Historical Background to Southwestern Ecological Studies

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The Southwest is justifiably famous as a focal area for North American natural history inquiry and discovery. Many of America's great conservationists and naturalists, President Theodore Roosevelt, Charles Sheldon, John Wesley Powell, and Aldo Leopold, were strongly influenced by its spectacular and diverse environments. In addition, many eminent biologists and ecologists were lured to work in the Southwest, C. Hart Merriam, E. W. Nelson, E. A. Goldman, Joseph Grinnell, Homer Shantz, Forrest Shreve, F. E. Clements, and more recently Walter P. Taylor, Carl L. Hubbs, Robert MacArthur, and Donald Tinkle. Four presidents of the Ecological Society of America worked and made their homes in Arizona (Shantz, Shreve, Charles Vorhies and Taylor; Burgess, 1977). As a result, much understanding of the continent's biogeography originated here with the work of Merriam, Shreve, Lee R. Dice, and their associates, students and successors.

The main reason the Southwest has contributed so greatly to knowledge of natural history is the juxtaposition of North American biomes so obvious in the region. Communities of plants and animals are often clearly demarcated by elevational gradients. Consequently, habitats in vastly different biomes may be readily sampled during a day's fieldwork. Reaching a similar diversity of habitats could literally require days of travel in other parts of the continent.

A second reason favoring Southwestern studies is the excellent historical record of this region, especially the extensive natural information obtained from relatively continous fossil records. There are Tertiary floras complete enough for interpretation of past elevations, climates, and other ecological features, as well as the lineages of existing species and even communities (Axelrod, 1958b, 1979). Fossil to recent pollen in sediments of closed drainage basins have added another paleobotanical technique for interpretations of change, or lack of it (Martin, 1963; Martin and Mehringer, 1965; Meyer 1973, 1975; many others). Complementary data are available from such diverse sources as ancient woodrat middens (Wells, 1978), vertebrate remains and other materials in cave deposits (Van Devender and Worthington, 1978; Van Devender *et al.* 1978), tree-ring chronologies (Fritts, 1974; Fritts *et al.*, 1979), and archaeological sites (Mehringer, 1967). Aridity of the region has preserved a remarkable amount of these data, and a vast amount of information is undoubtedly yet to be revealed. Another advantage to understanding Southwest environments is that we have descriptions of how things were prior to invasion of technological culture. This was made possible by the Southwest's relatively late and low density of occupation by Hispanic cultures, and an even later acquisition of its northern half by Anglo-Americans.

The chapters which follow illustrate that Southwestern ecosystems are distinctive because of the particular evolutionary history of their geographic locations. These communities and their component plant and animal species, however, are similar to their ecological equivalents in other parts of the world (Mabry *et al.*, 1977; Simpson, 1977; Orians and Solbrig, 1977). It is not surprising, therefore, to find that ecological studies have contributed not only to a record of the natural history of the region, but also to an understanding of general ecological principles of worldwide application. Thus, some investigations describe the natural history of organisms such as Saguaro Cactus (Niering *et al.*, 1963) and/or processes such as arroyo cutting (Cooke and Reeves, 1976), that are

either peculiar to, or particularly well illustrated in, the Southwest. Other, more general investigations in the region have illustrated or suggested basic ecological concepts or patterns for the first time,—concepts such as the life zones of Merriam (1890, 1898). Southwestern ecological studies have also incorporated theoretical and methodological biases prevalent in contemporary ecological studies conducted in areas outside the region. Late 19th and 20th Century ideas on predator control and wildlife management, for example, were applied to the Kaibab Plateau of Arizona with disastrous results from 1920 to 1939 (Rasmussen, 1941).

Historical development of our knowledge of the ecology of Southwestern ecosystems recapitulates a pattern frequently seen in development of ecological knowledge in other parts of the world. In general, Southwestern ecological studies fall into three overlapping periods of development: 1) *Exploration*, 2) *Inventory*, and 3) *Synthesis*. Those who studied and described the natural environment during each of these periods often were distinctive individuals, and formed the basis for much of the legend and lore of the region (see for example Corle, 1951). Their occupations, like those of their counterparts at other times and in other parts of the world, typically reflected their motives for being in the Southwest. Thus, natural history reports during the period of exploration (from 1807 to 1900) were prepared by trappers, personnel of military surveys, and physician-naturalists assigned to such surveys.

The inventory period (from 1850 to 1940) saw hunter-naturalists and collectors beginning the task of cataloging and preserving representatives of Southwestern plant and animal life. During this period, a movement with its origins in sportsmen's social clubs of the Northeastern United States spawned a group of wildlife advocates known as "conservationists" who also reported on the natural history of the West. Even as the cataloging process was just seriously beginning, these men fought to obtain laws and lands to protect wildlife species and wilderness areas that were already vanishing in the 1800s.

The synthetic period (from 1890 to the present) has been characterized by studies and publications of professional ecologists from academic, governmental and private institutions. Many of these professionals have made their homes in the Southwest, sharply distinguishing them from the largely transient researchers of previous periods. These scientists contributed greatly to maturation of ecology as a science. More recently, the work they started has been reflected in species inventories and habitat descriptions that typically accompany modern-day "environmental impact statements." Contemporary students of Southwestern ecology are trying to understand the causes of patterns initially described by these workers. Ecologists now use long- and short-term population, community, and ecosystem studies, as well as comparative and experimental approaches, to demonstrate how distribution and abundance of plants and animals are affected not only by variation in abiotic factors, but also by processes such as competition, predation, and nutrient availability.

The objective of this chapter is first to summarize contributions of investigators characteristic of each of the major periods of ecological development. Incidentally, it will be noted how their work reflected theoretical and methodological biases of the science of ecology at the time they conducted their research. Secondly, we summarize ways in which these studies contributed to our knowledge of natural history of the Southwest, and perhaps how they influenced in a more general way ideas concerning basic ecological principles beyond the region.

Exploration: Trappers, Military Surveys, and Physician-Naturalists.

Beaver trappers were important among the first people of Northern European extraction to enter the Southwest (Davis, 1982). Between 1823 and 1846, these so-called "mountain men" found an unsettled land sparsely occupied by people at a Neolithic stage of development. Except for a few outposts, pueblos or presidios at Santa Fe, Janos, Taos, Tubac, San Diego, and at the slightly more numerous missions, Hispanic presence was local and, with the important exception of introduced livestock, largely passive. So it also was with the beaver trappers who, disdainful of Spanish and later Mexican laws against their vocation, and even more of farming, mining, ranching, and other sedentary pursuits, left the wilderness and its inhabitants largely intact. Some, like James Ohio Pattie (1962), kept journals or narrated memoirs, thereby leaving valuable accounts of a soon-to-vanish wilderness.

As the United States expanded its boundaries westward, newly acquired lands had to be surveyed, mapped and described. This job fell to the military. Most survey parties had in attendance a physician who doubled as a botanist, zoologist, or naturalist. Although most early expeditions were limited to collecting and cataloging specimens, this in itself was a great contribution. Explorer-naturalists provided initial descriptions of species, upon which later, more detailed studies were based.

As early as 1807, military sorties had begun to penetrate the Southwest. In that year Maj. Zebulon Montgomery Pike (1810) "wandered" into Spanish territory by traveling through Plains grasslands up the Arkansas River to the Rocky Mountains, then south to Santa Fe on what was termed exploration. Pike and his party were detained, then escorted by Spanish militia from the region *via* the Rio Grande to El Paso, thence to Ciudad Chihuahua and eastward to be released. This trip revealed a vast, somewhat unexpected area, plus potential military routes west to California.

Stephen Harriman Long's Army Corps of Engineers returned in 1820 from an expedition to the Plains and Rocky Mountains through what is now New Mexico. Santa Fe was then the Southwest's trading center and capitol. Accompanied by such naturalists as Thomas Say (now honored by Say's Phoebe, *Sayornis sayi*) and Edwin James (*Hilaria jamesii, Eriogonum jamesii, Jamesia americana*) this expedition recorded a number of important new plants and animals including Limber Pine (*Pinus flexilis*) and the Rocky Mountain Mule Deer (*Odocoileus h. hemionus*). Biological discovery of the Southwest was underway.

The great soldier-explorer John C. Fremont led the next major expedition along the Old Spanish Trail. He moved from the west, and entered the Mohave Desert at Tehachapi Pass in 1844. Leading a detachment of topographical engineers and accompanied by Christopher "Kit" Carson, Fremont crossed southern Nevada, camping at what is now Las Vegas before continuing up the Virgin River into the Creat Basin Deserts of southwestern Utah. Fremont was a true naturalist

and collected numerous plants enroute including *Ambrosia dumosa, Coleogyne ramosissima, Pinus monophylla,* and *Populus fremontii.* Although much of his plant collection was later lost in winter snow and summer flood, extensive material remained. The plants were sent to John Torrey at Columbia University, who described them and named the cottonwood after Fremont. It was Fremont who appropriately coined the term "Great Basin" for much of the Intermountain West.

In the mid-1840's the United States acquired what is now the northern half of the American Southwest, Texas, southern California, and New Mexico (the last of which included what was to become Arizona), and military surveys began in earnest.[1] In 1846, while war with Mexico was in progress, Lt. William Hemsley Emory, a red-headed engineer assigned to Col. Stephen W. Kearney's "Army of the West," was commissioned to map from the "Rio Grande to the Pacific", with 14 topographical engineers. It was on this expedition that the Saguaro Cactus (*Cereus giganteus*) was first collected and made known to science. The Roundtail Chub (*Gila robusta*) from the Gila River was accurately illustrated in Emory's (1848) journal, although it was technically described from material collected elsewhere. Emory's journey was followed by three consecutive boundary surveys after the end of war in 1848, the last in 1855 again under Emory, now a major. A. L. Heerman, C. B. R. Kennerly, and Arthur Schott were scientists accompanying these surveys. They collected mammals, fishes, and plants for the U.S. National Museum to be housed at the newly built (1852) Smithsonian Institution. Journals were kept, botanical and zoological reports were submitted, and Congress authorized the printing of 3,000 copies of the reports (1859).

After collecting in Texas, Dr. S. W. Woodhouse, physician and naturalist, accompanied Capt. Lorenzo Sitgreaves' survey of northern New Mexico and Arizona in 1851. It was on that trip that Woodhouse described and named Abert's Squirrel (*Sciurus aberti*) after Lt. James William Abert who was John C. Fremont's brother-in-law and head of the Corps of Topographic Engineers. Abert himself had explored northeastern New Mexico, in 1845 prior to joining Emory's expedition to New Mexico, Arizona, and California in the following year. Woodhouse's travels took him up the Rio Grande from El Paso to the Rio Puerco and on to Laguna. The Sitgreaves party thence proceeded down the Zuñi River to Arizona. Along this last route two western big-river fishes, the Bonytail Chub and Roundtail Chub (*Gila elegans* and *G. robusta*) were discovered and named (Baird and Girard, 1853).

In 1853, C. B. R. Kennerly was again an attending physician and naturalist with Lt. A. W. Whipple's expedition attempting to find a railroad route along the 35th parallel. Accompanied by the German artist-naturalist Heinrich B. Möllhausen, they collected a vast quantity of material for the U.S. National Museum along the trail from Albuquerque to the Colorado River. Both Kennerly and Möllhausen later explored and collected along the Little Colorado and Colorado rivers under Lts. Beale and Joseph C. Ives (1857-1858), the former of Camel Corps fame.

Later military surveys attempted to be even more specific in nature. The G. M. Wheeler Survey of 1871-74 reported on geology of the region, as did the civilian John Wesley Powell Expeditions (Powell, 1875) to the Colorado Plateau and Colorado River and the F. V. Hayden Expedition (Hayden, 1873) to the north. Henry W. Henshaw, an ornithologist with the Wheeler party, collected extensively, especially in New Mexico, as did Joseph T. Rothrock, the U.S. Army botanist assigned to the survey. The botanist George Vasey made an extensive plant collection during the Powell survey, and he later became curator at the U.S. National Herbarium.

The last, and in many ways the most productive survey with a primary geographic mission, was the U.S. and Mexican Boundary Survey of 1892-93. It had as its physician and naturalist Edgar Alexander Mearns. He was primarily interested in mammals and published a treatise (Mearns, 1907) on the natural history of the Southwestern boundary with Mexico, and a descriptive catalog of its mammals. His collections of other organisms added substantially to our knowledge of the overall Western biota (*e.g.* fishes, Snyder, 1915; plants, Britton, 1889). Mearns continued as a collector and investigator in the United States and Mexico until his death from diabetes at age 61.

Although the primary purpose of these surveys was the pragmatic task of determining boundaries, finding railroad routes, and ascertaining geological wealth, the government also valued documentation of the region's living resources. Naturalists accompanying these surveys kept journals as did many of their commanders and engineering colleagues. Given the pristine conditions they encountered, their recordings and descriptions are now invaluable. These surveys became the forerunners of the Geological Survey of the U.S. Department of the Interior and the Biological Survey of the U.S. Department of Agriculture. The latter was first designated in 1889 as the Division of Economic Ornithology and Mammalogy of the USDA.

The surveys had increasingly changed from those of an exploratory nature to scientific expeditions, requiring their participants to have an ever greater scientific expertise. The army was not the best organization to direct detailed scientific endeavors, and after the Wheeler Survey it became apparent that science would best be served by multidisciplined teams of civilian professionals, like the Powell Surveys. Although a few major operations were organized to explore remote areas, the period of general exploration *per se* thus came to a close by about 1880. Surveys henceforth were limited to restricted geographic areas, selected not for their military or political importance, but because there was little biological knowledge of the area. Thus began the collecting period.

Inventory: Hunter-Naturalists, Collectors, and Conservationists.

Even before 1800, expeditions from Europe had been seeking out the world's remote places with the objective of locating new plants and animals. Many of these expeditions were led by big game hunters, some by retiring botanists, others by royalty, but all their findings were eagerly awaited by scientists of all kinds. Little was contributed to North American zoology by North American scientists prior to 1800

[1] *A most important exception to the military efforts was physician, ornithologist and botanist, William Gambel, who in 1841 discovered and collected many new species on a wagon trip along the Old Spanish Trail from Aliquin to California. Gambel was a friend of the great naturalist Thomas Nuttall, who described and named several important species for him, including Gambel Oak* (Quercus gambelii) *and Gambel's Quail* (Lophortyx gambelii).

Figure 6. *Clinton Hart Merriam about 1910 after he published Life-zones of the San Francisco Mountains, Arizona. Merriam was a collector and naturalist when he became the first Chief of the U.S. Office of Economic Mammalogy and Ornithology (later to become the U.S. Biological Survey) from 1879 to 1885. After 1885 he conducted numerous biological and anthropological investigations including a study of the status of the Fur Seal on the Pribiloff Islands and his work on the San Francisco Peaks. This latter work resulted in his famous classification of North American life-zones,—a system still in use in the Southwest today.*

(Myers, 1964). Formation of the Academy of Natural Sciences of Philadelphia in 1812 started to change this condition, and the vast biota of Eastern North America began to be studied in detail. With exploration of the Southwest, collecting increased, and institutions such as the Museum of Comparative Zoology at Harvard University espoused a policy of preserving large collections of organisms. Reports of discovery and description of new forms constituted much of the scientific literature in this period.

A large part in development of this phase of descriptive science in North America was played by the prominent Swiss zoologist Louis Agassiz. Although Agassiz scarcely dealt with Southwestern animals, his influence after emigrating still is reflected in the works of his academic descendants. As pointed out by Hubbs (1964), "few of the more active ichthyologists of the present day are unable to trace their lineage back to Jordan, and through him to Agassiz," and analogies hold for other biological disciplines as well.

Studies in the American Southwest were enhanced by establishment of the Smithsonian Institution in 1846, with its National Museum, and eventually (in 1890) the National Herbarium. That institution and the prestigious Academy of Natural Sciences of Philadelphia sponsored a large percentage of the published literature in the period from 1850 to 1875. Collections of animals and plants made during exploratory expeditions and surveys were housed in those repositories. Important collections of fishes for example, including much of the Southwest's known fauna, were described by Charles Fredrick Girard, alone or in co-authorship with Spencer Fulton Baird. The first of these men emigrated from France to study American fishes with Louis Agassiz. The second was selected as Assistant Secretary of the Smithsonian Institution in 1850, and brought in 1871 an early and vigorous beginning to the U.S. Fish Commission. That agency gave rise in turn to the Bureau of Fisheries, which was ultimately combined with the Bureau of Biological Survey to become the Fish and Wildlife Service. Edward Drinker Cope played much the same role as Baird and Girard in describing numerous reptiles and amphibians from the surveys (Cope, 1866), and in studying not a few fishes (Cope and Yarrow, 1875).

The policy of assignation of collectors to field stations by the Smithsonian Institution resulted in Dr. Elliot Coues' mission to Fort Whipple, Arizona, in 1864. His assignment was to collect and prepare specimens of wildlife from the Rio Grande to the Colorado River. This he did, and his *List of Birds of Fort Whipple, Arizona,* published by the Academy of Natural Sciences of Philadelphia in 1866, and his *Quadrupeds of Arizona,* published by the American Museum of Natural History in 1867, are the first scientific papers on Southwestern wildlife other than species descriptions. These works are even more impressive when one remembers that much of the material was obtained in unsettled territory inhabited only by military personnel and Indians. Coues was the first to report Bobwhite Quail (*Colinus virginiana*) in Arizona. The diminutive Coues' Whitetail Deer (*Odocoileus virginiana couesi*) inhabiting Arizona, New Mexico, Sonora, and Chihuahua, was appropriately named for him.

Although many collectors were primarily concerned with discovering and naming new species, all believed that they contributed greatly to the knowledge of natural history, and so they did. Although taxonomists are dependent on collections for their studies, ecologists, zoogeographers, phytogeographers, paleobiologists, and evolutionary biologists also depend on these resources for their research. David Starr Jordan (whose long and successful career included the latter part of the 19th and the early part of the 20th centuries) lauded these contributions in dedicating the 13th edition of the *Manual of Vertebrate Animals* in 1929 "To five of my early students, 'brought up on the Manual of Vertebrates'... and to five others, equally gifted, who lost their lives while engaged in field work." We owe a great deal to these early naturalists who frequently financed, organized, led, and died on their expeditions.

After the Civil War, settlement of the Southwest proceeded more rapidly. Although some like George Thurber began collecting plants around what is now Silver City, New

Mexico, in the 1850's, the 1870's saw several collecting trips to trans-Pecos Texas, and into New Mexico. A few like John G. Lemmon (and later his wife, Sara Plummer Lemmon) collected plants in southern California, the Mohave, Great Basin, and Sonoran deserts, and throughout Arizona when these areas were still relatively unsettled (Crosswhite, 1979). It was not until the 1880's, however, with suppression of the Apaches, that museum expeditions could be sent out in earnest for Arizona, Sonora, and Chihuahua. This was the peak of the survey and collecting period. Identification and description of subspecies as well as species proceeded actively. For the next 60 years racial characters as well as animal distributions were considered necessary parts of an understanding of the evolution and taxonomy of our biota. Investigators traveled by train and hired horse and wagon or else hiked to reach collecting sites; the most eminent scientists of the day participated.

The Death Valley Expedition under the Division of Economic Ornithology and Mammalogy and composed of no less than C. Hart Merriam, V. Bailey, Edward W. Nelson and others, covered the vast deserts of southern Nevada and southeastern California in 1891. Hence the names of White River Springfish (*Crenichthys baileyi*), Ash Meadows Poolfish (*Empetrichthys merriami*) and Desert Bighorn (*Ovis canadensis nelsoni*). Nelson, accompanied by Edward A. Goldman, initiated studies of mammals and birds in Mexico in 1892, also under the Division, and ended it in 1905-06 with a trip by pack animals through the entire length of Baja California (Goldman, 1951). Goldman went on to collect extensively throughout the Southwest and elsewhere in Mexico, and for the next 40 years his name was associated with more than 100 published works dealing with Southwestern animals and landscape descriptions. Nelson also collected throughout the Southwest. He first collected the native elk in Arizona (the so-called Merriam Elk), and later proved to be a most able administrator of the Biological Survey. In subsequent years, Barton W. Evermann and Cloudsley M. Rutter reported on fishes of the Colorado River basin in 1895, and Seth Eugene Meek began his studies of the fishes of Mexico (Meek, 1902, 1903, 1904), under the auspices of the Field Columbian Museum, now the Chicago Natural History Museum.

Collecting and compilation of descriptive information was not limited to the Field Museum, the U.S. National Museum and the Philadelphia Academy. The Museum of Vertebrate Zoology at Berkeley, the San Diego Natural History Museum, the University of Michigan Museum of Zoology, and as years passed, the Museum of Natural History at the University of Kansas, and others, sponsored collectors and housed specimens. Private collectors and collections flourished. A. W. Anthony collected in New Mexico in 1886 and again in 1889 for the Merriam collection. H. H. Rusby (1889) collected plants under pharmaceutical industry sponsorship in southwestern New Mexico and Arizona. Anthony's specimens went to the National Museum as a result of Merriam's employment as first head of the U.S. Biological Survey.

Most private collections eventually found their way to a university. This is fortunate in lieu of the fact that the Southwest has never had a regional or even a state-based depository for natural history material. Some of the most significant contributions were the D. R. Dickey collection of vertebrates. It was Dickey who financed the important trips of A. J. van Rossem in Sonora and southern Arizona, and some early travels of L. M. Huey in Baja California. The Herbert Brown (editor for the Tucson Citizen newspaper) Ornithological Collection (now at the University of Arizona) was another important contribution of the later 19th and early 20th centuries (Phillips *et al.*, 1964). W. H. Burt (1932, 1938) reported on his and other collections of mammals in Baja California and Sonora, respectively.

Vernon and Florence Merriam Bailey (C. H. Merriam's daughter) collected throughout New Mexico for the Bureau of Biological Survey from 1889 to 1924. Results of this long and fruitful effort are V. Bailey's *Mammals of New Mexico* (1931; recently reprinted as *Mammals of Southwestern United States*) and Florence Bailey's (1928) *Birds of New Mexico.* Scattered descriptions and new information on the Southwest's fishes were summarized in the monumental *Synopsis of Fishes of North America* by Jordan and Gilbert (1883), and in the even greater *Fishes of North and Middle America* by Jordan and Evermann (1896-1901). In the case of fishes, these works suppressed research for a number of years, with their completeness overshadowing needs for further studies (see *e.g.*,Hubbs, 1964). Results of the remarkably extensive biological exploration in Mexico by Nelson and Goldman did not appear until far later (*Lower California and Its Natural Resources* by Nelson, 1922; *Plant Records of an Expedition to Lower California* by Goldman, 1916, *Mexican Tailless Amphibians*. . .by Remington Kellogg, 1932; *Birds of North and Middle America* by Robert Ridgeway and Herbert Friedmann, 1901-1950; and *Biological Investigations in Mexico* by Goldman, 1951).

The extensive collections of E. O. Wooton, now in the U.S. National Herbarium, were gathered mostly from New Mexico in the late 1890's and early 1900's. They with other collections at the National Herbarium and New Mexico State University, were the basis fore the pioneer work by Wooton and Standley, entitled *The Flora of New Mexico* published in 1915. Meanwhile, P. C. Standley was collecting in Mexico preparatory to his five-part opus, *Trees and Shrubs of Mexico,* published between 1920 and 1926 by the Smithsonian Institution, while he was Associate Curator at the U.S. National Herbarium.

Other early Biological Survey collectors of note were the entomologists T. D. A. Cockerell and C. M. Barber (who amid myriad accomplishments sampled in the Sacramento Mountains and Mesilla Park areas of New Mexico), J. A. C. Rehn, and Walter P. Taylor. The latter is probably best known for his editorship of *The Deer of North America* (Taylor, 1956). Cockerell, like E. A. Goldman, Vernon Bailey, and other collectors, was also greatly interested in biogeography.

Synthetic Period: The Biogeographers.

In 1890, Clinton Hart Merriam (Fig. 6) published his *Results of a Biological Survey of the San Francisco Mountain Region and Desert of the Little Colorado, Arizona,* thereby ushering in a unique life-zone concept of delineating habitats. This system, which equated elevational zones with biogeograpic realms within the North American continent (Fig. 3) proved extremely useful in the Southwest where it was developed. Initially used by Merriam's Bureau of Biological Survey colleagues, it has been generally applied in descriptions of habitats for more than 80 years (see *e.g.* Lowe, 1964). Development of a common language to describe habitats facilitated efforts at additional ecological surveys by the

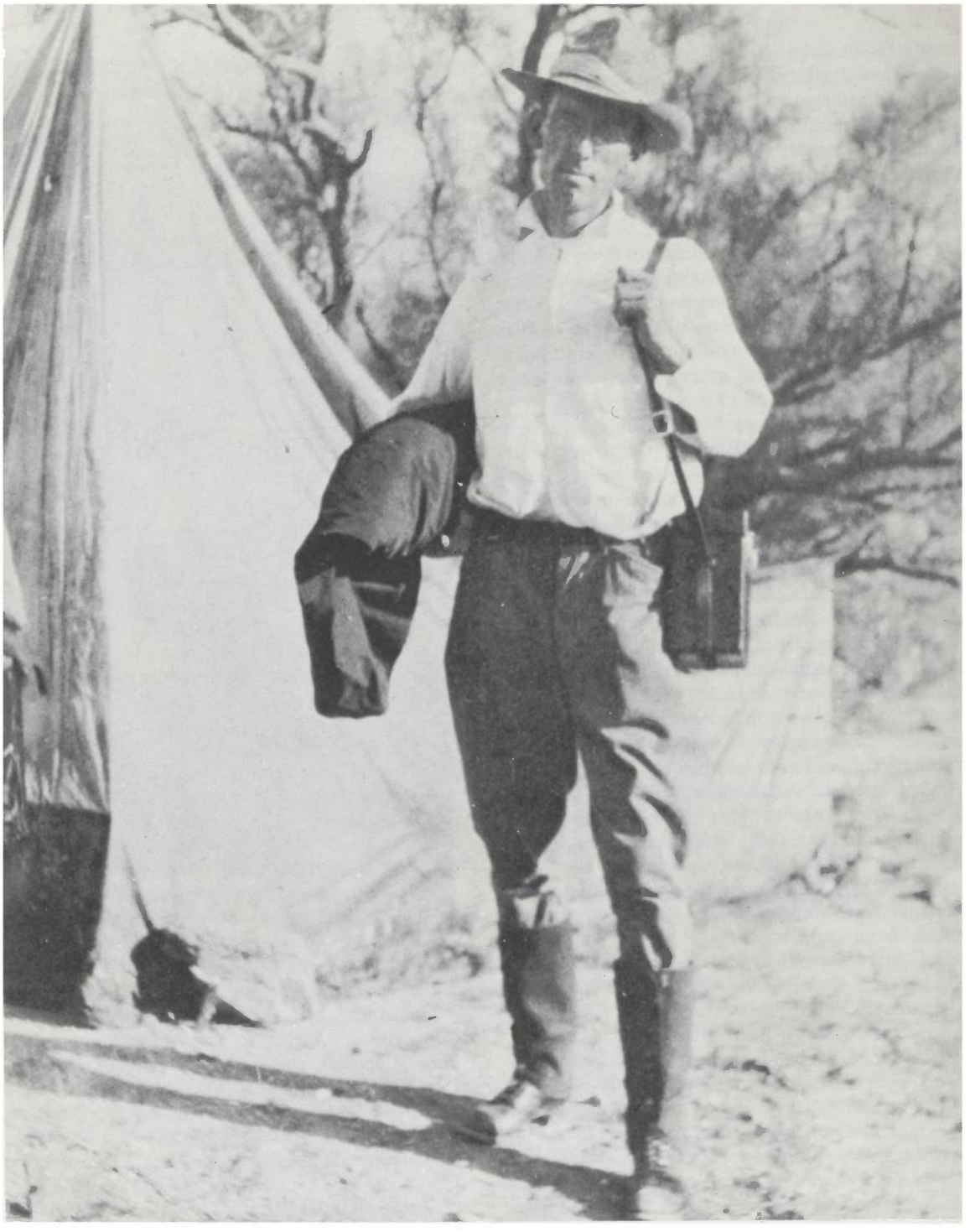

Figure 7. *Forrest Shreve about 1940. Shreve truly provided the key to our understanding of the North American deserts. A prolific as well as intuitive botanist, Shreve's work on the effects of climate on plant distribution made him one of the great ecologists of our time. Photograph courtesy of Mrs. Margaret Shreve Conn.*

Bureau, resulting in Cockerell publishing *Life-Zones in New Mexico* (1897, 1898), and V. Bailey publishing a *Biological Survey of Texas* (1902), *Life-Zones and Crop-Zones of New Mexico* (1913) and other works, in and outside of the Southwest. Other worthy surveys tying terrestrial vertebrates to prescribed life-zones were accomplished by Joseph Grinnell, another Merriam advocate working with the University of California. In our region these surveys resulted in a publication entitled *The Biota of the San Bernardino Mountains* (1908), an account of the San Jacinto Mountain area with H. S. Swarth (1913) and an account of the lower Colorado River (1914). E. Raymond Hall also published information on the life-zones of Nevada in his monumental *Mammals of Nevada* (1946).

These and numerous other early efforts first resulted in a correlation of plants and animals occurring in Southwestern environments. By the 1920's, correlations with climatic variables were recognized on a continental basis (Merriam, 1898; Shreve, 1917; Shantz and Zon, 1924; Shelford and Shreve, 1926). It now remained only to continue to implement the use of vegetative descriptions within the life-zone system on a more intensive basis.

This endeavor was largely underway by the 1930's. A. A. Nichol (1937) described and mapped Arizona's natural environments, Tharp (1939) summarized those in Texas, and Melvin Morris (1935) mapped Colorado's natural vegetation.

Gloyd (1937) dealt with reptiles in southern Arizona. Swarth (1929) and Phillips (1939) designated "faunal areas" on the basis of birds. Studies reviewed by Lowe (1964) dealt with geographic regions based on congruent distributional ranges of several animal groups. Furthermore, the Mexican half of the Southwest was being inventoried, mapped, and described in the context of vegetational zones or biomes. The Carnegie Institution of Washington funded Forrest Shreve's (Fig. 6) great work on arid lands (1934, *et seq.*) in the United States and Mexico. Similarly, H. S. Gentry (1942) was cataloging and describing the tropical and sub-tropical vegetation of southern Sonora and Sinaloa. D. D. Brand's (1936, 1937) descriptions and maps of northwest Mexico, Harde LeSueur's (1945) work on the vegetation of Chihuahua, E. G. Marsh's largely unpublished investigations of Cuatro Ciénegas and elsewhere in Coahuila (Hubbs and Miller, 1965; Minckley, 1969; Pinkava, 1979), C. H. Muller's (1939, 1947) studies in Nuevo Leon and Coahuila, and Elzada U. Clover's (1937) work on the lower Rio Grande in Texas, all were accomplished in the 1930's. This was also a period of great productivity in the fields of natural history and ecology in general. The successional and climax principles of Weaver and Clements (1938), the biome concepts of Shelford (1932, 1945), Pitelka (1941), and Lee R. Dice (1939, 1943) used in this book, were also products of that decade. Wieslander's (1932-1940) remarkable vegetation maps of California at 1:125,000, Forest Shreve's (1951) brilliant treatment of the Sonoran Desert, E. Lucy Braun's (1950) treatise on the Eastern Deciduous Forest, and Weaver and Albertson's (1956) analysis of grasslands of the Great Plains were all products of the 1930's.

Study and interpretation of wetlands and their biota in the Southwest lagged behind similar terrestrial pursuits. However, an event in 1894 in Williams, Arizona, the birth of Carl Leavitt Hubbs (Fig. 8) was to insure additional search for knowledge of Southwestern fishes despite the doldrums following publication of *Fishes of North and Middle America*. After a childhood in southern California, Hubbs was influenced by Loye Holmes Miller and George Bliss Culver to enter Stanford University, where under the tutelage of David Starr Jordan and C. H. Gilbert he became one of the leading naturalists in North America, a position he retained even after his death in 1979 (Norris, 1974; Pister, 1979). Hubbs' efforts along with those of his student, son-in-law, and colleague, Robert Rush Miller resulted in one of the largest collections of freshwater fishes in the World at the University of Michigan Museum of Zoology, a large percentage of which are from the American Southwest. Their work on fishes contributed greatly to our knowledge of biogeographic relations in Western deserts and elsewhere. Hubbs' early collecting in streams and lakes of the arid West with John

Figure 8. *Carl L. Hubbs about 1954. Although Hubbs' contributions to fish management, systematics, and research were continentwide, his interest in palaeoclimate resulted in a great contribution to understanding Southwest fish evolution. Photograph by Lewis W. Walker.*

Otterbein Snyder led him back to the region. Hubbs, Miller, and their families traced ancient shorelines, delineated former watercourses, and studied the remarkable relict fish populations of isolated pools and streams, deriving hydrographic interpretations of climate, geology, and biology, which stand as a challenge to even the most astute geologists of today (Hubbs and Miller, 1948; Miller, 1948, 1959; Hubbs *et al.*, 1974; and many others). Their dedication to systematics, conservation, and natural history of Western fishes was exceptional, yet the Southwest's wetland environments went largely unnoticed until very recently—mostly until the last two decades. Indeed, the wetland section presented in this volume is the first holistic treatment of these valuable and neglected resources.

The late 1930's and early 1940's was a high-water-mark period of general natural history studies. The job of resource inventory must, however, continue to better interpret and understand our natural history heritage, and to communicate information and ideas of what is and what has been. This is the purpose of this publication and its companion map—to communicate the accumulated knowledge of Southwestern ecology and biogeography.