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Pollen Analysis and Woodrat Middens: Re-evaluation of Quaternary Vegetational History in the American Southwest

Stephen A. Hall

This article critically examines the usefulness and importance of woodrat middens (clumps of plant materials from woodrat dens cemented by dried urine) as supplements to pollen analysis in reconstruction of quaternary vegetational history in the American Southwest. Due to post-depositional weathering processes, pollen is occasionally absent, is found in concentrations too low to be sufficient, or is inadequately preserved in arid-land sediments to supply adequate, conclusive temporal information about past plant landscapes. Woodrat middens are important tools that can and should be used to fill in the gaps in reconstructing the vegetation of the Quaternary; however, caution must be exercised because there are significant limitations and pitfalls.

Pollen studies in the American Southwest began in 1935, when Paul Sears examined samples of Holocene alluvium collected by Ernst Antevs from Tsegi Canyon, near Kayenta, northeastern Arizona. The sampled alluvium contained abundant pollen, showing the potential for pollen analysis of arid-land sediments (Sears 1937, 1961). At that time, the field of pollen analysis was some two decades old. Sears's study was the first attempt in North America to look at fossil pollen from deposits outside the bogs and lakes of glaciated terrains. He also observed that

> ...no safe conclusions can be drawn from this region on the basis of pollen analysis alone. The erosion history of the entire region must be developed. Terraces and buried soils abound and their relationships must be established as a necessary step in the application of pollen analysis of silt deposits (Sears 1937: 65)

Sears's conclusion, sixty years later, still rings true. Although only fourteen papers on Southwestern pollen analysis had been published by 1959, increased

Stephen A. Hall is a professor in the Department of Geography at the University of Texas at Austin, Austin, TX 78712.

popularity of pollen work in the following decades led to numerous applications to sediments of diverse origin, including of materials from archeological sites. By 1984, the number of pollen studies of archeological sites for cultural resource management projects amounted to 45 percent of all of the pollen studies in the Southwest, which at that time totaled more than 540 titles (Hall 1985b). Early pollen studies were interpreted as indicating a glacial-age vegetation dominated by ponderosa pine forests extending to low elevations out into the Great Plains. Postglacial vegetation was characterized by dwindling tree populations and a wet mid-postglacial climate (Martin 1963; Martin and Mehringer 1965). Later pollen studies have shown these initial interpretations to be incorrect, that glacial-age lowland vegetation was an *Artemisia* steppe and that the postglacial vegetation was a desert grassland with a hot-dry mid-Holocene climate (Hall 1985a).

The biogeographic significance of fossilized woodrat middens was discovered in the Mojave Desert of southern Nevada (Wells and Jorgensen 1964). Middens are clumps of plant materials from a woodrat den cemented by dried urine. Subsequently, the identification of plant remains from woodrat middens has taken on a significant role in reconstructing late-Quaternary phytogeography in the arid Southwest. By 1985, more than seventy studies on the analysis of fossilized midden material had been published, compared with 188 papers in pollen-based paleoecology (Webb and Betancourt 1990: 85-86; Hall 1985a: 96). A brief history of woodrat-midden studies was presented in Betancourt et al. (1990: 2-6), at which time 1,113 middens, or two or more fragments from single middens, had been radiocarbon-dated (Webb and Betancourt 1990). An excellent review and summary of the studies of fossilized woodrat middens in the Southwest was presented in the book *Packrat Middens: The Last 40,000 Years of Biotic Change,* edited by Betancourt, Van Devender, and Martin (1990; see review by Hall 1992). Many of the following comments and observations on the strengths and biases of woodrat-midden studies were taken from this useful book.

Den-building rodents of the genus *Neotoma* are represented in the Southwest and adjacent Mexico by nine species (E. R. Hall 1981). These species are called woodrats in the zoological, range management, and biological literature, although they are also known as "packrats," a local name given to them because of their strong instincts to collect objects for their dens. Woodrat is the common term in the broad literature and is used in this review.

Critique of Pollen and Woodrat-Midden Analysis

Pollen Preservation

Pollen analysis is the most mature method applied worldwide to reconstruction of vegetational and paleoecological history. In southwestern deserts, however, the use of pollen-based studies for interpreting vegetation history has been held back by the sparseness of deposits that contain abundant, well preserved pollen. Although numerous depressions and playas occur throughout the desert landscape, pollen grains, if present at all, are often poorly preserved. Because poor preservation can bias a pollen assemblage, a great deal of attention over the years has been paid to the circumstances of pollen deterioration.

It has been noted that intact pollen grains enter virtually all depositional environments, but that over time the grains become deteriorated by post-depositional weathering processes. Several criteria exist to assess the degree of deterioration; hence, the reliability of pollen assemblages (Hall 1981a, 1995; Bryant et al. 1994). These criteria are: (1) low concentrations or numbers of pollen grains per unit of sediment analyzed; (2) high percentages of grains that cannot be identified due to their poor preservation; (3) high percentages of corroded grains; and (4) a low number of pollen taxa in an assemblage. The criteria are discussed in detail by Bryant and Hall (1993).

Poor preservation leads to difficulty in identifying pollen grains under the microscope. As a consequence, pollen percentages will be biased in favor of grains that can be recognized. Also, not all pollen deteriorates at the same rate. Conifer pollens, such as pine and spruce, tend to persist longer in an assemblage during weathering processes than do nonconifer pollen grains. Thus, when pollen-bearing sediments are weathered over time, an assemblage may come to be dominated by conifer pollen, producing artificially high percentages of pine and spruce, a phenomenon observed by Bachhuber (1971), Hall (1981a), and Hall and Valastro (1995). In some circumstances where weathering processes affect pollen-bearing sediments continuously through time, such as in rockshelter environments, progressive deterioration of pollen has been observed. Pollen-grain destruction is greater with depth in the deposit, hence with time (Hall 1991).

Poor preservation of pollen occurs in all arid-land depositional environments in which the sediments have been subjected to weathering processes. In some circumstances, however, pollen preservation is excellent. The very best pollen preservation occurs in fossil woodrat middens, similar in quality to that seen in Tauber pollen traps and dry-cave coprolites. The excellent condition of pollen in middens is one of the reasons why woodrat middens are valuable paleoenvironmental resources in the Southwest.

Pollen Representation

An important task in pollen analysis is determining the relationship between plants in the vegetation and the amount of pollen they produce. Some plants, such as pines, produce more pollen in proportion to their abundance in the landscape. For example, at Chaco Canyon, New Mexico, surface sediment contains about 20 percent *Pinus* pollen, even though pine trees are miles away. Other plants, such as mesquite and creosote, produce very small amounts of pollen. Pollen analysts take these varying relationships of pollen-plant abundance into account. Modern pollen assemblages from soil surfaces and from Tauber traps are used to establish modern pollen-modern vegetation analogs, providing the correction factors necessary to interpret vegetation even though over- and under-represented taxa are present, such as the surface samples at Chaco Canyon. At Chaco, one would expect to have more than 20 percent *Pinus* pollen in an assemblage before the presence of pine trees could be inferred. Clearly, a few pine pollen grains would not be evidence for the past presence of pine trees in the local vegetation.

Midden Fossils: Presence-Only

Woodrat middens are a different story. The advantage of fossil woodrat middens is that a single pine needle, if it is not a contaminant from an older or younger midden, would firmly indicate the presence of a pine tree within thirty meters of that location (modern woodrat home range). Midden analysts have adopted the use of diagrams, mimicking pollen diagrams, that show relative abundance of identified plant parts in middens through time. A fossil midden with 500 pine needles does not indicate that the abundance of pine trees is any greater than that of a midden with five pine needles. Varying numbers of needles only indicate the presence of one pine tree. The same is true for all other taxa as well. The presence of hundreds of twigs, leaves, or seeds of a species in a midden is more indicative of a woodrat's diet than of the abundance of that species in the local vegetation. Thus, species-abundance diagrams are misleading. Plant remains identified from fossil woodrat middens provide a floral list from the local escarpment, and nothing more.

Woodrat Filter Effect

Woodrat behavior exerts a strong filter effect on plant species that are represented in dens and preserved in middens. Woodrats do not randomly collect plants from their thirty-meter home range. They select specific plants for food storage, for nesting, and for den construction. The classic monograph, *The Wood Rats of Colorado: Distribution and Ecology,* documented in great detail their food and den construction preferences (Finley 1958). In summary of the study, Finley (1958: 545-546) stated

> All wood rats in Colorado subsist mostly on relatively coarse, leafy vegetation and cactus pulp, supplemented by seeds, fruits, and other parts of plants. *N. cinerea* and *mexicana* prefer the foliage of soft-leaved shrubs, forbs, and montane conifers, whereas *albigula* and *micropus* prefer the succulent pulp of cactus and the foliage of junipers and xerophytic shrubs and forbs....Two sympatric species of wood rats sometimes occupy the same rock den, probably in succession rather than simultaneously. Such dual use of the same shelter by *mexicana* and *albigula* can be recognized by the distinctive middens left by each species.

Finley's observation that different woodrat species leave behind distinct middens bears directly on fossil-midden studies.

More recent studies show the same results. A study of woodrat populations at Woodhouse Mesa, in northern Arizona, found that plant remains in woodrat middens were more closely related to woodrat diet than to local plant communities (Dial and Czaplewski 1990). In an innovative experiment, Dial (1988) removed a species from its den and recorded what happened:

> When one species replaced another at a den site, obvious changes began to appear in the accumulated plant clippings. After a period of den occupancy by the new species, the predominant plant species collected by the previous occupant became progressively less obvious. After a year had passed, evidence of the original occupant was completely obscured. For example, a year after *N. devia* replaced *N. stephensi* at den 13, plant clippings around the den changed from dried juniper twigs and foliage (the hallmark of *N. stephensi*) to mostly *Ephedra* twigs (preferred by *N. devia*).(Dial and Czaplewski 1990: 53).

Clearly, a turnover in woodrat species resulted in a dramatic shift in plant species in middens, which, in the fossil record, could be mistaken for a change in prehistoric vegetation or climate.

An extreme case of the woodrat filter effect is the Stephens' woodrat (*Neotoma stephensi*), which is a dietary specialist that requires juniper-tree foliage. Ninety percent of its yearly diet is juniper, mostly *Juniperus monosperma*, and usually from a single tree. Because of its preference for juniper foliage, plants in their middens also have a comparatively low correspondence to the diversity of local plant communities (Vaughan 1990). Today, the Stephens' woodrat ranges throughout the central part of the Southwest, although its range may have been different in the past. Thus, a fossil midden dominated by juniper twigs can be the result of a woodrat diet. Furthermore, the juniper targeted by a woodrat can be an isolated individual along a rocky escarpment that is a relict from the past. If this is the case, the presence of large numbers of juniper twigs in a midden, although of biogeographical interest, is misleading with regard to vegetation and paleoclimate reconstruction.

Rocky-Escarpment Vegetation

Fossil woodrat middens are preserved at protected sites along rocky escarpments. As a consequence, plant macrofossil records represent escarpment plant communities. Rocky escarpments are special microhabitats in the desert, characterized by thin, stony soils, steep north- and south-facing slopes, and sometimes seeps from perched water tables, all of which interact to produce variable plant communities. These narrow, restricted plant communities differ significantly from vegetation occupying broad upland expanses and wide-valley slopes where soils are thicker and finer in texture. For example, creosote is generally restricted to broad, flat colluvial-alluvial surfaces and is seldom found today along rocky escarpments; it is perhaps surprising that creosote occurs at all in middens. Although woodrats build houses at the base of shrubs and cacti in these broad upland and lowland areas, their middens are not protected from rain and snow and are not preserved as fossils.

Escarpments may also harbor plant relicts for millennia in protected rocky habitats after changes in regional climate and vegetation. The apparent persistence of juniper woodlands at lowland sites in the desert during the Holocene may be explained by the presence of relict stands and individuals of junipers along escarpments.

Chronology: Pollen Profiles vs. Middens

One misleading aspect of most midden studies is that the radiocarbon-dated middens are reported in print as a single diagram arranged by time, similar to a pollen diagram. However, unlike pollen diagrams, which represent a single core or stratigraphic section, the middens may have come from a wide area with differing microhabitats, instead of occurring all in one place. The temporal distribution of middens is erratic, too, with each dated part of a midden representing a thin slice of time with large gaps in between. For example, the initial study at Chaco Canyon of nineteen different middens spanning 10,600 years looks convincing when brought together in a single diagram (Betancourt and Van Devender 1981). Yet, when the distribution of middens over an area of fifty square kilometers through time is illustrated in maps (Figures 1 and 2), the reader is left wondering: How representative are the macrofossil data from those middens? At Chaco Canyon, the older fossil middens are from west-facing Atlatl Cave, where today plants thrive at a seep from a perched water table. Some fossil middens are from xeric south-facing escarpments of the central canyon. Other fossil middens are from east-facing slopes of tributary canyons. These diverse escarpment environments harbor distinct plant communities today. It is reasonable to conclude that a similar diversity of plant communities exited in the past. As a consequence, plant macrofossil content of middens may reflect both temporal and geographic differences in environments. Thus, apparent changes in a plant macrofossil record through time may be a result of different microhabitats represented by the fossil midden localities.

Fossil Middens: Biased Sampling

Perhaps the most serious issue facing the field worker is sampling. Given a large number of middens in an area and a limited amount of funding available for radiocarbon dating, how does a researcher decide which midden to study? The answer to this question is, unfortunately, that middens containing exotic, non-local plants are targeted for collecting, while middens containing only plant species found in the modern flora are bypassed (Grayson 1993: 215). What this means is that desert middens containing obvious remains of juniper twigs or pine needles are collected, while those without are not collected. Is it a sur-

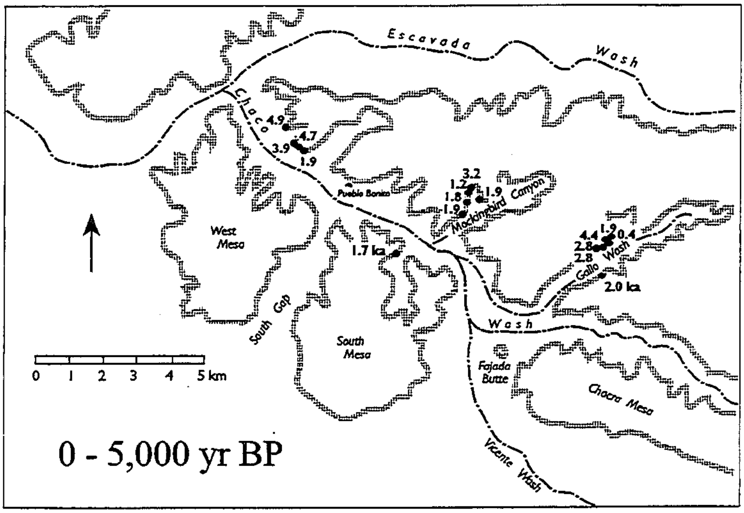

Figure 1. Woodrat Middens, Chaco Canyon, 0 to 5,000 Years Before Present

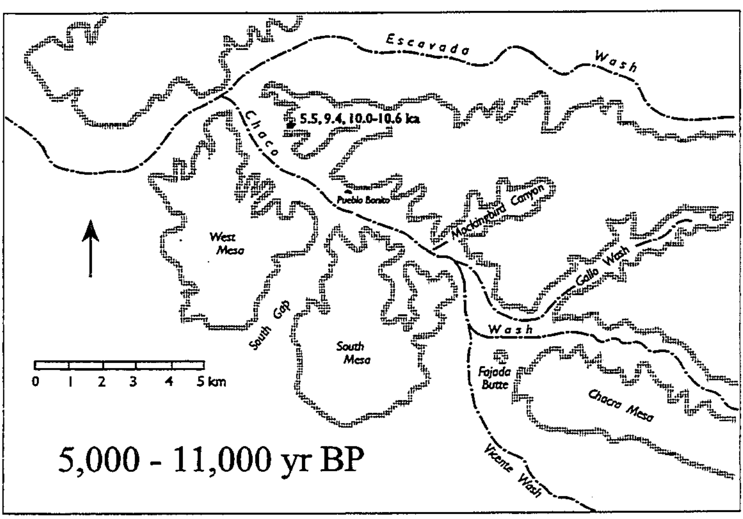

Figure 2. Woodrat Middens, Chaco Canyon, 5,000 to 11,000 Years Before Present

prise that so many middens are from a pinyon-juniper woodland? This systematic error in sampling is an obvious mistake and has resulted in a serious biasing of virtually all midden data, the extent of which may never be known.

In *Packrat Midden,* Webb and Betancourt (1990: 85) referred to the field-sampling bias:

> In the early enthusiasm for packrat midden research, as with any new technique, special research interests dominated the collection of data. As a result, basic sampling assumptions required for a synthesis of the total midden record have not been explored.

This statement suggests that specific types of middens have been the focus of field collecting—perhaps some strongly indurated middens with conifers, or, on the other end of the spectrum, loose, obviously young middens without conifers. We can only wonder, for example, whether or not low-elevation middens with pinyon and juniper are representative of all the middens formed during that particular time period. If all of the middens in a given area were sampled, a 100 percent survey, would there be middens without pinyon and juniper of the same age as middens with pinyon and juniper? If that were the case, how would it change our interpretations of past vegetation and climate?

Fossil Middens: Unique Preservation

Pollen grains and plant macrofossils in middens are often perfectly preserved because of the dried-urine cement that binds the plant materials together and the dry, sheltered sites that protect the middens from being dissolved away by moisture from rain and snow. Because of the excellent preservation, pollen grains can be identified accurately, and accordingly, pollen assemblages and their percentages have a greater reliability than do pollen percentages from deposits where grains are poorly preserved.

In addition, the excellent preservation of plant parts in fossil middens allows species-specific identifications that are seldom possible in other types of deposits, except dry caves and perpetually water-saturated sediments associated with lakes and mires. The species- and generic-level of identification of plant macrofossils is often at a much better taxonomic resolution than is possible with pollen grains, mostly identifiable at genus and family level. Good examples of this dichotomy are illustrated by *Juniperus* and *Quercus,* where pollen can identify only the genus, while twigs, seeds, leaves, and acorns can be identified to species. Another good example is the grass family Poaceae, where pollen can seldom resolve beyond the family, while whole stems can be identified to species (even better than grass phytoliths, which can only be identified to groups of genera). Another important difference in identification potential is with pines. In the Southwest, some pines can be identified by their pollen (if well preserved), such as ponderosa (*Pinus ponderosa*) and limber (*P. flexilis*). Pollen of bristlecone pine (*P. aristata*) and the pinyon pines (*P. edulis, P. remota, P. cembroides*) are distinct from ponderosa and limber pines but are difficult to distinguish from each other. On the other hand, needles from all the pines, including the pinyons, are identifiable to species, especially if needle bundles are not broken up. Another advantage of plant macrofossils from middens is that many seeds and leaves of insect-pollinated annuals are preserved and identifiable, while pollen grains from these flowers are generally not found in pollen assemblages. Also, insect-pollinated flowers produce small amounts of pollen, compared to the enormous amounts of pollen released by wind-pollinated plants. As a result, pollen grains from insect-pollinated species are rare or absent in pollen assemblages, not just in woodrat middens, but also from nearly all environments.

Pollen Analysis of Fossil Middens

Pollen analysis of fossil woodrat middens, even with the above limitations, provides valuable information on plant communities that has not been obtained from looking only at macrofossils. The first pollen analysis of fossil woodrat middens was by J. E. King. He analyzed middens from the Sonoran Desert of eastern Arizona and adjacent California (Van Devender and King 1971; King and Van Devender 1977). In twenty-two middens, King identified forty-seven pollen taxa. From the same middens, eighty-four macrofossil taxa were identified; only eighteen of them were in common. Pollen analysis added twenty-nine taxa to the floral list from the middens that were not represented by macrofossils, including such important taxa as Poaceae, *Abies, Picea, Celtis, Ulmus, Populus, Salix,* and *Ephedra torreyana* and *Ephedra viridis* types. From the study, King concluded that

> ...the macrofossil record in any one midden is geographically limited. It is similar to a photograph of one's backyard, incredibly detailed but not always representative of the rest of the city. The combination of macrofossils and pollen, however, provides the specific identification of species and communities that once existed at the site, yet places them within the framework of the larger regional pollen rain. (King and Van Devender 1977: 203)

One of the important lessons from the King and Van Devender study is illustrated by the presence of *Artemisia* in the fossil middens. About half the middens had very low abundance (rare to uncommon) of identifiable remains of white sage (*Artemisia ludoviciana*) and big sagebrush (*Artemisia tridentata*); seven of the middens lacked *Artemisia* macrofossils altogether. They concluded that white sage and big sagebrush, based on macrofossils, were insignificant in the local plant community. In contrast, *Artemisia* pollen occurred in every midden and, in fact, was one of the five most abundant pollen taxa in the entire record, especially in the Pleistocene middens. While the macrofossils were interpreted as a pinyon-juniper-oak woodland, the pollen record showed that the vegetation also included a large component of *Artemisia,* which was not picked up by macrofossil analysis.

The next major study of pollen from fossil woodrat middens came from Chaco Canyon. Here, an earlier investigation of pollen from alluvium provided an opportunity for an independent check on the midden pollen and macrofossil records. The Chaco pollen records both from alluvium and middens indicated a treeless shrub desert grassland vegetation, while the macrofossils indicated a pinyon-juniper woodland vegetation. Seemingly, both views could not be right. However, at low-elevation sites in the southwestern deserts, isolated trees and small stands of trees, especially pinyon pines and single-seed junipers, are often found as outliers along rocky escarpments. Such is the case today at Chaco Canyon. Junipers and a few pinyons are restricted to escarpments, where the escarpment microhabitat allows them to survive. This must have been the situation at Chaco Canyon in the past as well. The pinyon and juniper macrofossils from middens reflected the presence of isolated trees along escarpments, while the surrounding upland and lowland vegetation was a desert shrub grassland. This reconstruction, although not accepted by midden analysts who prefer a more literal interpretation of macrofossils, accommodated all of the plant data, pollen and macrofossil alike. Of course, if we accept the reconstruction that the prehistoric vegetation was a desert shrub grassland with a few pinyons and juniper along escarpments, then we must also modify models of prehistoric land use, especially models that call for regional "deforestation" by prehistoric inhabitants (Hall, 1977, 1981b, 1982, 1986, 1988; Betancourt and Van Devender, 1981).

Quaternary Vegetation

The following issues are taken from Hall (1985), who synthesized southwestern vegetation history from the pollen-analysis literature up through 1984, and from Betancourt et al. (1990), wherein a series of chapters summarized southwestern vegetation history from fossil woodrat-midden literature up through 1987. Even though a few important pollen and woodrat-midden studies have been subsequently published, the overall picture of vegetation history presented by pollen and by midden macrofossils remains generally unchanged from the Hall (1985) and Betancourt et al. (1990) summaries.

Late Pleistocene and Holocene Vegetation

Late-Wisconsin pollen records from the Chihuahuan and Sonoran deserts showed a consistent, general pattern that, during the last glacial maximum, the vegetation was an *Artemisia* grassland. By 14,000 years ago, as climate warmed, pinyons dropped out of the low-elevation terrain and were replaced by a drier Chenopodiaceae-Asteraceae shrub grassland. Throughout the Holocene, low-elevation desert regions were dominated by desert-shrub grassland vegetation. The mid-Holocene was characterized by a decrease in grasses and an increase in shrubs due to the hot, dry climate during that period. In the Colorado Plateau during the late Wisconsin, open forests of spruce and fir occurred at higher elevations, and an *Artemisia*-pinyon woodland occurred on lower sites.

Vegetation reconstructions based on plant macrofossils from woodrat middens differed dramatically from those based on pollen analysis. Virtually all studies of low-elevation glacial-age middens (Chihuahuan and Sonoran deserts) were interpreted as a pinyon-juniper-oak woodland. At 11,000 years ago, a major shift in plant communities occurred, with the movement of pinyon trees to higher elevations and, throughout the Holocene, a northward migration of pinyons into the Colorado Plateau and beyond. During the Holocene, desert species began to occupy low elevations, forming a desert scrub vegetation by 8,000 years ago, with the dropping out of junipers by 7,000 years ago. Modern desert plant communities were established during the past 4,000 years. At high elevations in the Colorado Plateau, late-Wisconsin vegetation was a spruce-fir forest. In low-elevation areas, there occurred a mixture of limber pine-

Douglas fir-spruce-white fir-Rocky Mountain juniper *Artemisia* grassland vegetation, specifically lacking pinyon and ponderosa pine. During the Holocene, conifers moved to higher-elevation sites, and pinyon pines invaded from the southern deserts, resulting in the development of a pinyon-juniper woodland throughout the Colorado Plateau.

Discussion of Vegetation Reconstructions

The only major point of agreement between pollen and midden records is that, during the last glacial maximum, trees were growing at elevations lower than they do now. In the glacial-age Chihuahuan and Sonoran deserts, pollen indicated an *Artemisia* grassland, in contrast to plant macrofossils that were interpreted as pinyon-juniper-oak woodlands.

Insect and vertebrate faunal studies, however, agreed with the pollen record, indicating glacial-age grasslands. Insect fossils in glacial-age middens at Big Bend, Texas, have affinities to faunas occurring today in Great Plains grasslands, indicating that the *Artemisia* grasslands documented in West Texas may have extended south into what is now the northern Chihuahuan Desert during the last glacial maximum (Elias and Van Devender 1990; Elias 1994: 214-215; Hall and Valastro 1995). Glacial-age vertebrate faunas from the same regions also indicated grassland vegetation (Harris 1985, 1993; Graham 1987). The reader may well ask: Why were plant macrofossils from middens indicating a pinyon-juniper-oak woodland, while numerous studies of pollen, insects, and vertebrates indicated grassland vegetation? For reasons discussed in this article, the pinyon-juniper-oak macrofossils from middens may represent isolated individuals or small populations of trees along rocky escarpments that were not characteristic of the overall regional vegetation. The insect fauna from Holocene middens also diverged from the plant macrofossil record; the insects indicated a vegetation dominated by desert grasslands instead of desert shrublands (Elias and Van Devender 1990).

Ironically, the conclusion that the late-Wisconsin vegetation of the Colorado Plateau was a limber pine-Douglas fir-spruce-white fir-Rocky Mountain juniper *Artemisia* grassland is based on the presence of these conifers in some low-elevation midden sites and the evidence from pollen records for a widespread *Artemisia* grassland (Betancourt 1990: 281-282). What type of vegetation is a limber pine-Douglas fir-spruce-white fir-Rocky Mountain juniper *Artemi-*

sia grassland? As in the situation with the evidence from the Chihuahuan Desert, it is likely that low-elevation expanses of the Colorado Plateau were characterized by an *Artemisia* grassland, while some conifers grew along rocky escarpments.

An interesting facet of the Wisconsin midden record is the absence of ponderosa pine (*Pinus ponderosa*) and Colorado pinyon pine (*P. edulis*) from the Colorado Plateau. Today, ponderosa pine occurs widely throughout the western United States, and it seems unusual that it would not show up in glacial-age midden records. On the other hand, *P. ponderosa* pollen is distinctive and has been identified in lake deposits of Wisconsin age in the Chuska Mountains in the heart of the Colorado Plateau (Wright et al. 1973). Why it is rarely found in woodrat middens is not yet known. It occurs in Holocene middens; perhaps the species of woodrat inhabiting the region during the Wisconsin avoided collecting ponderosa pine due to the unappealing chemistry of its needles. Another enigma is the absence of glacial-age midden records of Colorado pinyon pine. *P. edulis* pollen also has been documented in full-glacial lake sediments in the Chuska Mountains (Wright et al. 1973). Again, the Wisconsin-age woodrats may have been avoiding pinyon pines, just as with ponderosa pine. In a recent study, however, needles of *P. edulis* from a woodrat midden in north-central Arizona are directly-dated 13,670 +1,160/-1,010 years BP. Cinnamon and Hevly (1988) concluded that the new record of pinyon pine shows that pinyons were not absent from the region during the late Pleistocene and that the widespread range of pinyons in the western United States today may have spread from isolated populations scattered in canyon systems.

Before woodrat middens were noticed by paleoecologists, plant macrofossils from lakes and mires were used to evaluate local wetland plant communities (Argus and Davis 1962; Baker 1965; Baker et al. 1989). In most cases, information from fossil seeds and other plant remains supplemented the pollen record, informing the analyst of which plant species were growing at and near the site of deposition. Seeds and other remains of aquatic plants provide insight on the nature of changing lacustrine environments during basin infilling and fluctuating water tables. Remains from upland plants indicated the local presence of plant species. While plant macrofossils from organic-rich deposits contain pivotal information on plant species inhabiting local wet-ground sites and adjacent uplands, they were generally limited from indicating the regional upland vegetation; the picture of what the regional vegetation looks like was painted by pollen analysis. Plant macrofossils from woodrat middens are analogous to those from lacustrine deposits, and, accordingly, they are representative of local plant communities rather than regional vegetation.

Woodrat Middens as Nonrenewable Resources

Fossilized woodrat middens are unique. Once destroyed, the vast amount of information they contain is lost forever. I and my colleagues are appalled at the destructive collecting of fossilized middens that we have seen in the field. We have visited midden sites in New Mexico after they had been collected by others and have found large chunks of broken midden strewn on the ground. In some cases, there is nothing or very little of the original midden left in place.

Woodrat middens have value far beyond the identification of a few exotic plant fossils. Middens are sources of material for studies of stable isotopes, genetics, biochemistry, insects, vertebrates, mollusks, pollen grains, fungal spores, and other micro-remains. Without doubt, there are new, future applications that are not yet imagined. Furthermore, how does one check and modify the studies of previous workers if the middens are destroyed?

Who owns fossil middens? Since most of the studies involve middens on federal- or state-owned and managed land, "we" own the middens. A parallel can be made with archaeological sites, also unique nonrenewable resources (who owns archaeological sites?). Furthermore, what is the responsibility of the researcher concerning the use and care of fossil middens? One would think that the individual who studies middens would feel a strong responsibility to preserve these valuable resources. (To be fair, I should hastily add that not all midden workers destroy middens; some middens I and others have visited very recently that had been sampled years ago are in excellent condition.) With some individuals, however, a sense of personal responsibility does not seem to be important, considering the destruction of middens that has already occurred.

What is to be done? Perhaps fossil middens should be treated in the same way by which we manage archaeological sites. Woodrat middens could be inventoried, mapped, evaluated in the field, given numbers, and registered with an environmental-management office of a branch of the federal or state government. Permission to study and collect would have to be cleared and monitored. Anything collected from fossil middens, just as with artifacts from archaeological sites, would be curated and made available for study by others. Alas, if an individual were intent upon busting apart woodrat middens searching for exotic plant species, it would continue to occur, just as archaeological sites are still vandalized. But, in the end, perhaps education will prevail and middens will be preserved for future study and applications.

Conclusion

It is clear to this reviewer that, because of field-sampling problems and the presence-only nature of midden data, plant macrofossils from woodrat middens are less suitable for use in reconstructing regional vegetation than initially thought. Indeed, the interpretations of fossil middens that appear in the literature seldom match the evidence for past vegetation that comes from pollen records, insect assemblages, and vertebrate faunas. On the other hand, because of the excellent preservation of plant remains and the species- and genus-level of taxonomic information that they provide, midden fossils can help the pollen analyst determine what species are represented by pollen grains. Also, fossil middens are unique, nonrenewable sources of valuable paleophytogeographic information from the southwestern deserts that is not forthcoming from other lines of research. Because of their uniqueness and importance, fossil woodrat middens should be conserved.

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