Thoughts on the Evolution of Southwestern Desert Reptiles

Thomas R. Van Devender

Research Scientist
Arizona-Sonora Desert Museum
2021 North Kinney Road
Tucson, Arizona 85743

(This article is based upon a presentation made to the Tucson Herpetological Society on 20 March 1990.)

At one time I was President of the first herpetological society in Tucson and had the distinction of having the society vote to disband while I was President. It looks like you have a more viable organization now than the first go around.

What I'd like to do is to show some pretty pictures and give you some thoughts on the evolution of the deserts of North America and some of the animals you know and love and their roles in all of this.

Tumamoc Hill here in Tucson has a nice Sonoran Desert community and we know it because it is in our backyard. However, when one looks closely at the Sonoran Desert, and really any of the deserts of North America, you see unique morphological adaptations. There are plants with spines, lizards with spines, and other things that are special about desert species.

As to origins of these deserts, you have to go back to the early part of the Tertiary to put this into a time perspective. The extinction of the dinosaurs at the end of the Cretaceous was about 65 million years ago. The early Tertiary was a long, warm, tropical period for North America and most of the world. Before we had deserts, we had tropical vegetation. At that time, broadleaf or tropical deciduous forest were present practically coast to coast across North America with very little regional differentiation.

In the Eocene (35 to 45 million years ago) fossils of tortoises, crocodiles and palms were found on Ellesmere Island, which is today and was then, north of the Arctic Circle. The fossils are even more interesting considering the six months of darkness at such high latitudes. Are hibernation and aestivation the modern descendants of dormancy in tropical Arctic regimes?

As to the reptiles and amphibians, a different kind of primitive fauna lived in those early tropical vegetation types. Some of the early herps were tortoises, *Stylemys nebraskensis* from the Oligocene, an ancestral gopher tortoise, and primitive families of reptiles such as the night lizards (Xantusiidae), the skinks (Scincidae), the anguids (Anguidae), and the closely-allied Xenosauridae. The snake fauna was dominated by a ground boas in the subfamily Erycinae - not large species like *Boa constrictor*. *Lichanura trivirgata* (rosy boa) and *Charina bottae* (rubber boa) are the surviving members of the group. *Eryx* itself is now found in desert areas in Africa and the Middle East.

Tropical means a warm climate with rain during some part of the warm season. With the exception of rainforest, tropical communities have a dry season ranging from a few to more than six months. During the dry seasons, plants and animals are faced with with desiccation and heat as they are in more arid environments. Paleobotanist Daniel Axelrod of California proposed the idea that the plants of the Sonoran Desert or their ancestors evolved in dry tropical forest communities. For example, Alamos in southern Sonora, Mexico, receives 40 to 50 inches of rain a year but also has a very dry period from January to July. As you move north in Sonora, as near Ures on the Rio Sonora, tropical deciduous forest gives way to drier Sinaloan thornscrub. Here the plant communities are much more open and the plants are more drought stressed during the dry season.

Several processes were involved in the transition from the archaic, tropical biota of the early Tertiary tropics to what we have today. In the late Oligocene and early Miocene (15-30 million years ago) a number of new herps immigrated to North America across the Bering Strait from Asia. As late as the early Miocene (20-25 million years ago), there palm trees were still growing in Alaska. New herp families including the Bufonidae, Ranidae, Colubridae, Elapidae, and Viperidae appeared for the first time in the fossil record and began major evolutionary radiations.

Major geological events in the early to middle Miocene were important in modernizing the biota. The Rocky Mountains and the Sierra Madre Occidental were uplifted to great heights for the first time. The Rocky Mountains in particular were high enough to interfere with the upper circulation of the atmosphere. Today most of our weather of North America is tied down to the axis of the Rocky Mountains. For the first time different weather patterns developed for major regions. Eastern, mid-continent, Rocky Mountains, southwest, and west biomes developed as environmental extremes including aridity (grasslands, deserts, tundra) and cold (woodlands, conifer forests, tundra), became limiting.

The middle Miocene uplift of the Rocky Mountains had several effects on biota of North America. One was segregating out species tolerant of cold and aridity from more tropical species to form new communities. In many of the groups that are now common and successful, there were dramatic evolutionary radiations. The Miocene was a revolutionary period with a dramatic turnover in the biota - from archaic to modern.

Several years ago, I met Dave Barker who's Master's thesis was on the ridgenose rattlesnake (*Crotalus willardi*). From his work he had concluded that this species was the most primitive of the rattlesnakes. From my perspective, considering the Miocene uplift of the Sierra Madre Occidental, I would not view it as the most primitive but of a younger origin. To me the forests and woodlands of the Sierra Madre are derived habitats compared to lowland tropics. If it lives on the top of a mountain, it should be a younger species than a tropical lowland relative. Species of *Sistrurus* and lowland tropical *Crotalus* should be older species present before the uplift. However, the Sierra Madre is older than Sonoran Desert so that the evolution of the sidewinder (*C. cerastes*) could have occurred millions of years later than the ridgenose rattlesnake. In a similar example, lowland tropical subspecies of *Lampropeltis triangulum* (milksnake; *amaura*, *annulata*, *conanti*, *nelsoni*, *sinaloae*) are probably more primitive than montane (*arcifera*, *dixoni*, *smithi*) or Great Plains/Rocky Mountains (*celaenops*, *gentilis*, *multistriata*, *taylori*) forms.

A couple of events shaped the evolution of the Sonoran Desert biota including with the rifting of the Baja California Peninsula from mainland Mexico in the middle to late Miocene beginning about 12 million ago. Cabo San Lucas on the southern tip (21°N) was attached to the mainland in the state of Jalisco (20°30" N). The land mass split off and moved 275 miles to the north-northwest. At times it was a series of islands. Isolation of the biota, moving to higher latitudes, and general trends in increasing cool aridity resulted in a unique evolutionary arena. Examples of Baja species include the rosy boa (*Lichanura trivirgata*) and chuckwalla (*Sauromalus obesus*). The rosy boa is interesting because it is both from an archaic ground boa and a desert-adapted species.

Beginning in the middle Miocene about 15 million years ago there was general increase in aridity. By the latest Miocene (5 to 8 million years ago) the Sonoran and Chihuahuan deserts were in existence according to Axelrod. Thus species such as saguaro (*Carnegiea gigantea*), sidewinder, and regal horned lizard (*Phrynosoma solare*) could be as much as 5 million years old! The aridity peak resulted in the separate evolution of eastern and western herps in some tropical groups. For example, both the barefoot gecko (*Coleonyx switaki*) of California and Baja California and the Big Bend gecko (*C. reticulatus*) in Texas and northern Mexico were derived from a tropical ancestor very similar to *C. mitratus* of tropical Mexico.

The Pliocene was the time of the iguana. The sequence we've gone through began with widespread tropics, the uplift of the mountains, and a gradual increase of aridity forming the deserts. Several important things happened to the deserts subsequently. In the Pliocene (2 to 4 million years ago) it again became very warm and moist. Recent pollen work done in northern Canada, found pollen and macrofossils of five needle pines (*Pinus*) and tulip trees (*Liriodendron*) in Pliocene deposits at at 80° North. Now that's a long way from the desert but the absence of permafrost in the Arctic would indicate warm conditions for the globe and a tremendous northward expansion of the Neotropics. Pliocene fossils of *Iguana iguana* collected in the Anzo Borrego badlands of southern California certainly indicate more tropical conditions. Warmer climates with little water tied up in continental glaciers resulted in very high sea levels, the Gulf of California extended all the way to the Los Angeles area. There is even some geologic evidence that there was a connection with the Pacific isolating the L.A.-San Diego-Baja California area into an island. Other climatic implications of a warm Pliocene, would be expansion of the eastern Sonoran Desert with saguaros at least to Las Vegas and of the Vizcaino-Baja California desert to San Diego, Los Angeles, or Santa Barbara! In turn, the Mediterranean winter-rainfall chaparral would have been pushed further up the coast.

Beginning about two million years ago, in the Pleistocene, a series of ice ages profoundly affected the climate and biota of the earth. Giant continental glaciers were in large areas of North America, Europe, and South America. To give an example, New York City and the Great Lakes were under two miles of ice. The glaciers themselves produced secondary climatic changes reflected in biotic shifts over the entire globe. Much of the energy in sunlight hitting the surface of a glacial is reflected due to its very high *albedo* (a measure of reflectivity) - leaving them as cold air sinks. Winds and weather redistribute cold and heat on the earth's surface. Changes in one area will be felt elsewhere. For example, colder air at high latitudes could indirectly be involved in increased winter rainfall in the Sonoran Desert or drier climates in Central America, the Sahara, or Australia!

When palynologists, people that study fossil pollen, studied lake sediments in Europe, the eastern United States, and eventually in the Southwest (the San Augustin Plains in New Mexico, and the Wilcox Playa in Arizona), they found pollen of a very different vegetation types than today in muds 10,000 to 15,000 years in age. In 1965, Paul Martin at the University of Arizona concluded from his pollen work that vegetation was lowered about 3,300 feet below what it is today during the last glacial period. A vegetation lowering of this magnitude would leave little room for ice age deserts.

Another product of having glacial periods is that ranges of a number of herps were split on either side of the continental divide giving rise to two species - termed a vicariance event. One species pair is the Trans-Pecos ratsnake (*Elaphe subocularis*) and the Baja California ratsnake (*E. rosaliae*). The desert banded geckos, *Coleonyx brevis* in the Chihuahuan Desert, and our local gecko, *C. variegatus* in the Sonoran Desert are closely related. The desert horned lizard (*Phrynosoma platyrhinos*) from Sonoran and Mohave deserts and the round-tailed horned lizard (*P. modestum*) of the Chihuahuan Desert, are an interesting east-west species pair. *Phrynosoma modestum* is a small species that earns its living mimicking rocks. The juveniles of the two species are much more similar than the adults. *Phrynosoma modestum* is more derived and probably reflects an evolutionary process called "paedomorphism" or "neoteny", i.e. the new species matures at a smaller size, retains juvenile characters as an adult, and loses adult characteristics.

At this point I'd like to present some of the paleoecological evidence I have personally obtained, focussing on the fossil records of reptiles and amphibians. In 1872, the United States was still exploring the western part of the country and searching for transcontinental railroad routes to connect California with the East. A U.S. Army expedition under the command of a Lt. Wheeler passed through New Mexico and Utah. The herpetologist on the expedition named Yarrow (of Yarrow's spiny lizard fame) discovered a hard, dark organic deposit. He took it back to Washington and had chemical tests done on it, finding how much ash and lithium it contained. He and his associate Spencer Baird (of Baird's ratsnake and sparrow fame), then the Assistant Secretary of the Smithsonian Institution, decided that the deposit was the work of the chuckwalla (*Sauromaulus obesus*). Since Baird was the scientific describer of the chuckwalla (as *Euphryne obesus*) that lent credence to their opinion, included in the herpetology section of the Wheeler survey report. The only worry was that chuckwallas were not known to occur in Utah. In a footnote, Edward Drinker Cope, the famous herpetologist and vertebrate paleontologist, disagreed and said the deposits were the work of packrats!

Packrats or wood rats (*Neotoma* ssp.) are medium-sized rats that collect objects and bring them back to their houses. They have a home range of about 30 to 50 m, so they don't go very far. When they live in dry rockshelters or caves, they may cement portions of their collections together forming hard deposits called middens. The deposits will be preserved as long as they are dry and have been radiocarbon dated as far back as 51,000 years ago. They have proven to be a remarkable source of fossils from the deserts themselves — other sources of fossils are rare. Packrats collect a great variety of organic materials. Most are plant macrofossils including well-preserved needles, leaves, twigs, spines, seeds, etc. A variety of animal remains including occasional bones, teeth, scales, and feathers of small of vertebrates and common arthropod remains in the middens are transported to the rockshelter by raptorial birds or small mammalian predators. They potentially are from larger sampling areas than the plant fossils.

So what? We've got these little piles of crap from the desert which are well preserved and can be identified to species. Radiocarbon dating allows us to string them into time sequences. If the samples are from one area, the fossil assemblages provide detailed records of change through time. Geologically, 50,000 years is not a long time compared to the 65 million years since the end of the Cretaceous that we began talking about. However, it's enough to give us a good idea of the dynamics of desert communities during the shift from a glacial to an interglacial climate.

The southern Chihuahuan Desert in Chihuahua, Durango, and Coahuila, Mexico, is known as the Bolsón de Mapimí. In Dave Morafka's doctoral work, he defined a more southern division, the Saladan, in Zacatecas and San Luis Potosí. It's really too wet to be included in the desert, but is certainly a Chihuahuan Biotic Province. The area between Saltillo and Torreón has broad valleys with playa basins that were huge fresh water lakes during the last ice age. The Chihuahuan fringe-toed lizard (*Uma exsul*) lives on the sand in this playa. This lizard is an eastern disjunct related to our *Uma* of the Colorado River Valley in Arizona, California, and northern Mexico. Morafka considers the Chihuahuan species to be primitive and ours to be more advanced. Their isolation probably predates the Pleistocene.

On the limestone slopes in the Bolsón de Mapimí at 26°N, you find incredibly rich succulent communities. I've collected packrat middens from caves in the area as old as about 12,000 to 13,000 years. In the last glacial period, pinyon pine and juniper grew on these slopes with Chihuahuan Desert succulents in mixed biotic communities. Several interesting animals were identified from the middens. The Texas alligator lizard (*Gerrhonotus liocephalus*) expanded its range to lower elevations; the modern environment is too hot and dry for it. I also identified the bones of the canyon lizard (*Sceloporus merriami*), that is still common on the nearby rocks. The coming and goings of ice age climates and woodland trees probably had little effect on this Chihuahuan endemic.

The Big Bend National Park at 30°N is separated from the Sierra del Carmen in Coahuila on the Mexico by the Rio Grande. The elevation of about 2000 ft. on the river is the lowest, hottest, driest portion of the Chihuahuan Desert. In comparison most elevations in the Bolsón de Mapimí are above 4000 ft., El Paso is at 3900 ft., Tucson is at 2400 ft., and Yuma is at 400 ft. I have middens from sites from near Rio Grande Village in the Park and from Maravillas Canyon in Black Gap Wildlife Refuge that go back 45,000 years. Prior to 11,000 years ago in the last glacial period, a pinyon-juniper-oak woodland grew on the limestone slopes. Some Chihuahuan Desert plants such as lechuguilla (*Agave lechuguilla*) were in the woodland but fewer than in the Bolsón de Mapimí.

Interesting ice age faunal records from Big Bend middens include the Bolson tortoise (*Gopherus flavomarginatus*). Today this is a threatened species restricted to a small area in the Bolsón de Mapimí. It is being intensively studied and managed for its survival. From 12,000 to 20,000 years ago, this tortoise was living in Maravillas Canyon. The slopes supported a woodland vegetation much more mesic than is found in its modern range. Paul Martin at the Desert Laboratory, University of Arizona, believes that its decline was the result of prehistoric hunters. Incidentally, the same deposits yielded a bone of the California condor (*Gymnogyps californianus*). Shell fragments of a second tortoise in the same cave belonged to Wilson's tortoise (*Geochelone wilsoni*). This extinct species was first discovered in Freisenhahn Cave near San Antonio, Texas. *Geochelone wilsoni* was a small tortoise with a very high-domed, ridged carapace found in late Pleistocene deposits from central Texas to the Big Bend north to southern New Mexico, and southern Oklahoma.

Some other interesting herps identified from the ice age middens in the Big Bend are the the Texas alligator lizard, the round-tailed horned lizard, western hook-nosed snake (*Gyalopion canum*), blackhead snake (*Tantilla rubra*), milksnake (*Lampropeltis triangulum*), and everybody's favorite pet, the grey-banded kingsnake (*L. mexicana*). The interesting thing about finding Texas alligator lizard, *Gyalopion*, *T. rubra*, and *L. mexicana* in the Big Bend during the last glacial period, is that they are mainly Mexican species. If the ice age winters had been much colder than today's, they would have been displaced southward into Mexico. However, the fossil record provides strong evidence for an equable climate, meaning that summers were cooler and winters were warmer than today, allowing for biotic mixtures not found today or only in narrow ecotones.

With *Lampropeltis mexicana* above, notice I use "*mexicana*" and not "*alterna*" because I don't think they're different species. The evidence in Bill Gartska's paper used to separate the species is weak and unconvincing. You should look into it before uncritically accepting and using *L. alterna*. The subspecies *alterna* is found from Coahuila to the Big Bend, the Davis Mountains, and all the way to the El Paso area in Texas. It has a reduced dorsal pattern with alternating blotches. The subspecies *blairi* is found east of the Big Bend at the southern edge of the Edwards Plateau from Rock Springs and Del Rio west to the Davis Mountains. Although Ernest Tanzer lumped the two subspecies based on a mixed litter and a crude poll of collectors, the forms are distinct subspecies. Data supporting the validity of *blairi* as a subspecies are in Dennie Miller's masters thesis at Sul Ross University which was published by the Chihuahuan Desert Research Institute. Individuals with the *blairi* pattern enter the Big Bend from the east in Black Gap and in the desert ranges in the Park. Ice age climates were more like those of central Texas. During each glacial, *blairi* moved into the Big Bend. Populations in places like the Christmas Mountains near Luna Vista northeast of the Park, have complex genetic mixes reflecting repeated incursions of *blairi* into *alterna*. The incredibly variable color patterns in this population are probably a reflection of historical gene flow and not necessarily due to local adaptive pressures.

About 25 miles east of El Paso, Texas, the Hueco Mountain State Park at 32°N is a nice place to visit. In the northern Chihuahuan Desert creosotebush (*Larrea divaricata*) and Torrey yucca (*Yucca torreyana*) are still present but limestone slopes support fewer succulents Packrat middens in caves in the Hueco Mountains provide fossil records for the past 42,000 years. As elsewhere, pinyon-juniper-oak woodland was on the slopes until about 11,000 years ago, although few Chihuahuan plants were present.

One of the interesting ice age faunal records in the middens was the short-horned horned lizard (*Phrynosoma douglassi*). Although it is common in higher elevation grasslands, woodlands, and forest from the northern Sierra Madre Occidental in Chihuahua north through the Rockies as far as British Columbia, it is a fairly rare animal in Texas. It is common in the massive Sacramento Mountains of south-central New Mexico. In Texas it's restricted to the Davis and Hueco Mountains (a recent discovery). The midden fossils indicate that under cooler conditions, this animal expanded its range across valleys and to ranges that are now too harsh for it.

Ranges of other species like the rock rattlesnake (*Crotalus lepidus*) have apparently been more stable and not contracted during interglacials. The Hueco Mountain animals are an unusual tan color reflecting long term isolation in a small mountain range and evolution of a local race or deme. Another interesting fossil record from the El Paso area is of desert tortoise (*Xerobates agassizi*). Although there are a few places where it will get up into juniper woodland, and perhaps pinyons, most populations in the Sonoran and Mohave deserts are in desertscrub, or in thornscrub and tropical deciduous forest in Sonora and Sinaloa. Modern observations of tortoises in woodland are mostly in areas where woodlands occur at unusually low elevations. The desert tortoise records from the northern

Chihuahuan Desert are all from pinyon-juniper-oak woodland samples from 4500 to 5500 ft. elevation and 300 miles east of their present range. Shelter Cave on Bishop's Cap, just north of El Paso in New Mexico, and excavated by the California Institute of Technology in the 1930's, yielded rich collection of tortoise bones and epidermal scutes from the excavation is now housed in the Los Angeles County Museum.

The distribution of creosotebush is the best single indicator of the warm deserts of North America. The midden fossils tell us that creosotebush did not reach the El Paso area until about 4,000 to 5,000 years ago, marking the establishment of the present distribution of deserts. Four thousand years ago brings us into recorded history, — the first pyramids were being built in Egypt, the foundations of Rome were being laid. It's really not that long ago.

Now I'd like provide a few records from the Sonoran Desert. Here in Tucson we live in the Arizona Upland subdivision with paloverde-saguaro desertscrub communities. This part of the desert is well-watered, with high biomass and diversity. As one goes west into the Colorado River Valley, rainfall decreases, temperatures increase, and desert conditions become harsher. I will discuss a couple of packrat midden sites along that gradient and present the paleovegetation and herp records.

In the Waterman Mountains near the Silver Bell mine, just across the Avra Valley west of Tucson, I have a series of middens out of vertical crevices in limestone ridges that go back 22,000 years. Again, Sonoran Desert plants were absent from ice age communities, replaced by a woodland/chaparral. The woodland was dominated by a singleleaf pinyon (*Pinus monophylla*), two types of juniper (*Juniperus*), Joshua tree (*Yucca brevifolia*), big sagebrush (*Artemisia tridentata*-type), and Arizona rosewood (*Vauquelinia californica*). I identified a dermal osteoderm of a Gila monster (*Heloderma suspectum*) from a 22,000 year old woodland sample. Although today it's primarily a desert animal, it is occasionally found up to 6,000 or 7,000 ft. (D. Bertelsen, pers. comm.). It has remained in the Watermans as the vegetation changed around it.

Four middens from Picacho Peak, north of Tucson, ranged in age from 9,400 to 13,000 years. They were exceptional because bones were abundant, particularly the vertebrae of small snakes. A total of 26 herp, small mammal, and bird taxa were identified. An interesting record was the desert horned lizard (*Phrynosoma platyrhinos*) which reaches its eastern limits in the area in the hottest, driest creosotebush communities in the valley bottoms. The regal horned lizard lives in higher desertscrub and desert-grassland and the short-horned horned lizard is in woodland and forest in the mountains. The Picacho Peak record of *P. platyrhinos* was from a pinyon-juniper sample dated at 11,000 years in age. Its presence in a different vegetation is interesting. However, if you go up in northwestern Arizona, it lives in singleleaf pinyon woodlands today (G.L. Bradley, pers. comm.). Again it has been in the Picacho Peak area as the local communities shifted from woodland to desert.

Banded geckos were also in the 11,000 year sample. In fact all of the 14 reptile and amphibian species in the fauna are desert animals that only enter woodland or chaparral at the upper limits of their ranges. During the last glacial period, woodland/chaparral was their typical habitat, open and not desertscrub - a very dramatic conclusion! Twenty years ago, vertebrate paleontologists would identify a Gila monster and say "Ah-ha, here we have a desert." However, midden assemblages with plants and animals in association have shown the lower vertebrates are much more adaptable than we ever thought.

Now moving to Alamo Canyon in the Ajo Mountains of Organ Pipe Cactus National Monument, from a 9600 year old juniper midden I identified a vertebra of *Chionactis palarostris* (Sonoran shovel-nosed snake). This is interesting because it is a regional endemic, ranging from the Monument south to the coast of Sonora, and it was from a juniper sample. Today occasional redberry junipers (*Juniperus erythrocarpa*) in the Ajo's are found well above the habitat of *C. palarostris*. There may be a problem inferring the animal-plant association in the midden because the midden rockshelter was high in the mountains and an owl could have flown down into the valley bottom to feed. It's interesting to know it's been in Organ Pipe 5,000 years longer than the organ pipe cactus (*Stenocereus thurberi*).

Moving further west, we arrive at the Tinajas Mountains, the last range east of the Colorado River. Tinajas refer to permanent water pools in the rocks. Tinajas Altas, or high tanks, was an important stop on the old Camino del Diablo from Organ Pipe to Yuma. The elevation at the base of the rocks is 600 to 700 ft. with few plants and no trees on the slopes. Even saguaro, blue paloverde (*Cercidium floridum*), and velvet mesquite (*Prosopis velutina*) are restricted to riparian habitats along desert washes. Packrat middens from the Tinajas Altas Mountains dating back to more than 43,000 years record singleleaf pinyon as low as 1500 ft. and California juniper (*Juniperus californica*) down to 800 ft.

That's pretty amazing but some of the things that are with them are interesting too. Creosotebush twigs from a California juniper-Joshua tree sample in the Tinajas Altas mountains were directly radiocarbon dated at 18000 years ago, at the height of the last glaciation when the Laurentide Ice Sheet reached its maximum southward extent. Remember that creosotebush only reached the Hueco Mountains in the northern Chihuahuan Desert about 4500 years ago. In contrast it could have been in the lower Colorado River Valley throughout the glacial periods. We began this by talking about the evolution of desert communities and species in response to geological events in North America in the Miocene. Creosotebush is an exception that evolved in a South American species that immigrated to North America.

The bones out of these lower elevation sites are from fairly typical desert species like the chuckwalla, rosy boa, sidewinder, and banded gecko. As elsewhere the desert herps were apparently less affected by glacial climate changes than the plants, and were widespread in ice age woodlands. Now this is interesting because, as recently as the 1970's, herpetologists typically explained the evolution of their beasts as occurring when "They were pushed off into Mexico during the ice ages, differentiated, and then had come back north as climate warned in the interglacials." The late Donald Tinkle and Royce Ballinger in their monograph on the evolution of species and subspecies in the genus *Uta* invoked this argument. Well, the packrat midden fossils have told us that for the most part that didn't happen - that side-blotched lizards (*Uta stansburiana*) stayed in most of their modern desert range as the vegetation changed around them.

We are now getting the picture that the long-lived trees and shrubs been more sensitive to climatic change than many desert animals. These are the structural dominants of the plant communities that you see when you see a forest, woodland, or a Joshua tree desertscrub. Other plants with shorter life spans such as desert grasses and annuals didn't change much. Ranges of many desert reptiles and arthropods have been extremely stable. Thus, a desert community in a broad sense is a complicated ecological web with many layers, each with their own differential responses to climatic changes.

The lowest, driest, hottest deserts in North America are in the Lower Colorado River Valley. Simple desertscrub communities are formed by widely spaced, small creosotebush, white bursage (*Ambrosia dumosa*), and big galleta grass (*Hilaria rigida*). Rocky slopes support few plants and have surely been used as "moonscapes" in Hollywood movies. Ken Cole who worked on Tumamoc Hill analyzed middens from the Picacho Peak area (another one) in California just north of Yuma. Creosotebush communities without junipers were still on the slopes 13,000 years ago at the end of the last glacial. Even here there was change in the desert communities because Sonoran Desert plants were replaced by Joshua tree and Whipple yucca (*Yucca whipplei*), Mohave Desert species.

Another parameter that comes into this story is sea level. When you tie up large amounts of water as ice in glaciers it comes from the oceans. Sea level was about 300 ft lower than it is today at the full-glacial. Land exposed at the head of the Gulf of California would have been new desert. Thus, woodland invaded the upper 2000 to 4000 ft. of the Sonoran Desert while a modest area was exposed at sea level. What the packrats have given us is an amazingly detailed record for rocky slopes from the deserts themselves for the last 45,000 years. That's enough to get us from the last ice age to the present interglacial, and through a series of steps leading up to our modern environment.

Proxy data from deep sea sediments provides a relatively continuous record of climatic fluctuations during the last million years. Oxygen isotope ratios from the shell carbonates from marine plankton provide a general reflection of global temperatures or of the amount of water tied up as ice in continental glaciers. In the last 400,000 years there have been 6 or 7 glacial/interglacial cycles of change. Until a few years ago, it was thought that there had been only four ice ages in the Pleistocene; this is found in all the old geology and biology texts. The current thinking is that we've had more like 15 or 20 cycles in the last 1.8 million years. What this means is that for each interglacial saguaros have migrated north, and during each glacial, singleleaf pinyon grew on rocky slopes from Tucson to the Tinajas Altas Mountains. Community composition changed continually through each cycle as some species responded and others are more stable.

The next time you are in a beautiful desert community take a moment to consider that it represents a very complex evolutionary history. Although my example is for an organ pipe cactus community in the Monument, other desert areas throughout the Southwest reflect similar processes, histories, and relationships. The plants are growing on volcanic rocks that probably formed in the middle Tertiary (25 to 30 million years ago). The structural events that created the hills and mountains probably occurred in the middle Miocene (15 million years ago). When you look at evolutionary time scales, the saguaro, organ pipe cactus, and other Sonoran Desert species, if we are correct, evolved by the late Miocene (5 to 8 million years ago). *Lichanura trivirgata* is a modern desert species evolved from early Tertiary North American stock while *Chionactis palarostris* is a highly-derived species in a New World radiation that began after colubrids immigrated from Asia in the late Oligocene or early Miocene. What the packrats have told us is that these desert species have not all been in this place since they evolved; this is just the current community. While the reptile species could easily be as old as the saguaro, other groups such as heteromyid rodents have had more rapid evolutionary rates. The pocket mice (*Perognathus*) on the slope are much younger as species.

On time scales of thousands of years, the packrats tell us how this community got to be the way it is today. Many of the modern desert reptiles, arthropods, and short-lived plants were present in the ice age. At that time a California juniper-Joshua tree woodland was on the slope. Beginning 11,000 years ago, Sonoran Desert species displaced south into Mexico during the glacial began returning to the area about 11,000 years ago. Saguaro and brittlebush (*Encelia farinosa*) were the first arrivals. Juniper disappeared about 8900 years ago. The modern community formed about 4000 years ago with the arrival of organ pipe cactus and foothills paloverde (*Cercidium microphyllum*). Within the 4000 years or so of the modern Sonoran Desert regime there have been lesser climate fluctuations - cooler, wetter and hotter, drier periods. Today we are living in the hottest, driest period since the last interglacial more than 80,000 years ago - deserts are at their maximum. Even in a healthy, pristine community like this organ pipe cactus desertscrub, composition, structure, abundances, and biomass have been affected by several major droughts and hard freezes this century. Some fast growing plants like brittlebush recover quickly; many do not.

Thirty years ago, when a biologist visited the desert and said "Ah-ha, look at these ancient things and unique life forms. This must be a stable place relatively immune to the climate changes seen elsewhere," they would have been wrong. Our work has indicated that desert communities are not stable, but very dynamic with species ranges and community composition and structure changing continuously. The common assumption of an equilibrium state in ecological modeling would rarely be justified. Climatic fluctuations on scales from hours to millennia result in continuous "reshuffling" of the community "deck." Communities are very individualistic groups of species whose association may or may not be an old one.

Question/Answer Period

Any thoughts on the climate we've seen here in the past 5 or 6 years? An uncanny repetition of hot, dry weather from March through November with the same phenomena each year since 1985.

There has been a lot of concern about global warming and all I can say is that climate seems different since I moved here and is unusually hot. The past two summers have been pretty unbelievable. However, desert climates are so variable it's difficult to speculate on a few years observations.

The winters have not been that variable but in March the temperatures sky rocket.

From my work, I know what things have been like for the past 40,000 years but it's difficult to predict the future. Frankly, if we do go into global warming with a 2 to 3°C increase in annual global temperatures, I don't think we have had anything in our history like that unless in the Pliocene was that warm. The present biota hasn't experienced anything like that in a very long time.

How far back have you found *Phrynosoma solare* (regal horned-lizard) or *Bufo alvarius* (Sonoran desert toad)?

There is *P. solare* identified from the Deadman Cave in the Santa Catalina Mountains but the deposits are not very well dated. I think it's probably 8,000 or 9,000 years old. I haven't found *Bufo alvarius* in the middens but there is a Pliocene record from Benson that's about two million years old. I identified *B. alvarius* from a sedimentary deposit at Rancho la Brisca in north-central Sonora. It's about 150,000 years in age from the last interglacial, the Sangamon.

I'm usually working from the positive side of the fossil record.

When I get *P. platyrhinos* I discuss it. Animals not found in the midden are difficult to evaluate. The desert iguana (*Dipsosaurus dorsalis*) could have arrived in the Picacho Peak area and not have been present in ice age woodlands.

Have you grown the seeds from the packrat middens and if so how do they compare to those plants now?

I haven't tried to grow the seeds although some of the prickly pears look good enough - presumably they are dead.

Recently I tallied up the vertebrates, arthropods and plants and so far we have identified 410 species that are older than 10,000 years. Species are identified by matching to modern reference specimens and I find no difference in external morphology. That is balanced against a very few records of extinct species in this time period. The extinction of large tortoises (*Geochelone*), were probably due to man's activities according to Paul Martin's views. One species of spider beetle (*Ptinus*) and a species of rabbit brush (*Chrysothamnus*) were described from midden specimens. If they have gone extinct (they may yet be discovered living), they haven't evolved into new forms, and were dead ends. From an evolutionary standpoint species haven't changed very much in the last 40,000 years; the species we see today is the same as it was in the late Pleistocene.

Do the things in the middens layer out and do all the data from the different sites fit together?

The law of superposition in stratigraphy states that the youngest things are on the top and the oldest are on the bottom. Packrats don't obey that rule. Sometimes I think packrats can urinate upside down. We have sites where the radiocarbon dates in a series are completely reversed. If there is a hole in the midden, the packrats will plug it up out of sequence. The actual stratigraphic setting doesn't matter for what I do since I clean the sample, look at what is inside it, and run a radiocarbon age on it. Its actual stratigraphic setting doesn't matter.

The general sequences which we get out of the middens are remarkably similar from place to place across the Southwest. I have found blue paloverde growing on hot rocky slopes from about 4,000 to 9,000 years ago; in 5 or 6 Sonoran Desert sites; today it's restricted to washes in all of them. Foothills paloverde arrived later in all places. Pinyon pines disappeared from desert slopes from the Big Bend and Hueco Mountains of Texas to the Waterman, Ajo, and Tinajas Altas Mountains of Arizona, to the Whipple Mountains of eastern California very close to 11,000 years ago.

It seems your data supplies good evidence for Paul Martin's argument regarding Pleistocene extinctions because the small things aren't changing.

Well, I think there is a better correlation. The extinction of the large mammals was over by about 11,000 years ago. Although I see a major change in vegetation and climate at that time, a drier woodland lingered for several thousand years beyond that extinction in the deserts. In the summer-rainfall Chihuahuan Desert, grassland developed after the ice age woodlands and before the modern desertscrub. In Africa, savannas support greater large mammal populations than tree communities. So, the timing of the major climatic changes is off by several thousand years here.

Most of your middens are in the desert. Do you find them up in the mountains?

I don't get up there very often but they have been found in mountains. Geoff Spaulding has found them at 9,000 ft in Nevada. I found them at about 5,000 ft on Pontatoc Ridge in the Santa Catalina Mountains near an old mine. But don't go there as it is dangerous place. Middens ranging from 18,000 to 11,000 years in age yielded an Arizona cypress (*Cupressus arizonica*) forest assemblage with Douglas fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), and two pinyons. The forest was something like Bear Canyon in the Santa Catalinas today, but it must have been fairly local. Middens from higher elevations on the Colorado Plateau and in the Great Basin had mixed-conifer forest assemblages with blue spruce (*Picea pungens*), Douglas fir, limber pine (*Pinus flexilis*) and Great Basin bristlecone pine (*P. longaeva*) instead of pinyon-juniper-oak woodland or chaparral. The surprising thing is that the ponderosa pine was a very rare tree during the last ice age and today it is the most abundant and wide spread forest tree in the western United States. The pine forest zone was absent from the ice age gradient; mixed-conifer forest directly abutted pinyon-juniper woodland. Ponderosa pine has apparently migrated from our area or southern New Mexico north to British Columbia in the last 10,000 years.

Are those northern deserts more recent than our desert here?

The northern deserts are a little more of a problem. They are mainly defined by big sagebrushes (*Artemisia tridentata*) and relatives which have affinities with the Asian Steppes. I don't know when they got here and whether their evolutionary histories are similar to those of the warm deserts. The uplift of the Sierra Nevada was later than the Rockies creating an intense rainshadow in the Great Basin and Mohave Deserts. There has been a lot of evolution later in those areas.

Have you ever found tortoise scats in middens?

Yes, I thought I had one from the Hueco Mountains near El Paso. I dated it at 33,000 years ago. However, when Dick Hansen did a cuticle analysis on it, all it had in it were agave fragments - a very unlikely tortoise diet. It could have been from an extinct peccary.
