CONSTANCE I. MILLAR
Institute of Forest Genetics
U.S. Forest Service
Pacific Southwest Research Station
Albany, California

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Tertiary Vegetation History

ABSTRACT

The Tertiary period, from 2.5 to 65 million years ago, was the time of origin of the modern Sierra Nevada landscape. Climates, geology, and vegetation changed drastically in the Sierra Nevada during this time, and analyses of this period provide both context for and insight into vegetation dynamics of the current and future Sierra. During the early Tertiary, warm-humid, subtropical to tropical conditions prevailed on the low, rolling plains of the area now the Sierra Nevada. Fossil taxa with tropical adaptations and affiliations were widespread throughout the region. In the Sierra Nevada, ginkgo *(Ginkgo biloba),* avocado *(Persea),* cinnamon *(Cinnamomum),* fig *(Ficus),* and tree fern *(Zamia)* were common. At the end of the Eocene epoch, about 34 million years ago, global climates changed rapidly from warm-equable to cool-seasonal temperate conditions. In response, vegetation also shifted enormously; cool-dry-adapted conifers and hardwoods, which had been refugial during the early Tertiary in upland areas of the Great Basin–Idaho region, migrated into newly hospitable habitats of the Sierra Nevada. These floras contained many of the taxa now native to the Sierra, plus relicts from the subtropical forests of the earlier Tertiary and species adapted to temperate conditions with summer rain—mixes that seem incompatible under modern conditions. Until late in the Pliocene epoch (about 1 million years ago), adequate but diminishing rainfall distributed through the year supported many taxa now extinct in the Sierra Nevada. By the late Tertiary, in response to continued drying, winter cooling, and increasing summer drought, and to gradual uplift of the Sierra Nevada, replacement of early Tertiary floras by modern taxa and associations had occurred. With the development of a Mediterranean climate by the late Pliocene, floras of the Sierra Nevada became segregated ecologically into elevational, latitudinal, and orographic zones.

An important message for ecosystem management from a study of the Tertiary flora of the Sierra Nevada is that, although vegetation has changed drastically over 65 million years, the rate has been very slow. Human impacts in the Sierra are potentially of a similar magnitude to these evolutionary changes but can occur at rates many times faster; such changes may be more rapid than plants are likely able to adapt to. Another management implication is that currently native species in the Sierra Nevada have existed in the past under drastically different climatic and environmental conditions than at present, have had very different distributions, and have occurred in mixes not seen in the recent past. Thus, assumptions about the behavior of native species in the future under unknown climates and/or novel management regimes should not be based solely on the behaviors of species in current environments. Unforeseen responses are likely, whether “positive” (population health, expansion, productivity), “negative” (population decline, extirpation), or novel. The most appropriate management action is to maintain diverse, healthy forests with conditions favoring resilience to unpredictable but changing future climates and management regimes. Plans that require landscapes to reach precise vegetation targets are likely to fail. Management programs that build flexibility, reversibility, and alternative pathways are more likely to succeed in an uncertain future.

INTRODUCTION

The Tertiary period is a slice of Earth’s history, roughly defining the time between the extinction of the dinosaurs and the beginning of Northern Hemisphere continental glaciation, from 65 million years ago (denoted as 65 Ma) to about 2.5 Ma (table 5.1). This was a period of major change in global climates and of significant mountain building, overall moving from warm-mild and moist-equable regimes to seasonally dry and cool climates. The Mediterranean dry summer typical of California today was unknown until late in the Tertiary. The Tertiary was the time of initial uplift of the Sierra Nevada and volcanism in the Cascade Mountains. Accompanying these physical changes were radical transformations in the vegetation assemblages that covered the landscapes.

The human time scale for land management stretches 100–200 years into the future at its most imaginative. Why would

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SNEP look back 65 million years? The Tertiary provides an important larger context for understanding modern landscape relationships in the Sierra Nevada. The Tertiary was the time of revolutionary development of the modern vegetation, climates, and landscape. At the onset of the Tertiary, there were humid subtropical climes in California, typical of vast periods of time prior to the Tertiary. Species such as ginkgo, avocado, figs, and palms dominated broad plains and low mountains in the area that is now the Sierra Nevada. By the mid-Tertiary, plants with affinities to modern taxa—pines, firs, oaks, and cottonwoods—appeared to be more widespread in the region of the developing Sierra Nevada. By the close of the Tertiary, most modern species and many modern vegetation assemblages were present and stratified into elevational zones. Although species and plant communities shifted in response to fluctuating conditions of the Quaternary period, which followed, these shifts were minor relative to the major evolutionary and continental-scale dynamics of the Tertiary. Thus the Tertiary sets the stage for the present.

The present flows seamlessly from the past. Knowing the origins and broad context of our flora informs our understanding and appreciation of the dynamics of current Sierra Nevada ecosystems—why species grow where they do, under what environmental and ecological conditions they have grown, what relationships have existed among plant associates, how biota respond to environmental change, and what potentials exist for rapid and dramatic natural vegetation change. Since many of our current taxa first appeared in California under different climates and evolved under very different environmental conditions, the past informs us about ecological responses that we are not able to infer from present dynamics.

OBJECTIVES

The purposes of this chapter are to:

- briefly review and assess the methods used to reconstruct the Tertiary vegetation of the Sierra Nevada
- develop a chronological overview of Tertiary geology, climate, and vegetation for the Sierra Nevada
- present floral lists and maps from published reports on Tertiary fossil deposits of the Sierra Nevada and neighboring regions and
- summarize points relevant to ecosystem management of the Sierra Nevada

The time frame for this chapter is the Tertiary period, as I define the boundaries from 65 Ma to 2.5 Ma (table 5.1), with focus on the Miocene and Pliocene epochs. Although a thorough understanding of the biogeographic and phylogenetic origins of modern Sierra species requires studying their presence in fossil floras throughout western North America and beyond, the focus here is on what was and what was not in the Sierra Nevada during the Tertiary. Thus, the geographic focus is the greater Sierra Nevada region and parts of western and central Nevada, specifically the area defined by the fossil floras chosen for inclusion here (figure 5.1).

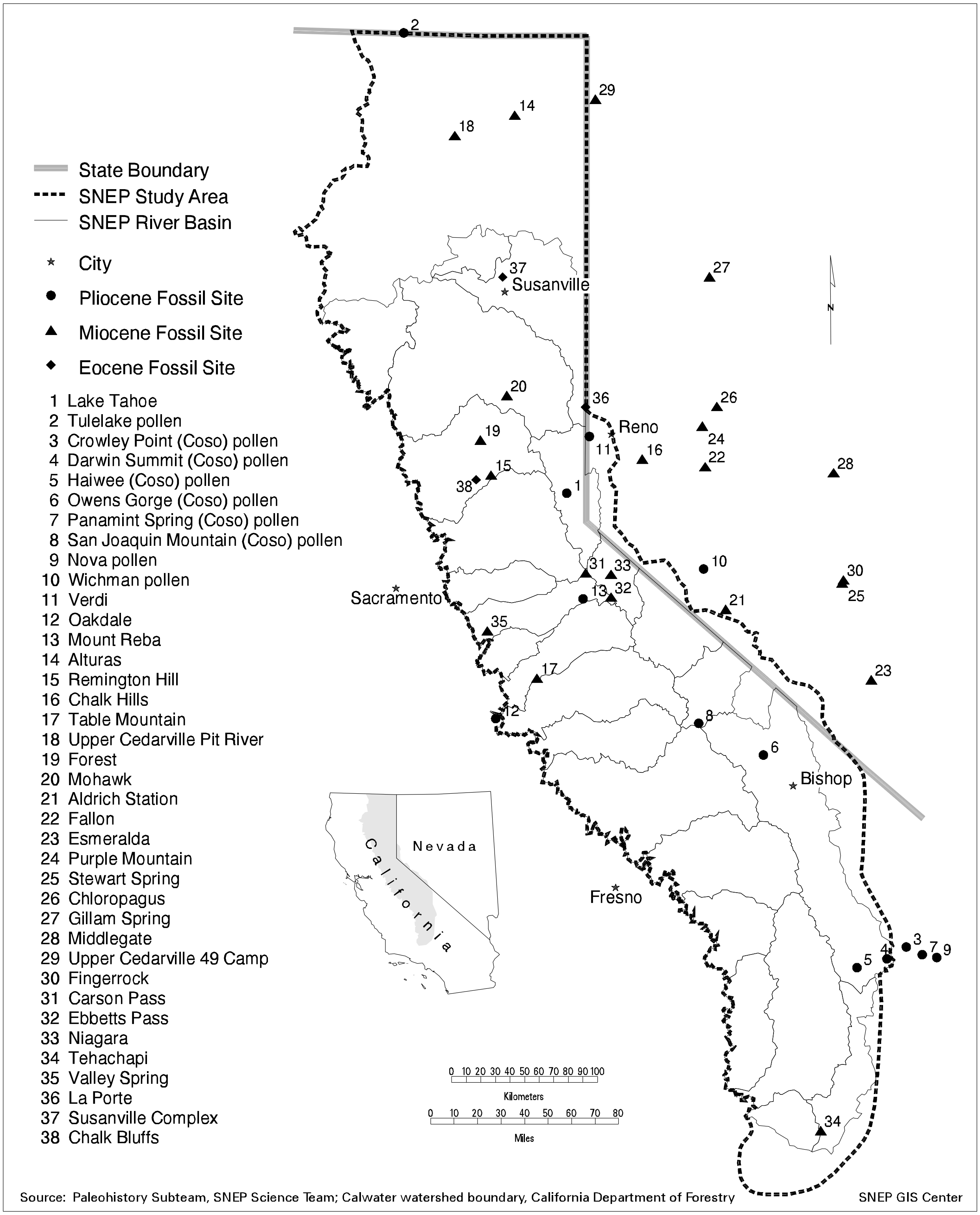
TABLE 5.1

Geological time chart for the Quaternary and Tertiary periods of the Cenozoic Era, showing approximate ages and durations of epochs (Odin 1982; Shackleton and Opdyke 1977; Swisher and Prothero 1990; Woodburne 1987).

Period	Epoch	Millions of Years Ago (Ma)
Quaternary	Holocene	0–0.01 (last 10,000 years)
	Pleistocene	0.01–2.5
Tertiary		
Neogene	Pliocene	2.5–7
	Miocene	7–26
Paleogene	Oligocene	26–34
	Eocene	34–54
	Paleocene	54–65

ASSUMPTIONS

1. This review is not intended to be exhaustive or comprehensive. Literature citations to more in-depth analyses are provided.
2. The focus is on plants and vegetation primarily, geology and climate secondarily; animals are not considered.
3. Confidence in knowledge decreases as we look further into the past; the biases of the fossil record and interpretation are discussed. Historical reconstruction is fraught with speculation.
4. Systematics and dating of the original interpretations of fossils are accepted unless subsequent revisions specific to the flora were published, or unless subsequent publications cast doubt on identifications. Other than these revisions, no modernization of nomenclature or taxonomic revision is attempted. Taxonomic revisions often lead to significant reinterpretations of biogeographic and evolutionary events. Examples of these are given to indicate the tenuousness of interpretations and the dependence on accurate taxonomy.
5. Detailed projections by original authors about paleoclimate (especially specific temperatures) and paleoaltitudes are



Source: Paleohistory Subteam, SNEP Science Team; Calwater watershed boundary, California Department of Forestry

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FIGURE 5.1

Distribution of Tertiary floras in the Sierra Nevada and adjacent regions of western and central Nevada. Floras are numbered in approximate order of age (from young to old). *Note:* Floras 3–10 are pollen sites, interpretations are based on a very small number of grains, and species identifications may be incorrect. These sites should be treated with question.

often not summarized here. New methods have cast doubt on the validity of some specific interpretations. Those new techniques have not yet been applied to Sierran Tertiary floras. Thus, generalizations about climate and environment are conservatively given.

6. Knowledge gained by understanding the origins of modern vegetation in the Sierra Nevada is relevant to ecosystem management of the ecoregion.

REVIEW OF METHODS FOR RECONSTRUCTING TERTIARY VEGETATION

Time Periods

The classification of time into eras, periods, and epochs (the geological time chart) is somewhat arbitrary, implying that a continuous process, time, is divisible. "Since geological time is not salami, slicing it up has no particular virtue" (Vita-Finza 1973). Despite this fundamental contradiction, historic events do tend to occur more or less periodically, lending themselves to description in pieces rather than as a continuum. Periodicities of tectonic, climatic, and biotic events are not often synchronous, however, from place to place or between plant and animal events. Boundaries of time periods are thus specific to regions, to biotas, and to causes (climate, paleomagnetic events, biotic changes).

Classification into geologic time periods was especially important in early paleontologic interpretation. Before direct dating methods were available, age of a fossil flora was assigned based on geologic stratigraphy and correlation to other local fossil floras. Radiometric dating (Dalrymple and Lanphere 1969; Steiger and Jager 1977) has relieved the temptation to date by correlation, since—within tolerances and errors—fossil floras can be directly dated. This both improves the accuracy of assigning floras to periods in the geologic time chart and relieves pressure for relying on those assignments to periods, since many floras can be discussed by direct age rather than by period. However, although radiometric methods have been available for several decades, not all of the Tertiary fossil floras in the Sierra Nevada (originally dated by stratigraphic correlation) have been confirmed radiometrically, and many that have been confirmed were dated in the early years of radiometry, when techniques were less accurate than recent methods. Quaternary sites discussed in Woolfenden 1996, by contrast, are almost all radiometrically dated. With the increased availability of accurate radiometric dating, discussion about stratigraphic definitions of boundaries, once a topic of intense debate, has subsided.

I have included radiometric dates in this report where available. I do not defend a strict view of the dates for boundaries of epochs or eras, instead accepting that they are guidelines for orientation in the past. For convention, I adopt the Mesozoic:Cenozoic boundary at 65 Ma (Odin 1982), the beginning of the Northern Hemisphere ice ages for the Tertiary:Quaternary boundary at 2.5 Ma (Shackleton and Opdyke 1977; references in Thompson 1991), and combined North American floristic and land-mammal stages for the Tertiary epochs (table 5.1) (Odin and Curry 1985; Swisher and Prothero 1990; Wolfe 1981; Wood et al. 1941; Woodburne 1987). Workers in the field, including several reviewers of this chapter in manuscript, propose alternative dates for time periods. This underscores the fact that boundaries depend on which factors are considered significant in the history of the earth. I do not include here a review of alternative dating for the epochs of western North America.

Biases in Historical Interpretation

Misinterpretations of vegetation history occur due to inherent biases in the fossil record, errors in understanding the record, and cumulative errors due to subsequent analysis. Each of these is discussed in turn.

Biases in the Fossil Record

The single most frustrating reality about reconstructing past events is that there are gaps in the fossil record. These occur due to limited exposures in time and space of fossil-bearing rocks and sediments of successively older ages. For the Sierra Nevada, exposure of Tertiary rocks is uneven. No fossil-bearing deposits of the earliest Tertiary (Paleocene) are known; Eocene and Oligocene fossil floras are limited in extent and are present mostly in the northern Sierra; Miocene and Pliocene records are somewhat more numerous. Even for the middle to late Tertiary, however, much better representation occurs in adjacent western and central Nevada. Fortunately, these floras contain many species that later appear in the Sierra Nevada and thus provide important material from the perspective of the Sierra Nevada.

Tertiary records in western North America are primarily impression macrofossils, that is, imprints left when leaves, twigs, or fruits (macro-organs) were deposited in wetland sediments (lake bottoms, bogs, marine environments, or other wetlands). Occasionally, petrified organs and tissues are found. In these, chemical replacement of living tissues has occurred, leaving a nearly identical replica of the internal and external anatomy of the organ or tissue (usually wood or cones). From a regional perspective, macrofossil deposits bias the sampling in that they overrepresent wetland species (willows [Salix], cottonwoods [Populus], etc.) that are adjacent to depositional sites and underrepresent upland species. Sampling is assumed to be limited to plants growing about 1 km (0.62 mi) from the site of deposition (Gregory 1994). Beyond this distance, smaller leaves are preferentially preserved over large leaves, as are thick, tough leaves over fragile ones. By and large, conifer remains are readily preserved if they get into a deposit. Their usual ecological position in the uplands, however, may limit their representation in the deposit. For all these reasons, the number of specimens of a single type occurring in a fossil deposit is usually not correlated with its abundance in the environment, and many contemporaneous species may be left out of the deposit altogether. Several other biases due to preservation of individual macrofossil specimens, referred to collectively as taphonomic bias, distort the sampling and recovery of species from macrofossil deposits (Greenwood 1992; Spicer 1989; Wolfe and Upchurch 1986).

Macrofossils also occur in the arid parts of the Sierra Nevada region in wood rat middens (Betancourt et al. 1990). These do not date to the Tertiary and are not considered here.

The other important plant remains from the Tertiary are pollen grains and other microfossils. Wind- and waterborne pollen is preserved in wetland sediments of lakes and bogs. Pollen in these sediments is usually recovered from long cores bored through lake sediments. Sampling like this has a significant advantage over macrofossil deposits in that a continuous stratigraphic record through time may be obtained, with much better control on species mixes, stratigraphic orientation, and changes over time than lakeside macrofossil deposits can offer. Pollen samples infrequently have been taken from solid exposed sediments rather than from a core, a technique that eliminates or reduces the opportunity to analyze a continuous record.

Pollen sampling is a common method for Quaternary analysis, but only recently has it been applied to Tertiary sediments. The Tulelake core (Adam et al. 1990; Adam et al. 1989) is the only published continuous core for the Sierra Nevada region that extends into the Tertiary, although other deep cores are currently under analysis. Most notable is the Owens Lake study, which provides continuous analysis of a sediment core into the early Pleistocene (Owens Lake Core Study Team 1995).

Pollen floras suffer different kinds of systematic biases from those of macrofossil deposits. Species with abundant and wind-borne pollen grains are disproportionately represented. Of these, there is a bias related to distance, in that pollen travels different distances depending on species. For example, because of its size and shape, 95% of giant sequoia (Sequoiadendron giganteum) pollen falls within 500 m (1,500 ft) of a native forest source (Anderson 1990), whereas pine (Pinus) pollen can travel hundreds of kilometers and still be an abundant type in a pollen sample. Biases due to size of the depositional basin also occur. Pollen grains of different species degrade with time, and differential preservation is especially important in old samples, such as Tertiary pollen cores. For several of these reasons, pine, fir, and spruce may dominate the pollen record in numbers disproportionate to their representation in the original flora. Methods to calibrate these biases are routinely applied (Overpeck 1985; Prentice 1985).

Other kinds of microfossils are often identified along with pollen in Quaternary samples. These include diatoms, chrysophyte cysts and scales, radiolarians, coccoliths, ostracods, and occasionally foraminifera (in saltwater basins). Charcoal and some macrofossils (leaf tissue) may also be included in lake sediment cores. Charcoal can provide information about fire occurrence.

Biases in Reading the Record

Analysis of any fossil flora hinges critically on accurate systematic interpretation of specimens. Opportunities for misidentifying macrofossils are abundant, because of poor preservation (e.g., only part of a leaf or cone was imprinted or intact), changes in size, shape, or structure due to preservation, distant relationship to modern taxa (there is no living analog), hybridization, and natural variation in the species. Because so much interpretation depends on correct identification, old fossil floras have been reviewed and their systematics revised; these revisions have sometimes been as dramatic as assigning a specimen to a different kingdom from that in the original publication. Individual paleobotanists vary in their willingness to make identifications, with some assigning specimens confidently to species and others listing only family or genus. Methods have been developed to assess physiognomy of fossil remains independent of taxonomic identification (described below), thus circumventing the dependence on correct systematic identification for some kinds of analysis.

Microfossils also may be misidentified, but the risk is lower in part due to the lack of diagnostic characters for identifying pollen to lower taxonomic levels and the reduced temptation to try. Thus, pollen is often identified only to genus, sometimes even to a combined family level (e.g., TCT, *Taxodiaceae-Cupressaceae-Taxaceae*). The lack of species diagnostics limits the usefulness of pollen analysis in studies that require knowledge of individual species.

Some fossil floras have been independently analyzed for macrofossils and for pollen. These provide the opportunity to compare information from the two data sets and assess the relative effectiveness of one or the other method. The Chalk Bluffs fossil flora near Nevada City (figure 5.1; table 5.2; appendix 5.1, list 3), originally described by an extensive macrofossil list (MacGinitie 1941), was reevaluated for pollen taxa by Leopold (1983, 1984). This analysis revealed the biases of both approaches. Pollen did not diagnose individual species and was unable to record taxa from four families found in macrofossils, yet it added taxa from eight families not recorded in the macrofossils. The additional taxa were mostly wind-pollinated species. Despite the differences in representation of individual taxa, the vegetation and climatic interpretation of the flora was similar between the two methods, that is, that this assemblage was a rich subtropical forest in a warm, moist climate. A significant addition from the pollen was the presence of taxa from the pine family (pine [Pinus], fir [Abies], spruce [Picea]), with implications discussed later. Other comparisons of Tertiary pollen and macrofossil floras have yielded greater discrepancies (e.g., only 38% correlation of taxa among methods for a Washington flora [Reiswig 1983], 18% correlation for a northwestern California flora [Barnett 1983]).

TABLE 5.2

Paleogene fossil floras of the Sierra Nevada and surrounding regions, listed in approximate order of age (young to old).

Flora Name	Location	Present Elevation	Latitude and Longitude	Age	Ma	Number of Species	Reference
La Porte	La Porte, CA	1,200 m 3,900 ft	39°42' N 120°W	Early Oligocene	33[a]	41	Potbury 1935
Susanville Complex	Susanville, CA	1,500 m 4,875 ft	40°30' N 120°40' W	Middle Eocene		22[b]	Knowlton 1911; Wolfe and Hopkins 1967
Chalk Bluffs	Colfax, CA	1,000 m 3,250 ft	120°52' N 39°15' W	Early Eocene		71	MacGinitie 1941; Leopold 1983

[a] Age is radiometrically confirmed.
[b] The number of species is questionable.

Biases in Analysis

A floral list, either macrofossil or microfossil, provides the raw data for subsequent analysis. For Tertiary floras, the main analysis has been to infer paleoclimates, paleoaltitudes, and ecological relationships of vegetation assemblages. These analyses have sometimes been quite specific, attempting to define mean annual temperatures, ranges of temperatures, effective temperatures, and annual precipitation at the fossil sites, as well as elevations above sea level. There are two general approaches to environmental analysis of fossil floras: those that rely on floristic comparison (analog approach), and those that rely on morphological relationships with environment (physiognomy approach).

Floristic analysis (Axelrod 1966, 1968; Axelrod and Bailey 1969) attempts to describe Tertiary conditions (plant communities and their ecological relationships) on the basis of taxonomic composition. The approach is basically qualitative and intuitive, and it involves comparing modern species to fossil species. Modern relatives are assigned corresponding to species in the fossil deposit, and known ecological requirements of modern species are used to build a composite description of past conditions. This approach requires both high accuracy in species identification and trust in the concept of uniformitarianism—the assumption that modern species do not differ in ecological response and requirements from their fossil representatives and thus provide reliable and relatively precise indicators of paleoenvironments.

Although analogs and uniformitarian models are common in paleontology and are routinely applied in Quaternary analysis, they have been criticized for reconstruction of older environments (e.g., Bryson 1985; MacGinitie 1962; Wolfe 1971; Wolfe and Hopkins 1967). The primary bases for criticism are: (1) These models depend on accurate taxonomic identification to species level, which is doubtful for the Tertiary; (2) the potential evolutionary change within species lineages renders comparisons of ecological relationships between current and fossil groups invalid; (3) the models confuse “vegetation” with “taxon,” assuming that a vegetation assemblage has a characteristic response to an environment, whereas, in fact, individual taxa respond; (4) some environmental situations have no analog, because current climates and ecological conditions do not represent the full range of those that existed in the past; and (5) the reproducibility of results by other workers has been low.

An alternative approach based on the observation that leaf morphology varies with climate has proved useful for interpreting fossil floras that have many angiosperm taxa. This approach takes advantage of empirical relationships between leaf physiognomy and climate, notably the positive correlation of the percentage of species with entire-margined leaves in an assemblage with the mean annual temperature and equability of vegetation type (tropical rain forest, subtropical forest, deciduous oak forest, etc.). This measure has been applied to fossil assemblages since the early twentieth century (Bailey and Sinnott 1916) and has been developed more fully for Tertiary interpretations by Wolfe and his colleagues (Wolfe 1971; Wolfe and Hopkins 1967). The significance of this approach is that climatic interpretations are independent of species identifications, known empirical relationships are used, quantitative values are derived, and results are reproducible. From climate information, inferences about paleoelevations have also been made.

Univariate leaf-margin analysis is not adequate to represent fossil floras fully (Axelrod and Bailey 1969; Wolfe 1971), and other characters have been used to supplement interpretations. Recently, Wolfe (1993) developed multivariate approaches that take advantage of combined data sets to estimate temperatures and elevations of Tertiary fossil environments. These methods were applied to a critical reevaluation of the Florissant flora in Colorado, a well-known Tertiary deposit (Gregory 1994). The reevaluation indicated that climatic estimates based on multivariate approaches yield quite different values than both floristic comparisons and univariate leaf physiognomy methods (Gregory 1994).

Results at Florissant with the multivariate methods suggest that climatic interpretation of the Sierran Tertiary floras may need significant revision. For this reason, in this report I do not summarize the detailed climatic interpretations of earlier literature. Further, since the Sierra Nevada has been dominated by conifer vegetation types, which are not amenable to the leaf physiognomy methods in general, we need to take a broader view of climate implications of the deposits. The approach here is to indicate generally the ecological conditions and elevations suggested by the fossil species in the assemblages and to encourage revision of interpretations for older floras.

TERTIARY HISTORY OF THE SIERRA NEVADA

Although the Tertiary was the time of origin for modern California vegetation, this is not to say that the taxa that are distinctively Sierran originated during this period or in California (Millar and Kinloch 1991). Many lineages did undergo significant evolution in California during this period. Many taxa that are today Sierran were in other parts of North America during the early Tertiary and often occurred in assemblages with no modern analogs. Rather, the primary significances of the Tertiary were the changes in distributions of many taxa and the major environmental changes (climate and mountain building) that catalyzed these changes. The environmental changes and the resulting plant responses led to almost complete replacement of vegetation types in the Sierra Nevada and to restructuring of species mixes, geographic distribution, and elevational zones of vegetation types.

Although early work stressed the cohesiveness of vegetation assemblages (e.g., geofloras [Axelrod 1958]), biologists now almost universally accept that taxa respond individualistically to environments (Botkin 1990; Frankel and Soule 1981; Grumbine 1994; Hansen et al. 1991; Kaufman 1993). Vegetation assemblages are transient collections of taxa unified by a common environment and the intersection of biogeographic histories. This is not to say that taxa do not influence each other in space and time; ecosystem science focuses on just these interactions. At historical scales, however, migratory movements and population colonizations and extirpations are primarily related to the behavior of individual taxa.

The many plant species and complex vegetation assemblages in the Sierra Nevada are significant components of biodiversity in the region (Davis and Stoms 1996; Shevock 1996). From the historical perspective, these species and assemblages can be viewed as relicts of earlier periods and prior environmental events, with contributions from different parts of North America, exhibiting evolutionary responses to an increasing aridity and seasonality that began in the mid-Tertiary. The following sections summarize major events in the Sierra Nevada through the epochs of the Tertiary. Vegetation dynamics are inferred from Tertiary deposits in the Sierra Nevada and adjacent regions of Nevada (figure 5.1; tables 5.2–5.4). Systematic compositions of these fossil floras (using unrevised nomenclatures) are given in appendix 5.1, lists 1–34 (in alphabetical order by flora name).

Paleocene and Eocene

During the earliest Tertiary, the region of the present Sierra Nevada was mostly low plains to low hills, dominated by old marine sediments. In the north, the region was a low plain with a river 5 km (3 mi) wide crossing near the area of Susanville today. Southward, the region consisted of low, rolling hills, with smaller rivers draining across most of the present Sierran axis (Armentrout et al. 1979). In the region of Mount Whitney, the land rose to its highest altitude, which was still quite low compared to current Sierran elevations. The western edge of the Sierra Nevada formed the Eocene Pacific Ocean coastline for all but the northern portion (figure 5.2) (Axelrod 1968; Minckley et al. 1986).

Interior to the Sierra Nevada was a large upland region that stretched throughout the northern Great Basin and intermountain areas of Idaho, western Wyoming, and western Colorado (Axelrod 1968; Ruddiman and Kutzbach 1989; Wolfe 1987). This was the only important upland region of western North America, extending to elevations over 1,225 m (4,000 ft) (Axelrod 1968) or, by Gregory's recent interpretation (1994), to 2,500 m (8,000 ft) in Colorado. This high plateau was dominated by volcanic centers and large lakes, and many of the fossil floras in the region are contained in calderas and depositional basins. This upland was unusual not only for western North America but also for temperate latitudes worldwide. As such it was an important relictual area for temperate montane taxa and a source of taxa to the Sierra Nevada in later epochs (references in Millar 1993).

Climates for the Sierra Nevada during the Paleocene and Eocene, as inferred from several sources, were different from current climates and from those in epochs before the Tertiary. Although warm-equable climates had typified the late Mesozoic (McGowran 1990; Parrish 1987; Wolfe and Upchurch 1986), temperate latitudes of the early Tertiary experienced unusually high temperatures (figure 5.3) and rainfall (references in Wolfe 1990). The trends toward increasing humidity started in the early Paleocene and continued into the Eocene, reaching maximums by the early Eocene (Savin 1977; Wolfe 1985). Major fluctuations in temperature (greater in magnitude than those of the Pleistocene) characterized the Eocene (figure 5.3), causing conditions in California to alternate between tropical and subtropical (references in Millar 1993). Truly temperate conditions (seasonally cool and dry) did not exist in California except perhaps in a few limited upland areas, and no true deserts or arid areas are known to have existed at this time in the region of the Sierra Nevada (Axelrod 1979). Except in the uplands of the northern Great Basin and Idaho, humid subtropical conditions existed in a broad zone throughout temperate latitudes in North America (Millar 1993; Wolfe 1978) throughout the early Tertiary.

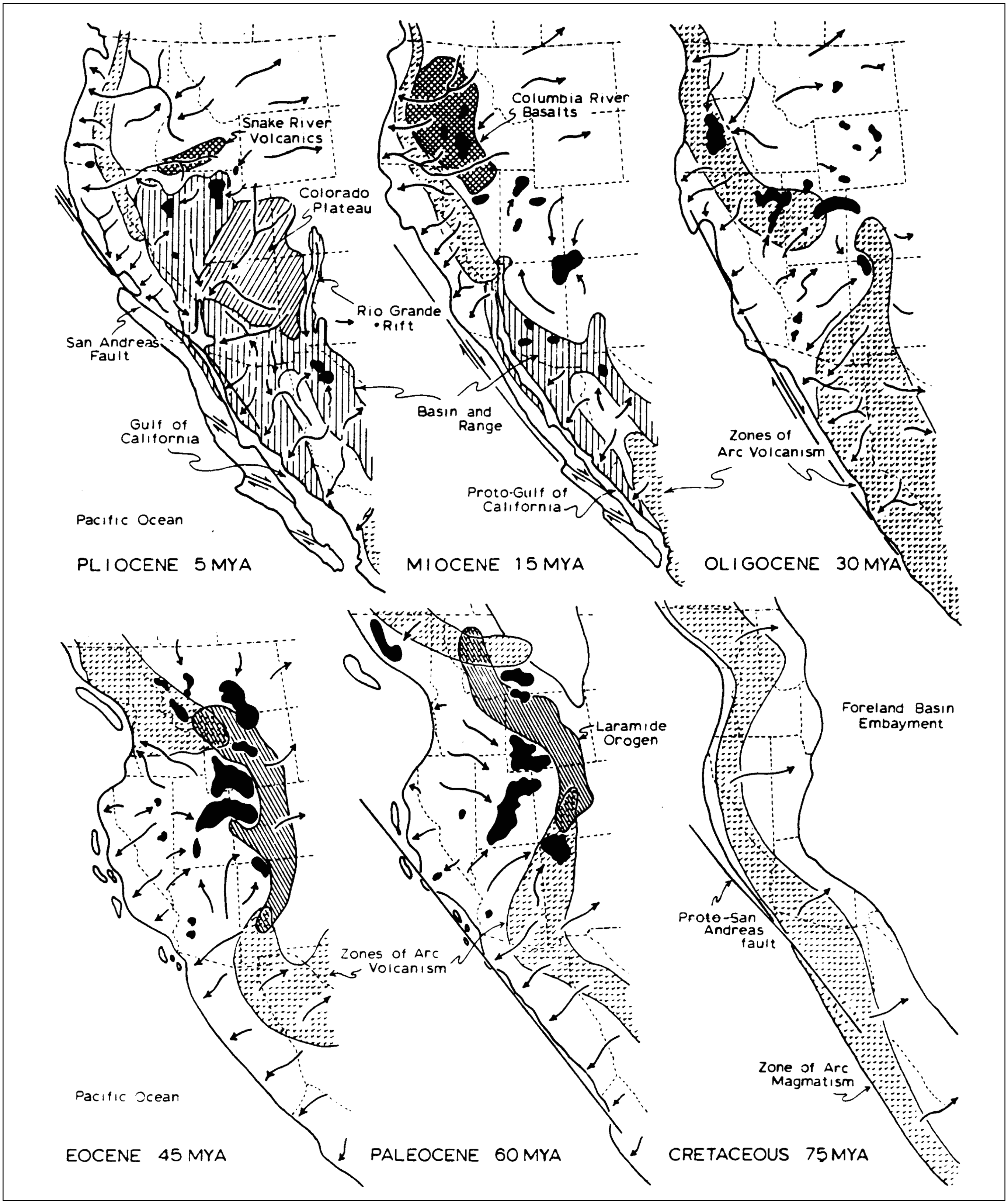


FIGURE 5.2

Tertiary coastline of western North America (from Minckley et al. 1986).

In general, the vegetation of California (like vegetation throughout most of temperate North America) reflected the tropical/subtropical climates of the early Tertiary. Starting in the earliest Paleocene, diverse tropical angiosperm species appeared with increasing representation throughout the warm-humid intervals of the Paleocene and Eocene. Subtropical assemblages are known to have expanded in temperate zones worldwide from this time, extending to 70° N latitude (Friis et al. 1987; Tiffney 1985; Wolfe 1985). Plant communities from Eocene locations were similar taxonomically and physiognomically to current rain forests of eastern Asia (e.g., Malaysia) and southern Mexico.

The Sierra Nevada has only two fossil floras from this period (table 5.2; figure 5.1). There are not many more terrestrial deposits for all of California, since most rocks of this age in California are marine sediments. These, along with the early Oligocene La Porte flora (table 5.2; appendix 5.1, list 14), occur in northern California and western central California, and they record rich, diverse, and—compared to modern California—exotic forests. Chalk Bluffs (appendix 5.1, list 3), near Colfax, California, records one of the richest Eocene floras of western North America, with seventy-one species, in families and with foliar adaptations that could only indicate humid subtropical conditions. Few taxa in the macrofossil record overlap species in the present Sierra Nevada. Rather, they contain species of viburnum (Viburnum), avocado (Persea), magnolia (Magnolia), fig (Ficus), and many others with warm-humid affinities. Similar subtropical taxa with warm-humid physiognomic adaptations (large leathery leaves, entire margins, drip points) occur in the smaller Susanville Complex flora (appendix 5.1, list 26) and the early Oligocene La Porte flora (appendix 5.1, list 14). The only gymnosperms, represented in very low diversity in the macrofossil record, were similarly warm-humid-adapted. They included a cycad (Zamia), and possibly a yew (Taxus) species.

The additional assessment of the Chalk Bluffs deposit for pollen added a floral component that was absent in the macrofossil record. In very small proportions, pine, spruce, and fir pollens were identified, suggesting that these species blew in from distant areas that remained habitable to conifers in the otherwise incompatible subtropical environments. Except for Chalk Bluffs, conifer taxa have not been recorded from any other Sierran sites of this age, and pines were recorded from only one other Eocene deposit in California (Axelrod and Raven 1985). Indeed, pines and possibly other conifers in general seem to have retreated to hospitable refugia during the early Tertiary. At the global level, these refugia were at very high and low latitudes and in the few upland regions that existed in temperate latitudes, such as the volcanic plateau of the Great Basin–Idaho uplift (Millar 1993). Limited

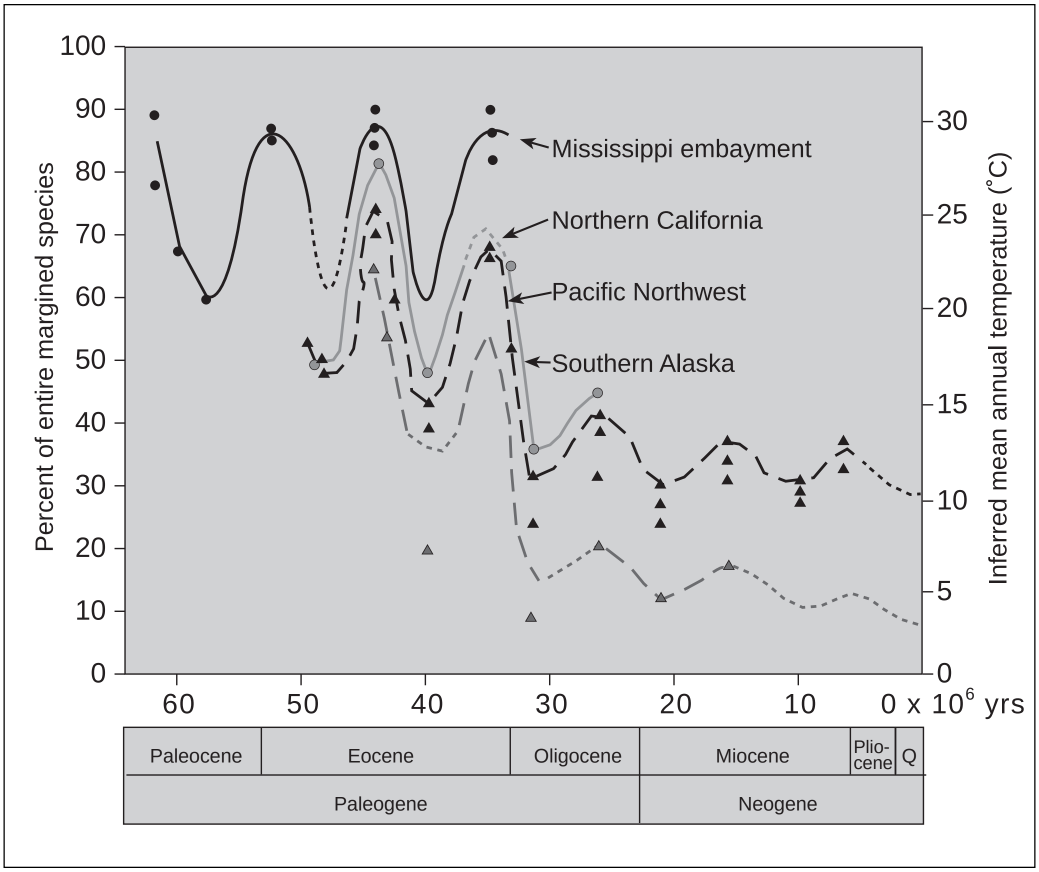


FIGURE 5.3

Tertiary paleotemperatures estimated from foliar physiognomy (from Wolfe 1978).

TABLE 5.3

Miocene fossil floras of the Sierra Nevada and surrounding regions, listed in approximate order of age (young to old).

Flora Name	Location	Present Elevation	Latitude and Longitude	Age	Ma	Number of Species	Reference
Alturas	Alturas, CA	1,350 m 4,390 ft	41°30' N 120°35' W	Late	8.1[a]	7	Axelrod 1944b
Remington Hill	Nevada City, CA	1,180 m 3,840 ft	39°17' N 120°45' W	Late	9.5	32	Condit 1944
Chalk Hills	Virginia City, NV	1,785 m 5,800 ft	39°23' N 119°33' W	Late		28	Axelrod 1962
Table Mountain	Columbia, CA	677 m 2,200 ft	38°02' N 120°23' W	Late		28	Condit 1944
Upper Cedarville Pit River	Canby, CA	1,350 m 4,390 ft	41°22' N 121°4' W	Late		21	LaMotte 1935, 1936
Forest	Sierra County, CA	1,500 m 4,875 ft	39°30' N 125°52' W	Late		9	Knowlton 1911; Chaney 1944
Mohawk	Plumas County, CA	1,500 m 4,875 ft	39°46' N 120°38' W	Middle		13	Knowlton 1911; Axelrod 1944b
Aldrich Station	Yerington, NV	?1,970 m ?6,400 ft	38°27' N 118°54' W	Middle	11[a]	35	Axelrod 1956
Fallon	Fallon, NV	1,200 m 3,900 ft	39°20' N 119°3' W	Middle	12.6	22	Axelrod 1956
Esmeralda[b]	Coaldale, NV	1,590 m 4,900 ft	38° N 117°46' W	Middle	12.7[a]		Axelrod 1940
Purple Mountain	Wadsworth, NV	1,275 m 4,140 ft	39°35' N 119°4' W	Middle	13	36	Axelrod 1976, 1995
Stewart Spring	Stewart Valley, NV	1,655 m 5,500 ft	38°36' N 117°59' W	Middle	13–14[a]	43	Wolfe 1964; Schorn 1984
Chloropagus	Hot Springs Mountains, NV	1,385 m 4,500 ft	39°42' N 118°57' W	Middle	13.9[a]	22	Axelrod 1956
Gillam Spring	Gillam Spring, NV		40°30' N 118°57' W	Middle	15	63	Axelrod and Schorn 1994
Middlegate	Clan Alpine Mountains, NV	1,415 m 4,600 ft	39°17' N 118°2' W	Middle	15.9[a]	43	Axelrod 1956, 1976, 1986
Upper Cedarville 49 Camp	49 Camp, NV	1,500 m 4,875 ft	41°36' N 119°55' W	Middle	16	43	LaMotte 1935, 1936; Chaney 1959
Fingerrock	Cedar Mountain, NV	1,754 m 5,700 ft	38°37' N 117°58' W	Middle	16.4	22	Wolfe 1964
Carson Pass[b]	Kirkwood, CA	2,550 m 8,290 ft	38°41' N 120° W	Middle			Axelrod 1977
Ebbetts Pass[b]	Markleeville, CA	2,660 m 8,645 ft	38°32' N 119°48' W	Middle			Axelrod 1977
Niagara[b]	Markleeville, CA	1,800 m 5,850 ft	38°40' N 119°48' W	Middle			Axelrod 1977
Tehachapi	Tehachapi, CA	1,538 m 5,000 ft	35°14' N 118°14' W	Middle	17.1[a]	70	Axelrod 1939; Chaney 1944
Valley Spring	Mokelumne, CA	215 m 700 ft	38°19' N 120°46' W	Middle	19.9[a]	17	Axelrod 1944b

[a] Age is radiometrically confirmed.
[b] The available literature does not give full species list information for the flora.

exposures of Eocene fossil-bearing rocks in the Great Basin–Idaho uplift area constrain our understanding of the distributions of these more temperate taxa (e.g., taxa adapted to seasonally cool and dry climates) in the regions that directly surround the Sierra Nevada.

Collectively, the limited plant record from the early Tertiary in the Sierra Nevada, together with other Eocene floras from western North America, gives a picture of warm-humid-adapted forests with high diversity, spread throughout the region of the Sierra Nevada. Many taxa represented in these floras currently occur in tropical rain forests of eastern Asia, and they are unable to tolerate frost, drought, or severe temperature fluctuations. Abrupt changes (rather than slow or no changes) in vegetation type occurred in the early Tertiary only near the edge of the major interior upland plateau, probably near the edge of the western Great Basin (Axelrod 1977). In this upland region, taxa existed that later appear in the Sierra Nevada and California mountains (Axelrod 1977).

Oligocene

The Oligocene remained a period of relative quiescence geologically for the Sierra Nevada, despite general uplift of the entire range, retreat of the coastline along the western margin of the Sierra, and local volcanic activity. Explosive volcanic activity and mountain building occurred, however, in the region of the Great Basin–Idaho uplands (McKee 1979; Stewart 1978).

The Oligocene was a time of major climatic transition in California and throughout temperate Northern Hemisphere latitudes. Climatic events that occurred during this epoch triggered the subsequent modernization of the Sierra Nevada forests. Although the dates, geographic extent, and causes remain questions of scientific interest and debate, little doubt exists that a major climatic change occurred near what is now considered the Eocene:Oligocene boundary, about 34 Ma (table 5.1) (references in McGowran 1990; Parrish 1987; Prothero 1994; Wolfe 1978). This climatic event, sometimes referred to as the terminal Eocene event (Wolfe 1978), was the most profound of the Tertiary. Inferred from many data sources, average temperatures in temperate latitudes at this time declined drastically (up to 13°C [23.4°F] in some areas over only one million years) (figure 5.3) and stayed low (although not as low, and with minor fluctuations) throughout the rest of the Tertiary.

Accompanying this radical temperature drop was a shift to drier, more seasonal climates and to wider annual temperature ranges. The average range of temperatures is estimated to have been over 25°C (45°F), twice the present range (Wolfe 1971). Continental ice sheets occurred for the first time in the Tertiary during the Oligocene (McGowran 1990), although no glaciers are known to have formed in the Sierra Nevada until the onset of the Pleistocene.

The terminal Eocene event was marked by widespread disappearances and extirpations of the Eocene subtropical and tropical floras from middle latitudes worldwide (Wolfe 1978). Complementary expansions of cool-adapted conifers and angiosperms are recorded in many deposits of this age. These conifers may in fact have been reoccupying sites in middle latitudes that they had dominated in the late Mesozoic but had been forced out of by the pervasive warm-humid conditions of the early Tertiary (e.g., for pines, Millar 1993).

The Sierra Nevada has only one fossil deposit from the Oligocene, the La Porte flora of northern California (figure 5.1; appendix 5.1, list 14), and this is early enough to have affinities to the periods discussed earlier. The Sierra Nevada record, therefore, does not have the temporal resolution to

TABLE 5.4

Pliocene fossil floras of the Sierra Nevada and surrounding regions, listed in approximate order of age (young to old).

Flora Name	Location	Present Elevation	Latitude and Longitude	Age	Ma	Number of Species	Reference
Lake Tahoe pollen	Tahoe City, CA	1,900 m 6,175 ft	39°10' N 120°9' W	Late	1.9[a,b]		Adam 1973
Tulelake pollen	Tulelake, CA	1,240 m 4,030 ft	42° N 121°30' W	Late	3–2[a]		Adam et al. 1990; Adam et al. 1989
Crowley Point (Coso) pollen	Inyo Mountains, CA	1,180 m 3,840 ft	36°21' N 117°33' W	Late		25	Axelrod and Ting 1960
Darwin Summit (Coso) pollen	Inyo Mountains, CA	1,600 m 5,200 ft	36°17' N 117°42' W	Late		13	Axelrod and Ting 1960
Haiwee (Coso) pollen	Coso Mountains, CA	1,355 m 4,400 ft	36°14' N 117°56' W	Late	2.2[a]	37	Axelrod and Ting 1960
Owens Gorge (Coso) pollen	Bishop, CA	2,000 m 6,500 ft	37°33' N 118°37' W	Late	3.2[a]	30	Axelrod and Ting 1960
Panamint Springs (Coso) pollen	Inyo Mountains, CA	600 m 1,950 ft	36°18' N 117°26' W	Late		18	Axelrod and Ting 1960
San Joaquin Mountain (Coso) pollen	Mammoth Lakes, CA	2,954–3,052 m 9,600–9,920 ft	37°45' N 119°7' W	Late		23	Axelrod and Ting 1960
Nova pollen	Panamint Mountains, CA	800 m 2,600 ft	36°17' N 117°19' W	Late		22	Axelrod and Ting 1960
Wichman pollen	Wichman, NV	1,600 m 5,400 ft	38°42' N 119°4' W	Late		14	Axelrod and Ting 1960
Verdi	Verdi, NV	1,477 m 4,800 ft	39°31' N 119°58' W	Early	5.7[a]	19	Axelrod 1958
Oakdale	Oakdale, CA	77 m 250 ft	37°47' N 120°42' W	Early	6	16	Axelrod 1944a
Mount Reba[c]	Bear Valley, CA	2,615 m 8,600 ft	38°31' N 120°1' W	Early	7	>6	Axelrod 1976, 1977

[a] Age is radiometrically confirmed.
[b] This is a minimum age; the radiometric date is for the lava flow that overlies the pollen deposit.
[c] The available literature does not give full species list information for the flora.

trace at a fine scale the major transitional events indicated earlier. Because of this, the exact timing of climate change and vegetation response in the early mid-Tertiary cannot be determined for the Sierra Nevada.

Miocene and Pliocene

The Miocene and Pliocene epochs span the last half of the Tertiary, or about 23 million years. Fossil records are relatively abundant throughout this period, climate and mountain building are complex, and floristic relationships are significant to an understanding of modern vegetation patterns. We summarize these epochs together for this report, since no major transitions mark the Miocene:Pliocene boundary.

Uplift and mountain building of the Sierra Nevada accelerated during the Miocene, as evidenced by an increase in block faulting during this time. The range was not yet a moisture barrier to westerlies carrying ocean-laden air. The ocean that extended into the present Central Valley of California was reduced to a large inland sea bay, connected in several places to the ocean (figure 5.2). Its eastern shoreline extended along the middle third of the present Sierran axis (Axelrod 1968). By the mid-Miocene (16–18 Ma), Columbia River basalt was flowing, creating ample opportunities for fossil preservation in the still-high Great Basin–Idaho upland. Uplift of this region continued, estimated at another 920 m (3,000 ft), with higher regions in the south (Nevada) and lower in the north. Many fresh water lakes were formed during this uplift, which also proved important for fossil deposition.

Block-fault uplift of the Sierra Nevada continued through the Pliocene, with scattered volcanic activity along the eastern and, to a lesser extent, western margins. Huber (1981) estimated that, by the late Pliocene (3 Ma), the height of the central Sierra Nevada was about 2,100 m (6,825 ft). Much of the uplift of the Sierra Nevada apparently occurred after 1.9 Ma (Winograd et al. 1985), and the ranges were much less effective barriers to wet air masses from the west prior to that time. Formation of the major southeastern valleys (the Owens and Searles Valleys) may have been tied to the onset of mafic volcanism and basin-range faulting between 3 and 4 Ma (Duffield et al. 1980).

Following the major change in the climates of western North America (and elsewhere) during the Eocene-Oligocene transition, climates never again turned warm-humid and tropical in temperate western North America. There were, however, significant changes from the conditions of the Oligocene, and fluctuations in climate occurred throughout the rest of the Tertiary. From the cool-cold, strongly seasonal conditions inferred for Sierra-like regions of western North America during the Oligocene, average temperatures increased in the early Miocene, and rainfall decreased. This early Miocene warming was followed by a cooling and drying trend and increasing provincialization, which continued (with fluctuations) through the middle and late Miocene (Raven and Axelrod 1978). The late Miocene seems to have been cooler than the middle, with evidence for dry summer climates beginning in Nevada by the late Miocene (Wolfe 1969). This is the first evidence for the Mediterranean climates and arid climates of the Sierra Nevada; prior to this, rainfall seems to have occurred year-round (Axelrod 1973, 1979; Raven and Axelrod 1978). Nevertheless, certain parts of the Sierra Nevada (e.g., near Lake Tahoe [Adam 1973]) seem to have retained more summer rain than at present until at least 1.9 Ma.

Although no major climatic, geologic, or floristic transitions mark the beginning of the Pliocene, this epoch was a period of decreased average rainfall and gradual decline in temperatures. The drying was related mostly to a change in the seasonality of precipitation, with summer drought increasing in length and severity. The full Mediterranean pattern typical of California and most of the Sierra Nevada developed only in the late Pliocene. The climate patterns may be related to increases in high-pressure areas, decreases in global temperatures, glaciation at high latitudes—all conditions during the later Pliocene that signaled the development of Pleistocene climate patterns. The middle of the Pliocene may have been the driest part of the Tertiary in California (Raven and Axelrod 1978), although some sites in the western interior of North America show evidence of greater levels of effective moisture than in modern times (Thompson 1991). Clearly there were significant fluctuations in climate during this period (e.g., Adam et al. 1990; Adam et al. 1989). By the end of the Pliocene, climates were distinctly cooler and wetter throughout the Sierra Nevada, with the estimated increase in rainfall 25–40 cm (10–15 in) above that of the mid-Pliocene (Axelrod 1977).

From the standpoint of scientific method, the Pliocene is a period that overlaps the focuses of Tertiary botany and Quaternary science, since deep pollen cores (previously restricted to the Quaternary) are increasingly penetrating Pliocene (and even Miocene) sediments. Since the methods and questions of the disciplines have differed somewhat, the Pliocene becomes rich with information from both scientific communities. When interpreting reports from the two disciplines, it is important to note that events may be described at different temporal, spatial, and conceptual scales. Quaternary scientists who investigate Tertiary phenomena focus especially on high frequency events (e.g., those with periods of 1,000 years or less) (Delcourt and Delcourt 1991, hierarchical models of time and space). Quaternary science methods are capable of looking at temporally continuous floristics and fine resolution in the temporal scale of climate; they have a strong focus on external forcing factors for detailed climate reconstruction. Quaternary scientists, however, continue to rely heavily on uniformitarian assumptions about species ecology, making the (probably valid) assumption that evolutionary change was not significant during the Holocene or even late Pleistocene. For the Pliocene, this assumption may be inappropriate, and floristic comparisons based on response-surface analyses may not be well calibrated to successively older taxa.

Analysis of continuous records of microfossils (pollen and diatoms) in parts of California make the dating of climate events and high-frequency fluctuations more precise. An example from northeastern California, on the Modoc Plateau, is the Tulelake core, with continuous records into the late Pliocene (figure 5.1; table 5.2; appendix 5.1, list 29) (Adam et al. 1990; Adam et al. 1989). During the period from 3.0 Ma to 2.12 Ma, fluctuations in the Sierra Nevada climate are recorded from the Tulelake core. From 3.0 to 2.9 Ma, the climate was cool, whereas from 2.9 to 2.6 Ma, warmer conditions prevailed (as much as 5°C [9°F] higher than current conditions). Evidence for severe summer drought also exists. From 2.48 to 2.12 Ma, the Tulelake basin dried, and floristic compositions (e.g., sagebrush [Artemesia]) increased, probably reflecting colder conditions as well. A shift to cool, moist conditions around 2.0 Ma is inferred from diatoms.

Vegetation dynamics of the Miocene and Pliocene of the Sierra Nevada and adjacent regions are complex. Although this undoubtedly reflects the major environmental transitions of the time, it is probably also an artifact of the better records from younger ages. I discuss in turn the Miocene-Pliocene vegetation history under three more-or-less-chronological themes:

1. Early extinctions and vegetation replacements resulting from the Eocene:Oligocene climatic event,
2. High diversity through the middle to late Miocene correlated with summer rain, and
3. Migrations, species turnovers, increasing provincialization, zonation, and late Miocene extinctions due to decreasing summer rainfall through the Miocene-Pliocene.

Early Extinctions and Replacements

Since the Oligocene is poorly recorded in the Sierra Nevada, the response of vegetation to the major climatic transitions of the Eocene:Oligocene can be read only from the later record. Many Tertiary records from the mid-Miocene in the Sierra Nevada and western Nevada show enormous turnovers in vegetation relative to earlier (Eocene) deposits (compare table 5.2 and appendix 5.1, lists 3 and 26 to table 5.3 and appendix 5.1, lists 1, 5, 8, 9, 11, 15, 16, 22, 25, 28, 30, 32). The most dramatic changes are the loss of warm-humid-adapted angiosperms and the appearance of cool-temperate-adapted conifers and angiosperms (Axelrod 1977, 1986; Axelrod and Schorn 1994; Raven and Axelrod 1978; Schorn 1984; Wolfe 1969). Almost all of the key subtropical and tropical taxa (e.g., Diospyros, Ficus, Engelhardtia, Magnolia, Viburnum, Cinnamomum, Persea) that are known from Sierran and other western North American Eocene floras are missing from the fossil deposits of the mid-Tertiary. In both floristics and foliar physiognomy (percentage of entire-margined leaves), the adaptations changed from tropical to temperate (Wolfe 1969). In general, the losses of taxa from the Sierra Nevada represent major regional and even continental extirpations: many taxa (or their nearest relatives) that occurred in California during the Eocene are found now in tropical Mexico and others only in eastern Asia (Axelrod 1977; Raven and Axelrod 1978).

Replacing these subtropical taxa, by the mid-Miocene, were abundant conifer species of the Pinaceae (Pinus, Abies, Picea), Cupressaceae (Chamaecyparis, Thuja, Juniperus), and Taxodiaceae (Sequoiadendron, Sequoia) and angiosperm species such as Alnus, Fraxinus, Populus, Salix, Arbutus, Quercus, and Ceanothus (e.g., appendix 5.1, lists 1, 5, 8, 9, 11, 15, 22). In addition to taxa currently native to the Sierra Nevada, these Miocene forests contained temperate-adapted taxa now native to other parts of North America. These included conifers and angiosperms currently native to non-Sierran provinces of California (e.g., Chamaecyparis, Sequoia, Picea, Thuja, coastal species of Quercus), as well as species that now grow in eastern North America (e.g., Carya, Ulmus, Juglans, Liquidambar).

Many of these temperate-adapted taxa appear to have been present during the early Tertiary on the volcanic plateau of the Great Basin–Idaho uplift, which seems to have served as a refugial island during the warm, humid phases of the early Tertiary (Axelrod 1968, 1986; Axelrod and Raven 1985; Millar 1993; Millar and Kinloch 1991). These taxa would have been closely adjacent to the Sierra Nevada, capable of migrating westward relatively rapidly into the range as Oligocene and early Miocene climates opened hospitable habitats in the Sierra Nevada (Axelrod 1977). Prior to basin and range extension, these two regions were closer together than at present (Fiero 1991).

High Diversity of Miocene Floras

One consequence of these biogeographical changes was that, although temperate taxa replaced tropical ones in the Sierra Nevada by the mid-Miocene, diversity of the new flora was high, apparently much higher even than at present in the Sierra Nevada. Not only was the total diversity of species high (many currently native species plus taxa not now in the Sierra), but also the vegetation associations were highly diverse and different from those of the present. For instance, in the Purple Mountain flora of western central Nevada (mid-Miocene) (appendix 5.1, list 22), the following species occurred together in one deposit: false cypress (Chamaecyparis), red and white firs (Abies cf. magnifica and A. cf. concolor), Santa Lucia fir (A. cf. bracteata), western white pine (Pinus cf. monticola), Brewer's spruce (Picea cf. breweriana), giant sequoia (Sequoiadendron cf. giganteum), madrone (Arbutus), live oak (Quercus cf. chrysolepis), cottonwood (Populus), and willow (Salix) (Axelrod 1976). At the Upper Cedarville locality of northwestern Nevada (mid-Miocene) (appendix 5.1, list 30), false cypress, Ginkgo, redwood (Sequoia cf. sempervirens), red fir, ponderosa pine (Pinus cf. ponderosa), nutmeg (Torreya), madrone, chestnut (Castanea), beech (Fagus), hickory (Carya), ash (Fraxinus), Tilia, and elm (Ulmus) grew together (LaMotte 1936). The Chalk Hills forest of western central Nevada (late Miocene) (appendix 5.1, list 4) contained false cypress, white fir, foxtail pine (Pinus cf. balfouriana), Douglas fir (Pseudotsuga cf. menziesii), giant sequoia, madrone, Rhododendron, hickory, and oak (Quercus) (Axelrod 1962).

By modern standards these and most other Sierran middle to late Miocene floras strike us as unusual in that they contain mixes of "incompatible" species. For instance, the cooccurrence of foxtail pine (subalpine), Port Orford cedar (warm-humid), giant sequoia (middle elevation, mixed conifer, fire-adapted), rhododendron (cool-mesic), hickory (continental, well-distributed rainfall), and scrub live oak (xeric) challenges our ability to imagine the Tertiary habitat. Although biases in the fossil record (such as single floras appearing contemporaneous from the stratigraphy but actually representing many years of accumulation) may skew interpretations, these diverse vegetation assemblages recur commonly enough to indicate that the associations were actually this diverse and ecologically complex by modern standards.

An explanation for the high species and association diversities is that, although climates of the Sierra Nevada and western Nevada were temperate by the Miocene, rainfall remained distributed throughout the year (Axelrod 1977; Axelrod and Schorn 1994; Wolfe 1969). A common requirement, or tolerance, of the species in these assemblages is summer rainfall. From several lines of evidence, summer rainfall appears to have persisted late into the Miocene, although the trend was toward decreasing summer rain during this period. Summer rainfall would offer permissive conditions for subtropical taxa that were remnants of the early Tertiary (e.g., Ginkgo at Upper Cedarville [appendix 5.1, list 30]; Viburnum and Persea at Tehachapi [appendix 5.1, list 28]; Magnolia at Mohawk [appendix 5.1, list 16]) as well as temperate broad-leaved species not native to California now (hickory, beech, chestnut, honey locust [Robinia]) and temperate conifers and angiosperms that can tolerate these conditions. Temperate climate with summer rainfall thus contributed to the high diversity of Miocene floras.

Response to Decreasing Summer Rainfall and Warmer Summers

The main catalyst for vegetation change in the late Tertiary appears to have been the trend to decreasing summer rainfall, which culminated in the well-developed Mediterranean pattern of present-day California. Lack of distribution of rainfall throughout the year, especially when associated with high temperatures during the growing season, is extremely stressful to plants. It requires specific adaptations and is apparently intolerable to many taxa. One pattern that appears from this climate trend is increasing provincialization and zonation of assemblages. Although there are few early Tertiary deposits in the Sierra Nevada, their composition parallels the many Eocene fossil floras from throughout western North America. Notable about these floras, in addition to their general subtropical or tropical adaptations, is their low degree of regional or local differentiation (Wolfe 1969). In the Sierra Nevada, little evidence of provincial development exists by the mid-Miocene. By the late Miocene and the Pliocene, floras of western North America, including those in the Sierra Nevada, had become increasingly differentiated, by region, latitude, and elevation (Wolfe 1969). Cooler winters may also have contributed to differentiation.

Although mid-Miocene floras had remained highly diverse by virtue of adequate summer rain, decreasing summer precipitation in the later Miocene and the Pliocene narrowed the adaptive zones for these species, segregating them into habitats specific to the needs of individual taxa. Thus the "incompatible mixtures" of species from the mid-Miocene started to segregate into the "compatible mixtures" of modern associations, with the result that floras became more depauperate. Compared to modern standards, the mid-Miocene floras reflect more than earlier Miocene floras the locally specific conditions (e.g., elevation, orography, local climate) currently influencing species distributions and ecosystem dynamics in the Sierra Nevada.

Another consequence of increasing summer drought was migration or shifting distributions of species. The diverse forests of the mid-Miocene in Nevada, which contained taxa that are now found in subalpine, mixed conifer, and coastal environments, appear to have contributed taxa that moved west and found suitable habitats in the Sierra Nevada by the late Miocene and the Pliocene. For example, foxtail pine, present in several early and middle Miocene floras in Nevada but absent from California in the early Tertiary, appears to have migrated westward to the Sierra Nevada and western California. It remains a relict in only two regions in California that persist in having summer rain today: the southern Sierra Nevada and the Klamath Province (Axelrod 1977). As the conifer taxa moved west and up into the Sierra Nevada, the Nevada basins and ranges lost these "montane" conifers and were colonized by piñon/juniper species, which spread rapidly across this area in the early Pliocene. Increasing aridity eventually forced even these conifers to higher elevations, and sage/bitterbrush dominated the dry basins. The effect on Sierra Nevada floras is exemplified by the Mount Reba flora of the central Sierra Nevada. Situated now at 2,625 m (8,600 ft) but probably lower in the early Pliocene, the deposit contains live oak, tan oak (Lithocarpus cf. densiflora), Douglas fir, cypress (Cupressus), white fir, and giant sequoia (appendix 5.1, list 17) (Axelrod 1976). By the early Pliocene, these taxa were no longer present in western Nevada, although they had been in earlier Miocene floras. Presumably many of these species were extirpated in western Nevada and had migrated westward into the Sierra, where they found more suitable habitats.

Contributing also to the modernization of the Sierra Nevada forests was gradual extinction or extirpation of many species adapted to warm winters and summer rainfall. By the late Miocene and the Pliocene, subtropical/tropical and temperate hardwoods requiring summer rain were mostly gone (e.g., Chalk Hills [appendix 5.1, list 4]; Oakdale [appendix 5.1, list 19]; Verdi [appendix 5.1, list 33]), and warm-humid conifers (Port Orford cedar, redwood, Thuja) and other taxa that are now coastal (Brewer's spruce [Picea cf. breweriana], Santa Lucia fir [Abies cf. bracteata]) were declining in representation. Relicts from the early Tertiary persisted longer on the west side of the Sierra Nevada than on the east side (Raven and Axelrod 1978). On the west slope, a rich oak woodland was present in the early Pliocene (e.g., Oakdale flora [appendix 5.1, list 19]) that still contained summer-rain species, such as Celtis, Persea, Robinia, Sapindus, and Umbellularia, which were gone from the eastern Sierra by that time (Axelrod 1977). These extirpations left diversity lower than in the early to middle Miocene forests and left communities both more differentiated and more adapted to summer drought. In sum, vegetation diversity was lower by the late Tertiary in part due to elimination of species now allied with taxa in eastern North America and eastern Asia and in part due to segregation into climate zones elevationally and latitudinally in the Sierra Nevada.

These patterns over the late Miocene and the Pliocene are well documented in a set of continuous sediments at Gillam Spring, northwestern Nevada (Axelrod and Schorn 1994). A rapid change in species diversity and abundance centered around 15 Ma is recorded in three stratigraphically continuous localities (appendix 5.1, list 11; figure 5.4). The compositions of the florules shift from being dominated in the oldest stratum by deciduous hardwoods allied to taxa of the eastern United States and eastern Asia to being dominated in the youngest stratum by conifers and summer-drought-adapted mountain hardwoods.

The last phase of the Tertiary was marked by climates that by some indications were warmer than at present in the Sierra Nevada and possibly not as dry. Between 2 and 3 Ma in the Tulelake samples (Adam et al. 1990), pine and Taxodiaceae-Cupressaceae-Taxaceae (assumed to be incense cedar or juniper) dominate, whereas the modern vegetation is sagebrush shrub. Increasing summer drought eliminated most of the sclerophyllous vegetation from western Nevada and stratified Sierran conifers both elevationally and by slope (west or east side of the crest). That the Mediterranean climate pattern had not become as intensified in the earliest Pleistocene (1.9 Ma) as at present, however, is suggested by the lingering persistence of spruce near Lake Tahoe (appendix 5.1, list 13) (Adam 1973).

The general vegetation trends described for the second half of the Tertiary can be seen in the distributions for select individual taxa (figures 5.5–5.22). Many conifers now native to the Sierra Nevada had much broader Tertiary distributions, were not stratified into the vegetation groups we now recognize, and/or were present only in western Nevada during the Tertiary. This can be seen for several species currently in the upper montane and subalpine zones (red fir [figure 5.5]; bristlecone pine [Pinus cf. longaeva] [figure 5.6]; foxtail pine [Pinus cf. balfouriana] [figure 5.7]; western white pine [figure 5.8]; western hemlock [Tsuga cf. heterophylla] [figure 5.9]). It is also seen for conifers that currently occur in mixed conifer and primarily west-side Sierran forests (white fir [figure 5.10]; incense cedar [figure 5.11]; sugar pine [Pinus cf. lambertiana] [figure 5.12]; ponderosa [P. cf. ponderosa] and Jeffrey [P. cf. jeffreyi] pines [figures 5.13, 5.14]; Douglas fir [figure 5.15]; and giant sequoia [figure 5.16]). Many oaks similarly had broad distributions in the Sierra and western Nevada during the Miocene and Pliocene (black oak [Quercus cf. kelloggii] [figure 5.17]; white oak [Q. cf. lobata] [figure 5.18]).

Several species were broadly distributed in the middle Tertiary, eventually became extirpated from the Sierra Nevada, but now occur in coastal California habitats. These include false cypresses and Santa Lucia fir (figure 5.19), Brewer's spruce (figure 5.20), coast redwood (figure 5.21), and coast live oak (Quercus cf. chrysolepis) (figure 5.22). Blue oak (Q. douglasii) and scrub oak (Q. dumosa), both widespread now, occur in surprisingly few Tertiary deposits (figure 5.23).

The importance of taxonomic identification and revision to interpretation of biogeography and evolution can be demonstrated with two examples. Howard Schorn (letter to the author, July 1995) is revising many of the Tertiary floras from Nevada and the Sierra Nevada and provides the following information. As a generalization, the revision of taxonomy indicates no Pseudotsuga, Larix, or Thuja in the Nevada–Sierra Nevada area during the Tertiary. The many fossils that previously indicated the presence of Douglas fir (figure 5.15) are in fact now identified primarily to Abies and Tsuga, with none to Douglas fir. Thus, the biogeographic origins of Douglas fir must not parallel the history described above for many of the present-day Sierran conifers. Rather than originating on the upland plateau of Nevada, Douglas fir must have moved into the Sierra Nevada from another bioregion.

Similarly, Schorn's revisions (letter to the author, July 1995, and manuscript in preparation) indicate that, although abundant Abies is recorded in Tertiary deposits, no white fir (Abies concoloroides) is firmly identified from the Sierra Nevada or Nevada until the Pliocene about 6–8 Ma, and then only in the vicinity of Reno, Nevada. This contrasts with earlier descriptions (figure 5.10), which suggest white fir was widespread through this region during the Tertiary. Schorn identifies most of the white fir fossils as red fir (A. magnifica) instead. These revisions markedly change interpretations of the origins of these two taxa: white fir, like Douglas fir, apparently was not part of the upland Nevada mixed conifer forests and did not enter the Sierra Nevada from the east. Conversely, red fir was much more abundant and widespread throughout Nevada Tertiary forests than previously indicated (figure 5.5), and apparently did co-occur in the upland region as part of the diverse Miocene and Pliocene forests.

These examples underscore the importance of correct taxonomic identifications and the need for widespread revision of old fossil floras with new methods.

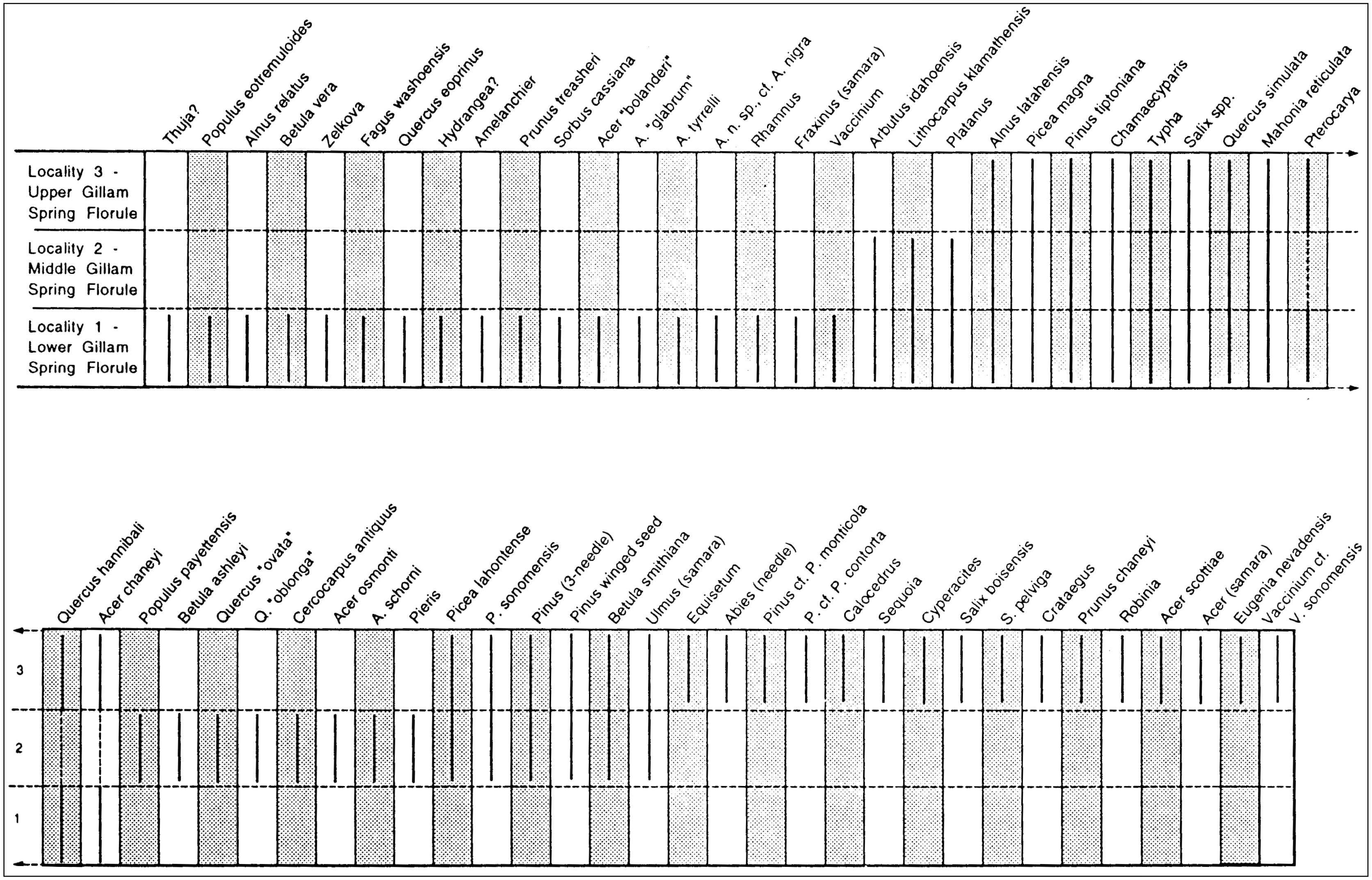
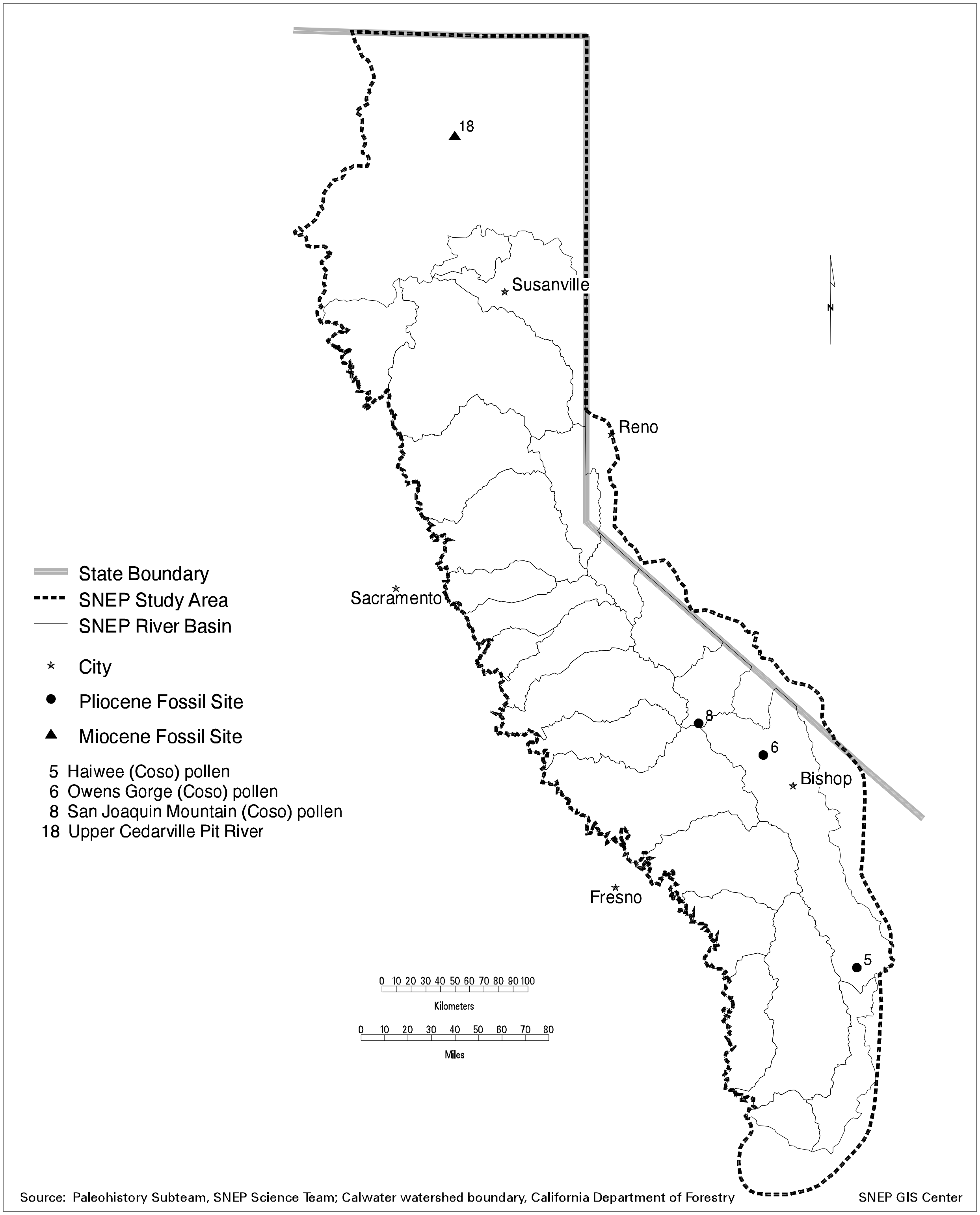


FIGURE 5.4

Rapid change in species diversity and abundance recorded at three stratigraphically continuous mid-Miocene sites at Gillam Spring, Nevada (from Axelrod and Schorn 1994).



Source: Paleohistory Subteam, SNEP Science Team; Calwater watershed boundary, California Department of Forestry

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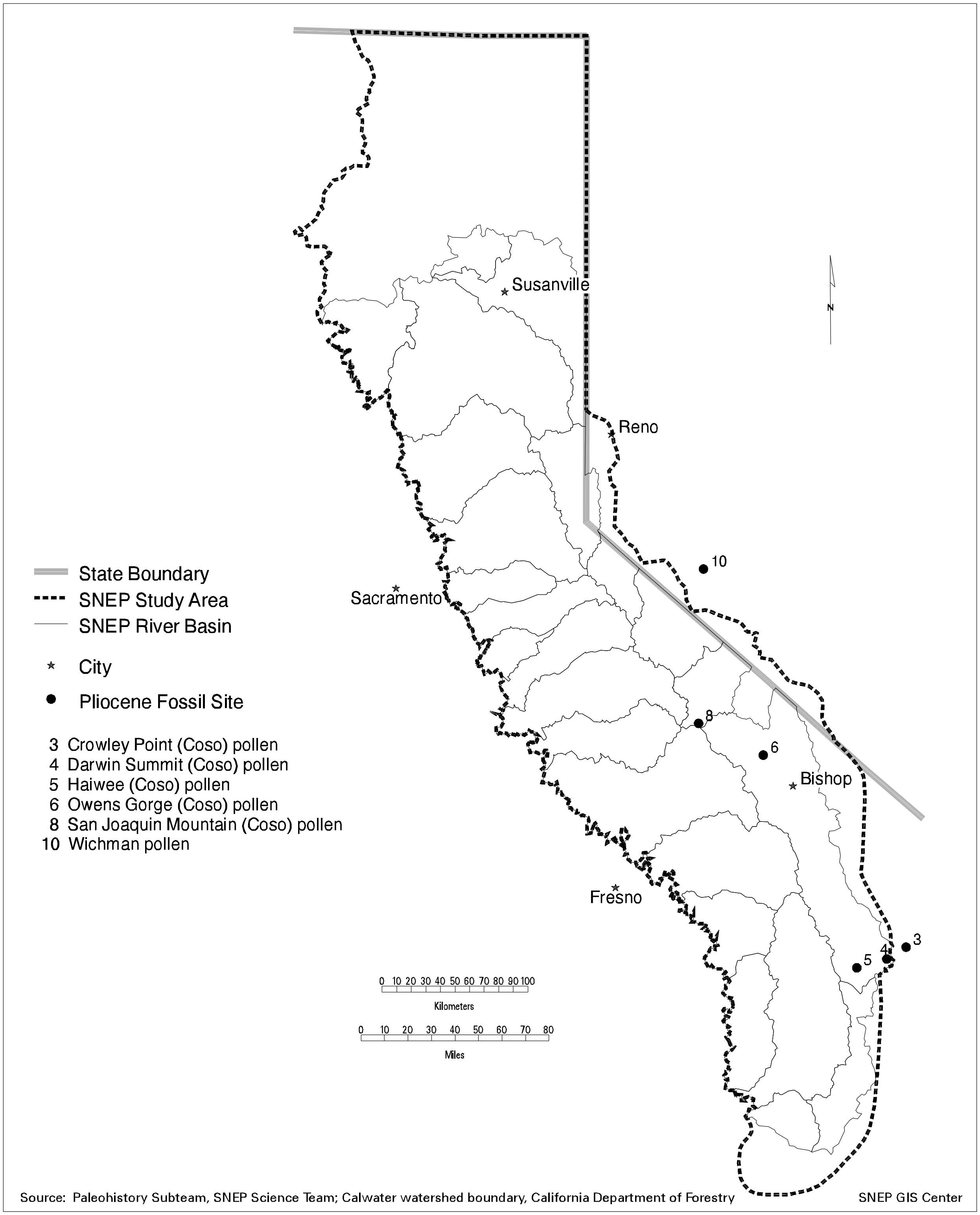
FIGURE 5.5

Distribution of red fir *(Abies* cf. *magnifica)* in the Sierra Nevada and adjacent Nevada as recorded in Tertiary fossil deposits. *Note:* Floras 5, 6, and 8 are pollen sites, interpretations are based on a very small number of grains, and species identifications may be incorrect. These sites should be treated with question. Unpublished revisions by Howard Schorn of the University of California, Berkeley, Museum of Paleontology (letter to the author, June 1995) indicate that all *Abies concolor* fossils indicated for Tertiary Nevada–Sierra Nevada are in fact red fir.



Source: Paleohistory Subteam, SNEP Science Team; Calwater watershed boundary, California Department of Forestry

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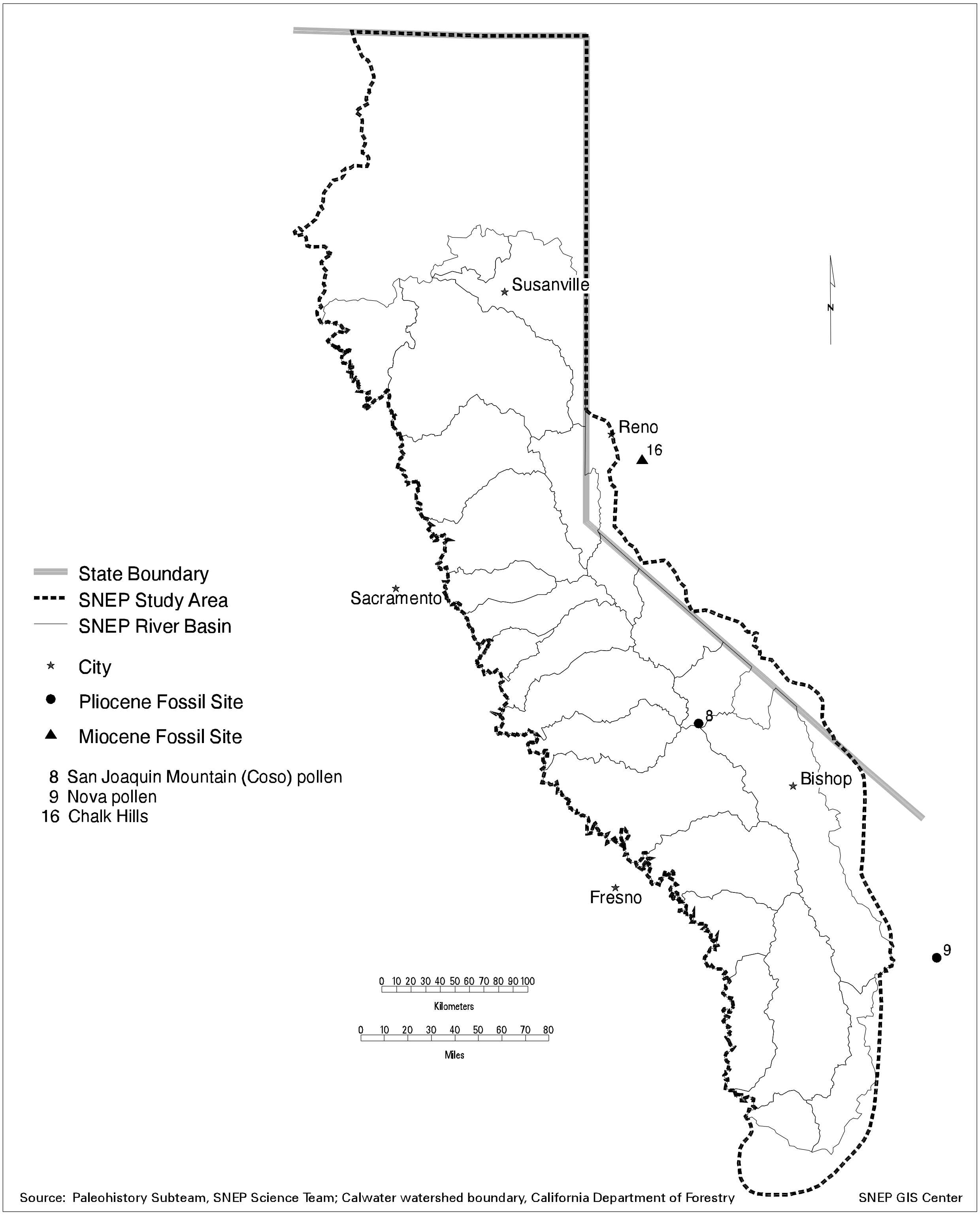
FIGURE 5.6

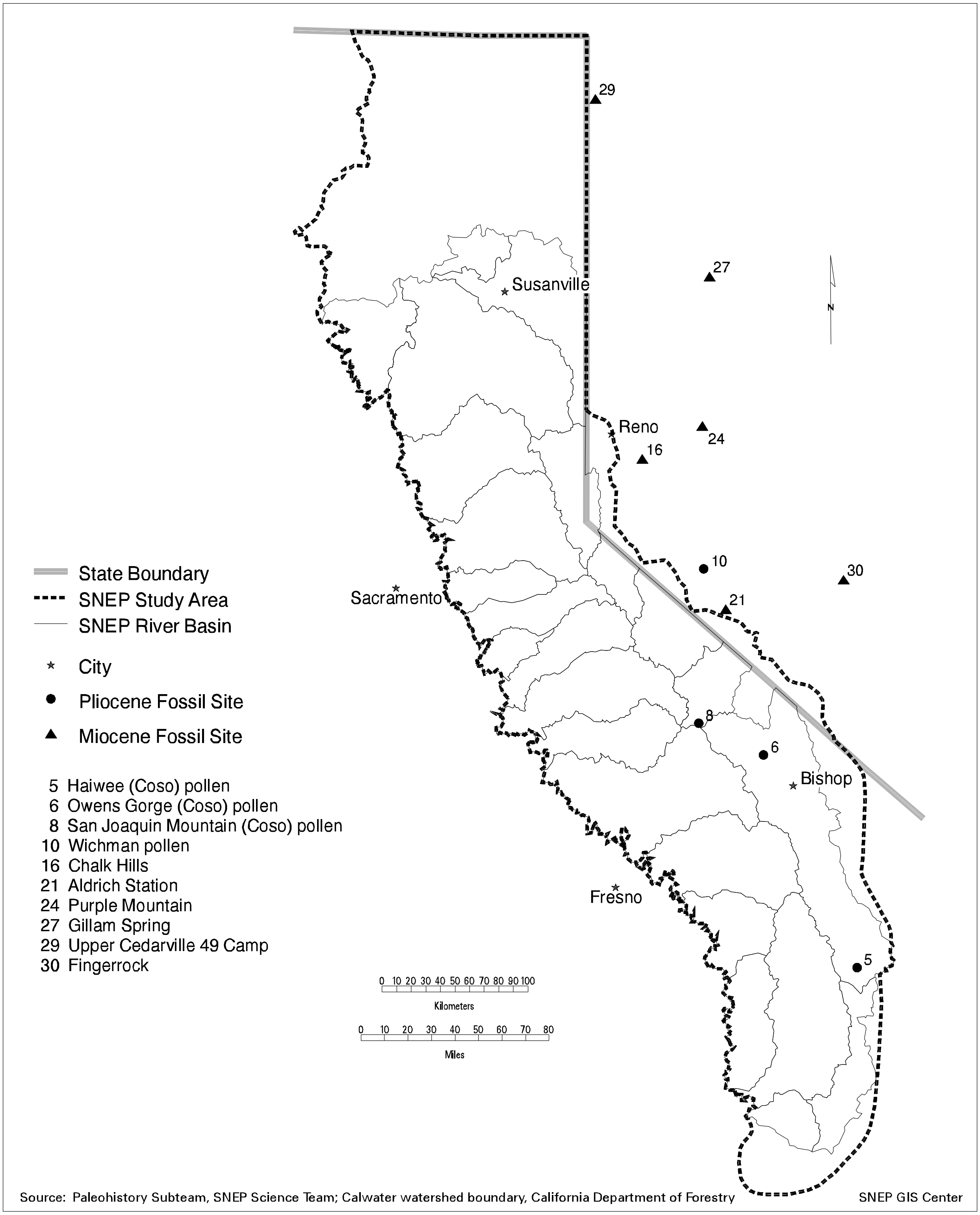
Distribution of bristlecone pine *(Pinus* cf. *longaeva)* in the Sierra Nevada and adjacent Nevada as recorded in Tertiary fossil deposits. *Note:* Floras 3–6, 8, and 10 are pollen sites, interpretations are based on a very small number of grains, and species identifications may be incorrect. These sites should be treated with question.



Source: Paleohistory Subteam, SNEP Science Team; Calwater watershed boundary, California Department of Forestry

FIGURE 5.7

Distribution of foxtail pine *(Pinus* cf. *balfouriana)* in the Sierra Nevada and adjacent Nevada as recorded in Tertiary fossil deposits. *Note:* Floras 8 and 9 are pollen sites, interpretations are based on a very small number of grains, and species identifications may be incorrect. These sites should be treated with question.



Source: Paleohistory Subteam, SNEP Science Team; Calwater watershed boundary, California Department of Forestry

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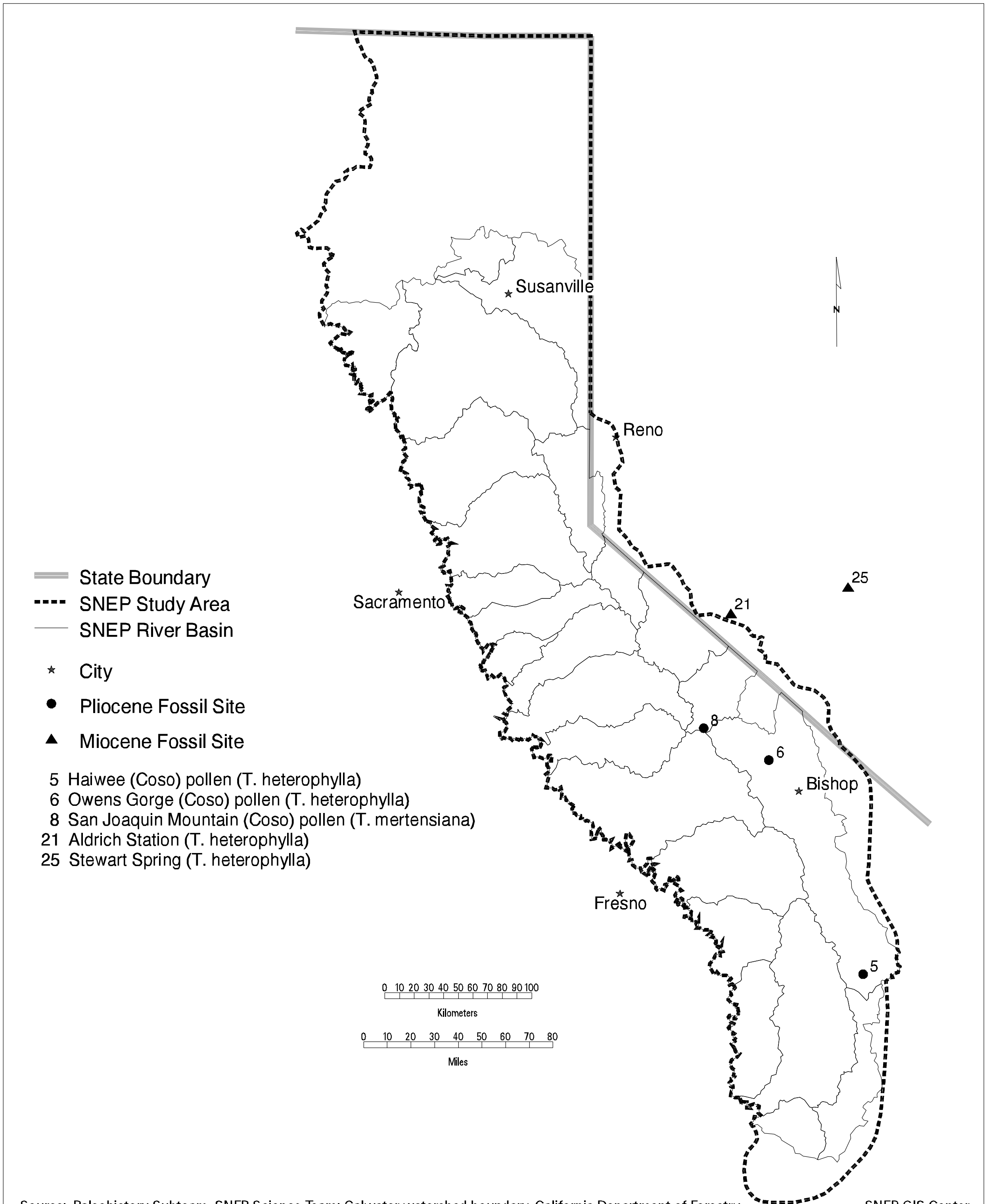
FIGURE 5.8

Distribution of western white pine *(Pinus* cf. *monticola)* in the Sierra Nevada and adjacent Nevada as recorded in Tertiary fossil deposits. *Note:* Floras 5, 6, 8, and 10 are pollen sites, interpretations are based on a very small number of grains, and species identifications may be incorrect. These sites should be treated with question.



Source: Paleohistory Subteam, SNEP Science Team; Calwater watershed boundary, California Department of Forestry

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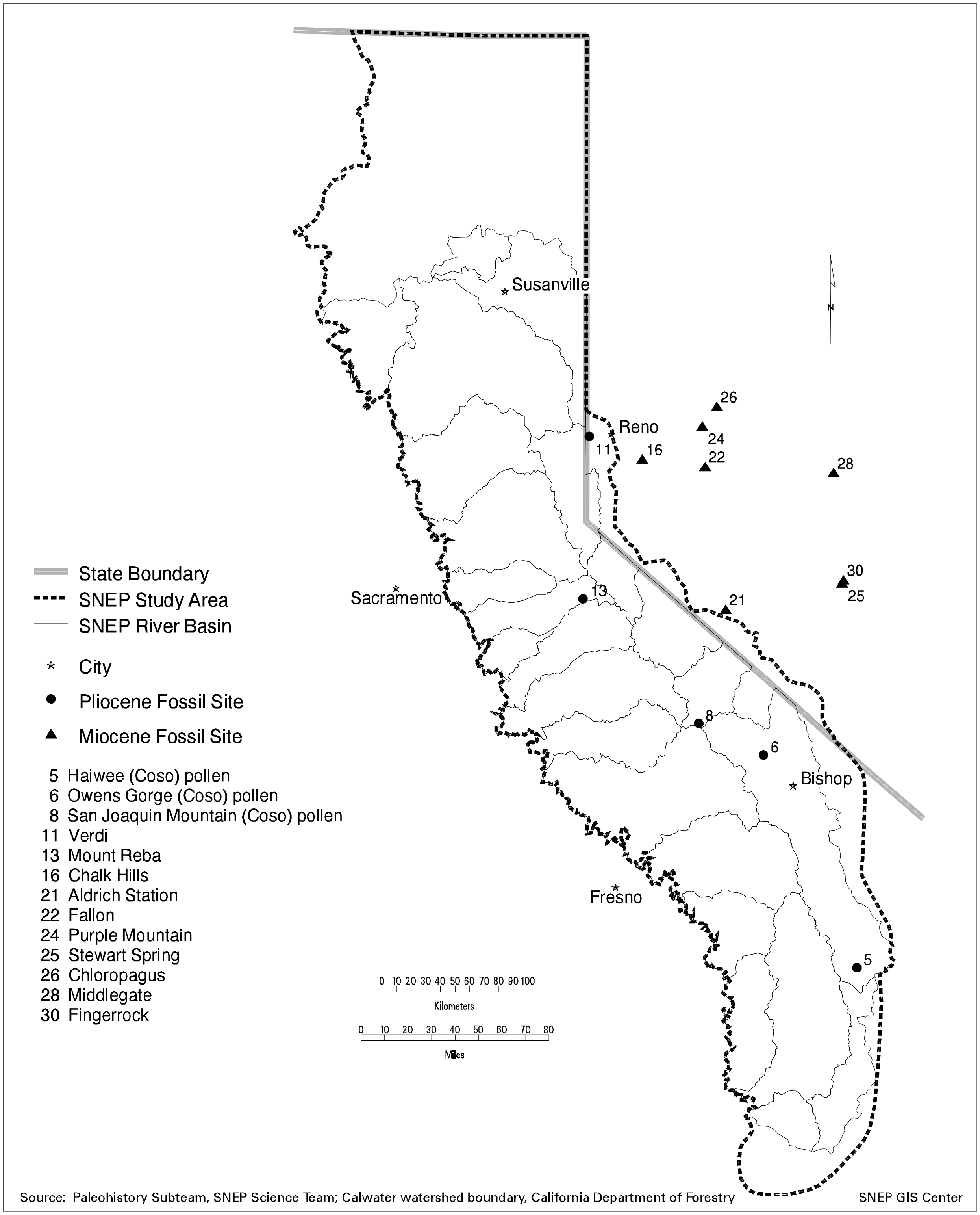
FIGURE 5.9

Distribution of hemlock *(Tsuga)* in the Sierra Nevada and adjacent Nevada as recorded in Tertiary fossil deposits. *Note:* Floras 5, 6, and 8 are pollen sites, interpretations are based on a very small number of grains, and species identifications may be incorrect. These sites should be treated with question.



Source: Paleohistory Subteam, SNEP Science Team; Calwater watershed boundary, California Department of Forestry

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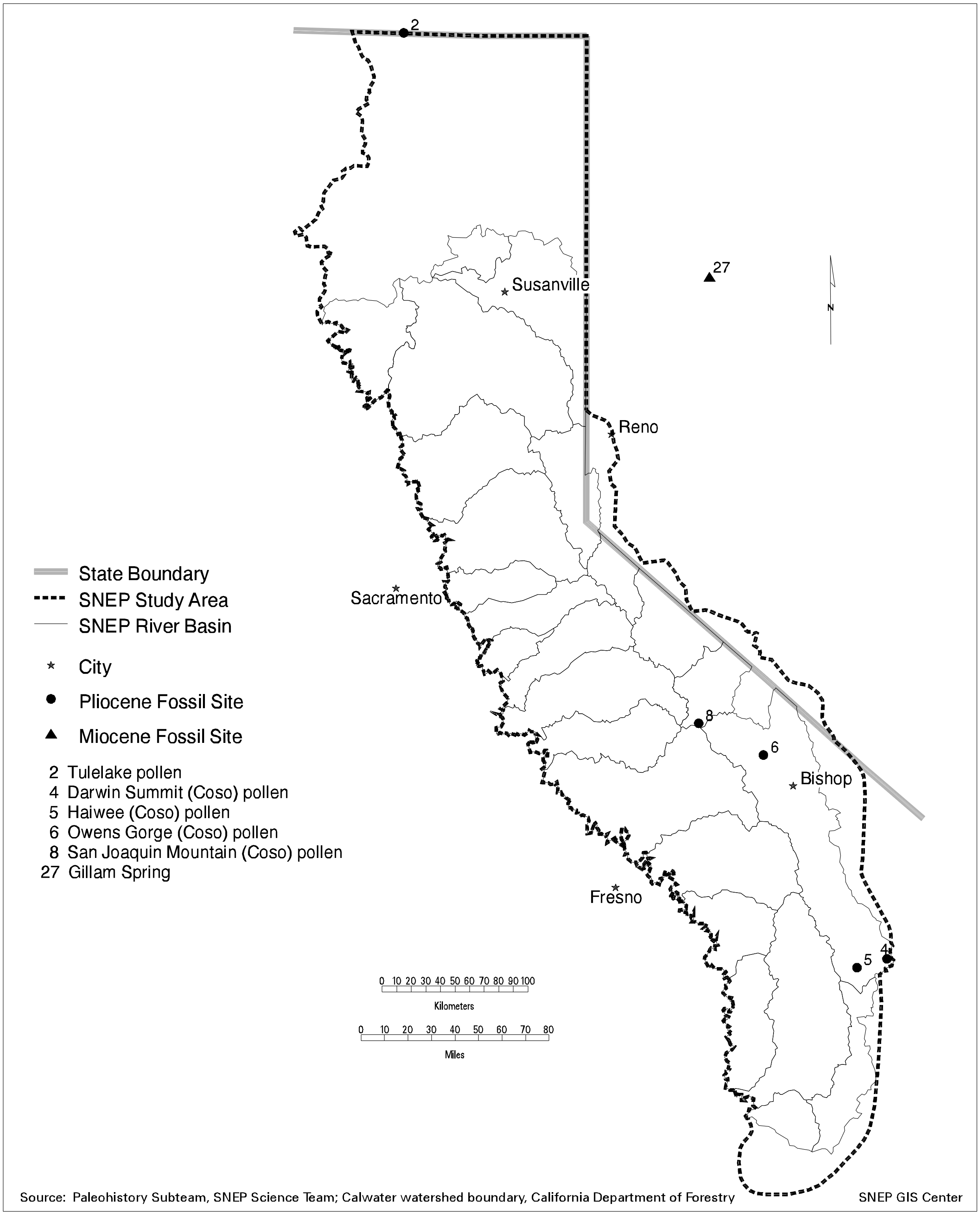
FIGURE 5.10

Distribution of white fir *(Abies* cf. *concolor)* in the Sierra Nevada and adjacent Nevada as recorded in Tertiary fossil deposits. *Note:* Floras 5, 6, and 8 are pollen sites, interpretations are based on a very small number of grains, and species identifications may be incorrect. These sites should be treated with question. Unpublished taxonomic revisions by Howard Schorn of the University of California, Berkeley, Museum of Paleontology (letter to the author, June 1995) indicate that there is no white fir in this bioregion except in the Reno, Nevada, area (Verdi) during the Tertiary. The fossils originally described as white fir now are primarily identified as red fir.



Source: Paleohistory Subteam, SNEP Science Team; Calwater watershed boundary, California Department of Forestry

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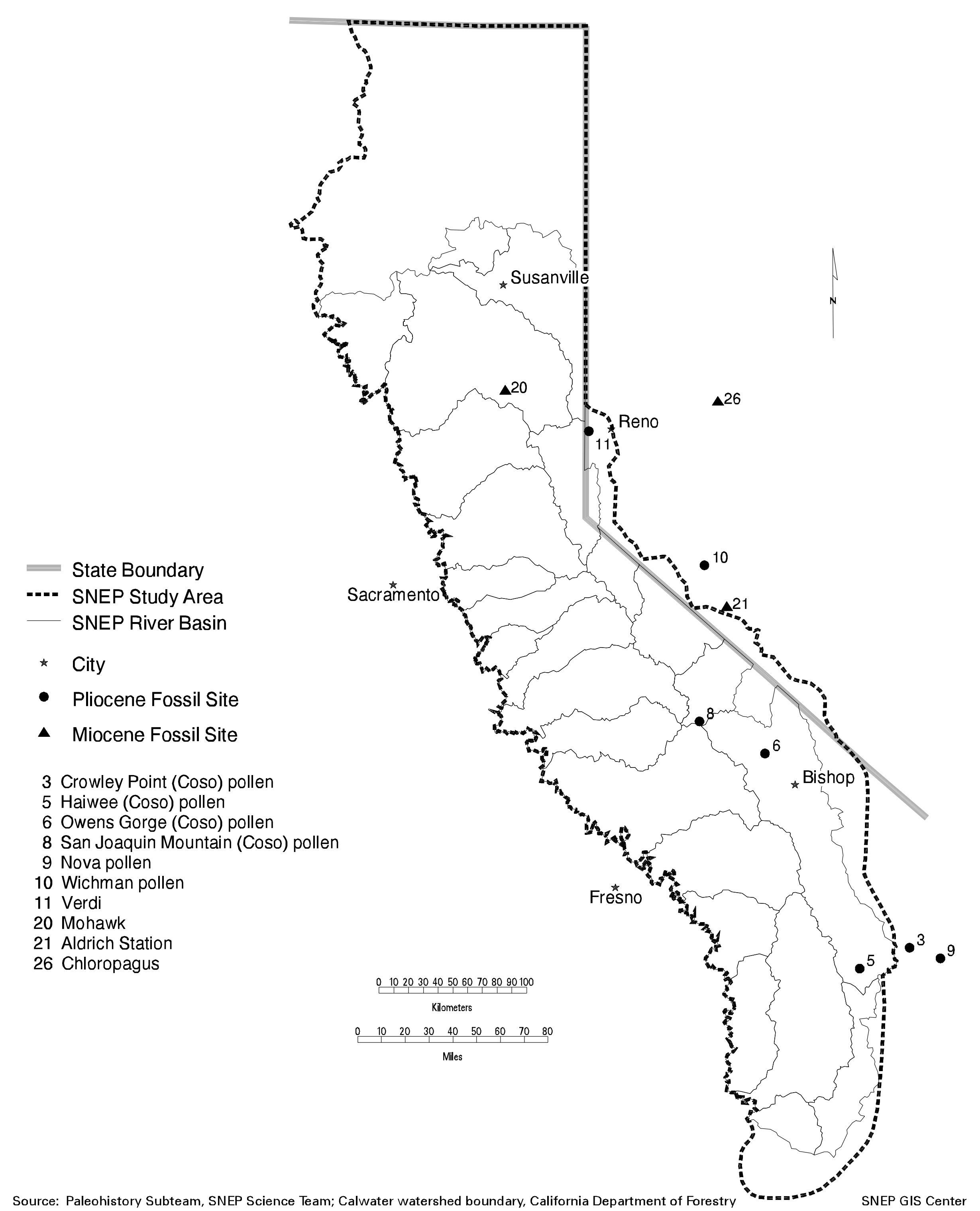
FIGURE 5.11

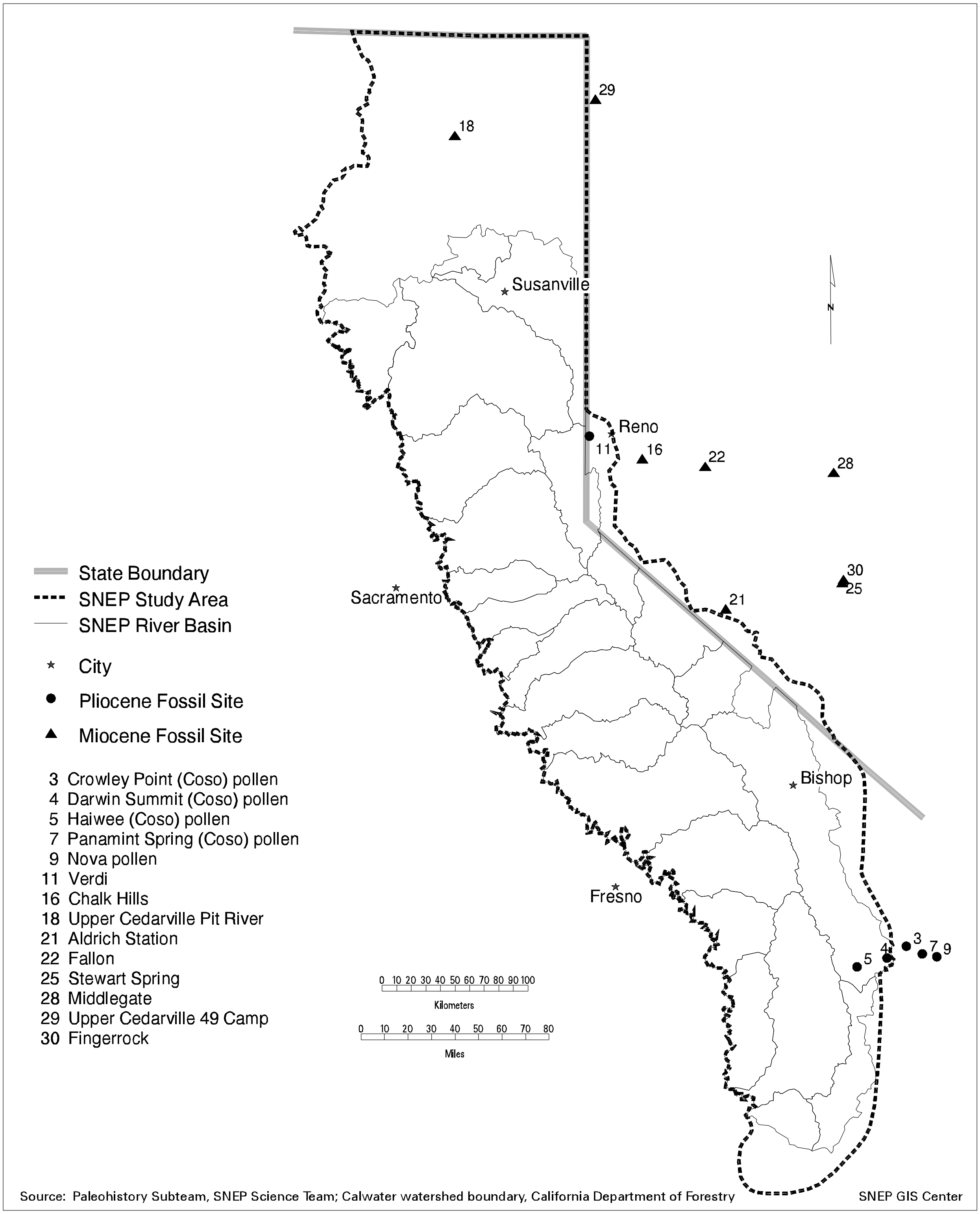
Distribution of incense cedar *(Calocedrus* cf. *decurrens)* in the Sierra Nevada and adjacent Nevada as recorded in Tertiary fossil deposits. *Note:* Floras 2, 4–6, and 8 are pollen sites, interpretations are based on a very small number of grains, and species identifications may be incorrect. These sites should be treated with question.



Source: Paleohistory Subteam, SNEP Science Team; Calwater watershed boundary, California Department of Forestry SNEP GIS Center

FIGURE 5.12

Distribution of sugar pine *(Pinus* cf. *lambertiana)* in the Sierra Nevada and adjacent Nevada as recorded in Tertiary fossil deposits. *Note:* Floras 3, 5, 6, and 8–10 are pollen sites, interpretations are based on a very small number of grains, and species identifications may be incorrect. These sites should be treated with question.



Source: Paleohistory Subteam, SNEP Science Team; Calwater watershed boundary, California Department of Forestry

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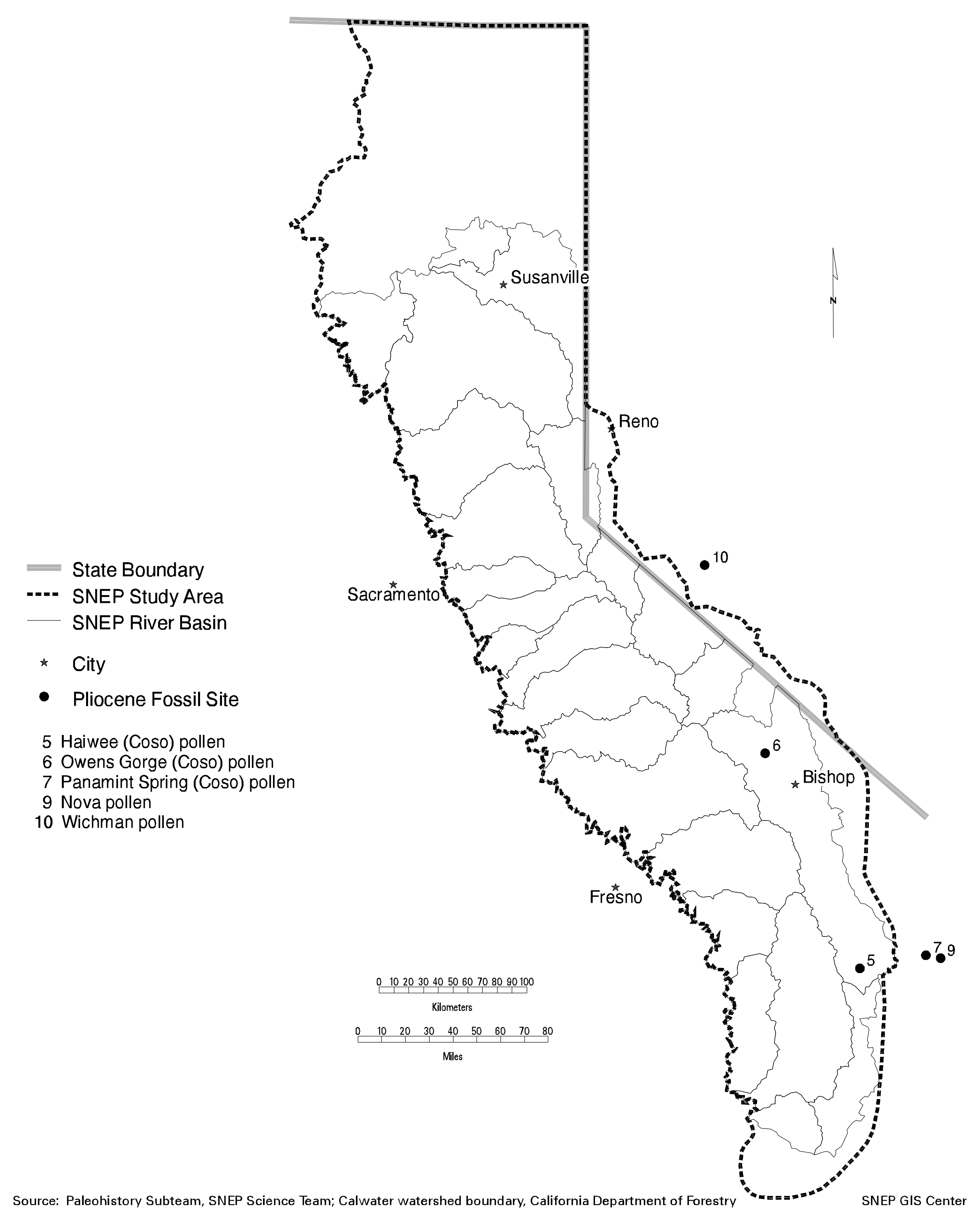
FIGURE 5.13

Distribution of ponderosa pine *(Pinus* cf. *ponderosa)* in the Sierra Nevada and adjacent Nevada as recorded in Tertiary fossil deposits. *Note:* Floras 3–5, 7, and 9 are pollen sites, interpretations are based on a very small number of grains, and species identifications may be incorrect. These sites should be treated with question.



Source: Paleohistory Subteam, SNEP Science Team; Calwater watershed boundary, California Department of Forestry

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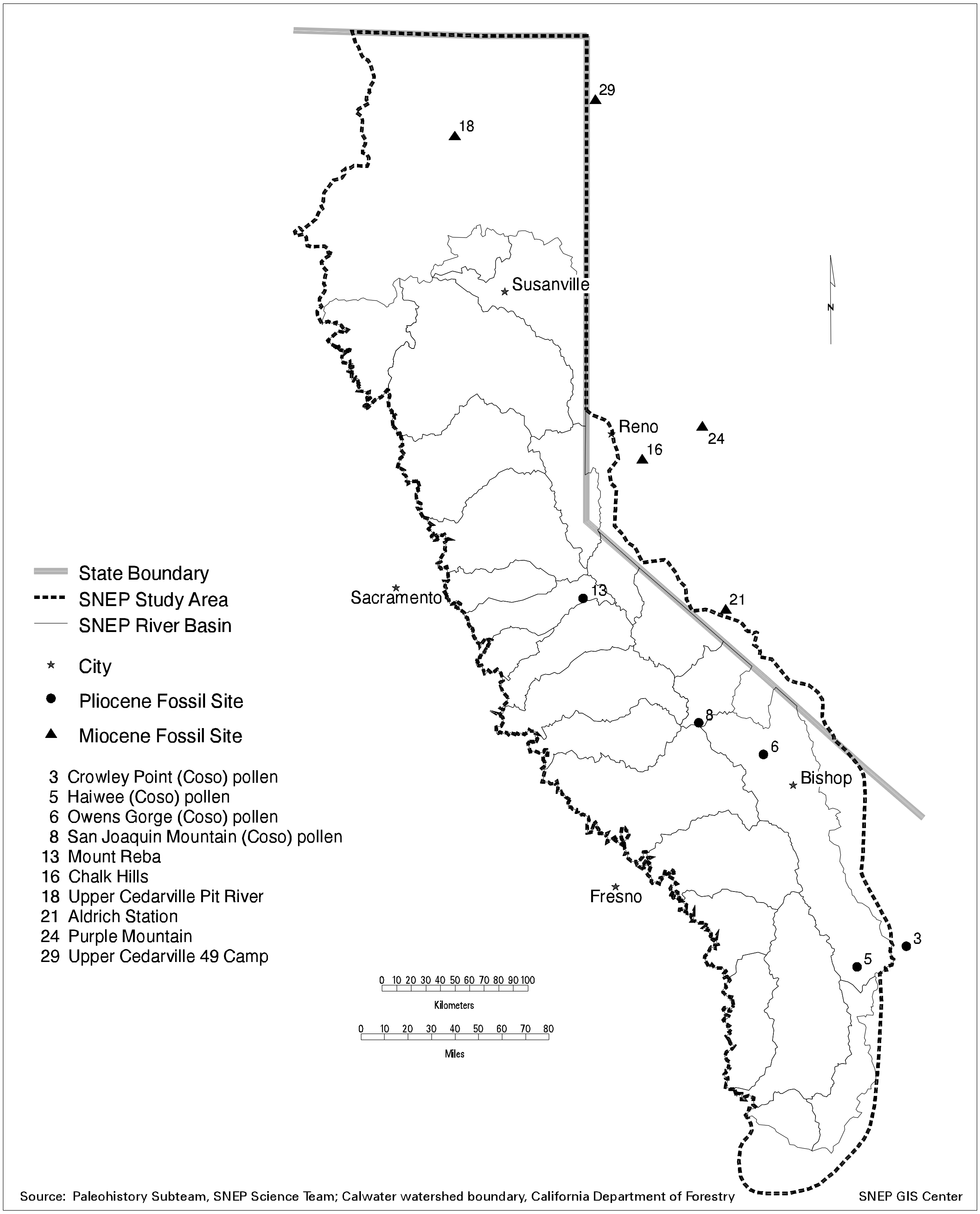
FIGURE 5.14

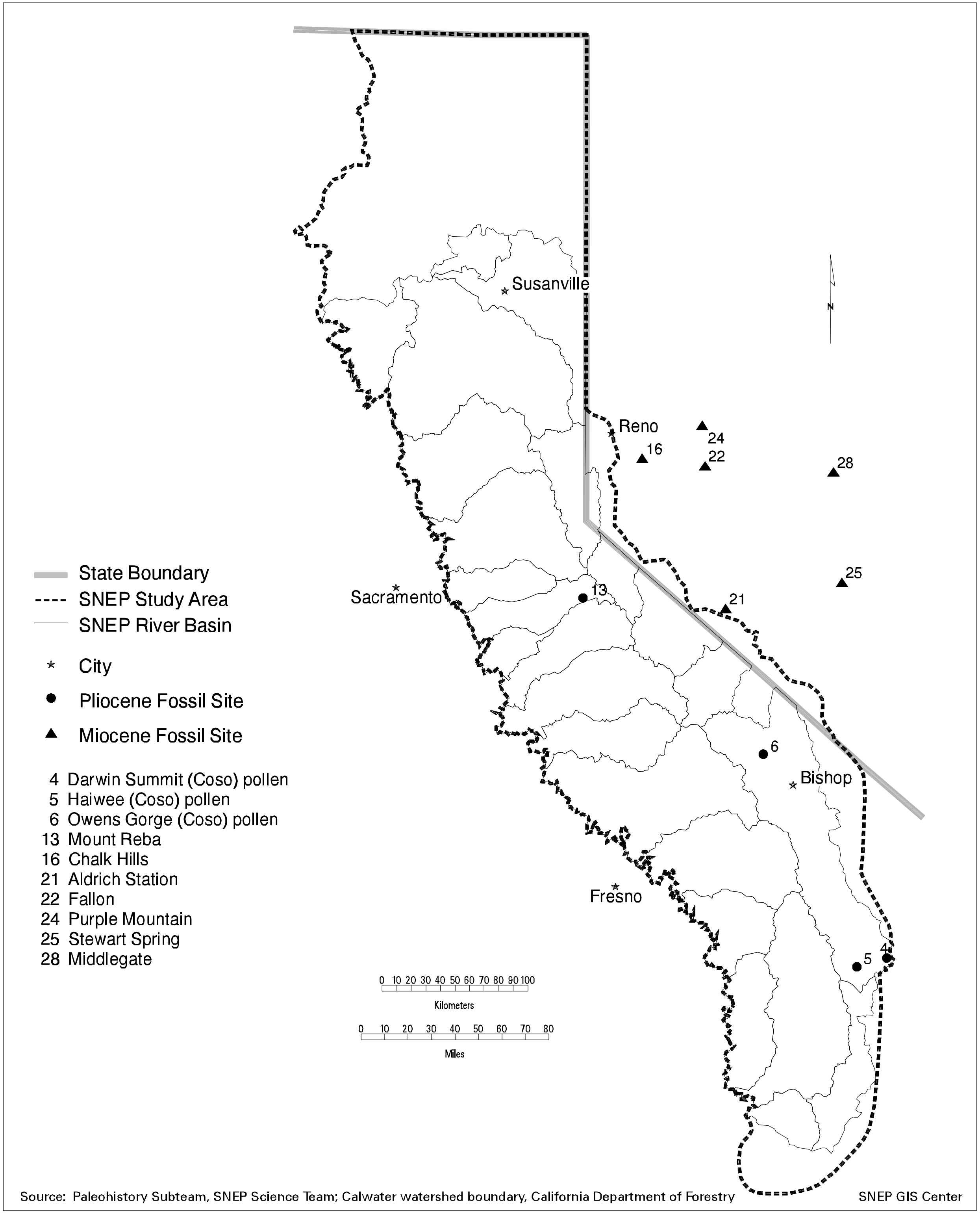
Distribution of Jeffrey pine *(Pinus* cf. *jeffreyi)* in the Sierra Nevada and adjacent Nevada as recorded in Tertiary fossil deposits. *Note:* Floras 5–7, 9, and 10 are pollen sites, interpretations are based on a very small number of grains, and species identifications may be incorrect. These sites should be treated with question.



Source: Paleohistory Subteam, SNEP Science Team; Calwater watershed boundary, California Department of Forestry

FIGURE 5.15

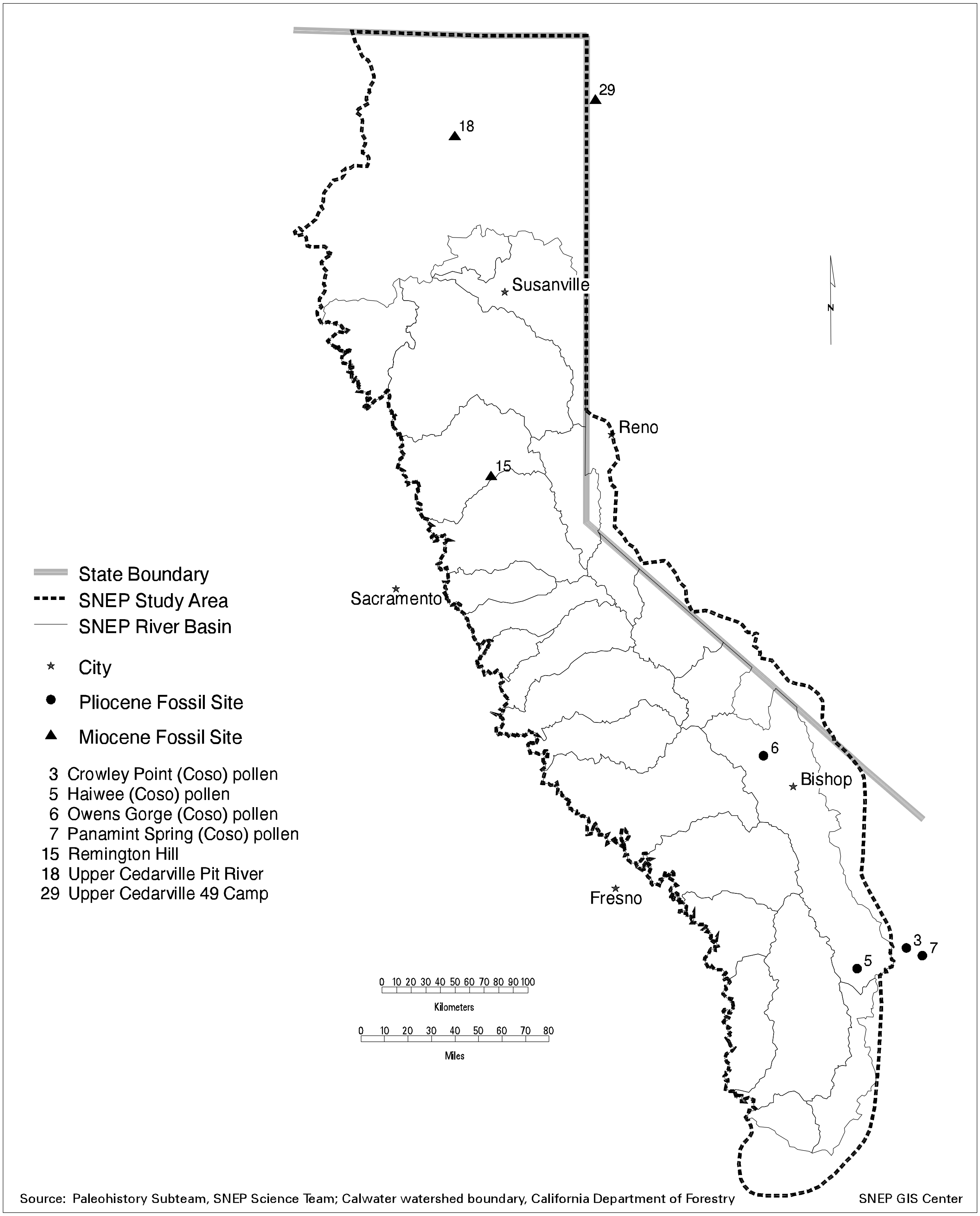
Distribution of Douglas fir *(Pseudotsuga* cf. *douglasii)* in the Sierra Nevada and adjacent Nevada as recorded in Tertiary fossil deposits. *Note:* Floras 3, 5, 6, and 8 are pollen sites, interpretations are based on a very small number of grains, and species identifications may be incorrect. These sites should be treated with question.



Source: Paleohistory Subteam, SNEP Science Team; Calwater watershed boundary, California Department of Forestry

FIGURE 5.16

Distribution of giant sequoia *(Sequoiadendron* cf. *giganteum)* in the Sierra Nevada and adjacent Nevada as recorded in Tertiary fossil deposits. *Note:* Floras 4–6 are pollen sites, interpretations are based on a very small number of grains, and species identifications may be incorrect. These sites should be treated with question.



Source: Paleohistory Subteam, SNEP Science Team; Calwater watershed boundary, California Department of Forestry

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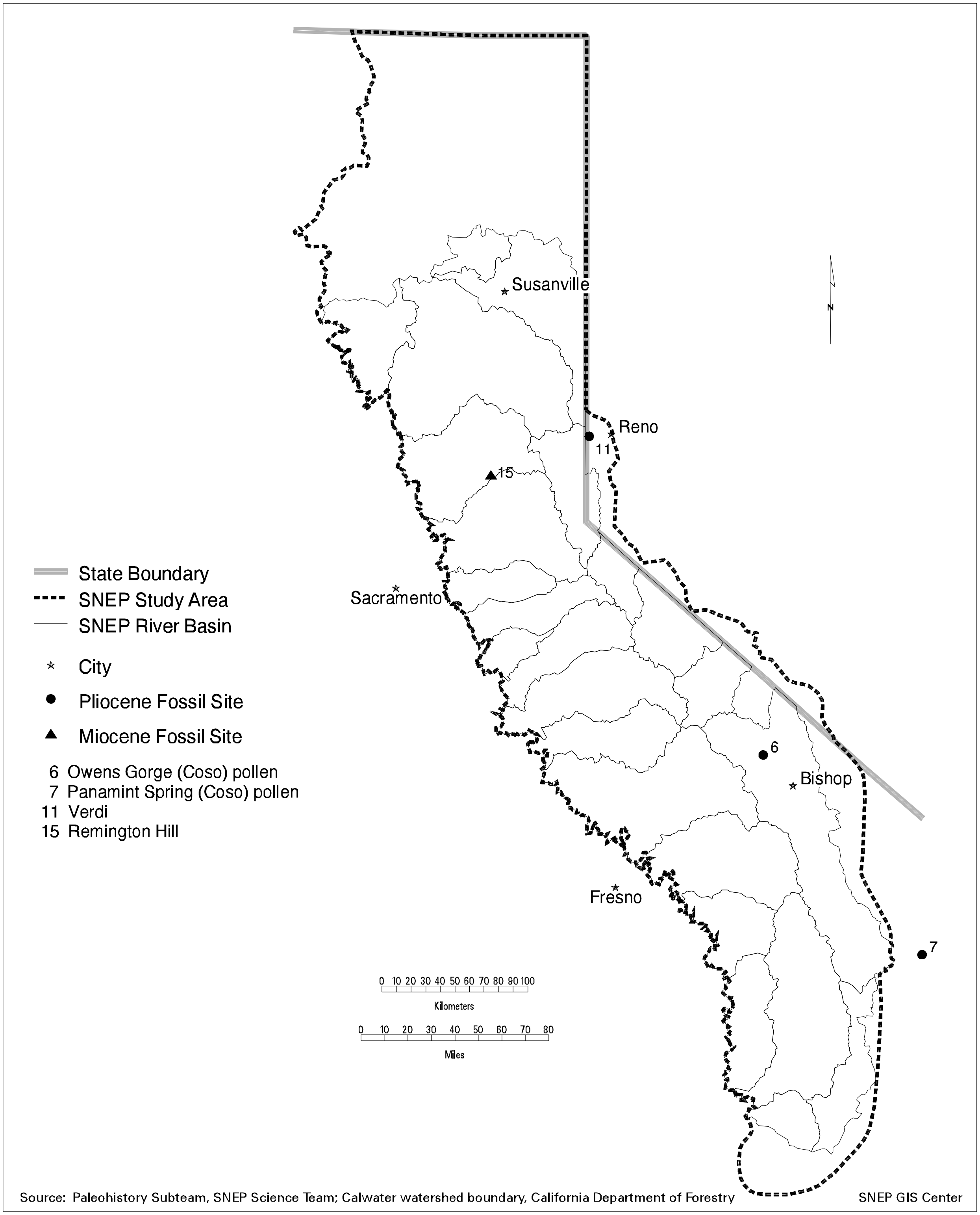
FIGURE 5.17

Distribution of black oak *(Quercus* cf. *kelloggii)* in the Sierra Nevada and adjacent Nevada as recorded in Tertiary fossil deposits. *Note:* Floras 3 and 5–7 are pollen sites, interpretations are based on a very small number of grains, and species identifications may be incorrect. These sites should be treated with question.



Source: Paleohistory Subteam, SNEP Science Team; Calwater watershed boundary, California Department of Forestry

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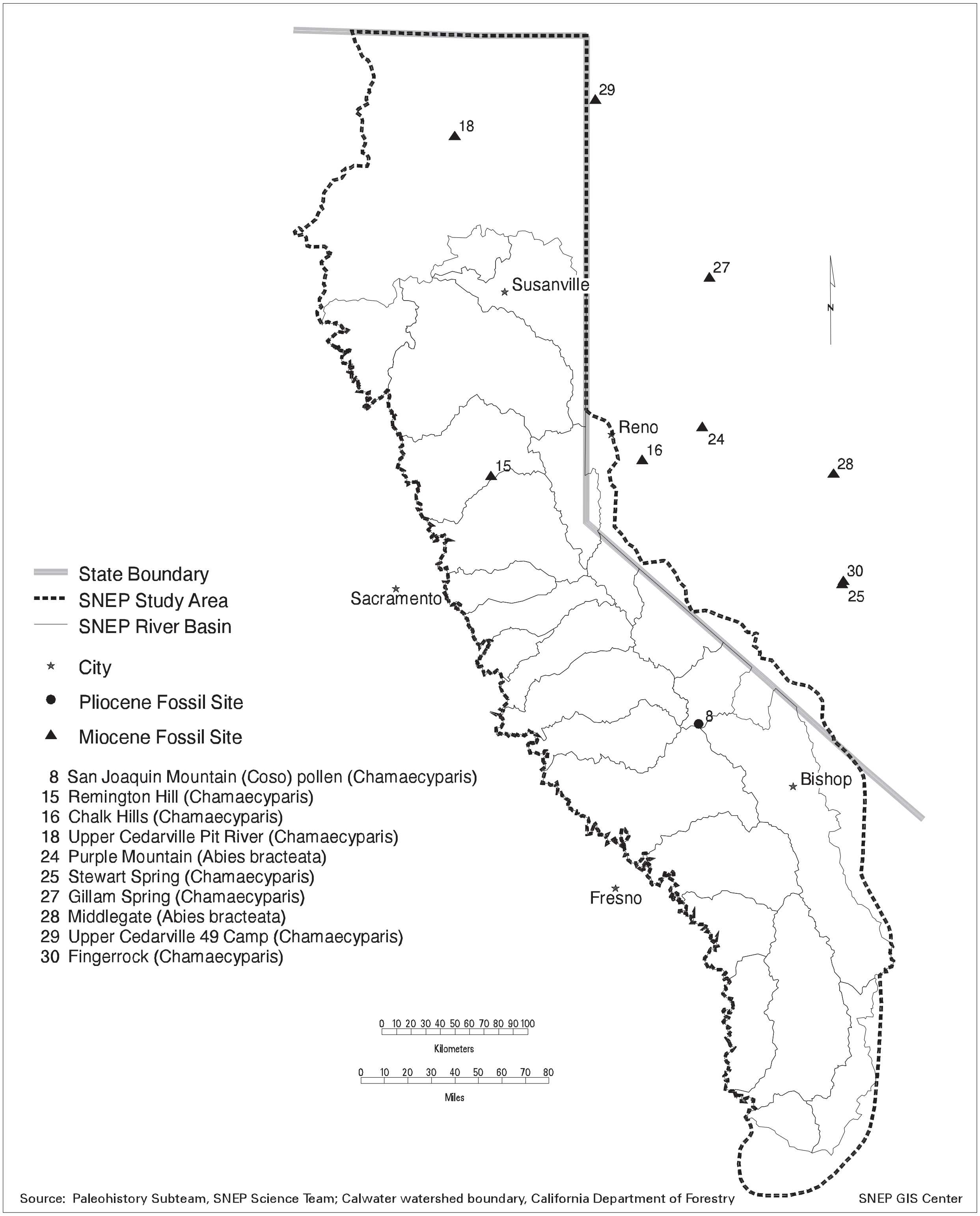
FIGURE 5.18

Distribution of white oak *(Quercus* cf. *lobata)* in the Sierra Nevada and adjacent Nevada as recorded in Tertiary fossil deposits. *Note:* Floras 6 and 7 are pollen sites, interpretations are based on a very small number of grains, and species identifications may be incorrect. These sites should be treated with question. Wolfe and Tanai (1987) indicate that the Verdi site actually is an *Acer* not oak.



Source: Paleohistory Subteam, SNEP Science Team; Calwater watershed boundary, California Department of Forestry

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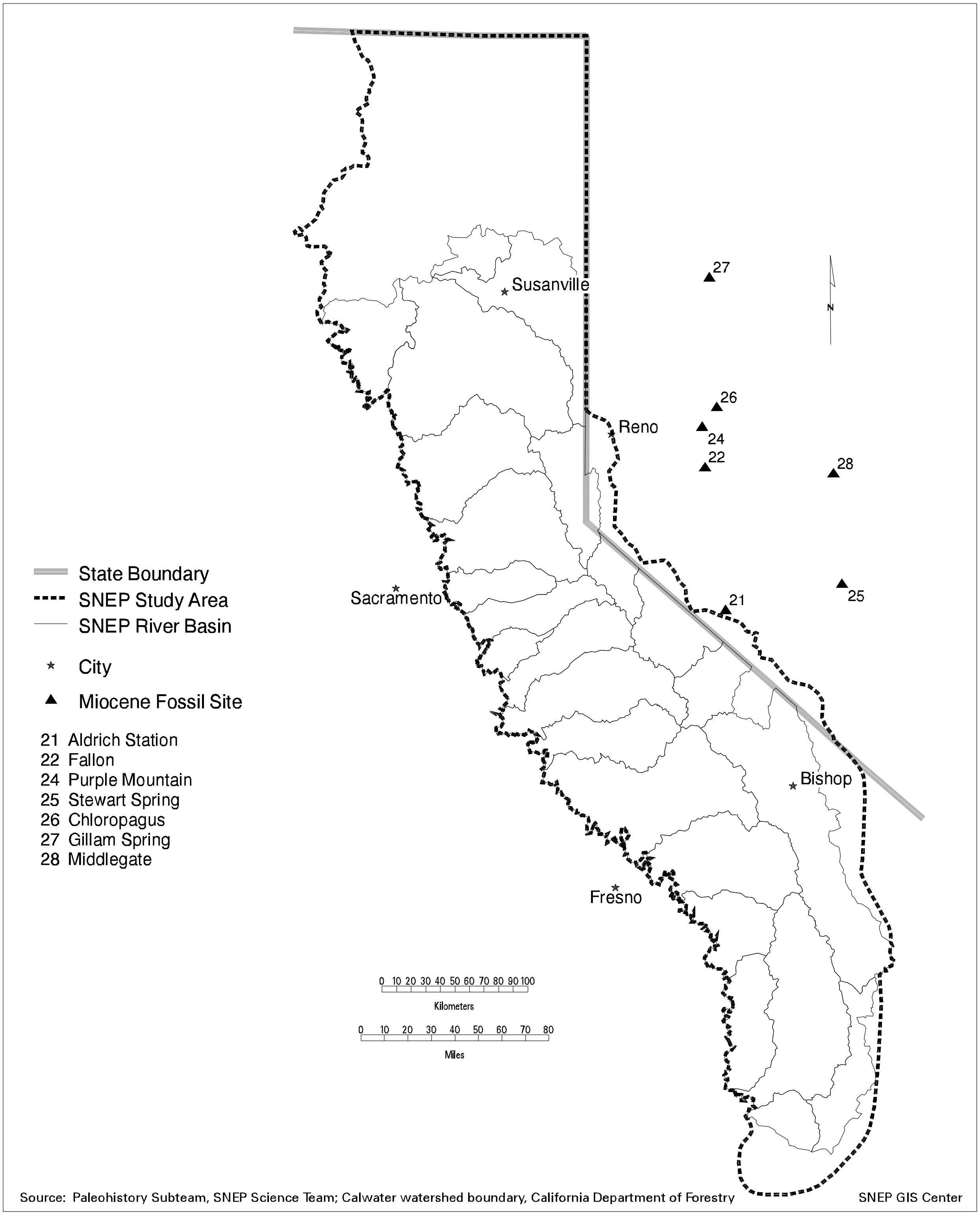
FIGURE 5.19

Distribution of Santa Lucia fir *(Abies bracteata)* and false cypresses *(Chamaecyparis)* in the Sierra Nevada and adjacent Nevada as recorded in Tertiary fossil deposits. *Note:* Flora 8 is a pollen site, interpretations are based on a very small number of grains, and species identifications may be incorrect. This site should be treated with question.



Source: Paleohistory Subteam, SNEP Science Team; Calwater watershed boundary, California Department of Forestry

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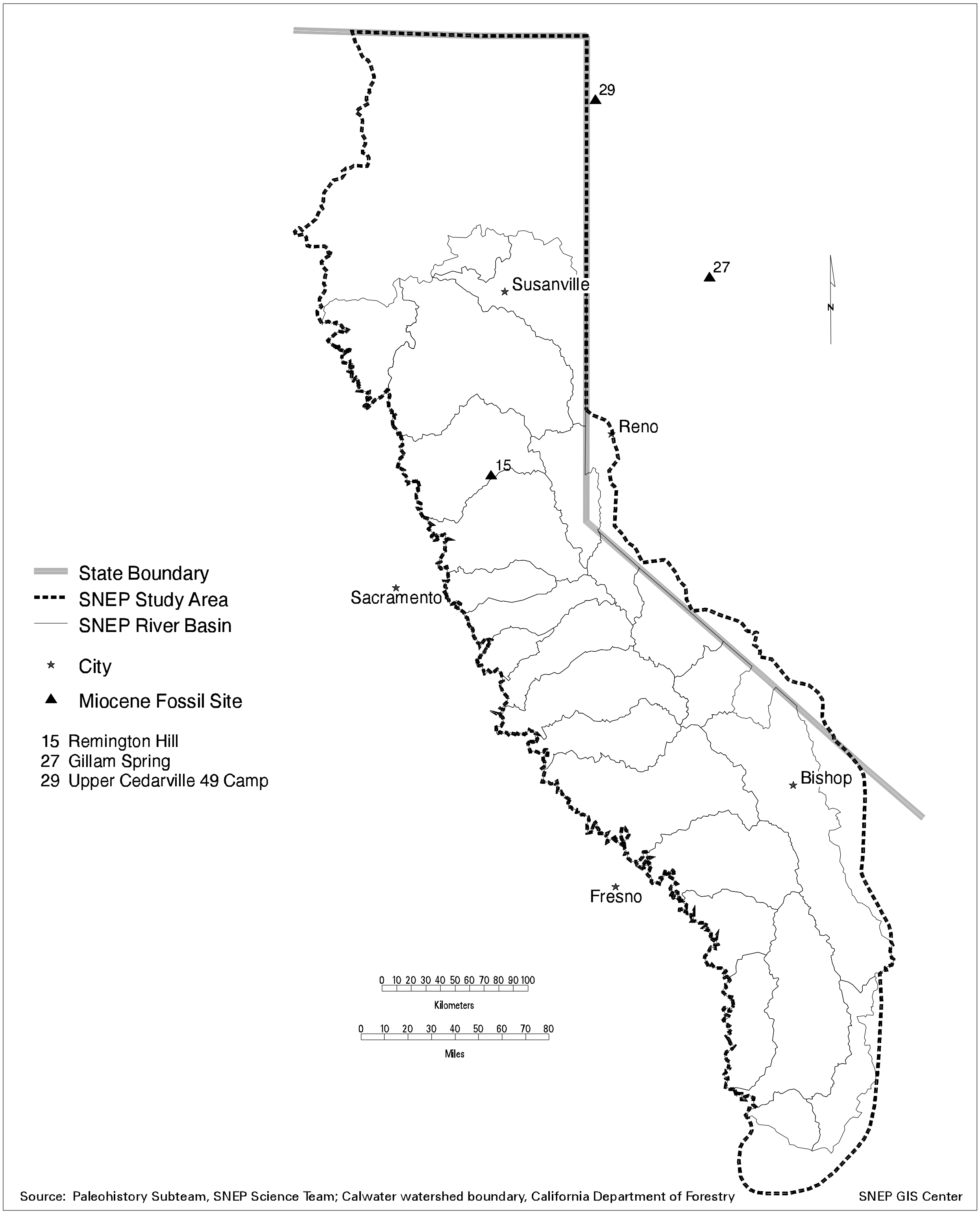
FIGURE 5.20

Distribution of Brewer's spruce *(Picea* cf. *breweriana)* in the Sierra Nevada and adjacent Nevada as recorded in Tertiary fossil deposits.



Source: Paleohistory Subteam, SNEP Science Team; Calwater watershed boundary, California Department of Forestry

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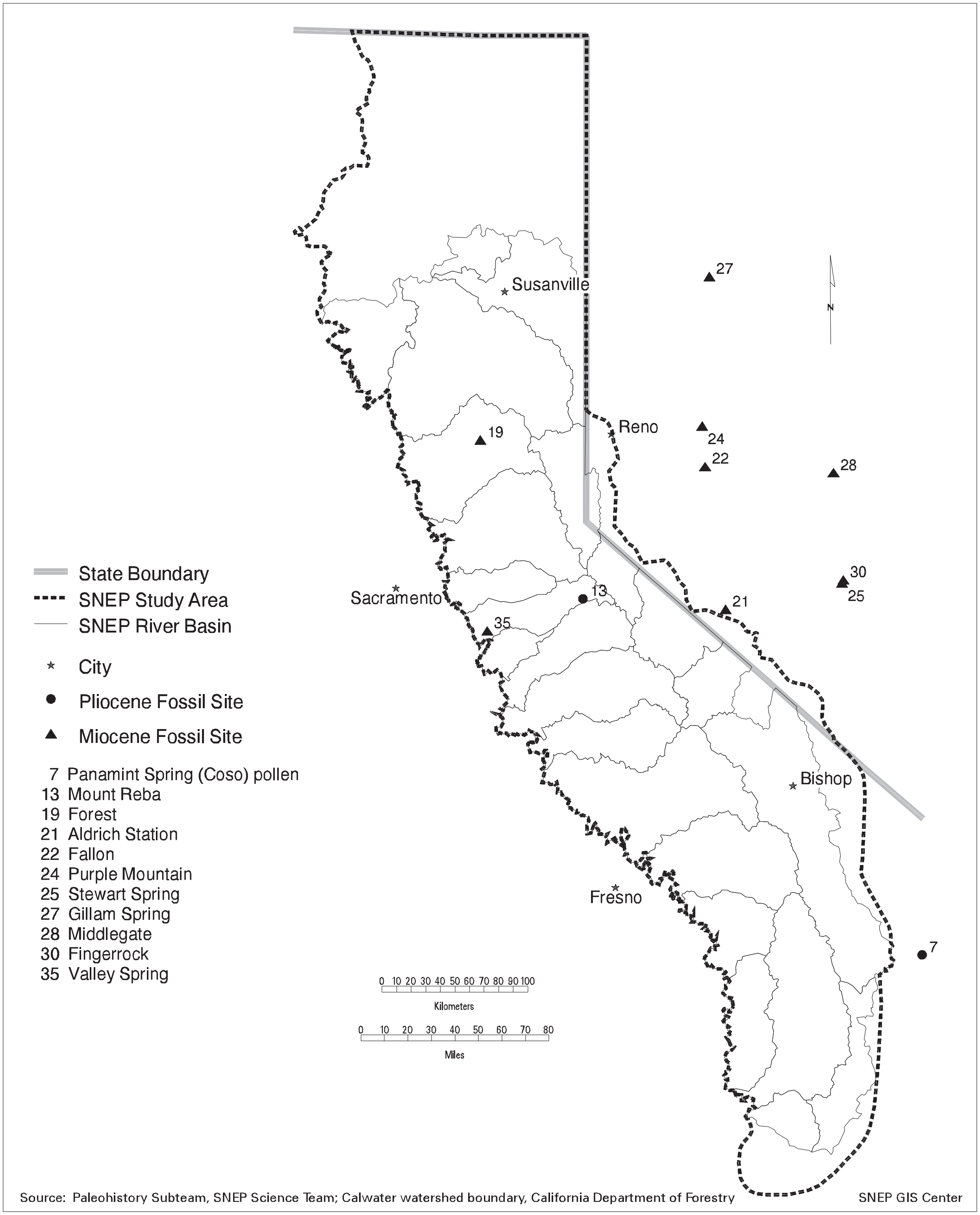
FIGURE 5.21

Distribution of coast redwood *(Sequoia* cf. *sempervirens)* in the Sierra Nevada and adjacent Nevada as recorded in Tertiary fossil deposits.



Source: Paleohistory Subteam, SNEP Science Team; Calwater watershed boundary, California Department of Forestry

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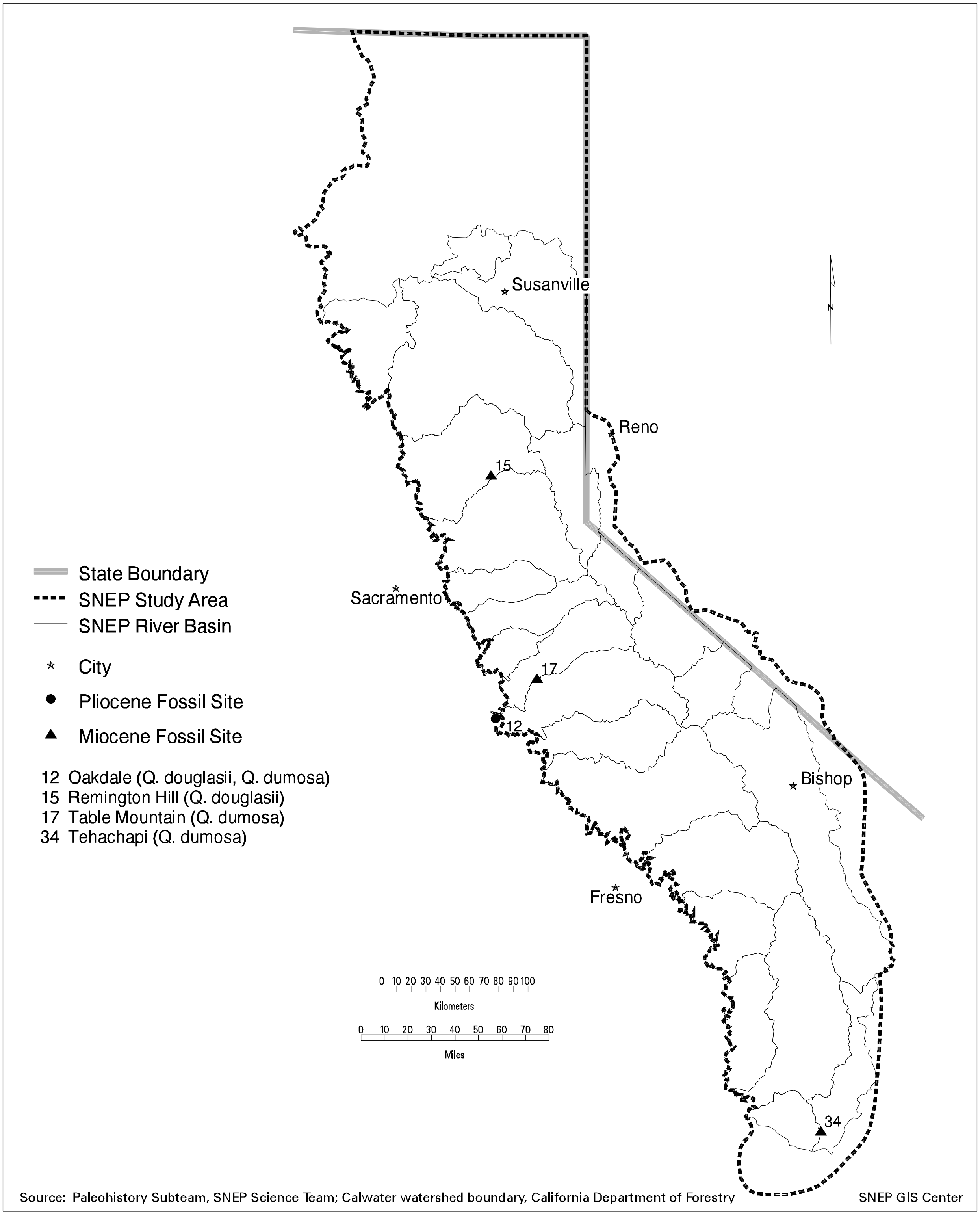
FIGURE 5.22

Distribution of coast live oak *(Quercus* cf. *chrysolepis)* in the Sierra Nevada and adjacent Nevada as recorded in Tertiary fossil deposits. *Note:* Flora 7 is a pollen site, interpretations are based on a very small number of grains, and species identifications may be incorrect. This site should be treated with question.



Source: Paleohistory Subteam, SNEP Science Team; Calwater watershed boundary, California Department of Forestry

FIGURE 5.23

Distribution of blue oak *(Quercus douglasii)* and scrub oak *(Q. dumosa)* in the Sierra Nevada as recorded in Tertiary fossil deposits.

MANAGEMENT IMPLICATIONS

From the study of Tertiary vegetation dynamics we derive several lessons, but one is central: ecosystems change. The theme of ecosystem change is dominant throughout SNEP's assessments and analyses (Anderson and Moratto 1996; Franklin and Fites-Kaufmann 1996; Kinney 1996; Skinner and Chang 1996; Stine 1996; Woolfenden 1996). Land management does not occur in a static biotic or physical environment; every management action is like a leap into white water. Understanding that ecological (and social) systems are in flux, that they change in sometimes predictable and sometimes chaotic ways, at scales from minute to large, improves our chances for setting and reaching realistic objectives for management of natural ecosystems.

Successful land managers learn to work optimally within the flow of natural change, or at least to understand the consequences of moving against currents. SNEP analyses emphasize both spatial (Davis and Stoms 1996; Franklin and Fites-Kaufmann 1996; Skinner and Chang 1996) and temporal (Kinney 1996; Skinner and Chang 1996; Woolfenden 1996) scales of change. Ecological processes cluster in nested levels, from short to long term, small to large scale (Delcourt and Delcourt 1991). Knowledge of Tertiary evolution and of the development of our modern landscape emphasizes the millennial scale of change within which we view smaller-scale natural ecosystem dynamics, elucidates the responses of modern species to climates we do not experience at present, and underlines some of the transient and individualistic aspects of many current assemblages of plants and animals. We must place our understanding of human impacts, sustainability, and conservation within this context of change.

Many of the SNEP analyses focus on the nature of agents of change that derive from within ecosystems and operate at short time scales (e.g., competition, disturbance, natural selection, succession) (Chang 1996; Ferrell 1996; Franklin and Fites-Kaufmann 1996; Menke et al. 1996; Skinner and Chang 1996). Simultaneously, forces external to ecosystems and/or operating on longer time scales (e.g., climate effects like El Niño, changes in orbital patterns of the earth, changes in the earth's axis relative to the sun, sunspots) interact to influence vegetation dynamics. Taxa endure and are influenced by these larger effects as well as the short-term forces. We must assume that, to some degree, the past dynamics of species in the Sierra Nevada represent potential behaviors of these external forces.

Several implications for land management in the Sierra Nevada derive from this chapter. The most important is a scale lesson and derives from a comparison of the rate and magnitude of change that humans impose with the rate and magnitude of change on an evolutionary scale. Although 65 million years have witnessed drastic changes in Sierran ecosystems, taken at a millennial or centennial (human) scale the pace of evolutionary change is very slow. Humans, by contrast, in a matter of decades have effected vegetation changes in the Sierra Nevada as large as or larger than these long-term evolutionary changes. Rate of environmental change is extremely important to species viability, distribution, and persistence, as adaptation and evolution can track environmental change at only relatively slow rates. The challenge to managers is to mimic rates and magnitudes of natural change and to prevent magnitudes of change comparable to the Tertiary from occurring in a matter of decades or centuries.

It is also important to consider the implications for native species that are a result of changes that have occurred over evolutionary time. Tertiary environments and climates supported species assemblages for which there seem to be no modern analogs, although the species are currently native. Vegetation associations containing these species occurred in mixes and distributions that are unknown in the Sierra today. Thus, it would be inaccurate to assume that the behavior of current taxa under current (or recent historic) climates represents the full range of those species' responses (including species dynamics, population extirpations, and range expansions). It may also be inaccurate to assume that currently native species will behave in future climates as they have behaved in the recent past. Although climatologists do not confidently predict the direction and magnitude of climate change in the Sierra Nevada over the next fifty or one hundred years (Stine 1996), there is relative agreement that climates will change and that there will be more frequent and extreme fluctuations in climate (see Woolfenden 1996). Sierran taxa may react to these fluctuations in individualistic and unpredictable ways. Unforeseen responses are likely, whether "positive" (population health, expansion, productivity), "negative" (population decline, extirpation) or novel (unprecedented response).

Natural reactions under new climates may be further affected by land-management practices and produce unexpected vegetation responses. Under conditions of such uncertainty a land manager's best responses might be:

- Do not assume that species will continue to respond exactly as they have in the recent past or at present.
- Recognize that population extirpations and range shifts have occurred in response to climate changes in the past and are likely to occur in the future.
- Plan for more frequent and severe fluctuations in climate than in the recent past.
- Assume that land management will interact with species' natural responses, adding an element of unknown magnitude.

Maintaining diverse, healthy forests with conditions favoring resilience to unpredictable but changing future climates and management regimes is the most appropriate management response. Planning that depends on landscapes reaching precise vegetation targets is likely to fail. Management programs that build flexibility, reversibility, and alternative pathways are more likely to succeed in uncertain futures.

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APPENDIX 5.1

Systematic Composition of the Tertiary Sierra Nevada Floras

The floras are listed in alphabetical order. Species names in parentheses are the closest modern affinities to fossil taxa.

LIST 1

Aldrich Station flora, western central Nevada, mid-Miocene (Axelrod 1956).

- Equisetales
  - Equisetaceae
    - *Equisetum alexanderi*
- Gymnosperms
  - Cupressaceae
    - *Thuja dimorpha (plicata)*
  - Pinaceae
    - *Abies concoloroides (concolor)*
    - *Picea magna (polita, neoveitchii)*
    - *Picea sonomensis (breweriana)*
    - *Pinus florissanti (ponderosa)*
    - *Pinus wheeleri (monticola, lambertiana)*
    - *Pseudotsuga sonomensis (menziesii)*
    - *Tsuga sonomensis (heterophylla)*
  - Taxodiaceae
    - *Sequoiadendron chaneyi (giganteum)*
- Angiosperms
  - Berberidaceae
    - *Mahonia marginata (beali)*
    - *Mahonia reticulata (repens)*
  - Betulaceae
    - *Alnus smithiana (tenufolia)*
  - Caprifoliaceae
    - *Symphoricarpos wassukana (oreophilius)*
  - Celastraceae
    - *Pachystima nevadensis (myrsintes)*
  - Fagaceae
    - *Quercus hannibali (chrysolepis)*
    - *Quercus simulata (myrsinaefolia)*
  - Hippocastanaceae
    - *Aesculus ashleyi (parryi)*
  - Leguminosae
    - *Amorpha oblongifolia (californica)*
    - *Sophora spokanensis (japonica)*
  - Myricaceae
    - *Comptonia parvifolia (asplenifolia)*
  - Oleaceae
    - *Fraxinus acornia (velutina)*
  - Platanaceae
    - *Platanus paucidentata (racemosa)*
  - Rhamnaceae
    - *Rhamnus precalifornica (californica)*
  - Rosaceae
    - *Amelanchier apiculata (utahensis)*
    - *Cercocarpus antiquus (betuloides)*
  - Salicaceae
    - *Populus alexanderi (trichocarpa)*
    - *Populus payettensis (angustifolia)*
    - *Populus sonorensis*
    - *Populus subwashoensis (temula, grandidentata)*
    - *Salix knowltonii (lemmonii)*
    - *Salix payettensis (exigua)*
  - Sapotaceae
    - *Burmelia beaverana (lanuginosa)*
  - Ulmaceae
    - *Ulmus moorei (crassifolia)*
    - *Zelkova nevadensis (serrata)*

LIST 2

Alturas flora (macrofossil), northeastern California, late Miocene (Axelrod 1944b).

- Angiosperms
  - Salicaceae
    - *Populus alexanderi (trichocarpa)*
    - *Populus payettensis (angustifolia)*
    - *Populus pliotremuloides (tremuloides)*
    - *Salix truckeana (nigra)*
    - *Salix vanorensis (caudata)*
    - *Salix wildcatensis (lasiolepis)*
  - Ulmaceae
    - *Ulmus moragensis (speciosa)*

LIST 3

Chalk Bluffs flora (macrofossil and pollen), western central Sierra Nevada, California, early Eocene (Leopold 1983; MacGinitie 1941).

- Pteridophytes
  - Cyatheaceae
    - *Hemitelia pinnata*
  - Schizaeaceae
    - *Lygodium kaulfussi*
- Gymnosperms
  - Cycadaceae
    - *Zamites californica*
- Angiosperms
  - Aceraceae
    - *Acer aequidentatum*
  - Aesclepiadaceae
    - *Asclepiadites laterita*
  - Anacardiaceae
    - *Rhus mixta*
  - Apocynaceae
    - *Nerium hinoidea*
    - *Tabernaemontana chrysophylloides*

Betulaceae
  Alnus peria
Burseraceae
  Canarium californicum
Caprifoliaceae
  Viburnum variabilis
Celastraceae
  Celastrus preangulata
Cercidiphyllaceae
  Cercidiphyllum elongatum
Combretaceae
  Terminalia estamina
Compositae
  Calycites mikanoides
Cornaceae
  Cornus kelloggii
Ebenaceae
  Diospyros retinervis
Euphorbiaceae
  Acalypha aequalis
  Mallotus riparius
Fagaceae
  Castanopsis longipetiolatum
  Quercus distincta
  Quercus eoxalapensis
  Quercus nevadensis
Hamamelidaceae
  Hamamelites voyana
  Liquidambar californicum
Icacinaceae
  Phytocrene sordida
Juglandaceae
  Carya sessilis
  Engelhardtia nevadensis
Lauraceae
  Cinnamomum acrodromum
  Cinnamomum dilleri
  Cryptocarya praesamarensis
  Laurophyllum fremontensis
  Laurophyllum litseaefolia
  Neolitsea lata
  Persea praelingue
  Persea pseudo-carolinensis
Leguminosae
  Dalbergia rubra
  Desmodium indentum
  Inga ionensis
  Pongamia ovata
  Strongylodon falcata
  Vouapa geminifolia
Liliaceae
  Smilax labidurommae
Magnoliaceae
  Magnolia dayana
Meliaceae
  Cedrela eolancifolia
Menispermaceae
  Hyperbaena diforma
Moraceae
  Artocarpus lessigiana
  Ficus densifolia
  Ficus goshenensis
Myrtaceae
  Calyptranthes myrtifolia
Nymphaeaceae
  Nelumbium lacunosum
Nyssaceae
  Nyssa californica
Oleaceae
  Fraxinus yubaensis
Palmae
  Sabalites californicus
Platanaceae
  Platanophyllum angustiloba
  Platanophyllum angustiloba var. *serrata*
  Platanophyllum whitneyi
  Platanus appendiculata
  Platanus coloradensis
Rhamnaceae
  Rhamnidium chaneyi
  Rhamnus calyptus
  Rhamnus plenus
Rosaceae
  Chrysobalanus eoicaco
  Vauquelinia exigua
Sabiaceae
  Meliosma truncata
Salicaceae
  Salix ionensis
Sapindaceae
  Cupania oregona
  Thouinopsis myricaefolia
Saxifragaceae
  Hydrangea californica
Simarubaceae
  Ailanthus lesquereuxi
Theaceae
  Gordonia egregia
Ulmaceae
  Chaetoptelea pseudo-fulva
Vitaceae
  Cissus pyriformus

Additions to the Chalk Bluffs flora from pollen identifications (Leopold 1983, 1984):

Gymnosperms
  Pinaceae (very small fraction; inblown)
    Abies
    Picea
    Pinus
Angiosperms
  Bombacaceae
    diverse genera
  Juglandaceae
    Juglans
    Carya
    Engelhardtia
    Platycarya
  Hamamelidaceae
    Liquidambar
  Icacinaceae
    Phytocrene
  Melicaceae
    Cedrela
  Platanaceae
    Platanus
  Schizaeaceae
    Anemia
  Tiliaceae
    diverse genera

LIST 4

Chalk Hills flora (macrofossil), western central Nevada, late Miocene (Axelrod 1962; Howard Schorn, letter to Constance I. Millar, July 1995).

Gymnosperms
  Cupressaceae
    Chamaecyparis linguaefolia (lawsoniana)
    Cupressus/Juniperus
  Pinaceae
    Abies concoloroides (concolor)
    Pinus balfouroides (balfouriana) (per Axelrod 1986)
    Pinus florissanti (ponderosa)
    Pinus wheeleri (monticola)
    Pseudotsuga sonomensis (menziesii)
    Tsuga (mertensiana)
  Taxodiaceae
    Sequoiadendron chaneyi (giganteum)
Angiosperms
  Berberidaceae
    Mahonia reticulata (nervosa, repens)
  Betulaceae
    Alnus smithiana (tenufolia)
    Betula thor (papyrifera)
  Ericaceae
    Arbutus matthesii (menziesii)
    Rhododendron gianellana (occidentale, albiflorum)

- Fagaceae
    - *Castanopsis sonomensis (chrysophylla)*
    - *Quercus simulata (myrsinaefolia)*
- Juglandaceae
    - *Carya bendirei (ovata)*
- Rhamnaceae
    - *Ceanothus chaneyi (integerrimus)*
    - *Ceanothus leitchii (velutinus)*
    - *Rhamnus precalifornica (californica)*
- Rosaceae
    - *Amelanchier alvordensis (alnifolia)*
    - *Holodiscus idahoensis (microphyllus, dumosus)*
    - *Prunus moragensis (emarginata)*
- Salicaceae
    - *Populus eotremuloides (trichocarpa)*
    - *Populus pliotremuloides (tremuloides)*
    - *Populus washoensis (grandidentata, tremula* var. *davidiana)*
    - *Salix knowltoni (lemmonii)*
    - *Salix laevigatoides (laevigata)*
    - *Salix owyheeana (hookeriana)*
- Saxifragaceae
    - *Ribes stanfordianum (sanguineum, nevadense)*

LIST 5

Chloropagus flora (macrofossil), western central Nevada, mid-Miocene (Axelrod 1956).

- Gymnosperms
    - Cupressaceae
        - *Juniperus nevadensis (utahensis, californica)*
        - *Thuja dimorpha (plicata)*
    - Pinaceae
        - *Abies concoloroides (concolor)*
        - *Picea sonomensis (breweriana)*
        - *Pinus wheeleri (lambertiana)*
    - Taxaceae
        - *Torreya nancyana (californica)*
- Angiosperms
    - Berberidaceae
        - *Mahonia marginata (beali)*
        - *Mahonia reticulata (repens)*
    - Fagaceae
        - *Quercus hannibali (chrysolepis)*
        - *Quercus simulata (myrsinaefolia)*
        - *Quercus wislizenoides (wislizenii)*
    - Leguminosae
        - *Cercis carsoniana*
        - *Robinia californica (neo-mexicana)*
    - Rosaceae
        - *Amelanchier apiculata (utahensis)*
        - *Cercocarpus linearifolium (ledifolius)*
    - Salicaceae
        - *Populus alexanderi (trichocarpa)*
        - *Populus payettensis (angustifolia)*
        - *Populus subwashoensis (tremula, grandidentata)*
        - *Salix knowltoni (lemmonii)*
        - *Salix payettensis (exigua)*
        - *Salix wildcatensis (lasiolepis)*
    - Typhaceae
        - *Typha lesquereuxi (latifolia)*

LIST 6

Crowley Point (Coso) flora (pollen), eastern central California, late Pliocene (Axelrod and Ting 1960). *Note:* This flora is a pollen site, interpretations are based on a very small number of grains (67), and species identifications may be incorrect. This flora should be treated with question.

- Gymnosperms
    - Cupressaceae
        - *Juniperus occidentalis*
        - *Juniperus osteosperma*
    - Pinaceae
        - *Pinus aristata* or *flexilis*
        - *Pinus lambertiana*
        - *Pinus* cf. *monophylla*
        - *Pinus ponderosa*
        - *Pseudotsuga taxifolia*
- Angiosperms
    - Berberidaceae
        - *Mahonia* sp.
    - Caprifoliaceae
        - *Symphoricarpos oreophilus*
    - Cornaceae
        - *Cornus californica*
        - *Cornus sessilus*
    - Fagaceae
        - *Quercus kelloggii*
    - Rhamnaceae
        - *Ceanothus cordulatus*
        - *Ceanothus integerrimus*
        - *Rhamnus crocea*
    - Rosaceae
        - *Cercocarpus betuloides*
        - *Rosa* sp.
    - Salicaceae
        - *Populus trichocarpa*
        - *Salix exigua*
        - *Salix lasiandra*
        - *Salix lasiolepis*
    - Saxifragaceae
        - *Ribes nevadense*
        - *Ribes viscosissimum*
    - Sterculiaceae
        - *Fremontia californica*
    - Ulmaceae
        - *Ulmus alata*

LIST 7

Darwin Summit (Coso) flora (pollen), eastern central California, late Pliocene (Axelrod and Ting 1960). *Note:* This flora is a pollen site, interpretations are based on a very small number of grains (17), and species identifications may be incorrect. This flora should be treated with question.

- Gymnosperms
    - Cupressaceae
        - *Calocedrus decurrens*
        - *Juniperus osteosperma*
    - Pinaceae
        - *Pinus aristata* or *flexilis*
        - *Pinus* cf. *monophylla*
        - *Pinus ponderosa*
    - Taxodiaceae
        - *Sequoiadendron giganteum*
- Angiosperms
    - Betulaceae
        - *Betula fontinalis*
    - Caprifoliaceae
        - *Symphoricarpos albus*
    - Cornaceae
        - *Cornus nuttallii*
    - Juglandaceae
        - *Pterocarya* sp.
    - Rhamnaceae
        - *Ceanothus cordulatus*
    - Salicaceae
        - *Salix lasiolepis*
    - Saxifragaceae
        - *Ribes roezlii*

LIST 8

Fallon flora (macrofossil), western central Nevada, mid-Miocene (Axelrod 1956).

- Gymnosperms
  - Cupressaceae
    - *Juniperus nevadensis (utahensis, californica)*
    - *Thuja dimorpha (plicata)*
  - Pinaceae
    - *Abies concoloroides (concolor)*
    - *Picea sonomensis (breweriana)*
    - *Pinus florissanti (ponderosa)*
  - Taxaceae
    - *Torreya nancyana (californica)*
  - Taxodiaceae
    - *Sequoiadendron chaneyi (giganteum)*
- Angiosperms
  - Berberidaceae
    - *Mahonia marginata (beali)*
    - *Mahonia reticulata (repens)*
  - Betulaceae
    - *Betula thor (papyrifera, occidentalis)*
  - Ericaceae
    - *Arbutus matthesii (menziesii)*
  - Fagaceae
    - *Quercus hannibali (chrysolepis)*
    - *Quercus simulata (myrsinaefolia)*
    - *Quercus wislizenoides (wislizenii)*
  - Leguminosae
    - *Sophora spokanensis (japonica)*
  - Oleaceae
    - *Fraxinus alcorni (velutina)*
  - Rosaceae
    - *Cercocarpus linearifolius (ledifolius)*
  - Salicaceae
    - *Populus eotremuloides (trichocarpa)*
    - *Populus subwashoensis (tremula, grandidentata)*
    - *Salix knowltoni (lemmonii)*
    - *Salix payettensis (exigua)*
  - Typhaceae
    - *Typha lesquereuxi (latifolia)*

LIST 9

Fingerrock flora (macrofossil), southwestern Nevada, mid-Miocene (Wolfe 1964).

- Gymnosperms
  - Cupressaceae
    - *Chamaecyparis nootkatensis*
  - Pinaceae
    - *Abies (concolor)*
    - *Picea magna*
    - *Pinus (monticola)*
    - *Pinus (ponderosa)*
  - Taxodiaceae
    - *Glyptostrobus* sp.
- Angiosperms
  - Aceraceae
    - *Acer bolanderi*
    - *Acer (macrophyllum)*
  - Berberidaceae
    - *Mahonia reticulata (repens)*
  - Betulaceae
    - *Alnus relata*
    - *Betula thor*
  - Cyperaceae
    - *Cyperacites* sp.
  - Ebenaceae
    - *Diospyros*
  - Ericaceae
    - *Arbutus traini (menziesii)*
  - Fagaceae
    - *Quercus (chrysolepis)*
    - *Quercus pseudolyrata*
    - *Quercus simulata (chrysolepis? myrsinaefolia)*
  - Juglandaceae
    - *Carya bendirei (tonkinensis)*
  - Platanaceae
    - *Platanus bendirei*
  - Salicaceae
    - *Populus lindgreni (heterophylla)*
  - Ulmaceae
    - *Ulmus newberryi*
    - *Zelkova oregoniana*

LIST 10

Forest flora (macrofossil), southern central Sierra Nevada, California, late Miocene (Chaney 1944; Knowlton 1911).

- Angiosperms
  - Aceraceae
    - *Acer arcticum*
    - *Acer* sp.
  - Fagaceae
    - *Quercus pseudo-chrysolepis (chrysolepis)*
    - *Quercus steenstrupiana?*
    - *Quercus transgressus*
  - Liliaceae
    - *Smilax diforma (rotundifolia)*
  - Platanaceae
    - *Platanus paucidentata (racemosa)*
  - Salicaceae
    - *Salix hesperia (lasiandra)*
  - Ulmaceae
    - *Ulmus californica (americana)*

LIST 11

Gillam Spring flora, northwestern Nevada, mid-Miocene (Axelrod and Schorn 1994). Species lists are by age of florules (upper = youngest; lower = oldest).

Upper Gillam Spring Florule

- Equisetales
  - Equisetaceae
    - *Equisetum*
- Gymnosperms
  - Cupressaceae
    - *Calocedrus*
    - *Chamaecyparis*
  - Pinaceae
    - *Abies*
    - *Picea lahontense*
    - *Picea magna*
    - *Picea sonomensis*
    - *Pinus (contorta)*
    - *Pinus (monticola)*
    - *Pinus* (three-needle)
    - *Pinus tiptonia*
  - Taxodiaceae
    - *Sequoia*
- Angiosperms
  - Aceraceae
    - *Acer chaneyi*
    - *Acer scottiae*
  - Berberidaceae
    - *Mahonia reticulata*
  - Betulaceae
    - *Betula smithiana*
  - Ericaceae
    - *Arbutus idahoensis*
    - *Vaccinium (sonomensis)*
  - Fagaceae
    - *Quercus hannibali*
    - *Quercus simulata*
  - Juglandaceae
    - *Pterocarya*
  - Oleaceae
    - *Fraxinus*

- Rosaceae
  - *Crataegus*
  - *Prunus chaneyi*
  - *Robinia*
- Salicaceae
  - *Salix*
  - *Salix boisensis*
  - *Salix pelviga*
- Typhaceae
  - *Typha*
- Ulmaceae
  - *Ulmus*

Cyperacites?
Eugenia nevadensis?

Middle Gillam Spring Florule

Gymnosperms
- Cupressaceae
  - *Chamaecyparis*
- Pinaceae
  - *Picea lahontense*
  - *Picea sonomensis*
  - *Pinus* (three-needle)
  - *Pinus tiptonia*

Angiosperms
- Aceraceae
  - *Acer osmonti*
  - *Acer schorni*
- Berberidaceae
  - *Mahonia reticulata*
- Betulaceae
  - *Alnus latahensis*
  - *Betula ashley*
  - *Betula smithiana*
- Ericaceae
  - *Arbutus idahoensis*
- Fagaceae
  - *Lithocarpus klamathensis*
  - *Quercus (ovata)*
  - *Quercus (oblonga)*
- Platanaceae
  - *Platanus*
- Rosaceae
  - *Cercocarpus antiquus*
- Salicaceae
  - *Salix* (two spp.)
- Typhaceae
  - *Typha*
- Ulmaceae
  - *Ulmus*

Pieris?

Lower Gillam Spring Florule

Gymnosperms
- Cupressaceae
  - *Chamaecyparis* sp.
  - *Thuja?* sp.
- Pinaceae
  - *Picea magna*
  - *Pinus tiptonia*

Angiosperms
- Aceraceae
  - *Acer (bolanderi)*
  - *Acer chaneyi*
  - *Acer (glabrum)*
  - *Acer (nigra)*
  - *Acer tyrrelli*
- Berberidaceae
  - *Mahonia*
- Betulaceae
  - *Betula vera*
- Ericaceae
  - *Arbutus idahoensis*
  - *Vaccinium*
- Juglandaceae
  - *Fagus washoensis*
  - *Lithocarpus*
  - *Pterocarya*
  - *Quercus eoprinus*
  - *Quercus hannibali (chrysolepis)*
  - *Quercus simulata*
- Oleaceae
  - *Fraxinus*
- Platanaceae
  - *Platanus*
- Rhamnaceae
  - *Rhamnus*
- Rosaceae
  - *Amelanchier*
  - *Prunus cassianna*
- Salicaceae
  - *Populus eotremuloides (tremuloides)*
  - *Salix*
- Saxifragaceae
  - *Hydrangea?*
- Typhaceae
  - *Typha*
- Ulmaceae
  - *Zelkova*

LIST 12

Haiwee (Coso) flora (pollen), southeastern Sierra Nevada, California, late Pliocene (Axelrod and Ting 1960). *Note:* This flora is a pollen site, interpretations are based on a very small number of grains (123), and species identifications may be incorrect. This flora should be treated with question.

Gymnosperms
- Cupressaceae
  - *Calocedrus decurrens*
- Pinaceae
  - *Abies concolor*
  - *Abies grandis*
  - *Abies magnifica*
  - *Pinus aristata* or *flexilis*
  - *Pinus jeffreyi*
  - *Pinus lambertiana*
  - *Pinus* cf. *monophylla*
  - *Pinus monticola*
  - *Pinus murrayana*
  - *Pinus ponderosa*
  - *Pseudotsuga taxifolia*
  - *Tsuga heterophylla*
- Taxodiaceae
  - *Sequoiadendron giganteum*

Angiosperms
- Betulaceae
  - *Alnus rhombifolia*
  - *Betula fontinalis*
  - *Corylus californica*
- Caprifoliaceae
  - *Sambucus glauca*
- Cornaceae
  - *Cornus nuttallii*
- Fagaceae
  - *Quercus kelloggii*
  - *Quercus wislizenii*
- Garryaceae
  - *Garrya* sp.
- Juglandaceae
  - *Juglans nigra*
- Papaveraceae
  - *Dendromecon rigida*
- Rhamnaceae
  - *Ceanothus cordulatus*
  - *Ceanothus integerrimus*
- Rosaceae
  - *Amelanchier alnifolia*
  - *Holodiscus dumosa*
  - *Rubus parviflorus*
- Salicaceae
  - *Salix exigua*
  - *Salix lasiandra*
- Saxifragaceae
  - *Ribes cereum*
  - *Ribes montigenum*
  - *Ribes nevadense*
  - *Ribes roezlii*

- Sterculiaceae
  - *Fremontia californica*
- Ulmaceae
  - *Zelkova* sp.

LIST 13

Lake Tahoe flora (pollen), central Sierra Nevada, California, late Pliocene (Adam 1973).

- Gymnosperms
  - Pinaceae
    - *Abies*
    - *Libocedrus*
    - *Picea*
    - *Pinus*
    - *Pseudotsuga*
    - *Tsuga*
- Angiosperms
  - Amaranthaceae
    - *Amaranthus?*
  - Betulaceae
    - *Alnus*
    - *Betula*
  - Caryophyllaceae
  - Chenopodiaceae
    - *Sarcobatus*
  - Compositae
    - *Artemesia*
  - Cornaceae
    - *Cornus*
  - Cyperaceae
  - Ericaceae
  - Euphorbiaceae
    - *Euphorbia*
  - Fagaceae
    - *Quercus*
  - Gramineae
  - Juglandaceae
    - *Juglans*
  - Loranthaceae
    - *Arceuthobium*
  - Malvaceae
  - Oleaceae
    - *Fraxinus*
  - Onagracaceae
    - *Oenothera?*
  - Polygonaceae
    - *Eriogonum*
    - *Polygonum*
  - Ranunculaceae
  - Rhamnaceae
  - Rosaceae

LIST 14

La Porte flora (macrofossil), western central Sierra Nevada, California, early Oligocene (Potbury 1935).

- Pteridophytes
  - Polypodiaceae
    - *Polypodites* sp.
- Gymnosperms
  - Cycadaceae
    - *Zamia mississippiensis* var. *macrophylla* (spp.)
  - Taxaceae
    - *Cephalotaxus californica (argotaenia)*
- Angiosperms
  - Apocynaceae
    - *Tabernaemontana intermedia (lanceolata, rupicola)*
  - Aquifoliaceae
    - *Ilex oregona (paraguensis)*
  - Cornaceae
    - *Cornus kelloggii* (spp.)
  - Dilleniaceae
    - *Davilla intermedia (aspera, rugosa)*
  - Euphorbiaceae
    - *Acalypha serrulata (schlechtendahliana)*
    - *Aleurites americana (triloba)*
    - *Euphorbiophyllum multiformum (Drypetes alba)*
    - *Microdesmis occidentalis (casearifolia)*
  - Fagaceae
    - *Quercus nevadensis (hainanensis)*
    - *Quercus suborbicularia* (spp.)
  - Hamamelidaceae
    - *Liquidambar californicum (styraciflua)*
  - Lauraceae
    - *Cinnamomum acrodromum (mercadoi)*
    - *Cinnamomum dilleri (pedunculatum)*
    - *Laurophyllum intermedium (Misanteca capitata)*
    - *Laurophyllum raminervum* (*Ocotea* sp.)
    - *Ocotea eocernua (cernua)*
    - *Persea praelingue (lingue)*
    - *Persea pseudo-carolinensis (podadenia)*
  - Leguminosae
    - *Leguminosites falcatum (Prioria copaifera)*
    - *Lonchocarpus coriaceus (hondurensis)*
    - *Mimosites acutifolius (Pithecolobium corymbosum)*
    - *Sophora repandifolia* (spp.)
  - Liliaceae
    - *Smilax goshenensis (mexicana)*
  - Menispermaceae
    - *Cissampelos rotundifolia (pareira)*
    - *Hyperbaena diforma (smilacina)*
  - Moraceae
    - *Ficus goshenensis (bonplandiana)*
  - Palmae
    - *Sabalites rhapifolius (Rhapis flabelliformis)*
  - Rhamnaceae
    - *Rhamnidium chaneyi (elaeocarpum)*
  - Sabiaceae
    - *Meliosma goshenensis (panamensis)*
  - Sapotaceae
    - *Chrysophyllum conforme (mexicanum)*
  - Sterculiaceae
    - *Sterculia ovata (blancoi, lanceolata)*
  - Styracaceae
    - *Styrax curvatus (argenteum)*
  - Tiliaceae
    - *Columbia occidentalis (longipetiolata)*
  - Ulmaceae
    - *Ulmus pseudo-fulva (mexicana)*
  - Verbenaceae
    - *Petrea rotunda (arborea, volubilis)*

LIST 15

Middlegate flora (macrofossil), western central Nevada, mid-Miocene (Axelrod 1956, 1976, 1986).

- Equisetales
  - Equisetaceae
    - *Equisetum alexanderi* (sp.)
- Gymnosperms
  - Cupressaceae
    - *Thuja dimorpha (plicata)*
  - Pinaceae
    - *Abies concoloroides (concolor)*
    - *Abies scherrii (bracteata)* (Axelrod 1976)
    - *Picea magna (polita, neovietchii)*
    - *Picea sonomensis (breweriana)*
    - *Pinus (ponderosa)* (Axelrod 1986)
  - Taxodiaceae
    - *Sequoiadendron chaneyi (giganteum)*
- Angiosperms
  - Aceraceae
    - *Acer alvordensis (macrophyllum)*
    - *Acer arida (grandidentatum)*
    - *Acer middlegatei (saccharinum)*
    - *Acer minor (negundo)*
  - Anacardiaceae
    - *Rhus alvordensis (glabra)*
  - Berberidaceae
    - *Mahonia marginata (beali)*
    - *Mahonia reticulata (repens)*

- Betulaceae
  - *Betula thor (papyrifera, occidentalis)*
  - *Betula vera (lenta)*
- Ericaceae
  - *Arbutus prexalapensis (xalapensis)*
- Fagaceae
  - *Quercus hannibali (chrysolepis)*
  - *Quercus simulata (myrsinaefolia)*
  - *Quercus wislizenoides (wislizenii)*
- Lauraceae
  - *Persea coalingensis (podadenia)*
- Leguminosae
  - *Robinia californica (neo-mexicana)*
- Myricaceae
  - *Comptonia parvifolia (asplenifolia)*
- Nymphaeceae
  - *Nymphaeites nevadensis* (*Nymphaea* spp.)
- Oleaceae
  - *Fraxinus coulteri (oregona, americana)*
  - *Fraxinus millsiana (anomala)*
- Platanaceae
  - *Platanus dissecta (orientalis)*
  - *Platanus paucidentata (racemosa)*
- Rhamnaceae
  - *Ceanothus precuneatus (cuneatus)*
- Rosaceae
  - *Cercocarpus antiquus (betuloides)*
  - *Cercocarpus holmesii (paucidentatus)*
  - *Crataegus middlegatei (chrysophlla, erythropoda)*
  - *Crataegus pacifica (euneata, monogyna)*
  - *Prunus morganensis (emarginata)*
- Salicaceae
  - *Populus eotremuloides (trichocarpa)*
  - *Populus payettensis (angustifolia)*
  - *Populus pliotremuloides (tremuloides)*
  - *Salix hesperia (lasiandra)*
  - *Salix knowltoni (lemmonii)*
  - *Salix truckeana (gooddingii)*
  - *Salix wildcatensis (lasiolepis)*
- Styraceaceae
  - *Styrax middlegatei (californica)*
- Typhaceae
  - *Typha lesquereuxi (latifolia)*

LIST 16

Mohawk flora (macrofossil), northern Sierra Nevada, California, mid-Miocene (Axelrod 1944; Knowlton 1911).

- Gymnosperms
  - Pinaceae
    - *Pinus (lambertiana)*
- Angiosperms
  - Betulaceae
    - *Alnus* sp.
  - Ericaceae
    - *Arbutus matthesii (menziesii)*
  - Fagaceae
    - *Quercus payettensis*
  - Hamamelidaceae
    - *Liquidambar (styraciflua)*
  - Juglandaceae
    - *Carya egregia (ovata)*
    - *Juglans (californica)*
  - Lauraceae
    - *Laurus californica*
    - *Persea pseudo-carolinensis (podadenia)*
  - Magnoliaceae
    - *Magnolia dayana*
  - Rhamnaceae
    - *Berchemia multinervis (scandens)*
  - Salicaceae
    - *Populus eotremuloides (trichocarpa)*
    - *Salix hesperia (lasiandra)*

LIST 17

Mount Reba flora (macrofossil) (partial list), western central Sierra Nevada, California, early Pliocene (Axelrod 1976, 1977).

- Gymnosperms
  - Cupressaceae
    - *Cupressus (cashmeriana)*
  - Pinaceae
    - *Abies (concolor)*
    - *Pseudotsuga (menziesii)*
  - Taxodiaceae
    - *Sequoiadendron (giganteum)*
- Angiosperms
  - Fagaceae
    - *Lithocarpus (densiflora)*
    - *Quercus (chrysolepis)*

LIST 18

Nova flora (pollen), eastern central California, late Pliocene (Axelrod and Ting 1960). *Note:* This flora is a pollen site, interpretations are based on a very small number of grains (77), and species identifications may be incorrect. This flora should be treated with question.

- Gymnosperms
  - Cupressaceae
    - *Juniperus osteosperma*
  - Ephedraceae
    - *Ephedra nevadensis*
  - Pinaceae
    - *Abies* sp.
    - *Pinus attenuata*
    - *Pinus balfouriana*
    - *Pinus jeffreyi*
    - *Pinus lambertiana*
    - *Pinus* cf. *monophylla*
    - *Pinus ponderosa*
- Angiosperms
  - Betulaceae
    - *Alnus rhombifolia*
    - *Corylus californica*
  - Juglandaceae
    - *Juglans californica*
    - *Juglans rupestris*
    - *Pterocarya* sp.
  - Rhamnaceae
    - *Ceanothus cordulatus*
    - *Rhamnus californica*
  - Rosaceae
    - *Cercocarpus betuloides*
    - *Holodiscus* sp.
  - Salicaceae
    - *Populus angustifolia*
    - *Salix exigua*
    - *Salix lasiolepis*
  - Ulmaceae
    - *Ulmus alata*

LIST 19

Oakdale flora (macrofossil), western central Sierra Nevada, California, early Pliocene (Axelrod 1944a).

- Angiosperms
  - Berberidaceae
    - *Mahonia marginata (fremontii)*
  - Ericaceae
    - *Arctostaphylos oakdalensis (mariposa)*
  - Fagaceae
    - *Quercus dispersa (dumosa)*
    - *Quercus douglasoides (douglasii)*
    - *Quercus wislizenoides (wislizenii)*

- Lauraceae
  - *Umbellularia salicifolia (californica)*
- Leguminosae
  - *Robinia californica (neo-mexicana)*
- Rhamnaceae
  - *Ceanothus precuneatus (cuneatus)*
- Rosaceae
  - *Photinia sonomensis (arbutifolia)*
- Salicaceae
  - *Populus alexanderi (trichocarpa)*
  - *Populus paucidentata (acuminata)*
  - *Populus pliotremuloides (tremuloides)*
  - *Salix wildcatensis (lasiolepis)*
- Sapindaceae
  - *Sapindus oklahomensis (drummondii)*
- Saxifragaceae
  - *Ribes mehrtensis (quercetorum)*
- Ulmaceae
  - *Celtis kansana (reticulata)*

LIST 20

Owens Gorge (Coso) flora (pollen), eastern central Sierra Nevada, California, late Pliocene (Axelrod and Ting 1960). *Note:* This flora is a pollen site, interpretations are based on a very small number of grains (162), and species identifications may be incorrect. This flora should be treated with question.

- Gymnosperms
  - Cupressaceae
    - *Calocedrus decurrens*
  - Pinaceae
    - *Abies concolor*
    - *Abies magnifica*
    - *Pinus aristata* or *flexilis*
    - *Pinus jeffreyi*
    - *Pinus lambertiana*
    - *Pinus monticola*
    - *Pinus murrayana*
    - *Pseudotsuga taxifolia*
    - *Tsuga heterophylla*
  - Taxodiaceae
    - *Sequoiadendron giganteum*
- Angiosperms
  - Aceraceae
    - *Acer glabrum*
  - Betulaceae
    - *Corylus californica*
  - Caprifoliaceae
    - *Symphoricarpos albus*
  - Cornaceae
    - *Cornus californica*
    - *Cornus nuttallii*
  - Fagaceae
    - *Quercus agrifolia*
    - *Quercus breweri*
    - *Quercus kelloggii*
    - *Quercus lobata*
    - *Quercus wislizenii*
  - Juglandaceae
    - *Juglans cinera*
    - *Juglans nigra*
    - *Pterocarya* sp.
  - Salicaceae
    - *Salix exigua*
    - *Salix lasiandra*
    - *Salix lasiolepis*
    - *Salix nuttallii*
  - Saxifragaceae
    - *Ribes monteginum*
  - Sterculiaceae
    - *Fremontia californica*

LIST 21

Panamint Springs (Coso) flora (pollen), eastern central Sierra Nevada, California, late Pliocene (Axelrod and Ting 1960). *Note:* This flora is a pollen site, interpretations are based on a very small number of grains (45), and species identifications may be incorrect. This flora should be treated with question.

- Gymnosperms
  - Pinaceae
    - *Pinus attenuata*
    - *Pinus coulteri*
    - *Pinus jeffreyi*
    - *Pinus* cf. *monophylla*
    - *Pinus ponderosa*
- Angiosperms
  - Cornaceae
    - *Cornus nuttallii*
  - Fagaceae
    - *Castanopsis chrysolepis*
    - *Quercus kelloggii*
    - *Quercus lobata*
  - Garryaceae
    - *Garrya* sp.
  - Juglandaceae
    - *Juglans californica*
    - *Juglans rupestris*
  - Oleaceae
    - *Fraxinus velutina*
  - Rosaceae
    - *Holodiscus* sp.
  - Saxifragaceae
    - *Ribes cereum*
  - Sterculiaceae
    - *Fremontia californica*
  - Typhaceae
    - *Typha latifolia*
  - Ulmaceae
    - *Ulmus alata*

LIST 22

Purple Mountain flora (macrofossil), western central Nevada, mid-Miocene (Axelrod 1976, 1995).

- Gymnosperms
  - Cupressaceae
    - *Chamaecyparis sierrae (lawsoniana)*
  - Pinaceae
    - *Abies concoloroides (concolor)*
    - *Abies klamathensis (shastensis)*
    - *Abies scherrii (bracteata)*
    - *Picea magna (polita)*
    - *Picea sonomensis (breweriana)*
    - *Pinus quinifolia (monticola)*
    - *Pseudotsuga sonomensis (menziesii)*
  - Taxodiaceae
    - *Sequoiadendron chaneyi (giganteum)*
- Angiosperms
  - Aceraceae
    - *Acer columbianum (glabrum)*
    - *Acer middlegateii (saccharinum)*
    - *Acer oregonianum (macrophyllum)*
  - Berberidaceae
    - *Mahonia reticulata (pinnata-insularis)*
    - *Mahonia simplex (japonica, lomariifolia)*
  - Betulaceae
    - *Betula lacustris (papyrifera)*
  - Ericaceae
    - *Arbutus matthesii (menziesii)*
  - Fagaceae
    - *Castanopsis sonomensis (chrysophylla)*
    - *Lithocarpus klamathensis (densiflorus)*
    - *Quercus hannibali (chrysolepis)*
  - Leguminosae
    - *Amorpha oklahomensis (fruticosa)*

- Rhamnaceae
    - *Ceanothus leitchii (velutinus)*
    - *Rhamnus precalifornica (californica)*
- Rosaceae
    - *Amelanchier alvordensis (alnifolia)*
    - *Cercocarpus antiquus (betuloides)*
    - *Cercocarpus holmesii (paucidentatus)*
    - *Heteromeles sonomensis (arbutifolia)*
    - *Holodiscus idahoensis (glabrescens)*
    - *Lyonothamnus parvifolia* (extinct sp.)
    - *Sorbus* sp. *(aucuparia)*
- Salicaceae
    - *Populus eotremuloides (trichocarpa)*
    - *Populus payettensis (angustifolia)*
    - *Populus pliotremuloides (tremuloides)*
    - *Salix knowltonii (lemmonii)*
    - *Salix* sp. *(melanopsis)*
    - *Salix* sp. *(nigra)*
    - *Salix wildcatensis (lasiolepis)*

LIST 23

Remington Hill flora (macrofossil), western central Sierra Nevada, California, late Miocene (Condit 1944).

- Gymnosperms
    - Cupressaceae
        - *Chamaecyparis gracilis (lawsoniana)*
    - Taxodiaceae
        - *Sequoia langsdorfii (sempervirens)*
- Angiosperms
    - Aceraceae
        - *Acer negundoides (negundo)*
    - Berberidaceae
        - *Mahonia malheurensis*
    - Caprifoliaceae
        - *Viburnum platyspermum (ellipticum)*
    - Ericaceae
        - *Arbutus matthesii (menziesii)*
        - *Arctostaphylos martzi (manzanita)*
        - *Leucothoe* sp. *(davisiae)?*
    - Fagaceae
        - *Quercus douglasoides (douglasii)*
        - *Quercus prelobata (lobata)*
        - *Quercus pseudo-lyrata (kelloggii)*
        - *Quercus remingtoni (morehus)*
        - *Quercus simulata (myrsinaefolia)*
        - *Quercus winstanleyi (aliena)*
        - *Quercus wislizenoides (wislizenii)*
    - Hamamelidaceae
        - *Liquidambar pachyphyllum (styraciflua)*
    - Hippocastanaceae
        - *Aesculus preglabra (glabra)*
    - Juglandaceae
        - *Juglans pseudomorpha (nigra)*
    - Lauraceae
        - *Persea pseudo-carolinensis (borbonia)*
        - *Umbellularia salicifolia (californica)*
    - Liliaceae
        - *Smilax diforma (rotundifolia)*
    - Platanaceae
        - *Platanus paucidentata (racemosa)*
    - Rhamnaceae
        - *Berchemia multinervis (scandens)*
        - *Ceanothus precuneatus (cuneatus)*
    - Rosaceae
        - *Crataegus newberryi (pinnatifida)*
        - *Prunus petrosperma (ilicifolia)*
    - Salicaceae
        - *Populus alexanderi (trichocarpa)*
        - *Populus pliotremuloides (tremuloides)*
        - *Populus prefremontii (fremontii)*
        - *Salix hesperia (lasiandra)*
    - Sapindaceae
        - *Ungnadia clarki* (spp.)
    - Ulmaceae
        - *Ulmus californica (americana)*
    - Vitaceae
        - *Vitis bonseri*

LIST 24

San Joaquin (Coso) flora (pollen), eastern central Sierra Nevada, California, late Pliocene (Axelrod and Ting 1960). *Note:* This flora is a pollen site, interpretations are based on a very small number of grains (59), and species identifications may be incorrect. This flora should be treated with question.

- Gymnosperms
    - Cupressaceae
        - *Calocedrus decurrens*
        - *Chamaecyparis lawsoniana*
        - *Juniperus occidentalis*
    - Pinaceae
        - *Abies concolor*
        - *Abies grandis*
        - *Abies magnifica*
        - *Pinus aristata* or *flexilis*
        - *Pinus balfouriana*
        - *Pinus lambertiana*
        - *Pinus monticola*
        - *Pinus murrayana*
        - *Pseudotsuga taxifolia (menziesii)*
        - *Tsuga mertensiana*
    - Taxaceae
        - *Taxus brevifolia*
- Angiosperms
    - Aceraceae
        - *Acer circinatum*
    - Anacardiaceae
        - *Rhus diversifolia*
    - Juglandaceae
        - *Carya* sp.
    - Rhamnaceae
        - *Ceanothus cordulata*
        - *Rhamnus crocea*
    - Salicaceae
        - *Salix lasiolepis*
        - *Salix scouleriana*
    - Saxifragaceae
        - *Ribes cereum*
        - *Ribes nevadense*

LIST 25

Stewart Spring flora (macrofossil and pollen), western central Nevada, mid-Miocene (Wolfe 1964 [macrofossil]; Schorn 1984 [pollen]).

- Gymnosperms
    - Cupressaceae
        - *Chamaecyparis (nootkatensis)*
        - *Juniperus nevadensis (californica, utahensis)*
    - Pinaceae
        - *Abies (concolor)*
        - *Larix (occidentalis)*
        - *Picea (breweriana)*
        - *Picea magna*
        - *Pinus (edulis)*
        - *Pinus (monticola)*
        - *Pinus (ponderosa)*
        - *Tsuga (heterophylla)*
    - Taxodiaceae
        - *Sequoiadendron*[a]
- Angiosperms
    - Anacardiaceae
        - *Astronium mawbyi*
        - *Rhus (integrifolia)*
        - *Schinus savegei (gracilepis)*
    - Berberidaceae
        - *Mahonia reticulata (repens)*
    - Betulaceae
        - *Betula* sp. *(lacustris)*
    - Caprifoliaceae
        - *Sambucus* sp.

- Cyperaceae
  - *Cyperacites* sp.
- Eleagnaceae
  - *Eleagnus cedrusensis (utils)*
- Ericaceae
  - *Arbutus traini (menziesii)*
  - *Arctostaphylos (masoni)*
- Fagaceae
  - *Quercus cedrusensis*
  - *Quercus (chrysolepis)*
- Garryaceae
  - *Garrya axelrodi (elliptica)*
- Graminae
  - *Poacites* sp.
- Juglandaceae
  - *Carya*[a]
  - *Juglans (major)*
- Oleaceae
  - *Fraxinus millsiana*
- Rhamnaceae
  - *Colubrina* sp.
- Rosaceae
  - *Amelanchier (cusicki)*
  - *Cercocarpus (antiquus)*
  - *Holodiscus fryi (dumosus)*
  - *Lyonothamnus parvifolius*
  - *Peraphyllum (vaccinifolium)*
  - *Prunus* sp.
  - *Rosa* sp.
  - *Sorbus (acuparia)*
- Salicaceae
  - *Populus cedrusensis (brandegeei)*
  - *Populus (tremuloides)*
  - *Populus (trichocarpa)*
  - *Populus washoensis (grandidentata? bonatti?)*
  - *Salix pelviga*
- Sapindaceae
  - *Sapindus* sp.
- Saxifragaceae
  - *Philadelphus nevadensis*
  - *Ribes webbi (cereum)*
- Ulmaceae
  - *Ulmus*[a]
  - *Zelkova*[a]

[a] Pollen taxon is additional to macrofossil list.

LIST 26

Susanville Complex flora (macrofossil), northeastern Sierra Nevada, California, mid-Eocene (Knowlton 1911; Wolfe and Hopkins 1967).

Oreodaphne litsaeformis

- Angiosperms
  - Araliaceae
    - *Aralia lasseniana*
  - Fagaceae
    - *Quercus moorii*
    - *Quercus olafensi*
  - Juglandaceae
    - *Juglans rugosa*
  - Lauraceae
    - *Cinnamomum scheuchzeri*
    - *Laurus californica*
    - *Laurus grandis*
  - Leguminosae
    - *Leguminosites* sp.
  - Magnoliaceae
    - *Magnolia hilgardiana*
    - *Magnolia ingelfieldi*

LIST 27

Table Mountain flora (macrofossil), western central Sierra Nevada, California, late Miocene (Condit 1944).

- Gymnosperms
  - Pinaceae
    - *Pinus pretuberculata (attenuata)*
- Angiosperms
  - Aceraceae
    - *Acer bolanderi (acuminata)*
  - Anacardiaceae
    - *Rhus mensae (laurina)*
  - Aquifoliaceae
    - *Ilex opacoides (opaca)*
  - Berberidaceae
    - *Mahonia prelanceolata (lanceolata)*
  - Cornaceae
    - *Cornus ovalis (alternifolia)*
    - *Nyssa elaenoides (sylvatica)*
  - Ericaceae
    - *Arbutus matthesii (menziesii)*
    - *Rhododendron sierrae (rockii)*
  - Fagaceae
    - *Quercus bockeei* (Asian type)
    - *Quercus convexa (engelmannii)*
    - *Quercus dispersa (dumosa)*
  - Juglandaceae
    - *Carya typhinoides (cordiformis)*
  - Lauraceae
    - *Persea coalingensis (borbonia)*
    - *Umbellularia salicifolia (californica)*
  - Leguminosae
    - *Cercis buchananensis (canadensis)*
    - *Gleditsia* (spp.)
    - *Robinia californica (neo-mexicana)*
  - Magnoliaceae
    - *Magnolia californica (grandiflora)*
  - Oleaceae
    - *Forestiera buchananensis (neo-mexicana)*
  - Platanaceae
    - *Platanus dissecta (racemosa)*
  - Rhamnaceae
    - *Berchemia multinervis (scandens)*
  - Rosaceae
    - *Cercocarpus antiquus (betuloides)*
    - *Crataegus newberryi (pinnatifida)*
  - Salicaceae
    - *Salix californica (breweri)*
  - Saxifragaceae
    - *Philadelphus nevadensis (lewisii)*
  - Ulmaceae
    - *Celtis kansana (reticulata)*
    - *Ulmus californica (americana)*

LIST 28

Tehachapi flora (macrofossil), southern Sierra Nevada, California, mid-Miocene (Axelrod 1939; Chaney 1944).

- Equisetales
  - Equisetaceae
    - *Equisetum* sp.
- Filicales
  - Polypodiaceae
    - *Pteris calabazensis*
- Gymnosperms
  - Cupressaceae
    - *Cupressus mohavensis (arizonica)*
  - Pinaceae
    - *Pinus lindgreni (cembroides)*
- Angiosperms
  - Anacardiaceae
    - *Rhus obovata (virens)*
    - *Rhus preintegrifolia (integrifolia)*
    - *Rhus sonorensis*
  - Berberidaceae
    - *Mahonia mohavensis (fremontii)*

- Burseraceae
  - *Bursera* sp.
- Caprifoliaceae
  - *Viburnum* sp. *(stenocalyx)*
- Ericaceae
  - *Arbutus mohavensis (peninsularis)*
  - *Arbutus prexalapensis (xalapensis)*
  - *Arctostaphylos mohavensis* (sp.)
- Euphorbiaceae
  - *Euphorbia mohavensis (hindsiana)*
- Fagaceae
  - *Quercus browni (chrysolepis)*
  - *Quercus convexa (engelmanni)*
  - *Quercus declinata (tomentella)*
  - *Quercus dispersa (dumosa)*
  - *Quercus pliopalmeri (paleri)*
  - *Quercus turneri (arizonica)*
- Juncaceae
  - *Juncus* sp.
- Lauraceae
  - *Persea* sp. *(hartwegii)*
  - *Umbellularia dayana (californica)*
- Leguminosae
  - *Amorpha oblongifolia (californica)*
  - *Diphysa californica (suberosa)*
  - *Leucanea californica (microcarpa)*
  - *Pithecolobium miocenicum (dulce)*
  - *Pithecolobium mohavense (mexicanum)*
  - *Prosopis pliocenica (juliflora)*
  - *Robinia californica (neo-mexicana)*
- Melicaceae
  - *Cedrela oregoniana* (sp.)
- Moraceae
  - *Ficus* sp. *(palmeri)*
- Myricaceae
  - *Myrica mohavensis (mexicana)*
- Oleaceae
  - *Foresteria* sp. *(reticulata)*
  - *Fraxinus mohavensis (macropetala)*
- Palmaceae
  - *Erythea californica (brandegeei)*
  - *Sabal miocenica (uresana)*
- Rhamnaceae
  - *Ceanothus precrassifolius (crassifolius)*
  - *Ceanothus precuneata (cuneatus)*
  - *Colubrina lanceolata (arborea)*
  - *Condalia mohavensis (lycoides)*
  - *Karwinskia californica (humboldtiana)*
  - *Rhamnus precalifornica (californica)*
- Rosaceae
  - *Cercocarpus antiquus (betuloides)*
  - *Cercocarpus preledifolius (ledifolius)*
  - *Chamaebatiaria creedensis (millefolium)*
  - *Holodiscus elliptica (discolor)*
  - *Lyonothamnus mohavensis (floribundus)*
  - *Photinia (Heteromeles)* sp. *(arbutifolia)*
  - *Platanus paucidentata (racemosa)*
  - *Prunus masoni (lyoni)*
  - *Prunus preandersonii (andersonii)*
  - *Prunus prefasciculata (fasciculata)*
  - *Prunus prefremontii (fremontii)*
  - *Rosa miocenica (mohavensis)*
- Salicaceae
  - *Populus alexanderi (trichocarpa)*
  - *Populus lesquereuxi (angustifolia)*
  - *Populus pliotremuloides (tremuloides)*
  - *Populus prefremontii (fremontii)*
  - *Populus sonorensis (monticola)*
  - *Salix coalingensis (lasiolepis)*
  - *Salix kernensis (bonplandiana)*
- Sapindaceae
  - *Dodonea californica (viscosa)*
- Sapotaceae
  - *Bumelia florissanti (lanuginosa)*
- Saxifragaceae
  - *Philadelphus bendirei (lewisii)*
- Sterculiaceae
  - *Fremontia trilobata (californica)*
- Typhaceae
  - *Typha lesquereuxi* (sp.)
- Ulmaceae
  - *Celtis kansana (reticulata)*

LIST 29

Tulelake flora (pollen), northeastern California, late Pliocene (Adam et al. 1990; Adam et al. 1989).

- Gymnosperms
  - Cupressaceae
    - TCT *(Taxodiaceae-Cupressaceae-Taxaceae)* (probably *Juniperus occidentalis* or *Calocedrus decurrens*)
  - Pinaceae
    - *Pinus*
- Angiosperms
  - Chenopodiaceae-Amaranthus
  - Compositae
    - *Artemisia*
  - Cyperaceae
  - Fagaceae
    - *Quercus*
  - Poaceae

LIST 30

Upper Cedarville 49 Camp flora (macrofossil), northwestern Nevada, mid-Miocene (Chaney 1959; LaMotte 1935, 1936).

- Lycopods
  - Lycopodiaceae
    - *Lycopodium prominens (obscurum)*
- Gymnosperms
  - Cupressaceae
    - *Chamaecyparis gilmoreae (nootkatensis)*
  - Ginkgoaceae
    - *Ginkgo adiantoides (biloba)*
  - Pinaceae
    - *Abies laticarpus (magnifica)*
    - *Pinus monticolensis (monticola)*
    - *Pinus russelli (ponderosa)*
    - *Pseudotsuga masoni (menziesii)*
  - Taxaceae
    - *Torreya bonseri (californica)*
  - Taxodiaceae
    - *Sequoia langsdorfii (sempervirens)*
- Angiosperms
  - Aceraceae
    - *Acer merriami (macrophyllum)*
    - *Acer negundoides (negundo)*
    - *Acer osmonti (glabrum)*
  - Araliaceae
    - *Oreopanax conditi (taubertianum)*
  - Berberidaceae
    - *Odostemon simplex (nervosus)*
  - Betulaceae
    - *Alnus carpinoides (rubra)*
    - *Ostrya oregoniana (virginiana)*
  - Cercidiphyllaceae
    - *Cercidiphyllum crenatum (japonicum)*
  - Ericaceae
    - *Arbutus matthesii (menziesii)*
  - Fagaceae
    - *Castanea lesquereuxi (pumila)*
    - *Castanopsis chrysophylloides (chrysophylla)*
    - *Fagus washoensis (longipetiolata)*
    - *Quercus consimilis (myrsinaefolia)*
    - *Quercus distincta (agrifolia)*
    - *Quercus pseudo-lyrata (kelloggii)*
  - Juglandaceae
    - *Carya egregia (ovata)*
  - Lauraceae
    - *Umbellularia oregonensis (californica)*
  - Leguminosae
    - *Cercis spokanensis (occidentalis)*
    - *Leguminosites vicicarpus*
  - Menispermaceae
    - *Cebatha heteromorpha (triloba)*
  - Oleaceae
    - *Fraxinus* sp. *(oregona)*

- Platanaceae
  - *Platanus dissecta (racemosa)*
- Rosaceae
  - *Crataegus newberryi (pinnatifida)*
  - *Prunus masoni (integrifolia)*
  - *Sorbus chaneyi (alnifolia)*
- Rutaceae
  - *Ptelea miocenica (trifoliata)*
- Salicaceae
  - *Populus eotremuloides (trichocarpa)*
- Sapindaceae
  - *Sapindus oregonianus (mukorossi)*
- Saxifragaceae
  - *Ribes* sp. *(lacustre)*
- Sparganiaceae
  - *Sparganium praesimplex (simplex)*
- Tiliaceae
  - *Tilia aspera (mandshurica)*
- Ulmaceae
  - *Ulmus speciosa (americana)*

LIST 31

Upper Cedarville Pit River flora (macrofossil), northern Sierra Nevada, California, late Miocene (LaMotte 1935, 1936).

- Gymnosperms
  - Cupressaceae
    - *Chamaecyparis gilmoreae (nootkatensis)*
  - Ginkgoaceae
    - *Ginkgo adiantoides (biloba)*
  - Pinaceae
    - *Abies laticarpus (magnifica)*
    - *Pinus russelli (ponderosa)*
    - *Pseudotsuga masoni (menziesii)*
- Angiosperms
  - Betulaceae
    - *Alnus carpinoides (rubra)*
  - Ericaceae
    - *Arbutus matthesii (menziesii)*
  - Fagaceae
    - *Castanea lesquereuxi (pumila)*
    - *Castanopsis chrysophylloides (chrysophylla)*
    - *Fagus washoensis (longipetiolata)*
    - *Quercus consimilis (myrsinaefolia)*
    - *Quercus distincta (agrifolia)*
    - *Quercus pseudo-lyrata (kelloggii)*
  - Juglandaceae
    - *Carya egregia (ovata)*
  - Lauraceae
    - *Umbellularia oregonensis (californica)*
  - Oleaceae
    - *Fraxinus* sp. *(oregona)*
  - Platanaceae
    - *Platanus dissecta (racemosa)*
  - Rosaceae
    - *Prunus masoni (integrifolia)*
  - Rutaceae
    - *Ptelea miocenica (trifoliata)*
  - Sapindaceae
    - *Sapindus oregonianus (mukorossi)*
  - Tiliaceae
    - *Tilia aspera (mandshurica)*

LIST 32

Valley Springs flora (macrofossil), western central Sierra Nevada, California, mid-Miocene (Axelrod 1944b).

- Gymnosperms
  - Pinaceae
    - *Pinus* sp.
  - Taxaceae
    - *Torreya* sp.
- Angiosperms
  - Aceraceae
    - *Acer bolanderi (acuminata)*
    - *Acer* cf. *negundoides (negundo)*
  - Berberidaceae
    - *Mahonia hollicki*
  - Betulaceae
    - *Alnus merriami*
  - Fagaceae
    - *Quercus convexa (engelmannii)*
    - *Quercus hannibali (chrysolepis)*
    - *Quercus simulata (myrsinaefolia)*
  - Lauraceae
    - *Persea pseudo-carolinensis (borbonia)*
    - *Umbellularia salcifolia*
  - Moraceae
    - *Ficus microphylla*
  - Platanaceae
    - *Platanus dissecta (racemosa)*
  - Rhamnaceae
    - *Ceanothus (rigidus)*
  - Rosaceae
    - *Lyonothamnus mohavensis (floribundus)*
  - Salicaceae
    - *Salix californica (breweri)*
  - Sapindaceae
    - *Sapindus oklahomensis (drummondii)*

LIST 33

Verdi flora (macrofossil), western central Nevada, early Pliocene (Axelrod 1958).

- Gymnosperms
  - Pinaceae
    - *Abies concoloroides (concolor)*
    - *Picea* (pollen, Howard Schorn personal communication cited in Adam 1973)
    - *Pinus florissanti (ponderosa)*
    - *Pinus prelambertiana (lambertiana)*
    - *Pinus pretuberculata (attenuata)*
- Angiosperms
  - Characeae
    - *Chara verdiana* (spp.)
  - Ericaceae
    - *Arctostaphylos verdiana (nevadensis)*
  - Fagaceae
    - *Quercus prelobata (lobata)*[a]
    - *Quercus renoana (engelmannii)*
    - *Quercus wislizenoides (wislizenii)*
  - Grossulariaceae
    - *Ribes galeana (roezlii)*
  - Naiadaceae
    - *Potamogeton verdiana* (spp.)
  - Nymphaeceae
    - *Nymphaeites nevadensis*
  - Rhamnaceae
    - *Ceanothus precuneatus (cuneatus)*
  - Rosaceae
    - *Prunus moragensis (emarginata)*
  - Salicaceae
    - *Populus alexanderi (trichocarpa)*
    - *Populus pliotremuloides (tremuloides)*
    - *Populus subwashoensis (tremula davidiana)*
    - *Salix boisiensis (scouleriana)*
    - *Salix truckeana (gooddingii)*

[a] Now identified as *Acer* (Wolfe and Tanai 1987).

LIST 34

Wichman flora (pollen), northern central Nevada, late Pliocene (Axelrod and Ting 1960). *Note:* This flora is a pollen site, interpretations are based on a very small number of grains (37), and species identifications may be incorrect. This flora should be treated with question.

- Gymnosperms
  - Pinaceae
    - *Pinus attenuata*
    - *Pinus flexilis* or *aristata*
    - *Pinus jeffreyi*
    - *Pinus lambertiana*
    - *Pinus monticola*
- Angiosperms
  - Anacardiaceae
    - *Rhus diversilobus*
  - Betulaceae
    - *Alnus rhombifolia*
  - Cornaceae
    - *Cornus nuttallii*
  - Fagaceae
    - *Quercus breweri*
  - Juglandaceae
    - *Juglans cinerea*
  - Rhamnaceae
    - *Ceanothus cordulatus*
  - Rosaceae
    - *Cercocarpus ledifolius*
    - *Rubus parviflorus*
  - Saxifragaceae
    - *Ribes nevadense*

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