



Illuminating the lack of consensus among descriptions of earth history data in the North American deserts: A resource for biologists

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ppg.sagepub.com**Joseph S. Wilson**

Utah State University, USA

James P. Pitts

Utah State University, USA

Abstract

Understanding the timing of mountain building and desert formation events in western North America is crucial to understanding the evolutionary history of the diverse arid-adapted biota that is found there. While many different, often conflicting descriptions exist regarding geobiotic change in western North America, little work has been done to synthesize these various viewpoints. In this paper we present several case studies that illustrate the differences in the various explanations, based on geological and paleobiological data, detailing mountain uplift and desertification in western North America. The majority of the descriptions detailing mountain building in this area fall into two major periods of uplift, the Laramide uplift (~70–50 Ma) and the Neogene uplift (~15–2 Ma), yet it remains unclear which of these events was responsible for the formation of the modern mountains. Like the descriptions of mountain building, various accounts exist detailing the timing of desert formation. Some authors suggest that the deserts existed as far back as 15 Ma while others propose that desert formation occurred as recently as 10,000 years ago. Based on this review of the literature, we suggest that the data on Cenozoic geomorphological evolution of the North American desert landscape is still too coarse and filled with gaps to allow for the development of a robust model of landscape evolution. Instead, this work demonstrates the need for biologists studying the North American biota to realize just how problematic some of the earth history data and models are so that they can build this uncertainty into biogeographic reconstructions.

Keywords

arid lands, desert biogeography, desertification, historical biogeography, mountain uplift, North America

1 Introduction

Evolution in the North American deserts has long interested biogeographers and biologists because of the region's diverse topography and its equally diverse biota. Understanding the causes of diversification in these areas is crucial to evolutionary and historical biogeographical

reconstructions. Many recent studies have explored the historical biogeography of the

Corresponding author:

Joseph S. Wilson, Utah State University, Department of Biology, 5305 Old Main Hill, Logan, Utah 84322, USA

Email: joseph.wilson@usu.edu

Nearctic warm deserts by determining the phylogenetic patterns of a variety of taxonomic groups and comparing those patterns to historical geological and climatic events (eg, Epps *et al.*, 1998; Orange *et al.*, 1999; Marshall and Liebherr, 2000; Riddle *et al.*, 2000a; 2000b; Zink *et al.*, 2001; Jaeger *et al.*, 2005; Riddle and Hafner, 2006). Often, the driving force behind diversification is investigated by relying on a combination of phylogenetic analysis, molecular dating analysis and earth history reconstructions (eg, Crisci *et al.*, 2003; Ayoub and Riechert, 2004; Posadas *et al.*, 2006). Because a large body of literature exists detailing the strengths and limitations of both phylogenetic techniques, as well as molecular dating techniques (eg, Felsenstein, 2004; Rutschmann, 2006), it is generally understood that the results of these analyses are imperfect reconstructions of evolutionary history. Little or no work has been done, however, synthesizing the various, often conflicting, descriptions of geobiotic change in western North America. The lack of a cohesive review seems have caused a misunderstanding among some biologists that past geological events are well defined both structurally and temporally. This, however, is not necessarily the case.

Because the geological literature is often multifaceted, the information pertinent to historical biogeographical and evolutionary reconstructions can be elusive to biologists. Due to this inaccessibility, biologists regularly cite only a single or a limited number of studies on which they base their evolutionary hypotheses, which can lead to erroneous narratives detailing the causes of diversification. Additionally, biologists often cite primarily biologically based analyses rather than geologically based papers when describing the geobiotic changes that led to diversification in their study system. Furthermore, many of the sources most often used are from the late 1970s or earlier (eg, Axelrod, 1957; 1979; Morafka, 1977; Webb, 1977). In fact, 75% of the studies dealing with historical

biogeography in the Nearctic deserts published in *Molecular Ecology* in the past five years cited one of these older papers, or papers that relied on these older papers as the main indicator of past climatic and geological changes. While these references should not be discounted based on their publication date alone, it must be noted that these studies presented indirect evidence from fossil data on the uplift of mountain ranges, and subsequent aridification of the West. Furthermore, these studies were written early in the developing discipline of plate tectonics, so newer information about geological events is available, that sometimes conflicts with the older studies. Before robust evolutionary and biogeographical reconstructions can be made, an understanding of the variability that exists in the descriptions of earth history data needs to be acknowledged and incorporated into these scenarios.

In this paper we present several case studies that illustrate the differences in the various explanations regarding geobiotic change in the North American deserts. We report the findings of both geologists and biologists, both historical and modern, on orogenic (mountain building) events and desert formation in the western Nearctic. We have included references detailing the history of both the hot and cold deserts, as well as neighboring shrub-steppe arid regions. Many of these studies discuss the timing of the mountain building and desert formation events by geologic epoch only (eg, middle Miocene). In an effort to give a clear picture of the timing of events leading to the formation and evolution of the deserts, we have provided estimated dates for these cases. The dates are derived from the Geologic Time Scale produced by the Geological Society of America in 1999 and are provided to represent a generalized age, not a specific date. Because desert formation is often attributed to mountain building events, we will first explore the literature regarding mountain building in western North America, followed by discussions dealing with desert formation.

The goal of this paper is not to give a definitive date of mountain uplift, nor is it to determine exactly when the deserts formed or emphatically state what geological processes, if any, led to the current desert biota. The data on Cenozoic geomorphological evolution of the North American desert landscape is still too coarse and filled with gaps to allow for the development of a robust model of landscape evolution. Our goal is to demonstrate the knowledge gap that is yet to be bridged between earth scientists and biologists. We demonstrate the need for North American biologists and biogeographers to realize the problems with some of the earth history data and models so that they can build this uncertainty into biogeographic hypotheses and reconstructions. Furthermore, because the ever-growing mountain of geological and paleoecological literature is jargon-based, as is the literature in any field, we have provided short summaries of the changes that the desert regions experienced, from their origin to modern times.

II Mountain uplift

The timing of mountain uplift is important to biologists and biogeographers in two major ways. First, rising mountains can isolate populations and lead to allopatric evolution, where the two populations occur in separate, non-overlapping geographic areas. Second, mountain ranges have drastic effects on the climate of both the windward and leeward sides of the range. Often, the timing of these mountain building events is crucial to the biogeographic explanations proposed by North American biologists and biogeographers (eg, Riddle *et al.*, 2000a; 2000b; Jaeger *et al.*, 2005; Douglas *et al.*, 2006).

The majority of the mountains in western North America are part of the American Cordillera that includes the Rocky Mountains, the Coastal mountain ranges, the Sierra Madre ranges, and others (Dickinson, 2004; Figure 1). One major event in the evolution of the

American Cordillera was the Laramide Orogeny, which was a period of active mountain building. The timing of this uplift is contested. Some authors propose that the majority of the activity was from the late Cretaceous (~70 Ma) through the Paleocene (~50 Ma; English and Johnston, 2004). Other authors, however, argue that much of the uplift occurred earlier, from as early as the middle Triassic (~200 Ma; Dickinson, 2004) to the early-late Cretaceous (~90 Ma; Umhoefer, 2003). Regardless of the exact timing, the Laramide uplift is overwhelmingly thought to be responsible for the formation of much of the western American Cordillera (Coney *et al.*, 1980; de Cserna, 1989; Oldow *et al.*, 1989; Ferrusquia-Villafranca, 1993; House *et al.*, 1998; Umhoefer, 2003; English and Johnston, 2004; Dickinson, 2004; Cecil *et al.*, 2006; Ferrari *et al.*, 2007).

In contrast to these explanations of ancient mountain building, many other authors advocate the existence of a second, younger uplift that began in the middle Neogene (~15 Ma). Following the Laramide uplift, widespread erosion occurred through the late Eocene (~30 Ma), which left much of western North America marine basins or emergent regions of low relief (Hay, 1984; Ruddiman *et al.*, 1989). Beginning in the middle Miocene (~15 Ma), much of the American West experienced widespread uplift, with a majority of the elevation being added since the latest Miocene (~7 Ma; King, 1958; Segerstrom, 1962; Smiley, 1963; Christensen, 1965; Cohn, 1965; McKee, 1972; Morafka, 1977; Marchand and Allwardt, 1981; Huber, 1981; Naeser *et al.*, 1983; Ruddiman *et al.*, 1989; Dumitru, 1990; Burchfiel *et al.*, 1992; Christiansen and Yeats, 1992).

While it seems that the idea of this younger widespread Neogene uplift (starting ~15 Ma) is the current paradigm in geology (Hay and Soeding, 2002), there are several differing accounts detailing when this uplift occurred. Many authors have suggested that the majority of the uplift occurred in the middle to late

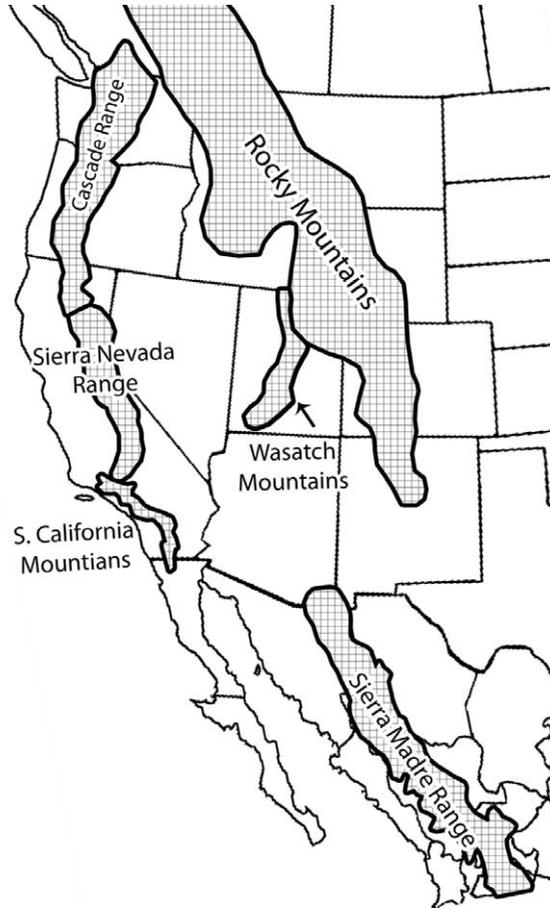


Figure 1. Map of the major North American mountain ranges (the North American Cordillera)

Miocene (~15–7 Ma; King, 1958; Segerstrom, 1962; Cohn, 1965; Morafka, 1977; Marchand and Allwardt, 1981; Huber, 1981; Naeser *et al.*, 1983; Ruddiman *et al.*, 1989; Dumitru, 1990; Burchfiel *et al.*, 1992; Christiansen and Yeats, 1992). Other authors proposed that the bulk of the uplift took place in the Pliocene and Quaternary (~5 Ma to present; Axelrod, 1962; Christensen, 1965; Kennett and Thunell, 1975; 1977; Amand and Roquemore, 1979; Huber, 1981; Kennett, 1981; Thorne, 1986; Cambray and Cadet, 1994; Straub and Schmincke, 1998; Clark *et al.*, 2005). Although it may seem insignificant to make a distinction between a mid- to

late Miocene uplift and a late Pliocene uplift, these differences may be crucial to many historical biogeographic analyses that are seeking to explain the causes of diversity in the North American deserts. Often, the distinction is made between Pleistocene climate change and Neogene mountain building in exploring the diversification of desert-adapted taxa (eg, Riddle *et al.*, 2000a; 2000b; Jaeger *et al.*, 2005; Douglas *et al.*, 2006). If the Neogene mountain building did not occur until the late Pliocene, the isolation of species caused by that vicariant event may be indistinguishable from isolation by global cooling and glaciation. Many

authors have indicated that the initiation of global cooling, which led to ice age glaciation, began long before the Pleistocene. Dates given for the onset of glaciation in the Northern Hemisphere range from about 9 Ma to 3 Ma (eg, Wolf and Thiede, 1991; Haug and Tiedemann, 1998). Hay and Soeding (2002) suggest that the cooling trend began as far back as the Eocene (~40 Ma).

The orogeny of the American Cordillera, whether it occurred during the Laramide uplift, in Neogene events, or both, has often been credited as the driving force behind the formation of the Nearctic deserts (eg, Latham and Ricklefs, 1993; Qian, 2001a; 2001b; Jaeger *et al.*, 2005). Ruddiman and Kutzbach (1989), through numerical modeling of uplift, showed how climate changed from a no-mountain scenario to one with medium-sized mountains, and to one with present-day mountains. Their experiments suggest that precipitation decreases over central North America in the rain shadow of the developing mountains (Ruddiman and Kutzbach, 1989). The authors suggested that results of uplift-sensitivity experiments support ideas about the importance of mountain uplift in producing both local and regional climatic effects (Ruddiman and Kutzbach, 1989).

Interpretation of paleobiological data suggests that the late Cenozoic uplift was responsible for the development of North America's arid environments (Axelrod, 1950; Webb, 1977; Axelrod and Raven, 1985; Graham, 1993; 1999; Katinas *et al.*, 2004). Surprisingly, there is no paleobiological literature that indicates the Laramide uplift caused any aridification in North America. In fact, most climate reconstructions suggest that much of North America, including present desert areas, changed from a subtropical forest to a subhumid woodland-savanna in the late Eocene and Oligocene times (~40–24 Ma; Axelrod, 1950; Webb, 1977).

While the evidence overwhelmingly supports the idea that there were two major episodes of mountain building in western North America,

the Laramide uplift and the Neogene uplift (Figure 2), only the latter is currently thought to have influenced the formation of the deserts. Caution should be used, however, by biologists seeking to cite this Neogene uplift as a causal factor for their biogeographic studies without accounting for the range of dates given for this event. The inconsistencies in the dates for the major uplift of North American mountain ranges could be, in part, due to individual ranges uplifting at different times rather than all forming simultaneously.

In order to explore the precision in the timing of individual ranges, we discuss the uplift of the Sierra Nevada ranges as an example.

Uplift of the Sierra Nevada ranges

The uplift of the Sierra Nevada mountain ranges is thought to be instrumental in the desertification of most of western North America (Ruddiman *et al.*, 1989). There are many interpretations, however, of when these mountains arose. Cecil *et al.* (2006), in their study on the thermochronology of the Sierra Nevada ranges, proposed that a period of relatively rapid uplift of the Sierras occurred during the late Cretaceous to early Cenozoic (70–50 Ma) followed by a period of erosional smoothing that lasted through the Neogene (~2 Ma). Umhoefer (2003) disagreed, suggesting that the period of uplift began much earlier (125 Ma) when the Sierra Nevada arc was pushed eastward over the North American crust.

Many authors disagree with the claim that the majority of uplift was completed through Laramide processes, instead suggesting that most mountain ranges experienced uplift primarily in the Neogene (Christensen, 1965; Axelrod, 1980; Huber, 1981; Dumitru, 1990). Several geological studies suggest that much of the uplift of the Sierra Nevada ranges occurred during the past 10 million years with a majority occurring between 5 and 3 Ma (Huber, 1981; Marchand and Allwardt, 1981; Clark *et al.*,

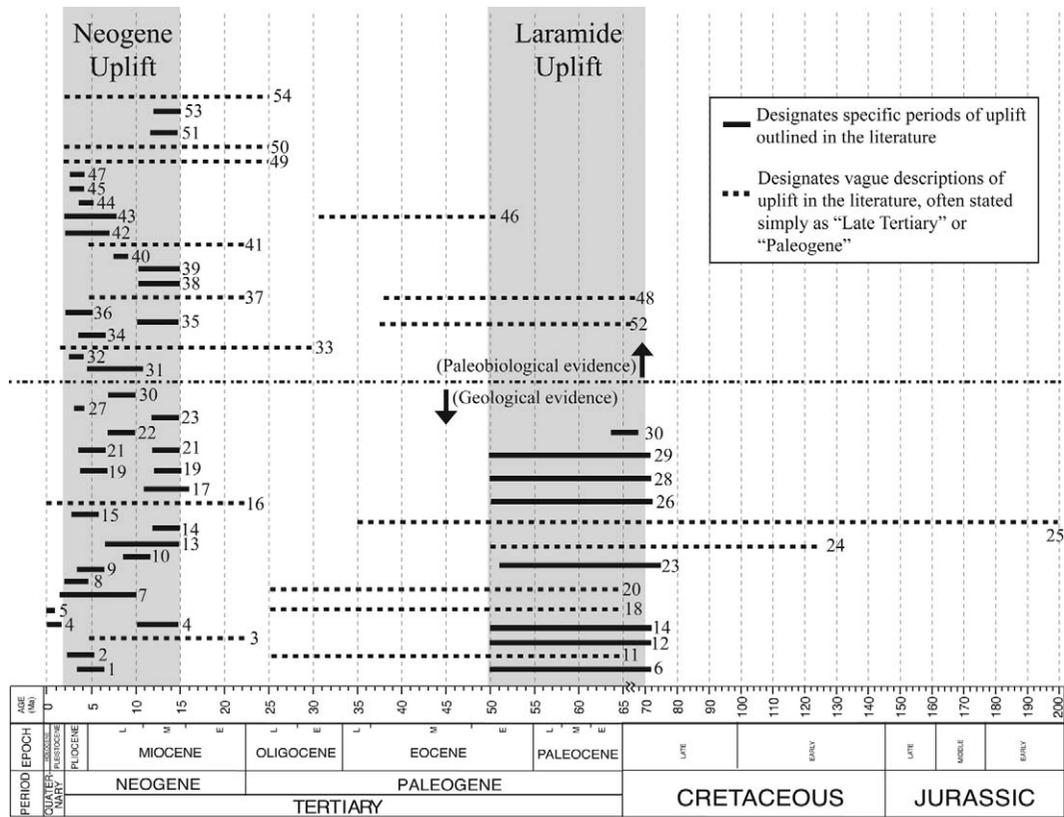


Figure 2. Depiction of the various descriptions of mountain building in western North America with the two major periods of uplift marked in grey. The Laramide uplift has been defined temporally by several authors (eg, English and Johnston, 2004). Based on the geological and paleobiological data, we suggest that the Neogene uplift occurred primarily from 15 to 2 Ma. The solid lines represent specific periods of uplift described in the literature. The dashed lines represent vague descriptions of uplift described in the literature. Numbers to the right of each line correspond to the reference from which the dates were given. Several authors suggested two different dates for mountain uplift, in these cases both dates were marked on the figure. References are separated by type of evidence used in the analysis. Geologically based papers are: 1 Segerstrom (1962); 2 Christensen (1965); 3 McKee (1972); 4 Kennett and Thunell (1975; 1977); 5 Amand and Roquemore (1979); 6 Coney *et al.* (1980); 7 Huber (1981); 8 Kennett (1981); 9 Marchand and Allwardt (1981); 10 Naeser *et al.* (1983); 11 de Cserna (1989); 12 Oldow *et al.* (1989); 13 Ruddiman *et al.* (1989); 14 Dumitru (1990); 15 Thompson (1991); 16 Burchfiel *et al.* (1992); 17 Christiansen and Yeats (1992); 18 Ferrusquia-Villafranca (1993); 19 Cambray and Cadet (1994); 20 Wernicke *et al.* (1996); 21 Straub and Schmincke (1998); 22 Reiners *et al.* (2002); 23 Pederson *et al.* (2002); 24 Umhoefer (2003); 25 Dickinson (2004); 26 English and Johnston (2004); 27 Clark *et al.* (2005); 28 Cecil *et al.* (2006); 29 Ferrari *et al.* (2007); 30 Pelletier (2007). Paleobiologically based papers are: 31 Axelrod (1940); 32 Axelrod (1948); 33 Axelrod (1950); 34 Axelrod (1957); 35 King (1958); 36 Axelrod (1962); 37 Smiley (1963); 38 Cohn (1965); 39 Morafka (1977); 40 Webb (1977); 41 Axelrod (1980); 42 Axelrod and Raven (1985); 43 Thorne (1986); 44–45 Leopold and Denton (1987); 46 Wing (1987); 47 Thompson (1991); 48 Gregory and Chase (1992); 49 Graham (1993); 50 Graham (1999); 51 Wolfe *et al.* (1995); 52 Wolfe *et al.* (1998); 53 Van Devender (2000); 54 Katinas *et al.* (2004).

2005). Wernicke *et al.* (1996) disagreed with these findings, suggesting that the Sierra Nevada ranges may have maintained or lost elevation in Neogene rather than have been uplifted. Pelletier's (2007) modeling experiments showed that both the Laramide model of uplift and the Neogene model could have been influential in the formation of modern mountains.

Multiple paleobotanical studies also support the Neogene model of Sierran uplift, yet they give a broader range of dates for this event than the geological studies. Axelrod (1962) reported that changes in the pollen record are consistent with major uplift during the late Miocene and Plio-Pleistocene (2 Ma). In addition to these pollen records, fossil floras indicate that the Sierra Nevada gained elevation in Mio-Pliocene times, causing east-west differences in floras in areas that previously housed similar floras on both sides of the present Sierra Nevada range (Axelrod, 1957). Wolfe *et al.* (1995), however, suggested that the basin and range adjacent to the Sierra Nevada ranges may have dropped about 1.5 km from former high altitudes from about 20 to 13 Ma which may have been the cause of the difference in fossil floras.

The uplift of the Sierra Nevada ranges undoubtedly contributed to the formation of both the Great Basin and the Mojave deserts, yet, like the descriptions of the other mountain ranges in western North America, the timing of the uplift remains unclear. It appears that the geological data regarding mountain uplift, although vitally important to biologists and biogeographers, must be used with caution given the wide array of explanations about when and how the mountains arose. Biogeographical and evolutionary studies often attempt to associate species or lineage divergence with historical events like mountain building. Because there is a broad range of dates given for the orogenic events in western North America, we suggest that biologists consider these events as occurring sometime in a range of acceptable dates. For the Neogene uplift we suggest, based on the literature, that any

evolutionary events occurring between ~ 15 and ~ 2 million years ago could be considered associated with recent mountain building in western North America. For the Laramide uplift, although generally beyond the scope of most evolutionary or biogeographical analyses, we suggest that divergences dating between 125 and 50 Ma could be associated with this uplift based on the variety of dates given for this event.

2 The Baja California peninsula

Mountain uplift is not the only type of historical event important to biogeography and evolution. Many other geological processes have often been credited as being the driving force behind diversification in the North American deserts. Because of its unique biogeographic history, as well as its distinctive biota, Baja California has received a great deal of attention from biogeographers and evolutionary biologists. The Baja California peninsula was formerly connected to the Mexican mainland, and is generally accepted to have split from the mainland around 6 Ma (Oskin and Stock, 2003a; 2003b; 2003c). Some authors have suggested that the separation began earlier during middle Miocene times (~ 15 Ma; Curray and Moore, 1984; Lonsdale, 1991; Carreño and Helenes, 2002). Marine deposits insinuate that some areas in the northern part of the Gulf of California were low enough to receive seawater by the middle Miocene (Helenes and Carreño, 1999). Other geological evidence suggests that the southern part of the Gulf of California remained connected to the Mexican mainland until about 5 Ma; therefore, the water in the northern part of the gulf that was present in the middle Miocene must have entered by a different way than at present (Helenes and Carreño, 1999), perhaps through a mid-peninsular seaway.

Although several lines of evidence exist supporting the existence of a mid-peninsular seaway, often called the Vizcaino seaway, various dates have been proposed for when this

seaway may have existed. Lindell *et al.* (2006) investigated the evidence for a mid-peninsular (Vizcaino) seaway in Baja California and concluded that evolutionary relationships based on molecular data of lizards, snakes, mammals, birds, and spiders supported the idea that a mid-peninsular seaway temporarily bisected Baja California. Upton and Murphy (1997), during a molecular study of side-blotched lizards, suggested that the mid-peninsular region of Baja California was submerged at about 1 Ma, resulting in a temporary connection between the Gulf of California and the Pacific Ocean. Lindell *et al.* (2005; 2006), however, argued that an older scenario for the mid-peninsular seaway of Baja California (2–3 Ma) might better explain the geographical location among breaks of individual genealogies. Murphy and Aguirre-Leon (2002) implied that mid-peninsular seaways have been in existence multiple times, but most recently about 3 Ma, and these seaways had receded by the early Pleistocene. Helenes and Carreño (1999) studied the sediment of the area and proposed the existence of a seaway in the central Baja California peninsula at around 10 Ma. Still others suggested that there may not have been a mid-peninsular seaway, arguing that the evidence supporting a seaway is circumstantial at best (Grismer, 2002).

The Baja California peninsula has been the focus of countless biogeographical studies. While the references cited in the above section are not a comprehensive list, they illustrate that there is controversy even for the timing of the formation of the Baja California peninsula and that authors should use caution when relying on a single source for the geologic aspects of their biogeographical reconstructions.

III Desert formation

Lack of consensus in the proposed dates of mountain building events have made determining the timing and sequence of desert formation difficult. Understanding the timing of the

development of North America's deserts can be crucial in understanding the evolution of the diverse arid-adapted biota that is found in these areas. Because desert climates are not ideal for fossilization, a good fossil record detailing the sequence of climatic changes leading to desert formation is lacking. Webb (1977) believed much of North America gradually dried out, shifting from a tropical savanna to a more arid environment beginning in the early Cenozoic (65 Ma). No mechanism was proposed that would lead to a decrease in humidity and precipitation. Recent advances in fields of palynology and the study of packrat (*Neotoma* spp.) middens have provided more data detailing climate change in the deserts (Betancourt *et al.*, 1990). The timescales at which these data, especially packrat middens data, can be useful for historical biogeography are quite limited. As with mountain uplift, there are differing opinions on the dates of the formation of the North American deserts (Figure 3). While there are various descriptions of the deserts and their boundaries, in the following sections we will use the boundaries described by Omernik (1987; Figure 4).

I The Sonoran Desert

Axelrod (1979), in his noteworthy paper on the origin and evolution of Sonoran Desert vegetation based on fossil floras, clearly demonstrated the changes in vegetation this region experienced through time. He stated that the Sonoran Desert was a humid savanna during the Cretaceous (before 65 Ma). The region slowly began to dry out into dry savanna and dry tropical forest with pockets of tropical forest and cloud forest by the late Paleocene and early Oligocene (55–33 Ma; Axelrod, 1979). Then, during the late Eocene (35 Ma) local semi-arid areas were present that probably supported semi-desert vegetation. By the Miocene (8 Ma) many near-modern semi-desert species were already present (Axelrod, 1979). However, Axelrod (1979) stated that semi-desert aspects were present only

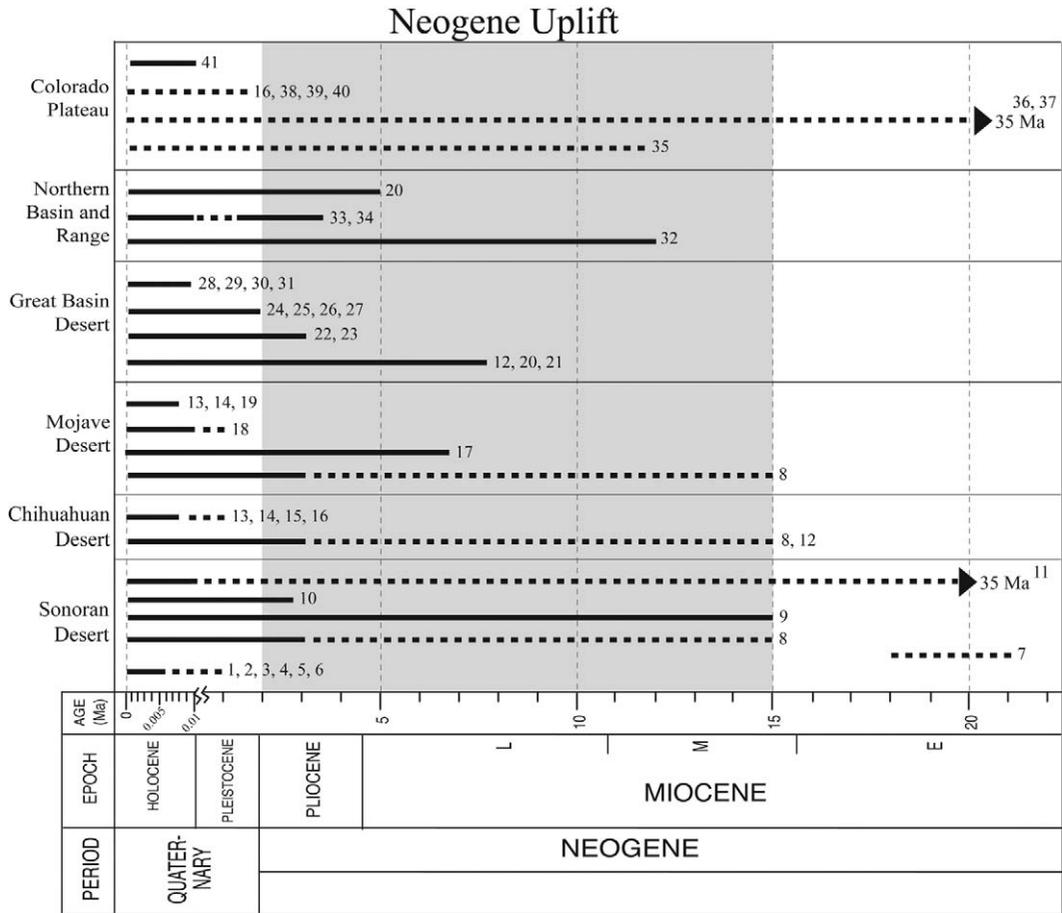


Figure 3. Depiction of the various descriptions of desert formation in western North America with the Neogene uplift marked in grey. The solid lines represent accounts from the literature describing desert-like climates or vegetation. The solid line is not meant to suggest that the area has been a desert continually from the beginning of the solid line through the present. Instead, the line represents the oldest date that desert vegetation is reported from an area. The dashed lines represent descriptions from the literature that show arid or near-desert conditions were present at least in some parts of the region. Number(s) to the right of each line correspond to the reference from which the information was presented. References used in this figure are: 1 Hall (1985); 2 Hall *et al.* (1989); 3 Van Devender (1990); 4 Van Devender *et al.* (1990); 5 Anderson and Van Devender (1995); 6 Hunter *et al.* (2001); 7 Moore and Jansen (2006); 8 Morafka (1977); 9 Van Devender (2000); 10 Phillips and Comus (2000); 11 Axelrod (1979); 12 Webb (1977); 13 Van Devender (1977); 14 Hunter *et al.* (2001); 15 MacKay and Elias (1992); 16 Elias *et al.* (1995); 17 Thorne (1986); 18 Koehler *et al.* (2005); 19 Spaulding (1991); 20 Axelrod (1940); 21 Davis and Moutoux (1998); 22 Wolfe (1990); 23 Axelrod (1948); 24 Moutoux (1995); 25 Litwin *et al.* (1999); 26 Madsen *et al.* (2001); 27 Woolfenden (2003); 28 Bryne *et al.* (1979); 29 Thompson and Kautz (1983); 30 Mehringer (1985); 31 Thompson (1990); 32 Owen Davis (unpublished data); 33 Leopold and Denton (1987); 34 Thompson (1991); 35 Ruddiman *et al.* (1989); 36 Wolfe *et al.* (1998); 37 Gregory and Chase (1992); 38 Soreng and Van Devender (1989); 39 Anderson *et al.* (2000); 40 Jackson *et al.* (2005); 41 Sharpe (2002).



Figure 4. Map of the North American deserts and arid lands using boundaries described by Omernik (1987)

in local edaphic sites and in local rain shadows or dry valleys during the Oligocene and Miocene. Also, extant desert vegetation only appeared as a broad regional habitat after the Pleistocene time (after 10,000 years ago). In summary, the progression of fossil floras provides incontrovertible evidence that the Sonoran Desert developed gradually, and that desert-adapted taxa have been accumulating in the Sonoran region since the late Cretaceous (Axelrod, 1979).

Phillips and Comus (2000), however, disagree with Axelrod. They argued that the diversity and endemism of modern plant assemblages point to the idea that the Sonoran Desert formed more recently during the Pliocene-Pleistocene (2 Ma). Others suggest that the Sonoran Desert formed during a drying trend in the middle Miocene (15–8 Ma; Van Devender, 2000). Furthermore, molecular phylogenetics of an arid-adapted plant crinklemat (*Tiquilia*) suggested that a major

divergence for the genus occurred about 20 Ma, indicating that a desert must have existed, at least in some areas, at the time (Moore and Jansen, 2006). Because the Sonoran Desert houses a diverse and often endemic suite of plants and animals, many biologists have assumed that this region must be quite old (Axelrod, 1979; Moore and Jansen, 2006). Currently, the explanation given by Axelrod (1979) seems to be the most accepted description of the evolution of the Sonoran Desert.

The history of the Sonoran Desert is further complicated by the proposed presence of a Miocene-Pliocene ($\sim 8\text{--}4$ Ma) northern extension of the Gulf of California known as the Bouse Sea or Bouse Embayment (Metzger, 1968; Lucchitta, 1972; Blair, 1978; Eberly and Stanley, 1978; Boehm, 1984; Ingle, 1987; Buising, 1990; McDougal *et al.*, 1999; Carreño and Helenes, 2002), which covered large expanses of the low-elevation areas. The size of this embayment, however, is not well established. Some authors suggest that water covered only the Salton Trough region in southern California north through the Coachella Valley (Lucchitta, 1972; Boehm, 1984; Ingle, 1987; McDougal *et al.*, 1999). Others propose that the sea stretched farther north reaching Lake Mead in southern Nevada and covered a large part of southern Arizona (Metzger, 1968; Blair, 1978; Eberly and Stanley, 1978; Buising, 1990; Carreño and Helenes, 2002). Carreño and Helenes (2002) suggested that the Bouse Sea varied in size reaching southern Nevada and covered much of southern Arizona only in the late Miocene (~ 8 Ma), and receding to the Coachella Valley of California and areas around Yuma Arizona by the early Pliocene (4 Ma). Authors also disagree on the source of the Bouse Sea. While many authors suggest that the Bouse Sea was a marine extension of the Gulf of California, others suggest that the area was a non-marine embayment fed by the Colorado River (Spencer and Patchett, 1997; Poulson and John, 2003). Regardless of whether it was

marine or fresh water, the Bouse Sea created a barrier isolating the Baja California peninsula and the westernmost part of southern California from the remainder of the Sonoran Desert.

Much of the data available concerning the Sonoran Desert deals with more recent regional environmental changes. Evidence from packrat middens shows that many sites were not desert-like in full glacial times, having a cooler, more mesic climate with evergreen woodland dominating (Hall *et al.*, 1989; Van Devender *et al.*, 1990; Anderson and Van Devender, 1991; McAuliffe and Van Devender, 1998). Many other areas, however, maintained hot desert-like characteristics throughout the Pleistocene glacial cycles (Van Devender, 1990; Van Devender *et al.*, 1990; Hunter *et al.*, 2001). As rainfall increased during the Pleistocene (Van Devender *et al.*, 1990), numerous pluvial lakes formed across western North America, including the Sonoran Desert (Figure 5). During the late Pleistocene ($\sim 80,000$ years ago) and through much of the Holocene, a portion of the Salton Trough was a freshwater lake (Lake Cahuilla) that reached its maximum size and depth about 500 years ago (Stokes *et al.*, 1997; Gobalet and Wake, 2000). The large sand dunes found in the Coachella valley of California, which now house several endemic taxa, were likely formed near the shores of this lake during this time (Stokes *et al.*, 1997).

While it is generally stated that the modern Sonoran Desert came into existence sometime after the Pleistocene (eg, Axelrod, 1979), the dates given for this event vary greatly, and often contradict each other. Anderson and Van Devender (1995) found that some floral elements of the modern Sonoran Desert have been established for the last 10,000 years, but modern floral assemblages appeared sometime prior to 5400 years ago. Other authors proposed that cool, wet environments were present in the middle Holocene, and relatively modern desert scrub took over by about 4000 years ago (Hall *et al.*, 1989; McAuliffe and Van Devender, 1998). Interestingly, Anderson and Van Devender (1991) suggested that the

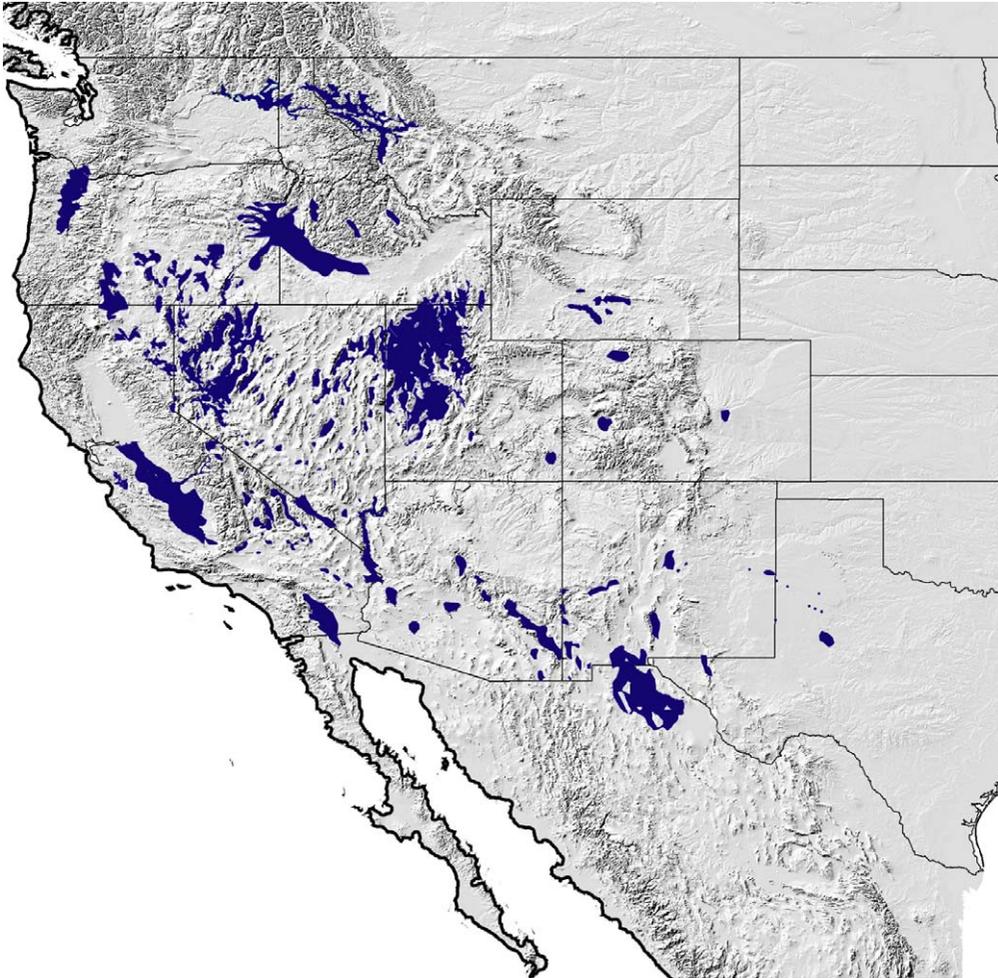


Figure 5. Map of western North America showing the proposed pluvial lakes that were present during the Pleistocene (1.8 Ma to 10,000 years ago). Placement of pluvial lakes is based on descriptions by Feth (1961), Allen (2005) and Grapes *et al.* (2008).

climate of today is the most xeric in the entire Sonoran Desert record. Hall (1985) proposed, however, that fossil pollen analyses imply aridity exceeding that of the present beginning 7500 years ago and ending by 4700 years ago.

2 The Chihuahuan Desert

While the Sonoran Desert is often thought of as the center of origin for many desert-adapted taxa

based on Axelrod's (1979) work, other authors believe the origin of modern desert taxa could be centered in the Chihuahuan Desert. Morafka (1977) suggested that the Mexican Plateau and the Chihuahuan Desert, in particular, should be considered as a centre of origin of desert biota, because this area has been geologically and climatically stable since the middle Miocene (~ 15 Ma) based on herpetological data. Furthermore, these data suggested that a vast

desert region existed during the middle Miocene (15 Ma) that Morafka (1977) called Mojavia. Mojavia included areas where the modern Chihuahuan, Sonoran, and Mojave Deserts exist today. This region split into the modern North American deserts by the late Pliocene (~ 2 Ma), due to the uplift of the Continental Divide (Rocky Mountain–Sierra Madre Occidental axis), and the enlargement of the Gulf of California. Webb (1977) agreed that the vertebrate-fossil record during the middle and late Miocene (15–5 Ma) also provides evidence that an arid savanna mammalian assemblage was centered in the Chihuahuan Desert and other portions of the Mexican Plateau. By the late Pliocene (~ 2 Ma), the climate in the Chihuahuan Desert was comparable to the present (Morafka, 1977). While there is ample evidence that the Chihuahuan Desert region was drying during the Miocene, it is unclear how far-reaching this desertification was. Microfossil floras from central Mexico, for example, show that cooler climates existed during the late Miocene (~ 8 Ma) relative to the present (Graham, 1987).

During the Pleistocene, cooler wetter climates were present in much of the Chihuahuan Desert. Like the Sonoran Desert, Chihuahuan Desert fossil assemblages dated to the Pleistocene imply that a mesic woodland dominated much of the landscape (MacKay and Elias, 1992; Pendall *et al.*, 1999; Holmgren *et al.*, 2003). Because of increased rainfall and cooler temperatures, many large pluvial lakes were present in the area during parts of the Pleistocene (Figure 5). This Pleistocene woodland was eventually replaced by a more arid desert grassland. Some authors place this transition at about 8000 years ago (Van Devender, 1977; MacKay and Elias, 1992), while others suggest that the transition occurred more recently, after 4000 years ago (Hunter *et al.*, 2001; Holmgren *et al.*, 2003). Although it is clear that many portions of the Chihuahuan Desert housed mesic woodlands during the late Pleistocene, fossil arthropod remains from packrat middens suggest that at

least some refugium for desert biota also existed during this time (Elias *et al.*, 1995).

3 The Mojave Desert

Various types of data present a conflicting story of the Mojave desert during the Miocene. While Axelrod (1979) hypothesized the modern desert flora evolved in isolated arid patches and migrated northward as the climate continued to dry, some authors suggest that a dry grassland environment was already present in the Mojave Desert by the middle Miocene. Fossil grasses found in the Mojave Desert suggest that by as early as the Miocene (~ 20 Ma) Mediterranean chaparral-type grasslands had established in the region (Tidwell and Nambudiri, 1989). Fossilized arthropods also present this picture showing that climates in the Mojave Desert consisted of grassland with scattered patches of woodland during the Miocene (Park and Downing, 2001). Along the Pacific Coast, the climate during the middle Miocene (15 Ma) became warmer (Flower and Kennett, 1994). Arthropod and vertebrate fossils from this time suggest that the region had high temperatures, received more moisture than today, and consisted mainly of open grasslands scattered with small playa lakes (Merriam, 1919; Park and Downing, 2001). Paleobotanical evidence presents yet another picture, suggesting that the area consisted primarily of oak woodland rather than grassland (Axelrod, 1981; Thorne, 1986).

The differences in the description of the Miocene Mojave Desert may be due to slight elevational differences in fossil deposition sites. In the modern Mojave, adjacent areas that are separated by less than 100 m in elevation harbor drastically different plant communities (personal observation). It is likely that the landscape of the Mojave was a mix of oak woodland and open grasslands in the Miocene. Precipitation decreased in the late Miocene and aridity peaked about 5–8 Ma causing the increase of semi-desert habitats (Thorne, 1986).

Other evidence points to a more recent origin of the Mojave Desert. Thorne (1986), in a study of the vegetation of the Mojave Desert, suggested that the late Pliocene-Pleistocene uplift of the Sierran, Transverse, and Peninsular Ranges created the regional rain-shadow deserts. Amand and Roquemore (1979), however, stated that the uplift of the southern Sierra and the development of Basin and Range topography of the northern Mojave Desert took place more recently, mainly since the Middle Pleistocene.

Additional evidence that this region was in a rain shadow during the Pleistocene comes from glacial-age fossils from the Mojave Desert, which indicate the existence of widespread xeric steppe-woodlands (Koehler *et al.*, 2005). Pluvial lakes covered many areas in the Mojave Desert during various parts of the Pleistocene (Figure 5; eg, Amand and Roquemore, 1979; Brown and Rosen, 1995; Hooke, 1999) and are associated with sand dunes that exist today (Britten and Rust, 1996). These dune systems house a unique and often endemic biota (Hardy and Andrews, 1979; Rust *et al.*, 1983; Pavlik, 1985; Rust, 1986; Pitts *et al.*, 2009). Many authors have implied that the sand dunes of the Mojave Desert are less than 10,000 years old (Norris and Norris, 1961; Sharp, 1966; MacDonald, 1970; Mehringer, 1986). Pavlik (1989), however, suggested that there is strong evidence that some kind of dune habitat existed in portions of the Mojave before the Pleistocene. The Pleistocene woodlands in the Mojave Desert were replaced with desert or arid grassland vegetation in the late-middle Holocene (~7000 years ago; Van Devender, 1977; Spaulding, 1990; 1991; Hunter *et al.*, 2001).

4 The Great Basin Desert

The hot deserts of North America have received much of the recent attention from historical biogeographers (eg, Marshall and Lieberr, 2000; Riddle *et al.*, 2000a; 2000b; Zink *et al.*, 2001; Jaeger *et al.*, 2005; Riddle and Hafner,

2006), yet the Great Basin Desert has nearly as old a history as the hot deserts. Pollen records and fossilized plants from the Great Salt Lake indicate desert vegetation from the late Miocene (8 Ma) to the early Pliocene (5 Ma; Axelrod, 1940; Davis and Moutoux, 1998). During the middle Miocene, Redwood forest in the northern Great Basin and Columbia Plateau were replaced with arid shrub-steppe primarily due, presumably, to drying caused by uplift of the Sierras (Axelrod, 1940). Vertebrate fossils also suggest that by the late Miocene a scrub or steppe-adapted Great Basin fauna had expanded to nearly its present range (Webb, 1977).

Pliocene (5–2 Ma) deposits from Cache Valley, Utah (extreme northeastern Great Basin), include equivalents of many of the modern shrubs indicating warmer temperatures (2–4°C) and 6 cm more rain annually than the present (Wolfe, 1990). Fossil floras also indicate that a mild and warm semi-arid climate was present in the western United States during this time (Axelrod, 1948). Not all paleobotanical evidence from the Great Basin tells the same story. Pliocene (5–2 Ma) pollen assemblages from Beaver, Utah (southeastern Great Basin), for example, show that pine-dominated vegetation dominated the area (Thompson, 1991). Wernicke *et al.* (1988) suggested that the Great Basin has increased substantially in area during the last 15 Ma by extension of many faults, which enabled the expansion of an arid-adapted flora through Pliocene and Pleistocene (5–0.1 Ma; Davis and Moutoux, 1998).

Because the Great Basin Desert is a cold desert, and because it is higher in latitude than the regional hot deserts, it is often assumed that any desert-adapted elements in the Great Basin biota were replaced by a mesic Pleistocene biota. This is not necessarily the case. Early Pleistocene pollen records from the Great Basin, as well as climate reconstructions, suggest higher temperatures and lower precipitation than modern times (Moutoux, 1995; Davis and Moutoux, 1998). Even during full glacial times much of

the area was dominated by an arid shrub-steppe (Davis and Moutoux, 1998; Litwin *et al.*, 1999; Madsen *et al.*, 2001; Woolfenden, 2003).

Like the other North American deserts, many valleys in the Great Basin Desert were covered with large pluvial lakes during parts of the Pleistocene (Figure 5). These Pleistocene lakes led to the development of many Great Basin sand dunes (Britten and Rust, 1996), which, like the other dune systems in the West, can be considered islands of diversity (Pavlik, 1985).

Plant fossils from packrat middens suggest that a drier climate occurred over most of the southwest in the mid-Holocene (7000–5000 years ago; Bryne *et al.*, 1979; Thompson and Kautz, 1983; Mehringer, 1985). Many sites across the Great Basin, however, indicate that near modern plant communities have been present from ~11,000 years ago (Thompson, 1990).

5 The Snake River Plain/Northern Basin and Range

While the Great Basin Desert seems to have been established by the middle Miocene, the arid shrub-steppe environments north of the Great Basin, classified by Omernik (1987) as two distinct areas, the Snake River Plain and the Northern Basin and Range, may have had a more recent origin. The Snake River Plain was formed as the North American Plate moved across a mantle plume (the Yellowstone Plume) beginning about 17 Ma (Hanan *et al.*, 2008). As the Plate moved across the mantle plume, the land was uplifted directly above the plume leaving a lower-elevation subsidence in its wake (Owen Davis, unpublished data). This lower-elevation plain provided a habitat for arid adapted shrub-steppe plants like sagebrush to establish. Owen Davis (unpublished data) recovered pollen samples from drill cores in southern Idaho that indicated the presence of sagebrush steppe as far back as 12 Ma in the Snake River Plain.

In contrast to the evidence of Miocene arid steppe environments, vertebrate fossils from this

area indicate the presence of a deciduous forest with patches of more open, shrubby woodland during this time (Webb, 1977). Further evidence gained by comparing oxygen isotopes with faunal evidence supports the thought that the Miocene climate of the Snake River Plain and Northern Basin and Range was warm and moist with cool summers and mild winters (Smith and Patterson, 1994).

Several authors have suggested a more recent evolution of shrub-steppe environments on the Snake River Plain/Northern Basin and Range compared to the similar environments of the Great Basin Desert. Palynological evidence from this area indicates that the origination of an increasingly arid-steppe environment occurred in the middle Pliocene (3.5 Ma; Leopold and Denton, 1987; Thompson, 1991). Other palynological data, however, show that pine-fir-spruce assemblages dominated parts of this area in the early Pliocene (5 Ma), later transitioning to increased steppe environments by the late Pliocene (2 Ma), then back to pine-fir dominated landscapes in the middle Pleistocene (~1 Ma; Thompson, 1991).

6 The Colorado Plateau

There has been some debate as to when the Colorado Plateau and the surrounding mountain ranges gained the majority of their current elevation, and, therefore, developed the rain shadow in which the region now sits. For example, Ruddiman *et al.* (1989) stated that most of the net uplift on the Colorado Plateau has occurred since 12–10 Ma. Pederson *et al.* (2002) suggested that the Plateau experienced two periods of uplift. Early Cenozoic events (55 Ma) provided the majority of the uplift, with a second set of small episodes occurring in the mid- to late Cenozoic (25 Ma) that provided only slight elevation gains. Middle to late Eocene (35 Ma) pollen records support Pederson *et al.* (2002) indicating that the Colorado Plateau had surface elevations as high as or higher than today (Wolfe

et al., 1998; Gregory and Chase, 1992). Webb (1977) admitted the difficulty in discussing the late Miocene mammal fauna (8 Ma) of the Colorado Plateau, because of the diversity of fossils found there, but the evidence points to the presence of a mesic forest on much of the Colorado Plateau, with isolated patches of drier environments.

The Pleistocene climatic cycles undoubtedly affected the plant communities of the Colorado Plateau. Fossil evidence suggests that evergreen woodland dominated much of the Colorado Plateau, along with patches of grassland and shrubland (Soreng and Van Devender, 1989; Elias *et al.*, 1992; Anderson *et al.*, 2000; Jackson *et al.*, 2005). The early Holocene brought a warmer more xeric ecosystem (Sharpe, 2002), yet evidence also suggests that precipitation was much higher than modern times (Betancourt, 1990; Sharpe, 2002).

IV Summary and conclusion

The geologic history of western North America is as varied as explanations that exist describing the formation of this diverse landscape. We have made an attempt to illustrate the differing views from the vast body of literature that exists regarding this subject, but the debate goes on concerning the causation and timing of the formation of the Nearctic desert regions. One must assume that all of the data presented are accurate, and, therefore, it seems that the uplift of the American Cordillera, and the subsequent formation and differentiation of the various deserts, cannot be explained by a single event. It is interesting and worth mentioning that while the Laramide orogeny certainly occurred, there is no evidence that this major uplift created a rain shadow and caused the type of aridification that the Neogene events apparently produced. This could be because the Laramide events did not elevate the terrain enough to alter climatic processes, or it could be because subsequent erosion

was rapid enough that no long-term biotic change was recorded in the fossil record.

Paleobiological evidence suggests that the Neogene uplift events created a rain-shadow effect over most of western North America, and, therefore, led to the formation of the different desert regions. The formation of these distinct desert regions seems to be a major driving factor in the diversification of a unique North American arid-adapted biota. While the current literature does not demonstrate exactly when the mountains rose, or when and how the deserts formed, this review reveals the fact that geological time estimates need to be treated as just that, estimates. Biologists attempting to understand the historical biogeography of western North America would be wise to report dates of geological events with confidence intervals and error associated with them just as they do with molecular divergence time estimates. Based on the various dates given for mountain building and desert formation (Figures 2 and 3), we suggest that evolutionary events dating anywhere between 15 and 2 Ma could be considered associated with mountain building or desert formation activity.

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