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Cover images: Views of the Rainbow Basin (top), the Barstow Formation (middle) and the Cajon Valley Formation (bottom).

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The middle Miocene in southern California: Mammals, environments, and tectonics of the Barstow, Crowder, and Cajon Valley formations—Field Trip of the North American Paleontological Convention, June 22, 2019

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OVERVIEW AND PURPOSE

The Mojave Region preserves a rich and continuous Miocene mammal-fossil record that formed during a time of significant tectonic activity and climate change. We will visit exposures of the Crowder, Cajon Valley, and Barstow formations to look at the evolution of three different sedimentary basins through the middle Miocene. Participants will learn how depositional environments and habitats changed through time in relation to tectonics and climate and how they influenced patterns of mammal diversity and biostratigraphy.

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I. SCHEDULE AND ROAD LOG

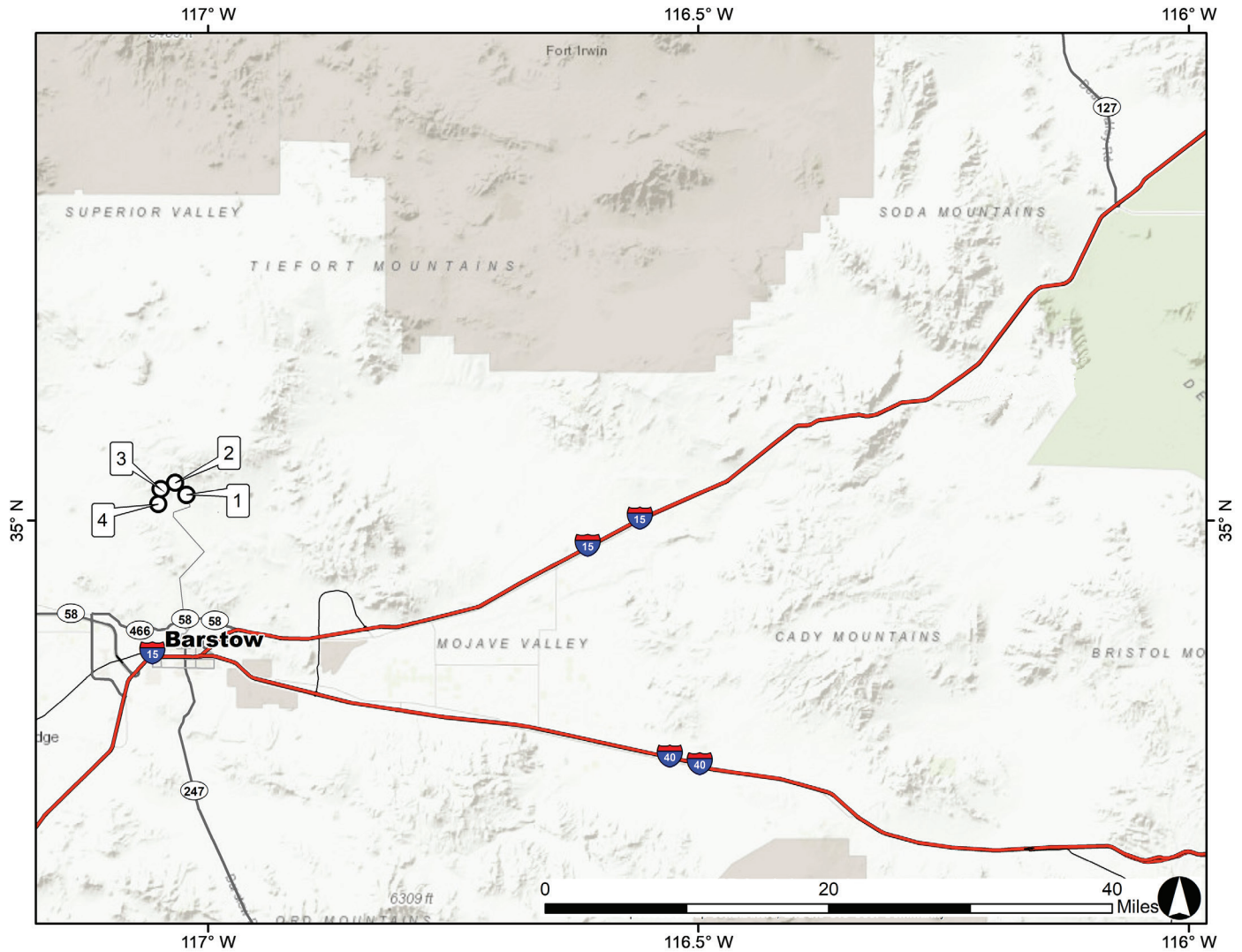
8:30 am—Depart for Rainbow Basin, Mud Hills, north of Barstow (~1.5-hour drive)

Follow I-215 North toward Barstow. Merge onto I-15 North, and follow north through Cajon Pass toward Barstow. Take exit 181 for L Street. Turn right onto Main Street. Turn left onto North 1st Avenue, then turn left onto Irwin Road. Turn left onto Fossil Bed Road. Turn right onto the Rainbow Loop Road and keep left on Owl Canyon Road toward Owl Canyon Campground.

10:00 am—Stop 1. Owl Canyon Campground (Restrooms and water)—Introduction to the middle Miocene Barstow Formation. The lower part of the Barstow

Formation is exposed at Owl Canyon Campground. From the campground, we can see lacustrine deposits, sandstone, and conglomerate of the Owl Conglomerate Member. Here, deposits of Facies Association 1 (sandstone and conglomerate) and Facies Association 2 (thin-bedded siltstone, claystone, marl) are separated by a fault.

Walk through section in Owl Canyon trail toward the syncline axis. We will pass through four of the six macrofacies in the Barstow Formation (Facies Associations 1, 2, 3, and 5 of [Loughney and Badgley 2017](#)), most separated from one another by faults. Note the numerous minor faults that offset marker beds (including the Skyline and Dated Tuffs) through the canyon. Note ripple marks, insect traces, and mammal tracks in the tilted sandstone



Map showing field trip Stops 1–4 in the Barstow Formation.

bed just off the trail.

11:00 am—Drive around Rainbow Loop

Head south down Owl Canyon Road and turn right onto the Rainbow Loop Road. Note changes in lithology as we drive along the loop road.

Stop 2. Rainbow Basin—View of the Barstow syncline axis in Rainbow Basin. The lower part of the Upper Member (Facies Association 5) of the Barstow Formation is exposed in the syncline axis above the Skyline Tuff, a prominent marker layer. Rainbow Basin is a popular spot for geology mapping exercises for southern California schools. Return to vehicles and continue around Rainbow Loop. Note offset along the Rainbow Fault, that separates Facies Associations 4 and 5.

Stop 3. Cal-Uranium Prospect Canyon—Park and walk upsection through exposures of middle Barstow

Formation (Facies Association 3), visit old Frick Quarry. The Middle Member of the Barstow Formation is best exposed in the central Mud Hills. Thin-bedded sandstone, siltstone, claystone, and marl represent marginal lacustrine deposits. Sandstone and mudstone beds become thicker upsection and represent near-channel floodplain deposits that comprise most of Facies Association 3. These deposits grade upwards into stacked sandstone beds that form cliffs along the skyline (Facies Association 4). Many of the large fossil localities developed by the American Museum of Natural History are located in this part of the Mud Hills. Continue up Skyline Trail.

Stop 4. Overview of Rainbow Basin—Views of the stacked sandstone beds of Facies Association 4 that represent a significant change in depositional style and changes in basin drainage patterns. To the southwest across the valley are the Waterman Hills, location of

the detachment fault and metamorphic core complex. Detachment faults are deep-seated normal faults that produce significant extension that eventually exposes part of the upper mantle (a metamorphic core complex). This type of structural development is characteristic of the Basin and Range province, where widespread detachment faulting produced numerous asymmetrical basins.

12:30 pm—Return to Owl Canyon Campground for lunch

Head east on Fossil Bed Road and continue to Owl Canyon Campground.

1:30 pm—Depart for Cajon Pass (~1.25-hour drive)

Head south on Owl Canyon Road, turn left on onto Rainbow Loop road and left again on Fossil Bed Road. to exit the Rainbow Basin Natural Area. Turn right onto Irwin Road, then turn right on 1st Avenue. Turn right onto Main St., and left onto L Street in order to merge onto I-15 S. We will follow I-15 south for 48.5 miles.

Approximately five miles before we arrive in Cajon Pass (past Oak Hill Road), note that we are proceeding down section through the Old Alluvium of Noble (1954), the Shoemaker Gravels, the Phelan Peak Formation, the Miocene Cajon Valley and Crowder formations underlain by the Oligocene Vaqueros Formation, to the late Cretaceous Cosy Dell Formation. The exposed stratigraphic history spans 70 Ma (Woodburne 1991).

Take Exit 131 for CA-138 W (turn right at junction). After 0.5 mile, turn right onto Santa Fe Fire Road. Bear right (north-northwest) onto dirt road USFS Route 3N53. Turn right (north) on the east side of the BNSF railroad bridge and cross a sand wash, then a gully. We will continue for ~1.5 miles and stop before the BSNF tracks to arrive at Stop 5.

2:45 pm—Stop 5. *Davis Ranch, Cajon Valley Formation Unit 3*. DO NOT CROSS TRACKS—Introduction to the middle Miocene Cajon Valley (18.0–12.7 Ma) and Crowder (17.5–7.1 Ma) formations (see Fig. 4 in section III for regional geologic map).

Biostratigraphy and magnetostratigraphy (Woodburne and Golz 1972, Reynolds 1991, Liu 1990) suggests that the deposition of the 2440-m-thick Cajon Valley Formation spans a period from 18 Ma to 12.7 Ma. The Cajon Valley Formation in the southwestern Mojave preserves diverse mammalian fossils and records faunal response to environmental changes during Miocene Climatic Optimum warming (MCO; ~17–14 Ma). Unit 3 generally contains Hemingfordian (He) North American Land Mammal Age (NALMA) vertebrate fossils, while Unit 5 generally

contains Barstovian (Ba) NALMA vertebrate fossils.

Here, we are in Unit 3 of the Cajon Valley Formation where pulses of arkosic sandstone are interspersed with red pedogenic horizons (or poorly developed paleosols). Measured and sampled sediments from a northern and southern section of Units 3 and 5 of the Cajon Valley Formation record two different paleoenvironments within the basin: an arid, upslope habitat (northern section) and a ponded basin center habitat (southern section). Smiley et al. (2018) analyzed phytolith assemblages (plant microfossils), carbon isotopic composition of preserved soil organic matter, and elemental geochemistry of pedogenic horizons within each section in order to reconstruct local environmental change through time. Here at Davis Ranch we see exposures in the northern, or arid upslope, section.

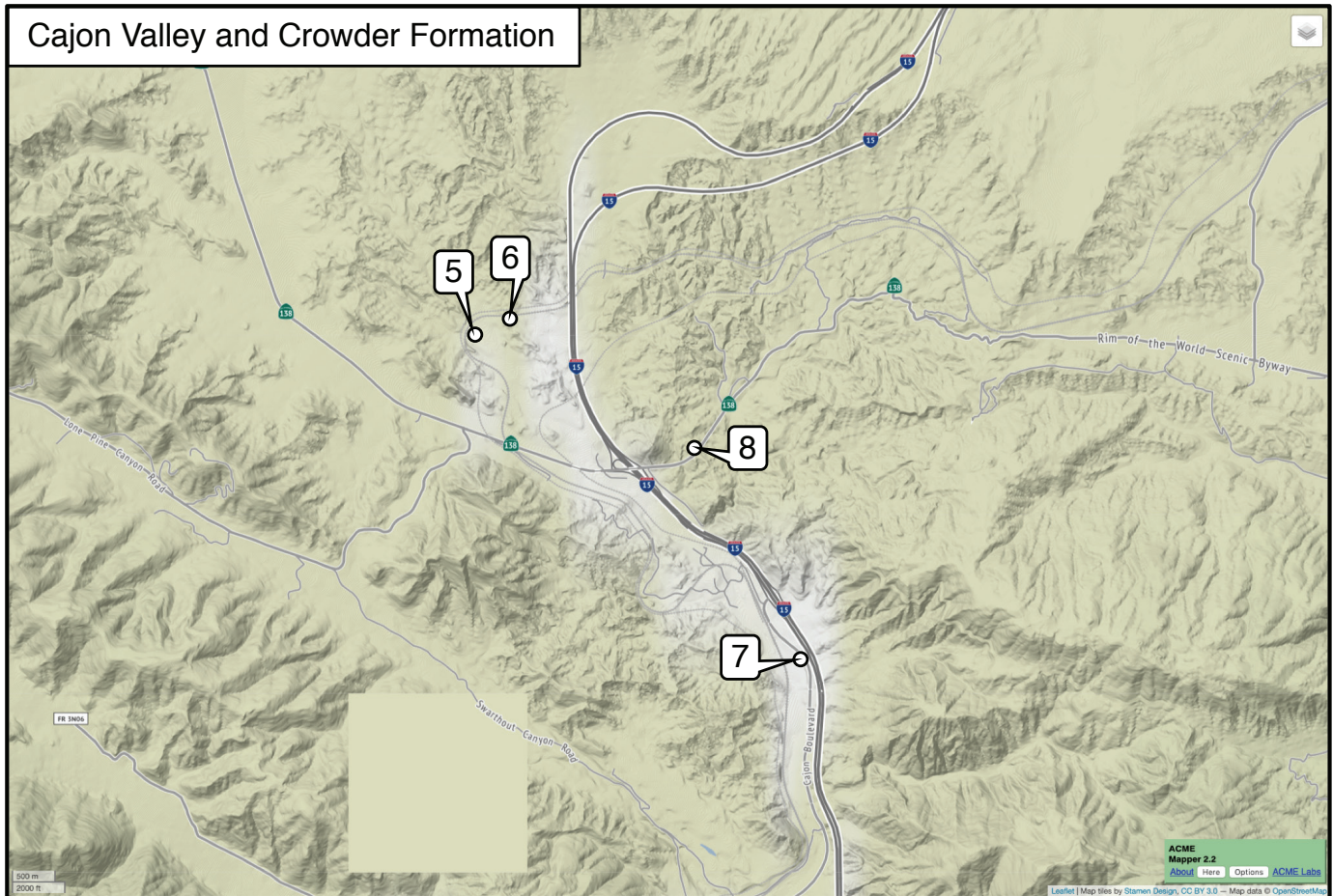
Paleosol colors may imply soil development and weathering under differing drainage patterns or climatic regimes. Red-colored paleosols suggest deep oxidation of ferromagnesian minerals under relatively dry conditions (Woodburne and Golz 1972). Gray or brown paleosols might indicate oxidation under moist conditions, such as slow drainages with structural blockages.

The transition from Unit 3 to Unit 5 in the Cajon Valley Formation approximates the transition from Hemingfordian to Barstovian NALMA, although a few localities in uppermost Unit 3 have produced Barstovian mammals. Cajon Valley Formation Unit 4 is a clastic wedge of limited extent that is locally absent.

We will drive east along the south side of the BNSF tracks to Stop 6. As we drive along the BNSF tracks, we will observe this transition in time and associated changes in the sediments exposed in railroad cuts, reflecting past environmental change. Park in cleared area.

3:15 pm—Stop 6. *Davis Ranch, Cajon Valley Formation Unit 5*. DO NOT CROSS TRACKS—Pedogenic horizons across the tracks are gray to brownish-gray; compare them with the brick-red pedogenic horizons at the previous stop. Cajon Valley Formation Unit 6 is exposed north along Baldy Mesa Road. Magnetostratigraphy suggests that deposition of Cajon Valley Unit 6 ceased about 12.7 Ma (Liu 1990). Opening of the Cajon Valley Basin was apparently linked to rotation of the San Gabriel Block at the east end of the Western Transverse Ranges (Dickinson 1996). Basin filling stopped with cessation of rotation (Woodburne 2015). To the north, the Cajon Valley Formation is truncated by an erosional unconformity or fault contacts.

Reverse direction and retrace to Santa Fe Fire Road. Turn left on Santa Fe Fire Road to get back to CA-138.



Map showing field trip Stops 5–7 in the Cajon Valley Formation and Stop 8 in the Crowder Formation.

Turn left onto CA-138, heading east and proceed toward I-15. Enter I-15 southbound, but stay in the right lane to exit shortly at Cleghorn Road. Turn right (southwest) onto Cajon Boulevard. Approximately 0.5 miles pass the left bend in the road, turn left (east) onto the pavement of Route 66 and park.

3:30 pm—*Stop 7. View of southern section*—Discuss stratigraphy of the Cajon Valley Formation. Here, we see the southern section of the Cajon Valley Formation, with Unit 5 sediments clearly exposed in the outcrop. Note the preserved freshwater limestone and lignite beds. These units, along with the local presence of fossil aquatic gastropods support the interpretation of marsh land or ponded depositional environment in the center of the basin. One of the most fossil-rich sites for small mammals in the Cajon Valley Formation is found near the top of this section, containing the only record of the relatively large-bodied heteromyid *Harrymys maximus* in the region (Lindsay and Reynolds 2015).

From this viewpoint, we see the stratigraphic

exposures of the Cajon Valley Formation in the foreground:

View N35°W, 0.7 miles: Red pedogenic horizons of Cajon Valley Formation, Unit 3 (He) at the Dipslope Locality (Reynolds 2015).

View N45°W, 0.7 miles: Transition to white, purple and green sandstones of Cajon Valley Formation, Unit 5 (Ba).

View N85°W, 0.4 miles: Chalicothere Cut, Cajon Valley Formation, lower Unit 5 (Ba; Coombs and Reynolds 2015).

View S80°W, 0.3 miles: Cajon Lignite Cut, Cajon Valley Formation, middle Unit 5 (Ba).

The broader stratigraphic context of the Cajon Valley Formation spans Cretaceous marine sediments to the Quaternary. The Cretaceous Cozy Dell Formation (Morton and Miller 2003) that contains bones of elasmosaur, a late Cretaceous indicator fossil (Lucas and Reynolds 1991), is found in outcrops to the south and west. The Oligocene to Miocene marine Vaqueros Formation (Morton

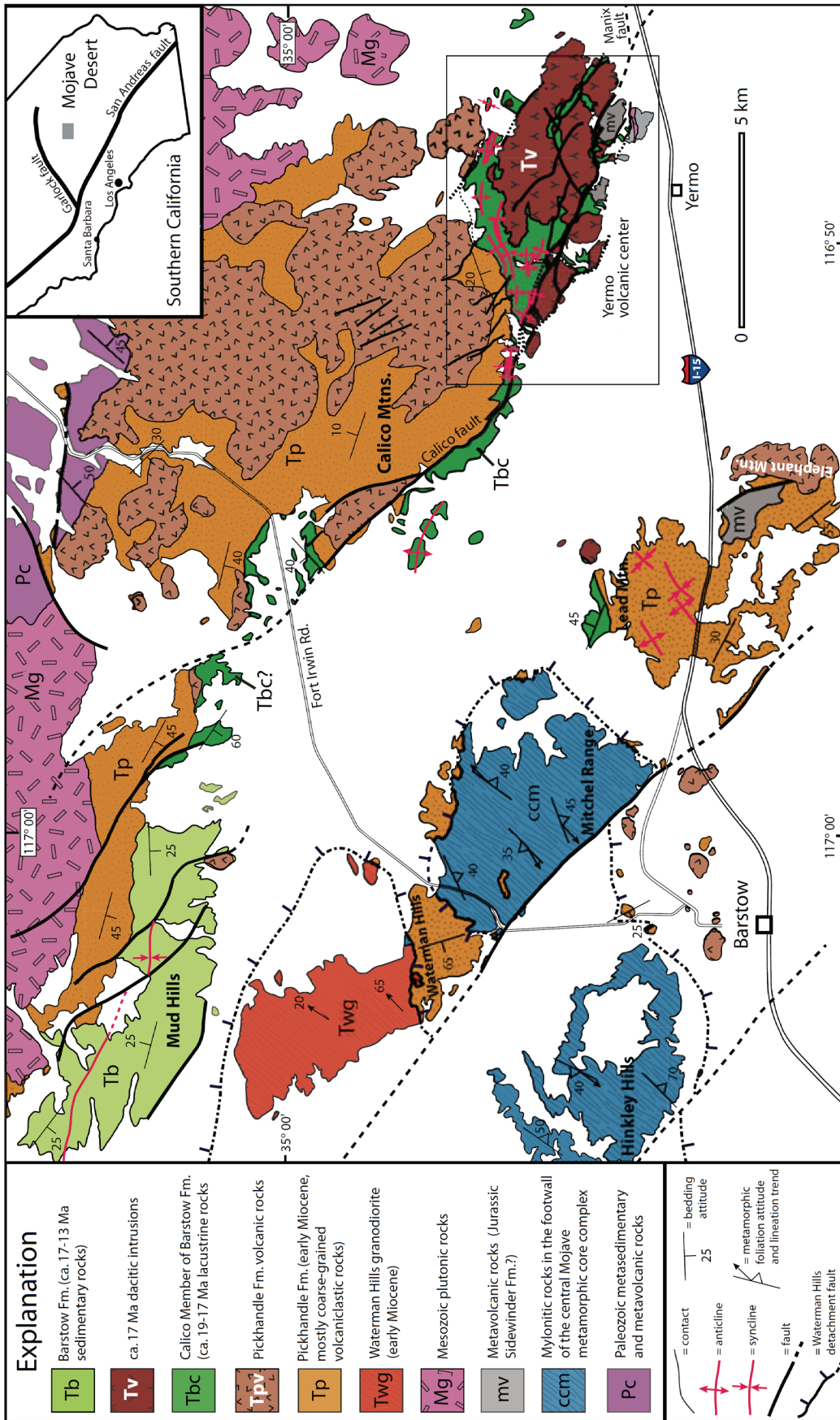


Figure 1. Map of the central Mojave Desert near Barstow, California. Outcrops of the Barstow Formation occur in the Mud Hills and Calico Mountains. Modified from Singleton and Gans (2008).

and geologic formations (Woodburne 2004). The large-mammal fauna of the Barstow Formation includes 13 canid species, eight species of equids, seven species of camelids, and six antilocaprid species, as well as several species of amphicyonids, oreodonts, tayassuids, felids, palaeomyricids, rhinocerotids, and proboscideans. The small-mammal fauna includes 10 heteromyid species, six murid species, three species of geomyoid rodents, two species of sciurids, as well as soricids, leporids, talpids, and erinaceids (Table 1; Pagnac et al. 2013).

In the Mud Hills, the Barstow Formation is divided into three members: the Owl Conglomerate, Middle, and Upper members (Fig. 2; Woodburne et al. 1990). These deposits become finer grained upwards from the conglomerate and sandstone of the Owl Conglomerate Member to the mudstone-dominated sequences of the Upper Member. In the nearby Calico Mountains (Fig. 1), the Calico Member encompasses lacustrine deposits (Singleton and Gans, 2008) that are roughly correlative with the Owl Conglomerate Member (Loughney and Badgley 2017). Several prominent tuff layers (volcanic ash deposits) occur throughout the Barstow Formation that serve as stratigraphic markers in the Mud Hills, in particular the Skyline Tuff that separates the Middle and Upper members (Woodburne et al. 1990). Deposition in the Mud Hills occurred between ~19 and 13 Ma (Woodburne et al. 1990); the sequence is dated through biostratigraphy (Lindsay 1972, Pagnac 2009), magnetostratigraphy (Woodburne 1996), and radiometric ($^{40}\text{K}/^{40}\text{Ar}$, $^{40}\text{Ar}/^{39}\text{Ar}$, and U-Pb) dating of marker tuffs (MacFadden et al. 1990, Miller et al. 2013). In the Calico Mountains, the age of Barstow deposits is estimated to be between 19 and 17 Ma based on $^{40}\text{Ar}/^{39}\text{Ar}$ dating of intrusive igneous rocks and breccia of the Yermo volcanic center (Fig. 1).

The Barstow Basin includes multiple formations that record the history of basin filling through the early to middle Miocene. The major sedimentary facies of the Barstow Formation and related deposits are typical of an extensional-basin sequence. The Barstow Formation unconformably overlies the early Miocene Pickhandle and Mud Hills formations, which comprise breccia derived from previously deposited volcanic rocks, fluvial, and lacustrine deposits (Ingersoll et al. 1996, Fillmore and Walker 1996). Extension along the Waterman Hills detachment fault (Fig. 1) and volcanism in the central Mojave Region began around 24 Ma (Glazner et al. 2002). The Pickhandle and Mud Hills formations represent syn-extensional deposits that formed during the early history of the Barstow Basin, between ~24 and 19 Ma, whereas

the Barstow Formation is largely post-extensional (Ingersoll et al. 1996, Fillmore and Walker 1996).

Loughney and Badgley (2017) identified six facies associations (FA) in the Barstow Formation that represent the dominant environments forming at the time of deposition in the Mud Hills (Table 2). A facies association is a group of facies united by their lithological features and are characteristic of specific depositional environments (Miall 2016). Conglomerate and sandstone of FA 1 represent alluvial-fan deposits and are contemporaneous with thin-bedded lacustrine deposits of FA 2 (Stop 1), which thicken eastward toward the Calico Mountains. During this early stage of the Barstow Basin (Fig. 3A), one or more shallow, saline-alkaline lakes occupied the basin, surrounded by wooded grassland (Park and Downing, 2001). Evidence for salinity and alkalinity derive from the presence of zeolite, sulfate, and borate minerals, bedded gypsum, and the faunal composition of arthropod fossil assemblages (Park 1995, Park and Downing 2001). Few vertebrate fossils occur in FA 1 in the Mud Hills (Woodburne et al. 1990). Nodules from FA 2 in the Calico Mountains produce well-preserved plant and arthropod fossils, including fairy shrimp, biting midges, water fleas, and diving beetles, that occur in modern saline-alkaline lakes of the Great Basin (Park and Downing 2001).

Sandstone and mudstone beds of FA 3 represent channel and proximal-channel floodplain deposits of meandering streams that developed as subsidence in the basin decreased (Loughney and Badgley 2017). Assemblages of phytoliths (microscopic plant-silica bodies) indicate that palms and woody dicots were abundant in the closed-canopy riparian environments that dominated this part of the basin around ~16.5 to 15.5 Ma (Loughney et al. 2019). The abundance of fossils and diversity of mammals increase in this facies association, coinciding with the Hemingfordian–Barstovian NALMA boundary at ~16 Ma (Fig. 2): 37 species of large mammals and 13 species of small mammals are known from FA 3 (Pagnac et al. 2013). The environments of FA 3 represent habitats that supported diverse mammal communities, as well as depositional settings that also had high preservation potential, which contributed to the increase in mammal diversity (Loughney 2018). FA 4 is dominated by stacked sandstone beds that crop out in the central Mud Hills (Stops 3 and 4). These beds represent the channel and near-channel deposits of braided streams. Mammal diversity was lower in FA 4 than in FA 3, although several rich and biostratigraphically important localities occur in this facies association (Woodburne et al. 1990, Pagnac, 2009, Pagnac et al. 2013).

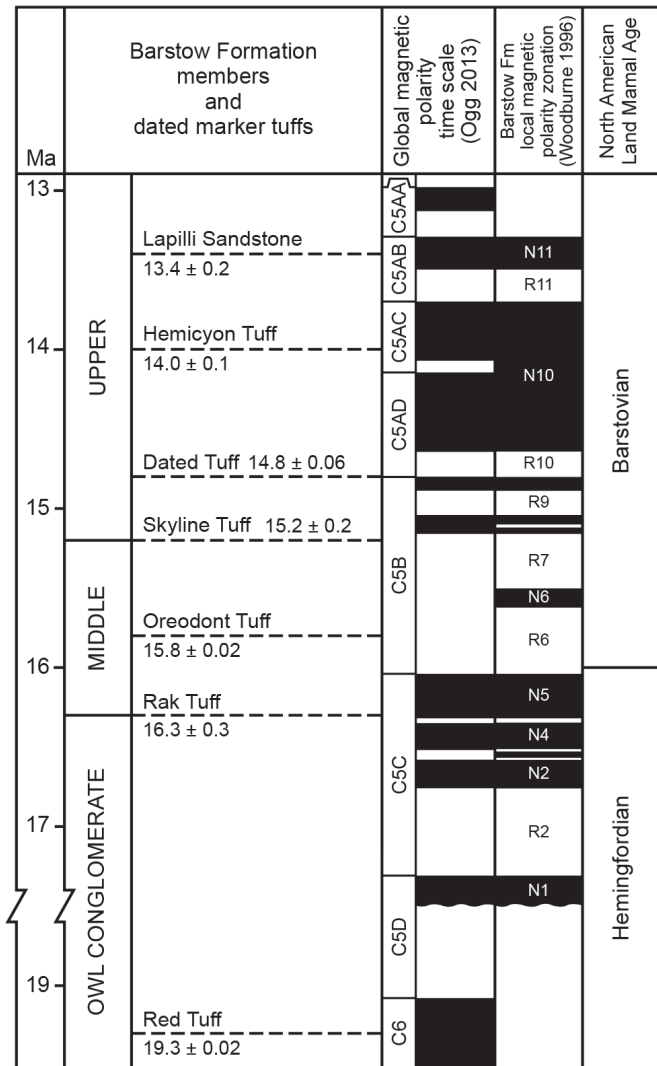


Figure 2. Age and lithostratigraphic divisions of the Barstow Formation in the Mud Hills. From Loughney and Badgley (2017).

FA 5 includes drab-colored ashy mudstone and red-colored mudstone that represent poorly drained and well-drained floodplain deposits, respectively (Table 2). FA 5 interfingers with FA 6, which is exposed only in the western Mud Hills. FA 6 is composed of mudstone and interbedded marl layers (clay-rich carbonate) that represent well-drained floodplain and ephemeral wetland deposits. Open-canopy habitats formed in the Barstow Basin during the late stages of basin history (after ~15 Ma; Fig. 3B), when subsidence and sedimentation rates were low. Phytolith assemblages from FA 5 are dominated by morphotypes of woody dicots with a minor grass component. Open-habitat grass morphotypes are abundant in assemblages from FA 6, and the abundance of palm morphotypes varies from low to high among

samples, indicating that water sources were ephemeral or highly localized (Loughney et al. 2019). These assemblages indicate the presence of wooded grasslands that formed around spring-fed wetlands in the Barstow Basin (Fig. 3B).

The number of fossil localities increases substantially in the Upper Member compared to the Middle and Owl Conglomerate members. The abundance of fossils and localities relates to the depositional environments in the basin at the time of deposition (Loughney and Badgley 2017). Environments must be suitable habitats for mammals and also be able to preserve vertebrate body fossils. As the basin evolved, rates of subsidence and sedimentation decreased, allowing stable, vegetated habitats to develop. Increasingly heterogeneous habitats in the Barstow Basin also influenced the preservation of fossils, as more diverse depositional settings formed in FA 5 and FA 6 than in FA 3 and FA 4.

III. PALEOENVIRONMENTS AND FAUNAS OF THE CROWDER AND CAJON VALLEY FORMATIONS (text and figures modified from Smiley et al. 2018)

The Crowder and Cajon Valley formations (Fig. 4) represent long documented records through the middle Miocene that have been well-prospected for fossils. Fossil collection in the Crowder and Cajon Valley formations has occurred over the last five decades, with notable recovery of small-mammal fossils due to extensive screen-washing efforts. To date, 56 identified taxa of small ($n = 33$) and large ($n=23$) mammals are known from the two formations (Tables 3 and 4; Woodburne and Golz 1972; Reynolds 199, Reynolds et al. 2008). Highly fossiliferous assemblages of both large and small mammals, in addition to several dated tuffs, make the Barstow Formation of the western Mojave Desert a useful reference for biostratigraphic and chronostratigraphic correlation with the Crowder and Cajon Valley formations. Mammalian assemblages of the Crowder and Cajon Valley formations overlap biostratigraphically with those of the Barstow Formation and record older Hemingfordian faunas that coincided with early MCO warming (Figs. 5 and 6). Age determination based on biostratigraphic correlation, faunal zones from the Barstow Formation, and paleomagnetic stratigraphy indicate that the Crowder Formation was deposited between 17.5 and 7.1 Ma or younger (Reynolds et al. 2008), and the Cajon Valley Formation between 18.0 and 12.7 Ma; however, fossils do not occur throughout the entire depositional histories of these basins (Woodburne and Golz 1972, Winston 1985, Weldon 1986, Liu 1990, Reynolds et al. 2008).

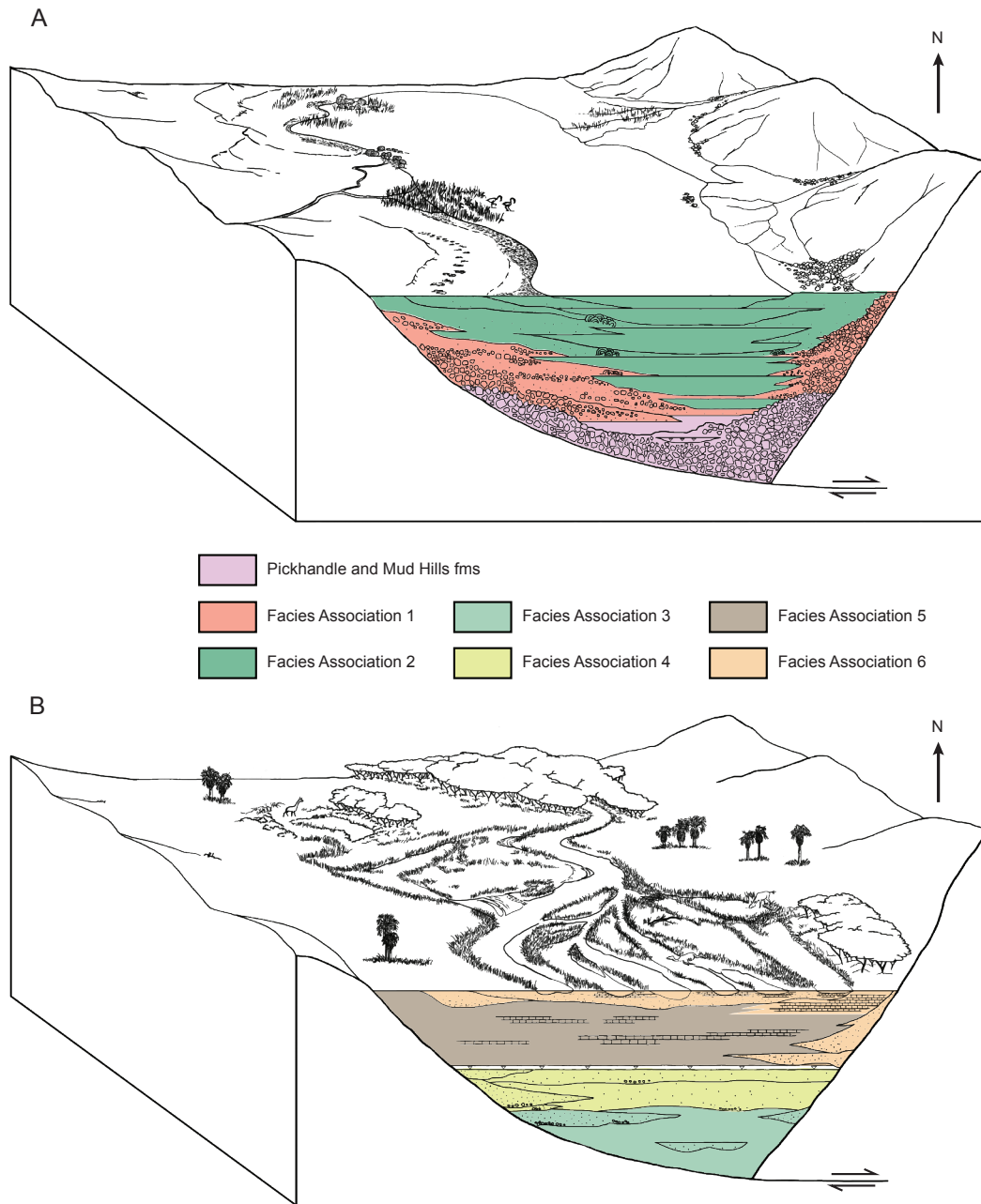


Figure 3. Schematic block diagrams showing environments of the Barstow Formation during (A) early and (B) late basin history. Not to scale. From Loughney and Badgley (2017).

Sediments of both the Crowder and Cajon Valley formations are primarily arkosic sandstones and conglomerates that were deposited unconformably over crystalline basement rocks or the early Miocene Vaqueros Formation, a marine conglomerate and sandstone locally exposed below the Cajon Valley Formation (Noble 1954, Dibblee 1967, Woodburne and Golz 1972, Morton and Miller 2003). Paleoelevations of these formations are not known; however, regional geological history indicates that uplift northwest and northeast of Cajon

Pass supplied sediment to the Crowder and Cajon Valley formations, which were deposited on a low-relief surface proximal to the coast prior to the late Miocene uplift of the Transverse Ranges (Meisling and Weldon 1989; Woodburne 1991).

The composite section of the Crowder Formation contains 980 m of terrestrial sandstones and conglomerates alternating with fine-grained sandstone and siltstone beds (Foster 1980, Winston 1985). The Cajon Valley Formation is approximately 2440 m thick and primarily

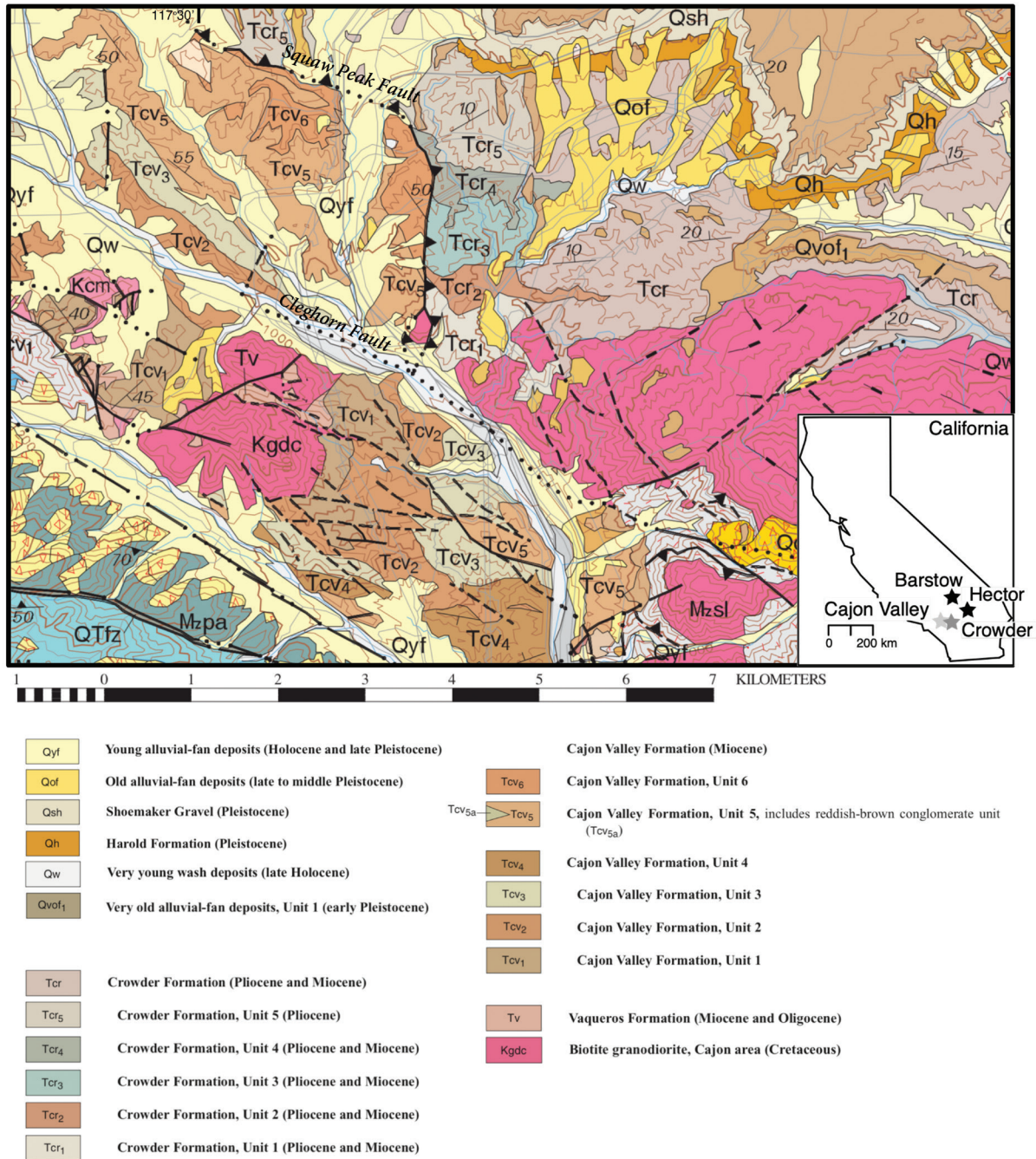


Figure 4. Geologic map showing the Cajon Valley and Crowder formations and the Squaw Peak Fault at Cajon Pass, San Bernardino County, California. Map and legend extracted from USGS Geologic Map: San Bernardino 30' x 60' Quad (from Morton and Miller 2003).

composed of siltstone, arkosic sandstone, and conglomerate with greater lithologic variation (e.g., lignite and limestone present) and sediment induration than the Crowder Formation (Woodburne and Golz 1972, Meisling and Weldon 1989). Based on lithologies, clast composition, sedimentary structures, and bedforms, the depositional environments for the Crowder and Cajon Valley formations are interpreted as fluvial in nature, with

features most closely resembling braided channel and floodplain systems in extensional basins (Woodburne and Golz 1972, Foster 1980, Winston 1985, Meisling and Weldon 1989). Fining-upward lithologies and the presence of lignites and limestone beds in the southeastern portion of the Cajon Valley Formation imply gradual infilling of basins over a southwest-draining paleoslope (Foster 1980, Weldon, 1986, Meisling and Weldon 1989).

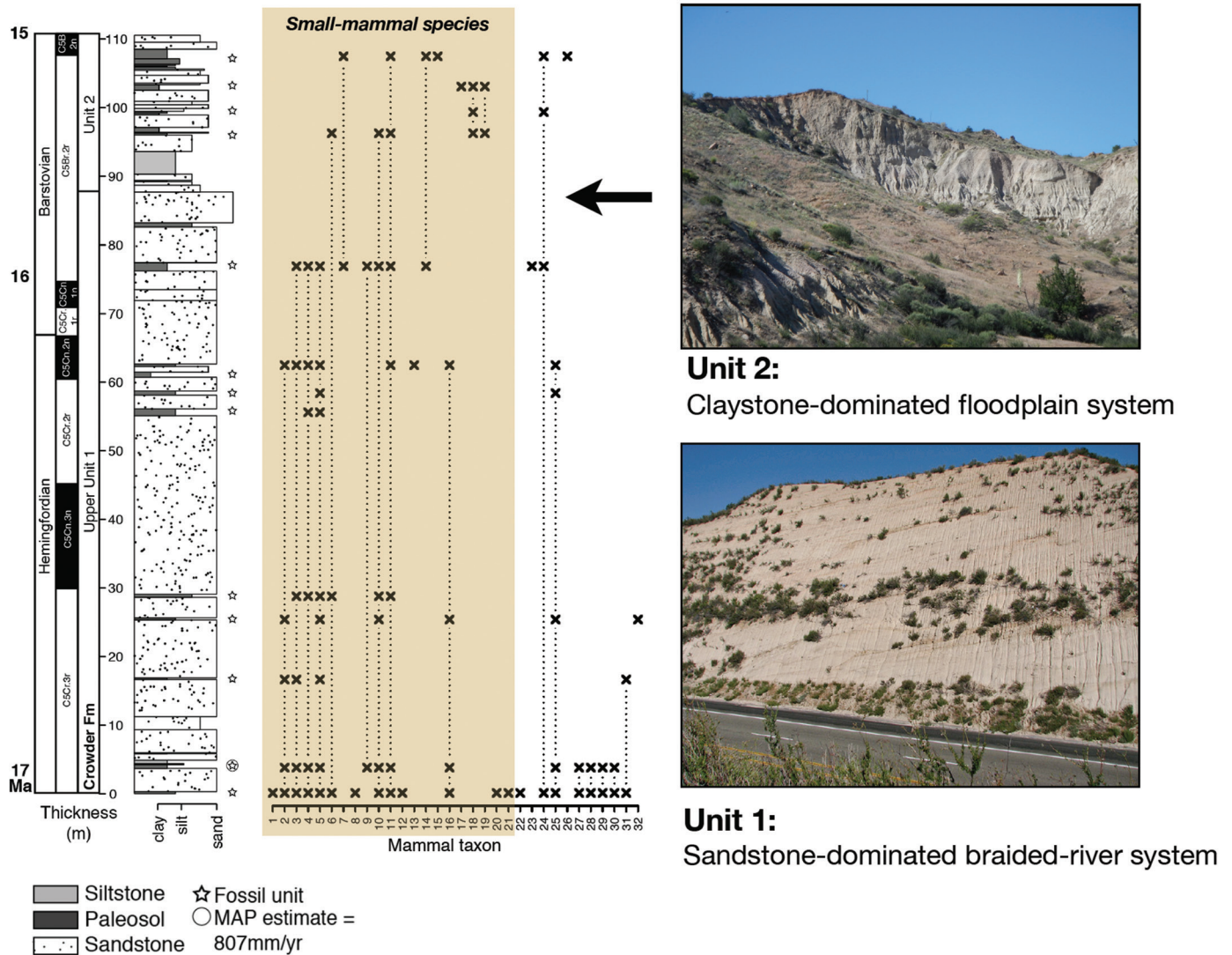


Figure 5. Stratigraphic section for the Crowder Formation, Upper Unit 1 and Unit 2. Temporal correlation with the NALMA and global geomagnetic polarity timescales (Woodburne 1987, Gradstein et al. 2004) is shown. Fossil occurrences of taxa listed in Table 3 are indicated by an x in relation to the stratigraphic section and biostratigraphic ranges (dotted lines) are assumed to range through the first and last occurrences of taxa within the formation. The black arrow indicates the interval of most pronounced environmental and faunal change. Ages of the sedimentary strata and fossil localities are inferred from paleomagnetic data from Winston (1985) and Weldon (1986), and biostratigraphy and paleomagnetic age interpretations from Reynolds et al. (2008). Figure modified from Smiley et al. (2018).

In the Crowder and Cajon Valley formations, mammal fossils are typically associated with finer-grained sandstone and siltstone beds that often contain clays, evidence of root traces, and other pedogenic features (Figs. 5 and 6; Winston 1985, Reynolds, 1991).

The middle Miocene was a significant interval of local to regional landscape and climate change, including tectonic extension and the development of topographic complexity in western North America and the MCO warming period, that coincided with peak mammal diversity for the entire Basin and Range Province. The Crowder and Cajon Valley formations provide new paleoenvironmental

and faunal information, most notably during the initial MCO warming for which records are currently sparse in western North America. The integration of phytolith, carbon isotope composition of preserved soil organic matter, and paleosol-derived precipitation proxies provide a detailed reconstruction of spatially and temporally varying paleoenvironmental conditions within the two basins and in relation to faunal assemblages (Smiley et al. 2018). These formations record mesic (MAP= \sim 800 mm yr⁻¹) ecosystems, the development of increasingly arid conditions, the existence of relatively open grassland ecosystems, and the earliest potential evidence of

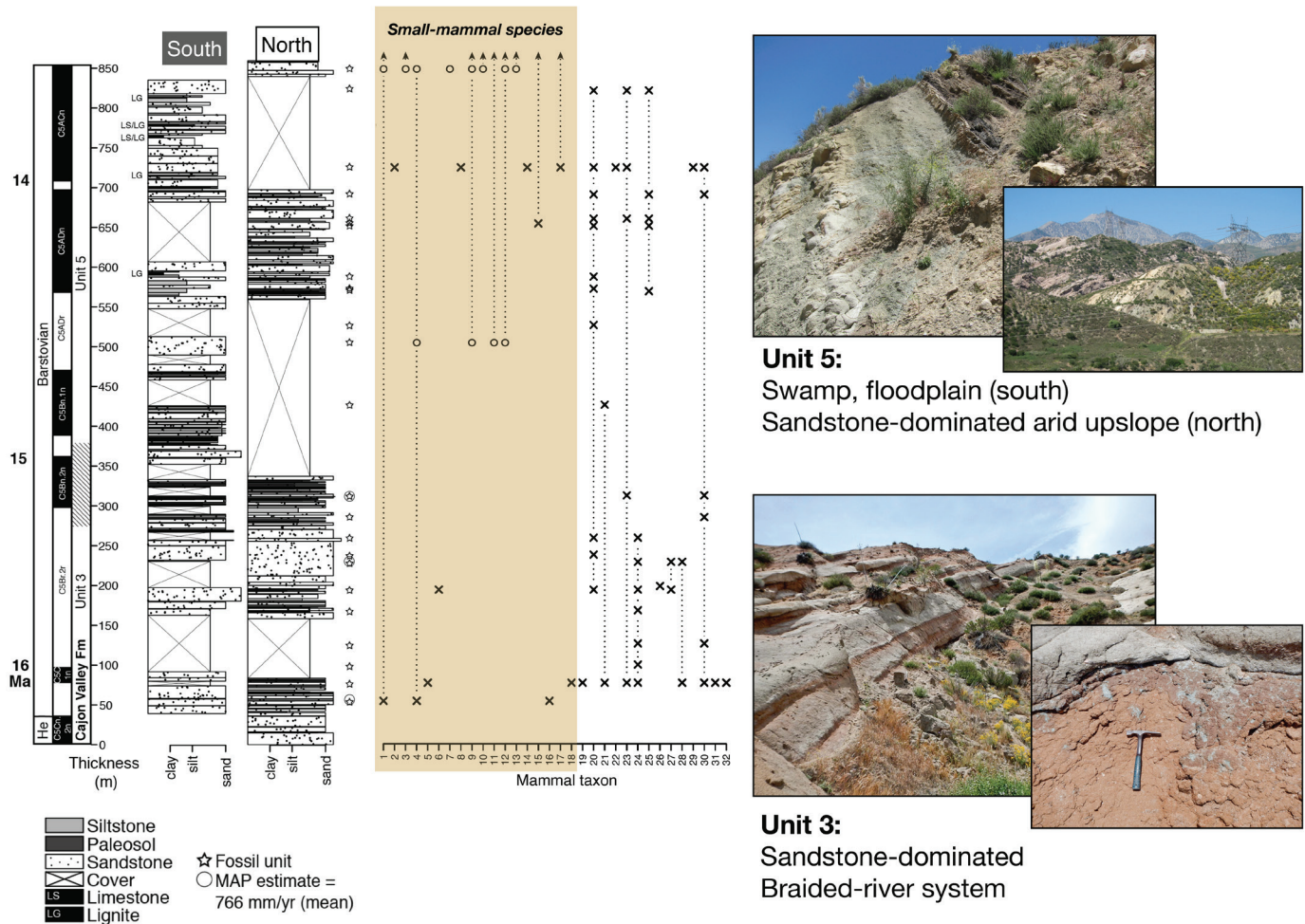


Figure 6. Southeastern and northwestern stratigraphic sections for the Cajon Valley Formation Units 3 and 5 (gradual transition between units indicated by hashed lines). Temporal correlation with the NALMA and global geomagnetic polarity timescales (Woodburne 1987, Gradstein et al. 2004) is shown. Known (x) and approximate (o) fossil occurrences of taxa (as listed in Table 4) are presented in relation to the stratigraphic section. Biostratigraphic ranges (dotted lines) are assumed to range through the first and last occurrences of taxa within the formation. Arrows indicate fossil occurrences stratigraphically higher than the measured section (Upper Unit 5 and Unit 6). Ages of the sedimentary strata and fossil localities are based on biostratigraphy in Woodburne and Golz (1972) and from paleomagnetic data and age interpretation in Liu (1990). Figure modified from Smiley et al. (2018).

C4 grasses within the Mojave Desert region and more broadly across the Basin and Range Province. Spatial heterogeneity of C4 grasses between the Crowder and Cajon Valley basins supports the hypothesis that expansion of C4 ecosystems was influenced by local factors instead of global climate and CO₂ drivers (Fox and Koch 2003, Edwards et al. 2010, Strömberg and McInerney 2011, Cotton et al. 2012, Chen et al. 2015).

The Mojave Desert has the longest, most continuous record of mammalian diversity in the Great Basin, and the Crowder and Cajon Valley formations document distinct depositional environments and faunal assemblages compared to the nearby Barstow Formation. Mammalian response to environmental change is evident in the

Crowder Formation, which records faunal turnover and declining diversity of small mammals in relation to a drying trend in the basin. Low faunal similarity between the Crowder, Cajon Valley, and Barstow formations imply high spatial turnover in species composition (Table 5), while diverse assemblages, especially of small mammals, in the Crowder and Barstow formations and certain paleosol units of the Cajon Valley Formation indicate high local diversity. Both contributed to increased regional diversity and document the history of mammalian diversity during past warming and landscape change.

Recent paleoecological research has assessed the stable isotope composition of both large (Feranec and Pagnac 2013, Feranec and Pagnac 2017) and small

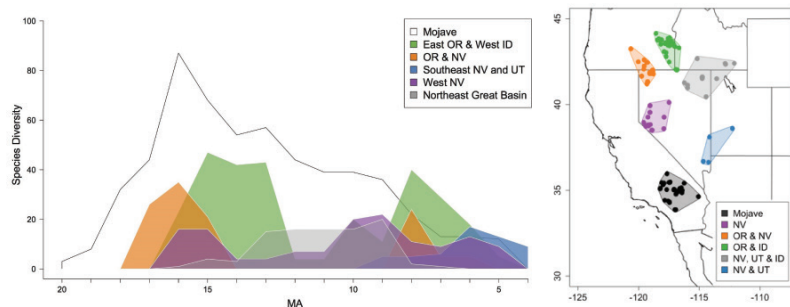


Figure 7. Overlapping species diversity of mammals (left panel) for the six subregions of the Basin and Range Province (right panel). For the interval from 18 to 14 Ma, mammal diversity increased in three regions simultaneously (the Mojave region, northwestern Nevada and southern Oregon, and southwestern Idaho and eastern Oregon). Figure modified from [Badgley et al. 2015](#).

All Miomap Fossil Localities

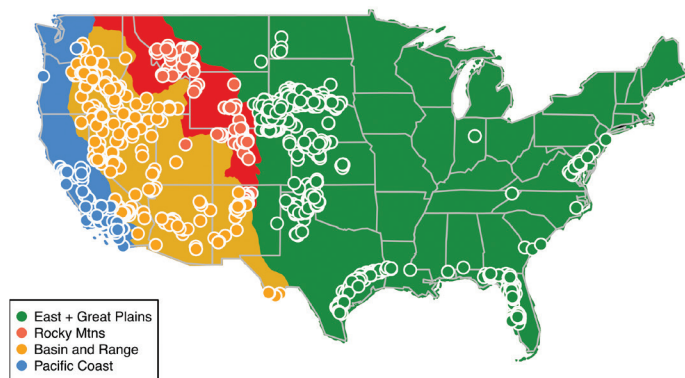


Figure 8. Map of fossil localities for North America mammal (data extracted from the MIOMap database; [Carrasco et al. 2007](#)). Colors correspond to four different geologic provinces, with the Basin and Range Province highlighted in yellow.

mammals ([Smiley 2016](#), Smiley et al. in prep) from the Crowder and Cajon Valley formations. Large-mammal isotopic studies support the idea that the C₄ vegetation was localized and not widespread at the time. C₄ plants (presumably grasses) were present by 14.3 Ma and were an emerging food source for equids in the Crowder Basin (est. 18% of diet; [Feranec and Pagnac 2013](#)), but the same signal was not found in equids from nearby Cajon Valley Formation ([Feranec and Pagnac 2017](#)). The stable isotopic composition of rodents records the consumption, and thus presence, of C₄ vegetation in both the Crowder and Cajon Valley formations as early as 17 Ma (Crowder Formation) and 15 Ma (Cajon Valley Formation); however, there is a high degree of isotopic variability within assemblages from single stratigraphic horizons. Within-assemblage rodent isotopic variability—up to 7‰—is more variable than the isotopic composition of preserved soil organic matter or of large mammals, suggesting that rodents capture more fine-grain variation in vegetation than do other proxies. This high degree of variability could be attributed to the small home ranges and rapid metabolism and tooth formation of rodents ([Hynek et](#)

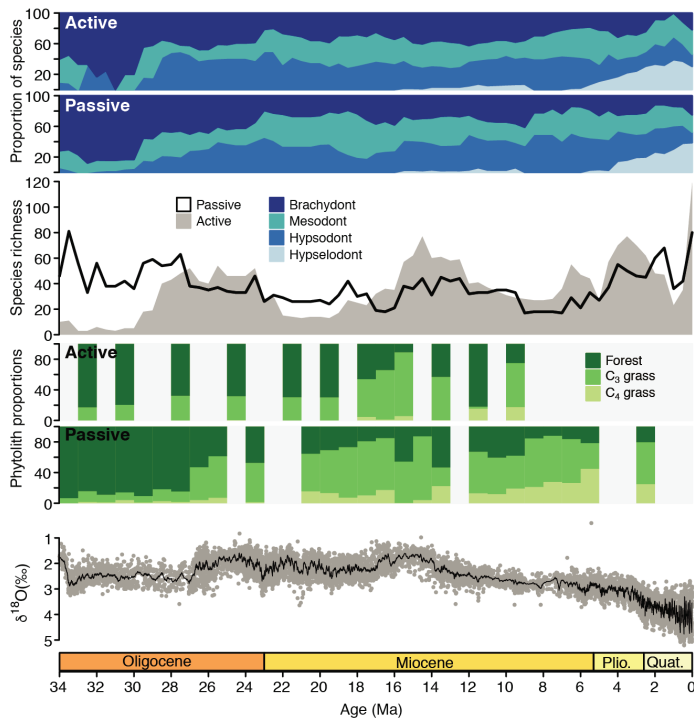


Figure 9. Climatic and biotic changes in North America over the past 35 myr. The global temperature trend is from the benthic foraminiferal oxygen-isotope record. Notable warming during the Middle Miocene was followed by long-term cooling and Quaternary glacial cycles. Global climate influenced vegetation (inferred from the phytolith record) differently in the active (montane west) versus the passive (Great Plains) regions of North America. Although both regions exhibited a Neogene increase in grasses, the decline of forest ecosystems occurred earlier in the passive region. Between 34 and 28 Ma, 22 and 18 Ma, and 2 and 1 Ma, rodent diversity was higher in the passive region, whereas from 17 to 13 Ma, 7 to 5 Ma, and 5 to 3 Ma, diversity was much higher in the active region. The contrast in diversity between active and passive regions was greatest during the Middle Miocene Climatic Optimum (17–14 Ma). Much of the diversity change among rodents coincided with changes in faunal composition. Corresponding changes in dietary ecology are demonstrated by the increase in high-crowned species (hypsodont and hypselodont) toward the present day. This increase preceded the expansion of grasslands in both regions, suggesting that adaptation to more abrasive diets was initially driven by volcanic ash in soils or grit on plants rather than increased consumption of grass. (From [Badgley et al., 2017](#); see original publication for data references.)

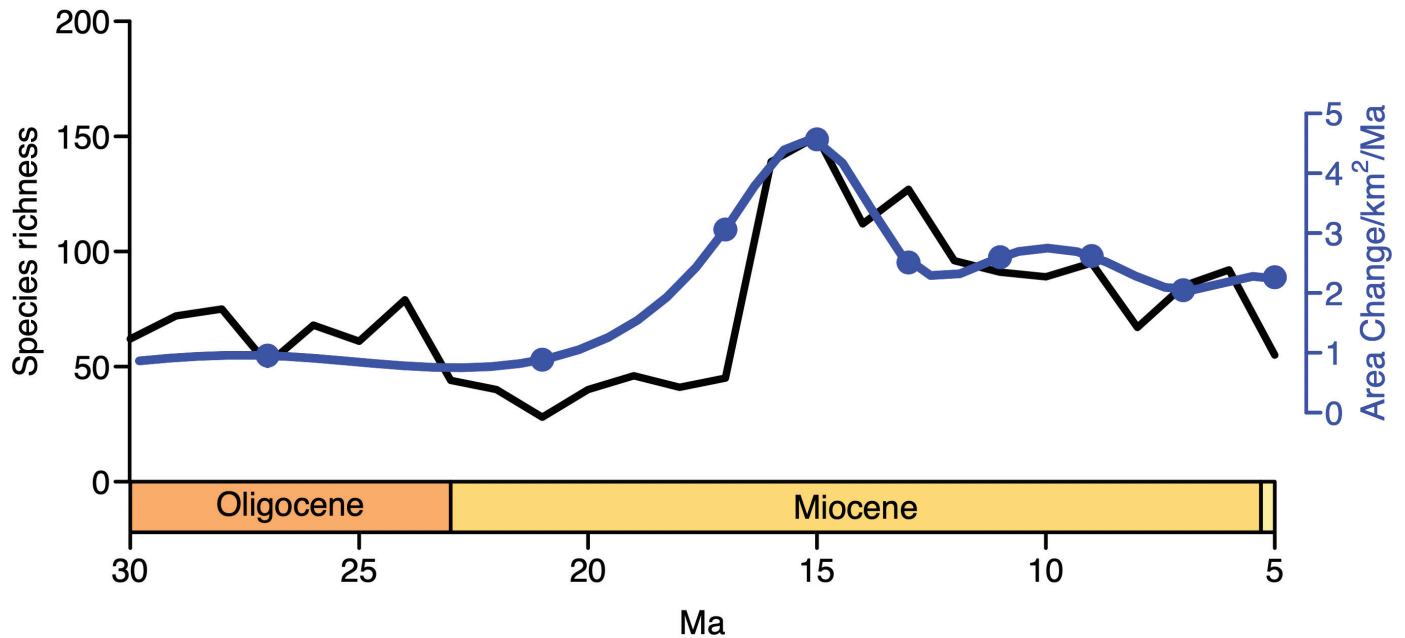


Figure 10. Species richness from the fossil record of mammals (black line) in the Basin and Range Province is tightly correlated (Spearman's $r = 0.77$, $p = 0.013$) with the regional rate of tectonic extension (blue line; data from Bahadori et al. 2018).

al. 2012, Smiley et al. 2016). Rodents increase their consumption of C4 vegetation through the history of deposition in the Crowder and Cajon Valley formations. This baseline shift in dietary niche through the MCO warming occurred across and within families, genera, and species—in particular, in the diverse and fossil-rich granivorous (seed-eating) Heteromyidae family—and precedes ecomorphological change in dentition (e.g., hypsodonty or tooth area). In contrast, rodent species did not diverge significantly in their isotopic niches, determined based on carbon and oxygen isotopic composition, implying notable and stable dietary niche overlap through the record, even when small-mammal diversity was elevated locally (Smiley et al. in prep).

IV. REGIONAL CONTEXT OF MIOCENE MOJAVE DIVERSITY

The most complete continental fossil record spanning the MCO within western North America occurs in the Mojave Desert of southern California (Fig. 7). Work over several decades has generated a rich fossil record from this region, including abundant small-mammal remains from three primarily middle Miocene formations. The Barstow, Crowder, and Cajon Valley formations are temporally well constrained through biochronological, radiometric, and paleomagnetic dating methods (Weldon 1986, Liu 1990, MacFadden et al. 1990). These formations record local processes within the larger Basin and

Range Province. Each basin is an archive of the influences of tectonic activity and climate change on mammal diversification and paleoecology at the local scale. In addition, paleoenvironmental data from sedimentary units in each formation serve to illuminate local-scale environmental changes and habitat heterogeneity during the MCO (e.g., Loughney and Badgley 2017, Smiley et al. 2018, Loughney et al. 2019). Continuous stratigraphic coverage among formations in the Mojave during the interval of intensified tectonic activity and climate change represents a critical record for the diversification history of mammals that is poorly represented elsewhere in the Basin and Range Province.

A primary motivation for studying the influence of tectonic activity and climate change on diversity at the basin scale is to understand the processes that generate and maintain high diversity in topographically complex regions today and in the past. Today, species richness for many different plant and animal groups is elevated in high-relief regions across all continents, including the Basin and Range Province (Badgley et al. 2017, Antonelli et al. 2018). Stepping back through time, the fossil record of mammals from 30 to 5 Ma in the Basin and Range Province is geographically and temporally dense, including eight orders of mammals spanning proboscideans to rodents. While gaps do exist in space, time, and taxonomy, the fossil record in this region is one of the best sampled and studied for Neogene mammals globally (Fig.

8). Contrasting the adjacent mammalian fossil records of the tectonically active Basin and Range Province and the tectonically quiescent Great Plains (Fig. 9) forms the basis of several studies into the evolutionary, ecological, and geohistorical processes driving regional patterns of diversity and diversification. In particular, the fossil record has been used to investigate the strengthening and weakening of the Topographic Diversity Gradient (TDG) in relation to tectonics, landscape and climate change, and species ecology through the Neogene.

Notable trends in the regional data include a peak in mammal diversity from 18 to 14 MA, producing a strong TDG (Barnosky and Carrasco 2002, Kohn and Fremd 2008, Finarelli and Badgley 2010, Badgley et al. 2014). A strong correlation between species richness and tectonic extension, as quantified by the rate of area gain, suggests a role of tectonic activity in driving regional diversity patterns (Fig. 10). In addition to elevated diversity during this period, diversification rates increased. In particular origination rates, which include contributions from both in situ speciation and immigration, are significantly higher than elsewhere in the record (Finarelli and Badgley 2010, Smiley 2018).

The macro and microfossil record of plants over the Neogene reveal a history of climatic drying and transition from forest dominated to grassland dominated ecosystems. Studies of these macrofloras have provided floral lists, estimates of MAT, MAP and in some cases paleo-elevation for the fossil sites. More recently, great strides in our understanding of the regional plant fossil record have been gained in large part due to the study of plant microfossils known as phytoliths. These silica bodies produced in plant tissues can be preserved in the geological record, often in pedogenic horizons and in association with mammalian fossils, and can reveal the vegetation types and structure of local ecosystems (Dunn et al. 2015, Strömberg et al. 2018). Major shifts in the taxonomic and ecological composition of the mammalian fossil record align with global to regional shifts in climate and vegetation (Fig. 9). For example, both rodents and large mammals show an increase in molar crown height in relation to the expansion of grassland ecosystems and regional aridification through Neogene (Janis et al. 2004, Jardine et al. 2012).

The regional view of diversity through time can be divided into fossil-rich subregions to assess both subregion diversity and turnover across the Basin and Range Province through time (Fig. 7). Doing so, a significant portion of the middle Miocene record comes from the Mojave subregion as well as the Northwestern region near

the Snake River Plain, both of which undergo significant landscape change due to tectonic extension and volcanism. Similarity in faunal composition (i.e., the number of species shared) from subregion to subregion is variable through time, reflecting changes in the pattern of species distributions in relation to potential barriers or connective corridors of suitable habitat and climate (Badgley et al. 2015). Whereas a decay in faunal similarity with distance or reduced similarity between subregions with strong geographic barriers between them is expected, a strong relationship between subregional faunal similarity and 1) paleodistance and 2) paleotopography is only found during the middle Miocene from 18 to 14 Ma (Smiley et al., in prep). This broad-scale pattern is reflected in the Mojave by the major differences in taxonomic composition from basin to basin (Table 5). These relationships suggest a strong influence of tectonic activity and climate warming (MCO) on faunal composition and turnover across spatial scales during this period. Loss of a geographic signal in faunal similarity later in the record could correspond with mammalian tracking of regional changes in vegetation, in particular the shift from mosaic to more widespread grassland ecosystems. The relative contributions of these various drivers to diversification dynamics and patterns of faunal turnover over time are currently an area of active study.

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Table 1. Faunal list of mammals from the Barstow Formation. After Lindsay (1972) and Pagnac et al. (2013).

Order Lagomorpha	Order Carnivora
Family Leporidae	Family Felidae
Subfamily Archaeolaginae	<i>Nimravides marshi</i>
<i>Hypolagus</i>	<i>Pseudaelurus intrepidus</i>
Order Rodentia	Family Canidae
Family Sciuridae	Subfamily Hespercyoninae
<i>Miospermophilus</i> sp.	<i>Osbornodon fricki</i>
<i>Nototamias ateles</i>	Subfamily Borophaginae
<i>Petauristodon jamesi</i>	<i>Cynarctoides acridens</i>
<i>Petauristodon minimus</i>	<i>Paracynarctus kellogi</i>
Family Castoridae	<i>Euoplocyon brachygnathus</i>
Subfamily Castoroidinae	<i>Microtomarctus conferta</i>
<i>Monosaulax pansus</i>	<i>Tomarctus hippophaga</i>
Family Eomyidae	<i>Tomarctus brevirostris</i>
<i>Leptodontomys stirtoni</i>	<i>Protomarctus optatus</i>
Family Geomyidae	<i>Cynarctus galushai</i>
<i>Mojavemys alexandrae</i>	<i>Aelurodon asthenostylus</i>
<i>Phelosaccomys</i> sp.	<i>Paratomarctus temerarius</i>
Family Heteromyidae	<i>Protepicyon raki</i>
<i>Diprionomys</i> sp.	Subfamily Caninae
<i>Cupidinumus boronensis</i>	<i>Leptocyon leidyi</i>
<i>Cupidinimus eurekaensis</i>	Family Amphicyonidae
<i>Cupidinimus halli</i>	Subfamily Amphicyoninae
<i>Cupidinimus lindsayi</i>	<i>Cynelos sinapius</i>
<i>Mioheteromys crowderensis</i>	<i>Pliocyon medius</i>
<i>Mookomys altifluminus</i>	<i>Amphicyon ingens</i>
<i>Peridiomys</i> sp.	<i>Amphicyon</i> sp.
<i>Perognathus furlongi</i>	Family Ursidae
<i>Perognathus minutus</i>	Subfamily Hemicyoninae
<i>Proheteromys formicarum</i>	<i>Plithocyon barstowensis</i>
<i>Proheteromys lophatus</i>	Family Mustelidae
<i>Proheteromys sulculus</i>	Subfamily Mustelinae
Family Muridae	<i>Brachypsalis pachycephalus</i>
<i>Copemys barstowensis</i>	<i>Plionictis ogygia</i>
<i>Copemys esmeraldensis</i>	<i>Miomustela</i> sp.
<i>Copemys longidens</i>	Family Procyonidae
<i>Copemys pagei</i>	Subfamily Bassaricinae
<i>Copemys russelli</i>	<i>Bassariscus antiquus</i>
<i>Copemys tenuis</i>	Order Artiodactyla
Order Erinaceomorpha	Family Tayassuidae
Family Erinaceidae	Subfamily Tayassuinae
<i>Lanthanotherium sawini</i>	<i>Hesperhys vagrans</i>
Order Soricomorpha	<i>Dyseohyus fricki</i>
Family Soricidae	<i>Cynorca occidentale</i>
<i>Limnoecus tricuspis</i>	Family Oreodontidae
<i>Paradomnina</i> cf. <i>relictus</i>	Subfamily Ticholeptinae
Family Talpidae	<i>Merychyus smithi</i>
<i>Domminoides</i> sp.	<i>Brachycrus laticeps</i>
	<i>Mediochoerus mojavensis</i>

Table 1 (cont.). Faunal list of mammals from the Barstow Formation. After Lindsay (1972) and Pagnac et al. (2013).

Family Camelidae
Subfamily Protolabinae
<i>Protolabis barstowensis</i>
<i>Protolabis</i> sp.
<i>Michenia mudhillsensis</i>
<i>Michenia</i> sp.
Subfamily Miolabinae
<i>Paramiolabis tenuis</i>
<i>Paramiolabis singularis</i>
<i>Paramiolabis minutus</i>
<i>Miolabis fissidens</i>
Subfamily Aepycamelinae
<i>Aepycamelus alexandrae</i>
<i>Aepycamelus</i> sp.
Family Antilocapridae
Subfamily Cosorycinae
<i>Merycodus joraki</i>
<i>Merriamoceros coronatus</i>
<i>Paracosoryx alticornis</i>
<i>Merycodus necatus</i>
<i>Ramoceros brevicornis</i>
<i>Cosoryx furcatus</i>
Family Palaeomerycidae
Subfamily Dromomerycinae
<i>Rakomeryx raki</i>
<i>Dromomeryx jorakinus</i>
Order Perissodactyla
Family Equidae
Subfamily Anchitheriinae
<i>Hypohippus affinis</i>
<i>Archaeohippus mourningi</i>
<i>Megahippus mckennai</i>
Subfamily Equinae
<i>Parapliohippus carrizoensis</i>
<i>Merychippus isonesus</i>
<i>Scaphohippus sumani</i>
<i>Scaphohippus intermontanus</i>
<i>Acritohippus styloidontus</i>
Family Rhinocerotidae
Subfamily Aceratheriinae
<i>Aphelops</i> sp.
Family Gomphotheriidae
Subfamily Gomphotheriinae
<i>Gomphotherium</i> sp.
Family Mammutidae
Subfamily Mammutinae
<i>Zygodolophodon</i> cf. <i>proavus</i>
<i>Zygodolophodon</i> sp.

Table 2. Facies associations (FA) of the Barstow Formation. After Loughney and Badgley (2017).

	Lithological description	Interpretation
FA 6	Weakly to moderately pedogenic siltstone, thin-bedded marl layers, sandstone	Spring-fed and ephemeral wetland deposits
FA 5	Bentonitic and tuffaceous siltstone with weakly developed pedogenic features, numerous marl layers	Poorly to well-drained floodplain deposits
FA 4	Stacked, multi-story sandstone beds with conglomeratic bases, siltstone	Channel and proximal-channel deposits of braided streams
FA 3	Sandstone and siltstone interbedded with nodular marl layers	Proximal-channel deposits of meandering streams
FA 2	Thin-bedded fine-grained sandstone, siltstone, claystone, and biogenic marl, gypsum locally present	Playa lake and marginal lacustrine deposits
FA 1	Amalgamated coarse-grained sandstone and conglomerate	Channels deposits of alluvial fans

Table 3. Mammalian faunas of the Crowder Formation.*Data extracted from the Paleobiology Database.

Small Mammals		Dietary Category*	Large Mammals		Dietary Category*
	Heteromyidae				
1	<i>Perognathus minutus</i>	granivore-browser	22	Antilocapridae – cf. <i>Merycodus</i> sp.	browser-grazer
2	<i>Paratrogomys whistleri</i>	granivore-browsers	23	Palaeomerycidae – <i>Sinclairiomeryx</i> sp.	browser
3	<i>Mookomys “altifluminus”</i>	granivore-browser		Equidae	
4	<i>Perognathus furlongi</i>	granivore-browser	24	<i>Archaeohippus mourningi</i>	browser
5	<i>Proheteromys sulculus</i>	granivore-browser	25	<i>Parapliohippus carrizoensis</i>	grazer-browser
6	<i>Balantiomys crowderensis</i>	granivore-browser	26	“ <i>Merychippus</i> ” (large)	grazer-browser
7	<i>Cupidinimus halli</i>	granivore-browser	27	Tayassuidae – <i>Cynorca</i> sp.	herbivore-omnivore
	Sciuridae			Camelidae	
8	<i>Protospermophilus</i> sp.	granivore-frugivore	28	<i>Procamelus</i> sp.	browser
9	<i>Tamias</i> sp.	granivore-frugivore	29	<i>Michenia agatensis</i>	browser
10	<i>Miospermophilus</i> sp.	granivore-frugivore	30	<i>Miolabis tenuis</i>	browser
11	<i>Petauristodon</i> sp.	granivore-frugivore	31	<i>Hesperocamelus</i> sp.	browser
	Zapodidae		32	Rhinocerotidae – <i>Menoceras</i> sp.	browser
12	<i>Megasminthus</i> sp.	herbivore			
13	<i>Plesiosminthus</i> sp.	herbivore			
	Cricetidae				
14	<i>Copemys tenuis</i>	herbivore			
15	<i>Copemys pagei</i>	herbivore			
16	Heterosoricidae – <i>Paradomnina relictus</i>	insectivore			
17	Leporidae – <i>Hypolagus</i> sp.	grazer-browser			
	Ochotonidae				
18	<i>Russellagus</i> sp.	herbivore			
19	<i>Hesperolagomys</i> sp.	herbivore			
	Mustelidae				
20	<i>Miomustela</i> sp.	carnivore-omnivore			
21	<i>Leptarctus</i> sp.	omnivore			

Table 4. Mammalian faunas of the Cajon Valley Formation. *Data extracted from the Paleobiology Database.

Small Mammals		Dietary Category*	Large Mammals		Dietary Category*
	Heteromyidae		19	Antilocapridae	browser-grazer
1	<i>Cupidinimus sp.</i>	granivore-browser	20	Camelidae	browser
2	<i>Harrymys maximus</i>	granivore-browser	21	Chalicotheriidae – <i>Moropus sp.</i>	browser
3	<i>Perognathus furlongi</i>	granivore-browser		Equidae	
4	<i>Proheteromys sulculus</i>	granivore-browser	22	<i>Acritohippus styloidontus</i>	grazer-browser
5	Sciuridae		23	<i>Archaeohippus mourningi</i>	browser
6	<i>Petauristodon</i> , large sp.	granivore-frugivore	24	<i>Parapliohippus carrizoensis</i>	grazer-browser
7	<i>Petauristodon</i> , small sp.	granivore-frugivore	25	<i>Scaphohippus intermontanus</i>	grazer-browser
8	<i>Petauristodon uphami</i>	granivore-frugivore	26	Merycoidodontidae – <i>Brachycrus buwaldi</i>	herbivore
	Cricetidae		27	Moschidae – Blastomerycine	browser-grazer
9	<i>Copemys longidens</i>	herbivore		Palaeomerycidae	
10	<i>Copemys sp. cf. C. russelli</i>	herbivore	28	<i>Bouromeryx americanus</i>	browser
11	<i>Copemys tenuis</i>	herbivore	29	<i>Bouromeryx sp.</i>	browser
	Eomyidae		30	Rhinocerotidae	browser
12	<i>Pseudadjidaumo stirtoni</i>	herbivore	31	Tayassuidae – <i>Dyseohyus sp.</i>	herbivore-omnivore
	Geomyidae		32	Ursidae – <i>Ursavus sp.</i>	herbivore-carnivore
13	<i>Mojavemys lophatus</i>	browser	Unit 6 taxa: <i>Cupidinimus halli</i> (granivore-herbivore), <i>C. lindsayi</i> (granivore-herbivore), <i>Miospermophilus</i> (granivore-frugivore), <i>Spermophilus sp. cf. S. primitivus</i> (granivore-frugivore), <i>Mojavemys alexandrae</i> (browser), <i>Parapliosaccomys</i> (browser), <i>Hypolagus fontinalis</i> (grazer-browser)		
14	Heterosoricidae – <i>Paradomnina relictus</i>	insectivore	Unit 5, above stratigraphic section: <i>Aepycamelus alexandrae</i> (browser), <i>Dyseohyus fricki</i> (herbivore-omnivore), <i>Scaphohippus sumani</i> (grazer-browser)		
15	Talpidae	insectivore			
16	Leporidae – <i>Hypolagus sp.</i>	grazer-browser			
17	Erinaceidae – <i>Lanthanotherium sp.</i>	insectivore-carnivore			
18	Mustelidae – <i>Leptarctus ancipidens</i>	omnivore			

Table 5. Results from bootstrap analysis of faunal similarity: the number of shared species between the Crowder and Cajon Valley formations is significantly lower than expected based on a random resampling of the combined taxonomic pool (see Smiley et al., 2018 for more details). *The number of unique taxa expected under null expectations according to the bootstrapped distribution of faunal similarity values.

Minimum shared	Bootstrapped Distribution*	Observed Value	
	mean (95% CI)	<i>Crowder</i>	<i>Cajon Valley</i>
Total taxa	21 (17-25)	7	9
Small-mammal taxa	14 (10-17)	5	7
Large-mammal taxa	7 (5-10)	2	2

Maximum shared	Bootstrapped Distribution*	Observed Value	
	mean (95% CI)	<i>Crowder</i>	<i>Cajon Valley</i>
Total taxa	24 (21-27)	14	17
Small-mammal taxa	16 (13-18)	9	12
Large-mammal taxa	8 (6-10)	5	5

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