GEOLOGIC HISTORY
OF THE
GIANT SEQUOIA
and the Coast Redwood

Gary D. Lowe

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Cover:
Sequoiadendron chaneyi Axelrod 1956, Aldrich Station, Mineral County, Nevada. Branched foliate shoot. Longest branch is 3.4 cm from fork to tip. Specimen courtesy Harold F. Bonham, August 1974.
FOREWORD

The mission of the North America Research Group is to encourage responsible stewardship of Earth’s paleontological resources; and to promote scientific research, communication, and public education. nargpaleo.org

Around a campfire in the Summer of 2004 a group of fossil hunters collaborated on how to contribute to science while pursuing their passion. The North America Research Group (NARG) was formed shortly afterward with eight founding members. Since inception, and in a very short period of time, NARG has grown into a diverse and dynamic group of people sharing a mutual respect and passion for geoscientific study and fossil collecting. Our membership of around a hundred ranges from 10 to 80 years in age. This adventurous assemblage of individuals has an amazing variety of backgrounds, interests, hobbies, educations, and professions; including paleontology, geology, botany, zoology, oceanography, and the arts.

NARG sponsors the NW FossilFest in Hillsboro, Oregon and participates in many programs and events devoted to public education. We strive to follow local, state, and federal regulations when collecting fossil resources. We collaborate with university scientists and government agencies to enhance and promote collection and research. Significant specimens are donated to recognized museums to insure they remain in the scientific and public domain.

As part of NARG’s mission to promote scientific research, communication, and public education a series of Special Publications is being undertaken. NARG members are non-professional experts at locating, recovering and preserving fossil specimens — affectionately called “fossil search and rescue.” Although we are affiliated with University of Oregon, Oregon State University, Western Oregon University, and South Dakota School of Mines and Technology, among others, we are not employed by them or otherwise researching for them. As our discoveries become a valuable part of the known paleontological history, a vehicle for sharing this information becomes necessary. Likewise, other general or special interest material from graduate and undergraduate theses not making it into “main stream” could find its way to short book-length publications sponsored by NARG. When NARG member Phil Knutson, an amateur paleobotanist himself, learned of the “Geologic History of the Giant Sequoias” by author Gary D. Lowe, he suggested NARG could publish copies for the scientific community. Further, this would support our mission of promoting scientific research,
communication, and public education in the field of paleontology. Thus, we present the first in a series of Special Publications.

As NARG approaches the 10th year of success, a second Special Publication highlighting our discoveries and projects is currently in development. Future publications of original material of appropriate nature such as research projects, identification guides, and field collecting guides by other authors will be considered. To find out more about the North America Research Group (NARG), visit us online at nargpaleo.org. NARG is structured as an IRS non-profit public charitable organization 501(c)(3).

Aaron D. Currier
NARG President
July 8, 2013

This second printing adds the Lost Creek assemblage of the Bridge Creek flora of central Oregon that was overlooked due to comments in earlier publications on this flora, and further elucidates the Oligocene occurrence of Sequoiadendron as well as a few scattered edits and corrections. Some of the queries posed by readers have been addressed through deliberate prefatory quotation mining.
Early twentieth century photograph of LPF#1, Lund Petrified Forest, Washoe County, Nevada (photo postcard by J. H. Eastman). This middle Miocene (15.75 Ma) petrified forest is thought to be dominantly comprised of upright Sequoiadendron boles (Bonham 1969, Erwin, et al. 2005).

Petrified wood contributes little to this review of the geologic history of the giant sequoia. Many genera in the family Cupressaceae, particularly the former Taxodiaceae, produce wood that is almost indistinguishable. Fossil wood from these trees is properly placed in the form genus Sequioioxylon, and includes wood from Sequoiadendron, Sequoia, Metasequoia, Taxodium, Glyptostrobus and others.
The giant sequoia of the Sierra Nevada has affected the American mind, and indeed that of the literate world, since its discovery was first published in the April 30, 1853 issue of the *Calaveras Chronicle*, the weekly newspaper published in Mokelumne Hill, the contemporary county seat of Calaveras County, California. The giant sequoia is considered a national treasure with its natural stands seeing protection at the Federal, State, local, and tribal levels.

The incorporation of this tree into American culture was apparent when Josiah D. Whitney, California State Geologist, noted in 1868, “No other plant ever attracted so much attention or attained such a celebrity within so short a period. The references to it in scientific works and journals already number between one and two hundred.” This literary trend continues a century and a half later.

Geologists and paleontologists are not immune to the influence of the magnificence of the giant sequoia. In his 1947 introductory/popular paleobotany book, *Ancient Plants and the World They Lived In*, Henry N. Andrews, Jr., Associate Professor at Washington University, and the staff paleobotanist at the Missouri Botanical Gardens, noted, “if any plant may be considered as the ‘sacred tree of America,’ it is most certainly the sequoia.”

In the popular imagination sequoia meant the giant sequoia, now botanically classified as *Sequoiadendron giganteum* (Lindl.) J. Buchholz 1939. The giant sequoia had been classified in the genus *Sequoia* since 1854. The coast redwood, *Sequoia sempervirens* (D. Don) Endlicher 1847, was not popularly called sequoia, merely redwood.

This geologic history of the giant sequoia is a blend of historical geology and the history of geology. The reader will encounter the names of many of the scientists - geologists, botanists, and paleobotanists - who have contributed to an understanding of the geologic history of the giant sequoia, a geologic history not independent of the coast redwood.

The approach taken herein deviates from the historic norm, where the geologic history of the giant sequoia is portrayed as linear back into the Mesozoic. In a relative sense, an extreme position is taken, though based entirely on the published record. This was the general mindset current with Daniel I. Axelrod, the discoverer of the Tertiary giant sequoia, when he included the following quote in a 1980 publication:

> Extreme positions are of extreme value. They induce the reader to think along different lines. They break his conformist habits. - Feyerabend (1970).
Fossil impressions of *Sequoia langsdorffii* (Brongniart) Heer in a Swiss mudstone. Oswald Heer, a Swiss naturalist and geologist, first correctly assigned fossil forms to the genus *Sequoia* in 1855 (compiled from *Flora Helvetiae*, Plate 21).

The volume in which Endlicher named the genus *Sequoia* (*Synopsis Coniferarum*) closes with 50 pages of fossil conifers. Included among Endlicher’s fossil conifers is Adolphe-Theodore Brongniart’s 1828 *Taxites langsdorffii*. Though so similar in apparent morphology “Endlicher failed to recognize the resemblance of these leafy shoots to those of Sequoia sempervirens which he had described for the first time on a preceding page” (Chaney 1951). The fossil form depicted by Heer has since been assigned a new name, *Sequoia abietina*, reflective of the close similarity of the fossil leaves to the dominate leaf form of the living tree, and to the leaves of the firs, the genus *Abies*, and because of nomenclatural priority resulting from reassignment of *Phyllites abietina* Brongniart 1822 in Cuvier and Brongniart 1822 (Knobloch 1964).
GEOLOGIC HISTORY OF THE GIANT SEQUOIA and the COAST REDWOOD

Scraps of branches with leaves hardly distinguishable from those of the existing Californian trees are frequently met with in Tertiary and Mesozoic sediments, and with them occasionally occur cones too imperfectly preserved to afford satisfactory evidence of more than superficial agreement with those of the recent species. The task of deciphering the past history of plants, particularly of the Conifers, is accompanied by many difficulties and insidious temptations. It is clear from a critical examination of many of the recorded instances of fossil Sequoias that the generic name has been frequently used by writers without adequate grounds. The fragmentary specimens available to the botanical historian cannot as a rule be subjected to microscopical investigation, and even a partial acquaintance with the similarity of the foliage of different types of living Conifers is sufficient to convince the student of the need of self-control in the identification of the fossils.

Sir Albert C. Seward 1911.

The genus *Sequoia* was established in 1847 by Austrian botanist Stephen F. L. Endlicher for the coast redwood (previously classified as in the genus *Taxodium*) growing along the west-central North American coast from the southernmost 20 miles of Oregon to about sixty miles south of Monterey in California (many references, e.g., Lowe 2012a). Five years later in early 1853, when very few botanists even knew the new Linnaean name *Sequoia*, the giant sequoia was discovered in the central Sierra Nevada (Lowe 2012b). The new tree was described by English botanist John Lindley near the end of the year as a new genus, but was assigned to the genus *Sequoia* about six months later by French botanist Joseph Decaisne. Because of close anatomical similarities the giant sequoia remained classified as a member of the genus *Sequoia* for the next 85 years, until 1939, when the giant sequoia was assigned to the new genus *Sequoiadendron* by American botanist Joseph T. Buchholz. The anatomical similarities that required 85 years to sort out in the living trees rarely are discernable in the fossil record and necessitate discussing the geologic history of both genera.

Conifers are primarily classified based on the external and internal morphology and anatomy of their seed cones. The seed cones and other anatomical features, such as leaf morphology, are considered to be distinctive of species. Thus, in separating *Sequoiadendron* from *Sequoia*, Buchholz used many anatomical and developmental differences between the two species. In both genera, the leaves and cone scales are attached to their supporting structure in a spiral. Not all of the features used in living
plant classification are preserved in the fossil record; most of the time very few features beyond the mere external morphology of scattered plant parts are preserved. Rarely are different plant parts found connected in any individual fossil. Even more rarely are entire plants found, and then only the smaller ones. Sometimes the different parts are found associated together in the same deposit through which a connection is assumed.

At first glance leaf morphology is one anatomical difference between the genera *Sequoia* and *Sequoiadendron* that is readily apparent to any observer. The type specimen of *Sequoia sempervirens* illustrated by David Don in 1828 (as *Taxodium sempervirens*) bears prominent flattened needlelike leaves with the needle leaves longest in the middle portion of each twig. Also present at the base of the twig to which the needlelike leaves are attached are scale-like leaves (appressed) that are also present on the twig ending in a seed cone. The needlelike leaves are spirally arranged, and have their attached bases at the twig twisted to bring the needles into a flattened row on either side of the twig, i.e., it runs a short distance down the axis of the branch instead of terminating at the point of attachment (decurrent), thus appearing to be in an alternate arrangement. John Lindley’s type specimen of *Sequoiadendron giganteum* has densely spirally arranged awl-shaped to scale-like leaves that spread at the tip. Specimens with either, or both, needlelike or scaly-leaves are present in the fossil record.

The fossil record is generally enriched in the leaves of deciduous species as opposed to non-deciduous species, because of the greater availability of deciduous leaves for transport along the short distances to the sites where the fossils were preserved. Living *Sequoia* and *Sequoiadendron* are both non-deciduous, or evergreen, and only shed a portion of their branchlets each year. Presumably this was true in the fossil species. The modern trees shed their leaves by a process called cladoptosis, the dropping of discrete leafy branchlets. This was first observed in the literature by James Stark in 1876 and summarized by Addicott (1982). In *Sequoia*, the cast-off branchlets exhibit from one to as many as five seasons of growth. Most of the cast-off branchlets were only on the tree for three years. Or, as noted by Stark, the branchlets “are generally simple, but occasionally they are compound.” In *Sequoiadendron* the cast-off branchlets have from one to several years growth. These dropped branchlets are generally what are seen in the fossil record, but occasionally larger branchlets are preserved having been removed from the tree by some other process.
Left – David Don’s type specimen of *Sequoia sempervirens* and Right – John Lindley’s type specimen of *Sequoiadendron giganteum*. (see source references in Lowe 2012a). The original names were used on their figures. From these beginnings the fossil record would be interpreted.

The first fossil forms to be correctly assigned to the genus *Sequoia* were leafy twig remains from the Miocene of Switzerland described in 1855 by Oswald Heer (frontpiece).

Two years after the giant sequoia was assigned to the genus *Sequoiadendron*, Japanese paleobotanist Shigeru Miki assigned fossil leafy twig remains similar, but clearly not identical, to Heer’s from the Pliocene of Japan to a new genus he named *Metasequoia*. Three years later, in 1944, Chinese forester Tsang Wang discovered living plants that
within a few years were determined to be identical to the Miki’s fossil material. Before 1939, all sequoia-like fossils were either assigned to the genus *Sequoia* or to a genus established for the purpose (e.g., *Sequoites*, *Elatocladus*, and others). In 1951, paleobotanist Ralph W. Chaney published substantial revisions of the classifications of fossils from western North America assigned to sequoia-like genera based on the establishment of the genus *Metasequoia*. The genus *Metasequoia* is frequently mentioned, but not specifically discussed in this geologic history of the giant sequoia.

All of this naming and renaming has occurred because these three tree genera have overlapping morphological features and, due to their similarities, are now grouped together in the subfamily Sequoiioideae in the family Cupressaceae. Until recently, the three related Sequoiioideae genera, the sequoias, were grouped together with other similar conifers in a family of their own, the Taxodiaceae. The other former members of the now defunct family Taxodiaceae have also been reclassified based on detailed morphologic and genetic similarities. Fortunately, the names of the genera are held sacred under the established rules. The names of some of the other genera of the former Taxodiaceae will occasionally be referred to: the swamp cypresses, *Taxodium*, *Glyptostrobus*, and the closely allied *Cryptomeria*; *Metasequoia*; and the ancient genus *Cunninghamia*.

Considering all the confusion when determining the relatedness of the living trees, it is quite understandable that even greater confusion has plagued the studies of the small fragments of the trees preserved in the fossil record. Fossils can occur in any of several types, or modes of preservation, depending on their original growth habit, the habitat in which the plant grew, and the later geologic history of the fossil. Among these are compressions, impressions, mummifications, petrifications, various stages of coalification, and a few others.

The early botanists working with fossil plants, who would later specialize as paleobotanists, utilized readily discernable visible features, mainly leaf and cone impressions and compressions. The names of these investigators recur time and again in the geologic history of the giant sequoia: Kaspar Maria von Sternberg (1761-1838), known as the “father of paleobotany;” Adolphe-Théodore Brongniart (1801-1876), who reported the first fossils that would eventually be included among the sequoias; Charles Léo Lesquereux (1806-1889), who dominated collecting and identifying fossil plants in the mid-continent western territories of the United States; Oswald von Heer (1809-1883), who assigned the first fossil form to the genus *Sequoia* and set the stage for generations of confusion; Franz Eugen Geinitz (1814-1900), who first
described the fossil that, for a while, would be known as *Sequoia reichenbachii*; John Strong Newberry (1822-1892), who, while working in the American far west, first saw a rock slab covered with imprints that would ultimately be identified as *Metasequoia*; and William Morris Fontaine (1835-1913), who mainly worked with eastern American Mesozoic plants.

Transitioning American paleobotany into the early twentieth century were; Davis Pearce Penhallow (1854-1910), working in Canada; Frank Hall Knowlton (1860-1926), who studied Pacific Northwest and Alaskan material and generated comprehensive catalogues; and Edward Wilbur Berry (1875-1945), who was geographically widespread in his research and summarized at a popular level the first century of study in his 1923 book “Tree Ancestors.”

Twentieth century notables included Roland Wilbur Brown (1893-1961), who worked on fossils from the Great Plains and Rocky Mountains; Ralph Works Chaney (1890-1971), who, as previously noted, revised the fossil sequoia in western North America; Harry Dunlap MacGinitie (1896-1987) studied many sites in the western United States, particularly the Florissant Fossil Beds in Colorado, and provided the first comprehensive description of *Sequoia affinis*; and Daniel Isaac Axelrod (1910-1998), who identified the first morphologically modern fossil giant sequoia, in the Miocene of western Nevada, southern Idaho, and easternmost California, and named it for his friend and mentor: *Sequoiadendron chaneyi*.

Notice that the above listing does not include any extant, or living, paleobotanists involved in understanding the geologic history of the giant sequoia and the coast redwood. Their life’s work is ongoing.

F. H. Knowlton, published in 1919, as U. S. Geological Survey, Bulletin 696, a second edition of his 1898 “A Catalogue of the Mesozoic and Cenozoic Plants of North America.” Knowlton lists 37 discreet named species of *Sequoia* and another 24 listed merely as *Sequoia sp*. By the time that Robert Smith LaMotte revised the catalogue through 1937 (USGS Bull. 924) the number of accepted Mesozoic and Cenozoic named species of *Sequoia* had slipped to 22. Of course, as noted above, in 1937 the giant sequoia was still classified in the genus *Sequoia* while the genus *Metasequoia* had not yet been identified and named. After Chaney’s 1951 revisions, the number of named species of western North American sequoia had fallen to three; one species in each of the Cretaceous (*Sequoia dakotensis* Brown 1937), Tertiary (*Sequoia affinis* Lesquereux 1876), and Quaternary (*Sequoia sempervirens* (Don in Lambert) Endlicher 1847). Each of these geologic time periods were also
each allotted one species of Metasequoia \((M.\ cuneata,\ \text{Cretaceous};\ M.\ occidentalis,\ \text{Tertiary};\ M.\ \text{glyptostroboides},\ \text{Quaternary})\).

Chaney informally reassigned the several scaly-leaved species to the genus Sequoiadendron, but his main focus was with the fossil forms with flattened needlelike leaves and in separating out the Metasequoia from the western North American fossil record. As a result of Chaney’s revisions, one can interpret that there were two species of Sequoiadendron recognized: In the Cretaceous, Sequoiadendron reichenbachii; and the modern Sequoiadendron giganteum. By 1951, when Chaney published his revisions of the Sequoia fossil record, Sequoiadendron had not yet been found in the Tertiary.

Eventually two species of Sequoia were thought to occur in Europe. As mentioned above, the first fossil sequoia was reported in 1855 from the Miocene of Switzerland by Oswald Heer (Sequoia langsdorffii, text frontpiece). This fossil was a form with flattened needlelike leaves, attached to the two sides of a twig, called distichous foliage (from the Greek: \textit{dis} – two separate, or apart and \textit{tich} – a wall; two leaves separated by the twig). A few years later, in 1863, Heer reported the scaly leaved variety, named Sequoia couttsiae, in deposits he also thought to be Miocene in Devon, southwest England. Like so many aristocratic scientists of the nineteenth century, Heer was overly attuned to his own point of view and the superiority of his observations and interpretations. Heer’s dogmatic fixation with the presence of Sequoia as defining the Miocene took decades to unravel.

The genus Sequoia is first definitively (?) identified in eastern Asia in late Eocene of northeast China and from the Miocene of south China (Ma, et al. 2005). Possible migration pathways were occasionally present. Easternmost Asia was connected to North America from the late Cretaceous until late in the Tertiary (Parrish 1987). No occurrences of the genus Sequoia are known from the Yukon Territory westward through Alaska to northeastern Siberia. However, the probably deciduous genera Metasequoia, Glyptostrobus, and Parataxodium are known from this area (Crane 1987). Eastern Asia was also isolated from Europe in the early Paleocene through the late Eocene by the intervening Turgai Strait/West-Siberian Seaway (Akhmetiev and Beniamovski 2009).

As discussed in the following chapter, claims have been made to the occurrence of Sequoia in Asia much earlier, in the lower Cretaceous. With the exception of this last mentioned very early claimed occurrence, the presence of Sequoia in Asia and its possible importance in showing a connection between North American and European occurrences will not be further discussed due to paucity in information.
The names given to several standard divisions of geologic time have been freely used up to this point. However, the range of geologic time, in millions of years before the present (Ma), and the sequence of divisions, needs defining in order to follow the geologic history of the giant sequoia. The geologic time chart used in this discussion is presented below.
Sequoia jeholensis Endô
OR
Elatocladus leptophyllus Wu

An early Cretaceous (122-135 Ma) sequoia-like fossil from the Yixian Formation of Liaoning Province, China.
THE SEQUOIA FOSSIL RECORD

Are they remnants, sole and scanty survivors of a race that has played a grander part in the past ...? Have they had a career, and can that career be ascertained or surmised, so that we may at least guess whence they came, and how, and when?  Asa Gray 1872.

As previously mentioned, the conifers are primarily classified based on the morphology and anatomy of the seed cones. Seed cones and leafy twigs are rarely encountered attached together in the fossil record, though they are fairly frequently found associated with each other in the same fossil deposit. Sometimes a close association is confused with a unity of attachment.

Without the cones it can be impossible to ascertain if a fossil form is from a plant in the same genus as a living species. Even with a cone, examining only the external morphology doesn’t completely narrow down the classification. This is even more the case with fossil leaves. The best that can be said is that the fossil is like the living genus, thus sequoia-like.

The geologic record of the family Cupressaceae begins by the early Mesozoic (Farjon 2005). The oldest fossils of members of the subfamily Sequoioideae first occur in deposits dated from the Cretaceous.

The Cretaceous

The earliest fossil plant that is said to be a sequoia, as opposed to being a plant distantly related, comes from the lower Cretaceous Yixian Formation of China that includes the Jehol biota. (Age interpretations and local geographic names have changed since this fossil was studied, a point not noted in all subsequent publications.) Many of the fossils in this formation are magnificently preserved, including evidence of the soft parts that typically are not preserved. This fossil form was named Sequoia jeholensis Endô in 1951 (Endô and Chaney 1951). However, there were no cones reported, and regardless of how similar the leaves and their attachment to the twig are to the modern Sequoia, they cannot positively be classified as a member of the genus Sequoia without seed cones. There is a wide array of form genera in the paleontologic record for situations where a fossil looks like something, but can’t actually be classified. More up to date literature refers to these fossils as Elatocladus leptophyllus Wu (e.g., Wu 1999), the genus Elatocladus having been established by Thore G. Halle in 1913 for just such form fossils.
A mid-Cretaceous (98-112 Ma) scaly-leaved sequoia-like variety, *Sequoia condita* Lesquereux, occurs in the coastal floodplain deposits of the Cheyenne Sandstone of south central Kansas along the eastern shore of the Cretaceous North American Seaway (Berry 1921; Huang and Dilcher 1994; Retallack and Dilcher 2012).

North America in the mid-Cretaceous, at about the time that the coastal wetland *Sequoia condita* was preserved in the Cheyenne Sandstone. The approximate land area and the Cretaceous North American Seaway are shown. After Smith, et al. 1994.

*Sequoia condita*, from Berry (1921)
Cones and foliage are locally very abundant in the Cheyenne Sandstone. The internal anatomy of these fossil “sequoias” has not been investigated so as to determine how they might relate to other fossil and living genera. Many of the fossils are empty casts that the foliage or cone had once occupied. Huang and Dilcher (1994) point out that, “one difference … is that the surface of the cone scale is nearly rounded in *Sequoia condita* and rhombic” in the living *Sequoia sempervirens*, and other similar fossil forms, suggesting that these are not members of the genus *Sequoia*. Berry’s 1921 observation should be stressed, that, “In the absence of attached cones the foliage might be referred to any one of several genera,” including the living genera *Widdringtonites* (sic), *Juniperus*, and *Glyptostrobus*, and the extinct genus *Sphenolepsis*. Berry’s list should be extended to include the extinct genus *Geinitzia* and the extant *Sequoiadendron*.

In 1842, Franz Geinitz identified a fossil with scaly leaves as being Araucaria-like in the lower upper Cretaceous of Bohemia and named it *Araucarites reichenbachi* Geinitz. Heer in his studies in Greenland and Spitsbergen, in seven volumes titled “Flora Fossilis Arctica,” published between 1868 and 1883, recognized the presence Geinitz’s scaly-leaved twig’s in the Arctic fossil floras. Heer, having the advantage of the further study and reclassification of the coast redwood, as well as the discovery of the giant sequoia, renamed these fossils *Sequoia reichenbachi* (Geinitz) Heer. This was an era of over-populating the fossil record with species based on slight differences, so it is no wonder that Heer also recognized four other scaly-leaved sequoia species that Chaney (1951) reassigned to *Sequoia reichenbachi*. Heer had also described five needle-leaved sequoias, two of which Chaney reclassified as *Metasequoia*, one as *Glyptostrobus*, one as *Taxodium*, and one as a pine.

“*Sequoia reichenbachi* (Geinitz) Heer” (?) from the lower upper Cretaceous near Sofia, Bulgaria. Length of fossil approximately 39 mm.
Some of Heer’s scaly-leaved sequoias were recognized in the upper Cretaceous of the New Jersey coast at the mouth of the Hudson River by Edward W. Berry (1905, 1906, and 1911). Predominant among the fossils were leafy twigs assigned to *Sequoia reichenbachi*, but also cones of J. S. Newberry’s *Sequoia gracillima*, that Lesquereux had considered as being in the genus *Glyptostrobus*. Berry later (1911) added Heer’s *Sequoia concinna* to the New Jersey coastal Cretaceous flora having collected cones that he compared to a cone Arthur Hollick (1906) had reassigned from its original description as “provisionally a flower of Eucalyptus.” As the reader may surmise, some fossils are very confusingly preserved.

Concerning the leafy twigs of *Sequoia reichenbachi*, Berry (1905b, 1923) wrote:

“The magnificent specimen of sequoia with the large cone and the needle-like curved leaves shown in the figure, (line drawing reproduced on the facing page) is from the clays near Cliffwood, N.J., where the twigs are among the most abundant fossils, looking like elegant lithographs against the background of dove-colored clay. This species had cones almost exactly like those of the living California tree and the foliage was also very similar.”

The rock formations of the upper Cretaceous of coastal New Jersey continue across the Hudson River, occurring also on Staten Island. The microscopic structure of the leafy twigs of *Sequoia reichenbachi*, were studied by Hollick and Jeffrey (1909), who reported “examination of their internal structure has demonstrated that they do not belong to that genus, …, and hence the generally accepted generic name must be abandoned. … The species is also clearly not referable to the genus *Araucarites* … (as assigned by Geinitz, see above) but belongs in the genus *Geinitzia* Endlicher … we have therefore adopted for the name of this species the new combination *Geinitzia reichenbachi* (Gein.).”

In an article titled, “A Brief Sketch of Fossil Plants,” in the 1905 Annual Report of the New Jersey State Geologist, Berry (1906) stated that, “In the vicinity of Cliffwood bluff grew many Sequoias, distant ancestors of the ‘big trees’ of California. The clays are full of their twigs, and hundreds of their cones have been washed out by the waves during winter storms.” Fortunately, many of these cones ended up in the United States National Museum collection where they could be later studied using more advanced technology.

The Cliffwood, New Jersey petrified cones from the US National Museum collection were anatomically studied by LaPasha and Miller (1981) and were found to be sufficiently dissimilar to the cones of the
Edward W. Berry’s idealized ancestral ‘big tree’ of California - “Sequoia Reichenbachii, A widespread Cretaceous species, restored from numerous specimens from New Jersey clays” (Berry 1905b).

living genera *Sequoia, Sequoiadendron, Metasequoia*, and other (formerly) Taxodiaceous genera, both living and extinct, as to comprise a different, and new genus. The cone anatomy combines features present in all three of the genera of the Sequoioidae and *Cunninghamia*, the genus with a long geologic record and far down the genetic nucleotide sequencing molecular phylogenetic trees of Kusumi, et al. (2000) and Gadek, et al. (2000). The New Jersey *Sequoia reichenbachii*, so enamored by Berry as the “ancestral ‘big tree’ of California”, are neither *Sequoia*, nor *Sequoiadendron*.

As in the middle Creteceous of Kansas discussed above, the late/upper Cretaceous was also characterized by genera of the Sequoioidae living near the shores of the North American Seaway. The preserved sequoias include foliage fragments of both the scaly-leaved and the flattened needle-leaf types and “cones of widely different but intergrading size,” all originally assigned to the species *Sequoia dakotensis*.

The *Sequoia* cones are “well-preserved mud casts,” with the mud infilling between the former cone scales. There is no preserved organic material on which to base identifications. The cone scales are represented by the voids. These *Sequoia* cones occur, along with the more abundant
Metasequoia cones, in the stream and marsh sediments that filled in the North American Seaway in the area of western Alberta and Montana and western North Dakota and southward to eastern Wyoming and western South Dakota.

Sequoiod cones have also been recovered from the late Cretaceous of Australia and Sweden. The internal anatomy of these cones is a combination of the characteristics of taxodiaceous features. Several of the late Cretaceous cones from Sweden combine characteristics of the genera *Sequoia* and *Sequoiadendron* and have been assigned to a genus named *Quasisequoia* (Srinivasan and Friis 1989). This genus is as important in the later geologic record of Europe, as are the genera *Sequoia*, *Glyptostrobus*, and *Taxodium*.

With respect to the ancestry of the former Taxodiaceae, Miller (1977) and LaPasha and Miller (1981) note, and Thomas and Spicer (1987) concurs, “All the modern genera except *Sequoiadendron* have been reported from the Mesozoic.” These investigations abrogate Florin’s (1963) summary of the former Taxodiaceae “distribution … in time and space.” This is an important observation that has generally not been taken into consideration in phylogenetic research.
The Tertiary

Plate tectonics and continental drift are well established geologic facts that need not be summarized here. Regardless of how climates and habitats were responding to the movement of the ever-shifting continents, and the planet its orbit, the Cretaceous ended with a bang. The loss of life forms was literally astronomical. The mid-continent US/Canada border region experienced an approximately seventy percent extinction in fossil leaf types after the 66.5 Ma Cretaceous-Tertiary boundary (Johnson 1992). Among the survivors were species in the Cupressaceae subfamily Sequoioideae.

The late Cretaceous depositional environments in which the fossils are found extended into the lower Paleocene, preserving numerically fewer fossils. However, before continuing with the sequoias along the borders of the mid-continental seaway of North America the Tertiary of Europe will be briefly examined.

The Tertiary Sequoias of Europe

Oswald Heer’s flat needle-leafed Sequoia langsdorffii (Brongniart) Heer from the Miocene of Switzerland that was first published in 1855 has been mentioned above. Since Heer’s day, this species has been found in the sedimentary basins of the Tertiary European archipelago in deposits ranging in age from the upper Eocene to the upper Miocene (Mai 1998). Sequoia langsdorffii (Brongniart) Heer was also found in the Miocene of Iceland and Greenland where it was thought to have populated a land bridge connecting North America and Europe, a well documented feature named the Greenland-Scotland Transverse Ridge, the GSTR (Denk and Zetter 2011); allowing Sequoia access to Europe.

European Tertiary sedimentary deposits also preserved a scaly-leaved type of Sequoia, along with Taxodium and Glyptostrobus. Heer first described the scaly-leaved Sequoia from lignite deposits on England’s southwest peninsula at Bovey Tracy in Devon in 1862. He named this species Sequoia couttsiae. This species was also found nearby in the upper Eocene of Hamstead and in the London Clay of the same age. Later Sequoia couttsiae was found to be a widely distributed plant throughout the Tertiary basins of southern Europe.

In his revisions of the genus Sequoia, Chaney (1951) had left Sequoia langsdorffii (Brongniart) Heer in Europe alone. All of the European fossils that were illustrated in publications, and all the specimens that he had been able to examine, he considered to be “true sequoias.” Metasequoia fossils had not been found in Europe, with the
possible exception of a site (Isle of Skye, Scotland) with questionable pollen. Years later, *Metasequoia* leaves were found along the GSTR, east of Iceland, in the Eocene of the Faroe Islands (Rasmussen and Koch 1963). This occurrence suggests that *Metasequoia* may have been present elsewhere in Europe. Its presence in Europe, along with the confusion from Heer’s overuse of *Sequoia langsdorffii* prompted a revision of the genus *Sequoia* in Europe. Tertiary species were reassigned to *Sequoia abietina* (Brongniart 1822) Knobloch 1964 due to the characteristic distichous abies-like leaves and priority (Knobloch 1968).

*Sequoia abietina*, from the Miocene of Europe (2.0 cm coin for scale for both).

Left – Maramures, Romania.

Right – Zülpich, Germany.

(extracted from brown coal/lignite)

Following Knobloch’s revision of the flat needle-leafed sequoia, and the establishment of the genus *Quasisequoia* from the late Cretaceous of Sweden, Kunzmann (1999) reexamined the European Tertiary species *Sequoia couttsiae* (Heer). Kunzmann found that the cones and many leaf microscopical features were, like Srinivasan and Friis’s genus *Quasisequoia*, a combination of the characteristics of the genera *Sequoia* and *Sequoiadendron*. Some of the features were previously reported by Chandler (1962), but not used as a basis of establishing a new genus. Florin’s (1963) summary of the past distribution of the Sequoioideae is also invalidated for the Tertiary.

Kunzmann renamed the European Tertiary scaly-leaved type of sequoia *Quasisequoia couttsiae* (Heer 1862) Kunzmann 1999 and notes that the species ranged from the upper Paleocene to the upper Miocene of central, western, and southeastern Europe in sediments deposited in wetlands such as coastal plains, riparian forests and lake shores and that *Quasisequoia* often was preserved in swamp deposits where *Taxodium* and *Glyptostrobus* were prominently present.

With the demise of the Cretaceous occurrence of *Sequoiadendron* from the geologic record, and the reassignment of the European Tertiary swamp margin fossil species to *Quasisequoia couttsiae*, the geologic history of the giant sequoia can no longer consider European records. The scanty Asian records of the genus *Sequoia* are insufficient to ascertain their place in the geologic history of the genus *Sequoia* and *Sequoiadendron* is not reported in Asia. It is to North America that we must turn for the geologic history of the giant sequoia.
Tertiary European “Sequoias.”

**Sequoia abietina** (Brongniart 1822)
Knobloch 1964
Rupelian (early Oligocene)
Lower part of the Calcaires de Vachères (Chalks of Vachères)
Manosque-Forcalquier Basin
Alpes-de-Haute Province
Southeast France
(2.0 cm coin for scale).

**Quasisequoia couttsiae** (Heer 1862) Kunzmann 1999
early Miocene Most Formation
North Bohemian Brown Coal Basin
Bilina Coal Mine
Czech Republic
(2.0 cm coin for scale).
Sequoia affinis Lesquereux 1876 from the Stonerose Interpretive Center quarry near Republic, Washington. Specimen courtesy of Paul Adams, Portland, Oregon. (2.0 cm coin for scale).
**Sequoia affinis** of Western North America

In 1951 Ralph W. Chaney revised the status of the western North American fossil Taxodiaceae (now Sequoioideae). Chaney assigned all of the North American Tertiary Sequoia to the species *Sequoia affinis* Lesquereux. The Tertiary fossil *Sequoia* comes from 25 to 30 published and a few unpublished localities (see map below). The total number of leaf specimens of *Sequoia affinis* recorded in reports is fewer than six hundred. The majority of these are tabulated in Appendix A and the illustrated specimens are used in this review. At some of the published localities petrified wood of sequoia is more abundant than leaves, but is not discussed here.

The locations in the western United States and Canada where *Sequoia affinis* Lesquereux 1876 has been found. - 1a, Driftwood Canyon, B.C.; 1b, McAbee, B.C.; 1c, Falkland, B.C.; 1d, Republic, WA; 2, Yellowstone National Park, WY; 3, Rainbow, UT; 4, Thunder Mountain, ID; 5, Copper Basin, NV; 6, Missoula, MT; 7, Mormon Creek, MT; 8, Beaverhead basins, MT; 9, Florissant, CO, 10, Ruby River Basin, MT; 11, Lost Creek, OR; 12, York Ranch, MT; 13, Haynes Creek, ID; 14, Lyons, OR; 15, Blue Mountains, OR; 16, Troutdale, OR; 17, Remmington Hill, CA; 18, Neer's Hill/Taylor Mountain, CA; 19, Petrified Forest, CA; 20, Portola Valley, CA. Lettered locations A through K – see Appendix A.
The genera *Metasequoia*, *Taxodium*, and *Glyptostrobus* were dominate members of Paleocene plant communities in the coal forming swamps and other wetland areas in the lowlands of the mid-continent of North America, where the final remains of the Cretaceous North American Seaway was being filled in through sedimentation. These three genera, particularly *Metasequoia*, were also members of the plant community bounding paleolakes in the area now forming the “interior plateau” of British Columbia and northernmost portions of eastern Washington (map locations 1a-1d). These lakes were nestled in the volcanic terrain of the late early Eocene (49-52 Ma) Okanagan Highlands, extending for 600 miles from just below present latitudes of 48°N to about 55°N. Among the upland vegetation present in this terrain was *Sequoia affinis* (Arnold 1955), referred to by most workers as *Sequoia sp.* (Wehr and Schorn 1992; Dillhoff, et al. 2005; Greenwood et al. 2005).

*Sequoia* was not a clearly recognizable member of the fossil community preserved in the Paleocene sedimentary rocks deposited during the final closure of the former mid-continent seaway (Brown 1962; Bell 1949). Partially overlying the western margin of this former seaway, the rock record has yielded fossil floras with upland species, especially in the Eocene Sepulcher and Lamar River formations of northern Yellowstone National Park (map location 2). In addition to the standing tree “stumps” of the fossil forest, Knowlton (1899) reported twelve locations with fossils of the distichous leafy twigs of the coast redwood type. Unfortunately, the number of specimens and other details were not mentioned. At one of these locations, “abundant” scaly-leafed specimens, were also collected. All of the specimens collected by Knowlton were examined by Chaney, and he assigned all of them to the species *Sequoia affinis*, including Knowlton’s scaly-leafed *Sequoia couttsiae* (not illustrated by Knowlton) as being a scaly-leafed *Sequoia affinis* due to the similar heteromorphic nature of the coast redwood. More recent work classifies this and similar material as *Glyptostrobus* (Brown 1962; MacGinite 1974).

Three hundred miles to the south of the Eocene Yellowstone uplands, in the sedimentary basins of the developing middle Rocky Mountains, the Evacuation Creek member of the middle Eocene (48-50 Ma) Green River Formation (map location 3) has yielded a single sequoia fossil, a frond with ten or more leafy twigs. This specimen is described as, “the foliage is not distinguishable from that of living *Sequoia sempervirens*.” MacGinite (1969) also considered that this specimen “is somewhat more robust than that of typical *Sequoia affinis* from Florissant,” Colorado where he extensively studied this species.
(MacGinite 1953; to be discussed later). He considered the Green River Formation specimen to be similar to, but not, *Sequoia affinis*. The specimen has a few “typical” scaly leaves at the branch end of this frond.

The single *Sequoia affinis* specimen from the Green River Formation deposited in middle Eocene Lake Uinta in easternmost central Utah, must have been growing in nearby highlands in the immediate area to the north or east. Nearer the western rim of the drainage basin contributory to the lake, the middle Eocene (45 Ma) Thunder Mountain Caldera (Axelrod 1998a; map location 4) in south-central Idaho and the slightly later middle Eocene (41.5 Ma) Copper Basin (Axelrod 1966; Henry 2008; map location 5) in northeastern Nevada supported relatively abundant *Sequoia affinis*.

*Sequoia affinis* is found in the late Eocene at four locations. One in central western Montana near Missoula (est. 36.6 Ma, map location 6) and two in southwestern Montana; one in the Mormon Creek basin near the Ruby River Reservoir in Madison County (35.46 Ma, map location 7) and the other in the Beaverhead basins (Christensen Ranch, 34.5 Ma, and Horse Prairie, 34.05 Ma; illustrated fossils unsorted; average, 34.28 Ma, map location 8) to the west in Beaverhead County.

![Scaly leaved *Sequoia affinis* from the late Eocene (Chadronian, est. 34-36 Ma; Wing 1987) Muddy Creek basin, one of the Beaverhead Basins of southwestern Montana (Becker 1969) and representative of material from map location 8.](image)

(Short twig at top of view, 1.4 cm.)
The fourth late Eocene locality yielding Sequoia affinis fossils is the spectacular Florissant Fossil Beds National Monument, Colorado (Meyer 2003; map location 9) from the very end of the Eocene (34.07 Ma). The sequoia fossils from Florissant that Lesquereux brought back in 1874 provided the type specimens he described in 1876 and were extensively studied by MacGinitie (1953).

Sequoia affinis from the latest Eocene Florissant Fossil Beds, Colorado (Sequoia map, location 9). Right, fertile shoot with seed cones; left, distichous foliage. For more spectacular fossils see Meyer 2003 (2.0 cm coin for scale).
Two early Oligocene aged deposits in southwestern Montana, that can be seen from each other, have yielded *Sequoia affinis*. The northern one is named for the Ruby River basin (33.88 Ma, map location 10) and the other is from across the Ruby River (York Ranch, 32.63 Ma, map location 12). A third early Oligocene deposit is some 75 miles to the west, across the continental divide, at Haynes Creek, south of Salmon, Idaho (30.6 Ma, map location 13). Oligocene *Sequoia affinis* is found in central Oregon in the Lost Creek florule (33 Ma) of the Bridge Creek Flora of the John Day Formation and in western Oregon, along Thomas Creek (approximately 30 Ma) near the town of Lyons. (Map locations 11 and 14. See Appendix A for specifics).

Bottom and right, “typical” *Sequoia affinis* from the “late” Oligocene Lyons Flora, Thomas Creek, near Lyons, northwestern Oregon (map location 14). Upper left, *Metasequoia occidentalis*. Photo, courtesy Philip Knutson, Salem, Oregon.

The Miocene *Sequoia affinis* locations shown on the map include six for which insufficient information could be found. The Nevada location is discussed in a later section. Data from three Miocene locations are tabulated in Appendix A: two in Oregon (Blue Mountains, map location 15; and Troutdale, map location 16) and one in California at Remmington Hill (map location 17).

Two age bracketed *Sequoia affinis* leaf localities are associated with the Pliocene Sonoma Volcanics one in the north central end of the City of Santa Rosa, California (5 Ma, map location 18) and at the other at the nearby Calistoga Petrified Forest (3.4 Ma, map location 19). The youngest location considered is in the Pleistocene Santa Clara Formation near Portola, California (map location 20). The Pliocene and Pleistocene fossils are the most nearly indistinguishable from the extant *Sequoia sempervirens*. 
Leafy twig of *Sequoiadendron chaneyi* middle Miocene (12.5 Ma)
Fallon Flora, Nevada (map location 4). (2.0 cm coin for scale).
THE *SEQUOIADENDRON* FOSSIL RECORD

Or are they now coming upon the stage … to play a part in the future? Asa Gray 1872.

The earliest fossil record of the genus *Sequoiadendron* comes from the early middle Miocene (18.5 Ma) Middlegate/Eastgate Basin of western Nevada. The Miocene species was assigned to *Sequoiadendron chaneyi* Axelrod 1956, first reported that year from the locality at the base of Aldrich Hill, on the east margin of Coal Valley, approximately 40 miles south of Yerrington, Nevada. Two additional localities were reported that year that yielded *Sequoiadendron chaneyi*: one in the Dead Camel Mountains, near Fallon, and the other at the southern end of the Clan Alpine Mountains near Middlegate. It was noted that “*Sequoiadendron chaneyi* is represented by numerous impressions of small twigs …, all of which can not be distinguished from similar structures produced by the living Sierra redwood, *Sequoiadendron giganteum*, (Axelrod 1956).

There are nine published localities where *Sequoiadendron chaneyi* has been found (Appendix B) shown on the map below.

Locations in Nevada, California, and Idaho where *Sequoiadendron chaneyi* Axelrod 1956 has been found. NV: 1, Middlegate Basin; 2, Fingerrock Wash; 3, Purple Mountain; 4, Fallon; 6, Aldrich Station; 7, Chalk Hills; 9, Minden-Gardnerville; ID: 5, Trapper Creek: CA: 8, Mt. Reba. Lettered locations A through D – see Appendix B.
At these nine published localities a total of 108 foliage specimens and eight cones are tabulated. Seven of the fossil localities are in western Nevada; one in southeastern most Idaho; and two from the western edge of the Great Basin in California. A slightly younger occurrence is in the Pliocene (5 Ma) deposits easterly of the Minden/Gardnerville area in westernmost Nevada. *Sequoiadendron giganteum* is represented in a few Pleistocene floras relatively near where they now occur, but are not considered here.

The assemblage of fossil plants at many of the above mentioned localities and the assemblages at additional localities have been used to understand the geologic history of the forest community in which the giant sequoia is found (Axelrod 1959, 1976).

**Sequoiadendron Problematica**

In the fossil record the leaves of the sequoias have historically been described as those with flat needlelike leaves and those with scale-like leaves. The similarity of the twigs of the scaly-leafed *Sequoia, Sequoiadendron, Glyptostrobus* and other genera was mentioned several times when discussing the Cretaceous and the Cenozoic sequoias. This similarity has resulted in no end of confusion and can be summarized through the following quotes:

“In the absence of attached cones the foliage might be referred to any one of several genera” (Berry 1921).

“the foliar material (of the North American) *Glyptostrobus oregonensis* cannot be separated with certainty from that of *G. europaeus* (Chaney and Axelrod 1959);

“similar specimens, but without cones were previously identified as *Glyptostrobus oregonensis* ... There is the possibility that the *Glyptostrobus* material may also be Sequoia” (Becker 1966);

“The sterile twigs of *Glyptostrobus* are morphologically identical with leaves of *Quasisequoia couttsiae* (Heer) Kunzmann and often co-occur in fossil sites” (Teodoridis and Sakala 2008);

Determination of what plant the leaves represent is a major difficulty when investigating fossil plant assemblages, especially those with few examples, sometimes only one, of the fossil type to be determined. The identifications are critical to an interpretation of the record, and occasionally seems to have at times relied on an interpretation of the other species in the fossil habitat. Examples follow where fossil scale-like leaves have caused difficulty.
An Oligocene Occurrence of Sequoiadendron?

In 1986, Axelrod stated “Sequoiadendron is now known from the Late Oligocene of south-central Idaho, and from the Miocene of southern Idaho and western Nevada.” Fossil localities were not provided. In 1978, Axelrod included an Oligocene location on his map showing the Tertiary distribution of Sequoia and Sequoiadendron. In his 1976 publication on the history of coniferous forests in California and Nevada, among Paleogene floras, he had included both the Coal Creek flora (no age provided) and the Thunder Mountain flora (stated as >29 Ma) of Idaho.

In 1937 Roland Brown collected fossil plants from the Dewey Gold Mine and vicinity at Thunder Mountain, Idaho, and referred the material to the lower Miocene. The Arthur Holmes Geologic Time Scale of 1933 placed the base of the Miocene at 32 Ma, consequently lower Miocene material was considered as approaching 32 Ma in age. Advances in dating techniques adjusted the base of the Miocene to 26.2 Ma in the 1947 edition of the Holmes Geologic Time Scale, rendering Brown’s near 32 Ma Thunder Mountain material late Oligocene. In 1961 the base of the Miocene was adjusted to 25 Ma (Kulp 1961) with no resulting change in a late Oligocene age assignment for Thunder Mountain. Contrary to the mid 1970s, in 1968 Axelrod had considered Thunder Mountain to be middle Eocene and included Sequoiadendron in the flora.

In the summer of 1964, Axelrod collected fossil leaves at Thunder Mountain and received additional material from B. F. Leonard and W. Hamilton of the USGS. In 1985 renewed mining in the area exposed additional fossil leaf bearing outcrops where Axelrod collected in mid 1986, 1987, and 1988. Before this activity, in late 1985, Axelrod submitted his manuscript quoted above, “The Sierra Redwood
Axelrod’s specimen summary for the 1964 collections does not include sequoia-like twig fragments. However, a single, scaly leaved twig fragment (11.5 mm) is listed in the Dewey Mine florule (Axelrod 1998a, Pl. 7, Fig. 9). This was possibly the specimen collected in 1967 by H. Ehrenspeck and identified that year by J. A. Wolfe, both with the USGS, as *Sequoia affinis* (Leonard and Marvin 1982). This single specimen was the only one available from Thunder Mountain on which Axelrod (1968) could assign material to *Sequoiadendron*. The locality collected in 1964/1967 was buried under mine waste when visited in the late 1980s, however, the new locality yielded an additional 47 branchlets and two cones. These new specimens included some with needlelike leaves, resulting in all of the material being assigned to *Sequoia affinis*, without mention of Wolfe’s previous identification, with the almost canonical provision, “This species differs from the living *Sequoia sempervirens* in its smaller cones and branchlets with shorter needles and a greater tendency to produce scale leaves” (Axelrod 1998a).

The Thunder Mountain caldera infill is dated to about 45 Ma; middle Eocene (Leonard and Marvin 1982). The middle Eocene (Axelrod 1968) Coal Creek flora remains unpublished, and includes 70 specimens of *Sequoiadendron* (397190-397259 in the UCMP database), collected and identified by Axelrod in 1966, with 86 branch fragments and 4 cones, in addition to 48 branch fragments of *Sequoia* on 40 specimens (397150-397189), but cannot be considered in this literature review. However, the scaly leaf problematica clearly influenced Axelrod’s interpretations.

**An Abandoned Occurrence of *Sequoiadendron*.**

In 1964, Axelrod included *Sequoiadendron chaneyi* in the Buffalo Canyon Flora (18.0 Ma) of western Nevada, as one of the eight then known occurrences of this species. By 1975 the species presence was excluded at Buffalo Canyon (Axelrod 1976). This position was maintained when the report on the Buffalo Canyon Flora was published (Axelrod 1991). Another member of the Cupressaceae, *Chamaecyparis linguaefolia*, was included in the 1975 plant list.

Among the living plants, some of the polymorphic leafy twigs of *Sequoiadendron giganteum*, the scale leaves, look very much like the scaly leafy twigs of *Chamaecyparis lawsoniana* (Frajon 2005). Some leaves of both *Sequoiadendron giganteum* and *Chamaecyparis lawsoniana* can also look very much like some of the leaves of Junipers. In the fossil record, many of the preservations are less than ideal.
Chamaecyparis lingueaefolia was not included in the Buffalo Canyon Flora report (Axelrod 1991). A new species Chamaecyparis cordillerae was identified when the Miocene (18 Ma) floras of the Middlegate Basin were described (Axelrod 1985). When describing the Buffalo Canyon Flora (Axelrod 1991), only 19 and 27 km (12 and 17 mi.) distant from the two Middlegate Basin floras, Chamaecyparis cordillerae and Juniperus desatoyana, a new species, were included. The description of Chamaecyparis cordillerae makes note that “A single branchlet, temporarily ‘lost’ among the numerous specimens of Juniperous … is certainly Chamaecyparis.” Junipers were not included in the 1975 list of Miocene conifers in the Great Basin area. Dubious preservation and limited fossil material can result in years of uncertainty.

49 Camp, Nevada: No Sequoia At All

The problem of correctly identifying the scaly leaves found as fossils has plagued many localities. LaMotte (1936) assigned leafy material at the middle Miocene Upper Cedarville flora (49 Camp, Loc. 97) of northwestern most Nevada (Sequoia affinis map locality I) to Sequoia langsdorffii (region wide reassigned in 1951) and an incertae sedis to Lycopodium prominens (a club-moss, a pteridophyte).

Chaney (1951) reassigned all of the 49 camp scaly leaved material to Glyptostrobus oregonensis Brown, because, “The foliage is more scaly than that of S. affinis” and because it was “a species common in the Miocene of adjacent areas to the north.” Since Sequoiadendron was unrecognized in the Miocene at the time of both LaMotte’s and Chaney’s investigations, the same logic can be used to reassign some of this material (sight unseen) to Sequoia langsdorffii. Nonetheless LaMotte’s use of the name S. langsdorffii requires the presence of distichous needle forms to be comparable to Heer’s material, since Heer’s material does not include scaly-leaved forms. At least one of LaMotte’s specimens should have been assigned to S. affinis by Chaney, or his new Metasequoia occidentalis reassignments, if appropriate.

Axelrod and Schorn (1994) recognized both S. affinis and G. oregonensis at Gillam Spring, Nevada (15 Ma), about 41 miles southeast of Camp 49. The Gillam Spring site is only 2 to 3 miles from the Lund Petrified Forest recognized as standing Sequoiadendron “stumps” (Bonham, 1969; Erwin, et al. 2005).

Axelrod (1985) also revised Wolfe’s (1964) Glyptostrobus from Fingerrock Wash in Mineral County, Nevada, to Sequoiadendron, based on stratigraphic position and the presence of Sequoiadendron cones in the revised location (not illustrated). Clearly, more work is needed.
Less expanded needle-like to fully scale-like leaf forms of *Sequoia dakotensis* (Cretaceous-Paleocene); *Sequoia affinis* (post Paleocene Tertiary); and *Sequoiadendron chaneyi* (Neogene) in the geologic record.

1a, Driftwood Canyon, B.C.; 1b, McAbee, B.C.; 1c, Falkland, B.C.; 1d, Republic, WA; 2, Yellowstone National Park, WY; 3, Rainbow, UT; 4, Thunder Mountain, ID; 5, Copper Basin, NV; 6, Missoula, MT; 7, Mormon Creek, MT; 8, Beaverhead basins, MT; 9, Florissant, CO; 10, Ruby River Basin, MT; 11, Lost Creek, OR; 12, York Ranch, MT; 13, Haynes Creek, ID; 14, Lyons, OR; 15, Blue Mountains, OR; 16, Troutdale, OR; 17, Remmington Hill, CA; 18, Neer’s Hill/Taylor Mountain, CA; 19, Petrified Forest, CA; 20, Portola Valley, CA.
LEAF FORMS of *Sequoia affinis* IN THE FOSSIL RECORD


**Scale-Like vs. Needlelike Leaves In The Fossil Record**

Returning now to *Sequoia affinis*, a summary of the occurrence of flat needlelike leaves and those with scale-like leaves is necessary. Chaney (1951) used the term ‘distichous’ for the needlelike foliage of *S. affinis* and referred the reader to MacGinitie’s forthcoming (1953) description of *S. affinis* from Florissant, Colorado. MacGinitie used the descriptor ‘decurrent’ for the needlelike leaves. Distichous was defined previously, and means there are two rows on opposite sides of an axis. Decurrent means that the leaves extend downward from the base along the stem. To this MacGinitie added “or appressed,” that means lying flat against the stem, “appressed leaves shorter.” The appressed leaves are those usually called scale-like. For the original Florissant *Sequoia affinis* specimens described by Lesquereux, Erling Dorf (quoted in Chaney 1951) noted that the collection “include(s) a full range from scaly, non-distichous, to needle-like, distichous (leaves), plus a good many attached cones. … In the Florissant collections … there is just as much distichous, needle-like foliage as scaly foliage.” Chaney noted that, “the collectors’ preference may also be a consideration in the abundance of scaly shoots” and gives “an exaggerated idea of the proportion of scaly shoots.”

Appendix A lists the illustrated twig specimens of *Sequoia affinis* in the published record. At some locations the twig specimens are somewhat described, or a description can be inferred from the report discussion. The illustrated, described, or inferred specimens are assumed to be representative of the *Sequoia affinis* fossils at each locality. In Appendix A the fossils are categorized as to their general leaf form; those with scale-like leaves (i.e., generally less expanded leaves, as defined later, to full awl-shaped scale-like leaves) and those with needle-like leaves (i.e., generally more expanded leaves). Where possible, the categorized leaf forms are biased toward the original description in the report.Twig specimens with either staminate (pollen) cones or pistillate (seed) cones, or unattached cones, are listed separately.

In Appendix A the total of each of the two leaf forms are summed for each location, and summarizes the leaf forms as the percent with less expanded to scale-like leaves at each location, exclusive of those with
cones (i.e., infertile shoots). The percent of the less expanded to scale-like leaves at each location in the fossil record is plotted to show the progression of leaf form over geologic time in Ma on the facing page. The plot also shows the available record for the Cretaceous (and probably Paleocene) *Sequoia dakotensis* and the wholly scale-like leaves of *Sequoiadendron chaneyi*.

The non-random, progressive variation in the percent of less expanded to scale-like leaves through time in the geologic record necessitates interpretation. To do this we first turn to the living trees and then to overarching global events.

**Contributions From Nearest Living Relatives**

For the first century of North American paleobotany, assessment of the paleoclimatic characteristics in the vicinity of the depositional environment of a fossil flora focused on comparing Tertiary plant communities to the ecologic requirements of the modern equivalents of as many fossil forms as possible. This environmental reconstruction process is referred to as the Nearest Living Relative technique. Habitat reconstruction is not the purpose here, but rather an examination is made of the nearest living relatives of *Sequoia affinis* and *Sequoiadendron chaneyi* to see what the living plants, *Sequoia sempervirens* and *Sequoiadendron giganteum*, can contribute to an understanding of the geologic history of the fossil forms. The possible contributions of the fossil wood is not considered.

In briefly discussing *Sequoia sempervirens*, John M. Bigelow (1854) made the first notice of the fact that “the foliage of this tree is dimorphous.” Other botanists occasionally also made notice of this fact, but the first actual published investigation of the presence of flat needlelike leaves and scale-like leaves was by Alice Eastwood in 1895 at the California Academy of Sciences. Consequently, the nineteenth century paleobotanists were essentially not informed as to this fact and placed their fossils in a multitude of species. In 1909, Willis Linn Jepson noted “*Sequoia sempervirens*, leaves … in the top of adult trees … (are) strikingly suggestive of those of the Big Tree (*Sequoiadendron giganteum*)”.

The clearest published observation of the foliage of *Sequoia sempervirens* was made by Chaney in his 1951 monograph:

Anyone who has studied the foliage of *S. sempervirens*, especially on the dry borders of its range, must have observed that it has a larger proportion of scaly and small-needled shoots than in the heart of the Redwood Belt. Whole trees may occasionally be seen on which the foliage is scaly. Furthermore, all trees
Leaf forms of living *Sequoia sempervirens* as a function of water availability induced stress.

bear scaly shoots at their growing tips, where cones are most abundant. A climatic or growth factor may be involved in the often scaly aspect of *S. affinis*.

Recent studies have brought further clarification to the foliage of *Sequoia sempervirens* (Jennings 2002 and Koch, et al. 2004). Studies related to tree height have shown that leaf morphology (quantified as the leaf mass per unit area, LMA) is a function of the negative water pressure (akin to suction) in the xylem (sap wood) of the tree. The LMA is higher (leaves of the same weight are smaller) at lower sap wood water pressure, that, in turn lowers the positive water pressure in the leaves (turgor). The lowering of the water pressure in the leaves prevents leaves from expanding, a well known consequence of drought (Taiz and Zeiger 2002). In *Sequoia sempervirens* this means that newly emerging leaves are not able to grow and expand from their initial scale-like form to flat needlelike leaves present in moist habitats or lower down on taller trees.
Koch, et al. (2004) provided a dramatic example of the affect of drought, as expressed in tree height, on leaf morphology. A branch from the upper crown at a height of over 90 meters with scaly leaves was rooted in wet soil under full light like that at the top of the tree. The next flush of growth was comprised of flat needlelike leaves. Similar physiological responses were operative in the early Eocene (51.5 Ma) *Sequoia affinis* preserved in the Tranquil Shale McAbee Flora of British Columbia, as shown below.

*Sequoia affinis* from the Zugg I Mineral Claim near Cache Creek, British Columbia. This fossil shows a flush of growth under more moist conditions following a period of growth under a water deficit. Specimen courtesy of John A. Fraser, Ashcroft, British Columbia.

(2.0 cm coin for scale).

Farjon (2005) noted that, “the leaves in Cupressaceae are polymorphic in all species.” *Sequoiadendron giganteum* is no exception. This may account for the early identification of *Sequoiadendron* in the Buffalo Canyon Flora, Nevada, noted above. However any physiologic contributions to understanding the fossil record have not been fully worked out.

Modern physiological investigations of *Sequoia sempervirens*, and similar morphological expression in the fossil record, indicate that Ralph Chaney was correct when he surmised that, “A climatic or growth factor may be involved in the often scaly aspect of *S. affinis*.”
Sequoia affinis’s GLOBAL CENOZOIC CLIMATIC SETTING

Geology dictates the lie of the land, and climate controls how the design of the world accommodates to life. But climate itself is in thrall to geology. Richard Fortey 2004.

After the dust settled following the instantaneous end of the Cretaceous, the global climate during the Paleocene continued the wet and warm conditions that had prevailed during the late Cretaceous. Global temperature began to rise near the end of the Paleocene, culminating in the Initial Eocene Thermal Maximum. The climate then began to cool, somewhat irregularly, falling below the temperatures of the Paleocene by the end of the early Eocene. Global temperature continued to decline at about the same rate until near the end of the middle Eocene. At the middle-late Eocene boundary temperatures rapidly declined, crossing a biotic threshold, and finally bottoming out, temporarily, just after the Eocene-Oligocene boundary. During the earliest Oligocene, global climate cooled even more significantly and very quickly, making a “great break,” known in Europe as La Grande Coupere (Prothero 1994), in the history of life on Earth during the Cenozoic. (Cenozoic climates have been the focus of numerous investigations and can merely be summarized here. See for example Zachos, et al. 2001; Bender 2013).

The global climatic change in the early Oligocene was reflected not only in lowered temperature but also in changing precipitation quantities and distribution. Colder temperatures dominated much of the Oligocene. The climate somewhat warmed through the late Oligocene and there were periods of increased global aridity, particularly at the Oligocene-Miocene boundary. The warming trend continued into the early Miocene and peaked in the early middle Miocene, between 16 and 14 Ma, in a period called the “Middle Miocene climatic optimum,” or occasionally the “Global Thermal Maximum.” The global warming however, never reached the temperatures evident before the middle-late Eocene transition. Overall, global climate was continuing to cool, and did so dramatically following the thermal maximum. The late Miocene was a time of transition to much cooler and drier conditions, with a slight warming at the Miocene-Pliocene boundary (5.1 Ma). The Pliocene was a short period before the global climate plummeted into the “ice age” climate of the Pleistocene.

In western North America, Sequoia affinis was a part of an interior upland plant community where temperatures were lower than global
averages. In the middle to late Eocene, continental climate exaggerated the global temperature changes, and increasing seasonal dryness produced the most extreme paleobotanical change of the Cenozoic – loss of the tropical forests (Prothero 1998; Wing 1998). Near the end of the Eocene, at the Florissant, Colorado fossil locality (34.07 Ma), where *Sequoia affinis* was first identified, the altitude may have been over 8,000 feet (Hay, et al. 2002), with a mean annual temperature of 13°C (55°F), several degrees below the global average of about 17°C (63°F). Site specific climatic interpretations vary widely even at one location and are of limited use here. However, global average temperatures can be used for a general comparison, as a climate proxy, to track changes in the leaf morphology of *Sequoia affinis*, as shown in the following chart.

*Sequoia affinis* leaf morphology and average global temperatures over the course of the Cenozoic.
The Oligocene had a duration of about 10.9 million years, from about 33.9 Ma to 23.03 Ma. The early Oligocene global cooling, from 33.2 to 32.8 Ma, Europe’s “Le Grande Coupure,” with glaciation in Antarctica, triggered massive vegetational changes including significant extinctions and plant migrations in much of the world. Easterly of the highlands where *Sequoia affinis* was growing, evidence from depositional environments, paleosols, fossil terrestrial snails, and fossil plants, all show a trend toward cooling and drying (Prothero 1994, 1998). As temperatures fell during the early Oligocene, cooler habitats favorable for *Sequoia affinis* would also have extended to lower elevations to the westerly of the interior uplands where *Sequoia affinis* is found in the middle to late Eocene. A westward migration of *Sequoia affinis* could be recorded in the tentatively late Oligocene deposits of western Oregon in the Lyons, Willamette, and Rujada floras (respectively, locations 14, D, and E in Appendix A).

The extreme global cold period resulting in the early Oligocene changes in vegetation may have lasted only a million years (Miller, et al. 1991), to as little as 300,000 years (Zachos, et al. 2001), in geological time, a mere “cold snap.” This early Oligocene cold period effectively eliminated the last of the Eocene tropical plants from western North America through a combination of extinction, migration, and isolation in lower latitudes (Wolfe 1992). Later in the early Oligocene a more protracted cold period, with renewed glaciation in Antarctica, began and lasted about 4 million years. The Oligocene cold snap had eliminated those plants that could not adapt and the floristic response to the 4 million year cold period across the early/late Oligocene boundary seems less severe based on overall floristic response (Prothero 1998). After 4 million years of Antarctic glaciation, the late Oligocene was a period warming, however Antarctic glaciation was once again renewed across the Oligocene/Miocene boundary, with further global cooling and drying.

Though the “middle” Oligocene cold period may not have had an additional affect on the angiosperms surviving the early Oligocene cold snap (excepting subgeneric-level modernization, Wing 1987), this may not have been the case among gymnosperms, particularly in the family Cupressaceae, of which Sequoioideae is a subfamily, that underwent speciation. Examples are that the earliest fossil record of the genus *Juniperus* is from the early Oligocene (stated as Eocene/Oligocene boundary) in central Europe (Farjon 2005) and of *Calocedrus* from the early Oligocene Butler Basin assemblage of the Bridge Creek Flora of Oregon (Meyer and Manchester 1997). Earlier appearing genera (e.g., *Thuja*) also appear to have gone through a flush of speciation after the Eocene/Oligocene boundary (Peng and Wang 2008).
Tree structured phylogenetic (genealogical) relationships of the Cupressaceae have been worked out by several investigators (Kusumi, et al. 2000; Gadek, et al. 2000). A time frame has been established for the phylogenetic trees using molecular clock models partially calibrated using the fossil record (Mao, et al. 2012; Crisp and Cook 2011). In summary, the time (geologic age, Ma) when closely related living gymnosperm branches began to diversify (called the crown age), has a median age of 32 Ma (Crisp and Cook 2011), significantly close to the early Oligocene global cold snap (33.2 to 32.8 Ma).

The Oligocene/Miocene boundary (23.6 Ma) was another period of Antarctic glaciations. The lower Miocene witnessed a slight warming trend. *Sequoia affinis* could have been restricted during this time to more favorable habitats resulting in a higher percentage of needlelike leaves seen in Neogene deposits, or, as Chaney (1959), Axelrod (1966) and Fields (1993) have suggested, a new species, more akin to *Sequoia sempervirens*, may have emerged, OR, the early Oligocene climatic deterioration may have had an even bigger affect. In 1967, J. A. Wolfe (1967, in Leonard and Marvin 1982) stated “*Sequoia affinis* indicates a Paleogene age,” thus, precluding Neogene (Miocene and Pliocene) occurrences.
NEAREST LIVING RELATIVES REVISITED

Evolution, being on the whole a population turnover, is ordinarily a gradual process, except for certain chromosomal processes that may lead to the production of a new species-individual in a single step. … there is no doubt as to the prevalence of geographic (allopatric) speciation and (in plants) polyploidy as the prevailing forms of speciation. Ernst Mayr 2001.

In his excellent monograph on The Fossils of Florissant, Herbert W. Meyer (2003) suggested that, “Sequoia affinis may have been ancestral to Sequoia sempervirens, but it also may have been the ancestor of the modern Sequoiadendron giganteum. … Of the two, Sequoia clearly shows the closest similarity to the fossil species from Florissant.” For Sequoia affinis to have been ancestral to either, or both, modern species the basic building blocks of ancestry, chromosomes, had to have gone through a favorable set of historical changes resulting in better adapted, yet alone survivable, descendents.

All three of the genera in the Sequoiadeae: Sequoia, Metasequoia and Sequoiadendron, are monoecious, producing male and female cones on the same tree. The pollen is dispersed by wind and the female cones are both cross- and self-pollinated. This is essentially a distribution biased random process.

Eight of the nine genera that were “traditionally” grouped in the Taxodiaceae, including Sequoiadendron, possess 11 paired chromosomes (chromosome number = n) in their somatic cells (main body, as opposed to reproductive, cells), for a diploid number, 2n, of 22, when the chromosomes are unpaired during meiosis for reproduction. The total number of genes in the unpaired (i.e., haploid set) chromosomes is referred to as the genome. For the eight “traditional” Taxodiaceae mentioned, the genome number is the same as the diploid number; 22. Genome (chromosomal) duplication is the presence of more than two genomes (sets of chromosomes) per somatic cell nucleus, and is referred to as polyploidy.

Sequoia sempervirens is unique among conifers, with 66 chromosomes in its somatic cells, the only hexaploid conifer (6x11 =66). Only four conifers are polyploid, including Sequoia, for a total of about 1.5% of conifer species. However, among other land plants, polyploidy is widespread. In flowering plants (angiosperms) 47-70% are polyploids (Grant 1963; Masterson 1994), and among the pteridophytes (ferns and allies) the number of polyploid species is close to 95% (Ahuja 2005).

The origin of Sequoia sempervirens, and hence its hexaploid state, was reviewed by Yang, et al. (2012) and is helpful in accessing Meyer’s
suggestion of *Sequoia affinis* as a common ancestor of both living *Sequoia* and *Sequoiadendron*. Morphological and cytological studies have resulted in several proposed hypothesis for the origin of the living *Sequoia*’s hexaploidy (Stebbins 1948; Li 1987, 1988; Ahuja and Neale 2002; Ahuja 2005). The following summarizes Yang’s review of the works of these authors:

Stebbins (1948) was the first to report that *Sequoia sempervirens* was a hexaploid. He inferred that *Sequoia* originated by hybridization between *Metasequoia* and some probably extinct taxodiaceous plant. Li (1987, 1988) suggested *Metasequoia* and *Sequoiadendron* or ancestors of the two genera as the parental species of *Sequoia*. [Here, ancestors should be emphasized and defined as similar genera, now extinct, since none of the Cretaceous taxodiaceous fossils have been demonstrated to be *Sequoiadendron*. As stated by Miller (1977) and LaPasha and Miller (1981) – “All the modern genera except *Sequoiadendron* have been reported from the Mesozoic.”] The most up to date work concerning the origin of hexaploidy in *Sequoia sempervirens* is that of Ahuja and Neale (2002, 2005) and Ahuja (2005, 2009). These authors have provided several possible hybridization modes to explain the hexaploidy. Their conclusions are, “It is not known when the polyploid coast redwood evolved from its diploid ancestors and which are its putative progenitors, living or extinct” and “Sequoia remains an enigmatic hexaploid (either an autoallohexaploid, or a segmental allohexaploid, or a partially diploidized autohexaploid.”

From their phylogenetic studies Yang, et al. (2012) concluded, “Unfortunately, clues for the origin of *Sequoia* may have been blurred in the long evolutionary history, given that the earliest fossil record of this genus can be dated back to the early Cretaceous.” The Cretaceous fossil referred to is the form fossil (leaf and twig impressions only) *Sequoia jeholensis* Endô / *Elatocladus leptophyllus* Wu from early in the lower Cretaceous discussed previously. It should be noted that the earliest fossils of *Metasequoia* date from the lower upper Cretaceous (LePage, et al. 2005), some 40 Ma after the claimed *Sequoia* fossils, at best complicating the suggested Mesozoic hybridization origins. Yang, et al. (2012) went further, offering the following possible explanation: “nevertheless, the inconsistent relationships among *Metasequoia*, *Sequoia* and *Sequoiadendron* revealed by different data sets could be an important sign of reticulate evolution among the three genera, even though it is difficult to deduce how and when *Sequoia* originated.”

Though the origin of the genus *Sequoia* has been obscured by the limitations of the fossil record and its application, the goal here is to evaluate how the *Sequoia sempervirens* genetic studies are helpful in accessing Meyer’s suggestion that *Sequoia affinis* might have been a common ancestor of the living species of both *Sequoia* and *Sequoiadendron*. This assessment relies on the ramifications of all of the
several suggestions that have been put forth and allows development of a speculative evolutionary model.

*Sequoia affinis* is found in sediments preserved in the depositional basins of the volcanic uplands of western North America. In the early to middle Eocene, the global climate was tropical, including of course the geographic range of *Sequoia affinis*. As oceanic currents adjusted to the openings and closings of circulation routes, and atmospheric circulation changed in response to changes in both ocean dynamics and land mass elevations, climates adjusted accordingly. By the end of the middle Eocene the global tropical climate ended and more distinct continental, altitudinal, and latitudinal effects were formulating. By the end of the Eocene, the changes had occurred over many millions of years allowing any adaptations in *Sequoia affinis* to occur. As demonstrated at the Florissant Fossil beds, some populations of *Sequoia affinis* stayed at higher elevations, though they may have migrated southward to lower latitudes (Florissant is the southernmost Paleogene occurrence of *Sequoia affinis*). As previously mentioned, other populations may have migrated to lower elevations as favorable habitat expanded downward to less interior locations.

One possible adaptation may be evidenced by the “Redwood Trio” stump at Florissant that indicates that *Sequoia affinis* reproduced vegetatively, just like *Sequoia sempervirens*, from basal stem sprouts (Meyer 2003). Both the fossil and the extant species also reproduced by seed production. By comparison, in living *Sequoiadendron* vegetative reproduction is known only in younger, injured trees (Weatherspoon 1990), and then rarely. Natural vegetative reproduction is not reported in *Metasequoia* (Williams 2005).

The paired reproductive mode of *Sequoia* might indicate that polyploidy developed in the genus *Sequoia* by the end of the Eocene. In Ahuja’s (2005) assessment, *Sequoia* “might have been nature’s incomplete experiment in evolving polyploidy in a conifer with a caveat; there was a mid-course correction by establishing an additional mode of reproduction, the vegetative propagation, for the survival of a rare polyploid in a conifer!” Crepet and Niklas (2009) add that paired “reproductive mechanisms (are) particularly efficacious for the survival of a species in environments experiencing episodic or random physical disturbance.” The latter is a good generalization of the extreme volcanic terrain in the geographic range of Paleogene *Sequoia affinis*.

Since chromosomal, or genome, duplication (polyploidy) is a hereditary process, it is not specific to *Sequoia sempervirens* or the gymnosperms, where it is rare. Examples of the influences of polyploidy must be sought among the angiosperms. Any effects, beneficial or
detrimental, demonstrated by a polyploid in one group of plants can be similar in another (Levin 2002). Crepet and Niklas (2009) when mentioning Sequoia sempervirens’ exceptionalism as “one of the very few known naturally occurring polyploid conifers” stated, “It is perhaps also informative to note that, among (living) angiosperms, polyploidy tends to increase toward higher elevations and latitudes. Thus, it is possible that polyploid plants have an ecological advantage in cold environments.” Considered in a cause and effect manner, it is equally likely that the reproductive stresses resulting from the colder and dryer conditions that spanned the middle and late Eocene and culminated in the early Oligocene “cold snap” climatically ‘forced’ some plants to undergo genome duplication, thereby becoming polyploids, in the more severe climates of higher elevations and latitudes.

Mentioned above was Ahuja’s (2005) opinion that Sequoia’s polyploidy “might have been nature’s incomplete experiment in evolving polyploidy.” Ahuja and Neale (2002, 2005) considered Sequoia “either an autoallohexaploid, or a segmental allohexaploid, or a partially diploidized autohexaploid.” The names of each of these possible mechanisms to achieve hexaploidy come from the ancestral components (meiotic configurations) in the resulting polyploid itself: auto, self or within, meaning that the genome duplication arose from within the same species population; allo, different or other, meaning the genome duplication arose from hybridization with another species; and autoallo meaning both self and other in the meiotic configurations. Ahuja (2005) emphasized Sequoia sempervirens being an autoallohexaploid as a working assumption. The “incomplete experiment” derived from considering Sequoia as possibly being a “partially diploidized autohexaploid.” Each of these mechanisms will be assessed.

Of the three types of polyploidism suggested as possibly applying to Sequoia – autoallohexaploid, segmental allohexaploid, or a partially diploidized autohexaploid – the middle one can be dispensed with. The state of a species being a segmental allohexaploid is fairly discounted by Sybenga (1996, summarized in Levin 2002) who “questioned the idea that segmental alloploids persist in nature. He contends that although they may be formed by hybridization between related species followed by chromosome doubling, recombination between homologous chromosomes eventually will turn them into autopolyploids or less often into allopoloids.” Ahuja (2009) indicates that Sequoia is not strictly an allopoloid. The allohexaploid state explored by Ahuja and Neale (2002) necessitated that three distinct species be available for chromosomal interaction, of which only two plausible choices exist in the later fossil record as discussed below.
Thus, given Sybena’s and Ahuja’s later considerations, three evolutionary paths are available for *Sequoia affinis* to reach the hexaploid state found in *Sequoia sempervirens*. All three pathways involve two rounds of chromosomal doubling, but only two of these involve an initial chromosomal doubling within a *Sequoia affinis* population and both result in an autotetraploid *Sequoia affinis* subpopulation. Along one of these two paths the autohexaploid state is eventually reached by self-hybridization of *Sequoia affinis* tetraploids with *Sequoia affinis* diploids in the parent *Sequoia affinis* population. Along the other pathway to hexaploidy the autoallohexaploid state is reached through a *Sequoia affinis* tetraploid – alien species hybrid. The third pathway also ends in an autoallohexaploid state, but does not involve an initial chromosomal doubling and will be discussed later.

**Initial Chromosomal Doubling and the Climatic Record**

All three pathways to achieve hexaploidy in *Sequoia sempervirens* explored by Ahuja and Neale (2002, 2005) involve two rounds of chromosomal doubling. The time gap between the first doubling episode and the second is indeterminate and probably variable. Two of the possible pathways to hexaploidy involve an initial round of chromosomal doubling and result in a tetraploid subpopulation. Given that *Sequoia affinis* was in a midlatitude inland upland area undergoing significant climatic change, it is probably meaningful to note that in their summary of polyploidy, D’Amato and Durante (2005) point out that, “In growing plants, a sudden drop in atmospheric temperature at metaphase blocks cells dividing in the shoot apex, thereby producing autotetraploid cells.” This is what Ramsey and Schemske (1998) reported as “a failure of the reduction division in meiosis,” i.e., the chromosomes do not become unpaired and separate during reproductive cell division, an unreduced gamete. What if the drop in temperature is prolonged?

The progressively cooling and drying environment throughout the 18 million years of the middle to late Eocene, that ultimately caused the extinction of the majority of the land mammal genera and loss of the tropical/subtropical forests in the lowlands, undoubtedly had protracted periods of sub-lethal cold in the uplands that would affect reproductive processes throughout the habitat of *Sequoia affinis*. A long term continuance of the cold driven chromosomal doubling process may have been necessary across the general population of *Sequoia affinis* in order for tetraploidy to become a stable feature. The percentage of the overall population in a tetraploidal state possibly would have been higher at higher altitudes and latitudes. As summarized by Levin (2002)
“Chromosomal doubling may be accompanied by increased resistance to cold temperatures.”

In the drying environment, the tetraploid members of the population may also have had a survival advantage. “Chromosomal doubling can have a substantial impact on plants’ water relations ... (because) chromosomal doubling is likely to increase leaf diffusive resistance (and) because transpiration rates are a negative function of diffusive resistance, they are likely to be lower in polyploids than diploids,” thus lowering transpiration rates and the water demand (Levin 2002).

Concurrently, within the population-wide development of an autotetraploid subpopulation, many of the earlier autotetraploids would have been going through the genetic processes where the genome becomes restructured as a diploid rather than as a polyploid, a process called diploidization. Multigeneration garden tests of short lived plants has elicited the conclusion that “the greater the progression of diploidization the more difficult it is to discern” (Levin 2002). Ahuja (2005) made note that, “In spite of its antiquity, Sequoia has not undergone the evolutionary process of complete diploidization, involving both changes in cytological behavior and genetic constitution, to achieve a diploid-like state.” Ahuja’s comment was derived from living Sequoia sempervirens, a current descendent of that process.

The 300,000 year long early Oligocene global cold snap undoubtedly destroyed some geographical populations of Sequoia affinis and may have differentially affected the remaining parental diploid members of other populations in some areas. The cold snap could have induced multiple pulses of development of autotetraploid members. These genetically younger autotetraploid members would not necessarily have been morphologically and adaptively identical to genetically older autotetraploid subpopulations and would probably have had a different habitat controlled geographic distribution.

**Hybrids, Chromosomal Doubling, and More Hybrids**

The scenarios proposed by Ahuja and Neale (2002, 2005) and Ahuja (2005, 2009) to explain the hexaploidy in Sequoia sempervirens could have operated in response to post middle Eocene cooling or to the early Oligocene “cold snap” forcing tetraploidal subpopulation of Sequoia affinis to develop. The tetraploidal individuals could hybridize within the residual diploidal and/or recently diploidized subpopulation of Sequoia affinis resulting in another subpopulation with three pairs of chromosomes in the nucleus (i.e., a triploid subpopulation) that could then have been forced to undergo a second round of chromosomal
doubling in the more severe climate, as appropriate, of the early Oligocene “cold snap” or the Oligocene/Miocene boundary cold period, depending on timing. This second chromosomal doubling event would result in a subpopulation of autohexaploid descendents.

However, there is a possible problem with positing a triploid subpopulation as required under each of Ahuja and Neal’s mechanisms. “The union [pollination] of a [cold induced] unreduced (2n) gamete [either from the pollen or ovule] with a haploid (n) gamete [a normal reproductive cell] yields a triploid (3n) individual.” However, “plants with odd-numbered ploidy are generally nearly sterile” (Futuyma 2005). Since apparent sterility can also encompass survivability of fertilized ovum through the early developmental stage, there can be a climatic factor involved. The operative limitation of “generally nearly sterile,” could be overcome in favorable habitats and by sheer numbers over hundreds of thousands or millions of years.

The preceding scenario could have worked throughout the range of Sequoia affinis or could have been restricted to only a portion of its range. In overall warmer/moister habitats at lower altitudes or latitudes within the geographic range of the autohexaploidal Sequoia affinis, or a descendent, the population would exhibit a more expanded leaf form. Contemporaneous cellular processes, the aforementioned changes in cytological behavior and genetic constitution (meiotic stabilization), could result in a “partially diploidized autohexaploid” population, Ahuja (2005)’s “incomplete experiment.”

The first of the two suggested paths to an autoallohexaploid state of Sequoia sempervirens initially requires the internal (auto) chromosome duplication discussed above leading to a partial population of tetraploid individuals. Under the mechanisms proposed by Ahuja and Neal (2002) and Ahuja (2005), the tetraploid members of the population would then have had to have hybridized with a different species.

In all of the phylogenetic references quoted so far, the genus Sequoia has been assumed to be a Mesozoic hybrid between extinct or precursor members of the traditional Taxodiaceae. Generally these have been loosely called Metasequoia and Sequoiadendron, even though the Sequoiadendron fossil record does not extend back in time to the Mesozoic (Miller 1977; LaPasha and Miller 1981) and the fossil record of Sequoia may antedate that of Metasequoia by some 40 Ma.

If the assumption is made that Metasequoia and Sequoia were distinct diploid entities (as are the majority of modern conifers) on tropical Earth from at least the early late Cretaceous through to the middle-late Eocene (biotic threshold) boundary, then a model can be developed where the hexaploidal nature of Sequoia sempervirens began
Copreservation of *Sequoia affinis* and *Metasequoia occidentalis* in the Cenozoic of western North America and the distribution of *Sequoiadendron chaneyi* and *Metasequoia occidentalis*.

through hybridization later in geologic time. Two of Ahuja and Neal (2002)'s scenarios to yield an autoallohexaploid subpopulation require the presence of a second species with which to hybridize. *Sequoia affinis* is copreserved with *Metasequoia occidentalis* at several fossil sites, fourteen of which are shown on the accompanying maps.
The first map (upper left) covers the early through middle Eocene. Of the eleven sites where *Sequoia affinis* is found, all seven of the northernmost localities in the Okanagan Highlands, preserve fossils of both *Sequoia affinis* and *Metasequoia occidentalis*. Sometimes fossil twigs of both are found on the same hand specimen. The climate was tropical with no known climatic forcing events. There are no known fossils that exhibit distinctly identifiable morphologic features that would suggest the presence of a hybrid in the population. *Metasequoia* is present unaccompanied by *Sequoia* at the singular location near the west coast. At the southern extent of the range of *Metasequoia*, the two genera are not copreserved. This might suggest that there was a separation of habitat tolerances, and *Sequoia affinis* extends further south past the range of *Metasequoia occidentalis*.

The late Eocene up to the earliest Oligocene, before the 300,000 year “cold snap,” shown on the second map (upper right), is represented by four fossil sites. There are only a third as many sites as before the late Eocene. The three northern sites copreserve *Sequoia affinis* and *Metasequoia occidentalis* and the single southern site preserves only *Sequoia affinis*. This could represent a southward habitat separation as was suggested for the early to middle Eocene record. Morphologic hybrids have not been found in the late Eocene fossil record.

On the third map (lower left), four of the five Oligocene localities after the 300,000 year “cold snap,” show copreservation of both species. Again no morphological hybrid forms have been reported. The two overlapping locality symbols on the Oligocene map at the Idaho/Montana border, one with copreservation of the two species and one without, continues to show a possible habitat separation in the uplands that may have become established in the middle to late Eocene (first map). *Metasequoia* is fairly widespread westerly of the Oligocene uplands, with and without copreservation of *Sequoia*.

For the duration of the presence of *Metasequoia* in North America into the Miocene, there is no copreservation with *Sequoia affinis* (fourth map, lower right). It is during the Miocene that the more westerly populations of *Sequoia affinis* could have been restricted to moister habitats resulting in a higher percentage of expanded needlelike leaves or, as Chaney (1959), Axelrod (1966) and Fields (1993) have suggested, a new species, more akin to *Sequoia sempervirens* may have emerged.

The third suggested path to an autoallohexaploid state of *Sequoia sempervirens* (Ahuja and Neal 2002) does not involve an initial chromosomal doubling. The third pathway begins with a round of *Sequoia affinis* diploid – alien species (*Metasequoia*) hybridization followed by this pathway’s initial round of chromosomal doubling, then
another round of hybridization by two possible routes. The chromosomally doubled descendents (tetraploid individuals) of the first hybridization must once again hybridize with either a *Sequoia affinis* diploid or with members of the earlier alien species (*Metasequoia*) with which hybridization occurred. Here too, the possible problem with triploid fertility arises. At risk of over emphasizing the fact, there is no evidence of morphologic hybrids found in the fossil record. Either, or both, of the two types of second stage hybrids must then go through another episode of chromosomal doubling. Though theoretically possible it seems like this third pathway to hexaploidy in *Sequoia sempervirens* is a proper place to apply Occam’s Razor.

With the absence of morphological hybrids in the copreserved Cenozoic populations of *Sequoia affinis* and *Metasequoia occidentalis*, there is no direct evidence to support either of Ahuja and Neale (2002)’s two pathways to autoallohexaploidy as a basis to explain hexaploidy in *Sequoia sempervirens*. The autopolyploidal mechanism seems much more plausible, as it can occur within a single species ancestral population, and it does not require genetic interaction with another genus/species. Therefore, there would be no morphological hybrids to leave a fossil record. Furthermore, “autopolyploids may have unique to transgressive tolerances and traits that may allow the exploitation of habitats beyond the limits of their diploid progenitors” (Gottschalk 1976, quoted in Levine 2002), suggesting the ability to adapt to changing climatic conditions in a subpopulation that may have tracked suitable habitat out of the uplands to survive.

Either morphologic hybrids in the fossil record have escaped notice, or *Sequoia sempervirens* is that *Sequoia* tetraploid – *Sequoia* diploid hybrid: Chaney’s (1959), Axelrod’s (1966) and Fields’ (1993) new species, more akin to *Sequoia sempervirens*, a pre-*Sequoia sempervirens*, unrecognizable as a morphologic hybrid due to having been derived through the autopolyploidal pathway and not yet completely diploidized.

*Sequoia affinis*,
autohexaploid, OR
pre-*Sequoia sempervirens*?
Early Pleistocene.
Santa Clara Fm.
Santa Cruz Mountains,
California.

(Lower right twig stem, 2.6 cm.)
Full Diploidization Following Initial Chromosomal Doubling

Throughout the range of *Sequoia affinis*, not every location where the fossil species is found would have experienced the same microclimatic conditions and changes. Nor would all of the surviving older autotetraploid members been identical in their morphological and physiological features. Some autotetraploid subpopulations must have had features allowing for their survival and reproduction in their particular habitat, even where their progenitor populations had completely failed. Older autotetraploid subpopulations would have been undergoing diploidization longer than younger autotetraploid subpopulations, possibly allowing for different populations to development under a range of environmental factors.

Previously, when discussing possible autoploidy mechanisms in *Sequoia affinis* that may have lead to pre-*Sequoia sempervirens*, it was noted that the post middle Eocene cooling or the early Oligocene “cold snap” could climatically force the emergence of a tetraploidal subpopulation of *Sequoia affinis*. Further, it was noted that the tetraploidal individuals could hybridize within the residual diploidal population, thereby yielding a triploid generation of individuals that were “generally nearly sterile,” or may have had low early developmental survivability, and that these constraints could be overcome through sheer numbers and favorable environmental conditions over hundreds of thousands or millions of years.

Under other environmental conditions, the constraints of the triploid progeny may not have been the case. In such cases “the tetraploid is reproductively isolated, and it is therefore a distinct biological species” (Futuyma 2005).

In the late Eocene (36 Ma), *Sequoia affinis* with slightly over half scaly-leaf forms was relatively abundant in the sedimentary Breaverhead basins (Appendix A location 8) of southwestern Montana (Becker 1969). These basins were located on the arid east flank of the Challis volcanic terrain, in “a narrow rain shadow in the central Rocky Mountains” (Retallack 2007). Fossils from the early Oligocene Ruby River Basin, about 40 miles distant to the east (Appendix A location 10), yielded only scaly-leaved twig fossils that were initially assigned to *Glyptostrobus*. The fossils were later reassigned to *Sequoia affinis* based on a similarity of the staminate (male) cone fossils to similar fossils from Florissant.

The male cones from the Ruby River Basin illustrated by Becker (1966) are smaller in relation to the attached twig diameter than are the male cones from Florissant shown by MacGinitie (1953) and by Chaney (1951). These male cones are closer in their outward appearance to those
of Sequoiadendron giganteum than to those Sequoia sempervirens as seen in their habitats and as illustrated by Farjon (2005).

In favor of Sequoiadendron evolving from a late Eocene to early Oligocene scaly-leaved population of Sequoia affinis in a relatively arid environment, like the southwestern Montana record, comes from another one of Sequoiadendron giganteum’s exceptionalisms. When Pittermann, et al. (2012) characterized the habitat affinities of all living Cupressaceae, they found, exclusive of the two most specious genera, Cupressus and Juniperous, and the xeric Callitroids, that of the remaining species of the Cupressaceae, “the majority inhabit mesic habitats. With the exception of Sequoiadendron giganteum, the early diverging Cupressaceae occupy mesic-hydric habitats.”

In a strict sense, Sequoiadendron could not have been an early diverging Cupressaceae because “All the modern genera except Sequoiadendron have been reported from the Mesozoic” (Miller 1977, LaPasha and Miller 1981). However, full diploidization of a drought specialized Sequoia affinis tetraploid could have occurred in later Oligocene and earliest Miocene under more stabilized arid climatic conditions as the rain shadow of the Cascade Mountains merged with that of the Central Rocky Mountains (Retallack 2007). The earliest occurrence of a stabilized genus might possibly be seen in Sequoiadendron chaneyi of the late early Miocene, a period much drier than the mesic-hydric habitats of the early diverging Cupressaceae.

The genetics of Sequoia affinis and Sequoiadendron chaneyi are unlikely ever to be able to be directly investigated. However, Ambrose, et al. (2009) concluded from their studies of tall trees that their data “suggest that wood and hydraulic properties of both redwood species may have evolved under different and perhaps drier conditions than these species experience today.” This conclusion is clearly favorable for considering the evolution of Sequoiadendron and Sequoia sempervirens through climatic forcing in populations of Sequoia affinis.

Furthermore, in support of a close genetic affinity between Sequoiadendron giganteum and Sequoia sempervirens, as pointed out by Rejmánek (2013), a “recent Cupressaceae phylogeny based on nucleotide sequences from plastid, mitochondrial, and nuclear DNA, Sequoia and Sequoiadendron are always closer to each other than (either is) to Metasequoia (Mao et al. 2012). This may support there near contemporaneous derivation from a common ancestor, after which each followed its separate developmental pathway.
CONE SIZE DISPARITY

Cones develop over an extended period of time. Development starts with inception of a cone. … The period from … the time they reach full size is one of relatively massive growth. The growth is mostly in the cone scales and the cone axis that supports them. Graham R. Powell 2009.

Ovules (seed precursors) [are] associated with bracts which form the cone scales. There is a gradient in the number of bracts, from Metasequoia with 16-28, Sequoia with 18-25, to Sequoiadendron with 28-45. All three species produce sterile bracts at the apex of the cone, as well as a few at the cone base. [There is] considerable intercalary growth at the base of the bract … [and there] is also a gradient in the contribution of the intercalary growth to the cone scale among the genera. Most of the changes during cone development are due to this intercalary growth. Aljos Farjon, 2005.

The female cones of Sequoia affinis from the middle Eocene through the Miocene represented in the paleobotanical literature range in size roughly from an axial length of 0.8 to 1.9 cm and a width of from 0.5 to 1.1 cm. Cones in the lower end of this range have not been reported for Sequoia sempervirens. The female cone of Sequoia affinis from Haynes Creek, Idaho, as illustrated by Axelrod (1998b), has the same outward appearance as, and falls in the size range of, those from Florissant. Both the Ruby River Basin and the Haynes Creek sites are early Oligocene (30 Ma), shortly after the early Oligocene cold snap. Both these wholly scaly subpopulations of Sequoia affinis were precursors to Sequoiadendron, there were still nearly 12 million years to develop additional anatomical features in response to significant climatic changes. These climatic changes include periods of increased global aridity, particularly at the Oligocene-Miocene boundary and the ensuing warming trend that continued through the early Miocene, before the appearance of indisputable Sequoiadendron in the fossil record. The first appearance of Sequoiadendron chaneyi is in the upper lower Miocene around 18.5 Ma in the Middlelegate basin of west-central Nevada.

The size of the female cones of Sequoia affinis, is generally noticeably smaller than those of Sequoia sempervirens, but there is a slight overlap in cone size between the largest Sequoia affinis cones and the smallest Sequoia sempervirens cones. However, the cone size of Sequoia affinis is dramatically smaller than that generally attributed to Sequoiadendron giganteum cones.

Sequoia sempervirens blooms between late November and early March, although flowering is usually over by the end of January. The
cones mature during the autumn after flowering and are typically from 1.27 to 2.85 cm in axial length (*Sequoia affinis* cone axial length is 0.8 to 1.9 cm). Both longer and shorter cones can be found. The cones open from early September until late December and shed their seeds soon after opening (Roy 1965).

In *Sequoiadendron giganteum* pollination usually occurs between the middle of April and the first of May when the conelets are only two to three times as large in diameter as the twigs on which they are borne. By the end of the first growing season the conelets are about one-third of the mature cone size, i.e., from 1.69 to 2.96 cm in axial length. The mature, second growing season cones, are 5.1 to 8.9 cm in axial length (Schubert and Beetham 1957). Longer and shorter first year and mature cones can readily be found.

The lower end of the size range of *Sequoiadendron giganteum* first year cones overlaps the axial length of the cones of both extant *Sequoia sempervirens* and extinct *Sequoia affinis*. There is a 0.2 cm (15.7%) overlap with *Sequoia affinis* and a 0.4 cm (25.3%) overlap with *Sequoia sempervirens*. Late development, unopened, *Sequoia sempervirens* cones can be visually indistinguishable from first year *Sequoiadendron giganteum* cones.

Left - Early Eocene *Sequoia* sp., cf. *Sequoia affinis*. Coalified compression of fertile and infertile twigs from the Zugg I Mineral Claim near Cache Creek, British Columbia. Larger cone axial length 1.05 cm. Specimen courtesy John A. Fraser, Ashcroft, British Columbia. Right – Partially permineralized decayed cone (approximately 3.7 cm) of *Sequoiadendron chaneyi* from the middle Miocene (12.5 Ma) Fallon Flora. (2.0 cm coin for scale).
Cone development requires a constant supply of water and nutrients. Development of second growing season maturation of cones in *Sequoiadendron*, could be in direct response to an interruption in the water and nutrient supply. Since “drought-resistance necessitates the development of smaller conduits (in the tree’s xylem), it follows that xylem-specific (hydraulic) conductivity declines” (Pitterman, et al. (2010). With a lowering of water transport rate and consequent nutrient delivery, cone growth would be slowed, resulting in delayed maturation.

The female cones of *Sequoia affinis* from the late Eocene (estimated average age of 34.3 Ma; Lielke, et al. 2012) Beaverhead Basins of southwestern Montana (Becker 1969) are reported as occurring as “dissociated, stalked female cones” and as on “fertile branches with attached … cones in various stages of development.” The slightly younger Ruby Basin flora (33.9 Ma; Lielke, et al. 2012) lacks female cones altogether, though *Sequoia affinis* fossils are by no means abundant (Becker 1966). As noted above the male cones in the Ruby Basin suggest those of *Sequoiadendron*. Within sight of the Ruby Basin flora, at the younger York Ranch flora (32.6 Ma; Lielke, et al. 2012), where *Sequoia affinis* fossils are also abundant, Becker (1973) reported that, “The absence of female cones is in striking contrast to their occurrence at the Beaverhead Basin sites where cones were dominant among *Sequoia* remains.”

The abscission of fertile shoots bearing female “cones in various stages of development” has not been noticed at other localities. The shedding of immature cones could suggest that the need for cone retention in order to reach maturity was already developing in the southwestern Montana *Sequoia affinis* populations but that the delaying of the abscission process was not fully congruous.

Development of the larger, second growing season maturation of cones in *Sequoiadendron*, and retention on the tree for 20 years or longer, has a survival advantage in a drier habitat. With serotinous cones, the seeds are restricted from distribution until conditions are most favorable for reproduction.

Cone size increase in *Sequoia/Sequoiadendron* could be a climatic response. Axelrod (1980) has suggested that “the trend to larger cones” (in *Pinus radiata*) “may have been an “adaptation to increasing summer drought during the later Cenozoic.” The genus *Pinus* is complex, with 97 species divided into two subgenera, four sections, and 14 subsections among which the geologic history varies widely. *Pinus radiata* is in the subsection Oocarpae that first appears in the fossil record in the Miocene. *Sequoiadendron* also first appears in the fossil record in the Miocene in
an area of more severe summer drought (Mulch, et al. 2007) than *Pinus radiata*.

Axelrod (1980) also concluded that an enlarged cone size has been shown to have had little to do with the evolution of cone predators in pines, including *Pinus radiata*, or other conifers. Axelrod specified Abies, Larix, Picea, Pinus (as a whole), Pseudolarix, Pseudotsuga, and Tsuga, all of which extend back at least into the late Paleocene and Eocene. In each of these conifers, the cone predators consume the seeds. In living *Sequoiadendron* the mammalian cone predator consumes the cone scales and only incidentally the seeds. *Sequoiadendron* doesn’t appear in the fossil record until the Miocene, whereas, the first appearance of the tree squirrels in North America was *Douglassciurus jeffersoni* in the latest Eocene, (mid-Chadronian, 36 Ma), in the White River Beds of Montana, Wyoming, and Saskatchewan (Emry and Korth 1996, 2001). Cone size increase in *Sequoiadendron* could well be partially a response to the predation, however, the current mammalian cone predator, the Douglas Squirrel (*Tamiasciurus douglassi*), does not specialize in *Sequoiadendron* cone predation, and only has a fossil record extending back to the Pliocene (Steele 1999).

Eight cones of *Sequoiadendron chaneyi* have been illustrated in reports from four sites and range in size roughly from an axial length of 2.1 to 5.2 cm and a width of from 1.3 to 3.5 cm. The cones from the 13 Ma Purple Mountain locality (Appendix B, location 3) are about a third the size of the others and were once thought by Axelrod (1964) to possibly represent a different species. A ninth *Sequoiadendron chaneyi* cone is reported by Erwin, et al. (2001) with an axial length of reported as 1.5 cm from the Washoe Lands Plant site (~5 Ma; Cashman, et al. 2009). These few cones of *Sequoiadendron chaneyi* are within the size range of the cones of *Sequoiadendron giganteum* if first year cones are included in the assessment.

The ranges in cone size with habitat variations have not been reported for *Sequoia sempervirens* and *Sequoiadendron giganteum*. The third living member of the living Sequoiadeae, *Metasequoia*, has been studied more extensively since its discovery in the 1940s. The cone sizes of fossil *Metasequoia* in the Oligocene Bridge Creek flora from Oregon have been shown to vary across reconstructed habitats from 2.4 to 3.5 cm in length from one assemblage and from 1.2 to 1.7 cm at another assemblage, and “may reflect differences in habitat types as they do in modern *Metasequoia* forests, where larger cones are correlated with (plants adapted to) drought resistant sites and smaller cones are from moister sites” (Meyer 2005; Li 1999). Perhaps a similar relationship is found in *Sequoiadendron chaneyi*, where the previously mentioned cones
from the Purple Mountain locality are one third the size of *Sequoiadendron chaneyi* cones from the other locations and “are preserved in a dark gray to black shale … suggesting that the site was swampy” (Axelrod 1995), a condition atypical of western Nevada in the Miocene.

Partially ferriferous mineral lined cast of a leafy twig and a faint impression of an approximately 3.5 cm cone of *Sequoiadendron chaneyi* from an ash-fall tuff within one meter above of the lacustrine deposits in which the 12.5 Ma Fallon Flora is preserved. (2.0 cm coin for scale).
Percent Infertile Shoots With Less Expanded to Scale-like Leaves Among Figured Specimens and Descriptive Locations.

Environmental Change Threshold Resulting In Middle/Late Eocene Boundary Extinctions.

Major Plant Group Extinctions.

Loss of Over 25% of Land Mammal Genera.

Development of New Better Adapted Species.

"La Grande Coupure" - Literally, the "Great Cut."

"The Great Break" Between the Old and the New.

The Second Environmental Threshold Exceeded Resulting in Extinction of the Last Vestiges of Warm Adapted Land Mammals and Plants; Development of Modern Forms.

"C" Oligocene climatic deteriation 33.2 to 32.8 Ma

Essentially Uniformly Warm Humid Conditions Extending From Late Cretaceous.

Prothero's "Greenhouse of the Dinosaurs"

Developmental path to Sequoiadendron Sequoia affinis as "ancestral to both" Sequoia sempervirens and Sequoiadendron giganteum suggested by Meyer (2003).

'D' Sequoia dakotensis Paleogene Developmental path to Sequoia sempervirens.

'A' Sequoia affinis Paleogene Neogene 'Newly Recognized' Neogene Sequoia Field (1993)

Sequoia and Sequoiadendron in the Changing World Scene (as exhibited among figured specimens).
SUMMATION

I would like to persuade colleagues to take seriously the possibility that ...the initiator of speciation is never biotic interaction but is always physical (environmental) change. Elisabeth S. Vrba 2005.

A purpose of this meta-analysis of the history of the giant sequoia and the coast redwood has been to show the plausibility of the suggestion put forth by Herbert W. Meyer (2003) that, “Sequoia affinis may have been ancestral to Sequoia sempervirens, but it also may have been the ancestor of the modern Sequoiadendron giganteum,” the suggestions made by Chaney (1959), Axelrod (1966) and Fields (1993) that a “new species” of Sequoia is seen in Neogene deposits, and Wolfe’s statement (1967 in Leonard and Marvin 1982) that, “Sequoia affinis indicates a Paleogene age,” precluding Neogene occurrences.

The chart on the facing page portrays the previously presented progression of the less expanded to scaly Sequoia affinis leaf forms through time showing the relationships with various global climatic events and shows where Sequoiadendron chaneyi and a Sequoia pre-sempervirens may lay with respect to the Sequoia affinis leaf form temporal distribution.

Sequoia affinis was widely distributed during the Eocene in the highlands of the Northern and Central Rockies. The early Eocene had been a time of global tropical to subtropical climate. Under these conditions, northern and higher elevation areas were somewhat less tropical, with upland vegetation distinct from that of lower areas.

Through the middle Eocene the global climate commenced cooling and drying. During the late Eocene the global climate cooled dramatically. The time breaks dividing the upper, middle, and late Eocene are each defined where a biotic threshold was exceeded. The fossil record shows that the prevailing leaf morphology of Sequoia affinis was tending toward drought resistant types over the course of time.

The western interior of the North American continent was even cooler than global average, and drier. As the climate cooled and dried, Sequoia affinis would have expanded its range, tracking into the new cooler, lower elevation areas. West of the interior highlands the climate was moister than further into the continent to the east of the Rockies. Consequently, Sequoia affinis would have expanded its range further to the westward than eastward.

After the end of the Eocene the climate cooled yet further. “The [early] Oligocene deterioration … was the most extreme paleobotanical change in all of the Cenozoic” (Prothero 1991). The late Oligocene and
Miocene witnessed warming and cooling trends, ending at the middle Miocene Global Thermal Maximum, after which dramatic cooling once again set in.

The Oligocene and Miocene showed worldwide diversification of gymnosperms with extinction of earlier types (base taxon) and appearance of new derived forms (Crisp and Cook 2010; Pitterman, et al. 2012). There is no reason to suspect that *Sequoia affinis* was immune to such changes.

Later populations of *Sequoia affinis* that remained nearer the higher elevations of the Eocene populations would have experienced the greatest influence of the cooling. Cold induced chromosomal processes exist that promote genetic changes in some of the subsequent generations resulting in adaptation of the surviving new members to the colder and drier conditions, retaining and enhancing the climatically favorable drought resistant anatomical traits. Reproductive success among the new members and incompatibility with the core population preserves their new hardiness as a reproductively isolated new species. Under the prolonged persistence or intensification of the cooling, the newly adapted species survives while the climate change completely eliminates the non-adapted members of the source population.

*Sequoia affinis* populations that had tracked more optimal conditions westward down out of the highlands would have experienced less extreme cold. Other genetic processes were operable under less severe conditions. Cross breeding between adapting generations and the source population, or possibly with genetically compatible cohabitating species, resulted in a chromosomally complex species. Continued down the generations, the soil/plant water hydraulically variable anatomical traits of the original population were retained, expressed at different situations in an individual and across the species range.

Furtherance of chromosomal process consolidates the genes expressed in the adaptations in one habitat into a new species and in another habitat the chromosomal consolidation is yet to be completed in a different species. Over the course of 15 million years, the biologic changes occur in response to the changing climate, thus yielding, the present dryer/colder adapted genus *SEQUIOIADENDRON*, persisting as *SEQUIOIADENDRON GIGANTEUM*, and the moister/warmer adapted *SEQUOIA SEMPEVIRENS*.

There is no final truth in paleontology. Every new observer brings something of his or her own: a new technique, a new intelligence, even new mistakes. Richard Fortey, 2000.
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I was mindful of a colleague who once wrote to me to say how much he appreciated an earlier book I wrote – because he found the references useful. Anything to please. Michael C. Corballis 1991.

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UCMP, 2013, University of California Museum of Paleontology Database, Specimen Search (http://ucmpdb.berkeley.edu/).


APPENDIX A

THE *Sequoia affinis* FOSSIL RECORD
Appendix A
Sequoia affinis Lesquereux 1876

Expanded: Distichous - bi-facially flattened, two ranked, longer, wider, more widely spaced needles
Less Expanded: Shorter, narrower, more appressed (lying flat), spirally arranged, subulate (awl shaped) needles
Scyly: Scale-like, spirally arranged needles

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2 | 12 | 12 | By location | 1 | By description | Yellowstone NP, Wyoming | Knowlton 1898 (by location); Wing 1987 |
| | 1 | 1 | | | Sepulcher Fm. | Dorf 1964 (illust) |

3 | 0.00 | 48.18 | 1 | 1 | 1 | Pl. 5, Fig. 1 | MacGinitie, 1969 | DeVore & Pigg 2009 |
### Appendix A, continued

**Sequoia affinis Lesquereux 1876**

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### Appendix A, continued

**Sequoia affinis Lesquereux 1876**

<table>
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<th>Number</th>
<th>Sterile</th>
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<td>Number (male) (female)</td>
<td>Illustrated Cones</td>
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<td>Reference (if different)</td>
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#### OLIGOCENE

| 10 | 3 | Ruby River Basin (paper & blocky shales), southwestern Montana | 1 | Pl. 10, Fig. 1 | Becker 1961 | Wing 1987 |
| 1 | 1 | Pl. 10, Fig. 2 | As Glyptostrobus, reassigned Becker 1966 |
| 1 | 1 | Pl. 10, Fig. 3 | Fritz, et al. 2007 |
| 1 | 1 | Pl. 1, Fig. 1 | Becker 1966 |
| 1 | 1 | Pl. 1, Fig. 2 | Counterpart to Pl. 1, Fig. 1 |
| 100.00 | 33.88 | Total | 4 | 1 |

| 11 | 6 | Lost Creek florule, Bridge Creek Flora, John Day Formation Oregon | Meyer and Manchester, 1997 | Dillhoff, et al., 2009 |
| 1 | 1 | Pl. 2, Fig. 8 |
| 1 | 1 | Pl. 2, Fig. 9 |
| 50.00 | 33 | Total | 1 | 1 |

| 9 | Pl. 12, Figs. 3-1 | Becker 1973 |
| 3 | Pl. 13, Figs. 3, 4, 5 |
| 1 | Pl. 13, Figs. 6, 7 |
| 1 | Pl. 13, Figs. 8 |
| 1 | Pl. 13, Figs. 9 |
| 1 | Pl. 13, Figs. 10 |
| 1 | Pl. 13, Figs. 11 |
| 1 | Pl. 13, Figs. 12 |
| 1 | Pl. 13, Figs. 13 |
| 1 | Pl. 13, Figs. 14 |
| 1 | Pl. 14, Fig. 1 |
| 1 | Pl. 14, Fig. 2 |
| 1 | Pl. 14, Fig. 3 |
| 1 | Pl. 14, Fig. 4 |
| 1 | Pl. 14, Fig. 5 |
| 1 | Pl. 14, Fig. 6 |
| 1 | Pl. 14, Fig. 7 |
| 31.25 | 32.63 | Total | 11 | 5 | 14 | 0 |

(NALMA - Whitneyan, 30.8 - 33.3 Ma, Wing 1987.)
### Appendix A, continued

**Sequoia affinis Lesquereux 1876**

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#### OLIGOCENE, continued

| 13 | 45 | Haynes Creek, eastern Idaho | | 1 | 100.00 | Pl. 5, Fig. 9 | Axelrod 1998b |
| 14 | 28-32 | Lyons, western Oregon | | 1 | 100.00 | Pl. 1, Fig. 4 | Meyer 1973 |
| **Not Included - D** | 30 | Williamette, western Oregon | | "Undescribed" | | | |
| **Not Included - E** | 3 | Rupeada, western Oregon | | "late Oligocene" | | | |
| **Not Included - F** | 4 | Salmon, Idaho | | "late Oligocene" | | | |

#### MIocene

| 4 | 50.00 | Upper Cedarville (49 Camp), NV | | 1 | Pl. 3, Fig. 1 | A. Lycopodium Wood | LaMotte 1936 |

All leaf material reassigned to Glyptostrobus oregonensis by Chaney 1951 not illustrated.
### Appendix A, continued

**Sequoia affinis Lesquereux 1876**

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#### MIOCENE, continued

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| 16 | 1 | 1 | Troutdale, western Oregon | Chaney 1944 |
| 0.00 | 9 | Total | 1 |

| 17 | 5 | Remmington Hill, central Sierra Nevada, California | Axelrod 1985 |
| 0.00 | 8 | Total | 1 |

#### PLEISTOCENE

**Not Included - J**

**"Pliocene"**

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| 19 | 141 | Sonoma Flora, northeast of Santa Rosa, California |
| 0.00 | 3.4 | Total | 1 | 0 |

#### PLEISTOCENE

**Not Included - K**

**"Reisocene"**

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*Note: The table continues with additional entries and references.*
APPENDIX A – Sequoia affinis - References


Hannibal, H., 1911, A Pliocene flora from the Coast Ranges of California: Bull. of the Torrey Botanical Club, V. 38, pp. 329-332, Plate 15, n. 3.


LaMotte, R. S., 1936, The Upper Cedarville Flora of Northwestern Nevada and Adjacent California: in Middle Cenozoic Floras of Western North America: Carnegie Institution of Washington, Contributions to Paleontology, Publication 455, pp. 57-142.


APPENDIX B

THE *Sequoiadendron chaneyi* FOSSIL RECORD
A note on spelling: *S. chaneyii* vs. *S. chaneyi*

The use of a double, “ii” to spell *S. chaneyii* is how Axelrod spelled the name in his most recent taxonomic publication (Axelrod 1995) on the Purple Mountain flora, when he was 85 years old. This is technically correct under *The International Code of Botanical Nomenclature*, if you assume that the “y” at the end of the name Chaney is a consonant. If, however, the “y” is considered a vowel, as Axelrod evidently did when he introduced the species in 1956, when he was 46, and followed through with in his 1962, 1964, 1980, and 1985 taxonomies, then the name would end with a single “i.” I have followed this convention in this second printing, because the name with the single “i,” *S. chaneyi*, was the formal name in the 1956 taxonomy, when the species was introduced as a “n. sp.” Furthermore, in the 1995 publication the spelling change was not properly corrected in the synonymy, where the double “ii” is incorrectly indicated to be in the earlier publications, and on Plate 9, the spelling is both “iI” and “ii.” Regardless, both endings, “i” and “ii,” may be incorrect, because Axelrod stated that “It is a pleasure to name this species for Ralph W. Chaney in recognition of his important contribution to our knowledge of the redwoods of the past.” Thus it can be assumed that Chaney neither discovered nor described the fossil *Sequoiadendron*. Under the *Code*, the genitive ending (“i” or “ii”) is used when “the species has been described or distinguished by the botanist whose name it takes,” otherwise the name is an adjective form; *anus*, *a*, or *um*. Consequently, the name should have been either, *S. chaneyum*, *S. chaneya*, or *S. chaneyanus*, which is where I will let this sit.
Appendix B
Sequoiadendron chaneyi Axelrod 1956

Leaves short appressed (lying flat), spirally arranged, subulate (awl shaped) needles
scale-like, spirally arranged needles

Holotype The single specimen used as the basis of the original published description of a taxonomic species.

Paratype A specimen belonging to the original series, but not the holotype.

Hypotype Specimen is an example of an already described or named species, whether from the same locality or from another deposit, and for which one gives a new description and a new figure.

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<td>Illustrated</td>
<td>Illustrated</td>
<td>Illustrated</td>
<td>Reference</td>
<td>(if different)</td>
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OLIGOCENE
Not Included
Mentioned by Axelrod (1986, p. 28) as occurring in the late Oligocene of south central Idaho.
Quietly reassigned to Sequoia affinis (Axelrod 1998a) and to the middle Eocene (45 Ma).
See Appendix A, location 4, and text section "Problematica."

MIOCENE

1
Middlelegate/Eastgate Basin, NV
18.5 3
(15.5, Wolfe, et al. 1997) 1
Pl. 25, Fig. 4 M Hypotype
Axelrod 1986
M
6
1
Pl. 4, Fig. 18 M Hypotype
Axelrod 1986
E
20
1
Pl. 18, Fig. 1 E Hypotype
Axelrod 1986
E
1
Pl. 19, Fig. 2 E Hypotype
Axelrod 1986
E
1
Pl. 18, Fig. 3 E Hypotype
Axelrod 1986
E
1
Pl. 19, Fig. 4 E Hypotype
Axelrod 1986
E
1
Pl. 19, Fig. 1 E Hypotype
Axelrod 1986
E
2
Pl. 19, Fig. 2 E Hypotype
Axelrod 1986
E
1
Pl. 19, Fig. 3 E Hypotype
Axelrod 1986
E
1
Pl. 19, Fig. 4 E Hypotype
Axelrod 1986
E
1
Pl. 19, Fig. 5 E Hypotype
Axelrod 1986
E
Total 11 3

2
Firgerrock Wash, NV
16 2
Wolfe 1964 As Glyptostrobus
(15.5, Wolfe, et al. 1997) 1
Pl. 1, Fig. 8
1
Pl. 1, Fig. 11
"Several cones" Axelrod 1985 Reassigned to S.c.
Total 2

Not Included - A (Locality not published) Reported as Glyptostrobus
Glam Spring, NV Axelrod & Schorn 1994

3
Purple Mountain (complex), NV
13 25
Axelrod 1995 Hypotype
1
Pl. 8, Fig. 9 Hypotype
1
Pl. 8, Fig. 10 Hypotype
1
Pl. 8, Fig. 11 Hypotype
1
Pl. 8, Fig. 12 Hypotype
1
Pl. 9, Fig. 1 Hypotype
1
Pl. 9, Fig. 2 Hypotype
1
Pl. 9, Fig. 9 Hypotype
Oldest sub-locality includes 2 foliage and 2 cone fragments of Glyptostrobus oregonensis.
Axelrod (1964) once considered that, "At Purple Mountain it is represented by abundant foliage, and also two cones which are about one third the size of those representing S.chaneyi and the living S. giganteum; at that locality we appear to have a new species.
Total 4 3

Not Included - B (no foliage)
Lund Petrified Forest, NV
15.7 average era assignments
Ensm, et al. 2005 Wood
Marpign 1993 Wood
### Appendix B, continued

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<th>Sterile Shoots</th>
<th>Sterile Cones</th>
<th>Staminate Shoots</th>
<th>Staminate Cones</th>
<th>Postulate Shoots</th>
<th>Postulate Cones</th>
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<td>Axelrod 1956</td>
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<td>(14. Wolfe et al. 1997)</td>
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| 5              |               |                  |                  |                  |                 | 12.4   | 10              | 1                 | Aldrich Station, NV | Axelrod 1956 |      |
|                |               |                  |                  |                  |                 |        | (12.4 to 13.3, Wolfe et al. 1997) | 1                 | Pl. 4, Fig. 25 | Holotype |         |
|                |               |                  |                  |                  |                 |        | 1               | Paratype          |          |           |       |
|                |               |                  |                  |                  |                 |        | 1               | Paratype          |          |           |       |
|                |               |                  |                  |                  |                 |        | Total           |                   | 6                    | 1         |           |       |

| 6              |               |                  |                  |                  |                 | 9.7    | 21              | 1                 | Trapper Creek, ID | Axelrod 1964 | Armstrong, et al. 1975 |
|                |               |                  |                  |                  |                 |        |                 | 1                 | Pl. 7, Fig. 17 | Hypotype |         |
|                |               |                  |                  |                  |                 |        | 1               | Hypotype          |          |           |       |
|                |               |                  |                  |                  |                 |        | 1               | Hypotype          |          |           |       |
|                |               |                  |                  |                  |                 |        | Total           |                   | 3                    | 1         |           |       |

| 7              |               |                  |                  |                  |                 | 9      | 9               | 1                 | Chalk Hills, NV | Axelrod 1962 |                  |
|                |               |                  |                  |                  |                 |        | (12.5, Wolfe et al. 1997) | 1                 | Pl. 43, Fig. 3 | Hypotype |         |
|                |               |                  |                  |                  |                 |        | 1               | Hypotype          |          |           |       |
|                |               |                  |                  |                  |                 |        | 1               | Hypotype          |          |           |       |
|                |               |                  |                  |                  |                 |        | Total           |                   | 3                    | 1         |           |       |

**Not Included - C**

|                |               |                  |                  |                  |                 | 7      | "Abundant foliage" with logs |                   | Frenchman Dam, CA | Durrell 1987 | Not illustrated |
|                |               |                  |                  |                  |                 |        |                  |                  | Axelrod 1980 | Not illustrated |       |

| 8              |               |                  |                  |                  |                 | 7      | 3               | 1                 | Mt. Reba, CA | Axelrod 1980 |                  |
|                |               |                  |                  |                  |                 |        |                 | 1                 | Pl. 4, Fig. 4 | Hypotype |         |
|                |               |                  |                  |                  |                 |        | 1               | Hypotype          |          |           |       |
|                |               |                  |                  |                  |                 |        | 1               | Hypotype          |          |           |       |
|                |               |                  |                  |                  |                 |        | Total           |                   | 3                    | 1         |           |       |

**PLIOCENE**

| 9              |               |                  |                  |                  |                 | 5      | "several" | 1                 | Minden/Gardnerville, NV | Schorn 2001 | Not illustrated |
|                |               |                  |                  |                  |                 |        |                  | 1                 | Erwin, et al. 2001 | Anonymous website |       |
|                |               |                  |                  |                  |                 |        | Total           |                   | 2                    | 1         |           |       |

**Not Included - D**

|                |               |                  |                  |                  |                 | 2.2    |                  |                  | Coso (pollen flora), CA | Axelrod and Ting 1962 |       |
APPENDIX B – Sequoiadendron chaneyi - References


Concerning the former Taxodiaceae, “All the modern genera except Sequoiadendron have been reported from the Mesozoic.” Charles N. Miller, Jr. (1977).

“With the exception of Sequoiadendron giganteum, the early diverging Cupressaceae occupy mesic-hydric habitats.” Pittermann, Stuart, Dawson, and Moreau (2012).

“There may even have been two Tertiary Sequoias, a coastal species from which S. sempervirens has been derived, and an interior upland species, S. affinis, which became extinct at the end of the Miocene.” Ralph W. Chaney (1959).

“Sequoia affinis may have been ancestral to Sequoia sempervirens, but it also may have been the ancestor of the modern Sequoiadendron giganteum.” Herbert W. Meyer (2003).

Geologic History of the Giant Sequoia and the Coast Redwood, NARG - North America Research Group (Paleontology)’s Special Publication No. 1, summarizes the fossil record of these two trees. Cued by the above quotations, this geologic history breaks from the century old interpretation of an ancient, Mesozoic, origin of the giant sequoia and makes a multi disciplinary evaluation of the plausibility of both trees having derived from the extinct Tertiary species, Sequoia affinis, in a less remote geologic time, when there were as yet but few recent forms of plants and animals entering the geologic record.