# Early Miocene Cape Blanco Flora of Oregon

By L.F. Emerson, G.J. Retallack, and B.G. Hughes

**The Bulletin of the Museum of Natural History of the University of Oregon**
Museum Bulletin No. 29, August 2022

The Bulletin of the Museum of Natural History of the University of Oregon is published to increase the knowledge and understanding of the natural history of Oregon. Original articles in the fields of Archaeology, Botany, Ethnology, Geology, Paleontology, and Zoology appear irregularly in consecutively numbered issues. Contributions arise primarily from the research programs and collections of the University of Oregon Museum of Natural and Cultural History. However, in keeping with the basic purpose of the publication, contributions are not restricted to these sources and are both technical and popular in character.

Communications concerning manuscripts or previous issues of the Bulletin should be addressed to the Museum of Natural and Cultural History, University of Oregon, Eugene OR 97403, or by email to mnhbulletin@uoregon.edu.

Volume and Technical editor — Dana M. Reuter

Layout Designer — Isa Ramos

# Early Miocene Cape Blanco Flora of Oregon

By L.F. Emerson, G.J. Retallack, and B.G. Hughes

The Bulletin of the Museum of Natural History of the University of Oregon
Museum Bulletin No. 29, August 2022

# CONTENTS

**Provenance of the Tuff**

# CONTENTS

# ILLUSTRATIONS

**Figure** **Page**

# ILLUSTRATIONS

## ABSTRACT

Deposition of the shallow marine sandstone of Floras Lake was interrupted by a transient deltaic progradation of redeposited volcanic tuff, which contains the Cape Blanco flora. Dating by $^{40}Ar/^{39}Ar$ on fresh plagioclase constrains the age of the plant-bearing tuff to 18.24 ± 0.86 Ma, because we interpret this age of eruption and landscape loading with ash, as within only a few years of redeposition. Several plausible sources of the tuff can be identified from caldera eruptions in the Cascade Volcanic Arc. The relation between the early Miocene Cascade volcanic arc and the Klamath Terrane has been fixed since the early Miocene, and the high $Cr_2O_3$ in the sandstones is an indication that the source area for the sandstone of Floras Lake was the Klamath Terrane. Fossil leaves and other plant organs of 33 species of the Cape Blanco flora represent floral diversity and paleoclimate of coastal Oregon during the early Miocene. The flora includes a variety of thermophilic elements from California, including coast redwood (*Sequoia affinis*), and avocado (*Persea pseudocarolinensis*), and is numerically dominated by live oak (*Quercus hannibalii*), and chinquapin (*Chrysolepis sonomensis*). The size and proportion of serrate margins of the fossil leaves are evidence of mean annual temperature of ~14 º C and a mean annual precipitation of ~223 cm/yr for the Cape Blanco flora. Comparison of the Cape Blanco flora with the Temblor flora of California and the Seldovia flora of Alaska reveals a latitudinal gradient of ~ 0.6 º C/degree latitude, compared with a gradient of ~0.3 º C/degree latitude from isotopic composition of marine foraminifera of the northeast Pacific Ocean. Both results confirm that the late early Miocene mean annual temperature at 45º north latitude was 4-5 º C warmer than today.

## INTRODUCTION

Miocene time may be considered a climatic analog for projected global warming by the year 2100 (Retallack et al., 2016). Modeling of ongoing greenhouse warming predicts atmospheric $CO_2$ levels of 600-850 ppm by the year 2100 (Ciais et al., 2013). This is comparable with the early and middle Miocene atmospheric $CO_2$ inferred from stomatal indices of fossil leaves 612 ± 24 ppm from the stomatal index of fossil *Ginkgo* leaves in Idaho (Breecker and Retallack, 2014). Carbon dioxide and temperature are well correlated today and in many different geological records, and are evidence that the Miocene was warmer than today (Wolfe, 1979; Böhme 2003, Cosgrove et al., 2002, Kürschner et al., 2008). The late early Miocene is between the Mi-1 Glaciation and Mid-Miocene Climatic Optimum as revealed by oxygen isotopic study of marine foraminifera (Zachos et al., 1994, 2001). New paleotemperature estimates from foliar physiognomy of an early Miocene flora therefore serve as an additional guide for the magnitude and distribution of global heat when Earth's atmosphere contains more $CO_2$.

Coastal location makes the Cape Blanco flora important for paleoclimatic and floristic assessment (Figs. 1-2), because previously documented Miocene floras of Oregon, USA, (Table 1) are inland at high elevation and within a rain shadow zone (Ashwill, 1983; Retallack, 2004a). Coastal records provide a link between marine records of global climate (Zachos et al., 2001) and inland climate records (Wolfe, 1994; Retallack, 2007; Retallack et al., 2016). Regional reconstruction of paleoclimate is important to the testing of climate models (Wing and Greenwood, 1993; Wing et al., 2005, Sewall and Sloan, 2006), as well as tectonic reconstructions that call upon climate as a potential driver (Ruddiman, 1997). Furthermore, paleotemperatures for fossil floras at sea level allow interpretation of terrestrial-lapse-rate-based studies of paleoelevations (Axelrod, 1968; Forest et al., 1999), and better reconstructions of paleolatitudinal temperature gradients (Miller et al., 2006).

### GEOLOGIC SETTING

The Cape Blanco flora was found within a 7.5 m thick rhyodacitic tuff within the unconformity bound, early Miocene, marine sandstone of Floras Lake (Figs 3-5). This sandstone contains fossil marine snails and clams, as well as stenohaline sand dollars, both above and below the plant-bearing pumiceous tuff (Addicott, 1980, 1983; Armentrout, 1980). The Cape Blanco flora was discovered and briefly characterized by Wolfe (1994), and noted by Leithold and Bourgeois (1983).

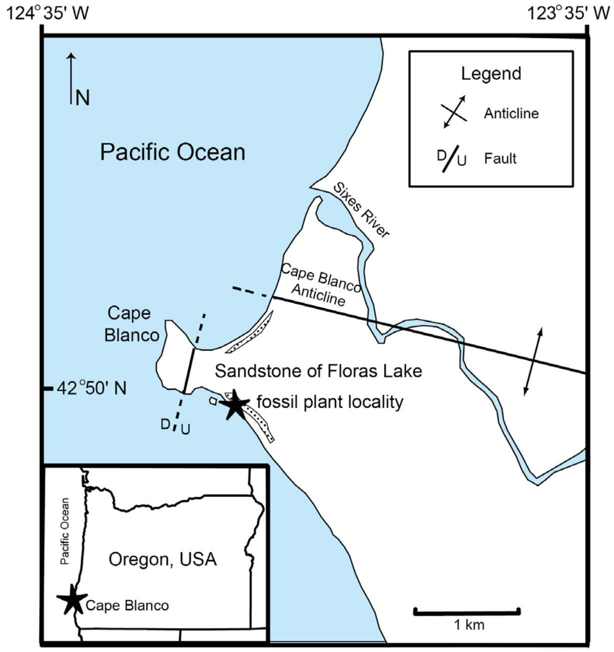

**Figure 1:** Location map for sandstone of Floras Lake, and fossil plant locality, simplified from Kelsey (1990) and Addicott (1980). For detailed bedrock geology refer to Dott (1962) and for detailed terrace maps refer to Kelsey (1990).

Cape Blanco is the westernmost point of the Oregon coast, and the sea cliffs southeast of the cape expose a sequence of Eocene to Holocene sedimentary rocks on the south limb of an east/west trending anticline (Armentrout, 1980). The axis of the anticline is 1 km north of the cape (Fig. 1). Cape Blanco lies near the intersection of three geologic provinces (Fig. 2): (1) the subducting Gorda plate, (2) the accreted and metamorphosed Mesozoic Klamath Terrane, and (3) Cenozoic marine basins of the Coast Ranges. Cape Blanco has the shortest trench-normal distance of the Oregon coast (Miller et al., 2001) and the age of the Gorda Plate at the trench west of Cape Blanco is 6 Ma (Wilson, 1989). The accreted Mesozoic rocks of a broadly defined Klamath Terrane have their most northerly coast outcrop near Cape Blanco. The Siletzia terrane, thought to underlie the Cenozoic sediments of the Oregon Coast Range and Willamette Valley, has its most southward extent just north of Cape Blanco (Wells et al., 1998).

The northernmost exposure of accreted Mesozoic rocks along the Oregon Coast is near Cape Blanco (Kelsey, 1990), and the Jurassic Otter Point sandstones and mudstones (Dott, 1962, 1971; Koch, 1966) form resistant rocks of the headland and sea stacks offshore. Unconformably overlying the Otter Point Formation are Cenozoic deposits that have been offset by north-trending normal faults (Dott, 1962) and folded by the Cape Blanco anticline (Diller, 1902; Kelsey, 1990). The southern limb of the east-west trending anticline exposes a long sequence of southeast-dipping sedimentary rocks; Eocene Roseburg formation shale (Armentrout et al., 1983, Bandy, 1950), early Miocene sandstone of Floras Lake (Addicott 1980, 1983; Armentrout 1980), late Miocene Empire sandstone (Armentrout et al., 1983; Diller 1902), Plio-Pleistocene Port Orford sandstone (Baldwin 1945), and a flight of Pleistocene marine terraces (Bockheim et al., 1992, 1996; Diller, 1902; Janda, 1969; Kelsey, 1990). The dip of each unconformity-bound unit (Durham 1953) decreases with age, so the structure has been continuously active during and since deposition of the sandstone of Floras Lake (Kelsey, 1990). The fault at the neck of the cape brings down late Miocene, Empire Formation sandstone, which forms the light-colored cliffs that are the source of Cape Blanco's name (Dott, 1962).

This study focuses on the 158 m thick Burdigalian (Addicott 1976) sandstone of Floras Lake (Fig. 3), which is punctuated by a 7.5-meter-thick tuff bed (Fig. 4). Previous early Miocene age estimates were based on molluscan biostratigraphy (Addicott 1976, 1980, 1983; Allison and Addicott, 1976; Moore, 1963; Moore and Addicott, 1987). Those assemblages are interpreted as beach to shallow shoreface deposits along a NW trending rocky coast. Leithold and Bourgeois (1983) also subdivided the sandstone of Floras Lake into four subunits: the basal conglomeratic sandstone unit, the middle pebbly sandstone unit, the tuff, and the upper sandstone unit (Fig. 3). The fining-upward trend may record a transgressive sequence with increase in depositional depth from intertidal at the bottom to below stormweather wave base at the top (Addicott, 1983; Leithold and Bourgeois, 1983). Our close examination of the plant-bearing tuff bed aimed to interpret the paleoenvironment and preservation of the fossil flora.

## SEDIMENTARY PALEOENVIRONMENT

METHODS: Exposures south of Cape Blanco are sea cliffs between vegetated landslides (Fig. 5). Our stratigraphic sections (Figs. 3-4) were measured using the eye-height method and grain-size and meter-scale observations of sedimentary structures

**Table 1.** Oregon Neogene fossil floras

| Flora | Reference | Age | Ma | Status |
|---|---|---|---|---|
| Lolo Pass | Wolfe & Tanai 1987 | latest Miocene | 5 | Site only |
| Alvord Creek (many sites) | Chaney et al., 1944 | late Miocene | 10 | Site and taxonomy |
| Troutdale (many sites) | Chaney et al., 1944, Wolfe 1994 | late Miocene | 10 | Site and paleoclimate |
| Unity | Retallack 2004a | late Miocene | 11 | Site and taxonomy |
| Vibbert | Ashwill 1983 | late Miocene | 12 | Site and taxonomy |
| Faraday | Wolfe 1994; Wolfe & Tanai 1987 | late Miocene | 12 | Site and paleoclimate |
| Liberal | Wolfe 1994 | late Miocene | 13 | Site and paleoclimate |
| Molalla | Wolfe 1994 | late Miocene | 13 | Site and paleoclimate |
| Vinegar Creek | Wolfe & Tanai 1987 | Mid-to-late Miocene | 14 | Mention only |
| Mascall (many sites) | Chaney & Axelrod 1959 | middle Miocene | 16 | Site and taxonomy |
| Blue Mountain (many sites) | Chaney & Axelrod 1959 | middle Miocene | 16 | Site and taxonomy |
| Beulah | Axelrod 1964 | middle Miocene | 16 | Site and taxonomy |
| Pelton | Ashwill 1983 | middle Miocene | 16 | Site and taxonomy |
| Stinking Water (many sites) | Chaney and Axelrod 1959 | middle Miocene | 16 | Site and taxonomy |
| Succor Creek (many sites) | Graham 1963; Niklas et al. 1978 | middle Miocene | 16 | Site and taxonomy |
| Trout Creek (many sites) | Graham 1963 | middle Miocene | 16 | Site and taxonomy |
| Weyerhauser | Wolfe 1994; Wolfe & Tanai 1987 | late Miocene | 17 | Site and paleoclimate |
| Jamison | Wolfe & Tanai 1987 | early-mid Miocene | 17 | Site only |
| Baker | Wolfe & Tanai 1987 | early-mid Miocene | 17 | Site only |
| Hidden Lake | Wolfe & Tanai 1987 | early-mid Miocene | 17 | Site only |
| Little Butte Creek | Wolfe & Tanai 1987 | early-mid Miocene | 17 | Site only |
| Skull Spring | Wolfe & Tanai 1987 | early-mid Miocene | 17 | Site only |
| Sparta | Wolfe & Tanai 1987 | early-mid Miocene | 17 | Site only |
| Cape Blanco | this paper | early Miocene | 18 | Site, taxonomy, paleoclimate |
| Eagle Creek (many sites) | Wolfe 1994 | early Miocene | 18 | Site and paleoclimate |
| Collawash (many sites) | Wolfe 1994 | early Miocene | 20 | Site and paleoclimate |
| Forman Point | Ashwill 1983 | early Miocene | 21 | Site only |
| Fish Creek Road | Fields 1996 | early Miocene | 22 | Site only |
| Cascadia | Fields 1996 | early Miocene | 22 | Site only |
| Sandstone Creek | Fields 1996 | early Miocene | 22 | Mention only |

confirmed the descriptions of Leithold and Bourgeois (1983). Grain size and sedimentary structures were recorded for the tuff bed with 0.1 m precision.

## OUTCROP OBSERVATIONS:

The 7.5 m tuff is a thick, gray, erosion resistant unit composed of a series of even and parallel tabular beds that vary in thickness from a few millimeters to nearly a meter (Fig. 4). Sand-sized grains are sub-angular, and granules are mainly pumice. We divide the tuff into three units; lower, middle, and upper (Figs 4, 5). These units are evaluated separately and then combined to construct a depositioal model for the tuff bed.

The lower tuff unit (0-515 cm) is composed of parallel laminated thin (0.2 cm to 2 cm) beds (Fig. 5C-D). These beds are massive with the exception of a small 3 cm trough cross bed and a 30 cm exposure of ripple cross lamination. There are two distinct bed types within the lower tuff unit based on grain size: uniform and bimodal. Uniform beds are sandy and very well to moderately well sorted. Bimodal beds contain sand and fine pebble gravel (up to 2 cm) pumice grains. Bimodal beds fracture conchoidally and do not split evenly on bedding planes. The lower contact of the tuff is obscured.

The middle tuff unit (515-580 cm) is well sorted, sub-angular, coarse-grained, trough cross-bedded sandstone (Figure 5C-D). The bi-directional cross-

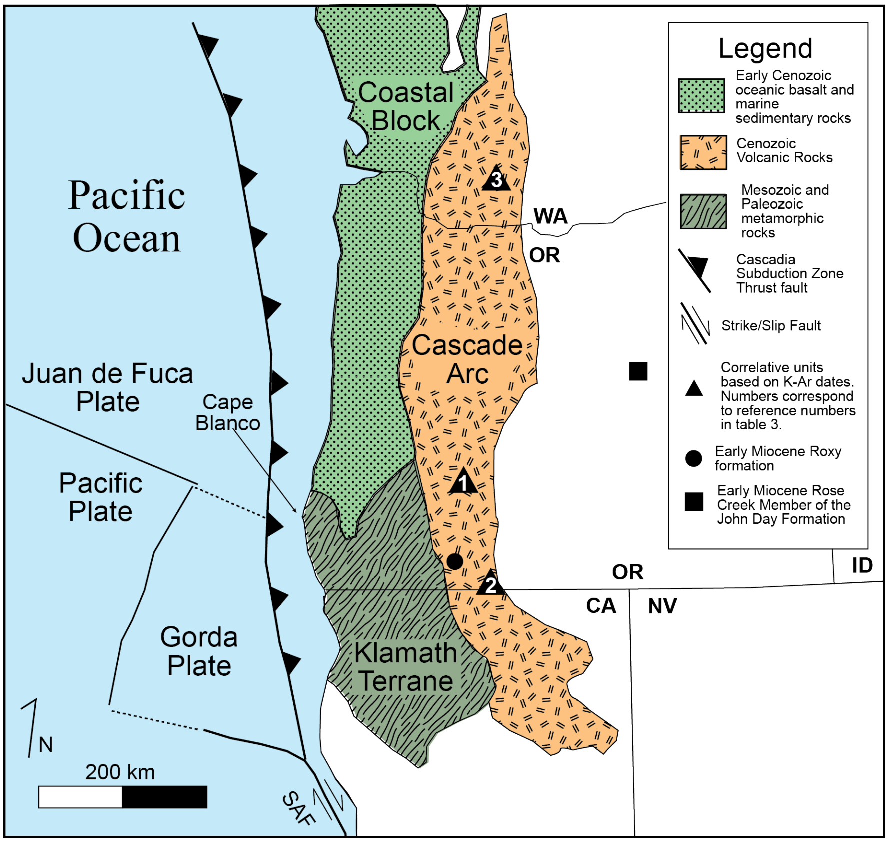

**Figure 2:** Map of the Pacific Northwest showing tectonic terranes relevant to the history of Cape Blanco. Continental province base map modified from Wells and Heller (1988) and oceanic plate boundaries modified from Dziak et al. (2001). Multiple samples are included in the correlation points because they are too close together to differentiate at this scale. SAF: San Andreas Fault, OR: Oregon, WA: Washington, CA: California, NV: Nevada, ID: Idaho.

bedding is truncated at a high angle and the contact with the underlying lower tuff is abrupt and erosional.

The upper tuff unit is subdivided into three sub-units, including a central fossil-bearing unit. The sub-units are: lower tuff (580 to 615 cm), middle shale with fossil leaves (615-655 cm), and upper tuff (655-750). The lower sub-unit of the upper tuff. is 15 cm of massive siltstone overlain by 5 cm of parallel-laminated coarse-grained thin beds similar to the basal tuff. The lower contact is gradational and the siltstone has a few interbedded very fine sand beds with some lenses of coarser sand to granule material. The middle sub-unit is a massive cherty shale, which fractures into small blocks. The contact between the lower and middle sub-units is abrupt. The upper sub-unit is a medium-grained parallel-laminated sandstone with beds varying from 0.5 cm to 15 cm thick. The contact between the upper and middle sub-units is abrupt and planar. The contact between the tuff and overlying marine sandstone has load casts (Fig. 5A).

## OUTCROP INTREPRETATIONS

The sedimentary structures, rounded granules, predominantly sand-sized sediments, and thin planar beds in the lower sub-unit of the tuff unit indicate remobilization of sediment rather than direct pyroclastic base surge or airfall on land or into water. These sediments lack dune forms of base surge and graded beds typical of airfall into water (Cas and Wright, 1987). The coarse sand is evidence that the sediment was remobilized through traction by water. Evidence of bioturbation is absent indicating rapid deposition, and given the difficulty of fracturing the rock along bedding planes and absence of parting lineation, it is likely that the beds were deposited within the lower flow regime (Tucker, 2003). Such criteria are met in the swash zone

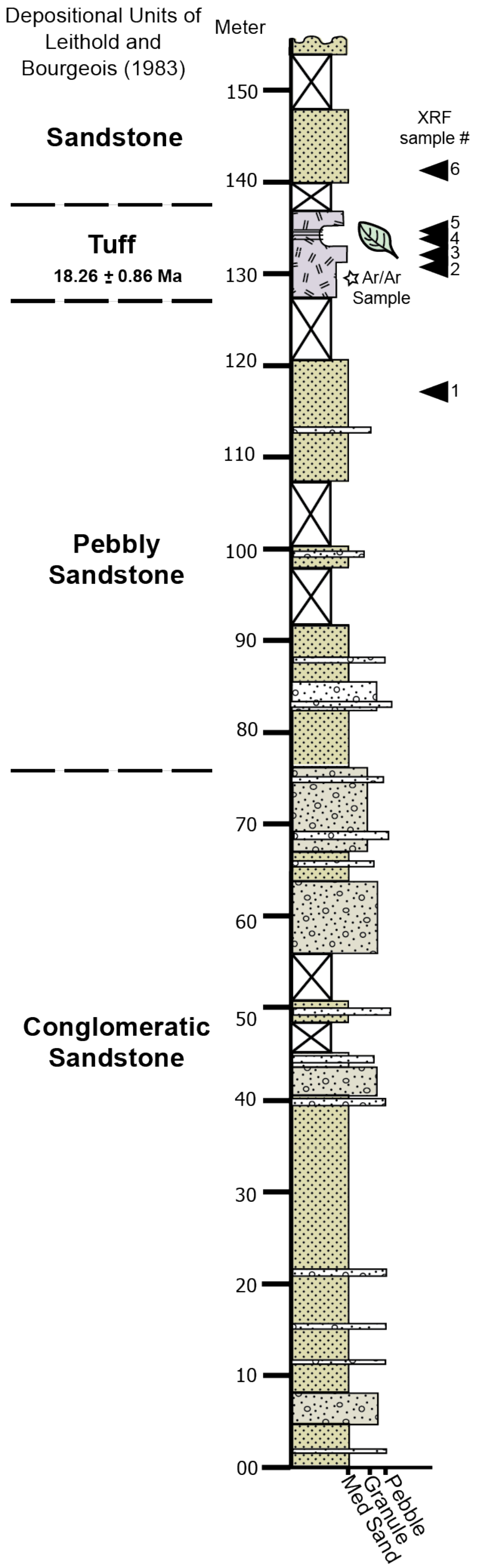

**Figure 3:** Stratigraphic section of sandstone of Floras Lake with sample locations for XRF. Leaf symbol indicates the location of the fossil flora. Unexposed portions of the section are marked by crossing lines.

along the shoreline (Clifton et al., 1971). Trough cross bedding in the middle part of the tuff are from dunes of channelized flow (Selley, 2000). We interpret the trough cross-bedded facies as a barred nearshore system (Hunter et al., 1979), or a channel on a prograding delta (Reading and Collinson, 1996). The massive cherty shales are interpreted as pond or lagoonal deposits that trapped fine-grained sediment and floating leaves. The association of swash zone, channeled flow, and lagoon indicate deposition in a small barred estuary or a delta.

The 7.5 m thickness of the tuff layer suggest that it was the product of at least a moderate size eruption, especially considering the distance to likely Cascade Range sources. Grain size and uniformity suggest this tuff bed was in the distal zone of volcanic deposition (Vessel and Davies, 1981; Scott, 1988), which can extend from 40-120 km downstream from the volcanic source (Smith, 1988; Orton, 1996).

Abundant pumice is evidence that the tuff was derived from a Plinian style volcanic eruption (Cas and Wright, 1987). Such an eruption would have provided a large amount of easily remobilized sediment to drainage networks supplying sediment to this shallow marine system. Such rapid inputs of sediment can quickly fill available accommodation space at the paleoshoreline and cause shallowing and progradation. Stream aggradation was observed at Mt. St. Helens following the 1980 eruption (Scott, 1988). In Guatemala following the 1902 eruption of Volcan Santa Mariá, volcanically derived sediment raised the riverbed 10-15 m, and an elongate platform prograded 7 km (Kuenzi et al., 1979). An aggrading stream may have dammed smaller drainages creating small lakes. Such lakes assist in the mechanical size sorting of the remobilized volcanic products by impounding the coarser fractions and leaving ash and leaves in suspension. When the lakes were subsequently breached by headwall erosion, or a large precipitation event, large plugs of ash and leaves could have been remobilized downstream. We suggest an increased sediment supply as the mechanism for shallowing as opposed to volcanically induced uplift proposed by Leithold and

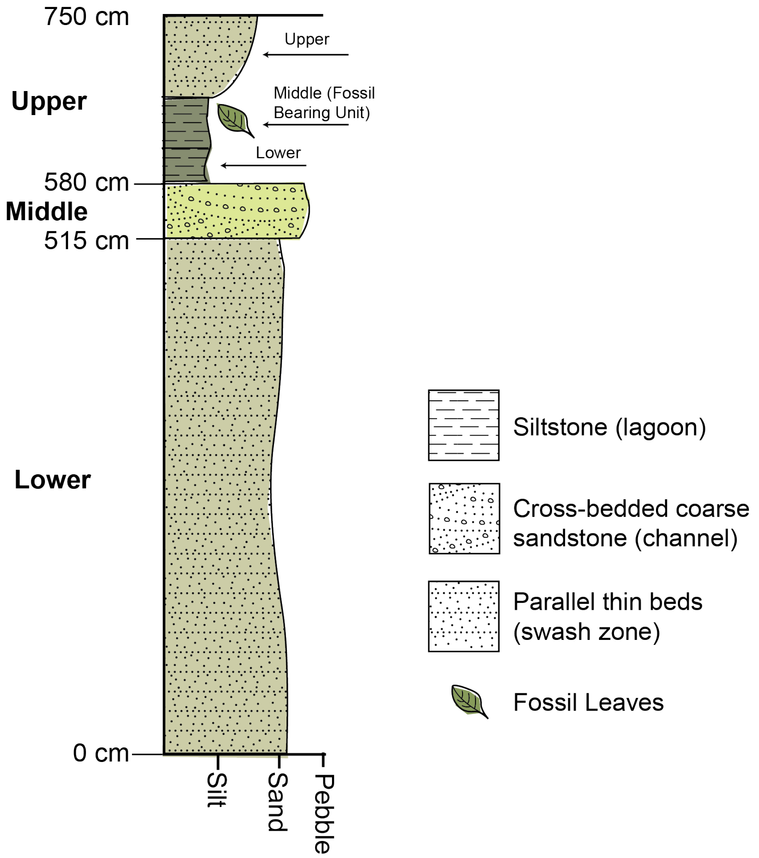

**Figure 4:** Stratigraphic section of tuff with three zones; upper, middle, and lower. Leaf symbol indicates location of fossil bearing unit.

Bourgeois (1983), because the distance to a plausible source of the tuff in the Cascade Range is at least 100 km.

### $^{40}$AR/$^{39}$AR DATING OF THE TUFF

METHODS: Two fresh tuff samples were collected in the lower subunit of the tuff and sent for analysis by Robert Duncan and John Huard at Oregon State University. A sample of plagioclase phenocrysts and hornblende phenocrysts each with a total mass of 50-100 mg as well as FCT-3 biotite monitors (standard age of 28.03 ± 0.18 Ma after Renne et al., 1994) were wrapped in Cu-foil and stacked in evacuated quartz vials and irradiated with fast neutrons for 6 hr in the core of the 1MW TRIGA reactor at Oregon State University. Incremental heating experiments were performed using the MAP215/50 mass spectrometer. The measured argon isotopes ($^{40}$Ar, $^{39}$Ar, $^{38}$Ar, $^{37}$Ar, and $^{36}$Ar) were corrected for interfering Ca, K, and Cl, nuclear reactions (McDougall and Harrison, 1999) and for mass fractionation. Apparent ages for individual temperature steps were calculated using ArArCALC software (Koppers, 2002) assuming an initial atmospheric $^{40}$Ar/$^{39}$Ar value of 295.5, and reported uncertainty ($2\sigma$) includes error in regression of peak height measurement, in fitting the neutron flux measurements (J-values), and uncertainty in the age of the monitor. The $^{40}$Ar/$^{36}$Ar normal isochron intercepts confirm that there was no excess Ar in the samples. Plateau ages are the average of concordant step ages, comprising most of the gas released, weighted by the inverse of their standard errors. The decay constants used were $\lambda\varepsilon = 0.581\text{E-}10/\text{yr}$ and $\lambda\beta = 4.963\text{E-}10/\text{yr}$.

RESULTS: Of the two samples, only plagioclase yielded a reliable plateau age (Fig. 6, Table 2). The hornblende age was unreliable because of a low amount of original K. The weighted plateau age of plagioclase is 18.24 ± 0.86 with a MWSD of 0.82. The plagioclase age values for each step are within

**Figure 5:** Photographs of tuff in the early Miocene, sandstone of Floras Lake near Cape Blanco after **(A-B)** and before excavation **(C-D)**, showing divisions of the tuff and distribution of the fossiliferous shale.

the error range of all other steps indicating a valid age determination.

## PROVENANCE OF THE TUFF

METHODS: X-ray florescence analysis was used to quantify chemical differences between the tuff and the surrounding sandstone, and to identify a possible volcanic source for the tuff eruption. We sampled the least weathered rock available within the tuff, and approximately 10 meters above and below the tuff (Fig. 3). The whole-rock samples were then analyzed by ALS Chemex of Vancouver, BC, using CANMET standard SDMS2, with FeO by Pratt titration.

The X-ray florescence results in weight percent ages were not normalized for material lost on ignition (LOI) and results are shown in Table 3. There was a higher loss on ignition (LOI) from the tuff samples (sample numbers: 2, 3, 4 and 5), compared with marine sandstones. This difference may be related to devitrification and hydration of volcanic glass in the interval between airfall and redeposition, or a greater amount of organic matter in the tuff.

RESULTS: The plant-bearing tuff is chemically distinct from the adjacent marine sandstones, and the tuff can be classified as a dacite (Fig. 7) using the total alkali and silica method of Le Bas et al. (1992). Change in the sediment supply system is observed by comparing the average and standard error of the four tuff values with the measurements from the adjacent sandstones. Between the tuff and the sandstone below all oxides were outside the 95% confidence interval of an average of tuff values. Thus the tuff overwhelmed material from the depositional source area, and the change in sediment supplied to the system was abrupt. Element oxide values for the sandstone above the tuff were also significantly different from the tuff. Thus, once the volcanic material was flushed through, the system returned to pre-eruptive conditions. Some dilution of the sediments by controlled redeposition of small amounts of tuff did occur because elemental oxide values for the sandstone above the tuff fall between the values for the tuff and the sandstone below. Most of the tuff was deposited without significant mixing with local sediment, but small amounts of tuff continued to be eroded into shallow marine sandstone after the eruption.

Given age constraints for the tuff, its source was a part of the 100 km wide predominantly andesitic volcanic belt that spanned the western Cordillera of North America (Christiansen and Yeats, 1992), referred to in Oregon as the Early Western Cascades (Priest et al., 1983). Although data on early Miocene Cascade volcanism is limited (Sherrod and Smith, 2000), information that permits correlation is of two types. The first type is geologic maps that combine sparse radiometric dating with stratigraphic position to determine age (Fig. 2). Rocks of early Miocene age are present in the southern Washington Cascades (Hammond, 1980; Swanson, 1989), but the most likely correlation is with the compositionally diverse but generally siliceous Roxy Formation of the Southern Oregon Cascades (Hladky, 1994, 1996, 1999a, 1999b). The radiometric dates that constrain the age of the Roxy Formation are 2-3 million years older than the Floras Lake tuff, though younger potentially correlative units may have been removed by erosion. The second line of evidence for correlation are geochemical and geochronological studies (du Bray et al., 2006; Hammond, 1980; Mertzman, 2000; Verplanck, 1985). These studies include samples (Table 4) that may correlate with the tuff bed. The criteria used for identification were that the samples have radiometric dates with two sigma error ranges that overlap with the Floras Lake tuff date and that the samples are classified as andesite or dacite (Le Bas et al., 1992). The possible correlations are all located within the Cascade Volcanic Arc (Figure 2).

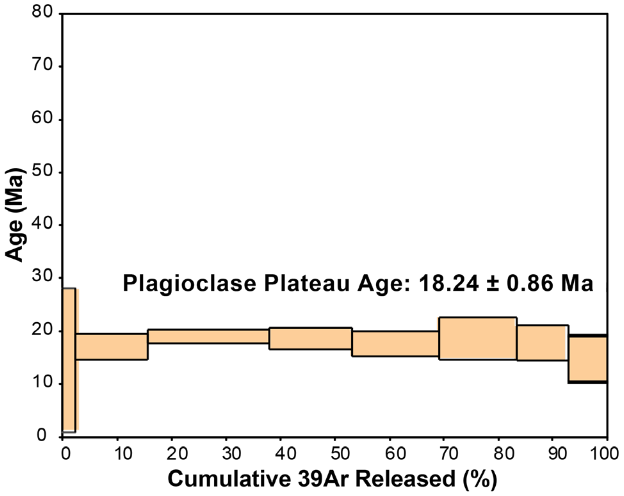

**Figure 6:** Plagioclase cumulative argon release plateau. Weighted Plateau age 18.24 ± 0.86 Ma; Total Fusion 17.88 ± 1.03; Normal Isochron 16.28 ± 2.55; Inverse Isochron 18.45 ± 1.23; MSWD 0.82. The weighted plateau age is favored because it has the smallest error.

Quaternary Plinian eruptions of the Cascades produced tephra fallout patterns primarily to the east and deposits rarely reach the coast (Sarna-Wojcicki et al., 1991). Sedimentary units that may correlate with the tuff bed are therefore more likely to be found on the leeward side of the Cascade range. Of comparable age is the Rose Creek Member of the volcaniclastic Eocene to Miocene John Day Formation in Central Oregon (Albright et al., 2008). The Rose Creek Member contains a number of ashfall tephra beds (Hunt and Stepleton, 2004) that may have had the same source eruption as the tuff at Cape Blanco.

Also of note is the amount of chromium in the sandstones (Table 3). The amount of chromium in the adjacent sandstones is much higher than in the tuff. The presence of detrital chromite in sandstone has been used as evidence of onset and development of collision in India and Pakistan because the uplift exposed ultramafic source rocks (Garzanti et al., 1996, Warwick et al., 1998). Elevated concentrations of Cr in mudstones have also been used to identify ultramafic provenance (Garver and Scott, 1995). The Klamath Terrane contains widespread ultramafic ophiolites (Harper, 1984) and the high chromium in the sandstones of Floras Lake, excluding the tuff, indicates that the catchment area for the sandstone of Floras Lake likely included the Klamath Terrane.

**Table 2.** Analytical Data for Radiometric Dates

| Sample | Plateau age (Ma) | 2σ error | Total fusion age (Ma) | 2σ error | MSWD | Normal isochron age (Ma) | 2σ error | $^{40}$Ar/$^{39}$Ar normal isochron | 2σ error | J |
|---|---|---|---|---|---|---|---|---|---|---|
| Plagioclase | 18.24 | 0.86 | 17.88 | 1.03 | 0.82 | 16.28 | 2.55 | 309.66 | 172.16 | 0.0021259 |
| Hornblende | 11.43 | 6.36 | 13,78 | 9.82 | 0.26 | 5.89 | 14.85 | 301.58 | 14.62 | 0.0021169 |

**Table 3.** Chemical composition of the Cape Blanco tuff by XRF[a]

| Sample | SiO2 | $Al_2O_3$ | $Fe_2O_3$ | CaO | MgO | $Na_2O$ | $K_2O$ | $Cr_2O_3$ | $TiO_2$ | MnO | $P_2O_5$ | SrO | BaO | FeO | LOI. | Tot. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 6 | 71.61 | 14.07 | 4.15 | 2.31 | 2.26 | 2.42 | 2.42 | 0.01 | 0.51 | 0.02 | 0.09 | 0.04 | 0.07 | 3.01 | 6.32 | 93.66 |
| 5 | 70.42 | 15.94 | 3.41 | 1.48 | 2.59 | 3.61 | 1.94 | 0 | 0.40 | 0.03 | 0.08 | 0.02 | 0.07 | 1.18 | 10.3 | 99.45 |
| 4 | 69.91 | 16.10 | 3.61 | 2.26 | 2.96 | 2.89 | 1.59 | 0 | 0.46 | 0.03 | 0.08 | 0.03 | 0.06 | 1.37 | 12.1 | 98.70 |
| 3 | 71.51 | 15.46 | 3.29 | 1.72 | 1.96 | 3.38 | 2.05 | 0 | 0.42 | 0.05 | 0.09 | 0.02 | 0.07 | 1.16 | 9.99 | 98.85 |
| 2 | 70.47 | 16.46 | 3.34 | 1.68 | 2.77 | 2.79 | 1.81 | 0 | 0.47 | 0.03 | 0.08 | 0.02 | 0.07 | 1.51 | 12.25 | 98.86 |
| 1 | 71.83 | 13.25 | 4.47 | 2.29 | 2.44 | 2.56 | 2.11 | 0.05 | 0.72 | 0.04 | 0.09 | 0.05 | 0.09 | 1.99 | 4.26 | 99.74 |
| an.err. | 2.71 | 0.83 | 0.4 | 0.22 | 0.18 | 0.11 | 0.13 | - | 0.06 | 0.03 | 0.04 | - | - | - | 0.35 | n/a |
| tuff av. | 70.58 | 15.99 | 3.41 | 1.79 | 2.58 | 3.16 | 1.85 | 0 | 0.44 | 0.04 | 0.08 | 0.03 | 0.07 | 1.3 | n/a | n/a |
| st.dev. | 0.33 | 0.21 | 0.07 | 0.17 | 0.22 | 0.20 | 0.10 | 0 | 0.02 | 0 | 0 | 0 | 0 | 0.08 | n/a | n/a |

[a] Analysis results with analytical error (an. er.) reported from 10 replicate samples, mean of the four tuff samples (tuff av.) and standard deviation of tuff samples (st.dev.). The stratigraphic location of samples is shown on figure 3. Dashes indicate that analytical error data was not available.

---

## FOSSIL PLANT COLLECTION

METHODS: Abundant new material (687 specimens) was collected for this study from a single quarry in six trips including students of paleobotany classes totaling 102 person-hours. Rock was removed from the quarry in 40 cm x 40 cm x 40 cm blocks and then broken down into fist sized pieces. The fossiliferous tuffaceous siltstone is cherty, with a fracture pattern that made exposure of complete leaves difficult. The majority of leaf fossils were within a single massive, 40 cm thick grey cherty shale and an underlying 10 cm of coarse sand to granule pumiceous tuff bed. Coniferous needle litter was predominantly found in the basal, coarse grained, pumice conglomerate. Fossils that had promise of identifiable features were collected and brought to the laboratory for further analysis.

In the laboratory, morphotypes were created to document diversity in the flora. The morphotypes were based on the part of the leaf preserved, level of preservation, venation, size, and margin state. As the fossils were considered in the laboratory, each was assigned to a morphotype and a total of 115 morphotypes were established. To ensure that the full diversity of the assemblage was captured we created a rarefaction curve (Fig. 8) to show the rate of new morphotype establishment. When much additional material revealed few new morphotypes, we were satisfied that we had captured the diversity present in the fossil flora. Well preserved morphotypes were subsequently assigned fossil names by reference to an extensive literature on Neogene floras of the western U.S., and in many cases morphotypes were merged where transitional examples warranted. This resulted in a tally of 33 species, including one pteridophyte, three conifers, at least one monocot and 28 angiosperms. Photographs of fossils were taken using a Nikon DS90 camera with a macro lens and cable release mounted on a camera stand. Images were adjusted for brightness and contrast using Adobe Photoshop 9.0.

No new species were described as a part of this study. Nor do we attempt comprehensive synonymy of each species, showing only the first reference which we consider valid. Specimens included in this study are from two collections; the majority were collected by the authors, as described above, and are housed in the Condon Collection of the Museum of Natural and Cultural History, University of Oregon (UOF specimen numbers and online

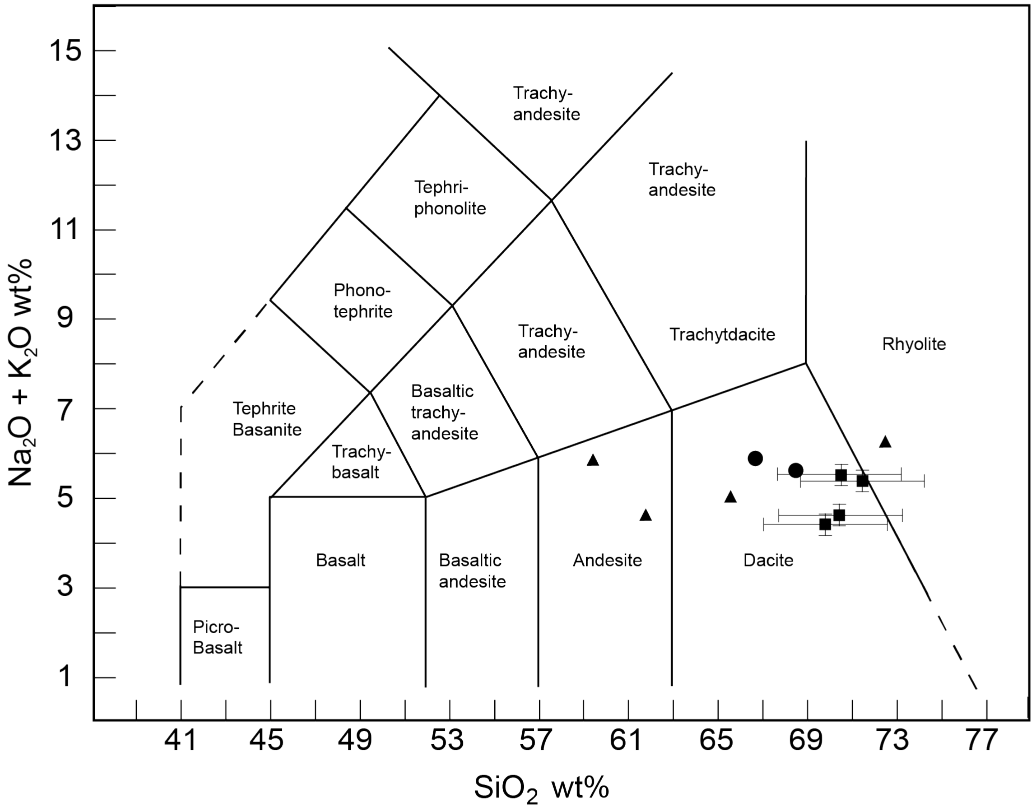

**Figure 7**: Total alkali-silica diagram showing classifications from Le Bas et al (1992). Squares are tuff data, error bars are the analytical error, for the $Na_2O + K_2O$ the error was summed. Circles are from Verplanck (1985) and triangles are from Mertzman (2000) and correspond with Cascade samples that have Ar/Ar dates that overlap with the Cape Blanco specimens. Errors were not reported and the plotted values are normalized to account for reported totals (Verplanck 1985) and LOI (Mertzman 2000).

**Table 4.** Possible volcanic sources for the Cape Blanco tuff

| Sample | Reference | Age (Ma) | Ma error (2σ) | Age method | TAS classification (after LOI correction) |
|---|---|---|---|---|---|
| 97-54Z | Mertzman 2000 | 17.1 | 0.8 | K-Ar | andesite |
| 97-55 | Mertzman 2000 | 17.6 | 0.7 | K-Ar | rhyolite |
| JM97-16 | Mertzman 2000 | 17.6 | 0.6 | K-Ar | dacite |
| M3-36 | Verplanck 1985 | 17.8 | 0.2 | K-Ar | dacite |
| FRL#4816(a) | Hammond 1980 | 18,4 | 0.3 | K-Ar | n/a |
| FRL#4816(b) | Hammond 1980 | 18.9 | 0.3 | K-Ar | n/a |
| M3-38 | Verplanck 1985 | 19.0 | 0.2 | K-Ar | dacite |
| FRL#4817(a) | Hammond 1980 | 19.4 | 1.0 | K-Ar | n/a |
| 97-53 | Mertzman 2000 | 19.6 | 0.6 | K-Ar | andesite |
| FRL#4817(b) | Hammond 1980 | 20.0 | 1.0 | K-Ar | n/a |

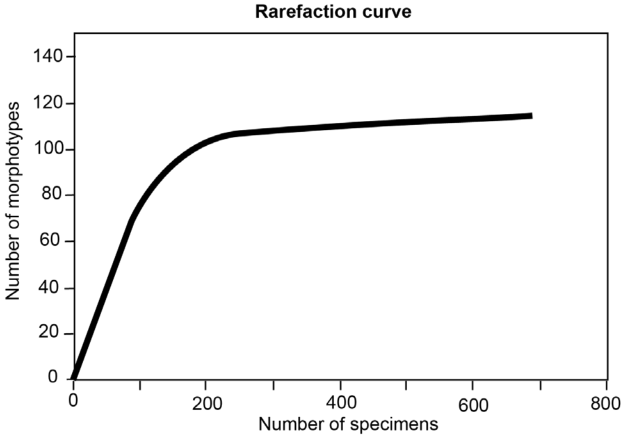

**Figure 8**: Rarefaction curve documenting the decrease in new morphotype discovery with increasing specimens. The flat portion of the graph demonstrates that the morphological diversity present in the flora was captured by our collections.

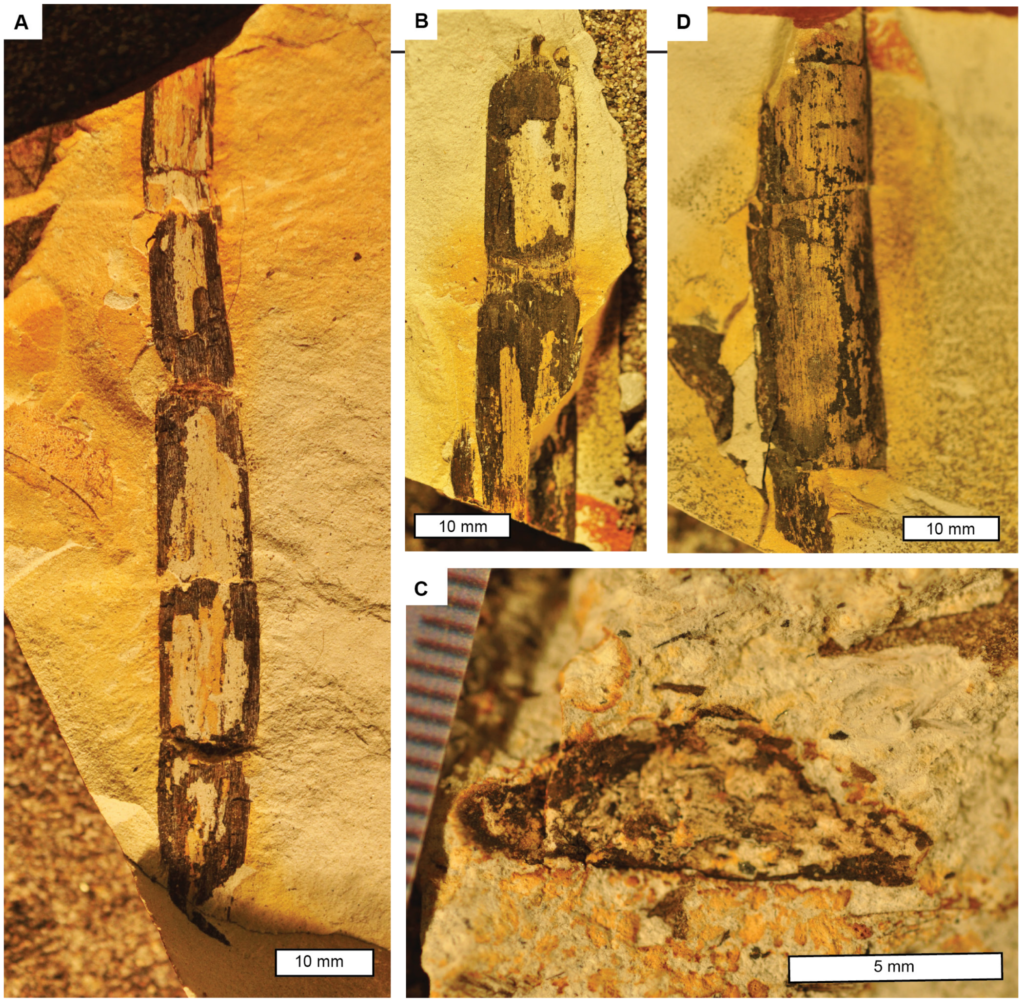

**Figure 9**: Cape Blanco fossil horsetails **A-D**. *Equisetum miocenicum* Graham 1963; **A**, culm UOF38088A; **B**, leafy culm UOF38068; **C**, rhizome UOF38103; **D**, cilmpinna fragment UOF38107.

portal paleo.uoregon.edu). The Condon Collection specimens were supplemented by 73 specimens collected by Jack Wolfe, and now in the Museum of Natural History of the Smithsonian Institution, Washington D.C. (USNM specimen numbers and online portal http://collections.nmnh.si.edu/search/paleo/).

We recognize the similarity of many of these fossil species with extant plants and indicate nearest living relatives, largely assigned by previous workers, to aid in the floristic interpretation of the flora. The systematic assignments of dicotyledonous angiosperms are organized by order following the classification of the Angiosperm Phylogeny Group (2016).

## SYSTEMATIC PALEOBOTANY

### DIVISION EQUISETOPHYTA
### CLASS EQUISETOPSIDA
### ORDER EQUISETALES
### FAMILY EQUISETACEAE
### *EQUISETUM MIOCENICUM*

1963 *Equisetum miocenicum* Graham, p. 933, fig. 17.

REFERRED SPECIMENS: UOF38068 (Fig.9A); UOF38088A (Fig. 9B); UOF38103 (Fig.9C), UOF38107 (Fig.9D).

DESCRIPTION: *Equisetum* is recognized by longitudinally ridged axes, separated by transverse joints at the nodes. Stems were 1-2 cm wide with nodes every 2.5 cm, and adpressed leaves are 2 mm across at the base. This wide-stemmed horsetail with wide leaves is like the living *Equisetum telmataeia* still found on the Oregon coast. Other Neogene *Equisetum* differ in narrow stems and leaves (*E. alexanderi* Brown 1936; *E. octangulatum* Smith 1938), more like living *Equisetum sylvaticum* and *E. arvense*.

### DIVISION GYMNOSPERMAE
### CLASS PINOPSIDA
### ORDER PINALES
### PINALES *INCERTAE SEDIS*

REFERRED SPECIMENS: charcoal UOF38091 (Fig. 10L), UOF38093, UOF38094, UOF38095; shredded wood UOF38104

DISCUSSION: Compressed wood is coalified, thick and elongate, and may show splayed tracheids,but lacks the equant, rounded shape of charcoal. Modern wood of cedar (*Thuja*), and pine (*Pinus*), shreds in a comparable way as it weathers. Many equant charcoal pieces up to a few centimeters in the long axis direction were found in the coarse grained pumiceous layer of the tuff at Cape Blanco. Vessels could not be identified in either the shredded or charcoalified wood suggesting that it is all coniferous. There was a range in sizes from a cm (UOF38093), to a piece that was more than 10 cm in diameter (UOF38092), from a small tree.

### FAMILY CUPRESSACEAE
### *SEQUOIA AFFINIS*

1876 *Sequoia affinis* Lesquereux, p. 584.

REFERRED SPECIMENS: partial ovulate cone unit? UOF38090B (Fig.10A), foliar spurs UOF42105B (Fig. 10B, F), OUF42310 (Fig. 10C), UOF38096B (Fig. 10D), UOF38105B (Fig. 10E).

DISCUSSION: This taxon includes specimens of lanceolate, acute, divergent needles arranged helically around slender axes (Fig. 10C-E), as well as other specimens with comparable leaves adpressed to diverging axes (Fig. 10B, F). Also tentatively assigned to *Sequoia* is an isolated cone unit, because of its sharp angulation of its short base from a strongly wrinkled apophysis (Fig. 10A). All these remains were found in the coarse pumiceous uppermost tuff with charcoal and wood fragments.

The fossil species *Sequoia affinis* in the extended sense of Chaney (1950) has long been used for foliage as old as Paleocene similar to living *Sequoia sempervirens* Endlicher, the coast redwood (Lowe, 2013). The only other species of fossil *Sequoia* accepted by Chaney (1950) is Late Cretaceous *S. dakotensis*, which has a smaller cone and distichous needles, unlike the Cape Blanco fossils.

While foliage of *Sequoia affinis* and *S. sempervirens* are similar, the cones of *S. affinis* are only 50-70 % the size of cones of the living species (Meyer, 2003). Most *Metasequoia* and *Sequioadendron* needles are wider and longer (Lowe, 2013), and molecular evidence supports the idea that these genera hybridized to form the genus *Sequoia* (Yang et al., 2012). *Sequoia sempervirens* is a forest giant of the Coast Range of northern California, but one large tree grew near Waldport, Oregon, between 1720 to 1820 years ago (Gavin et al., 2013).

### FAMILY PINACEAE
### *PINUS CARMELENSIS*

2000 *Pinus carmelensis* Axelrod, p. 20; pl. 2, figs. 1, pl. 3, fig. 1.

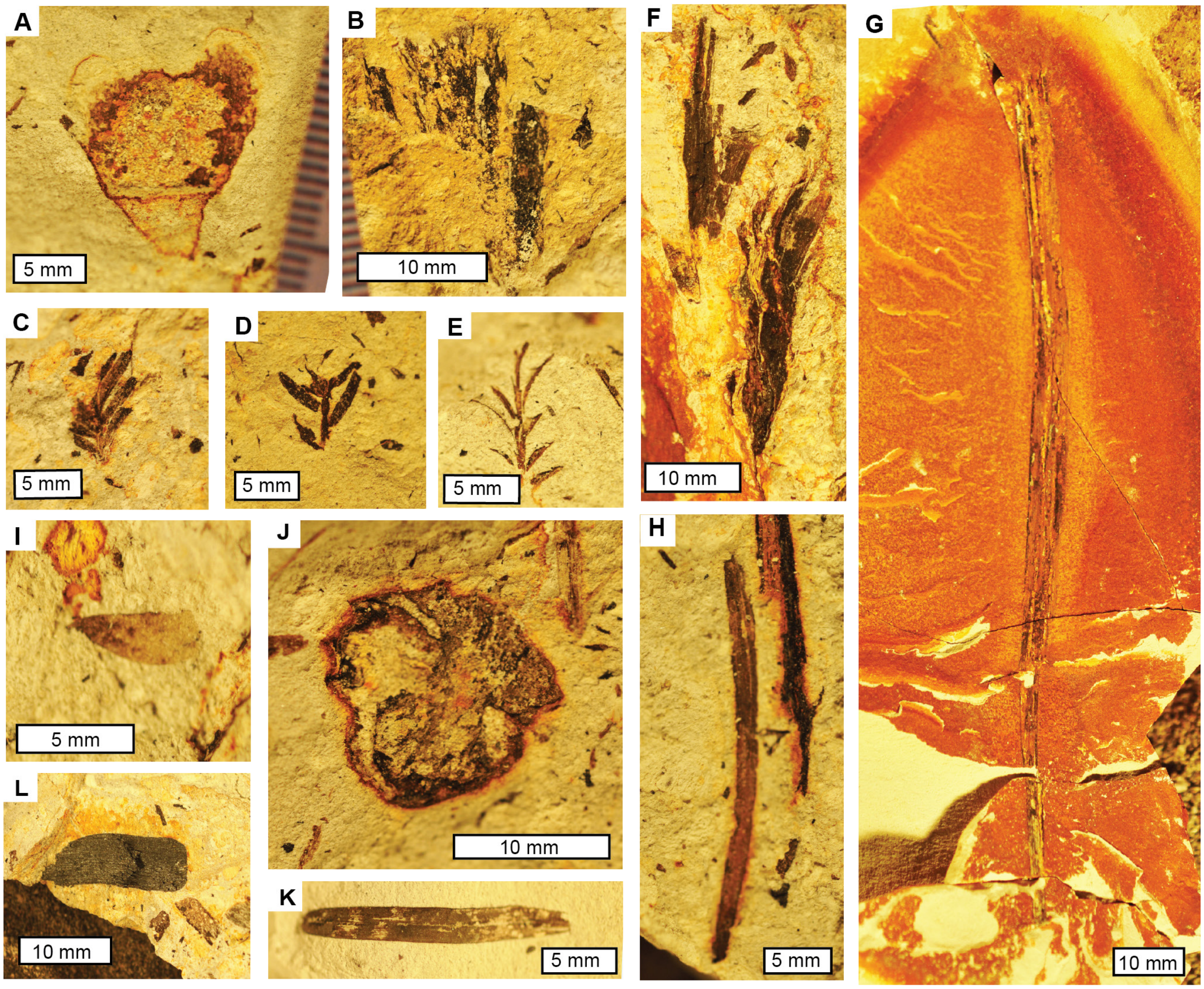

**Figure 10**: Cape Blanco fossil conifers: **A-E.** *Sequoia affinis*; **F-H**, *Pinus carmelensis*; **I-K**, *Picea sookensis*; **L**, conifer charcoal; **A**, ovulate partial cone unit UOF38090B; **B**, foliar spurs UOF42105B; **C**, foliar spur UOF42310; **D**, foliar spur UOF38096B; **E**, foliar spur UOF38105B; **F**, short shoots with fascicle sheaths UOF38103; **G**, three-needle complete fascicle UOF38089B; **H**, needles UOF38116; **I**, winged seed UOF42088; **J**, cone cross-section UOF38115A; **K**, needle UOF42033A; **L**, charcoal UOF38091.

REFERRED SPECIMENS: fascicle of three needles UOF38089B (Fig. 10G); short shoot showing fascicle sheath UOF38103 (Fig. 10F), isolated needles UOF38116 (Fig. 10H).

DISCUSSION: *Pinus carmelensis* is best represented by a complete three-needle fasicle with basal sheath at least 27 mm long (Fig. 10F-G). The needles are 15 cm long and 2 mm wide, and arranged radially within the bundle. Longitudinal ridges run the length of the needle to give them a diamond shaped cross section.

*Pinus ponderosoides* and *P. macginitei* also are long-needled, 3-needle pines, but have narrower needles and a longer fascicle sheath (Axelrod 1986). Another three-needle fossil pine is *Pinus andersoni* found permineralized in chert, with needles at least 6 cm long, but unknown for fascicle sheath and needle tips (Stockey, 1984). *Pinus ballii* (Brown, 1934) also has three needle fascicles, but they lack a basal sheath and the needles are only 2.5 cm long.

Axelrod (2000) considered *Pinus taeda* and *P. caribaea* the closest living relative, but these have shorter fascicle sheaths (USDA, 2009; Wildscreen Arkive, 2018). The closest living relative to *Pinus carmelensis* is *Pinus ponderosa* var *benthamiana* Hartweg (ponderosa pine; Lauria 1996), widespread in central California coast ranges (Wofford et al.,

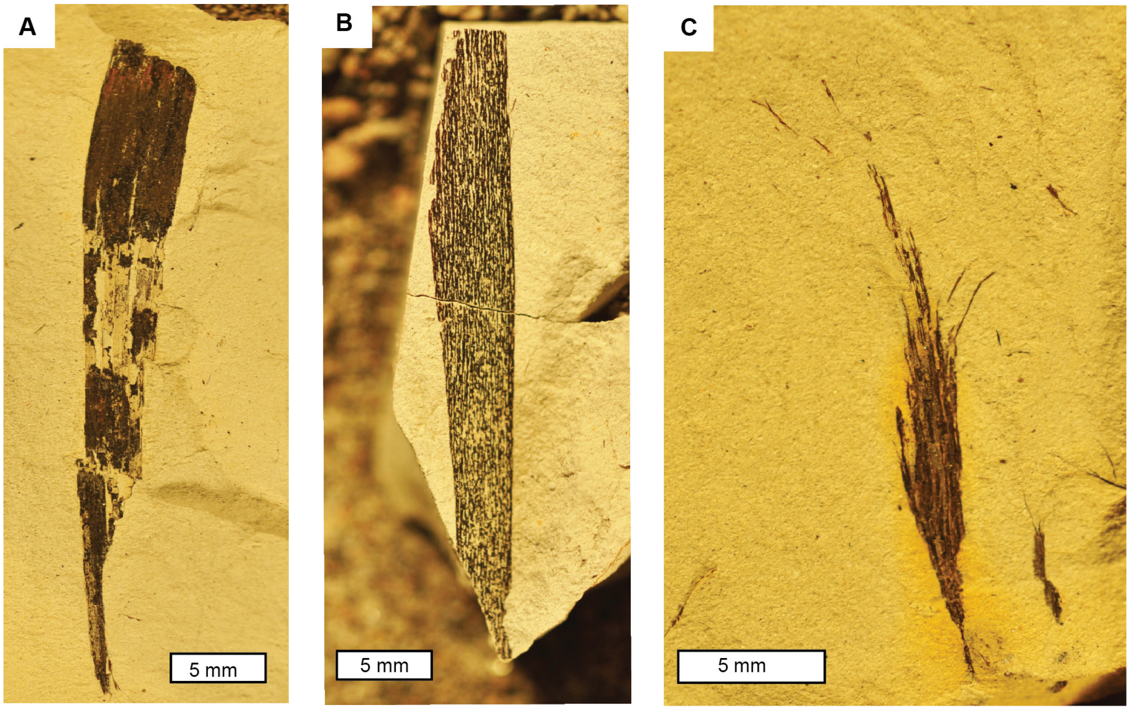

**Figure 11**: Cape Blanco fossil grasses: **A-C**, Poaceae gen et sp. indet. **A**, pleated leaf, UOF38108A; **B**, leaf UOF42277B; **C**, frayed culm UOF38101B.

2014), unlike other varieties of *P. ponderosa* found further inland (Youngblood et al., 2004).

### *PICEA SOOKENSIS*

1935b *Picea sookensis* LaMotte, p. 55, pl.1, fig.1.

REFERRED SPECIMENS: winged seed UOF42088 (Fig. 10I), cone cross-section UOF38115A (Fig.10J), needle UOF42033A (Fig. 10K).

DISCUSSION: Spruce is represented by a single winged seed (Fig. 10I), and cone cross section (Fig. 10J), and perhaps also by wide, revolute needles (Fig. 10K). The winged seed is only 6 mm long and has a very thin, unwrinkled wing.

The cone units have thick bases but thin and ribbed to fimbriate apophyses, unlike the thick, rigid apophyses of most other genera of conifers and other fossil species of *Picea*: *P.harrimanii*, *P. breweriana*, *P.lahontense*, *P. wolfei*, *P. diettertiana*, *P. banksii*, *P. sonomensis*, and *P. mariana* (Le Page, 2001). These other species also have larger seeds than the Cape Blanco specimen (Axelrod, 1995a, 1995b; Le Page 2001). The fossil species *Picea columbiensis*, *P. quilchensis* and *P. tranquilensis* are based only on needles that are smaller than those found at Cape Blanco (Penhallow, 1908).

The closest living relative to *Picea sookensis* is *Picea sitchensis* (sitka spruce), which also shares thin, flexible to fimbriate apophyses. *Picea sitchensis* is a forest dominant of northeastern Pacific coastal mountains from the Aleutian Islands south to northern California (Holliday et al., 2010).

### DIVISION ANGIOSPERMAE
### CLASS MONOCOTYLEDONAE
### ORDER POALES
### FAMILY POACEAE
### POACEAE gen. et sp. indet

REFERRED SPECIMENS: leaf group UOF38108A (Fig. 11A),

DISCUSSION: Some leaves 2-5 mm wide have longitudinal parallel venation, with marked pleating (Fig. 11A-B). No connected stems, nodes, or sheaths were found. Another specimen with numerous arching fine threads from a stem (Fig. 11C) may be a frayed stem or leaf.

### CLASS DICOTYLEDONAE
### ORDER LAURALES
### FAMILY LAURACEAE
### *PERSEA PSEUDOCAROLINENSIS*

1878 *Persea pseudo-carolinensis* Lesquereux, p.

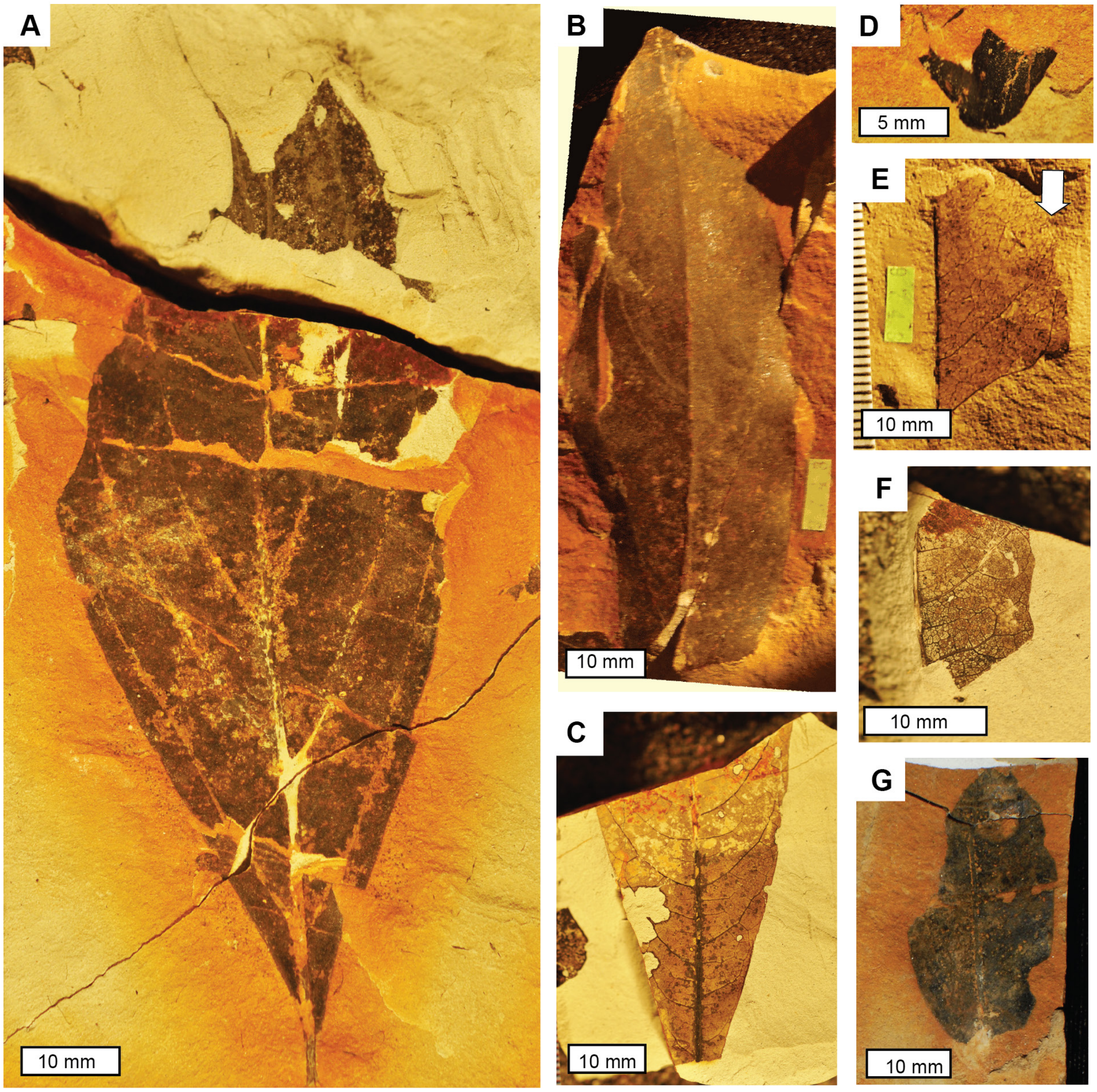

**Figure 12**: Cape Blanco fossil laurels and barberry: **A**, *Persea pseudocarolinensis*; **B-D**, *Umbellularia oregonensis*; **E-G**, *Mahonia trainii*; **A**, leaf, UOF115013; **B**, leaf USNM645803; **C**, leaf base UOF42207B; **D**, umbel bracts UOF42264A; **E**, leaflet fragment with sharp tooth at arrow USNM645804; **F**, leaflet fragment UOF42189A; **G**, leaflet USNM645805.

19-20; pl. 7, figs. 1, 2.

REFERRED SPECIMEN: UOF115013 (Fig.12A).

DISCUSSION: Long arching secondary veins are the unique identifier for this species, which has the festooned brochidromous venation, and entire margins typical of laurels.

This species had a complicated taxonomy in the early part of the twentieth century, but we follow the specific concept of Chaney and Axelrod (1959). *Persea coalingensis* and *P. lanceolata* are smaller, narrower and have a more acute apex than *P. pseudocarolinensis* (Axelrod, 1950a, 1964; Chaney and Axelrod, 1959). Study of DNA from Miocene (16 Ma) *Persea pseudocarolinensis* from Clarkia, Idaho, shows a closer relationship with sassafras (*Sassafras albidum* (Nuttall) Nees) than with living avocado (*Persea americana* Miller), but also shows that the genus *Persea* is polyphletic, so that transfer of the fossils to the genus *Sassafras* is not warranted at this time (S. Kim et al., 2004).

Whether related to *Sassafras* or *Persea*, modern relatives of this fossil are from warmer climates to the south. *Persea americana* is native to Mexico,

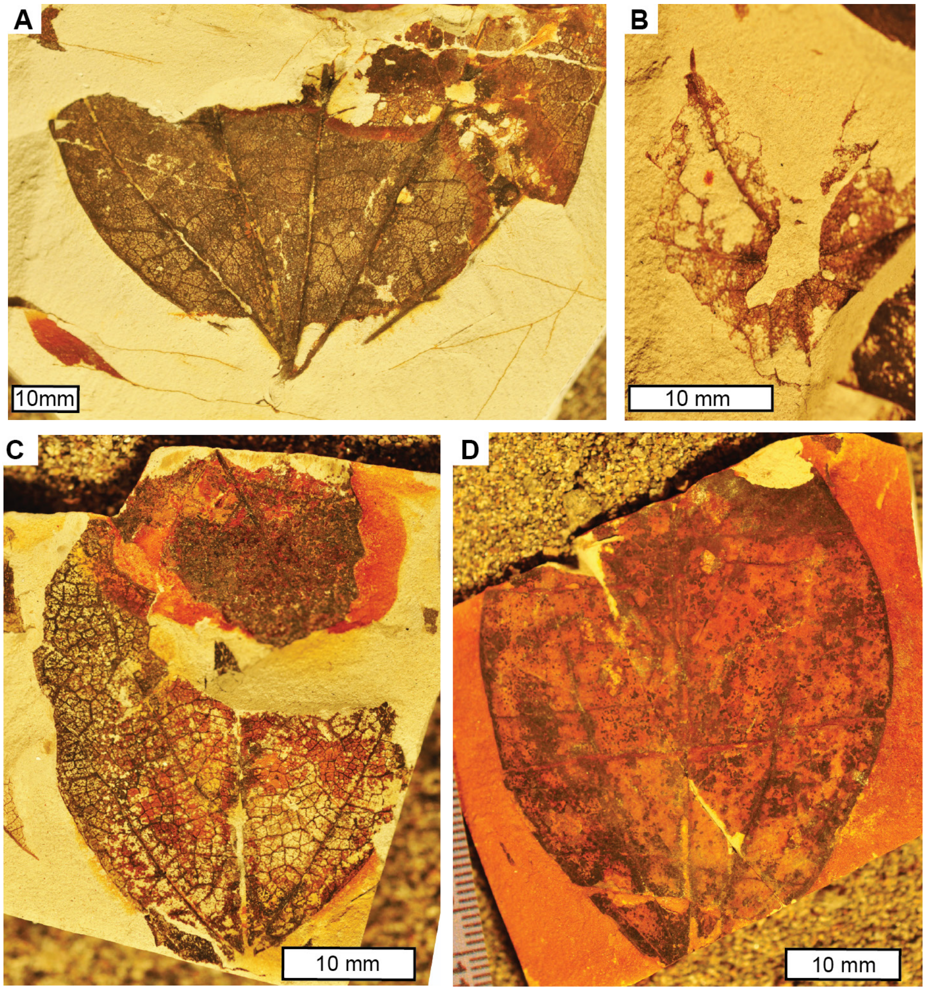

**Figure 13:** Cape Blanco fossil sycamore, pipli and witch hazel: **A-B**, *Platanus paucidentata*; **C-D**, *Exbucklandia oregonensis*; **E-F**, *Hamamelis merriamii*; **A**, leaf base UOF38054B; **B**, stipule UOF42406A; **C**, leaf base UOF42335, **D**, leaf base UOF115015B; **E**, leaf UOF42181A; **F**, leaf apex UOF42267.

---

and probably other parts of Mesoamerica, but was dispersed by humans even in prehistoric times (Galindo-Tovar et al., 2008). *Sassafras albida* and *Persea carolinensis* are widely distributed in southeastern United States from Florida to southern Michigan and into eastern Texas (Nie et al., 2007).

### *UMBELLULARIA SALICIFORMIS*

1952 *Umbellularia saliciformis* (Knowlton and Cockerell) LaMotte, p. 349.

REFERRED SPECIMENS: leaf SI645803 (Fig. 12B), leaf base UOF42207B (Fig. 12C), umbel bracts UOF42264A (Fig.12D).

DISCUSSION: These are lanceolate to spathulate, entire-margined leaves with festooned brochidromous venation arching to concordance with the margin (Fig. 12B-C), as is typical of laurels. These leaves are coriaceous and mildly recurved, but lack the checkerboard areolation of associated live oaks. Also possibly attributable to this fossil species are radial bracts (Fig. 12D), like those that subtend the tight umbels of Oregon myrtlewood (*Umbellularia californica*), a likely living relative.

LaMotte (1952) has a broad concept of *Umbellularia saliciformis* including several other named species, but not the narrow-leaved *U. dayana* (Knowlton, 1926), nor the oblanceolate to elliptical *U. eocenica* (Brown, 1940).

The likely living relative, *Umbellularia californica* (Hooker and Arnold) Nuttall now grows throughout western California and into southwestern Oregon (Goralka and Langenheim, 1995).

## ORDER RANUNCULALES
## FAMILY BERBERIDACEAE
### *MAHONIA TRAINII*

1936 *Mahonia trainii* Arnold, p. 62; pl. 3, figs. 4, 6, 8.

REFERRED SPECIMENS: leaflet fragments SI645804 (Fig 12E), UOF42189A (Fig.12F), USNM645805 (Fig.12G).

DISCUSSION: The secondary veins on *Mahonia* are festooned brochidodromous with the first loop occurring roughly half way between the primary vein and the margin. Tertiary veins form an irregular polygonal reticulate mesh with rectangular areoles. The long axis of the rectangular areoles is at a high angle to the primary vein. One fragment shows a spinose marginal tooth (arrow in Fig. 12E). These identifying characteristics were sufficient to determine a generic assignment for these fragments.

Teeth much larger than apparent from our fragments are found in living *Mahonia oregonensis* and the following fossil species: *M. reticulata* (Brown, 1936), *M. eocenica* (=”*Odostemon eocenica*” Brown 1934), *M. simplex* (Arnold, 1936), *M. hakeaefolia* (Arnold, 1936), *M. hollicki* (Arnold, 1936), *M. macginitiei* (Axelrod, 1985), *M. marginata* (Axelrod, 1987), *M. harneyensis* (Axelrod, 1987), *M. grimmii* (Güner and Denk, 2012), and *M. mioasiatica* (Huang et al., 2016). Also distinct for elongate tapering leaflets are the living species *Mahonia lanceolata* and the following fossil species *Mahonia malheurensis* (Arnold 1936), *M. mohavensis* (Axelrod, 1939), *M. prelanceolata* (Condit, 1944b), and *M. creedensis* (Axelrod, 1987). *Mahonia somaensis* has comparable leaf shape but palmate basal secondaries like living *Mahonia nervosa* (Güner and Denk, 2012), rather than pinnate secondaries.

A modern equivalent to *Mahonia trainii* suggested by Arnold (1936) is *Mahonia lanceolata* Bentham (Mexican grape holly) of the Mexican states of Oaxaca to Hidalgo (Y.D. Kim et al., 2004).

## ORDER PROTEALES
## FAMILY PLATANACEAE
### *PLATANUS PAUCIDENTATA*

1930 *Platanus paucidentata* Dorf, p. 95, pl. 10, figs. 4,9, pl. 11,m fig. 1, pl. 12, fig. 1.

REFERRED SPECIMENS: leaf base UOF38054B (Fig. 13A), stipule UOF42406A (Fig. 13B).

DISCUSSION: Fragments of leaf bases have what appear to be palinactinodromous primary veins (basal secondaries dichotomizing again) of *Platanus*.

The sparse teeth and short distance to palinactinodromous branching of our specimens and of *Platanus paucidentata* are unusual among sycamore leaves, and distinguish them from the following well characterized fossil species: *Platanus bendirei* (Wolfe, 1964; Wolfe and Tanai, 1980; Fields, 1996), *P. exaspera* (Meyer and Manchester, 1997), *P. condonii* (Meyer and Manchester, 1997), *P. dissecta* (Berry 1934), *P. acerifolia* (Sanborn, 1947), *P. appendiculata* (MacGinitie, 1941), and *P. coloradensis* (MacGinitie, 1941). *Platanus angustiloba* has even narrower, more deeply incised lobes than *P. paucidentata* (Axelrod, 2000), and such incision would extend to the level apparent on our fragments. *Platanus* leaves can be confused with those of *Acer*, but *Acer* is actinodromous, a condition found in few species of *Platanus* (Dorf, 1930; Meyer and Manchester, 1997).

*Platanus paucidentata* has narrow lobes unlike living *Platanus occidentalis* (American sycamore), *P. mexicana* (Mexican sycamore), or *P. rzedowski* (Rzedowski’s plane), and is more sparsely dentate than *P. gentryi* (Gentry’s plane). The most similar living leaves are those of *Platanus racemosa* (California sycamore), which ranges throughout California into northern Baja California (Nixon and Poole, 2003; Feng et al., 2005).

## ORDER SAXIFRAGALES
## FAMILY HAMAMELIDACEAE
### *EXBUCKLANDIA OREGONENSIS*

1920 *Cercis oregonensis* Chaney, p. 177, leaf only, pl. 16, fig. 3-4.

1946 *Exbucklandia oregonensis* (Chaney) Brown, fruits and seeds only, p. 348, text-fig 4-6.

REFERRED SPECIMENS:
partial leaves UOF42335 (Fig.13C), UOF115015B (Fig. 13D).

DISCUSSION: These fragments have asymmetrical ovate leaves, with basal actinodromous secondary veins and brochidodromous secondaries. These veins do not sweep into a marginal vein as in superficially similar leaves of *Calkinsia*, *Hovenia*, *Pflafkeria*, *Ceanothus*, *Viburnum*, or *Cercidiphyllum* (Wolfe, 1968, 1977; Meyer and Manchester, 1997).

*Exbucklandia oregonensis* is mainly represented

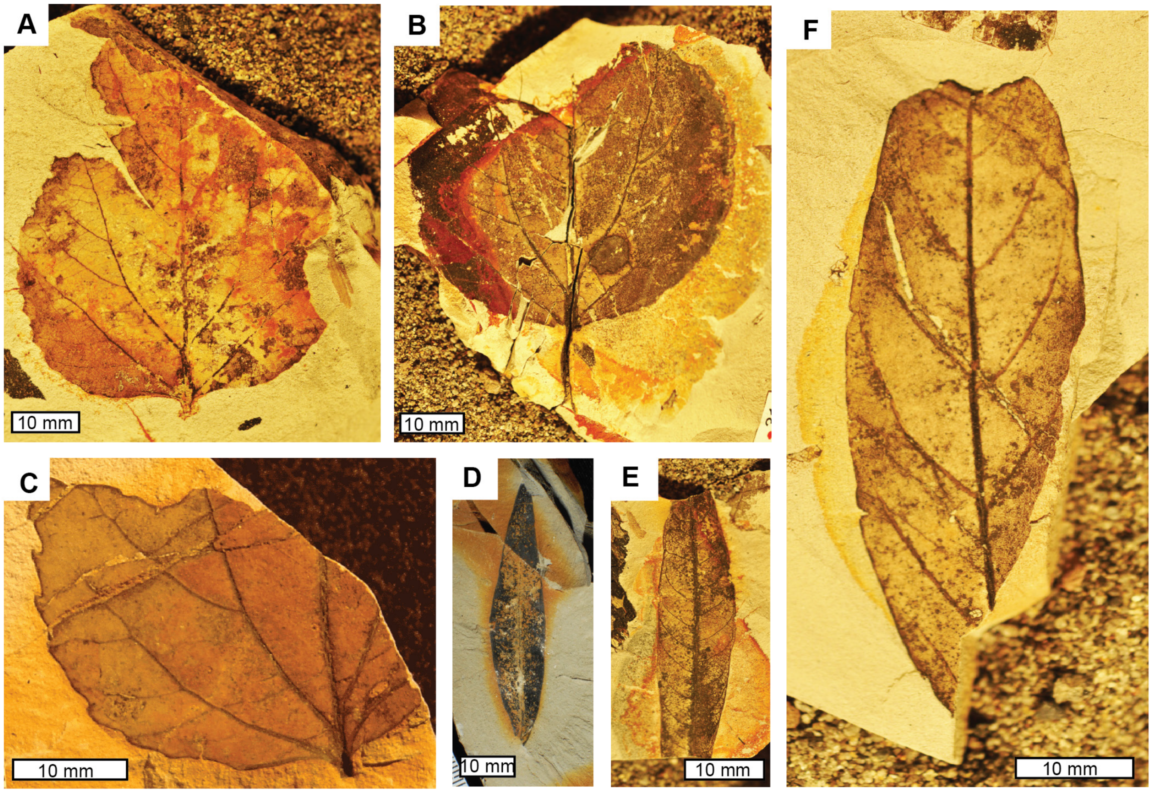

**Figure 14**: Cape Blanco fossil poplars and willows: **A-B**, *Populus eotremuloides*; **C**, *Populus lindgrenii*; **D-E**, *Salix succorensis*; **F**, *Salix laevigatoides*; **A**, leaf UOF38119B; **B**, leaf UOF38118A; **C**, leaf base USNM645810; **D**, leaf USNM645812; **E**, leaf UOF42122A; **F**, leaf UOF38136A.

by fruits and seeds (Brown, 1946; LaMotte, 1952), but fossil leaves also have been widely reported (Chaney, 1920; Meyer, 1973; Baghai and Jorstad, 1995). This is the only fossil species known from North America, and differs from Chinese fossils including the larger *E. guangxiensis* (Huang et al., 2017), ovate-cordate *E. tengchongensis* (Wu et al., 2009), and narrow, apically acuminate *E acutifolia*, which is widest well below the level preserved on our leaves (Huang et al., 2017).

There are three living species of *Exbucklandia*, including cordate to truncate *E. populnea*, and narrow ovate *E. tonkinensis*, but our fossil leaves are ovate like *E. longipetala* H. T. Chang (changbanmatihe) of the southern Chinese provinces of Guizhou and Guangxi (Huang et al., 2017).

### ORDER MALPHIGIALES
### FAMILY SALICACEAE
### *POPULUS EOTREMULOIDES*

*1898 Populus eotremuloides* Knowlton, p. 725; pl. 100, figs. 1, 2; pl. 101, figs. 1, 2.

REFERRED SPECIMENS: leaves UOF38119B (Fig.14A), UOF38118A (Fig. 14B).

DISCUSSION: Suprabasal actinodromous primary venation is a diagnostic character of the broad morph of mature and late season leaves of *Populus*, but not necessarily the narrow morph of juvenile and early season leaves (Eckenwalder, 1980).

Only broad morphs were recognized as *Populus* at Cape Blanco, and these are distinct from narrow morphs such as *Populus bonhamii*, *P. cedrusensis*, *P. creedensis*, *P. cinnamomoides*, *P. hernandezi*, *P. lesquereuxii*, *P. mutreloides*, *P. payettensis*, *P. silvae*, and *P. tidwellii* (Axelrod, 1939, 1985, 1987, 1991, 1995a, 1995b; Ramirez and Cevallos-Ferriz, 2000; Manchester et al., 2006).

Our leaves are asymmetric, with thin basal secondaries giving rise to longer tertiaries on one side than another, unlike symmetrical leaves such as *Populus alexanderi* (Dorf, 1930; Chaney, 1938), *P. balsamoides* (Condit, 1938), *P. dentiacuminata* (Ramirez and Cevallos-Ferriz, 2000), *P. emersoni*

(Condit, 1938), *P. pliotremuloides* (Chaney, 1938; Axelrod, 1985), *P. prefremonti* (Dorf, 1930; Axelrod, 1944a), *P. voyana* (Chaney and Axelrod, 1959), and *P. wilmattae* (Manchester et al., 2006). Our specimens from Cape Blanco also lack the large teeth of *Populus washoensis* (Axelrod, 1944a; Condit, 1944b; Chaney and Axelrod, 1959). *Populus sonorensis*, and *P. parcedentata* are less obviously toothed and have secondaries diverging at a wider angle (Axelrod, 1939, 1944b-c, 1950b-c) than either of the poplars at Cape Blanco. *Populus lamottei* is a smaller leaf with more closely spaced secondaries (Chaney and Elias, 1938). Very similar leaves to our *Populus eotremuloides* are figured by Chaney and Axelrod (1959, pl.17, fig.4), and Axelrod (1985, pl. 20, fig. 6; 1991, pl. 6, fig. 1, 8). The two *Populus* species observed at Cape Blanco are distinguished by their leaf margin, with *P. eotremuloides* entire to very finely serrate, and *P. lindgreni* crenate to toothed.

*Populus eotremuloides* has serration comparable with that observed on leaves of black cottonwood (Chaney and Axelrod, 1959), *Populus trichocarpa* (Torr. & A Gray ex Hooker), which is sometimes regarded as a subspecies of *Populus balsamifera* Linnaeus (Barakat et al., 2007), and is widely distributed in western North America from northern California to southern Alaska (Gornall and Guy, 2007).

### *POPULUS LINDGRENII*

1898 *Populus lindgreni* Knowlton, p. 725; pl. 100, fig. 3.

REFERRED SPECIMEN: leaf base USNM645810 (Fig.14C).

DISCUSSION: The suprabasal actinodromous venation of *Populus lindgrenii* extends at a wide angle to the primary vein and the margins have wide teeth (LaMotte, 1936).

Buechler et al. (2007) included *Populus voyana* Chaney and Axelrod (1959) in *P. lindgrenii* and regarded differences in petiole and midrib thickness used by Chaney and Axelrod (1959) to separate *P. voyana* as natural variation within the species. Fields (1996) did not document *P. lindgrenii* at Succor Creek, but supported separation of *P. voyana*. We assigned our specimen to the name with priority, *P. lindgrenii*, because the teeth of our specimen most closely resembles *P. lindgrenii* of LaMotte (1936, pl. 4, fig.1), Sanborn (1947, pl. 6, fig. 4), and Chaney and Axelrod (1959 pl. 17, fig 2). Chaney and Axelrod (1959) suggested that the nearest living relative to *Populus lindgrenii* may be *P. heterophylla* Linnaeus, and also concur with Fields (1996) that *P. voyana* is more like *P. tremuloides* (aspen). *Populus heterophylla* (swamp cottonwood) is widely distributed in coastal lowlands of eastern North America from Massachusetts to Louisiana and inland floodplains of Ohio and southern Michigan (Searcy and Ascher, 2001).

### *SALIX LAEVIGATOIDES*

1950a *Salix laevigatoides* Axelrod, p. 55; pl. 2, fig. 10.

REFERRED SPECIMENS: leaf UOF38136A (Fig. 14F).

DISCUSSION: The diagnostic characters of *Salix* are lanceolate leaves with semicraspedodromous to brochidodromous secondary venation and reticulate tertiary venation. Axelrod (1950a) did not offer a formal diagnosis of this species, and a supplementary diagnosis can be offered as follows.

Leaves firm in texture; margin chiefly entire, may be finely serrate; leaf narrowly lanceolate; 3.5 to 11.4 cm long; 1.2 to 2.6 cm wide; elliptic to ovate; midrib thick; secondaries more than 7 pairs, thin, alternate, arising from midrib at high angle, secondary veins brochidodromous to semicraspedodromous; tertiary veins orthogonal reticulate.

*Salix* is diverse in the fossil record back to the Eocene (Collinson, 1992). Many Neogene *Salix* species have a serrated margin unlike our specimen, and the following species can be excluded on this basis: *Salix californiana* (Condit, 1944b), *S. desatoyensis* (Axelrod, 1995a), *S. edenensis* (Axelrod, 1950b), *S. florissantii* (Berry, 1934), *S. hesperia* (Chaney and Axelrod, 1959). *S. inquirenda* (Axelrod, 1995a), *S. kempfii* (Ashlee, 1932), *S. paradisensis* (Brown, 1949), *S. payettensis* (Axelrod, 1944e), *S. pelvida* (Axelrod, 1995a), *S. ramaleyi* (Meyer, 2003), *S. spokanensis* (Brown, 1936), *S. truckeana* (Axelrod, 1950b), *S. venosiuscula* (Chaney and Axelrod, 1959). Oblong leaf shape excludes *S. owyheeana* (Chaney and Axelrod, 1959) and *S. wildcatensis* (Axelrod, 1995a), obovate shape distinguishes *Salix boisiensis* (Chaney and Axelrod, 1959), *S. williamsii* is short oblanceolate (Brown, 1949), *S. edenensis* is narrow oblanceolate (Axelrod, 1950b), and three species, *S. churchillensis*, *S. kernensis* and *S. vaccinifolia*, are narrow linear (Axelrod, 1939, 1940, 1995a). Axelrod (1995a, p.

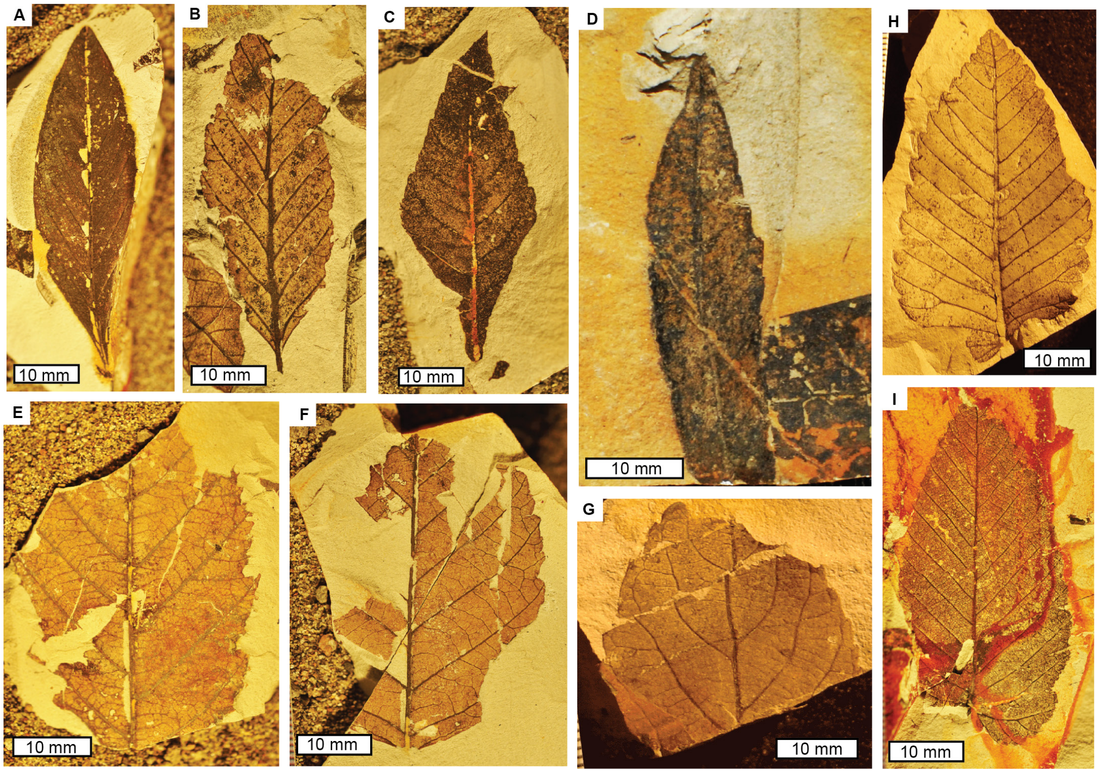

**Figure 15**: Cape Blanco fossil mahogany, ash, elms, birch and alder: **A**, *Cercocarpus nevadensis*; **B-D**, *Sorbus idahoensis*; **E**, *Corylus macquarrii*; **F-G**, *Alnus harneyana*; **H-I**, *Ulmus speciosa*; **A**, leaf UOF42121B; **B**, leaf UOF42406B; **C**, leaflet UOF38053A; **D**, leaflet USNM645807; **E**, leaf UOF42025A; **F**, leaf UOF42024B; **G**, leaf SI645813; **H**, leaf USNM645814; **I**, leaf UOF42408.

44) provides a key to seven Miocene species, which we followed to assign the entire and erose margined lanceolate *Salix* specimens from Cape Blanco to *S. laevigatoides*.

The nearest living form to *Salix laevigatoides* is *Salix laevigata* Bebb of California, Nevada, Arizona, and southernmost Oregon (Argus, 2007).

### *SALIX SUCCORENSIS*

1959 *Salix succorensis* Chaney and Axelrod, p. 154; Pl. 16, fig. 8.

REFERRED SPECIMENS: leaves USNM645812 (Fig. 14D), UOF42122A (Fig. 14E).

DISCUSSION: The large length to width ratio, small size, entire margin, and 45º angle of secondary departure are characters unique to *Salix succorensis*, and distinguish it from other narrow, entire-margined species such as *S. churchillensis* (Axelrod, 1995a), *S. edenensis* (Axelrod, 1950b), *S. kernensis* (Axelrod, 1939), *S. pelviga* (Axelrod (1985), *S. storeyana* (Axelrod, 1995a), and *S. vaccinifolia* (Axelrod, 1940). The specimens from Cape Blanco are a very good match for the leaf figured by Buechler et al. (2007), which has an entire margin. This echoes the comments of Fields (1996, p 411) who describes the margin as "faintly or non-toothed". However, the figured specimen of Chaney and Axelrod (1959) shows teeth, whereas the Cape Blanco specimens are entire-margined.

Modern species most closely resembling *Salix succorensis* are *S. nigra* Marshall, and *S. longipes* Anderson (Chaney and Axelrod 1959), which was later reassigned to *S. caroliniana* (USDA 2009). *Salix nigra* is widespread in eastern North America from Quebec to Minnesota and south to Texas and Florida, but *S. caroliniana* is found from Pennsylvania to Kansas and south to Texas and Florida (Argus, 2007).

### ORDER ROSALES
### FAMILY ROSACEAE
### *CERCOCARPUS NEVADENSIS*

1991 *Cercocarpus nevadensis* Axelrod, p. 51; pl. 17, figs. 6-13.

REFERRED SPECIMEN: UOF42121B (Fig 15A).

DISCUSSION: This distinctive small leaf is represented by only two complete specimens from Cape Blanco. Other Neogene fossil *Cercocarpus* include *C. antiquus* with more closely spaced secondary veins, *C. ovatifolius* with wider leaves, *C. cuneatus* and *C. eastgatensis* with steeply upswept secondaries, and *C. linearifolius* and *C. holmesii* with very narrow leaves (Axelrod, 1944e, 1950c, 1985, 1991).

The modern species most similar to *C. nevadensis* was reported as *Cercocarpus betuloides* Nuttall by Axelrod (1991), which has since been reassigned to *Cercocarpus montanus* or mountain mahogany (USDA 2009). *Cercocarpus montanus* is a shrub widespread in the United States west of Louisiana to Minnesota, and is a useful browse plant for livestock and deer (Brotherson et al., 1984; USDA, 2009). Among the varieties of living *Cercocarpus montanus*, our fossil leaves are most like *C. montanus* var. *paucidentatus*, found in central Arizona and New Mexico south to Mexico City, Mexico (Lis, 1992).

### *SORBUS IDAHOENSIS*

1985 *Sorbus idahoensis* Axelrod, p. 169; pl. 29, figs. 2, 6-7, 10.

REFERRED SPECIMENS: leaflets UOF42406B (Fig. 15B), UOF38053A (Fig. 15C), USNM645807 (Fig.15D).

DISCUSSION: Although based on only three specimens, these leaflets are unique because of their strongly serrate margin, narrow lanceolate shape, and irregular auxiliary veins between secondaries.

*Sorbus diversifolia* and *S. nupta* have leaflets more deeply dissected than our specimens (Cockerell, 1910). *Sorbus alvordensis* MacGinitie (1933) and *S. harneyensis* Axelrod (1944e) are similar in size and shape but have acute, forward-directed teeth like those of oak. *Sorbus chaneyi* LaMotte (1936) and *S. mcjannetii* (Axelrod, 1991) have different proportions with almost elliptical leaflets. *Sorbus cassiana* has narrower linear leaflets (Axelrod, 1995b).

Axelrod (1985) suggests European mountain ash (*Sorbus aucuparia*) as a modern equivalent, but that species has more symmetrically elliptical leaflets. A better match for the acuminate apex of the Cape Blanco specimens is American mountain ash (*Sorbus americana* Marshall), widespread in eastern North America from Georgia north to Quebec, and inland from Minnesota to Wisconsin, Illinois, and Tennessee (USDA, 2009).

## FAMILY ULMACEAE
### *ULMUS SPECIOSA*

1898 *Ulmus speciosa* Newberry, p. 80; pl. 45, figs. 3, 4.

REFERRED SPECIMENS: USNM645814 (Fig. 15H), UOF42408 (Fig. 15I).

DISCUSSION: Doubly serrate *Ulmus* has been distinguished from singly serrate *Zelkova*, but that difference is inconsistent, and Tanai and Wolfe (1977, p.3) offer the following differentiae. “In *Zelkova*, the tertiary veins are typically thin, widely spaced, and fork conspicuously midway between the secondary veins, in contrast to *Ulmus* in which the tertiary veins are thick, more widely spaced, and at least half the tertiary veins are unbranched”.

The keys of Tanai and Wolfe (1977) and of Meyer and Manchester (1997) were followed in assigning our specimens to *Ulmus speciosa*. The tertiary venation, and prominent asymmetrical bases observed in our specimens are identical to *Ulmus speciosa*. Axelrod (1991) was not satisfied with the key of Tanai and Wolfe (1977) and includes *U. owhyeeana* within *U. speciosa*. Meyer and Manchester (1997) also distinguish *U. chaneyi* for large leaves with subsidiary teeth on both the apical and basal sides of most of the primary teeth, and smaller narrow leaves comparable with *U. paucidentata.*

Meyer and Manchester (1997) consider that the most similar living species to *Ulmus speciosa*, is *U. americana* Linnaeus, which is native to North America from Saskatchewan south to Texas and eastward to the east coast (USDA, 2009).

## ORDER FAGALES
## FAMILY BETULACEAE

Leaves of the birch family have compound serrate margins and typically straight secondary veins. Here we differentiate large leaves with widely spaced secondaries, and three-ordered serrate margin into *Alnus harneyana*, and the small leaves into Betula thor. There are some similarities with Corylus, which has distinctive high relief venation and leaf base supplied by parallel tertiary veins (Wolfe and and Tanai, 1980). The genera *Alnus* and

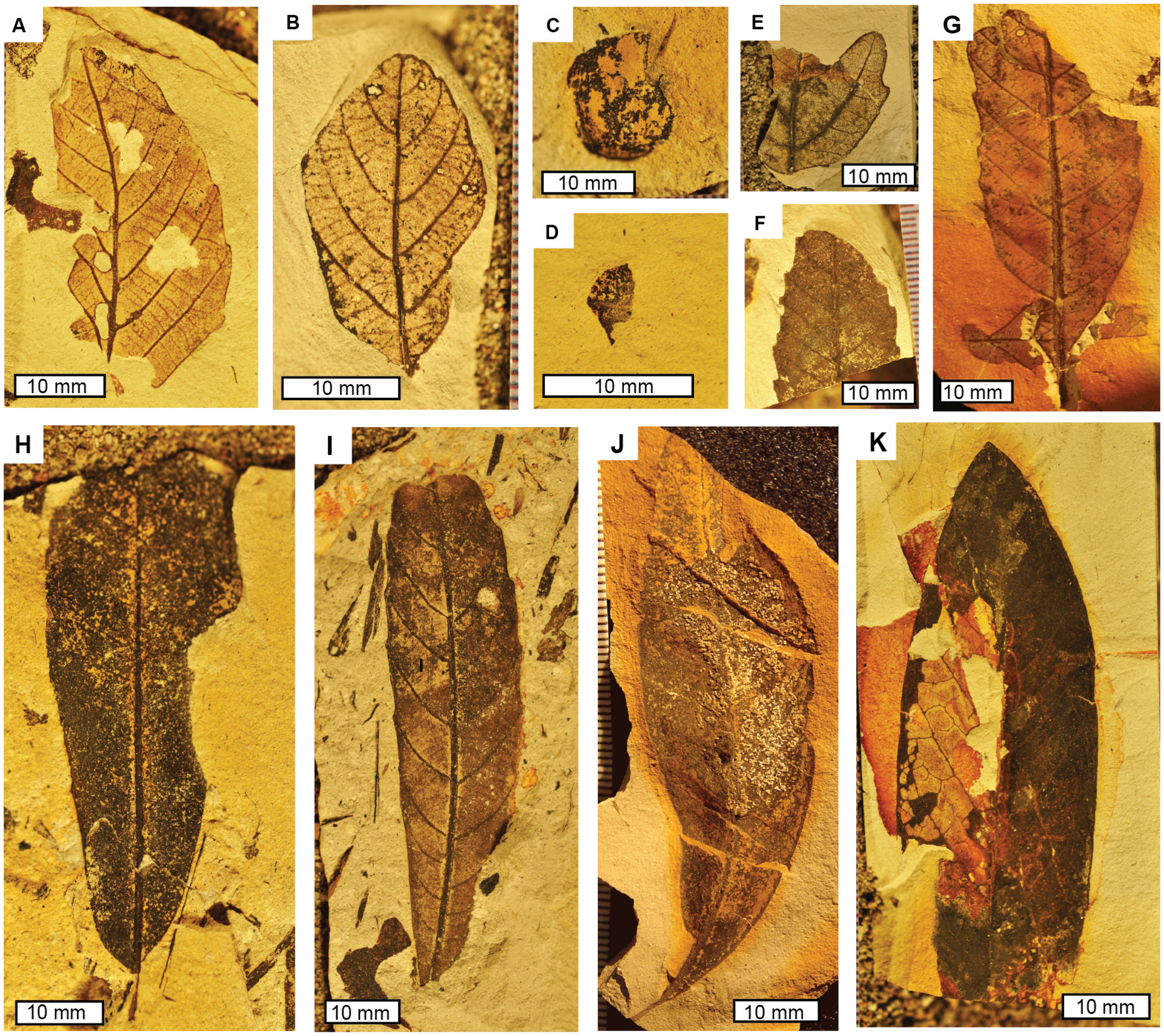

**Figure 16**: Cape Blanco fossil beech and oaks: **A-C**, *Fagus washoensis*; **D**, *Quercus* sp. indet.; **E**, *Quercus prelobata*; **F-G**, *Quercus simulata*; **H**, *Quercus hannibalii*; **I**, "*Lithocarpus*" *nevadensis*; **J-K**, *Chrysolepis sonomensis*; **A**, leaf UOF42078A; **B**, leaf UOF38057A; **C**, cupule UOF42387B; **D**, immature acorn UOF42401A; **E**, leaf UOF42138A; **F**, leaf UOF42142B; **G**, leaf SI645811; **H**, leaf UOF42105A; **I**, leaf UOF42088; **J**, leaf USNM645808; **K**, leaf UOF38056A.

*Betula* were distinguished by Chaney and Axelrod (1959, p. 158) as follows, "(a) the leaves of *Alnus* are characterized by strong subsecondaries which diverge from the abaxial side of the secondaries in the outer part of the blade, whereas if subsecondaries are present in *Betula* they are only weakly developed; (b) in leaves of comparable size, *Betula* has more numerous and more closely spaced secondaries than *Alnus*; (c) in shape *Alnus* is generally wider in the lower half of the blade, not near the middle of the blade like *Betula*; (d) the marginal outline is more even in *Betula* than in *Alnus*." Axelrod (1985) stressed the need to consider the whole leaf, but lamented the rarity of complete fossil leaves of Betulaceae. Fossil Betulaceae have been much debated in the literature (Wolfe 1966; Axelrod, 1985; Fields, 1996) but a useful review of the family has yet to be presented. Our fossil leaves are membranaceous and many are torn, indicating less resistance to transport than associated leaves.

### *ALNUS HARNEYANA*

1959 *Alnus harneyana* Chaney and Axelrod, p. 158-159: pl. 21, figs. 3-9

REFERRED SPECIMENS: UOF42024B (Fig. 15F), USNM645813 (Fig. 15G).

DISCUSSION: A subcoriaceous to membranaceous texture, straight and uniform secondaries, and rounded teeth all mark this species. The fine details of venation were preserved in the Cape Blanco specimens, but no complete leaves were recovered. Many leaf base fragments were found that match the description of Chaney and Axelrod (1959).

Among other Neogene fossil alders, the most similar is *Alnus fairi* which has more teeth between the secondary veins than our fossils, and is ovate rather than elliptical (Wolfe, 1966). *Alnus heterodonta* has blunter compound teeth, and *A. newberryi* has well-spaced narrow to glandular teeth, and an acuminate apex (Meyer and Manchester, 1997). More finely dentate and sharply pointed compound teeth are found in *Alnus adumbrata* (Wolfe, 1966), *A. carpinoides* (LaMotte, 1936), *A. corrallina* (LaMotte, 1952), *A. corylina* (Wolfe 1966, including *A. cappsii*, *A. barnesii*, and *A. schmidtae* according to Axelrod, 1985), *A. evidens* (Wolfe, 1966), *A. fossilis* (Chaney and Axelrod, 1959), *A. healyensis* (Wolfe, 1966), *A. hollandiana* (Chaney and Axelrod, 1959), *A. largei* (Wolfe, 1966), *A. latahensis* (Axelrod, 1991 including "*A. relatus*"), *A. merriami* (Axelrod, 1944d), *A. microdontoides* (Axelrod, 1998), and *A. rubroides* (Axelrod, 1944d). *Alnus latahensis* (Axelrod, 1991), and *A. spokanensis* (Axelrod 1995a) are both narrower leaves with secondary veins swept more steeply forward. *Alnus pyramidensis* is large (more than 18 cm long) and obovate (Axelrod, 1991).

The extant species suggested by Chaney and Axelrod (1959) and Axelrod (1985) as closely resembling *Alnus harneyana* is *Alnus tenuifolia* (thinleaf alder). This name is now a variety of the modern species, *Alnus incana* (Linnaeus) Moench ssp. *tenuifolia* (Nuttall) Breitung, and its range is western North America from New Mexico north to Saskatchewan and Nunavut, and California to Alaska (USDA 2009).

### *BETULA THOR*

1926 *Betula thor* Knowlton, p. 35; pl. XVII, fig 3

REFERRED SPECIMEN: UOF42025A (Fig. 6A)

DISCUSSION: Small size, elliptical shape, serrate margins, and deep teeth characterize this species (Chaney and Axelrod, 1959).

Several species originally described as *Betula* have since been transferred to *Alnus* (Wolfe, 1966; Meyer and Manchester, 1997). Ovate shape and less deep teeth are found in *Betula angustifolia* (Meyer and Manchester, 1997), *B. idahoensis* (Smith, 1939), *B. multinervis* (Condit, 1938), *B. praenigra* (Berry, 1916), and *B. vera* (Chaney and Axelrod, 1959). *Betula nanita* is a very small, probably immature leaf, with secondary veins at low angle to the midrib (Chaney, 1920). *Betula lacustris* is similar in vein density and tooth incision but widely deltoid in outline (MacGinitie, 1933; Smith, 1941).

Most living birch leaves have a deltoid or orbicular shape unlike *Betula thor*, which is most like *Betula nigra* Linnaeus (Chaney and Axelrod, 1959), or river birch, found today in the southeastern United States from Texas to Minnesota, Maine and Florida (USDA, 2009).

## FAMILY FAGACEAE

Fossil leaves of oak and beech have moderate relief suggestive of coriaceous texture, secondary veins terminating in teeth or directly into the margin, and orthogonal areoles of well lignified high-order veins (Jones, 1986; Manchester and Dilhoff, 2004).

### *CHRYSOLEPIS SONOMENSIS*

1985 *Chrysolepis sonomensis* (Axelrod) Axelrod, p. 144, pl. 10, figs. 1-3

REFERRED SPECIMENS: USNM645808 (Fig. 16J), UOF38056A (Fig. 16K)

DISCUSSION: These entire margined, medium-sized, lanceolate leaves with thick midribs and clear tertiary venation are common in the Cape Blanco flora, and widespread in Miocene floras of Nevada (Axelrod, 1985, 1991). These leaves are superficially similar to *Magnolia*, such as *M. latahensis* (Y.D. Kim et al., 2004), which differ in less regularly spaced secondary veins and denser tertiary venation. Miocene *Chrysolepis convexa*, including type material of "*Castanopsis perplexa*" Brown (1940), has a smaller elliptical leaf with rounded apex (Axelrod, 1985).

The most similar modern species suggested by Axelrod (1985) for this fossil species is *Chrysolepis sempervirens* (Kellog) Hjelmquist (bush chinquapin), which ranges from California to Oregon and Nevada (USDA 2009).

### *FAGUS WASHOENSIS*

1936 *Fagus washoensis* La Motte, p.119, pl.8, figs. 2, 3, 5.

REFERRED SPECIMENS: leaf UOF42078A (Fig. 16A), UOF38057A (Fig. 16B), possible valvate cupule UOF42387B (Fig.16C)

DISCUSSION: The Cape Blanco specimens are singly serrated with regular tooth spacing; apical and basal sides of the teeth convex; sinus rounded; apex simple. Secondaries diverge from primary from 30-60º and are craspedodromous straight to each tooth apex. A plausible cupule shows apical splits and has prickly appendages, but is fragmentary, and so uncertain (Fig. 16C).

We follow Fields (1996), who synonymized two *Fagus* species based on the existence of a size gradation between them, and so did not recognize the smaller *Fagus idahoensis* of Chaney and Axelrod (1959). The type specimen of "*Fagus*" *bonnevillensis* Chaney (1920) has more strong curved secondary veins than *Fagus* (Meyer and Manchester, 1997). Leaves of *Fagus pacifica* (Meyer and Manchester, 1997) are larger (47-83 mm long) and *F. langevinii* (Manchester and Dillhoff, 2004) even larger (52-193 mm), and both are obovate, rather than ovate like our specimens. *Fagus lambertensis* (Berry, 1916) is almost as wide as long and has more closely spaced secondary veins. *Pseudofagus idahoensis* is a larger leaf and has subsidiary teeth not seen in our specimens (Smiley and Huggins, 1981).

The most similar modern plant to *Fagus washoensis* is American beech, *Fagus grandifolia* Ehrhardt, which is found in eastern North America from Quebec south to Florida, and Ontario south to Texas, with outlying populations in Utah (USDA, 2009).

### *"LITHOCARPUS" NEVADENSIS*

1985 *Lithocarpus nevadensis*
Axelrod, p. 145; pl. 8 figs. 8-10; pl. 24, figs. 1-7.

1991 *Lithocarpus nevadensis*
Axelrod, p. 38; pl. 9, figs. 4-5.

1995b *Lithocarpus nevadensis*
Axelrod, p. 49; pl. 15, fig. 6.

REFERRED SPECIMENS: UOF42088 (Fig. 16I).

DISCUSSION: "*Lithocarpus nevadensis*" was separated from similar *Quercus* species by Axelrod (1985). This fossil may be better assigned to the genus *Notholithocarpus* proposed by Manos et al. (2008) to distinguish North American tanoak from Asian *Lithocarpus*, because *Notholithocarpus* has leaves with unbranched secondary veins extending into teeth like our fossils, and also "*Lithocarpus*" *klamathensis* (Axelrod, 1944d). North American *Notholithocarpus* is distinct from Asian leaves of *Lithocarpus*, which have branched secondary veins and are entire to only partly toothed, with acuminate leaf apices (Jones, 1986). The primary differences between "*L.*" *nevadensis* and *Quercus simulata* are the spacing of the teeth, which are further apart in "*L.*" *nevadensis*, and the shape of the secondary veins which are curved in "*L.*" *nevadensis*, and straight in *Q. simulata*. These observations are in addition to the differences outlined by Axelrod (1991, p 38) of "*L.*" *nevadensis* having a more coriaceous texture and blunter teeth. "*Lithocarpus*" *klamathensis* (Axelrod 1944d) has a wider leaf tapering to a more acute apex, unlike the slender tapering leaf of "*L.*" *nevadensis*.

The most similar modern species to "*Lithocarpus*" *nevadensis* is *Notholithocarpus densiflorus* (Hook. and Arnold) Manos et al. (2008) of Oregon and California (USDA, 2009).

### *QUERCUS HANNIBALII*

1930 *Quercus hannibali* Dorf, p. 86; pl. 8, figs. 8-11

REFERRED SPECIMEN: UOF42105A (Fig. 16H)

DISCUSSION: These coriaceous, entire-margined, lanceolate leaves have a thick midrib contrasting with weak secondaries, and the tertiary vein mesh is so dense that individual tertiary veins are difficult to distinguish.

Chaney and Axelrod (1959) differentiate sublanceolate *Quercus hannibalii* from oval to ellipsoidal leaves of *Q. dayana* with differences in venation, and from *Q. simulata* by lack of teeth. In *Quercus hannibalii* there is a slight curve where secondary veins meet the midrib, and tertiary veins are mostly percurrent, as they are in Cape Blanco specimens. *Quercus hannibalii* has been synomymized with *Q. pollardiana* by Axelrod (1995b), but ovate leaves of *Q. pollardiana* are crenate to serrate (Axelrod, 1995b, 2000; Retallack, 2004a). *Quercus pasadori*

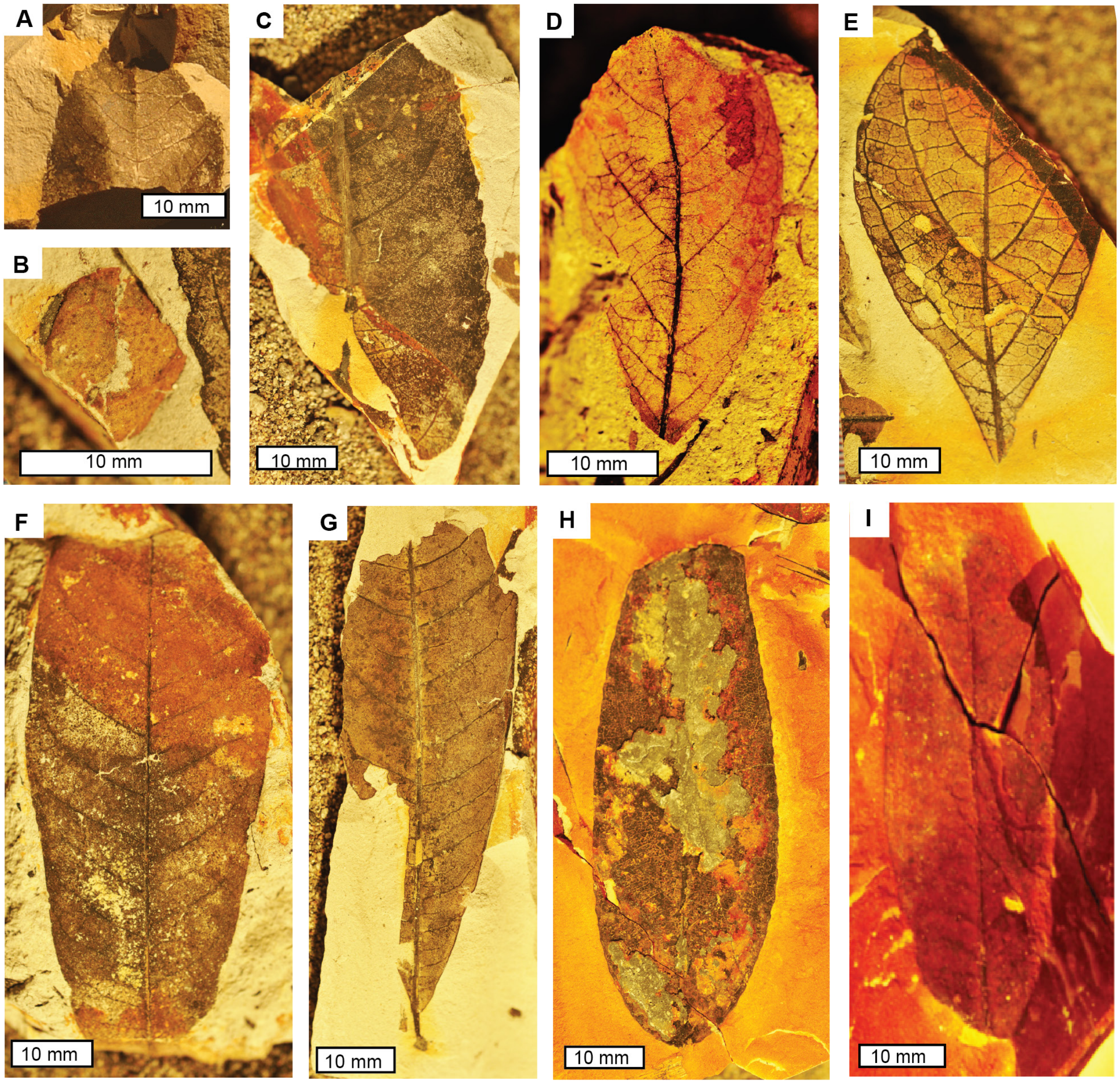

**Figure 17**: Cape Blanco fossil pecan, salal, rhododendron and madrone: **A-B**, *Carya bendirei*; **C-E**, *Gaultheria primorica*; **F-G**, *Rhododendron sierra*; **H-I**, *Arbutus xalapoides*; **A**, USNM645806; **B**, UOF42358B; **C,** UOF42358A; **D**, UOF42113A; **E**, UOF422206A; **F**, UOF42251A; **G**, UOF42206A; **H**, UOF115014B; **I**, UOF42374A.

(Axelrod, 2000) and *Q. orindensis* (Dorf, 1930; Axelrod, 1938) are smaller leaves that are broadly ovate to oval leaves (Axelrod, 2000). *Quercus turneri* is a small ovate leaf, with acute apex (Axelrod, 1939). Also distinct are entire-margined, oblanceolate leaves of *Quercus smileyana* (Chaney and Axelrod, 1959). *Quercus oberlii* is narrow elliptical to linear (Buechler et al. 2007). These are entire-margined leaves are like those of living live oaks, and are very distinct from spiny sclerophyllous “holly” oaks, chartaceous “chestnut” oaks, and deeply lobed “white” and “red” oaks (Jones, 1986).

The modern plant most similar to *Quercus hannibalii* is *Quercus vaccinifolia* Kellog, or huckleberry oak, found in Oregon, California and Nevada (USDA, 2009).

### *QUERCUS PRELOBATA*

1944a *Quercus prelobata* Condit, p. 43; pl. 7, figs. 3, 4

REFERRED SPECIMEN: UOF42138A (Fig. 16E)

DISCUSSION: *Quercus prelobata* is a fossil oak distinguished by rounded lobes (Chaney and Axelrod, 1959). A whole leaf was not recovered from

Cape Blanco, but complete mid-leaf lobes were collected which contribute to our confidence in this assignment. *Quercus prelobata* is generally a small leaf (Retallack, 2004a), but the size range of this species was expanded by Buechler et al (2007) to include leaves up to 14.5 cm long. Fungal fruiting bodies discussed by Buechler et al (2007) were not observed on the Cape Blanco specimens.

Round-lobed oak leaves are generally regarded as "white oaks" (Jones, 1986), distinct from acute-lobed oak leaves, such as Miocene *Quercus pseudolyrata* (Condit, 1944a). Other round-lobed oak leaves, such as *Quercus winstanleyi* are obovate and less deeply lobed than *Q. prelobata* (Condit 1944a; Chaney, 1944a, 1944b). *Quercus douglasoides* and *Q. moragensis* are small leaves with only three very broad lobes on each side (Condit, 1944b; Axelrod, 1944b, 1944d). *Quercus duriuscula* has lobes rounded at the end, but subtriangular rather than domed in outline (Dorf, 1938).

*Quercus prelobata* is found in few Miocene floras (Axelrod, 1944c, 1950a; Chaney and Axelrod, 1959; Retallack, 2004a), and is similar to many species of white oaks (Jones, 1986). In overall size and dissection of the lobes *Q. prelobata* is most like living *Quercus lobata*, the valley oak, or roble, of California (USDA, 2009).

### *QUERCUS SIMULATA*

1898 *Quercus simulata* Knowlton, p. 728-729; pl. 101, figs. 3, 4; pl. 102, figs. 1, 2.

REFERRED SPECIMENS: UOF42142B (Fig. 16F), USNM64581 (Fig. 16G).

DISCUSSION: *Quercus simulata* is a common component of Miocene floras and has been the subject of multiple taxonomic revisions and reassignments (MacGinitie, 1933; Chaney and Axelrod, 1959; Axelrod, 1985, 1995a, 1995b; Meyer and Manchester, 1997; Buechler et al., 2007). A thorough discussion is provided by Fields (1996, pages 363-379), who develops the concept of a "*Quercus simulata* morphoplex". The primary problem with this species is substantial morphological variation from toothed to entire margined specimens. The Cape Blanco specimens of *Q. simulata* have teeth with spines and straight secondary veins.

Fields (1996, p. 375) lists 17 modern species that various authors have suggested resembled *Quercus simulata*. Chaney and Axelrod (1959) compared it with several species of Asiatic oaks, and of these, our leaves are most similar to living sawtooth oak, *Quercus acutissima* Carruthers, of Japan and southeast Asia, but now cultivated from Masschusetts south to Florida (Whittemore, 2004; USDA, 2009).

## FAMILY JUGLANDACEAE
### *CARYA BENDIREI*

1959 *Carya bendirei* (Lesquereux) Chaney and Axelrod, p. 155; pl. 19, fig 1-5.

REFERRED SPECIMEN: leaf apex USNM645806 (Fig. 17A), husk valves UOF42358B (Fig. 17B).

DISCUSSION: The primary recognition criteria are the curved secondary veins which diverge from the primary at a ~90º angle. Obovate shape, fine serration, transition from brochidodromous to craspedodromous, and thin leaf substance are also diagnostic (Chaney and Axelrod, 1959; Axelrod, 1991). Also found on the same slab as a leaf fragment was a split pecan-like fruit husk (Fig. 17B), but attributing it to the same species is uncertain because *Carya bendirei* was established on the basis of leaves (Chaney and Axelrod, 1959).

Fossil *Carya egregia* has wider leaflets more symmetrically lanceolate (LaMotte 1936). *Carya typhinoides* has smaller ovate leaves (Condit, 1944b). *Carya libbeyi* has leaflets with acuminate apex and lanceolate shape (Meyer, 2003). Reexamination of "*Hicoria pretexana*" (Berry, 1916), found closer similarity with living *Carya aquatica* and *C. tomentosa* (Stults and Axsmith, 2015), with more strongly acuminate apex than seen in our apical fragment. "*Carya*" *antiquorum* also has an acuminate tip and lacks successive branching of the secondary veins near the margin characteristic of *Carya* (Manchester, 1987). There is also a fossil record of nuts with separate specific epithets: *Carya washingtonensis*, *C. florissantensis* (Manchester, 1987) and *C. tennesseeensis* (Huang et al., 2014) are nuts twice the size of the husks found with our specimens. DNA analysis of modern species reveals that North American and Asian clades of *Carya* are distinct clades, although there were at least two distinct intercontinental exchanges indicated by fossil fruits during the Eocene and Miocene (Zhang et al., 2013)

Most modern species of *Carya* have an acuminate leaf apex (USDA, 2009), unlike complete leaves of *C. bendirei* (Chaney and Axelrod, 1959). *Carya cordiformis*, *C. glabra*, and *C. ovata* have ovate to lanceolate leaves (USDA, 2009), more symmetrical than fossil *C. bendirei*. The closest living leaves to *Carya bendirei* are found in *Carya texana* Buckley (black hickory), which also has relatively narrow nuts like our specimen (Fig. 17B). *Carya texana* ranges from Texas to Kansas and Illinois to Georgia (USDA, 2009).

### ORDER ERICALES
### FAMILY ERICACEAE
### *ARBUTUS XALAPOIDES*

1950b *Arbutus prexalapensis* Axelrod, p.113, pl.3, fig.11-14.

1952 *Arbutus xalapoides* LaMotte, p. 73.

REFERRED SPECIMENS: leaves UOFD42374A (Fig. 17D), UOF115014B (Fig. 17E).

DISCUSSION: These are coriaceous, ovate, entire-margined to weakly crenate leaves with rounded apex. Secondary veins are thick near the midrib, but taper strongly halfway to the margins, leading to dome-like wrinkling between proximal secondary veins and obscure distal secondary veins.

Modern and fossil *Arbutus menziesii* (Hannibal, 1911; Mason, 1934), and our fossils from Cape Blanco are entire-margined unlike dentate fossil leaves attributed to *Arbutus*: *A. idahoensis* (Axelrod, 1991, 1995a, 1995b), *A. matthesii* (LaMotte, 1936; Axelrod, 1995a, 1995b), *A. opaca* (Smith, 1941), and *A. trainii* (MacGinitie, 1933; Axelrod, 1991). *Arbutus mohavensis* (Axelrod, 1939) has a single lateral tooth, and also is distinguished by short, obovate outline. *Arbutus stewartii* (Axelrod, 1987) is elliptical rather than ovate, but otherwise similar to our specimens.

Serrated leaves distinguish living strawberry tree (*Arbutus unedo*) found around most of the Mediterranean Sea (Sealy and Webb, 1950), but introduced to North America (USDA, 2009). *Arbutus xalapensis* and *A. arizonica* have elliptical leaves, smaller than our specimens, which are most like obovate leaves of living *Arbutus menziesii* Pursh (Pacific madrone), now distributed from California to British Columbia (USDA 2009).

### *RHODODENDRON SIERRAE*

1944b *Rhododendron sierrae* Condit p. 87, pl. 20, fig. 6.

REFERRED SPECIMENS: leaves UOF42251A (Fig. 17F), UOF42206A (Fig. 17G).

DISCUSSION: The secondary veins of these coriaceous, entire-margined leaves are at high divergence angle and uniform spacing, but have brochidodromous loops close to the leaf margin. Complete leaves illustrated by Condit (1944b) are obovate, with a long tapering base.

*Rhododendron weaveri* leaves are elliptical and smaller (Wolfe, 1966). *Rhododendron chaneyi* (Brown, 1946) and *R. deweyense* (Axelrod, 1998) have obtuse leaf bases, whereas our specimens are cuneate at the base. Miocene *Rhododendron sp.* of MacGinitie (1933) is linear lanceolate and has secondary veins at a lower angle to the midrib than in our specimens. The reliable fossil record of *Rhododendron* goes back to the Paleocene, and its center of diversity is in China (Collinson and Crane, 1978; Wang and Tiffney, 2001).

*Rhododendron sierrae* is a larger leaf than most living *Rhododendron* species (especially those commonly called azaleas) and has obovate leaves unlike the lanceolate leaves of *R. maximum* (USDA, 2009). *Rhododendron sierrae* resembles modern *Rhododendron macrophyllum* D. Don ex G. Don (coast rhododendron), of western North America from northern California through British Columbia (Thompson et al., 1999; USDA, 2009).

### *GAULTHERIA PRIMORICA*

2007 *Gaultheria primorica* Pavylutkin, p.305, fig. 7, pl. 3, fig. 1, 2.

REFERRED SPECIMENS: leaves UOF42358A (Fig. 17C), UOF42113A (Fig. 17D) UOF42231A (Fig. 17E).

DISCUSSION: These coriaceous leaves have strongly marked eucamptodromous secondary veins and weakly percurrent to perpendicular tertiary veins. They are entire margined to weakly crenate, and ovate to obovate, with a truncate base that lacks strong secondary veins. Looping secondary veins are well back from the margin, and the basal secondaries extend more than a third of the length of the leaf.

Other fossil leaves with eucamptodromous secondaries and perpendicular tertiaries are *Parrotia brevipetiolata* (Meyer and Manchester, 1997) and *Cordia oregona* (Chaney and Sanborn, 1933), but those leaves have parallel and more numerous secondary veins. Our fossils show markedly non-parallel secondary veins and less regular tertiary veins, most like *Gaultheria primorica* (Pavlyutin, 2007). The North American fossil record of *Gaultheria* is limited to two specimens from the Latah flora

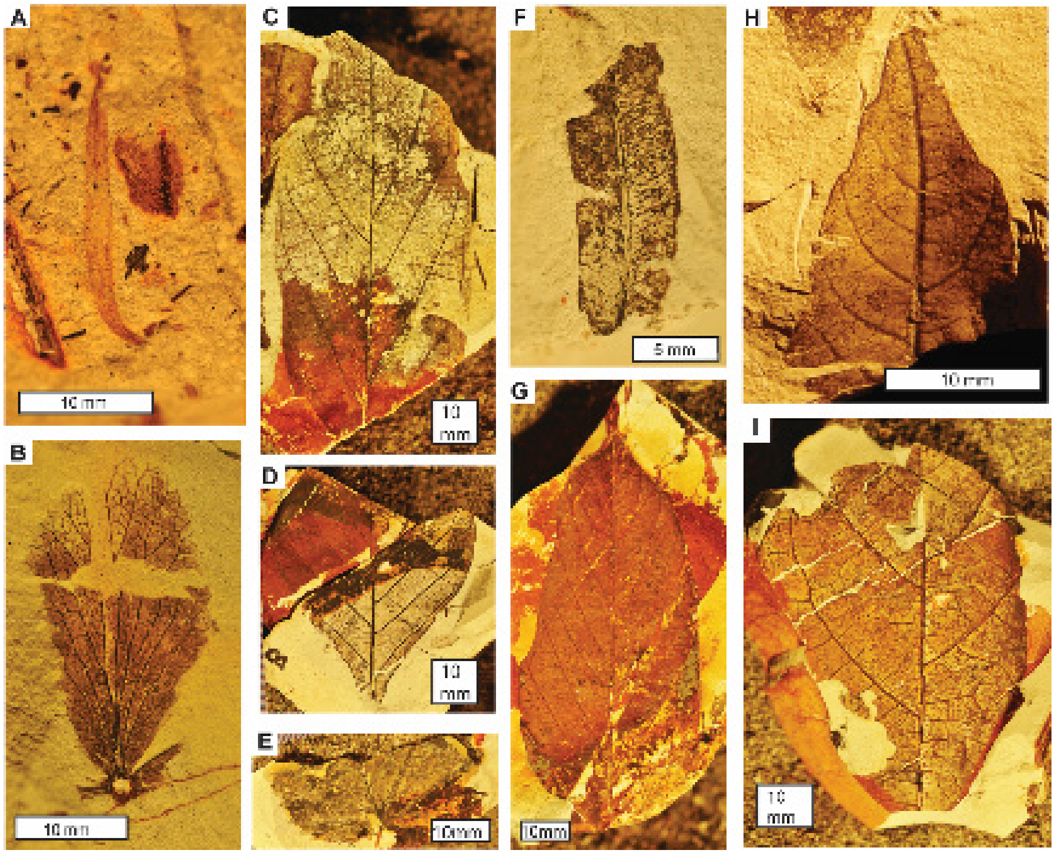

**Figure 18**: Cape Blanco fossil hydrangea, basswood, viburnum, and unidentified: **A**, Unidentified angiosperm; **B-D**. *Hydrangea bendirei*; **E-G**, *Tilia pedunculata*; **H-I**, *Viburnum lantanafolium*; **A**, leaf UOF38115B; **B**, flower sepal UOF42273B; **C**, leaf UOF42251A; **D**, leaf base UOF42221A; **E**, leaf base UOF42180B; **F**, fertile bract UOF42260; **G**, leaf UOF42380B; **H**, leaf apex USNM645809; **I**, leaf UOF42263.

that were originally described as *Arbutus matthesii* (Brown 1936) and then later transferred to *Gaultheria pacifica* Brown (Brown 1946). These fossils differ from ours in their serrate margin.

Five living species of *Gaultheria* in North America are smaller leaved than our fossil, which is most like the remaining species, *Gaultheria shallon* Pursh (salal), a common coastal shrub from California north to Alaska (USDA, 2009).

### FAMILY TILIACEAE
### *TILIA PEDUNCULATA*

1920 *Tilia pedunculata* Chaney, p. 179, pl. 19, figs. 3-4.

REFERRED SPECIMENS: leaf base UOF42180B (Fig. 18E), bract UOF42253 (Fig.18F), leaf UOF42380B (Fig. 18G).

DISCUSSION: A single specimen of a narrow bract (Fig. 18E) has the characteristic disorganized venation of *Tilia pedunculata* Chaney (Meyer and Manchester, 1997, pl. 40, fig. 6). Also found were dentate leaves with craspedodromous secondaries and asymmetrical cordate base (Figs. 18F-G) broadly comparable with *Tilia aspera*, which LaMotte (1935a) considered conspecific with *T. pedunculata* bracts in the early Miocene Eagle Creek flora and middle Miocene 49 Camp flora. In the Oligocene Bridge Creek floras of Oregon there are two species of *Tilia* bracts, *T. circularis* and *T. pedunculata*, and three species of *Tilia* leaves, *T. aspera*, *T. fossilensis*, and *T. lamottei*, but it is uncertain which belong with each other (Meyer and Manchester, 1997). Our early Miocene *Tilia* leaves associated with bracts of *Tilia pedunculata* are included in that species, rather than the larger and wider Oligocene leaf species

*T. aspera*.

Unlike our specimens, *Tilia williamsii* is camptodromous and entire-margined (Sanborn, 1947). Our leaves show some similarity with associated leaves of *Viburnum lantanafolium* Berry (1929), which has different semicraspedodromous and non-parallel secondary veins (Oliver, 1934; Chaney and Axelrod, 1959).

Living *Tilia tomentosa* with deltoid leaves is distinct from our specimens, and *Tilia americana* varieties *americana* and *heterophylla* are also almost as wide as long (USDA, 2009). Wide leaves also distinguish European and Asian cultivars of *Tilia* (linden or lime trees) introduced to the United States. Our elongate ovate leaves are most like *Tilia americana* Linnaeus var. *caroliniana* (Miller) Castiglioni (Carolina basswood), found from Texas and Missouri through Tennessee and North Carolina and south to Florida (USDA, 2009).

### ORDER CORNALES
### FAMILY HYDRANGEACAEAE
### *HYDRANGEA BENDIREI*

1902 *Hydrangea bendirei* (Ward) Knowlton, p. 309.

REFERRED SPECIMENS: sepal UOF42273B (Fig. 18B), leaves UOF42251A (Fig. 18C), UOF42221A (Fig. 18D)

DISCUSSION: A single sepal 18 mm long and 12 mm wide has the radiating venation of *Hydrangea*, and bases of additional sepals reveal the characteristic tetramerous symmetry (Fig. 18A). Associated leaves are semicraspedodromous with numerous percurrent veins and finely dentate margin (Figs. 18B), though entire margined and decurrent near the base (Fig. 18C).

Fossils of *Hydrangea fraxinifolia* have sepals that are orbicular, and narrow leaves with acuminate tip (Meyer, 2003). Orbicular sepals also distinguish *Hydrangea knowltonii* (Manchester et al., 2015) and *H. alaskana*, which vary in having three or four sepals (Hollick, 1925). *Hydrangea californica* has sepals that are subquadrate (MacGinitie, 1941). The sepals of *Hydrangea incerta* are only a third the size of our specimens (Cockerell, 1908). *Hydrangea russellii* is based only on leaves which are about twice the size of our specimens, and with quilt-like relief of the lamina (Chaney and Sanborn, 1933). Our specimens are most like *Hydrangea bendirei* from the middle Miocene of the Columbia Plateau, with leaf bases that range from truncate to cuneate (Chaney and Axelrod, 1959; Smiley et al., 1975).

Living North American *Hydrangea arborescens* and *H. radiata* have leaves with cordate base and *H. quercifolia* is deeply lobed. Our specimens are most like *Hydrangea cinerea* (ashy hydrangea) of the southeastern United States from Oklahoma to Illinois and Georgia and north to Massachusetts (USDA, 2009).

### ORDER DIPSACALES
### FAMILY ADOXACEAE
### *VIBURNUM LANTANAFOLIUM*

1929 *Viburnum lantanafolium* Berry, 1929, p 264; pl. 60, fig. 6.

REFERRED SPECIMENS: leaf apex USNM645809 (Fig. 18H), leaf fragment UOF42263 (Fig. 18I).

DISCUSSION: These fragments have distinctive non-parallel craspedodromous secondaries that lead into low blunt teeth widely spaced along the margn. Tertiary venation is well marked, and weakly percurrent.

Many Cretaceous and early Tertiary leaves have been assigned to *Viburnum*, but associated fruits show they were unrelated (Manchester, 2002). Among Neogene fossil species of *Viburnum*, prominent teeth distinguish *V. grahamii* (Fields 1996 p. 515). Trilobate shape distinguishes *Viburnum whitebirdensis* (Ashlee, 1932) and *V. ribesiforme* (La Motte, 1944). Strong basal tertiary veins distinguish *Viburnum thomae* and "*Ficus*" *quisumbingi* is a larger leaf with more prominent teeth (Chaney and Sanborn, 1933). More complete leaves of *Viburnum lantanafolium* like our specimens have been figured by Berry (1929), Oliver (1934), and Brown (1936).

Most modern North America species of *Viburnum* have prominently dentate margins, but our entire-margined to sparsely dentate leaf is most like *Viburnum nudum* Linnaeus (Possum haw), found in the southeastern United States from Texas to New York and Florida (USDA, 2009).

### DICOTYLEDONAE *GEN. ET SP.*
### *INCERTAE SEDIS*

REFERRED SPECIMEN: leaf UOF38115B (Fig. 18A).

DISCUSSION: A small lanceolate entire-margined leaf has brochidodromous secondary veins that diverge from a stout midrib at high angle. The petiole curves strongly as if it were borne horizon

**Table 5**: Cape Blanco flora fossil quantities and similar modern plants

| Fossil species | Parts | No | Nearest living relative |
|---|---|---|---|
| *Equisetum miocenicum* Graham 1963 | stem | 4 | *Equisetum telmataeia* (northern giant horsetail) |
| *Sequoia affinis Lesquereux* 1855 | leaf, cone | 3 | *Sequoia sempervirens* (coast redwood) |
| *Pinus carmelensis* Axelrod 2000 | leaf | 4 | *Pinus ponderosa var. benthamiana* (ponderosa pine) |
| *Picea sookensis* LaMotte 1935 | Seed, cone | 25 | *Picea sitchensis* (sitka spruce) |
| Charcoal | charcoal | 14 | Conifer charcoal |
| Frayed wood | wood | 8 | Conifer wood |
| *Poaceae sp. indet.* | leaf, spike | 9 | Wide-leaf grass |
| *Persea pseudocarolinensis* Lesquereux 1878 | leaf | 12 | *Persea carolinensis* (avocado) |
| *Umbellularia oregonensis* Chaney 1925 | leaf, calyx | 2 | *Umbellularia californica* (Oregon myrtlewood) |
| *Mahonia trainii* Arnold 1936 | leaf | 10 | *Mahonia lanceolata* (Mexican grapeholly) |
| *Platanus paucidentata* Dorf 1930 | leaf | 3 | *Platanus racemosa* (California sycamore) |
| *Exbucklandia oregonensis* (Chaney) Brown 1946 | leaf | 10 | *Exbucklandia longipetala* (changbanmatihe). |
| *Populus eotremuloides* Knowlton 1898 | leaf | 20 | *Populus balsamifera* (balsam poplar) |
| *Populus lindgrenii* Knowlton 1898 | leaf | 7 | *Populus heterophylla* (swamp cottonwood) |
| *Salix laevigatoides* Axelrod 1950 | leaf | 30 | *Salix laevigata* (red willow) |
| *Salix succorensis* Chaney and Axelrod 1959 | leaf | 6 | *Salix nigra* (black willow) |
| *Cercocarpus nevadensis* Axelrod 1991 | leaf | 2 | *Cercocarpus montanus* (mountain mahogany) |
| *Sorbus idahoensis* Axelrod 1985 | leaf | 4 | *Sorbus americana* (American mountain ash) |
| *Ulmus speciosa* Newberry 1898 | leaf | 12 | *Ulmus americana* (American elm) |
| *Alnus harneyana* Chaney and Axelrod 1959 | leaf | 3 | *Alnus incana* (gray alder) |
| *Betula thor* Knowlton 1926 | leaf | 3 | *Betula papyrifera* (paper birch) |
| *Chrysolepis sonomensis* (Axelrod) Axelrod 1985 | leaf | 49 | *Chrysolepis chrysophylla* (golden chinquapin) |
| *Fagus washoensis* LaMotte 1936 | leaf, calyx | 6 | *Fagus grandifolia* (American beech) |
| “*Lithocarpus*” *nevadensis* Axelrod 1985 | leaf | 19 | *Notholithocarpus densiflorus* (tanoak) |
| *Quercus hannibalii* Dorf 1930 | leaf, acorn | 63 | *Quercus chrysolepis* (canyon live oak) |
| *Quercus prelobata* Condit 1944 | leaf | 3 | *Quercus lobata* (Oregon live oak) |
| *Quercus simulata* Knowlton 1898 | leaf | 16 | *Quercus acutissima* (sawtooth oak) |
| *Carya bendirei* (Lesquereux) Chaney and Axelrod 1959 | leaf | 5 | *Carya texana* (black hickory) |
| *Arbutus xalapoides* LaMotte 1952 | leaf | 2 | *Arbutus menziesii* (madrone) |
| *Rhododendron sierrae* Condit 1944b | leaf | 8 | *Rhododendron macrophyllum* (rhododendron) |
| *Gaultheria primorica* Pavylutin 2007 | leaf | 40 | *Gaultheria shallon* (salal) |
| *Tilia pedunculata* Chaney 1920 | leaf, bract | 23 | *Tilia Americana var. caroliniana* ( basswood) |
| *Hydrangea bendirei* Knowlton 1902 | leaf, flower | 2 | *Hydrangea cinerea* (ashy hydrangea) |
| *Viburnum lantanafolium* Berry 1929 | leaf | 2 | *Viburnum nudum* (possumhaw) |
| *Dicotyledonae gen. et sp. indet.* | leaf | 1 | Herbaceous weed? |

tally on a vertical axis.

The size and shape of this leaf is reminiscent of *Salix churchillensis* Axelrod (1991) the venation does not loop up into the blade to simulate a marginal vein. The secondary veins on this leaf are cladodromous to brochidodromous. *Arctostaphylos fergusoni* (Axelrod, 1950a), *Vaccinium sonomensis* (Axelrod, 1944d), and *V. sophoroides* (Chaney and Axelrod, 1959) are comparably small leaves, but wider and elliptical. Other broadly comparable leaves are *Cercocarpus linearifolia* (Axelrod, 1950a), *C. praeledifolius* (Berry, 1929), *Condalia mohavensis* (Axelrod, 1939), and *Dodonea californica* (Axelrod, 1950b), which are longer with stronger orthogonal secondary veins. These are all shrub and tree genera, but the strong basal curvature of our specimen, lacking in all these comparisons, suggests an herbaceous plant, with a single erect axis. The botanical nature and modern affinities of this fossil are unknown.

## VEGETATION RECONSTRUCTION

The Cape Blanco flora includes at least 28 unique angiosperm leaf forms, most of them identifiable to the species level, as well as one horsetail, three conifers, and at least one monocot. Table 5 shows the numbers of specimens of each form, as well as the most similar extant plant summarized from the foregoing discussion.

PHYTOGEOGRAPHY: The assemblage of leaves observed in the Cape Blanco flora is a combination of forms that are well documented and commonly observed in the Miocene of the Pacific Northwest (Chaney and Axelrod 1959; Smiley et al., 1975; Buechler et al., 2007) and a few exotic forms (Chaney and Axelrod, 1959; Meyer and Manchester, 1997; Huang et al., 2017). The dominance of oaks, for example, is observed in many Miocene localities and has been used as evidence for the onset of drying and cooling climate in western North America (Axelrod, 1985, 1995a, 1995b). Also common and diverse in Miocene floras are Betulaceae, Juglandaceae, and Rosaceae, which are all present at Cape Blanco.

Four distinct groups of fossils in the Cape Blanco assemblage can be recognized from the geographic distribution of their nearest living relatives (Table 5). A first group is indigenous species similar to those found today in the region around Cape Blanco. These include the following 12 species similar to modern plants in the Oregon Coast Range: *Equisetum miocenicum*, *Picea sookensis*, *Pinus carmelensis*, *Umbellularia oregonensis*, *Populus eotremuloides*, *Salix laevigatoides*, *Alnus harneyana*, *Chrysolepis sonomensis*, *"Lithocarpus" nevadensis*, *Arbutus xalapoides*, *Rhododendron sierrae*, and *Gaultheria primorica*.

A second group of southwestern species now found in California or Mexico, includes the following 6 species: *Sequoia affinis*, *Mahonia trainii*, *Platanus paucidentata*, *Cercocarpus nevadensis*, *Quercus hannibalii*, and *Quercus prelobata.*

A third group of species with living relatives found in the southeastern United States, includes the following 11 species *Persea pseudocarolinensis*, *Populus lindgreni*, *Salix succorensis*, *Sorbus idahoensis*, *Ulmus speciosa*, *Betula thor*, *Fagus washoensis*, *Carya bendirei*, *Tilia peduncularis*, *Hydrangea bendirei*, and *Viburnum lantanafolium*.

A fourth group of exotic species with living relatives only in southeast Asia, includes the following 2 species: *Exbucklandia oregonensis* and *Quercus simulata*.

The group of species still living near Cape Blanco is encouraging from the perspective of vegetation changes due to global warming, because it implies that common elements of coastal spruce forests and salal scrub will persist with anticipated climate change (Retallack et al., 2016). The California-Mexico group, in contrast, is similar to northern California coast redwood forest and oak forests of the northern Great Valley of California (Barbour et al., 2007). This group is evidence that important elements of these plant communities migrated north of their current range during early Miocene paleoclimatic warming, as perhaps they will again. The southeastern North American group is also conspicuous, and not unexpected, because Miocene floras of the Columbia Plateau have long been known to include southeastern elements (Chaney and Axelrod, 1959). The southeastern connection has been confirmed by DNA sequencing of exceptionally well preserved fossil leaves from Clarkia, Idaho, including *Liriodendron* (Baghai, 1988), *Magnolia* (S. Kim et al., 2004), and *Taxodium* (Soltis et al. 1992). A humid warm corridor at middle altitudes during the early to middle Miocene may have connected the southeastern and northwestern United States, because Miocene humid climate (Alfisol) paleosols were extensive at moderate elevations, but arid climate (Aridisol) paleosols were widespread in intermontane valleys (Sheldon, 2003; Retallack, 2007, 2009). Nor is the exotic East Asian element a surprise (Chaney and Axelrod, 1959; Wu et al., 2009; Huang et al., 2017). Genera still endemic to the western United States, but with much greater specific diversity in Asia include *Mahonia* (Y. D. Kim et al., 2004), *Carya* (Zhang et al., 2013), *Rhododendron* (Collinson and Crane, 1978; Wang and Tiffney, 2001), *Gaultheria* (Middleton, 1991; Pavylutin, 2007), *Tilia* (Manchester, 1994) and *Viburnum* (Winkworth and Donoghue, 2005). Asian migration routes through Beringia are also invoked to explain the Miocene appearance in North America of elephants (Lambert and Shoshani, 1998), beardogs (Hunt, 2002), gelocid deer (Webb, 2008), and gavials (Whiting et al., 2016). The Cape Blanco flora is a unique Miocene assemblage with large-leaved taxa requiring greater warmth than at present, as well as indigenous temperate Miocene plants.

Many of the larger leaves from Cape Blanco have prominent midribs and a coriaceous texture, suggesting an evergreen habit as in live oaks, rather than deciduous. Broadleaf evergreens along with the large number of oaks of the Cape Blanco flora falls within the notophyllous broad-leaved evergreen forest of Wolfe (1979), suggesting a mean annual temperature between 13 º C and 20 º C. Although the presence of conifers suggests lower temperatures, they are occasionally present in the notophyllous broad-leaved evergreen, or 'oak-laurel' forests of Wolfe (1979). A more likely explanation for rarity of conifers in the Cape Blanco flora is that they lived on hillslopes above a coastal lagoon surrounded by broadleaf trees.

PALEOECOLOGY: Living relatives of the Cape Blanco flora include dominant species of several modern vegetation types: the *Picea sitchensis* (sitka spruce) coastal forest and *Gaultheria shallon* (salal) coastal shrubs of Oregon (Franklin and Dyrness, 1988), and the *Sequoia sempervirens* (coast redwood) forest of coastal mountains, and *Quercus lobata* (valley oak) woodland of the northern Great Valley of California (Barbour et al., 2007).

Sitka spruce evergreen forests include salal as an understorey shrub, but salal forms an extensive monodominant scrub on the outermost coastal terraces and slopes above beaches or rock headlands (Franklin and Dyrness, 1988). Other modern plants of Oregon salal community with similar species in the Cape Blanco flora are *Equisetum telmataeia*, and wide-leaved grasses. On higher slopes of sitka spruce forests the following modern species have relatives in the Cape Blanco flora: *Umbellularia californiana*, *Rhododendron macrophyllum*, *Arbutus menziesii*, *Alnus rubra* and *Populus trichocarpa* (Franklin and Dyrness, 1988). Early successional forms within these forests include the following modern species with similarities to the Cape Blanco flora: *Alnus rubra*, and *Gaultheria shallon* (Franklin and Dyrness, 1988).

The coast redwood forests of California extend 20 km into southern Oregon (Franklin and Dyrness, 1988), some 80 km south of Cape Blanco, but a single tree grew to maturity between 1720 and 1820 years ago near Waldport, Oregon, (Gavin et al., 2013), which is 260 km north of California. Other plants of California coast redwood forest similar to fossils from the Cape Blanco flora include other conifers (*Pinus ponderosa*), hardwoods (*Arbutus menziesii*, *Notholithocarpus densiflorus*, *Quercus chrysolepis*, *Umbellularia californica*), wetland trees (*Populus trichocarpa*, *Salix laevigata*), and shrubs (*Cercocarpus montanus*, *Gaultheria shallon*, and *Rhododendron macrophyllum*: all in cpLowB-WS of Barbour et al., 2007).

Valley oak (*Quercus lobata*) is not only characteristic of woodlands of the northern Great Valley, but found in the inland zone of the northern coast redwood forest, along with conifers (*Sequoia sempervirens*, *Pinus ponderosa*), hardwoods (*Arbutus menziesii*, *Quercus chrysolepis*, *Umbellularia californica*), wetland trees (*Populus trichocarpa*, *Salix laevigata*), and shrubs (*Alnus incana* var. *tenuifolia*, and *Cercocarpus montanus*: all in ipLoBWS of Barbour et al., 2007).

The closest ecological analog of the Cape Blanco flora is thus with the northern fringe of the California coast redwood community, but the presence of many modern coastal taxa in the fossil flora is encouraging for their persistence in a regime of anticipated global warming when coast redwoods may migrate northward (Retallack et al., 2016). Comparison with the California coast redwood community is not exact because the Cape Blanco flora includes avocado (*Persea*) and Asian exotic plants (*Exbucklandia*), but similar plants may also be replicated in the future as plants of gardens and parks become naturalized (Boersma et al., 2006). Coastal fog is a critical environmental control of the modern California coastal redwood community, and has been declining more in California than Oregon with increased summer maximum temperature from

1951-2008 (Johnstone and Dawson, 2010). The anomalously warm year of 2005 in Oregon showed delayed early-season upwelling but stronger late-season upwelling of cold water, and consequent fog, consistent with predictions of global warming models (Barth et al. 2007).

PALEOTOPOGRAPHY: Paleoelevation of the Cape Blanco flora based on sedimentology is sea level, because the tuffaceous beds prograded into shallow marine and beach sands, and were then overlain by comparable sandstones with marine fossils (Figs. 3-5). Topographic relief of at least 70 m is revealed by sea stacks of Jurassic Otter Point Formation and pebbles in the sandstone of Floras Lake (Armentrout, 1980; Leithold and Bourgeois, 1983). There are also indications from the flora itself of a mountainous hinterland and local river margins or wetlands. Modern wetland species similar to fossil plants in the Cape Blanco flora include *Equisetum telmataeia*, *Populus trichocarpa*, and *Salix laevigata* (Franklin and Dyrness, 1988; Barbour et al, 2007). On the other hand, the dominant conifers are similar to *Picea sitchensis*, *Sequoia sempervirens*, and *Pinus ponderosa*, which grown on well drained soils of alluvial terraces and slopes. Valley oak (*Quercus lobata*) is now found on inland portions of the coast redwood belt (Barbour et al., 2007), perhaps indicating valleys to deliver comparable leaves to the Cape Blanco flora.

TAPHONOMY: The Cape Blanco flora is taphonomically unusual. Some fossil leaf deposits are fossil leaf litters preserved on a paleosol (Retallack and Dilcher, 1988, 2012; Retallack, 2018), and many others are preserved in shales of large meromictic lakes (Ferguson, 1985; Spicer, 1991). There are no root traces in the deposit, nor are the fossiliferous gray siltstones varved and fissile (Figs. 3-5). The massive siltstones at Cape Blanco have some leaves that are folded, fragmented, skeletonized, and cutting across bedding planes like leaves in leaf litter (Figs. 12B, 12E-F, 16A), but others are spread out flat as in lacustrine deposits (Figs. 14A, 15H, 16J, 17F). These fossil leaves in massive siltstone can be contrasted with basal pumice bearing tuffs that have most of the conifer and charcoal remains (Fig.10A-E, H-K). Such differences in modern leaves in sedimentary environments (Gastaldo, 1989, Gastaldo et al., 1989) are evidence for traction deposition of the comminuted charcoal and conifer remains in fluvial levees or crevasse splays. In contrast the more or less intact fossil leaves collected from Cape Blanco had a range of sizes and shapes suggesting that no systematic exclusion of forms occurred. For the leaf-bearing siltstones, we envisage a locally ponded environment of the distal portion of a mudflow from volcanic ash, as observed after modern eruptions (Kuenzi et al.,1979; Scott, 1988). This mechanism of rapid deposition would not have mechanically sorted and fragmented remains as thoroughly as in the basal conifer and charcoal bed, but did sweep up leaf litter. As shown by modern studies of leaf litter taphonomy (Burnham, 1989; Greenwood, 1992; Ellis and Johnson, 2013; Retallack, 2018), there may be a bias toward more coriaceous and sclerified leaves in the Cape Blanco flora, reflecting the exclusion of herbaceous and spring ephemeral plants.

## PALEOCLIMATIC IMPLICATIONS

PHYSIOGNOMIC METHOD: The shape and size of modern leaves has been shown to correlate with temperature and precipitation (Bailey and Sinnott, 1916; Wolfe 1993; Wilf et al., 1998). The relationships are based on the whole composition of the flora, with the proportion of species with serrated margins deceasing with warmer temperatures (Bailey and Sinnott, 1916) and leaf size increasing with increased precipitation (Wilf et al., 1998). One advantage of the physiognomic method is that it is ataxonomic, and emphasizes overall leaf shape and margin character without addressing venation or other taxonomically significant features.

Two techniques of physiognomic interpretation are multivariate analysis of a suite of leaf morphologic characters associated with many climate parameters (Wolfe, 1993), and univariate analysis of a single morphological feature correlated with a single measured climate variable. Both methods have advantages and disadvantages, the multivariate method can yield more data, yet suffers from lack of transparency, variables that co-vary, and difficulty in defining the error of results. The univariate method is straight forward and transparent, but may not extract the full measure of data from the flora. Both methods suffer from a lack of theoretical underpinning and thus solely rely on empirical observations. Here we apply the two most robust univariate analysis, those that estimate mean annual temperature and mean annual precipitation, to the Cape Blanco Flora. A least squares linear regression of leaf margin state and mean annual temperature allows for estimates of ancient mean annual temperature. The relationships are robust and differ only slightly in different parts of the world: East Asia (Wolfe, 1979; Wing and Greenwood, 1993; Su et al., 2010), Bolivia (Gregory-Wodzicki, 2000), Australia (Greenwood et al., 2004), North and South America (Wilf, 1997), and Central and North America (Miller et al., 2006). The Central and North American calibration of Miller et al. (2006) is most appropriate and comprehensive for the Cape Blanco flora.

There are 28 angiosperm leaf forms in the Cape Blanco flora, 12 of them have entire margins. Using the equation of Miller et al. (2006), where *T* is leaf estimated mean annual temperature (°C), and F is the fraction of species in the flora that have entire margins.

$$T = 29.0 \cdot F + 1.32$$

Mean annual temperature of the Cape Blanco Flora estimated in this way was 13.7 ± 4.6 º C (the error is from the nomogram of Miller et al., 2006). This result corresponds well with the floristic indications of comparable modern vegetation in northern California. The current mean annual temperature at Cape Blanco is ~11 º C (Wolfe, 1993).

The mean annual paleoprecipitation (*P* in cm) at Cape Blanco can be estimated in a similar fashion following Wilf et al. (1998), using parameter *S* which is the sum of the percentage representation in the flora of mesophylls (4500-18225 mm$^2$), macrophylls (18225-164025 mm$^2$), and megaphylls (>164025 mm$^2$) in the flora, as follows.

$$P = 3.77 \cdot S + 47.0.$$

The percent of mesophylls and larger in the Cape Blanco flora is 46.7%, and this gives a mean annual precipitation of 223 cm (+ 95 cm, -68 cm). This is more than the 195 cm per year observed today at Cape Blanco (Wolfe, 1993).

OTHER EARLY MIOCENE FLORAS: Our results for paleotemperature can be compared with other floras of the same geological age for two other late early Miocene floras from the west coast of North America: the ~18 Ma, Temblor (Renney, 1972), and Seldovia (Wolfe and Tanai, 1980) floras (Fig. 19). Coastal floras are ideal for comparison with sea surface temperatures because their interpretation is not complicated by paleoaltitude or rain shadow effects.

The Temblor flora was recovered from the Temblor Formation at a locality 9 miles north of Coalinga, California, USA, which Renney (1972) regarded as middle Miocene and ~15.5 Ma. The stratigraphy of the region has since been revised and based on lithology, the plant fossil beds described by Renney (1972) correlate with the estuarine facies tract of Bridges and Castle (2003). This updates the age of the fossil flora to 17.5 ± 1 Ma based on regional bounding surfaces and their correlation to the global sea level curve of Haq et al. (1987). The estuarine facies tract is the second of five facies tracts that range from incised valley to subtidal.

The Seldovia Point flora (Wolfe and Tanai, 1980) was recovered from multiple localities within the late early Miocene Tyonek Formation (Calderwood and Fackler, 1972), in the Kenai Peninsula, Alaska. Based on stratigraphic position and correlation, the age of the formation is late early Miocene to early Middle Miocene (16 to 18 Ma). Low gradient fluvial deposition along with the formation thickness, areal extent, and duration of deposition, all suggest that the unit was deposited near sea-level (Wolfe and Tanai 1980).

The margin type for fossil plant species from the Temblor and Cape Blanco floras was recorded, and the percent of entire margins was calculated. The determination of character state was from figures and descriptions of Renney (1972). Wolfe and Tanai (1980) reported the percentage of entire species for the Seldovia Point flora. Based on the number of entire leaves, leaf mean annual temperature (Miller et al., 2006) was calculated (Table 6).

EVIDENCE FROM MARINE OXYGEN ISOTOPES: The early Middle Miocene (15.5 to 16.5 Ma, N-8) benthic foraminifera compilation (n=83) of Savin et al. (1985) was used to estimate late early Miocene sea surface temperature. To follow the calcite/water $\delta^{18}O$ temperature equation of Erez and Luz (1983), it was necessary to estimate the isotopic composition of the early Miocene ocean at the sample latitudes ocean by using equation one of Zachos et al. (1994) and adding a -0.5 ‰ ice volume correction. Zachos et al. (1994) used the same ice volume correction value for their early Oligocene study. The sea surface temperature estimates are the circle symbols on the plot of absolute latitude verses temperature (Fig. 20). The entire global dataset is used because the northeastern Pacific region Miocene has been little sampled by deep sea drilling (e.g., Woodruff and Savin, 1989). The Holocene temperature measurements also used data compiled by Savin et al. (1985) and followed the same method of sea surface estimation, however no ice volume

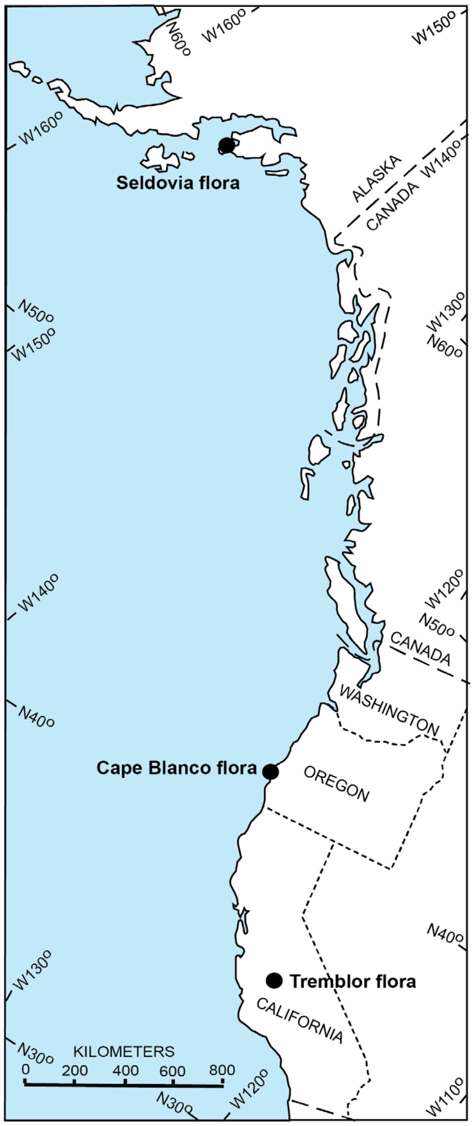

**Figure 19**: Cape Blanco flora compared with other early Miocene floras at different latitudes today.

**Table 6**: Paleotemperature estimated from fossil floras following Miller et al. (2006)

| Location | Tremblor | Cape Blanco | Seldovia |
|---|---|---|---|
| Latitude north (°) | 36 | 43 | 59 |
| Total forms | 31 | 28 | 54 |
| Entire margined species | 21 | 12 | 9 |
| Leaf mean annual temperature (°C) | 21.0 | 13.7 | 6.2 |
| Error (2σ) after Miller et al. (2006) | 3.8 | 4.6 | 2.6 |

correction was used. Modern weather station data for the west coast of North America (Bryson and Hare, 1974) and South America (Schwerdtfeger, 1976) are also plotted on Fig. 20A.

EARLY MIOCENE TEMPERATURE GRADIENTS: The four global data sets are plotted with modern latitude on the x-axis and temperature (º C) on the y axis, Figure 20A. A subset of the global data sets was also analyzed. The Northern Hemisphere, temperate latitude (23.3 º N to 66.6 º N), portions of the data sets, and their least squares linear regressions are shown in Figs 20B and 20C.

Linear regressions of the four global data sets showed very different slopes for marine (0.3) and coastal (0.6), and student t-test confirmed with greater than 99.9% confidence that these slopes were distinct.

The Northern Hemisphere temperate latitude subset, however, is more interesting. The fossil leaf slope and the modern temperature slope could not be differentiated with greater than 95% confidence.

The Miocene and Holocene isotope slopes could not be differentiated from each other with greater than 90% confidence, but they were different than the modern and leaf slopes. The offsets of the slope-coincident regressions are 5.2 ºC for the leaf versus modern 4.2 ºC for the Miocene versus Holocene isotopes as measured at 45 ºN. In both cases the Miocene measurements are warmer.

The global data set when considered from a latitude perspective fails to yield compelling results, probably because the northern and southern hemispheres have fundamentally different land and ocean distributions. Furthermore, to accurately model the temperature gradient from equator to pole data should be evenly distributed among the latitudes and this is not the case with the isotopic and leaf data sets.

The most robust result of this study is that the offset between the Miocene leaf and modern regressions (5.2 ºC) and the Miocene isotope and Holocene isotope regressions (4.2 ºC) is within one degree Celsius. This magnitude of temperate increase matches the temperature increase predicted for the interval 2013 to 2100 (Ciais et al., 2013).

The coincident slopes of the modern and fossil data sets are also of note. That the fossil leaf and modern weather station data have the same latitudinal gradient ~ -0.6 º C/degree latitude suggests that fossil leaves are an accurate climate predictor. The coincident slopes for the isotope data suggest that the equations used to convert measured $\delta^{18}O$ to sea surface temperature in ºC may have a large control of the ºC results or that the Miocene and Holocene oceans had the same latitudinal temperature gradient.

But, which gradient is correct, the one based on marine oxygen isotopes or on fossil-leaves? It is likely that both are correct. The ocean temperature is moderated both by the high heat capacity of water and ocean currents, which are dominated by the cold southerly California Current (Freeland et al., 2003; Johnstone and Dawson, 2010). This current creates the distinctive summer-dry seasonality of Oregon (Dallman, 1998; Barth et al., 2007), which can be recognized well back into the Miocene (Retallack, 2004b). Air has a lower heat capacity than water, and so its temperature is more sensitive to energy differences between the equator and pole. This discrepancy may explain why the land-based measurements have a steeper latitudinal temperature gradient. The coincident offset in the temperatures between the oceans and land may be due to the climate buffering capacity of $CO_2$ which increased the heat capacity of the atmosphere and can, through atmospheric circulation, transfer heat between the oceans and continents resulting in a similar overall temperature increase.

The recognition of shallower gradients in isotopic data calls for caution when using these data to predict polar and tropical land temperatures, as they may be over and under predicted, respectively. The possibility of warmer low latitudes during Miocene time challenges models where the global heat budget is predominantly accommodated by an increase in high latitude temperature (Crowley and Zachos 2000; Nikolaev et al. 1998).

The Miocene remains an important time for understanding global climate change because tectonic arrangements during Miocene time were similar to today (Herold et al. 2008), however two major changes with the potential to drastically change ocean circulation, the closure of the Panamanian isthmus (Duque-Caro, 1990), and the opening of the Bering Strait (Marincovich and Gladenkov, 1999), preclude direct comparisons. Promising modeling results (Motoi et al., 2005) have begun to address and quantify the results of ocean circulation differences between the early Miocene and today.

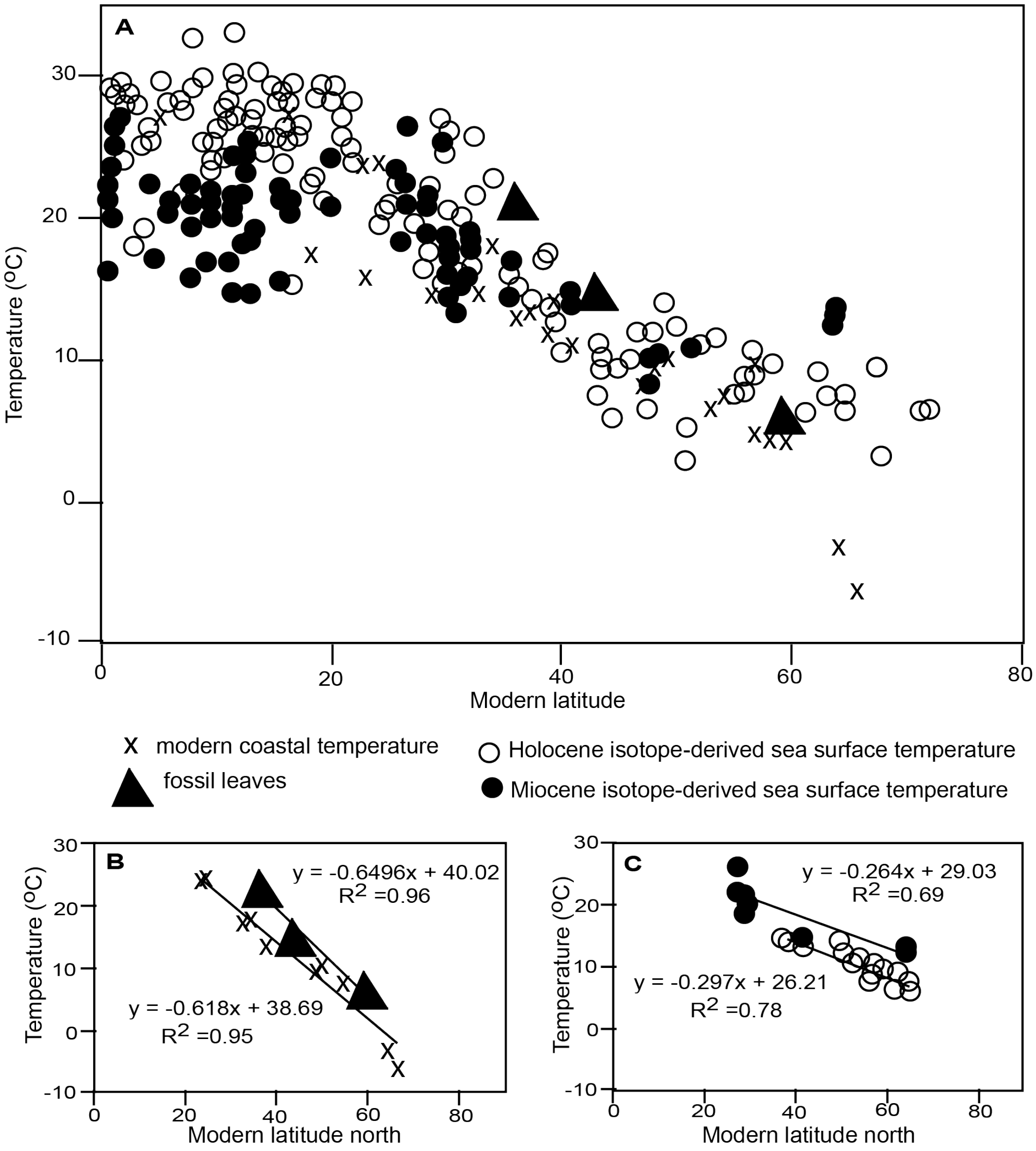

**Figure 20**: Temperature data. A; global data plotted with absolute value of latitude, B; Northern Hemisphere temperate fossil leaf data and modern temperature station measurements with linear regressions of the two data sets, C; Northern Hemisphere temperate sea surface estimates with linear regressions of the two data sets.

## CONCLUSIONS

At 18.26 ± 0.86 Ma, during the early Miocene, a rhyodacitic eruption in the Western Cascades blanketed the Klamath terrain with pumice and ash, which overwhelmed a catchment leading to a local coastal progradation. Leaves of the trees growing at that time were carried along with the ash and deposited in a lagoon near the shore. These fossils have been identified following a long tradition of Miocene paleofloristic paleobotany in the Pacific Northwest (Chaney and Axelrod, 1959; Smiley et al., 1975). Based on the size and margin state of the leaves (Wilf et al., 1998; Miller et al., 2006), a mean annual temperature of ~14º C and a mean annual precipitation of ~223 cm/yr can be estimated for the Cape Blanco flora, compared with 11º C and 195 cm today (Wolfe, 1993). Cape Blanco paleotemperature can also be compared with comparable paleotemperature estimates from the Temblor flora of California (Renney, 1972) and the Seldovia flora from Alaska (Wolfe and Tanai, 1980), as well as paleotemperatures estimated from oxygen isotopic analysis of benthic foraminifera (Savin et al., 1985). The leaf data estimate a latitudinal gradient of ~ 0.6º C/degree latitude, and the isotopic predicted gradient is ~0.3 º C/degree latitude. Both results agree that the mean annual temperature at 45º latitude north was 4-5 º C warmer than today in the late early Miocene.

Both paleobotanical and oxygen isotope methods estimate that the late early Miocene in the northern hemisphere was ~5º C warmer than today. This magnitude increase is the same as models predict occurring by 2100 (Ciais et al., 2013). The predicted atmospheric $CO_2$ in 2100 is also the same as is estimated for the late early Miocene, 612 ± 24 ppm (Breecker and Retallack, 2014). The global data set was inconclusive and the temperate Northern Hemisphere had to be considered independently for compelling results to be obtained. The latitudinal gradients predicted by fossil leaf measurements did not match those from the sea. This may reflect differences in temperature of the ocean and the land which remain a forceful driver of Mediterranean seasonality in Oregon (Dallman, 1998; Barth et al., 2007).

## ACKNOWLEDGEMENTS

Robert Duncan and John Huard at Oregon State University completed the mineral separation and laboratory analysis for the $^{40}$Ar/$^{39}$Ar date. Joshua Roering and Edward Davis offered much useful advice. Win McLaughlin provided photographs of specimens in the Smithsonian Institution, and Jon Wingerath catalogued them for this study. For fossil excavation we are particularly indebted to students of successive paleobotany classes: Jill Bailey, Todd Braje, Ian Betteridge, Jesse Brink, Christopher Capucci, Giselle Conde, James Coulombe, Don Day, Timothy De Groote, Tobias Dietz, Megan Evans, Francis Finnan, James Freeman, Eric Goodwin, Clare Gordon, Dale Hanson, Christopher Hedeen, Nathan Hemphill, Stacey Johnson, Joel Lavin, Dana Ledford, Michelle Lips, Brent Love, Johan Matsumura, Gavin McCarthy, Shannon McDowell, Shane Mellott, Christine Metzger, Tricia Miller, Drew Mirante, Robert Murray, Katherine Neall, Jennifer Oberst, Kevin O'Dea, William Patty, Christopher Pearl, Tom Peryam, Tracy Piccinnino, Scott Powers, Edward Rackley, Scott Robinson, Selina Robson, Michelle Rucker, Eric Sach, Ben Shapiro, Lance Schendel, Dominick Schiavione, Colgan Smith, Ann Tattersall, Jeannette Taylor, Alexandra Tiepel, Peter Tollan, Abigail Turner, Kelli Van Norman, Deborah Varty, Jared Weybright, Jonathan Wynn, and Keli Yeats. Diane Erwin and Steven Manchester provided exceptionally useful reviews of the manuscript.

## REFERENCES

Addicott, W. O. 1976. Neogene molluscan stages of Oregon and Washington, pp. 95-115 in A. E. Fritsche, H. J. Ter Best, and W. W. Wornardt (eds.), The Neogene Symposium. Society of Economic Paleontologists and Mineralogists, Pacific Section, San Francisco.

Addicott, W. O. 1980. Miocene stratigraphy and fossils, Cape Blanco, OR. Oregon Geology 42: 87-98.

Addicott, W. O. 1983. Biostratigraphy of the Marine Neogene Sequence at Cape Blanco, Southwestern Oregon. U.S. Geological Survey Professional Paper 774-G: G1-G19.

Albright L. B., M. O. Woodburne, T. J. Fremd, C. C. I. Swisher, B. J. MacFadden, and G. R. Scott. 2008.

Revised Chronostratigraphy and Biostratigraphy of the John Day Formation (Turtle Cove and Kimberly Members), Oregon, with Implications for Updated Calibration of the Arikareean North American Land Mammal Age. Journal of Geology 116: 211-237.

Allison, R. C., and W. O. Addicott. 1976. The North Pacific Miocene Record of *Mytilus* (*Plicatomytilus*), a New Subgenus of Bivalvia. U. S. Geological Survey Professional Paper 962: 1-21

Angiosperm Phylogeny Group. 2016. An update of the angiosperm phylogeny group for the orders and families of flowering plants: APG IV. Botanical Journal Linnaean Society 181: 1-20.

Argus, G.W. 2007. *Salix* (Salicaceae) distribution maps and a synopsis of their classification in North America, north of Mexico. Harvard Papers in Botany 12: 335-368.

Armentrout, J. M. 1980. Cenozoic Stratigraphy of Coos Bay and Cape Blanco, Southwestern Oregon, pp. 175-216 in K. F. Oles, J. G. Johnson, A. R. Niem, and W. A. Niem (eds.), Geologic Field Trips in Western Oregon and Southwestern Washington. Oregon Department of Geology and Mineral Industries Bulletin 101.

Armentrout, J. M., D. A. Hull, J. D. Beaulieu, and W. W. Rau. 1983. Correlation of Cenozoic stratigraphic units of Western Oregon and Washington. Oregon Department of Geology and Mineral Industries Oil and Gas Investigation 7: 1-87.

Arnold, C. A. 1936. Some fossil species of *Mahonia* from the Tertiary of Eastern and Southeastern Oregon. Contributions from the Museum of Paleontology University of Michigan 5(4): 55-66.

Ashlee, T. R. 1932. A contribution to the Latah flora of Idaho. Northwest Science 4: 69-82.

Ashwill, M. 1983. Seven fossil floras in the rain shadow of the Cascade Mountains, Oregon. Oregon Geology 45: 107-111.

Axelrod, D. I. 1938. A Pliocene flora from the Mount Eden beds, southern California, pp. 125-183, in R.W. Chaney, M.K. Elias, D. I. Axelrod, and C. Condit (eds). Miocene and Pliocene floras of North America. Carnegie Institution of Washington Publication 476.

Axelrod, D. I. 1939. A Miocene flora from the western border of the Mohave Desert. Carnegie Institution of Washington Publication 516: 1-129.

Axelrod, D. I. 1940. The Pliocene Esmeralda flora of west-central Nevada. Journal of the Washington Academy of Sciences 30: 163-174.

Axelrod, D. I. 1944a. The Black Hawk Ranch flora, pp. 91-101 in R. W., Chaney (ed.), Pliocene floras of California and Oregon. Carnegie Institution of Washington Publication 553.

Axelrod, D. I. 1944b. The Mulholland Flora, pp. 103-128 in R. W., Chaney (ed.), Pliocene floras of California and Oregon. Carnegie Institution of Washington Publication 553.

Axelrod, D. I. 1944c. The Oakdale Flora, pp. 147-165 in R. W., Chaney (ed.), Pliocene floras of California and Oregon. Carnegie Institution of Washington Publication 553

Axelrod, D. I. 1944d. The Sonoma Flora, pp. 167-206 in R. W. Chaney (ed.), Pliocene floras of California and Oregon. Carnegie Institution of Washington Publication 553.

Axelrod, D. I. 1944e. The Alvord Creek flora, pp. 225-262, in R. W. Chaney (ed.), Pliocene floras of California and Oregon. Carnegie Institution Washington Publication 553.

Axelrod, D. I. 1950a. A Sonoma florule from Napa, California, pp. 23-71 in D. I. Axelrod (ed.), Studies in Late Tertiary paleobotany. Carnegie Institution of Washington Publication 590.

Axelrod, D. I. 1950b. Further studies of the Mt Eden flora, southern California, pp. 121-158 in D. I. Axelrod (ed.), Studies in Late Tertiary paleobotany. Carnegie Institution of Washington Publication 590.

Axelrod, D. I. 1950c. The Anaverde flora of southern California, pp. 75-119 in D. I. Axelrod (ed.), Studies in Late Tertiary paleobotany. Carnegie Institution of Washington Publication 590.

Axelrod, D.I. 1964. The Miocene Trapper Creek Flora of Southern Idaho. University of California Publications in Geological Sciences 51: 1-148.

Axelrod, D. I. 1968. Tertiary Floras and Topographic History of the Snake River Basin, Idaho. Geological Society of America Bulletin 79: 713-734.

Axelrod, D. I. 1985. Miocene Floras from the Middlegate Basin, West-Central Nevada. University of California Publications in Geological Sciences 129: 1-209.

Axelrod, D. I. 1986. Cenozoic history of some western American pines. Missouri Botanical Garden Annals 73: 565-641

Axelrod, D. I. 1987. The late Oligocene Creede flora, Colorado. University of California Publications in Geological Sciences 13: 1-235.

Axelrod, D. I. 1991. The early Miocene Buffalo Canyon Flora of Western Nevada. University of California Publications in Geological Sciences 136: 1-76.

Axelrod, D. I. 1995a. The middle Miocene Pyramid flora of Western Nevada. University of California Publications in Geological Sciences 137: 1-50.

Axelrod, D. I. 1995b. The Miocene Purple Mountain Flora of Western Nevada. University of California Publications in Geological Sciences 139: 1-62.

Axelrod, D.I. 1998. The Eocene Thunder Mountain flora of central Idaho. University of California Publications in Geological Sciences 142: 1-55.

Axelrod, D. I. 2000. A Miocene (10-12 Ma) evergreen laurel-oak forest from Carmel Valley, California. University of California Publications in Geological Sciences 145: 1-34.

Baghai, N.L. 1988. *Liriodendron* (Magnoliaceae) from the Miocene Clarkia flora of Idaho. American Journal of Botany 75: 451-464.

Baghai, N. L., and R. B. Jorstad. 1995. Paleontology, paleoclimatology and paleoecology of the late middle Miocene Musselshell Creek flora, Clearwater County, Idaho. A preliminary study of a new fossil flora. Palaios 10: 424-436.

Bailey, I. W., and E. W. Sinnott. 1916, The climatic distribution of certain types of angiosperm leaves. American Journal of Botany 3: 24-39.

Baldwin, E. M. 1945. Some revisions of the late Cenozoic stratigraphy of the Southern Oregon Coast. Journal of Geology 53: 35-46.

Bandy, O. L. 1950. Some later Cenozoic Foraminifera from Cape Blanco, Oregon. Journal of Paleontology 24: 269-281.

Barakat, A., P. K. Wall, S. DiLoreto, and J. E. Carlson. 2007. Conservation and divergence of microRNAs in *Populus*. BMC Genomics 8: 481 (1-16).

Barbour, T. Keeler-Wolf, and A.A. Schoenherr (eds.) 2007. Terrestrial vegetation of California. University of California Press, Berkeley, 712 pp.

Barth, B.A. Menge, J. Lubchenko, F. Chan, J.M. Bane, A.R. Kiriincich, M.A. McManus, K.J. Nielsen, S.D. Pierce, and L. Washburn, 2007. Delayed upwelling alters nearshore coastal ocean ecosystems in the northern California current. U.S. National Academy of Sciences Proceedings 104, 3719-3724

Berry, E.W. 1916. The flora of the Citronelle Formation. US Geological Survey Professional Paper 98: 193-208.

Berry, E. W. 1929. A revision of the flora of the Latah Formation. U.S. Geological Survey Professional Paper 154-H: 225-265.

Berry, E. W. 1934. Miocene plants from Idaho. U. S. Geological Survey Professional Paper 185-E: 97-125.

Bockheim, J. G., H. M. Kelsey, and J. G. Marshall. 1992. Soil development, relative dating, and correlation of Late Quaternary marine terraces in southwestern Oregon. Quaternary Research 37: 60-74.

Bockheim, J. G., J. G. Marshall, and H. M. Kelsey. 1996. Soil-forming processes and rates on uplifted marine terraces in southwestern Oregon, USA. Geoderma 73: 39-62.

Boersma, P. D., S. H. Reichard, and A. N. Van Buren (eds). 2006. Invasive species of the Pacific Northwest. University of Washingto Press, Seattle, 287 pp.

Böhme, M. 2003. The Miocene Climatic Optimum: evidence from ectothermic vertebrates of Central Europe. Palaeogeography Palaeoclimatology Palaeoecology 195: 389-401.

Breecker, D.O., and G. J. Retallack. 2014. Refining the pedogenic carbonate atmospheric $CO_2$ proxy and application to Miocene $CO_2$. Palaeogeography Palaeoclimatology Palaeoecology 406:1-8.

Bridges, R. A., and J. W. Castle. 2003. Local and regional tectonic control on sedimentology and stratigraphy in a strike-slip basin: Miocene Temblor Formation of the Coalinga area, California, USA. Sedimentary Geology 158: 271-297.

Brotherson, J. D., D. L. Anderson, and L. A. Szyska. 1984. Habitat relations of *Cercocarpus montanus* (True Mountain Mahogany) in Central Utah. Journal of Range Management. 37: 321-324.

Brown, R. W. 1934. The recognizable species of the Green River flora. U. S. Geological Survey Professional Paper 185-C: 1-68.

Brown, R. W. 1936. Additions to some fossil floras of the western United States. U. S. Geological Survey Professional Paper 186-J: 163-206.

Brown, R. W. 1940. New species and changes of name in some American fossil floras. Washington Academy of Sciences Journal 30: 344-356.

Brown, R. W. 1946. Alterations in some fossil and living floras. Washington Academy of Sciences Journal 36: 344-355.

Brown, R.W. 1949. Pliocene plants from Cache Valley, Utah. Journal of the Washington Academy of Sciences 39: 224-229.

Bryson, R. A., and F. K. Hare. 1974. Climates of North America. Amsterdam, Elsevier, 420 p.

Buechler, W. K., M. T. Dunn, and W. C. Rember. 2007. Late Miocene Pickett Creek Flora of Owyhee County, Idaho. Contributions from the Museum of Paleontology University of Michigan 31: 305-362.

Burnham, R. J. 1989. Relationships between standing vegetation and leaf litter in a paratropical forest: implications for paleobotany. Review of Palaeobotany and Palynology 58: 5-32.

Calderwood, K. W., and W. C. Fackler. 1972. Proposed stratigraphic nomenclature for Kenai Group, Cook Inlet Basin, Alaska. American Association of Petroleum Geologists Bulletin 56: 739-754.

Cas, R. A. F., and J. V. Wright. 1987. Volcanic Successions Modern and Ancient. London, Allen & Unwin, 528 pp.

Chaney, R.W. 1920. The flora of the Eagle Creek Formation. Walker Museum Contributions 2: 115-181.

Chaney, R.W. 1938. The Deschutes Flora of Eastern Oregon, Miocene and Pliocene Floras of Western North America, pp. 185-216, in R.W. Chaney, M.K. Elias, D. I. Axelrod, and C. Condit (eds). Miocene and Pliocene floras of North America. Carnegie Institution of Washington Publication 476.

Chaney, R. W. 1944a. The Dalles flora, pp. 285-321 in R. W., Chaney (ed.), Pliocene floras of California and Oregon. Carnegie Institution of Washington Publication 553.

Chaney, R. W. 1944b. The Troutdale flora, pp. 323-351 in R. W., Chaney (ed.), Pliocene floras of California and Oregon. Carnegie Institution of Washington Publication 553.

Chaney, R.W. 1950. A revision of fossil *Sequoia* and *Taxodium* in western North America based on the recent discovery of *Metasequoia*. American Philosophical Society Transactions 40: 171-263.

Chaney, R. W., and D. I. Axelrod. 1959. Miocene floras of the Columbia Plateau. Carnegie Institution of Washington Publication 617: 1-237.

Chaney, R.W. and M. K. Elias. 1938, Late Tertiary flora from the High Plains. pp. 1-72, in R.W. Chaney, M.K. Elias, D. I. Axelrod, and C. Condit (eds). Miocene and Pliocene floras of North America. Carnegie Institution of Washington Publication 476.

Chaney, R. W., and E. I. Sanborn. 1933. The Goshen flora of west central Oregon. Carnegie Institution of Washington Publication 439: 1-103.

Christiansen, R. L., and R. S. Yeats. 1992. Post-Laramide geology of the U.S. Cordilleran region, pp. 261-406 in B. C. Burchfiel, P. W. Lipman, and M. L. Zoback (eds.), The Cordilleran Orogen: Conterminous U.S. Geological Society of America, Geology of North America G-3.

Ciais, P., C. Sabine, G. Bala, L. Bopp, V. Brovkin, J. Canadell, A. Chhabra, R. DeFries, J. Galloway,

M. Heimann, C. Jones, C. Le Quéré, R. B. Myneni, S. Piao, and P. Thornton. 2013. Carbon and other biogeochemical cycles, p. 465-570 in T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, and P. M. Midgley (eds.), Climate Change 2013: The Physical Science Basis. Cambridge University Press, Cambridge.

Clifton, H. E., R. E. Hunter, and L. R. Phillips. 1971. Depositional structures and processes in the non-barred high-energy nearshore. Journal of Sedimentary Petrology 41: 651-670.

Cockerell, T. D. A. 1908. The fossil flora of Florissant, Colorado. American Museum of Natural History Bulletin 24: 71-110.

Cockerell, T. D. A. 1910. Descriptions of Tertiary plants. American Journal of Science 29: 76-78.

Collinson, M. E. 1992, The early fossil history of Salicaceae: a brief review. Royal Society of Edinburgh Proceedings Biological Sciences 98: 155-167.

Collinson, M.E. and P. R. Crane. 1978. *Rhododendron* seeds from the Palaeocene of southern England. Botanical Journal of the Linnean Society 76: 195-205.

Condit, C. 1938. The San Pablo flora of west central California, pp. 219-268 in R. W. Chaney, M. K. Elias, D. I. Axelrod, and C. Condit (eds.), Miocene and Pliocene Floras of western North America. Carnegie Institution of Washington Special Publication 476.

Condit, C. 1944a. The Remington Hill flora, pp. 21-39 R. W. Chaney, M. K. Elias, D. I. Axelrod, and C. Condit (eds.), Miocene and Pliocene Floras of western North America. Carnegie Institution of Washington Special Publication 476.

Condit, C. 1944b. The Table Mountain flora, pp. 57-90 in R. W. Chaney, M. K. Elias, D. I. Axelrod, and C. Condit (eds.), Miocene and Pliocene Floras of western North America. Carnegie Institution of Washington Special Publication 476.

Cosgrove, B. A., E. J. Barron, and D. Pollard. 2002. A simple interactive vegetation model coupled to the GENESIS GCM. Global and Planetary Change 32: 253-278.

Crowley, T. J., and J. C. Zachos. 2000. Comparisons of zonal temperature profiles for past warm time periods, pp. 50-76 in B. T. Huber, K. G. Macleod, and S. L. Wing (eds.), Warm Climates in Earth History. Cambridge, Cambridge University Press.

Dallman, P. R. 1998. Plant life in the world's Mediterranean climates: California, Chile, South Africa, Australia, and the Mediterranean basin. Univ of California Press, Berkeley, 255 pp.

Diller, J. S. 1902. Topographic development of the Klamath Mountains. United States Geological Survey Bulletin 196: 1-63.

Dorf, E. 1930. Pliocene floras of California. Carnegie Institution of Washington Publication 412: 1-108.

Dorf, E. 1938. A late Tertiarty flora from southwestern Idaho, pp. 75-124 in R. W. Chaney, M. K. Elias, D. I. Axelrod, and C. Condit (eds.), Miocene and Pliocene Floras of western North America. Carnegie Institution of Washington Special Publication 476.

Dott, R. H. 1962. Geology of the Cape Blanco Area, southwestern Oregon. Ore Bin 24: 121-133.

Dott, R. H. 1971. Geology of the southwestern Oregon coast west of the 124th meridian. Oregon Department of Geology and Mineral Industries Bulletin 69: 1-63.

du Bray, E. A., D. A. John, D. R. Sherrod, R. C. Evarts, R.M. Conrey, and J. Lexa. 2006. Geochemical database for volcanic rocks of the Western Cascades, Washington, Oregon, and California, U.S. Geological Survey Data Series 155: 1-49.

Duque-Caro, H. 1990. Neogene stratigraphy, paleoceanography and paleobiogeography in northwest South America and the evolution of the Panama Seaway. Palaeogeography Palaeoclimatology Palaeoecology 77: 203-234.

Durham, J. W. 1953. Miocene at Cape Blanco, Oregon. Geological Society of America Bulletin Abstracts 64: 1504-1505.

Dziak, R.P., Fox, C.G., Bobbitt, A.M. and Goldfinger, C. 2001. Bathymetric map of the Gorda plate: Structural and geomorphological processes inferred from multibeam surveys. Marine Geophysical Research 22(4): 235-250.

Eckenwalder, J. E. 1980. Foliar heteromorphism in *Populus* (Salicaceae), a source of confusion in the taxonomy of tertiary leaf remains. Systematic Botany 5: 366-383.

Ellis, B., and K. R. Johnson. 2013. Comparison of leaf samples from mapped tropical and temperate forests: Implications for interpretations of the diversity of fossil assemblages. Palaios 28: 163-177.

Erez, J., and B. Luz. 1983. Experimental paleotemperature equation for planktonic foraminifera. Geochimica et Cosmochimica Acta 47: 1025-1031.

Feng, Y., S. H. Oh, and P. S. Manos. 2005. Phylogeny and historical biogeography of the genus *Platanus* as inferred from nuclear and chloroplast DNA. Systematic Botany 30:.786-799.

Ferguson, D. K. 1985. The origin of leaf-assemblages: new light on an old problem. Review of Palaeobotany and Palynology 46: 117-188.

Fields, P. F. 1996. The Succor Creek Flora of the middle Miocene Sucker Creek formation, southwestern Idaho and eastern Oregon; Systematics and Paleoecology Unpublished PhD thesis, Michigan State University, East Lansing, 675 pp.

Forest, C. E., J. A. Wolfe, P. Molnar, and K. A. Emanuel. 1999. Paleoaltimetry incorporating atmospheric physics and botanical estimates of paleoclimate. Geological Society of America Bulletin 111: 497-511.

Franklin, J. F., and C. T. Dyrness. 1988. Natural vegetation of Oregon and Washington. Oregon State University press, Corvallis, 452 pp.

Freeland, H. J., G. Gatien, A. Huyer, and R. L. Smith. 2003. Cold halocline in the northern California Current: an invasion of subarctic water. Geophysical Research Letters, 30: 1141.doi: 10.1029/2002GL016663

Galindo-Tovar, M.E., N. Ogata-Aguilar, and A.M. Arzate-Fernández, 2008. Some aspects of avocado (*Persea americana* Mill.) diversity and domestication in Mesoamerica. Genetic Resources and Crop Evolution 55: 441-450.

Garver, J. I., and T. J. Scott. 1995. Trace elements in shale as indicators of crustal provenance and terrane accretion in the southern Canadian Cordillera. Geological Society of America Bulletin 107: 440-453.

Garzanti, E., S. Critelli, and R. V. Ingersoll. 1996. Paleogeographic and paleotectonic evolution of the Himalayan Range as reflected by detrital modes of Tertiary sandstones and modern sands (Indus transect, India and Pakistan). Geological Society of America Bulletin 108: 631-642.

Gastaldo, R. A. 1989. Preliminary observations on phytotaphonomic assemblages in a subtropical/temperate Holocene bayhead delta: Mobile Delta, Gulf Coastal Plain, Alabama. Review of Palaeobotany and Palynology 58: 61-83

Gastaldo, R. A., S. C. Bearce, C. W. Degges, R. J. Hunt, M. W. Peebles, and D. L. Violette. 1989. Biostratinomy of a Holocene oxbow lake: a backswamp to mid-channel transect. Review of Palaeobotany and Palynology 58: 47-59.

Gavin, D.G., M. Anderson, and J.J. Roering. 2013. Potential Late-Holocene disjunction of *Sequoia sempervirens* on the Central Oregon Coast. Northwest Science 87:.81-94.

Goralka, R.J. and J.H. Langenheim. 1995. Analysis of foliar monoterpenoid content in the California Bay Tree, *Umbellularia californica*, among populations across the distribution of the species. Biochemical Systematics and Ecology 23: 439-448.

Gornall, J. L., and R. D. Guy. 2007. Geographic variation in ecophysiological traits of black cottonwood (*Populus trichocarpa*). Candian Journal of Botany 85: 1202-1213.

Graham, A. 1963. Systematic Revision of the Sucker Creek and Trout Creek Miocene Floras of Southeastern Oregon. American Journal of Botany 50: 921-936.

Greenwood, D. R. 1992. Taphonomic constraints on foliar physiognomic interpretations of Late Cretaceous and Tertiary palaeoclimates. Review of Palaeobotany and Palynology 71: 149-190.

Greenwood, D. R., P. Wilf, S. L. Wing, and D. C. Christophel. 2004. Paleotemperature estimation using leaf-margin snalysis: Is Australia different? Palaios 19: 129-142.

Gregory-Wodzicki, K. M. 2000. Relationships between leaf morphology and climate, Bolivia: implication for estimating paleoclimate from fossil floras. Paleobiology 26: 668-688.

Güner, T.H. and T. Denk. 2012. The genus *Mahonia* in the Miocene of Turkey: Taxonomy and biogeographic implications. Review of Palaeobotany and Palynology 175:.32-46.

Hammond, P. E. 1980. Reconnaissance Geologic Map and Cross Sections of Southern Washington Cascade Range. Department of Earth Sciences Portland State University, scale 1:125,000.

Hannibal, H. 1911. A Pliocene flora of the Coast ranges of California. Torrey Botanical Club Bulletin 38: 329-342.

Haq, B. U., J. Hardenbol, and P. R. Vail. 1987. Chronology of fluctuating sea levels since the Triassic. Science 235: 1156-1167.

Harper, G. D. 1984. The Josephine ophiolite, northwestern California. Geological Society of America Bulletin 95: 1009-1026.

Herold, N., Seton, M., Müller, R.D., You, Y. and Huber, M., 2008. Middle Miocene tectonic boundary conditions for use in climate models. Geochemistry, Geophysics, Geosystems, 9(10): Q10009, doi:10.1029/2008GC002046.

Hladky, F. R. 1994. Geologic Map of the Lakecreek Quadrangle, Jackson County, Oregon. Oregon Department of Geology and Mineral Industries Geological Map Series GMS-88, scale 1:24,000.

Hladky, F. R. 1996. Geology and Mineral Resources of Grizzly Peak Quadrangle, Jackson County, Oregon. Oregon Department of Geology and Mineral Industries Map Series-106, scale 1:24,000.

Hladky, F. R. 1999a. Geology and Mineral Resources Map of the Brownsboro Quadrangle, Jackson County, Oregon. Oregon Department of Geology and Mineral Industries Map Series-109, scale 1:24,000.

Hladky, F. R. 1999b. Geology and Mineral Resources of the Rio Canyon Quadrangle, Jackson County, Oregon, Oregon Department of Geology and Mineral Industries Map Series GMS-108, scale 1.24,000.

Hollick, A. 1925. A new fossil species of *Hydrangea*. Torrey Botanical Club Bulletin 52: 21-23.

Holliday, J.A., K. Ritland, and S. N. Aitken. 2010. Widespread, ecologically relevant genetic markers developed from association mapping of climate-related traits in Sitka spruce (*Picea sitchensis*). New Phytologist 188: 501-514.

Huang, J., T. Su, J. Lebereton-Anberrée, S. T. Zhang, and Z. K. Zhou. 2016. The oldest *Mahonia* (Berberidaceae) fossil from East Asia and its biogeographic implications. Journal of Plant Research 129: 209-223.

Huang, J., G.-L. Shi, T. Sua, and Z.-K. Zhou. 2017. Miocene *Exbucklandia* (Hamamelidaceae) from Yunnan, China and its biogeographic and palaeoecologic implications. Review of Palaeobotany and Palynology 244: 96-106

Huang, Y. J., Y. S. C. Liu, and M. Zavada 2014. New fossil fruits of *Carya* (Juglandaceae) from the latest Miocene to earliest Pliocene in Tennessee, eastern United States. Journal of Systematics and Evolution 52: 508-520.

Hunt, R. M. 2002. Intercontinental migration of Neogene amphicyonids (Mammalia, Carnivora): appearance of the Eurasian beardog *Ysengrinia* in North America. American Museum Novitates 3384: 1-53.

Hunt, R. M., and E. Stepleton. 2004. Geology and paleontology of the Upper John Day beds, John Day River Valley, Oregon: Lithostratigraphic and biochronologic revision in the Haystack Valley and Kimberly Areas (Kimberly and Mt. Misery Quadrangles). American Museum of Natural History Bulletin 282: 1- 90.

Hunter, R. E., H. E. Clifton, and R. L. Phillips. 1979. Depositional processes, sedimentary structures, and predicted vertical sequences in barred nearshore systems, southern Oregon Coast. Journal of Sedimentary Petrology 49: 711-726.

Janda, R. J. 1969. Age and correlation of marine terraces near Cape Blanco, Oregon. Geological Society of America Annual Meeting Abstracts and Program 3: 29-30.

Johnstone, J.A., and Dawson, T.E. 2010. Climatic context and ecological implications of summer fog decline in the coast redwood region. U.S. National Academy of Science Proceedings 107, 4533-4538

Jones, J.H. 1986. Evolution of the Fagaceae: the implications of foliar features. Annals of the Missouri Botanical Garden 73: 228-275.

Kelsey, H. M. 1990. Late Quaternary deformation of marine terraces on the Cascadia Subduction Zone near Cape Blanco, Oregon. Tectonics 9: 983-1014.

Kim, S., D. E. Soltis, P. S. Soltis, and Y. Suh. 2004. DNA sequences from Miocene fossils: an ndhF sequence of *Magnolia latahensis* (Magnoliaceae) and an rbcL sequence of *Persea pseudocarolinensis* (Lauraceae). American Journal of Botany 91: 615-620.

Kim, Y.D., S.H. Kim, and L. R. Landrum. 2004. Taxonomic and phytogeographic implications from ITS phylogeny in *Berberis* (Berberidaceae). Journal of Plant Research 117: 175-182.

Knowlton, F. H. 1898. A report of the fossil plants of the Payette Formation, pp. 721-735 in W. Lindgren (ed.), The Mining Districts of the Idaho Basin and the Boise Ridge, Idaho. 18th Annual Report of the United States Geological Survey Part 3.

Knowlton, F.H. 1901. Fossil plants, pp. 285-309 in J. C. Merriam (ed.). A contribution to the geology of the John Day Basin, Oregon. Department of Geological Sciences University of California Bulletin 2: 285-309.

Knowlton, F. H. 1902. Fossil Flora of the John Day Basin Oregon. U. S. Geological Survey Bulletin 204: 1-150.

Knowlton, F. H. 1926. Flora of the Latah Formation of Spokane, Washington, and Coeur D' Alene, Idaho. U. S. Geological Survey Professional Publication 140A: 1-55.

Koch, J. G. 1966. Late Mesozoic stratigraphy and tectonic history, Port Orford-Gold Beach Area, Southwestern Oregon Coast. American Association of Petroleum Geologists Bulletin 50: 25-71.

Koppers, A. P. 2002. ArArCALC-software for $^{40}$Ar/$^{39}$Ar age calculations. Computers and Geosciences 28: 605-619.

Kuenzi, W. D., O. H. Horst, and R. V. McGhee. 1979. Effect of volcanic activity on fluvial-deltaic sedimentation in a modern arc-trench gap, southwestern Guatemala. Geological Society of America Bulletin 90: 827-838.

Kürschner, W. M., Z. Zvacek, and D. L. Dilcher. 2008. The impact of Miocene atmospheric carbon dioxide fluctuations on climate and the evolution of terrestrial ecosystems. U. S. National Academy of Sciences Proceedings 105: 449-453.

Lambert, W.D., Shoshani, J., 1998. Proboscidea, pp. 606-621 in C. M. Janis, K. M. Scott, and L. L. Jacobs (eds.), Evolution of Tertiary Mammals of North America, Terrestrial Carnivores, Ungulates and Ungulatelike Mammals, vol. 1. Cambridge University Press.

LaMotte, R. S. 1935a. The Miocene Tilias of weastern North America. Carnegie Institute of Washington, Publication 455: 49–56.

LaMotte, R. S. 1935b. An upper Oligocene florule from Vancouver Island. Carnegie Institute of Washington, Publication 455: 49–56.

LaMotte, R.S. 1936. The upper Cedarville flora of northwestern Nevada and adjacent California. Carnegie Institution of Washington Publication 455: 57-142.

LaMotte, R. S. 1944. Supplement to catalogue of Mesozoic and Cenozoic plants of North America, 1917-1937. U. S. Geological Survey Bulletin 924: 1-330.

LaMotte, R.S. 1952. Catalog of the Cenozoic plants of North America through 1950. Geological Society of America Memoir 51: 1-381.

Lauria, F. 1996. Typification of *Pinus benthamiana* Hartw. (Pinaceae), a taxon deserving renewed botanical examination. Annalen des Naturhistorischen Museums in Wien. Serie B für Botanik und Zoologie 95B suppl.; 427-446.

Le Bas, M. J., R. W. Le Maitre, and A. R. Woolley. 1992. The construction of the total alkali-silica chemical classification of volcanic rocks. Mineralogy and Petrology 46: 1-22.

Leithold, E. L., and J. Bourgeois. 1983. Sedimentology of the sandstone of Floras Lake (Miocene) transgressive, high-energy shelf deposition, SW Oregon, pp. 17-28 in D. K. Larue and R. J. Steel (eds.), Cenozoic Marine Sedimentation Pacific Margin, U.S.A. Los Angeles, Pacific Section Society of Economic Paleontologist and Mineralogists.

LePage, B. 2001. New species of *Picea* A. Dietrich (Pinaceae) from the middle Eocene of Axel Heiberg Island, Arctic Canada. Botanical Journal of the Linnean Society 135: 137-167.

Lesquereux, L. 1876. On some new species of fossil plants from the lignite formations. U. S. Geological and Geographic Survey of the Territories Annual Report 7: 363-389.

Lesquereux, L. 1878. Report of the fossil plants of the auriferous gravel deposits of the Sierra Nevada. Museum of Comparative Zoology Harvard College Memoir 6: 1-55.

Lis, R.A. 1992. Leaf architectural survey of *Cercocarpus* (Rosaceae) and its systematic significance. International Journal of Plant Sciences 153: 258-272.

Lowe, G.D. 2013. Geologic history of the giant *Sequoia* and the coast redwood. Beaverton Oregon, North American Research Group, 29 p.

MacGinitie, H.D. 1933. The Trout Creek flora of southeastern Oregon. Carnegie Institution of Washington Publication 416: 22-68.

MacGinitie, H. D. 1941. A middle Eocene flora from the central Sierra Nevada, California. Carnegie Institution of Washington Publication 534; 1-167 p.

Manchester, S. R. 1987. The fossil history of the Juglandaceae. Monographs in Systematic Botany of the Missouri Botanical Garden 21: 1-137.

Manchester, S.R. 1994. Inflorescence bracts of fossil and extant *Tilia* in North America, Europe, and Asia: patterns of morphologic divergence and biogeographic history. American Journal of Botany 81: 1176-1185.

Manchester, S. R. 2002. Leaves and fruits of *Davidia* (Cornales) from the Paleocene of North America. Systematic Botany 27: 368–382

Manchester, S.R. and R. M. Dillhoff. 2004. *Fagus* (Fagaceae) fruits, foliage, and pollen from the Middle Eocene of Pacific northwestern North America. Canadian Journal of Botany 82: 1509-1517.

Manchester, S. R., W. S. Judd, and B. Handley. 2006. Foliage and fruits of early poplars (Salicaceae: *Populus*) from the Eocene of Utah, Colorado and Wyoming. International Journal of Plant Science 167: 897–908.

Manchester, S. R., F. Grímsson, and R. Zetter. 2015. Assessing the fossil record of asterids in the context of our current phylogenetic framework. Missouri Botanical Garden Annals 100: 329-363.

Manos, P.S., C. H. Cannon, and S. H. Oh. 2008. Phylogenetic relationships and taxonomic status of the paleoendemic Fagaceae of western North America: recognition of a new genus, *Notholithocarpus*. Madrono 55: 181-190.

Marincovich, L. J., and A. Y. Gladenkov. 1999. Evidence for an early opening of the Bering Strait. Nature 397: 149-151.

Mason, H.L. 1934. Pleistocene flora of the Tomales Formation. Carnegie Institution of Washington Publication 415: 81-179.

McDougall, I., and T.M. Harrison. 1999. Geochronology and thermochronology by the $^{40}$Ar/$^{39}$Ar Method. New York, Oxford University Press, 269 pp.

Mertzman, S. A. 2000. K-Ar results from the southern Oregon-northern California Cascade Range.

Oregon Geology 62: 99-122.

Meyer, H. W. 1973. The Oligocene Lyons flora of northwestern Oregon. The Ore Bin 35: 37-53.

Meyer, H. W. 2003. The fossils of Florissant. Washington DC, Smithsonian, 258 p.

Meyer, H. W., and S. R. Manchester. 1997. The Oligocene Bridge Creek flora of the John Day Formation, Oregon. University of California Publications in geological Sciences 141: 1-195.

Middleton, D.J., 1991. Infrageneric classification of the genus *Gaultheria* L.(Ericaceae). Botanical Journal of the Linnean Society 106: 229-258.

Miller, I. M., M. T. Brandon, and L. J. Hickey. 2006. Using leaf margin analysis to estimate the mid-Cretaceous (Albian) paleolatitude of the Baja BC block. Earth and Planetary Science Letters 245: 94-114.

Miller, M. M., D. J. Johnson, C. M. Rubin, H. Dragert, K. Wang, A. Qamar, and C. Goldfinger. 2001. GPS-determination of along-strike variation in Cascadia margin kinematics: Implications for relative plate motion, subduction zone coupling, and permanent deformation. Tectonics 20: 161-176.

Moore, E. J., 1963, Miocene marine mollusks from the Astoria Formation in Oregon, U.S. Geological Survey Professional Paper 419: 1-109.

Moore, E. J., and W. O. Addicott. 1987. The Miocene Pillarian and Newportian (Molluscan) Stages of Washington and Oregon and their usefulness in correlations from Alaska to California. U. S. Geologic Survey Bulletin 1664: A1-A13.

Motoi, T., W.-L. Chan, S. Minobe, and H. Sumata. 2005. North Pacific halocline and cold climate induced by Panamanian gateway closure in a coupled ocean-atmosphere GCM. Geophysical Research Letters 32: doi:10.1029/2005GL022844.

Newberry, J. S. 1898. Later extinct floras of North America. U. S. Geological Survey Monograph 35: 1-295.

Nie, Z.L., J. Wen, and H. Sun. 2007. Phylogeny and biogeography of Sassafras (*Lauraceae*) disjunct between eastern Asia and eastern North America. Plant Systematics and Evolution 267: 191-203.

Nikolaev, S. D. 1998. Neogene-Quaternary variations of the ‘Pole-Equator’ temperature gradient of the surface oceanic waters in the North Atlantic and North Pacific. Global and Planetary Change 18: 85-111.

Nixon, K.C. and J. M. Poole. 2003. (Vol. 06, 2003-12) Revision of the Mexican and Guatemalan Species of *Platanus* (Platanaceae). Lundellia 6: 103-137.

Oliver, E. 1934. A Miocene Flora from the Blue Mountains, Oregon, Middle Cenozoic Floras of Western North America. Carnegie Institution of Washington Publication 455: 1-27.

Orton, G. J. 1996. Volcanic environments, pp. 485-567 in H. G. Reading (ed.), Sedimentary Environments: Processes, Facies and Stratigraphy. Oxford, Blackwell.

Pavlyutin, B. I. 2007. Predstaviteli nadporiakh Ericanae is oligosenovoj voznovskoj flory Primorskogo kraja. Botanicheskii Zhurnal 92: 293-307.

Penhallow, D.P. 1908. Report on Tertiary plants of British Columbia collected by Lawrence M. Lambe in 1906: together with a discussion of previously recorded Tertiary floras. Canada Department of Mines 1013: 1-167.

Preist, G. R., N. M. Woller, and G. L. Black. 1983. Overview of the Geology of the Central Oregon Cascade Range, pp. 3-28 in G. R. Preist, and B. F. Vogt (eds.), Geology and Geothermal Resources of the Central Cascade Range. Oregon Department of Geology and Mineral Industries Special Paper 15.

Ramírez, J. L., and S. R. Cevallos-Ferriz. 2000. Leaves of Salicaceae (*Salix* and *Populus*) from Oligocene sediments near Tepexi de Rodriguez, Puebla, Mexico. International Journal of Plant Sciences 161:.521-534.

Reading, H. G., and J. D. Collinson. 1996. Clastic Coasts, pp. 688-702 in H. G. Reading (ed.), Sedimentary Environments: Processes, Facies, and Stratigraphy. Oxford, Blackwell.

Renne, P. R., A. L. Deino, R. C. Walter, B. D. Turrin, C. C. Swisher, T. A. Becker, G. H. Curtis, W. D.

Sharp, and A.-R. Jaouni. 1994. Intercalibration of astronomical and radioisotopic time. Geology 22: 783-786.

Renney, K. M. 1972. The Miocene Temblor flora of west-central California. Unpublished MSc thesis, University of California Davis, 106 pp.

Retallack, G.J. 2004a. Late Miocene climate and life on land in Oregon within a context of Neogene global change. Palaeogeography Palaeoclimatology Palaeoecology 214: 97-123.

Retallack, G.J. 2004b. Late Oligocene bunch grassland and early Miocene sod grassland paleosols from central Oregon, U.S.A. Palaeogeography Palaeoclimatology Palaeoecology 207: 203-237.

Retallack, G. J. 2007. Cenozoic Paleoclimate on Land in North America. Journal of Geology 115: 271-294.

Retallack, G.J. 2009. Greenhouse crises of the past 300 million years. Geological Society of America Bulletin 121: 1441-1455.

Retallack, G.J. 2018. Leaf litter taphonomy from a Eucalyptus woodland near Sydney, Australia. Alcheringa: volume 43 pages 71-84.

Retallack, G. J. and D. L. Dilcher. 1988. Reconstructions of selected seed ferns. Annals of the Missouri Garden 75: 1010-1057.

Retallack, G. J. and D. L. Dilcher. 2012. Core and geophysical logs versus outcrop for interpretation of Cretaceous paleosols in the Dakota Formation of Kansas. Palaeogeography Palaeoclimatology Paleoecology 329-330: 47-63.

Retallack, G.J., D. G. Gavin, E. B. Davis, N. D. Sheldon, J. M. Erlandson, M. H. Reed, E. A. Bestland, J. J. Roering, R. J. Carson, and R. B. Mitchell. 2016, Oregon 2100: projected climatic and ecological changes. University of Oregon Museum of Natural and Cultural History Bulletin 26: 1-21.

Ruddiman, W. F. (ed.). 1997. Tectonic Uplift and Climate Change. New York, Plenum Press, 535 pp.

Sanborn, E.I. 1947. The Scio flora of western Oregon. Oregon State College Studies in Geology 4: 1-47.

Sarna-Wojcicki, A. M., K. R. Lajoie, C. E. Meyer, and D. P. Adam. 1991. Tephrochronologic correlation of upper Neogene sediments along the Pacific margin, conterminous United States, pp. 117-140 in R.B. Morrison (ed.), Quaternary nonglacial geology; conterminous U. S.. Boulder, Geological Society of America.

Savin, S. M., L. Abel, E. Barrera, D. Hodell, J. P. Kennett, M. Murphy, G. Keller, J. Killingley, and E. Vincent. 1985. The evolution of Miocene surface and near-surface marine temperatures: Oxygen isotopic evidence, pp. 49-82 in J. P. Kennett (ed.), The Miocene Ocean: paleoceanography and biogeography. Boulder, Geological Society of America.

Schwerdtfeger, W. 1976. Climates of Central and South America. Amsterdam-Oxford-New York, Elsevier Scientific Publishing Company, pp. 527.

Scott, K. M. 1988. Origins, behavior, and sedimentology of lahars and lahar-runout flows in the Toutle-Cowlitz River System. U.S. Geological Survey Professional Paper 1447-A: 1-74.

Sealy, J. R. and D. A. Webb. 1950. *Arbutus unedo* L. Journal of Ecology 38: 223-236.

Searcy, K. B., and R. Ascher, R. 2001. The first record of *Populus heterophylla* (swamp cottonwood, Salicaceae) in Massachusetts. Rhodora 103: 224-226.

Selley, R. C. 2000. Applied Sedimentology. San Diego, Academic Press, 521 pp.

Sewall, J. O., and L. C. Sloan. 2006. Come a bit closer: A high-resolution climate study of the early Paleogene Laramide foreland. Geology 34: 81-84.

Sheldon, N.D. 2003. Pedogenesis and geochemical alteration of the Picture Gorge subgroup, Columbia River basalt, Oregon. Geological Society of America Bulletin 115: 1377-1387.

Sherrod, D. R., and J. G. Smith. 2000. Geologic Map of Upper Eocene to Holocene Volcanic and Related Rocks of the Cascade Range, Oregon. U.S. Geological Survey, scale 1:500,000.

Smiley, J. Gray and L. M. Huggins 1975. Preservation of Miocene fossils in unoxidized lake deposits, Clarkia, Idaho; with a section on fossil Insecta by WF Barr and JM Gillespie. Journal of Paleontology 49: 833-844.

Smiley, C. J. and L. M. Huggins. 1981. *Pseudofagus idahoensis*, n. gen. et sp.(Fagaceae) from the Miocene Clarkia flora of Idaho. American Journal of Botany 68: 741-761.

Smith, G. A. 1988. Sedimentology of proximal to distal vocaniclastics dispersed across an active foldbelt: Ellensburg Formation (late Miocene), central Washington. Sedimentology 35: 953-977.

Smith, H.V. 1938. Some new and interesting late Tertiary plants from Sucker Creek, Idaho-Oregon boundary. Torrey Botanical Club Bulletin 65:.557-564.

Smith, H.V. 1939. A flora of eastern American aspect in the Miocene of Idaho. Torrey Botanical Club Bulletin 66:.465-481.

Smith, H.V. 1941. A Miocene flora from Thorn Creek, Idaho. American Midland Naturalist 25: 473-522.

Soltis, P. S., D. E. Soltis, and C. J. Smiley. 1992. An rbcL sequence from a Miocene *Taxodium* (bald cypress). U. S. National Academy of Sciences, USA 89: 449–451.

Spicer, R. 1991. Plant taphonomic processes, pp. 71-113 in P. A. Allison, and D. E. G. Briggs (eds), Taphonomy: releasing the data locked in the fossil record. Plenum, New York.

Stockey, R.A. 1984. Middle Eocene *Pinus* remains from British Columbia. Botanical Gazette 145: 262-274.

Stults, D.Z. and B. Axsmith. 2015. New plant fossil records and paleoclimate analyses of the late Pliocene Citronelle Formation flora, US Gulf Coast. Palaeontologia Electronica 18: 1-35.

Su, T., Xing, Y.-W., Liu, Y.-S., Jacques, F.M.B., Chen, W.-Y., Huang, Y.-J. and Zhou, Z.-K. 2010. Leaf margin analysis: a new equation from humid to mesic forests in China. Palaios 25, 234-238

Swanson, D. A. 1989. Geologic maps of the French Butte and Greenhorn Buttes Quadrangles, Washington, U. S. geological Survey Open-File Report 89-309, 3 Sheets p.

Tanai, T., and J. A. Wolfe. 1977. Revisions of *Ulmus* and *Zelkova* in the middle and late Tertiary of western North America. U. S. Geological Survey Professional Paper 1026: 1-11.

Thompson, R. S., K. H. Anderson, and P. J. Bartlein. 1999. Atlas of relations between climatic parameters and distributions of important trees and shrubs in North America. U. S. Geological Survey Professional Paper 1650C: 1-422.

Tucker, M. E. 2003. Sedimentary Rocks in the Field. West Sussex, Wiley, 234 pp.

USDA, NRCS. 2009. The PLANTS Database (http://plants.usda.gov, 6 April 2009). National Plant Data Center, Baton Rouge, LA 70874-4490 USA.

Verplanck, E. P. 1985. Temporal variations in volume and geochemistry of volcanism in the western Cascades, Oregon. Unpublished Ph.D. thesis, Oregon State University, Corvallis, 115 p.

Vessell, R. K., and D.K. Davies. 1981. Nonmarine sedimentation in an active fore arc basin. Society of Economic Paleontologist and Mineralogist Special Publication 31: 31-45.

Wang, N. and B. H. Tiffney. 2001. Seeds of *Rhododendron* (Ericaceae) from the Late Eocene of California. Palaeontographica B259: 245-254.

Warwick, P. D., E.A. Johnson, and I. H. Khan. 1998. Collision-induced tectonism along the northwestern margin of the Indian subcontinent as recorded in the Upper Paleocene to Middle Eocene strata of central Pakistan (Kirthar and Sulaiman Ranges). Palaeogeography Palaeoclimatology Palaeoecology 142: 201-216.

Webb, S. D. 2008. Revision of the extinct Pseudoceratinae (Artiodactyla: Ruminantia: Gelocidae). Florida Museum of Natural History Bulletin.48: 17-58

Wells, R. E., C. S. Weaver, and R. J. Blakely. 1998. Fore-arc migration in Cascadia and its neotectonic

Fore-arc migration in Cascadia and its neotectonic significance. Geology 26: 759-762.

Whiting, E. T., D. W. Steadman, and J. Krigbaum. 2016. Paleoecology of Miocene crocodylians in Florida: Insights from stable isotope analysis. Palaeogeography, Palaeoclimatology, Palaeoecology 451:.23-34.

Whittemore, A. T. 2004 Sawtooth oak (*Quercus acutissima*, Fagaceae) in North America. Sida Contributions to Botany 21: 447-454.

Wildscreen Arkive, 2018. Species (http://www.arkive.org/, 16 June 2018). Wildscreen USA, 888 17th Street NW, Washington DC 20006

Wilf, P. 1997. When are leaves good thermometers? A new case for leaf margin analysis. Paleobiology 23: 373-390.

Wilf, P., S. L. Wing, D. R. Greenwood, and C. L. Greenwood. 1998. Using fossil leaves as paleoprecipitation indicators: An Eocene example. Geology 26: 203-206.

Wilson, D.S. 1989. Deformation of the so-called Gorda Plate. Journal of Geophysical Research 94: 3065-3075.

Wing, S., L., and D. R. Greenwood. 1993. Fossils and fossil climate: the case for equable continental interiors in the Eocene. Royal Society of London Biological Sciences Philosophical Transactions B341: 243-252.

Wing, S. L., G. J. Harrington, F. A. Smith, J. I. Bloch, D. M. Boyer, and K. H. Freeman. 2005. Transient Floral change and Rapid Global Warming at the Paleocene-Eocene Boundary. Science 310: 993- 996.

Winkworth, R. C. and M. J. Donoghue. 2005. *Viburnum* phylogeny based on combined molecular data: implications for taxonomy and biogeography. American Journal of Botany 92: 653-666.

Wofford, A.M., Finch, K., Bigott, A. and Willyard, A. 2014. A set of plastid loci for use in multiplex fragment length genotyping for intraspecific variation in *Pinus* (Pinaceae). Applications in plant sciences 2(5); 140002.

Wolfe, J. A. 1964. Miocene floras from Fingerrock Wash, southwestern Nevada. U. S. Geologic Survey Professional Paper 454-N: 1-36.

Wolfe, J. A. 1966. Tertiary plants from the Cook Inlet Region, Alaska. U. S. Geological Survey Professional Paper 398-B: 1-29.

Wolfe, J. A. 1968. Paleogene biostratigraphy of nonmarine rocks in King County, Washington. U. S. Geological Survey Professional Paper 571: 1-33.

Wolfe, J.A. 1977. Paleogene floras from the Gulf of Alaska region. U. S. Geological Survey Professional Paper 997: 1-105.

Wolfe, J. A. 1979. Temperature parameters of humid to mesic forests of Eastern Asia and relation to forests of other regions of the Northern Hemisphere and Australasia, U. S. Geological Survey Professional Paper 1106: 1-37.

Wolfe, J. A. 1993. A method of obtaining climatic parameters from leaf assemblages. U. S. Geological Survey Bulletin 2040: 1-67.

Wolfe, J. A. 1994. Tertiary climatic changes at middle latitudes of western North America. Palaeogeography Palaeoclimatology Palaeoecology 108: 195-205.

Wolfe, J. A., and T. Tanai. 1980. The Miocene Seldovia Point Flora from the Kenai Group, Alaska. United States Geological Survey Professional Paper 1105: 1-52.

Woodruff, F., and S. M. Savin. 1989. Miocene deep water oceanography. Paleoceanography 4: 87-140.

Wu, J., B. Sun, B., Y. S. C. Liu, S. Xie, and Z. Lin. 2009. A new species of *Exbucklandia* (Hamamelidaceae) from the Pliocene of China and its paleoclimatic significance. Review of Palaeobotany and Palynology 155: 32-41.

Yang, Z-Y., J.H. Ran, and X-Q. Wang. 2012. Three genome-based phylogeny of Cupressaceae s.l.: Further evidence for the evolution of gymnosperms and southern hemisphere biogeography. Molecular Phylogenetics and Evolution 64: 452–470.

Youngblood, A., T. Max, and K. Coe. 2004. Stand structure in eastside old-growth ponderosa pine forests of Oregon and northern California. Forest Ecology and Management 199:.191-217.

Zachos, J., L. D. Stott, and K. C. Lohmann. 1994. Evolution of early Cenozoic marine temperatures. Paleoceanography 9: 353-387.

Zachos, J., M. Pagani, L. Sloan, E. Thomas, and K. Billups. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. Science 292: 686-692.

Zhang, J.-B., R.-Q. Li, X.-G. Xiang, S. R. Manchester, L. Lin, W. Wang, J. Wen, Z.-D. Chen. 2013. Integrated fossil and molecular data reveal the biogeographic diversification of the eastern Asian-eastern North American disjunct hickory genus (*Carya* Nutt.). PloS One 8.7: e70449.

MUSEUM
OF NATURAL
AND CULTURAL
HISTORY