.		T(25)	T(2)	3(3)	3(10)		2(22)
	A. utahensis			T(2)				
	Lathyrus sp.			2(6)	1(1)			
	Lupinus argenteus	3(17)	5(38)	10(40)	5(42)	4(20)	3(21)	6(24)
	L. caudatus		2(25)	6(18)	12(31)	17(20)	10(43)	9(40)
	L. sercieus					1(10)		9(8)
	Trifolium andersonii			1(14)	T(1)		1(13)	
Gentianaceae								
	Frasera speciosa				3(1)		T(4)	4(12)
	F. albomarginata							T(4)
Geraniaceae								
	Geranium fremontii		1(12)	3(18)	30(1)		T(4)	10(30)
	G. viscosissimum			10(2)				4(8)
Hydrophyllaceae								
	Hydrophyllum capitatum			1(4)			1(17)	
	Phacelia hastata			1(6)		1(20)	1(4)	3(6)
Lamiaceae								
	Agastache urticifolia				13(1)	3(30)		4(40)
	Monardella odoratissima				T(1)			T(2)
	Scuttelaria antirrhinoides							T(4)
Linaceae								
	Linum perenne		1(12)	2(22)	1(21)	3(10)	2(8)	T(4)

TABLE 5. Continued.

Family	Taxa	ARNO ATCO SIHY	ARNO ORHY	ARNO AGSP	ARAR AGSP	ARAR FEID POSA	ARAR FEID	ARLO FEID	ARWYO SIHY
Malvaceae									
	Sidalacea neomexicana								
	Sphaeralcea coccinea		T(6)						
Onagraceae									
	Epilobium angustifolium								
Orobanchaceae									
	Orobanche californica			T(2)					
Paeoniaceae									
	Paeonia brownii								
Polemoniaceae									
	Eriastrum sparsiflorum								
	Gilia congesta								
	Ipomopsis aggregata			1(2)	2(8)	T(5)			1(25)
	Leptodactylon pungens	5(8)		2(8)	4(4)	3(15)	1(5)		1(25)
	Phlox hoodii	5(16)	1(6)	6(23)	2(8)	5(5)		19(25)	3(50)
	P. longifolia	2(50)	1(60)	1(68)	1(63)	1(70)	1(55)		T(75)
	Polemonium carneum								
Polygonaceae									
	Eriogonum brevicaule								
	E. caespitosum		5(6)	1(2)	2(36)	5(20)		3(25)	T(25)
	E. heracleoides				7(4)		3(25)	4(75)	2(25)
	E. microthecum		T(12)	1(36)	2(40)	1(30)	T(5)		
	E. ovalifolium		1(19)	1(2)	T(12)	3(5)		T(25)	1(25)
	E. racemosum								
	E. umbellatum	T(8)	2(6)	1(10)	1(8)		1(5)		
Ranunculaceae									
	Delphinium andersonii	T(8)							1(50)
	Thalictrum fendleri								
Rosaceae									
	Geum triflorum								
	Potentilla glandulosa						2(5)		
	P. gracilis						7(5)		
	P. sp.								1(25)
Santalaceae									
	Commandra pallida			2(5)	1(4)	2(5)	1(15)		T(25)
Saxifragaceae									
	Heuchera parvifolia			T(2)	T(4)				
	Lithophragma bulbifera								
Scrophulariaceae									
	Castilleja chromosa	T(33)	T(12)	1(38)	2(32)	1(20)	3(55)		1(25)
	C. cusickii				T(4)		T(5)		
	C. flava								
	C. linariaefolia			2(2)					
	Pedicularis centranthera			1(2)	2(8)				
	Penstemon caespitosum								
	P. confusus					2(5)			
	P. eatonii								
	P. humilus					1(5)			
	P. palmeri								
	P. rydbergii	4(8)		T(2)	1(8)	T(5)	2(5)		
	P. sp.	2(16)	T(6)	1(23)	1(4)	2(25)	2(30)		T(50)
	P. speciosus			1(25)					
	P. watsonii	T(8)							
Violaceae									
	Viola sp.								

TABLE 5. Continued.

Family	Taxa	ARTR AGSP	ARTR FEID	ARVA AGSP	ARVA FEID	ARVA ELCI	ARVA SYOR AGSP	ARVA SYOR BRCA
Malvaceae								
	Sidalcea neomexicana					T(10)	1(4)	
	Sphaeralcea coccinea							
Onagraceae								
	Epilobium angustifolium			5(6)				
Orobanchaceae								
	Orobanche californica							
Paeoniaceae								
	Paeonia brownii							4(2)
Polemoniaceae								
	Eriastrum sparsiflorum							T(2)
	Gilia congesta							T(2)
	Ipomopsis aggregata			T(12)			1(4)	T(2)
	Leptodactylon pungens	6(17)		1(25)	1(1)			
	Phlox hoodii			4(10)	1(1)		1(4)	5(2)
	P. longifolia		T(25)	1(70)	1(39)	1(30)	1(70)	1(30)
	Polemonium carneum			2(2)		1(10)		
Polygonaceae								
	Eriogonum brevicaule			1(2)				
	E. caespitosum			2(10)				
	E. heracleoides		3(38)	3(2)	5(65)	2(10)	4(35)	4(50)
	E. microthecum			1(26)	1(3)		2(30)	T(2)
	E. ovalifolium			1(6)	1(12)		T(8)	1(2)
	E. racemosum				1(4)		1(8)	
	E. umbellatum		1(12)	1(27)	1(9)	1(20)	1(21)	3(12)
Ranunculaceae								
	Delphinium andersonii							1(2)
	Thalictrum fendleri							2(2)
Rosaceae								
	Geum triflorum						1(4)	
	Potentilla glandulosa			1(2)	2(6)	1(10)		4(12)
	P. gracilis		1(12)					1(6)
	P. sp.			T(2)	13(1)			
Santalaceae								
	Commandra pallida			1(20)			1(26)	T(2)
Saxifragaceae								
	Heuchera parvifolia						1(4)	7(2)
	Lithophragma bulbifera			T(2)				
Scrophulariaceae								
	Castilleja chromosa		T(12)	1(22)	3(36)	12(10)	2(17)	4(22)
	C. cusickii		T(25)	3(12)		1(10)		2(6)
	C. flava			T(2)				
	C. linariaefolia			3(6)			2(17)	1(6)
	Pedicularis centranthera			T(8)				
	Penstemon caespitosum				T(1)			
	P. confusus			1(2)				
	P. eatonii				T(1)			
	P. humilus							
	P. palmeri			1(2)				
	P. rydbergii		4(12)	3(8)	2(6)	7(10)	3(17)	2(12)
	P. sp.		2(25)	1(22)	2(21)	T(10)	1(17)	1(16)
	P. speciosus			2(14)			4(8)	
	P. watsonii			6(4)	T(1)		7(13)	
Violaceae								
	Viola sp.			T(10)	1(9)	T(10)	1(26)	T(18)

TABLE 5. Continued.

Family	Taxa	ARNO ATCO SIHY	ARNO ORHY	ARNO AGSP	ARAR AGSP	ARAR FEID POSA	ARAR FEID	ARLO FEID	ARWYO SIHY
Iridaceae									
	Sisyrinchium halophilum					2(5)			
Liliaceae									
	Allium acuminatum	2(8)		1(5)	T(4)	1(20)	T(20)	T(50)	T(25)
	Calochortus nuttallii	T(8)		T(10)	T(4)				
	Fritillaria atropurpurea			T(5)	T(4)	T(5)			
	Leucorinum montanum								
	Smilacina racemosa								
	Zigadenus panidulatus	T(8)					1(10)		

these community types have acted to increase the number of young shrub species present. The ARVA/FEID, ARVA/SYOR/AGSP, and ARVA/SYOR/BRCA community types display relatively equal proportions of young and old shrub species, which indicates that in the absence of disturbance these types will probably maintain their current shrub composition levels.

Ground cover parameters display significant differences between community types (Table 9). The percent of vegetation plus litter comprising the ground cover of a site is highest on the more mesic community types (e.g., ARTR/FEID, ARVA/SYOR/BRCA). Xeric community types (e.g., ARNO/ORHY, ARNO/AGSP, ARAR/AGSP) have significantly lower vegetation plus litter cover, which results in much greater percentages of bare ground and gravel cover on those types.

In a study of southern Idaho sagebrush communities, Jensen (1983) found that measured soil erosion loss was negatively correlated

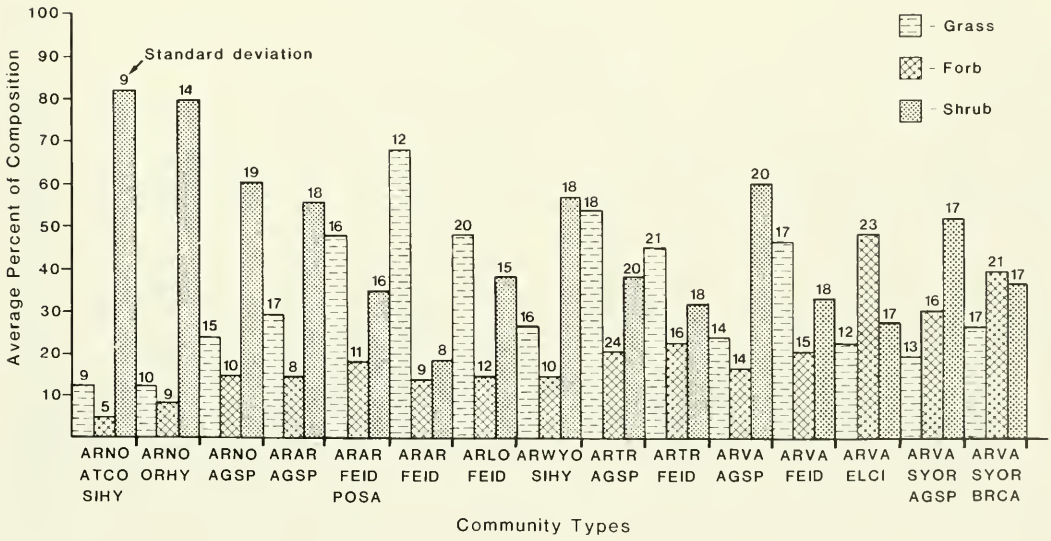

Fig. 2. Relative percent of total annual production contributed by grass, forb, and shrub growth forms within the sagebrush community types.

TABLE 5. Continued.

Family	Taxa	ARTR AGSP	ARTR FEID	ARVA AGSP	ARVA FEID	ARVA ELCI	ARVA SYOR AGSP	ARVA SYOR BRCA
Iridaceae								
	Sisyrinchium halophilum				1(1)			
Liliaceae								
	Allium acuminatum		2(12)	2(12)	1(21)	2(31)	2(17)	2(22)
	Calochortus nuttallii		T(12)	T(16)	T(3)		T(34)	
	Fritillaria atropurpurea			T(2)	T(3)			
	Leucorinum montanum			2(2)				
	Smilacina racemosa						10(4)	
	Zigadenus panidulatus			T(10)	T(1)		T(4)	T(2)

with vegetation and litter, and positively correlated with bare ground and gravel cover of a site. These relationships suggest that community types with *A. nova*, *A. arbuscula*, and *A. longiloba* as the dominant sagebrush species experience higher soil erosion losses than do *A. tridentata* ssp. *vaseyana*–dominated community types. Observations of soil erosion indicators (e.g., rilling, surface soil displacement) made over the sample sites support this assumption.

LITERATURE CITED

COOK, C. W., AND J. STUBBENDIECK, EDS. 1986. Range research: basic problems and techniques. Soc. for Range Manage., Denver, Colorado.

CRONQUIST, A., H. H. HOLMGREN, N. H. HOLMGREN, J. L. REVEAL, AND P. K. HOLMGREN. 1984. Intermountain flora. Vol. 4. New York Botanical Garden, Bronx, New York.

HARPER, J. L. 1977. Population biology of plants. Academic Press, New York.

HIRONAKA, M., M. A. FOSBERG, AND A. H. WINWARD. 1983. Sagebrush-grass habitat types of southern Idaho.

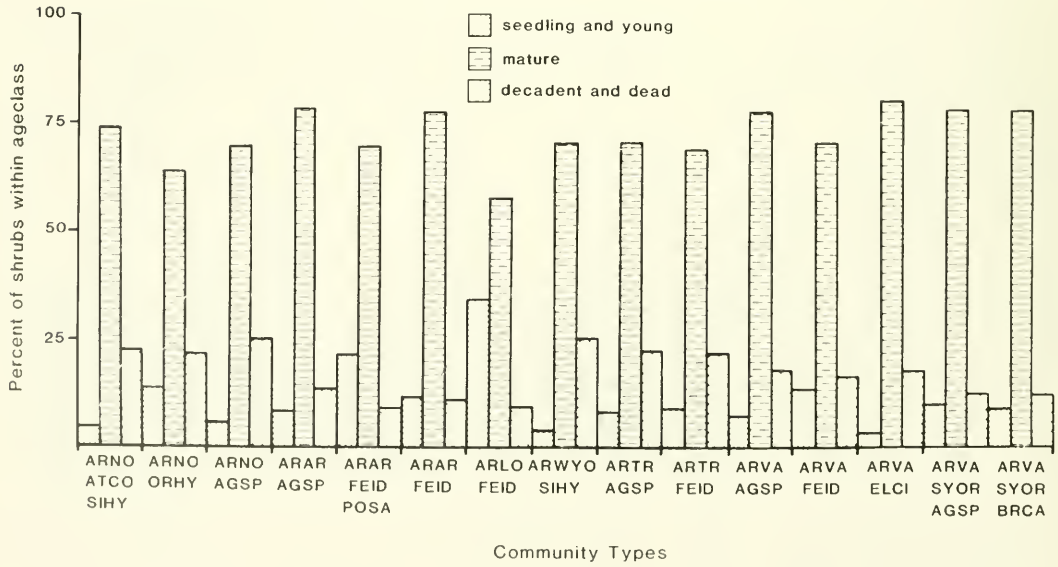

Fig. 3. Age-class distribution of shrub species within each sagebrush community type.

TABLE 6. A comparison of annual grass, forb, and shrub production by sagebrush community type.

Community Type	Grass production (kg/ha—dry wt.)			Forb production (kg/ha—dry wt.)			Shrub production (kg/ha—dry wt.)			Total production (kg/ha—dry wt.)		
	X	S	CV	X	S	CV	X	S	CV	X	S	CV
ARNO/ATCO/SIHY	50	32	64%	19	25	132%	362	145	40%	431	155	36%
ARNO/ORHY	43	32	76%	27	24	88%	364	194	53%	434	191	44%
ARNO/AGSP	102	61	60%	81	80	100%	307	164	53%	490	167	34%
ARAR/AGSP	133	72	54%	73	53	73%	349	202	58%	555	210	38%
ARAR/FEID/POSA	248	143	58%	81	57	70%	167	134	80%	496	183	37%
ARAR/FEID	423	158	37%	95	73	77%	109	57	52%	627	207	33%
ARLO/FEID	227	92	40%	78	80	100%	180	64	36%	485	111	23%
ARWYO/SIHY	173	87	50%	81	57	70%	341	106	31%	595	32	5%
ARTR/AGSP	355	357	100%	114	163	143%	255	148	58%	724	405	56%
ARTR/FEID	392	147	38%	249	222	89%	295	146	49%	936	290	31%
ARVA/AGSP	156	108	69%	135	150	111%	437	270	62%	728	349	48%
ARVA/FEID	343	156	45%	183	192	105%	258	231	89%	784	329	42%
ARVA/ELCI	260	136	52%	650	496	76%	316	226	72%	1226	576	47%
ARVA/SYOR/AGSP	187	120	64%	280	290	104%	233	106	45%	700	308	44%
ARVA/SYOR/BRCA	224	165	68%	536	543	101%	375	270	72%	1135	647	57%
		average	58%			96%			57%			38%

Note: X = mean; S = standard deviation; CV = coefficient of variation

TABLE 7. Comparison of percent shrub cover by species within the sagebrush community types studied.

Variable		Community type														
		ARNO ATCO SIHY	ARNO ORHY	ARNO AGSP	ARAR AGSP	ARAR FEID POSA	ARAR FEID	ARLO FEID	ARWYO SIHY	ARTR AGSP	ARTR FEID	ARVA AGSP	ARVA FEID	ARVA ELCI	ARVA SYOR AGSP	ARVA SYOR BRCA
Total shrub	x	19.3	21.9	16.0	20.4	16.5	11.6	23.3	18.8	21.2	16.3	24.2	18.6	16.0	25.0	22.5
cover	s	4.0	5.8	7.0	6.6	6.5	6.5	10.3	4.3	10.0	6.9	9.5	9.9	5.2	7.6	9.9
ARNO	x	16.1	19.3	14.8	1.0	2.0	—	—	—	—	—	—	—	—	—	—
cover	s	5.6	5.8	6.9	—	—	—	—	—	—	—	—	—	—	—	—
ARAR	x	—	—	1.0	19.0	15.8	10.1	2.0	2.0	—	1.0	1.0	3.6	—	2.0	—
cover	s	—	—	0	6.4	6.1	7.0	1.4	—	—	—	—	3.2	—	—	—
CHVI	x	1.6	9.4	1.8	1.8	1.0	4.2	2.5	2.2	—	4.0	2.0	3.3	2.5	1.6	1.4
cover	s	0.8	10.4	1.4	1.0	0	6.5	0.7	1.9	—	2.7	1.8	4.3	1.4	0.8	1.0
ARWYO	x	1.0	—	1.0	—	—	—	—	11.2	—	—	2.0	—	—	—	—
cover	s	—	—	—	—	—	—	—	4.7	—	—	—	—	—	—	—
ARTR	x	—	—	—	—	—	—	—	7.0	15.3	9.5	4.0	3.0	—	—	1.5
cover	s	—	—	—	—	—	—	—	—	12.3	7.5	2.8	1.8	—	—	0.7
ARVA	x	—	—	1.2	6.0	—	2.2	6.5	—	12.5	13.0	18.0	15.2	10.1	15.1	13.0
cover	s	—	—	0.5	1.4	—	2.4	4.9	—	10.6	0	8.6	10.6	6.3	6.8	7.6
SYOR	x	—	1.0	—	1.2	—	2.0	—	1.0	2.0	1.0	2.8	1.8	1.0	7.9	7.2
cover	s	—	—	—	0.5	—	—	—	—	—	—	2.0	1.2	0	5.6	7.9
PUTR	x	—	—	3.3	3.5	5	10	14	—	1.0	2.5	9.0	6.6	7.3	4.7	4.7
cover	s	—	—	1.5	3.5	—	11	—	—	—	2.4	5.8	4.9	8.3	4.6	4.0

Note: x = average percent cover on sites where the species occurs, s = standard deviation of the population where the species occurs.

TABLE 8. Comparison of shrub density and age class relationships by sagebrush community type.

Community type	Total shrubs per hectare		Relative percentage by age class: Seedling		Young		Mature		Decadent		Dead	
	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s
ARNO/ATCO/SIHY	23,991	5,911	0.0	0.0	5.0	4.8	73.3	10.6	14.8	7.5	6.9	4.6
ARNO/ORHY	32,473	16,410	0.1	0.3	14.1	24.9	64.0	20.6	15.7	10.0	6.0	5.2
ARNO/AGSP	30,195	14,085	0.2	0.8	5.5	4.8	69.5	12.2	19.2	9.8	5.6	6.4
ARAR/AGSP	35,237	11,350	0.5	1.8	7.4	9.8	78.8	16.6	9.8	7.9	3.4	5.4
ARAR/FEID/POSA	47,664	29,256	1.2	2.0	20.2	20.5	69.1	21.1	6.8	4.8	2.6	2.9
ARAR/FEID	36,680	21,916	3.4	5.0	7.7	14.9	77.4	19.4	6.3	5.1	4.9	5.8
ARLO/FEID	44,329	32,152	3.8	4.3	29.5	29.5	57.2	29.4	4.8	3.5	5.0	6.7
ARWYO/SIHY	20,865	10,565	0.0	0.0	4.3	4.5	70.7	3.0	18.0	2.6	7.0	2.0
ARTR/AGSP	10,091	2,519	0.0	0.0	8.2	18.1	70.5	28.3	6.8	5.4	14.3	13.2
ARTR/FEID	24,347	21,023	2.2	4.5	7.0	6.4	68.2	21.0	11.5	11.4	11.0	8.4
ARVA/AGSP	19,006	8,670	0.4	1.5	6.5	7.9	76.6	12.7	10.4	8.0	7.0	6.4
ARVA/FEID	21,112	10,871	3.7	8.3	10.4	16.8	69.6	23.4	5.8	5.8	10.6	15.0
ARVA/ELCI	10,256	4,205	0.1	0.3	2.9	3.9	80.4	13.4	10.7	9.6	6.1	4.4
ARVA/SYOR/AGSP	20,703	7,585	1.4	5.7	8.7	10.8	77.3	17.1	7.2	5.5	5.3	8.2
ARVA/SYOR/BRCA	17,474	7,149	1.1	2.6	8.0	10.8	77.4	18.1	4.7	4.7	6.7	7.0

Note: x = mean, s = standard deviation of the population.

TABLE 9. Relative percentage of total ground cover contributed by various parameters by sagebrush community type.

Ground cover parameter		ARNO ATCO SIHY	ARNO ORHY	ARNO AGSP	ARAR AGSP	ARAR FEID POSA	ARAR FEID	ARLO FEID	ARWYO SIHY	ARTR AGSP	ARTR FEID	ARVA AGSP	ARVA FEID	ARVA ELCI	ARVA SYOR AGSP	ARVA SYOR BRCA
% Veg + litter	(X)	36^{a}	39^{a}	44^{a}	$50^{a,b}$	$52^{a,b}$	60^{b}	$58^{a,b}$	$72^{b,c}$	$71^{b,c}$	82^{c}	59^{b}	78^{c}	64^{b}	63^{b}	78^{c}
	(S)	13	11	14	12	15	15	14	12	18	14	17	14	19	14	14
	(SE)	4	3	2	2	4	3	7	6	7	5	2	2	6	3	2
% Bare ground	(X)	$22^{b,c}$	24^{c}	$15^{a,b}$	10^{a}	$15^{a,b}$	$14^{a,b}$	$23^{a,b}$	$19^{a,b}$	$22^{a,b}$	$15^{a,b}$	$13^{a,b}$	12^{a}	$24^{b,c}$	$21^{b,c}$	$14^{a,b}$
	(S)	12	10	8	6	10	10	16	2	14	10	10	8	18	7	11
	(SE)	3	3	1	1	2	2	8	1	6	4	1	1	6	1	2
% Gravel	(X)	$34^{b,c}$	$33^{b,c}$	36^{c}	$31^{b,c}$	$26^{b,c}$	21^{b}	18^{a}	8^{a}	4^{a}	3^{a}	21^{b}	8^{a}	7^{a}	12^{a}	8^{a}
	(S)	7	13	15	15	16	17	18	9	5	5	14	11	8	11	10
	(SE)	2	3	2	3	4	4	9	4	2	2	2	1	3	2	2
% Cobblestone	(X)	9^{b}	$4^{a,b}$	$4^{a,b}$	9^{b}	$5^{a,b}$	1^{a}	$2^{a,b}$	$1^{a,b}$	$3^{a,b}$	$1^{a,b}$	7^{b}	1^{a}	$4^{a,b}$	$4^{a,b}$	1^{a}
	(S)	10	6	5	8	6	2	2	2	4	1	8	2	6	6	2
	(SE)	3	1	1	2	1	1	1	1	2	1	1	1	2	1	1

Note: Means having the same letter in superscript do not differ significantly as determined by the Tukey-HSD multiple range test interpreted at the 95% confidence level.

Bull. 35, University of Idaho For. Wildlife and Range Expt. Sta., Moscow.

JENSEN, M. E. 1983. Applicability of the Universal Soil Loss Equation for southeastern Idaho wildlands. Great Basin Nat. 43: 579–584.

———. 1988. Soil characteristics of mountainous northeastern Nevada sagebrush community types. Great Basin Nat. (in press).

JENSEN, M. E., L. S. PECK, AND M. V. WILSON. 1988. A sagebrush community type classification for mountainous northeastern Nevada rangelands. Great Basin Nat. 48(4): 422–433.

MUEGGLER, W. F., AND W. L. STEWART. 1980. Grassland and shrubland habitat types of western Montana. USDA For. Serv. Gen. Tech. Rept. INT-66, Intermt. For. and Range Expt. Sta., Ogden, Utah.

MUELLER-DOMBOIS, D., AND H. ELLENBERG. 1974. Aims and methods of vegetation ecology. John Wiley and Sons, New York.

NOAA. 1986. Climatological data annual summary—Nevada. Nat. Oceanic Atmos. Admin., Asheville, North Carolina.

NORUSIS, M. J. 1985. Statistical package for the social sciences. SPSS, Inc., Chicago, Illinois.

RISC. 1983. Guidelines and terminology for range inventories and monitoring. Report of the Range Inventory Standardization Committee. Soc. for Range Manage., Denver, Colorado.

STEVENS, R., AND E. D. MCARTHUR. 1974. A simple field technique for identification of some sagebrush taxa. J. Range Manage. 27: 325–326.

STURGES, D. L. 1977. Soil water withdrawal and root characteristics of big sagebrush. Amer. Midl. Nat. 98: 257–274.

USDA. 1969. Range environmental analysis handbook. USDA For. Serv., Intermountain Region, Ogden, Utah.

_____. 1975. Soil taxonomy. Soil Survey Staff. USDA Agric. Handb. 436. U.S. Govt. Printing Office, Washington, D.C.

WINWARD, A. H. 1980. Taxonomy and ecology of sagebrush in Oregon. Agric. Expt. Sta. Bull. 642. Oregon State University, Corvallis.

_____. 1983. Using sagebrush ecology in wildland management. *In:* K. L. Johnson, ed., First Utah Shrub Ecology Workshop Proceedings, 1983. Utah State University, Logan.

ZAMORA, B., AND P. T. TUELLER. 1973. *Artemisia arbuscula*, *A. longiloba* and *A. nova* habitat types in northern Nevada. Great Basin Nat. 33: 225–242.

ZAR, J. R. 1974. Biostatistical analysis. Prentice-Hall Inc., Englewood Cliffs, New Jersey.

A SAGEBRUSH COMMUNITY TYPE CLASSIFICATION FOR MOUNTAINOUS NORTHEASTERN NEVADA RANGELANDS

M. E. Jensen[1], L. S. Peck[2], and M. V. Wilson[3]

ABSTRACT.—A synecological study of sagebrush-dominated rangelands was conducted on the Humboldt National Forest, northeastern Nevada, between 1983 and 1986. A total of 372 relatively undisturbed sites were sampled for both vegetation and soil parameters, with 35 grass, 39 shrub, and 140 forb species identified. Plant species production data were used to develop a hierarchical, floristic-based community type classification with TWINSPAN. Seventeen sagebrush community types were identified in this analysis and named by their dominant shrub and grass species. The dominant sagebrush species of the community types are *Artemisia tridentata* ssp. *vaseyana* (5 community types), *A. tridentata* ssp. *wyomingensis* (3 community types), *A. tridentata* ssp. *tridentata* (2 community types), *A. arbuscula* (3 community types), *A. nova* (3 community types), and *A. longiloba* (1 community type). Multivariate analysis revealed that all community types contain significantly different plant species compositions. Shrub species are more effective in discriminating between community types than grass species, which, in turn, are more effective than forb species.

One approach toward rangeland plant community description in the Great Basin is the identification of habitat types (Daubenmire 1952, 1968). Habitat typing, which has traditionally been used in forest environments (Hoffman and Alexander 1976, Pfister et al. 1977), is being used increasingly to characterize rangelands [e.g., Zamora and Tueller (1973) in Nevada, Hironaka et al. (1983) in Idaho, and Mueggler and Stewart (1980) in Montana]. In this approach, climax plant communities are used as environmental integrators that permit the identification of environments (habitats) with similar biotic potentials throughout the landscape (Mueggler and Stewart 1980). Environments with the same potential to support a given climax plant community are classified within the same habitat type, regardless of current successional status. The application of habitat typing to western rangelands can present problems, however, due primarily to disturbance and the resulting lack of reference climax plant communities on the landscape.

Other approaches to rangeland plant community description include the range-site method commonly used by the USDA Soil Conservation Service, and the ecological-site method, which recently has been proposed as an alternative to range site or habitat type in identifying the basic unit of rangeland classification (RISC 1983). Much disagreement still exists as to what type of classification approach should be used in describing rangeland plant communities (Anderson 1983, Dyksterhuis 1983 and 1985, Daubenmire 1984, Hoffman 1985, Hall 1985).

Komarkova (1983) compared the habitat type approach to other methods of vegetation classification. She concluded that vegetation classifications resulting from the habitat-type approach tend to be very similar to those obtained from floristic-based methods. Komarkova also stressed that vegetation should be described first in terms of floristic relationships, without undue concern for successional status in developing initial floristic classifications for an area. This basic philosophy was followed in this study.

Little quantitative information exists concerning the mountainous rangeland plant communities of northeastern Nevada. Even less information is available for successional processes operable in such communities. Continued use of these lands by livestock, mineral, wildlife, and watershed interest groups dictates that plant community classifications be developed by land management agencies, even though a universal acceptable method for rangeland classification is not available. Such classifications are required if consistent assessments of the landscape's potential for management are to be made.

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The goal of this paper is to present a rangeland plant community classification for the Humboldt National Forest of northeastern Nevada. The classification groupings presented are referred to as community types, in that they are based upon floristic similarities in both the overstory and undergrowth layers present at a given site. These groupings are, however, approximately equivalent to the potential natural communities of an ecological site (RISC 1983) since they represent vegetation associations that are in dynamic equilibrium with current environmental conditions. This classification provides land managers with a communication tool that will improve their ability to describe an area's land-based potentials.

STUDY AREA AND METHODS

The study was conducted in the years 1983–1986 on the eight mountain ranges of the Humboldt National Forest, northeastern Nevada (Fig. 1). The study area is characteristic of higher-elevation rangelands of the Great Basin having semiarid climates. Elevation ranges between 1,800 m and 3,100 m, and average annual precipitation is approximately 33 cm.

A total of 372 rangeland sites were sampled to correlate soils to plant community types in an order 3 soil survey of the forest, in cooperation with National Cooperative Soil Surveys. Site selection was based on "subjective sampling without preconceived bias" as described by Mueller-Dombois and Ellenberg (1974). Reconnaissance of an area was made prior to site selection to inspect for the dominant soil families and sagebrush species present. Samples were taken on dominant soil polypedons that supported an apparently representative plant community for an area. This approach minimized the number of environmental ecotones described through avoidance of inclusions of dissimilar soils within a soil map unit. Relatively undisturbed sites were sampled, with areas of obvious disturbance (e.g., recent burn, heavy livestock use, compaction) being omitted. The vegetation communities described were the best expressions of late seral or climax plant community development present in the study area.

Sampling at each site was conducted within a 323-m^2 macroplot located to represent average vegetation and soil conditions. Annual biomass production was determined by plant species in ten 2.93-m^2 circular microplots located randomly in the macroplot. A weight-estimate method was used to determine plant species production, with two microplots being clipped at each site and cover estimates of production taken in the remaining microplots (Pechanec and Pickford 1937). Green weight production estimates were converted to dry weight values through use of conversion factors routinely used by Intermountain Region, U.S. Forest Service range personnel (USDA 1969).

Shrub species canopy cover was measured by the line intercept method (Canfield 1941) beneath five 15.2-m line transects. Transects were located randomly within the macroplot along the slope contour. Density of shrub species by age-class grouping was recorded by counting the total number of shrubs rooted within a 0.91-m belt oriented parallel to each line transect. Rooted frequency (Hyder et al. 1963) and ocular canopy cover estimates were obtained within five 25 × 50-cm quadrats located at 2.5-m intervals along each line transect. A total of 25 quadrats were measured within a macroplot. Cover assessments of soil surface parameters (e.g., bare soil, litter, gravel) were derived from sampling of five fixed points within each 25 × 50-cm quadrat.

The majority of plants were identifiable to the species level during the period of field sampling. Specimens of unknown plant species were collected for taxonomic verification. Sagebrush species and subspecies were identified using morphological characteristics (Winward 1980), with simple chromatographic tests based upon fluorescence in alcohol performed as a check on such classifications (Stevens and McArthur 1974). Taxonomic nomenclature follows Cronquist et al. (1984).

Soil descriptions were made within all macroplots using standard pedon description methods that facilitated classification to the family level of soil taxonomy (USDA 1975). Soils were described to a depth of 1.5 m or to a shallower depth if a restrictive layer was present (e.g., duripan, paralithic or lithic contact). Composite samples were collected for chemical analysis at each pedon at depths of 0–15 and 40–60 cm. Generalized site characterizations were made at each macroplot to indicate the geomorphic features present.

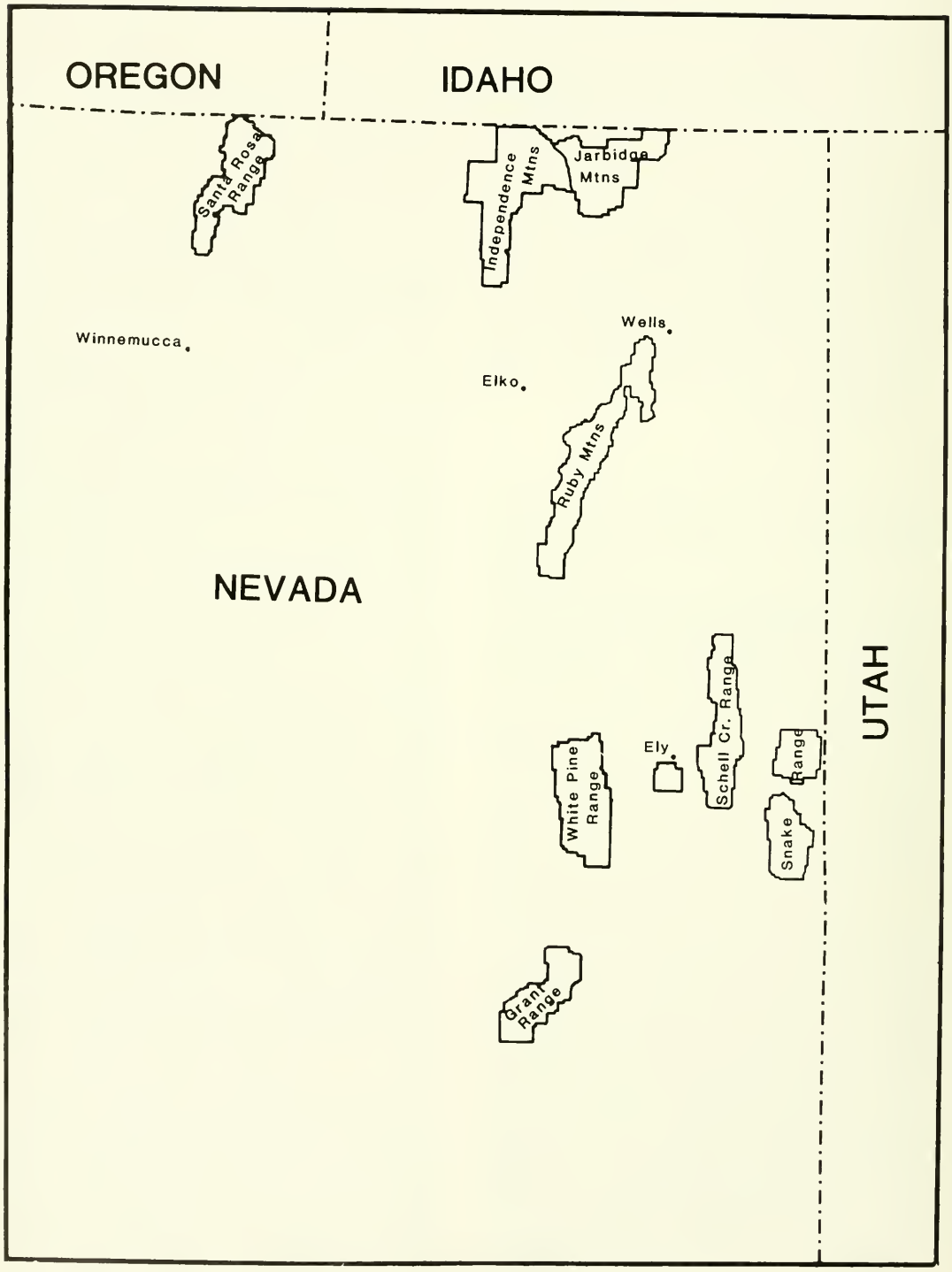

Fig. 1. The Humboldt National Forest of northeastern Nevada.

TABLE 1. Listing of dominant and indicator plant species found over the sagebrush communities studied.

GRASSES	SHRUBS	FORBS	
Agropyron spicatum	*Amelanchier alnifolia*	*Achillea millefolium*	*Halogeton glomeratus*
Agropyron trachycaulum	*Artemisia arbuscula*	*Agoseris glauca*	*Hackelia patens*
Bromus carinatus	*Artemisia frigida*	*Agastache urticifolia*	*Heliomeris multiflora*
Bromus inermis	*Artemisia longiloba*	*Arabis holboellii*	*Helianthella uniflora*
Bromus tectorum	*Artemisia nova*	*Arenaira kingii*	*Hydrophyllum capitatum*
Carex spp.	*Artemisia tridentata* ssp. *tridentata*	*Astragalus calycosus*	*Linum perenne*
Elymus cinereus	*Artemisia tridentata* ssp. *vaseyana*	*Astragalus purshii*	*Lomatium dissectum*
Festuca idahoensis	*Artemisia tridentata* ssp. *wyomingensis*	*Aster scopulorum*	*Lupinus argenteus*
Koelaria cristata	*Atriplex confertifolia*	*Balsamorhiza sagittata*	*Lupinus caudatus*
Oryzopsis hymenoides	*Chrysothamnus nauseosus*	*Castilleja chromosa*	*Mahonia repens*
Poa ampla	*Chrysothamnus viscidiflorus*	*Commandra pallida*	*Mertensia obliogifolia*
Poa fendleriana	*Cowania mexicana*	*Crepis acuminata*	*Opuntia polyacantha*
Poa nevadensis	*Ephedra nevadensis*	*Delphinium andersonii*	*Orobanche californica*
Poa pratensis	*Prunus virginiana* var. *melanocarpa*	*Epilobium angustifolium*	*Pedicularis centranthera*
Poa sandbergii	*Purshia tridentata*	*Erigeron argenteus*	*Penstemon watsonii*
Sitanion hystrix	*Symphoricarpos oreophilus*	*Eriogonum heracleoides*	*Phlox hoodii*
Stipa columbiana		*Eriogonum microthecum*	*Phlox longifolia*
Stipa comata		*Euphorbia albomorginata*	*Senecio integerrimus*
Stipa lettermanii		*Frasera speciosa*	*Senecio multilobatus*
Stipa thruberiana		*Geranium fremontii*	*Sedum stenopetalum*
		Geranium viscosissimum	*Wyethia amplexicaulis*
		Geum triflorum	*Stellaria jamesiana*

Two-Way Indicator Species Analysis, TWINSPAN (Hill 1979, Hill and Gauch 1980), was used to develop community type classifications for the sagebrush communities sampled. This is a polythetic, divisive, hierarchical classification technique similar to the Braun-Blanquet classification method in its emphasis on indicator species and production of an arranged species-sample data matrix (Gauch 1982).

All sites and species were included in initial TWINSPAN analyses utilizing, in turn, vegetation frequency, cover, and production attributes. Samples were tentatively assigned to a community type based upon their TWINSPAN cluster assignment. Each sample was then inspected to see if it contained abundances of indicator plant species similar to those contained by other samples in its assigned community type. Samples displaying low similarity to other samples in their community type were reassigned to a different community type when appropriate. A few samples were omitted from analysis since they displayed little similarity to other samples. The TWINSPAN analyses based upon frequency, cover, and production attributes produced similar arranged data matrices and indicator species lists. The analysis based upon production attributes yielded the clearest aggregation of samples into community types and was used to produce the final community type classification.

Phases of community types were determined through similar TWINSPAN analyses of each community type subset. Phases were described for community types displaying floristically dissimilar subgroupings that could be related to major differences in soil properties.

DECORANA (Hill 1979) was used to ordinate the plant species and samples of the TWINSPAN analysis to facilitate determination of environmental gradients that influence the distribution of community types. Multivariate analysis programs of SPSS (Norusis 1985) detected differences in overall vegetation composition between community types and determined which plant species were most effective in discriminating between community types.

RESULTS

A total of 218 plant species were found within the 372 rangeland sites sampled. The graminoids were represented by 35 species, the shrubs by 39 species, and the forbs by 140 species. Tree species were present in minor amounts on some sites with four species described. A listing of the major plant species present is provided in Table 1.

TABLE 2. List of sagebrush community types and abbreviated codes referred to in the text.

Abbreviated code	Community type
ARNO/ATCO/SIHY	*Artemisia nova/Atriplex confertifolia/Sitanion hystrix*
ARNO/ORHY	*A. nova/Oryzopsis hymenoides*
ARNO/AGSP	*A. nova/Agropyron spicatum*
ARAR/AGSP	*A. arbuscula/Agropyron spicatum*
ARAR/FEID/POSA	*A. arbuscula/Festuca idahoensis/Poa sandbergii*
ARAR/FEID	*A. arbuscula/Festuca idahoensis*
ARLO/FEID	*A. longiloba/Festuca idahoensis*
ARWYO/SIHY	*A. tridentata* ssp. *wyomingensis/Sitanion hystrix*
ARWYO/POSA	*A. tridentata* ssp. *wyomingensis/Poa sandbergii*
ARWYO/AGSP	*A. tridentata* ssp. *wyomingensis/Agropyron spicatum*
ARTR/AGSP	*A. tridentata* ssp. *tridentata/Agropyron spicatum*
ARTR/FEID	*A. tridentata* ssp. *tridentata/Festuca idahoensis*
ARVA/AGSP	*A. tridentata* ssp. *vaseyana/Agropyron spicatum*
ARVA/FEID	*A. tridentata* ssp. *vaseyana/Festuca idahoensis*
ARVA/ELCI	*A. tridentata* ssp. *vaseyana/Elymus cinereus*
ARVA/SYOR/AGSP	*A. t.* ssp. *vaseyana/Symphoricarpos oreophilus/Agropyron spicatum*
ARVA/SYOR/BRCA	*A. t. ssp. vaseyana/Symphoricarpos oreophilus/Bromus carinatus*

TWINSPAN classification based upon plant species production over all samples resulted in the identification of 15 sagebrush community types and 1 wet meadow complex (Fig. 1). Sagebrush community type names were derived by denoting the dominant shrub and grass species characteristic of each type (Table 2). Abbreviations for community names appear in Table 2. In all cases, such grass and shrub species were idenitified in the TWINSPAN analysis as being the principal indicator plant species for their respective community types. Forb species generally were not effective in separating community types, except at the phase level. Vegetation characteristics of these community types are discussed by Jensen et al. (1988).

The classification dendrogram developed from the TWINSPAN analysis of production shows the successive division of the data into more homogenous vegetation classification groupings (Fig. 2). The first TWINSPAN classification division separated most of the tall sagebrush communities (e.g., ARVA/AGSP, ARVA/FEID, ARTR/AGSP) from the low sagebrush communities (e.g., ARAR/AGSP, ARNO/ORHY). At the second classification division, the low sagebrush communities were split primarily into groupings that had *Artemisia arbuscula* or *A. nova* as the dominant shrub species. The tall sagebrush–dominated grouping was divided into a wet meadow community type and various sagebrush communities. The division process was continued until a given grouping displayed a dominant shrub and codominant grass species and a reasonable consistency of secondary species; that is, until a sagebrush community type was obtained.

TWINSPAN was effective in displaying apparent community types within the sagebrush communities sampled. It does not, however, indicate whether such community types differ significantly in their vegetation composition. Many studies in plant community classification utilize various ordination or clustering techinques to define plant communities and habitat types (Hironaka et al. 1983, Marks and Harcombe 1981, Mueggler and Stewart 1980, Youngblood et al. 1985); yet rarely are such classification groupings tested for significance (Strauss 1982). The TWINSPAN-generated classification produced sagebrush community types that are significantly different from each other in overall vegetation composition (Table 3). Community types displaying large separations in the TWINSPAN classification dendrogram (Fig. 2) tend to show high F ratios in this analysis.

A variety of plant species are effective in discriminating between the sagebrush community types (Table 4). The plant species presented in this table are also the primary indicator species of the TWINSPAN analyses. These results suggest that shrub and grass species tend to have greater significance than forb species in determining plant community types for the rangelands studied.

A key to the sagebrush community types is presented in Table 5. The indicator species

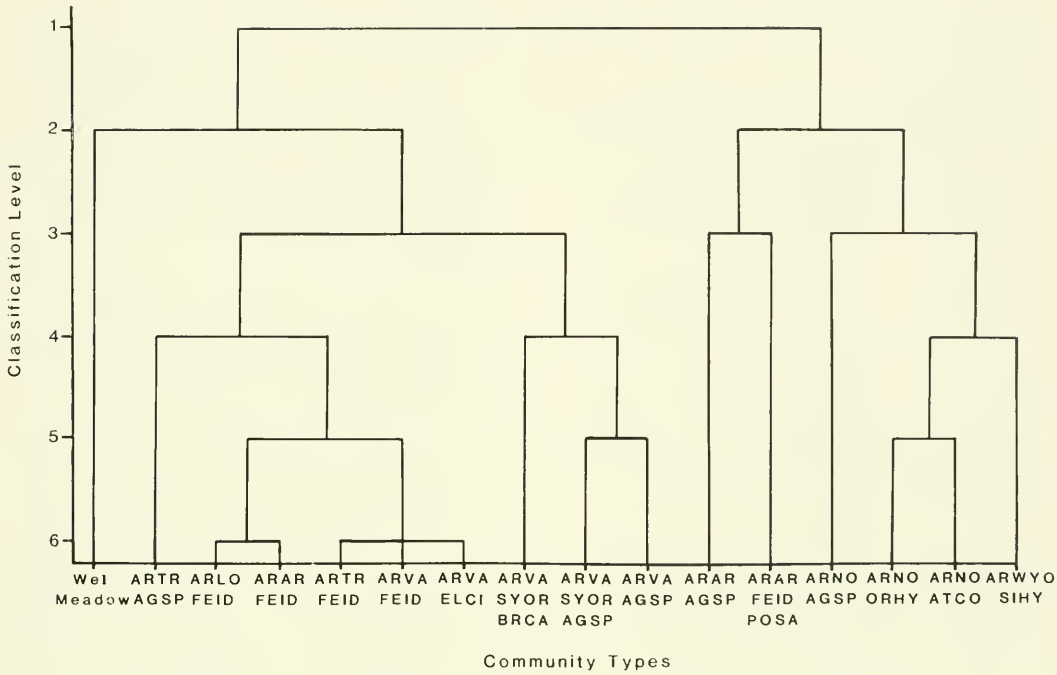

Fig. 2. TWINSPAN classification dendrogram of the sagebrush community types.

TABLE 3. Multivariate F ratios testing the hypothesis that pairs of sagebrush community types differ in their average vegetation composition.

Community type	Community Type: ARNO ATCO SIHY	ARNO ORHY	ARNO AGSP	ARAR AGSP	ARAR FEID POSA	ARAR FEID	ARLO FEID	ARWYO SIHY	ARTR AGSP	ARTR FEID	ARVA AGSP	ARVA FEID	ARVA ELCI	ARVA SYOR AGSP	ARVA SYOR BRCA
ARNO/ATCO/SIHY	—														
ARNO/ORHY	2	—													
ARNO/AGSP	2	2	—												
ARAR/AGSP	14	13	20	—											
ARAR/FEID/POSA	13	12	16	5	—										
ARAR/FEID	7	6	6	4	2	—									
ARLO/FEID	11	10	11	9	6	4	—								
ARWYO/SIHY	14	14	17	14	14	10	13	—							
ARTR/AGSP	26	25	28	27	25	17	19	24	—						
ARTR/FEID	34	33	39	37	33	19	22	27	2	—					
ARVA/AGSP	20	17	31	27	17	6	8	19	26	38	—				
ARVA/FEID	14	12	17	16	6	3	6	16	22	30	6	—			
ARVA/ELCI	6	6	6	7	6	6	6	7	13	14	6	6	—		
ARVA/SYOR/AGSP	17	15	20	21	15	6	8	18	24	33	6	6	7	—	
ARVA/SYOR/BRCA	15	14	16	18	12	6	9	17	23	31	10	6	6	6	—

Note: All values are significant at the 95% confidence level.

discussed in this table are those that best distinguished between vegetation groupings in the TWINSPAN analysis. The ARWYO/POSA and ARWYO/AGSP community types presented in Table 6 are not presented in the TWINSPAN dendrogram (Fig. 2) because of limited sampling in these types (i.e., two descriptions each). They are included in the scriptions each). They are included in the community type key since thay have been described in areas adjacent to this study (Hironaka et al. 1983) and may be more extensive in northern Nevada than our sampling indicates. The community type phases presented were derived through TWINSPAN analysis of individual community type subsets of the

TABLE 4. Listing of the 30 most useful plant species in discriminating between the sagebrush communities studied.

Order of significance	Species
1	*Artemisia tridentata* ssp. *tridentata*
2	*A. arbuscula*
3	*A. nova*
4	*A. tridentata* ssp. *wyomingensis*
5	*Festuca idahoensis*
6	*A. longiloba*
7	*A. tridentata* ssp. *vaseyana*
8	*Symphoricarpos oreophilus*
9	*Purshia tridentata*
10	*Elymus cinereus*
11	*Wyethia amplexicaulis*
12	*Agropyron spicatum*
13	*Poa sandbergii*
14	*Poa nevadensis*
15	*Poa fendleriana*
16	*Senecio multilobatus*
17	*Carex* spp.
18	*Agoseris glauca*
19	*Sitanion hystrix*
20	*Chrysothamnus nauseosus*
21	*Chrysothamnus viscidiflorus*
22	*Balsamorhiza sagittata*
23	*Lupinus argenteus*
24	*Helianthella uniflora*
25	*Oryzopsis hymenoides*
26	*Stipa columbiana*
27	*Bromus carinatus*
28	*Bromus tectorum*
29	*Geranium viscosissimum*
30	*Lupinus caudatus*

Note: All species listed display significant differences ($P < .05$) in abundance between sagebrush community types. Order of significance indicates the relative usefulness of a plant species in discriminating between community types, based upon its ability to reduce Wilks Lambda

original sample-species data matrix. Phases were designated when one or more secondary species showed consistent differences in distribution within a community type that could be related to variations in soil properties. Such differences were not sufficiently great, however, to warrant separate habitat type status.

The sagebrush community types display major differences with respect to soil and environmental features (Jensen 1988). Community types with *Artemisia nova* as the dominant shrub species tend to occur on Aridisol soil orders, while all other community types are primarily found on Mollisols (Table 6). Mollic epipedon thickness tends to be absent or low in community types dominated by *A. nova*, intermediate in community types dominated by *A. arbuscula*, *A. longiloba*, and *A. tridentata* ssp. *wyomingensis*, and highest

TABLE 5. Key to sagebrush community types of the Humboldt National Forest.

1. *Artemisia nova* is the dominant sagebrush species 2
— *Artemisia nova* is not the dominant sagebrush species 3
2(1). *Sitanion hystrix* and *Poa nevadensis* are the dominant grasses. *Atriplex confertifolia* and *Ephedra nevadensis* are generally conspicuously present ..... *Artemisia nova/Atriplex confertifolia/Sitanion hystrix* c.t.
— *Oryzopsis hymenoides* and *Sitanion hystrix* are the dominant grasses. *Atriplex confertifolia* and *Ephedra nevadensis* are lacking or present in small amounts ..... *Artemisia nova/Oryzopsis hymenoides* c.t.
— *Agropyron spicatum* is the dominant grass. *Poa sandbergii* is conspicuously present and may replace *A. spicatum* in dominance on some sites ..... *Artemisia nova/Agropyron spicatum* c.t.
3(1). *Artemisia arbuscula* is the dominant sagebrush species 4
— *Artemisia arbuscula* is not the dominant sagebrush species 5
4(3). *Agropyron spicatum* is the dominant grass. *Poa sandbergii* and *Poa fendleriana* are conspicuously present and may replace *A. spicatum* in dominance on some sites ..... *Artemisia arbuscula/Agropyron spicatum* c.t.
— *Festuca idahoensis* is the dominant grass. *Poa sandbergii* is conspicuously present and may replace *F. idahoensis* in dominance on some sites ..... *Artemisia arbuscula/Festuca idahoensis/Poa sandbergii* c.t.
— *Festuca idahoensis* is the dominant grass. *Agropyron spicatum* is conspicuously present with *Poa sandbergii* absent or present in only small amounts ..... *Artemisia arbuscula/Festuca idahoensis* c.t.
5(3). *Artemisia longiloba* is the dominant sagebrush species. *Festuca idahoensis* is the dominant understory grass with *Agropyron spicatum* occurring in varying amounts ..... *Artemisia longiloba/Festuca idahoensis* c.t.
— *Artemisia longiloba* is not the dominant sagebrush species 6
6(5). *Artemisia tridentata* spp. *wyomingensis* is the dominant sagebrush species 7
— *Artemisia tridentata* spp. *wyomingensis* is not the dominant sagebrush species 8
7(6). *Sitanion hystrix* is the dominant grass ..... *Artemisia wyomingensis/Sitanion hystrix* c.t.
— *Poa sandbergii* is the dominant grass ..... *Artemisia wyomingensis/Poa sandbergii* c.t.
— *Agropyron spicatum* is the dominant grass with *Festuca idahoensis* occurring in varying amounts ..... *Artemisia wyomingensis/Agropyron spicatum* c.t.

TABLE 5. Continued.

8(6). *Artemisia tridentata* spp. *tridentata* is the dominant sagebrush species 9

— *Artemisia tridentata* spp. *tridentata* is not the dominant sagebrush species 10

9(8). *Agropyron spicatum* is the dominant grass. *Bromus tectorum* is conspicuously present and may replace *A. spicatum* in dominance on some sites ..... *Artemisia tridentata/Agropyron spicatum* c.t.

— *Festuca idahoensis* is the dominant grass. *Agropyron spicatum* is present in varying amounts ..... *Artemisia tridentata/Festuca idahoensis* c.t.

10(8). *Artemisia tridentata* spp. *vaseyana* is the dominant sagebrush species. *Symphoricarpos oreophilus* is usually absent, or, if present, it does not contribute significantly to the shrub component (i.e., less than 3% canopy cover) 11

— *Artemisia tridentata* spp. *vaseyana* is the dominant sagebrush species. *Symphoricarpos oreophilus* is conspicuously present, or, if lacking, *Amelanchier alnifolia* is usally present 12

11(10). *Agropyron spicatum* is the dominant grass. *Poa fendleriana* and *Poa sandbergii* are conspicuously present and may share dominance with *A. spicatum* on some sites. *Festuca idahoensis* is usually absent, or, if present, it occurs in trace amounts. *Purshia tridentata* is commonly present in varying amounts ..... *Artemisia vaseyana/Agropyron spicatum* c.t.

(1). *Purshia tridentata* is absent, or, if present, it occurs in trace amounts. *Poa fendleriana* shares dominance with *Agropyron spicatum* on most sites ..... *Poa fendleriana* phase

(2). *Purshia tridentata* is conspicuously present, usually with canopy cover greater than 5%. *Poa fendleriana* shares dominance with *Agropyron spicatum* on most sites ..... *Purshia tridentata* phase

(3). *Purshia tridentata* is commonly present, usually with canopy cover greater than 3%. *Poa fendleriana* is absent, or, if present, it occurs in trace amounts. *Balsamorhiza sagittata* is the dominant forb on most sites ..... *Balsamorhiza sagittata* phase

— *Festuca idahoensis* is the dominant grass. *Agropyron spicatum* is commonly present, in varying amounts. *Purshia tridentata* is usually absent ..... *Artemisia vaseyana/Festuca idahoensis* c.t.

(1). *Purshia tridentata* is usually absent, or, if present, it occurs in trace amounts. *Lupinus caudatus* is commonly the dominant forb species. *Lupinus argenteus* is usually absent, or, if present, it occurs in trace amounts ..... *Lupinus caudatus* phase

(2). *Purshia tridentata* is usually absent, or, if present, it occurs in trace amounts. *Lupinus argenteus* is commonly the dominant forb species. *Lupinus caudatus* is usually absent, or, if present, it occurs in trace amounts ..... *Lupinus argenteus* phase

(3). *Purshia tridentata* is commonly present, usually with canopy cover greater than 5%. *Lupinus* species are not dominant forb components on most sites ..... *Purshia tridentata* phase

— *Elymus cinereus* is the dominant grass. Forb species are generally abundant, with *Balsamorhiza sagittata* and *Wyethia amplexicaulis* sharing dominance with *E. cinereus* on some sites ..... *Artemisia vaseyana/Elymus cinereus* c.t.

12(10). *Artemisia tridentata* spp. *vaseyana* is the dominant sagebrush species. *Symphoricarpos oreophilus* is conspicuously present, usually with canopy cover greater than 3%. *Balsamorhiza sagittata* is commonly present, in varying amounts 13

13(12). *Agropyron spicatum* is the dominant grass with *Poa fendleriana* conspicuously present. *Festuca idahoensis* may replace *A. spicatum* in dominance on some sites. Grass species occur in higher abundance than forb species on most sites ..... *Artemisia vaseyana/Symphoricarpos oreophilus/Agropyron spicatum* c.t.

— *Bromus carinatus* is the dominant grass. *Festuca idahoensis*, *Agropyron trachycaulum*, and *Elymus cinereus* are conspicuously present and may replace *B. carinatus* in dominance on some sites. Forb species occur with the same abundance as grasses on most sites ..... *Artemisia vaseyanna/Symphoricarpos oreophilus/Bromus carinatus* c.t.

(1). Grass species occur in equal or higher abundance than forb species on most sites. *Agropyron trachycaulum* is commonly the dominant grass species present. *Geranium viscosissimum* is usually absent, or, if present, it occurs in trace amounts ..... *Agropyron trachycaulum* phase

(2). Forb species occur in greater abundance than grass species on most sites. *Geranium viscosissimum* is commonly the dominant forb species present ..... *Geranium viscosissimum* phase

in community types dominated by *A. tridentata* ssp. *tridentata* and *A. tridentata* ssp. *vaseyana*.

Environmental gradients that influence community type distribution are evident in the ordination of average community type scores along two DECORANA axes (Fig. 3). The transition from community types dominated by *A. tridentata* ssp. *vaseyana* to *A. tridentata* ssp. *tridentata*, *A. arbuscula*, and *A. nova* displayed along axis 1 is considered to represent a gradient of decreasing soil

TABLE 6. Listing of the major sagebrush community types of the Humboldt National Forest with general site characterizations provided.

Community type	Sample size	Principal soil great group	Elevation range (m)	Slope (%) x	Slope (%) s	Soil depth (cm) x	Soil depth (cm) s	Thickness mollic epipedon (cm) x	Thickness mollic epipedon (cm) s
ARNO/ATCO/SIHY	12	Haplargids	1,829–2,225	23	20	90	32	0	
ARNO/ORHY	16	Paleorthids	1,859–3,048	15	11	77	28	0	
ARNO/AGSP	44	Calciorthids	1,829–3,048	20	13	81	32	16	16
ARAR/AGSP	27	Argixerolls	1,981–2,926	24	13	73	26	26	9
ARLO/FEID/POSA	19	Argixerolls	1,524–3,109	13	10	71	28	22	9
ARAR/FEID	19	Cryoborolls	1,768–2,438	13	9	74	26	28	9
ARLO/FEID	4	Argixerolls	1,829–1,981	6	3	81	26	29	4
ARWYO/SIHY	4	Haploxerolls	1,829–2,134	4	2	99	37	27	38
ARTR/AGSP	6	Haploxerolls	1,707–1,920	20	21	118	39	43	34
ARTR/FEID	8	Haploxerolls	1,615–2,103	16	13	132	35	48	26
ARVA/AGSP	63	Cryoborolls	1,829–3,048	24	16	104	38	37	21
ARVA/FEID	66	Cryoborolls	1,707–2,743	17	14	111	36	45	19
ARVA/ELCI	9	Cryoborolls	1,859–2,316	33	18	117	25	37	11
ARVA/SYOR/AGSP	23	Cryoborolls	2,012–2,743	26	16	117	39	43	16
ARVA/SYOR/BRCA	46	Cryoborolls	1,768–2,499	28	15	136	26	53	17

Note: x = mean, s = standard deviation.

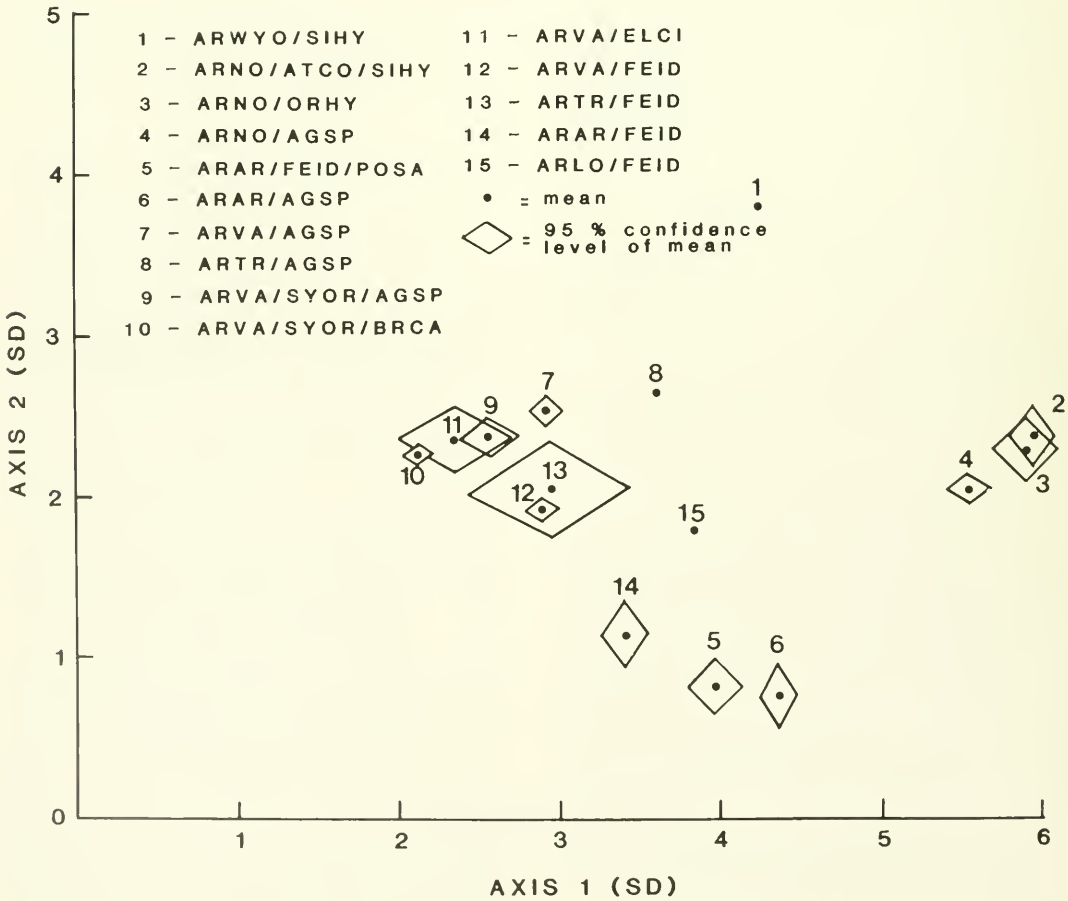

Fig. 3. Ordination of average community type scores along two DECORANA axes. The rectangles represent the 95% confidence interval of the mean with respect to each axis. Confidence intervals are not presented for the ARWYO/SIHY, ARTR/AGSP, and ARLO/FEID community types because of high variances associated with limited sampling in those types.

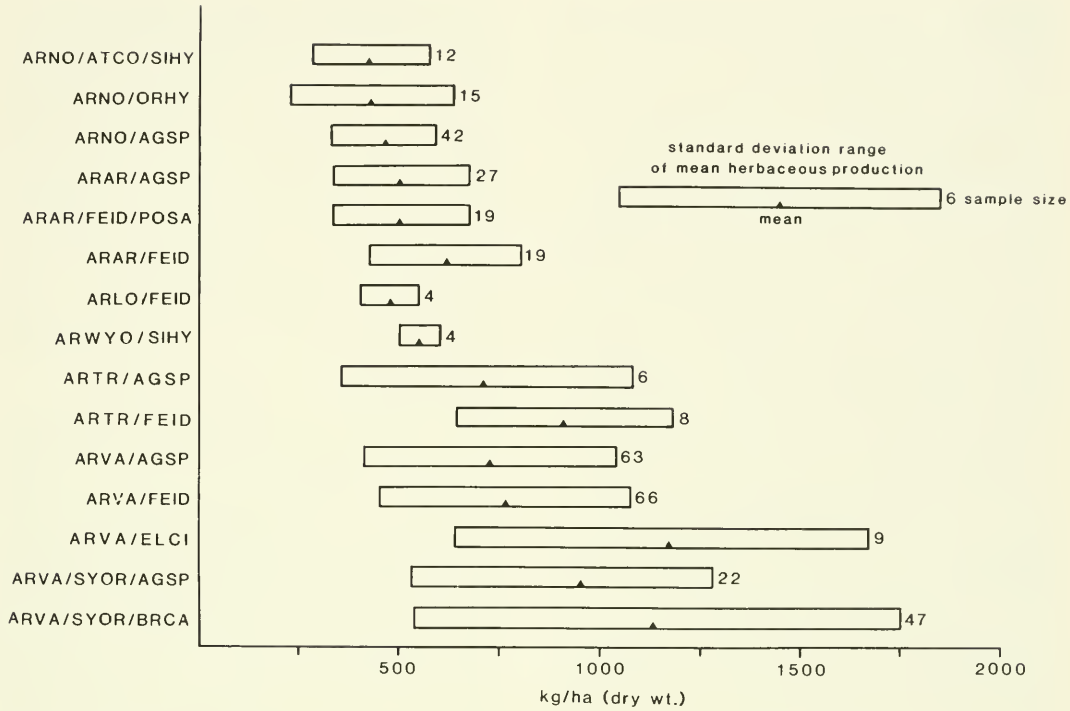

Fig. 4. Average annual dry weight production of the sagebrush community types. The standard deviation range represents one standard deviation of the sample above and below the observed mean value.

moisture and increasing soil temperature. This observation is supported by visual assessments of soil moisture status and soil temperature measurements collected at each site. Axis 2, based upon inspection of soil profile descriptions, is considered to represent a gradient of decreasing soil clay content and increasing soil depth.

Total annual production for the community types follows this apparent soil moisture gradient, with *A. tridentata* spp. *vaseyana*–dominated community types displaying highest production levels (Fig. 4). Production variability tends to be greatest on higher production sites, with the ARVA/SYOR/BRCA community type displaying the widest range in average production values. Such high variability in observed production within certain community types acts to limit their predictive significance for assessing site potentials on the landscape.

DISCUSSION

The sagebrush community types presented are similar to vegetation classification types identified by other researchers. Floristic compositions are relatively similar between our community types and comparably named habitat types identified in southern Idaho (Hironaka 1983). Of the 17 community types presented, 14 are comparably named in the southern Idaho classification. Only the ARNO/ATCO/SIHY, ARNO/ORHY, and ARVA/SYOR/BRCA community types of this study are not identified in that classification. This fact supports Komarkova's (1983) contention that floristic-based classification methods that use stand taxa composition as a basis for analysis produce similar results to the habitat-type approach. The low sagebrush community types presented are also similar to the low sagebrush habitat types identified in Nevada by Zamora and Tueller (1973). Similarities are apparent between our classification and the mountain big sagebrush associations described in Nevada by Mooney (1985) and Tueller and Eckert (1987). The community types described also relate closely to the potential natural communities of an ecological site (RISC 1983) in that they represent the

vegetation association that is in dynamic equilibrium with current environmental conditions present at a given site.

The desired result in both the habitat-type or range-site methods of classification is to produce groupings of land with similar inherent productivity and climax vegetation expression (RISC 1983). The fact that these two methods often produce different classifications of a given area is due primarily to differences in objectives. The objective of habitat typing is to produce groupings (habitats) with similar internal biotic potentials (Hoffman 1984). A habitat may occupy a wide range of soil, topographic, and climate conditions, provided the ecological sum of the environment (i.e., the ability to support one particular climax plant association) is the same (Daubenmire 1952). The identification of groupings with similar internal biotic potentials is also an objective in range-site classification (Hall 1985). Such groupings, however, tend to be more specifically defined than habitat types since another common objective in range-site classification is to delineate major differences in the production potential of a given climax plant association. As a consequence of this objective, a narrower range in soil, topographic, and climatic conditions is tolerated in a range site as contrasted to a habitat type. In both methods the land's capability to support a particular climax plant association is the primary criterion in classification. It seems reasonable, therefore, that a range site should encompass a finer division of the environment than a habitat type. In other words, a habitat type or phase of habitat type could be divided into a number of range sites dependent upon classification objectives.

The community types identified in this study reflect similar groupings to those that would be developed by a habitat-type approach. Since no existing classification system was available for the study area, a broad-level classification was considered most appropriate for this initial study. The community types could, however, be subdivided into range sites based upon the production and soils data collected. The variability in total production recorded over the community types with *Artemisia tridentata* ssp. *vaseyana* and *A. tridentata* ssp. *tridentata* as the dominant shrubs (Fig. 4) suggests that these types should be considered for subdivision into range sites.

West et al. (1978) suggest that the distribution of sagebrush species in Nevada is controlled primarily by climatic conditions present at a site. Similar observations have been made in other areas (Beetle and Johnson 1982, Hironaka 1979, Hironaka et al. 1983) and in this study. Young et al. (1985) state that sagebrush habitat types do not follow an orderly moisture temperature gradient in the landscape due to soil edaphic influences on community distribution. Passey et al. (1982) emphasize that soil properties modify the effects of climate on rangeland plant communities.

Because of the apparent interaction between climate and soil properties on rangeland plant community distribution, it is not surprising to find plant communities described in one area on different soils in a distant location. For example, dwarf sagebrush species of Idaho (*A. nova* and *A. arbuscula*) are described as usually occuring on soils that are either shallow (i.e., less than 50 cm depth) or, if moderately deep, have a restrictive layer (Hironaka et al. 1983). These same species are found to occupy much deeper soils in this study (Table 6). Lower precipitation on these community types in Nevada results in a wetting front that probably does not extend throughout the entire soil. Consequently, even though deeper soils may support these community types in this study, the actual depth exploited by plants for soil moisture is probably comparable to that described in Idaho. Such interactions between climate and soil make if difficult to predict rangeland soil properties based upon plant community composition.

LITERATURE CITED

ANDERSON, E. W. 1983. Ecological site/range site/habitat type—a viewpoint. Rangelands 5: 187–188.

BEETLE, A. A., AND K. L. JOHNSON. 1982. Sagebrush in Wyoming. University of Wyoming Agric. Expt. Sta. Bull. 779.

CANFIELD, R. H. 1941. Application of line interception method in sampling range vegetation. J. Forestry 39: 388–394.

CRONQUIST, A., H. H. HOLMGREN, N. H. HOLMGREN, J. L. REVEAL, AND P. K. HOLMGREN. 1984. Intermountain Flora. Vol. 4. New York Botanical Garden, Bronx, New York. 573 pp.

DAUBENMIRE, R. 1952. Forest vegetation of northern Idaho and adjacent Washington, and its bearing on concepts of vegetation classification. Ecol. Monogr. 22: 301–330.

_____. 1968. Plant communities: a textbook of plant synecology. Harper and Row, New York. 300 pp.

_____. 1984. Viewpoint: ecological site/range site/habitat type. Rangelands 6: 263–264.

DYKSTERHUIS, E. J. 1983. Habitat type: a review. Rangelands 5: 270–271.

_____. 1985. Follow-up on range sites and condition classes as based on quantitative ecology. Rangelands 7: 172–173.

GAUCH, H. G. 1982. Multivariate analysis in community ecology. Cambridge University Press, Cambridge, England. 298 pp.

HALL, F. C. 1985. Viewpoint: the habitat type controversy: two common concepts. Rangelands 7: 170–171.

HILL, M. D. 1979. TWINSPAN—a FORTRAN Program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Cornell University, Ithaca, New York. 29 pp.

HILL, M. D., AND H. G. GAUCH. 1980. Detrended correspondence analysis: an improved ordination technique. Vegetatio 42: 47–58.

HIRONAKA, M. 1979. Basic synecological relationships of the Columbia River sagebrush type. *In:* The sagebrush ecosystem: a symposium. April 1978, Utah State University, Logan.

HIRONAKA, M., M. A. FOSBERG, AND A. H. WINWARD. 1983. Sagebrush-grass habitat types of southern Idaho. Bull. 35, University of Idaho For. Wildlife and Range Expt. Sta., Moscow. 44 pp.

HOFFMAN, G. R. 1984. Habitat types: a supportive view. Rangelands 6: 264–266.

HOFFMAN, G. R., AND R. R. ALEXANDER. 1976. Forest vegetation of the Bighorn Mountains, Wyoming: a habitat type classification. USDA For. Serv. Res. Pap. RM–170, Rocky Mt. For. and Range Expt. Sta., Ft. Collins, Colorado. 38 pp.

HYDER, D. N., C. E. CONRAD, P. T. TUELLER, L. D. CALVIN, C. E. POULTON, AND F. A. SNEVA. 1963. Frequency sampling in sagebrush-bunchgrass vegetation. Ecology 44: 740–746.

JENSEN, M. E. 1988. Soil characteristics of mountainous northeastern Nevada sagebrush community types. Great Basin Nat. (in press).

JENSEN, M. E., L. S. PECK, AND M. V. WILSON. 1988. Vegetation characteristics of mountainous northeastern Nevada sagebrush community types. Great Basin Nat. 48(4): 403–421.

KOMARKOVA, V. 1983. Comparison of habitat type classifications to some other classification methods. *In:* Moir and Hendzel, coord., Proceedings of the workshop on southwwestern habitat types. April 1983, Albuquerque, New Mexico.

MARKS, P. L., AND P. A. HARCOMBE. 1981. Forest vegetation of the Big Thicket, southeast Texas. Ecol. Monogr. 51: 287–305.

MOONEY, M. J. 1985. A preliminary classification of high elevation sagebrush-grass vegetation in northern and central Nevada. Unpublished thesis, University of Nevada at Reno. 123 pp.

MUEGGLER, W. F., AND W. L. STEWART. 1980. Grassland and shrubland habitat types of western Montana. USDA For. Serv. Gen. Tech. Rept. INT-66, Intermt. For. and Range Expt. Sta., Ogden, Utah, 154 pp.

MUELLER-DOMBOIS, D., AND H. ELLENBERG. 1974. Aims and methods of vegetation ecology. John Wiley and Sons, New York. 547 pp.

NORUSIS, M. J. 1985. Statistical package for the social sciences. SPSS, Inc., Chicago, Illinois.

PASSEY, H. B., V. K. HUGIE, E. W. WILLIAMS, AND D. E. BALL. 1982. Relationships between soil, plant community, and climate on rangelands of the Intermountain West. Tech. Bull. 1669. USDA Soil Cons. Serv., Washington, D.C.

PECHANEC, J. F., AND G. D. PICKFORD. 1937. A weight estimate method for determinations of range or pasture production. J. Amer. Soc. Agron. 29: 894–904.

PFISTER, R. D., B. L. KOVALCHIK, S. F. ARNO, AND P. C. PRESBY. 1977. Forest habitat types of Montana. USDA For. Serv. Gen. Tech. Rept. INT-34, Intermt. For. and Range Expt. Sta., Ogden, Utah. 174 pp.

RISC. 1983. Guidelines and terminology for range inventories and monitoring. Report of the Range Inventory Standardization Committee. Soc. for Range Manage., Denver, Colorado. 13 pp.

STEVENS, R., AND E. D. MCARTHUR. 1974. A simple field technique for identification of some sagebrush taxa. J. Range Manage. 27: 325–326.

STRAUSS, R. E. 1982. Statistical significance of species clusters in association analysis. Ecology 63: 634–639.

STURGES, D. L. 1977. Soil water withdrawal and root characteristics of big sagebrush. Amer. Midl. Nat. 98: 257–274.

TUELLER, P. T., AND R. E. ECKERT. 1987. Big sagebrush (*Artemisia tridentata vaseyana*) and longleaf snowberry (*Symphoricarpos oreophilus*) plant associations in northeastern Nevada. Great Basin Nat. 47: 117–131.

USDA. 1969. Range environmental analysis handbook. USDA For. Serv., Intermountain Region, Ogden, Utah.

_____. 1975. Soil taxonomy. Soil Survey Staff, USDA Agric. Handb. 436. U.S. Govt. Printing Office, Washington, D.C.

WEST, N. E., R. J. TAUSCH, K. H. REA, AND P. T. TUELLER. 1978. Taxonomic determination, distribution, and ecological indicator values of sagebrush within the pinyon-juniper woodlands of the Great Basin. J. Range Manage. 31: 87–92.

WINWARD, A. H. 1980. Taxonomy and ecology of sagebrush in Oregon. Agric. Expt. Sta. Bull. 642, Oregon State University, Corvallis. 15 pp.

YOUNG, J. A., R. A. EVANS, AND R. E. ECKERT. 1985. Successional patterns and productivity potentials of the sagebrush and salt desert ecosystem. *In:* Developing strategies for rangeland management. National Academy of Science. Westview Press, Boulder, Colorado.

YOUNGBLOOD, A. P., W. G. PADGETT, AND A. H. WINWARD. 1985. Riparian community type classification of eastern Idaho–western Wyoming. USDA For. Serv. Regional Ecol. Note 85–01, Regional Office, Ogden, Utah.

ZAMORA, B., AND P. T. TUELLER. 1973. *Artemisia arbuscula*, *A. longiloba*, and *A. nova* habitat types in northern Nevada. Great Basin Nat. 33: 225-242.

COLORADO'S RARE FLORA

Steve L. O'Kane, Jr.[1]

ABSTRACT.—Distribution, status, habitat, elevational range, original literature citations, synonymy, and specimens deposited at Brigham Young University (BRY), University of Colorado (COLO), Colorado State University (CS), Denver Botanical Garden (KHD), Kansas State University (KSC), University of Kansas (KANU), Missouri Botanical Garden (MO), and the Rocky Mountain Herbarium (RM) are given for 79 species of rare Colorado plants. Species federally listed by the U.S. Fish and Wildlife Service under the Endangered Species Act, candidates for listing, and species that qualify as federal candidates because of limited range, small populations, or known threats are included. Suggested changes in status are offered where appropriate. Maps and tables indicating the Colorado range of these species are provided.

Colorado, because of its geologic history and elevational extremes, its diversity of geologic formations, soil types, topography, local climatic regimes, and floristic affinities (Kruckeberg 1986, Mason 1946a, 1946b, Stebbins and Major 1965, 1980, Welsh 1978a), is host to a number of rare endemic species. Some of these species are directly threatened by human activities that modify or eliminate habitat essential to the species. These threats include overgrazing by domestic livestock, road construction, off-road-vehicle (ORV) use, construction of irrigation ditches and canals, agricultural conversion, residential and summer home construction, chaining, spraying, seeding rangeland to introduced species, competition from exotic weeds, dam construction for hydroelectricity and water storage, and exploration for and extraction of oil, gas, minerals, and oil shale. Furthermore, rare species, by virtue of their narrow endemism or small populations, are more susceptible to stochastic or systematic human-caused extinction (Diamond 1984, Jablonski et al. 1985, Menges 1986, Terborg and Winter 1980, Wilcox 1980); a single catastrophic event could significantly impact or even extirpate them. Some rare species are the objects of intentional harm. Colorado's rare cacti, for example, are actively sought by collectors in this country and abroad.

The Endangered Species Act of 1973 provides protection for species that are threatened with extinction throughout all or a significant portion of their range (endangered) or that are likely to become endangered in the foreseeable future (threatened). Seven species in Colorado are listed as either endangered or threatened, and numerous taxa are under review for listing as endangered or threatened. The most recent list of Colorado's candidate species is contained in the U.S. Fish and Wildlife Service's (1985) list of candidate plant taxa. Endangered and threatened species are listed in the publication Endangered and Threatened Wildlife and Plants (USFWS 1987). The Colorado Natural Areas Program (CNAP) cooperates with the USFWS, through an Endangered Species Act, Section 6 agreement, in protecting rare plant species. CNAP maintains a data base for listed and candidate taxa, as well as for those species that are more common elsewhere but are rare in Colorado. CNAP's list of Colorado rare plants (CNAP 1988) is revised as new data are received. CNAP and USFWS files on rare species in Colorado, data from literature sources, and specimen label data from herbaria with important collections of Colorado specimens have been used to compile this report.

This paper addresses those species that (1) are listed as endangered or threatened, (2) are candidates or are qualified to be candidates for listing, and (3) are no longer candidates but are rare enough to be either reinstated or require constant surveillance to assure that they do not again become rare or threatened in the foreseeable future. Botanists, government agency personnel, ecologists,

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environmental consultants, and land developers can use this information to plan for projects that modify natural habitats, to assess the status of rare species contained in project areas, to prepare environmental impact statements, and to plan for fieldwork involving rare species.

The only publications specifically concerning Colorado's rare plants are Peterson's (1982) pamphlet on the plants listed as threatened or endangered and Ecology Consultant's (1979) compendium for the U.S. Forest Service of the rare species of Forest Service Region 6. These publications, now out of date, do not contain information on the availability of specimens for study. However, they have been extensively consulted in the preparation of this paper, as have reports on intensive inventories of individual species and of important botanical areas by CNAP, government agencies, environmental consultants, interested amateurs, university personnel, and The Nature Conservancy (e.g., Galatowitsch et al. 1988, Peterson and Baker 1982, O'Kane 1986, 1987a, 1987b, 1987c, 1987d, Harner and Associates 1984, Knight et al. 1986).

Specimens from eight herbaria were thoroughly examined and are reported herein: Brigham Young University (BRY), University of Colorado (COLO), Colorado State University (CS), Denver Botanical Garden (KHD), Kansas State University (KSC), University of Kansas (KANU), Missouri Botanical Garden (MO), and Rocky Mountain Herbarium (RM). A few specimens from herbaria not thoroughly searched are reported when known. Papers, reports, and books dealing with the rare flora of adjacent states are helpful sources of data for species crossing state borders. For Utah, Welsh et al. (1975), Welsh (1978b), Welsh and Chatterly (1985), and Welsh and Thorne (1979) are freely consulted. Dorn and Dorn (1980) and Ecology Consultants (1979) are used for Wyoming. New Mexico Native Plant Protection Advisory Committee (1984) is employed for data on New Mexico's rare plants. Mohlenbrock's book on the threatened and endangered plants of the United States (1983) provides useful information for several of Colorado's rare plants. Floras and monographs giving data on species distributions include: Harrington (1964) and Weber (1976, 1987) for Colorado; Kearney and Peebles (1960) for Arizona; Martin and Hutchins (1980) for New Mexico; Cronquist et al. (1977, 1984) and Welsh et al. (1987) for Utah; Dorn (1988) for Wyoming; Great Plains Flora Association (1986) for the Great Plains; Goodrich and Neese (1986) for the Uinta Basin; and Barneby (1964) for the genus *Astragalus*.

Inasmuch as this paper is a companion to Welsh and Chatterly's (1985) recent report on Utah's rare plants, the format used in their paper has been followed closely. Habitat, distribution, threats, elevational range, and federal status, as well as distributional maps, useful anecdotal information, and specimen citations are given for each species. The township and range of collection sites are from specimen labels if given, but are otherwise extrapolated from locality descriptions provided on the labels. Dates of collections are provided—month/day/year—to help in planning field surveys. Original literature citations for each species are included to facilitate location of technical descriptions. Although synonyms are provided, an exhaustive literature search has not been conducted to provide a definitive synonymy for each species.

The federal status of each taxon, as defined in the Endangered Species Act and as reported in U.S. Fish and Wildlife Service (1985), is as follows. Species listed as endangered or threatened are protected by specific laws. For Category 1 species the USWS has enough information available to support the appropriateness of being listed as endangered or threatened. Category 2 species are possibly appropriate to list as endangered or threatened, but more data are needed to support preparation of a listing package. Category 2* species meet the criteria of Category 2 but are presumed extinct. Category 3C species are no longer considered candidates for listing. Category 3B species are taxa that do not meet the act's definition of "species"; this usually means that the entity is either not a "good" taxon or that it is synonymous with a more abundant one. Recommendations are made, where appropriate, that species be considered for listing as threatened or endangered, that taxa currently not candidates be made Category 1 or 2 candidates, or that current candidates be down-graded to Category 3C or 3B.

Binomials and trinomials used here are not necessarily those recommended by authorities familiar with the taxa but are, rather,

those given in the Federal Register lists. Common names are primarily those given in CNAP (1988) with modifications from Welsh et al. (1987).

Figure 1 shows the townships in Colorado containing federally threatened or endangered taxa. Figure 2 shows townships containing candidate and recommended candidate taxa. Table 1 lists by species the county distribution of the rare species in Colorado. A species list arranged by county is found in Table 2. Maps showing the geographical range of each taxon are found in the Appendix.

COLORADO'S RARE FLORA

***Aletes humilis* C. & R.**, Contr. U.S. Nat. Herb. 7: 107. 1900.

Map 1

FAMILY.—Apiaceae (Umbelliferae).

FEDERAL STATUS.—Category 2.

The Larimer aletes occurs in nearly vertical habitats of Precambrian granite cliffs and isolated tors in the ponderosa pine and Douglas-fir zones of the lower foothills in the drainages of the Poudre River, Larimer County, where it is frequently found growing with *Heuchera* and *Pseudocymopterus*. Localities range in elevation from 2,100 to 2,380 m. Populations are in relatively inaccessible habitats that are little threatened by existing land management. Planned reservoir projects in the area, however, could threaten known populations and potential habitat. Several populations northwest of Fort Collins in Phantom Canyon are protected by The Nature Conservancy. The species has recently been reported from Albany County, Wyoming (Dorn 1988).

LARIMER COUNTY: T9N R71W: Wilken, Popp & Steingraeber 13973, 6/8/83 (CS); Hartman 11678 6/13/80 (RM); T11N R71W: Popp s.n., 6/29/83 (CS); T11N R72W: Neely 3542, 1986 (CS); Popp s.n., 6/29/83 (CS); Johnston & Lucas 1664–5, 6/8/78 (BRY, COLO, RM); Lucas s.n., 6/9/78 (COLO, RM); T12N R71W: Jones 41797, 6/9/65 (CS, RM); Popp s.n., 6/29/83 (CS, RM); Osterhout 4678, 5/24/12 (BRY, COLO, RM); Osterhout 2002, 7/19/99 (BRY, COLO, RM); Johnston & Lucas 1662, 6/7/78 (BRY, COLO); Weber & Jones 12392, 6/9/65 (COLO); Hartman 3077, 5/16/71 (RM); T12N R obscure: Goodding 8850, 4/02 (RM).

***Ambrosia linearis* (Rydb.) Payne**, N. Amer. Fl. 33: 27. 1922.

Map 2

FAMILY.—Asteraceae (Compositae).

SYNONYMS.—*Gaertneria linearis* Rydb., *Franseria linearis* Rydb.

FEDERAL STATUS.—Category 2.

The streaked ragweed is a rarely collected endemic of the eastern plains of Colorado. It is known to occur in sandy, seasonally moist soils. Few searches have been conducted for the species, and records are spotty, coming mostly from disturbed sites of railroad embankments and road borrow ditches. The taxon may be more common, as indicated by the county distribution of the few available records. Inventories are needed to ascertain its status.

LOCATION OBSCURE: Christ 948, 7/10/37 (CS). ELBERT COUNTY: T9S R64W: Austin 939, 8/7/35 (CS). EL PASO COUNTY: Location obscure, Ward 3371, 3/19/36 (CS). KIOWA COUNTY: T18S R51W: Penland 4686, 8/31/72 (COLO); T18S R52W: Stephens 62753, 9/28/72 (COLO, KANU); Stephens 54547, 6/10/72 (KANU). LINCOLN COUNTY: T17S R56W: Stephens 62695, 9/28/72 (KANU); Stephens 90540, 7/15/81 (KANU); Stephens 54616, 6/10/72 (KANU); T16S R58W: Ownbey 1325, 7/5/37 (COLO).

***Aquilegia micrantha* Eastw. var. *mancosana* Eastw.**, Proc. California Acad. Sci. (2) 4: 559. 1895.

Map 3

FAMILY.—Ranunculaceae (Hellaboraceae).

SYNONYM.—*Aquilegia micrantha* Eastw. f. *mancosana* (Eastw.) W. A. Weber.

FEDERAL STATUS.—Category 2*.

The Mancos columbine is known from two historical collections taken in or near Johnson Canyon, a side canyon of the Mancos River below Mesa Verde National Park. Recent searches of the canyon failed to locate populations of the taxon. The original collections were from damp, alkaline alcoves of cliff overhangs. Collections and sightings of spurless forms of *A. micrantha* have, however, been made elsewhere in the state. This variety needs to be examined taxonomically, as it probably represents only a spurless form of *A. micrantha*, in which case it should be downgraded to Category 3B.

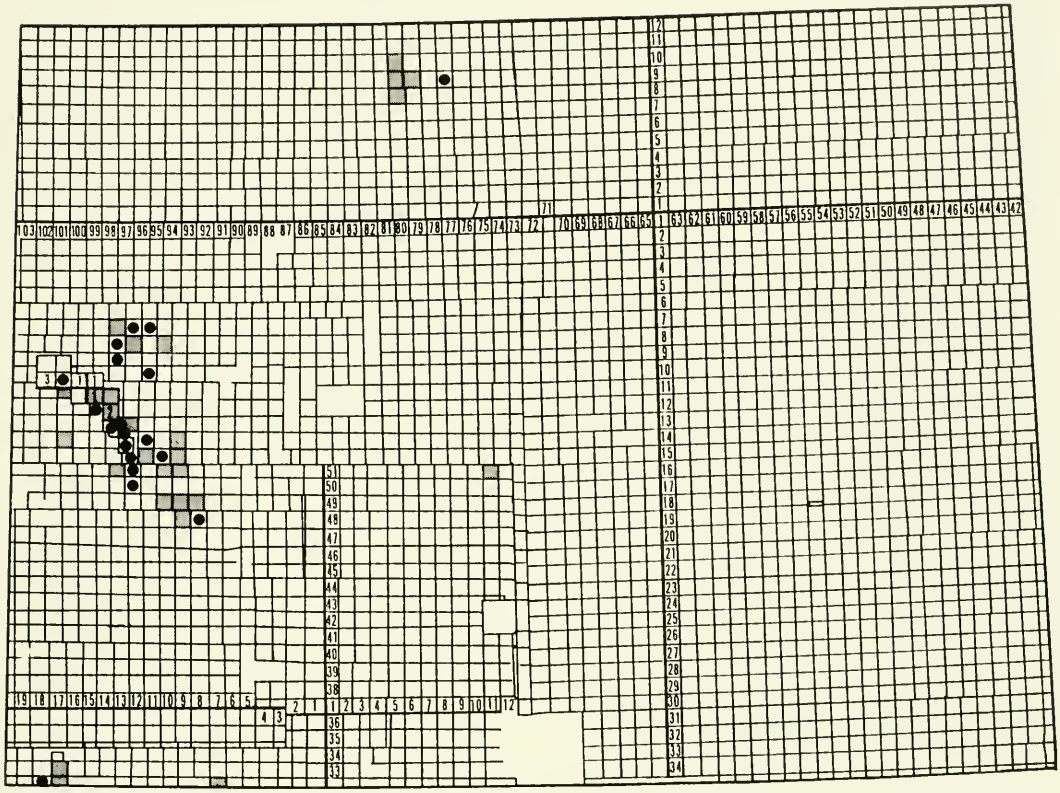

Fig. 1. Distribution of Colorado's federally endangered and threatened species by township. Locations based on specimen labels are shaded. Dots indicate locations based solely on CNAP data.

MONTEZUMA COUNTY: T33N R14W: Wetherill s.n., 6/1891 (CAS); Eastwood s.n., 9/1892 (Holotype: CAS).

***Artemisia argilosa* Beetle,** Rhodora 61: 84–85. 1959.

Map 4

FAMILY.—Asteraceae (Compositae).

SYNONYM.—*Seriphidium canum* (Pursh) W. A. Weber ssp. *viscidulum* (Osterh.) W. A. Weber sensu Weber.

FEDERAL STATUS.—Category 2.

Coaltown sagebrush grows in a small area in North Park, Jackson County. The taxonomic validity of this taxon is questioned (Leila Shultz, personal communication, Wittmann et al. 1988). This species may be a hybrid between *A. cana* ssp. *viscidula* and *A. longiloba*, both of which occur in North Park, albeit not growing with *A. argilosa* (Beetle 1959). According to Shultz, other specimens of the taxon may be found filed under *A. cana* ssp. *viscidula*. If the taxon should be found to be an unstabilized hybrid or proven to be synonymous with *A. cana* ssp. *viscidula* (*Seriphidium canum* ssp. *viscidulum*), its status should be downgraded to Category 3B. The species tends to grow on disturbed sites of alkaline mine tailings within flat expanses of sagebrush, *Atriplex*, and greasewood at ca 2,500 m in elevation.

JACKSON COUNTY: T6N R80W: Asplund 68–12, 8/24/68 (RM); Beetle & Palmer 12316, 11/12/56 (KANU, RM); Beetle 12872, 7/31/57 (Holotype: RM); Mahaffey s.n., 9/19/65 (CS); Mahaffey s.n., 9/19/65 (CS); Mahaffey & Harrington s.n., 9/19/45 (RM); Wiley-Eberle 454, 7/30/79 (CS); Wiley-Eberle et al. 824, 7/16/81 (CS).

***Asplenium andrewsii* A. Nels.,** Proc. Biol. Soc. Washington 17: 174–175. 1904.

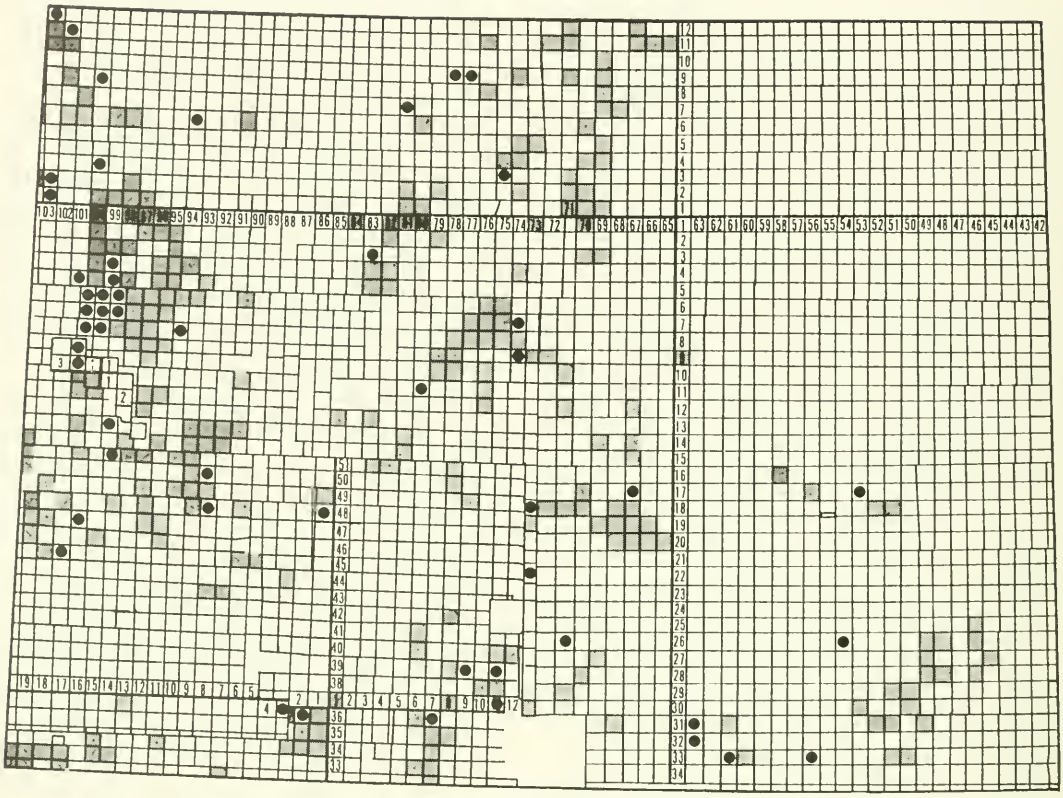

Fig. 2. Distribution of Colorado's current and recommended candidate rare plants by township. Locations based on specimen labels are shaded. Dots indicate locations based solely on CNAP data.

Map 5

FAMILY.—Aspleniaceae.

SYNONYM.—*A. adiantum-nigrum* L. of Colorado literature.

FEDERAL STATUS.—Category 2.

The black spleenwort is known from four widely disjunct populations: White Rocks in Boulder County, Colorado; Zion National Park, Utah; near Flagstaff in Coconino County, Arizona; and in Chihuahua, Mexico (McVaugh 1957). The White Rocks population grows in cracks of a light-colored rock outcrop. Development for gravel pits and housing developments may pose a threat to the species (Ecology Consultants 1979). Our material may be conspecific with *A. adiantum-nigrum* L. of Eurasia and Africa (Maxon 1912; Lellinger 1985), in which case it should be downgraded to Category 3B. This is one of the rarest species in the United States.

BOULDER COUNTY: T1N R69W: Andrews s.n., 8/05 (CS); Bethel & Andrews s.n., 8/05 (CS); Betts & Robbins 8340, 12/15/10 (COLO); Andrews s.n., 7/15/17 (COLO); Schramus s.n., 8/1/14 (MO).

Astragalus cronquistii **Barneby**, Mem. New York Bot. Gard. 13: 257–259. 1964.

Map 6

FAMILY.—Fabaceae (Leguminosae).

FEDERAL STATUS.—Category 2.

Cronquist milkvetch is known from Ute Mountain Ute tribal lands in the southwestern corner of Montezuma County, from adjacent Utah, and from Comb Wash in San Juan County, Utah. It occurs in shadscale communities in fine-textured soils derived from Mancos shale and the Morrison Formation. In Colorado it ranges in elevation from 1,475 to 1,750 m. Populations are currently threatened by road construction and gas exploration and by an impending system of canals. The species was recently discovered in Colorado.

Table 1. County distribution of Colorado's rare plants. A single asterisk indicates species endemic to Colorado. Locations are based on herbarium specimens except where double asterisks indicate county records based solely on CNAP data.

Species	County
Aletes humilis	Larimer
*Ambrosia linearis**	Elbert, El Paso, Kiowa, Lincoln
Aquilegia micrantha var. *mancosana**	Montezuma
Arabis vivariensis	Moffat
*Artemisia argilosa**	Jackson
Asplenium andrewsii	Boulder
Astragalus cronquistii	Montezuma
*Astragalus debequaeus**	Mesa
*Astragalus deterior**	Montezuma
Astragalus hamiltonii	Moffat
Astragalus humillimus	Montezuma
*Astragalus linifolius**	Delta, Mesa, Montrose
*Astragalus microcymbus**	Gunnison
*Astragalus osterhoutii**	Grand
Astragalus ripleyi	Conejos
*Astragalus schmolliae**	Montezuma
Astragalus wetherillii	Garfield, Mesa, Moffat, Montrose, San Miguel**
Atriplex pleiantha	Montezuma
Braya humilis ssp. *ventosa**	Chaffee, Gunnison, Park
Cirsium ownbeyi	Moffat
Cleome multicaulis	Saguache, Costilla Rio Grande, Alamosa
*Cryptantha aperta**	Mesa
Echinocereus triglochidiatus var. *inermis*	Mesa, Montrose
Erigeron kachinensis	Montrose
*Eriogonum brandegei**	Chaffee, El Paso, Fremont, Park
Eriogonum clavellatum	Montezuma
*Eriogonum pelinophilum**	Delta, Montrose
*Eutrema penlandii**	Park, Summit
Festuca dasyclada	Garfield, Rio Blanco
Festuca hallii	Huerfano, Larimer
*Frasera coloradensis**	Baca, Bent, Prowers, Las Animas
Gaura neomexicana ssp. *coloradensis*	Boulder, Larimer, Weld, Adams?
*Gilia penstemonoides**	Gunnison, Hinsdale Montrose, Ouray
*Hackelia gracilenta**	Montezuma
Haplopappus fremontii ssp. *monocephalus**	Fremont, Huerfano**, Otero**, Las Animas
Hymenoxys helenioides	Las Animas, Hinsdale
*Ipomopsis globularis**	Lake, Park, Summit
Ipomopsis polyantha var. *polyantha**	Archuleta
*Lesquerella congesta**	Rio Blanco
*Lesquerella parviflora**	Garfield, Rio Blanco
*Lesquerella pruinosa**	Archuleta
*Lomatium concinnum**	Delta, Gunnison, Montrose
Lomatium latilobum	Mesa
*Lupinus crassus**	Montrose
Lygodesmia doloresensis	Mesa
Mentzelia argillosa	Garfield
*Mentzelia densa**	Chaffee, Fremont
*Mimulus gemmiparus**	Grand, Jefferson, Larimer
*Mirabilis rotundifolia**	El Paso, Fremont, Pueblo
*Neoparrya lithophila**	Chaffee, Conejos, Huerfano, Rio Grande, Saguache
Oenothera acutissima	Moffat
*Oenothera kleinii**	Mineral
Parthenium alpinum	Weld
*Parthenium tetraneuris**	Chaffee, Fremont, Pueblo
Pediocactus knowltonii	La Plata
Penstemon albifluvis	Rio Blanco**
*Penstemon debilis**	Garfield
*Penstemon degeneri**	Custer**, Fremont
Penstemon gibbensii	Moffat, Rio Blanco
Penstemon grahamii	Rio Blanco
*Penstemon harringtonii**	Eagle, Grand, Routt, Summit
*Penstemon parviflorus**	Montezuma
*Penstemon penlandii**	Grand
*Penstemon retrorsus**	Delta, Montrose
*Phacelia formosula**	Jackson
*Phacelia submutica**	Garfield, Mesa
Phlox caryophylla	Archuleta, La Plata
*Physaria bellii**	Boulder, El Paso, Jefferson, Larimer
*Physaria obcordata**	Rio Blanco
Potentilla effusa var. *rupincola**	Boulder, Clear Creek, Larimer
*Ptilagrostis porteri**	Lake**, Park, Summit
*Rorrippa coloradensis**	Alamosa?
Saussurea weberi	Park, Summit
Sclerocactus glaucus	Delta, Garfield, Mesa, Montrose
Sclerocactus mesae-verdae	Montezuma
Senecio dimorphophyllus var. *intermedius*	Mesa, Montrose, Ouray
Sisyrinchium pallidum	Larimer, Park
Spiranthes diluvialis	Boulder, Jefferson, Weld?, Morgan?, El Paso?
*Thalictrum heliophilum**	Garfield, Mesa**, Rio Blanco

Montezuma County: T32N R20W: O'Kane, Anderson & Flemming 2027A, 5/8/85 (CS); Barneby 17803, 5/19/82 (BRY, COLO); Higgins & Welsh 13330, 5/25/83 (BRY); T33½N R18W: O'Kane & Anderson 2343, 5/15/86 (COLO, CS); T33N R20W: O'Kane et al. 2028A, 5/8/85 (CS); Goodrich & Atwood 18175, 5/17/83 (BRY).

TABLE 2. Colorado's rare plants listed by county. Locations are based on herbarium specimens except where an asterisk indicates records based solely on CNAP data.

ADAMS
Gaura neomexicana ssp. coloradensis?
ARCHULETA
Ipomopsis polyantha var. *polyantha*
Lesquerella pruinosa
Phlox caryophylla

ALAMOSA
Cleome multicaulis
Rorippa coloradensis?

BACA
Frasera coloradensis

BENT
Frasera coloradensis

BOULDER
Asplenium andrewsii
Gaura neomexicana ssp. *coloradensis*
Physaria bellii
Potentilla effusa var. *rupincola*
Spiranthes diluvialis

CHAFFEE
Braya humilis ssp. *ventosa*
Eriogonum brandegei
Mentzelia densa
Neoparrya lithophila
Parthenium tetraneuris

CLEAR CREEK
Potentilla effusa var. *rupincola*

CONEJOS
Astragalus ripleyi
Neoparrya lithophila

COSTILLA
Cleome multicaulis
Hymenoxys helenioides

CUSTER
*Penstemon degeneri**

DELTA
Astragalus linifolius
Eriogonum pelinophilum
Lomatium concinnum
Penstemon mensarum
Penstemon retrorsus
Sclerocactus glaucus

EAGLE
Penstemon harringtonii

ELBERT
Ambrosia linearis

EL PASO
Ambrosia linearis
Eriogonum brandegei
Mirabilis rotundifolia
Physaria bellii
Spiranthes diluvialis?

FREMONT
Eriogonum brandegei
Haplopappus fremontii ssp. *monocephalus*
Mentzelia densa
Mirabilis rotundifolia

TABLE 2. Continued.

Parthenium tetraneuris
Penstemon degeneri

GARFIELD
Astragalus wetherillii
Festuca dasyclada
Lesquerella parviflora
Mentzelia argillosa
Phacelia submutica
Sclerocactus glaucus
Thalictrum heliophilum

GRAND
Astragalus osterhoutii
Mimulus gemmiparus
Penstemon harringtonii
Penstemon penlandii

GUNNISON
Astragalus microcymbus
Braya humilis ssp. *ventosa*
Gilia penstemonoides
Lomatium concinnum

HEURFANO
Festuca hallii
*Haplopappus fremontii var. monocephalus**
Neoparrya lithophila

HINSDALE
Gilia penstemonoides
Hymenoxys helenioides

JACKSON
Artemisia argilosa
Phacelia formosula

JEFFERSON
Mimulus gemmiparus
Physaria bellii
Spiranthes diluvialis

KIOWA
Ambrosia linearis

LAKE
Ipomopsis globularis
*Ptilagrostis porteri**

LAS ANIMAS
Frasera coloradensis
Haplopappus fremontii ssp. *monocephalus*

LINCOLN
Ambrosia linearis

LA PLATA
Pediocactus knowltonii
Phlox caryophylla

LARIMER
Aletes humilis
Festuca hallii
Gaura neomexicana ssp. *coloradensis*
Mimulus gemmiparus
Physaria bellii
Potentilla effusa var. *rupincola*
Sisyrinchium pallidum

MESA
Astragalus debequaeus
Astragalus linifolius
Astragalus wetherillii

Table 2. Continued.

Cryptantha aperta
Echinocereus triglochidiatus var. *inermis*
Lomatium latilobum
Lygodesmia doloresensis
Phacelia submutica
Sclerocactus glaucus
Senecio dimorphophyllus var. *intermedius*
*Thalictrum heliophilum**

Moffat
Astragalus hamiltonii
Astragalus wetherillii
Cirsium ownbeyi
Arabis vivariensis
Oenothera acutissima
Penstemon gibbensii

Mineral
Oenothera kleinii

Montrose
Astragalus linifolius
Astragalus wetherillii
Echinocereus triglochidiatus var. *inermis*
Erigeron kachinensis
Eriogonum pelinophilum
Gilia penstemonoides
Lomatium concinnum
Lupinus crassus
Penstemon retrorsus
Sclerocactus glaucus
Senecio dimorphophyllus var. *intermedius*

Montezuma
Aquilegia micrantha var. *mancosana*
Astragalus cronquistii
Astragalus deterior
Astragalus humillimus
Astragalus schmolliae
Atriplex pleiantha
Eriogonum clavellatum
Hackelia gracilenta
Penstemon parviflorus
Sclerocactus mesae-verdae

Morgan
Spiranthes diluvialis?

Ouray
Gilia penstemonoides
Senecio dimorphophyllus var. *intermedius*

Table 2. Continued.

Otero
Haplopappus fremontii var. *monocephalus**

Park
Braya humilis ssp. *ventosa*
Eriogonum brandegei?
Eutrema penlandii
Ipomopsis globularis
Ptilagrostis porteri
Saussurea weberi
Sisyrinchium pallidum

Pueblo
Mirabilis rotundifolia
Parthenium tetraneuris

Prowers
Frasera coloradensis

Rio Blanco
Festuca dasyclada
Lesquerella congesta
Lesquerella parviflora
*Penstemon albifluvis**
Penstemon gibbensii
Penstemon grahamii
Physaria obcordata
Thalictrum heliophilum

Rio Grande
Cleome multicaulis
Neoparrya lithophila

Routt
Penstemon harringtonii

Saguache
Cleome multicaulis
Neoparrya lithophila

San Miguel
*Astragalus wetherillii**

Summit
Eutrema penlandii
Ipomopsis globularis
Penstemon harringtonii
Ptilagrostis porteri
Saussurea weberi

Weld
Gaura neomexicana ssp. *coloradensis*
Parthenium alpinum
Spiranthes diluvialis?

Astragalus debequaeus **Welsh,** Great Basin Nat. 45: 31–33. 1985.

Map 7

Family.—Fabaceae (Leguminosae).

Federal status.—Category 2.

The DeBeque milkvetch, recently described from Mesa County, grows among rocks in sandy soils of the Wasatch Formation and in clay soils derived from the Atwell Gulch Member of the Wasatch Formation. It is found in areas surrounded by pinyon-juniper woodlands at elevations ranging from 1,570 to 1,950 m. Known localities are just west of DeBeque in the Chimney Rock area and south of the Colorado River in the shallow canyons at the base of Horsethief Mountain. The species is similar to the pink-purple–flowered *A. eastwoodiae*, which is nearly sympatric and with which it may be conspecific.

Mesa County: T8S R97W: O'Kane 2369,

5/22/86 (CS); Anderson 85–83, 6/21/85 (BRY); T8S R98W: O'Kane 2374, 5/22/86 (CS, RM); Johnston 2520, 5/7/82 (COLO); T8S R99W: O'Kane & Anderson 2351, 5/20/86 (COLO, CS, NY); T9S R97W: Welsh, Welsh & Kass 22390, 5/11/85 (BRY); Anderson 85–15, 6/12/84 (BRY); O'Kane 2389, 5/25/86 (CS, NY); Welsh, Welsh & Kass 22802, 5/16/84 (COLO); Welsh, Welsh & Kass 22792, 5/16/84 (BRY, COLO); Welsh, Welsh & Kass 22792, 5/16/84 (Holotype: BRY; Isotypes: BRY, COLO, MO); Kass 1649, 5/16/84 (BRY); T9S R98W: O'Kane 2397, 5/26/86 (CS, RM).

***Astragalus deterior* (Barneby) Barneby,** Leafl. West. Bot. 7: 36. 1953.

Map 8

FAMILY.—Fabaceae (Leguminosae).

FEDERAL STATUS.—Category 3C.

The Cliff Palace milkvetch is endemic to a small area in Mesa Verde National Park near Anasazi cliff dwellings, where it grows in sandy soils of ledges and in cracks of slickrock. The species occurs between 2,040 and 2,135 m in elevation with pinyon and juniper. Superficially, this inconspicuous species resembles *A. naturitensis*, *A. cottamii*, and *A. monumentalis*. Its ochroleucous flowers are smaller than those of these species. *Astragalus naturitensis* has bicolored rather than ochroleucous flowers, and both *A. monumentalis* and *A. cottamii* have narrower pod septa and pink-purple petals. No threats are known; however, park use within its habitat should be monitored.

MONTEZUMA COUNTY: T34N R15W: Ratzloff & Colyer s.n., 5/31/78 (COLO); Isely, Erdman & Isely 8789, 5/21/64 (BRY); Welsh 1746, 5/31/62 (BRY); Welsh, Erdman & Moore 2132, 6/9/63 (BRY); Peabody & Sears 1464, 6/17/77 (BRY); Friedlander s.n., 6/15/80 (CS).

***Astragalus hamiltonii* C. L. Porter,** Rhodora 54: 159. 1952.

Map 9

FAMILY.—Fabaceae (Leguminosae).

SYNONYM.—*A. lonchocarpus* Torr. var. *hamiltonii* (C. L. Porter) Isely.

FEDERAL STATUS.—Category 2.

The Hamilton milkvetch is known in Colorado from a single population, discovered in 1987, of perhaps a score of individuals near Deerlodge Park in Dinosaur National Monument. The few other populations of the species occur in northwestern Uintah County and near the Utah-Colorado border about 16 km north of Bonanza, Utah, where it grows on soil derived from the Duchesne River Formation from 1,580 to 1,935 m in elevation. The Colorado population occurs at 1,756 m in sand of the interstices of a small, nearly barren outcrop of the Morrison Formation in a juniper–*Cercocarpus intricatus* woodland. The National Park Service protects this species in Colorado.

MOFFAT COUNTY: T6N R99W: O'Kane 2768, 5/17/87 (COLO, CS, Dinosaur Nat'l. Mon.).

***Astragalus humillimus* Gray ex Brandegee,** Bull. U.S. Geol. Surv. 23: 235. 1876.

Map 10

FAMILY.—Fabaceae (Leguminosae).

SYNONYMS.—*Tragacantha humillima* (Gray) O. Kze., *Phaca humillima* (Gray) Rydb.

FEDERAL STATUS.—Endangered.

The Mancos milkvetch is known from a few populations in San Juan County, New Mexico, and from the rims of mesas above the Mancos River canyon in Montezuma County, Colorado. The type locality in Montezuma County, discovered in 1875 by T. S. Brandegee, was not relocated until field searches were conducted in 1986 and 1987. The species inhabits pockets of sandy soil on exfoliating slickrock of the Point Lookout Member of the Mesa Verde Formation amidst pinyon-juniper woodlands at 1,700 to 1,770 m elevation. Populations in Colorado are small and, although not currently threatened, could be impacted by seismic exploration for deposits of oil and gas. This species may be exhibiting competitive exclusion with *A. cottamii* Welsh. These species are never found growing together in the same pocket of soil but may be found in immediately adjacent but slightly different habitat.

MONTEZUMA COUNTY: T33N R obscure: Brandegee 1087, 7/1861 (Type: GH, MO); T33N R17W: O'Kane 2342, 5/14/86 (COLO); Neely 3897, 4/4/87 (CS); Neely 3889, 4/3/87 (CS).

***Astragalus linifolius* Osterh.,** Bull. Torrey Bot. Club 55: 75. 1928.

Map 11

FAMILY.—Fabaceae (Leguminosae).

Synonyms.—*Ctenophyllum linifolium* Osterh., l.c., nom. nud. in syn., *A. rafaelensis* Jones sensu Rydb.

Federal status.—Category 2.

The Grand Junction milkvetch is known from a few populations in Delta, Mesa, and Montrose counties at elevations of 1,510 to 1,880 m on steep slopes of the Chinle and Morrison formations with pinyon, juniper, and sagebrush on the east side of the Uncompahgre Plateau. Until the late 1970s the species was known only from Osterhout's type locality near Grand Junction. No threats are known, but the impact of grazing on the species is not understood. The species is similar to *A. rafaelensis*, which occurs on the west side of the Uncompahgre Plateau. *Astragalus rafaelensis*, primarily found in and around the San Rafael Swell in Utah, differs by having pendant pods and shorter calyx teeth. *A. linifolius* may represent a variety of this species (Barneby 1964).

Delta County: T51N R13W: Weber 15307, 5/15/78 (BRY, COLO, RM). Mesa County: T1S R1W: Osterhout 6557, 6/18/26 (Holotype: RM, Isotypes: COLO, RM); T12S R100W: Atwood & Thompson 8742, 5/18/82 (BRY); Anderson s.n., 5/10/82 (COLO); T49N R18W: Wilken & Kelley 13955, 6/2/83 (BRY, CS); T51N R13W: Wilken, Ratzloff & Ellis 13533, 5/27/79 (CS). Montrose County: T48N R17W: Peterson & Kennedy 83–50, 6/2/83 (BRY, CS, RM); T51N R12W: Johnston, Ratzloff & Lucas 1559, 5/25/78 (COLO, RM); T51N R13W: Johnston, Ratzloff & Lucas 1587, 5/25/78 (BRY, COLO); Neese & Abbott 13553, 6/14/83 (BRY, CS, RM).

Astragalus microcymbus **Barneby,** Amer. Midl. Nat. 41: 499. 1949.

Map 12

Family.—Fabaceae (Leguminosae).

Federal status.—Category 2.

The skiff milkvetch eluded collectors for so many years that the species was thought to be a waif at the roadside type locality near Gunnison. Since the late 1960s, several small populations have been found south of the Gunnison River in a small area adjacent to South Beaver Creek (see Barrell 1969). The species has been observed colonizing an area seeded to crested wheatgrass. The effects of other habitat modifications, e.g., heavy grazing, are not known. Populations may be affected by ORV activity. *Astragalus microcymbus* grows in sagebrush communities in fine to moderately coarse soils usually derived from Cambrian granite on hillsides from 2,315 to 2,485 m in elevation. Due to its extreme rarity, this species should be listed as threatened.

Gunnison County: T49N R1W: O'Kane & Anderson 3270, 13/7/87 (RM); Weber 9144, 7/9/55 (BRY, CS, RM); Ripley & Barneby 7179, 7/20/45 (Holotype: CAS; Isotypes: COLO, GH, RSA); Johnston, Ratzloff & Lucas 1795, 7/11/78 (COLO, RM); Ratzloff s.n., 6/30/78 (COLO); Neese 15894, 7/15/84 (BRY, CS, RM); Neese 15855, 7/13/84 (BRY, CS); Neese 15857, 7/13/84 (BRY, CS); Neese 15892, 7/15/84 (BRY, CS); Neese 15845, 7/13/84 (BRY, CS, RM).

Astragalus osterhoutii **M. E. Jones,** Rev. Astrag. 251. 1923.

Map 13

Family.—Fabaceae (Leguminosae).

Synonym.—*Lonchophaca osterhoutii* (Jones) Rydb.

Federal status.—Category 2.

Osterhout milkvetch occurs in a few populations near Kremmling, Grand County, on clayey, seleniferous soils derived from shales of the Niobrara, Piene, and Troublesome formations on barren knolls and in sagebrush communities. Elevations range from 2,225 to 2,315 m. The species is an obligate selenophyte and is able to withstand harsh site conditions. Barneby (1964) reports Osterhout's type locality as "Hot Sulphur Springs." Osterhout's specimen label, however, merely states "Sulphur Springs." The taxon has not been located near Hot Sulphur Springs but has been collected near Sulphur Springs, a spring northeast of Kremmling and west of Hot Sulphur Springs. A proposed reservoir north of Kremmling could extirpate many of the known localities. Recent intensive inventories for the species have not significantly increased its known range. This species should be listed as endangered, and a listing package to that effect is pending approval (J. Anderson, personal communication).

Grand County: T1N R81W: Weber 4914, 7/2/49 (COLO, KANU); T2N R81W: Beath & Eppson s.n., 6/21/40 (RM); Eppson s.n., 7/10/47 (MO, RM); Weber 4915, 7/2/49 (COLO, KANU, RM); Neese & Grah 17181, 6/9/85 (RM); Neese & Grah 17145, 7/10/85

(RM); Peterson & Baker 83–402, 7/9/83 (CS); Osterhout 3038, 7/17/05 (Syntypes: COLO, RM); Osterhout 3253, 6/9/06 (Syntype: RM); Ripley & Barneby 10516, 7/16/50 (RM).

Astragalus ripleyi **Barneby,** Leafl. West. Bot. 6: 175. 1952.

Map 14

FAMILY.—Fabaceae (Leguminosae).

FEDERAL STATUS.—None.

The Ripley milkvetch is a tall, striking, yellow-flowered milkvetch of the Rio Grande Valley in Taos County, New Mexico, and from the lower drainages of the Conejos River, Conejos County, Colorado. In Colorado this milkvetch grows in grassy ponderosa pine savannas, pinyon-juniper woodlands, and sagebrush and rabbitbrush flats adjacent to streams and rivers at elevations of 2,500 to 2,700 m. Most localities have been severely impacted by heavy grazing. Plants avoid herbivory by growing within tall shrubs. Plants growing in the open, which are selectively eaten by livestock, wildlife, or both, are rarely seen. This species needs protection from grazing. Category 2 status is recommended.

CONEJOS COUNTY: T32N R7E: O'Kane & Anderson 2531, 7/13/86 (COLO, CS); T33N R6E: O'Kane & Anderson 2536, 7/13/86 (NY, RM); T33N R7E: Ramaley & Johnson 14747, 6/22/35 (COLO); Weber 7788, 7/18/52 (COLO, KANU, RM); T34N R7E: Anderson 87–165, 9/11/87 (COLO); Bye & Linares 12923, 7/10/84 (COLO); T35N R7E: O'Kane & Anderson 2619, 8/19/86 (COLO, CS, RM); T36N R6E: Weber & Salamun 12914, 7/14/65 (COLO); O'Kane & Anderson 2540, 7/13/86 (COLO, CS, RM); O'Kane & Anderson 2601, 8/18/86 (BRY, CS, RM).

Astragalus schmolliae **C. L. Porter,** Madroño 8: 100. Pl. 9, Figs. 4–7. 1945.

Map 15

FAMILY.—Fabaceae (Leguminosae).

SYNONYM.—*A. platycarpus* var. *montezumae* Barneby.

FEDERAL STATUS.—Category 2.

The Schmoll milkvetch grows in sandy loam on mesas, slopes, and in drainage bottoms in pinyon-juniper woodlands at 1,830 to 2,135 m in elevation. It is limited to a small area in Mesa Verde National Park. Although populations are few, they often have numerous individuals. Populations within the park should be monitored for impacts from park use. Potential habitat outside the park may be threatened by grazing and by road construction associated with Ute Mountain Ute Tribal Park development. The species is similar to *Astragalus lonchocarpus*, although it is foliose with all leaves regularly odd-pinnate with petiolate leaflets, whereas *A. lonchocarpus* has leaves mostly reduced to rachises. Alice Eastwood first collected fragmentary material of the species in 1890, but it was not described until 1945.

MONTEZUMA COUNTY: T33N R15W: Neely 4487, 7/10/87 (CS); T33½N R15W: Weber 4823, 6/13/49 (COLO, KHD); Sears 1462, 6/16/77 (BRY); Welsh 3026, 6/12/64 (BRY); Welsh 3024, 6/12/64 (BRY); Bader 26, 5/12/29 (BRY, COLO); Isely, Erdman & Isely s.n., 5/21/64 (BRY); Friedlander s.n., 6/15/80 (CS); Erdman 458, 5/28/64 (COLO); Friedlander 458, 6/5/65 (COLO); Eastwood s.n., 6/1890 (COLO); Welsh & Welsh 1550, 6/6/61 (BRY); Schmoll & Nusbaum 1555, 5/26/52 (Holotype: RM, Isotype: BRY); Nelson 10420, 5/12/25 (MO, RM).

Astragalus wetherillii **M. E. Jones,** Zoe 4: 34. 1893.

Map 16

FAMILY.—Fabaceae (Leguminosae).

SYNONYM.—Phaca wetherillii (Jones) Rydb.

FEDERAL STATUS.—Category 3C.

The Wetherill milkvetch is known from scattered localities in western Colorado. It grows in sagebrush, sagebrush-greasewood, oakbrush, and juniper communities on steep slopes, canyon benches, and talus under cliffs in sandy-clay to gravelly soils, usually of the Mancos and Wasatch formations, at elevations of 1,430 to 2,015 m. Jones (1923) reports an Eastwood observation from the canyon of the Colorado east of Moab, Grand County, Utah. This population, despite recent searches, has not been re-collected and may represent a waif carried downstream (R. Barneby, in correspondence to J. Anderson). Although relatively widespread, populations are infrequent and invariably consist of few individuals. Various populations are threatened by oil and gas development, overgrazing, road construction, and other habitat modifications. This taxon, because of small population sizes and known threats, should be considered a Category 2 species.

Garfield County: T5S R93W: Neese 11278, 5/2/82 (BRY, CS); O'Kane 2446; 6/26/86 (CS, RM); Weber 3326, 5/17/47 (CS, KANU, RM); Welsh & Higgins 6228, 6/13/67 (BRY); Welsh & Higgins 6235, 6/14/67 (BRY). Mesa County: Location obscure: Eastwood s.n., 5/1892 (Type: MO, RM); T8S R97W: Kass, Welsh & Welsh 1653, 5/16/84 (BRY, RM); Welsh, Welsh & Kass 22816, 5/16/84 (BRY, RM); T10S R97W: Kass, Welsh & Welsh 2023, 5/11/85 (BRY, RM); Welsh, Welsh & Kass 23377, 5/11/85 (BRY, RM).

Moffat County: T6N R91W: Harrington 7202, 6/12/53 (CS). Montrose County: T49N R9W: Payson 682, 6/15/15 (RM); Payson 82, 5/11/13 (RM). San Miguel County: Location obscure: Brewster s.n., n.d. (CS).

***Atriplex pleiantha* W. A. Weber,** Madroño 10: 189. 1950.

Map 17

Family.—Chenopodiaceae.

Federal status.—Category 2.

The Four Corners orach is a rare Navajo Basin endemic of Montezuma County and immediately adjacent New Mexico and Utah. It grows in salt desert scrub communities with *Atriplex* on nearly barren clay knolls derived from Mancos shale. In Colorado the taxon occurs from 1,490 to 1,650 m in elevation. This annual species experiences vast fluctuations in population density depending on annual precipitation. Populations are threatened by oil and gas exploration, ORV use, and, in New Mexico, coal mining. Threatened or endangered status is recommended.

Montezuma County: T32N R19W: Weber 4788, 6/12/48 (Holotype: COLO, Isotypes: CS, MO, RM); O'Kane, Anderson & Flemming 2022, 5/8/85 (CS); Weber 7651, 6/7/49 (COLO, KANU, MO); Anderson 85–35, 6/8/85 (BRY).

***Braya humilis* (C. A. Meyer) Robins. ssp. *ventosa* Rollins,** Rhodora 55: 114. 1953.

Map 18

Family.—Brassicaceae (Cruciferae).

Federal status.—Category 2.

Alpine braya occurs on tundra underlain with Leadville limestone or Manitou dolomite. Elevations range from 3,475 to 3,900 m. The species prefers slopes without late-lying snowbanks and is found in small, open microsites from which solifluction lobes capped with *Dryas octopetala* have slipped. This pioneer habitat provides a place where seeds can germinate and individuals can escape competition. Individuals are occasionally found on old roads associated with hardrock mining in its highly mineralized habitat. Despite the widespread occurrence of suitable habitat, the species is infrequent and consists of small populations (Neely and Carpenter 1986). Mining and ORV activity associated with old mining roads are the most significant threats to the species. This taxon may be synonymous with *B. humilis* var. *humilis* (Harris 1985), in which case, although a biologically interesting disjunct, it should be downgraded to Category 3B.

Chaffee County: T14S R81W: Neely 3170, 7/19/85 (CS, UTC); T15S R81W: Peterson, Johnston & Anderson 82–56, 8/17/82 (CS). Gunnison County: T13S R84W: Neely 3183, 7/24/85 (CS, UTC); T51N R3E: Neely 3174, 7/19/85 (CS, UTC); Neely 3174, 7/19/85 (CS, UTC); Neely & Carpenter 3311, 8/18/85 (CS, UTC); Neely & Carpenter 3310, 8/18/85 (COLO, UTC); T51N R4E: Neely 3220a, 7/26/85 (CS, UTC); Neely 3211, 7/25/85 (CS, UTC); Weber & Dixon 16332, 7/27/82 (COLO); Dixon 712, 7/21/81 (COLO); Johnston, Peterson & Anderson 2614, 8/18/82 (COLO). Park County: T8S R78W: Neely et al. 3141, 7/18/85 (CS, UTC); Yeatts 2069, 7/14/85 (KHD); Weber & Roloff 16328, 7/26/82 (BRY, COLO, CS, RM); Walter 28, 7/7/59 (CS); Weber & Rollins 6491, 7/7/51 (CS); O'Kane et al. 2171, 7/19/85 (CS); O'Kane 2144, 7/16/85 (CS); Rollins & Weber 51288, 8/7/51 (Isotypes: COLO, RM); Weber & Livingston 5153, 7/7/51 (COLO, RM); Weber 8753, 7/4/54 (COLO); T9S R78W: O'Kane 2152, 7/17/85 (CS); T10S R78W: Neely 3125a, 7/16/85 (CS, UTC).

***Cirsium ownbeyi* Welsh,** Great Basin Nat. 42: 200. 1982.

Map 19

Family.—Asteraceae (Compositae).

Federal status.—Category 2.

The Ownbey thistle is endemic to the eastern Uinta Mountains in Utah and Cross Mountain and Dinosaur National Monument in Moffat County, Colorado. In Colorado it occurs in sandy soils of riparian areas in otherwise dry canyons and, more typically, in

alcoves with seeps and under shaded cliffs. In alcoves it is usually associated with *Aquilegia micrantha*. The species, in Colorado, is known only from drainages of the Yampa and Green rivers on outcrops of the Morgan and Weber formations, and, less frequently, on Madison Limestone. Elevations range from 1,700 to 1,800 m. Inventories in 1987 and 1988 (S. O'Kane, personal communication, T. Naumann, personal communication) showed that the canyons of the Yampa River in Dinosaur National Monument, the center of the range of this species, contain many populations. Although populations are small, most are not threatened due to their inaccessibility to livestock and human activities.

MOFFAT COUNTY: T6N R98W: Northcutt & Bunin s.n., 9/19/78 (COLO); Neese & Smith 12051, 7/25/82 (BRY, RM); T6N R101W: O'Kane 2820, 5/19/87 (COLO, CS, Dinosaur Nat'l. Mon.); T6N R102W: O'Kane & Roszczewski 3168, 6/26/87 (COLO, CS, Dinosaur Nat'l. Mon.).

***Cleome multicaulis* Moçino & Sessé ex DC.**, Prod. 1: 240. 1824.

Map 20

FAMILY.—Capparidaceae.

SYNONYM.—*C. sonorae* A. Gray.

FEDERAL STATUS.—Category 2.

Slender spiderflower is a wetland species occurring around the margins of lakes, ponds, artesian wells, and sloughs in the San Luis Valley. *Cleome multicaulis* grows with *Carex*, *Juncus*, and *Triglochin* a few meters back from the water in the moderately moist zone between a ring of *Scirpus* standing in water below and alkaline *Sarcobatus* flats above. *Cleome* also occurred in southeastern Arizona, western Texas, New Mexico (a single collection), and south to Mexico City (the type locality). No modern collections outside the San Luis Valley, other than a recent one from Wyoming, are known. The Natrona County, Wyoming, collection (Dorn 1988) is from the margins of a man-made stock pond (R. Hartman, personal communication) where it was probably brought in by migrating waterfowl. Modification of wetland habitats is the greatest threat to the species.

ALAMOSA COUNTY: Location obscure: Bethel s.n., 7/1897 (CS, RM); Hapeman s.n., 7/30/18 (RM); T38N R10E: Dixon 2103, 7/5/72 (CS); T38N R11E: O'Kane, Anderson & Dixon 2450, 7/7/86 (CS, RM, WIS); O'Kane, Anderson & Dixon 2456, 7/7/86 (COLO, RM, WIS); T40N R11E: O'Kane & Anderson 2484, 7/8/86 (COLO, CS); O'Kane & Anderson 2487, 7/8/86 (CS, RM); Brandegee 1150, 8/1875 (COLO); Ramaley 15926, 8/3/36 (COLO); Ramaley 12216, 7/21/29 (COLO, RM); T40N R12E: Spellenberg & Zucker 7850, 8/4/84 (ASU, CS, ID, MO, NMC, NY, RSA, UNM); O'Kane & Anderson 2482, 7/8/86 (CS, NY, RM, WIS); O'Kane & Anderson 2469, 7/7/86 (COLO, CS, WIS). COSTILLA COUNTY: T30S R73W: O'Kane & Anderson 2493, 7/9/86 (COLO, RM, WIS); Ramaley 15745, 7/29/36 (COLO). RIO GRANDE COUNTY: T37N R8E: Johnson 76, 8/9/74 (CS); Robinson C–1, 8/23/68 (CS); T39N R8E: Ramaley 15645, 7/23/36 (COLO). SAGUACHE COUNTY: T42N R8E: Ramaley 13039, 8/14/31 (COLO); T43N R8E: O'Kane, Anderson & Dixon 2449, 7/14/86 (COLO, CS, WIS); Weber 11067, 7/12/60 (BRY, COLO).

***Cryptantha aperta* (Eastw.) Payson**, Bull. Torrey Bot. Club 30: 241. 1903. 14: 295. 1927.

Map 21

FAMILY.—Boraginaceae.

SYNONYM.—*Oreocarya aperta* Eastw.

FEDERAL STATUS.—Category 2*.

The Grand Junction cat's-eye, known only from the type locality collected in 1892 by Alice Eastwood, has not been rediscovered and may be extinct. Habitat in and around Grand Junction has been significantly altered or eliminated for agriculture and urban development. However, the herbarium label probably indicates the general locality, and the Grand Junction cat's-eye may still occur in the foothills surrounding the Grand Valley. Most *Cryptantha* species do not inhabit lowlands in this part of Colorado.

MESA COUNTY: Location obscure: Eastwood s.n., 6/27/1892 (Holotype: CAS, Isotype fragment: RM); Eastwood s.n. 5/17/92 (CALIF.).

***Echinocereus triglochidiatus* Engelm. var. *inermis* (K. Schum.) Arp**, Monatsschr. Kakt. 6: 150. 1896.

Map 22

FAMILY.—Cactaceae.

SYNONYMS.—*Echinocereus melanacanthus* (Engelm.) L. Benson sensu lat., *E. phoeniceus* Engelm. var. *inermis* Schum., *E. coccineus* Engelm. var. *inermis* (Schum.) Purpus.

FEDERAL STATUS.—Endangered.

The spineless hedgehog cactus, like the typical variety, has a stunning scarlet red flower. The spineless form has been subject to commercial exploitation. Other threats include chaining of rangeland, trampling by cattle, and habitat destruction for energy development. In Colorado the spineless variety occurs in Mesa, Delta, Montrose, and San Miguel counties and grows in pinyon-juniper woodlands, often in the duff and partial shade under pinyon and juniper trees at elevations of 1,800 to 2,800 m. Soils are coarse and shallow and are usually derived from sandstone, often the Dakota sandstone. Welsh et al. (1987) place this taxon in var. *melanacanthus* (Engelm.) L. Benson because there appears to be a cline from eastern Utah to western Colorado of plants with dense spines to those with no spines at all. In Colorado spineless plants have been observed growing with the spined form. The taxon might better be treated as a forma rather than as a variety (Wittmann et al. 1988, Welsh et al. 1987), in which case it should be downgraded to Category 3B.

MESA COUNTY: Location obscure: Osterhout 6572, 6/18/26 (COLO); T1S R2W: Weber, Wittman & Rector 16128, 5/31/82 (COLO); T13S R97W: Neese & Abbott 13577, 6/15/83 (BRY); T14S R101W: Arp 1019, 6/20/70 (COLO); Arp 1020, 6/20/70 (COLO). MONTROSE COUNTY: T51N R13W: Arp 1695, 8/4/71 (COLO, RM).

Erigeron kachinensis **Welsh & Moore,** Proc. Utah Acad. Sci. 45: 231. 1968.

Map 23

FAMILY.—Asteraceae (Compositae).

FEDERAL STATUS.—Category 2.

The kachina daisy is a Colorado Plateau endemic growing in hanging gardens, seeps, and shaded alcoves of otherwise dry slickrock canyons in San Juan County, Utah, and Montrose County, Colorado. It is often found with *Mimulus eastwoodiae* at about 1,575 m in elevation. The species is apparently very rare in Colorado, but new populations are infrequently found in both Colorado and Utah. The inaccessibility of much of its habitat provides the species some protection but also makes new populations difficult to locate.

MONTROSE COUNTY: T45N R18W: Ratzloff 107, 4/29/78 (COLO, CS); Ratzloff s.n., 8/17/78 (BRY); T46N R19W: Ratzloff & Crowe 218, 8/30/77 (COLO); Ratzloff s.n., 8/17/78 (BRY); Ratzloff s.n., 4/29/78 (BRY).

Eriogonum brandegei **Rydb.,** Fl. Rocky Mts. 220, 1061. 1917.

Map 24

FAMILY.—Polygonaceae.

SYNONYM.—*Eriogonum spathulatum* Gray var. *brandegei* (Rydb.) Stokes.

FEDERAL STATUS.—Category 2.

The Brandegee buckwheat was once known only from a small population collected by T. S. Brandegee near the Garden Park Dinosaur Quarry near Canyon City, Fremont County. Reveal and Davidse located a small population near Salida, Chaffee County, in 1967. Since then several large populations have been located around Salida, growing on barren slopes of lucustrine alluvium of the Dry Union Formation at elevations of 2,200 to 2,560 m. Searches at the Garden Park locality have yielded only one new population; here plants grow on the Morrison Formation at 1,760 to 1,975 m in elevation. The Arkansas River canyon, cut through igneous rocks, divides the two areas of occurrence by 50 miles. Reveal (1969) should be consulted for a description employing more important characters than those given in the original description. Bentonite mining threatens one of the two Garden Park populations, but the extensive populations near Salida have no current threats, except that increased development for mountain homes around Salida could pose a significant threat to the species in the future. A specimen taken from "South Park," Park County (Kelly 507), probably has an incorrect location. Repeated searches in South Park have located neither the species nor suitable habitat. Kelly, passing through South Park on his way to Cortez, probably collected the species near Salida. Letterman s.n., a particularly wooly pubescent collection taken in 1884, gives "Colorado Springs" as the collection locality.

CHAFFEE COUNTY: T50N R8E: O'Kane 2208, 7/31/85 (COLO, CS); O'Kane & Anderson 2219, 8/2/85 (CS); O'Kane & Anderson 2216, 8/1/85 (COLO, CS); O'Kane & Anderson 2215, 8/1/85 (COLO, CS); O'Kane & Anderson 2212, 8/1/85 (COLO, CS); T51N R8E: Johnston & Lucas 1888, 8/11/78 (RM); Johnston, Hendzel & Fager 2775, 10/12/83 (RM);

O'Kane 2192, 7/29/85 (CS); Neese 15929, 7/16/84 (BRY, CS, RM); Johnston 1864, 7/31/78 (COLO, CS); Reveal & Davidse 868, 8/22/67 (BRY, CS, RM). EL PASO COUNTY: Location obscure: Letterman s.n., 7/25/1884 (MO). FREMONT COUNTY: T17S R70W: Neese 15937, 7/17/84 (BRY, RM); Neese 15949, 7/17/84 (BRY); Neese 15946, 7/17/84 (BRY, CS, RM); Neese 15963, 7/18/84 (BRY); O'Kane 2196, 7/29/85 (CS); O'Kane & Anderson 2193, 7/29/85 (COLO, CS). PARK COUNTY?: Location obscure: Kelly 507, 6/28/47 (COLO).

Eriogonum clavellatum **Small,** Bull. Torrey Bot. Club 25: 48. 1898.

Map 25

FAMILY.—Polygonaceae.

FEDERAL STATUS.—Category 3C.

The Comb Wash buckwheat is a Colorado Plateau endemic growing on sites in Colorado identical to those supporting *Astragalus cronquistii*, with which it is occasionally found. The species occurs in shadscale communities on fine soils derived from the Mancos shale at about 1,750 m in elevation. Known occurrences in Colorado are threatened by road construction, by exploration for oil and gas, and by a proposed system of irrigation canals on the Ute Mountain Ute Reservation in the southwest corner of Montezuma County. The species is also known from adjacent San Juan County as far west as Comb Wash. This species, because of its limited range, few populations, and known threats, should be considered a Category 2 candidate for federal listing. Additional fieldwork for the species is needed.

MONTEZUMA COUNTY: T33½N R18W: O'Kane & Anderson 2344, 5/15/86 (COLO, CS); T33N R19W: Harrington 10103, 6/19/68 (CS).

Eriogonum pelinophilum **Reveal,** Great Basin Nat. 33: 120–122. 1973.

Map 26

FAMILY.—Polygonaceae.

FEDERAL STATUS.—Endangered.

The clay-loving buckwheat is limited to an area from Montrose to Delta and Hotchkiss where it grows on barren adobe hills derived from Mancos shale in *Artemisia nova* and *Atriplex corrugata* communities at elevations of 1,600 to 1,910 m. The species prefers shallow swales surrounded by shadscale where black sage is the dominant species. *Penstemon retrorsus*, a Category 1 species, is a common associate. Prior to 1984, *E. pelinophilum* was known only from the type locality near Hotchkiss, adjacent to a heavily grazed horse pasture. Intensive searches have since located several large populations. The species is threatened by livestock grazing, habitat modification for agriculture and housing developments, oil and gas exploration, the construction of irrigation ditches, and ORV activity.

DELTA COUNTY: T14S R94W: Gentry 2283, 7/23/55 (COLO); Neese 13236, 5/10/83 (CS); Ratzloff s.n., 6/21/78 (COLO); Reveal & Reveal 2780, 7/16/72 (Isotypes: BRY, COLO, MO, RM); T15S R94W: Neese 15792, 6/20/84 (CS); T51N R10W: Neese 15784, 6/20/84 (CS). MONTROSE COUNTY: T48N R9W: Neely 2950, 6/20/85 (CS, UTC); T48N R9W: Neely 2962, 6/20/85 (CS, UTC); Neely 2969, 6/20/85 (CS, UTC); T49N R8W: Neely 2983, 6/27/85 (CS, UTC); Neese 15968, 7/19/84 (CS); Neese 15800, 7/12/84 (CS); T49N R9W: Neese 15796, 6/22/84 (CS); Neese 15967, 7/19/84 (CS); T49N R10W: Neese 15795, 6/21/84 (CS); T51N R9W: Neely 2892, 6/16/85 (COLO, CS, UTC); Neely & O'Kane 2943, 6/19/85 (CS, UTC); O'Kane & Neely 2087, 6/19/85 (COLO, CS); O'Kane & Neely 2088, 6/19/85 (COLO, CS).

Eutrema penlandii **Rollins,** Contr. Gray Herb. 171: 51. 1950.

Map 27

FAMILY.—Brassicaceae (Cruciferae).

SYNONYM.—*Eutrema edwardsii* R. Brown ssp. *penlandii* (Rollins) W. A. Weber.

FEDERAL STATUS.—Category 3C.

Penland's eutrema, an alpine species of mossy bogs perched on outcrops of Leadville limestone or Manitou dolomite, grows in the Mosquito Range and on Hoosier Ridge. Elevations range from 3,660 to 4,260 m. The species is known from few populations, most of which are threatened because of their proximity to active mines or mining claims. Mining activities that alter hydrologic regimes can destroy the fragile alpine wetlands required by the species; e.g., habitat of a known population on Pennsylvania Mountain was recently ditched to supply water to a nearby mine. Populations generally consist of few individuals. Careful searches in 1986 of six known localities revealed that only two of these sites

still contained individuals of the species, albeit small size and the possibility that individuals may not appear in a given year may have prevented plants from being located. Because of rarity, small populations, fragile habitat, and current and potential threats, the species' status should be raised to Category 2.

Park County: T8S R77W: Hulten & Weber 11041, 7/10/59 (COLO); Johnston & Lucas 1351, 7/21/77 (RM); Lucas & Johnston s.n., 7/21/77 (CS); Penland 3909, 7/26/49 (GH); Penland 1305, 7/27/35 (COLO, GH); Weber & Rollins 51291, 8/8/51 (COLO, RM); T9S R78W: O'Kane 2157, 7/18/85 (CS); Weber 13343, 7/14/67 (COLO); T9S R79W: O'Kane & Anderson 2572, 8/6/86 (CS); T10S R78W: Weber 13315, 7/12/67 (COLO). Summit County: T8S R77W: Johnston, Lucas & Benjamin 1878, 7/27/78 (COLO).

***Festuca dasyclada* Hackel ex Beal,** Grasses N. Amer. 2: 602. 1896.

Map 28

Family.—Poaceae (Gramineae).

Synonym.—*Argillochloa dasyclada* (Hackel ex Beal) W. A. Weber.

Federal status.—Category 2.

The Utah fescue grows on outcrops of Green River shale on barren scree slopes or in sparsely vegetated communities dominated by *Pseudotsuga menziesii* at elevations of 1,890 to 2,745 m. The species is apparently rare in Utah. Colorado hosts many populations, but they are restricted to the Piceance Basin and to the Roan Plateau. The major threat to the species is the mining of oil shale, although ORVs, domestic livestock grazing, and road construction also impact the species. Unless oil shale extraction drastically increases in the future, the species is not threatened with significant habitat loss. An oil shale company has used the species for revegetation of disturbed sites. This species should be downgraded to Category 3C.

Garfield County: T4S R96W: Popp & Riefler 82–372, 7/13/82 (CS); T5S R95W: Harner s.n., 7/16/83 (COLO); Keammerer & Keammerer s.n., 7/28/78 (COLO); T5S R96W: Clark s.n., 8/82 (COLO); Kaemmerer & Kaemmerer s.n., 7/26/78 (COLO, RM); T6S R94W: Irvine & Chichester 193, 7/15/76 (BRY, COLO); Mase 1241, 7/16/81 (CS); T6S R95W: Nicholas 158, 7/17/81 (CS); Woods s.n., 7/7/81 (COLO); T7S R96W: Irvine 171, 7/5/76 (COLO, UTC); O'Kane & Anderson 2425, 6/11/86 (RM); Painter, Emrich & Bender 54, 7/17/78 (COLO, CS); T7S R97W: Irvine & Gregory 34, 7/75 (COLO); Painter, Emrich & Pease 25, 7/14/78 (COLO, CS, RM). Rio Blanco County: T3S R95W: Baker & Sigstedt 82–264, 7/2/82 (CS); Kelley, Baker & Sigstedt 82–19A, 6/30/82 (CS); Neese et al. 11979, 7/10/82 (BRY); Smith et al. 1814, 7/10/82 (BRY, COLO, RM, UTC); T4S R94W: Kelley & Sigstedt 82–71, 7/8/82 (CS); Neese et al. 11982, 7/10/82 (BRY); Weber 17810, 7/8/86 (COLO); Weber 15977, 6/21/81 (COLO); Wiley & England 429, 7/24/79 (BRY); Wilken 13567, 9/22/79 (CS); T4S R95W: Baker & Naumann 82–269, 7/6/82 (BRY, COLO, CS); Kelley & Sigstedt 82–61, 7/7/82 (CS); T5S R98W: Ellis & Hackney s.n., 7/13/80 (CS).

***Festuca hallii* (Vasey) Piper,** Bot. Gaz. 6: 296. 1881.

Map 29

Family.—Poaceae (Gramineae).

Synonyms.—*Melica hallii* Vasey, *F. scabrella* Torr. *in* Hook. sensu lat., *Festuca altaica* Trin. ssp. *hallii* (Vasey) Harms.

Federal status.—Category 2.

In Colorado, Halls fescue grows in alpine tundra with *Kobresia* and in subalpine grasslands. The highest stations for the species are found in Colorado. The species, once thought to be limited to Colorado, occurs across the northern Great Plains of North Dakota and Canada, extends down the Rocky Mountain Cordillera through Montana, Wyoming, and Colorado, and is apparently disjunct near Thunder Bay, Ontario (Dorn 1988, Harms 1985, Pavlick and Looman 1984). In Colorado the species is apparently rare and may be disjunct (Weber 1961, 1987). This taxon, because it is widespread and is apparently not threatened in a significant portion of its range, should be downgraded to Category 3C.

Location obscure: Hall & Harbour 621, n.d. (NY, US). Larimer County: T8S R76W: Weber & Pickford 9694, 8/25/56 (COLO). Huerfano County: T31S R68W: Weber & Wingate 15442, 7/6/78 (COLO, RM).

***Frasera coloradensis* (C. M. Rodgers) D. M. Post,** Madroño 10: 108. 1949.

Map 30

Family.—Gentianaceae.

Synonym.—*Swertia coloradensis* Rogers.

FEDERAL STATUS.—Category 2.

The Colorado gentian is endemic to southeastern Colorado where it grows on sparsely vegetated slopes and disturbed sites covered with gravel derived from Greenhorn limestone. It is associated with typical grassland species and, occasionally, with *Juniperus*. Elevations range from 1,220 to 1,650 m. The species is apparently negatively impacted by domestic livestock grazing. A recent survey in Colorado located several new populations; however, outcrops of Greenhorn limestone in adjacent New Mexico, where the species is expected, were not searched.

BACA COUNTY: T28S R46W: Kuhn 494, 6/23/87 (COLO); Kuhn 619, 9/2/87 (CS); Kuhn 541, 6/29/87 (CS); T28S R48W: Kuhn 527, 6/25/87 (CS); T28S R49W: Kuhn 522, 6/25/87 (COLO); T29S R50W: Kuhn 510, 6/24/87 (COLO); T30S R50W: Kuhn 556, 7/2/87 (CS); T31S R49W: Kuhn 554, 7/2/87 (CS); T33S R50W: Kuhn 553, 7/2/87 (CS); Johnston 2441, 6/16/81 (COLO); Johnston 2446, 6/16/81 (COLO); Locklear 7, 6/5/86 (COLO, KANU, NEB); Rogers 6423, 9/8/48 (COLO, MICH). BENT COUNTY: T26S R48W: Kuhn 548, 7/1/87 (CS); T26W R49W: Kuhn 524, 6/24/87 (CS); T27S R49W: Kuhn 523, 6/24/87 (COLO). LAS ANIMAS COUNTY: T29S R51W: Kuhn 511, 6/24/87 (COLO); T30S R53W: Kuhn 550, 7/1/87 (CS); T31S R51W: Kuhn 552, 7/1/87 (CS); Johnston 2450, 6/16/81 (COLO); Locklear 10, 9/9/86 (COLO, KANU, NEB); T31S R52W: Johnston 2449, 6/16/81 (COLO); Rogers 4951, 7/20/47 (COLO, MICH); T33S R51W: Rogers 6110, 6/29/48 (COLO, MICH). PROWERS COUNTY: T25S R46W: Harrington 3481, 7/13/47 (CS); Porter 4300, 7/13/47 (COLO, MO, RM); T26S R46N: Johnston 2424, 6/15/81 (COLO); Harrington 9864, 6/9/65 (CS); Locklear 9, 9/9/86 (KANU, NEB); Weber 5082, 8/28/49 (COLO); T26S R47W: Kuhn 549, 7/1/87 (CS); T27S R45W: McGregor 34856, 9/7/83 (KANU).

***Gaura neomexicana* Woot. ssp. *coloradensis* (Rydb.) Raven & Gregory,** Bull. Torrey Bot. Club 65: 114. 1938.

Map 31

FAMILY.—Onagraceae.

SYNONYM.—*Gaura coloradensis* Rydb.

FEDERAL STATUS.—Category 1.

The Colorado butterflyweed was previously known only from a small area near the Colorado-Wyoming border in Larimer and Weld counties and Sedalia in Adams County (J. Anderson, personal communication). Populations near the foothills in Larimer County have not been seen since 1944. Recent surveys, however, located several populations in Laramie County, Wyoming, the southwestern corner of Nebraska, and near the Colorado-Wyoming border in Weld County, Colorado. Two "populations" are known from Boulder County: just north of Boulder on a disturbed roadside and further east on the plains. The first consisted of a single individual and the latter was transplanted there in the late 1970s. The species is probably impacted by domestic livestock grazing, and several populations in Wyoming may be impacted by development at military installations. The species occupies moist meadows and gentle mid-slopes just above drainages and below the drier uplands at elevations from about 1,790 to 1,890 m. It is frequently associated with species of *Scirpus* and *Carex*.

BOULDER COUNTY: T1N R71W: Weber & Phipps 17471, 9/22/84 (COLO, CS, RM). LARIMER COUNTY: Location obscure: Cowan 1632, 7/1/95 (COCO, CS, US); Harrington 543, 8/4/44 (COLO, CS); T7N R68W: Cowan s.n., 7/8/1895 (Holotype: NY; Isotype: GH); Cowan & Crandall 1308, n.d. (ISC, NY). WELD COUNTY: T11N R67W: Neese 16023, 8/4/84 (BRY, CS); Neese, Peterson & Andrews 15969, 8/1/84 (CS); T12N R67W: Neese & Andrews 16057, 8/14/84 (CS); Porter 9690, 8/64 (DS, MSC, RM, RSA).

***Hackelia gracilenta* (Eastw.) I. M. Johnston,** Contr. Gray Herb. 68: 46. 1923.

Map 32

FAMILY.—Boraginaceae.

SYNONYM.—*Lappula gracilenta* Eastw.

FEDERAL STATUS.—None.

Hackelia gracilenta is endemic to a small area in Mesa Verde National Park where it grows in loamy or sandy soils of mesas, slopes, and drainage bottoms. It prefers the accumulated litter beneath stands of *Quercus gambelii* or pinyon and juniper. Elevations range from 1,830 to 2,010 m. No threats are known, but potential habitat outside the park in the Ute Mountain Ute Tribal Park may be threatened by grazing and by road construction for

park development. This species, like other Mesa Verde endemics of extremely limited distribution, should be considered a Category 2 species. Inventories of national park and adjacent tribal lands are needed.

MONTEZUMA COUNTY: T33.5N R15W: Friedlander s.n., 6/15/80 (CS); Friedlander s.n., 6/22/80 (CS); Mesa Verde Explorers' Camp 146, 7/6/44 (CS); Nelson 10414, 5/12/25 (MO, RM); Schmoll & Nusbaum 1660, 6/1/25 (RM); T34N R15W: Erdman 46, 6/16/59 (COLO); Buder 89, 6/8/29 (COLO); Eastwood s.n., 6/1890 (COLO); Reveal, Gentry & Davidse 843, 6/9/67 (COLO, KANU, NY, RM); Weber 8711, 6/9/54 (COLO).

***Haplopappus fremontii* A. Gray ssp. *monocephalus* (A. Nels.) H. M. Hall,** Gen. Haplopappus 87. 1928.

Map 33

FAMILY.—Asteraceae (Compositae).

SYNONYM.—*Oonopsis monocephala* A. Nels.

FEDERAL STATUS.—Category 2.

Haplopappus fremontii ssp. *monocephalus* has a relatively large range. Furthermore, it is probably not a good subspecies (G. Brown, personal communication, W. A. Weber, personal communication). Populations are known to contain both single- and multi-headed individuals. I have seen mixed specimens as well as specimens of the typical variety and var. *monocephalus* from the same locality collected by the same person on the same day. Status should be changed to Category 3B. The taxon grows in clayey soils, often derived from the Morrison Formation, in the juniper zone in south central and southeastern Colorado.

FREMONT COUNTY: T17S R70W: Neese 15948, 7/17/84 (CS); T18S R68W: Weber 8569, 5/21/49 (COLO); T18S R70W: Neese 15961, 7/18/84 (RM); T19S R69W: Weber & Hogan 17537, 8/24/85 (COLO, RM). LAS ANIMAS COUNTY: T31S R61W: Archibald s.n., 1902 (COLO); Archibald A257, 1900 (Isotypes: COLO, RM); T33S R60W: Brooks 14334, 7/11/79 (MO).

***Hymenoxys helenioides* (Rydb.) Cockerell,** Bull. Torrey Bot. Club 31: 481. 1904.

Map 34

FAMILY.—Asteraceae (Compositae).

SYNONYMS.—*Picradenia helenioides* Rydb., *Dugaldia helenioides* (Rydb.) A. Nels.

FEDERAL STATUS.—Category 2.

In Colorado the Intermountain bitterweed is found at elevations from 2,600 to 2,725 m where it grows on grassy floodplain terraces above creeks and below forested hillsides. This species resembles *Helenium (Dugaldia) hoopesii* Gray—hence the specific epithet—but differs from that taxon by its shorter stature, smaller capitula, and divided leaves. The species in Colorado is known from La Veta Pass, in Costilla County, and from near Slumgullion Pass, Hinsdale County. In 1987 John Anderson relocated these populations, which have not been seen since 1900 and 1940, respectively. Sangre de Cristo Creek near La Veta Pass is the type locality. Several populations are known from the Wasatch and Aquarius plateaus in central Utah, one from the Chuska Mountains of San Juan County, New Mexico (Anderson & Heil 87–174 ASU), and three from the Lukachukai Mountains of Apache County, Arizona (Anderson & Heil 87–126, 87–141 & 87–142 ASU). Arizona and New Mexico populations occur in openings in ponderosa pine–oak–aspen forests; in Utah the species grows on dry sagebrush-covered mounds within dry sedge meadows. Populations of the species invariably consist of few individuals, often fewer than a dozen. The habitat of the species, because of its high forage value, is usually grazed by domestic livestock. Because populations invariably consist of few individuals, are infrequently found across a large geographical area containing much potential habitat, have inviable pollen, and are found with both *Hymenoxys richardsonii* and *Helenium hoopesii*, *Hymenoxys helenioides* may be of sporadic hybrid origin (J. Anderson, unpublished data, personal communication).

COSTILLA COUNTY: T28S R70W: Anderson 87–105, 7/22/87 (COLO). T29S R71W: Rydberg & Vreeland 5495, 7/2/1900 (Holotype: NY, Isotype: RM); Anderson 87–116, 7/23/87 (CS). HINSDALE COUNTY: T44N R3W: Penland 1548, 7/7/40 (COCO).

***Ipomopsis globularis* (Brand) W. A. Weber,** Pflanzenreich, 4, Fam. 250: 120. 1907.

Map 35

FAMILY.—Polemoniaceae.

SYNONYMS.—*Gilia spicata* Nutt. var. *capitata* A. Gray, *G. cephaloidea* Rydb. of manuals, *G. globularis* Brand.

FEDERAL STATUS.—Category 3C.

Globe gilia is a showy endemic of the Mosquito Range, adjacent Hoosier Ridge, and Boreas Pass where it grows on barer spots in gravelly tundra and loose talus at elevations of 3,475 to 3,965 m. It is often interspersed with caespitose *Salix* species and *Dryas octopetala*. The habitat of this species is usually underlain with heavily mineralized Leadville limestone or Manitou dolomite. Mining and four-wheel-drive recreation present the major threats to the species. Although not in danger of immediate large-scale habitat loss, this species should be monitored for decreases in population size and for habitat destruction.

LOCATION OBSCURE: Brandegee s.n., 1871 (COLO); LAKE: T10S R79W: Lewis 1741, 8/3/80 (US). PARK COUNTY: T7S R77W: Lewis 1685, 7/31/80 (US); T8S R77W: Crandall s.n., 7/31/95 (CS); Johnston & Kurling 136, 7/31/75 (COLO); Johnston & Lucas 7, 7/21/77 (CS); Lewis 1578, 7/29/80 (US); Lewis 1872, 7/29/80 (US); Wojciechowski 1032, 7/23/80 (US); T8S R78W: Hall & Harbour 461, n.d. (Isotypes: GH, US); Huestis s.n., 8/14/05 (COLO, CS); Johnston 2369, 7/18/80 (COLO); Lewis 1505, 7/25/80 (US); Lewis 1767, 8/23/80 (US); O'Kane 2141, 7/16/85 (CS); O'Kane 2120, 7/15/85 (CS); O'Kane 2174, 7/19/85 (CS); Yeatts 2067, 7/14/85 (KHD); T9S R78W: O'Kane 2153, 7/17/85 (CS); T10S R78W: Neely 3068, 7/9/85 (CS); Neely & Johnston 3098, 7/16/85 (CS); T10S R79W: Pillmore s.n., 8/13/55 (CS). SUMMIT COUNTY: T7S R77W: Cowan 1810, 8/2/95 (CS); Cowan & Crandall s.n., 8/2/95 (CS); Nelson 1052, 8/1/72 (CS); Wojciechowski 1137, 7/31/80 (US); T8S R77W: Weber & Thornburg 4450, 8/31/48 (COLO, CS); T8S R78W: Komarkova s.n., 8/17/73 (COLO).

Ipomopsis polyantha* (Rydb.) V. Grant var. *polyantha, Bull. Torrey Bot. Club 31: 634. 1904.

Map 36

FAMILY.—Polemoniaceae.

SYNONYM.—*Gilia polyantha* Rydb. var. *polyantha*.

FEDERAL STATUS.—Category 2.

The Pagosa gilia is endemic to the area immediately surrounding Pagosa Springs where it grows on gray, fine-textured soils derived from Mancos shale in oak and ponderosa communities. Elevations range from 2,070 to 2,170 m. The few known populations have low population densities. Threats include residential and commercial development in the Pagosa Springs area associated with airport expansion, and increased recreational use of public lands in conjunction with two proposed ski facilities located nearby. Grazing may also impact the species. The species may be an early successional species, as it is occasionally seen growing on older road cutbanks. The effects of continual or catastrophic disturbance are not known. Field surveys are still needed to document the limited range of the species, but unless additional populations are found, it should be considered a candidate for listing as a threatened species.

ARCHULETA COUNTY: T34N R3W: O'Kane 2077, 8/5/85 (COLO, CS); T35N R1W: Harrington 8242, 6/13/56 (CS); Harrington 9981, 6/14/67 (CS); Higgins 3574, 7/3/70 (BRY); O'Kane 2079, 6/5/85 (CS); O'Kane & Anderson 2081, 6/5/85 (COLO, CS); Weber & Livingston 6334, 6/20/51 (COLO, CS, MO); T35N R2W: Bethel 7683, 7/2/17 (CS, RM); Bethel s.n., 6/29/20 (CS); Bethel, Willey & Clokey 4251, 6/30/21 (COLO, MO, RM); Smith 23, 7/20/1873 (COLO); Baker 538, 7/28/1899 (MO).

***Lesquerella congesta* Rollins**, Contr. Gray Herb. 214: 8. 1984.

Map 37

FAMILY.—Brassicaceae (Cruciferae).

FEDERAL STATUS.—Category 2.

The recently described Dudley Bluffs bladderpod is an extremely rare endemic of the Piceance Basin where it grows on barren outcrops of the Thirteen Mile Creek Tongue of the Green River shale where it abuts the Uinta Formation on ridgetops, benches, and snouts of ridges. The taxon inhabits harsh sites which, because of sparse vegetation, exposed topographic positions, and light-colored substrate, have a high-incident solar radiation. Sites are characterized by a pavement of small shale fragments. *Astragalus lutosus*, *Machaeranthera grindelioides*, and *Artemisia* are always present. Elevations range from 1,870 to 2,025 m. Habitat destruction associated with oil shale extraction is the greatest potential threat to the species. Recent surveys provide enough information to list the species as threatened or endangered.

Rio Blanco County: Location obscure: Weber 10895, 5/16/59 (COLO); T1N R98W: O'Kane 2418, 6/5/86 (COLO, GH); T1S R97W: O'Kane 2402, 6/2/86 (COLO, CS); O'Kane & Sigstedt 82–125, 5/19/82 (CS, RM); T1S R98W: O'Kane 2417, 6/5/86 (COLO, GH); Walker & Sigstedt 82–31, 5/31/82 (CS); Walker, Waters & Riefler 82–108, 6/2/82 (COLO, CS); T2S R97W: Baker & Naumann 82–191, 6/11/82 (CS); Rollins & Rollins 8394, 6/30/83 (Isotypes: COLO, CS, MO, RM).

Lesquerella parviflora **Rollins,** J. Arn. Arb. 64: 506–507. 1983.

Map 38

Family.—Brassicaceae (Cruciferae).

Federal status.—Category 2.

The Piceance bladderpod is endemic to outcrops of Green River shale in the Piceance Basin and escarpments of the Roan Plateau and Battlement Mesa. It grows on barren ridgetops above steep, shifting talus slopes and on unstable, oakbrush-covered side slopes. Elevations range from 1,905 to 2,625 m. Several populations growing adjacent to roads may be impacted by road maintenance and by ORVs leaving established rights-of-way. Oil shale extraction could severely affect several other populations. The type locality was recently patented by a shale-oil producer. The species, like *Lesquerella congesta*, *Penstemon debilis*, *Physaria obcordata*, and *Thalictrum heliophilum*, was discovered during botanical inventories of areas containing high-quality oil shale. A recent survey indicates that the species is more abundant and widespread on the Roan Plateau than previously thought (Mountain West Environmental Services 1987).

Garfield County: T5S R100W: Kelley 83–134, 8/3/83 (CS). Rio Blanco County: T1N R99W: O'Kane 2436, 6/15/86 (COLO); O'Kane 2433, 6/15/86 (COLO, BRY); O'Kane 2427, 6/14/86 (COLO, GH); T1S R96W: Baker & Naumann 82–231, 6/25/82 (CS, GH); T1S R100W: Kelley & Naumann 82–155, 7/22/82 (CS, GH); T2S R95W: O'Kane 2405, 6/3/86 (COLO, CS, RM); O'Kane 2403, 6/3/86 (COLO, NY); O'Kane 2407, 6/3/86 (COLO, BRY); T2S R96W: Walker & Naumann 82–213, 6/16/82 (CS); T2S R100W: O'Kane 2447, 6/28/86 (COLO, GH); T3S R99W: O'Kane & O'Kane 2095, 6/27/85 (CS); Rollins & Rollins 8395, 6/20/83 (BRY, CS, GH, RM); Wiley-Eberle 1021, 7/27/83 (CS, RM); T3S R100W: Baker & Sigstedt 82–308, 7/21/82 (Holotype: GH; Isotype: CS); Painter, Emrich & Pease 132, 7/24/78 (CS); Peterson & Naumann 82–4, 7/16/82 (COLO, CS, RM); Peterson et al. 1141, 7/5/78 (CS); Wilken 13866, 7/14/82 (COLO, CS, GH, RM). Mesa County: T8S R95W: Anderson 87–87, 7/15/87 (COLO, CS).

Lesquerella pruinosa **Greene,** Pitt. 4: 307–308. 1901.

Map 39

Family.—Brassicaceae (Cruciferae).

Federal status.—Category 2.

The Pagosa bladderpod is endemic to the area around Pagosa Springs where it grows in fine-textured soils derived from Mancos shale at elevations of 2,095 to 2,290 m. This area is being increasingly impacted by residential and commercial development associated with airport expansion, out-of-state vacationer homes, and land speculation related to two proposed ski areas near Wolf Creek Pass. The species is found on open shale slopes in oakbrush communities and, less frequently, open stands of ponderosa. Known threats and limited distribution qualify the species as a threatened species, although more fieldwork is needed before a final determination can be made.

Archuleta County: T34N R1W: Johnston & Lucas 1724, 6/21/78 (COLO, RM); O'Kane 2080, 6/5/85 (COLO, CS); O'Kane & Anderson 2072b, 6/4/85 (CS); T34N R2W: O'Kane 2068, 6/4/85 (COLO, CS); T34N R3W: O'Kane 2648, 4/5/87 (RM); O'Kane & Johnston 2078, 6/5/85 (CS); T35N R1W: Bethel s.n., 7/4/17 (CS, MO, RM); Bethel s.n., 6/30/21 (CS); Bethel, Willey & Clokey 4132, 6/29/21 (RM); Johnston & Lucas 1719, 6/20/78 (RM); O'Kane 2063, 6/4/85 (CS); Penland, Brown & Hartwell 2119, 6/15/48 (KHD); 035N R2W: Schmoll 1077, 6/16/24 (COLO, RM).

Lomatium concinnum **(Osterh.) Mathias,** Ann. Missouri Bot. Gard. 25: 276. 1937.

Map 40

Family.—Apiaceae (Umbelliferae).

Synonym.—*Cogswellia concinna* Osterh.

Federal status.—Category 2.

The Colorado desert-parsley is endemic to

the barren adobes and pinyon-juniper covered hills of Mancos shale from south of Montrose to Delta and Hotchkiss. The species grows in mat saltbush communities at elevations of 1,635 to 1,920 m and up to 2,120 m in pinyon and juniper. It is known to occur with *Penstemon retrorsus*, a Category 1 species, and *Eriogonum pelinophilum*, an endangered species. The species is threatened with habitat modification and destruction resulting from residential and agricultural development, canal systems, oil and gas exploration, and ORV use. Searches for this species are required to determine its status as few specimens exist, most of these being at least 75 years old.

DELTA COUNTY: Location obscure: Purpus 51, 5/1892 (F); Purpus 587, 5/1893 (F); T14S R91W: Neese 13245, 5/11/83 (BRY, CS); Osterhout 4515, 5/21/11 (Isotype: COLO); T14S R92W: Neese 13257, 5/11/83 (BRY, CS); T14S R93W: Ellis s.n., 5/27/78 (CS); T14S R94W: Neese 13267, 5/12/83 (BRY, CS, RM); T15S R93W: Neese 13262, 5/11/83 (BRY, CS). GUNNISON COUNTY: Location obscure: Baker 22, 6/6/01 (MO, RM). MONTROSE COUNTY: T49N R8W: Weber 7483, 5/30/52 (COLO). OURAY COUNTY: T R; Anderson and Fergeson 87–55, 6/1/87 (COLO, CS).

***Lomatium latilobum* (Rydb.) Mathias,** Ann. Missouri Bot. Gard. 25: 281. 1937.

Map 41

FAMILY.—Apiaceae (Umbelliferae).

SYNONYMS.—*Cynomarathrum latilobum* Rydb., *Aletes latiloba* (Rydb.) W. A. Weber.

FEDERAL STATUS.—Category 2.

The Canyonlands lomatium is a Navajo Basin endemic limited to the Entrada and Wingate sandstones at elevations of 1,538 to 1,570 m. The species is known from a few populations in Mesa County, Colorado, and Grand and San Juan counties, Utah, where it grows in sand and sandy silt on rimrock ledges in the pinyon-juniper zone. Occasionally plants are found as waifs in the canyons below as seeds are washed down. Because of its inaccessible habitat and the protection most populations receive in Colorado National Monument and Arches National Park, the species is not currently threatened with extinction. Because the species is known from very few populations, however, it should remain a candidate for listing until field surveys are completed and threats, if any, to other populations are identified.

MESA COUNTY: T1S R1W: Neese 13274, 5/13/83 (BRY, CS, RM); Siplivinsky 3298, 5/19/82 (COLO); T1S R2W: Rector 6, 7/12/80 (COLO); Ripley & Barneby 5443, 5/23/43 (RM); Weber 15804, 5/24/80 (COLO); T2S R2W: Anderson 372, 5/15/82 (BRY); T11S R102W: Anderson s.n., 7/19/84 (BRY); Rector s.n., 8/30/80 (COLO, CS, RM); Weber & Rector 16641, 5/26/83 (COLO, CS, RM); T12S R101W: Siplivinsky 5033, 8/29/82 (COLO).

***Lupinus crassus* Payson,** Bot. Gaz. 60: 376. 1915.

Map 42

FAMILY.—Fabaceae (Leguminosae).

FEDERAL STATUS.—Category 2.

The Paradox lupine is known only from western Montrose County where it grows at elevations of 1,530 to 1,825 m. The species is usually found growing beneath junipers on fairly open ground but may also be found in stands of mixed pinyon and juniper. Soils are usually sandy and are derived from the Chinle formation. Plants are, however, occasionally seen on loamy to clayey soils and even on adobe hills. This is a distinct taxon recognized by its succulent herbage and prostrate habit. Threats to the species include overgrazing, landfills, road construction, and oil and gas exploration and extraction.

MONTROSE COUNTY: T46N R15W: Beck & Siplivinsky 3606, 6/4/82 (COLO, CS); Payson 239, 4/21/14 (Holotype: RM; Isotypes: COLO, MO, RM); Payson 985, 6/1/17 (MO, RM); Peterson & Baker 83–49, 5/16/83 (BRY, COLO, CS); T47N R18W: Peterson & Kennedy 83–60, 5/18/83 (BRY, COLO, CS, RM); Peterson & Kennedy 83–58, 5/18/83 (BRY, COLO, CS); Peterson & Kennedy 83–57, 5/18/83 (BRY, COLO, CS, RM); T47N R19W: Weber & Wittman 16073, 5/29/82 (COLO); T48N R19W: Atwood & Thompson 8801, 5/20/82 (BRY); Conrad, Morris & Dunn 6627, 5/19/73 (BRY, COLO); Cox, Dunn & Fleak 1986, 6/10/70 (MO); Peterson & Kennedy 83–55, 5/18/83 (BRY, COLO, CS, RM); Ratzloff s.n., 5/13/78 (COLO); Ratzloff s.n., 5/13/78 (COLO); Walker 152, 6/21/12 (RM).

***Lygodesmia doloresensis* Tomb,** Syst. Bot. Monogr. 1: 48–50. 1980.

Map 43

FAMILY.—Asteraceae (Compositae).

FEDERAL STATUS.—Category 2.

The Dolores skeletonplant is a narrow endemic of the Dolores River canyon near the Colorado-Utah border at Gateway in Mesa County. It grows in reddish purple, sandy alluvium and colluvium of the Cutler formation between the canyon walls and the river in juniper, shadscale, and sagebrush communities at elevations of 1,400 to 1,435 m. A small population in adjacent Utah is reported (J. Anderson, personal communication). Populations of this species are severely impacted by domestic livestock grazing along narrow canyon reaches and in blackbrush flats of wider places in the canyon bottom. Individuals are limited to the protection of shrubs and clumps of *Opuntia*, and herbage projecting beyond this protection is immediately browsed. Few individuals are seen between shrubs, and then only on small sites inaccessible to livestock. Unless the little additional inventory needed indicates otherwise, this species should be listed as endangered.

MESA COUNTY: T15S R104W: O'Kane & Anderson 2092, 6/20/85 (CS); T50N R19W: Harrington 4426, 6/11/49 (CS); O'Kane & Anderson 2091, 6/20/85 (CS); Ratzloff 1655, 6/21/79 (COLO); T51N R19W: Anderson 85–82, 6/20/85 (BRY); Beck & Siplivinski 3669, 6/5/82 (COLO, CS, RM); Freeman & Wetter 1823, 5/18/83 (KANU); Harrington 3069, 5/27/47 (CS); O'Kane & Anderson 2090, 6/20/85 (CS).

***Mentzelia argillosa* J. Darl.**, Ann. Missouri Bot. Gard. 21: 153. 1934.

Map 44

FAMILY.—Loasaceae.

SYNONYM.—*Nuttalia argillosa* (Darl.) W. A. Weber.

FEDERAL STATUS.—Category 2.

The Arapien stickleaf is known from two small, widely separated areas of endemism. In Utah it is found at a few sites in Sanpete and Sevier counties growing on Arapien shale. In Colorado it grows only along escarpments of Green River shale on the Roan Plateau, Garfield County. The species occurs on steep, barren slopes of shifting talus at 1,830 to 2,560 m in elevation and is typically found with other oil shale endemics such as *Astragalus lutosus*, *Thalictrum heliophilum*, *Penstemon debilis*, and *Festuca dasyclada*. While the Utah distribution is not thoroughly known (Welsh 1985), the species has been well inventoried in Colorado and many localities are known. The major threat to the taxon is oil shale mining and retorting.

GARFIELD COUNTY: T5S R96W: Harner 1530, 8/82 (COLO); T6S R91W: Nicholas 197, 7/17/81 (CS); T6S R96W: Nicholas 46, 6/20/81 (CS); Weber & Clark 16359, 8/28/82 (BRY, COLO, CS, RM).

***Mentzelia densa* Greene**, Pitt. 3: 99. 1896.

Map 45

FAMILY.—Loasaceae.

SYNONYMS.—*Mentzelia multiflora* (Nutt.) A. Gray var. *densa* (Greene) A. Nels., *Nuttallia densa* (Greene) Greene, *Touteria densa* (Greene) Rydb.

FEDERAL STATUS.—Category 2.

The Royal Gorge stickleaf is limited to the drainages and main canyon of the Arkansas River between Cañon City and Cotopaxi, a distance of 25 miles, where it grows on steep, igneous canyon walls in mountain shrub communities at elevations of ca 1,900 to 1,990 m. Darlington enigmatically reports the species from "southern Colorado" by citing specimens from "Mesa County." Darlington does not place the species in the Arkansas canyon although Greene described the taxon from there. Specimens examined by Darlington are probably best ascribed to *M. multiflora* (O'Kane et al. 1988). Known localities are immediately adjacent to highways, but other threats are not known. Livestock probably have little impact on the species because of its inaccessible habitat. Inventories are needed to document the status of this species.

CHAFFEE COUNTY: T49N R9E: Baker, Earle & Tracy 14½, 6/19/1898 (MO). FREMONT COUNTY: Location obscure: Engelmann s.n., 9/1874 (MO); Redfield 466, 7/22/1872 (MO); T18S R70W: Osterhout 3334, 8/15/06 (RM); Osterhout 2094, 6/20/00 (NY); Shear 3782, 8/8/92 (NY); T18S R71W: Osterhout 6599, 6/22/26 (RM); T18S R72W: Harrington 7636, 7/8/54 (CS); Jones s.n., 6/29/13 (RM); T19S R73W: Brandegee s.n., 1872 (COLO); T48N R12E: O'Kane & Anderson 2204, 7/31/85 (CS).

***Mimulus gemmiparus* W. A. Weber**, Madroño 21: 423–425. 1972.

Map 46

FAMILY.—Scrophulariaceae.

FEDERAL STATUS.—Category 2.

This monkeyflower, unusual for the genus in that it does not reproduce sexually, is known from two areas of endemism, one near Tarryall Reservoir in Jefferson County and another consisting of a few populations in Rocky Mountain National Park. Interestingly, is has been located on the outwash from the recent Lawn Lake flood (B. Jennings, personal communication). The species reproduces by forming "gemmae" of swollen petiole bases containing a reduced plant axis. These gemmae fall free from the plant when leaves dehisce in the autumn. Flowers are rarely formed, and these are functionally sterile. This precise mode of reproduction is not known in any other plant species (J. Karron, personal communication). The species provides an opportunity to study the evolution of obligate asexual reproduction in an otherwise sexually reproducing genus. *Mimulus gemmiparus* grows in crevices of rock outcrops, often with dripping water, in the spruce-fir zone at elevations ranging from 2,560 to 3,050 m, often with other *Mimulus* species. Although very rare and unusual, no threats are known for the species.

GRAND COUNTY: T2N R74W: Douglass 74–1, 7/23/74 (COLO); Douglass 62–33, 6/29/62 (COLO); Karron 1, 8/15/82 (COLO); Nelson 6222, 8/2/50 (COLO); Willard 62119, 8/16/62 (COLO); Willard 61379, 8/12/61 (COLO); T4N R75W: Vickery 2735, 8/14/67 (MO). JEFFERSON COUNTY: T10S R71W: Karron 5, 9/6/82 (COLO); Murphy 322, 8/9/79 (COLO). LARIMER COUNTY: T5N R74W: Weber & Grove 14062, 7/8/70 (Holotype: COLO, Isotypes: CS, MO).

***Mirabilis rotundifolia* (Greene) Standl.**, Field Mus. Nat. Hist. Bot. Ser. 8: 305. 1931.

Map 47

FAMILY.—Nyctaginaceae.

SYNONYMS.—*Allionia rotundifolia* Greene, *A. polyatricha* Standl., *Oxybaphus rotundifolius* (Greene) Standl.

FEDERAL STATUS.—Category 2.

Mirabilis rotundifolia is endemic to an area along the Arkansas River between Cañon City and Pueblo where it grows on fine-textured, white hills eroded from the Timpas Formation, a Niobrara equivalent. It occurs at 1,550 to 2,200 m and is often found associated with *Frankenia*, *Juniperus*, *Pinus edulis*, and *Atriplex*. The species is threatened by mining for cement products and by residential expansion. The effects of grazing are not known, and surveys for the taxon are incomplete.

EL PASO COUNTY: T14S R67W: Loftfield 113, 7/18/24 (COLO). FREMONT COUNTY: T18S R70W: Brandegee 702, 7/28/1873 (UC); Brandegee 437, 8/13/1872 (Type: UC); T19S R68W: Locklear 11, 9/11/86 (COLO, NEB); Locklear 8, 6/17/86 (COLO, NEB). PUEBLO COUNTY: T20S R65W: Ewan 14177, 6/12/42 (COLO); T20S R66W: Ripley & Barneby 7663, 5/23/47 (NY); T21S R68W: Barneby 13004, 6/1/61 (NY).

***Neoparrya lithophila* Mathias**, Ann. Missouri Bot. Gard. 16: 393–394. 1929.

Map 48

FAMILY.—Apiaceae (Umbelliferae).

SYNONYM.—*Aletes lithophila* (Mathias) W. A. Weber.

FEDERAL STATUS.—Category 2.

Neoparrya lithophila was long sought in the "Heufano Mts." of northern New Mexico until it was rediscovered by W. A. Weber in 1957 on a volcanic dike near Silver Mountain in the vicinity of the Spanish Peaks, Huerfano County, Colorado. The species was found in Saguache County on the eastern edges of the San Juan volcanic area by C. E. Taylor in 1922. His specimens were filed under *Pseudocymopterus anisatus* at the U.S. Forest Service Herbarium until discovered by R. Hartman when the herbarium was moved to the Rocky Mountain Herbarium. Several populations have subsequently been located from northwest of Saguache to south of Alamosa. These populations occur on lava flows and outcrops of igneous rocks with *Artemisia*, *Ribes*, *Symphoricarpos*, and *Pinus*. An unusual population, growing on barren, nearly white silt-loam of the Dry Union Formation, was discovered near Salida in 1986 (O'Kane et al. 1988). The total elevational range of the species is 2,130 to 3,048 m. The species is not impacted by grazing because it grows on inaccessible rock outcrops with little forage value. No other threats, other than some habitat degradation of the Elephant Rocks population near Del Norte from recreational activities,

are known, and the species might best be downgraded to Category 3C.

Chaffee County: T49N R9E: O'Kane & Anderson 2218, 8/2/85 (COLO, CS). Conejos County: T34N R11E: O'Kane, Anderson & Dixon 2500, 7/10/86 (COLO, CS). Huerfano County: T27S R69W: Hartman 3101, 5/25/71 (RM); Johnston 1406, 8/1/77 (COLO); Parry 83, 9/1867 (Holotype: GH, Isotypes: MICH, MO); Weber & Gaudreau 10571, 6/29/57 (BRY). Rio Grande County: T40N R6E: Anderson s.n., 7/25/84 (COLO); Johnston 3038, 7/24/85 (RM); Johnston 3051, 7/24/85 (RM); Johnston 3041, 7/24/85 (RM); O'Kane & Anderson 2243, 8/8/85 (COLO, CS). Saguache County: T41N R6E: O'Kane & Anderson 2241, 8/8/85 (COLO, CS); T43N R7E: O'Kane 2245, 8/9/85 (COLO, CS); T45N R5E: Hartman 17360, 9/18/83 (COLO, RM); Hartman 17350, 9/18/83 (COLO, RM, CS); Hartman 17360, 9/18/83 (CS, RM); Johnston 3058, 7/25/85 (RM); Johnston et al. 2776, 10/12/83 (RM); O'Kane & Anderson 2222, 8/7/85 (COLO, CS); O'Kane & Anderson 2221, 8/7/85 (CS); Taylor 475, 7/10/22 (RM); Taylor 476, 7/6/22 (RM); T45N R6E: Johnston 3062, 7/25/85 (RM); Johnston 3063, 7/25/85 (RM).

***Oenothera acutissima* W. L. Wagner,** Syst. Bot. 6: 153–155. 1981.

Map 49

Family.—Onagraceae.

Synonym.—*O. flava* (A. Nels.) Garrett var. *acutissima* (W. L. Wagner) Welsh.

Federal status.—Category 2.

This evening-primrose is known in Colorado only from Moffat County where it grows in sandy, moist soils. It is found in seeps, adjacent to springs, along ephemeral watercourses, and in cracks of outcrops of the Uinta Mountain Group sandstones where microsites are more mesic. Surrounding vegetation may be ponderosa pine savanna, sagebrush, grass-forb, or mountain brush. Elevations range from 2,195 to 2,550 m. Known populations, because of nearby water and relatively lush forage, are impacted by domestic livestock grazing. The effects of this grazing are not known. Because the species is low-growing, light grazing could, in some situations, be beneficial, as it reduces the cover of taller species. Heavy grazing, with accompanying trampling, is probably detrimental to the species, especially around grassy springs. The species is also known from a few populations in adjacent Uintah and Daggett counties, Utah.

Moffat County: T6N R104W: Harrington 9924, 6/7/66 (CS); Neese 11806, 6/20/82 (BRY); T7N R101W: Brown s.n., 1938 (BRY); MacLeod & MacLeod s.n., 6/7/70 (COLO); MacLeod & MacLeod s.n., 7/2/70 (COLO); T7N, 102W: O'Kane & Neely 3052, 13/6/87 (COLO, MO, RM); T8N R102W: MacLeod 790, 8/8/69 (COLO); Wiley-Eberle 822, 5/14/81 (CS); Wiley-Eberle et al. 822, 6/3/81 (CS); T11N R103W: Peterson & Kennedy 83–360, 6/30/83 (BRY, CS).

***Oenothera kleinii* W. L. Wagner & Mill,** Syst. Bot. 9: 50. 1984.

Map 50

Family.—Onagraceae.

Federal status.—Category 2*.

The Wolf Creek evening-primrose is known only from the type collection from the Wolf Creek Valley overlook on the south side of Wolf Creek Pass. This subalpine area is dominated by subalpine fir and Engelmann spruce. Immediately following its discovery the population was destroyed by earthmoving equipment widening Highway 160. Inventories in the area have not located additional populations, and the species is presumed extinct, at least at the type locality. The taxon has affinities to other species of *Oenothera* in the Mojave Desert (W. L. Wagner, personal communication, W. A. Weber 1987) and may have been introduced in a highway seed mix, as several species from much lower altitudes are present on the site.

Mineral County: T37N R1E: Wagner & Wagner 4531, 9/18/81 (Isotypes: COLO, CS, MO, RM).

***Parthenium alpinum* (Nutt.) T. & G. var. *alpinum*,** Fl. N. Amer. 2: 285. 1840.

Map 51

Family.—Asteraceae (Compositae).

Synonym.—*Bolophyta alpina* Nuttall.

Federal status.—Category 3C.

The alpine feverfew is endemic to the plains of northern Weld County, Colorado, and to the southeastern quadrant of Wyoming. It forms small mats in clayey soils derived from mudstone. Cobbles eroded from conglomerate of overlying strata are often found on the soil surface. The species occurs at elevations

of 1,675 to 1,770 m in sparsely vegetated areas of blue grama grasslands. The effects of heavy grazing on the species are not known. Because of apparent rarity and lack of biological information, the taxon should be considered a Category 2 species until inventories indicate otherwise. This species (and the following species) illustrates the potential beneficial uses of rare plant genomes. *Parthenium alpinum, P. tetraneuris, and P. ligulatum* (a relatively rare species of the Uinta Basin) have been crossed with guayule (*P. argentatum*) as part of a study designed to transfer desirable traits, particularly cold tolerance, into this potentially valuable rubber-producing species (Hashemi et al. 1986, 1987).

WELD COUNTY: T11N R65W: Harmon 8919, 6/4/77 (CS); Harmon 8810, 6/4/77 (CS); Johnston & Lucas 1602, 5/30/78 (COLO, RM); Johnston & Lucas 1626, 5/31/78 (COLO, CS, RM); T11N R66W: Hartman 17370, 6/29/84 (RM); Hartman 17369, 6/9/84 (RM).

Parthenium tetraneuris **Barneby,** Leafl. West. Bot. 5: 19–22. 1947.

Map 52

FAMILY.—Asteraceae (Compositae).

SYNONYMS.—*Parthenium alpinum* (Nutt.) T. & G. var. *tetraneuris* (Barneby) Rollins, *Bolophyta tetraneuris* (Barneby) W. A. Weber.

FEDERAL STATUS.—Category 2.

The Arkansas River feverfew occurs on the rolling and dissected hills between Cañon City and Pueblo in Fremont and Pueblo counties. It grows at elevations of 1,500 to 1,710 m on limestone and shale derived from the Niobrara Formation in communities composed of various mixtures of pinyon, juniper, mountain mahogany, sagebrush, and *Frankenia*. A disjunct population near Salida, Chaffee County, grows on alluvium of the Dry Union Formation with *Eriogonum brandegei*, pinyon, and juniper at 2,225 m. Many populations are threatened by residential expansion, mining of limestone for cement production, and ORVs. The effects of grazing are not known. Inventories for the species are relatively complete, but the full extent of current and potential impacts needs to be determined.

CHAFFEE COUNTY: T50N R8E: Anderson 85–109, 8/1/85 (CS). FREMONT COUNTY: T14S R69W: Johnston & Wittman 2034, 6/10/79 (COLO); T18S R67W: Baker & Deardorff 83–123, 7/14/83 (CS); T18S R68W: Baker & Deardorff 83–124, 7/14/83 (CS); Baker & Deardorff 83–121, 7/14/83 (CS); Baker & Deardorff 83–120, 7/14/83 (CS); Baker & Deardorff 83–122, 7/14/83 (CS); Hermann 23600, 6/1/71 (CS, RM); Johnston & Lucas 1628, 6/1/78 (RM); Weber 4680, 5/21/44 (COLO, CS, KANU, RM); T19S R68W: Baker & Deardorff 83–119, 7/13/83 (COLO, CS); Baker & Deardorff 83–111, 7/11/83 (BRY, CS); Harrington 9856, 5/17/65 (CS, KSC); Johnston & Lucas 1630, 6/1/78 (COLO); Peterson & Kennedy 83–434, 7/12/83 (BRY, CS); Peterson & Kennedy 83–439, 7/13/83 (CS, RM); Peterson & Kennedy 83–433, 7/12/83 (CS); Ripley & Barneby 7662, 6/1/46 (RM); Wittmann & Wittmann 1575, 5/4/81 (COLO); T19S R69W: Peterson & Kennedy 83–416, 7/11/83 (CS, RM); Weber s.n., 5/60 (COLO). PUEBLO COUNTY: T19S R66W: Baker & Deardorff 83–125, 7/20/83 (CS); T19S R67W: Peterson & Kennedy 83–119, 7/13/83 (COLO, CS); Peterson & Kennedy 83–436, 7/12/83 (CS, RM); T20S R65W: Peterson & Kennedy 83–438, 7/12/83 (CS); Ripley & Barneby 8303, 5/23/47 (RM); T20S R66W: Baker & Kennedy 83–126, 7/21/83 (CS, RM); Peterson & Deardorff 83–447, 7/21/83 (BRY); Peterson & Kennedy 83–448, 7/21/83 (CS); Peterson & Kennedy 83–448, 7/21/83 (BRY); T20S R67W: Ripley & Barneby 7666, 6/1/46 (RM).

Pediocactus knowltonii **L. Benson,** Cac. and Succ. J. 32: 193. 1960.

Map 53

FAMILY.—Cactaceae.

SYNONYM.—*Pediocactus bradyi* L. Benson var. *knowltonii* (L. Benson) Backbg.

FEDERAL STATUS.—Endangered.

The Knowlton cactus is known from one naturally occurring population on the New Mexico–Colorado border in La Plata County, Colorado, and San Juan County, New Mexico. A small population in New Mexico near the type locality, consisting of eight individuals and presumably introduced by cactophiles fearful of the effects of Navajo Reservoir on the native population, has recently been reduced to three individuals by road construction (P. Knight, personal communication). Another "population" has recently been created in New Mexico from cuttings to study the

biology and to ensure the survival of the species. This species is among the rarest in North America as well as one of the most endangered. Cactus collectors as far away as Germany and Japan have poached the species for their cactus collections. The type locality, now owned by The Nature Conservancy, is fenced to exclude domestic livestock. The one hill that this species occupies is unusual in that it contains a mixture of *Juniperus osteosperma* and *J. scopulorum*. *Juniperus scopulorum* is not found elsewhere within miles of the population. Additionally, although at a relatively low elevation of 1,950 m, other montane species are found at the site. Soils are cobbly riverine alluvium. This species poses interesting questions concerning speciation and dispersal in the Cactaceae.

La Plata County: T32N R7W: Heil s.n., 5/18/78 (UNM); Peterson & Knight 83–7, 5/2/83 (CS).

Penstemon albifluvis **England,** Great Basin Nat. 42: 367. 1982.

Map 54

Family.—Scrophulariaceae.

Synonym.—*Penstemon scariosus* Pennell var. *albifluvis* (England) N. Holmgren.

Federal status.—Category 1.

The White River penstemon is known in Colorado only from several small populations on barren outcrops of Green River shale on Raven Ridge, Rio Blanco County. No herbarium specimens were located from the locality, but the record is certain as the Colorado Natural Areas Program and the Bureau of Land Management are currently conducting a population biology study of the species at this locality. The species, in Colorado, grows in pinyon-juniper communities. Welsh (1985) questions whether this taxon should be considered a candidate for listing, although he gives no justification for this view. A limited range and potential threats from oil shale production indicate that the species should remain a candidate until inventories show otherwise. The effects of grazing on the unstable substrate occupied by the species are not known.

Penstemon debilis **O'Kane & J. Anderson,** Brittonia 39: 412–416. 1987.

Map 55

Family.—Scrophulariaceae.

Federal status.—None.

The Parachute penstemon is known only from Mt. Callahan, above the town of Parachute, where it occupies the steep southern escarpment of the ridge crest, and from a small population on the Anvil Points near Rifle. It grows on unstable, nearly barren white talus of decomposing Green River shale with *Eriogonum lonchophyllum*, *Cymopterus hendersonii*, and *Galium coloradense*. Mount Callahan also hosts *Thalictrum heliophilum*, *Festuca dasyclada*, *Mentzelia argillosa*, and *Astragalus lutosus*, other oil shale endemics. One of the two subpopulations on Mt. Callahan, ca 90 ha total, is protected as a Colorado Natural Area. This taxon is likely limited to its currently known range as inventories of oil shale lands are relatively thorough. Because of extreme rarity, *P. debilis* should be listed as an endangered species. *Penstemon debilis* and *Pediocactus knowltonii* are among the rarest plants in North America.

Garfield County: T7S R96W: O'Kane & Anderson 2424, 6/11/86 (Holotype: COLO; Isotypes: ASU, BRY, CS, NY, RM, UTC); O'Kane 2443, 6/25/86 (KANU); Anderson 86–79, 6/25/86 (CS, SJNM); Anderson 86–118, 7/23/86 (COLO, RM).

Penstemon degeneri **Crosswh.,** Amer. Midl. Nat. 74: 434. 1965.

Map 56

Family.—Scrophulariaceae.

Federal status.—Category 2.

The Degener beardtongue is apparently endemic to the canyon of the Arkansas River from near Texas Creek to Cañon City and to Wet Mountain Valley, but few specimens are known. It grows in the duff of pinyon at elevations of 1,830 to 2,895 m. Until inventories are conducted, the species should be considered rare.

Fremont County: T18S R71W: Peterson & Kennedy 83–446, 7/14/83 (CS); Weber & Nelson 13360, 7/23/67 (COLO); T49N R12E: Harrington 7517, 7/5/54 (CS).

Penstemon gibbensii **Dorn,** Brittonia 34: 334. 1982.

Map 57

Family.—Scrophulariaceae.

Federal status.—Category 2.

The Gibbens beardtongue occurs in Sweetwater and Carbon counties, Wyoming, and, in

Colorado, from Browns Park in Moffat County and the Piceance Basin of Rio Blanco County. The species belongs to a polymorphic and difficult group of species that includes *P. penlandii* and *P. fremontii*. In Browns Park the species grows in sandy soils derived from the Browns Park Formation. Populations in the Piceance Basin grow on partially decomposed shale of the Green River Formation. *Penstemon gibbensii* is typically found with *Artemisia tridentata*, but it is also found in communities dominated by mountain mahogany and Utah juniper. Populations in Browns Park are threatened by heavy grazing. Piceance Basin populations may be threatened in the future by oil shale extraction; some populations have been impacted by road construction.

MOFFAT COUNTY: T10N R102W: Peterson et al. 1261, 7/20/78 (CS); T10N R103W: Wiley-Eberle s.n., 6/15/84 (CS); Neely 3668, 7/23/86 COLO, CS); Neely 3687, 7/23/86 (COLO, CS). RIO BLANCO COUNTY: T1N R97W: O'Kane 2409, 6/4/86 (BRY, NY); T1N R98W: O'Kane 2445, 6/26/86 (COLO); T1N R99W: O'Kane 2434, 6/15/86 (BRY, COLO, GH, NY,RM); T1S R97W: Peterson & Rollins 83–215, 6/20/83 (CS); O'Kane 2414, 6/4/86 (COLO, RM); T2N R98W: Baker & Naumann 82–184, 6/10/82 (CS); O'Kane 2441, 6/15/86 (COLO, NY, RM); O'Kane, Sigstedt & Peterson 82–322, 6/11/82 (CS); T2S R95W: O'Kane 2407, 6/3/86 (BRY, COLO, NY, RM); T2S R97W: Baker & Naumann 82–197, 6/11/82 (CS); T3S R95W: Kelley & Riefler 82–37, 7/2/82 (CS); T3S R98W: Peterson et al. 1178b, 7/6/78 (CS); T4S R95W: Kelley & Sigstedt 82–88A, 7/8/82 (CS).

***Penstemon grahamii* Keck in E. Graham,** Ann. Carnegie Mus. 26: 331. 1937.

Map 58

FAMILY.—Scrophulariaceae.

FEDERAL STATUS.—Category 1.

The Graham beardtongue, in Colorado, grows only west of Rangely on Raven Ridge, a floristically important outcrop of Green River shale that contains a number of endemic species. It is found with *Juniperus osteosperma*, *Cercocarpus intricatus*, and *C. montanus* at 1,780 m. The population, consisting of a few small subpopulations, is monitored by the Colorado Natural Areas Program and the Bureau of Land Management. The Colorado population is included in a Colorado Natural Area/BLM Area of Critical Environmental Concern. Elsewhere, the species is known from a few populations in Carbon and Uintah counties, Utah. The species is potentially threatened by oil shale mining because it grows on rich deposits of the Green River shale. The effects of grazing on the unstable habitat of this species are not known.

RIO BLANCO COUNTY: T2N R104W: Shultz & Shultz 5164, 5/28/81 (COLO); Weber et al. 1923, 5/27/79 (COLO).

***Penstemon harringtonii* Penland,** Madroño 14: 153. 1958.

Map 59

FAMILY.—Scrophulariaceae.

FEDERAL STATUS.—Category 2.

Harrington beardtongue occurs in a semicircular area adjacent to the Eagle, Colorado, and Blue rivers from near Vail to Dotsero, State Bridge, Kremmling, and to Green Mountain Reservoir. It grows in sands and fine sands in sagebrush communities at elevations of 2,165 to 2,475 m. Because it increases in open stands and decreases in closed stands of sagebrush, it appears to be an early successional species. The species is similar to *P. osterhoutii*, with which it is sympatric. *Penstemon osterhoutii* tends to occur just above the slightly more mesic sagebrush habitat of *P. harringtonii*. Inventories of habitat from Green Mountain Reservoir to Kremmling are relatively complete, but surveys elsewhere in the range are sketchy. Several populations, especially along the Blue River, are threatened by grazing and increased vacation-home and ski-resort construction. If expanses of habitat are found not to be threatened, the species should be lowered to Category 3C.

EAGLE COUNTY: T2S R82W: Harrington 8053, 6/28/55 (CS); Western Resource Development, Co. s.n., 6/22/82 (COLO); T4S R82W: Harrington 4935, 6/7/35 (CS); T4S R83W: Western Resource Development, Co. s.n., 6/22/82 (COLO); T5S R82W: Bunin 2, 6/17/85 (COLO); T5S R83W: Western Resource Development, Co. s.n., 6/24/82 (COLO). GRAND COUNTY: T1N R80W: Naumann 11, 6/29/84 (CS, RM); T1S R80W: Naumann 10, 6/28/84 (CS); Penland 4296, 6/19/52 (Isotypes: COLO, RM); T1S R81W: Harrington 8056, 6/28/55 (CS); Naumann 12, 6/29/84 (CS); Western Resource Development, Co.

s.n., 6/22/82 (COLO); T1S R82W: Wiley s.n., 6/4/79 (CS); Wiley s.n., 6/4/79 (CS). Routt County: T1S R84W: Norton & Norton s.n., 6/29/51 (CS). Summit County: T2S R79W: Weber & Wittmann 16300, 6/24/82 (RM).

Penstemon parviflorus **Pennell,** Contr. U. S. Nat. Herb. 20: 340. 1920.

Map 60

Family.—Scrophulariaceae.

Federal status.—Category 2*.

This species is known only from the type locality, "S. W. Colo., Mancos," collected by Alice Eastwood in 1890. No further clues to the type location are available because Eastwood's field books were destroyed in the 1906 San Francisco earthquake and fire. To my knowledge, no in-depth searches have been conducted for the species, although collectors have frequented the general area. The species is currently presumed extinct.

Montezuma County: T36N R13W: Eastwood s.n., 6/1890 (Isotypes: COLO, US, Phil. Acad. Sci.).

Penstemon penlandii **W. A. Weber,** Phytologia 60: 459–461. 1986.

Map 61

Family.—Scrophulariaceae.

Federal status.—None.

The Penland beardtongue is known only from a small area along a country road just northeast of Kremmling growing on seleniferous clay hills of the Troublesome Creek Formation at 2,300 m in elevation. It is sympatric with a small population of *Astragalus osterhoutii*. The effects of grazing on the species are not known. Also, the effects of increased recreational use of the area, should a nearby proposed reservoir be built, are not known.

Grand County: T2N R79W: Weber & Dahnke 17830, 7/30/86 (Holotype: COLO, Isotypes: MO, RM); Anderson 85–84, 7/1/86 (COLO).

Penstemon retrorsus **Payson ex Pennell,** Contr. U.S. Nat. Herb. 20: 373. 1920.

Map 62

Family.—Scrophulariaceae.

Federal status.—Category 1.

The adobe beardtongue occurs on barren grey adobe hills of the Mancos shale from near Montrose north to Delta and Paonia. It grows in sparsely vegetated communities dominated by *Artemisia nova*, *Atriplex confertifolia*, *A. corrugata*, and *Tetradymia spinescens* at elevations of 1,530 to 1,830 m on strongly gypsiferous clay soils. The species is sometimes found with *Eriogonum pelinophilum* and *Lomatium concinnum*, two other local Mancos shale endemics. Threats to the species include livestock grazing, habitat modifications due to agricultural and residential development, oil and gas exploration, construction of irrigation ditches, and ORV activity. Although the species is fairly abundant within its limited range, the presence of these threats indicates that it should remain a candidate for listing. If listed, it should be considered threatened.

Delta County: T14S R92W: Neese 13252, 5/11/83 (BRY, CS); Neese 15782, 6/19/84 (CS); Ratzloff s.n., 5/17/78 (COLO); T15S R92W: Ellis s.n., 5/28/78 (CS); T15S R98W: Neely 2981, 6/27/85 (CS, UTC). Montrose County: Location obscure: Dawson s.n., n.d. (COLO); T49N R8W: Rollins 2125, 5/24/38 (RM); Weber 7481, 5/28/78 (COLO, CS, MO, RM); Weber & Murray 12379, 5/18/65 (COLO); T49N R9W: Johnston, Ratzloff & Lucas 1553, 5/15/78 (COLO); Payson 673, 6/15/15 (RM); T50N R9W: Ellis 7215, 4/27/72 (COLO); T51N R9W: Neely 2894, 6/16/85 (CS, UTC).

Phacelia formosula **Osterh.,** Bull. Torrey Bot. Club 46: 54. 1919.

Map 63

Family.—Hydrophyllaceae.

Federal status.—Endangered.

The North Park phacelia is found on barren sandy slopes near the North Platte and Canadian rivers in North Park, a high-altitude basin in Jackson County lying between the Park Range on the west and the Medicine Bow Mountains on the east. The sandy soils of its habitat, derived from the Coalmont Formation, are easily shifted by prevailing winds and by the hooves of grazing animals. *Phacelia formosula* grows at ca 2,450 to 2,500 m in elevation and is associated with species of *Artemisia* and *Chrysothamnus*. In addition to being rare and local, the species may be threatened by domestic livestock grazing, by energy exploration, and by habitat modification for hay production. Studies currently being conducted by CNAP and the BLM are

designed to identify threats, if any, and the natural history of the species.

JACKSON COUNTY: T8N R80W: Peterson et al. 827, 6/4/81 (CS); T9N R79W: Atwood 1977, 7/16/69 (BRY); Atwood & Higgins 5830, 8/11/73 (BRY, RM); O'Kane 2096, 7/1/85 (CS); Osterhout 5794, 8/6/18 (Holotype: RM, Isotypes: GH, RM); Osterhout 312, 8/18/1894 (RM); Osterhout 7286, 8/6/30 (RM); Ripley & Barneby 9008, 7/5/47 (BRY); Weber & Wiley 15488, 8/13/79 (COLO); Wiley & Weber s.n., 8/13/79 (CS); T9N R80W: Peterson & Baker 814, 10/9/81 (CS); Peterson et al. 811, 10/8/81 (COLO, RM); Peterson et al. 812, 10/8/81 (CS); T10N R80W: O'Kane 2103, 7/2/85 (COLO, CS); Peterson & Baker 813, 10/9/81 (CS).

***Phacelia submutica* J. T. Howell,** Proc. California Acad. Sci. 4th Ser. 25: 370. 1944.

Map 64

FAMILY.—Hydrophyllaceae.

FEDERAL STATUS.—Category 2.

The DeBeque phacelia is limited to the Atwell Gulch and Shire Members of the Wasatch Formation at 1,540 to 1,890 m in elevation. It is found only within eight miles of DeBeque on both sides of the Colorado River where it grows on erosive, barren or sparsely vegetated, grey or dark brown, carboniferous clay soils with a high shrink-swell potential. Upon drying, these soils form deep cracks. Seeds of the species are "self planted" by falling into these cracks, which then close when wetted, thus covering the seeds. Associated species are infrequently scattered and are typical for xeric, clayey sites in the area. *Grindelia fastigiata* is nearly always an associate. Threats to the species include oil and gas exploration and extraction, ORV use, trampling by livestock, and road construction and improvement. Increased visitor use in the DeBeque area is expected if Roan Creek Reservoir is built. *Phacelia submutica* should be listed as a threatened species.

GARFIELD COUNTY: T7S R98W: Ellis & Hackney s.n., 5/13/82 (CS); T8S R97W: Johnston 2551, 5/21/82 (COLO); T8S R98W: Johnston 2542, 5/21/82 (COLO); Johnston 2547, 5/21/82 (COLO); O'Kane & Anderson 2349, 5/20/86 (CS). MESA COUNTY: T8S R97W: Barneby 12738, 5/17/55 (COLO); Johnston 2539, 5/21/82 (COLO); Johnston 2512, 5/7/82 (COLO); Osterhout 4726, 6/22/12 (CAS, COLO, RM); Osterhout 5978, n.d. (CAS RM); Osterhout 4458, 5/19/11 (Holotype: RM, Isotypes: COLO, NY, RM); Peterson & Baker , 4/27/82 (CS); Weber & Murray 12344, 5/15/65 (COLO, CS); Wingate & Weber 1365, 5/5/82 (KHD); T8S R98W: Kelley 83–20, 5/24/83 (CS); Kelley 83–16, 5/24/83 (BRY, CS, RM); T9S R96W: O'Kane 2380, 5/23/86 (BRY, COLO); O'Kane 2381, 5/24/86 (CS); O'Kane & Anderson 2364, 5/21/86 (COLO, CS); T9S R97W: Kelley 83–5, 5/12/83 (BRY, CS RM); T9S R98W: O'Kane 2396, 5/26/86 (COLO, CS); Peterson, Kelley & Walker 82–50, 5/22/82 (BRY, CS, RM); Peterson, Kelley & Walker 82–52, 5/22/82 (CS).

***Phlox caryophylla* Wherry,** Not. Nat. No. 146: 4. 1944.

Map 65

FAMILY.—Polemoniaceae.

FEDERAL STATUS.—Category 2.

Clove phlox is confined to an area from Pagosa Springs southeast and southwest to adjacent northern New Mexico where it grows in pinyon-juniper woodlands, sagebrush, and grassy meadows from 2,280 to 2,380 m in elevation. The species thrives in communities in mild disclimax, often along roads, but it is also found on pristine sites. Soils are clayey and are derived from the Mancos shale. Herbivores apparently do not utilize the species. Threats from increased residential and recreational use of the area associated with nearby proposed ski areas, an improved airport, and increased popularity of the area will probably not greatly impact the species because of its wide occurrence in its area of endemism and because the taxon can tolerate mild disturbance. Spraying of roadsides with herbicides, however, should be discontinued where the species occurs. This species should be downgraded to Category 3C.

ARCHULETA COUNTY: T34N R1W: Harrington 8076, 7/1/55 (CS); T34N R2W: Wilken 14425, 5/23/85 (CS); T35N R1W: Harrington 9979, 6/14/55 (CS); Johnston, Johnston & Johnston 2538, 5/16/82 (COLO); O'Kane 2062, 6/4/85 (CS); T35N R2W: Bethel 4967, 6/30/21 (CS); O'Kane 2055, 6/3/85 (CS); O'Kane 2056, 6/3/85 (CS); O'Kane 2067, 6/4/85 (COLO, CS); O'Kane & Anderson 2057, 6/3/85 (CS); Schmoll 1093, 6/15/24 (COLO, RM); T36N R1W: O'Kane 2054, 6/3/85 (CS);

T36N R2.5W: O'Kane et al. 2059, 6/3/85 (CS); T35N R8W: Porter 2031, 6/25/35 (RM).

Physaria bellii **Mulligan,** Canadian J. Bot. 44: 1662–1663. 1966.

Map 66

FAMILY.—Brassicaceae (Cruciferae).

FEDERAL STATUS.—Category 2.

Bell's twinpod, endemic to the Niobrara Formation, grows on fine-textured soils derived from black shale high in calcium in the southern part of its range and from light-colored, limey shale in the north. The species is scattered along the foothills and hogbacks from Fourmile Canyon near Boulder to Box Elder Creek north of Owl Canyon. One old collection, however, exists from Cheyenne Mountain near Colorado Springs (Churchill s.n. MO), and a 1988 report (J. Borland, personal communication, specimen verified by W. A. Weber) places the species southwest of Denver in Jefferson County on a small outcrop of Niobrara shale at the mouth of Deer Creek Canyon. As Cheyenne Mountain is composed of Pikes Peak Granite, it is likely that the collection locality is in error unless a disjunct population occurred at the foot of the mountain on Pierre Shale. Bell's twinpod is usually found in shrub communities dominated by *Rhus trilobata* and *Cercocarpus montanus* at elevations of 1,580 to 1,750 m. *Oryzopsis* and species of *Stipa* are common associates. Although not threatened everywhere in its range, threats to individual populations can be significant. Some populations are threatened by road construction and maintenance. The populations near LaPorte could be impacted by mining for cement products. The effects of grazing are not known.

BOULDER COUNTY: T1N R70W: Weber 3270, 4/10/47 (COLO, CS); T2N R70W: Naumann 2, 6/7/84 (CS); Neely 2514, 5/5/85 (CS, UTC); T2N R71W: Denham & Denham 1315, 4/16/67 (COLO); Gambill s.n., 5/7/84 (KHD); Mulligan & Crompton 2898, 8/24/64 (Isotype: COLO); Ramaley 1016, 5/30/05 (COLO); Rollins 7948, 5/24/79 (COLO, MO, RM); Weber 3372, 5/22/47 (COLO, CS); Wiegand & Upton 3320, 6/12/22 (MO); Wynn s.n., 5/10/83 (KHD); T3N R71W: Wilken 12887, 5/18/77 (CS). EL PASO COUNTY: T15S R67W: Churchill s.n., 6/22/12 (MO). LARIMER COUNTY: Location obscure: Osterhout 5616, 6/25/17 (COLO); T4N R70W: Popp s.n., 6/18/83 (CS); T4S R69W: Robinson s.n., 5/25/80 (COLO); T5N R69W: Naumann & Trout 4, 7/2/84 (CS); T6N R70W: Popp s.n., 6/29/83 (COLO); Schromberg s.n., 5/8/83 (COLO); T7N R69W: Naumann & Trout 3, 5/6/84 (CS); Popp s.n., 6/18/83 (CS); T8N R69W: Crandall 212, 5/14/1890 (CS); Crandall 425, 5/2/1896 (CS, MO); Crandall 427, 6/7/1898 (CS); Crandall 426, 5/7/1898 (CS); Wilken 14302, 5/6/85 (CS); T9N R69W: Lanham s.n., 6/8/80 (COLO); Neely 2734, 6/2/85 (CS, UTC); Popp s.n., 6/17/83 (CS); T10N R69W: Ramaley 2743, 6/14/07 (COLO).

Physaria obcordata **Rollins,** J. Arn. Arb. 64: 494–496. 1983.

Map 67

FAMILY.—Brassicaceae (Cruciferae).

FEDERAL STATUS.—Category 2.

The recently described Dudley Bluffs twinpod is limited to moderate or steep slopes in the Piceance Basin. The species is restricted to the Thirteen Mile Creek Tongue, which is embedded in the Uinta Formation, and to the more abundant Parachute Creek Member of the Green River shale. Soils are fine textured and usually have a large component of shale fragments. These soils, because of topographic position and sparse vegetation cover, are erosive. The species occurs in shrub communities containing various mixtures of *Amelanchier*, *Chrysothamnus*, *Atriplex*, and *Artemisia* at elevations of 1,815 to 2,270 m. The surrounding vegetation is pinyon-juniper woodland. Road and pipeline construction and maintenance have impacted and could potentially impact several populations. Herbicides should not be applied along stretches of county road known to contain the species. The species can colonize recently exposed shale slopes, but the effects of continued disturbance are not known. Oil shale mining on a large scale could significantly impact the species. Livestock do not utilize the species, but the effects of trampling the unstable habitat of the taxon are not known. Rarity and known and potential threats indicate that *P. obcordata* should be listed as a threatened species.

RIO BLANCO COUNTY: T1N R97W: O'Kane 2410, 6/4/86 (COLO, GH); T1N R98W: O'Kane 2419, 6/5/86 (COLO, GH); O'Kane & Anderson 2444, 6/26/86 (COLO, CS); T1N R100W: Walker & Riefler 82–361, 7/22/82

(CS, GH); Walker & Riefler 82–363, 7/27/82 (COLO, CS, GH); T1S R97W: O'Kane 2413, 6/4/86 (COLO, CS); O'Kane 2399, 6/2/86 (COLO, RM); T2S R97W: Baker & Naumann 82–209, 6/17/82 (CS, GH); Baker & Naumann 82–210, 6/17/82 (CS); Baker & Naumann 82–211, 6/22/82 (CS); Baker & Naumann 82–193, 1982 (CS, GH); Baker & Naumann 82–277, 7/8/82 (Holotype: GH, Isotypes: COLO, CS); Neese 11946, 7/9/82 (BRY); O'Kane 2412, 6/4/86 (BRY, COLO, RM); Rollins & Rollins 8390, 6/20/83 (COLO, CS, GH, RM); T3S R95W: Weber 17806, 7/8/86 (COLO).

***Potentilla effusa* Douglas ex Lehmann var. *rupincola* (Osterh.) Th. Wolf,** Bull. Torrey Bot. Club 26: 256. 1899.

Map 68

FAMILY.—Rosaceae.

SYNONYM.—*Potentilla rupincola* Osterh.

FEDERAL STATUS.—Category 2.

The Rocky Mountain cinquefoil, which grows among granitic rocks from ca 2,100 to ca 2,590 m in elevation, apparently occurs infrequently from Virginia Dale to Empire. Although no inventories have been conducted for the taxon, its range, as indicated by known herbarium specimens, is relatively large. Because it grows in inaccessible habitats, the species is probably not threatened. Unless inventories indicate otherwise, this taxon should be downgraded to Category 3C.

BOULDER COUNTY: T1S R73W: Payson 1558, 7/6/19 (COLO, RM). CLEAR CREEK COUNTY: T4S R74W: Shear 755, 8/19/1895 (RM); Tweedy 748, 7/15/03 (RM). LARIMER COUNTY: T4N R74W: Ashton 172, 7/27/30 (RM); T5N R73W: Osterhout 1497, 7/28/1897 (RM); T9N R74W: Osterhout 1323, 8/1893 (RM); T11N R71W: Kunkel s.n., 6/23/73 (COLO); Osterhout 5132, 7/4/14 (COLO, RM); Osterhout 2274, 9/7/00 (COLO, RM); Osterhout 1780, 7/21/1898 (Holotype: RM); Osterhout s.n., 7/20/1898 (RM, NY); Osterhout s.n., 7/19/1899 (RM); Osterhout 5524, 8/14/16 (RM); Osterhout 5602, 8/14/16 (RM); Weber & Jones 12392, 6/9/65 (COLO); T12N R71W: Stephens & Brooks 43467, 8/10/70 (KANU).

***Ptilagrostis porteri* (Rydb.) W. A. Weber,** Bull. Torr. Club 32: 599. 1905.

Map 69

FAMILY.—Poaceae (Gramineae).

SYNONYM.—*Ptilagrostis mongolica* Trucz. ex Trin. ssp. *porteri* (Rydb.) Barkworth.

FEDERAL STATUS.—Category 2.

The Porter needlegrass is endemic to the mountains flanking the north end of South Park where it grows in bogs with *Deschampsia*, *Salix*, and *Pentaphylloides*. The species is found on small microhabitats on the tops of hummocks formed from peat which elevate the species a few centimeters above the water table. Elevations range from 2,695 to 3,660 m. *Ptilagrostis porteri* is closely related to the Asiatic *P. mongholica*. Threats to the taxon include peat mining and the ditching of bogs for water diversion projects. The Geneva Park population has apparently been extirpated by peat mining. The effects of grazing are not known, but trampling by livestock probably disturbs the fragile microhabitat.

PARK COUNTY: T6S R75W: Giersch & Hickey 3102, 7/26/66 (COLO); Giersch s.n., 9/8/70 (COLO); Johnston 2511, 8/14/81 (COLO); T8S R74W: Johnston 2497, 8/13/81 (COLO); Johnston & Hendzel 2655A, 10/4/82 (COLO); Johnston & Hendzel 2655, 10/4/82 (COLO); T8S R77W: Marr s.n., 8/3/86 (COLO); T9S R72W: O'Kane 47, 8/28/84 (BRY, COLO, CS, RM); T9S R73W: Johnston & Hendzel 2658, 10/4/82 (COLO); O'Kane 53, 8/29/84 (COLO, CS, RM); Shubert 20–2, 7/20/54 (COLO, CS); Weber 12984, 9/25/66 (COLO); T9S R78W: Stevens 1, 9/3/59 (COLO, CS). SUMMIT COUNTY: T8S R78W: Price 403, 7/27/79 (COLO).

***Rorippa coloradensis* Stuckey,** Sida 4: 303–305. 1972.

Map 70

FAMILY.—Brassicaceae (Cruciferae).

FEDERAL STATUS.—Category 2*.

The Colorado watercress is known from a single collection, the type, collected by T. S. Brandegee in 1875. Stuckey (1972), by carefully reconstructing Brandegee's 1875 itinerary, surmised the collection locality to be "the vicinity of the lakes of the San Luis Valley" in Alamosa County. Searches by myself, J. Anderson, and H. Dixon in 1986, and periodically by others, did not relocate the species. Wetlands in the San Luis Valley are continually modified by systems of canals, the digging of artesian wells, and conversion for agriculture. This species is presumed extinct.

Location obscure: Brandegee 1069, 1875 (PH).

Saussurea weberi Hultén, Svensk Bot. Tidskr. 53: 200–202. 1959.

Map 71

Family.—Asteraceae (Compositae).

Synonym.—*S. alpina* DC. sensu Harrington.

Federal status.—Category 3C.

In Colorado this species is limited to the Mosquito Range and contiguous Hoosier Ridge where it grows on gravelly tundra slopes and amidst scree, often on solifluction lobes, at elevations of ca 3,200 to 4,355 m. It is most often found growing on exposed sites with poorly developed soils derived from Leadville limestone and Manitou dolomite. *Saussurea weberi* is also known from a few localities in west central Wyoming in Sublette and Fremont counties (Dorn 1988) and from west central Montana in Deer Lodge and Granite counties (Dorn 1984). Threats in Wyoming and Montana are not known, but in Colorado some populations are threatened by hard-rock mining in its mineral-rich area of endemism.

Park County: T8S R77W: Weber & Thornburg 4448, 8/31/48 (COLO); T8S R78W: Huestis s.n., 8/14/05 (Isotypes: COLO, RM); Penland 4254, 7/28/51 (BRY, COLO); T10S R78W: Neely 3070, 7/9/85 (CS); Weber 13304, 7/12/67 (COLO); T10S R79W: O'Kane & Anderson 2581, 8/6/86 (CS, NY, RM); Weber & Hogan 17508, 8/16/85 (COLO). Summit County: T6S R76W: Johnston 1479, 8/15/77 (COLO, RM); T8S R77W: Weber 4313, 7/24/48 (COLO).

***Sclerocactus glaucus* (K. Schum.) L. Benson**, Cact. Succ. J. (Los Angeles). 38: 53. 1966.

Map 72

Family.—Cactaceae.

Synonyms.—*Sclerocactus whipplei* (Engelm.) Britt. & Rose var. *glaucus* (J. A. Purpus) Welsh, *S. whipplei* (Engelm.) Britt. & Rose var. *roseus* (Clover) L. Benson sensu lat., *Echinocactus glaucus* K. Schum.

Federal status.—Threatened.

The Uinta Basin hookless cactus occurs in northeastern Utah as well as in Mesa, Garfield, Delta, and Montrose counties, Colorado. In Colorado the species grows on fine-textured soils that are often derived from the Mancos shale in shadscale, greasewood, and juniper communities at elevations generally near 1,550 m. Welsh (1987) considers this taxon to be a straight-spined form of *Sclerocactus whipplei* var. *roseus*, stating that "specimens with straight spines have long been known" and that "they differ in no other discernible way from the body of the species." Straight spines are "considered . . . to be taxonomically negligible." Plants with straight spines, as opposed to the usually hooked spines of *S. whipplei*, occur through much of the range of *S. whipplei*, although they are more common in eastern Utah and western Colorado. Whatever the taxonomic status of this controversial taxon, it is relatively widespread and abundant. Although threats to the taxon exist, e.g., poaching by cactus collectors and a proposed reservoir north of DeBeque, the species is threatened in only a fraction of its range and should, therefore, be reduced to Category 3C, or perhaps 3B, status.

Delta County: T14S R94W: Neese 13206, 5/9/83 (BRY); T15S R96W: Heil s.n., 10/76 (BRY). Garfield County: T7S R98W: Arp 1017, 6/20/70 (COLO); Kelley 83–6, 5/18/83 (CS); Weber 13978, 5/15/69 (COLO); T8S R97W: Arp 1006, 6/20/70 (COLO); Arp 1006, 6/20/70 (KHD). Mesa County: T1S R1E: Arp 1672, 7/8/71 (COLO); T1S R2E: Peterson 83–39, 5/11/83 (CS); T2S R2E: Baker 83–1, 5/11/83 (CS); Neese 13438, 5/27/83 (CS); Peterson & Kennedy 83–288, 5/10/83 (CS); T8S R97W: Kelley 83–14, 5/19/83 (CS); Weber 12353, 5/15/65 (COLO); T13S R97W: Neese & Abbott 13580, 6/15/83 (BRY). Montrose County: T51N R98W: Arp 1691, 9/4/71 (COLO).

***Sclerocactus mesae-verdae* (Boiss. & Davidson) L. Benson**, Leafl. West. Bot. 6: 163. 1951.

Map 73

Family.—Cactaceae.

Synonyms.—*Echinocactus mesae-verdae* (Boiss. & Davidson) L. Benson, *Coloradoa mesae-verdae* Boiss. & Davidson, *Pediocactus mesae-verdae* (Boiss. & Davidson) Arp.

Federal status.—Threatened.

The Mesa Verde cactus is limited, in Colorado, to Ute Mountain Ute tribal lands in the Four Corners area in Montezuma County where it grows on barren Mancos shale hills

and flats with *Atriplex corrugata* and *A. confertifolia* at elevations of 1,605 to 1,690 m. The species is also known from a few scattered stations in San Juan County, New Mexico. This taxon experiences a substantial degree of poaching from cactus collectors and is occasionally trampled by domestic livestock. ORV use of its barren habitat also accounts for some mortality, and it is threatened by oil and gas exploration and development.

MONTEZUMA COUNTY: T32N R17W: Peterson & Baker 83–16, 5/5/83 (CS); T33N R17W: Arp 1476, 9/6/70 (COLO); Peterson & Baker 83–10, 5/4/83 (CS); O'Kane & Jamieson 2631, 28/4/87 (RM); Weber s.n., 6/13/50 (COLO).

***Senecio dimorphophyllus* Greene var. *intermedius* T. M. Barkley,** Trans. Kansas Acad. Sci. 65: 363. 1962.

Map 74

FAMILY.—Asteraceae (Compositae).

FEDERAL STATUS.—Category 2.

The intermediate groundsel is known from three areas of endemism: the La Sal Mountains in Grand and San Juan counties, Utah; near the town of Mont Lewis in Sanpete County, Utah; and from the Uncompahgre Plateau in Mesa, Montrose, and Ouray counties, Colorado. The species, in Colorado, grows in wet meadows, often with *Pentaphylloides* and *Veratrum*, at elevations of 2,650 to 3,010 m. Surrounding vegetation is Engelmann spruce and aspen. The species is apparently infrequent and threats have not been identified. The effects of livestock grazing are not known. This taxon should remain a Category 2 species until thorough inventories are conducted.

MESA COUNTY: T51N R16W: Anderson 87–159, 9/1/87 (COLO). MONTROSE COUNTY: T46N R11W: Anderson 86–147, 8/28/86 (COLO); T47N R11W: Anderson 86–146, 8/28/86 (COLO, CS); T47N R12W: Anderson 86–145, 8/28/86 (COLO); T48N R14W: Anderson 86–142, 8/28/86 (COLO); Douglass 54–349, 6/23/54 (COLO). OURAY COUNTY: T46N R11W: Anderson s.n., 8/28/86 (COLO).

***Sisyrinchium pallidum* Cholewa & D. Henderson,** Brittonia 36: 361–362. 1984.

Map 75

FAMILY.—Iridaceae.

FEDERAL STATUS.—None.

Pale blue-eyed-grass is known from a few localities in central and north central Colorado and southern Albany County, Wyoming. The species grows in wet meadows with rich organic soils. Sedges, grasses, and other wetland species such as *Triglochin maritima*, *Juncus balticus*, *Primula incana*, and *Dodecatheon pulchellum* are common associates. Elevations range from 2,415 to 2,900 m. Populations in South Park may be threatened by the ditching of wetlands for water diversion projects. The species is apparently rare, but inventories for the taxon have not been conducted. The species, because it inhabits fragile wetland habitats and because it appears to be rare, should be considered a Category 2 species until inventories better document its status.

LARIMER COUNTY: T5N R74W: Cholewa 572, 7/12/80 (ID); T11N R76W: Wilken 14636, 7/9/86 (CS). PARK COUNTY: T7S R75W: Beetle 2101, 8/4/37 (RM); T7S R76W: Ramaley & Gambill 16878, 7/13/39 (COLO); Weber 17380, 7/20/84 (COLO, CS); Weber & Randolph 17380, 7/20/84 (COLO, CS); T8S R75W: Cholewa 448, 7/13/79 (ID), Cholewa 150, 7/13/78 (ID); Cholewa 437, 7/12/79 (MO); T8S R76W: Harrington 9084, 7/14/59 (CS); T10S R76W: Cholewa 454, 7/13/79 (MO); T11S R76W: Cholewa 450, 7/13/79 (ID), Cholewa 157 (ID); T12S R76W: Cholewa 456, 7/13/79 (Holotype: ID, Isotypes: CAN, CS, MO, NY, RM); Jennings s.n., 7/4/85 (CS).

***Spiranthes diluvialis* Sheviak,** Brittonia 36: 8–14. 1984.

Map 76

FAMILY.—Orchidaceae.

SYNONYM.—*Spiranthes porrifolia* Lindl. sensu Goodrich, Neese, and Welsh.

FEDERAL STATUS.—Category 2.

Diluvium lady's tresses is known from several widely disjunct localities in Colorado (Boulder and Jefferson counties and the "South Fork of the Platte"), Nevada (Lincoln County), and Utah (Daggett, Garfield, Tooele, Utah, Wayne, Salt Lake, and Weber counties). The species occupies wet meadows in floodplains and, at least in Colorado and Utah, does not tolerate heavy grazing (B. Jennings, personal communication, Sheviak 1984). Localities in Salt Lake, Tooele, and Utah counties, Utah, have been extirpated; a Boulder County, Colorado, population has

been impacted by grazing. The disjunct pattern of distribution indicates that the taxon may be found in suitable habitat in intervening areas. Sheviak (1984) states that, because of the complexity of the group, "a significant number of specimens may be misdetermined and the stations consequently undetected." Inventories are needed to ascertain the status of this taxon. Rydberg (1906) notes a locality for *Spiranthes porrifolia* from "Camp Harding, near Pike's Peak." The collection Rydberg consulted has not been located (B. Jennings, personal communication) but probably belongs to *S. diluvialis* as *S. porrifolia* is known only from west of Colorado (Cronquist et al. 1977).

LOCATION OBSCURE (Probably Weld or Morgan County): "South Fork of the Platte," H. Engelmann s.n., 9/1856 (MO). BOULDER COUNTY: T1S R70W: Jennings 86–9, 8/12/86 (COLO, CS, NYS, RM); Jennings 86–6, 7/30/86 (COLO, CS, NYS, RM); Jennings 86–7, 8/2/86 (COLO, CS, NYS, RM); Sharps s.n., 7/30/85 (COLO). JEFFERSON COUNTY: T3S R69W: B. Anderson 1827, 7/25/81 (KHD); Jennings s.n., 8/8/84 (CS); Root 85–55, 8/26/85 (KHD); T3S R70W: Bye 9769, 9/6/80 (COLO); Sheviak 224, bloomed in hort. (NYS), Sheviak 2313, 8/2/82 (NYS), Callas s.n., 8/17/84 (KHD); Gambill et al. s.n., 7/23/81 (COLO); Jennings s.n., 8/8/84 (CS); Sheviak, Jennings, Long & Wood 2257, 7/17/82 (Isotype: COLO); Smookler s.n., 8/18/80 (COLO).

Thalictrum heliophilum **Wilken & DeMott,** Brittonia 35: 156–158. 1983.

Map 77

FAMILY.—Ranunculaceae.

FEDERAL STATUS.—Category 2.

The sun-loving meadowrue grows on steep talus slopes and ridges covered with broken, shifting plates of the Parachute Creek Member of the Green River shale. Associated vegetation is very sparse, typically with scattered plants of *Cymopterus hendersonii*, *Holodiscus dumosus*, *Astragalus lutosus*, and *Chrysothamnus nauseosus*. The species is limited to the Piceance Basin, the Roan Plateau, and to the ridge east of Horse Mountain and south of the Colorado River. *Thalictrum heliophilum* is occasionally found with another oil shale endemic, *Lesquerella parviflora*. The population on Mount Callahan is found with *Festuca dasyclada*, *Mentzelia argillosa*, and *Penstemon debilis*. This site has been designated a Colorado Natural Area. Elevations range from 1,920 to 2,682 m. The species is unusual because it occupies windswept, harsh sites while its congeners prefer mesic, usually shaded conditions in the mountains. Oil shale companies have used the species for revegetation following shale extraction with great success. Inventories for the species are complete, and the decision whether or not to list the species as endangered or threatened depends, in part, on the likelihood of extensive oil shale extraction in the near future.

GARFIELD COUNTY: T5S R100W: Kelley 138, 8/3/83 (CS); T6S R95W: Nicholas 83, 6/20/81 (CS); T6S R96W: Harner 1918, 7/16/83 (COLO); T6S R97W: Mustard 3365a, 7/22/81 (COLO); T6S R98W: Camp, Dresser & McKee, Co. 3666, 7/8/82 (COLO); Mustard 2760, 6/3/81 (COLO); T7S R96W: O'Kane & Anderson 2421, 6/11/86 (COLO, NY, RM). RIO BLANCO COUNTY: T3S R99W: Allard & Walker 607, 8/26/81 (CS); Erdman s.n., 8/23/77 (COLO); Neese & Baker 11950, 7/10/82 (BRY); Popp & Waters 82–419, 8/2/82 (BRY, COLO, CS, RM); Waters s.n., 7/15/81 (CS); Wiley-Eberle 534, 7/17/80 (CS); T3S R100W: O'Kane 3226, 1/7/87 (COLO, MO, RM); Wilken 13864, 7/14/82 (Holotype: RM, Isotypes: BRY, COLO, CS, NY); T4S R100W: Baker & Naumann 82–286, 7/13/82 (BRY, CS, RM). Mesa County: T8S R95W; reported by Johnston in 1985 and J. Anderson in 1987.

OTHER RARE TAXA

The Colorado Natural Areas Program (1988) includes two additional taxa on its list of highest priority rare plants. At this time neither taxon is recommended for federal status as no threats are known that could significantly affect them. They are, however, biologically interesting endemics. These species are not included in Figures 1 and 2.

Arabis vivariensis **Welsh,** Great Basin Nat. 46: 261–264. 1986.

Map 78

FAMILY.—Brassicaceae (Cruciferae).

SYNONYMS.—*Arabis fernaldiana* Rollins var. *fernaldiana* sensu lat., *Boechera fernaldiana* (Rollins) Weber sensu lat.

FEDERAL STATUS.—None.

The park rockcress is endemic to Uintah County, Utah, and Dinosaur National Monument in western Moffat County, Colorado. The species grows on sandy soils derived from the Weber Formation in Colorado. In Utah, besides sandstone, it is known to occur on limestone (Welsh et al. 1987). Its habitat is the shade and duff beneath pinyon-juniper woodlands, these frequently with cryptogamic soils and often on steep canyon slopes. Elevations range from 1,525 to 2,150 m. Little is known about the taxon because it has only recently been the focus of a botanical inventory (Galatowitsch et al. 1988). Preliminary data from an inventory conducted in the spring of 1988 (T. Naumann, personal communication) indicate that the park rockcress may be more abundant in the canyons of Dinosaur National Monument than was previously thought. No current threats to the species are known, and the species is not recommended for federal status. Dinosaur National Monument management plans will include consideration of this species. *Arabis vivariensis* is similar to *A. fernaldiana* from Nevada but differs in having smaller flowers and a shorter style (Welsh et al. 1987).

MOFFAT COUNTY: T6N R101W: Neely 4069, 5/19/87 (COLO, CS, DINO); Neely 4053, 5/19/87 (COLO, DINO, RM); T6N R102W: O'Kane 2829, 5/19/87 (COLO, CS, DINO); Neely 4117, 5/28/87 (COLO, DINO, RM); T6N R103W: Neely 4204, 6/1/87 (COLO, DINO, RM); T6N R104W: O'Kane 3007, 6/1/87 (COLO, DINO, RM); O'Kane 3002, 6/1/87 (COLO, DINO, RM); T7N R103W: Neely 4224, 6/3/87 (COLO, DINO, RM); Neely 4405, 6/16/87 (BRY, COLO, DINO).

Gilia penstemonoides Jones, Zoë 4:279–280. 1893.

Map 78

FAMILY.—Polemoniaceae.

FEDERAL STATUS.—Category 3C.

The Black Canyon gilia has its center of distribution in the Black Canyon of the Gunnison and on Blue Mesa where it grows on igneous and metamorphic rocks of vertical cliff faces. The nature of the habitat of the species and its occurrence in Black Canyon of the Gunnison National Monument provide it with protection from factors that threaten other rare Colorado endemics. While not abundant, the taxon has a relatively large area of endemism.

GUNNISON COUNTY: Location obscure: Flowers 659, 6/12/61 (CS); Hall 553, 7/15/61 (CS); Hall 576, 7/18/61 (COLO); T47N R3W: Grey 41, 6/17/80 (COLO); Grey 158, 6/27/80 (COLO); Grey 196, 7/3/80 (COLO); Grey 520, 8/22/80 (COLO); Grey 212, 7/22/80 (COLO); Grey 157, 7/28/81 (CS); Grey 1426, 7/28/81 (CS); Johnston 1790, 7/10/78 (COLO); T48N R2E: Langenheim 4059, 8/12/55 (RM); T48N R4W: Grey 290, 7/9/80 (COLO); Grey 697, 8/19/80 (COLO); Grey 705, 8/19/80 (COLO); Grey 715, 8/21/80 (COLO); Grey 674, 8/19/80 (COLO); Grey 481, 7/21/80 (COLO); Weber 9356, 7/27/55 (COLO, CS, RM); T48N R5W: Grey 437, 7/18/80 (COLO); Grey 480, 7/21/80 (COLO); Grey 1188, 6/22/81 (CS); Grey 720, 8/21/80 (COLO); T49N R4W: Ripley & Barneby 10208, n.d. (NY). HINSDALE COUNTY: T44N R2W: Grey 746, 8/22/80 (COLO); Grey 930, 8/29/80 (COLO); Grey 939, 8/29/80 (COLO); Ratzloff 142, 8/23/78 (COLO). MONTROSE COUNTY: T47N R6W: Rollins 1995, 8/37 (NY, RM); T49N R7W: Grey 465, 7/20/80 (COLO); T50N R8W: Grey 454, 7/19/80 (COLO); Grey 714, 8/20/80 (COLO); Grey 464, 7/19/80 (COLO). OURAY COUNTY: T44N R7W: Osterhout 8365, 7/25/15 (RM).

NOTE ADDED IN PROOF

J. G. Harris, monographer of *Braya* (1985), recently annotated the specimens at CS (D. Wilken, personal communication). Material previously assigned to *Braya humilis* ssp. *ventosa* is now divided between *B. humilis* var. *glabella* and var. *humilis*. Although interesting long-distance disjuncts, neither taxon should be considered a candidate for U.S. Fish and Wildlife Service endangered or threatened status. Information on the status of specimens at other herbaria is not currently available; specimens at CS are as follows.

Braya humilis ssp. *humilis:* Neely 3211, 3125, 3174, 3220a, 3311, O'Kane 2144, 2152, 2171; Peterson et al. 82–56; Walter 28; Weber & Rollins 6491; Weber & Roloff 16328.

Braya humilis ssp. *glabella:* Neely 3170, 3174, 3183; Siems 1592, 7/31/87 "ca 15 mi WSW of Buena Vista" (CS) is a new collection.

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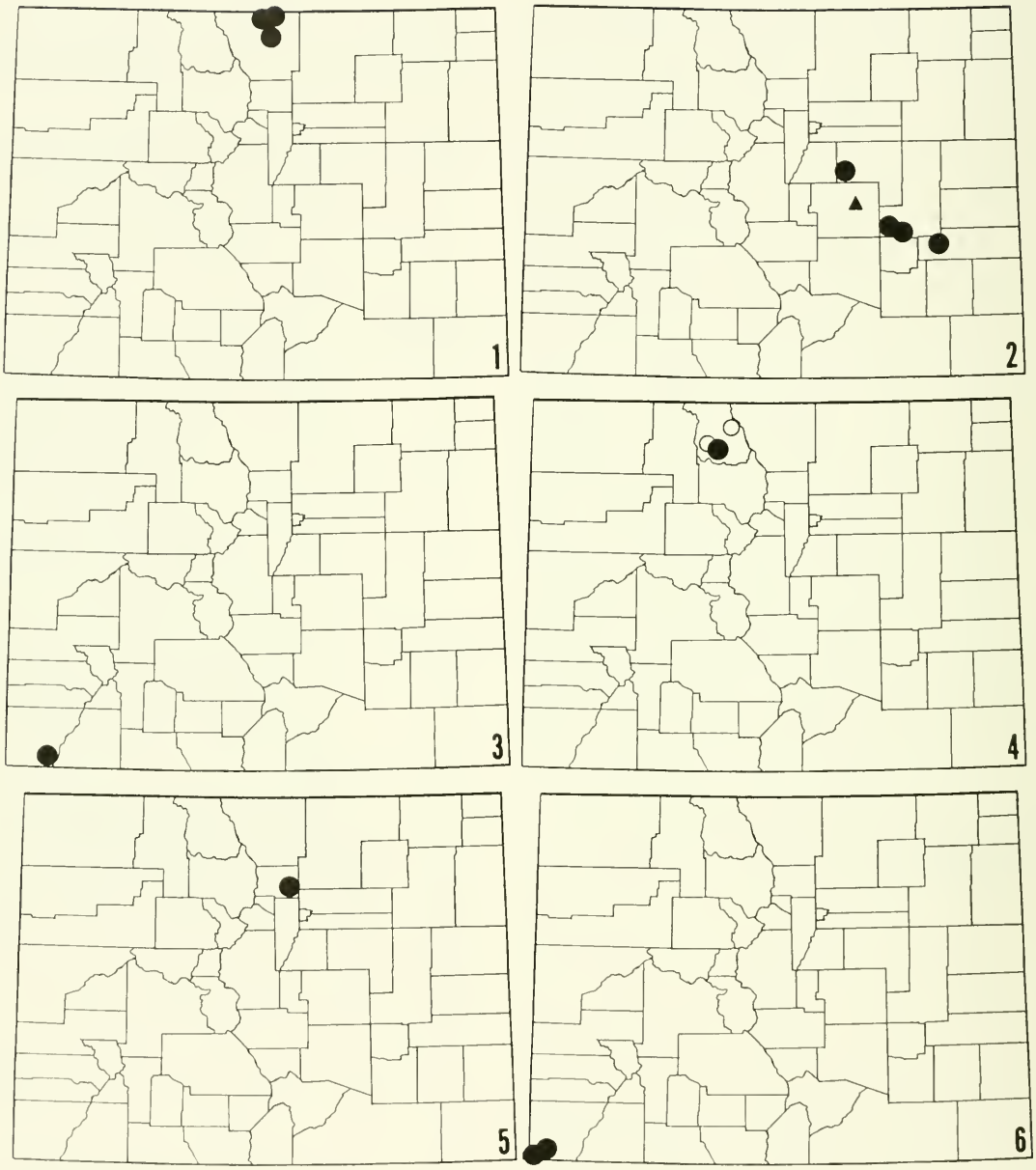
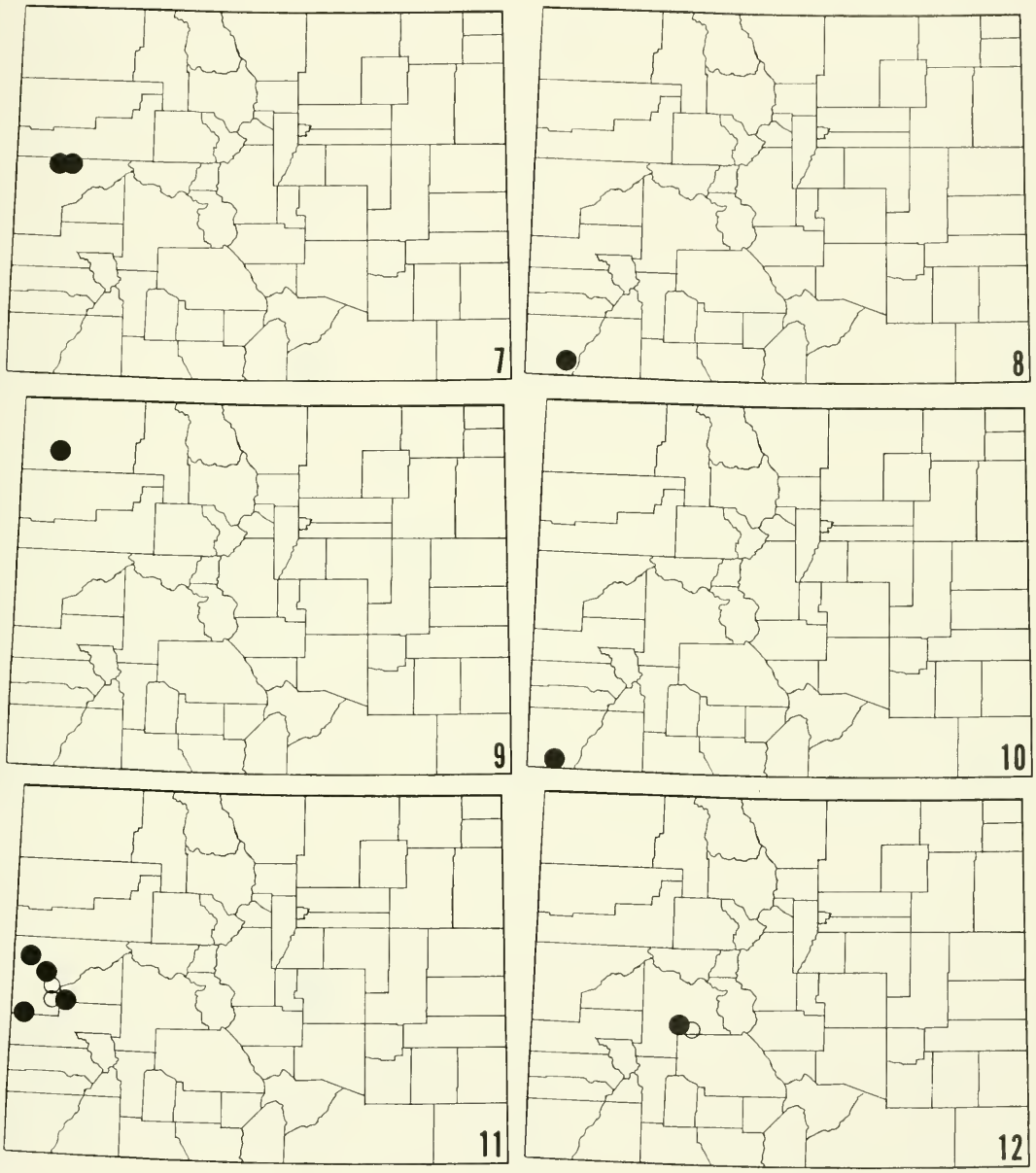
Appendix

The maps on the following pages show the geographical range of species treated in the text. Map symbols are as follows:

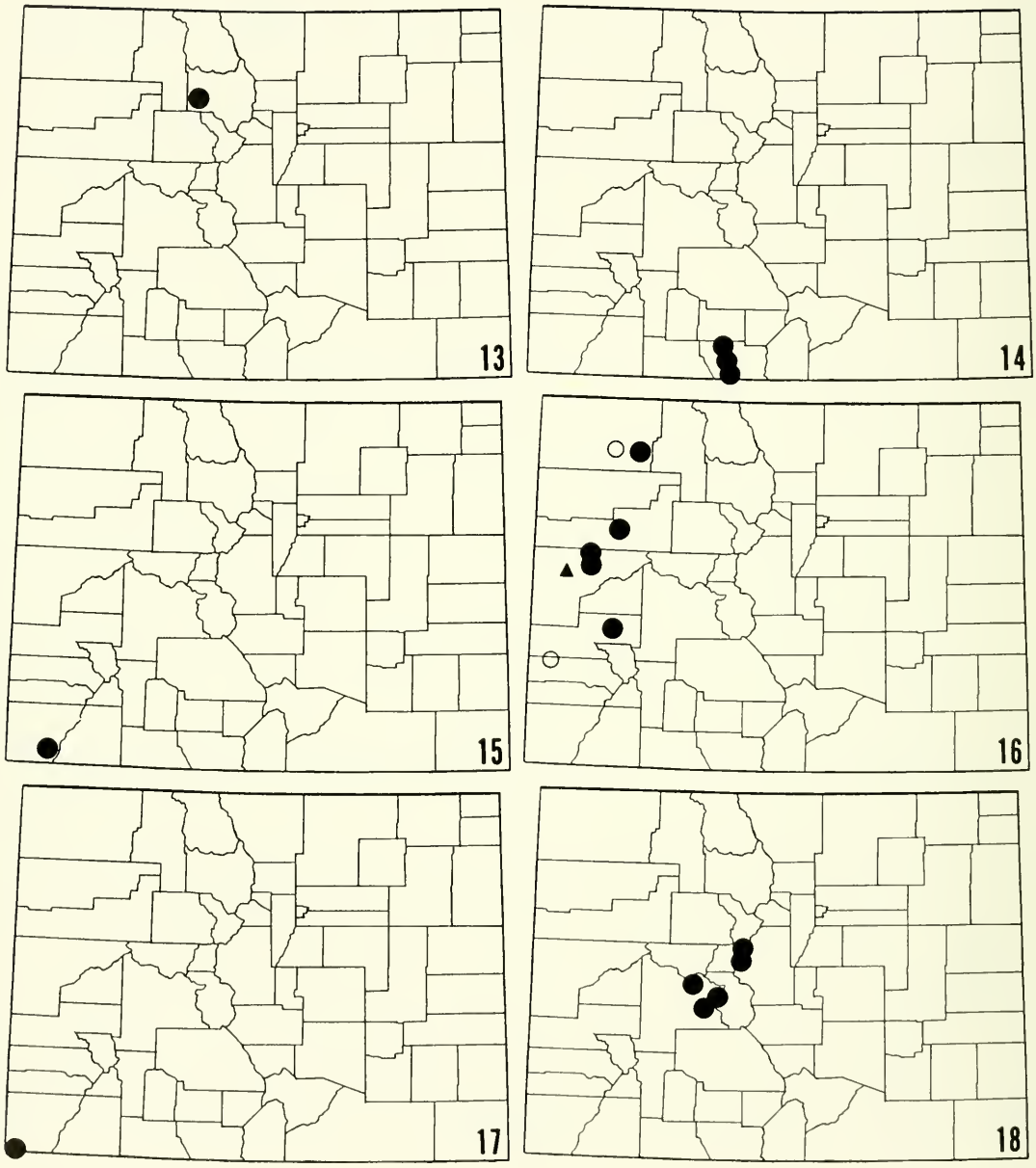
Solid circles	Unambiguous locations taken from herbarium specimens. Circles cover ca five townships and, therefore, may represent more than one collection locality.
Open circles	Locations based on field surveys for which no specimens exist. Data from the Colorado Natural Areas Program (CNAP) data base. Specimen-based localities always supercede CNAP reports. Circles cover ca four townships and, therefore, may represent more than one reported locality.
Triangles	Approximate locations based on herbarium records. Localities cannot with confidence be assigned to a particular township.
Star	Indicates a specimen-based record that can be placed only tentatively in a county.



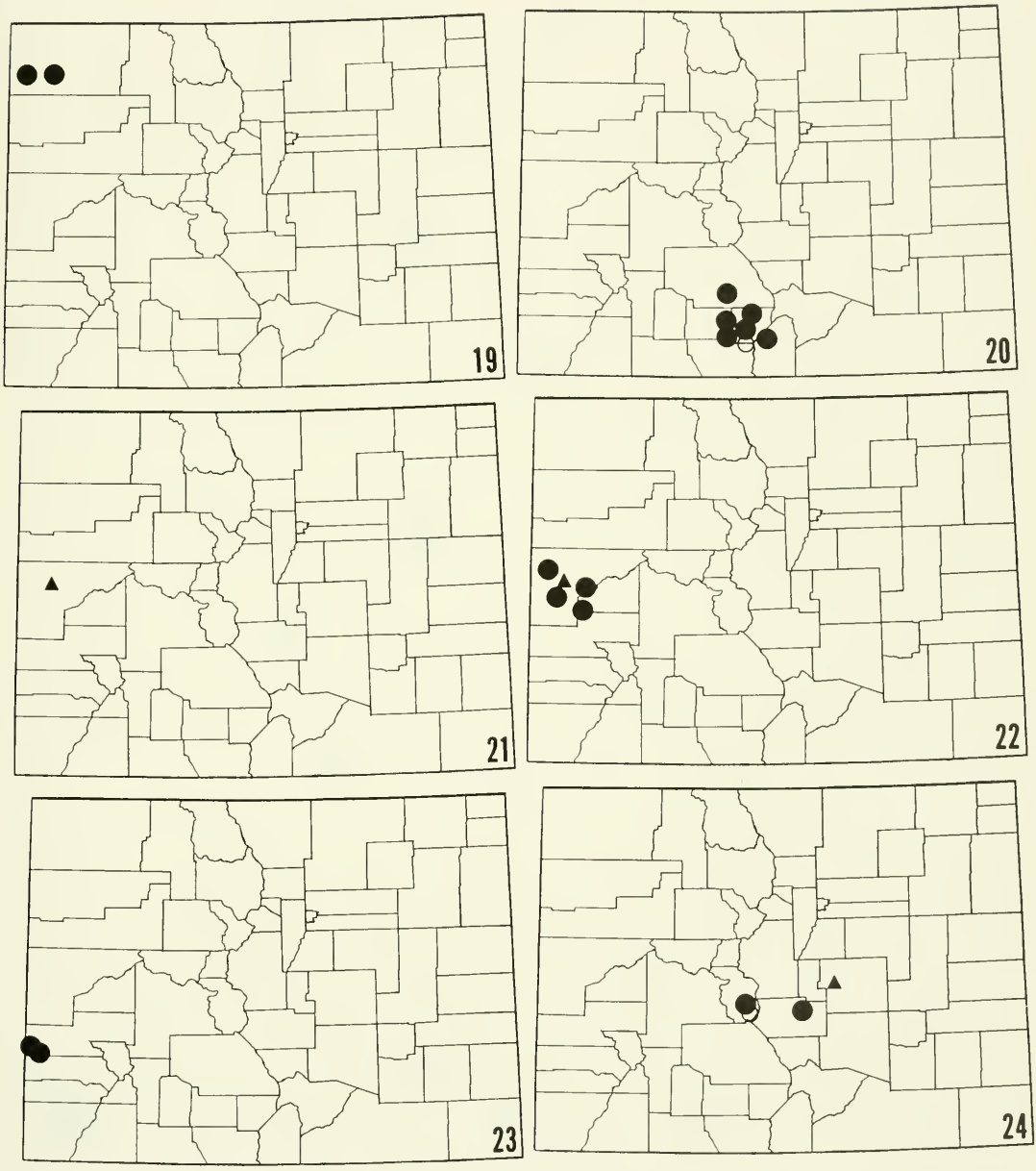
Maps 1–6. Distribution of (1) *Aletes humilis*, (2) *Ambrosia linearis*, (3) *Aquilegia micrantha* var. *mancosana*, (4) *Artemisia argilosa*, (5) *Asplenium andrewsii*, and (6) *Astragalus cronquistii*.



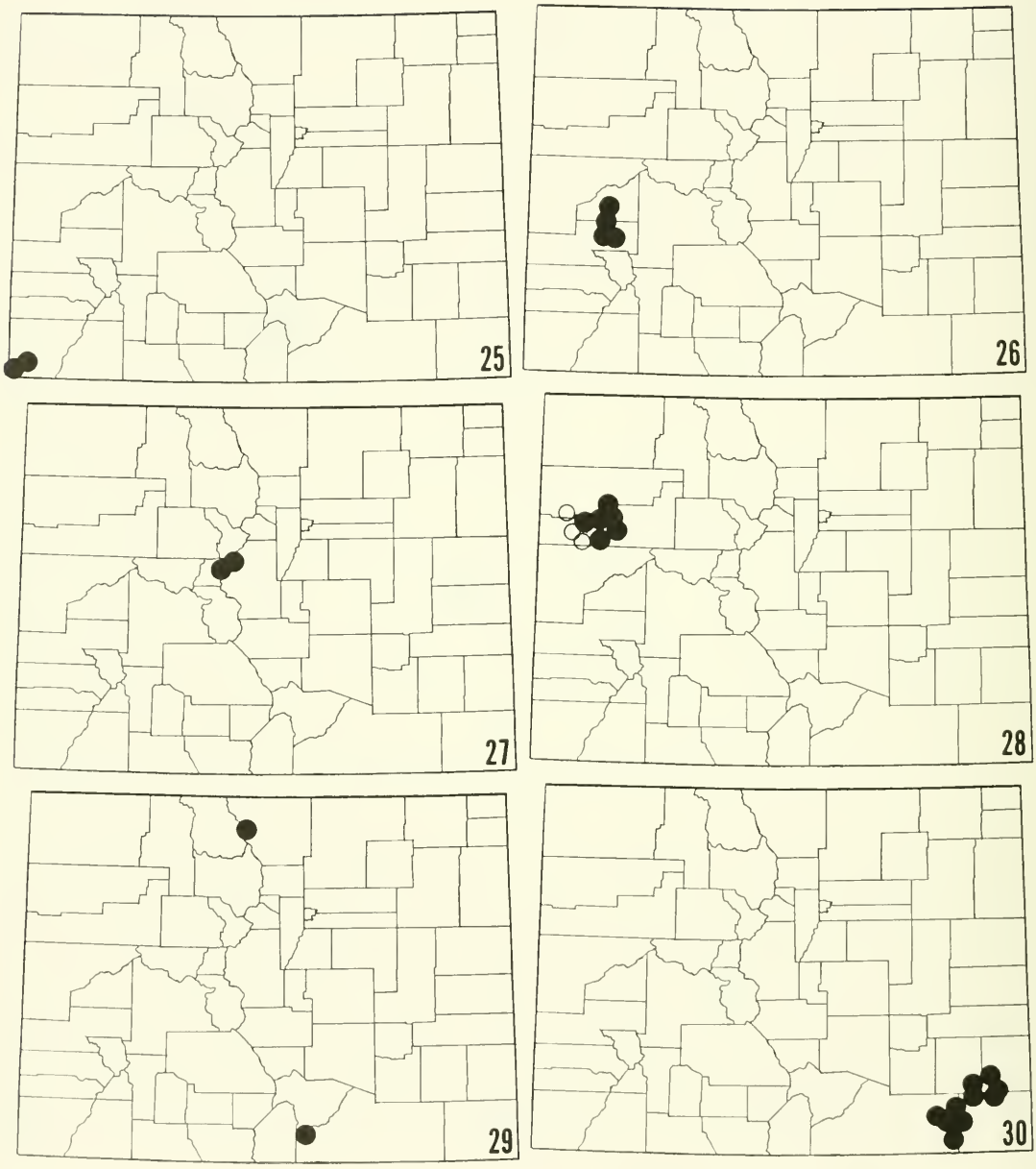
Maps 7–12. Distribution of (7) *Astragalus debequaeus*, (8) *A. deterior*, (9) *A. hamiltonii*, (10) *A. humillimus*, (11) *A. linifolius*, and (12) *A. microcymbus*.



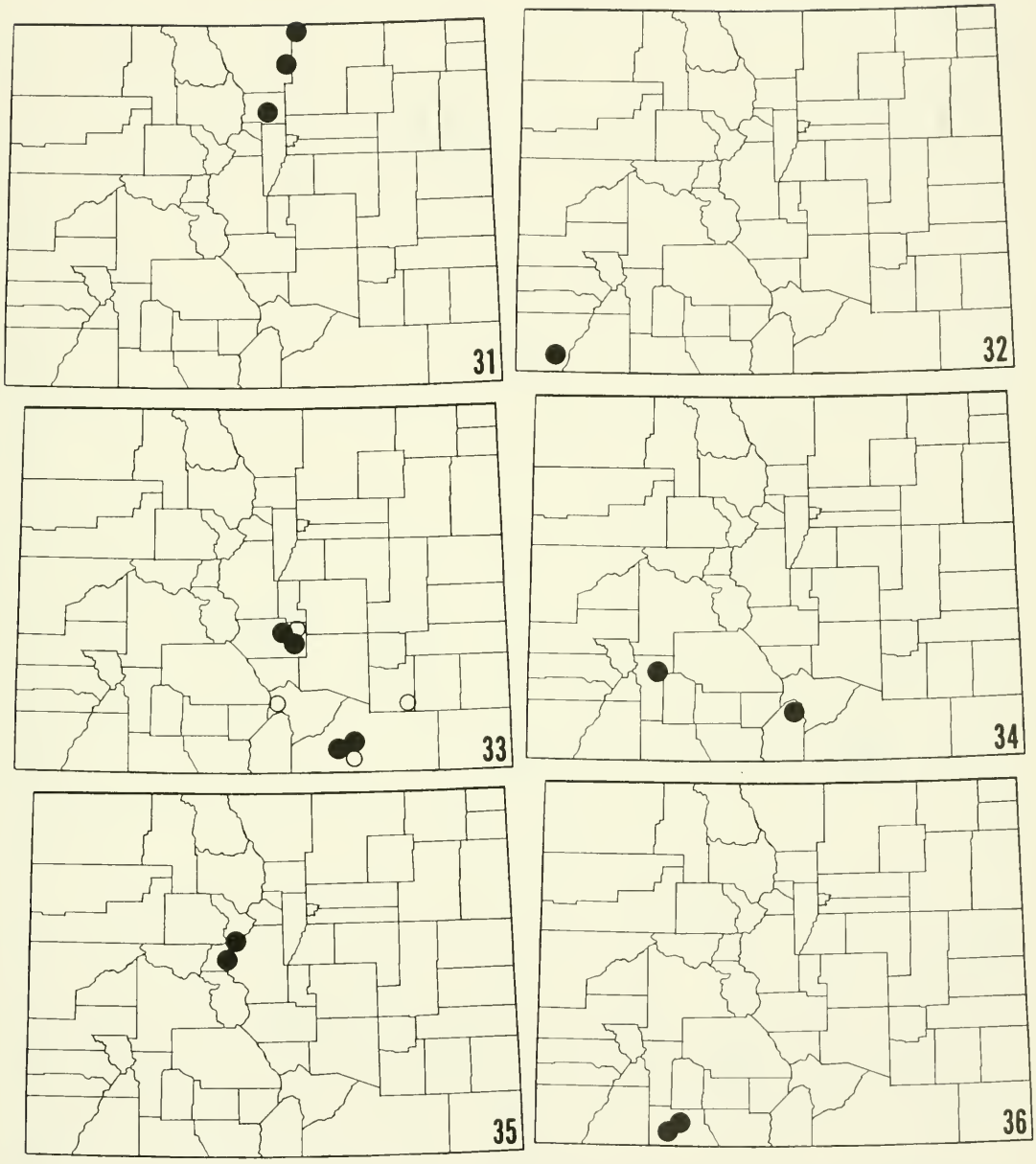
Maps 13–18. Distribution of (13) *Astragalus osterhoutii*, (14) *A. ripleyi*, (15) *A. schmolliae*, (16) *A. wetherillii*, (17) *Atriplex pleiantha*, and (18) *Braya humilis* ssp. *ventosa*.



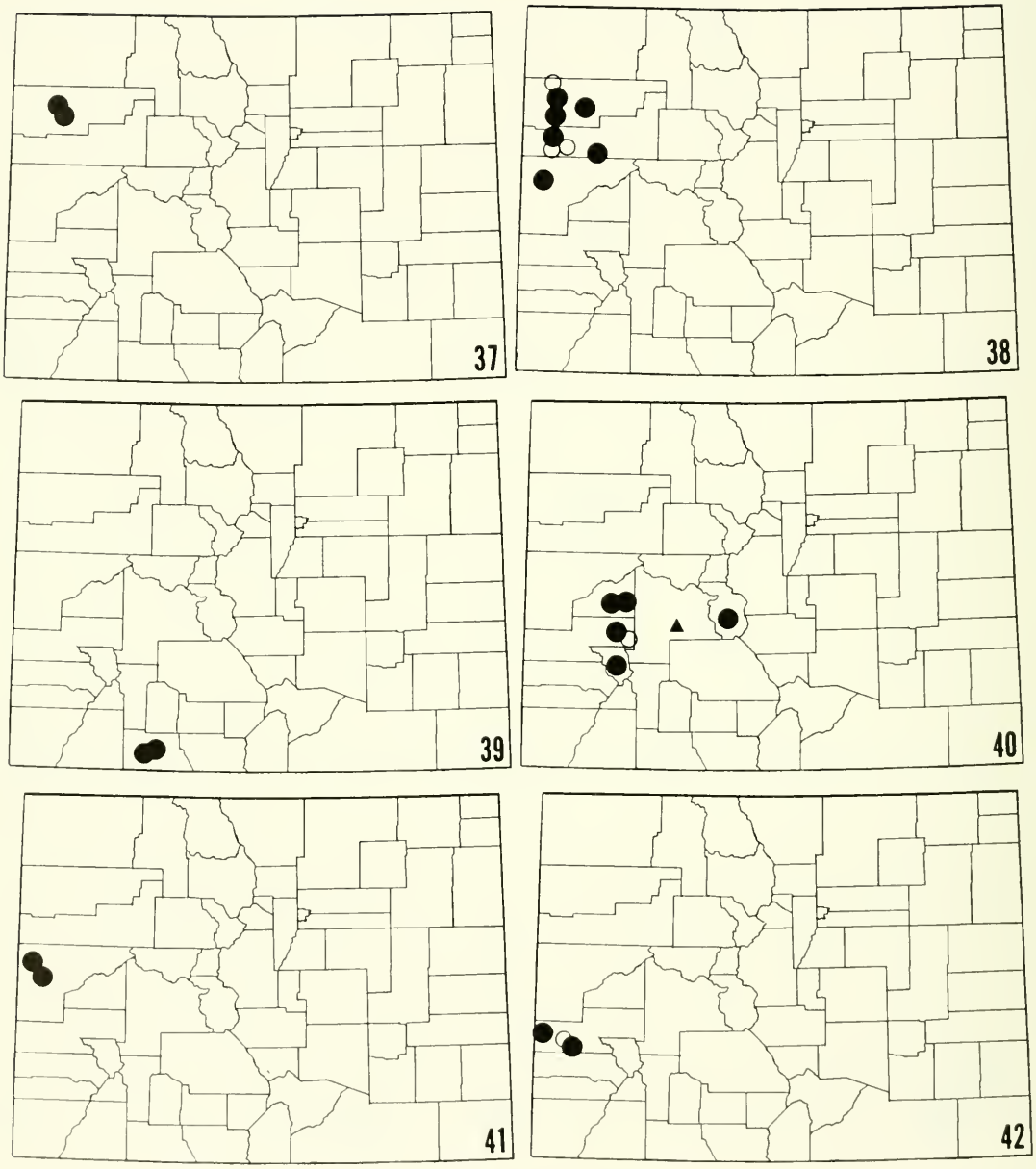
Maps 19–24. Distribution of (19) *Cirsium ownbeyi*, (20) *Cleome multicaulis*, (21) *Cryptantha aperta*, (22) *Echinocereus triglochidiatus* var. *inermis*, (23) *Erigeron kachinensis*, and (24) *Eriogonum brandegei*.



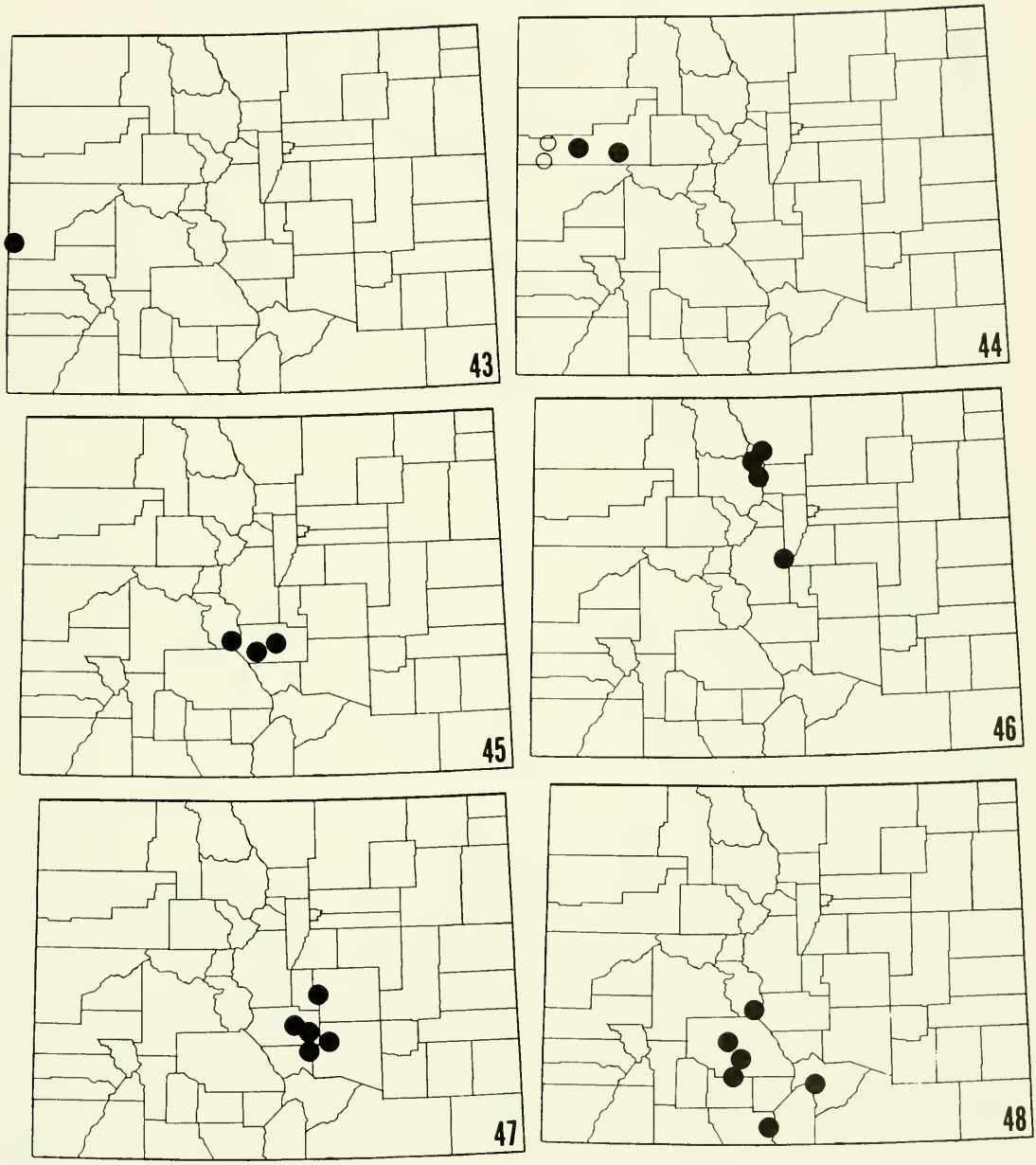
Maps 25–30. Distribution of (25) *Eriogonum clavellatum*, (26) *E. pelinophilum*, (27) *Eutrema penlandii*, (28) *Festuca dasyclada*, (29) *F. hallii*, and (30) *Frasera coloradensis*.



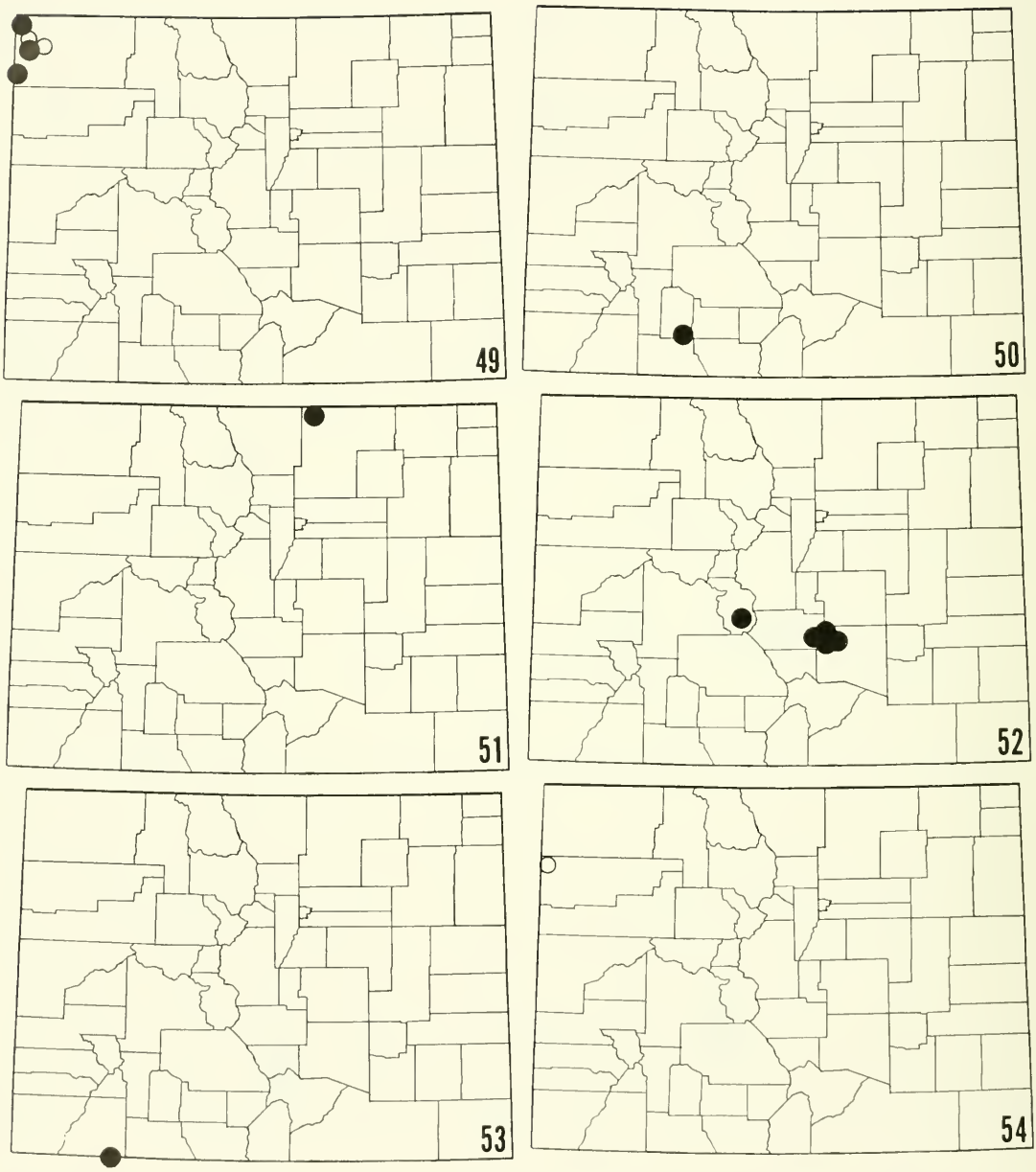
Maps 31–36. Distribution of (31) *Gaura neomexicana* ssp. *coloradensis*, (32) *Hackelia gracilenta*, (33) *Haplopappus fremontii* ssp. *monocephalus*, (34) *Hymenoxys heleioides*, (35) *Ipomopsis globularis*, and (36) *I. polyantha* var. *polyantha*.



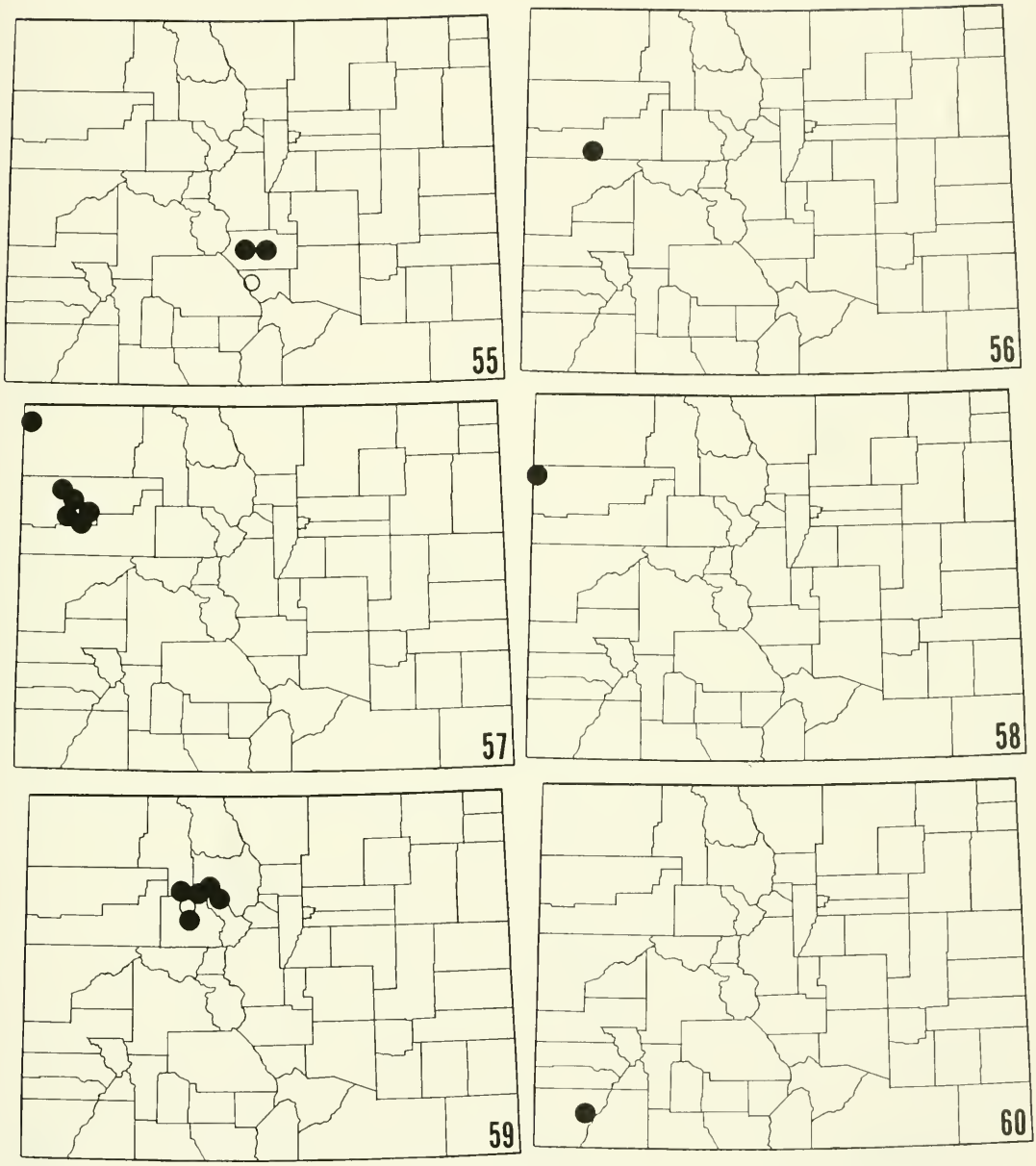
Maps 37–42. Distribution of (37) *Lesquerella congesta*, (38) *L. parviflora*, (39) *L. pruinosa*, (40) *Lomatium concinnum*, (41) *L. latilobum*, and (42) *Lupinus crassus*.



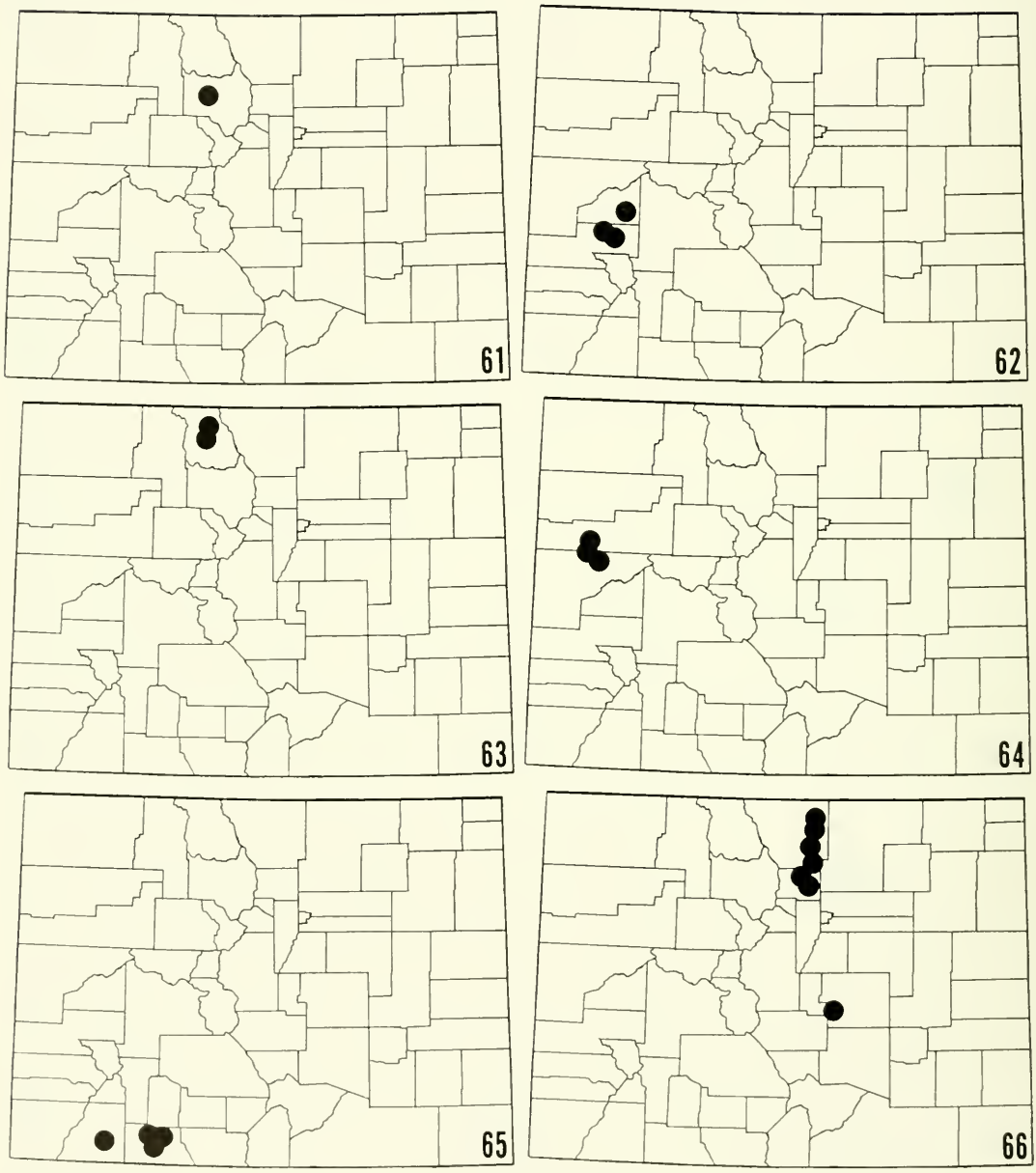
Maps 43–48. Distribution of (43) *Lygodesmia doloresensis*, (44) *Mentzelia argillosa*, (45) *M. densa*, (46) *Mimulus gemmiparus*, (47) *Mirabilis rotundifolia*, and (48) *Neoparrya lithophylla*.



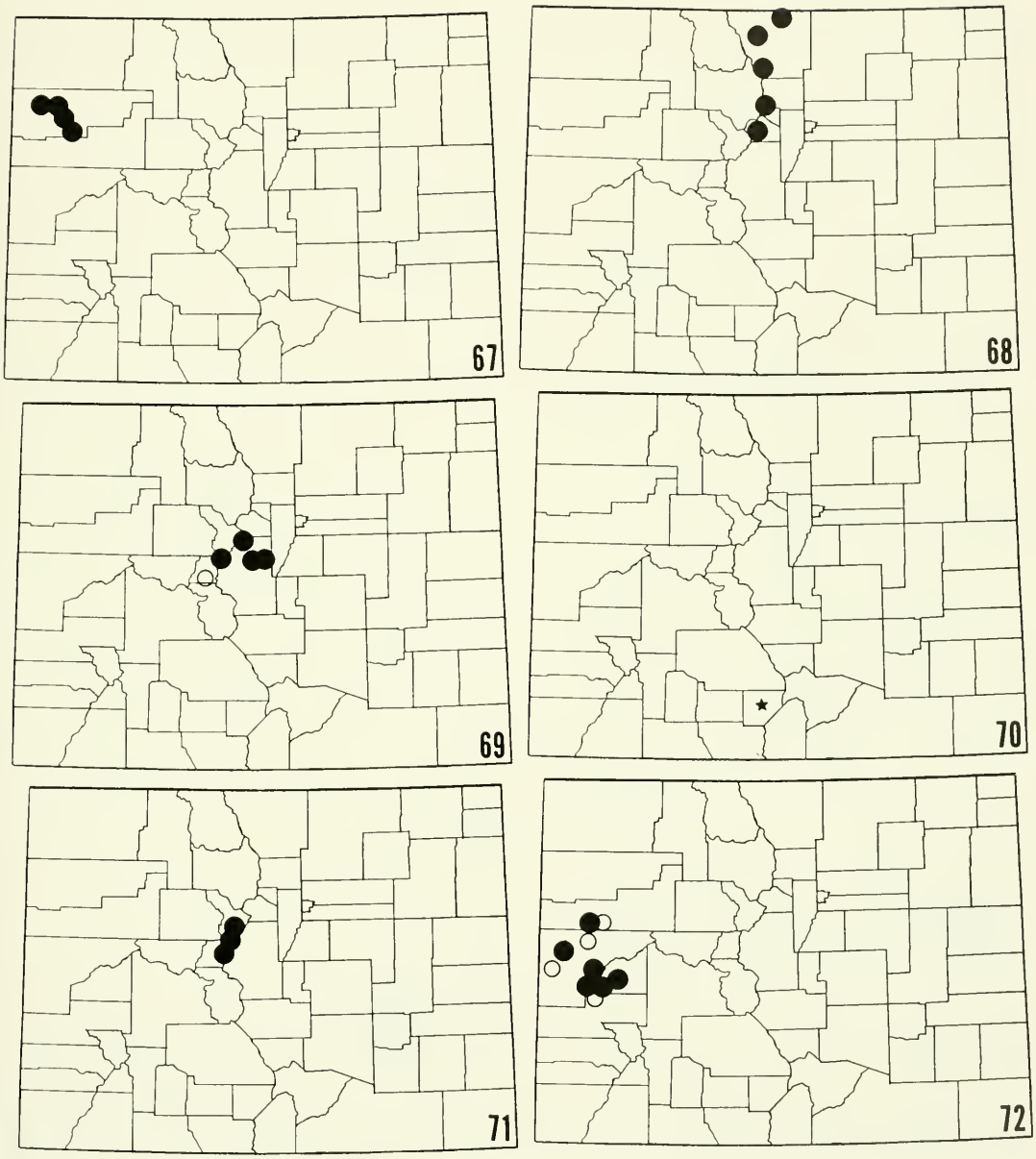
Maps 49–54. Distribution of (49) *Oenothera acutissima*, (50) *O. kleinii*, (51) *Parthenium alpinum*, (52) *P. tetraneuris*, (53) *Pediocactus knowltonii*, and (54) *Penstemon albifluvis*.



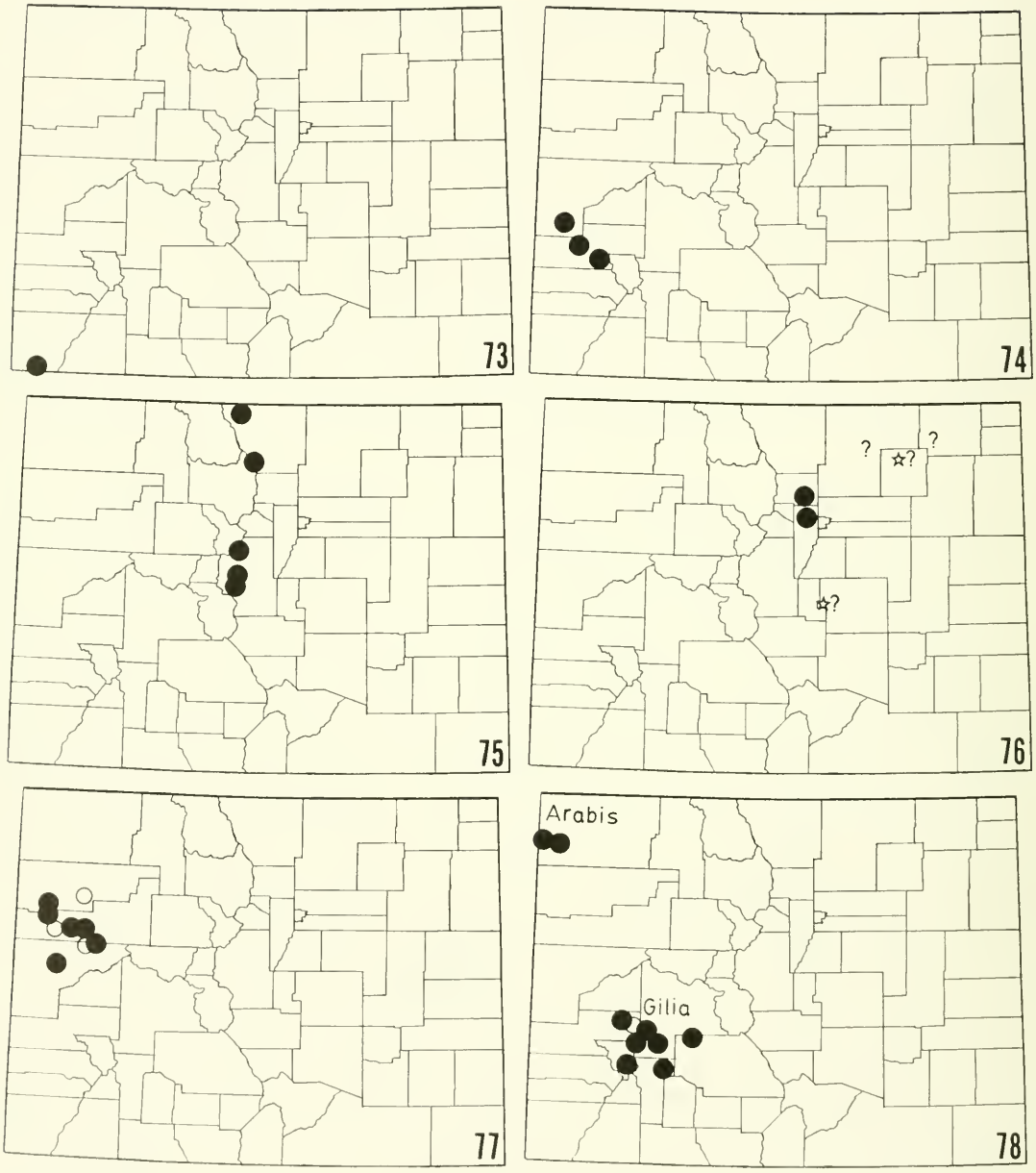
Maps 55–60. Distribution of (55) *Penstemon debilis*, (56) *P. degeneri*, (57) *P. gibbensii*, (58) *P. grahamii*, (59) *P. harringtonii*, and (60) *P. parviflorus*.



Maps 61–66. Distribution of (61) *Penstemon penlandii* (62) *P. retrorsus*, (63) *Phacelia formosula*, (64) *P. submutica*, (65) *Phlox caryophylla*, and (66) *Physaria bellii*.



Maps 67–72. Distribution of (67) *Physaria obcordata*, (68) *Potentilla effusa* var. *rupincola*, (69) *Ptilagrostis porteri*, (70) *Rorippa coloradensis*, (71) *Saussurea weberi*, and (72) *Sclerocactus glaucus*.



Maps 73–78. Distribution of (73) *Sclerocactus mesae-verdae*, (74) *Senecio dimorphophyllus* var. *intermedius*, (75) *Sisyrinchium pallidum*, (76) *Spiranthes diluvialis*, (77) *Thalictrum heliophilum*, and (78) *Arabis vivariensis* (upper left) and *Gilia penstemonoides*.

LITERATURE CITED

BARNEBY, R. C. 1964. Atlas of North American *Astragalus*. Mem. New York Bot. Gard. Vol. 13. 1,188 pp.

BARRELL, J. 1969. Flora of the Gunnison Basin. Natural Land Inst., Rockford, Ill.

BEETLE, A. A. 1959. New names with the section *Tridetatae* of *Artemisia*. Rhodora 61: 82–85.

COLORADO NATURAL AREAS PROGRAM. 1988. Colorado plant species of special concern—March 1988. Unpublished report, Colorado Natural Areas Program, Dept. Nat. Res., Denver, Colorado. 28 pp.

CRONQUIST, A., A. H. HOLMGREN, N. H. HOLMGREN, J. L. REVEAL, AND P. K. HOLMGREN. 1977. Intermountain flora. Vol. 6. Columbia University Press, New York. 584 pp.

———. 1984. Intermountain flora. Vol. 4. New York Bot. Gard., Bronx, New York. 573 pp.

DARLINGTON, J. 1934. A monograph of the genus *Mentzelia*. Ann. Missouri Bot. Gard. 21: 157–158.

DIAMOND, J. M. 1984. "Normal" extinctions of isolated populations. *In:* M. H. Nitecki, ed., Extinctions. University of Chicago Press, Chicago.

DORN, R. D. 1984. *Vascular plants of Montana*. Mountain West Pub., Cheyenne, Wyoming. 276 pp.

———. 1988. Vascular plants of Wyoming. Mountain West Pub., Cheyenne, Wyoming. 340 pp.

DORN, R. D. AND J. L. DORN. 1980. Illustrated guide to special interest vascular plants of Wyoming. Report published by U.S. Fish and Wildlife Service and Bureau of Land Management. 67 pp.

ECOLOGY CONSULTANTS. 1979. Proposed and recommended threatened and endangered plant species of the Forest Service Rocky Mountain Region. Report prepared for U.S. For. Serv. Region 2 in 1978 and expanded and corrected by B. C. Johnston 1979. 169 pp. + addenda.

GALATOWITSCH, S., T. NAUMANN, S. L. O'KANE, JR., AND B. E. NEELY. 1988. 1987 inventory of the plant species of special concern and the general flora of Dinosaur National Monument (annual progress report). Unpublished report, Colorado Natural Areas Program, Denver, Colorado. 24 pp. + appendices.

GOODRICH, S., AND E. NEESE. 1986. Uinta Basin flora. USDA For. Serv., Intermountain Reg.; USDA For. Serv., Ashley Nat. For.; USDI Bureau of Land Mgmt., Vernal Dist. 320 pp.

GREAT PLAINS FLORA ASSOCIATION. 1986. Flora of the Great Plains. University Press of Kansas, Lawrence. 1,392 pp.

HARMS, V. L. 1985. A reconsideration of the nomenclature and taxonomy of the *Festuca altaica* complex (Poaceae) in North America. Madroño 32: 1–10.

HARRINGTON, H. D. Manual of the plants of Colorado. Sage Books, Swallow Press, Inc., Chicago. 666 pp.

HARRIS, J. G. 1985. A revision of the genus *Braya* (Cruciferae) in North America. Unpublished dissertation, University of Alberta, Edmonton.

HASHEMI, A., A. ESTILAI, J. E. WEST, AND J. G. WAINES. 1988. Artificial hybridization of rubber-bearing guayule with cold-tolerant *Parthenium ligulatum*. Amer. J. Bot. 75: 197–204.

HASHEMI, A., J. E. WEST, AND J. G. WAINES. 1986. Chromosome pairing and pollen fertility in interspecific hybrids of species of *Parthenium* (Asteraceae). Amer. J. Bot. 73: 980–988.

JABLONSKI, D., K. W. FLESSA, AND J. W. VALENTINE. 1985. Biogeography and paleobiology. Paleobiology 11: 75–90.

JONES, M. E. 1923. Revision of North American species of *Astragalus*. Published by the author, Salt Lake City, Utah. 288 pp.

KEARNEY, T. H., AND R. H. PEEBLES. 1960. [1951]. Arizona flora. University of California Press, Berkeley. 1032 pp. + supplement.

KNIGHT, P. J., A. CULLY, B. JOHNSTON, AND S. L. O'KANE, JR. 1986. Status report on *Phlox caryophylla*. Unpublished report, Colorado Natural Areas Program, Denver. 31 pp.

KRUCKEBERG, A. R. 1986. An essay: the stimulus of unusual geologies for plant speciation. Syst. Bot. 11: 455–463.

LELLINGER, D. B. 1985. Ferns and fern-allies of the United States and Canada. Smithsonian Institution Press, Washington, D.C. 389 pp.

MARTIN, W. C., AND C. R. HUTCHINS. 1980. A flora of New Mexico. J. Cramer, Vaduz. 2 vols.

MASON, H. L. 1946a. The edaphic factor in narrow endemism. I. The nature of environmental influences. Madroño 8: 209–226.

———. 1946b. The edaphic factor in narrow endemism. II. The geographic occurrence of plants of highly restricted patterns of distribution. Madroño 8: 241–257.

MAXON, W. R. 1912. The relationship of *Asplenium andrewsii*. Contr. U.S. Natl. Herb. 16: 1–2, pl. 2.

MCVAUGH, R. 1957. *Asplenium adiantum-nigrum* in Mexico. American Fern. Journal 47: 135–137.

MENGES, E. S. 1986. Predicting the future of rare plant populations: demographic monitoring and modeling. Natural Areas J. 6: 13–25.

MOHLENBROCK, R. H. 1983. Where have all the wildflowers gone? MacMillan Pub. Co., Inc., New York. 239 pp.

MOUNTAIN WEST ENVIRONMENTAL SERVICES. 1987. Rare plant inventory interim report. Unpublished report, U.S. Bureau of Land Mgmt., Grand Junction, Colorado.

NEELY, E. E., AND A. T. CARPENTER. 1986. Size, structure, and habitat characteristics of populations of *Braya humilis* var. *humilis* (Brassicaceae): an alpine disjunct from Colorado. Great Basin Nat. 46: 728–735.

NEW MEXICO NATIVE PLANT PROTECTION ADVISORY COMMITTEE. 1984. A handbook of rare and endemic plants of New Mexico. University of New Mexico Press, Albuquerque. 291 pp.

O'KANE, S. L., JR. 1986. Floristic reconnaissance of the San Luis Valley. Unpublished report, Colorado Natural Areas Program, Denver, Colorado. 18 pp. + appendices.

———. 1987a. Status report for *Lesquerella parviflora*. Unpublished report, Colorado Natural Areas Program, Denver, Colorado. 27 pp. + appendices.

———. 1987b. Status report for *Phacelia submutica*. Unpublished report, Colorado Natural Areas Program, Denver, Colorado. 30 pp. + appendices.

———. 1987c. Status report for *Physaria obcordata*. Unpublished report, Colorado Natural Areas Program, Denver, Colorado. 25 pp. + appendices.

———. 1987d. Status report for *Thalictrum heliophilum*. Unpublished report, Colorado Natural Areas Program, Denver, Colorado. 27 pp. + appendices.

O'KANE, S. L., JR., D. H. WILKEN, AND R. L. HARTMAN. 1988. Noteworthy collections. Madroño 35: 72–74.

PAVLICK, L. E., AND J. LOOMAN. 1984. Taxonomy and nomenclature of rough fescues, *Festuca altaica*, *F. campestris* (*F. scabrella* var. *major*) and *F. hallii*, in Canada and the adjacent part of United States. Canadian J. Bot. 62: 1739–1749.

PETERSON, J. S. 1982. Threatened and endangered plants of Colorado. U.S. Fish and Wildlife Service Pub., Region 6, Denver, Colorado. 25 pp.

PETERSON, J. S., AND W. L. BAKER. 1982. Inventory of the Piceance Basin, Colorado: threatened and endangered plants, plant associations, and the general flora. 5 vols. Unpublished report, Bureau of Land Management, Denver, Colorado.

REVEAL, J. L. 1969. A revision of the genus *Eriogonum* (Polygonaceae). Unpublished dissertation, Brigham Young University, Provo, Utah.

RYDBERG, P. A. 1906. [1905]. Flora of Colorado. Bull. 100, Colorado Agr. Expt. Sta., Fort Collins, Colorado. 448 pp.

SHEVIAK, C. J. 1984. *Spiranthes diluvialis* (Orchidaceae), a new species from the western United States. Brittonia 36: 8–14.

STEBBINS, G. L. 1980. Rarity of plant species: a synthetic viewpoint. Rhodora 82: 77–86.

STEBBINS, G. L., AND J. MAJOR. 1965. Endemism and speciation in the California flora. Ecol. Monogr. 35: 1–35.

STUCKEY, R. L. 1972. Taxonomy and distribution of the genus *Rorippa* (Cruciferae) in North America. Sida 4: 279–430.

TERBORGH, J., AND B. WINTER. 1980. Some causes of extinction. *In:* M. E. Soulé and B. A. Wilcox, eds., Conservation biology: an evolutionary-ecological perspective. Sinauer Assoc., Sunderland, Minnesota.

U. S. FISH AND WILDLIFE SERVICE. 1985. Endangered and threatened wildlife and plants; review of plant taxa for listing as endangered or threatened species; notice of review. Fed. Reg. 50(188) 50 CFR Part 17: reprint edition pp. 1–57.

———. 1987. Endangered and threatened wildlife and plants. U.S. Government Printing Office, Washington, D.C. Pub. No. 50 CFR 17.11 & 17.12. 32 pp.

WEBER, W. A. 1961. Additions to the flora of Colorado. Univ. Colorado Stud., Series in Biology No. 7: 1–26.

———. 1976. Rocky Mountain flora. 5th ed. Colorado Assoc. Univ. Pr., Boulder, Colorado 479 pp. + addenda.

———. 1987. Colorado flora: western slope. Colorado Assoc. Univ. Pr., Boulder, Colorado. 530 pp.

WELSH, S. L. 1978a. Problems in plant endemism on the Colorado Plateau. Great Basin Nat. Mem. 2: 191–195.

———. 1978b. Endangered and threatened plants of Utah: a reevaluation. Great Basin Nat. 38: 1–18.

WELSH, S. L., N. D. ATWOOD, L. C. HIGGINS, AND S. GOODRICH. 1987. A Utah flora. Great Basin Nat. Mem. 9:1–894.

WELSH, S. L., N. D. ATWOOD, AND J. L. REVEAL. 1975. Endangered, threatened, extinct, endemic, and rare or restricted Utah vascular plants. Great Basin Nat. 35: 327–376.

WELSH, S. L., AND L. M. CHATTERLY. 1985. Utah's rare plants revisited. Great Basin Nat. 45: 173–236.

WELSH, S. L., AND K. H. THORNE. 1979. Illustrated manual of proposed endangered and threatened plants of Utah. Report published by U.S. Fish and Wildlife Service, Bureau of Land Management, and U.S. Forest Service, Denver, Colorado. 318 pp.

WITTMANN, R. C., W. A. WEBER, AND B. C. JOHNSTON. 1988. Flora of Colorado: computer-generated catalog. Alphabetical list of accepted names and synonyms for vascular plants, lichens, and bryophytes. Unpublished report, Museum, University of Colorado, Boulder.

FOOD HABITS OF YOUNG-OF-YEAR LARGEMOUTH BASS IN LAKE MEAD AND LAKE MOHAVE, ARIZONA-NEVADA

Gene R. Wilde[1] and Larry J. Paulson[2]

ABSTRACT.—Young-of-year largemouth bass from lakes Mead and Mohave fed upon crustacean zooplankton, insects (primarily chironomids), and fish. Largemouth bass smaller than 32 mm TL fed extensively upon zooplankton. In Lake Mead, transition to an insect-dominated diet occurred at 32 mm TL; transition to an insect-fish–dominated diet did not occur in Lake Mohave until a length of 56 mm was reached. Largemouth bass from Lake Mohave consumed significantly more zooplankton than did those from Lake Mead, but largemouth bass from Lake Mead consumed significantly more insects. Fish were most common in the diet of young-of-year largemouth bass larger than 52 mm TL.

Lake Mead was formed in 1935 by impoundment of the Colorado River along the Arizona-Nevada border. Largemouth bass, *Micropterus salmoides*, were introduced into Lake Mead from 1935 to 1940, and the lake soon developed a nationally recognized largemouth bass fishery (Moffett 1943, Wallis 1951). From 1935 until 1977 largemouth bass was the primary sport fish in the lake (Moffett 1943, Wallis 1951, Hoffman and Jonez 1973, Allan and Roden 1978). Allan and Roden reported that largemouth bass received 30 to 40% of angler effort and contributed 24.5 to 79.5% of the sport-fish catch in Lake Mead during the 20-year period, 1958–1977. Striped bass, *Morone saxatilis*, has been the primary sport fish in Lake Mead since 1977, but largemouth bass is still an important component of the fishery.

Lake Mohave was impounded in 1951 and lies immediately downstream from Lake Mead. Largemouth bass occurred in the Colorado River below Lake Mead before impoundment of Lake Mohave (Moffett 1942) and has since become the second most popular sport fish in the lake. From 1962 to 1977 largemouth bass contributed between 8.8 and 39.8% of the sport-fish catch in Lake Mohave (Allan and Roden 1978).

Despite the importance of largemouth bass to the sport fisheries of lakes Mead and Mohave, little is known of its biology in these lakes. The purpose of this paper is to describe and compare diets of young-of-year (YOY) largemouth bass in lakes Mead and Mohave.

METHODS

Young-of-year largemouth bass were collected from lakes Mead and Mohave by Nevada Department of Wildlife personnel during the spring (April–May) and summer (June–August) of 1976 to 1979. A total of 648 largemouth bass was collected from Lake Mead and 542 from Lake Mohave. Total lengths (TL) ranged from 6 to 150 mm.

For dietary analysis, stomachs were removed and each food item identified to the lowest possible taxon. Results for each year were expressed as mean number per occurrence and percent frequency of occurrence for each prey type. Empty stomachs were not included in the analyses. To study the association between diet and length (TL), we grouped fish less than 80 mm TL into 4-mm size classes; larger fish were included in an 80+ mm size class. We have pooled samples over the four-year study period and report herein unweighted means for mean number per occurrence and percent frequency of occurrence of major food items for each size class.

RESULTS

Zooplankton were the most frequently consumed and most numerous prey of YOY largemouth bass in lakes Mead and Mohave (Table 1). Rotifers were found in the stomachs of 16 largemouth bass in 1976 (11.3% frequency of occurrence) but were not found again during

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TABLE 1. Mean number per occurrence and percent frequency of occurrence (in parentheses) of prey in the diet of young-of-year largemouth bass.

	Lake Mead			
TL (mm)	N	Zooplankton	Insects	Fish
8				
12	13	40.8 (100)	3.0 (20)	
16	41	91.6 (100)	1.8 (11)	
20	33	70.0 (100)	1.0 (18)	
24	8	151.9 (100)	2.0 (25)	
28	34	76.9 (100)	2.0 (9)	
32	5	110.0 (50)	20.8 (50)	
36	4	29.5 (67)	30.3 (50)	
40	14	90.4 (63)	28.9 (50)	
44	16	109.6 (67)	5.8 (74)	
48	15	82.5 (47)	11.4 (66)	
52	16	47.1 (53)	18.7 (92)	
56	17	54.7 (34)	18.8 (51)	3.0 (30)
60	29	20.7 (37)	24.6 (74)	2.1 (37)
64	21	14.3 (55)	33.4 (42)	1.0 (20)
68	31	43.4 (24)	11.3 (81)	1.0 (9)
72	30	34.0 (28)	25.7 (45)	1.0 (46)
76	16	25.1 (45)	24.6 (90)	1.0 (15)
80	19	30.3 (32)	13.6 (57)	1.0 (43)
80+	57	21.8 (12)	10.4 (56)	1.2 (52)

Table 1. Continued.

	Lake Mohave			
TL (mm)	N	Zooplankton	Insects	Fish
8	2	28.5 (100)		
12	72	21.8 (100)	2.0 (8)	
16	77	74.5 (100)	1.0 (7)	
20	5	51.0 (100)		
24	19	162.1 (100)	1.0 (11)	
28	22	175.3 (100)	1.0 (3)	
32	43	133.2 (100)	1.0 (6)	
36	22	82.6 (75)	2.9 (51)	1.0 (8)
40	4	105.3 (100)	3.0 (50)	
44	11	488.9 (44)	3.1 (58)	2.5 (14)
48	29	159.0 (61)	7.3 (73)	
52	31	126.5 (84)	6.9 (54)	1.5 (10)
56	37	147.1 (41)	18.7 (65)	1.0 (24)
60	21	57.2 (27)	12.0 (60)	2.7 (26)
64	19	53.9 (38)	7.1 (30)	1.3 (33)
68	8	294.0 (17)	7.4 (77)	1.0 (23)
72	3		38.0 (50)	1.0 (100)
76	8		12.3 (43)	1.0 (57)
80	2			1.0 (100)
80+	39		8.9 (48)	1.6 (69)

our study. Crustacean zooplankton comprised the majority (> 99%) of the zooplankton consumed. The most commonly preyed upon species were the copepods *Cyclops vernalis*, *Diacyclops bicuspidatus thomasi*, *Diaptomus clavipes*, *D. reighardi*, and *D. siciloides* and the cladocerans *Bosmina longirostris*, *Ceriodaphnia lacustris*, *Daphnia galeata mendotae*, *D. pulex*, and *Scapholeberis kingi*. With the exception of *S. kingi*, all are common elements of the limnetic zooplankton of lakes Mead and Mohave (Paulson et al. 1980, Wilde 1984).

Zooplankton occurred in 100% of largemouth bass smaller than 32 mm TL in both lakes. At 32 mm TL, largemouth bass

TABLE 2. Spearman correlations (r_s) between total length (TL) and composition of the diet of young-of-year largemouth bass. Fish greater than 80 mm TL were not included in the analyses.

	Lake Mead	Lake Mohave
Mean number of zooplankton per stomach	−0.600**	−0.158
Frequency of occurrence of zooplankton	−0.884***	−0.936***
Mean number of insects per stomach	0.574*	0.904***
Frequency of occurrence of insects	0.676**	0.497*

* $p < .05$
** $p < .01$
*** $p < .001$

switched to an insect-dominated diet in Lake Mead; a similar transition did not occur in Lake Mohave until a length of 56 mm was reached. Frequency of occurrence of zooplankton in the diet of largemouth bass was negatively related to TL in both lakes (Table 2). Mean number of zooplankton was negatively related to TL in Lake Mead but not in Lake Mohave, reflecting the greater utilization of zooplankton in that lake. Overall, largemouth bass from Lake Mohave consumed significantly more zooplankton than did those from Lake Mead (Mann-Whitney U-test, $p < .05$).

Chironomid midges (larvae, pupae, and adults) were the most frequently consumed insects in lakes Mead and Mohave and represented 90% of the insects consumed by largemouth bass in both lakes. Other insect prey were, in order of importance, corixids, odonatids (primarily damselflies), coleopterans, miscellaneous dipterans, and ephemeropteran nymphs. Hydracarinids were infrequently consumed and are included in Table 1 as insects. In both lakes mean number and frequency of occurrence of insects in the diet were positively related to TL. Mean number of insects consumed was significantly greater in Lake Mead than in Lake Mohave ($p < .05$).

Fish were preyed upon by largemouth bass as small as 36 mm TL but were most common in the diets of individuals greater than 52 mm TL. Fishes consumed included largemouth bass, green sunfish (*Lepomis cyanellus*), and threadfin shad (*Dorosoma petenense*). Bluegill, *L. macrochirus*, although a common prey of largemouth bass in lakes Mead and Mohave (Moffett 1943, Allan and Roden 1978), were not found in any of the fish we examined.

DISCUSSION

The progression from zooplankton to insect- and fish-dominated diets observed in lakes Mead and Mohave is commonly reported for YOY largemouth bass (Kramer and Smith 1960, Applegate and Mullan 1967, Miller and Kramer 1971, Clady 1974, Timmons et al. 1981). In Lake Mead, largemouth bass switched to an insect-dominated diet at a smaller size (32 versus 56 mm TL) and consumed significantly more insects than in Lake Mohave. McCammon et al. (1964) suggested that composition of the diet of YOY largemouth bass reflects prey availability. Greater utilization of insects in Lake Mead may indicate a greater abundance of insects, especially chironomids, in that lake. Largemouth bass consumed significantly more zooplankton in Lake Mohave than in Lake Mead; this may result from greater density of zooplankton in Lake Mohave (Paulson et al. 1980), but it is more likely a consequence of lower insect abundance. Water level fluctuations expose a greater proportion of the littoral zone in Lake Mohave than in Lake Mead; these fluctuations can reduce the abundance of benthic invertebrates and, hence, their availability to game fishes (Hale and Bayne 1980).

Growth rate of YOY largemouth bass is positively related to size of prey consumed (Kramer and Smith 1960, Miller and Kramer 1971). First-year growth of largemouth bass in Lake Mead (201 mm TL) is approximately 10% greater than in Lake Mohave (178 mm TL, Allan and Roden 1978) and may result from the earlier and more extensive consumption of larger prey (insects) in Lake Mead. Applegate and Mullan (1967) found similar differences in diet and growth of YOY largemouth bass in Beaver and Bull Shoals reservoirs; first-year growth was greater in Beaver Reservoir where insects were available to "bridge the gap" between zooplankton- and fish-dominated diets.

Allan and Romero (1975) suggested that early survival of largemouth bass in Lake

Mead was limited by low availability of zooplankton. Since that study, nutrient loading into Lake Mead, especially via the Las Vegas Wash, has been greatly reduced. This has resulted in reduced phytoplankton abundance (Paulson and Baker, in press) and zooplankton density (Wilde 1984) in much of the lake. The Colorado River via discharge from Hoover Dam (Lake Mead) is the sole source of nutrient loading into Lake Mohave; phytoplankton abundance has decreased in Lake Mohave since the late 1970s (Paulson et al. 1980, Paulson unpublished data), and a reduction in zooplankton density seems likely given the generally strong relationship between phytoplankton and zooplankton abundance (McCauley and Kalff 1981). Our results show that crustacean zooplankton comprise the majority of the early diets of YOY largemouth bass in Lake Mead and Lake Mohave. Reductions in zooplankton density will likely have an adverse affect upon early growth and survival (Aggus and Elliot 1975) of largemouth bass in both lakes.

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LITERATURE CITED

AGGUS, L. R., AND G. V. ELLIOT. 1975. Effects of cover and food on year-class strength of largemouth bass. Pages 317–322 *in* R. H. Stroud and H. Clepper, eds., Black bass biology and management. Sport Fishing Institute, Washington, D.C.

ALLAN, R. C., AND D. L. RODEN. 1978. Fish of Lake Mead and Lake Mohave. Nev. Dept. Wildl. Biol. Bull. No. 7. 105 pp.

ALLAN, R. C., AND J. ROMERO. 1975. Underwater observations of largemouth bass spawning and survival in Lake Mead. Pages 104–112 *in* R. H. Stroud and H. Clepper, eds., Black bass biology and management. Sport Fishing Institute, Washington, D.C.

APPLEGATE, R. L., AND J. W. MULLAN. 1967. Food of young largemouth bass, *Micropterus salmoides*, in a new and old reservoir. Trans. Amer. Fish. Soc. 96: 74–77.

CLADY, M. D. 1974. Food habits of yellow perch, smallmouth bass and largemouth bass in two unproductive lakes in northern Michigan. Amer. Midl. Nat. 91: 453–459.

HALE, M. M., AND D. R. BAYNE. 1980. Effects of water level fluctuations on the littoral macroinvertebrates of West Point Reservoir. Proc. Ann. Conf. S.E. Assoc. Fish Wildl. Agen. 34: 175–180.

HOFFMAN, D. A., AND A. R. JONEZ. 1973. Lake Mead, a case history. Pages 220–233 *in* W. C. Ackerman, G. F. White, and E. B. Worthington, eds., Man-made lakes: their problems and environmental effects. Geophys. Monogr. Ser. No. 17.

KRAMER, R. H., AND L. L. SMITH, JR. 1960. First-year growth of the largemouth bass, *Micropterus salmoides* (Lacepede), and some related ecological factors. Trans. Amer. Fish. Soc. 89: 222–233.

MCCAMMON, G. W., D. LAFAUNCET, AND C. M. SEELEY. 1964. Observations on the food of fingerling largemouth bass in Clear Lake, Lake County, California. California Fish Game 50: 158–169.

MCCAULEY, E., AND J. KALFF. 1981. Empirical relationships between phytoplankton and zooplankton biomass in lakes. Canadian J. Fish. Aquat. Sci. 38: 458–463.

MILLER, K. O., AND R. H. KRAMER. 1971. Spawning and early life history of largemouth bass (*Micropterus salmoides*) in Lake Powell. Pages 73–84 *in* G. E. Hall, ed., Reservoir fisheries and limnology. Amer. Fish. Soc., Spec. Publ. No. 8.

MOFFETT, J. W. 1942. A fishery survey of the Colorado River below Boulder Dam. California Fish Game 28: 76–86.

———. 1943. A preliminary report on the fishery of Lake Mead. Trans. N. Amer. Wildl. Conf. 8: 179–186.

PAULSON, L. J., AND J. R. BAKER. In press. Management of fertility and productivity in Lake Mead. Proc. 7th Ann. Internat. Symp. N. Amer. Lake Manage. Soc.

PAULSON, L. J., J. R. BAKER, AND J. E. DEACON. 1980. The limnological status of Lake Mead and Lake Mohave under present and future powerplant operations of Hoover Dam. Lake Mead Limnol. Res. Cent. Tech. Rept. No. 1. 229 pp.

TIMMONS, T. J., W. L. SHELTON, AND W. D. DAVIES. 1981. Food of largemouth bass before and during the first three years after impoundment of West Point Reservoir, Alabama and Georgia. J. Tenn. Acad. Sci. 56: 23–27.

WALLIS, O. L. 1951. The status of the fish fauna of the Lake Mead National Recreational Area, Arizona-Nevada. Trans. Amer. Fish. Soc. 80: 84–92.

WILDE, G. R. 1984. Seasonal and spatial heterogeneity in the limnetic zooplankton community of Lake Mead. Unpublished thesis, University of Nevada at Las Vegas.

A MIXED POLLINATION SYSTEM IN *PENSTEMON PSEUDOSPECTABILIS* M. E. JONES (SCROPHULARIACEAE)

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ABSTRACT.—A population of *Penstemon pseudospectabilis* M. E. Jones (Scrophulariaceae) on Cave Creek in Cochise County, Arizona, was used in an experimental test of reproductive fitness with three caging treatments: all flying pollinators excluded, hummingbirds excluded, and no exclusion. Twenty plants were chosen and three shoots on each used in the experiment. The flowers were 25.6 (s.d. = 1.5) mm long, the end diameter was 8.5 (s.d. = 1.0) mm, the tube opening was 6.5 (s.d. = 1.0) mm, and the greatest diameter, 75% distal from the receptacle, was 10.1 (s.d. = 0.8) mm (N = 59). Floral nectar contained 11.7% (s.d. = 2.9%) fructose, 13.8% (s.d. = 2.7%) glucose, and 74.5% (s.d. = 5.4%) sucrose (N = 74). There was some evidence, significant only for fructose, that nectar-sugar composition varies between morning and evening. Larger floral dimensions were correlated with lower sucrose and higher hexoses. Casual observation showed *Xylocopa* sp., small bees, flies, and hummingbirds to be visitors. There was no sign of nectar robbing. Five percent of flowers set seed with all pollen vectors excluded, 44% with hummingbirds excluded, and 63% with no exclusion. Seed set per fruit was 2 with all excluded, 23 with hummingbirds excluded, and 46 with no exclusion. Mean seed set on pollinated flowers was 60, with a range of 2 to 192. Multiple linear regression showed the fraction of fruit setting seed when hummingbirds were excluded to be related to larger flower diameters and shorter flowers. With no pollinator exclusion, fruits setting seed were related to larger diameters and nectar fructose. For seeds per fruit, multiple regression gave similar, but less clear, results. We conclude that *P. pseudospectabilis* is pollinated by both bees and hummingbirds, with other pollinators not to be excluded as possible contributors. We found no hard evidence of selective forces currently at work.

In pollination biology, the weight of many observations has led to recognition of unique syndromes of morphological and nectar chemistry characteristics among plant taxa primarily pollinated by a given animal group (e.g., Baker and Baker 1983b, Faegri and van der Pijl 1971, Grant and Grant 1968). The chemical composition of floral nectars, especially the sugar composition, has received attention in this regard (Baker and Baker 1983a). However, demonstration of the selective forces implied by such adaptation is needed for insights to be more than pedagogical aphorisms.

Studies to assess the interaction of floral nectar sugars and reproductive fitness in natural populations are needed. The large western genus *Penstemon*, Scrophulariaceae, has a wide range of nectar-sugar composition and floral morphology and is pollinated by several classes of animals. It is an excellent taxon for experimental pollination biology (Baker and Baker 1983a, Crosswhite and Crosswhite 1981).

Penstemon pseudospectabilis M. E. Jones occurs from southeastern California to southwestern New Mexico in the desert or in open woodlands. The flower color has been variously described: pink (Jepson 1925), deep pink to rose-purple (Kearney and Peebles 1969), and pink, bearing darker guidelines in the throat (Martin and Hutchins 1981). The flowers are borne on numerous branching shoots arising from the basal rosette. The corolla tube is ampliate, reaching its greatest diameter at about three-fourths of the length distal of the receptacle. Nectaries are on the abaxial surfaces of the upper two free stamens near their bases (Straw 1966). The flower opening is large enough to accommodate some bees.

Straw (1956) describes some morphological and colorimetric characteristics leading to floral isolation in four penstemon species, and, in comparison, the flower of *P. pseudospectabilis* appeared to have some features of both bee- and hummingbird-pollinated species. It seemed appropriate, therefore, to test for mixed pollination systems. We here report on results of an exclusion experiment providing initial data on floral morphology, nectar-sugar composition, seed set, and the plant's dependence on different pollinators.

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MATERIALS AND METHODS

A population of *P. pseudospectabilis* in Cave Creek Canyon of the Chiricahua Mountains in Cochise County, Arizona, at about 1,370 m elevation was used for this study (Voucher: UTEP 22491). This population occurs within an open woodland on a south-facing slope and adjacent riparian and roadside areas of Cave Creek 150 m west of a U.S. Forest Service station. There appears to be little day-to-day human disturbance, but part of the population is within a fenced pasture occasionally used for horses or mules.

On 2 May 1987 we selected 20 plants for the study, each separated by at least 2 m. On each plant we chose three shoots for study. We made flower measurements and nectar collections. The following measurements were taken on one to six mature flowers on each stem using a millimeter ruler: length, corolla diameter at 25%, 50%, 75%, and 100% of the axis of the flower, and diameter of the opening. Nectar samples were taken from mature flowers on most shoots. Nectar was removed with a micropipette and placed on a filter paper disk to dry. We then stripped opened flowers from the shoots. The three treatments for our experiment were: (1) exclusion of all flying pollinators, (2) exclusion of hummingbirds, and (3) no exclusion to allow access by all pollinators. (The available pollinating fauna at Cave Creek, of course, varies greatly in numbers and composition during the season.)

On each plant one shoot was enclosed with an inverted half-gallon milk carton with cut-out sides over which a stocking was stretched (Radford et al. 1974). The stocking was drawn over the base and gently tied shut. Another was enclosed in a 30-cm diameter, 50-cm-tall cage of 5-cm chicken wire. The cages were supported by metal stakes driven into the ground. A third shoot was marked but left entirely open. After the exclosures were completed we remained to observe visitation by potential pollinators. No attempt was made to observe nocturnal activity of moths. The following day we again observed visitors, took additional nectar samples, and left the cages in place. On 19 June 1987 we returned, removed the cages, and harvested the shoots.

For each collected shoot the total number of fruits and the number of fruits with seed were counted. Starting from the bottom of the shoot, the first 10 fruits with seed were removed and dissected and seeds were counted.

Our methodology for sugar analysis by High-performance Liquid Chromatography (HPLC) was the same as in previous studies (Freeman et al. 1983, 1984, 1985, Reid et al. 1985). The paper disks holding dried nectar were placed in Parafilm (R) pouches with 20 μl of water. After five minutes eluted sugars were removed by squeezing the pouch and collecting the solution with a microsyringe. The sample was then injected into the chromatograph for analysis.

A Rainin Instrument Co. liquid chromatograph with a Knauer refractive index detector and an Alltech amino bonded silica column (5 μm particle size and 150 mm long) was used. The solvent was an acetonitrile: water (75:25 v/v) system flowing at 2.0 ml/min. For calibration, regressions based on response to sugar standards were established. The standard solution contains fructose, glucose, and sucrose, each 10% by mass, injected in volumes of 1, 2, 3, and 4 μl. The response of this system to sugar mass was nearly linear, and second order, least squares regressions were used for calibration curves. Regression coefficients of 0.9995 (d.f. = 1, $P < .02$) are obtained. A BASIC program by Reid computed relative percent by mass of each sugar from the chart responses.

Results were placed in data files and analyzed using Number Cruncher Statistical Software (Hintze 1985) and a BASIC program by Reid for the Kolmogorov-Smirnov test of normality (Sokol and Rohlf 1983). In comparing the floral tube and opening diameters to other variables such as nectar composition or seed set, we tested both diameter and diameter squared (proportional to area).

RESULTS AND CONCLUSIONS

The floral measurements are summarized in Table 1. Principal components analysis (Hintze 1985) of the floral measurements reveals that the first component (44% of the variance) is a positive correlate relation among five floral dimensions: length, diameter at 25% and 75% of length, opening, and end diameter. Thus, when one of these is larger, all are larger. The second component (19% of variance) is the independent variation of the diameter at 50% of length.

TABLE 1. Summary measurements for 59 *Penstemon pseudospectabilis* flowers. Pearson product-moment correlation coefficients significant at the P < .05 level are given. The standard deviation is indicated by s.d., range of measurements by ( ), and nonsignificant correlations are shown as n.s.

#	Measurement	Mean (mm)	s.d. (mm)	Correlation with measurement # 6	5	4	3	2
1	Length, 1	25.6 (22.0–28.0)	1.5	.293	.437	n.s.	n.s.	.426
2	Dia. at 25% of 1	4.0 (3.0–5.0)	0.3	.447	.426	.319	n.s.	
3	Dia. at 50% of 1	7.4 (5.5–9.0)	0.8	n.s.	n.s.	n.s.		
4	Dia. at 75% of 1	10.1 (8.0–12.0)	0.8	.582	.399			
5	Dia. of opening	6.5 (5.0–9.0)	1.0	.433				
6	Dia. at end	8.5 (6.0–11.0)	1.0					

TABLE 2. Summary data on the nectar-sugar composition of 74 floral nectar samples from *Penstemon pseudospectabilis* expressed as relative percent by mass of each sugar. Pearson product-moment correlation coefficients significant at the P < .01 level are given. All are normal in their distributions by the Kolmogorov-Smirnov test.

Sugar	Mean %	s.d. %	Correlation coefficient Sucrose	Glucose
Fructose	11.7	4.4	−0.955	0.881
Glucose	13.8	4.3	−0.958	
Sucrose	74.5	8.3		

Summary nectar-sugar data are given in Table 2. Freeman et al. (1984) found typical hummingbird nectar to contain 15% fructose, 11% glucose, and 74% sucrose, and gave 95% confidence limits for that property. The nectar of *P. pseudospectabilis* is similar and falls well within the domain of hummingbird nectars. While Freeman et al. (1984) showed hummingbird nectars often have somewhat more fructose than glucose (%F/%G = ca 1.4), the nectar of *Penstemon* studies here contained less (%F/%G = 0.8). This has been true of several *Penstemon* species studied (C. E. Freeman, unpublished data). The frequency distribution of percent composition by mass was normal (P < .01) by the Kolmogorov-Smirnov test (Sokol and Rohlf 1983).

Little data are available on the frequency distribution of nectar-sugar composition in different taxa, and it may be worth noting that such distributions are not always normal. The moth-pollinated species *Ipomopsis longiflora* has a skewed, nonnormal distribution in sucrose composition with a maximum above 90% sucrose (Freeman et al. 1985). An *Agave neomexicana* population at the upper limit of its altitudinal range has dispersed, nonnormal sugar compositions (Reid et al. 1985). The normality of distribution in *P. pseudospectabilis* does not rule out strong selective forces from pollinator preference, but it certainly provides no evidence for their presence. Indeed, present data on preference (Baker and Baker 1983a) and its elasticity with different food and water stresses does not permit more than the roughest of inferences. For example, Allen and Neill (1979) found that several hummingbird species regularly visit *Agave havardiana* for its abundant low-sucrose nectar (Freeman et al. 1983, Reid et al. 1985) in arid Big Bend National Park, Texas.

Twelve of the nectar samples were taken in the morning, and 41 were collected in late afternoon. Since the composition distributions were normal, we compared these for each sugar by ANOVA. Morning fructose was different from evening (F = 6.42, P = .001). However, glucose (F = 1.32, P = .26) and sucrose (F = 3.53, P = .06) were not significantly different. Temporal change in composition could affect pollinator activity, and this possibility requires further, more precise examination.

There were some significant correlations between floral morphology and sugar composition despite the relatively small variance in both these data sets. The area of the opening in the floral tube correlated with fructose (r = .517, P = .023), glucose (r = .541, P = .017), and sucrose (r = −.549, P = .015). The tube area 75% distal from the receptacle correlated

TABLE 3. Summary data on seed set in the *Penstemon pseudospectabilis* population. Treatment: A = shoot covered with stocking, B = shoot caged with 5-cm chicken wire, C = no exclosure. ( ) encloses the range.

Treatment	A	B	C
Mean fruits with seed/shoot	1.47	14.22	22.17
	(0–4)	(1–32)	(8–34)
Mean total fruits/shoot	25.23	31.17	35.33
	(7–51)	(19–44)	(23–49)
Fruits with seed/total fruits	0.06	0.45	0.63
	(0.0–0.16)	(0.05–0.74)	(0.0–0.94)
Mean seeds/fruit with seed	19.11	48.13	72.50
	(0.0–66.0)	(18.9–86.0)	(54.6–102.6)

with fructose ($r = .471$, $P = .042$), glucose ($r = .458$, $P = .048$), and sucrose ($r = -.463$, $P = .046$). Correlations with the end diameter and area were similar but somewhat lower and not significant at the 5% level. These relationships indicate that a larger, more open flower will have a lower sucrose composition.

We saw *Xylocopa* sp., small bees, flies, and several species of hummingbirds visit the flowers. The bees were not deterred by the 5-cm chicken wire, but the hummingbirds would not approach closer than a few dm. The *Xylocopa* approached the flowers from somewhat below and grasped the corolla with their forelimbs. Hanging briefly like a trapeze artist, they then forced their way partly into the floral tube, remained a few seconds, and left. In neither May nor June did we observe robbing or see torn flowers (Inouye 1983). Since *Xylocopa* lay eggs on large (1 cm) pollen pellets, it may be that pollen gathering was their primary objective in visiting these flowers.

Of the 20 plants originally selected, 2 appeared to have been disturbed, and the stocking on 1 additional shoot had a large hole. Thus, we determined seed set on 17 plant shoots excluding all pollinators, and 18 for those with a hummingbird exclusion cage and those with no exclusion.

It became apparent, upon examination of fruits, that the fresh fruit size was related to seed count. For 187 fruits we both counted seeds and measured greatest fruit diameter with a micrometer. After examining several relationships, we concluded that diameter cubed (Dcubed) gave the best correlation with number of seeds (N) for fruits greater than 2 mm: $N = 0.8 + 0.569*\text{Dcubed (mm)}$, $r = .902$, d.f. = 185, $P < .001$. No fruit smaller than 2 mm diameter contained seed. This relationship may be convenient in larger studies. Counting more than 23,000 seeds was a significant fraction of the effort in this work.

The seed set data were expressed in terms of seeds per fruit with seed, seeds per fruit, and fruits with seed per fruit to correct for differences in flowers per shoot (Table 3). In summary, 6% of flowers set seed with all flying pollinators excluded, 45% with hummingbirds excluded, and 63% with no exclusion. With all flying pollinators excluded, there were fewer than 2 seeds per fruit, 23 seeds with hummingbirds excluded, and 46 with no exclusion. The seed set with all flying pollinators excluded might be by selfing, through pollination by ants or other climbing insects, or our activities. Most of the seed set is from insect and hummingbird pollination. Overall, 580 (36%) of the 1,624 fruits set seed, and these had a mean seed set of 60, well below the maximum observed of 192. Clearly, the flowers in this test were not saturated by pollinators.

The seed set data were nonnormal in distribution, and we used nonparametric statistics to test differences among the treatments. We used both the Wilcoxon matched pairs test (assuming pairing since each plant tested had all three treatments) and the Mann-Whitney two sample test (assuming there was no significance to the pairing). Both tests showed all three treatments to be significantly different ($P < .01$) in all comparisons (fruits with seed/fruits, seeds/fruit with seed, and seeds/fruit). Thus, the effect of exclusion is highly significant.

Our final, and most speculative, analysis was to use multiple linear regression to explain two of the derived results, fruits with seed/fruits and seeds/fruit. We used the six measures of floral morphology and the percent by mass of each sugar as independent variables. The results are given in Table 4,

TABLE 4. Summary results of multiple linear regression analysis of *Penstemon pseudospectabilis* fruits with seed/fruits and seeds/fruit with the three treatments in comparison with the morphological and sugar composition data. The first four variables selected and the cumulative regression coefficient are given. The sign of the correlative relationship between each independent variable and the dependent variable is shown by + or −. Treatment: A = shoot covered with stocking, B = shoot caged with 5-cm chicken wire, C = no exclosure.

Variable analyzed: fruit with seed/total fruits			
Treatment =	A	B	C
Independent variable			
1	+sucrose	+dia. at 75% of 1	+dia. end
2	+dia. opening	+dia. at 25% of 1	+dia. opening
3	−length	+dia. at 50% of 1	+fructose
4	+dia. at 25% of 1	−length	+dia. at 75% of 1
Regression coefficient	0.779	0.816	0.687
Significance, P	< .001	< .001	< .01
Variable analyzed: seeds/fruit			
Treatment =	A	B	C
Independent variable			
1	+dia. at 25% of 1	+dia. at end	−length
2	−glucose	−length	+dia. at 75% of 1
3	−dia. at 50% of 1	+dia. at 75% of 1	+fructose
4	+dia. opening	+fructose	+dia. at 25% of 1
Regression coefficient	0.561	0.712	0.766
Significance, P	< .05	< .01	< .01

and, while they are statistically significant, they must be regarded as preliminary. There was less than 1% difference between using diameters and areas in the regressions, and no difference in the selection of variables.

Fruits setting seed on the stocking-covered shoots were positively related to sucrose. The other three variables, length (negatively correlated) and two diameters (positive), are not inconsistent with this. Fruits setting seed with hummingbirds excluded positively related to three areas (and diameters) and negatively correlated with length. This hints that bees are more effective pollinators of shorter, more open flowers. With no exclusion, the most significant variables were three measures of area near the distal end of the flower, and fructose. The positive correlation for fructose is also not inconsistent with the preference of hummingbirds as discussed above.

Results for seed set using multiple regression are somewhat similar, but occasionally cryptic. For the stocking-covered shoots, seed set was positively related to diameter at opening and at 25% of length. It was negatively related to diameter at 50% of length and glucose. The negative glucose correlation parallels one of positive sucrose. The hummingbird-excluded shoots were again supportive of a shorter, broader flower, with an additional positive correlation for fructose. Finally, the regression results for no exclusion are similar to those for hummingbird exclusion.

The results from this small experiment are remarkably supportive of the generalizations of pollination biology. They do not form an irrefutable chain of evidence, but they do lend detail to the complex mosaic of assertions made during recent decades. The data also support an assertion that careful experimentation in pollination biology will be numerically productive in testing and refining the rich insights of Herbert and Irene Baker and many others.

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LITERATURE CITED

ALLEN, T. M., AND R. L. NEILL. 1979. Avifaunal associates of *Agave havardiana* Trel. in Big Bend National Park. Trans. Proc. Series., Nat. Park Service No. 5: 475–478.

BAKER, H. G., AND I. BAKER. 1983a. A brief historical review of the chemistry of floral nectar. Pages 126–152 *in* B. Bentley and T. S. Elias, eds., The biology of nectaries. Columbia University Press, New York.

———. 1983b. Floral nectar sugar constituents in relation to pollinator type. Pages 117–141 *in* C. E. Jones and R. J. Little, eds., Handbook of experimental pollination biology. Van Nostrand Reinhold Co., New York.

CROSSWHITE, F. S., AND C. D. CROSSWHITE. 1981. Hummingbirds as pollinators of flowers in the red-yellow segment of the color spectrum with special reference to *Penstemon* and the "open habitat." Desert Plants 3: 156–170.

FAEGRI, K. AND L. VAN DER PIJL. 1971. The principles of pollination ecology. 2d ed. Pergamon Press, Oxford.

FREEMAN, C. E., W. H. REID, AND J. E. BECVAR. 1983. Nectar sugar composition in some species of *Agave* (Agavaceae). Madroño 30: 153–158.

FREEMAN, C. E., W. H. REID, J. E. BECVAR, AND R. SCOGIN. 1984. Similarity and apparent convergence in the nectar-sugar composition of some hummingbird-pollinated flowers. Bot. Gaz. 145: 132–135.

FREEMAN, C. E., W. H. REID, AND R. D. WORTHINGTON. 1985. Patterns of floral nectar-sugar composition of *Ipomopsis longiflora* (Polomoniaceae) near the contact zone of its subspecies *longiflora* and *australis*. Amer. J. Bot. 72: 1662–1667.

GRANT, K. A., AND V. GRANT. 1968. Hummingbirds and their flowers. Columbia University Press, New York.

HINTZE, J. L. 1985. Number cruncher statistical system, Version 4.2. Kaysville.

INOUYE, D. W. 1983. The ecology of nectar robbing. Pages 153–173 *in* B. Bentley and T. S. Elias, eds., The biology of nectaries. Columbia University Press, New York.

JEPSON, W. L. 1925. A manual of the flowering plants of California. University of California Press, Berkeley. 1,238 pp.

KEARNEY, T. H., AND R. H. PEEBLES. 1969. Arizona flora. University of California Press, Berkeley. xiii + 1,085 pp.

MARTIN, W. C., AND C. R. HUTCHINS. 1981. A flora of New Mexico. Cramer, Vaduz. xiii + 2,591 pps., 2 vols.

RADFORD, A. E., W. C. DICKISON, J. R. MASSEY, AND C. R. BELL. 1974. Vascular plant systematics. Harper and Row, New York. 891 pp.

REID, W. H., C. E. FREEMAN, AND J. E. BECVAR. 1985. Nectar-sugar variability in two species of *Agave* (Agavaceae). Southwest. Nat. 30: 443–445.

SOKAL, R. R., AND F. J. ROHLF. 1983. Biometry. 2d ed. W. H. Freeman and Co., San Francisco.

STRAW, R. M. 1956. Floral isolation in *Penstemon*. Amer. Natur. 90: 47–53.

———. 1966. A redefinition of *Penstemon* (Scrophulariaceae). Brittonia 18: 80–95.

AN *ERIGERON* FROM NEVADA AND A *PENSTEMON* FROM IDAHO

N. Duane Atwood[1] and Stanley L. Welsh[2]

ABSTRACT.—Described as new species are *Erigeron cavernensis* Welsh & Atwood from the Schell Creek Range and Currant Mountain, White Pine County, Nevada, and *Penstemon idahoensis* Atwood & Welsh from the Goose Creek drainage, Cassia County, Idaho.

Continued exploration of the American West yields new taxa almost on a yearly basis. The productive regions are those not explored previously due to difficulty of access or improper timing during previous exploration. Certain plants are difficult to discern other than when flowering, and many are not recognizably different except when flowers or fruit are present. The two species described herein were taken from poorly collected regions. They are small and not especially showy but distinctively attractive plants that grow in restricted habitat types. The *Erigeron* occurs at high elevations in limestone rubble and cliff crevices. The *Penstemon* is known only from peculiar white tuffaceous (?) outcrops along the Goose Creek drainage.

Erigeron cavernensis
Welsh & Atwood, sp. nov.

A Erigerone unciali Blake sensu lato differt in caulibus pubescentia hirsutis involucris brevioribus et caudicibus longioribus.

Perennial herbs from a branching subterranean caudex, the caudex branches clothed at their summits with marcescent ashy to black leaf bases; herbage copiously hirsute with multicellular trichomes; stems slender, erect, 1.7–6 cm tall; basal leaves (0.3) 0.8–2 (2.8) cm long, 1.5–6.5 mm wide, spatulate to oblanceolate, petiolate, obtuse apically; cauline leaves reduced upwards; heads solitary; involucres 3.5–4.5 mm high, 5–10 mm wide, subglandular, hirsute with multicellular hairs; bracts involucrate, somewhat thickened, purplish, the inner ones with scarious purplish margins; rays ca 16–23, purplish or white, 3.5–4.5 mm long; pappus double, the inner bristles ca 18–20, with shorter outer setae; achenes 2-nerved, hairy.

TYPE.—Nevada, White Pine County, Schell Creek Range, T15N, R66E, 25 air km SE of Ely, ca 2 km NE of summit of Cave Mountain, 3,172–3,233 m elev., limestone cliffs and rubble, *Pinus flexilis–P. longaeva* community, 18 July 1981, B. Welsh, S. Goodrich, and E. Neese 910 (Holotype BRY; Isotypes NY, RM, US, POM, UT, UNLV).

ADDITIONAL SPECIMENS.—Nevada, White Pine County, Schell Creek Range, T15N, R66E, 25 km due SE of Ely, near summit of Cave Mtn, at ca 3,264 m elev., crevices of limestone cliffs, bristlecone pine, limber pine, spruce community, 18 July 1981, E. Neese, S. Goodrich, B. Welsh 10778 (BRY); do, ca 3 km N of summit of Cave Mtn, at 3,233 m elev., limestone rubble and cliffs, limber pine, bristlecone, Engelmann spruce community, 18 July 1981, E. Neese, S. Goodrich, B. Welsh 10758 (BRY); Currant Mountain, on east slope below VABM 11513, T12N, R58E, Humboldt National Forest, between 3,050 and 3,355 m elev., in bristlecone pine community, 30 June 1987, N. D. Atwood and W. Swensen 13063 (BRY).

This is a handsome dwarf plant that is evidently allied to *E. simplex* Blake, from which it differs in its hirsute vesture, in its shorter-than-average involucres, and in the more elongate caudex branches. This latter feature might be an ecological response to the habitat in rubble and crevices. However, *E. simplex* Blake is also a plant of crevices in limestone, but the caudices are seldom well developed. The plant is named for its locality on Cave Mountain in the Schell Creek Range of Nevada. Naming of the plant at this time was stimulated by recognition of a second locality for the species on Currant Mountain, at the

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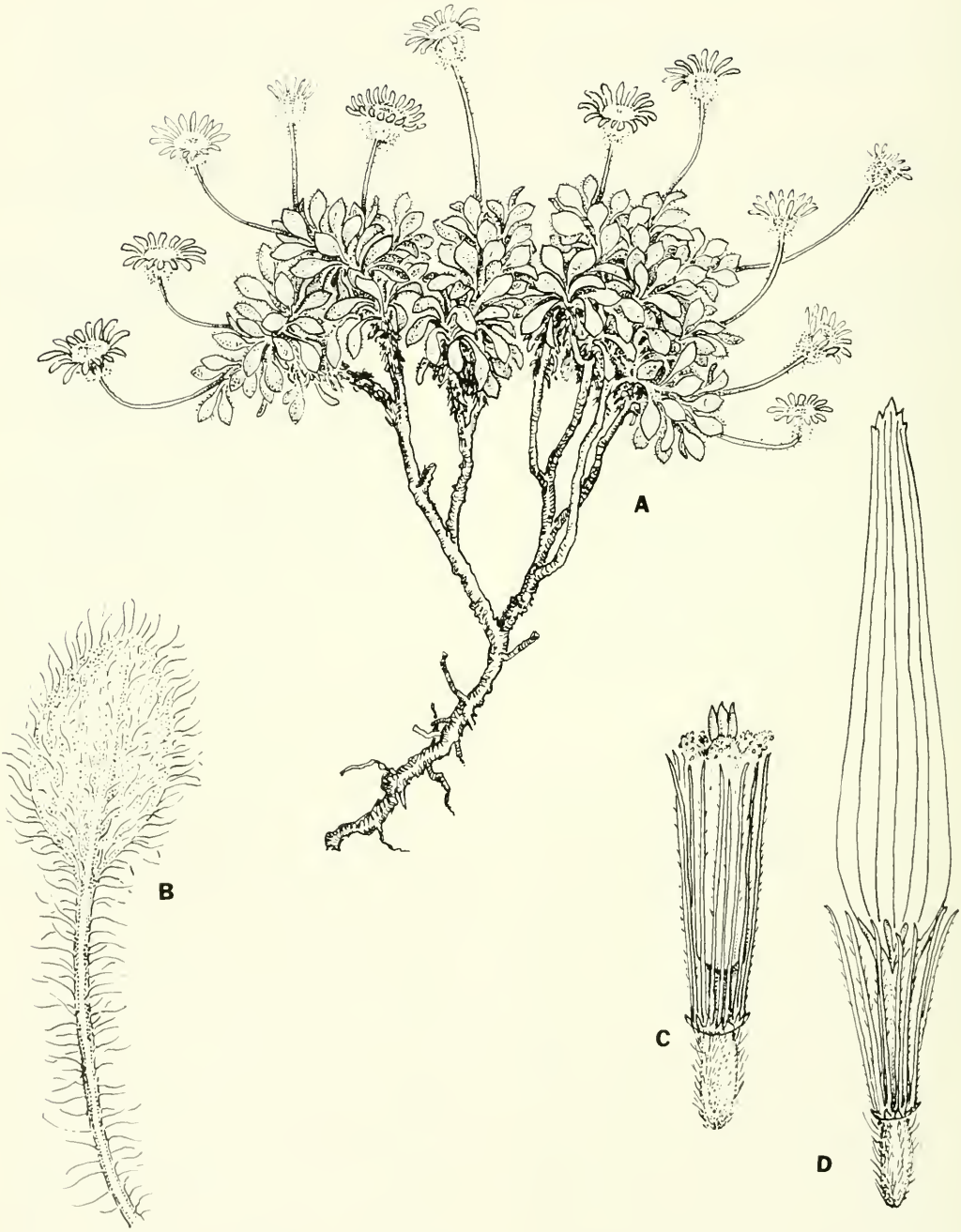

Fig. 1. A, *Erigeron cavernensis* Welsh & Atwood; B, leaf; C, disk flower; D, ray flower.

western margin of White Pine County. The voucher material for the second known locality was taken by N. D. Atwood and W. Swensen (see above).

Penstemon idahoensis
Atwood & Welsh, sp. nov.

Similis Penstemon scarioso Pennell section Glabri (Rydb.) Pennell sed glanduliferis

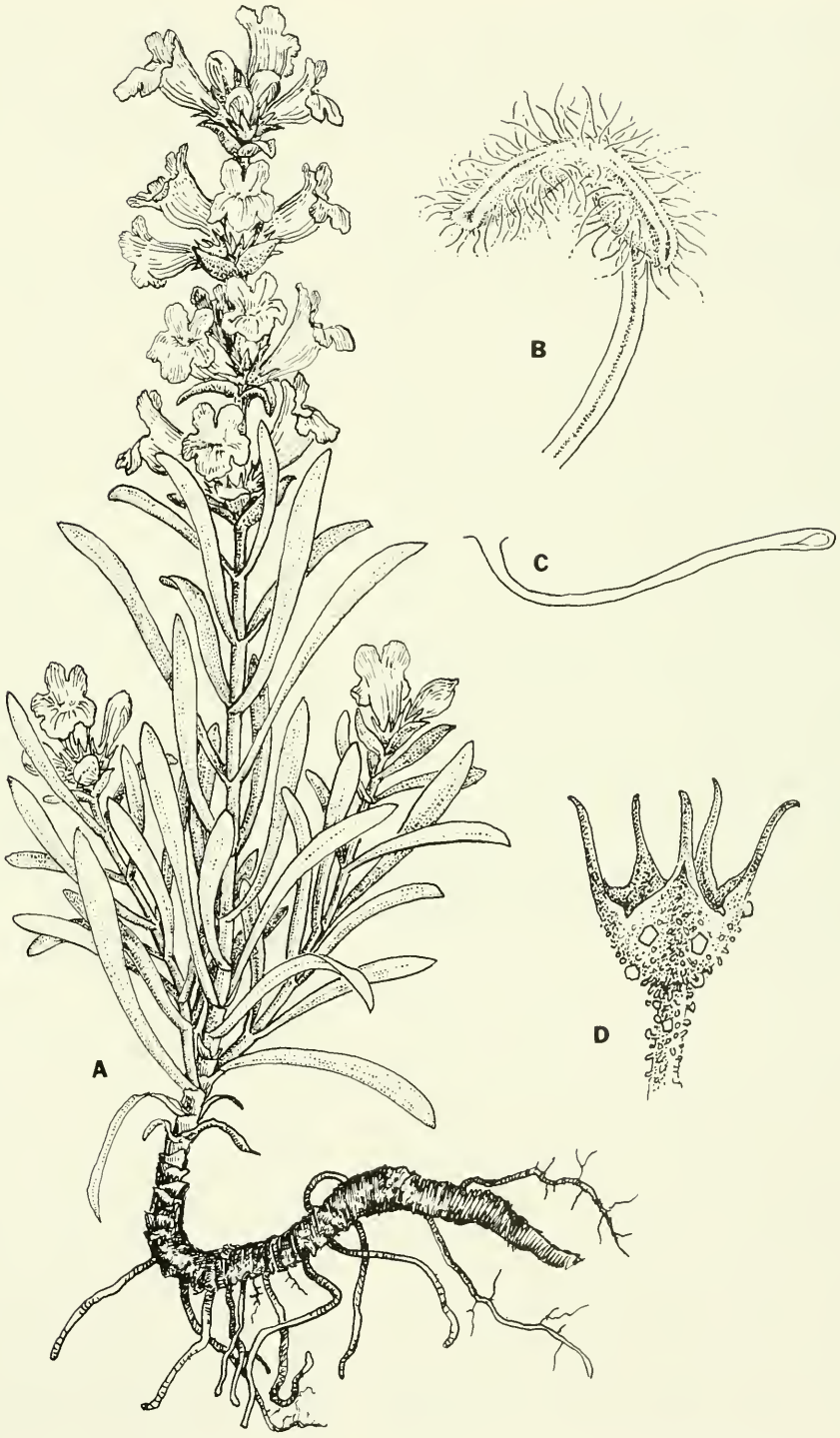

Fig. 2. A, *Penstemon idahoensis* Atwood & Welsh; B, stamen; C, staminode; D, calyx with sand grains adhering to the glandular surface.

omnino et detritis obtectis staminodia glabro et folia marginibus crassioribus differt.

Perennial herbs, 8–20 cm tall; stems several from a semiwoody caudex, ascending to erect, glandular; leaves entire, surficially glandular, glistening, bearing adherent soil particles, the margins revolute, thickened, sessile, the basal and lower cauline ones oblanceolate, 3.5–7 cm long, 1.4–4.2 (8) mm wide, the upper cauline ones linear to elliptical, 3.4–5.5 cm long, 2.4–5.3 mm wide; inflorescence glandular, congested, 3–9 cm long, secund, the cymes 1- to 5-flowered; calyx 5.4–8.5 mm long, glandular, the lobes 3–5 mm long, acuminate, inconspicuously scarious margined; corolla 1.7–2.1 cm long, ventricose-ampliate, blue to blue purple, glabrous externally, the palate glabrous, the lobes rounded, 2.6–4.5 mm long, undulate; fertile stamens included to slightly exserted, the anthers purplish, the sacs 1.5–2 mm long, divaricate, moderately white-bearded with slender flexuous hairs about equal to or surpassing the sac width, opening across the distal ends but not across the connective; staminode glabrous, included, bluish.

TYPE.—Idaho, Cassia County, T16S, R21E, S35 NW, 17 air mi SW of Oakley, 1 mi N of Idaho/Utah line, Goose Creek drainage, near Shoe Spring, in scattered juniper, 22 June 1982, D. Atwood (with S. Goodrich) 8958 (Holotype BRY; 13 isotypes distributed previously as *Penstemon*).

ADDITIONAL SPECIMENS.—Idaho, Cassia County T16S, R21E, S28 SW/SW, white tuffaceous outcrops, at 5,100 ft elev., 10 June 1985, D. Atwood [with R. Rosentrater 11163 (BRY)]; do, T16S, R221E, S2 SW, 14 air mi S of Oakley, Goose Creek, near Devine Canyon, 22 June 1982, D. Atwood [with S. Goodrich 8954 (BRY)].

This attractive species of penstemon is evidently confined to siliceous tuffaceous outcrops in Cassia County, Idaho, not far from the state boundary juncture of Utah, Nevada, and Idaho. The tuffaceous outcrop is evidently a portion of the Tertiary Salt Lake Formation. Fragments of the tuffaceous material, evidently siliceous in nature, cling to the glandular surface of the herbage but do not obscure the surface.

Relationship of this plant is apparently with members of section Glabri. The anthers are clothed with hairs that approximate the width of the sacs in length. Dehiscence is in the proximal portion of each sac only. In the protologue the species is compared to *P. scariosus*, which occurs along the high plateaus of Utah. The Idaho penstemon differs from that species as outlined in the protologue. It is named in recognition of the state of origin.

Illustrations of the two species are provided by Kaye Hugie Thorne, to whom our gratitude is expressed.

STATUS OF *THAMNOPHIS SIRTALIS* IN CHIHUAHUA, MEXICO (REPTILIA: COLUBRIDAE)

Wilmer W. Tanner[1]

ABSTRACT.—This is a study of the populations of *Thamnophis sirtalis* that occur in Chihuahua, Mexico, and the adjoining U.S. state of New Mexico. Reference is made to previous studies dealing with geographical and systematic relationships. Additional data are provided for the New Mexico subspecies (*dorsalis*), and the relationship of *T. s. parietalis* to the New Mexico population is discussed. The Chihuahua population is described as a new subspecies.

During the summer of 1899, Nelson and Goldman collected a specimen of *Thamnophis sirtalis* in north central Chihuahua. It was reported by Goldman (1951) to have been collected at Casas Grandes. Smith (1942) examined the specimen (USNM 46371) and referred it to the subspecies *Thamnophis sirtalis parietalis* (Say 1823). Smith's examination of this female specimen provides the following characters: scale rows 19-19-17, ventrals 152, tail incomplete, supralabials 7-7, infralabials 10-11, preoculars 1-1, and postoculars 3-3. It is further stated that the spots in the upper row are fused together, with those in the lower row confluent with the upper row but not with each other, and with spaces between red.

Since the Smith report, a number of studies have been made concerning the identity of specimens presumably collected in the Rio Grande basin (of which the Río Casas Grandes and Río Santa María in northern Chihuahua were a part during the recent pluvial period). Smith and Brown (1946), after an examination of the literature and available data, concluded that *T. ornata* (Baird 1859), which was supposedly collected between San Antonio and El Paso, Texas, was indeed a synonym of *T. s. parietalis*. Fitch and Milstead (1961) reexamined the status of *Thamnophis dorsalis* (Baird & Girard 1853) and concluded that *Thamnophis cyrtopsis* (Kennicott 1860) is a synonym of *Thamnophis sirtalis dorsalis*. Fitch and Maslin (1961), in their study of *Thamnophis sirtalis* in the Great Plains and Rocky Mountains, concluded that *dorsalis* was a synonym of *Thamnophis sirtalis ornata* Baird, referred the specimen from Casas Grandes, Chihuahua, to the subspecies *ornata*, and placed specimens from the Rio Grande valley of New Mexico, which had previously been designated as *Thamnophis sirtalis parietalis*, within the distribution area of *ornata*. Webb (1966), in his study by *Thamnophis cyrtopsis*, concluded that *Eutaenia dorsalis* is applicable to the upper Rio Grande population of garter snakes designated by Fitch and Maslin (1961) as *Thamnophis sirtalis ornata*.

In spite of much uncertainty concerning the type locality and the loss of the type specimen, Fitch (1980) accepted (with reservations) the subspecific name *dorsalis* as proposed by Webb for the population of *sirtalis* presently occurring in the Rio Grande valley of New Mexico.

Not until Van Devender and Lowe (1977) reported a series of *Thamnophis sirtalis* collected at or near Yepómera, in central Chihuahua, was there sufficient material to provide a basis for a study of the Chihuahua population. Since the study by Fitch and Maslin (1961), considerably more comparative material has become available from New Mexico. Through the courtesy of Dr. C. H. Lowe, I have had the privilege of examining the recently collected series of 13 specimens of *T. sirtalis* from Yepómera or nearby, 1 specimen from Nuevo Casas Grandes, and 3 specimens from near Galeana (one of these from Dr. R. Conant); in addition, USNM 46371 from Casas Grandes, Chihuahua, has been reexamined. A large series from New Mexico, loaned by Dr. W. G. Degenhardt, is now available. The series from Kansas (KU) and

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Utah (BYU) collections were also used as comparative material. Although there are many similarities to the population along the Rio Grande in central New Mexico, when compared to the population in central Chihuahua some significant variations are apparent (Tanner 1986). Differences are seen not only in some scale patterns, but also in color pattern. Furthermore, the Chihuahua population is several hundred miles removed from the nearest known populations in New Mexico and Texas. This isolation from the main body of this widespread species, which has apparently existed since the recent Ice Age, has resulted in character modifications sufficiently significant to recognize the Chihuahua population as a subspecies. It is, therefore, named in honor of one who has added much to the herpetology of southwestern United States and northwestern Mexico.

Thamnophis sirtalis lowei, n. subsp.

TYPE.—An adult female, UAZ 34879, Yepómera, Chihuahua, Mexico; collected 8 June 1972, by T. R. Van Devender. See Figure 1.

PARATYPES.—UAZ 34066, 34070, 34230, 34880–82, Yepómera; UAZ 34071, 3 km N Yepómera; UAZ 34067–69, 34399, 5 km N Yepómera; UAZ 34149, 6 km N Yepómera; UAZ 34434, 0.5 km N Nuevo Casas Grandes; USNM 46371, Casas Grandes, Chihuahua, Mexico.

DIAGNOSIS.—A subspecies similar to *T. s. parietalis* and *T. s. dorsalis* but with 21 rows of dorsal scales on the anterior part of the body, with the first reduction to 20 rows above the 10th to 19th ventral or the 10th to 19th scale posterior to the parietals in the middorsal stripe; ventrals male 158–166 (160.6), female 157–164 (160.7); subcaudals male 84–89 (86.5), female 73–78 (75.4); supralabials 7 or 8, infralabials 9–12. Color pattern (Fig. 1) similar to that of *T. s. parietalis* but differing noticeably from *T. s. dorsalis* as illustrated by Fitch and Maslin (1961, Fig. 4).

DESCRIPTION OF TYPE.—Top of head a dark olive brown, becoming darker on temporals, the expanded dark of temporal area narrowing to become a dark stripe 2–3 scale rows wide and sharply edging the middorsal cream-colored stripe, laterally being separated from the large dark spots by narrow longitudinal stripes of pink or reddish markings that usually surround the spots dorsally and laterally; ventrally the dark spots contact the light lateral stripe on the edge of the 3rd scale row. There are 66 lateral dark spots extending from nape to vent, distinct for the length of the body, but not extending onto the tail; dorsal stripe sharply defined and two scales wide, occupying the middorsal row and half of the adjacent rows, extending from parietals well onto tail before becoming indistinct near its end; lateral stripe distinct, but paler than dorsal and on rows 2 and 3; lower labials, chinshields, gulars, and anterior ventrals cream colored; ventrals a lead grey and without dark spots except for a few irregular shaped and spaced spots edging onto the ventrals from the first scale row.

Lepidosis generally normal for the species, with nasal divided, anterior section largest, one loreal, one preocular, 3–4 postoculars, 1+2 temporals, supralabials 7-7, infralabials 11-12 with 5-6 on right side divided, scale rows 21-19-17, reduction to 20 rows above 14th ventral, ventrals 157, subcaudals 78, anal single; except for the ventrals, subcaudals, head, and temporal scales, all scales have keels.

COMPARISONS.—The reduction to 20 scale rows may occur from the 10th to the 19th ventral, with an average for the series of 13.73 ventrals. In the middorsal stripe the reduction occurs between 10–20 scales posterior to the parietals, with an average of 13.9 scales. A comparison of these data to specimens of *sirtalis* from all other areas of distribution in the United States provides a reduction usually by or before the 8th ventral. A series of 61 specimens from the Rio Grande valley of New Mexico (Valencia, Bernalillo, Socorro, Sierra, and Rio Arriba counties) gives the following on the reduction of the scale rows: above the 5–11 ventral, average 7.7; below the 7–14 scale in the middorsal stripe posterior to the parietals, average 9.6.

The reduction to 20 scale rows in the New Mexico series provides more variation than in other populations or subspecies (Table 1). Actually *T. s. dorsalis* is an intermediate segment of the species between *T. s. parietalis* to the north and *T. s. lowei* to the south. This is reflected in the reduction of the scale rows, number of subcaudals, and slight increase in supralabials and infralabials.

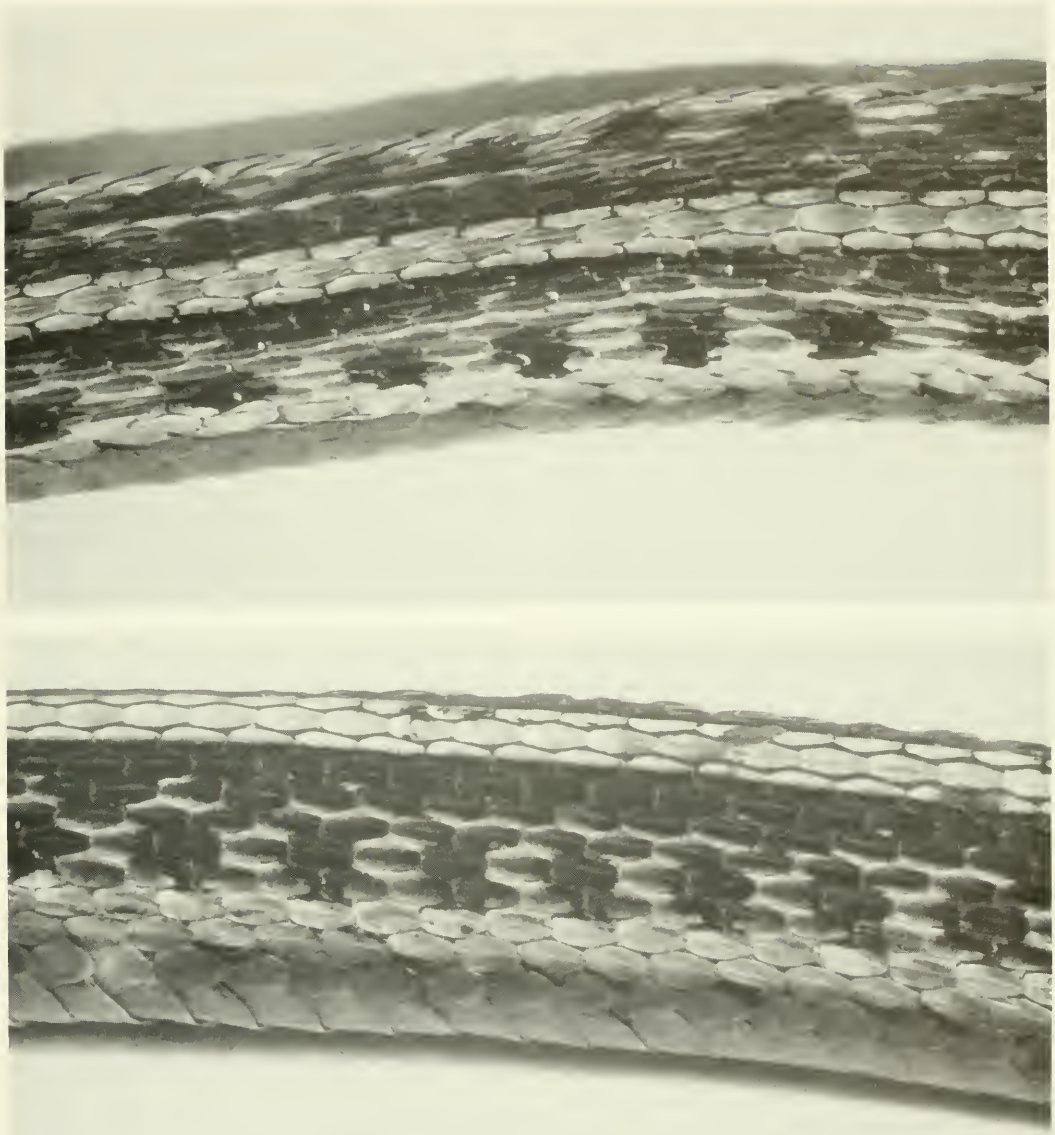

Fig. 1. A, dorsolateral view of the color pattern of the type of *Thamnophis sirtalis lowei*, UAZ 34879, taken at Yepómera, Chihuahua, Mexico, by T. R. Van Devender, 8 June 1972; B, dorsolateral view of a paratype of *Thamnophis sirtalis lowei*, UAZ 34881, Yepómera, Chihuahua, Mexico.

The color pattern is a variation between the diagrammatic drawings of Fitch and Maslin (1961) for *T. s. parietalis* (Fig. 3) and *T. s. ornata (dorsalis)* (Fig. 4). There is a reduction of the dark brown or black when compared to *T. s. parietalis* and considerably more than in *T. s. dorsalis* as previously described. A dark border two scales wide is lateral to the mid-dorsal stripe, in turn bordered by a narrow, broken, pink to reddish stripe, which usually separates the large lateral spots from the dark band between them and the dorsal stripe. In *T. s. dorsalis*, as described and figured by Fitch and Maslin (1961), the dark lateral spots are more often than not surrounded dorsally and laterally by the pink color, which may be a scale or more wide. In *T. s. lowei* there are irregular, small, dark extensions that may

TABLE 1. Scale pattern relationships between four subspecies of *T. s. sirtalis*. Scale row reductions occur above ventrals, with variations ranging from the 3rd to 19th.

Number examined	31	22	72	14
Subspecies	*s. sirtalis* (eastern U.S.)	*s. parietalis* (Kansas)	*s. dorsalis* (New Mexico)	*s. lowei* (Chihuahua)
Scale row reduction	3–8 (5.9)	5–10 (6.9)	5–11 (7.7)	10–19 (13.73)
Ventrals	♂ 10=144–159(152.0) ♀ 20–137–154(143.0)	11=152–161(157.3) 10=150–159(154.1)	17=159–178(166.0) 44=156–166(160.2)	3=158–166(160.6) 11=157–164(160.7)
Subcaudals	♂ 8=71–83(76.0) ♀ 18=55–70(63.7)	8=81–86(84.1) 8=69–77(74.3)	17=78–86(83.5) 32=65–78(72.6)	2=84–89(86.5) 5=73–78(75.4)
Supralabials	6–8 (7.0)	7–8 (7.08)	7–8 (7.15)	7–8 (7.43)
Infralabials	9–11 (9.77)	9–11 (9.85)	8–11 (10.0)	9–12 (10.2)

extend dorsally to connect the lateral spots to the dark band lateral to the median stripe. The dark lateral spots involve 4–7 scales and are separated from each other by at least one light (pink) scale. This is in contrast to most *dorsalis*, which have smaller spots involving 1–5 scales and more pink color between and dorsal to the spots (Fig. 2).

REMARKS.—Few species in North America have as wide a distribution as *Thamnophis sirtalis* (Fitch 1980). This has contributed to a series of variations not only in lepidosis but also in color pattern, resulting in the description of a number of subspecies. The study by Fitch and Maslin (1961) and the catalogue report by Fitch (1980) provide the most recent analysis of the species and establish a basis for a further examination of the populations now extant in the midsection of its distribution (Kansas, Colorado, Utah, Idaho, New Mexico, and Chihuahua, Mexico). The present study is concerned only with those populations occurring in Chihuahua and New Mexico.

The habitat requirements of *sirtalis* (streams, meadows, etc.) have produced in some areas (Rio Grande valley of New Mexico, Wasatch Front area of north central Utah, as well as central Chihuahua) a degree of isolation that appears to have limited these populations to little if any contact with populations in neighboring river valleys. This isolation has resulted since the recent pluvial period, and its effect on the variation between populations is only now, with an increase in available specimens, becoming evident. There is at present a wide area of desert separating the Chihuahua and New Mexico populations. Indications are that these populations have, through the slow desiccation since the recent Ice Age, been forced from the desert valleys to the more suitable mesic areas south or north of the northern basins of the Río Casas Grandes, and Río Santa María. Indications are that much of southern New Mexico originally served as a connection between populations in Chihuahua and New Mexico. At present the major concentration of the Chihuahua population appears to be in tributaries of the Río Papigochic near Yepómera and the basin of the Laguna de Babicora northwest of Gómez Farías. The populations in the Río Casas Grandes and Río Santa María are now seemingly restricted to areas south of Nuevo Casas Grandes and Galeana. Dams and diversions for agricultural purposes permit little stream flow to the north. Specimens UAZ 34434 from 0.5 km N of Nuevo Casas Grandes and USNM 46371 from Casas Grandes are similar to the population at or near Yepómera and may represent at present the northern extent of the *lowei* population. Furthermore, the southern headwaters of the Río Casas Grandes lie directly north of the Yepómera-Babicora area and may have provided for a natural migration lane from the Río Casas Grandes basin into the southern basins.

The population in the Río Santa María basin is presently isolated from the population in the Río Casas Grandes basin. Apparently, this has been the case since the desiccation separated the two basins, each now having separate closed lake basins terminating in separate inland dead lakes (Laguna de Santa María and

Laguna de Guzmán). This isolation has produced variation between the two *sirtalis* populations of Chihuahua. Three specimens from south of Galeana have fewer ventrals (151 and 152) and less pink laterally.

I have seen the three specimens from 1–3 miles S of Galeana. All other Chihuahua specimens have ventrals ranging from 154 to 166. In the one provided by Dr. Conant (1 mile S) the reduction to 20 scale rows and color pattern is similar to *lowei;* in the others the scale rows reduce above 7–9 ventral, and the color pattern is darker, with a noticeable reduction of the pink that tends to obscure the dark lateral spots so prominent in *lowei*. Until additional specimens are available, it is impossible to determine if the population in the Río Santa María basin has the basic characters relating it to either *lowei* or *dorsalis* or if it may represent a distinct population that should be recognized as a subspecies.

The subspecies *T. s. dorsalis* is, according to Fitch and Maslin (1961), Fitch (1980), and Stebbins (1985), recognizable by its color pattern. This subspecies designation at present includes only specimens occurring in the Rio Grande basin of New Mexico. An examination of New Mexico specimens, however, indicates that there are two distinct color patterns, one occurring in the southern counties (southeastern Valencia, Socorro, and Sierra) and one to the north (northwest Valencia, Bernalillo, and north into Rio Arriba). A typical color pattern for *dorsalis* (Fig. 2) consists of small spots above the lateral stripe, involving 1–5 scales and with a light space (with pink or blended colors) between them and a narrow dark stripe lateral to the middorsal stripe. This pattern gives specimens a much lighter ground color than is seen in specimens from northern New Mexico or in the subspecies *parietalis* or *lowei*.

In specimens from the northern counties, the pattern consists basically of a series of dark brown columns extending from the lateral line dorsad to fuse with a wide, dark area lateral to the dorsal stripe. Between these columns is a series of 3 or 4 oblong pink spots (Fig. 3). In only a few specimens are there additional light or pink spots radiating dorsad into the dark area as is common in *parietalis*. This pattern has a distinctness not often seen in other subspecies, but one that is easily related to *parietalis*.

In northeastern Valencia and extreme southern Bernalillo counties, some specimens do not conform to either of the above patterns. In this relatively narrow area, seemingly centered near Isleta and Los Lunas, specimens of either pattern and all gradations between occur. A typical intergrade has more pink and light colors between the spots that are partly or narrowly separated from the dark area lateral to the dorsal stripe. Some specimens have larger spots and a narrower dark area lateral to the dorsal stripe or various gradations in which lighter or darker patterns occur. Usually specimens with intergrading color patterns have more red in the pattern than *parietalis* and less than in *dorsalis*.

It is not a rarity for subspecies to have variable color patterns (*Sonora semiannulata* or *Lampropeltus getulus californiae*) nor to have narrow areas of intergradation. However, in this case there may have been other factors involved. All evidence indicates that *Thamnophis sirtalis* was once more widespread in south central United States and adjoining Mexico than at present. Based on present isolated populations in this wide area and data from the specimens available, one is inclined to wonder if the present population in the Rio Grande basin of New Mexico was derived from two *sirtalis* invasions into the basin.

There is reason to believe that much of Colorado and northern New Mexico was not a suitable habitat for *sirtalis* during the last pluvial period. This is not because of cool or cold temperatures, for *sirtalis* is well adapted to these conditions. Instead, it would seem that the mountains extending from southern Colorado into northeastern New Mexico served as a barrier during the Ice Age; thus, *sirtalis* may at that time have entered the Rio Grande valley by moving south along the western edge of the Great Plains. To the south an entirely different and suitable habitat must have been present, particularly in most of northern Chihuahua, western Texas, and southern New Mexico. These southern valleys served as catchment basins for the streams flowing south from New Mexico and north from the mountains in central and western Chihuahua. Apparently, *sirtalis* inhabited a wide area while these valleys were the recipient of major stream flow that provided suitable habitat along streams, lakes and adjoining meadows. As desiccation slowly changed

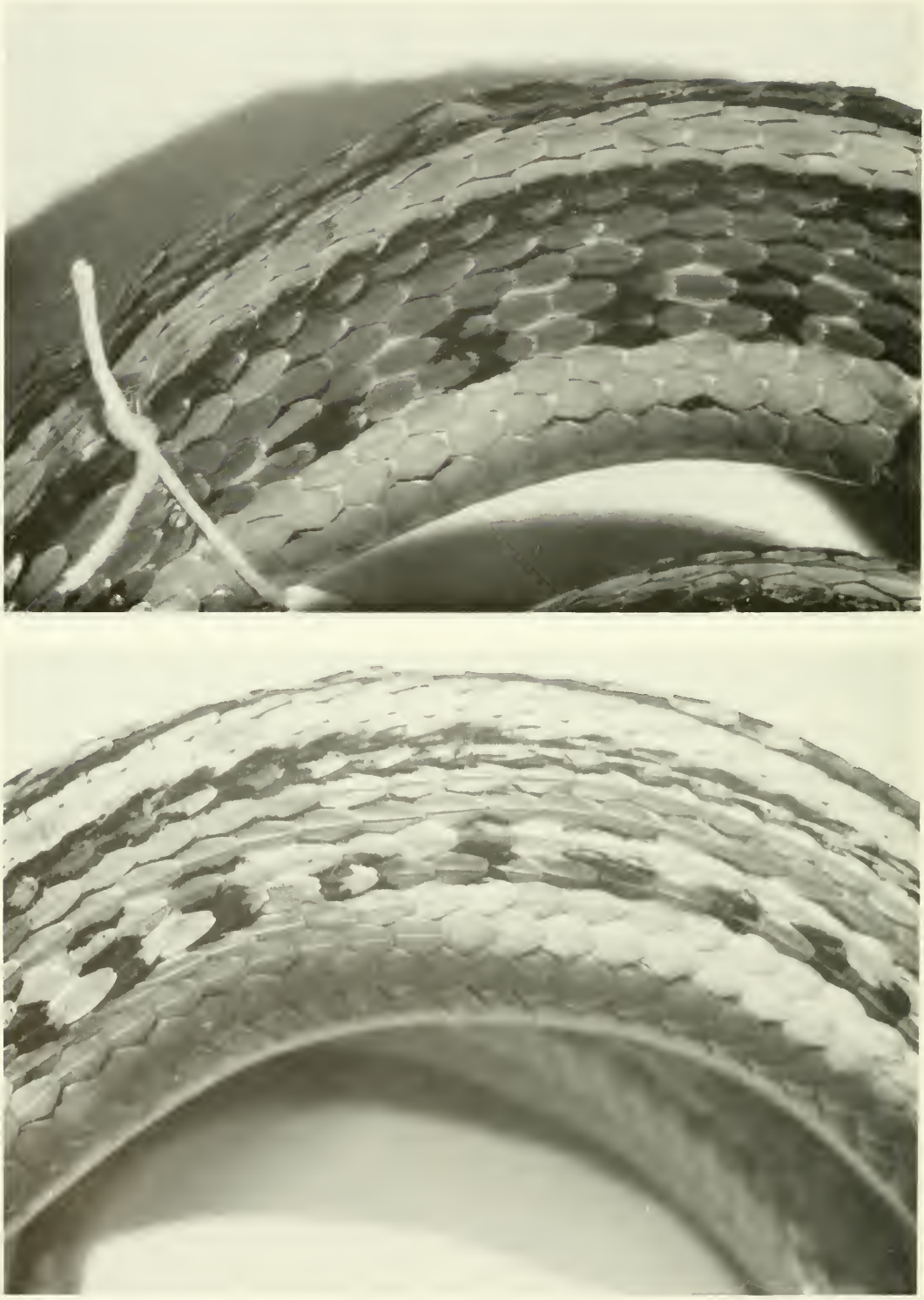

Fig. 2. Dorsolateral views of the color pattern of *Thamnophis sirtalis dorsalis:* A, UNM 15464, collected 3 miles S Isleta (Hwy. 47), Valencia County, New Mexico; B, UNM 32523, collected at Basque del Apache headquarters, Socorro County, New Mexico.

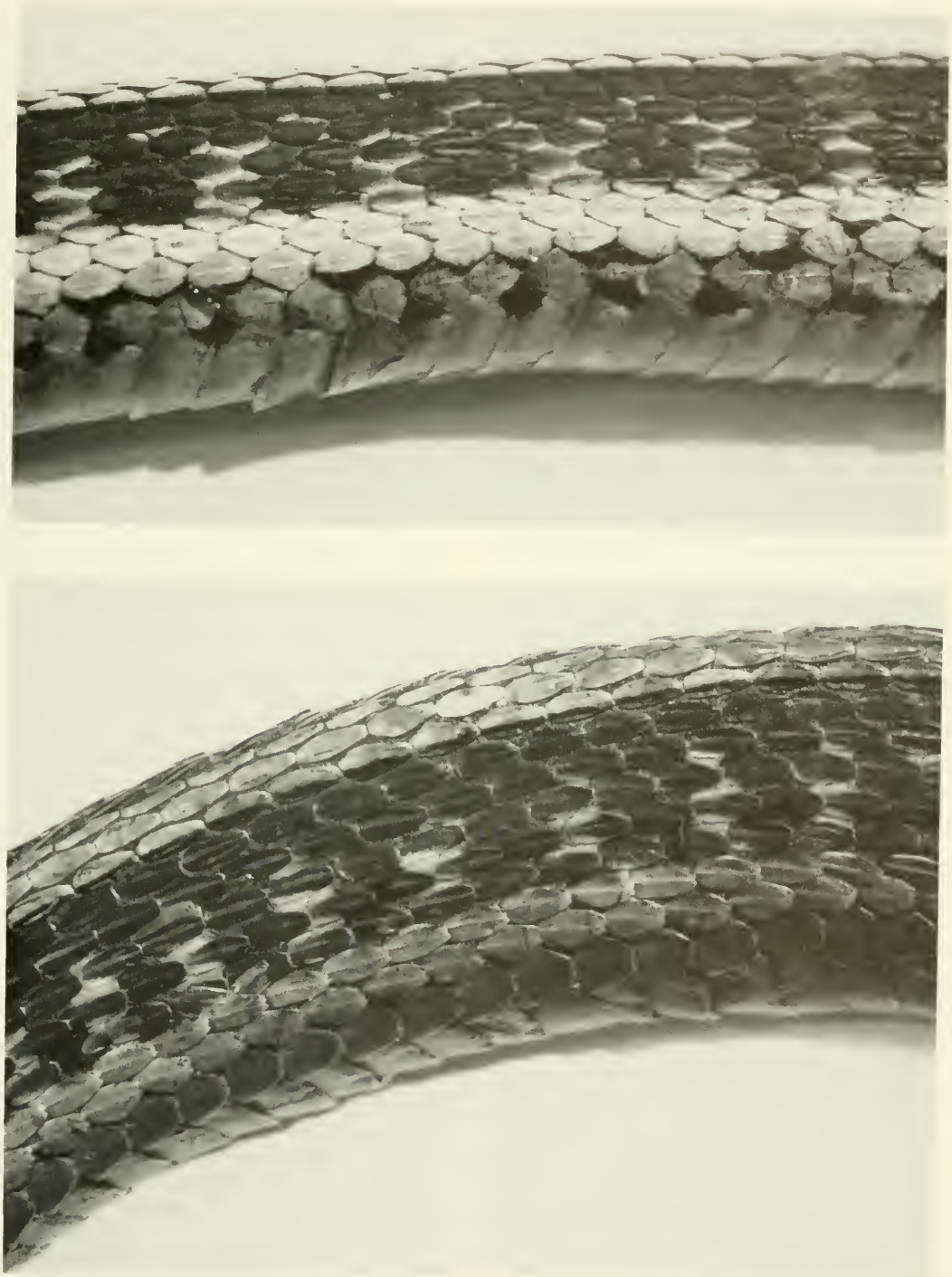

Fig. 3. Lateral and dorsolateral views of *Thamnophis sirtalis parietalis:* A, UNM 15583 2 miles S junction Hwy. 85/45, Bernalillo County, New Mexico; B, UNM 14697, 1.5 miles S junction NM Hwy. 54 and U.S. Hwy. 85, Valencia County, New Mexico.

this area into desert, *sirtalis* moved into the major drainage basins. In Chihuahua, two basins, Río Santa María and Río Casas Grandes, were inhabited and in southern New Mexico the Rio Grande to the north. It appears that the southern population of *sirtalis* was divided into north (Río Casas Grandes and Río Santa María) and south (Yepómera area) populations at an early date, and later the northern segment subdivided into the two river basins in northern Chihuahua.

The population in south central New Mexico (*dorsalis*) and the population in west central Chihuahua (*lowei*) show several relating characters. The color pattern is easily derived from either (*dorsalis* from *lowei* or *lowei* from *dorsalis*). Available data suggest that the ancestral population present during or immediately after the pluvial period was spotted, not with dark lateral columns as in the northern population of New Mexico or as is seen in some *parietalis*. Also, the dorsal rows are reduced to 20 rows more often at 9–11 ventrals than in the northern New Mexico population or *parietalis*.

The northern population seems closely related to *parietalis*. The similar color pattern may have come from *parietalis* entering the Rio Grande basin at a later period when conditions in northeastern New Mexico permitted a movement from eastern valleys (Arkansas or Canadian) into the headwaters of the Rio Grande. Such an invasion by *parietalis* would explain the color pattern differences and provide at least a tentative explanation for the divergence in pattern seen in the Rio Grande basin of central New Mexico.

If we conclude that the southern segment of the New Mexico population of *sirtalis* is a recognizable subspecies and retain it as the subspecies *dorsalis* based on what has been described by previous authors as a color pattern variable in the species, then it becomes necessary, based on available data, to deal with it as a subspecies and provide a diagnosis distinguishing it from *lowei*, to the south, and *parietalis*, to the north.

Thamnophis sirtalis dorsalis (Baird & Girard)
Rio Grande Garter Snake

DIAGNOSIS.—A subspecies with 19-19-17 or occasionally 21-19-17 scale rows, supralabials 7 or occasionally 8, ventrals 156–178, males 159–178 (166.0), females 156–166 (160.2), subcaudals 65–87, males 78–87 (83.5), females 65–78 (72.6), dorsal and lateral light stripes distinct on two scale rows, dorsal stripe edged laterally by a narrow dark area, irregular on its lateral edge, varying from 1 to 1 1/2 scales wide and with a wide area of pink or olive to light brown on both skin and scales separating the dark dorsal area from the small, lateral, dark spots (Fig. 2). Lateral spots small, involving 1–5 scales but not usually involving an entire scale, and usually in contact with the lateral stripe; ventrals and first row of scales with small, irregular, dark spots but not uniformly spaced.

DISTRIBUTION.—Sierra County: 18 specimens from Elephant Butte Reservoir are badly darkened by preservative. By submerging in clear fluid most show small lateral spots and a narrow dark edging lateral to the dorsal stripe. In a few the color pattern cannot be clearly seen. At least 13 can be determined to have the *dorsalis* color pattern (KU 5479–5497). Socorro County: 2 miles S Belen (UNM 17800); 7 1/2 miles S 1/2 mile W San Antonio (UNM 15965); Basque del Apache headquarters (UNM 32523, 35795). Valencia County: (UNM 383 no data); Isleta Marsh (UNM 14818–9, 14873); 3 miles S Isleta Hwy. 47 (UNM 15464–5); 2.4 miles S intersection Coors and U.S. 85 (UNM 19747); 8 miles N Belen Hwy. 6 (UNM 33922); (UNM 39597 no data). Bernalillo County: 3.5 miles S junction NM Hwy. 45 and US 85 (UNM 15212).

The specimens from southeast Valencia County have a color pattern characteristic of *T. s. dorsalis* as described by Fitch (1980). The lateral spots are small, involving 5 or fewer scales and spots not contacting the narrow dark margin lateral to the dorsal stripe. The body spots range from 75 to 88 and average 80 spots. This is a noticeable increase when compared to either *lowei* or *parietalis*.

The following specimens from Valencia and Bernalillo counties do not have the *dorsalis* color pattern as seen in Figure 3. I consider them to be either *dorsalis-parietalis* intergrades or a southern extension of *parietalis;* Valencia County: 2 miles N Los Lunas on Hwy. 85 (UNM 4631); marsh 4 miles N and 1/2 mile E Los Lunas (UNM 5224-6); 1 1/2 miles SE Belen (UNM 7606); 4 miles N Los Lunas (UNM 10897–9); 2 miles N Los Lunas (UNM 10962); 3 miles N Isleta marshes (UNM

15130); Los Lunas (UNM 11410); 14.7 miles from UNM S Hwy. 10 at Isleta Pueblo (UNM 11552); 1.5 miles S junction NM 45 and US 85 (UNM 14696–7); 4 miles N Peralta on Hwy. 47 (UNM 19777); 20 miles S Alb swamps along Hwy. 85 (UNM 19782); 10 miles N junction Hwys. 6 and 57 (UNM 31653–4); 3 miles N Lunas Hwy. 85 (UNM 32709); Hwy. 47 14 miles N junction 6 and 47 (UNM 37813). Bernalillo County: (UNM 375 no data); Albuquerque, Perea Rd. (UNM 384); 1 km N central on US 66 (UNM 5440); Albuquerque, W Rio Grande near Rt. 66 (UNM 8414); 2 miles S junction Hwys. 45 and 85 (UNM 15583); 3 miles SW Isleta along Hwy. 85 (UNM 5429–32); Pyle Beach, Albuquerque (UNM 10238–9); Isleta Indian Reservation (UNM 11063–4); 10 miles S Hwy. 66 on Hwy. 45 (UNM 11101); S Hwy. 55 bridge (UNM 11317–20); 9 miles N Albuquerque (UNM 12137); Beach Road NW Albuquerque (UNM 12314); Isleta Reservation (UNM 12209); Isleta Pueblo (UNM 12981); 3/4 mile S Coors intersection Hwy. 95 (UNM 12986); Hwy. E Coerales Bridge (UNM 14820); and 2 miles S junction Hwys. 85 and 45 (UNM 15583). Rio Arriba County: Espanola (UNM 31908); Riverside Lake, Espanola (UNM 36458–9).

The New Mexico populations do not vary significantly in scale patterns and are summarized as a unit in Table 1. Although the series is small for the subspecies *sirtalis* and *parietalis*, an east to west cline in all scale patterns is evident. In *dorsalis* and *lowei* the cline is north to south. These clines may be best expressed by percentages in the reduction of the dorsal scale rows to 19. The *sirtalis* from eastern U.S. all reduce by or before the 8th ventral; in 22 specimens from Kansas (*parietalis*), 1 reduces at the 10th ventral, the rest (95%) before the 10th; in 72 specimens of *dorsalis*, 10 reduce at the 10th ventral (approx. 14%), while all others at the 9th or before; and in *lowei* 93% reduce between the 10th to 19th ventral, with one reducing at the 9th. A relationship between *parietalis*, *dorsalis*, and *lowei* is not only indicated by the scale patterns but also by trends in color pattern, particularly in the similar pattern between the northern New Mexico populations and *parietalis* as well as *dorsalis* in southern New Mexico and *lowei* in Chihuahua.

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LITERATURE CITED

BAIRD, S. F. 1859. Reptiles of the boundary. *In:* Report of the United States and Mexican Boundary Survey. U.S. 34th Congress 1st session, Exec. Doc. (108), 2(2): 1–35.

BAIRD, S. F., AND C. GIRARD. 1853. Catalogue of North American reptiles in the Museum of the Smithsonian Institution. Part I. Serpents. Smithsonian Institute, Washington, D.C. 172 pp.

FITCH, H. S. 1980. *Thamnophis sirtalis* (Linnaeus). Pages 1–4 *in* Catalogue of American amphibians and reptiles, No. 270.

FITCH, H. S., AND T. P. MASLIN. 1961. Occurrence of the garter snake, *Thamnophis sirtalis*, in the Great Plains and Rocky Mountains. Univ. Kansas Publ. Mus. Nat. Hist. 13(5): 493–564.

FITCH, H. S., AND W. W. MILSTEAD. 1961. An older name for *Thamnophis cyrtopsis* (Kennicott). Copeia 1961: 112.

GOLDMAN, E. A. 1951. Biological investigations in Mexico. Smithsonian Misc. Colls., Washington, D.C. 115. xii + 476 pp.

KENNICOTT, R. 1860. Descriptions of N. Amer. serpents in the Mus. of the Smithsonian Inst., Washington, D.C. Proc. Acad. Nat. Sci. Philadelphia 12: 328–338.

SAY, T. 1823. *In:* Edwin James, account of an expedition from Pittsburgh to the Rocky Mountains. (Long's Expedition to Rocky Mountains.) Longman, Hurst, Rees, Orme and Brown, London. 344 pp. (in 3 volumes).

SMITH, H. M. 1942. The synonymy of the garter snakes (*Thamnophis*), with notes on Mexican and Central American species. Zoologica 27: 97–123.

SMITH, H. M., AND B. C. BROWN 1946. The identity of certain specific names in *Thamnophis*. *Herpetologica* 3: 73.

STEBBINS, R. C. 1985. Field guide to western reptiles and amphibians. Houghton Mifflin Co., Boston. xiv + 336 pp.

TANNER, W. W. 1985 [1986]. Snakes of western Chihuahua. Great Basin Nat. 45(4): 615–676.

VAN DEVENDER, T. R., AND C. H. LOWE, JR. 1977. Amphibians and reptiles of Yepómera, Chihuahua, Mexico. J. Herpetology 11(1): 41–50.

WEBB, R. G. 1966. Resurrected names for Mexican populations of black-necked garter snakes, *Thamnophis cyrtopsis* (Kennicott). Tulane Studies in Zoology 13: 55–70.

ENGELMANN SPRUCE CONE LOSSES CAUSED BY INSECTS IN NORTHERN UTAH IN A YEAR OF LOW CONE PRODUCTION

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ABSTRACT.—The impacts and timing of insect infestation were determined in developing Engelmann spruce cones throughout the summer of a year of low cone production in northern Utah. The major insects found were the western spruce budworm, *Choristoneura occidentalis* Freeman (Lepidoptera: Tortricidae); fir coneworm, *Dioryctria abietivorella* Grote (Lepidoptera: Pyralidae); and the spruce seed moth, *Laseyresia youngana* Kearfott (Lepidoptera: Olethreutidae). Insects reduced the survival of cones to 11.48 cones out of 100. The high percentage of seeds and cones lost to insect predation supported previous studies of a similar nature.

Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) is a widely distributed species of the western United States and Canada. It is a major component of Rocky Mountain high-elevation forests (Fowells 1965). Engelmann spruce seed and cones are subject to various insect predators, but much of the previous research on the seed and cone insects of spruce has been done on other spruce species such as white spruce (*Picea glauca* (Moench) Voss) in Canada. Additional research information is needed on the impacts of seed and cone insects on Engelmann spruce in Intermountain subalpine spruce/fir forests.

Insects are often major biotic agents, reducing seed survival in developing cones of conifers and, at times, destroying an entire seed crop. The amount of damage an insect species causes to a seed crop depends on the relative abundance of the insect population, the timing of the damage with respect to cone phenology, and the size of the cone crop. It has been suggested that cone crop periodicity is an adaptive mechanism reducing the impact of cone predators (Mattson 1971, Miller et al. 1984). This study examined the impact and timing of several seed and cone insects observed on Engelmann spruce in northern Utah during a year of low cone production.

MATERIALS AND METHODS

This study was conducted on the Utah State University Experimental Forest located on the Wasatch-Cache National Forest, approximately 15 km south of the Utah-Idaho border in Rich and Cache counties. The elevation ranged from 2,500 m to 2,700 m. The general moisture regime is semiarid, with most precipitation occurring as snow.

The predominant tree species are Engelmann spruce and subalpine fir (*Abies lasiocarpa* var. *lasiocarpa* [Hook.] Nutt.), which are late successional, climax species, and lodgepole pine (*Pinus contorta* var. *latifolia* Dougl. ex Loud.) and quaking aspen (*Populus tremuloides* Michx.), which form early successional stands. Open meadows are intermingled among the forested areas. Detailed ecological descriptions of the area are presented in Schimpf et al. (1980).

Sample trees were selected and tagged for periodic cone collections conducted throughout the growing season. Ten Engelmann spruce trees were chosen throughout the USU Experimental Forest on the basis of potential cone crop, climbing safety, and ease of access.

Ten cones per tree were collected every four weeks, beginning in late June and continuing until late September in 1986. In 1985 only one collection was made in late September. Each tree was climbed and branches were clipped until a sufficient sample size of cones was obtained. Two cones were randomly collected from each of five branches uniformly distributed in the upper third of the crown. Branches with cones, as well as any loose cones, were bagged, marked, and refrigerated until the cones were analyzed. The last

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TABLE 1. Percentage cone losses to frost and insects in 1985.

Mortality agent	Cones lost to agent %
Frost	72.18
Spruce seed moth	15.23
Western spruce budworm	3.97
Unidentified insects	6.40
Aborted	0.22
Unknown	1.99
Total	99.99

cone collection was obtained from fewer trees because some sample trees no longer had an adequate number of cones.

Half of the cones from each sample tree were dissected while the other half were placed into insect-rearing containers at room temperature. The percent of external cone damage and cone size were recorded; then the cones were cut longitudinally with a cone cutter. An ocular estimate of percentage of internal damage was made and recorded for each cone. Categories for coding percentage of damage were zero (0%), light (1–25%), low (26–50%), moderate (51–75%), and heavy (76–100%). The nature of the damage observed and the number and characteristics of any insects were recorded.

Rearing containers were constructed using three-gallon ice cream cartons with glass vials attached to the lids. Cones for each tree were placed in rearing containers, checked daily for emerging insects over the next three months, and then placed in a freezer at 0 C. The cold treatment simulated winter conditions and was designed to break diapause of any overwintering insects. After three months cones were removed from the freezer and returned to room temperature. Rearing containers were again checked for emerging insects. Adult insects obtained from rearing containers were frozen until proper identification could be made. Adult insects were keyed to species in the laboratory.

RESULTS AND DISCUSSION

In 1985 frost damage was responsible for 72% of the cone mortality (Table 1). Over half of the cones escaping the frost were infested with the spruce seed moth, *Laspeyresia youngana* (Kearfott) (Lepidoptera: Olethreutidae). Other mortality was attributed to

TABLE 2. Percentage of Engelmann spruce cones damaged by insects in 1986.

Collection date	Mortality factors	Percent dying
24 June	WSB	28.18
	Fir coneworm	12.08
	Cone abortions	2.68
	Unidentified insects	3.35
22 July	WSB	16.66
	Fir coneworm	19.56
	Spruce seed moth	15.21
	Cone axis midge	1.44
	Cone abortions	1.44
	Unidentified insects	5.07
21 August	WSB	14.85
	Fir coneworm	8.91
	Spruce seed moth	39.60
	Cone axis midge	3.96
	Unidentified insects	4.95
23 September	WSB	9.09
	Fir coneworm	6.81
	Spruce seed moth	54.54
	Cone axis midge	6.81
	Cone abortions	2.27
	Unidentified insects	9.09

external feeding by the western spruce budworm, *Choristoneura occidentalis* Freeman (Lepidoptera: Tortricidae), unidentified insects, and cone abortion.

In 1986 a greater diversity of mortality agents in the Engelmann spruce cones was observed (Table 2). At the time of the first collection, external feeding by western spruce budworm (WSB) was the major factor affecting cones. Other insects causing damage at other collection times included the fir coneworm, *Dioryctria abietivorella* (Grote) (Lepidoptera: Pyralidae), the spruce seed moth, and a spruce cone axis midge, *Dasineura rachiphaga* Tripp (Diptera: Cecidomyiidae) (Table 2).

WSB fed externally on the cones, impacting cone development early in the season. Rarely was WSB found to impact the developing seeds unless external feeding was extensive. In other studies extensive WSB outbreaks were found to impact foliage and many of the female buds and developing conelets (Dewey 1970, Frank and Jenkins 1987).

The spruce seed moth and fir coneworm are obligate seed and cone insects that feed internally on cones. The spruce seed moth was first described by Tripp (1954) and was previously considered to be a seedworm since larvae feed

TABLE 3. Ocular estimates of internal and external damage caused by insects to Engelmann spruce cones in 1986.

Collection	Zero (0%)	Light (1–25%)	Low (26–50%)	Moderate (51–75%)	Heavy (76–100%)
1	51.0[1]	36.2	10.7	1.3	0.6
	81.9	11.4	2.0	0.6	4.0
2	54.3	33.3	7.2	4.3	0.7
	26.1	63.7	8.7	1.4	0.0
3	64.3	21.7	12.8	0.9	0.0
	6.9	36.6	17.8	15.8	22.8
4	63.6	31.8	4.5	0.0	0.0
	4.5	15.9	36.4	34.1	9.1

[1]Top row values in each collection indicate external damage, while lower row values indicate internal damage.

almost entirely on seeds. The moth's life cycle is closely synchronized to the host phenology (Hedlin et al. 1980). Usually only one or two larvae inhabit a cone, but in this study more larvae per cone were occasionally found. When several larvae occupy the cone axis, they will separate themselves by packing frass between individuals (Hedlin 1974). Tripp and Hedlin (1956) noted that the number of larvae per cone depends on the number of cones available for attack, with more larvae persisting in a cone when fewer cones are present.

Early descriptions of fir coneworm are variable because *D. abietivorella* was often recorded as *D. abietella* (Denis & Schiffermuller), a similar coneworm species (Hedlin et al. 1980). This fir coneworm causes greater damage as its larvae tunnel indiscriminately through the cone scales and seeds. This coneworm species has been noted as a destructive insect in spruce, fir, and Douglas-fir (*Pseudotsuga*) cones (Keen 1958, Hedlin 1974, Hedlin et al. 1980).

Evidence of the spruce cone axis midge was apparent in the later cone collections. Positive identification of this species was made from adults obtained from rearing containers after the cold treatment. In a heavily infested cone, 15 to 20 larvae may converge in the cone axis, but, overall, little damage to the seeds occurs (Hedlin 1974, Hedlin et al. 1980). This study found similar results with less than 15% of the examined cones impacted by the spruce cone axis midge.

Variation in life cycles and feeding habits of a species is evident in the percentage of seed lost to the different species at each collection (Table 3). In the first collection (late June), only WSB and fir coneworm were evident. The early larval stages of fir coneworm feed on seeds at this time, while the spruce seed moth is just beginning to hatch from eggs. The spruce seed moth continues to destroy large percentages of seeds, feeding through early September until it overwinters. The fir coneworm, although found less frequently in the later collections, remains active throughout the growing season. The decline in the frequency of fir coneworm observed may be because some larvae exit cones to pupate on the ground in the late summer. The spruce cone axis midge, found in the later collections, was evident at that time because it moves into the axis to overwinter in late July. However, it impacts the cones earlier in the season as larvae feed on the ovuliferous scales.

To illustrate the impact of the species observed and relate them to cone phenology, we constructed a simple life table (Table 4). Starting with 100 cones, the life table shows the timing and relative impact of the insect species observed in this study. The life table illustrates that given 100 cones, only 11.48 escaped insect predation under the conditions observed in 1986.

Because only one collection was made in 1985, it is difficult to compare results of the two years. A frost on 23 June killed 72% of the Engelmann spruce cone crop in 1985. Of the cones surviving the frost 15% were infested with the spruce seed moth, 4% were damaged by WSB, and 6% were damaged by other insects. Nearly 100% of the cones collected were damaged by frost or insects (Table 1). These findings support other studies which report that variation in cone crop size greatly influences insect populations (Mattson 1971). Other studies have compared the percentage of cones lost to insects in years of different cone production levels (Hedlin 1964, Mattson 1971, Jenkins 1984). Typically, more cones are damaged in years of low cone production,

TABLE 4. Partial life table of mortality factors affecting cones of Engelmann spruce in 1986.

x Developmental stage	L_x x cones surviving	D_xF Mortality factors	D_x Number dying within x	100 q_x D_x as a percent of L_x	S_x Survival rate within x
Conelet I	100	WSB	19.44	19.44	
		Fir coneworm	15.44	15.44	
		Cone abortions	1.62	1.62	
		Other insects	3.35	3.35	
			39.85	39.85	.6015
Conelet II	60.15	Fir coneworm	11.76	19.56	
		Spruce seed moth	9.15	15.22	
		Cone axis midge	1.27	2.12	
		Other insects	3.05	5.07	
			25.23	41.97	.5805
Conelet III	34.92	Fir coneworm	3.11	8.91	
		Spruce seed moth	15.65	44.83	
		Other insects	1.73	4.95	
			20.49	58.69	.4132
Conelet IV	14.43	Fir coneworm	0.98	6.82	
		Other insects	1.97	13.64	
			2.95	20.46	.7955
Normal cones	11.48				

while in years of high cone production insects are satiated and excess cones escape predation. The periodic nature of cone crops has been suggested as an adaptive strategy evolved by trees to avoid seed and cone predation (Janzen 1969).

Other studies have reported such interactions between cone crop sizes and insect populations (Mattson 1971, Jenkins 1984, Miller et al. 1984). The fact that studies found more seeds escaping predation in years of high seed production has been offered as strong support for the adaptive mechanism of periodic mast crops in trees to avoid seed and cone predation.

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LITERATURE CITED

DEWEY, J. E. 1970. Damage to Douglas-fir cones by *Choristoneura occidentalis*. J. Econ. Entomol. 63: 1804–1806.

FOWELLS, H. A. 1965. Silvics of forest trees of the United States. U.S. Dept. Agric. Handb. 271. 762 pp.

FRANK, C. J., AND M. J. JENKINS. 1987. Impact of the western spruce budworm (Lepidoptera: Tortricidae) on buds, developing cones, and seeds of Douglas-fir in west central Idaho. Envir. Entomol. 16(1): 304–308.

HEDLIN, A. F. 1964. A six-year plot study on Douglas-fir cone insect population fluctuations. For. Sci. 10(1): 124–128.

———. 1974. Cone and seed insects in British Columbia. Envir. Can. For. Serv., BC-X-90. 63 pp.

HEDLIN, A. F., H. O. YATES, D. C. TOVAR, B. H. EBEL, T. W. KOERBER, AND E. P. MERKEL. 1980. Cone and seed insects of North American conifers. 122 pp.

JANZEN, D. H. 1969. Seed eaters versus seed size, number, toxicity and disperal. Evolution 23: 1–27.

JENKINS, M. J. 1984. Effect of western white pine cone production variability on mountain cone beetle population levels. Great Basin Nat. 44: 310–312.

KEEN, F. P. 1958. Cone and seed insects of western forest insects. U.S. Dept. Agric. Tech. Bull. 1169. 168 pp.

MATTSON, W. E. 1971. Relationship between cone crop size and cone damage by insects in red pine seed production areas. Canadian Entomol. 130: 617–621.

MILLER, G. E., A. F. HEDLIN, AND D. S. SMITH. 1984. Damage by two Douglas-fir cone and seed insects: correlation with cone crop size. J. Entomol. Soc. British Columbia. 81: 46–50.

SCHIMPF, D. J., J. A. HENDERSON, AND J. A. MACMAHON. 1980. Some aspects of succession in the spruce-fir zone of northern Utah. Great Basin Nat. 40(1): 1–26.

TRIPP, H. A. 1954. Description and habits of the spruce seedworm, *Laspeyresia youngana* (Kft.) (Lepidoptera: Olethreutidae). Canadian Entomol. 86: 385–402.

TRIPP, H. A., AND A. F. HEDLIN. 1956. An ecological study and damage appraisal of white spruce cone insects. For. Chron. 32: 400–410.

ELEVATIONAL CHANGES IN WOODY VEGETATION ALONG THREE STREAMS IN WASHINGTON COUNTY, UTAH

G. Merrill Webb[1] and Jack D. Brotherson[2]

ABSTRACT.—Patterns of change in the woody vegetation (trees and shrubs) of the riparian communities of three streams draining the slopes of the Pine Valley Mountains in Washington County, Utah, were examined. Thirty-nine study sites were established adjacent to the streams along an elevational gradient where vegetation, plant population, and species data were taken. Vegetation and species patterns varied with respect to elevation and geographical location. Vegetation of the high- and low-elevation areas was distinctly different, while that of the mid-elevations was transitional to both. Geographical patterns showed a north-south transition in vegetation between the Mojave and Great Basin deserts. Size-class distribution curves for 11 tree species showed varying degrees of survival with respect to age and location. Root sprouting was highly important in the reproductive effort of six of the trees. Species distribution patterns followed transriparian and intrariparian gradients within the riparian community.

Riparian areas are terrestrial zones associated with surface water that reveal, through the vegetative complex, the influence of that water (Platts 1978). Riparian communities are critical-use areas for a large segment of the human population and yet are often subjected to abuse by such users. The arid regions of southwestern Utah are presently experiencing rapid growth in human population. Because of the rising numbers of people and increased demands for water, the riparian communities of these desert regions will likely be heavily impacted.

Woody vegetation is an important environmental feature to small streams in desert areas because of its large size and overhanging canopies. Fisheries and wildlife biologists have suggested that riparian zones are critical habitats in maintaining populations of fish, birds, and small and big game animals (Ames 1977, Hubbard 1977). The overhanging canopies provide shade during the hot summer months, which helps to stabilize water temperatures, thereby benefiting all aquatic organisms (Behenke 1979).

These areas are also important sources of forage and water for domestic livestock (Phillips 1965, Cook 1966) and play an integral role in water quantity and quality (Horton and Campbell 1974). The early autumn leaf fall is a source of mineral nutrients and carbon for shredder organisms of the aquatic food chain (Russell-Hunter 1970).

The streams in southwestern Utah have historically provided water for irrigation and culinary or domestic use. Recreational uses, including fishing and boating, as well as wildlife uses, have been secondary in importance. But as the human population increases, demands for more water for culinary and recreational purposes will also increase, and competition will be greater for this important natural resource.

To establish baseline data on the conditions existent in the riparian habitat, we studied the woody plant species (trees and shrubs) associated with three streams in southwestern Utah with respect to species along an elevation gradient. Our purpose was to examine trees and shrubs associated with three riparian communities and to determine patterns of distribution with respect to elevation. The population dynamics of trees and shrubs along the elevational gradient were also investigated.

STUDY SITE

Our three study streams have their origin in the Pine Valley Mountain area, Washington County, Utah. The Pine Valley Mountains (3,200 m high) are largely composed of deroofed monzonite porphyry laccolith, which has an exposed extent of 181 km^2 and is Tertiary in age (Cook 1960). The soils along the streams are classified as Riverwash (USDA 1977) and consist of stratified, dominantly

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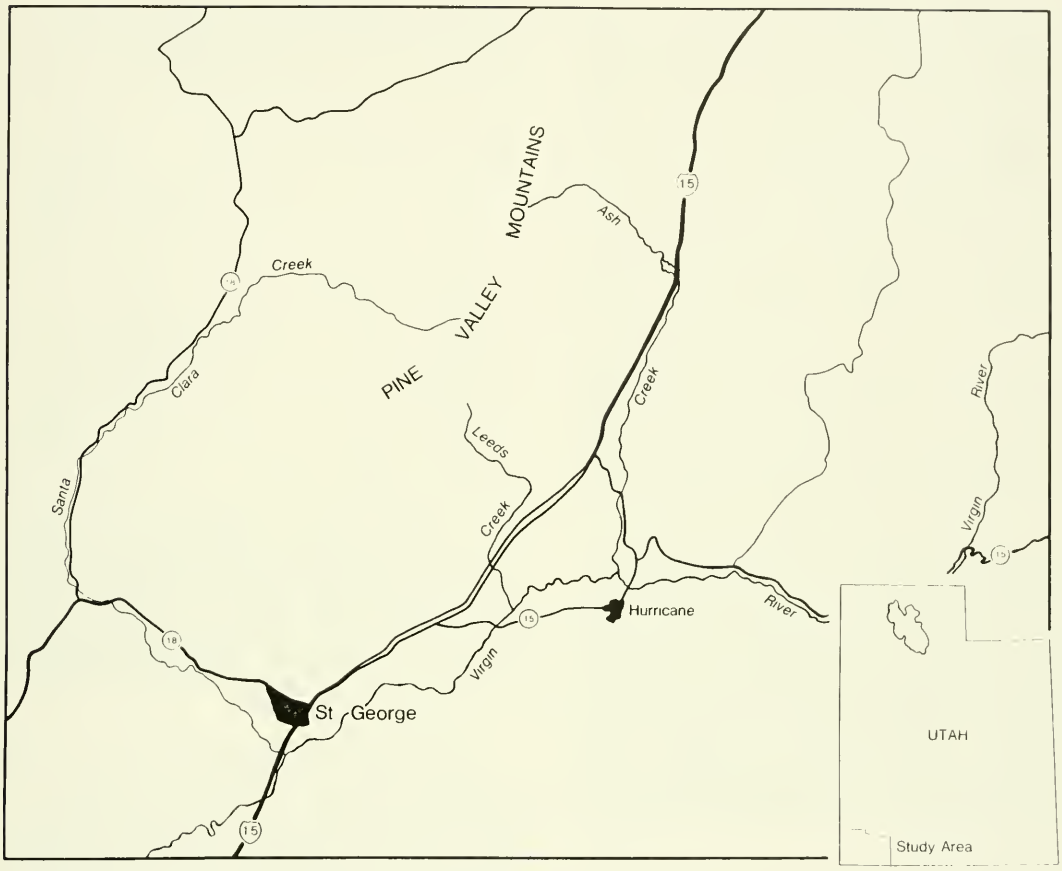


Fig. 1. Map of study location in Washington County, Utah.

coarse-textured, and gravelly, cobbly, or stony material in the washes and narrow drainageways. The material varies considerably over short distances and is moved from place to place during periods of high runoff. On the flood plains the soils are classified as Fluvaquents and Torrifluvents (USDA 1977). These are moderately well-drained to poorly drained, highly stratified soils ranging in texture from fine sands to silt loams. Layers of gravel and cobbles are common.

Ash Creek has its origin on the northeast side of the mountain at 2,418 m elevation near the small hamlet of New Harmony. The stream flows east and then south for 45 km, joining the Virgin River near LaVerkin at an elevation of 918 m, resulting in an elevational drop of 1,500 m. There is a single impoundment on this stream formed by U.S. Interstate Highway 15 about 8 km north of Pintura.

Leeds Creek originates on the south side of the mountain at an elevation of approximately 2,015 m and flows south 20 km past the town of Leeds to its confluence with the Virgin River at 837 m elevation. This is a 1178-m drop in elevation. A single impoundment on this stream, Quail Creek Dam, was constructed in 1984 and has now filled with water.

Santa Clara Creek originates on the north side of the Pine Valley Mountains at an elevation of 2,635 m and flows west past Veyo and then south past the towns of Gunlock and Santa Clara. It joins the Virgin River south of St. George at an elevation of 775 m. Total length of this stream is 68 km. Three impoundments as well as diversion dams alter and influence the flow of this stream.

Ash Creek and Santa Clara Creek flow through sections of steep lava rock canyons where the canopy extends from rim to rim in some segments. When the canyon (gorge) opens out, vegetation becomes more sparse.

Due to the influence of humans and the vagaries of weather, stream flows vary on all three streams. Some stream sections are dewatered below diversion dams, while at other times of the year the channels are scoured by raging torrents of flash floods. Summer lows for Ash Creek are 6.5 cfs and for Leeds Creek 1.5 cfs, while portions of Santa Clara Creek are entirely dewatered for irrigation. On the average, 78% of the stream flow is diverted for irrigation on all three streams; thus, on some stretches a sandy or rock-strewn stream bottom is all that exists (USDA 1977). Riparian vegetation, as a consequence, is subjected to extremes of flooding and drought conditions. All three streams are accessible by car and two have U.S. Forest Service campgrounds located near their headwaters. Portions of all three streams flow through private property with resultant grazing and human impacts.

Ash Creek flows through plant communities dominated by cottonwood, ash, and willow. Leeds Creek originates in a ponderosa pine–scrub oak habitat, flows through a zone of thick mountain brush and river birch, and then through a lower zone of willow and cottonwood. Santa Clara Creek has three distinct zones beginning with mountain shrub, then ash, and finally cottonwood and willow in its lower reaches.

Elevation within the study area ranges from 2,635 m down to 775 m. This wide range in elevation has a marked influence on the climate of the streams. For example, annual precipitation rates vary from a maximum of 500 mm a year in the higher elevations to 150 mm at the lowest elevations. Most precipitation occurs during winter and early spring when storms from the Pacific Ocean move across the intermountain area. A secondary precipitation maximum occurs in summer during July and August when occasional thunderstorms develop because of the moist air moving northward across the region from the Gulf of Mexico (USDA 1977).

METHODS

Thirty-nine study sites were established from August through December 1983 in the riparian zones of Ash Creek, Santa Clara Creek, and Leeds Creek. The number of study sites on each stream varied depending on the length of the stream. Sites were placed along an elevational gradient in 93-m increments from the mouth of the stream to its headwaters. A 31-m belt transect was established at each site across the flood plain as a study zone. Within this zone the following data were taken. Elevation was determined using USGS 7.5- and 15-minute topographic maps with 40- and 80-foot intervals, respectively. Trees were identified, and all individuals within the transect boundaries were counted and measured for diameter at breast height (DBH). Size-class distributions for each species were determined from the DBH data. Density of trees was determined by randomly selecting five individual trees and taking measurements to the nearest neighbor (Phillips 1959). Shrubs were identified and their frequencies determined by placing two 4.5 × 9-m quadrats along each side of the stream. The quadrats were placed parallel to the stream within the 100-m transect. Each 4.5 × 9-m quadrat was then subdivided into three 3 × 4.5-m units. Species were recorded as being present or absent within each of the 12 subunits.

Cluster analysis (Sneath and Sokal 1973) was applied to similarity index values (Ruzicka 1958) that were generated between all possible pair combinations of the vegetative stands. The analyses were based on unweighted pair-group clustering (UPGMA). The UPGMA method computes the average similarity of each unit to the cluster using arithmetic averages because it introduces less distortion than other methods (Kaesler and Cairns 1972). The vegetative stands were also ordinated and grouped into three-dimensional space following Orloci (1966).

Niche breadth and overlap values were computed for individual plant species (Colwell and Futuyma 1971). Species were then clustered from niche overlap values following Sneath and Sokal (1973). Niche breadth and overlap values were based on relative density figures for trees and relative frequency data for shrubs. Interspecific association patterns between plant species were computed using Cole's (1949) Index. Diversity indices were computed following Shannon and Weaver (1949) and MacArthur (1972). Plant nomenclature follows Welsh et al. (1987). Voucher specimens for plant species included in the study are deposited in the Brigham Young

TABLE 1. Prevalent species list for woody plants growing in the riparian zones of Ash Creek, Leeds Creek, and Santa Clara Creek in Washington County, Utah, along with relative dominance values for the trees and relative frequency values for the shrubs.

Species	P & F Index
TREES	
Populus fremontii	16.07
Fraxinus velutina	5.35
Salix laevigata	3.64
SHRUBS	
Baccharis glutinosa	4.06
Artemisia tridentata	3.35
Chrysothamnus nauseosus	3.05
Rhus trilobata	2.54
Salix exigua	2.37
Tamarix ramosissima	1.89
Rosa woodsii	1.68

University Herbarium, Provo, Utah. Prevalent species (those most frequently encountered during sampling) of the various plant communities are reported as equal to the average number of species per study plot (Warner and Harper 1972).

RESULTS AND DISCUSSION

Fifty-seven species of trees and shrubs representing 26 families were encountered in the study sites located within the riparian communities of Ash Creek, Leeds Creek, and Santa Clara Creek. Fifteen of these 57 were trees and 42 were shrubs. Two species, Russian olive (*Elaeagnus angustifolia*) and saltcedar (*Tamarix ramosissima*), are introduced. Saltcedar was abundant enough to have altered the streamside community in some areas. Three of the trees and seven of the shrubs turned out to be prevalent species (Warner and Harper 1972) (Table 1). Ten tree species were found on Ash Creek and 12 each on Leeds and Santa Clara creeks (Table 2). Tree species increased in numbers as elevation increased on Santa Clara Creek, while on Ash and Leeds creeks the number of species decreased as elevation increased. Shrubs had highest numbers at mid-elevation.

All species were not present on each stream, but when a single species occurred on more than one stream its relative importance varied from stream to stream (Table 2). For example, *Acer negundo, Celtis reticulata, Quercus gambelii, Artemisia ludoviciana, A. tridentata, Chrysothamnus nauseosus,* and *Guttierrezia sarothrae* showed high importance on Ash Creek and then decreased in importance south and west to Leeds and Santa Clara creeks. Conversely, *Salix laevigata, S. nigra,* and *Baccharis glutinosa* showed high importance on Santa Clara Creek and decreased in importance in a northeast direction to Leeds and Ash creeks. Generally, the first group (those most important on Ash Creek) tends to have Great Basin desert affinities, while the second group (those most important on Santa Clara Creek) shows Mojave Desert connections. The patterns suggest the existence of a floristic transition zone (Meyer 1978) within the geographical area through which these three streams flow. The region is environmentally diverse and is located so as to be transitional between the Great Basin and Mojave deserts (Welsh et al. 1987).

Pinus ponderosa, Populus angustifolia, Amelanchier alnifolia, Mahonia repens, and *Rosa woodsii* showed patterns similar to the Santa Clara Creek group, yet are clearly Great Basin in distribution. The similarity in the distribution patterns of the two groups is due to the occurrence of these latter species at high elevations in the Pine Valley Mountains near the headwaters of Leeds and Santa Clara creeks.

Elevations for the study sites along the three streams ranged from a low near St. George where Santa Clara Creek joins the Virgin River to a high in Pine Valley on the same stream, a difference of 1,313 m. The elevational distributions of the individual plant species growing along the three streams are shown in Figures 2 and 3. *Populus fremontii, Prosopis pubescens, Salix laevigata, S. nigra, S. exigua, Baccharis glutinosa, Tamarix ramosissima, Chrysothamnus nauseosus,* and *Pluchea sericea* were restricted to the lower reaches of all three streams. These species are often found in the riparian vegetation of perennial streams associated with the Mojave Desert. A second group, composed of *Abies concolor, Pinus ponderosa, Populus angustifolia, Symphoricarpos oreophilis, Salix bebbiana, Physocarpus monogynus,* and *Salix lutea,* was generally restricted to areas of high elevation near stream headwaters. Most other species were distributed at mid-elevational levels and can be considered transitional between the other two groups.

TABLE 2. Woody plant species found growing in the riparian zones of Ash Creek, Leeds Creek, and Santa Clara Creek in Washington County, Utah. The figures represent relative dominance values for the trees and relative frequency values for the shrubs.

Species	Ash Creek	Leeds Creek	Santa Clara Creek
		TREES	
Abies concolor	—	1.4	0.1
Acer negundo	6.7	7.1	0.3
Celtis reticulata	3.2	—	—
Elaeagnus angustifolia	0.1	—	—
Fraxinus velutina	11.1	10.1	10.3
Juniperus osteosperma	2.8	5.5	0.4
Juniperus scopulorum	0.1	14.1	0.9
Pinus edulis	—	0.1	—
Pinus ponderosa	—	6.6	14.9
Populus angustifolia	—	—	11.8
Populus fremontii	51.6	20.6	25.6
Quercus gambelii	11.0	16.7	3.5
Salix laevigata	12.2	1.6	20.6
Salix lasiolepis	—	10.0	3.8
Salix gooddingii	1.3	6.2	11.5
		SHRUBS	
Acer glabrum	—	—	0.2
Amelanchier alnifolia	1.4	2.4	3.0
Artemisia filifolia	0.8	—	—
Artemisia ludoviciana	11.1	0.6	0.4
Artemisia tridentata	12.7	8.9	3.8
Baccharis glutinosa	2.9	10.9	18.5
Betula occidentalis	—	9.1	5.2
Brickellia californica	17.9	1.6	—
Brickellia microphylla	—	—	0.2
Ceanothus greggii	—	2.4	—
Cercocarpus ledifolius	0.9	3.3	1.6
Chrysothamnus nauseosus	16.2	6.7	5.9
Clematis ligusticifolia	—	2.6	0.8
Cowania mexicana	0.8	0.2	—
Cornus stolonifera	—	4.7	5.1
Ephedra viridis	—	0.2	—
Eriodycton angustifolium	—	0.5	—
Garrya flavescens	—	2.8	—
Guttierrezia sarothrae	8.0	3.4	—
Mahonia repens	—	1.6	2.3
Opuntia sp.	—	0.2	0.2
Pachystima myrsinites	—	—	2.0
Physocarpus monogynus	—	—	0.2
Pluchea sericea	—	1.9	—
Prosopis glandulosa	—	2.7	—
Prunus fasciculata	4.1	1.4	—
Prunus virginiana	0.3	0.4	0.5
Purshia tridentata	1.2	0.2	—
Quercus turbinella	—	4.1	0.7
Rhus radicans	—	—	0.5
Rhus trilobata	6.0	2.1	8.3
Rosa woodsii	1.1	5.6	6.8
Rubia tinctoria	—	—	0.2
Salix bebbiana	0.6	—	—
Salix exigua	1.8	4.1	15.9
Symphoricarpos sp.	—	—	0.3
Tamarix ramosissima	6.8	2.6	7.6
Unknown species No. 1	—	—	3.4
Unknown species No. 2	2.1	—	—
Unknown species No. 3	—	—	2.0
Vitis arizonica	—	9.2	1.6
Yucca angustissima	—	0.2	—

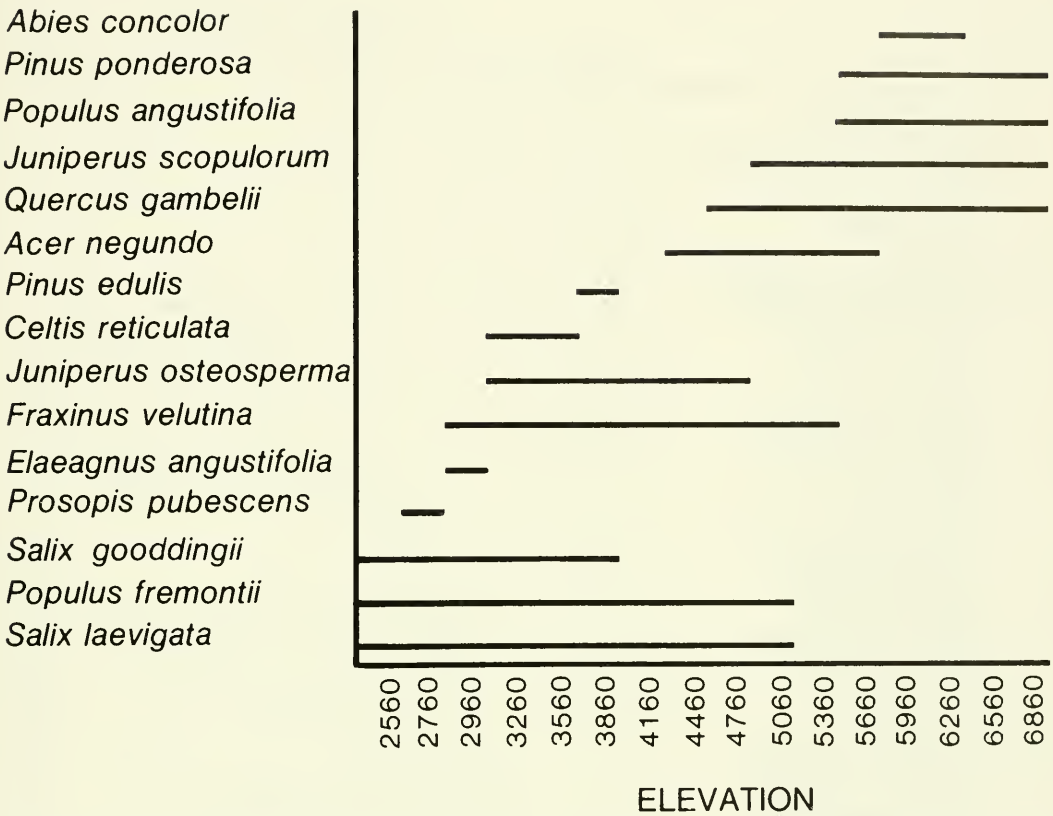


Fig. 2. The relationship of tree species to an elevational gradient along Ash, Leeds, and Santa Clara creeks in Washington County, Utah.

Indices of similarity (Ruzicka 1958) were computed on the basis of species relative density (trees) and relative frequency (shrubs) values for each study site in relation to all other study sites. The similarity between stands ranged widely from 0 to 73% and had an average of 32%. Cluster analysis (Sneath and Sokal 1973) of the similarity indices of the different study sites (Fig. 4) produced eight subclusters, which could be placed into three major groups, each of which contained stands from all three streams. The study sites within the major groups cluster mostly on the basis of stream geography and elevation (Fig. 4). For example, Group II, which contains the largest number of study sites, is composed of low- and mid-elevation stands. By contrast, Group I is composed of mid- and high-elevation stands, while Group III contains stands that are mid-elevation sites. The average elevation for Group II is 1,133 m, for Group III is 1,374 m, and for Group I is 1,748 m.

The relative importance of individual species contained within the cluster groups was computed (relative dominance values for trees and relative frequency values for shrubs) with respect to elevation (Table 3) in order to define the above patterns more precisely. Group I of Table 3 corresponds to Group II of Figure 4 and is composed of stands from the lower elevations. Group II of the table corresponds to Group III of Figure 4 and is composed of mid-elevation stands. Group III of Table 3 corresponds to Group I of Figure 4 and is composed of mid- and high-elevation stands. As expected, the species showed changing patterns of importance with respect to the elevation gradient (Table 3). For example, *Populus fremontii*, *Salix nigra*, *Baccharis glutinosa*, *Pluchea sericea*, *Salix exigua*, and *Tamarix ramosissima* were all low elevation in distribution. Important mid-elevation species included *Fraxinus velutina*, *Eriodycton angustifolium*, *Prunus fasciculata*, *Quercus*

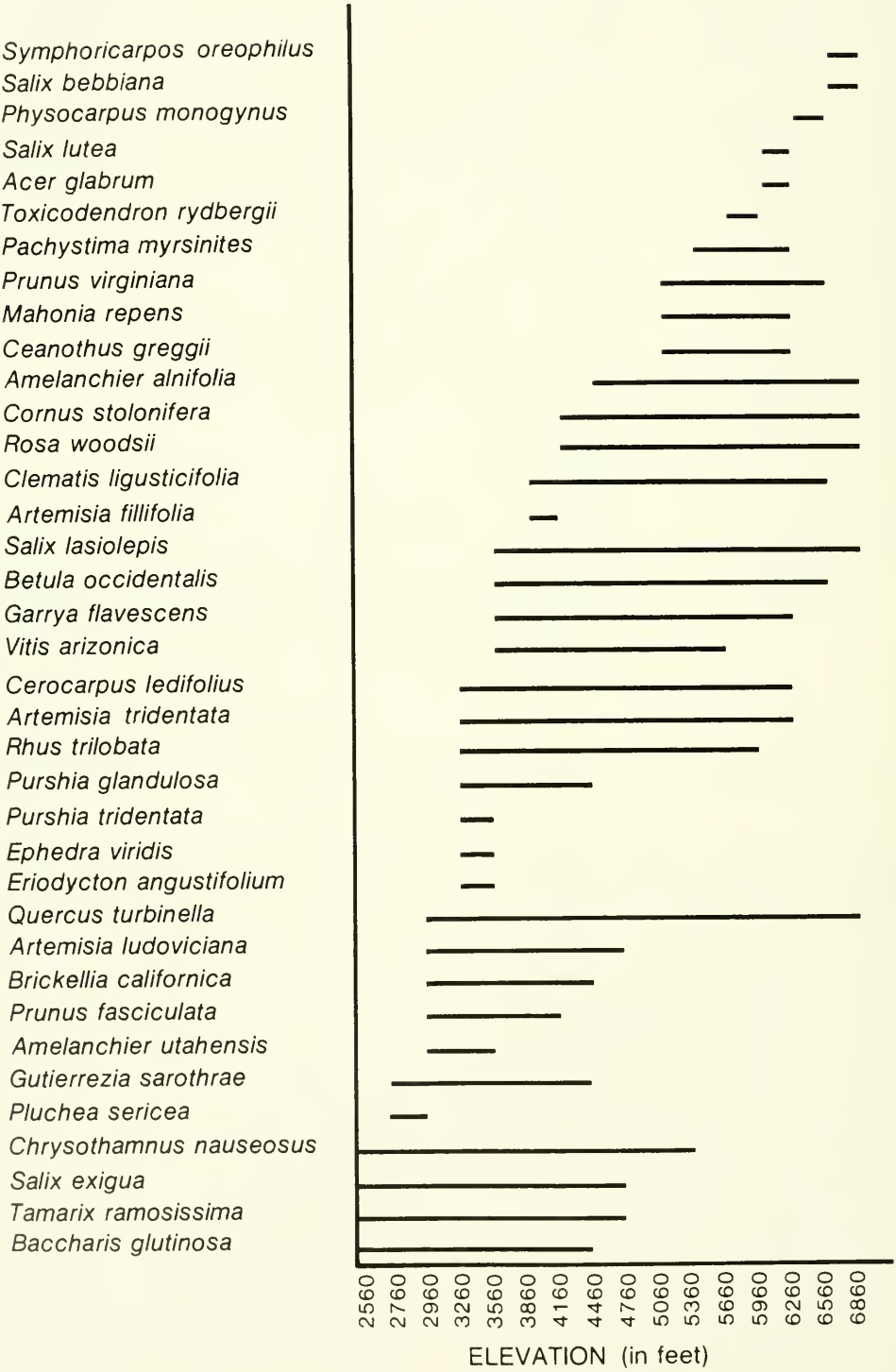


Fig. 3. The relationship of shrub species to an elevational gradient along Ash, Leeds, and Santa Clara creeks in Washington County, Utah.

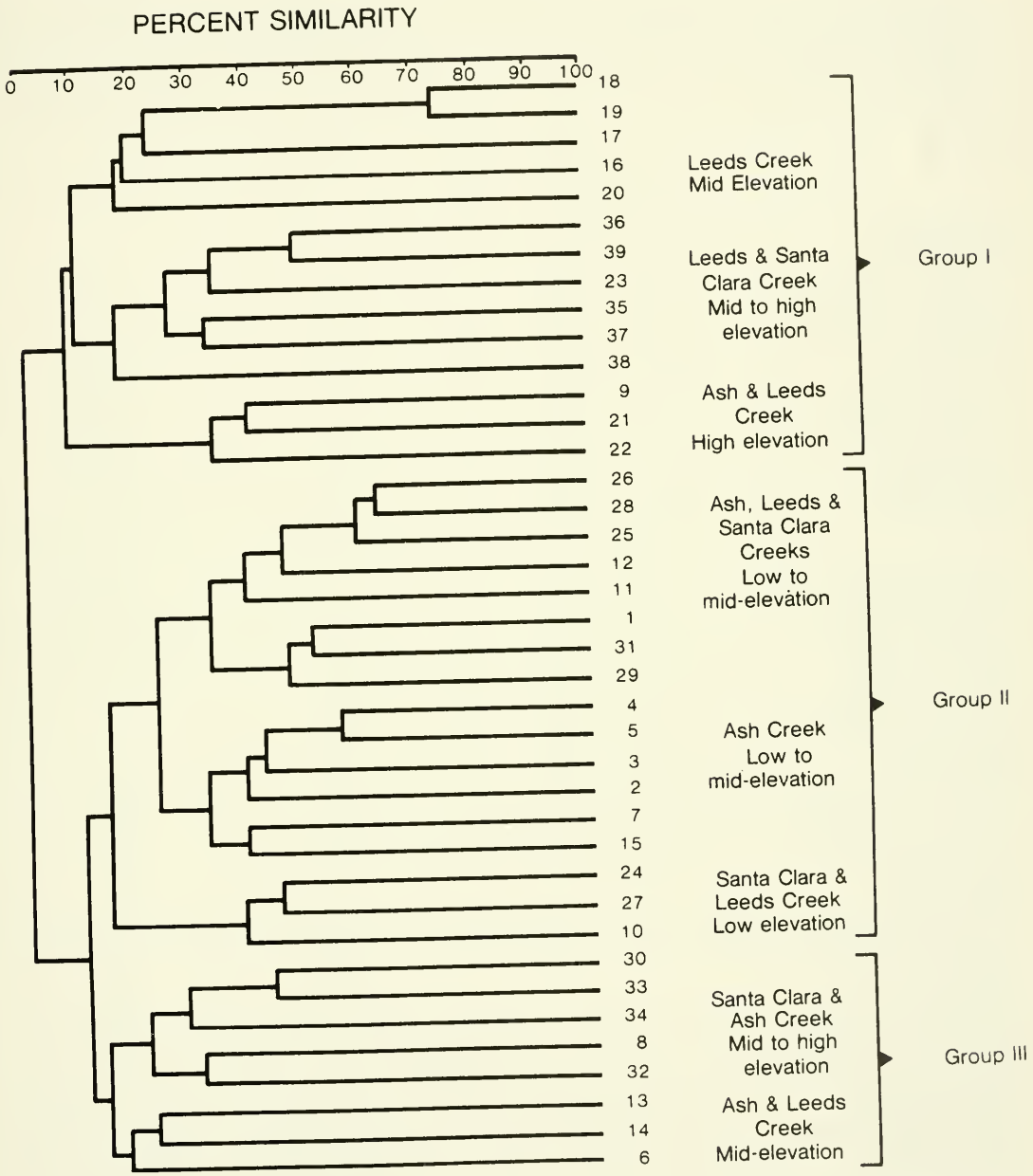


Fig. 4. Cluster dendrogram of study sites found along Ash, Leeds, and Santa Clara creeks in Washington County, Utah. Cluster is based on similarity of relative density values for tree species and relative frequency values for shrub species. Numbers 1–39 identify study sites.

turbinella, and *Rhus trilobata*. At the higher elevation sites *Abies concolor*, *Pinus ponderosa*, *Populus angustifolia*, *Juniperus scopulorum*, *Salix lasiolepis*, *Betula occidentalis*, and *Rosa woodsii* were the more important species. The species distribution patterns show that while some are restricted in distribution to a single elevational level (Figs. 2, 3), the majority peak in importance at specific points along the gradient and then decline as elevations change (Table 3).

Species whose relative density or relative

TABLE 3. Elevational patterns of woody plant species found growing in the riparian zones of Ash Creek, Leeds Creek, and Santa Clara Creek in Washington County, Utah. The figures represent relative dominance values for the trees and relative frequency values for the shrubs. Group I of the table corresponds to Group II of Figure 4 and is composed of stands from the lower elevations. Group II of the table corresponds to Group III of Figure 4 and is composed of mid-elevation stands. Group III of the table corresponds to Group I of Figure 4 and is composed of mid- and high-elevation stands.

	Group		
Species	I	II	III
		TREES	
Abies concolor	—	—	1.4
Acer negundo	—	7.9	2.2
Elaeagnus angustifolia	0.1	—	—
Fraxinus velutina	7.4	35.2	0.1
Juniperus osteosperma	0.1	6.2	11.3
Juniperus scopulorum	0.1	3.0	15.0
Pinus edulis	—	0.1	0.1
Pinus ponderosa	—	—	23.7
Populus angustifolia	—	—	13.5
Populus fremontii	65.1	7.1	0.1
Quercus gambelii	—	—	29.0
Salix laevigata	6.1	41.0	2.6
Salix lasiolepis	3.6	0.4	13.5
Salix gooddingii	15.6	2.2	—
		SHRUBS	
Acer glabrum	—	—	0.2
Amelanchier alnifolia	0.8	—	7.4
Artemisia filifolia	0.4	—	—
Artemisia ludoviciana	5.6	2.1	1.5
Artemisia tridentata	4.6	17.4	6.5
Baccharis glutinosa	24.2	8.1	—
Betula occidentalis	—	5.4	10.7
Brickellia californica	7.3	5.9	1.1
Brickellia microphylla	—	0.3	—
Ceanothus gregii	—	—	2.4
Celtis reticulata	1.7	—	0.4
Cercocarpus ledifolius	—	0.7	5.2
Chrysothamnus nauseosus	12.8	13.6	0.5
Clematis lingusticifolia	0.2	0.5	2.9
Cowania mexicana	0.2	0.4	0.2
Cornus stolonifera	—	—	10.3
Ephedra viridis	—	0.3	—
Eriodycton angustifolium	—	1.0	—
Garrya flavescens	—	1.1	2.0
Guttierrezia sarothrae	6.4	1.0	0.2
Mahonia repens	—	1.8	4.6
Opuntia sp.	—	—	0.4
Pachystima myrsinites	—	—	2.3
Physocarpus monogynus	—	—	0.2
Pluchea sericeae	1.6	—	—
Prosopis glandulosa	2.2	—	—
Prunus fasciculata	2.2	2.4	—
Prunus virginiana	—	—	1.7
Purshia tridentata	0.6	0.3	—
Quercus turbinella	1.1	4.7	1.9
Rhus radicans	—	—	0.6
Rhus trilobata	3.0	11.6	4.6
Rosa woodsii	—	4.2	11.2
Rubia tinctoria	0.2	—	—
Salix bebbiana	—	—	0.4
Salix exigua	14.1	11.3	—
Symphoricarpos sp.	—	—	0.3
Tamarix ramosissima	11.9	2.2	—
Unknown species No. 1	0.6	2.6	1.6
Unknown species No. 2	1.1	—	—
Unknown species No. 3	1.5	0.9	—
Vitis arizonica	0.6	4.9	8.4
Yucca angustissima	—	0.4	—

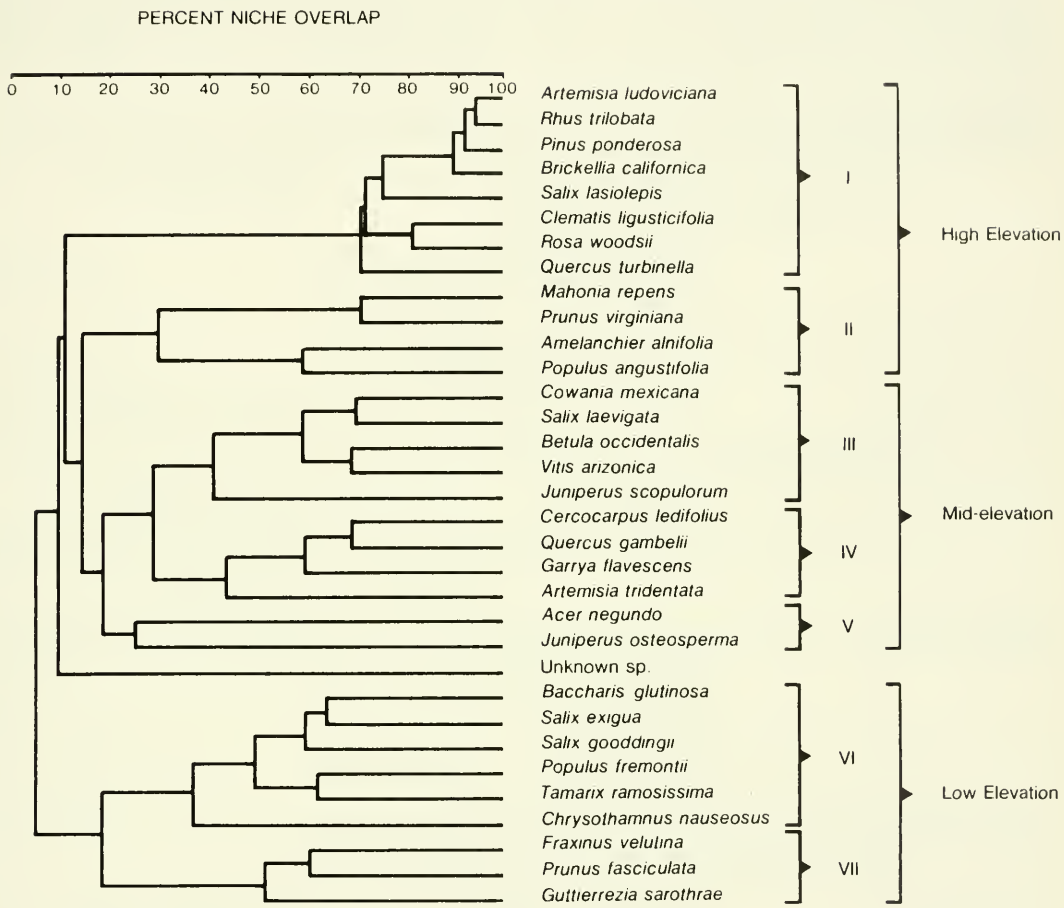


Fig. 5. Cluster dendrogram of plant species occurring along Ash, Leeds, and Santa Clara creeks in Washington County, Utah. Cluster is based on niche overlap values relative to a species geographical distribution.

frequency values across all sites exceeded 1.0% were clustered on the basis of niche overlap data (Colwell and Futuyma 1971) (Fig. 5) to more fully assess their geographical and elevational association patterns. Seven groups clustered together. Groups I and II consist of species generally found on high-elevation sites characterized by *Pinus ponderosa* and *Populus angustifolia*. Though these and their associated species occupy high-elevation sites along streams in the Pine Valley Mountains, elsewhere in the state they occupy mid-elevation areas. Groups III, IV, and V generally contain species from mid-elevation sites along the streams and are characterized by *Salix laevigata*, *Quercus gambelii*, and *Acer negundo*. Again, where these taxa are mid-elevation species in Washington County, they are mid- to low-elevation in other areas of Utah. Groups VI and VII contain mostly low-elevation species, both in southern Utah and in other parts of the state, and are characterized by *Salix nigra*, *Populus fremontii*, *Fraxinus velutina* and *Baccharis glutinosa*. When all species in the cluster are considered, it becomes clear that in moving from high-elevation to low-elevation groups, there is a general increase in the number of species included in those groups whose distributions are Southwest-desert related. Conversely, from the low- to the high-elevation groups, the high-elevation clusters include greater numbers of species whose distribution patterns have more northern affinities.

Cole's (1949) Index of interspecific association (Table 4) was used to define the interrelationships among the species more precisely.

TABLE 4. Results of Cole's Index analyses with respect to the interspecific association patterns of woody species found growing in the riparian zone of Ash Creek, Leeds Creek, and Santa Clara Creek in Washington County, Utah. All significance levels of the Chi-square tests above .05 are included. Numbers within the parentheses following the species names are Cole's interspecific association constants. They range from +1 to −1 with a +1 indicating high positive association and a −1 indicating non-association.

Species	Positive association	Negative association
Amelanchier alnifolia	*Cowania mexicana* (.46) *Mahonia repens* (.22) *Pinus ponderosa* (.39) *Populus angustifolia* (.22) *Prunus virginiana* (.22) *Quercus gambelii* (.46) *Salix lasiolepis* (.55)	*Baccharis glutinosa* (−1.0) *Populus fremontii* (−.61) *Salix laevigata* (−1.0)
Artemisia ludoviciana	*Brickellia californica* (.48) *Chrysothamnus nauseosus* (.44)	
Artemisia tridentata	*Cercocarpus ledifolius* (.29) *Garrya flavescens* (.16) *Rhus trilobata* (.45)	*Baccharis glutinosa* (−.80) *Salix exigua* (−.77) *Salix gooddingii* (−.79)
Baccharus glutinosa	*Populus fremontii* (.66) *Salix exigua* (.55) *Salix gooddingii* (.76) *Tamarix ramosissima* (.63)	*Cercocarpus ledifolius* (−1.0) *Cowania mexicana* (−1.0) *Juniperus scopulorum* (−1.0) *Quercus gambelii* (−1.0) *Rosa woodsii* (−1.0) *Salix lasiolepis* (−.75)
Betula occidentalis	*Clematis ligusticifolia* (.46) *Cowania mexicana* (.46) *Garrya flavescens* (.29) *Juniperus osteosperma* (.44) *Rosa woodsii* (.36) *Salix lasiolepis* (.70) *Vitis arizonica* (.59)	*Populus fremontii* (−.61) *Salix exigua* (−1.0)
Brickellia californica	*Guttierrezia sarothrae* (.42) *Prunus fasciculata* (.46) *Rhus trilobata* (.66)	
Cercocarpus lediflоius	*Cowania mexicana* (.46) *Garrya flavescens* (.29) *Prunus virginiana* (.22) *Quercus gambelii* (.59) *Rosa woodsii* (.53)	*Fraxinus velutina* (−.58) *Populus fremontii* (−.80) *Salix exigua* (−1.0) *Salix gooddingii* (−1.0)
Chrysothamnus nauseosus		*Cowania mexicana* (−1.0) *Pinus ponderosa* (−1.0) *Quercus turbinella* (−1.0) *Salix lasiolepis* (−1.0)
Clematis ligusticifolia	*Cowania mexicana* (.46) *Garrya flavescens* (.29) *Rosa woodsii* (.53) *Salix lasiolepis* (.85) *Vitis arizonica* (.59)	*Populus fremontii* (−.61) *Salix gooddingii* (−1.0) *Tamarix ramosissima* (−1.0)
Cowania mexicana	*Juniperus scopulorum* (.49) *Pinus ponderosa* (.39) *Populus angustifolia* (.33) *Quercus gambelii* (.46)	*Fraxinus velutina* (−1.0) *Populus fremontii* (−.80) *Salix exigua* (−1.0) *Salix gooddingii* (−1.0)

From the analysis two major groups are apparent (Fig. 6). Group 'A' contains two subgroups representing low- to mid-elevational sites. One subgroup centered around *Salix gooddingii* contains five species that reach their highest importance only on the low-elevation sites. The second subgroup contains species that are important on low- to mid-elevation areas. The pivotal species between these two subgroups is *Populus fremontii*. Group 'B'

TABLE 4. Continued

Cowania mexicana	*Rosa woodsii* (.84) *Salix lasiolepis* (.85) *Vitis arizonica* (.32)	*Tamarix ramosissima* (−1.0)
Fraxinus velutina	*Juniperus osteosperma* (.16) *Populus fremontii* (.35) *Prunus fasciculata* (.19) *Rhus trilobata* (.31)	*Pinus ponderosa* (−1.0) *Populus angustifolia* (−1.0) *Prunus virginiana* (−1.0) *Quercus gambelii* (−.79) *Rosa woodsii* (−.56) *Salix gooddingii* (−.52)
Garrya flavescens	*Quercus gambelii* (.55) *Salix lasiolepis* (.75) *Vitis arizonica* (.55)	
Guttierrezia sarothrae	*Populus fremontii* (.74) *Prunus fasciculata* (.40)	*Salix laevigata* (−1.0)
Juniperus osteosperma	*Prunus virginiana* (.32)	
Juniperus scopulorum	*Pinus ponderosa* (.39) *Populus angustifolia* (.44) *Rosa woodsii* (.80) *Salix lasiolepis* (.43)	*Populus fremontii* (−.75) *Salix gooddingii* (−1.0) *Tamarix ramosissima* (−1.0)
Mahonia repens	*Pinus ponderosa* (.69) *Prunus virginiana* (.72) *Quercus gambelii* (.66)	*Populus fremontii* (−1.0)
Pinus ponderosa	*Populus angustifolia* (.52) *Prunus virginiana* (.36) *Quercus gambelii* (.61) *Rosa woodsii* (.78) *Salix lasiolepis* (.57)	*Populus fremontii* (−1.0)
Populus angustifolia	*Quercus gambelii* (.66) *Rosa woodsii* (1.0)	*Populus fremontii* (−1.0)
Populus fremontii	*Salix exigua* (.19) *Salix gooddingii* (.30) *Tamarix ramosissima* (.35)	*Prunus virginiana* (−1.0) *Quercus gambelii* (−1.0) *Rosa woodsii* (−.86) *Salix lasiolepis* (−.55)
Prunus virginiana	*Quercus gambelii* (1.0)	
Quercus gambelii	*Rosa woodsii* (.69) *Salix lasiolepis* (.40)	*Salix exigua* (−1.0) *Salix laevigata* (−1.0) *Salix gooddingii* (−1.0) *Tamarix ramosissima* (−1.0)
Quercus turbinella	*Salix lasiolepis* (.63)	
Rosa woodsii	*Salix lasiolepis* (.57)	*Salix exigua* (−1.0) *Salix gooddingii* (−1.0) *Tamarix ramosissima* (−1.0)
Rhus trilobata	*Vitis arizonica* (.25)	*Salix gooddingii* (−.61)
Salix exigua	*Salix gooddingii* (.58) *Tamarix ramosissima* (.57)	*Salix lasiolepis* (−1.0)
Salix lasiolepis	*Vitis arizonicus* (.48)	*Salix gooddingii* (−.72) *Tamarix ramosissima* (−.75)
Salix gooddingii	*Tamarix ramosissima* (.87)	

contains species that are important at mid- and high-elevation areas. It is a complex cluster, and yet when examined closely, subgroups of geographical significance become apparent. For example, *Betula occidentalis* is the center of a mid-elevational subgroup generally restricted to Leeds Creek (Table 3). Possible explanations for the restricted nature of this subgroup to the Leeds Creek drainage are the lack of grazing on the watershed, the

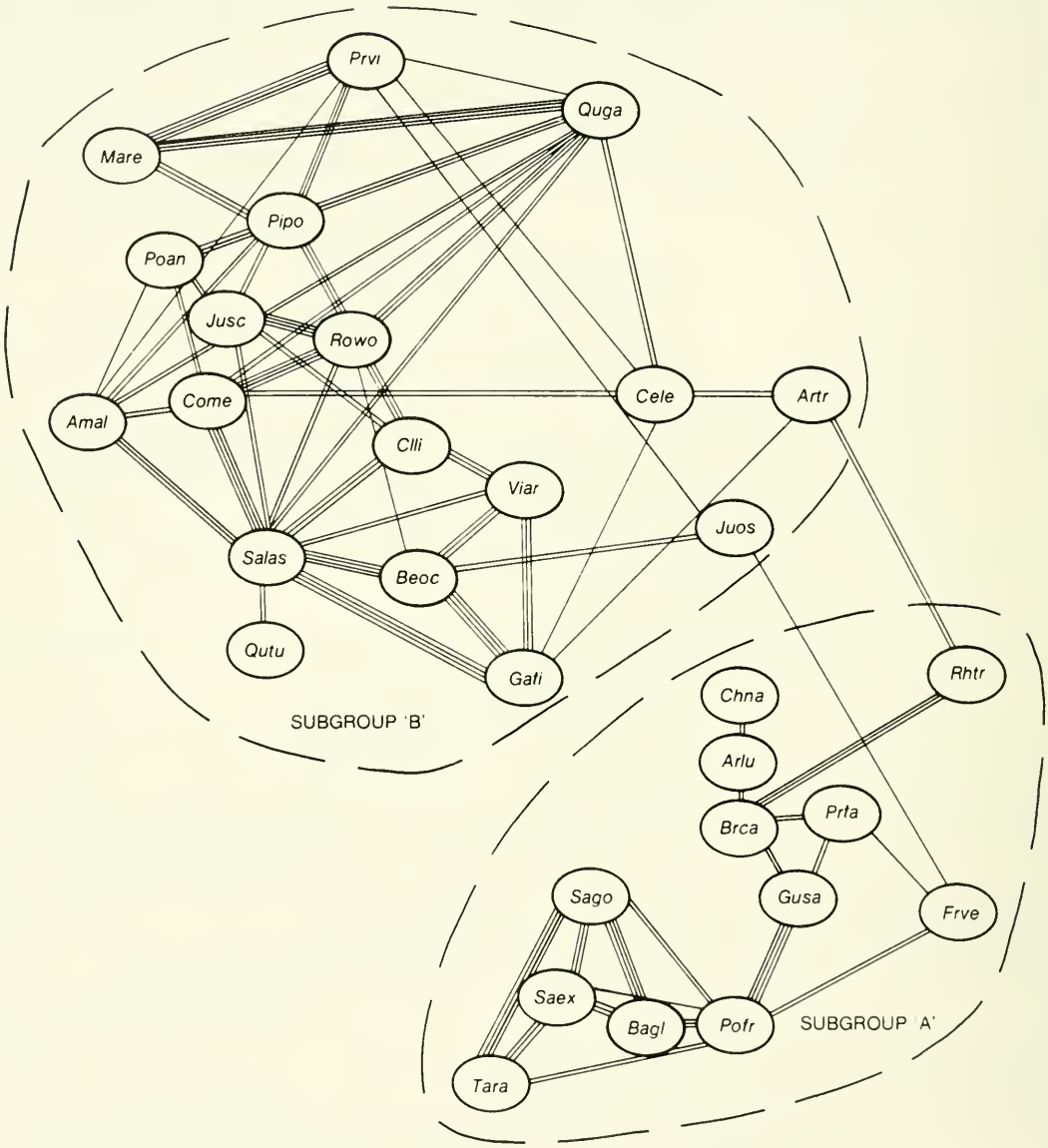


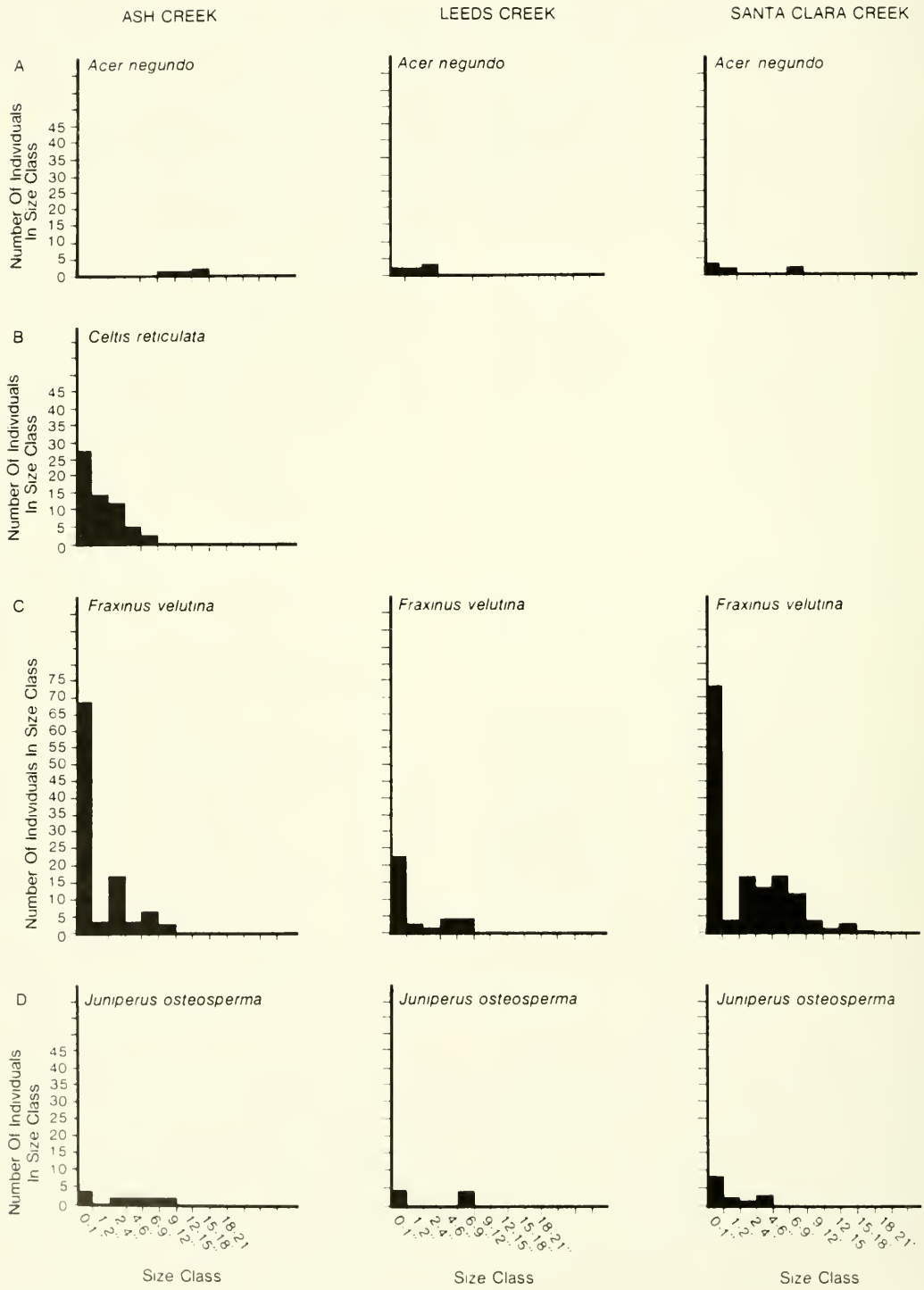
Fig. 6. Cluster of plant species associated with riparian communities of Ash, Leeds, and Santa Clara creeks in Washington County, Utah, as determined by Cole's (1949) Index. The more lines between the species, the greater the association. All associations are statistically significant ($p < .05$). Only those plant species with relative values of 1.0% are included in the analysis. Groups A and B are the subgroup clusters. Amal = *Amelanchier alnifolia*, Arlu = *Artemisia ludoviciana*, Artr = *Artemisia tridentata*, Bagl = *Baccharis glutinosa*, Beoc = *Betula occidentalis*, Brca = *Brickellia californica*, Cele = *Cercocarpus ledifolius*, Chna = *Chrysothamnus nauseosus*, Clli = *Clematis ligusticifolia*, Come = *Cowania mexicana*, Frve = *Fraxinus velutina*, Gafl = *Garrya flavescens*, Gusa = *Guttierrezia sarothrae*, Juos = *Juniperus osteosperma*, Juse = *Juniperus scopulorum*, Mare = *Mahonia repens*, Pipo = *Pinus ponderosa*, Pofr = *Populus fremontii*, Poan = *Populus angustifolia*, Prfa = *Prunus fasciculata*, Prvi = *Prunus virginiana*, Quga = *Quercus gambelii*, Qutu = *Quercus turbinella*, Rhtr = *Rhus trilobata*, Rowo = *Rosa woodsii*, Saex = *Salix exigua*, Sago = *Salix gooddingii*, Salas = *Salix lasiolepis*, Tara = *Tamarix ramosissima*, Viar = *Vitis arizonica*.

continuous flow of cold spring water in the stream, and cooler ambient air temperatures due to the northern exposures of the canyon walls along the upper reaches of the stream. A second subgroup of geographical significance is centered around *Pinus ponderosa* and is located on the upper reaches of Santa Clara Creek. Species included within this subgroup are plants whose distributions are characteristic of riparian, mountain brush, and aspen zones of the eastern Great Basin (Welsh et al. 1987).

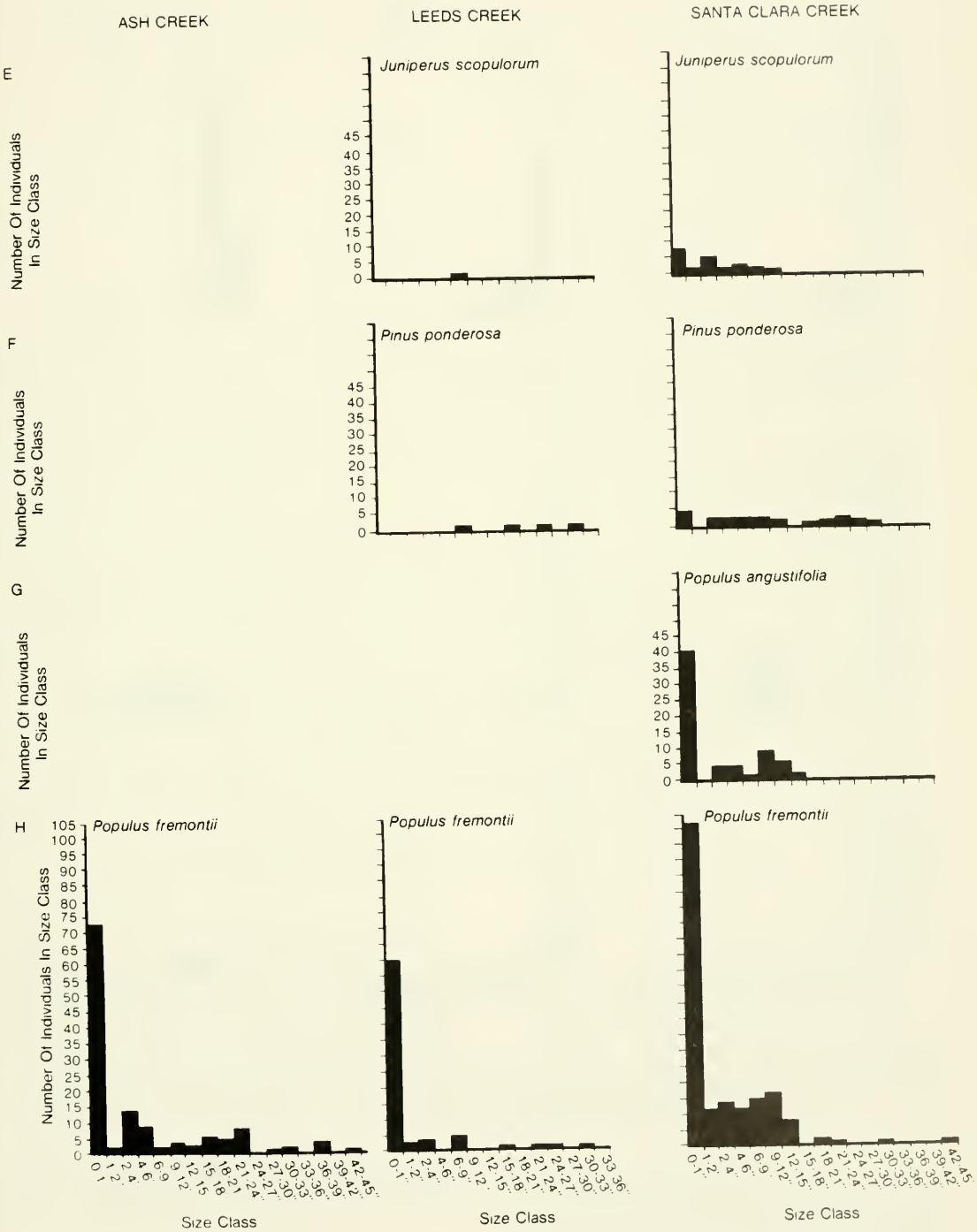
Size-class distributions for 11 of the tree species found in the riparian zones of the three streams are shown in Figures 7A–7K. Not all species were found within the sample plots on all three streams. For example, *Celtis reticulata* was restricted to Ash Creek, and *Populus angustifolia* was found only on the upper reaches of Santa Clara Creek. The absence of *Juniperus scopulorum* and *Pinus ponderosa* on Ash Creek is best explained by the fact that the headwaters of the creek occur at elevations below the habitat of these two species. Sampling was terminated because the stream played out and the creek bed became dry and difficult to delineate.

Examination of the size-class distribution curves for each species shows varying degrees of survival with respect to age and location. Species showing many young individuals in their populations include *Celtis reticulata*, *Fraxinus velutina*, *Quercus gambelii*, *Populus angustifolia*, *P. fremontii*, and *Salix laevigata* on Leeds Creek. Populations with a general lack of reproductive recruitment of young individuals are *Acer negundo* on Ash Creek, *Juniperus scopulorum* and *Pinus ponderosa* on Leeds Creek, and *Salix laevigata* and *S. gooddingii* on Ash and Santa Clara creeks. This variation in recruitment of young into some populations and not into others needs explanation. Modes of reproduction are known to influence seedling numbers entering a population (Irvine and West 1979). For example, our observations indicated that seedlings of *P. angustifolia*, *P. fremontii*, *Q. gambelii*, *S. laevigata*, *S. gooddingii*, and *F. velutina* often arise from root sprouts. Sprouting was most prolific in the stream channels where flooding effects were most severe. The high numbers of individuals in the first size class of most populations in the above species are a result of such sprouting. However, there is a noticeable decrease in the number of young trees in the second age class. These differences are likely due to periodic fluctuations in stream flow related to severe flooding from spring runoff and summer thunderstorms (Irvine and West 1979). Loss of plants in the second age class during flooding could be caused by inundation, uprooting and washing away of seedlings, seedling burial by fresh alluvial deposits, and direct injury due to movement of rocks and debris. An additional factor affecting these numbers may be grazing pressure by domestic cattle. Our observations indicated that on stream banks adjacent to private land, major portions of the streamside communities of Ash, Santa Clara, and lower Leeds creeks were subjected to such grazing. Studies by Boles and Dick-Peddie (1983), Glinski (1971), and Hamilton and Hamilton (1965) showed that the absence of cottonwood reproduction along streams in Arizona and New Mexico was due to overgrazing by cattle. Our observations further indicated that cattle were also grazing on young willow and ash seedlings. Literature (U.S. Forest Service 1937, Dayton 1931) substantiates these observations and indicates that such impact is greatest where cattle tend to concentrate.

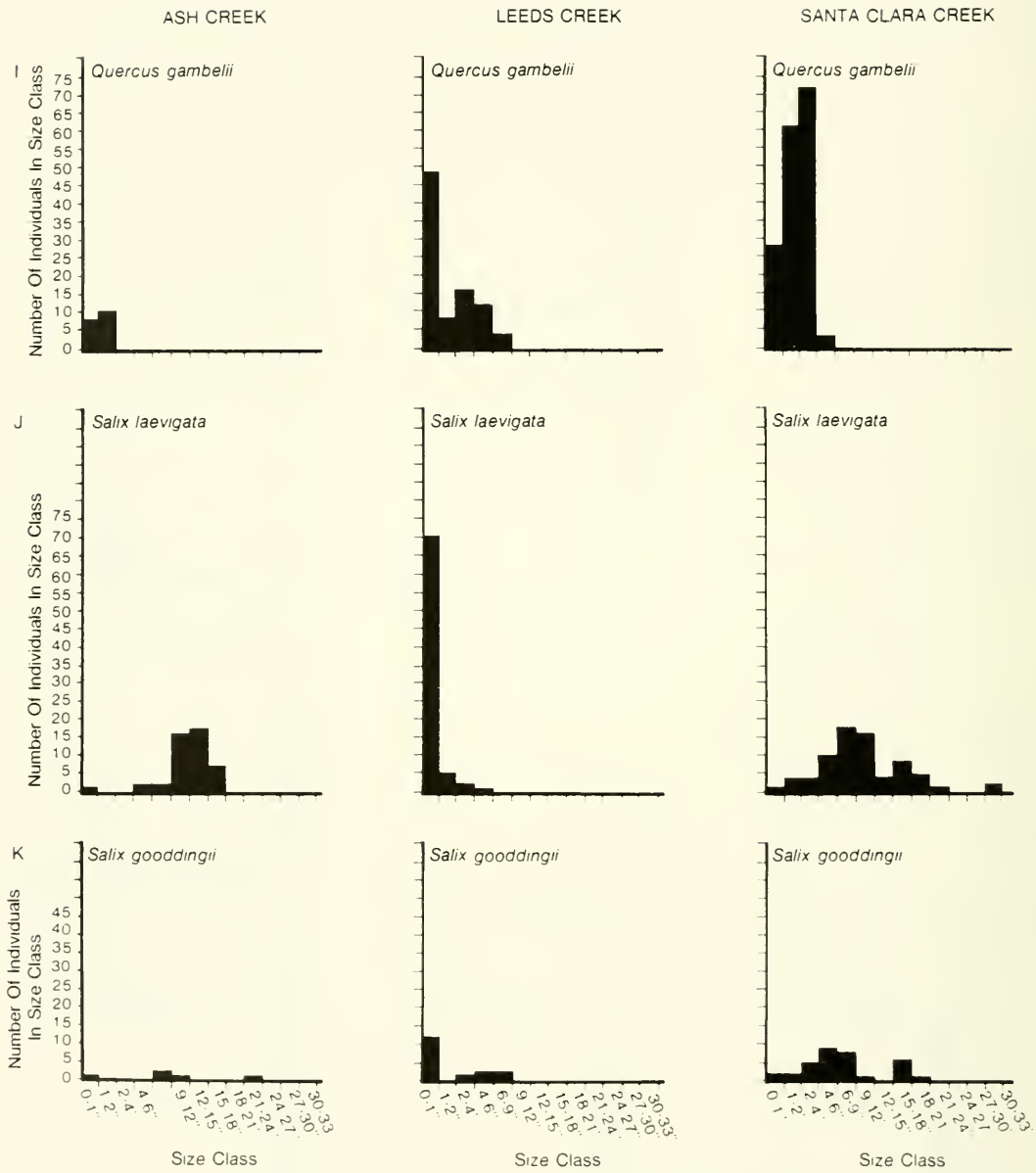
Johnson and Lowe (1985) describe two major environmental gradients with respect to riparian ecosystems of the Southwest: a transriparian continuum and an intrariparian continuum. The transriparian gradient extends from the aquatic habitat of the stream channel across the riparian zone and into the adjacent uplands. Across this gradient one traverses sequentially several vegetative zones based on water availability. The intrariparian gradient exists within the stream channel influence and extends from the mouth of a stream to its headwaters. Moving along this gradient from a stream's mouth to its headwaters one also traverses sequentially several vegetative zones. Each zone is dominated by species specific to that zone. It is worth noting that the influence of these two gradients can be observed in operation within the riparian communities of Ash, Leeds, and Santa Clara creeks. The major patterns discussed with respect to elevation changes along the streams constitute vegetative relationships defined by the intrariparian concept. The transriparian gradient is best exemplified on the lower elevation areas of the streams where higher



Figs. 7A–D. Histograms of population profiles by size class of *Acer negundo*, *Celtis reticulata*, *Fraxinus velutina*, and *Juniperus osteosperma* along Ash, Leeds, and Santa Clara creeks in Washington County, Utah.



Figs. 7E–H. Histograms of population profiles by size class of *Juniperus scopulorum, Pinus ponderosa, Populus angustifolia,* and *Populus fremontii* along Ash, Leeds, and Santa Clara creeks in Washington County, Utah.



Figs. 7I–K. Histograms of population profiles by size class of *Quercus gambelii*, *Salix laevigata*, and *Salix gooddingii* along Ash, Leeds, and Santa Clara creeks in Washington County, Utah.

percentages of the species are true riparian entities and tend to segregate along a soil moisture gradient away from the stream toward the adjacent upland. In the lower elevation areas along the streams the plant species growing within the riparian community are not generally shared with adjacent ecosystems; but, as elevations increase toward stream headwaters, greater numbers of species are shared in common with the biotic communities of the surrounding areas.

LITERATURE CITED

AMES, C. R 1977. Wildlife conflicts in riparian management: grazing. Pages 49–51 *in* Importance, preservation and management of riparian habitat: a symposium. USDA Forest Service Gen. Tech. Rept. RM-43. 217 pp.

BEHNKE, R. J. 1979. Values and protection of riparian ecosystems. Pages 164–167 *in* The mitigation symposium: a national workshop on mitigation losses of fish and wildlife habitats. Rocky Mountain Forest and Range Expt. Sta. USDA Forest Serv., Fort Collins, Colorado.

BOLES, P. H. AND W. A. DICK-PEDDIE. 1983. Woody riparian vegetation patterns on a segment of the Membres River in southwestern New Mexico. Southwest Nat. 28: 81–87.

COLE, L. C. 1949. The measurement of interspecific association. Ecology 30: 411–424.

COLWELL, R. K., AND E. J. FUTUYMA. 1971. On the measurement of niche breadth and niche overlap. Ecology 52: 567–576.

COOK, C. W. 1966. Factors affecting utilization of mountain slopes by cattle. J. Range Manage. 19: 200–204.

COOK, E. F. 1960. Geologic atlas of Utah—Washington Co. Bull. No. 70, Utah Geol. and Mineral Survey. University of Utah Press. 112 pp.

DAYTON, W. A. 1931. Important western browse plants. USDA Miscellaneous Publication No. 101. U.S. Goverment Printing Office, Washington, D.C. 213 pp.

GLINSKI, R. I. 1977. Regeneration and distribution of sycamore and cottonwood trees along Sonoita Creek, Santa Cruz Co., Arizona. Pages 116–123 *in* Importance, preservation and management of riparian habitat: a symposium. USDA Forest Service Gen. Tech. Rept. Rm. 43. 217 pp.

HAMILTON, W. J. III., AND M. F. HAMILTON. 1965. Breeding characteristics of yellow-billed cuckoos in Arizona. Proc. California Acad. Sci. 32: 405–432.

HORTON, J. P., AND C. J. CAMPBELL. 1974. Management of phreatophyte and riparian vegetation for maximum multiple use values. USDA Forest Serv. Res. Pap. RM-117. 23 pp.

HUBBARD, J. P. 1977. Importance of riparian ecosystems: biotic considerations. *In:* Importance, preservation and management of riparian habitat: a symposium. USDA Forest Service Gen. Tech. Rept. RM-43. 217 pp.

IRVINE, J. R., AND N. E. WEST. 1979. Riparian tree species distribution and succession along the lower Escalante River, Utah. Southwest Nat. 24: 331–346.

JOHNSON, R. R. AND C. H. LOWE. 1985. On the development of riparian ecology. Pages 112–116 *in* Riparian ecosystems and their management: reconciling conflicting uses. First North American Riparian Conference. Rocky Mountain Forest and Range Expt. Sta., USDA Forest Service Gen. Tech. Rept. RM-120. Tucson, Arizona.

KAESLER, R. L., AND J. CAIRNS. 1972. Cluster analysis of data from limnological surveys of the upper Potomac River. Amer. Midl. Nat. 88: 56–67.

MACARTHUR, R. H. 1972. Geographical ecology: patterns in the distribution of species. Harper and Row Publishers, New York. 269 pp.

MEYER, S. 1978. Some factors governing plant distributions in the Mojave-Intermountain transition zone. Pages 197–207 *in* Intermountain biogeography: a symposium. Great Basin Nat. Mem. No. 2. 268 pp.

ORLOCI, L. 1966. Geometric models in ecology. I. The theory and application of some ordination methods. J. Ecology 54: 193–215.

PHILLIPS, E. A. 1959. Methods of vegetation study. Holt, Rinehart, and Winston, Inc., New York. 107 pp.

PHILLIPS, T. A. 1965. The influence of slope gradient, distance from water and other factors on livestock distribution on National Forest cattle allotments of the Intermountain Region. Intermountain Forest and Range Expt. Sta. Impr. Notes. 10: 9–19. USDA Forest Serv., Ogden, Utah.

PLATTS, W. S. 1978. Livestock grazing and riparian/stream ecosystems: an overview. Pages 39–45 *in* O. B. Cope, ed., A forum on grazing and riparian/stream ecosystems. Trout Unlimited Inc., Denver, Colorado.

RUSSELL-HUNTER, W. D. 1970. Aquatic productivity: an introduction to some basic aspects of biological oceanography and limnology. The Macmillan Co., New York. 306 pp.

RUZICKA, M. 1958. Anwendund mathematisch-statistischer methoden in der Geobotanik (Synthetische bearbeitung von aufnahmen). Biolgia. Bratsil. 13: 647–661.

SHANNON, C. E., AND W. WEAVER. 1949. The mathematical theory of communication. University of Illinois Press, Urbana. 177 pp.

SNEATH, R. H. A., AND R. R. SOKAL. 1973. Numerical taxonomy: principles and practice of numerical classification. W. M. Freeman Co., San Francisco. 573 pp.

USDA. 1977. Soil survey of Washington County area, Utah. USDA Soil Conservation Service. U.S. Government Printing Office, Washington, D.C. 140 pp.

U.S. FOREST SERVICE. 1937. Range plant handbook. U.S. Government Printing Office, Washington, D.C.

WARNER, J. H., AND K. T. HARPER. 1972. Understory characteristics related to site quality for aspen in Utah. Brigham Young Univ. Sci. Bull., Biol. Ser. 16(2): 1–20.

WELSH, S. L., N. D. ATWOOD, S. GOODRICH, AND L. C. HIGGINS. 1987. A Utah flora. Great Basin Nat. Mem. No. 9. 894 pp.

NOTEWORTHY FLEA RECORDS FROM UTAH, NEVADA, AND OREGON

Harold J. Egoscue[1]

ABSTRACT.—Collections from several scattered western localities have (1) extended the ranges in Nevada of two sagebrush vole fleas, *Oropsylla bacchi johnsoni* and *Megabothris clantoni princei*, (2) provided a second record for Utah of the rarely collected flea, *Delotelis telegoni*, and (3) included additional examples of unusual and seldom reported host-flea relationships for the area.

The geographical distribution, ecology, host preferences, and seasonal occurrence of many western fleas are still imperfectly known. Presented here are range extensions, additional data about rare fleas, and uncommonly recorded host-flea associations.

Scientific and common names of mammals follow Hall (1981) except for *Sorex monticolus obscurus* (see Hennings and Hoffmann 1977). Fleas in the family Ceratophyllidae are according to a revision by Smit (Traub, Rothschild, and Haddow 1983). The name combination *Sternopsylla distincta texana* as new usage was first proposed by Johnson (1957).

One or more voucher specimens of most host species, except deer mice and the shrew listed as *Sorex* sp., were deposited in the University of Utah, Museum of Natural History, Salt Lake City. Hosts collected by me were caught in Museum Special snap traps except the spotted skunk, which was livetrapped. Fleas were permanently mounted on slides, and all but *Orchopeas sexdentatus* are presently in my possession.

Sorex merriami merriami Dobson

Epitedia stanfordi Traub, 1944. 1 ♀, Harney Co., Oregon: 16 km S of Crane, 1,318 m, 25 October 1984.

This host association is no doubt accidental; *E. stanfordi* was also collected here from *Lagurus curtatus*, *Peromyscus maniculatus*, *P. crinitus*, and *Reithrodontomys megalotis*, most of which are generally regarded as normal hosts for this flea. Flea records from the Merriam shrew are few. Specimens identified only as "common rodent fleas" were reported from *S. merriami* in central Washington (Johnson and Clanton 1954). Fleas specific to this soricid are unknown.

Sorex vagrans vagrans Baird

Epitedia stanfordi Traub, 1944. 1 ♂ 1 ♀, Tooele Co., Utah: mouth of South Willow Creek Canyon, east base Stansbury Mts., 8 km S of Grantsville, 1,610. 4 m, 21 February 1980.

Sorex monticolus obscurus Merriam

Corrodopsylla curvata obtusata (Wagner 1929). 1 ♀, Tooele Co., Utah: head of Mack Canyon, Stansbury Mts., 2,470.5 m, 28 September 1967; 1 ♀, outlet of North Willow Lake, Stansbury Mts., 2,562 m, 17 July 1968.

The first and only other published Utah records of *C. c. obtusata* are from the water shrew, *Sorex palustris*, collected in the Oquirrh Mts., Tooele Co. (Egoscue 1966). Several other species of small mammals including *Sorex monticolus* (then *S. obscurus*) caught in the same traplines there did not have this flea, thus leading me to wonder if *C. c. obtusata* might be host specific to water shrews in the intermountain area. This notion was dispelled by the Mack Canyon record ex *S. monticolus* collected on a dry, sagebrush hillside some distance from the nearest *S. palustris* populations. Left unexplained is why all *C. c. curvata* collected to date in Utah are from the Wasatch cordillera while every *C. c. obtusata* is from isolated mountains of the Bonneville Basin. Additional collecting is clearly recommended.

The taxonomic status of *C. c. obtusata* remains unresolved. Holland (1985 and elsewhere) strongly suggested that it be accorded full species status.

[1]Box 787, Grantsville, Utah 84029.

Sorex sp.

Corrodopsylla curvata curvata (Rothschild 1915). 16 ♂♂ 12 ♀♀, Salt Lake Co., Utah: Red Butte Canyon, Wasatch Mts., 1,830 m, July 1982.

The specific identity of the host (not saved) is in question, but it was not a water shrew. Twenty-eight fleas from either a dusky or a wandering shrew are highly unusual. Shrew fleas from Utah are rare in collections.

Tadarida brasiliensis mexicana (Saussure)

Sternopsylla distincta texana (C. Fox 1914). 10 ♀♀, White Pine Co., Nevada: Rose Guano Cave, west base of the Snake Range, 1,952 m, 24–26 August 1965; Idem., 1 ♂ 3 ♀♀, 5 October 1966; Idem., 1 ♂, 12 July 1967; Idem., but from guano collected on the cave floor, 1 ♂ 2 ♀♀, 4–5 July 1985.

Rose Guano Cave, sometimes referred to as Rosebud Cave, harbors a maternity colony of Brazilian free-tailed bats estimated to number several thousand. To my knowledge, these are the first records of *S. d. texana* from Nevada.

Ochotona princeps cinnamonea J. A. Allen

1. *Ctenopsyllus armatus* (Wagner 1901). 9 ♂♂ 9 ♀♀, Sevier Co., Utah: Johnson's Reservoir, 2,745 m, 31 May 1965. 2. *Megabothris abantis* (Rothschild 1905). 1 ♂, Idem., 31 May 1965. 3. *Amphalius runatus necopinus* (Jordan 1925). 1 ♀, Idem., 31 May 1965.

Ochotona princeps fuscipes A. H. Howell

1. *Ctenopsyllus armatus* (Wagner 1901). 3 ♂♂ 5 ♀♀, Kane Co., Utah: 3.2 km E of Navaho Lake, 2,745 m, 10 June 1965. 2. *Amphalius runatus necopinus* (Jordan 1925). 3 ♂♂, Idem., 10 June 1965.

Ochotona princeps lasalensis Durrant & Lee

1. *Ctenopsyllus armatus* (Wagner 1901). 7 ♂♂ 14 ♀♀, San Juan Co., Utah: Warner Ranger Station, La Sal Mts., 2,806 m, 21 May 1965. 2. *Amphalius runatus necopinus* (Jordan 1925). 1 ♀, Idem., 21 May 1965.

Ochotona princeps uinta Hollister

Ctenopsyllus armatus (Wagner 1901). 9 ♂♂ 16 ♀♀, Summit Co., Utah: Smith and Moorehouse Canyon, 1.6 km S of Smith and Moorehouse Guard Station, Uinta Mts., 2,745 m, 5–13 June 1965.

Stark (1958) had less than two dozen pika flea records to report from Utah. The rodent flea, *Megabothris abantis*, has been found with some regularity as a stray on *Ochotona* in Canada (Holland 1985), Utah (Stark 1958), and several other western states (Hubbard 1947).

Microdipodops megacephalus ambiguus Hall

Meringis hubbardi Kohls 1938. 1 ♂, Humboldt Co., Nevada: 14.5 km N of Winnemucca, 1,342 m, 30 July 1965.

Hubbard (1949b) reported this flea from kangaroo mice collected in northern Nevada but gave no specific localities. *Microdipodops* sp. rarely has fleas.

Microdipodops megacephalus nasutus Hall

Meringis hubbardi Kohls 1938. 2 ♂♂ 1 ♀, Mineral Co., Nevada: 1.2 km NE of Lucky Boy Pass Summit, Wassuk Mts., 2,455 m, 10–11 September 1980.

Although *M. hubbardi* has been found on a wide variety of small mammals, *Perognathus parvus* appears to be the preferred host. No Great Basin pocket mice were caught in association with kangaroo mice at either of the above-mentioned Nevada localities, although suitable habitat was present at both places.

Peromyscus maniculatus sonoriensis (Le Conte)

Delotelis telegoni (Rothschild 1905). 1 ♀, Utah Co., Utah: 7.2 km NE of the summit of Mt. Nebo, Wasatch Mts., 2,580 m, 31 July 1985.

The first Utah record of this rare flea was collected by D Elden Beck and reported by Stark (1958). My specimen came from a host trapped in an aspen-snowberry association with a heavy understory of grasses and herbaceous plants. Other small mammals caught here were *Sorex monticolus, Eutamias minimus, Microtus longicaudus*, and *Zapus princeps*.

Lagurus curtatus intermedius (Taylor)

1. *Oropsylla bacchi johnsoni* (Hubbard 1949). 6 ♂♂ 3 ♀♀, Eureka Co., Nevada: Garden Pass Summit, 56.3 km N of Eureka, 2,039 m, 22 July 1985. 2. *Megabothris clantoni princei* Hubbard 1949. 3 ♂♂ 10 ♀♀, Idem., 22 July 1985. 3. *Malaraeus telchinus* (Rothschild 1905). 1 ♀, Idem., 22 July 1985.

The 23 fleas listed above came from one host. None of several other kinds of rodents including deer mice collected here was infested with either *O. b. johnsoni* or *M. c. princei*. Garden Pass Summit is about midway between Vya, where Hubbard (1949a) found these two *Lagurus* fleas in extreme NW Humboldt Co., Nevada, and Johnson Pass, Tooele Co., the only place in Utah were *M. c. princei* has been collected (Egoscue 1977).

Spilogale putorius gracilis Merriam

1. *Orchopeas sexdentatus* ssp. 3 ♂♂ 9 ♀♀, Tooele Co., Utah: White Sage Flats, 1.6 km E of Simpson Buttes, 1,372.5 m, 18 November 1965. 2. *Anomiopsyllus amphibolus* Wagner, 1936. 5 ♂♂ 10 ♀♀, Idem., 18 November 1965. 3. *Meringis dipodomys* Kohls, 1938. 1 ♂ 3 ♀♀, Idem., 18 November 1965. 4. *Dactylopsylla ignota utahensis* (Wagner, 1936). 1 ♂ 4 ♀♀, Idem., 18 November 1965.

Fleas recovered from spotted skunks reflect their catholic food habits and investigative behavior; they have no fleas peculiar to them in the Great Basin.

All the fleas listed were collected from an adult male spotted skunk caught at a vacant kit fox den. This situation provides a classic example of the epidemiological involvement potential a small carnivore can have for acquiring and disseminating ectoparasites. Here we have a small mustelid living in the den of a canid and carrying four species of rodent fleas, all presumably picked up in the course of its recent foraging or denning activities. The kangaroo rat fleas could have come from the immediate vicinity where the skunk was captured, but the nearest woodrat and gopher populations were at least one mile distant. *Anomiopsyllus amphibolus* is a host-specific nest flea of *Neotoma*, suggesting that the skunk had recently spent time in a wood rat house.

ACKNOWLEDGMENTS

I thank T. Tomasi for providing the shrew fleas obtained during his research in Red Butte Canyon. Paul Lombardi collected the pika fleas. Robert E. Elbel, E. A. Shippee, and R. Bassard gave valuable assistance in the field; Elbel also critically read the manuscript.

LITERATURE CITED

EGOSCUE, H. J 1966. New and additional host-flea associations and distributional records of fleas from Utah. Great Basin Nat. 26(3–4): 71–75.

_____. 1977. The sagebrush vole flea, *Megabothris clantoni princei*, in western Utah, with comments on the distribution of *Megabothris* in the Bonneville Basin. Great Basin Nat. 37(1): 75–76.

HALL, E. R. 1981. The mammals of North America. John Wiley & Sons, New York. 2 vols. 1,181 pp.

HENNINGS, D., AND R. S. HOFFMANN. 1977. A review of the taxonomy of the *Sorex vagrans* species complex from western North America. Occas. Papers, Mus. Nat. Hist., Univ. Kansas 68: 1–35.

HOLLAND, G. P. 1985. The fleas of Canada, Alaska, and Greenland (Siphonaptera). Memoirs Ent. Soc. Canada No. 130. 631 pp.

HUBBARD, C. A. 1947. Fleas of western North America. The Iowa State College Press, Ames. 533 pp.

_____. 1949a. Additional data upon fleas of the sagebrush vole. Ent. News 60(7): 169–174.

_____. 1949b. Fleas of the state of Nevada. Bull. S. California Acad. Sci. 48(3): 115–128.

JOHNSON, M L., AND C. W. CLANTON. 1954. Natural history of *Sorex merriami* in Washington state. The Murrelet 35(1): 1–4.

JOHNSON, P. T. 1957. A classification of the Siphonaptera of South America with descriptions of new species. Ent. Soc. of Washington, Mem. No. 5. 298 pp.

STARK, H. E. 1958. The Siphonaptera of Utah. U.S. Dept. Health, Education and Welfare, Communicable Disease Center, Atlanta, Georgia. 239 pp.

SMIT, F. G. A. M. 1983. Pages 1–36 *in* R. Traub, M. Rothschild, and J. Haddow, The Rothschild collection of fleas. The Ceratophyllidae: key to genera and host relationships. University Press, Cambridge, England. 288 pp.

FOODS AND WEIGHTS OF THE ROCK PTARMIGAN ON AMCHITKA, ALEUTIAN ISLANDS, ALASKA

William B. Emison[1] and Clayton M. White[2]

ABSTRACT.—We examined the crop contents from 129 Rock Ptarmigan (*Lagopus mutus*) collected between 1967 and 1971 on Amchitka, Aleutian Islands, Alaska. On a yearly basis two plant species, *Empetrum nigrum* and *Equisetum arvense*, made up 87% of the diet. Only in July and August were they less than 90% of the diet, and in those months they constituted 65% of the diet. During the warmer months (May–October) when a variety of plant species were available, the Amchitka ptarmigan fed upon growth forms of plants high in nutritive value (particularly *Equisetum* strobili). Its main winter food was the vegetative portions of *Empetrum*, one of the few abundant evergreen vascular plants on the island.

The Rock Ptarmigan (*Lagopus mutus*), is one of the most abundant and widely distributed terrestrial vertebrate herbivores residing permanently in arctic and subarctic regions. Its circumpolar distribution covers most of the northern regions of Europe, Asia, and North America and extends southward as far as northern Japan and the Pyrenees Mountains of northern Spain. Throughout this extensive range, the Rock Ptarmigan is primarily a browser upon leaves, twigs, and buds of various plants (cf. Cramp and Simmons 1980). In many areas it is sympatric, at least for part of the year, with the Willow Ptarmigan (*Lagopus lagopus*) and may also share available food resources with other, primarily mammalian, browsing animals. However, neither Willow Ptarmigan nor terrestrial herbivorous mammals occur in the western Aleutian Islands.

In contrast to many other areas where Rock Ptarmigan occur, Amchitka Island in the western Aleutians (Fig. 1) consists of a small land area, in which the climate is maritime with little winter snow accumulation in the lower elevations and a somewhat depauperate flora (Hulten 1960). Many foods reportedly eaten by Rock Ptarmigan in other areas (Gelting 1937, Watson 1964, Weeden 1969, Gardarsson and Moss 1970, Cramp and Simmons 1980) are rare or absent. In particular, birch (*Betula*) and alder (*Alnus*), which make up 90% (dry weight) of the winter diet of central Alaskan birds (Weeden 1969), are not on Amchitka; and willows (*Salix*), which are sometimes eaten by Rock Ptarmigan in other areas, are rare on the island. Other unusual features of Rock Ptarmigan on Amchitka include its moult (Jacobsen et al. 1983) and its breeding phenology (White et al. 1977). This paper describes the food and shows weights of the Rock Ptarmigan on Amchitka Island.

MATERIALS AND METHODS

Between August 1967 and October 1971, crop contents were removed from 129 Rock Ptarmigan collected on Amchitka (Table 1). In most cases a specimen was processed on the day of collection as follows: at the time of collection the date, location, time, general weather condition, general ground condition (dry, wet, snow covered, etc.), and flock size were recorded; the specimen was then taken to the field laboratory where the crop and its contents were removed and placed in a bottle containing 8% formalin. The bird was then weighed and gonad measurements made. About 75% of the collected birds were aged by the method of Weeden and Watson (1967).

The preserved crop contents were sorted into component food species, thoroughly dried at 80 C, and weighed to the nearest 0.001 gram. Samples of vegetation from one bird were used to determine nitrogen and phosphorus content. These samples were removed from the crop, sorted, and air-dried in the field laboratory before shipment (no

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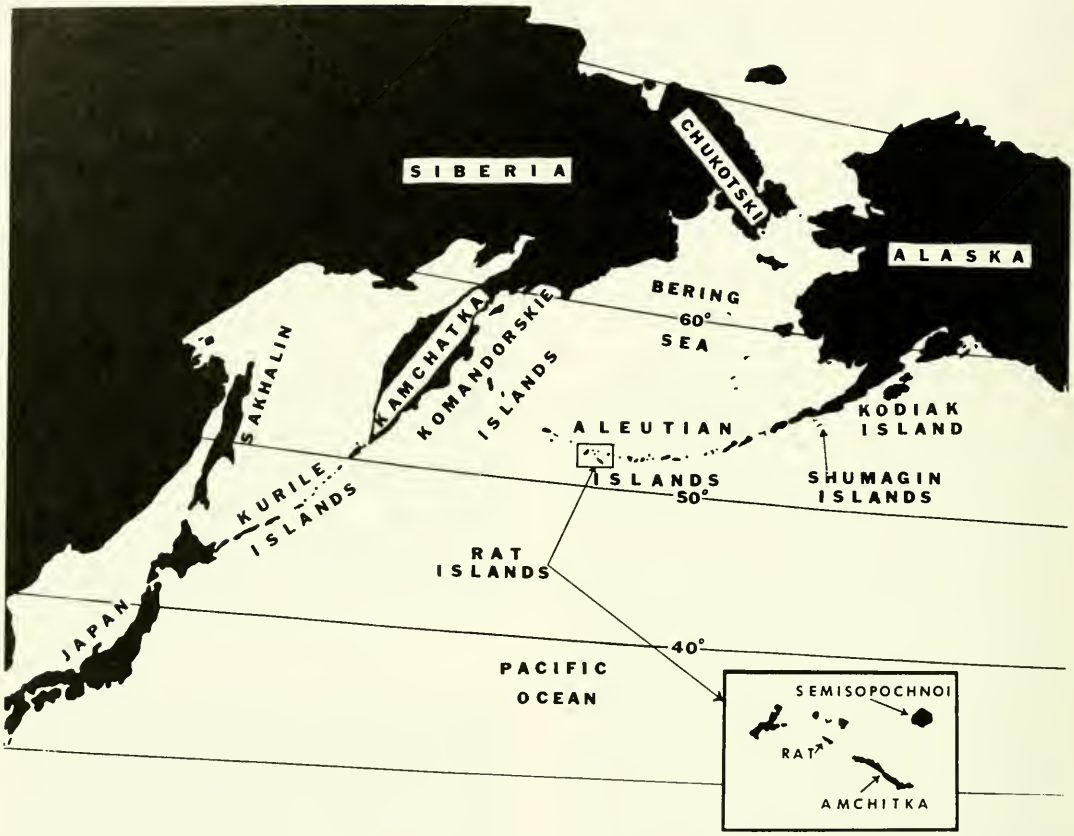

Fig. 1. Rat Islands and surrounding Bering Sea and north Pacific Ocean areas.

preservatives used). They were analyzed by Donald W. Fisher at the U.S. Geological Survey, Water Quality Laboratory, Washington, D.C.

RESULTS

Body weights

Weights in relation to collection dates of adult and juvenile females and of adult and juvenile males are shown in Figures 2 and 3.

Foods

Yearly foods: The year-round diet of Rock Ptarmigan on Amchitka was composed primarily of two plant species, *Empetrum nigrum* (crowberry) and *Equisetum arvense* (horsetail). Together these constituted 89% to 97% (dry weight) of the total diet in all months except July and August, when they formed about 65% of their diet (Fig. 4). On a yearly basis these two plants formed 87% of the diet (Table 2).

Food plants and their growth patterns: In the following discussions, abundances of plants were based both on personal observations and on abundance and ground coverage studies by C. C. Amundsen (unpublished manuscript and 1977) of important plant species in various habitats on Amchitka.

Empetrum nigrum was an evergreen plant that occurred over the entire island and formed extensive mats several cm high. It probably had the greatest gross biomass of any of the island species (Amundsen 1971, 1977) and, at least visually, was the dominant vascular plant on Amchitka. Berries were produced in profusion in May and were mature in August. Ptarmigan ate most berries in August and tapered off through the autumn and early

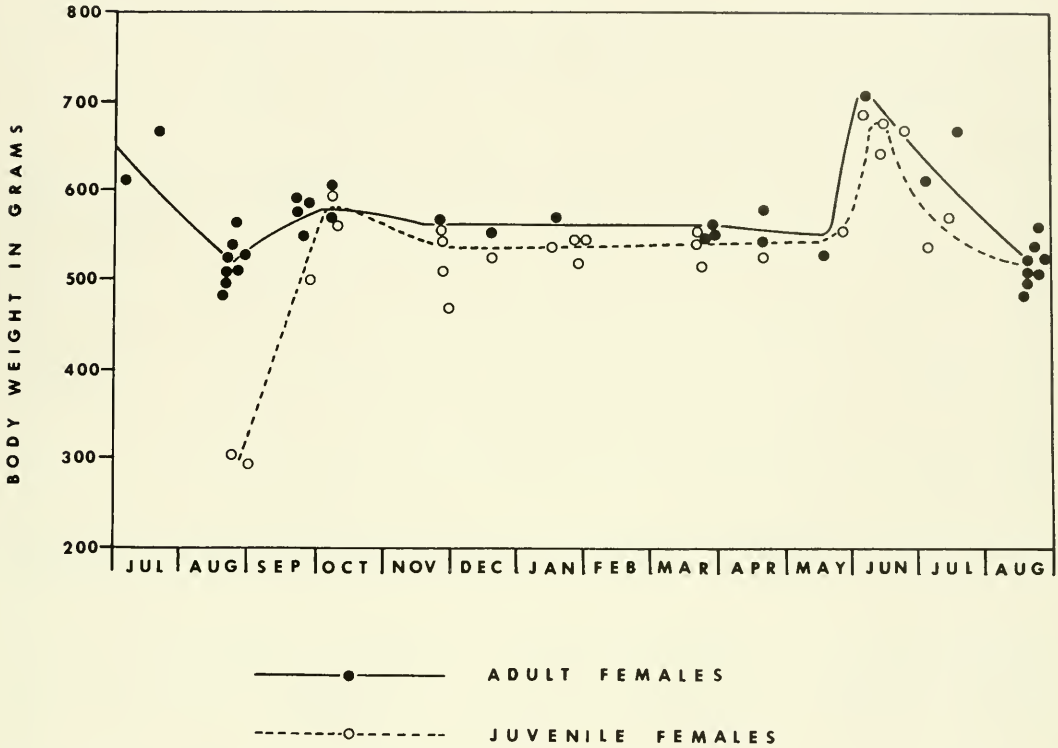

Fig. 2. Seasonal changes in body weight (less crop weight) of female Rock Ptarmigan on Amchitka Island, Alaska. Birds in their second August (and older) are classed as adults. Lines fitted by inspection.

TABLE 1. Number of Rock Ptarmigan collected from Amchitka Island for crop content analyses.

	Number of Rock Ptarmigan collected					
Sampling period	1967	1968	1969	1970	1971	Total
January–February		6		13		19
March–April				11	7	18
May		15	1			16
June			10	7	1	18
July				4	8	12
August	11		5			16
September–October	1		11		2	14
November–December			12	4		16
						129

winter months (Fig. 4) as berries become scarce. Leaves and twigs of *Empetrum*, available throughout the year, were mainly eaten in July and during winter (November–April). *Empetrum* usually protruded above the shallow winter snows. Although it was probably the most abundant vegetation even during warmer months (May–October), it was only eaten in quantity during June and July, when new growth was occurring. During the rest of summer other plants or growth forms were eaten.

Equisetum arvense was locally common, but in most habitats its abundance did not approach that of *Empetrum*. It occurred mainly in lush riparian meadows, on sand dunes, and on disturbed gravel areas on the low plateaus. Its two distinct growth forms

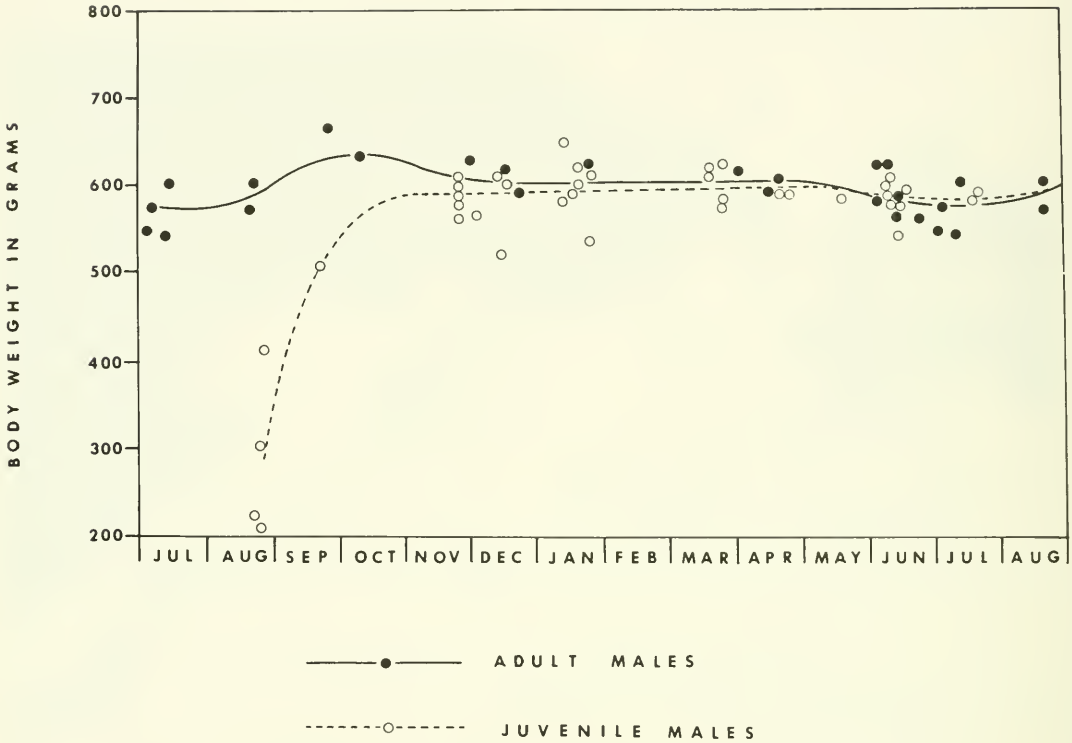

Fig. 3. Seasonal changes in body weight (less crop weight) of male Rock Ptarmigan on Amchitka Island, Alaska. Birds in their second August (and older) are classed as adults. Lines fitted by inspection.

TABLE 2. Percent composition of Rock Ptarmigan crop contents (dry weight) on a yearly basis (all months weighted equally).

Food plants	Percent of diet
Empetrum nigrum	62
Equisetum arvense	25
Ferns	2
Lupinus nootkatensis	2
Carex spp.	2
Sibbaldia procumbens	1
Ranunculus occidentalis	1
Cerastium spp.	1
Miscellaneous* and unidentified	4

*Includes parts of plants of the genera *Anemone*, *Cassiope*, *Cornus*, *Polygonum*, *Potentilla*, *Rubus*, *Salix*, and *Vaccinium*.

consisted of a fertile, erect stem with a single fruiting cone (strobilus) at the apex, and a sterile stem with many branches and tiny appressed leaves.

The sporangia of the fertile plant matured in early June (Shacklette 1969), and soon thereafter the stems and strobili appeared quite withered. Although timing of the appearance above ground of new strobili did not conform to that of *E. arvense* in other areas, it was the only species of *Equisetum* present (Hulten 1968, Shacklette 1969). In the typical life cycle of *E. arvense* the strobili, although fully formed, overwinter under the soil. However, on Amchitka some new strobili emerged to just above the soil in dense grasses (particularly in the riparian meadows) in September, and thus overwintered until the following spring when stems elongated and sporangia begin maturing (Amundsen, personal communication). Even though *Equisetum* strobili were relatively difficult to obtain during autumn and winter, ptarmigan fed extensively upon them in September–October and continued to eat substantial quantities throughout the winter (Fig. 4). In May and June, when the stems elongated and sporangia began maturing, the strobili were conspicuous and abundant in some habitats and were correspondingly abundant in ptarmigan crops. After the sporangia matured in June, the

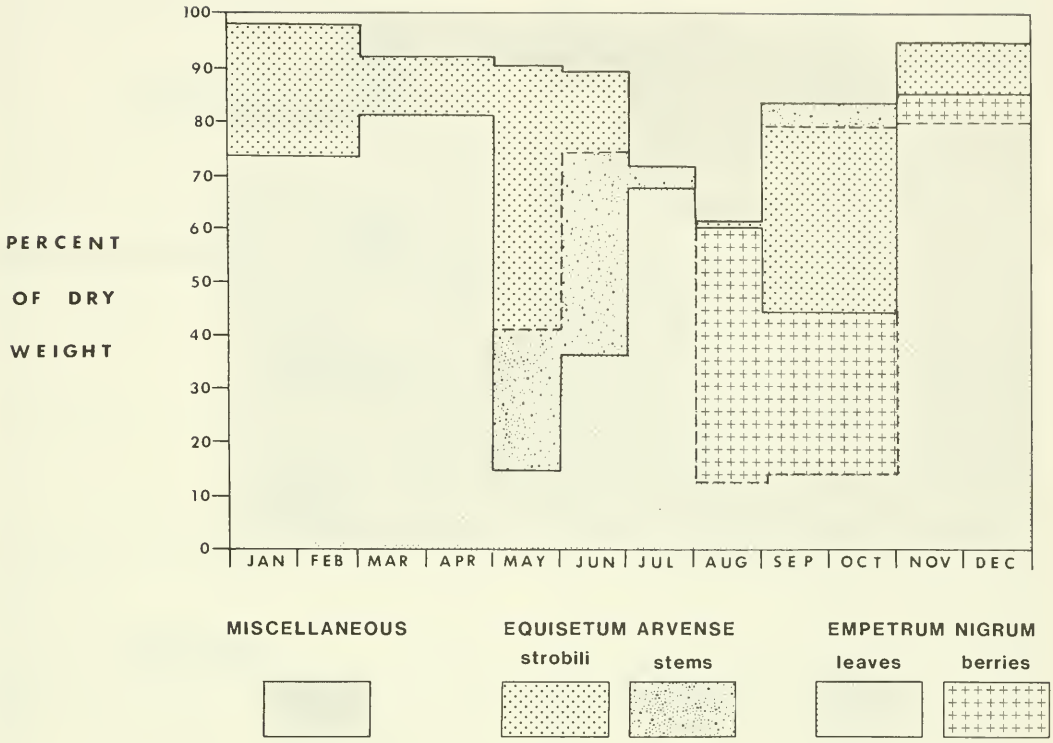

Fig. 4. Percentages of major food plants in the crop contents of Rock Ptarmigan on Amchitka Island, Alaska. The results are expressed in two-month periods for Jan–Feb, Mar–Apr, Sep–Oct, and Nov–Dec; and in one-month periods for May, Jun, Jul, and Aug.

plants withered, and strobili were not eaten between late June and the emergence of some new cones in September.

The new sterile plants of *Equisetum* emerged in late April, and ptarmigan fed heavily on the tips of the new growth (apical meristems) during May and early June (Fig. 4). After the plants branched out in late June they were rarely eaten, but a few newly grown tips appeared in crops of ptarmigan in September–October. Sterile plants withered in the autumn and were not a food source until the following spring when new plants again emerged.

Analyses of plant remains taken from the crop of a female collected on Amchitka in late April showed that *Equisetum* strobili contained 2.54% nitrogen and 0.42% phosphorus, while *Empetrum* vegetation had only 1.25% nitrogen and 0.14% phosphorus.

Plants other than *Empetrum* and *Equisetum* were seldom eaten by ptarmigan except during July and August (Fig. 5). New leaves of *Lupinus nootkatensis* (common in disturbed gravel areas) were fed upon mainly in June (trace) and July, and older leaves were less commonly taken in August–October. The flowers of *Carex macrochaeta* (one of the most abundant sedges) were eaten in June and July, and *Carex achenes* occasionally occurred in crops from August through December. Leaflets of ferns, which were probably either *Athyrium felix-femina* or *Dryopteris dilatata* (common in riparian meadows), were eaten in July–August. Achenes and a few leaves of the locally common buttercup (*Ranunculus occidentalis*) were eaten in August, and a few crops also contained some flowers in July. *Cerastium* (common in disturbed areas) capsules filled with seeds were eaten in limited quantities in September–October. The evergreen leaves of *Sibbaldia procumbens* (uncommon in disturbed areas such as old roadbeds) were eaten in small amounts from November through May. *Salix* and *Polygo-*

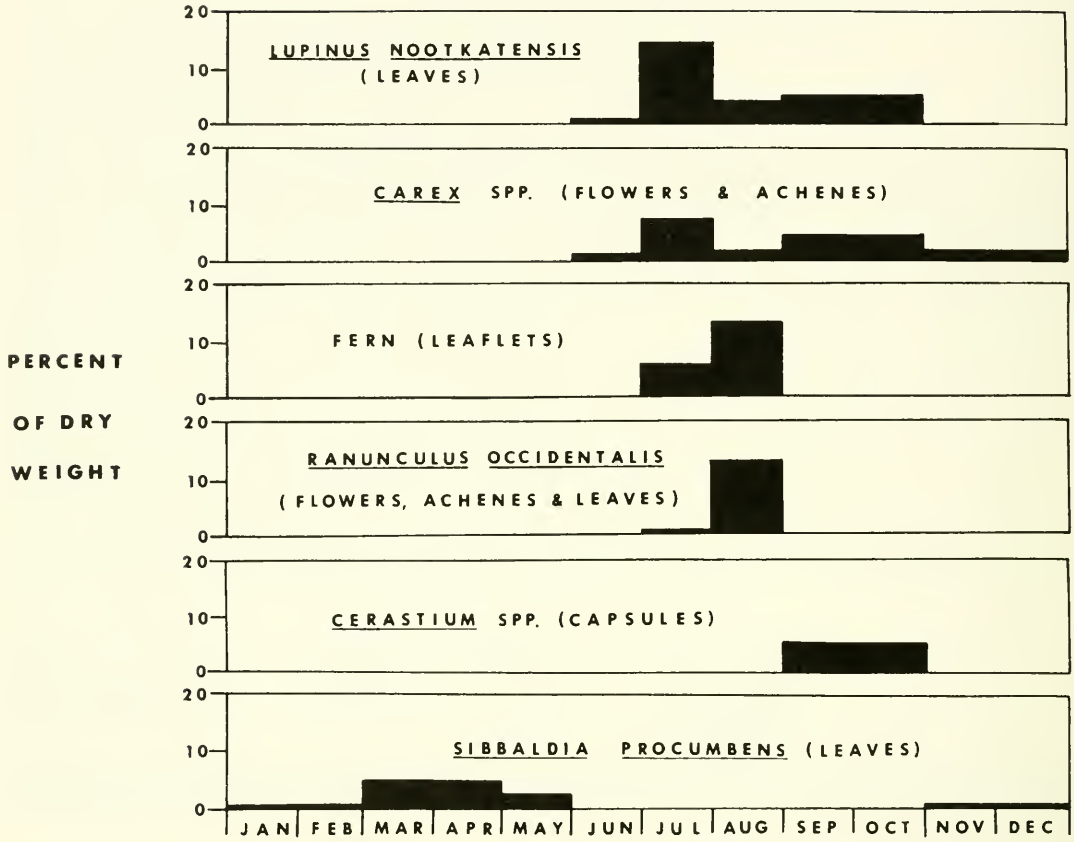

Fig. 5. Percentages of miscellaneous plants in the crop contents of Rock Ptarmigan on Amchitka Island, Alaska. The results are expressed in two-month periods for Jan–Feb, Mar–Apr, Sep–Oct, and Nov–Dec; and in one-month periods for May, Jun, Jul, and Aug.

num rarely occurred in crops, probably because they were rare on the island.

DISCUSSION

The diet of the Rock Ptarmigan on Amchitka Island was very simple, consisting of only two main foods, *Empetrum nigrum* and *Equisetum arvense*. During winter (November through April) its main food was the vegetative portions of *Empetrum*, one of the few abundant evergreen vascular plants on the island. The less abundant and more difficult to obtain *Equisetum* strobili also were taken throughout these months, but in smaller quantities than *Empetrum*. This pattern of winter feeding was similar to that of Rock Ptarmigan populations studied in other widely separated areas, such as central Alaska (Weeden 1969, Moss 1973, 1974), Greenland (Gelting 1937), Iceland (Gardarsson and Moss 1970), and Scotland (Watson 1964). All of these studies showed that winter foods consisted of one to three plants occurring abundantly in the winter habitat.

Summer foods, although more varied, were generally composed of either reproductive structures or parts of plants undergoing growth. Examinations of the crop contents of Amchitka Rock Ptarmigan taken between early May and mid-October revealed that developing strobili and apical meristems of *Equisetum* were being eaten. This resulted in two peaks of *Equisetum* consumption, one in May and June before the plants matured and the other in September–October when new strobili began appearing. Between these two peaks (in July and August) only mature growth

forms of *Equisetum* were available, and these were rarely eaten. At this time *Equisetum* was replaced in the diet by new *Empetrum* vegetation, *Empetrum* berries, and various other plants, most of which were exhibiting either new growth or mature fruits. Such selective feeding during the growing season is well documented for ptarmigan populations in other areas and has been shown to be related to the high nutritive values of plants undergoing growth and development (Gelting 1937, Moss 1968, Gardarsson and Moss 1970). In Iceland, where *Equisetum arvense* and *Empetrum nigrum* both occur, detailed chemical analyses by Gardarsson and Moss (1970) revealed that during May *E. arvense* strobili were considerably more nutritious and digestible than were leaves and shoots of *E. nigrum*. Considered to be of importance were the high percentages of nitrogen and phosphorus. Samples of *Equisetum* strobili and *Empetrum* vegetation taken from the crop of a female collected on Amchitka in late April were analyzed for both nitrogen and phosphorus and the results were similar to those of Gardarsson and Moss (1970). Thus, during the warmer months (May–October) when a variety of plant species were available, the Amchitka ptarmigan fed upon growth forms of plants high in nutritive value.

The body weights of all ages and sexes of ptarmigan collected on Amchitka increased during September and October. Another period of rapid weight increase occurred in females during June when they were forming and laying eggs; during June and July females weighed more than males. Other than during these two periods the average adult body weights remained either unchanged or declined. Both periods of weight increases coincided with the two periods of maximum intake of nutritious *Equisetum* strobili. This pattern of body weight changes was similar to that of the Svalbard Rock Ptarmigan in the high latitudes (77–81°N) north of Norway (Steen and Unander 1985). However, the increase in the September–October weights was much greater in the Svalbard Rock Ptarmigan, presumably because they lay down heavy deposits of fat prior to periods of continuous darkness during winter (Mortensen and Blix 1985).

When major food plants eaten in each of five different geographic areas (Amchitka Island, Scotland, Iceland, Greenland, and central Alaska) were compared, it was apparent that the Rock Ptarmigan was a flexible species capable of exploiting a variety of plant species, although within any one area it was considerably more selective. There appeared to be three major factors involved in winter food selection. (1) The abundance and availability of a suitable winter food. Generally, important winter foods were also some of the most important plants, in terms of abundance, in the winter habitat. (2) The nutritive value of winter plants. In some areas where more than one suitable food plant occurred abundantly, the more nutritious species predominated in the diet. This was shown to be the case in Iceland where *Salix*, *Betula*, *Empetrum*, and *Calluna* all occurred commonly, but the birds fed mainly on *Salix*, which was the highest quality food. (3) The presence of a closely related competitor within the winter habitat of the Rock Ptarmigan. In Iceland and Greenland where the Rock Ptarmigan was the only species of *Lagopus* present, the major winter food was *Salix*. However, in central Alaska where the Willow Ptarmigan was also present, the Rock Ptarmigan subsisted on *Betula*, while the Willow Ptarmigan fed on *Salix*.

Based upon examination of the foods eaten between April and November by Rock Ptarmigan in these studies, it appeared that plant abundance and nutritive values continued to be important factors influencing food selection, but that competition was of little importance because of nesting habitat separation between the two ptarmigan species (Weeden 1969). While a variety of plants and plant parts were eaten during these months, it was significant that parts of plants high in digestibility and nutritive value were selected; this was particularly evident at times when growth and development of young birds was occurring and when females were forming and laying eggs. In Iceland, Greenland, and central Alaska selection was primarily for *Polygonum* bulbils, but on Amchitka where this plant was rare, selection was for *Equisetum* strobili. However, in Scotland, plants high in digestibility and nutritive value were not available, but despite this, the Rock Ptarmigan was capable of maintaining breeding populations (Moss 1968). Thus, the Rock Ptarmigan was an adaptable species in terms

of food requirements and was successful in areas where the nutritive values of winter foods were low (as on Amchitka), where winter food competition with Willow Ptarmigan occurred (as in central Alaska), or where the year-round foods were relatively low quality (as in Scotland).

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LITERATURE CITED

AMUNDSEN, C. C. 1971. Dynamics of the terrestrial ecosystem vegetation of Amchitka Island, Alaska. BioScience 21: 614–622.

——. 1977. Terrestrial plant ecology. Pages 203–226 *in* M. L. Merritt and R. G. Fuller, eds., The environments of Amchitka Island, Alaska. U.S. Energy Research and Development Administration, TID-26712.

CRAMP, S., AND K. E. L. SIMMONS, EDS. 1980. Handbook of the birds of Europe, the Middle East and North Africa. Vol 2. Hawks to bustards. Oxford University Press, Oxford, England.

GELTING, P. 1937. Studies on the food of the east Greenland ptarmigan especially in its relation to vegetation and snow cover. Medd. Gronland. 116: 1–196.

GARDARSSON, A., AND R. MOSS. 1970. Selection of food by Icelandic ptarmigan in relation to its availability and nutritive value. Pages 47–71 *in* A. Watson, ed., Animal populations in relation to their food resources. British Ecol. Soc. Symp. No. 10.

HULTEN, E. 1968. Flora of Alaska and neighboring territories. Stanford University Press, Stanford, California.

JACOBSEN, E. E., JR., C. M. WHITE, AND W. B. EMISON. 1983. Molting adaptations of Rock Ptarmigan on Amchitka Island, Alaska. Condor 85: 420–426.

MORTENSEN, A., AND A. S. BLIX. 1985. Seasonal changes in the effects of starvation on metabolic rate and regulation of body weight in Svalbard Ptarmigan. Ornis Scand. 16: 20–24.

MOSS, R. 1968. Food selection and nutrition in ptarmigan (*Lagopus mutus*). Symp. Zool. Soc. London 21: 207–216.

——. 1973. The digestion and intake of winter foods by wild ptarmigan in Alaska. Condor 75: 293–301.

——. 1974. Winter diets, gut lengths, and interspecific competition in Alaskan ptarmigan. Auk 91: 737–746.

SHACKLETTE, H. T. 1969. Vegetation of Amchitka Island, Aleutian Islands, Alaska. U.S. Geological Surv. Professional Paper 648.

STEEN, J. B., AND S. UNANDER. 1985. Breeding biology of the Svalbard Rock Ptarmigan *Lagopus mutus hyperboreus*. Ornis Scand. 16: 191–197.

WATSON, A. 1964. The food of ptarmigan (*Lagopus mutus*) in Scotland. The Scottish Naturalist. 71: 60–66.

WEEDEN, R. B. 1969. Foods of Rock and Willow ptarmigan in central Alaska with comments on interspecific competition. Auk 86: 271–281.

WEEDEN, R. B., AND A. WATSON. 1967. Determining the age of Rock Ptarmigan in Alaska and Scotland. J. Wildl. Manage. 31: 825–826.

WHITE, C. M., F. S. L. WILLIAMSON, AND W. B. EMISON. 1977. Avifaunal investigation. Pages 227–260 *in* M. L. Merritt and R. G. Fuller, eds., The environment of Amchitka Island, Alaska. U.S. Energy Research and Development Administration, TIO-26712.

POPULATION CYCLES OF WAHWEAP MILKVETCH ON THE HENRY MOUNTAINS AND SEED RESERVE IN THE SOIL

M. H. Ralphs[1] and V. L. Bagley[2]

ABSTRACT.—A population outbreak of Wahweap milkvetch (*A. lentiginosus* var. *wahweapensis* Welsh) occurred in the Henry Mountains area of southeastern Utah in 1985 and 1986, causing extensive locoweed poisoning in cattle grazing these winter ranges. Weather conditions supporting this population outbreak included above average precipitation in the fall of 1984 and 1985, which presumably allowed germination of seed lying dormant in the soil. Above average spring precipitation in the subsequent year supported the population growth. Part of the population died in the summer of 1985, and nearly all plants died in the summer of 1986. Historically, population outbreaks occurred every six to eight years: 1949, 1957, 1965, 1973, 1979, and 1985–1986. Correlation with weather records indicated that population outbreaks occurred in years of high spring and total annual precipitation. Wahweap milkvetch seed lying dormant in the soil ranged from 940 to 4,346 seed/m^2 where old stands occurred, and 20 to 40 seed/m^2 where old plants were not evident. Sufficient seed remains in the soil to cause future population outbreaks.

Locoweed poisoning of livestock is the most widespread poisonous plant problem in the western United States (Kingsbury 1964). It is a particularly difficult problem because of the cyclic nature of *Astragalus* species on desert and semidesert rangeland. When environmental conditions are favorable, populations of some species explode and dominate entire regions (James et al. 1968, Williams et al. 1979, James and Nielsen 1987), causing extensive livestock losses, i.e., poor livestock performance, reduced weight gains, impaired reproduction, and deaths. Even though the genus *Astragalus* is generally characterized by narrow endemism associated with arid microsites (Barneby 1964), population outbreaks may be associated with specifically timed periods of high precipitation (Marsh 1909).

A population outbreak of Wahweap milkvetch (*A. lentiginosus* var. *wahweapensis* Welsh) (nomenclature follows Welsh et al. 1985) occurred in the Henry Mountains area of southeastern Utah in the spring and summer of 1985 and spring of 1986. This caused great concern among stockmen because of the potential for locoweed poisoning. The desert and foothill areas surrounding the Henry Mountains are used as winter and spring range for large numbers of cattle and sheep. The green, actively growing Wahweap milkvetch generally does not cause problems because other green forage is available during the late spring. Poisoning occurs from cattle grazing the dry, senescent plants during the winter and early spring. Thus, poisoning lags the population outbreaks by one to two years.

A grazing study was conducted during the winter of 1987 to evaluate cattle grazing behavior with respect to the dry, senescent Wahweap milkvetch plants to determine when, how much, and why cattle graze locoweed (Ralphs et al. 1988). Part of the study that is reported in this paper describes the weather conditions associated with the most recent population outbreak. Outbreaks of Wahweap milkvetch during the last fifty years were also related to historical weather patterns. Seed in soil was evaluated to determine potential for future population outbreaks.

MATERIALS AND METHODS

Wahweap milkvetch is a localized variety of freckled milkvetch or spotted locoweed (*Astragalus lentiginosus* Dougl. ex Hook.). Freckled milkvetch is a large polymorphic complex comprising 36 varieties (Barneby 1964). It grows from a caudex with incurved ascending stems 1.5–6 dm high. Leaflets are small, elliptic to ovate, 4–20 mm. It has a short raceme with 11–30 pink-purple to blue colored flowers. Pods are bilocular, inflated, and oblong, 12–26 mm long and 5–20 mm

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thick, and purple to red-tinged mottled, becoming stiff, papery, or almost leathery. Welsh et al. (1987) classifies the plants in the Henry Mountains area as Wahweap milkvetch (*A. lentiginosus* var. *wahweapensis* Welsh). It is distinguished from varieties *araneosus* (Sheldon) Barneby and *diphysus* (Gray) Jones by transparent or diaphanous pods and moderately elongate racemes. It grows in the pinyon-juniper or mixed-desert shrub vegetation types from 1,860 to 2,135 m on the Henry Mountains and Four Mile Bench in Kane County (Welsh et al. 1987).

Wahweap milkvetch grew in dense concentrations on the benches of the Henry Mountains in 1985 and 1986. Dense concentrations were limited to the semidesert, stony clay loam range site. It was especially dense on gravel and cobble outcroppings. Vegetation on this site was dominated by galleta grass [*Hilaria jamesii* (Torr.) Benth], shadscale [*Atriplex confertifolia* (Torr. & Frem.) S. Wats], and broom snakeweed [*Gutierrezia sarothrae* (Pursh) Britton & Rusby]. Minor grasses included Indian ricegrass (*Stipa hymenoides* Roem. & Schult), squirreltail [*Sitanion hystrix* (Nutt.) J. G. Smith], and blue grama [*Bouteloua gracilis* (HBK) Lag.). This range site was limited to the gravelly benches surrounding the Henry Mountains.

Wahweap milkvetch was also observed in localized areas in the semidesert, sandy loam range site along Coleman Draw. Vegetation included a sparse overstory of Utah juniper [*Juniperus osteosperma* (Torr.) Little] and understory dominated by galleta grass, rabbitbrush (*Chrysothamnus* spp.), and a variety of forbs.

The weather conditions (daily precipitation, maximum and minimum temperature, and soil moisture) relating to this most recent population outbreak were obtained from the Buck Canyon remote weather recording station, which is located in the higher elevation of the Wahweap milkvetch zone (2,130 m) about 64 km southwest of Hanksville, Utah.

Ranchers in the Henry Mountains area were interviewed in 1987 to determine when Wahweap milkvetch outbreaks had occurred in the past. Continuous weather records were collected from the Hanksville weather recording station for the past fifty years to see if weather patterns were related to Wahweap milkvetch outbreaks. Hanksville is located at a lower elevation than the bench areas where Wahweap milkvetch occurred and thus had lower precipitation and more extreme temperatures, but the weather patterns should be similar.

Soil cores were taken in the spring of 1987 to determine density of Wahweap milkvetch seed lying dormant in the soil. A 4 × 12.5-cm hand soil sampler was used to extract soil cores to 3-cm depth. Core samples were taken at 1-m intervals along transects established on two range sites at three locations. Transects were established at the King Ranch on cobble outcroppings and at the base of their slope. Another set of transects were established on the flat, gravelly bench tops of the stony clay loam site at the King Ranch and Applebush Bench. Transects were also established on the sandy loam site at the King Ranch and Coleman Draw. Old Wahweap milkvetch plants were not present on the sandy loam site at the King Ranch. Wahweap milkvetch stalks were present on one set of transects at Coleman Draw but were absent on the other set of transects.

RESULTS AND DISCUSSION

Weather Requirements

Over 40 mm of precipitation was recorded in October of 1984 and over 150 mm in the fall of 1985 at the Buck Canyon recording station (Fig. 1). We speculate that this moisture was sufficient to germinate Wahweap milkvetch seed lying dormant in the soil. Precipitation in the spring of 1985 was over 100 mm, and over 130 mm in the spring of 1986. Soil moisture recorded at 20-cm depth indicated that soil moisture was not limiting throughout the spring of 1985 or 1986 (Fig. 2). Soil moisture stress was less than 1 bar, indicating nearly saturated soil throughout the spring growing season. Mean spring temperature was above average for both years. It appears that weather conditions were suitable for germination and establishment of Wahweap milkvetch, and supported the population outbreak in 1985 and 1986.

A large number of the Wahweap milkvetch plants died during the summer of 1985, and very few survived the summer of 1986. There was an abundance of weathered black plants that grew in 1985 and brown senescent plants that grew in the spring of 1986. No living

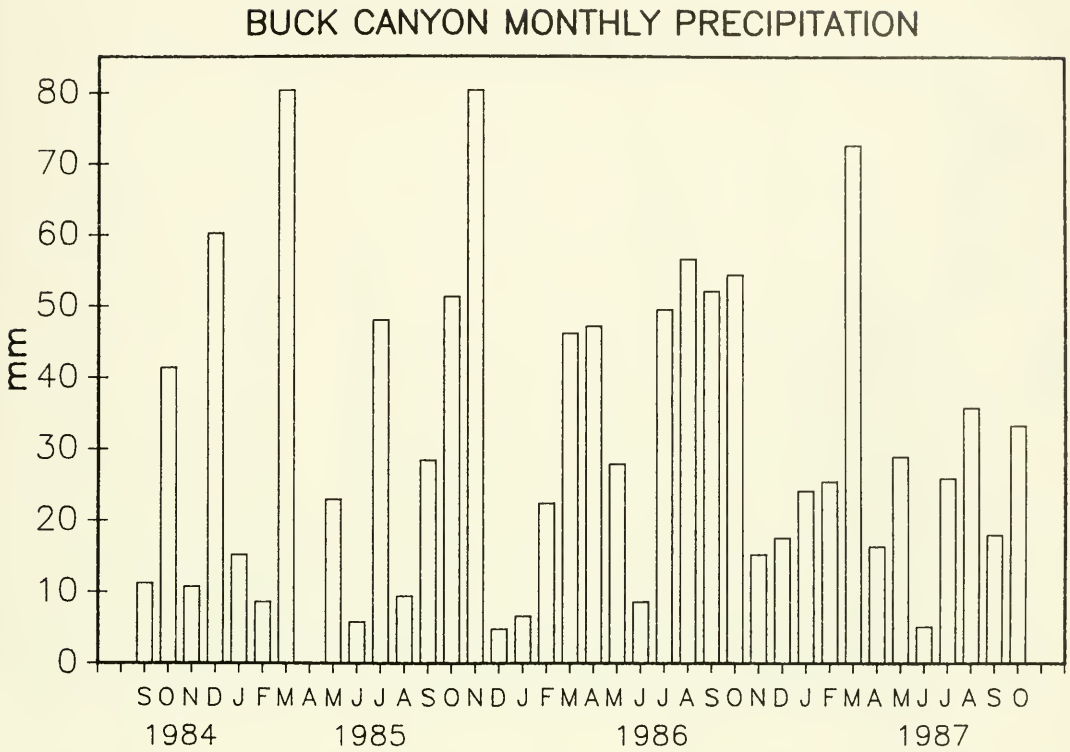

Fig. 1. Monthly precipitation at Buck Canyon remote weather recording station at 2,130-m elevation on the Henry Mountains.

plants or seedlings were observed in the fall of 1986 during the preparation and initiation of the grazing study. Very few living plants were observed on the gravelly benches in the spring of 1987, although a few plants were observed in localized areas along sandy washes. Precipitation was fairly high in the fall of 1986, but mean monthly temperatures were much lower than in the previous year. Weather conditions apparently were not suitable for germination and establishment of a new crop of Wahweap milkvetch in the fall of 1986.

The varieties of freckled milkvetch are classified as perennials (Barneby 1964, Welsh et al. 1988), but they often function as biennials. Welsh (1988) described the life cycle of potential perennials on arid or semiarid sites:

> Perennials also tend to germinate in autumn, following storms of late summer and early autumn. They persist like annuals through the winter and some will flower as annuals in the first springtime of their existence. Many do not flower in the first year, continue active growth as long as water is available, become dormant in the hot dry portions of the year, and often grow again in the autumn. In the spring of the second year they are sufficiently mature to produce flowers and fruit. If the spring of the second year is dry and moisture is inadequate, many of the potentially perennial plants die, having been functionally biennial. When conditions of moisture are adequate, however, those that have survived to flower in the second year become dormant following fruiting and persist to the spring of the third year. Seldom is precipitation adequate for continued perennation of more than a few years.

Ziemkiewicz and Cronin (1981) also stated that environmental factors influence germination and survival of juvenile locoweed plants and largely determine population densities. Late summer and fall precipitation and warm temperatures are apparently necessary for germination of Wahweap milkvetch. Abundant spring precipitation is necessary for continued growth and production of a population outbreak.

Population Cycles

Ranchers reported the occurrence of Wahweap milkvetch outbreaks in 1949, 1957,

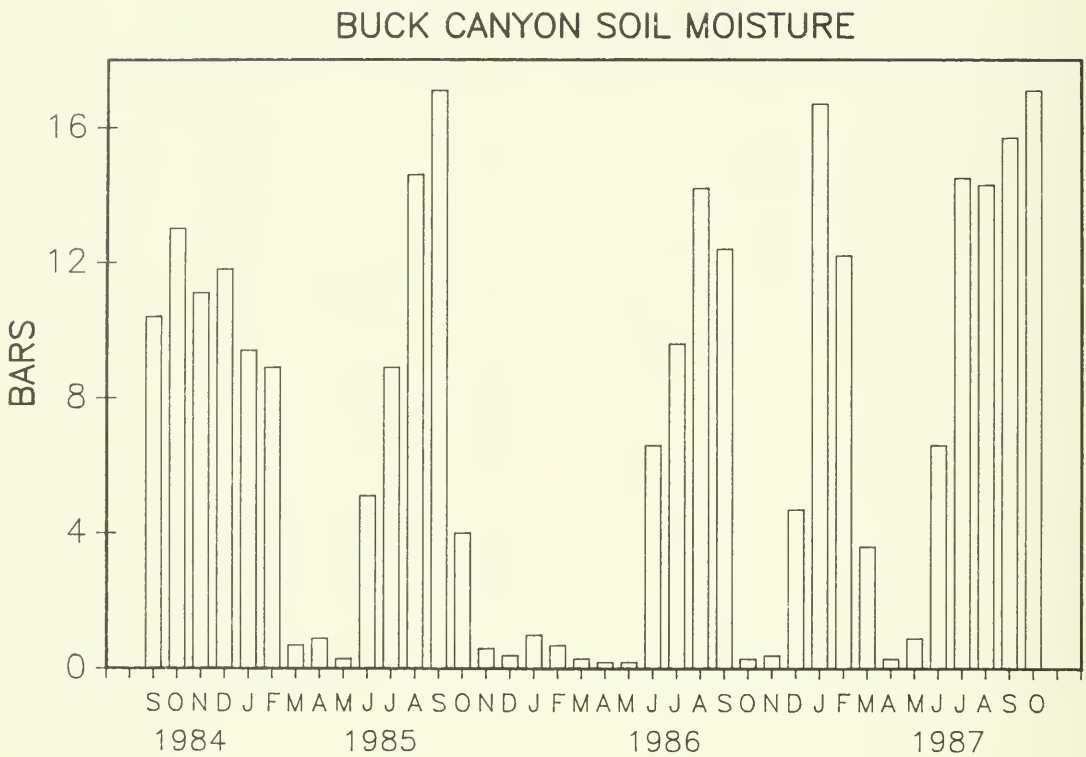

Fig. 2. Soil moisture stress at 20-m depth at the Buck Canyon remote weather station at 2,130-m elevation on the Henry Mountains.

1965, 1973, 1979, and 1985–1986 (Fig. 3). Population outbreaks occurred every six to eight years. Wahweap milkvetch grew in years of high total precipitation, except for 1973 (Fig. 3), during which it grew but not abundantly. The fall of 1972 was extremely wet, with over 130 mm of precipitation being recorded in Hanksville. The abundant fall precipitation may have carried over and supported a moderate population of Wahweap milkvetch in 1973. Spring precipitation was above average in every year Wahweap milkvetch outbreaks were reported (Fig. 4). Wahweap milkvetch grew in most years of peak spring precipitation.

Seed Reserve in Soil

Wahweap milkvetch seed was most abundant on the stony clay loam site (Table 1). The cobble outcroppings and base of the outcroppings had the highest seed density, 4,346 and 3,119 seed/m^2 respectively. Old dead Wahweap milkvetch plants from the recent population were very abundant on the cobble outcroppings. The flat gravel benches of the stony clay loam site had 650 and 1,300 seed/m^2 at the King Ranch and Applebush Bench, respectively. Old senescent Wahweap milkvetch plants were also present on these sites.

Wahweap milkvetch seed density was much lower on the sandy loam site (20 to 40 seed/m^2) where old plants were not present. Where old senescent plants were present, there were 940 seed/m^2. It is logical to assume that where plants were abundant during the previous two years, seed density in the soil is likely to be very high if the plants matured and produced seed. It is interesting to note that Wahweap milkvetch seed existed in soil where the plants were not present.

Seed density of other locoweed species in soil ranges from 400 to 1,500 seed/m^2 (Ralphs and Cronin 1987). Germination of spotted locoweed seed and seed of other locoweeds is very low (Ziemkiewicz and Cronin 1981, Baskin and Quarterman 1969, Green 1973,

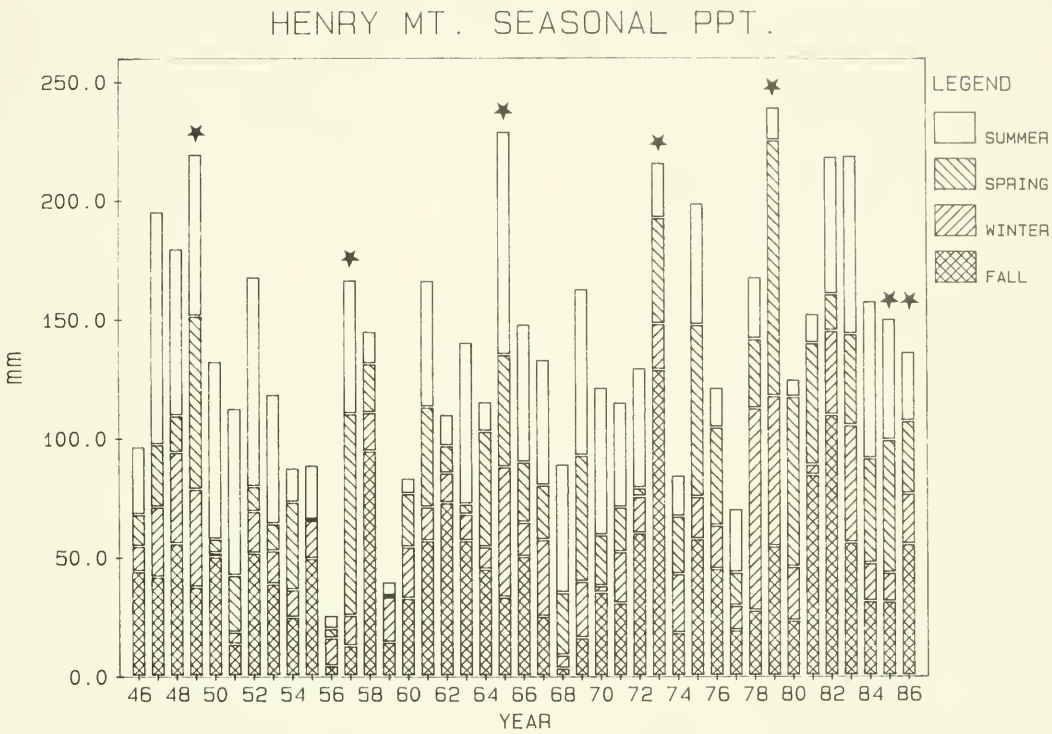

Fig. 3. Seasonal and total annual precipitation (expressed on a water year basis, October–September) recorded at Hanksville, Utah. Mean annual precipitation ($\bar{x}$) was 5.53 inches. * indicates years of Wahweap milkvetch outbreaks.

TABLE 1. Density of Wahweap milkvetch seed in soil on the Henry Mountains.

Location	Site	N	Seed/m^2 ± SE	% frequency of samples containing seed
King Ranch	semidesert stony clay loam			
	cobble outcropping	20	4346 ± 24	100
	base of slope	20	3119 ± 12	85
	bench	20	650 ± 240	65
	semidesert sandy loam	20	20 ± 14	20
Applebush	semidesert stony clay loam	20	1300 ± 347	60
Coleman Draw	semidesert sandy loam			
	old plants present	10	940 ± 308	80
	old plants not present	10	40 ± 27	20

Payne 1957, Ralphs and Cronin 1987). However, almost all seed are viable and will remain in soil and lie dormant for many years (Ralphs and Cronin 1987, Barneby 1964). There is probably sufficient seed of Wahweap milkvetch in the soil of the stony clay loam range site on the benches of the Henry Mountains to germinate and establish populations when weather conditions are favorable and create future population outbreaks.

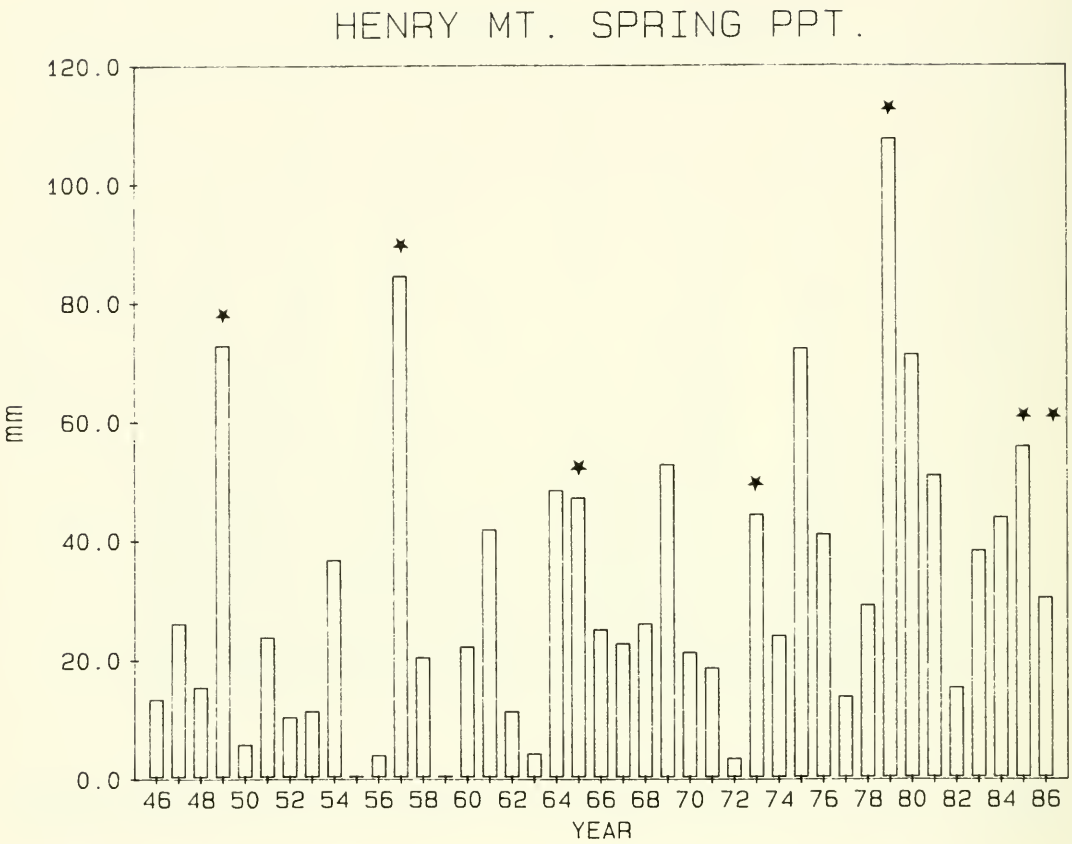

Fig. 4. Spring precipitation (April–June) recorded at Hanksville, Utah. Mean spring precipitation ($\bar{x}$) was 1.25 inches. * indicates years of Wahweap milkvetch outbreaks.

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LITERATURE CITED

BARNEBY, R. C. 1964. Atlas of North American *Astragalus*. The New York Botanical Garden, New York.

BASKIN, C. C., AND E. QUARTERMAN. 1969. Germination requirements of seeds of *Astragalus tennesseensis*. Bull. of the Torrey Botanical Club 96: 315–321.

GREEN, T. W. 1973. Factors affecting the ecology of *Astragalus cibarius* and *Astragalus utahensis* with emphasis on the role of insects. Unpublished dissertation, Utah State University, Logan, Utah.

JAMES, L. F., K. L. BENNETT, K. G. PARKER, R. F. KEELER, W. BINNS, AND B. LINDSAY. 1968. Loco plant poisoning in sheep. J. Range Manage. 21: 360–365.

JAMES, L. F. AND D. B. NIELSEN. 1987. Locoweeds: assessment of the problem on western U.S. rangelands. *In:* L. F. James, M. H. Ralphs, and D. B. Nielsen, eds.,The ecology and economic impact of poisonous plants on livestock production, Westview Press, Boulder, Colorado.

KINGSBURY, J. M. 1964. Poisonous plants of the United States and Canada. Prentice-Hall, Englewood Cliffs, New Jersey.

MARSH, C. D. 1909. The loco-weed disease of the plains. USDA Bur. Anim. Ind. Bull. 112.

PAYNE, G. F. 1957. Certain aspects of the ecology and life history of the poisonous plant, white pointloco (*Oxytropis sericea* Nutt.). Unpublished dissertation, Texas A & M University, College Station.

RALPHS, M. H., AND E. H. CRONIN. 1987. Locoweed seed in soil: density, longevity, germination, and viability. Weed Sci. 35: 792–795.

RALPHS, M. H., L. F. JAMES, D. B. NIELSEN, D. C. BAKER, AND R. J. MOLYNEUX. 1988. Cattle grazing spotted locoweed on the Henry Mountains. J. Animal Sci. 66 (12).

WELSH, S. L. 1988. *Astragalus* and *Oxytropis:* definitions, distribution, and ecological parameters. Pages 1–10 *in* L. F. James, A. D. Elbein, R. J. Molyneux, and C. D. Warren, eds., Swainsonine and related glycosidase inhibitors. Iowa State University Press, Ames.

WELSH, S. L., N. D. ATWOOD, S. GOODRICH, AND L. C. HIGGINS. 1987. A Utah flora. Great Basin Nat. Mem. 9: 340–381.

WILLIAMS, M. C., L. F. JAMES, AND B. O. BOND. 1979. Emory milkvetch (*Astragalus emoryanus* var. *emoryanus*) poisoning in chicks, sheep, and cattle. Amer. J. Vet. Res. 40: 403–406.

ZIEMKIEWICZ, P. F., AND E. H. CRONIN. 1981. Germination of seed of three varieties of spotted locoweed. J. Range Manage. 34: 94–97.

FOOD HABITS AND NEST CHARACTERISTICS OF BREEDING RAPTORS IN SOUTHWESTERN WYOMING

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ABSTRACT.—Food habits and nest site features of the Golden Eagle (*Aquila chrysaetos*), Prairie Falcon (*Falco mexicanus*), Red-tailed Hawk (*Buteo jamaicensis*), and Ferruginous Hawk (*B. regalis*) were studied near Medicine Bow, Wyoming, during 1981 and 1982. Foods consisted primarily of leporids and sciurids. The Wyoming ground squirrel (*Spermophilus richardsonii*) dominated the diet of Prairie Falcons, while Golden Eagles preyed on leporids more than did the other raptors. Diet overlap ranged from 59 to 99% between the species. Mean height of Golden Eagle nests was greater than nest height of other species. Most raptor nests (78%) were not visible from other active nests and were in view of roads. Prairie Falcons were the most specialized and Ferruginous Hawks the most versatile raptor species in terms of food habits and use of nest sites.

Ecologists recognize raptors as indicators of environmental quality because raptor populations are among the first to noticeably decline when habitats are either lost or degraded (Hickey 1969, Newton 1979). Energy and agricultural developments in the western United States may have negative impacts on populations of breeding raptors (Phillips et al. 1984). Development can cause loss of nest sites and foraging sites, nest abandonment, and death due to shooting or electrocution by transmission lines (Becker and Ball 1983, Evans 1983, U.S. Bureau of Land Management 1979, Howard and Gore 1980).

Interaction such as nest site selection and use of prey between raptor species in a community could be altered by changes that occur as a result of human impact. If this is true, population surveys may not provide adequate information on changes in raptor communities.

Our purpose was to examine how four diurnal birds of prey partition the food and nest site resources in southwestern Wyoming, an area of proposed wind energy development. The species were: Golden Eagle (*Aquila chrysaetos*), Prairie Falcon (*Falco mexicanus*), Red-tailed Hawk (*Buteo jamaicensis*), and Ferruginous Hawk (*B. regalis*).

The questions we asked were: (1) What are the prey items of each species? (2) What overlap in prey occurred among them? (3) What were the nest site characteristics of each of the four raptor species? (4) Could community partitioning be inferred from data on prey used and nest site selection?

STUDY AREA

The 712-km^2 study area was predominantly mixed sagebrush habitat in Albany and Carbon counties, southeastern Wyoming. Topography varied from gently undulating prairie to steep ridges, canyons, and sandstone outcrops. Elevations ranged from 1,993 to 2,234 m.

Big sagebrush (*Artemisia tridentata*) was the dominant shrub. Other common shrubs included Douglas and rubber rabbitbrush (*Chrysothamnus visciniflorus* and *C. nauseosus*), black sagebrush (*A. nova*), silver sagebrush (*A. cana*), and mountain mahogany (*Cerocarpus montanus*). In addition, snowberry (*Symphoriocarpus montanus*) grew along ridges, while black greasewood (*Sarcobatus vermiculatus*) and saltbush (*Atriplex* spp.) were in alkali depressions. Ponderosa pine (*Pinus ponderosa*) and juniper (*Juniperus* spp.) occurred on ridge slopes. Cottonwood (*Populus* spp.) and willow (*Salix* spp.) dominated riparian areas.

The semiarid climate was characterized by cool temperatures, low precipitation, and high evaporation (U.S. Bureau of Reclamation 1980). Most annual precipitation (27.5 cm) occurred in the spring and early summer

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months as rainfall. Annual temperature averaged 14 C. January temperatures averaged 8 C while July temperatures averaged 18 C. Westerly winds averaged 24 km (U.S. Bureau of Reclamation 1980).

Methods and Materials

Raptor nests were located by systematic flights over the area in 1979 and 1980. Ground searches were also conducted. A previous study (Oakleaf 1978) provided locations of many nests. To determine if nesting was successful, we monitored active raptor nests weekly from April through August in 1981 and 1982 or until fledging occurred.

Food Habits

Prey remains and regurgitated pellets were collected during weekly visits from within and below each nest with eggs or young. Pellets were separated into bone fragments, feathers, and hairs. Cranial material was identified with a skull key (Glass 1973). A study skin collection of local mammal species was prepared to identify prey remains collected from nests. Skeletons were cleaned and used to identify bones. Hair was identified by following the methods of Moore et al. (1974).

Estimates of raptor food habits by pellet analysis were probably biased toward overestimation of large prey items (Sherrod 1978). For instance, one large rabbit may have been consumed by several nestlings and so be represented in more than one pellet. Therefore, caution was taken in interpreting results of diet comparisons between species (see Greene and Jaksic 1983 for a discussion).

Nest Sites

Nest site locations were plotted on 7.5-min U.S.G.S. topographic maps. Characteristics of the nest sites of each species were measured in August and September after young birds had fledged. Nest substrate type (cliff, tree, pillar) and diameter at breast height of trees (dbh) were recorded. Nest height was estimated visually. Aspect and nest exposure were determined by compass. Degree of slope, nest elevation, and distance of the nest to nearest permanent water and dirt or paved road were recorded from topographic maps.

Analytical methods.—Statistical analyses were conducted with SPSS (Nie et al. 1975). Food niche breadth (diet diversity) was calculated for each species using Levins' (1968) formula:

$$B = 1/\sum p_i^2$$

where p_i was the relative occurrence of prey i in the diet. Index values ranged from 1 to n, where 1 indicated the narrowest value for food niche breadth.

Diet overlap was calculated using Pianka's (1973) formula:

$$O = p_i q_i / (\sum p_i^2 \sum q_i^2)^{1/2}$$

where p_i equaled the relative frequency of taxon i in the diet of one raptor species, and q_i was the relative frequency in the diet of the second raptor species. This index ranged from 0 (no overlap) to 1 (complete overlap in diets).

Cliffs and trees were the only nest substrates common to all raptors. Therefore, only cliff and tree nests were used in the calculations of nest substrate similarity. Throughout this paper the level of statistical significance was $P \leq .05$.

Results

Food Habits

A total of 951 pellets and prey remains were collected and identified (Table 1). Prey items were identified to species where possible. Prey of these raptors based on number of prey items included 90% mammals and 10% birds. Leporids (white-tailed jack rabbit, *Lepus townsendii*, and desert cottontail, *Sylvilagus audubonii*), Wyoming ground squirrels, thirteen-lined ground squirrels, and white-tailed prairie dogs were the mammals most commonly taken by the raptors (Table 1). Sage grouse was the most common avian prey of Golden Eagles, while passerines were more common in the diets of the other raptors.

Wyoming ground squirrels dominated Prairie Falcon diets, both in frequency of occurrence (59%) and biomass (53%). White-tailed prairie dogs ranked second, contributing 19% to frequency of occurrence and 38% of the biomass (Table 1). Thus, 98% of the Prairie Falcon diet was mammals.

Golden Eagles took 40% leporids, 27% prairie dogs, and 18% ground squirrels. In terms of total biomass, leporids accounted

TABLE 1. Diet of four raptors in 1981 and 1982. Numbers in parentheses indicate first nests and second pellets analyzed. (The symbol tr indicates the total less than 1%).

Prey Species	Prairie Falcon (22-137)			Golden Eagle (43-486)			Red-tailed Hawk (13-91)			Ferruginous Hawk (30-237)		
	N[a]	%F[b]	%B[c]	N	%F	%B	N	%F	%B	N	%F	%B
Leporidae	11	6.5	7.0	221	39.5	61.5	31	29.8	64.4	56	20.1	48.4
Wyoming ground squirrel *(Spermophilus richardsonii)*	99	58.9	53.0	101	18.0	5.4	36	34.6	14.3	98	35.3	16.2
Thirteen-lined ground squirrel *(S. tridecemlineatus)*	2	1.2	tr	1	tr	tr				5	1.8	tr
White-tailed prairie dog *(Cynomys leucurus)*	32	19.0	38.0	153	27.3	18.1	21	20.2	18.5	60	21.6	21.9
Other mammalia	1	.7	.4	34	6.0	11.0	8	7.7	.5	28	10.1	11.5
Total mammalia	145	86.3	98.4	510	89.8	96.0	96	92.3	97.7	247	88.9	98.0
Bird	23	13.7	1.6	48	8.7	3.8	8	7.7	2.3	31	11.3	1.9
Fish				2	.6	.2						
Total prey items	168			560			104			278		

[a]Number of prey items.
[b]Percentage frequency of occurrence.
[c]Percentage biomass based on total volume of pellets.

for 62% while prairie dogs and ground squirrels contributed 18% and 5%, respectively (Table 1).

Ferruginous Hawks took 37% ground squirrels, 22% prairie dogs, and 20% leporids. Leporid biomass (48%) contributed more to the total biomass estimate than prairie dog (22%) or ground squirrel (16%). Diet of the Red-tailed Hawk was likewise dominated by mammals.

Diet Comparisons

Interspecific comparisons of diet as explained by diet diversity indices were similar in both years. Ferruginous Hawks had the most diverse diet (4.74), while Prairie Falcons specialized on ground squirrels (1.53). Golden Eagle diversity was 4.63 and Red-tailed Hawk 4.21. In both years, Ferruginous Hawks and Red-tailed Hawks shared the greatest overlap in diet, while Prairie Falcons and Golden Eagles had the least similar diets (Table 2).

Chi-square tests of heterogeneity were used to compare differences in numbers of different prey classes taken by each raptor between 1980 and 1981. There were significant differences between years ($P \leq .05$) in the diet of Prairie Falcons and Golden Eagles. These results support the hypothesis that these birds take prey in an opportunistic fashion.

Using chi-square contingency tables to compare diets of pairs of raptors, we found Prairie Falcon diets differed ($P \leq .05$) from each of the other three raptors in 1981 and 1982. Prairie Falcons took a relatively low proportion of leporids and a high proportion of ground squirrels when compared to the other raptors.

Diets of Golden Eagles and Ferruginous Hawks were significantly different in both years. Golden Eagles ate larger prey items such as leporids, while Ferruginous Hawks took ground squirrels.

Nest Site Characteristics

Golden Eagles nested in significantly higher nests than the other raptor species (Table 3). Red-tailed Hawk nests in trees were higher than tree nests of Ferruginous Hawks. When comparing only cliff nests for the four species, we found no significant differences in nest height.

Cliffs were the most common substrate type. All nests of Prairie Falcon (13), except one in a tree, were on cliffs. Sixty percent of the Golden Eagle nests were on cliffs, while 40% of the Red-tailed Hawks and 30% of the Ferruginous Hawks nested on cliffs. All other Red-tailed Hawk nests were in trees, while 44% of the Ferruginous Hawk nests were on pillars and 26% in trees.

Mean nest aspect for all species was 300

Table 2. Diet overlap indices for raptor species calculated with Pianka's (1973) formula.

	1981			1982		
	Golden Eagle	Red-tailed Hawk	Ferruginous Hawk	Golden Eagle	Red-tailed Hawk	Ferruginous Hawk
Prairie Falcon	.589	.880	.894	.558	.799	.932
Golden Eagle		.829	.865		.930	.816
Red-tailed Hawk			.986			.960

degrees. Seventy-eight percent of most Ferruginous Hawk nests faced westerly (78%), yielding a mean aspect of 278 degrees. Golden Eagle nests commonly faced northwesterly (47%) while 33% faced southeasterly. Mean nest aspect was significantly different from random for Ferruginous Hawks and Golden Eagle nests alone and for the raptor assemblage as a whole.

Most raptors (78%) nested out of sight of another raptor nest. A significant proportion (77%) nested within sight of a road. Ferruginous Hawks had the widest diversity of nest substrates (B = 3.03) (Levins 1968). Prairie Falcons used the narrowest diversity of nest substrates (B = 1.15), while Golden Eagles (B = 2.12) and Red-tailed Hawks (B = 1.92) were intermediate. Using Pianka's (1973) niche overlap formula, we found that Ferruginous and Red-tailed Hawks shared the highest overlap in their use of nest substrates (0.937), while Red-tailed Hawks and Prairie Falcons were least similar (0.618). Ferruginous Hawks and Golden Eagles overlapped the most on their use of nest habits (0.918), while Red-tailed Hawks and Prairie Falcons were least similar (0.382). Red-tailed and Ferruginous Hawks also had a high overlap (0.904).

Discussion

Raptors are generally very opportunistic, selecting a wide variety of prey (Jaksic and Braker 1983, Sherrod 1978, Smith and Murphy 1973). The year-to-year food habits of raptors in the Medicine Bow assemblage, however, exhibit differing degrees of opportunism (Table 1). Prairie Falcons were the most specialized raptor, feeding primarily on prairie dogs and ground squirrels. Other studies, however, have shown that Prairie Falcons have a diverse diet (Smith and Murphy 1973). Ferruginous Hawks at Medicine Bow were generalists in terms of diet diversity; however, in Utah, Ferruginous Hawks had a more specialized diet (Smith and Murphy 1973).

Characteristics of the nest sites used by the four raptor species were very similar (Table 3); however, variation in nest substrate did occur. The only significant differences among the species were greater mean nest and nest substrate heights for Golden Eagles. Golden Eagle nest trees (mainly ponderosa pine) accounted for this difference. Golden Eagles and Prairie Falcons used the same nest sites interchangeably as did Ferruginous and Red-tailed Hawks. Nest site availability may have been constrained by the proximity of other territorial pairs of breeding raptors (Newton 1979).

Our results are comparable to others that show Ferruginous Hawks to be the most versatile in their use of nest substrates (Olendorff 1973, Gilmer and Stewart 1983). Generally, Ferruginous Hawk nest sites are associated with an elevated observation site such as a tree or hill (Janes 1985). Smith and Murphy (1973) found Ferruginous Hawks restricted their use of nest substrates in Utah. These conflicting results were likely due to study area differences. The Utah study area was a desert basin with junipers on the foothills, and Ferruginous Hawks nested in trees or on the ground. Our study area was a shortgrass prairie in which Ferruginous Hawks utilized a greater diversity of nest substrates. Conversely, Prairie Falcons had the narrowest nest substrate breadth and nested almost exclusively on cliffs (Olendorff 1973, Smith and Murphy 1973, Cade 1982). In Iowa, Bednarz and Dinsmore (1982) found Red-tailed Hawks nested in taller trees (17 m) with larger dbh (49 cm). Their study area, however, was comprised of larger trees along fields and in riparian habitats.

In this study the mean aspect of all nests was 300 degrees. In central Utah the majority of raptor nests had a westerly orientation (Smith and Murphy 1973). Lokemoen and Duebbert (1976) speculated that nest placement on certain exposures allowed incubating

TABLE 3. Nest characteristics of Prairie Falcons, Golden Eagles, and Red-tailed and Ferruginous Hawks from southeastern Wyoming, 1981–1982. Sample size in parentheses following first listing of bird species.

Variables	x	s.e.	Range
Substrate height (m)			
Prairie Falcon (14)	7.12	0.79	3.66– 13.10
Golden Eagle (30)	11.23	1.25	3.05– 39.62
Red-tailed Hawk (10)	8.99	0.98	4.57– 13.72
Ferruginous Hawk (23)	5.51	0.55	1.52– 12.19
Nest tree dbh (cm)			
Prairie Falcon	25.50	2.09	7.50– 45.50
Golden Eagle	75.40	9.91	53.50–161.00
Red-tailed Hawk	63.83	14.08	28.50–127.50
Ferruginous Hawk	34.30	1.41	31.00– 38.00
Nest height (m)			
Prairie Falcon	5.27	0.66	2.74– 10.97
Golden Eagle	8.38	1.02	2.13– 30.48
Red-tailed Hawk	7.25	0.81	3.66– 10.97
Ferruginous Hawk	4.55	0.39	1.52– 9.45
Nest elevation (m)			
Prairie Falcon	2098.88	11.58	2009–2152
Golden Eagle	2088.79	14.92	2012–2432
Red-tailed Hawk	2140.31	35.54	2036–2438
Ferruginous Hawk	2098.42	10.44	2012–2176
Slope (°)			
Prairie Falcon	23.21	2.86	7.00– 45.00
Golden Eagle	23.10	2.01	1.00– 45.00
Red-tailed Hawk	22.90	3.19	6.00– 39.00
Ferruginous Hawk	14.26	2.24	1.00– 45.00
Distance water (km)			
Prairie Falcon	0.24	0.04	0.10– 0.65
Golden Eagle	0.32	0.05	0.05– 1.20
Red-tailed Hawk	0.27	0.06	0.05– 0.60
Ferruginous Hawk	0.34	0.06	0.01– 1.30
Distance road (km)			
Prairie Falcon	0.50	0.08	0.20– 1.30
Golden Eagle	0.45	0.06	0.08– 1.50
Red-tailed Hawk	0.34	0.13	0.10– 1.45
Ferruginous Hawk	0.44	0.07	0.05– 1.15

Ferruginous Hawks to rise quickly into prevailing winds. This may have been applicable to the Medicine Bow area as prevailing winds were from the west (U.S. Bureau of Reclamation 1980). Mosher and White (1976) suggested that directional exposure of Golden Eagle nests prevents temperature stress of developing chicks. Our results showed a bimodal aspect for 30 Golden Eagle nests (326 degrees and 196 degrees). These aspects would have protected the nests from the wind and intense sunlight.

While factors such as number of perch sites, nest substrate, and substrate height can be associated with each raptor species (Janes 1985), the raptor species in the community also influence nest site selected. Likewise, prey selection is in part related to the presence of other raptors. The raptors studied near Medicine Bow, Wyoming, therefore utilize available food and nest sites. Within the habitat they became a bird assemblage based on the resources that are present. Changes, therefore, in food or sites for nests are likely to impact on the assemblage, not just individual species.

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Literature Cited

Becker, D. M., and I. J. Ball. 1983. Prairie falcon (*Falco mexicanus*). Pages 138–153 *in* J. S. Armbruster, ed., Impacts of coal surface mining on 25 migratory bird species of high federal interest. U.S. Fish Wildl. Serv. FWS/OBS–83/35. 348 pp.

Bednarz, J. C., and J. J. Dinsmore. 1982. Nest-site and habitat of Red-shouldered and Red-tailed Hawks in Iowa. Wilson Bull. 94: 31–45.

Cade, T. J. 1982. The falcons of the world. Comstock/Cornell University Press, Ithaca, N.Y. 188 pp.

Evans, D. L. 1983. Ferruginous hawk (*Buteo regalis*). Pages 109–123 *in* J. S. Armbruster, ed., Impacts of coal surface mining on 25 migratory bird species of high federal interest. U.S. Fish Wildl. Serv. FWS/OBS–83/35. 348 pp.

Gilmer, D. S., and R. E. Stewart. 1983. Ferruginous hawk populations and habitat use in North Dakota. J. Wildl. Manage. 47: 146–157.

Glass, B. P. 1973. A key to the skulls of North American mammals. 2d ed. Oklahoma State University, Stillwater. 59 pp.

Greene, H. W., and F. M. Jaksic. 1983. Food-niche relationships among sympatric predators: effects of level of prey identification. Oikos 40: 151–154.

Hickey, J. J., ed. 1969. Peregrine falcon populations: their biology and decline. University of Wisconsin Press, Madison. 596 pp.

Howard, R. P., and J. B. Gore, eds. 1980. Workshop on raptors and energy developments. Bonneville Power Admin., U.S. Fish Wildl. Serv., Idaho Power Co., Idaho Chapter of the Wildl. Soc., Boise. 125 pp.

Jaksic, F. M., and H. E. Braker. 1983. Food-niche relationships and guild structure of diurnal birds of prey: competition versus opportunism. Canadian J. Zool. 61: 2230–2241.

Janes, S. W. 1985. Habitat selection in raptorical birds. Pages 159–188 *in* M. L. Cody, ed., Habitat selection in birds. Academic Press, New York. 558 pp.

Levins, R. 1968. Evolution in changing environments. Princeton University Press, Princeton, New Jersey. 120 pp.

Lokemoen, J. T., and H. F. Duebbert. 1976. Ferruginous hawk nesting ecology and raptor populations in northern South Dakota. Condor 78: 464–470.

Moore, T. D., L. E. Spence, and C. E. Dugnolle. 1974. Identification of the dorsal guard hairs of some mammals of Wyoming. Wyoming Game and Fish Dept. Bull. No. 14. 177 pp.

Mosher, J. A., and C. M. White. 1976. Directional exposure of Golden Eagle nests. The Canadian Field Naturalist 90: 356–359.

Newton, I. 1979. Population ecology of raptors. Buteo Books, Vermillion, South Dakota. 399 pp.

Nie, N. H., C. H. Hull, J. G. Jenkins, K. Steinbrenner, and D. H. Bent. 1975. Statistical package for the social sciences. 2d ed. McGraw-Hill Book Co., New York. 675 pp.

Oakleaf, B. 1978. Medicine Bow raptor nesting survey. Wyoming Game and Fish Department Rep., Cheyenne.

Olendorff, R. R. 1973. The ecology of the nesting birds of prey of northeastern Colorado. U.S. Int. Biol. Program. Grassland Biome Tech. Rept. No. 211, Colorado State University, Fort Collins. 233 pp.

Phillips, R. L., T. P. McEneaney, and A. E. Beske. 1984. Population densities of breeding golden eagles in Wyoming. Wildl. Soc. Bull. 12: 269–273.

Pianka, E. R. 1973. The structure of lizard communities. Ann. Rev. Ecol. Syst. 4: 53–74.

Sherrod, S. K. 1978. Diets of North American Falconiformes. Raptor Res. 12: 49–121.

Smith, D. G., and J. R. Murphy. 1973. Breeding ecology of raptors in the eastern Great Basin of Utah. Brigham Young Univ. Sci. Bull., Biol. Ser. 18: (3)1–76.

U.S. Bureau of Land Management. 1979. Snake River birds of prey special research report. U.S. Dept. Int., Bur. Land Manage., Boise District, Idaho. 142 pp.

U.S. Bureau of Reclamation. 1980. Special investigations of the wind-hydroelectric energy integration study, Medicine Bow, Wyoming. Dept. Interior, Lower Missouri Region, Denver, Colorado. 26 pp.

RODENT WEIGHTS IN MODIFIED PINYON-JUNIPER WOODLANDS OF SOUTHWESTERN NEW MEXICO

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ABSTRACT.—Changing habitat structure in pinyon (*Pinus edulis*)–one-seed juniper (*Juniperus monosperma*) stands by (1) pushing trees down with a bulldozer and leaving them in place, (2) pushing, then piling and burning slash, or (3) thinning to a spacing of 6.1 m and leaving slash did not affect weights of individuals of nine rodent species. Previous studies have shown that habitat modifications influence kinds of species and numbers of individuals, but changes in total rodent biomass are a function of sizes of different species occupying different habitats, not changes in weights of individuals.

Studies reporting small mammal population changes resulting from habitat alterations are common. Considering only pinyon-juniper woodlands, for example, small mammal density changes due to overstory removal have been reported for Utah (Baker and Frischknecht 1973), Colorado (O'Meara et al. 1981), Arizona (Turkowski and Reynolds 1970), and New Mexico (Severson 1986a).

Information relative to treatment effects on small mammal biomass is less common. Grant et al. (1977, 1982), working on shortgrass prairie, examined effects of water, nitrogen, and grazing treatments on small mammal biomass; and Smith and Urness (1984) studied small mammal biomass and densities on native and altered foothill ranges in Utah. Sullivan (1979) reported weights of individual deer mice (*Peromyscus maniculatus*) from burned and unburned forest in British Columbia. Generally, however, studies reporting effects of habitat treatment on individual weights are lacking. Such information can provide a basis for comparing relative condition of individuals in different habitats and, when considered with densities, can furnish a more complete data base for analysis of effects of habitat manipulation on biomass distribution for energy flow studies (e.g., predator-prey relationships).

This paper describes influences of three pinyon-juniper overstory treatments and untreated control stands on rodent biomass and mean individual weights 13 to 18 years after treatment. Effects of these treatments on rodent densities were reported in an earlier paper (Severson 1986a).

STUDY AREA

This study was conducted on the Fort Bayard Allotment, Gila National Forest, 16 km east of Silver City, New Mexico. Important trees and shrubs are pinyon (*Pinus edulis*), one-seed juniper (*Juniperus monosperma*), alligator juniper (*J. deppeana*), gray oak (*Quercus grisea*), and hairy mountain mahogany (*Cercocarpus breviflorus*). Abundant herbaceous species include blue grama (*Bouteloua gracilis*), sideoats grama (*B. cutipendula*), and globemallow (*Sphaeralcea* spp.). Elevation ranges from 1,806 to 2,070 m. Annual precipitation averages 393 mm, with 55% falling as rain from July through September. Mean annual temperature is 12.8 C, with mean monthly extremes of 3.5 C (January) and 22.6 C (July).

Three pinyon-juniper control treatments and untreated plots, where trees were not disturbed, were randomly established in each of two blocks, one in 1965 and the other in 1970, to determine effects on deer and elk habitat use. Treatments included thinning (pinyons and junipers were cut to a minimum spacing of 6.1 m and left in place), bulldozing (all pinyons and junipers were pushed over and left in place), and bulldozing/piling/burning (all pinyons and junipers were pushed over and piled with a bulldozer, then burned). All plots were about 120 ha.

Pinyon-juniper densities averaged 359, 664, 52, and 74 stems/ha on the untreated, thinned, bulldozed/piled/burned, and bulldozed only plots, respectively, in 1983. Densities of other small trees and shrubs that were

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not controlled, primarily gray oak and hairy mountain mahogany, were 834, 481, 302, and 474 stems/ha in each respective treatment (Severson 1986a). Vegetation of treated areas is more completely described by Short et al. (1977) and Severson (1986b).

METHODS

Each plot was divided into six sampling areas, and a set of two transects was randomly placed in each. Beginning points of transects were 50 m apart and extended in opposite directions. Each plot and area were buffered by 100- and 35-m zones, respectively, to insure that transects were no closer than 200 and 70 m between plots or between areas, respectively. Transects consisted of 17 trapping locations spaced 10 m apart. Each location contained two traps—a standard rat trap and a museum special. Traps were baited with a mixture of peanut butter, oatmeal, and an ant repellent, dimethylphthalate (Anderson and Ohmart 1977). Traps were run in one transect within each plot segment in September 1981, the other in September 1982, and the first set again in September 1983. Three transects were trapped in each treatment for four consecutive days; then the traps were moved to the remaining three transects and run for the next four consecutive days. Traps were left set for 24-hour trap sessions and were checked daily. Captured individuals were tagged, double-wrapped in plastic bags, frozen, identified, and weighed after each trapping period. Specimens were weighed in plastic bags, and bag weights deducted, to insure that they were not affected by moisture loss due to freezing.

ANALYSES

A two-factor (treatments within blocks) multivariate analysis of variance with years as repeated measures was used to test the hypothesis that there were no differences in total weights of all small mammals trapped among treatments or among years. Weights of individuals were analyzed with a one-way analysis of variance to test the hypothesis that there were no differences in weights of individuals within each sex and age class among treatments. Four tests were possible for each species since adults and subadults of each sex were analyzed separately. Only those treatments in which three or more individuals of each species/sex/age class were trapped were included in the analysis. Among-years and between-block differences were tested for adult male and female white-throated woodrats (*Neotoma albigula*) and for adult male and female brush mice (*Peromyscus boylii*). None of these eight tests yielded significant results; therefore, we pooled blocks and years for analysis of individual weights.

Multivariate and one-way analyses of variance were conducted using SPSS/PC+ (Norusis 1986a, 1986b). Mean separation was done using Least Significant Differences method via SPSS/PC+ for individual small mammal weights among treatments (from one-way ANOVA) and via Multiple Comparison Procedures (developed by R. King, Rocky Mtn. For. and Range Expt. Sta., Fort Collins, Colorado) for total weights from multivariate ANOVA.

RESULTS AND DISCUSSION

Total biomass of trapped animals was significantly higher ($P < .05$) on the thinned (41.4 kg) and bulldozed-only (42.2 kg) treatments. These two treatments, along with the bulldozed/piled/burned treatment, supported the highest numbers (Severson 1986a). Total biomass on the bulldozed/piled/burned treatments (32.3 kg) was significantly lower because the larger rodents, woodrats (*Neotoma* spp.), were less abundant than on the other two treatments. The smaller species that favored more open habitats, e.g., white-footed mouse (*Peromyscus leucopus*), southern grasshopper mouse (*Onychomys arenicola*), and Ord's kangaroo rat (*Dipodomys ordii*), were relatively more abundant on bulldozed/piled/burned plots (Severson 1986a). Untreated areas produced the lowest total weight (23.5 kg) as well as the fewest animals (Severson 1986a).

Total weight of all rodents trapped in 1981 was 42.2 kg. It increased to 65.8 kg in 1982 but decreased to 31.4 in 1983. This trend generally followed total numbers trapped (381, 849, and 279 individuals in each respective year). All weights among years differed significantly ($P < .05$). The mean weight per individual was lower in 1982, but this is likely attributed to proportionately fewer trappings of the larger

TABLE 1. Mean individual weights of rodent species by sex and age classes, from four pinyon-juniper control treatments, Fort Bayard, New Mexico.

Species	Sex[1]	Age[2]	Pinyon-juniper treatment: Untreated	Thinned	Bulldozed/piled/burned	Bulldozed only
			grams			
Ord's kangaroo rat (*Dipodomys ordii*)	F	AD	46.6 ± 2.7(5)[3]	49.1 ± 6.5(3)	51.8 ± 5.1(3)	48.4 ± 2.1(5)
	M	AD	52.0 ± 5.5(5)	51.8 ± 5.0(3)	51.6 ± 3.5(14)	47.3 ± 3.8(5)
	F	SA	36.2 ± 6.6(3)	37.6 ± 2.4(4)		
White-throated woodrat (*Neotoma albigula*)	F	AD	172.0 ± 18.6(31)	173.7 ± 20.2(49)	176.4 ± 17.0(37)	176.3 ± 19.5(57)
	M	AD	195.7 ± 23.0(30)	201.7 ± 24.1(54)	201.0 ± 30.9(48)	207.4 ± 21.0(63)
	F	SA	124.8 ± 26.8(35)	130.2 ± 22.0(40)	127.2 ± 20.8(42)	129.9 ± 24.7(45)
	M	SA	136.8 ± 22.1(16)	134.8 ± 24.3(32)	130.7 ± 29.3(20)	138.6 ± 29.5(36)
Mexican woodrat (*Neotoma mexicana*)	M	AD		220.9 ± 23.4(6)		196.7 ± 32.3(4)
Stephen's woodrat (*Neotoma stephensi*)	F	AD	164.3 ± 28.2(4)	162.9 ± 17.8(9)		153.0 ± 10.8(7)
	M	AD	180.5 ± 21.8(4)		177.6 ± 14.9(7)	167.9 ± 14.2(4)
	F	SA		122.6 ± 28.8(6)		129.3 ± 29.8(4)
Southern grasshopper mouse (*Onychomys arenicola*)	F	AD			27.4 ± 3.6(10)	30.9 ± 5.5(12)
	M	AD			26.2 ± 1.4(12)	24.4 ± 1.1(3)
	F	SA	18.4 ± 2.1(6)		21.2 ± 2.9(15)	20.9 ± 2.8(9)
	M	SA			21.8 ± 2.2(22)	20.1 ± 7.7(5)
Brush mouse (*Peromyscus boylii*)	F	AD	31.9 ± 5.2(13)	31.3 ± 4.8(25)	31.0 ± 6.2(11)	29.1 ± 5.4(20)
	M	AD	26.3 ± 2.3(15)	25.8 ± 3.0(35)	26.6 ± 4.6(19)	26.4 ± 3.2(35)
	F	SA	22.0 ± 4.7(3)	21.5 ± 4.4(16)	20.5 ± 4.6(10)	21.1 ± 4.7(12)
	M	SA	19.8 ± 3.4(9)	21.2 ± 3.6(17)	22.4 ± 3.3(4)	21.3 ± 2.5(16)
Rock mouse (*Peromyscus difficilis*)	F	AD		30.2 ± 2.3(3)		28.9 ± 1.7(4)
White-footed mouse (*Peromyscus leucopus*)	F	AD		30.5 ± 3.2(6)[4]	37.7 ± 3.0(16)[4]	
	M	AD	29.2 ± 2.0(4)	28.4 ± 1.5(6)	29.3 ± 2.7(21)	25.2 ± 4.3(4)
Pinyon mouse (*Peromyscus truei*)	F	AD	33.0 ± 7.0(8)	34.2 ± 3.8(16)		
	M	AD	27.3 ± 2.7(10)	28.2 ± 2.1(17)		
	M	SA	21.8 ± 1.9(5)	20.9 ± 3.0(7)		
Western harvest mouse (*Reithrodontomys megalotis*)	F	AD			13.5 ± 3.5(7)	14.3 ± 1.8(14)
	M	AD	11.8 ± 0.7(3)	12.1 ± 0.9(4)	12.4 ± 1.2(12)	12.9 ± 1.2(13)
	M	SA			8.7 ± 2.8(6)	10.1 ± 0.7(13)

[1]F = female, M = male.
[2]AD = adult, SA = subadult.
[3]Mean ± standard deviation (sample size).
[4]Means are significantly different ($P < .05$).

woodrats (62%, 39%, and 63% in each respective year).

Mean weights of individuals within sex and age classes were generally not significantly different among treatments ($P < .05$; Table 1). Of the 28 tests, only one (female, adult white-footed mouse) demonstrated a significant difference between treatments; those from the bulldozed/piled/burned plots were heavier than those from thinned plots ($P < .05$; Table 1).

Habitat modifications can influence kinds of species and number of individuals (Severson 1986a). Total rodent biomass can also be affected, but generally as a function of sizes of different species occupying different habitats. Changing habitat, such as eliminating or altering overstory, does not appear to

influence weights of individual animals. These results are in general agreement with those of Sullivan (1979).

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LITERATURE CITED

ANDERSON, B. W., AND R. D. OHMART. 1977. Rodent bait additive which repels insects. J. Mamm. 58: 242.

BAKER, M. F., AND N. C. FRISCHKNECHT. 1973. Small mammals increase on recently cleared and seeded juniper rangeland. J. Range Manage. 26: 101–103.

GRANT, W. E., E. C. BIRNEY, N. R. FRENCH, AND D. M. SWIFT. 1982. Structure and productivity of grassland small mammal communities related to grazing induced changes in vegetative cover. J. Mamm. 63: 248–260.

GRANT, W. E., N. R. FRENCH, AND D. M. SWIFT. 1977. Response of a small mammal community to water and nitrogen treatments in a shortgrass prairie ecosystem. J. Mamm. 58: 637–652.

NICKERSON, M. F., G. E. BRINK, AND C. FEDDEMA. 1976. Principle range plants of the central and southern Rocky Mountains: names and symbols. USDA Forest Serv. Gen. Tech. Rept. RM–20. 121 pp.

NORUSIS, M. J. 1986a. SPSS/PC+ for the IBM PL/XT/AT. SPSS Inc., 444 N. Michigan Ave., Chicago, Illinois.

———. 1986b. Advanced statistics, SPSS/PC+ for the IBM PC/XT/AT. SPSS Inc., 444 N. Michigan Ave., Chicago, Illinois.

O'MEARA, T. E., J. B. HAUFLER, L. H. STELTER, AND J. G. NAGY. 1981. Nongame responses to chaining of pinyon-juniper woodland. J. Wildl. Manage. 45: 381–389.

SEVERSON, K. E. 1986a. Small mammals in modified pinyon-juniper woodlands, New Mexico. J. Range Manage. 39: 31–34.

———. 1986b. Woody plant reestablishment in modified pinyon-juniper woodlands, New Mexico. J. Range Manage. 39: 438–442.

SHORT, H. L., W. EVANS, AND E. L. BOEKER. 1977. The use of natural and modified pinyon pine–juniper woodlands by deer and elk. J. Wildl. Manage. 41: 453–459.

SMITH, C. B., AND P. J. URNESS. 1984. Small mammal abundance on native and improved foothill ranges, Utah. J. Range Manage. 37: 353–357.

SULLIVAN, T. P. 1979. Demography of populations of deer mice in coastal forest and clear-cut (logged) habitats. Canadian J. Zool. 57: 1636–1648.

TURKOWSKI, F. J., AND H. G. REYNOLDS. 1970. Response of some rodent populations to pinyon-juniper reductions on the Kaibab Plateau, Arizona. Southwest. Natur. 15: 23–27.

SPRING DENITRIFICATION RATES IN SOILS OF FOUR EASTSIDE SIERRA NEVADA PLANT COMMUNITIES[1]

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ABSTRACT.—Denitrification rates in soils of four subalpine plant communities in the Sierra Nevada were determined by the acetylene blockage method. The study area included riparian, meadow, forest, and barren sites. Data were collected during dawn-to-dusk measurements in April 1987. Soil atmosphere samples were analyzed for N_2O content using gas chromatography. Generally, temporal variability in denitrification rate within each plant community was insubstantial. Denitrification rate and soil temperature were found to be significantly correlated only in the riparian and barren sites. Of the four communities, the riparian site was found to have the lowest rate of denitrification overall. However, differences among sites in denitrification rate could not be conclusively attributed to variation in soil temperature, moisture, organic matter, total C and N, C:N ratio, NO_3-N, or pH.

Past research has yielded conflicting conclusions regarding soil denitrification rates and the parameters affecting them. Nevertheless, several studies agree that spatial and temporal variability in denitrification rates exists (Burford and Stefanson 1973, Dowdell and Smith 1974, Biggar 1978, Ryden et al. 1978, Folorunso and Rolston 1984, Robertson and Tiedje 1984, Mosier et al. 1986a).

While denitrification is a process generally believed to be inhibited by the presence of oxygen, even very dry soils have anaerobic pockets in which denitrification occurs. Soil moisture is believed to affect denitrification rates by governing the diffusion of oxygen and thus the number of anaerobic sites (Alexander 1977, Rolston 1981). Soil temperature may alter the effect of soil moisture on denitrification rates (Mosier et al. 1986b) by modifying N_2O solubility in water (Blackmer et al. 1982).

Contrary to the data presented by Focht (1978) and Terry and Tate (1980), Hussey et al. (1985) suggested that there is a positive relationship between the number of denitrifying bacteria and denitrification rates. Soil organic matter content is often positively correlated with denitrification (Stefanson 1973, Dowdell and Smith 1974, Rolston et al. 1982, Parkin 1987). However, Muller et al. (1980) found no correlation between denitrification and organic C, total N, or exchangeable NH_4. Some studies have demonstrated that soil NO_3 concentration does not limit denitrification (Ryden and Lund 1980, Bremner and Blackmer 1981).

The acetylene blockage method has proven a feasible technique for measuring field denitrification rates (Balderston et al. 1976, Yoshinari et al. 1977, Yeomans and Beauchamp 1978, Ryden et al. 1979a, Ryden et al. 1979b). During denitrification, NO_3 is reduced to N_2 by the reaction

$$NO_3 \rightarrow NO_2 \rightarrow N_2O \rightarrow N_2.$$

The presence of acetylene (C_2H_2) inhibits the reduction of N_2O to N_2, thus permitting measurement of the soil atmosphere concentration of N_2O. Balderston et al. (1976) concluded that the effects of C_2H_2 are reversible and that measurement of N_2O is an acceptable method for the determination of denitrification rates and quantities in either soil or water.

Most research on denitrification rates has been conducted in the laboratory or on agricultural soils. This study was designed to provide baseline data on field denitrification rates in soils of four plant communities of a subalpine Sierra Nevada watershed. These measurements were concentrated during mid-April 1987 in order to quantify denitrification during seasonal snowmelt flushing of the soil profile.

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MATERIALS AND METHODS

Site Description

The study site containing the four plant communities is located at an elevation of 2,134 m near the base of an 80-ha watershed on the east slope of the Carson Range in Nevada immediately over the crest from the Lake Tahoe Basin (39°7′28″N, 119°52′47″W). The plant communities include a riparian, meadow, forest, and barren site. A dense stand of *Alnus tenuifolia* dominates the riparian site, but *Cornus stolonifera*, *Juncus* sp., *Agrostis* sp., and *Poa sandbergii* are also present. The principal vegetation of the meadow site consists of *P. sandbergii*, *Agrostis* sp., and *J. ensifolius*. *Abies concolor* and *Pinus jeffreyi* dominate the forest site, and the barren site is devoid of any vegetation.

Field Equipment and Procedures

Three soil chambers, constructed according to the design of Denmead (1979) as modified by Greenlee (1985), were installed in each of the four plant communities. Acetylene was supplied to the soil atmosphere through probes consisting of drip irrigation tubing perforated on one side at 5-cm intervals and inserted 1 m into the ground (Greenlee 1985). Four probes were installed per chamber. The 12 probes on each site were simultaneously supplied with C_2H_2.

Acetylene was continuously supplied to the soil at a rate of 600 ml/min. The addition of C_2H_2 to the soil began 30 min prior to the start of the sampling period to permit its diffusion into the profile. The evacuation of N_2O from the chambers and its adsorption onto 5Å molecular sieve material was accomplished as described by Greenlee (1985). Nitrous oxide gas samples were suctioned from the chambers through vials containing the molecular sieve material. This occurred during alternate hours from 6:00 a.m. to 7:00 p.m. at a rate of approximately 300 ml/min (Ryden et al. 1979b). After each sampling period the vials of molecular sieve material were capped and replaced. Chamber covers were removed to facilitate aeration between each sampling period.

Soil moisture and soil and air temperatures were measured at the midpoint of each one-hour sampling period. Soil moisture was measured with a Campbell Pacific Neutron Model 503DR hydroprobe moisture depth gauge (CPN Corp., Pacheco, California). A neutron access tube, constructed of 0.13-cm thin-walled aluminum tubing with a 4.83-cm I.D., was installed near the chambers in each plant community by augering holes of slightly larger diameter and then backfilling. The probe was lowered down the tube, and readings were taken every 15 cm to a depth of 105 cm below the soil surface. Soil temperature was measured at depths of 5, 10, and 25 cm using three Reotemp Model H bimetal coil thermometers per chamber (Reotemp Instrument Corp., San Diego, California). Air temperature was measured 0.5 m above the ground.

Five soil subsamples were collected near each chamber to a depth of 20 cm and combined into one composite sample per chamber. These samples were kept on ice until arrival at the lab, oven-dried at 38 C for 48 hours, and ground to pass through a No. 10 (2-mm opening) sieve. Soil texture was determined by the hydrometer method; organic matter and total C by the Walkley-Black method, colorimetric and titration modifications, respectively; total N by macro-Kjeldahl digestion; NO_3-N by use of a specific ion electrode after extraction with $CaSO_4$; and pH by glass electrode on a 1:1 mixture (by weight) of soil and distilled water (American Society of Agronomy 1965). All analyses were done by A & L Agricultural Laboratories (Memphis, Tennessee). Total C and N values were used to calculate C:N ratios.

Soil water samples were collected at 10- and 25-cm depths from two lysimeters installed near the chambers in each plant community. These samples were transported on ice to the Desert Research Institute (Reno, Nevada), where $N0_3$ analyses were done using cadmium reduction (U.S. Environmental Protection Agency 1979).

Laboratory Equipment and Procedures

Laboratory procedures were based on those described by Ryden et al. (1978) as modified by Greenlee (1985). Nitrous oxide gas samples of 0.5 ml were injected into a gas chromatograph column of 80/100-mesh Porapak Q material (500 cm long by 0.21 cm I.D.) heated to 50 C. Argon was the carrier gas with a flow rate of 25 ml/min. Nitrous oxide was detected by a ^{63}Ni electron capture detector

heated to 350 C. Standards of 13.2 ppm N_2O were run after every sample. Each sample and each standard was injected at least twice, or until values were within 10%, and an average value calculated. Quantification of sample N_2O peak heights was based on comparison with standard peak heights. The field equipment set-up was duplicated in the lab using the standard N_2O tank as the gas source in order to calculate recovery rates. Recovery rates were approximately 70%.

Statistical Methods

All data were subjected to analyses of variance, and differences among means were evaluated using the LSD test ($\alpha = .10$). Log normal transformation was performed on all denitrification values as proposed by Parkin et al. (1988), and the arcsine transformation on soil organic matter, total C and N, and C:N ratio values. The analyses included comparisons among sampling periods within each plant community for denitrification rate and soil temperature at each measurement depth, and comparisons among plant communities for all variables. Also, a stepwise regression was performed to evaluate the relationship between denitrification rate and soil temperature within each plant community. The Statistical Analysis System (SAS Institute Inc., Cary, North Carolina) was used for all statistical analyses.

RESULTS

Overall, denitrification rates within each plant community did not vary appreciably among sampling periods. The lone exception was in the forest site, where a significantly lower rate was observed during the 6:00 to 7:00 p.m. sampling period. There was a positive correlation between denitrification rate and soil temperature at the 25 cm depth in the riparian site ($r^2 = .22$, $p = .03$), while denitrification rate and soil temperature at the 10 cm depth were negatively correlated in the barren site ($r^2 = .25$, $p = .02$). Denitrification rate and soil temperature were not significantly correlated in these two sites at any other depth of temperature measurement. Furthermore, there was no apparent relationship between these two parameters, regardless of temperature measurement depth, in the meadow or forest site.

The mean denitrification rate in the riparian site was significantly lower than those of the forest or barren sites by approximately 9% in either comparison (Table 1). The meadow site exhibited an intermediate rate that did not differ significantly from that of any other site. The soil of the forest site was frozen during these measurements, but the effect on denitrification was negligible. Soil temperature differences were substantial between the forest and barren sites, but the denitrification rates were essentially equivalent. Percent soil moisture by volume differed significantly among all sites. Lower denitrification rates were generally associated with higher soil moisture contents, but no conclusive relationship could be established from these data. Mean air temperatures ranged from 5 C at the barren site to 9 C at the meadow site, while intermediate values were observed at the other two sites.

Soil content of organic matter and total C and N were significantly greater in the riparian site than in the other sites examined (Table 2). Conversely, the values for these three parameters were generally lowest in the barren site. Among the four plant communities, C:N ratios generally paralleled denitrification rates, with the C:N ratios and denitrification rates being lower in the riparian and meadow sites and higher in the forest and barren sites. Soil NO_3-N differences among sites, although in some cases significant, were small. Nevertheless, sites with higher NO_3-N concentrations exhibited lower denitrification rates overall. The soil of the forest site was significantly more acidic than that of the other sites, but soil reaction within the range of values observed had no apparent effect on denitrification. Soil texture in all four plant communities was classified as either loamy sand or sandy loam. Soil water analyses for NO_3 indicated low concentrations in all sites of ≤ 0.002 mg/l.

DISCUSSION AND CONCLUSIONS

Many studies have shown soil denitrification rates to be affected by soil temperature, soil moisture, or both (Black 1968, Blackmer et al. 1982, Fillery 1983, Greenlee 1985, Mosier et al. 1986b). This study reveals a site-dependent relationship between soil denitrification and temperature with a positive

TABLE 1. Soil denitrification rate, temperature, and moisture in four subalpine Sierra Nevada plant communities.[a]

Site	Denitrification rate ug/m²/hr	Soil temperature °C 5 cm	10 cm	25 cm	Soil moisture % by volume at 45 cm
Riparian	88.6b	7a	6a	4b	50a
Meadow	90.9ab	8a	7a	5a	42b
Forest	97.2a	−1b	0b	0c	18d
Barren	97.8a	6a	6a	5a	21c

[a]Means sharing a common letter do not differ significantly according to the LSD test at $\alpha = .10$.

TABLE 2. Selected chemical properties of soils in four subalpine Sierra Nevada plant communities.[a]

Site	Organic matter %	Total C %	Total N %	C:N ratio	NO_3-N ppm	pH
Riparian	8.0a	4.9a	0.29a	18.5b	3a	6.5b
Meadow	4.0b	2.5b	0.13b	20.3b	3a	6.8b
Forest	3.0b	1.8b	0.05bc	36.5a	2b	5.6a
Barren	3.0b	1.5b	0.04c	33.7a	2b	6.3b

[a]Means sharing a common letter do not differ significantly according to the LSD test at $\alpha = .10$.

correlation and a negative correlation in the riparian and barren sites, respectively, but no apparent relationship between these two parameters in the meadow and forest sites. Mosier et al. (1986b) found that relatively low soil temperatures (12–24, 8–19, and 6–16 C for 5-, 10-, and 20-cm depths, respectively) contributed to low N_2O emission rates even when soil moisture conditions were near or above field capacity. Soil temperatures in the four plant communities examined here may have been below the threshold at which temperature predictably influences denitrification. Furthermore, the effects of soil moisture may have also been suppressed by these low temperatures. Thus, at these temperatures denitrification occurred, but it is unlikely that the variation in rates is solely attributable to soil temperature or moisture differences within or among sites.

Among the four plant communities, only the riparian site differed significantly in denitrification rate, but none of the other soil parameters investigated could be conclusively identified as a causal factor in the lower rate measured at this site. Studies by Ryden (1981) and Haider et al. (1987) suggest that plant absorption of NO_3 may limit denitrification. In this study, however, the lower denitrification rate of the riparian community could not be logically attributed to NO_3 uptake by the dense mountain alder stand occupying this site since soil NO_3-N concentration was not lower than those of the other sites.

The results presented here suggest that soil parameters other than those examined may have a significant impact on denitrification in wildland soils. Denitrifying bacterial populations may have been a factor of importance in the four plant communities investigated in this study, although other studies (Focht 1978, Terry and Tate 1980, Hussey et al. 1985) have presented conflicting conclusions regarding this parameter. It is obvious from the disparity in the results of denitrification studies that further research is necessary to delineate the causal relationships in the temporal and spatial denitrification variability of wildland soils.

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LITERATURE CITED

ALEXANDER, M. 1977. Introduction to soil microbiology. John Wiley and Sons, New York.

AMERICAN SOCIETY OF AGRONOMY. 1965. Methods of soil analysis. C. A. Black, ed. American Society of Agronomy, Madison, Wisconsin.

BALDERSTON, W. L., B. SHERR, AND W. J. PAYNE. 1976. Blockage by acetylene of nitrous oxide reduction in *Pseudomonas perfectomarinus*. Appl. Environ. Microbiol. 31: 504–508.

BIGGAR, J. W. 1978. Spatial variability of nitrogen in soils. Pages 201–211 *in* D. R. Nielson and J. G. MacDonald, eds., Nitrogen in the environment. Vol. 1. Academic Press, New York.

BLACK, C. A. 1968. Soil-plant relationships. John Wiley and Sons, New York.

BLACKMER, A. M., S. G. ROBBINS, AND J. M. BREMNER. 1982. Diurnal variability in rate of emission of nitrous oxide from soils. Soil Sci. Soc. Amer. J. 46: 937–942.

BREMNER, J. M., AND A. M. BLACKMER. 1981. Terrestrial nitrification as a source of atmospheric nitrous oxide. Pages 151–170 *in* C. C. Delwiche, ed., Denitrification, nitrification and atmospheric nitrous oxide. John Wiley and Sons, New York.

BURFORD, J. R., AND R. C. STEFANSON. 1973. Measurement of gaseous losses of nitrogen from soils. Soil Biol. Biochem. 5: 133–141.

DENMEAD, O. T. 1979. Chamber systems for measuring nitrous oxide emission from soils in the field. Soil Sci. Soc. Amer. J. 43: 89–95.

DOWDELL, R. J., AND K. A. SMITH. 1974. Field studies of the soil atmosphere: II. Occurrence of nitrous oxide. J. Soil Sci. 25: 231–238.

FILLERY, I. R. P. 1983. Biological denitrification. Pages 33–64 *in* J. R. Feeney and J. R. Simpson, eds., Gaseous loss of nitrogen from plant soil systems. Nijhoff/Junk, The Hague.

FOCHT, D. D. 1978. Methods of analysis of denitrification in soils. Pages 433–490 *in* D. R. Nielson and J. G. MacDonald, eds., Nitrogen in the environment. Vol. 2. Academic Press, New York.

FOLORUNSO, O. A., AND D. E. ROLSTON. 1984. Spatial variability of field-measured denitrification gas fluxes. Soil Sci. Soc. Amer. J. 48:1214–1219.

GREENLEE, D. L. 1985. Denitrification rates of a mountain meadow near Lake Tahoe. Unpublished thesis, University of Nevada at Reno.

HAIDER, K., A. MOSIER, AND O. HEINEMEYER. 1987. The effect of growing plants on denitrification at high soil nitrate concentrations. Soil Sci. Soc. Amer. J. 51: 97–102.

HUSSEY, M. R., Q. D. SKINNER, J. C. ADAMS, AND A. J. HARVEY. 1985. Denitrification and bacterial numbers in riparian soils of a Wyoming mountain watershed. J. Range Manage. 38: 492–496.

MOSIER, A. R., W. D. GUENZI, AND E. E. SCHWEIZER. 1986a. Field denitrification estimation by nitrogen-15 and acetylene inhibition techniques. Soil Sci. Soc. Amer. J. 50: 831–833.

———. 1986b. Soil losses of dinitrogen and nitrous oxide from irrigated crops in northeastern Colorado. Soil Sci. Soc. Amer. J. 50: 344–348.

MULLER, M. M., V. SUNDMAN, AND J. SKUJINS. 1980. Denitrification in low pH spodosols and peats determined with the acetylene inhibition method. Appl. Environ. Microbiol. 40: 235–239.

PARKIN, T. B. 1987. Soil microsites as a source of denitrification variability. Soil Sci. Soc. Amer. J. 51: 1194–1199.

PARKIN, T. B., J. J. MEISINGER, S. T. CHESTER, J. L. STARR, AND J. A. ROBINSON. 1988. Evaluation of statistical estimation methods for lognormally distributed variables. Soil Sci. Soc. Amer. J. 52: 323–329.

ROBERTSON, G. P., AND J. M. TIEDJE. 1984. Denitrification and nitrous oxide production in successional and old-growth Michigan forests. Soil Sci. Soc. Amer. J. 48: 383–389.

ROLSTON, D. E. 1981. Nitrous oxide and nitrogen gas production in fertilizer loss. Pages 127–149 *in* C. C. Delwiche, ed., Denitrification, nitrification and atmospheric nitrous oxide. John Wiley and Sons, New York.

ROLSTON, D. E., A. N. SHARPLEY, D. W. TOY, AND F. E. BROADBENT. 1982. Field measurement of denitrification: III. Rates during irrigation cycles. Soil Sci. Soc. Amer. J. 46: 289–296.

RYDEN, J. C. 1981. N_2O exchange between a grassland soil and the atmosphere. Nature 292: 235–237.

RYDEN, J. C., AND L. J. LUND. 1980. Nature and extent of directly measured denitrification losses from some irrigated vegetable crop production units. Soil Sci. Soc. Amer. J. 44: 505–511.

RYDEN, J. C., L. J. LUND, AND D. D. FOCHT. 1978. Direct in-field measurement of nitrous oxide flux from soils. Soil Sci. Soc. Amer. J. 42: 731–737.

RYDEN, J. C., L. J. LUND, AND D. D. FOCHT. 1979a. Direct measurement of denitrification loss from soils: I. Laboratory evaluation of acetylene inhibition of nitrous oxide reduction. Soil Sci. Soc. Amer. J. 43: 104–110.

RYDEN, J. C., L. J. LUND, J. LETEY, AND D. D. FOCHT. 1979b. Direct measurement of denitrification loss from soils: II. Development and application of field methods. Soil Sci. Soc. Amer. J. 43: 110–118.

STEFANSON, R. C. 1973. Evolution patterns of nitrous oxide and nitrogen in sealed soil-plant systems. Soil Biol. Biochem. 5: 167–169.

TERRY, R. E., AND R. L. TATE III. 1980. Denitrification as a pathway for nitrate removal from organic soils. Soil Sci. 129: 162–166.

U.S. ENVIRONMENTAL PROTECTION AGENCY. 1979. Methods for chemical analysis of water and waste. EPA–600/470–020. Cincinnati, Ohio.

YEOMANS, J. C., AND E. G. BEAUCHAMP. 1978. Limited inhibition of nitrous oxide reduction in soil in the presence of acetylene. Soil Biol. Biochem. 10: 517–519.

YOSHINARI, T., R. HYNES, AND R. KNOWLES. 1977. Acetylene inhibition of nitrous oxide reduction and measurement of denitrification and nitrogen fixation in soil. Soil Biol. Biochem. 9: 177–183.

ADDITIONAL RECORDS OF THE SPOTTED BAT (*EUDERMA MACULATUM*) FROM CALIFORNIA

Vernon C. Bleich[1] and Andrew M. Pauli[2]

ABSTRACT.—Additional records of the spotted bat (*Euderma maculatum*) from Inyo County and Shasta County, California, are reported. The latter record represents the northernmost locale for this species in California.

A live adult male spotted bat (*Euderma maculatum*) with a fractured humerus was found on the ground at Lone Pine, Inyo County, California, on 10 August 1986. It later died in captivity. The specimen (CSULB 11834) was prepared as a skin with skull, fluid-preserved carcass, and stained glans penis and is deposited in the Mammal Collection at California State University, Long Beach. Standard measurements are: total length, 111 mm; tail length, 51 mm; hind foot, 11 mm; ear, 41 mm; forearm, 49 mm. The spotted bat had previously been reported from the Owens Valley, 60 miles north of Lone Pine at Bishop, Inyo County (Constantine et al. 1979).

Vegetation in the Owens Valley is typical of the Great Basin, consisting primarily of sagebrush (*Artemisia tridentata*), saltbush (*Atriplex* spp.), greasewood (*Sarcobatus vermiculatus*), and rabbitbrush (*Chrysothamnus nauseosus*). The Owens Valley is in the rainshadow of the Sierra Nevada and is extremely arid.

Another spotted bat was found alive in a garage at a residence in Palo Cedro, Shasta County, California, on 14 March 1983 and was taken to the Redding Office of the California Department of Fish and Game where the identification was confirmed by T. P. Stone. Final disposition of that specimen is unknown. This record extends the reported distribution of this species about 245 km NW from Reno, Washoe County, Nevada (Hall 1935), and 400 km SW from the Alvord Basin, Harney County, Oregon (McMahon et al. 1981). Vegetation at Palo Cedro consists largely of oak savannah (*Quercus* spp.); the area is more mesic than the Owens Valley.

We thank E. and M. Muniz for calling our attention to the Lone Pine specimen and D. G. Huckaby for preparing it for deposition in the CSULB Mammal Collection.

LITERATURE CITED

CONSTANTINE, D. G., G. L. HUMPHREY, AND T. B. HERBENICK. 1979. Rabies in *Myotis thysanodes*, *Lasiurus ega*, *Euderma maculatum* and *Eumops perotis* in California. J. Wildl. Dis. 15: 343–345.

HALL, E. R. 1935. Occurrence of the spotted bat at Reno, Nevada. J. Mammal. 16: 148.

MCMAHON, E. E., C. C. OAKLEY, AND S. P. CROSS. 1979. First record of the spotted bat (*Euderma maculatum*) from Oregon. Great Basin Nat. 41: 270.

WATKINS, L. C. 1977. *Euderma maculatum*. Mammal Species 77: 1–4.

WILLIAMS, D. F. 1986. Mammalian species of special concern in California. California Department of Fish and Game, Sacramento. 111 pp.

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