NINE

Deep History of the Sonoran Desert

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HE SONORAN DESERT is the most tropical of North America's four deserts. Its climate is essentially frost-free, and it enjoys two rainy seasons annually: summer monsoonal rains that originate from the warm Gulf of California and Tropical Eastern Pacific Ocean and cold winter storms that move into our region from the North Pacific. The Sonoran Desert's structurally diverse vegetation, which includes the visually dominant columnar cacti and leguminous trees, differs dramatically from those of the shrub-dominated Great Basin, Mojave, and Chihuahuan Deserts. It has direct climatic, geographic, and biological connections with tropical communities to the south in Mexico. In a single day's travel, naturalists can begin in Sky Island coniferous forests of southern Arizona along Interstate 19 and travel through oak woodland, grassland, desertscrub, thornscrub, and tropical deciduous forest habitats along Mexico's Highway 15 in Sonora, experiencing the remarkable transition from temperate zone communities to the New World tropics. This vegetation gradient gives us a sense of the Sonoran Desert's connection with the tropics

but does not really explain it. The explanation lies in the tropical ancestry of this desert's flora, deep in evolutionary time.

A WALK THROUGH TIME

The Sonoran Desert that we see today, with its characteristic assemblages of plants and animals, is quite recent from the perspective of geologic time. In fact, it and the other North American deserts are among the youngest biotic communities on the continent. The development of the unique regional climates and the evolution of characteristic desertadapted plants and animals are thought to have combined to form a proto-Sonoran Desert by about 8 million years ago (mya) in the late Miocene. Since that time, this desert has contracted and expanded many times in response to cooling and warming regional climatic shifts (especially during the Pleistocene glacial and interglacial episodes), refining and redefining itself multiple times. The most recent expansion of the Sonoran Desert into southern Arizona and southeastern California occurred

only about 9000 years ago, with the modern communities of plants and animals completing their assembly about 4500 years later. This chapter is a walk through the past 65.5 million years, known as the Cenozoic era, examining the conditions that led to the development of the Sonoran Desert and exploring the forces that shaped its dynamic history.

The Paleocene Epoch

(65.5 to 56 mya)

In the Paleocene epoch, soon after the extinction of the dinosaurs (about 65 mya), most of North America was covered with widespread temperate evergreen floras with limited regional variation, and modern, tropical rainforests to the south. The Atlantic Ocean had already opened, separating the Western Hemisphere from Eurasia and Africa, although in North America the biogeographical ties to the Old World remained strong and obvious among both plants and animals. The mild climates promoted humid forests with strong Asian affinities; primitive ferns (Anemia), cycads (Dioon, Zamia), and palms grew as far north as Alaska. During this time, the flowering plants (angiosperms), whose spectacular evolutionary radiation began in the Late Cretaceous. became increasingly important in the forests, displacing archaic cycads, tree ferns, and some conifers. The earliest fossil grasses are from the time of the Mesozoic-Cenozoic transition. about 65 to 70 million years ago. These were probably broad-leafed forest grasses, similar and ancestral to the modern bamboos.

The Eocene Epoch

(56 to 33.9 mya)

In North America in the Eocene, coastal regions were warm (tropical palms grew in northwestern Washington and Canada), and deciduous trees became increasingly common, providing the first evidence of dry seasons. The landscape now included tropical deciduous forests, in which trees dropped their leaves in response to drought. During these drought periods, sunlight passing through the leafless canopy heated and dried the surface of the ground. Many new species of plants and animals evolved in this habitat, adapting to these new heat and moisture regimes.

The origin of cacti is thought to have occurred during the Eocene in such dry tropical forests. Fossils of an alligator (Allognathosuchus), a softshell turtle (Trionyx), a primitive tortoise (Geochelone), a primitive monitor lizard (Varanidae), a ground boa (Boidae), and many small mammals from Ellesmere Island in northeastern Canada, then at 78° north latitude, indicated that the world was very warm. The result was dramatic shifts in the biota as more advanced forms displaced archaic ones. It was also during the Eocene that South America split from Antarctica, opening the Drake Passage and initiating the first circum-Antarctic current, which in turn led to regional cooling and eventual development of the Antarctic ice cap some 20 million years later, in the Miocene.

The Oligocene Epoch

(33.9 to 23 mya)

By the Oligocene, western North America had become increasingly cooler and drier in response to tectonic events that created major mountain ranges. Many groups of angiosperms, including the grasses that became an important taxonomic group in arid lands, had achieved relatively modern diversity. Gopherus, the genus of the modern desert and gopher tortoises, appeared, as did modern genera of lizards, including skinks, and beaded lizards and Gila monsters. The Oligocene snake fauna was dominated by small ground boas related to the living rubber boa and desert rosy boa of western North America and the sand boas (Eryx spp.) of Africa. The lizards common today in the Sonoran Desert (members of the families Iguanidae and Teidae—iguanas and whiptails), and the common snakes (colubrid snakes such as bull snakes and kingsnakes, and pitvipers), were uncommon or absent at these early dates.

GEOLOGIC TIME SCALE

ERA	PERIOD		EPOCH	TIME (beginning)
	Quaternary		Holocene	11,700 ybp
Cenozoic			Pleistocene	2.6 mya
	Tertiary	Neogene	Pliocene	5.3 mya
			Miocene	23 mya
		Paleogene	Oligocene	33.9 mya
			Eocene	56 mya
			Paleocene	65.5 mya
Mesozoic	Cretaceous			145 mya
	Jurassic			201 mya
	Triassic			252 mya
Paleozoic	Permian			299 mya
	Carboniferous		Pennsylvanian	323 mya
			Mississippian	359 mya
	Devonian			419 mya
	Silurian			444 mya
	Ordovician			485 mya
	Cambrian			541 mya
Precambrian	Alandariyaan Alandariyaan Alandariyaan Alandariya Alandariya Alandariya Alandariyaan Alandariyaan Alandariyaan			4500 mya

Dates based on time scales of the Geological Society of America and the International Commission on Stratigraphy. The age of the beginning of the Holocene is in dispute. (mya = million years ago; ybp = years before present)

The Miocene Epoch

(23 to 5.3 mya)

A series of enormous volcanic eruptions from the mid-Oligocene to the mid-Miocene (about 30-15 mya) changed the climates and established the modern biogeographic provinces of North America (see chapter 10 for a more complete discussion of these processes and terminology). The Rocky Mountains were uplifted to new heights by the accumulation of over a mile (1.5 km) of volcanic rock. A 0.6-mile-thick (1-km) layer of rhyolitic ash fell in the Sierra Madre Occidental in northwestern Mexicoon top of another 0.6-mile (1-km) layer of early Tertiary-period andesites. As regional uplift pushed them even higher, the mountains interrupted the flow of the upper atmosphere for the first time. Tropical moisture from both the Pacific Ocean and the Gulf of Mexico was blocked from the mid-continent, drving the modern Great Plains and the Mexican Plateau of north-central Mexico. Harsher climates segregated drought- and cold-tolerant species into new environmentally limited biomes, including tundra, conifer forests, and grasslands, and restricted them along elevational and latitudinal environmental gradients. The Miocene also was a time when major evolutionary radiations began in many of today's most successful groups of plants and animals, including the sunflower family and modern grasses, as well as toads, iguanid and teid lizards, colubrid snakes, and pitvipers.

The "Miocene Revolution"

After the rise of the great Sierra Madre range in Mexico and the resulting changes in climate, tropical forests were largely restricted to the coastal lowlands of Mexico and Central America. There, newly evolved species joined preexisting ones in tropical deciduous forest. And, along the lower-elevation, drier edges of tropical deciduous forest there evolved a new biome—tropical thornscrub. Thornscrub can be viewed as a transitional state between tropical deciduous forest and desertscrub of the Sonoran Desert; its vegetation is shorter and sparser than tropical forest and it does not require as much moisture. During the Miocene, thornscrub might well have been the regional vegetation in drier areas to the north that now make up the Sonoran Desert. Thus, thornscrub species are likely to have been the ancestors of many of today's Sonoran Desert plants and animals.

The Sonoran Desert began to take shape during a drying trend in the mid-Miocene (15– 8 mya). Much of the desert's vegetation, however, predates the Sonoran Desert itself, having evolved in climates that also required adaptations to aridity. For example, guayacan, organ pipe cactus, palo brea, senita, and tree ocotillo likely evolved in thornscrub. Other plants, such as desert ironwood, foothill palo verde, and saguaro, evolved in place along with the rise of the Sonoran Desert.

Another important chapter in the history of the Sonoran Desert concerns the formation of the Baja California Peninsula. Before 6 million years ago, all the land that is now Baja California and Baja California Sur was part of the Mexican mainland. Activity along the East Pacific Rise spreading center (later to become the San Andreas Fault) caused the Gulf of California to open as the Baja California Peninsula moved northwestward (see chapter 10). The timing of the peninsula's separation is somewhat controversial, although recent estimates put it at about 6 million years ago. Of course, the new peninsula was already populated with tropical plants and animals from the mainland, and these gradually evolved into many regional endemics, among them the famous boojum tree or cirio, a close relative of the ocotillos. Today, the isolated islands on both sides of the peninsula in the Pacific Ocean and the Gulf of California, many of which are geologically young, are the most active evolutionary arenas in the Sonoran Desert Region and have many endemic species.

The Pliocene Epoch

(5.3 to 2.6 mya)

During the latest Miocene and earliest Pliocene, geological forces again altered landscapes and climate regimes, resulting in warmer climates worldwide. As glaciers and polar ice melted, sea level rose and inundated the Earth's coastal lowlands. With tropical circulation patterns enhanced by warmer oceans, tropical forests of western Mexico probably expanded, reaching farther north than they do today in Sonora; likewise, the Sonoran Desert in Arizona and California extended farther, perhaps as far as southern Nevada.

The Pleistocene and Holocene Epochs

(2.6 mya to today)

The warmth of the Pliocene ended abruptly at the beginning of the Pleistocene, about 2.6 million years ago, as the Earth entered a new climatic era that far surpassed the mid-Miocene in cool, continental conditions. A dozen or more glacial episodes ("ice ages") have been identified from the Pleistocene. Glacial episodes lasted around 100,000 years and were about 5 to 10 times longer than interglacials (the warm periods between ice ages), which lasted only 10,000 to 20,000 years. Officially, the end of the Pleistocene is defined as the beginning of the Holocene, nearly 12,000 years ago. However, it should be understood that the Holocene is simply the present interglacial period and that the cyclic environmental fluctuations of the Pleistocene probably have not ended (unless anthropogenic-driven climate change completely reshapes the glacialinterglacial periodicity that has been around for 2.6 million years, the past 2000 of which have been recognized recently as the Anthropocene because of the major influence of humans on the environment).

In the last glacial period (the Wisconsin Glacial), the massive Laurentide continental glacier covered most of Canada and extended as

far south as New York and Ohio. As much as 2 miles (3 km) of ice covered the Great Lakes and New York City area. Boreal forest with spruce and jack pine moved southward, displacing the mixed deciduous forests of the eastern United States. Glaciers covered the tops of the Rocky Mountains and the Sierra Nevada in the western United States and the Sierra Madre del Sur in south-central Mexico. Now-dry playa lakes in the Great Basin were full of water. Enough water was tied up in ice on land to lower sea level 325 to 400 feet (100-120 m). It is estimated that this lowered sea level exposed 7720 to 11,600 square miles (20,000-30,000 sq km) of salty land that is now submerged in the Gulf of California.

Plant remains in ancient packrat middens document the presence of woodland trees and shrubs in the Southwest during the last half of this glacial period (from 60,000 to about 11,000 years ago) in areas that had been desert during the previous interglacial period (and are desert today). Woodlands with singleleaf pinyon, junipers, scrub oak, and Joshua tree were widespread in what is now the Arizona Upland subdivision of the Sonoran Desert. Today's isolated (and species-poor) chaparral communities in central Arizona, mostly in a northwest–southeast band below the Mogollon Rim, are remnants of ice age chaparral connections with California.

During the cooler and wetter Wisconsin Glacial period, Sonoran Desert plants such as creosotebush were probably restricted to disparate populations in dry microsites within chaparral and pinyon-juniper-oak woodlands, largely below 1100 feet (300 m) elevation in the Colorado River Valley and the southern Chihuahuan Desert. Creosotebush probably arrived in North America from Argentina (where its likely ancestor, *L. divaricata*, occurs today) via longdistance dispersal by birds sometime between the late Pliocene and Middle Pleistocene, and it spread gradually throughout the Southwest where, today, there are three morphologically similar but genetically distinct chromosomal races in the Chihuahuan, Sonoran, and Mojave Deserts. With the onset of Holocene warming, the woodlands of southern Arizona's valleys began to move northward and up mountain slopes, to be gradually replaced by desertscrub and grassland species from the south. Although species such as brittlebush and saguaro returned to Arizona soon after the beginning of the present interglacial (the Holocene) between 10,000 and 12,000 years ago, the Sonoran Desert did not re-form until about 9000 years ago, as the last displaced woodland plants retreated upslope or to the north. The full, modern community composition was not achieved until about 4500 years ago, when foothill palo verde, ironwood, and organ pipe cactus arrived from their refuges in the south. However, a semblance of the modern community that we recognize today as the Sonoran Desert must have recurred many times during the Pleistocene interglacials, only to retreat or disburse to warmer, southern climates as each glacial period returned. In the Sonoran Desert Region, modern desert communities probably have been present for only about 5 percent of the 2.6 million years of the Pleistocene, while glacial-period woodlands in the lowlands persisted for about 90 percent of this period.

Tropical Interglacials

Surprisingly, the vertebrate fossil record suggests that some Pleistocene interglacial climates were more tropical than today's Holocene epoch. The fishing village of El Golfo de Santa Clara is near the mouth of the Colorado River in northwestern Sonora. Middle to Late Pleistocene fossils in sandstone outcrops near this village document the ancient Colorado River delta and reflect a climate that was warmer and likely had much more summer rainfall and humidity than today. Greater summer rainfall would suggest that tropical oceans were warmer than they are today, in contrast to most of the Pleistocene, when ocean waters were colder. The Pleistocene fauna from this area included such mammals as antelope, a

horses, proboscidians (elephant relatives), and a tapir (Tapirus). The giant anteater, capybara (Neochoerus), and ground sloths in the fauna were members of at least 10 families of mammals that had immigrated into North America after the establishment of the Panamanian land bridge, either in the mid-Miocene or late Pliocene (scientists are still debating the closure date of the Panama Seaway) as part of the "Great American Interchange." In contrast, the imperial mammoth (Mammuthus imperator), a hyena (Chasmaporthetes johnstoni), and jaguar were more recent Eurasian immigrants. The nearest populations of giant anteater today are 1800 miles (3000 km) to the south in the humid, tropical lowlands of Central America! Other fossils in the El Golfo Pleistocene fauna include the Sonoran Desert toad, slider turtle, boa constrictor, and the large, extinct California beaver (Castor cf. C. californicus). The Sonoran Desert toad is a regional endemic, while the slider and boa constrictor occur today in Sonora in wetter, more tropical areas to the south. Today, of course, the El Golfo area is part of the hyperarid Gran Desierto de Altar.

bear, camels (dromedaries and llamas), cats,

Sonoran Desert Mammoths?

Some years ago, a Mayo Indian found a very large bone in the bank of the arroyo behind his house in Teachive, a village in coastal thornscrub in southern Sonora. For him, as it has been for others who have discovered fossil mammoth bones throughout North America and Europe for centuries, it was puzzling and perhaps frightening. What animal could be so much larger than a deer or a cow? Why has no one seen these monsters? Many a legend was born to explain them and their disappearance.

Today we know that between 11,000 and 12,000 years ago, at the end of the last glacial period, nearly two-thirds of the large mammals of North America went extinct. Common, widespread grazers, including horses and mammoths, disappeared at the very time that spruce and pine retreated and grasslands

expanded in the Southwest. Paul S. Martin, late geoscientist at the University of Arizona, forcefully presented the case that human hunters caused widespread extinctions within a few hundred years after their entry into North America from Siberia via the Bering Strait. The theory of "overkill" of "naïve" large mammals is controversial, and some suggest that changes in climate may have caused the extinctions. However, the paleobotanical record provides little evidence of climatic changes severe enough to have resulted in the extinction of so many large animals over such a broad, diverse area in a few centuries. The well-preserved plant remains in old packrat middens provide additional insights. A species could respond to a major climatic change by: (1) adapting genetically (even to the point of speciation), (2) going extinct, or (3) adjusting its geographical distribution. Beginning nearly 12,000 years ago (the start of the Holocene), during the transition out of the Wisconsin Glacial Episode and into modern climate regimes, there are essentially no records of speciation or extinction in plants or small animals. Most species simply shifted their geographic and elevational ranges. Moreover, woodland plants survived in desert lowlands for several thousand years after the megafaunal extinctions and before the expansion of the Sonoran Desert. The biotic communities of North America have had fewer large herbivores in the last 11,000 years than at any time in the last 20 million years! The impacts of these herbivores on tropical deciduous forest, thornscrub, and the Sonoran Desert were undoubtedly profound-but we might never fully understand the ecological roles of these missing animals and why they went extinct.

WHOSE CHILD IS THIS?

The flora of the Sonoran Desert, and its ancestral roots to the south, clearly illustrate the tropical origin of this region. As noted above, the area we call "Sonoran Desert" today likely supported tropical deciduous forest from the Eocene to the early Miocene, and then thornscrub later in the Miocene—both biomes that today are restricted to tropical Mexico and farther south. Many Sonoran Desert species reach their southern limits in thornscrub, a biome that many people believe is the structural, biotic, and historical link to tropical deciduous forest. But, with the exception of organ pipe cactus and a few others, the paucity of Sonoran Desert species shared with the tropical deciduous forests challenges the popular idea that "tropical deciduous forest is the mother of the Sonoran Desert." Instead, thornscrub could more accurately be called the "mother" of the Sonoran Desert, and tropical deciduous forest its "grandmother" or "great aunt"!

WHAT DOES THE FUTURE HOLD?

Projections from global climate models indicate that temperatures in the Southwest will likely increase by 5.4°F to 10.8°F (3°C-6°C) over this century, due largely to man-made causes, primarily increased carbon dioxide in the atmosphere due to the burning of fossil fuels and deforestation. Predictions of whether precipitation will increase or decrease in the Southwest are still in conflict. However, the most recent work suggests decreasing winter rainfall and shifts in timing of the summer monsoons. Models used to examine how plants may respond to projected climate change indicate that increases in temperature will lead to movement of plant species up mountain slopes, leading to an increased area of desertscrub and grassland and a decrease in the area occupied by pine forest and mixed conifer forest, the biomes situated at the top of the highest mountains. And, in fact, it has been shown that this is already happening (e.g., in the Santa Catalina Mountains). The National Weather Service has kept continuous temperature and rainfall data for the Tucson Basin since 1949. The mean annual temperature for the 30-year period between 1950 and 1980 was 67.98°F (20°C), and for the next 30-year period (1981-2011) it was 69.73°F (21°C). Mean annual air temperatures exceeded the 1949-2011 mean

for 12 of the last 13 years. Mean annual temperature increased on average by 0.45°F (0.25°C) per decade from 1949 to 2011. Mean annual rainfall has been below the 1949–2011 mean for 13 of the last 20 years in that period. If climates continue to warm as projected, species will need to shift their present distributions or adapt to warmer conditions rapidly.

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