
Miocene floristic change at 15 Ma, Nevada to Washington, U.S.A.

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Mid-Miocene floras from the western interior regularly have numerous exotics allied to broad-leaved deciduous hardwoods and conifers now in the eastern United States and Asia. Successive floras from local areas show that exotics were eliminated first from western Nevada, later in Oregon and Washington to the north where precipitation was higher, as it is today. Precipitation requirements of allied modern species suggest that the exotics were reduced significantly at 15 Ma as summer rainfall (May-August) decreased to < 35 per cent of the annual total. The decrease seems attributable to the spread of the East Antarctic ice sheet (15 Ma) and resultant cold water upwelling that produced drier summers. Commencing 8-7 Ma, the spread of the West Antarctic ice sheet and Arctic polar ice, with resultant further cold water and drier summers, continued to reduce exotics and confine them to relict sites in mild coastal areas down to the close of the Tertiary.

Key-words—Palaeoecology, Floristic change, Miocene, U.S.A.

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सारांश

नेवादा से वाशिंगटन (संयुक्त राज्य अमेरिका) तक 15 एम-ए० वर्ष के आस-पास मध्यनूतन युगीन वनस्पतिजातीय परिवर्तन

डेनियल आई० एक्सलरॉड

पश्चिमी देशाभ्यन्तरीय मध्य-मध्यनूतन वनस्पतिजातों में निरन्तर कोनिफर एवं चौड़ी-पत्ती वाले पर्णपाती कठोरकाष्ठ वाले अनेक विदेशी अवयव मिले हैं। ये अवयव अब पूर्वी संयुक्त राज्यों एवं एशिया में भी मिलते हैं। स्थानीय क्षेत्रों के उत्तरोत्तर वनस्पतिजातों से व्यक्त होता है कि विदेशी अवयवों का पहले पश्चिमी नेवादा से तथा बाद में ओरिगन एवं वाशिंगटन से उत्तर की ओर स्थानांतरण हो गया था जहाँ कि इस समय की ही तरह अधिक वर्षा होती थी। अन्य सम्बद्ध वर्तमान प्रजातियों की पानी की आवश्यकता से प्रस्तावित होता है कि 15 एम-ए० वर्ष के आस-पास जब ग्रीष्मकालीन वर्षा में 35 प्रतिशत कमी हुई तब इन विदेशी वर्गों की संख्या में उल्लेखनीय कमी हो गई। वर्गों में यह कमी पूर्व अंटार्कटिक हिमाच्छादन तथा फलस्वरूप ग्रीष्म ऋतु में परिवर्तित ठंडे पानी के कारण भी हो सकती है। इसके पश्चात् इस पूर्व अंटार्कटिक हिमाच्छादन तथा ठंडे पानी के प्रभाव से इन विदेशी वर्गों की संख्या में और कमी हो गई तथा तृतीयक कल्प के अन्त तक ये उपयुक्त तटीय क्षेत्रों तक ही सीमित रह गये।

MIOCENE FLORAL SEQUENCES

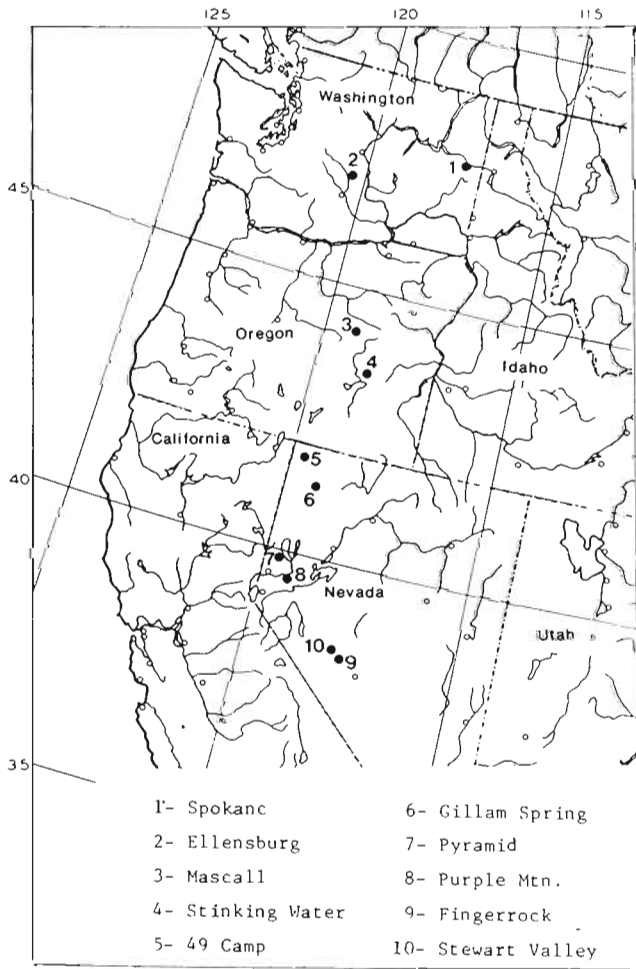
Miocene floras distributed for over 1,100 km from southwest Nevada to eastern Washington show that exotic deciduous hardwoods and conifers allied to those now in eastern United States and Asia disappeared first at the south, later in the north (Text-figure 1).

Nevada

Southwestern Nevada—The Fingerrock and Stewart Valley (formerly termed Stewart Spring) floras described by Wolfe (1964; Schorn, in prep. for Stewart Valley; Axelrod, for larger Fingerrock flora, UC Davis collection) occur in southwestern Nevada.

The Fingerrock flora is dated at 16.4 Ma by andesite flows and breccias directly above and below the flora in the upper Gilbert Andesite, with the age of the uppermost breccia 15.1 Ma. The Stewart Valley floras occur in the Savage Canyon formation that unconformably overlies Gilbert Andesite (Schorn *et al.*, 1989). Mammals of Barstovian age are in the basal sediments of the Savage Canyon Formation. The lower floras are as old as 14.6-14.8 and the higher floras probably range up to 14.0 Ma or somewhat less.

The Fingerrock has a number of broadleaved



Text-figure 1—Location of Miocene floras to which reference is made.

deciduous hardwoods representing eastern exotic taxa. Among these are species of *Acer* (3 sp.), *Alnus*, *Betula*, *Carya*, *Diospyros*, *Eugenia*, *Gymnocladus*, *Malus*, *Photinia*, *Populus*, *Quercus* (2 spp.), *Robinia*, *Sophora*, *Ulmus* and *Zelkova*, some of which (*) are especially abundant and probably were subdominants of the vegetation. Associates included species of *Abies*, *Picea*, *Pinus*, *Tsuga*, *Chamaecyparis*, *Acer*, *Amelanchier*, *Mahonia*, *Ribes*, and *Sorbus*. Members of broad-leaved evergreen sclerophyll forest, notably *Arbutus*, *Cercocarpus*, *Garrya*, *Lithocarpus* and *Quercus*, are also present.

The Fingerrock section yielded two florules at the initial site in Juniper Draw, but the specimens were mixed originally (Wolfe, 1964). Two florules also occur along Golddyke road 1.5 km east. In each area, the younger florules, separated by scarcely 30-40 m stratigraphically, are not so rich in exotic deciduous hardwoods, broadleaved sclerophyll taxa (*Arbutus*, *Garrya*, *Cercocarpus*, *Lithocarpus*,

Quercus, *Mahonia*) are more abundant and so are conifers that include species of *Calocedrus*, *Juniperus*, *Sequoiadendron* and *Thuja* not recorded at the original lower site in Juniper Gulch.

None of the deciduous hardwoods of eastern alliance that characterize the Fingerrock florules have been recovered from the well-sampled Stewart Valley flora. Taxa of Madrean alliance, such as, *Arbutus*, *Garrya*, *Juglans*, *Lyonothamnus*, *Populus*, *Quercus*, *Rhus* (*Schmaltzia*) and *Sapindus*, all similar to species now in Arizona-Mexico and California, are represented. This flora has a number of conifers that formed a mixed conifer forest on bordering, cooler slopes. These included species of *Abies*, *Chamaecyparis*, *Picea* (winged seeds very abundant), and *Pinus* together with *Amelanchier*, *Arctostaphylos*, *Holodiscus*, *Philadelphus*, *Prunus*, *Ribes* and *Salix*.

Of the 44 species in the siliceous shales of the Lower Fingerrock flora, 21 exotics represent 48 per cent of the species.

West-central Nevada—Two floras in this area are the Pyramid near the lake of that name and the Purple Mountain near Fernley, 40 km south. The Pyramid flora is preserved in diatomite interbedded with andesite and basalt flows. The Pyramid is dated at 15.6 Ma and the lower Purple Mountain at 14.7 or 14.8 (in Bonham, 1969).

The Pyramid flora is wholly dominated by exotic deciduous hardwoods distributed among *Acer* (4 spp.), *Aesculus*, *Alnus* (3 spp.), *Betula* (2 spp.), *Ostrya*, *Pterocarya*, *Cladastris*, *Quercus*, *Sophora* and *Taxodium*. These dominated the lake shore area for they account for over 1,300 of the 1,400-odd identified specimens. The 17 exotics in this flora of 41 species represent 44 per cent of the species; fewer Pyramid exotics than at Fingerrock reflect the much larger Fingerrock sample. Bordering slopes supported species of two vegetation zones. Broad-leaved sclerophyll forest species of *Arbutus*, *Chrysolepis* and *Lithocarpus* occupied warmer sites. Cooler slopes provided conditions favourable for a mixed conifer forest of *Abies*, *Calocedrus*, *Picea*, *Pinus*, with associates of *Amelanchier*, *Fraxinus*, *Populus*, *Ribes*, *Rosa* and *Sorbus*. Remains of both zones are rare in the flora probably because they occupied well drained slopes and alluvial fans of the bordering dacitic plugs that towered over the basin.

The Purple Mountain flora (Axelrod, ms.) is represented by nine florules distributed stratigraphically for fully 600 m. Exotic deciduous hardwoods in the lower two florules include species of *Acer*, *Betula*, *Gymnocladus*, *Quercus*, and *Glyptostrobus*. They account for a total of 49 specimens distributed among nine species that

represent only 0.87 per cent of the total flora of 5,600 specimens. Of the 65 woody species in the flora, the nine exotics represent 14 per cent of the species. All the florules are dominated by species of vegetation zones that occur in the Pyramid flora but are rare there. Mixed conifer forest at Purple Mountain included *Abies*, *Larix*, *Picea*, *Pinus*, *Pseudotsuga*, *Tsuga*, *Torreya* and *Sequoiadendron* with associates of *Amelanchier*, *Ceanothus*, *Leucothoe*, *Prunus*, *Rosa* and *Vaccinium*. Its broad-leaved sclerophylls included *Arbutus*, *Chrysolepis*, *Cercocarpus*, *Heteromeles*, *Lithocarpus* and *Lyonothamnus* that largely occupied warmer sites on the broad volcanic plain where the flora lived.

Northwestern Nevada—The 49-Camp flora occurs in diatomite associated with tuffaceous sediments of the High Rock Sequence, dated at 16 Ma (Bohnam, 1969). These sediments have been traced eastward where they unconformably overlie Canyon Rhyolite, and in Long Valley and High Rock Canyon have yielded mammalian faunas of Barstovian age (faunal lists in Bohnam, 1969).

The 49-Camp flora (LaMotte, 1936) has 21 exotics distributed in *Acer*, *Ailanthus*, *Carya*, *Cedrela*, *Cercidiphyllum*, *Cocculus*, *Fagus*, *Nyssa*, *Ptelea*, *Oreopanax*, *Populus*, *Quercus*, *Sassafras*, *Tilia* and *Ulmus*. Of the 38 woody species in the flora (revised), exotics make up 55 per cent of the assemblage. Associates included members of a mixed conifer forest with *Abies*, *Chamaecyparis* and *Pinus* as well as *Acer*, *Fraxinus*, *Populus*, *Prunus* and *Rosa*. A few broad-leaved evergreen sclerophyll species are present, notably *Arbutus* and *Quercus*.

The Gillam Spring flora (UC Davis collection) situated 70 km southeast, comes from lake beds of High Rock Sequence that rest unconformably on Canyon Rhyolite (Bohnam, 1969). Two florules are present, separated by about 40 m stratigraphically and a distance of 1.6 km. The lower florule, associated with coarse clastics, has an abundant exotic oak (*Quercus eoprinus*), and the common Miocene *Quercus simulata*, both of which required moist sites. Associated in this lower florule are species of *Acer*, *Pinus* (2-needled), *Chamaecyparis*, *Picea* (only a single seed), *Prunus* and *Quercus* (cf. *Q. chrysolepis*). By contrast, the upper florule is dominated by scores of winged seeds of *Picea*. Other mixed conifer forest species include *Abies*, *Calocedrus*, *Chamaecyparis*, *Pinus* and *Sequoia* with associates of *Mahonia*, *Prunus* and *Salix*. This upper florule has eight exotics, all quite rare, being represented by one or two specimens of *Acer* (2), *Alnus*, *Crataegus*, *Glyptostrobus*, *Robinia* and *Ulmus*. They account for a total of eight species in a florule of 30 taxa, and represent 26 per cent of the

assemblage. The exotic species include a total of 17 specimens among the 1,500 collected in this upper florule—numerically specimens of the exotics represent only 1.1 per cent of the flora.

This floral sequence closely parallels that in the lower Purple Mountain flora where rare exotics are rapidly displaced by members of a rich mixed conifer forest and broad-leaved sclerophyll vegetation.

Oregon

Two floras in central Oregon that provide a basis for comparison are the Mascall and Stinking Water (Chaney, 1959). The Mascall is dated at 15.8 Ma (Evernden & James, 1964), whereas the Stinking Water overlies basalts dated at 13.4 Ma and nearby lake beds yield the Juntura mammalian fauna of Clarendonian age (Shotwell, 1963).

The large Mascall flora represents a swamp-cypress forest with deciduous hardwoods and conifers converging the bordering slopes.

Among the exotics are such conifers as *Cephalotaxus*, *Ginkgo*, *Keteleeria*, *Metasequoia* and *Taxodium*, with associates of *Acer*, *Alnus*, *Betula*, *Carya*, *Cercidiphyllum*, *Diospyros*, *Fagus*, *Fraxinus*, *Gymnocladus*, *Hydrangea*, *Hamamelis*, *Laurophyllum*, *Liquidambar*, *Ostrya*, *Persea*, *Pterocarya*, *Quercus*, *Sassafras*, *Ulmus* and *Zelkova*. Specimen counts indicate that these make up 82 per cent of 10,000 specimens, with 48 exotics accounting for 70 per cent of the 68 woody species.

The Stinking Water flora from sites 120 km southeast, has fewer exotics. These include 14 species distributed in *Glyptostrobus*, *Keteleeria*, *Acer*, *Cedrela*, *Gymnocladus*, *Hydrangea*, *Ptelea*, *Pterocarya*, *Quercus*, *Smilax* and *Ulmus*. Although they account for 58 per cent of the 2,300 specimens recorded, the exotics make up only 35 per cent of the woody flora of 39 species.

Washington

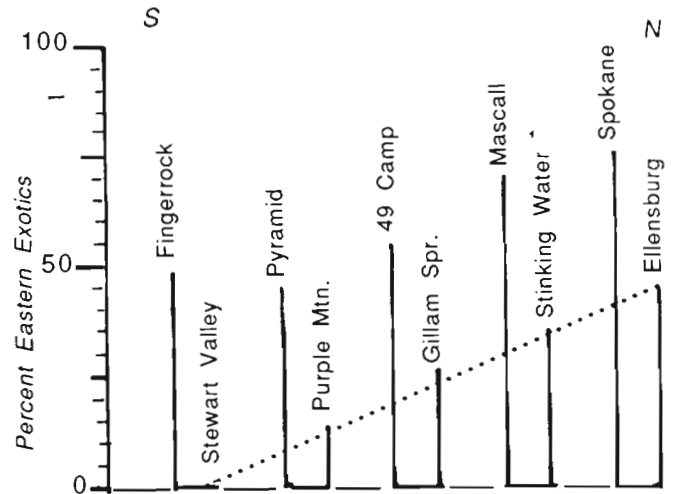
The rich Latah flora at Spokane (Knowlton, 1926; Chaney, 1959, p. 109, revised list) is interbedded with Columbia River Basalt dated at 15.8 Ma (Reidel & Hooper, 1989). The flora includes numerous exotics. Among these are such conifers as *Cephalotaxus*, *Fokienia*, *Ginkgo*, *Keteleeria* and *Taxodium*. Exotic dicots include species of *Acer*, *Alnus*, *Betula*, *Castanea*, *Cocculus*, *Comptonia*, *Exbucklandia*, *Fagus*, *Hydrangea*, *Ilex*, *Liquidambar*, *Liriodendron*, *Persea*, *Machilis*, *Magnolia*, *Sophora*, *Ulmus* and *Zelkova*. These total 50 of the 67 woody species, or about 75 per cent of the woody flora. Unfortunately, numerical counts of species abundance were not made for this flora which was

The Ellensburg flora, situated 250 km to the southwest, is preserved in sediments conformably above the Wenas Basalt (14 Ma) and includes the rich Tyrrell florule in its lower portion (Smiley, 1963). It was dated from a tuff at 10.9 Ma (Evernden & James, 1964), but this disagrees with mammalian evidence (Smiley, 1963, p. 202) that Clarendonian age mammals occur well above the florule which suggests it probably is of Late Barstovian age (i.e., 14-13.6 Ma). Exotics in the Tyrrell florule are represented by species of *Acer*, *Alnus*, *Carya*, *Crataegus*, *Celtis*, *Ilex*, *Liquidambar*, *Nyssa*, *Passiflora*, *Paulownia*, *Persea*, *Platanus*, *Ptelea*, *Quercus*, *Robinia* and *Zelkova*. The 17 exotics include a total of 1,286 specimens among the 1,662 in this florule. The exotics, distributed among 38 woody species, represent 44 per cent of the florule.

DISCUSSION

In the Miocene of western North America, sequential floras from generally local areas distributed north-south in the lee of the present Sierra Nevada and Cascade ranges, show a major trend in representation of exotic taxa. Floras dated at 16-15 Ma are rich in exotics allied to species now in the eastern United States and Asia. The record shows that these increased to the north, with the Mascall and Latah (Spokane) floras the richest in exotics. Post-15 Ma floras record the rapid elimination of eastern exotics at the south by 14.8 Ma, yet they were still important in floras to the north. The general relations charted in Text-figure 2 show the percentage of exotic species in the floras.

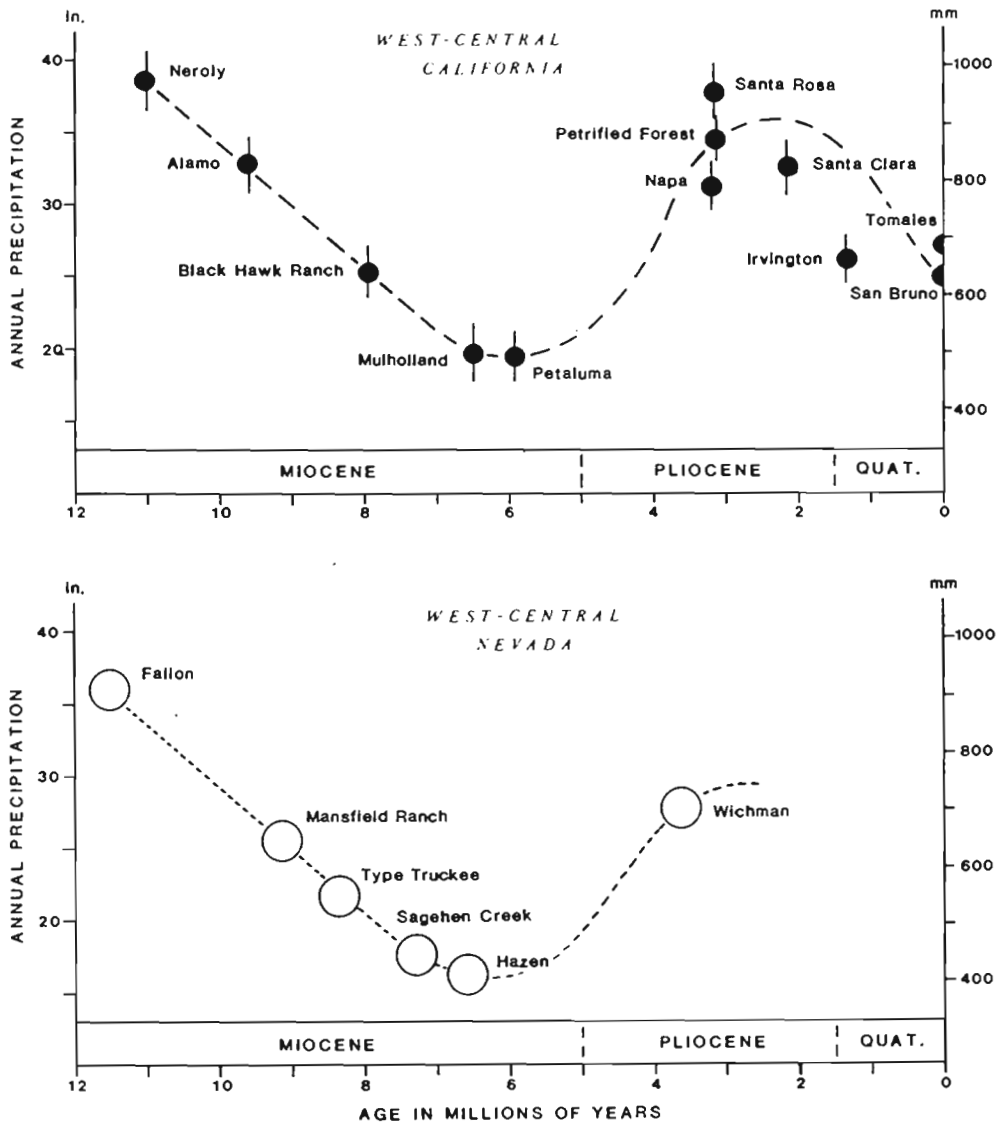
The progressive increase of exotics to the north reflects higher precipitation there, much as today. The decrease in exotics following 15 Ma resulted from the reduction in summer rainfall. At present, in areas of deciduous hardwoods on the western Great Plains (Longitude 95° W), in Iowa, Missouri and Oklahoma, warm season precipitation (May-August) averages 380-455 mm (15-16 inches). As it decreases to the west, deciduous hardwoods allied to those in the western Miocene floras are rapidly reduced and disappear. The relations suggest that as ample precipitation fell below a critical level of 75-90 mm (3.0-3.5 inches) each summer month, the diversity and abundance of deciduous hardwoods rapidly decreased (Axelrod, 1992). This is implied also by climatic data for areas of northeastern Turkey (Rise) and Soviet Georgia (nr. Sukumi) where deciduous hardwoods also find their distributional limits where summer precipitation is 35-40 per cent of the yearly total.



Text-figure 2—Percentage of exotic species in the floras. The progressive northward increase of exotics in post-15 Ma floras reflects higher summer precipitation there.

The increase in summer precipitation northward, as inferred from the higher representation of exotics there, probably is not the result of a topographic effect. The Sierra Nevada was not appreciably elevated until ≈ 5 Ma (Axelrod, 1980a; Unruh, 1991). The Miocene volcanics of the Cascades were not deformed until the later Tertiary and its volcanos (Mt. Shasta to Mt. Rainier) were constructed in the Quaternary (Baldwin, 1976).

The reduction in exotic species at 15 Ma represents a basic climatic relationship. The marine record shows that temperature decreased significantly in the deep ocean in the middle Miocene (Savin *et al.*, 1975). This resulted in the flourishing of deep-water diatoms and in the deposition of thick diatomite in California (summary in Reed, 1951; Woodring *et al.*, 1940; Bramlette, 1949). This event reflects the spread of the East Antarctic ice sheet at 15 Ma (Kennett, 1977). With cold water flowing northward into all ocean basins, upwelling along the west coast resulted in decreased summer rainfall. Saturated air masses moving onto the continent were being warmed and hence were more stable and less likely to produce summer rain. The cooling trend was supplemented at *circa* 8-7 Ma by the spread of the West Antarctic ice field and by glaciation in the Coast Ranges of Alaska-British Columbia and in the arctic basin. This time corresponds to the driest part of the Tertiary in coastal California and also in Nevada (Text-figure 3), as judged by the relations of such floras as the Mulholland and Petaluma in California, and the Truckee floras (Hazen, Sagehen Creek) in western Nevada. By this time only a few exotics were persisting as relicts in the mild coastal strip.



Text-figure 3—Floristic trends showing the driest part of the Tertiary in central California and western Nevada (from Axelrod, 1980b).

Further evidence that the Miocene floristic changes in the area from Nevada to Washington reflect climatic modification is indicated by the close correspondence with the Neogene floristic changes reported for Alaska (Wolfe, Hopkins & Leopold, 1966; Wolfe, 1981). In that area the transition between the Seldovian-Homerian stages is at 15 Ma and that between the Homerian and Clamgulchian occurred at 8 Ma. That comparable floristic changes occur on other continents, and especially in the western Mediterranean at these times, is a problem for future investigation.

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