

EVOLUTION OF THE CALIFORNIAN CLOSED-CONE PINE FOREST

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ABSTRACT

Fossil closed-cone pines similar to Californian species that now inhabit maritime and interior areas were already established as distinct adaptive groups in Miocene time. Their fossil associates suggest that floristically the closed-cone pine forests are part of the Madro-Tertiary Geoflora. Species ancestral to the pines and their associated endemics evidently represented members of a highly temperate phase of the geoflora that reached the coastal strip in Oligocene time. The pines and their associates probably did not evolve in insular isolation, but in the temperate uplands in the interior. As more extreme climates developed there, the pine forests migrated coastward to survive under mild maritime climate, and also southward where related species persist in the uplands of Mexico under highly temperate climate.

INTRODUCTION

Closed-cone pines of California and Baja California contribute to forests dominated by trees of generally small size that have persistent cones. They comprise two divergent adaptive groups, maritime and interior. The maritime species (*Pinus muricata*, *P. radiata*, *P. remorata*) form stands that are scattered discontinuously along the outer coast and on islands from near Trinidad Head south for 1,100 miles to Cedros Island (fig. 1). *P. muricata* has the greatest range, extending from the far north (Trinidad Head) to the far south (Cedros Island). *P. radiata* occurs near Año Nuevo Point, at Monterey-Carmel, San Simeon-Cambria, and on Guadalupe and Cedros¹ islands where it is represented by the variety *binata*. *P. remorata* is on Santa Cruz and

1. This report of its Cedros Island occurrence is based on specimens in the U.C.L.A. Herbarium (southernmost grove, Haines and Hale, 1939), and also the type specimen of *Pinus muricata* var. *cedrosensis* Howell (Calif. Acad. Sci.).

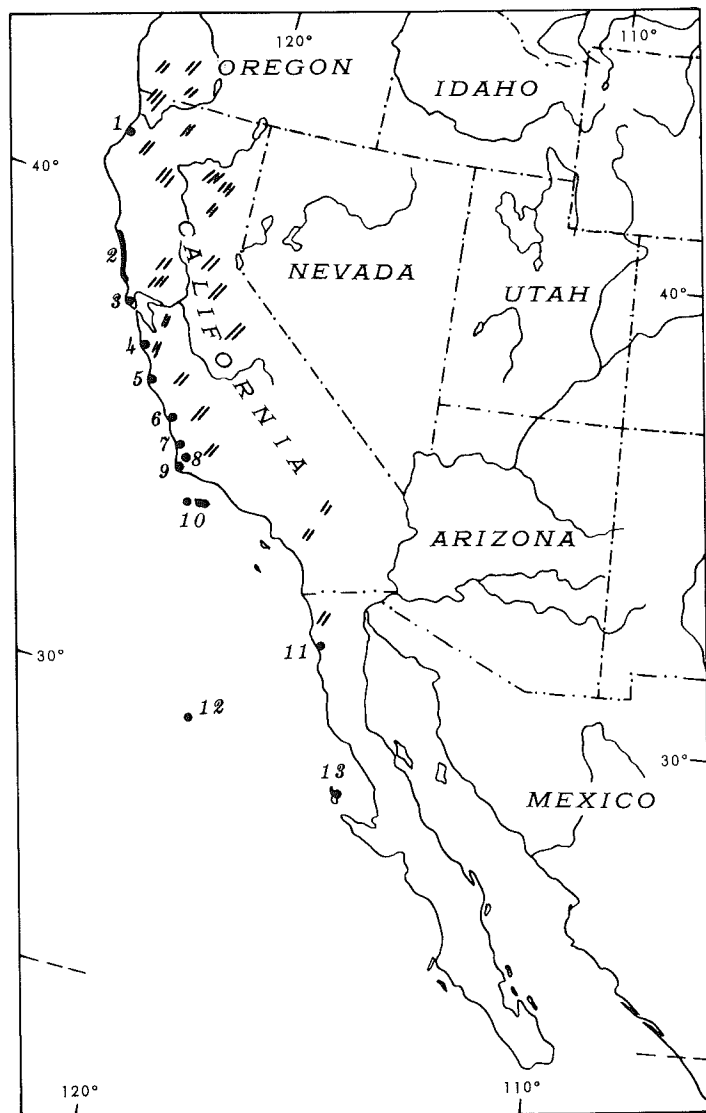


Fig. 1. Present distribution of closed-cone pines (areas exaggerated). Patches of maritime pines occur at 1—Trinidad Head; 2—Ingelnook - Point Arena; 3—Inverness Ridge; 4—Año Nuevo Point; 5—Monterey-Carmel; 6—Cambria-San Simeon; 7—San Luis Range; 8—La Purisima Hills-Burton Mesa; 9—west end of Santa Ynez Mountains; 10—Santa Cruz and Santa Rosa islands; 11—near San Vicente; 12—Guadalupe Island; 13—Cedros Island. The lined areas away from the coast show approximately the distribution of the interior species, *Pinus attenuata*.

Santa Rosa islands, on Cedros Island², and on the mainland near Lompoc, California (Pine Canyon; Lompoc oil field) and near San Vicente, Baja California (one mile west of mouth of Cañon de las Pinitas). *P. attenuata*, the sole living member of the interior alliance, occupies well-drained middle mountain slopes scattered from southwestern Oregon southward in the Coast Ranges and Sierra Nevada (to Mariposa County), with relict stands in southern California (San Bernardino Mountains, Santa Ana Mountains) and northern Baja California (east of Ensenada).

Analysis of the geologic history of the pines is made difficult by two circumstances. First, the sample available for study is exceedingly limited because the pines from rocks older than late Pleistocene usually are represented by only one or two specimens at each site, and the cones are not always complete. That the fossil record of the group should be meager is wholly consistent with the ecologic occurrence of the trees that comprise its two divergent adaptive groups. The species (*Pinus radiata*, *P. muricata*, *P. remorata*) now confined to the coastal strip and the islands have had such an occurrence throughout most of their recorded history. Although the structures (cones, needles, wood) that were contributed by the forest to sites of deposition on floodplains, at lake margins, and in lagoonal to littoral areas during the Tertiary no doubt formed rich deposits, this record was largely destroyed by uplift and erosion that accompanied the middle Pleistocene orogeny that affected the entire region (Reed, 1933; Jahns, et al., 1954; King, 1958). Thus it is wholly to be expected that remains of closed-cone pines in rocks that are of lower Pleistocene and greater age would be represented chiefly by occasional cones transported into basins and preserved in offshore deposits. It is also to be expected that the richest records that might be preserved would be those in the relatively undisturbed coastal deposits of upper Pleistocene age, which have provided several excellent sites, notably the Tomales (Mason, 1934), Carpinteria (Chaney and Mason, 1933) and Willow Creek (Chaney and Mason, 1930) floras. On the other hand, the interior species (*P. attenuata*) that represents the alliance now inhabits dry, well-drained slopes in mountainous areas. Since the fossil record indicates that a pine (*P. pretuberculata*) scarcely distinguishable from it occupied similar sites during the late Miocene (Condit, 1944) and Pliocene (Axelrod, 1937, 1958a), it would hardly be expected to contribute importantly to a fossil record

2. Records of its Cedros Island occurrence are represented by specimens identified as *Pinus muricata* var. *cedrosensis* Howell, filed in the herbaria at San Diego Mus. Nat. Hist., Calif. Acad. Sci., and Univ. Calif., Berkeley.

accumulating in lowland basins of deposition in the interior. Since the fossils are represented by very few specimens, the degree of variation of these older fossil pines is virtually unknown; and since the living species display variation in cone morphology, and notably so in *Pinus muricata*, it may not always be possible to determine the closest relative of a fossil species that is based on limited or fragmentary material. This might lead to errors in identification, and hence to misconceptions in terms of reconstructing phylogenetic relations. And second, since the species can produce fertile hybrids today, and presumably were able to do so in the past, occasional cones might be expected in the record that represent natural hybrids. If unrecognized, the cone of a fossil hybrid could distort the evidence in terms of analyzing the interrelations of the species (see discussion under *P. masonii* and *P. attenuata*).

In his pioneering studies of the history of the forest, Mason (1932, 1934) was well aware of the limitations posed by the problem of interpreting its history and evolution. As he has emphasized, since any hypothesis of the evolution of a modern group of species represented in the fossil record is based on fragmentary evidence, and notably so in the present case, tentative suggestions concerning their early history may be expected to require modification as new fossils become available. During the past 30-odd years only a few additional fossil cones have been added to the few previously known from rocks older than upper Pleistocene. Together with new tectonic, stratigraphic, and paleobotanic data they furnish evidence that suggests a considerably different evolutionary history for the forest than that proposed by Mason.

The new occurrences of fossil closed-cone pines that provide a basis for analyzing the evolutionary history of the forest include the following (see section on Systematic Paleontology):

Pinus radiata Don

1. Potrero Canyon, Pacific Palisades, in beds probably equivalent to Timms Point silt. Early Pleistocene.
2. Crystal Springs Lake, south of San Francisco, in basal beds of Santa Clara formation. Early Pleistocene.
3. Rancho La Brea, Los Angeles. Late Pleistocene.
4. One mile south of Fleishacker Pool, San Francisco, in Thornton Beach formation. Early Pleistocene.
5. Point Sal Ridge, in Orcutt formation. Late Pleistocene.

Pinus muricata Don

1. Near Wilmington, California, in upper San Pedro formation. Early Pleistocene.
2. Point Sal Ridge, in Orcutt formation. Late Pleistocene.

Pinus remorata Mason

1. Potrero Canyon, Pacific Palisades, in beds probably equivalent to Timms Point silt. Early Pleistocene.

2. Near Wilmington, California, in upper San Pedro formation. Early Pleistocene.

Pinus masonii Dorf

1. One mile north of Mussel Rock, San Francisco, in lower Merced formation. Middle Pliocene.
2. Santa Paula Creek, Ventura basin, in upper Pico formation. Late Pliocene.
3. Punta Gorda, 10 miles northwest of Ventura, California, in upper Pico formation. Late Pliocene.

Pinus lawsoniana Axelrod

1. Mussel Rock, San Francisco, in forest bed unconformably below the basal marine beds of the Merced formation. Early middle Pliocene, or older.
2. Santa Barbara, Monterey formation. Middle or upper Miocene.

Pinus pretuberculata Axelrod

1. Road cut at north end of Klamath Falls, Oregon, in beds of Pliocene age.

Apart from these new records that aid in interpreting the history of the forest, more recent geologic and paleontologic information in areas where pre-late Pleistocene closed-cone pines were earlier recovered indicates that previous age assignments for *P. masonii* Dorf must be revised. The localities for this species, which has been considered the oldest member of the alliance and possibly ancestral to the four living California pines (Mason, 1932), were earlier considered to be of lower Pliocene age. It is now known that they are in rocks of Plio-Pleistocene (Merced formation, two miles north of Mussel Rock) and upper Pliocene (Pitas Point, six miles northwest of Ventura) age.

AGE

The stratigraphic range of the closed-cone pines now known shows that both the *Pinus attenuata* and *P. radiata* alliances extend down into the Miocene, and the *P. muricata* line forms a continuum into the middle Pliocene at a minimum (fig. 2). Since the fossil cones of *P. pretuberculata* (*P. attenuata*), *P. lawsoniana* (*P. radiata*), and *P. masonii* (*P. muricata*) can scarcely be distinguished from those produced by living species, they probably have been distinct for a considerably longer time. The fossil equivalent of *P. remorata*, which has not yet been recovered from rocks below the Plio-Pleistocene transition, probably also extends well down into the Tertiary to judge from its distinctive morphology (small cones; cones normal to stem; cones rather symmetrical in outline; cone-scales plane; stems very brittle).

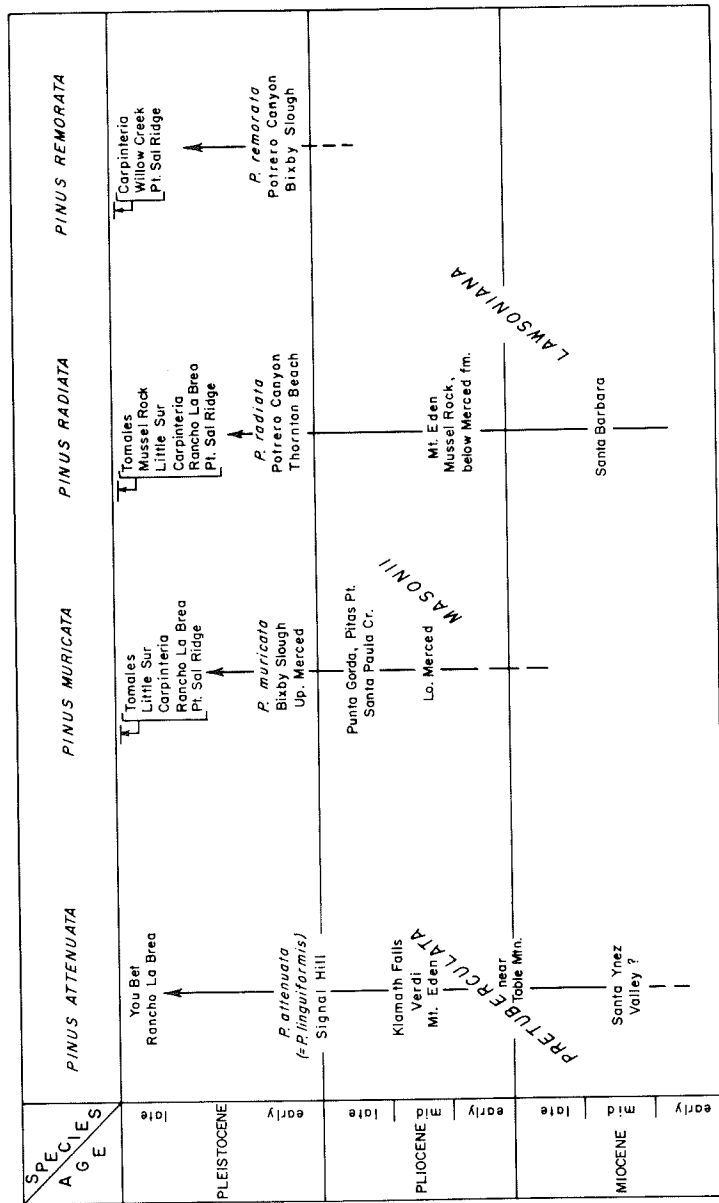


Fig. 2. Ages of localities where closed-cone pines have been recovered. The evidence suggests that essentially modern species were in existence by the Miocene.

The available records suggest that both the maritime and interior species that comprise the closed-cone pine alliance were evolving slowly during the middle and later Tertiary. This is paralleled by the comparatively slow rates of evolution indicated by fossil pines found elsewhere in the United States, and also in Europe. A number of American fossil pines were already very similar to living species in the Cretaceous and early Tertiary, as shown by the following list:

Fossil species	Similar living species	Occurrence	Age
clementsii	resinosa	Springfield, Minn.	late Cretaceous
Chaney			
crossii	aristata	Copper Basin, Nev.	late Eocene
Knowlton			
florissantii	ponderosa	Florissant, Colo.	early Oligocene
Lesquereux		Germer Basin, Ida.	mid-Eocene
prelambertiana	lambertiana	Del Mar, Calif.	mid-Eocene
Axelrod			
wheeleri	monticola	Bull Run, Nev.	late Eocene
Cockerell			
undescribed species	balfouriana	Thunder Mt., Ida.	mid-Eocene
undescribed species	murrayana	Bull Run, Nev.	late Eocene

Near-modern species were also established in Europe by the early Tertiary, and many are recorded in the Miocene and Pliocene (see Gaussen, 1960). Among these are the following, of which those marked by an asterisk are members of the section *Insignes*, to which the closed-cone pines belong:

Fossil species	Similar living species	Age
andrai Coemans	strobis aff.	late Cretaceous
hordacea Rossm.	strobis	Eocene
resurgens	taeda	Oligocene
heidingeri Unger		
gracilis Saporta	patula	Oligocene
paleodrymos Saporta	merkusii	Oligocene
thomasiana (Goepf.) Reich.	laricina	Oligocene
massalongii Sismonda	nigra	Oligocene
parvula Saporta	sylvestris	Oligocene
aquensis Saporta	echinata	Oligocene
coquandii Saporta	*brutia	Oligocene
hagenii Heer	*halepensis	Miocene

<u>Fossil species</u>	<u>Similar living species</u>	<u>Age</u>
goethana Al Braun	*rigida	Miocene
saturnii Unger	*serotina	late Pliocene
horrida Menzel	*virginiana	late Pliocene
oviformis Endlicher	*pinaster	late Pliocene

The section *Insignes* is composed of about 20 species that live in western Europe (*Pinus brutia*, *P. halepensis*, *P. pinaster*, *P. pitysua*), eastern United States (*P. banksiana*, *P. clausa*, *P. pungens*, *P. rigida*, *P. serotina*, *P. virginiana*), western United States (*P. attenuata*, *P. muricata*, *P. radiata*, *P. remorata*, *P. murrayana*, *P. contorta*), and Mexico (*P. oocarpa*, *P. greggii*, *P. patula*, *P. pringlei*). The occurrence of species of the alliance in the eastern United States and western Europe is understandable because the middle and later Tertiary floras of these regions are very similar, and the older Tertiary floras of Greenland, Iceland, and Spitzbergen provide a link between them. Europe and eastern North America represent two areas characterized by derivative forests of the Arcto-Tertiary Geoflora that migrated southward from higher latitudes following Eocene time (Gardner, in Gardner and Ettingshausen, 1879; Chaney, 1940). Apart from several pines now in the eastern United States that have Tertiary records in western Europe, many angiosperms in the middle and later Tertiary floras of Europe also find their nearest equivalents only in the eastern United States, and most of them are associated with the pines. Among these are fossil plants similar to *Taxodium distichum*, *Acer rubrum*, *Berchemia volubilis*, *Betula lenta*, *Carpinus caroliniana*, *Carya alba*, *C. ovata*, *Celtis occidentalis*, *Diospyros virginiana*, *Fagus grandiflora*, *Juglans nigra*, *Liriodendron tulipifera*, *Lindera benzoin*, *Liquidambar styraciflua*, *Morus rubra*, *Persea carolinensis*, *Platanus occidentalis*, *Populus balsamifera*, *Quercus prinus*, *Robinia pseudoacacia*, *Sassafras officinale*, and *Ulmus americana*. They largely became extinct in western Europe during the early Quaternary.

The evolutionary stability of woody angiosperms that contributed to the forests of the middle and later Tertiary is paralleled by the pines to judge from the rich record available in Europe (see Gaussen, 1960). It is highly critical that in Europe members of the section *Insignes* were already established as near-modern species in the Oligocene (*Pinus brutia*, *P. halepensis*) and Miocene (*P. rigida*), and also by the early Pliocene (*P. serotina*, *P. virginiana*), if not earlier. Since some of these species in Europe have their nearest relatives in the eastern United States, it is apparent that their earlier evolution extends well down into the Tertiary—a relation consistent with evidence provided by the available record of closed-cone pines in California.

The essentially modern character of Miocene species (*Pinus pretuberculata*, *P. lawsoniana*) of closed-cone pines indicates that splitting of the ancestral form into different adaptive groups occurred prior to the middle Miocene. In view of the absence of fossils of pre-Miocene age that represent the group, the nature of the ancestral species that gave rise to living members of the alliance is not now known. Mason (1932) considered *P. masonii* (cf. *P. muricata*) closest to the ancestral form of the group, chiefly because it was the oldest species then known. However, it is now apparent that these specimens from the Merced and Pico formations are not early Pliocene, but transitional Pliocene-Pleistocene in age. Further, fossil cones that are very similar to those of *P. radiata* and *P. attenuata* are now known from Miocene rocks (fig. 2). It seems probable that *P. remorata* may be more nearly like the ancestral form than *P. masonii* (*P. muricata*). This is suggested by its more central position in a taxonomic sense with respect to other members of the closed-cone pine group (*Peninsulares*) in which the evolutionary trend appears to have been toward larger and more asymmetric cones, and to cones with thicker and raised to hooked umbos. It is apparent that solution of the problem of the age and nature of the ancestral species must await the discovery of cones in pre-Miocene rocks.

INSULAR ISOLATION AND SPECIATION?

Mason (1934, pp. 137-140) developed the hypothesis that "the closed-cone pine forests are of insular origin and owe their distinctiveness to isolation afforded by such a habitat." Since all the data that were marshalled to support this view are equivocal, the evidence Mason presented will be discussed prior to suggesting an alternate hypothesis for the evolution of the species that contribute to the forest.

1. "In the modern flora, the first characteristic that points to an insular origin is the high degree of endemism prevailing among the forest species" (Mason, 1934, p. 137). He notes that 58 per cent of the species of woody plants in the closed-cone pine forests are endemic to the California floristic province, and of these 29 per cent are restricted to the closed-cone pine forests.

Endemism is not peculiar to insular regions, but occurs in continental areas as well. We need only recall the concentration of marked endemics in central (Hupeh-Szechuan) and southern (Yunnan) China (Wang, 1961; Takhtajan, 1957). Many of them ranged widely across Holarctica during the past, and they have survived in restricted upland areas characterized by a highly temperate, essentially frostless climate. As for an insular origin being indicated by the high degree of endemism among the forest

species, a number of the outstanding endemics of the insular flora (i.e., *Ceanothus arboreus*, *Lyonothamnus floribundus*, *Prunus lyonii*, *Quercus tomentella*) that occur with the pines today, and whose fossil equivalents were associated with them during the Miocene and Pliocene, have had a long continental history (Axelrod, 1939, 1958b). Such a relation is not unique, but is paralleled by insular and near-insular floras throughout the world (Axelrod, 1960, pp. 277-293). As suggested by Hooker (1867), who noted that the present endemics in the laurel forests in the uplands of the Canary and Madeira islands have a good representation in the Miocene and Pliocene floras of southwestern Europe, many insular species appear to have been preserved by isolation in local areas where mild climate of high equability has favored their persistence. Thus the present concentration of endemic species in the closed-cone pine forest need not necessarily indicate that they evolved in insular isolation.

2. Mason (1934, p. 138) points out that for endemic species to develop, barriers must exist so that specific characters can become established, and that this is best accomplished by isolation. Since most of the endemics in the closed-cone pine forest have closely related species elsewhere in the Coast Ranges, some isolation in the past is required. "...this does not necessarily indicate insular isolation, but it seems probable that water barriers were present... [chiefly because] no land barrier of a type that could exist in a region of such uniform climate as that of the coast of California would be sufficient to check the movement of these many related plants."

We can agree that isolation is required for differentiation of the coastal pines and their associated endemics because climate in the coastal strip was similar to that on the islands, and hence a barrier is necessary for genetic isolation between the mainland and maritime populations. However, if we accept the explanation of evolution in insular isolation, then we must also deny the ability to migrate over distances of only a few miles, which seems unlikely. It may be recalled that since the ice sheets retreated scarcely 8,000 years ago, all the arctic islands were populated across 150-200 miles of open sea by a circumboreal flora. In addition, the subantarctic islands have been colonized by a similar flora since the last glacial, and over broad tracts of open ocean. Thus it would appear that if species ancestral to closed-cone pines and their associated endemics were initially transported to islands situated only a few miles offshore, where climate was similar to that on the coastal strip, migrants would continue to arrive and there probably would be no genetic isolation.

3. Mason's next point (1934, p. 138-139) concerns the relations of the floras on the islands off southern California to those on the mainland, particularly in the closed-cone pine forests. He

notes that several species find their southern extensions on the islands, and he asserts that they occur on the southern mainland only in localities that were Tertiary islands. He points out that the discontinuous distribution of pines and cypresses also suggest such a relation. They are recorded in all the larger late Pleistocene floras; yet in many of the areas where the forests lived one or more of the pines or cypresses is not now present, as at Tomales, Carpinteria, and Rancho La Brea. Further, in some areas where land was present the conifers have disappeared, yet sediments close by contain their remains, as on the San Francisco Peninsula and at Bodega Head to the north. He concludes that "these facts strongly indicate that the discontinuous coastal pine forests had a common origin, and that it was probably insular."

The data are consistent with the belief that the forests had a common origin, and that the pines were widely spread along the coastal strip and on the islands. The fossil floras of late Pleistocene age (Tomales, Little Sur, Carpinteria, Willow Creek, Rancho La Brea) are more like one another than are the modern derivative forests today. They demonstrate that a forest of rather similar composition occupied the coastal strip into the latest Pleistocene, as recently as 12,000 years ago. Their present discontinuous occurrence seems chiefly due to the Xerothermic period, which brought a drier and a more intemperate climate to the coastal strip and disrupted the continuity of the forest and of its species (Axelrod, 1966). Thus the present differences as compared with those of the Pleistocene may owe not to insular evolution, but to segregation and restriction of plants to the few highly temperate sites with sufficient rainfall that were available for their survival. Their present or former occurrence at localities that may have been Pleistocene or Pliocene islands does not provide support for an insular origin. Actually, geologic evidence (see below) suggests that most of the mainland localities where the forests now occur were not parts of Pliocene islands. Furthermore, the pines also occupied the mainland (near Santa Paula; also in Mount Eden flora) probably because climate there was highly temperate. The pines presumably occurred wherever there were islands, as well as all along the outer coast. Thus, insular isolation is not demonstrated by the distributional evidence and does not seem required for the evolution of this group (see below).

4. Mason (1934, p. 139-140) asserts that there is a correlation between the ranges of the living pines and areas that were late Cenozoic islands. "In all localities in the Pliocene and in the Pleistocene where fossil records of closed-cone pines are known, the site of deposition is along one of the major fault lines of the California Coast Ranges. Likewise, they are in all cases located along the fault near a block that has been positive

throughout the Pliocene at least. . . . The fact remains that they are confined today to areas that were islands throughout most of the Tertiary and particularly in the Pliocene."

Considerably more is now known about the geologic history of the coastal strip. Most of the faults to which Mason makes reference are much younger than the closed-cone pines, whose history extends well down into the Miocene at a minimum (fig. 2). A survey of the areas adjacent to the present groves indicates (see new Geologic Map of California, scale 1:250,000):

a. Trinidad Head. This site is underlain by Cretaceous rocks and veneered with Quaternary marine deposits that are cut by younger faults. No evidence for insular isolation.

b. Point Arena-Inglenook. Most of the groves are on Quaternary marine deposits that lap against Cretaceous rocks. No major faults mapped in this area, and no evidence for insular isolation.

c. Inverness Ridge. Insularity is chiefly post-Pliocene because dipping marine Pliocene formations lie on tilted and eroded marine Miocene rocks which lap onto a thin wedge of quartz diorite that was largely subsea during their deposition. Nearest land was three to five miles east, along a ridge that extended southeasterly through the present site of San Francisco Bay, connecting with the mainland.

d. Año Nuevo Point. San Gregario fault behind the grove probably is middle Pleistocene. It brings the middle Pliocene marine Purisima formation against the marine Monterey which laps against Cretaceous and older rocks. They formed the mainland two to three miles east during the Pliocene, when present area of the grove on the Monterey formation was subsea.

e. Monterey-Carmel. The area includes folded and faulted late Miocene marine rocks resting on Paleocene-Cretaceous marine rocks and on granite. Area to southeast is laced by faults, some of which slice Quaternary deposits. If isolated, it was by not more than three to four miles.

f. San Simeon-Cambria. Cretaceous rocks are overlain by slightly warped upper Quaternary marine deposits cut by younger faults. No evidence for insularity.

g. Purisima Hills. This anticline is composed of a continuous section of middle Miocene to Plio-Pleistocene marine rocks overlain by the early Pleistocene nonmarine Paso Robles formation, all of which are folded. The Paso Robles and older rocks are overlain unconformably by the Orcutt sand which is also folded (dips of 20°) at the west end of the range, and has a radiocarbon age of 26,700 years. The forest occupied the area after mid-Pleistocene deformation at the earliest, and probably later. No evidence for insularity; thrust fault on south side of hills cuts lower Pleistocene rocks.

The *Pinus muricata* grove in Pine Canyon is on the marine Sisquoc formation of upper Miocene to lower Pliocene age, which

was uplifted during the mid-Pleistocene orogeny. Since the area was a site of marine deposition (Orcutt sand) during the upper Pleistocene (Arnold and Anderson, 1907; Woodring and Bramlette, 1950), the grove became established there after Pine Canyon was entrenched into the Orcutt sand (dated by radiocarbon at 26,700 years), down into the Sisquoc formation.

h. San Luis (Pecho) Range. These hills are composed of folded upper Miocene marine rocks that rest on a Cretaceous basement. Nearby lower Pleistocene marine rocks are folded and cut by younger faults. Insularity probably occurred in Pliocene, with nearest land a few miles east.

i. Northern Channel Islands. The islands were the site of a marine basin of deposition that extended east to include the area of the Santa Monica Mountains during the Miocene. In the Pliocene, uplift formed a low east-west trending peninsula that included the present island area and the Santa Monica Mountains which was joined to the mainland at the east. The Northern Channel Islands became separated from the mainland as the mid-Pleistocene orogeny depressed the western part of the peninsula. *Pinus lawsoniana* (at Santa Barbara) was already living in this area before the present islands were in existence, and *P. masonii* (Ventura basin) lived on the mainland when the peninsula was present.

j. San Vicente, Baja California. Three small groves west and southwest of San Vicente occur on (1) Cretaceous volcanic rocks of the Alisitos formation that lie on granodiorite and on (2) marine Paleocene (Sepultura formation) rocks. No evidence for insularity.

k. Cedros Island. The island is composed of Cretaceous, Miocene, and Pliocene marine rocks that rest on a crystalline basement. Insularity apparently developed in late Pliocene time as a result of faulting, to judge from conglomerates in the section.

As for the Pliocene species, their occurrences do not provide evidence for effective insular isolation.

a. Merced formation. This formation was deposited in a basin bounded on the east by northwest-trending hills that occupied the present site of San Francisco Bay, and on the west by a northwest-trending peninsula that separated the Merced from the marine Purisima basin to the south (Louderback, 1951). Thus the cones transported into the Merced basin were deposited only three or four miles from land at a maximum. As for the cones in the forest bed that underlies the marine Merced, they were deposited on the east shore of the northwesterly trending peninsula that was connected with the mainland to the southeast.

b. Pico formation. The cones (*Pinus masonii*) from the upper Pico near Pitas Point and Punta Gorda on the coast northwest of Ventura evidently were transported from hills at the site of the

ancestral Transverse Ranges directly north which were not an island. As for the cones (*P. masonii*) near Santa Paula, study of the sediments (Crowell, 1957) shows that they were derived together with shallow-water marine fossils and a deer phalanx from the Transverse Ranges a few miles north that was part of the mainland.

c. Monterey formation. The cones (*Pinus lawsoniana*) preserved in the formation at Santa Barbara presumably were carried into the basin from hills to the north, at the site of the Santa Ynez Mountains, which were connected with the mainland to the east (Corey, 1954).

Any relation between the evolution of closed-cone pines and Pliocene and Pleistocene islands is therefore doubtful. Furthermore, since the history of the forest extends well down into the earlier Miocene at a minimum, evolution of the pines predates the structural features (faults, positive blocks) that have been called on for their development.

5. Finally, Mason points out that "the homogeneity of the species content of the forest, and the absence of other contemporaneous plant assemblages in the Pleistocene of the coastline further support the hypothesis.... If the facts of... [the Pleistocene history of the redwood forest] are correctly drawn, we can attribute its absence from the records of the closed-cone pine forests to the predominantly insular habitat of these forests" (Mason, 1934, p. 140).

The redwood and closed-cone pine forests are scarcely associated today, and then only marginally where closed-cone pine forest reaches its inland limit a mile or two from the coast. The pine forests live at lower altitudes and nearer the coast, in sites where fog is more persistent in summer and where frost is less frequent. Since fossil plant deposits are composed preponderantly of species that lived at the site of deposition (Chaney, 1927), remains of a redwood forest situated two to three miles upstream from a coastal site of plant accumulation would contribute only rarely to the record being built up by a closed-cone pine forest living at the coast. This is consistent with the rare occurrence of logs and chips of redwood which were transported from the nearby mountains to the Carpinteria site (Axelrod, 1966), and also with the general absence of redwoods along the entire outer coast where climate was highly temperate. Furthermore, geologic evidence demonstrates that the late Pleistocene floras at Tomales, Little Sur, Point Sal Ridge, Carpinteria, and Rancho La Brea, all of which are dominated by closed-cone pine forest, were not insular—as Mason (1934, p. 140) has implied. The absence of redwood in them (rare at Carpinteria) seems readily explained by the highly temperate climate that characterized the coastal strip where these forests lived close to sea level. To judge from the distribution of redwood forest in areas near closed-

cone pine forest today, it probably occupied hills bordering most of these late Pleistocene sites where closed-cone pine forests occur, inhabiting valleys and moister slopes sufficiently remote (two to three miles) so that its structures are recorded only rarely.

EVOLUTION IN TEMPERATE UPLANDS

Having pointed out the difficulties with Mason's hypothesis that closed-cone pines and their associated endemics may have evolved in insular isolation, it is now appropriate to propose an alternate explanation for their evolution. Whereas evidence does not now decisively indicate the nature of the ancestral pine, floristic data provide a clue to the time when the divergent species may have become established. The closed-cone pines belong to the group *Peninsulares* (Martinez, 1945) which includes species now in Mexico. *Pinus oocarpa* and *P. pringlei* have cones not greatly different from those of *P. remorata*; and *P. greggii* and *P. patula* produce cones generally similar to those of *P. attenuata*. During the Miocene and Pliocene, closed-cone pines in California were associated with plants whose descendants now occur in Mexico. Furthermore, many of the trees and shrubs that live with the pines in California are descendants of the Madro-Tertiary Geoflora which had become established over northern Mexico and the southwestern United States by the early Tertiary (Axelrod, 1958b). Although the lowlands of coastal California were dominated by broadleaved evergreen forests representing the Neotropical-Tertiary Geoflora in the Eocene and Paleocene, the Madro-Tertiary Geoflora commenced to invade southern California from the drier interior during the Eo-Oligocene transition. In view of these relations, two suggestions may be made as to the probable later history of the California pines of the *Peninsulares* group.

The first possibility is that a pine ancestral to all the Californian species may have entered the region with the geoflora in the early Oligocene. This species then divided into two major adaptive groups, forerunners of the interior (*Pinus attenuata*) and maritime (*P. muricata*, etc.) species, as the Madro-Tertiary Geoflora reached coastal southern California near the close of the early Tertiary.

Two objections may be raised with respect to such a history. First, it has been noted that two of the Californian species closely resemble pines now chiefly in central to southern Mexico. This poses the problem of the evolution of the Mexican pines from an ancestral species in the Californian region. Second, the hypothesis calls for differentiation in a rather restricted region. To judge from their modern distribution, the basis of speciation in *Pinus* has been ecological differentiation, associated at some time with spatial isolation. The habitats now occupied by *P. radiata*, *P.*

muricata, and *P. remorata* are different (see below), yet are generally similar in that they are temperate and coastal. The habitats do not appear to be different enough for speciation to have taken place while they were living adjacent to one another. This is especially true of the coastal region for there is a far greater diversity of rock and climatic type there today than there was in pre-Miocene time when, it is believed, the species were evolving.

The second alternative is that several divergent lines were already established by the time the ancestors of each of the modern species reached the coastal slope. This means that evolution would have occurred during migration toward the coast, with speciation in response to diverse conditions in the temperate uplands occupied by the Madro-Tertiary Geoflora. On this basis, the group *Peninsulares* may have diversified in the interior, so that when the species that are now maritime reached coastal California they were sufficiently distinct to maintain their ecological differences. A hint of this is seen today in areas where different species of closed-cone pines occur in proximity. For example, there is an ecological separation of *Pinus remorata* and *P. muricata* in Pine Canyon on Burton Mesa, with *P. remorata* confined to flat-lying Orcutt sand and *P. muricata* chiefly to the slopes of diatomite of the Sisquoc formation below it; the species appear to hybridize in the narrow zone of contact. *P. remorata* also occurs five miles northeast, in the Lompoc oil field in the foothills of the Purisima Hills on the east side of State Highway 1, where it is confined to coarse grained rocks of the Careaga sandstone; *P. muricata* is widely distributed in the Purisima Hills, on different rock types. *P. muricata* and *P. radiata* display comparable relations at Monterey, with *P. muricata* confined to the thin soil at the crest of Huckleberry Hill above Monterey Pine, and with rare hybrids forming at the zone of contact. A similar relation exists near Año Nuevo Point, where *P. radiata* and *P. attenuata* are in proximity, with the latter on drier, more exposed sites. Edaphic differences also appear to account for the separation of pure stands of *P. remorata* and *P. muricata* near San Vicente, Baja California. The stands of *P. muricata* at Cerro Colorado and across the stream valley are on highly altered volcanic (rhyolite pyroclastics, andesite, basalt) rocks, but the grove of *P. remorata* about two miles south of it—in the entrenched meander one mile west of the mouth of Cañon de las Pinitas—is on marine sandstone and ash beds of the Sepultura formation. Two miles east, in Cañon de las Pinitas, the groves include many trees that are “intermediate”, and they occur on unaltered volcanic rocks (rhyolite tuff and breccia, andesite, basalt). Whether the groves of *P. muricata* and *P. remorata* on Santa Cruz Island are also separated by differences in underlying rock and soil is not now known though the preceding observations—coupled with the diversity of rock type known to exist there—indicate that their distribu-

tion may be controlled by edaphic factors. The preceding relations suggest that *P. attenuata* may have evolved on the drier, somewhat more intemperate margins of the Madro-Tertiary woodland. Once established, it was able to maintain its adaptation and more nearly separate distribution, as did its southern relatives, *P. patula* and *P. greggii*.

These suggestions are consistent with the occurrence of a dominant closed-cone pine forest in the coastal strip of southern California by the middle Miocene. This is supported by the abundance of pines in the lower part of the Wilmington core (Gray, in Martin and Gray, 1962) which Dr. W. S. Ting reports are of the closed-cone group (oral communication, April, 1965). The associated flora is typically Madro-Tertiary in composition, and floras in the nearby coastal area to the east (Puente formation) and north (Modelo, Topanga formations) contain Madro-Tertiary species of *Cercocarpus*, *Fremontodendron*, *Juglans*, *Karwinskia*, *Lyonothamnus*, *Pinus*, *Platanus*, and *Quercus*, together with relicts (*Annona*, *Ficus*, *Persea*, *Sabal*) of the Neotropical-Tertiary Geoflora. But in the interior, the Mint Canyon (Axelrod, 1940) and Tehachapi floras (Axelrod, 1939) reveal semiarid oak woodland, chaparral, and thorn forest vegetation. Closed-cone pines have not been found there. If they still occupied interior areas, they presumably were in the more temperate uplands. This inference is consistent with the middle Pliocene occurrence of *Pinus lawsoniana* (cf. *P. radiata*) in hills bordering the Mount Eden basin south of Beaumont in interior southern California (see section on Systematic Paleontology).

Present evidence thus suggests that closed-cone pine forest may represent a highly temperate phase of the Madro-Tertiary Geoflora that had become established in the coastal strip prior to the Miocene. The data seem consistent with the inference that the pines probably were isolated from their nearest relatives in Mexico by increasing aridity over southwestern North America during and following the Oligocene. Since all the pines lived under highly temperate climate in the early Tertiary, and most of them have survived under such conditions, the present California closed-cone pine forest may best be regarded as a relict community of the Madro-Tertiary Geoflora which has persisted under mild maritime conditions.

This interpretation is consistent with the historical relations of the distinctive endemics that are essentially restricted to the insular region with the pines. *Ceanothus arboreus*, *Cercocarpus alnifolius-traskiae*, *Lyonothamnus floribundus*, *Prunus lyonii*, and *Quercus tomentella* were represented by closely related species in the interior during the Miocene, and three of them (*Ceanothus*, *Cercocarpus*, *Prunus*) have related species in the uplands of Mexico. Some of the Miocene fossil species in the interior have leaves that are consistently smaller than those produced by

the living insular species. Pliocene species from stations nearer the coast are essentially intermediate in size between those produced by the Miocene and the related modern endemic species. This may mean that the species with small- and intermediate-sized leaves were confined to the more intemperate (cooler, or drier) sites, and that those with large leaves represent species that were adapted to highly temperate upland areas as well as to maritime and insular sites. On this basis, it is suggested that during the middle and later Tertiary angiosperm species closely related to the present insular endemics occupied different environments on the mainland, and that they were gradually eliminated there by the trend toward more intemperate climate. The larger-leaved forms that appear to have evolved under highly temperate climate have persisted on the islands, and locally in the coastal strip. Together with the pines, they may be regarded as a phase of the Madro-Tertiary Geoflora that evidently was confined to the coastal region late in its history.

Fossil evidence indicates that an essentially continuous closed-cone pine forest blanketed the outer coast and islands during the late Pleistocene, and as recently as 14,500 to 12,000 years ago. The forest was then more homogenous in composition than the modern groves, and the present narrow endemics had much wider distributions. Breakup of the more continuous forest, and restriction of its species to highly localized sites, seems to have resulted from the coastward spread of hot dry climate during the Xerothermic (Altitheimal) period. As discussed elsewhere (Axelrod, 1966), climate during this stage favored the migration of desert and semidesert species from the interior to the outer coast and to the islands of southern California, and the establishment of interior southern California chaparral and woodland species in the outer coastal area and also well to the north in central California. The Xerothermic period thus brought a hotter, drier, more intemperate climate to the coastal strip, a climate wholly unsuited for closed-cone pine forest. Patches of the forest persisted only in the most temperate sites where there was sufficient rainfall along the outer coast and on the islands, having been eliminated elsewhere by unfavorable climate during the very recent (ca. 8,000-3,000 B.P.) past.

SUMMARY

New evidence relating to the history of the Californian closed-cone pine forest indicates a greater age for its species, and suggests a different mode of evolution than previously proposed. Present data lead to the hypothesis (a) that the modern pines and their associated endemics are derivatives of the Madro-Tertiary Geoflora, (b) that pines of the group *Peninsulares* were already evolving in the early Tertiary, giving rise to species whose de-

scendants are now in Mexico and California, (c) that initially, species evolution was a response to ecologic diversity, (d) that the ancestral species and their derivatives were adapted to highly temperate climate in the interior uplands, occupying different sites, (e) that the pines and their associates had already assumed near-modern form by the Miocene, (f) that the Californian and central Mexican species of the group *Peninsulares* were gradually isolated by expanding intemperate climate over southwestern North America following the Eocene, with the surviving species finding a refuge in the mild, highly temperate coastal strip of California and in the uplands of Mexico, (g) that in California the later Tertiary forest and associated Madro-Tertiary plants were distributed continuously along the coast and on the islands, and persisted locally in the interior uplands where climate was highly temperate, (h) that the forest shifted north and south along the outer coast in response to alternating glacial-interglacial climates, and (i) that the forest was broken into discontinuous patches and disrupted floristically by the hot dry climate of the Xerothermic period, confining it to local moist sites of highly temperate climate together with other relicts of the geoflora.

SYSTEMATIC PALEONTOLOGY

The cones of Tertiary closed-cone pines are scarcely distinguishable from those produced by living species. The question may therefore be raised as to why they are not assigned names of modern trees. It seems best to apply separate names to the Tertiary species for several reasons (also see Chaney, 1954). First, these pines are known only from ovulate cones--there is no record of wood, fascicles, needles, or staminate cones. It seems probable that in the Tertiary these organs may not have been identical with those of living species, and hence might provide a basis for their separation. In this regard it is noted that the three-needled form of *Pinus radiata* appears to have evolved from a typically two-needled species during the Quaternary (Chaney and Mason, 1933). Thus by assigning a distinct name to a Tertiary pine (or angiosperm) and noting its modern affinity, we can indicate its relations without committing ourselves to an opinion of identity that cannot be established. Considering the continuum of life through the past, it finally does become a matter of opinion as to whether a fragment from a tree (a cone, or a leaf) preserved on a slab of rock represents a modern species or not.

Second, although most living species range down into the Pleistocene, there are sufficient differences between even Pleistocene and modern communities to suggest that they did not live under identical conditions. When we turn to the Pliocene, there usually is good evidence of close relationship between fossil

and living species, yet Pliocene communities illustrate greater differences between their ecological conditions and those under which the modern are found. Still greater discrepancies in environment are apparent if we compare Miocene or Oligocene floras and related modern forests. This evidence becomes important when taken in conjunction with evolutionary studies which reveal the dynamic nature of the hereditary process under the influence of changing environment: It militates against the preservation of exact similarity over even brief periods of geologic time. The relations suggest that the floristic differences between Tertiary and modern floras, which express different environmental conditions, probably indicate that the Tertiary species were different genetically. To judge from modern plants, such genetic differences regularly are accompanied by minor morphological variations (size of plant; nature of bark or root system; color of leaves or cones; color, size, shape, and arrangement of other organs; type of pubescence, if present; etc.) that provide useful and valid characters for distinguishing living species (or varieties) that occupy different environments, but which can scarcely be expected to be preserved in the fossil record. Leaf size is one of the few characters that may reflect important environmental (and presumably genetic) change, and it has provided a useful basis for designating differences between Miocene and Pliocene species. Examples of decreased leaf size in response to diminished rainfall and winter temperature following the Miocene have been described for Pliocene species of *Acer*, *Arbutus*, *Cercocarpus*, *Fagus*, *Lyonothamnus*, *Populus*, *Prunus*, *Quercus*, *Rosa*, *Ulmus*, and other genera (see Chaney, 1938, 1944; Axelrod, 1941, 1956, 1958b). They appear to reflect major environmental differences to judge from their associates, and also from the ecologic occurrences of their living analogues. Thus by assigning separate names to Tertiary species we can imply that they probably are not precisely the same as their nearest descendants, even though the few fossil structures (leaves, seeds, or cones) on which these species are necessarily based can scarcely be distinguished from those produced by their closest living descendants.

Third, the assignment of a modern name to a single structure (seed, or leaf, or cone) of a Miocene or Oligocene fossil plant necessarily implies that all the divergent morphologic characters that distinguish the living species have evolved at the same rate since that time at least—a conclusion that can scarcely be supported by fossil evidence.

Fourth, the assignment of a separate name to a fossil species emphasizes its temporal and stratigraphic separation from its nearest modern analogue, and thus adds a valuable time dimension that would be lacking if living species like Monterey pine (*Pinus radiata*), maui oak (*Quercus chrysolepis*), or box elder (*Acer negundo*) were identified in rocks of Miocene age.

All of the new records of closed-cone pines are discussed below. In considering them, it has been necessary to examine all fossils that previously have been assigned to the group. Supplementary data with respect to the geologic occurrences of some of these species are noted, and more recent evidence of their age is also included in the discussion.

Pinus attenuata Lemmon
(Pl. 6, fig. 1)

- Pinus attenuata* Lemmon. Metcalf, Amer. Forestry, 29: 172, fig. 1, 1923 (*Oakland*).
Mason, Carnegie Inst. Wash. Pub., 346: 148, pl. 2, fig. 2, 1927 (*You Bet*).
Pinus linguiformis Mason, Madroño, 2: 50, pl. 1, fig. 5, 1932 (*near Signal Hill*).
Pinus tuberculata Gordon. Knowlton, Wash. Acad. Sci., 6: 85 (part), 1916 (*Rancho La Brea*).
Pinus muricata Don. Mason, Carnegie Inst. Wash. Pub., 346: 147, pl. 3, fig. 1 only, 1927 (*Rancho La Brea*).

The partially carbonized, complete cone figured by Metcalf was recovered at 30th Street and Telegraph Avenue, Oakland, California, 42 feet below the surface. The proximal part of the specimen has been lost, so it is not now possible to ascertain with certainty its taxonomic relations. To judge from the illustration, and from the opinion expressed by W. L. Jepson (in Metcalf), it appears to be a valid record of *Pinus attenuata*. Its geologic occurrence indicates that it is late Pleistocene. On the basis of the ecologic requirements of the living species, the fossil suggests a climate with cooler winters and warmer summers than at Oakland today; it probably lived during an interglacial stage.

Chaney and Mason collected a complete cone of *Pinus attenuata* from late Pleistocene terrace gravel deposits capped by a ferruginous conglomerate at You Bet, near Grass Valley, California. The overlying iron-stained conglomerate is just below an old soil zone, and its color is due to leaching from above (H.D. MacGinitie, written communication, March 1965). As noted by Mason (1927), there appears no difference between the fossil cone and those produced by the living species.

The cone of *Pinus linguiformis* Mason was recovered from a bed of black clay at a depth between 800 and 900 feet at the Los Alamitos pump station of the Long Beach Water Works, about one-half mile northeast of Signal Hill. The geologic map for the Signal Hill Oil Field (Dudley, 1954) shows that the cone occurs close to the contact between the Pico and San Pedro formations, indicating that it is from strata that straddle the Plio-Pleistocene boundary.

The cones of *Pinus attenuata* produced by southern California populations, which occur in the Santa Ana Mountains (Sugarloaf Peak, Santiago Peak) and San Bernardino Mountains (City Creek Road), differ from those in central and northern California in having more prolonged, hooked umbos. Cones of the southern California trees are sufficiently similar to *P. linguiformis* to indicate that it is *P. attenuata*, or at least a species so similar to it that they cannot now be distinguished on the basis of the material (one cone) available for study.

In discussing *Pinus linguiformis*, Mason (1932) noted that it shows relationship to *P. attenuata* in shape, in the relatively few prolonged scales, and in the massive cone size. He also noted that *P. linguiformis* resembles an attenuate form of the *P. masonii-muricata* complex, though it is more massive and has fewer scales which are more tongue-like. Thus he suggested that it may represent an intermediate form between *P. masonii* and the living *P. attenuata*, giving rise to the latter in the middle Pleistocene. Since *P. attenuata*, (as *P. pretuberculata*) was already in existence as an essentially modern species in the Pliocene (Axelrod, 1958a) and in the late Miocene (Condit, 1944), it is apparent that *P. attenuata* could not have evolved from *P. linguiformis* during the Pleistocene. Furthermore, as noted below (see *P. masonii* discussion) some of the resemblances between cones of *P. muricata* and *P. attenuata* may be due to hybridization, and not to any recent phylogenetic relation between these species.

Knowlton examined and described, but did not illustrate, two cones from Rancho La Brea that he identified as *Pinus attenuata*. They were also determined by Frost as *P. tuberculata* (*P. attenuata*), and he figured (pl. 15, figs. 1, 2) the smaller one together with a winged seed: both of these specimens represent *P. muricata*. The other cone was figured by Mason (1927, pl. 3, fig. 1), and he identified it as *P. muricata*, though in a later paper (Mason, 1932, p. 50) he noted that it was too massive to be included in that species and suggested that it probably represented *P. linguiformis* (= *P. attenuata*). Examination of a number of open cones of *P. attenuata* indicates that the smaller ones produced by that species are very similar to the fossil, and it is therefore identified as *P. attenuata*.

Study of the cones of *Pinus xattenuradiata*, a natural hybrid between *P. radiata* and *P. attenuata* in the Santa Cruz Mountains near Swanton, shows that some of the cones of the F₂ generation³

3. Acknowledgement is due Dr. W. B. Critchfield, Pacific Southwest Forest and Range Experiment Station, who kindly loaned me for comparison with the Rancho La Brea fossil a number of cones from F₂ trees of *P. xattenuradiata* that are growing at the Institute of Forest Genetics, Placerville, California.

closely resemble the fossil here referred to *P. attenuata*. Whether the fossil represents a hybrid between *P. attenuata* and *P. radiata* can not be demonstrated, but such a relation is possible because both parents are at Rancho La Brea. In this connection it is noted that the fossil could possibly represent a cross between *P. radiata* and *P. muricata*. Unfortunately, cones from such a hybrid are not now available for study: a hybrid between these species at the Institute of Forest Genetics, Placerville, is still too young to produce cones. In any event, assignment of the fossil to a hybrid source now seems undesirable because there is only one fossil cone and the degree of cone variation of the tree that produced it is wholly unknown.

Collection: U.C. Mus. Pal., Paleobot. ser., hypotypes nos. 20540 (Oakland), 133 (You Bet), 446 (Signal Hill); Los Angeles Co. Mus. (Rancho La Brea).

Pinus lawsoniana sp. nov.
(Pl. 1, figs. 1-2)

Pinus insignis Douglas. Lawson, U.S. Geol. Surv., Geol. Atlas of the U.S., San Francisco Folio 193; 101, 1915.

Pinus pretuberculata Axelrod, Carnegie Inst. Wash. Pub., 476: 166, pl. 3, fig. 3 only, 1937 (Mount Eden flora).

Description: Cones 8.0-10.5 cm long, 7 cm wide proximally; asymmetrically long ovate; scales on outer, proximal side swollen and rounded, those on inner side slightly swollen to nearly plane. Impressions of winged seeds visible on cone scales, with slender wings somewhat over 1 cm long and asymmetrically acute distally.

Discussion: These figured cones, collected by A.C. Lawson in 1895, were identified by W.L. Jepson as *Pinus radiata*, as may be seen on the card in Jepson's handwriting which is filed with these fossils. Lawson (1915, p. 101) referred to the cones as *P. insignis*, a synonym of *P. radiata*, and described their occurrence as follows: "Between the basement volcanic rocks and the basal beds of the Merced is a wedge of post-Franciscan pre-Merced alluvium, now firmly cemented, composed almost wholly of fragments derived from the underlying volcanic rocks. Upon this ancient alluvium lies a layer of forest material, less than a foot thick, comprising carbonized wood, bark, matted leaves, and pine cones of the species *Pinus insignis*, and above this are the marine beds [of the Merced]." Since this site now underlies a city trash dump which is a cut-and-fill operation, additional material cannot be collected here.

A minimum age for the cones is indicated by their stratigraphic position, unconformably below the marine Merced, the basal part of which is transitional lower to middle Pliocene (Glen, 1959).

This species is named in honor of Andrew C. Lawson, the eminent geologist who first collected these cones during his investigation of the geology of the San Francisco Bay region.

Restudy of the Mount Eden fossils originally assigned to *Pinus pretuberculata* indicates that two very different pines were included in the type material. The small cone (Axelrod, 1937, pl. 3, fig. 4) appears to be a pine of the *P. attenuata* (*P. tuberculata*) alliance, as discussed below. However, the larger crushed specimen (pl. 3, fig. 3) and several other poorly preserved specimens in the collection seem to represent a different entity. They are obovate, and the cone scales on the best specimen (pl. 3, fig. 3) seem to have been rounded or swollen prior to distortion by compaction. Some of the tips of the scales bear a small mark where there was a deciduous prickle, and there is no evidence to show that the umbos were triangular or hooked. The material thus seems to represent a species allied to *P. radiata*.

It is not possible today to reconstruct the reason for including two widely different cones in the original description of *Pinus pretuberculata*. In part this was, no doubt, due to the fact that they are poorly preserved; they probably would not have been described as new species today. Another part of the error probably was due to a paleoecologic bias on my part. Since an explanation could not have been offered for the presence of a pine allied to a maritime species in an otherwise largely interior flora, the possibility that a pine of present day coastal occurrence may have lived there probably was not even entertained, or at least was immediately rejected. The concept of the temperate climate (Bailey, 1964) provides a basis for understanding how coastal species may have lived on slopes in the Mount Eden basin. The relation is paralleled by the distribution of the pine forests on Guadalupe and Cedros islands today, where conditions are highly temperate owing to their maritime position and to persistent summer fog that shelters them in the uplands. In connection with the presence of a highly temperate climate in the Mount Eden uplands, it is recalled that several other species in the flora are allied to plants (i.e., *Ceanothus spinosus*, *Prunus lyonii*, *Juglans californica*, *Rhus integrifolia*) that are typically insular or coastal in distribution today. It has been suggested that they were able to live in the area because the Santa Ana Mountains and Puente Hills to the west had not yet been elevated appreciably, and hence mild moderating maritime climate reached into the interior.

Collection: U. C. Mus. Pal., Paleobot. ser., holotypes no. 20533, paratypes nos. 20534-20538; U. C. Herbarium, sheet no. 400303 (*Mussel Rock*); Los Angeles Co. Mus., hypotype no. L 1306/1014/688; U. C. Mus. Pal., Paleobot. ser., homeotype no. 961 (*Mount Eden flora*).

New Occurrence

Santa Barbara. Mason (1949, p. 357) referred to two cones of *Pinus radiata* in the possession of Dr. Asbjorn P. Ousdal, a surgeon in Santa Barbara now deceased, and stated that they are from rocks of Pliocene age. I have examined these cones and agree that they represent a species scarcely distinguishable from *P. radiata*. However, Ousdal reported to me (1939) that they were recovered during road excavation in the city, and from the Monterey formation of Miocene age. Since the cones are strongly silicified, an occurrence in the Monterey seems consistent with his report. Furthermore, Ousdal was an amateur fossil collector for many years, and particularly concentrated on gathering marine mammal bones (chiefly whales) which occur in the Monterey. Since it has a distinctive lithology and cannot be confused with any other formation in the area, it seems highly probable that the cones come from the Monterey, and are therefore Miocene.

Ousdal's collection of fossils was distributed to both the University of California and the Museum of Natural History at Santa Barbara, but the cones could not be located at either institution (Spring, 1965).

Pinus masonii Dorf
(Pl. 5, figs. 1-2, 4-5; pl. 6, fig. 2)

Pinus masoni Dorf, Carnegie Inst. Wash. Pub., 412: 70, pl. 5, fig. 4, 1933; Mason, Madroño, 2: 49, pl. 1, fig. 4 (this is the same specimen figured by Dorf), 1932 (*upper Merced formation*).

Dorf, Carnegie Inst. Wash. Pub., 412: 70, pl. 5, figs. 5-6, 1933 (*upper Pico formation*).

The type material of this species was recovered at two localities. The specimen figured by Dorf from the Merced formation, which was refigured by Mason, was collected from steeply dipping rocks at a locality two miles north of Mussel Rock (also reported as one and one-half miles south of Fleishacker Pool). This gives it a position in the lower part of the upper Merced which is transitional Plio-Pleistocene in age (Lawson, 1915; Glen, 1959), though the locality was considered lower Pliocene by Mason (1932, p. 49) and by Dorf (1933, p. 6).

The second locality for *Pinus masonii* is on the coast at Pitas Point, six miles northwest of Ventura in the upper Pico formation. Initially regarded as lower Pliocene (Mason, 1932, p. 49; Dorf, 1933, p. 6), the cones come from the upper Pico formation (Jennings and Troxel, 1954), in rocks that yield foraminifera of late Pliocene age.

The cones of *Pinus masonii* from the Merced and Pico localities were considered by Mason to represent a species very similar to *P. muricata*, with which they were believed to form a continuum in time. In considering the relations of *P. muricata* to *P. masonii*, Mason noted that the cones from the Merced and Pico localities differ appreciably in the nature of the umbos. The Pico specimens are more nearly like the "norm" of *P. muricata* since their umbos are low pyramidal. The Merced cone differs from the Pico specimens in that the scales on the outer side form a triangular and attenuated beak, not a low pyramid. Mason reports that this range of variation is occasionally found in *P. muricata*, but that this extreme of variation does not characterize the species. However, recent field studies and examination of a number of collections of *P. muricata* cones illustrates that those with umbos that have triangular, attenuated (often recurved) beaks are not uncommon: They occur frequently in the populations near San Vicente, on Santa Cruz Island, and also are common in the stands in the Purisima Hills and in the San Luis (Pecho) Range. This variation in *P. muricata* includes cones that are dominantly elongate in outline (as compared with typically ovate to oval for *P. muricata*), and the scales have thick, raised, strongly hooked umbos that often are recurved proximally (as compared with typically broadly pyramidal umbos for *P. muricata*). Occasionally these cones of *P. muricata* so closely resemble those of *P. attenuata* that they cannot be distinguished from them.

It has not previously been suggested that this variation may have resulted from hybridization with *P. attenuata* during the colder stages of the Pleistocene, times when *P. attenuata* ranged to the coast. It is critical that there are records of both *P. attenuata* and *P. muricata* fossils in the coastal strip during the Pleistocene, and they lived in proximity. Pollen of both *P. attenuata* and *P. muricata* is well represented in the Merced rocks of transitional Plio-Pleistocene age that have yielded the *P. attenuata*-like cone of *P. masonii*. Further, *P. attenuata* (as *P. linguiformis*, near Signal Hill) and *P. muricata* (at Wilmington) are both in the San Pedro formation of lower Pleistocene age in coastal southern California. *P. attenuata* has also been recovered from alluvial fan deposits of late Pleistocene age at Oakland, California, not many miles removed from the late Pleistocene deposits at Tomales Bay where *P. muricata* is recorded. At the present time *P. attenuata* reaches close to the coast near Año Nuevo Point (where it hybridizes with *P. radiata*), and is elsewhere in the Santa Cruz (near Ben Lomond), Santa Lucia (Cuesta Pass), and Santa Ana mountains (Sugarloaf Peak), all localities near the coast. It is also critical that *P. attenuata* evidently was in the Purisima Hills north of Lompoc only a few decades ago, and that it apparently has since been destroyed by fire. A branch with long fascicles of three needles (U.C.L.A. Herbarium no. 6176)

representing *P. attenuata* was collected there by Loye Miller in 1924; typical large cones of *P. attenuata* were recovered from the summit of the pass directly north of Lompoc in the thirties (U.C.L.A. Herbarium no. 2113) but identified as *P. muricata* by Carl Wolf; and a collection (Sample B) of 6 cones secured there in 1940 by Carl Epling (U.C.L.A. Herbarium) also bears all the diagnostic features of *P. attenuata*—not *P. muricata*.

It appears to be significant that typical *Pinus muricata* cones, which generally are oval and small, can be found only on old mature trees or on large trees burned in the past. Younger trees are now producing more attenuated cones which are rather like those of *P. attenuata*, yet also have the characters of *P. muricata*. To judge from the cones, the young trees may represent a hybrid in which there has been an infiltration of *P. attenuata* characteristics. The present trees seem better adapted to the dryness of the site and climate than does the older form—a characteristic to be expected from a cross with *P. attenuata*.

These relations raise the possibility that the cone from the upper Merced (refigured here, pl. 6, fig. 2) may represent a hybrid between *Pinus attenuata* and *P. muricata*, a relation consistent with the occurrence of pollen of both species in the same section. Although such an origin for the cone cannot be demonstrated, it has nonetheless seemed desirable to present the evidence which suggests that it may have had such a history.

Collection: U. C. Mus. Pal., Paleobot. ser., holotypes no. 308 (locality 159, upper Merced formation); paratypes nos. 306, 307 (locality 161, upper Pico formation, Pitas Point, six miles northwest of Ventura).

New Occurrences

1. *Lower Merced.* An excellent cone collected from the lower Merced is asymmetrical in outline, with prominent triangular apophyses at the tips of the scales on the upper, outer side of the cone. The specimen measures 6.9 cm long and 6.7 cm wide, and is asymmetrically ovate. It can scarcely be distinguished from the normal cones produced by the living *Pinus muricata*.

The cone was recovered at locality PA-36 (U.C. Mus. Pal.), situated in section 14, 1220 feet south, 10° east of benchmark 538, San Francisco South Quadrangle, U. S. Geol. Surv., 7½ minute series, 1947. It has a stratigraphic position close to the boundary between the Etchegoin-San Joaquin faunal "stages," and hence is transitional middle-upper Pliocene in age. The site is closely associated with marine invertebrate locality B6331 (U.C. Mus. Pal.).

Collection: U. C. Mus. Pal., Paleobot. ser., hypotype no. 20532 (locality PA-36, lower Merced).

2. *Santa Paula Creek*. During their field studies of sedimentary structures in rocks of the Ventura basin, Drs. John C. Crowell and Edward L. Winterer collected parts of two carbonized pine cones in rocks that crop out 220 feet north of the steel bridge in Santa Paula Creek, situated three miles north of town (Crowell, 1957, p. 999). The site is in steeply dipping strata of the Pico formation which at this locality yield foraminifera of late Pliocene age. Associated with the cones were a medium phalanx of a deer, broken shells of shallow water mollusks, and deep water foraminifera. The former were all transported into deeper water offshore, from a source area in the hills to the north.

The carbonized cones are comparatively small due to shrinkage and compression. The proximal part of the largest specimen is 2.1 cm long and 2.9 cm wide, and is incomplete (pl. 5, fig. 4). Both specimens have well-preserved cone scales, with low pyramidal umbos that still have a few sharp prickles like those on cones of the living *Pinus muricata* from which they can scarcely be distinguished.

Collection: U. C. Mus. Pal., Paleobot. ser., hypotype no. 20380, homeotype no. 20381 (Santa Paula Creek).

3. *Punta Gorda, Ventura Co.* This specimen is a flattened cone measuring 4.5 cm long and 3.5 cm wide. It is asymmetrically ovate in outline, and has low pyramidal umbos on the scales on the upper, outer side of the cones. It is well matched by cones of the living *Pinus muricata*.

The specimen was collected by A. M. Piper at Punta Gorda, one mile west of Rincon Oil Field in the upper Pico formation of upper Pliocene age (Jennings and Troxel, 1954). It has somewhat smaller cone scales than those of *Pinus masonii* Dorf from the same formation four miles to the southeast along the coast.

Collection: Calif. Acad. Sci., locality 2133, hypotype no. 12738 (Punta Gorda).

Pinus muricata Don

(Pl. 5, fig. 3; pl. 6, figs. 3-4; pl. 7, figs. 1-9)

Pinus muricata Don. Mason, Madroño, 2: 51, pl. 1, fig. 3, 1932; Chaney and Mason, Carnegie Inst. Wash. Pub., 415: 54, pl. 4, fig. 1 (same specimen as Mason's, above); pl. 5, fig. 3, 1933 (*Carpinteria flora*).

Mason, Carnegie Inst. Wash. Pub., 415: 147, pl. 6, fig. 2, 1934 (*Tomales flora*).

Langenheim and Durham, Madroño, 17: 38, fig. 3h, 1963 (*Little Sur flora*).

Mason, Carnegie Inst. Wash. Pub., 346: 148, pl. 3, figs. 4-5 (figs. 4-5 are the same as those identified and figured by Frost as (*Pinus tuberculata*), 1927 (*Rancho La Brea*)).

Pinus attenuata Lemmon. Knowlton, J. Wash. Acad. Sci., 6: 85 (part), 1916 (*Rancho La Brea*).

Pinus tuberculata Gordon. Frost, Univ. Calif. Pub. Bot., 14: 75, pl. 15, figs. 1-2, 1927 (*Rancho La Brea*).

All the records cited above are of late Pleistocene age. The *Carpinteria* flora has been dated by radiocarbon as older than 38,000 years (Fergusson and Libby, 1964), and the *Tomales* has been dated (Berger and Libby, unpublished) as 29,050 ± 1100 years. The age of the *Little Sur* flora is also late Pleistocene to judge from its occurrence on one of the lower coastal terraces, and is possibly only 10,000 years to judge from chemical evidence of age of the associated freshwater molluscs (*in* Langenheim and Durham, 1963). The *Rancho La Brea* deposit is late Pleistocene, but different materials recovered from it indicate that the fossils were not entrapped contemporaneously. The greatest age is provided by *Quercus agrifolia* leaves dated by radiocarbon as 32,350 ± 1400 years (Berger and Libby, unpublished) the youngest by cypress wood dated as 14,400 ± 300 years (Howard, 1960).

Collection: Santa Barbara Mus. Nat. Hist., hypotypes nos. 2, 3 (*Carpinteria*); U. C. Mus. Pal., Paleobot. ser., hypotype no. 454 (*Tomales*); Univ. Illinois Paleobot. coll., hypotype no. L-7 (*Little Sur*); Los Angeles Co. Mus. (*Rancho La Brea*).

New Occurrences

1. *Bixby Slough, Wilmington*. In 1921, W. S. W. Kew collected several fragmentary cones from the upper San Pedro formation due west of Wilmington and south of Bixby Slough, in low hills on both sides of the Pacific Electric tracks at locality 282, Redondo Quadrangle. Their occurrence in the San Pedro formation indicates that they are early Pleistocene in age (Woodring, Bramlette & Kew, 1946).

Three carbonized specimens of *Pinus muricata* are in the collection, but they are mostly incomplete and somewhat broken and eroded. The cones are small, measuring up to 6.5 cm long. Two of them display the small triangular apophyses on the cone scales that are typical of the species.

Collection: U. C. Mus. Pal., Paleobot. ser., hypotype no. 20526; homeotypes nos. 20541, 20542.

2. *Point Sal Ridge*. In connection with his study of the processes of dune formation along the coastal strip between Point Sal and Oceano, Jerry L. Matthews discovered well-preserved pine cones in the Orcutt formation (or Orcutt sand). He accompanied me to the site late in August, 1965, at which time a large collection was made, and the area was visited again in November when additional material was secured. Two species are definitely represented in the collection. *Pinus muricata* cones are most abundant. A total of 25 complete to nearly complete cones were recovered, and an additional 43 were observed in varying states of destruction that were not retained for study.

P. radiata cones are less common, and include a total of five, none of which is wholly complete. A nearly symmetrical cone with very thin scales may represent *P. remorata* (see below), but it is too incomplete to be certain of its identity; it has nonetheless been retained in the collections for future reference.

An exceptionally well exposed section of the Orcutt formation crops out in the major (unnamed) canyon that drains west to Mussel Point, just north of the northwest end of Point Sal Ridge. Although the geologic map of the area (Woodring and Bramlette, 1950) does not depict the extension of the formation down the canyon as far as the plant-bearing beds, the Orcutt is exposed continuously from the westernmost outcrop shown on their map down the canyon to the cliffs where it overlies the Monterey formation.

The locality is 4,800 feet upstream from Mussel Point, and cones and wood occur throughout the 80-foot section exposed in the canyon walls.

As described by Woodring and Bramlette (1950), the Orcutt formation is the oldest and most extensive terrace deposit in the Santa Maria region, having been deposited on a broad surface extending southward into the Lompoc region, sloping gently from the foot of the mountains to the sea. The formation is somewhat deformed, and on the flanks of anticlines it dips as high as 12°. In the vicinity of the plant locality, the Orcutt is essentially horizontal and fully 100 feet thick. It is composed chiefly of poorly sorted, somewhat current-bedded, massive, yellow- to orange-stained coarse sandstones. The sandstones are interrupted by discontinuous gravel lenses three to six inches thick, with generally small (one-half to one inch) clasts of a variety of rock types derived from the bordering region. Dark gray to blue-black clay and mudstone beds are prominent in the section. They have narrow lateral extent, vary from three to six inches up to a maximum of 12 to 15 feet thick, and evidently represent ephemeral pond and swamp deposits. Locally there are thin (one to four feet), discontinuous, finely laminated silt and diatomaceous beds associated with fine sandstones, and they appear to have formed in shallow lakes.

The general depositional setting of the formation seems to have been much like that on the floodplain of the Santa Maria River today, which enters the ocean two miles north. Prior to extensive cultivation over the lowlands, the floodplain of this river had many small swamps, ponds, and lakes scattered over its surface. Since the plant-bearing beds are now at an altitude of from 400 to 480 feet, the summit of Point Sal Ridge rose about 800 feet above the south margin of the site of plant accumulation. The grove of pines that contributed to the record presumably covered its slopes, reaching down to the floodplain. To the west of the present coast the formation no doubt interfingered with

marine beds, paralleling its relations at Burton Mesa to the south (Woodring and Bramlette, 1950, p. 51).

Structural relations in the adjacent area show that the Orcutt overlies the folded lower Pleistocene Paso Robles formation with angular discordance, and hence indicates its upper Pleistocene age. A tapir tooth recovered from the formation about a mile east of the plant locality in Corralitos Canyon is of Pleistocene age (Stirton and Wedde, 1929). A few fresh water molluscs collected from the formation are also consistent with this age, though they are not diagnostic in terms of narrow age assignment (Woodring and Bramlette, 1950, pp. 52, 180). Wood is abundant in the formation at the cone locality, and gives a radiocarbon age of $26,700 \pm 800$ years (Berger and Libby, unpublished).

The fossil cones of *Pinus muricata* from the Orcutt formation are remarkably well preserved, having undergone no alteration and scarcely any compression. The smaller ones are 3.5-4.0 cm long and 3.5 cm wide, and the largest ones are 6.0 cm long and 4.5 cm wide. They are ovate, strongly asymmetrical, and the scales have prominent triangular apophyses on the outer side and some of them are markedly attenuate and reflexed. The fossil cones are rather similar to those produced by mature trees of *P. muricata* in the adjacent region. The nearest *P. muricata* stands to the fossil locality are (1) 20 miles north in the San Luis Range, and (2) 18-20 miles southwest on Burton Mesa and Purisima Ridge. Comparison of the fossils with suites of cones from these trees shows that none of the fossils have cone scales with relatively low or inconspicuous apophyses, as do some of those on the modern trees, and the fossils also tend to be more asymmetric. It has also been noted that the fossils have cone scales that are much more conspicuously triangular and raised than are those formed today by *P. muricata* on Inverness Ridge, north of San Francisco. It is apparent that before we can understand more fully the evolutionary history of the races that characterize the living species, larger suites of fossil *P. muricata* (and *P. masonii*) cones must be collected from other localities for comparison with cones produced by living populations.

Collection: U. C. Mus. Pal., Paleobot. ser., hypotypes nos. 20398-20408, homeotypes, nos. 20409-20416.

Pinus pretuberculata Axelrod
(Pl. 2, fig. 2)

- Pinus pretuberculata* Axelrod, Carnegie Inst. Wash. Pub., 476: 166, pl. 3, fig. 4 only, 1937 (*Mount Eden flora*).
Condit, Carnegie Inst. Wash. Pub., 553: 74, pl. 14, fig. 1, 1944 (*near Table Mountain*).
Axelrod, Univ. Calif. Pub. Geol. Sci., 34: 227, pl. 18, figs. 3-4, 11-13, 1958 (*Verdi flora*).

Restudy of the type specimens of *Pinus pretuberculata* from the Mount Eden flora shows that two species of pine are represented. One of the figured specimens (pl. 3, fig. 3) and several poorly preserved cones are obovate in shape. To judge from the nature of the umbos, which appear to have been rounded, they evidently represent a pine allied to *P. radiata* (see discussion under *P. lawsoniana*).

The other specimen (pl. 3, fig. 4) has small raised umbos much like those that are developed on the inner side of *Pinus attenuata* cones today. However the cone is not complete, and it can also be matched by cones of *P. muricata*. Until more complete material is available from the Mount Eden formation, the affinities of this specimen must remain somewhat in doubt. That it more probably represents a cone allied to *P. attenuata* than *P. muricata* is suggested by its resemblance to the cones that have been recovered from near Tuolumne Table Mountain and at Verdi. The cone scales of all these specimens are so similar that they may be considered to represent the same entity. The Table Mountain specimen is sufficiently complete to show that it represents the proximal third of a cone of the *P. attenuata* alliance, with large hooked scales on the outer side of the structure. It is well matched by cones produced by central California populations of *P. attenuata*. The three specimens in the Verdi flora display scales like those of the Table Mountain and Mount Eden specimens, and fascicles of a three-needled pine in the Verdi flora are very similar to those of *P. attenuata*.

Collection: Los Angeles Co. Museum, holotype no. 1014/696; (*Mount Eden*); U. C. Mus. Pal., Paleobot. ser., hypotype no. 2720 (*Table Mountain*); U. C. Mus. Pal., Paleobot. ser., hypotypes nos. 1972-1975; homeotype no. 1971 (*Verdi*).

New Occurrence

Klamath Falls, Ore. A cone of *Pinus pretuberculata* collected by Russell Pengelly in a new highway cut at the north end of Klamath Falls, Oregon, occurs in a pumiceous lense associated with volcanics. Dr. G. D. Hanna reports (oral communication, March 1965) that freshwater molluscs in the associated section appear to be of Pliocene age. The cone measures 8 cm long and 4 cm wide, is long-attenuate, and has asymmetrical knobs on the upper scales on the proximal outer side. The cone is closely similar to those produced by the living *P. attenuata*.

Collection: Calif. Acad. Sci., locality 36585, hypotype no. 12739.

Pinus radiata Don

(Pl. 2, figs. 1, 3; pl. 3, figs. 1, 3-4;
pl. 4, fig. 1; pl. 8, figs. 1-2)

Pinus radiata Don. Mason, Carnegie Inst. Wash. Pub., 346: 147, pl. 1, fig. 2, 1927; Mason, Carnegie Inst. Wash. Pub., 415: 148, pl. 6, fig. 3; pl. 7, fig. 3, 1934 (*Tomales flora*).
Chaney and Mason, Carnegie Inst. Wash. Pub., 415: 55, pl. 4, fig. 2; pl. 5, figs. 4, 9, 1933 (*Carpinteria flora*).
Langenheim and Durham, Madroño, 17: 38, fig. 3h, 1963 (*Little Sur flora*).

These occurrences are all late Pleistocene in age. As noted above (see *Pinus muricata*), the Tomales flora has been dated by radiocarbon as 29,050 ± 1100 years, and the Carpinteria is older than 38,000 years. The Little Sur flora occurs on one of the lower coastal terraces and may be as young as 10,000 years to judge from chemical evidence of the associated freshwater molluscs (Langenheim and Durham, 1963, p. 36).

Collection: U. C. Mus. Pal., Paleobot. ser., hypotypes nos. 456, 457, 20546. (*Tomales*); Santa Barbara Mus. Nat. Hist., hypotypes nos. 4,5,6 (*Carpinteria*); U. C. Mus. Pal., Paleobot. ser., homeotypes nos. 20543-20545 (*Carpinteria*); Univ. Illinois, Paleobot. coll., hypotype no. L-8 (*Little Sur*).

New Occurrences

1. *Rancho La Brea.* Two cones of Monterey pine are now known from Rancho La Brea. The larger one (pl. 2, fig. 1), measuring 7.5 cm long and 8.0 cm wide, with an asymmetrically ovate outline and swollen, smoothly rounded umbos on the proximal scales on the outer side of the cone, was discovered in the miscellaneous paleobotanical collections at the University of California. The other smaller one (pl. 3, fig. 1), 6.5 cm long and 7.4 cm broad, is from Pit 67 at Rancho La Brea.

As noted above (see *Pinus muricata*), the age of the fossil plants at Rancho La Brea varies, though all are late Pleistocene. In view of the climatic indications of *P. radiata*, it is presumed to have lived there during a glacial-pluvial stage.

Collection: U. C. Mus. Pal., Paleobot. ser., hypotypes nos. 20382, 20383 (*Rancho La Brea*).

2. *Potrero Canyon.* This site is along Coast Highway 101 just north of the Los Angeles-Santa Monica boundary, at the mouth of Potrero Canyon in Pacific Palisades. Several unaltered pine cones and numerous manzanita seeds were collected here in 1949 by J. J. Hoppinger when they were uncovered during excavation for the installation of a storage tank for a gasoline station.

The nearly horizontal, well-cemented fossiliferous bed is a pebbly conglomerate filled with broken mollusc shells associated with coarse sandstone and a thin limestone. The beds form the base of the Pleistocene section in this area, rest unconformably on Pliocene marine rocks, and have been considerably faulted. The plants occur in the same bed that yielded the invertebrate fauna at locality 31 discussed by Woodring (*in* Hoots, 1931, p. 120), and are within 25 feet of it. Valentine (written communication 1965) reports that the fauna at locality 31 represents colder water than the late Pleistocene fauna 0.85 miles farther up Potrero Canyon (Valentine, 1956). The fauna was considered initially by Woodring to be transitional Plio-Pleistocene in age, but later suggested that it is equivalent to the Lomita marl and Timms Point silt of early Pleistocene age (Woodring, et al., 1946, p. 104). A new fauna from apparently the same horizon was recently collected (U.C.L.A. locality 5297) in Rustic Canyon 2800 feet northeast of locality 31. It includes all the species recorded in the fauna of locality 31, as well as other species; and like the latter, this new fauna has several species that occur in the Timms Point but not in the younger rocks of this area (oral communication Takeo Suzuki, November, 1965).

The plant collection includes the proximal third of an unaltered cone of *Pinus radiata* and also an impression of another one preserved in conglomeratic sandstone, a cast of which is figured (pl. 4, fig. 1). The cones are 7.0 (estimated) to 9.0 cm long and 4.6 to 5.0 cm wide. The umbos on the proximal part of the outer side are swollen, rounded, and smooth, like those on *P. radiata* today.

Collection: U. C. Mus. Pal., Paleobot. ser., hypotype no. 20384; homeotype no. 20385.

2. Crystal Springs Reservoir. Three complete Monterey pine cones and three fragmentary specimens, as well as the upper half of a cone of *Picea sitchensis*, were recovered by Mr. William Glen at the base of the Santa Clara formation on the west side of Crystal Springs Reservoir, five miles southwest of San Mateo. As indicated in his report (Glen, 1961), the basal part of the Santa Clara formation that yields the fossils is a lignitic, poorly indurated, gray mudstone one to two feet thick that grades up into conglomerate and sandstone. The formation rests with angular discordance on the highly brecciated Calrea limestone member of the Franciscan formation which lies against the San Andreas fault that here follows the axis of the reservoir and trends north-northwest. The locality is between Upper and Lower Crystal Springs Reservoir, 300 yards north, and 45° west of the entrance to the rock quarry operated by Skyline Materials, Plant No. 1.

The carbonized cones of *Pinus radiata* are comparatively small owing to shrinkage in the mudstone. They measure 7.4 to 8.2 cm long and 5.0 to 5.3 cm broad. The cones are asymmetrical and have smooth, swollen umbos on the upper side of the outer part

of the cone. They cannot be distinguished from those produced by the living species.

The Santa Clara formation has been considered late Pliocene and Pleistocene in age. In discussing this problem, Savage (1951) and Glen (1961) note that some of the confusion results from the fact that more than one formation may be included in the unit, that no type section has yet been designated, and that most of the fossil collections recovered from it are quite small and hence inadequate for close age assignment. The Santa Clara flora (Dorf, 1933), which occurs 23 miles south-southeast of the cone locality, appears to be early Pleistocene to judge from the occurrence of spruce cones in it. The locality at Crystal Springs Reservoir was regarded as probably late Pliocene by Glen, though the spruce cone suggests that it may be younger. In the type Merced formation 15 miles north-northwest, a palynological study (Axelrod and Ting, manuscript) shows that spruce is rare (a few grains) at localities up to a horizon 35 feet stratigraphically above the upper gastropod beds, where it is abundant. On the assumption that its abundance means that the trees were near at hand, then the cone from Crystal Springs Reservoir probably indicates that the deposit is Pleistocene because the upper gastropod beds in the Merced have been considered to be of this age by all investigators (see Glen, 1959).

The cone of *Pinus sitchensis* is incomplete, with only the basal half or two-thirds of the structure represented. It measures 3.5 cm long and 2.0 cm wide, and is closed owing to submersion in water. The cone is composed of numerous overlapping, paper-thin scales. The exposed parts of the scales are slightly ridged vertically, and the distal edges are irregularly frayed or toothed. The specimen cannot be separated from cones of the living *P. sitchensis* (Bongard) Carriere, which now lives on the cooler coastal strip 135 miles north, from near Fort Bragg northward into Alaska (U. C. Mus. Pal. homeotype no. 20390).

Collection: U. C. Mus. Pal., Paleobot. ser., hypotypes nos. 20386, 20387; homeotype nos. 20388-20389, 20547.

4. Thornton Beach. Collections of cones of *Pinus radiata* have been recovered from peaty beds exposed on the beach 4,400 feet south of the south end of Fleishacker Pool, San Francisco. They are indistinguishable from those of the living Monterey pine, with swollen and rounded apophyses on scales of the upper, outer side of the cone.

Detailed stratigraphic work in the area by Mr. N. Timothy Hall, Department of Geology and Geophysics, University of California, Berkeley, has revealed that the peaty beds are at the base of the Thornton Beach formation (new) which comprises 635 feet of steeply dipping sandstone and conglomerate that rest unconformably on the upper Merced, and which were included in it by previous workers. The base of the formation is 160 feet above the upper gastropod beds of the upper Merced according to Hall.

Associated with the peaty beds are *Equus* and *Tanupolama*, which are Irvingtonian in age. They indicate that at a maximum the beds are not older than Kansan.

Collection: Calif. Acad. Sci., locality 30519 (three cones), locality 29442 (six cones); U. C. Mus. Pal., Paleobot. ser., hypotype no. 20528, homeotype nos. 20529-20531.

5. *Point Sal Ridge.* Five cones of *Pinus radiata* have been recovered from the Orcutt formation in the deep (unnamed) canyon at the northwest base of Point Sal Ridge, situated 12 miles west of Santa Maria (for geologic occurrence, see *P. muricata*). None of the cones is complete. They were weathered prior to collecting, and owing to their fragile nature were broken somewhat more in the process of excavation.

The incomplete cones are from 7.0 - 7.5 cm wide and are estimated to have been at least 8.0 cm long. The scales on the upper, outer side of the cone have large, conspicuously swollen, smooth umbos. The fossils are well matched by the cones produced by *Pinus radiata* and are--so far as can be determined from the incomplete specimens--more like the norm of the population at Cambria, which is distinguished by larger cones than the trees at Monterey. In this connection it is recalled that Chaney and Mason (1933, p. 55) have pointed out that the *P. radiata* cones from Carpinteria also are more nearly of the size of the cones from Cambria than those from Monterey.

Collection: U. C. Mus. Pal., Paleobot. ser., hypotypes nos. 20417-20418, homeotypes nos. 20419-20421.

Pinus remorata Mason

(Pl. 3, fig. 2; pl. 4, figs. 2-4; pl. 5, fig. 6;
pl. 8, fig. 3)

Pinus remorata Mason, Madroño, 2: 52, pl. 1, fig. 1, 1932; Chaney and Mason, Carnegie Inst. Wash. Pub., 415: 10, pl. 6, figs. 1-2, 1930 (*Willow Creek flora, Santa Cruz Island*).

Chaney and Mason, Carnegie Inst. Wash. Pub., 415: 56, 1933 (*Carpinteria flora*).

The previously reported cones of this species are from localities of late Pleistocene age in southern California. The Willow Creek flora of Santa Cruz Island has been dated by radiocarbon as $14,200 \pm 250$ years B.P. (Fergusson and Libby, 1963). The Carpinteria is older than 38,000 years to judge from radiocarbon evidence (Fergusson and Libby, 1964).

Chaney and Mason (1933) recovered two water-worn cones of *Pinus remorata* in the Carpinteria deposit, embedded in conglomerate that Mason (1949, p. 359) considers to represent a marine beach. He suggests that the cones may have been transported across the 30 mile wide Santa Barbara Channel from Santa Cruz Island where the species is well represented in the Willow Creek

flora, and where it also lives today. He proposed this interpretation for two reasons. First, he believes that the species has always had an insular occurrence. Second, he points out that "the very prolific way in which *P. remorata* bears its cones would seem to demand that if it grew near enough to the Carpinteria site for two cones to enter, many more cones would certainly have entered with them and their preservation would have been insured by the asphaltum matrix of the deposit."

Geologic evidence (Putnam, 1942) shows that all of the exposed fossiliferous Carpinteria deposit was laid down in a stream valley. Since the deposit considered by Mason to represent a marine beach is a gravel bar deposited by a stream, it would appear that the cones probably were transported to the site from trees that lived upstream from the deposit. Although fossil evidence indicates that *Pinus remorata* was a rare species in the area during Carpinteria deposition, the relation is wholly consistent with the occurrence of *Juniperus californica*, *Arctostaphylos glauca*, and *Pinus* cf. *sabiniana* in the flora. They point to a more temperate climate in the nearby region than that to which *P. remorata* is adapted, and it may well account for the rarity of the species there.

At the present time *Pinus remorata* is known from three sites on the mainland. A few trees are in Pine Canyon on Burton Mesa several miles northwest of Lompoc. They are near the crest of the terrace 200 yards southwest of the southeast gate to Vandenberg airbase, occupying the Orcutt sand that unconformably overlies diatomaceous shale of the Sisquoc formation. *P. remorata* was not noted below the terrace, where *P. muricata* is dominant. Trees that appear to be intermediate (hybrids?) between them are common in and close to the zone of contact, but not below it. The second site for *P. remorata* is about five miles northwest of Pine Canyon, in the Lompoc oil field which is situated in the foothills of the Purisima Hills. Here the trees occur on the coarse-grained Careaga sandstone. *P. muricata* is in the adjacent region, but is not as restricted in terms of substrate, for it occurs on diatomite, sandstone, and conglomerate representing several formations of different ages. The third site for *P. remorata* is in Baja California about 10 miles southwest of San Vicente, on the coastal plain one mile west of the mouth of Cañon de las Pinitas. This small grove occurs on Paleocene sandstone, conglomerate, and ash beds, together with several other species that are chiefly of insular occurrence.

On the basis of his studies in the 'forties, Mason (1949, p. 360) proposed that infiltration of genes of *Pinus remorata* into the mainland populations of *P. muricata* is indicated by the stature of the trees and habitat preference of the grove in Pine Canyon near Lompoc. He suggested that this resulted from transport of *P. remorata* pollen from Santa Cruz and Santa Rosa islands, situated 50 miles southeast. This proposal appears to be based in

part on his assumption that *P. remorata* has never had a continental history. The Pleistocene fossil record shows that it has occurred in coastal southern California at Potrero Canyon, near Wilmington, at Carpinteria, and probably at Point Sal Ridge. Furthermore, relict groves of *P. remorata* still occur at Pine Canyon on Burton Mesa and in the Purisima Hills. Although there appear to be hybrids between *P. remorata* and *P. muricata* in these areas, and also in Baja California (Cañon de las Pinitas, ten miles southwest of San Vicente), it seems probable that the *P. muricata* populations are swamping out those of *P. remorata* chiefly because the former are more vigorous and better adapted to present climatic conditions.

Collection: U. C. Mus. Pal., Paleobot. ser., hypotype nos. 416, 417 (*Willow Creek*); Santa Barbara Mus. Nat. Hist., homeotype no. 7 (*Carpinteria*).

New Occurrences

1. *Potrero Canyon.* The collection from this site (for geologic occurrence, see *Pinus radiata*) includes six essentially unaltered cones that represent *P. remorata*. They are from 4.0 to 8.5 cm long and 4.5 to 5.5 cm wide, obovate in outline, and symmetrical in shape. The cone scales are thin like those of the normal cones produced by the species and their surface features appear to be indistinguishable from those of the living pine.

The abundance of these cones and manzanita seeds in the basal beach deposit of the lower Pleistocene indicates that they were entombed close to the shore.

Collection: U. C. Mus. Pal., Paleobot. ser., hypotype nos. 20391-20394; homeotype nos. 20395-20396.

2. *Bixby Slough, Wilmington.* In the collection recovered by W.S.W. Kew from the upper San Pedro formation west of Wilmington (see discussion under *Pinus muricata*), there is a small, nearly symmetrical, closed cone with apparently thin plane scales that seems to represent *P. remorata*. As shown on pl. 5, fig. 6, the cone is somewhat incomplete, measuring about 3.4 cm long and 2.3 cm broad.

Collection: U.C. Mus. Pal., Paleobot. ser., hypotype no. 20527.

3. *Point Sal Ridge.* In the collection from the Orcutt formation, exposed in the deep canyon just north of Point Sal Ridge (for occurrence, see *Pinus muricata*), there is a cone that may represent *P. remorata*. It is not complete, yet it seems more nearly to represent this species than *P. muricata*. The oval cone is 5.5 cm long and 4.5 cm wide and is nearly symmetrical. As far as can be determined, the cone scales are thin and plane, like those of the living *P. remorata*. The cone is very similar to those recorded from Potrero Canyon. The possibility has been considered that it may represent no more than one extreme of the

variation of *P. muricata* at the locality. However, none of the numerous cones from the Orcutt formation approach this fossil in morphology. All of the *P. muricata* cones have well developed, triangular, raised umbos: none is intermediate between *P. muricata* and the presumed *P. remorata* in respect to cone umbos. Furthermore, this fossil that appears to be *P. remorata* is not strongly asymmetrical like all of the *P. muricata* cones with which it is associated.

The occurrence of three species of closed-cone pines at the Orcutt locality is not unique, but has been reported previously for the Carpinteria flora (Chaney and Mason, 1933).

Collection: U. C. Mus. Pal., Paleobot. ser., hypotype no. 20422.

Unconfirmed Records

1. A cone of *Pinus muricata* is reported by Scott (1927) from the Santa Clara formation near Portola, in the foothills west of Stanford University. Until it has been re-examined (it is now in storage at Stanford University), it seems best to list the occurrence here.

2. Scott (1927) reports the occurrence of two cones of *Pinus attenuata* in Miocene rocks 13 miles north of Santa Barbara. These cones are also in storage at Stanford and should be re-examined.

3. Mason (1934, p. 49) reports that *Pinus radiata* occurs in nearly flat-lying beds that rest on the dipping Merced formation at Mussel Rock, on the coast south of San Francisco. The whereabouts of the cone is not now known. Its stratigraphic occurrence shows the deposit is of Pleistocene age, and a small mammalian fauna of late Pleistocene age (Peabody, 1945) occurs in the same section.

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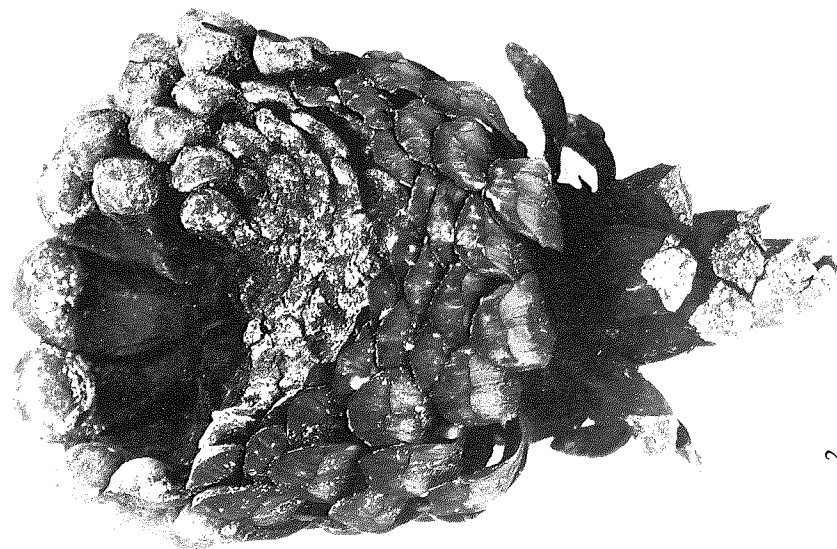
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Plate 1

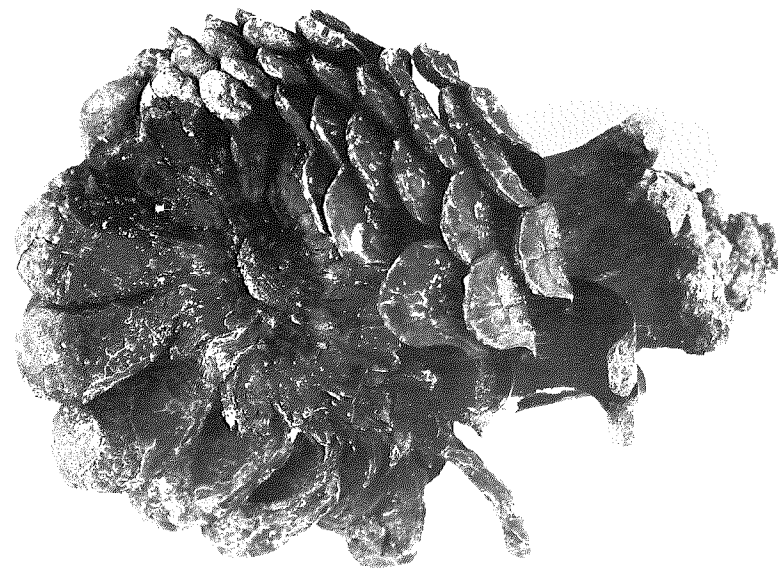
Fossil Closed-cone Pines

Fig. 1. *Pinus lawsoniana* Axelrod. Holotype, U. C. Mus. Paleobot. ser., no. 20533. Forest bed below type Merced formation, Mussel Rock, San Francisco. Collected by Andrew C. Lawson, 1895.

Fig. 2. *Pinus lawsoniana* Axelrod. Paratype, U. C. Mus. Paleobot. ser., no. 20534. Forest bed below type Merced formation, Mussel Rock, San Francisco. Collected by Andrew C. Lawson, 1895.



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