# Pollen Analysis and the Cenozoic

## Ancient climate and vegetation can be studied by comparison of modern and fossil pollen rains.

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The record of past plant communities provided by the fossil pollen and spore content of sediments is useful in the study of climatic and environmental change. Palynologists (pollen and spore specialists) can study pollen rains quantitatively. A reflection of major ecological, evolutionary, geological, and archeological events can be found in changes in the pollen stratigraphic record. Although not all sedimentary deposits contain fossil pollen—surprisingly enough, not even certain beds rich in fossil leaves, fruits, and vertebrate remains—a given sedimentary deposit is more likely to contain these microfossils than to contain any other plant remains. The chemically resistant outer walls of pollen and spores are the most abundant fossils of terrestrial origin. Their singular abundance has led to the widespread use of fossil-pollen data in practical stratigraphic problems such as petroleum exploration.

The relative abundances of different kinds of pollen are plotted against geologic time, and the graphic record is known as a pollen diagram. Before going on to a discussion of the results of late Cenozoic pollen studies in western North America, we will point out certain problems which arise in the interpretation of pollen diagrams (*1*).

### A Paleoecological Research Method

Under the title "Pollen analysis as a paleoecological research method," Cain (*2*, *3*) reviewed the major difficulties of palynological study. Some of the difficulties have diminished since the publication of new pollen diagrams and as a result of the many recent studies of modern pollen rains. One difficulty no longer so troublesome as a source of misinterpretation is the problem of long-distance transport of pollen.

Dramatic examples of long-distance pollen transport are common and raise the question of whether such foreign pollen might obscure the reconstruction of past plant communities and past climates. For instance, westerly winds carry pollen from North America into the mid-Atlantic (*1*). Peat bogs in the treeless Faeroe Islands yield pollen of exotic woody plants, including *Alnus*, *Betula*, *Pinus*, and *Tilia*, which grow 420 to 585 kilometers east of the islands (*1*). Pollen of the Southern Hemisphere beech, *Nothofagus*, has been found in postglacial-age peat of Tristan da Cunha, a remote island in the South Atlantic 4500 kilometers east of the nearest beech forests in South America (*4*). Such long-distance transport introduces exotic pollen into different climatic and vegetation zones. But experience has shown that in general this foreign pollen does not obscure the local pollen rain, which, as a rule, drowns out the fraction of pollen brought from greater distances. Although long-distance transport must account for all of the pollen captured in collecting devices exposed over the ocean or polar regions, very little pollen of distant origin is found in forest regions where local pollen production is great.

In regions of extreme relief, a small but significant amount of pollen from particularly abundant pollen producers may drift from one vegetation zone into another. Exotic pollen can also be expected in samples from the arctic tundra, from the subtropical deserts, and in other extreme environments of slow plant growth and relatively low pollen production. The effect of long-distance transport can be evaluated by careful study of the modern pollen rain. For example, we find pine pollen (0.5 to 12 percent) in sediment at the bottom of stock tanks of the Sonoran Desert and desert grassland (see Fig. 1). The stock-tank samples came from localities lying 15 to 50 kilometers from the nearest pine woodland in adjacent mountains. Obviously, no climatic change is indicated by the presence of 1 to 10 percent of pine pollen in fossil deposits in desert grassland. Fossil deposits with a much higher content of pine pollen are another matter; pine-pollen counts in excess of 50 percent in fossil deposits are comparable to the modern pollen rain from montane pine-oak woodland and pine forest (Fig. 1).

*Secondary pollen.* A more subtle source of error in the ecological interpretation of pollen counts is contamination by pollen reworked from older deposits. In Europe the pollen of temperate-forest trees was discovered in the oldest late-glacial lake clays. Accepting this discovery as evidence that temperate plants grew along the edge of the receding ice margin, certain palynologists postulated a warm temperate climate during the initial phase of deglaciation. A major revision in this interpretation of ice-margin conditions was required by the additional discoveries that the temperate-forest tree pollen included Tertiary genera, that this same forest pollen occurred in glacial till as well as in lake clays, and that it apparently had washed into proglacial lakes as the ice sheet melted.

As a result of these discoveries, the notion was discarded that temperate-forest trees might have grown next to the melting ice sheet, and the temperate-forest tree pollen is considered to be rebedded (*5*).

In Massachusetts, glacial till examined by Davis (*6*) was barren, but varved clay was comparatively rich in pollen. The occurrence of occasional Tertiary pollen types in the varved clay led Davis to suspect that rebedding might account for a relatively large amount of the pollen present, and she thus considered the varved-clay pollen counts unsuitable for paleoclimatic interpretation.

Problems of rebedding might be expected to complicate interpretation of pollen diagrams from floodplain allu-

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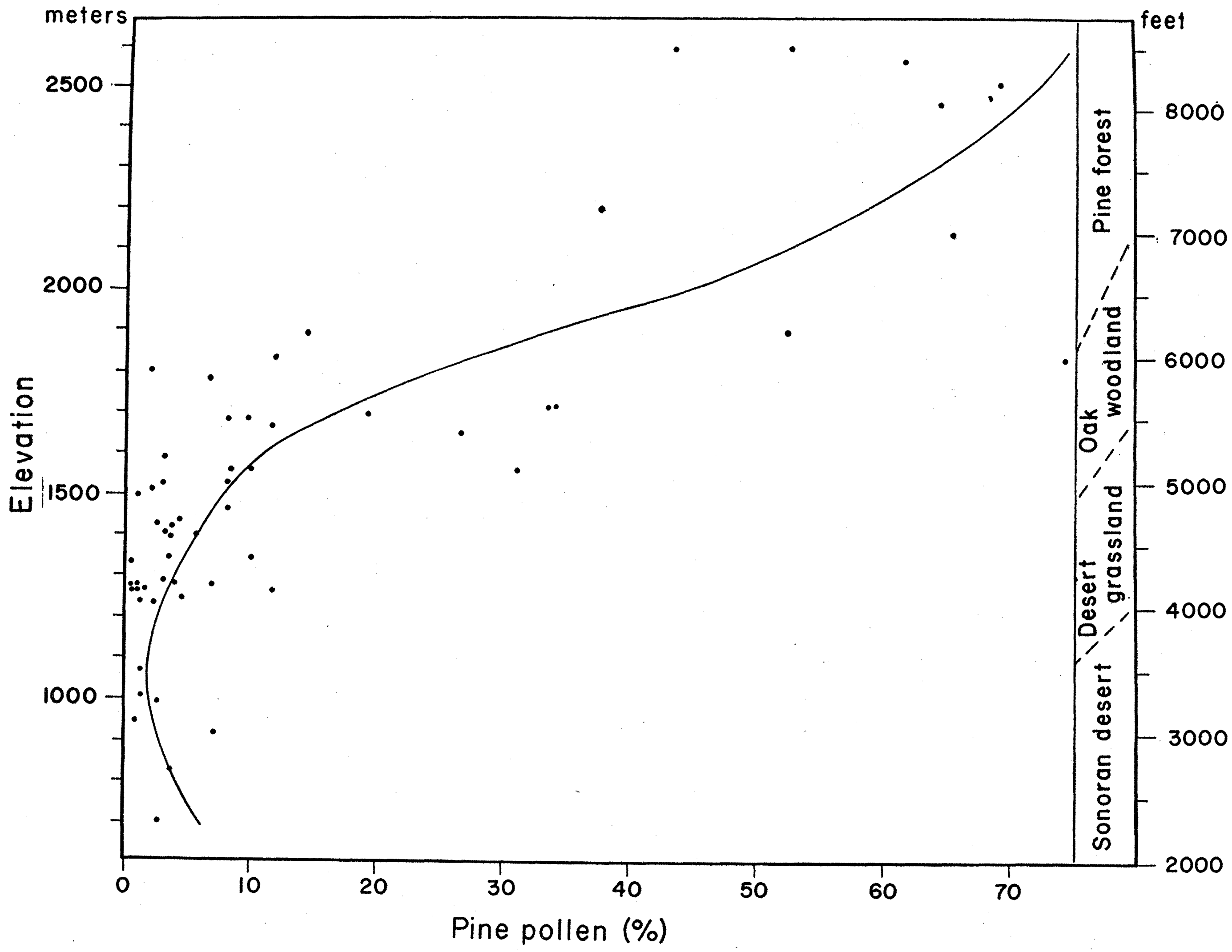

Fig. 1. Graph showing the relationship between elevation, vegetation, and relative abundance of pine pollen in Arizona, based largely on pollen samples from livestock tanks, from 59 collections made between Flagstaff and the Mexican border.

vium. In arid regions a large portion of the postglacial climatic and prehistoric fossil record can be found in banks of sediment exposed in dissected floodplains (arroyos). If eroding headwater outcrops contain abundant pollen, there is great likelihood of redeposition downstream. No evidence of rebedding was found in the analysis of postglacial-age alluvium from Arizona (*7*) and New Mexico (*8*), but the presence of a profusion of rebedded Tertiary pollen grains in sediment from alluviated valleys in Wyoming made paleoclimatic study of these sediments impossible (*9*).

In present-day bottom sediments of Lake Michigan and in Chicago city tap water, Hough (*10*) found well-preserved Devonian spores. Contamination by rebedding may even occur artificially; Paleocene microfossils in lignite added to drilling mud were inadvertently injected into Pleistocene sands during drilling of a core in the San Augustin Plains of New Mexico (*11*). It is evident that the indestructibility of pollen and spores is not always an asset!

*Problems of identification.* Evolutionists and ecologists accustomed to studying species or species populations may be dismayed to find that, "as palynological technique stands now, it is in most cases impossible to determine a fossil sporomorph further down than a genus or group of species" (*12*). Repeated attempts to overcome this difficulty have met with little success. A recent claim of accurate species identification within the genera *Pinus, Quercus, Salix,* and *Abies* (*13*) is not likely to prove an exception. The fact that palynologists are unable to inventory the *species* composition of fossil plant communities makes innovations in the use of pollen-spore data especially desirable. One new method widely used is determination of the ratio of tree pollen to nontree pollen. This ratio is valuable in distinguishing among forest, savanna, grassland, and desert communities.

Identification of pollen in older deposits is more difficult. Unfamiliar pollen and spore types are more numerous in the earlier than in the later Cenozoic. Ultimately, a number of such types will be assigned to living genera, especially to genera of tropical distribution whose pollen is little known at present. Other unfamiliar grains represent pollen or spores of extinct plant species.

Secular changes in pollen morphology can be traced occasionally. From the Upper Cretaceous to the mid-Tertiary, the inner wall (endexine) of the *Ctenolophon*-type pollen increased in thickness (*14*). On the other hand, the morphology of many genera (*Alnus, Betula, Carya*) has remained essentially unaltered from the early Tertiary to the present (*15*).

*Uniformitarianism.* Fossil plant species and their living relatives are assumed to have similar ecological requirements. Belief in the principle that the present is an ecological—as well as a geological—key to the past is strengthened by the observation that Cenozoic fossil floras seldom contain disharmonious mixtures of genera. An exception which occasions considerable soul-searching is the case of *Ephedra* (*16*). Pollen of this arid land shrub would not be expected in early Tertiary and late Mesozoic forest floras, where it has frequently been reported (*14–18*), sometimes in abundance (*14*). Are we to imagine that *Ephedra*, presently a shrubby heliophyte of the desert and dry woodland, once grew in the shade of mesic Tertiary forests?

Commonly, *Ephedra* grows on dunes and other well-drained sandy soils, including dunes of at least one region of moist climate (Brittany). Possibly it formerly occupied sandy shores along floodplains and lakes surrounded by mesic Tertiary forests. In speculating about this provocative case one should not lose sight of the fact that Tertiary forest floras generally make sense in terms of what we know of living forest associations.

*Modern pollen rains.* To recognize natural plant communities from their pollen rains, the palynologist examines the pollen-spore content of moss polsters, fresh alluvium, soil surfaces, and bottom samples of artificial ponds (including open-top cattle tanks scattered throughout the Western range), reservoirs, lakes, and marine estuaries. Data on modern pollen rains are very useful in the ecological interpretation of ancient pollen rains and the reconstruction of ancient plant communities.

As a further refinement the palynologist may cooperate with the ecologist in a comparison of pollen rains with the composition of adjacent plant communities. In the region of the San Augustin Plains, the quantity of juniper, pine, and oak pollen caught on petrolatum slides was more closely related to the basal area of tree trunks than to other estimates of plant cover, such as relative density or relative coverage (*19*). The basal area of trees producing especially abundant pollen (*Pinus, Betula, Corylus*) or very little pollen (*Acer, Magnolia*) may be very difficult to predict from the local pollen rain of these trees.

Quantitative comparisons of ancient and modern plant communities are not original with the palynologist. In a pioneering statistical study Chaney (*20*) attempted to reconstruct community composition of the rich Bridge Creek leaf flora (mid-Tertiary of Oregon) through quantitative investigation of a possible modern forest equivalent, Muir Woods of California. At Muir Woods he counted the number of leaves per square foot in a stream bed. He then related leaf-fall data to abundance of *Sequoia, Alnus, Quercus, Umbellularia,* and other adjacent trees and shrubs. Such critical comparison of modern and fossil leaf content of sediments is no different from the method used by palynologists in the attempt to recognize ancient forest communities. This type of comparison is impossible, however, if the modern communities needed for study have been obliterated or greatly reduced. For this reason, if for no other, natural scientists interested in in the meaning of pollen diagrams have a stake in the preservation of natural vegetation types still relatively unaltered by man.

*Relative and absolute counts.* While many refinements in the interpretation of fossil percentages can be made through close study of the pollen fallout of forests and other natural plant formations, the paleoecologist cannot use relative pollen percentages to compute the regional abundance of different plant species. In part the difficulty lies in the nature of percentage data, which incorporate a mathematical constraint, recognized by Pearson (*21*) as the spurious correlation. There is a strong tendency toward inverse relationships (significant negative correlations) between the more abundant pollen types in a pollen profile. A change in frequency of occurrence of one pollen type may not reflect a change in abundance or in pollen production or in local distribution for that particular plant species. For example, if the absolute pollen production of one common plant species increases while that of the others remains constant, the summed percentages for the latter must decrease. If the abundance and absolute pollen production of all the plant species increases or decreases equally, there can be no change in the pollen percentages. Can the spurious effect be removed by appropriate statistical treatment?

Palynologists seldom subject their percentages to formal correlation analysis; exceptions are analyses of cores from the Valley of Mexico (*22*) and of spores in Pennsylvanian-age coal beds. In the latter case Gray and Gunnel (*23*) recognized that a significant negative correlation between the abundant genera *Laevigatosporites* and *Lycospora* was neither an ecological nor a stratigraphic effect. In computing simple paired correlations for the four most abundant genera in cores from the Valley of Mexico, Sears and Clisby (*22*) found that pine, which accounts for over 70 percent of the fossil tree pollen, is negatively correlated with oak, alder, and fir. They endeavored to explain the correlation in ecological terms—pine indicating cool dry climates and oak, alder, and fir indicating an increase in moisture.

To eliminate the spurious correlations in the analysis of percentage data, Mosimann (*24*) has proposed use of the compound multinomial distribution and multivariate beta distribution. Applying this method to the Valley of Mexico cores, Mosimann found that when the spurious effect is subtracted, the negative correlation between pine and oak and pine and alder is reduced and that between pine and fir vanishes. A reappraisal of Pleistocene climates in the Valley of Mexico is needed. Palynologists seriously concerned with statistical correlations should become aware of the spurious correlation pointed out by Pearson, and all inverse relationships between dominant types in pollen diagrams should be viewed with this effect in mind.

When it can be determined, the absolute pollen rain offers a direct means of escaping spurious correlations and of obtaining an estimate of community composition. The absolute pollen rain is the amount of pollen per unit area landing during a known time interval. Such data are gathered throughout short time intervals by aerobiologists studying pollen fallout; they are very useful in describing pollen phenology. Unfortunately, the paleoecologist seldom knows the exact annual sedimentation rate in his section. Only in exceptional cases, such as in annually laminated deposits or in sediments very carefully dated by the radiocarbon method, is it possible to compute the absolute pollen deposition in fossil sediments. Meanwhile, palynologists must proceed empirically, with relative percentages plotted as pollen diagrams, and hope the results are not seriously misleading.

*Sample source.* An important development in palynology is the growing interest in nonlacustrine sediments. Lake mud, peat, and other highly organic materials have been the traditional source of sediment for pollen analysis. Marine sediments may be equally suitable (see Fig. 2). Alluvial floodplain deposits in both humid and arid areas have yielded late Pleistocene pollen profiles of paleoclimatic interest (*7, 8, 25*). Cave earth may contain abundant pollen (*26*), and pollen in dung from dry caves in Chile and Arizona yields a record of the diet of certain extinct ground sloths (*27*). Trash mounds and other prehistoric cultural debris may provide pollen evidence of man's use of plants and man's effects on natural vegetation in the vicinity. Additional promising sources of pollen include fossil soils (*28*), glacial ice (*29*), and certain sand dunes (*7*). Evidently, then, pollen and spores persist in sediments of more types than were once thought suitable for their preservation.

## The Western Tertiary

With the exception of Traverse's monograph (*30*) on the Brandon lignite (Oligocene) in Vermont, no major work on Tertiary palynology has been published recently in North America. Traverse has determined the frequency of occurrence of different plant genera and has discussed ecology in terms of pollen percentages, as analysts of Pleistocene pollen do. Although a few paleobotantists (*31*) question the validity of quantitative study of Tertiary plant microfossils, we see no serious obstacle to basing ecological and stratigraphic conclusions on careful, accurate pollen counts.

*A marine profile.* Analysis of a 960-meter sediment core from Wilmington, in the Los Angeles area of southern California, is shown in Fig. 2. The shales and sandstones, dated by associated foraminifera, represent most of Upper Miocene time and extend into the Lower Pliocene. Despite the thickness of the section and the length of time represented (several million years), there is little change in the pollen diagram. The major fluctuation illustrated is in the value for pine, which reached 50 percent or more at 1800- and 900-meter levels, with a lesser peak at about 1440 meters.

The evidence for Tertiary evolution of savannas, grassland, and desert is generally based on fossil remains of xerophytic trees and shrubs, such as at present border or occupy arid habitats (*32*). The reason for this is that megafossils of the low shrubs and delicate herbs which should have been among the dominants in xeric plant communities are seldom found. On the other hand, pollen and spores of many herbs and of certain shrubs can be expected in great abundance in sediments from arid lands, a fact that should be of great help to plant geographers attempting to establish the origin of the desert.

In the case of the Wilmington core, pollen of herbs and of certain low shrubs appeared in fairly great abundance, including pollen of the Gramineae, Chenopodiaceae, Compositae, Malvaceae, Onagraceae, Nyctaginaceae, and Polemoniaceae and pollen of *Ephedra* (Fig. 2). To our knowledge, neither the Polemoniaceae nor the Nyctaginaceae had been recorded previously in the Tertiary. The herb pollen record indicates the presence of arid plant communities as early as the late Miocene.

With the exception of *Ulmus, Liquidambar,* and *Carya* (all of infrequent occurrence), all the genera identified in the Wilmington core have living representatives in California. There was no palynological evidence of an arid tropical thorn-forest element (*Bursera, Sabal, Ficus, Leucaena, Pithecolobium*), recognized by the presence of megafossils in coastal Californian Mio-Pliocene floras (*32*). On the other hand, many of the thorn-forest genera are zoophilous, and their pollen would rarely appear in sediments. Perhaps for this reason, pollen of arid tropical genera did not appear in the analysis of the Wilmington core.

The paleoecological and floristic history of the Pacific slope has been established from the record of scattered megafossil floras, each of which may represent a short span of geological time. Pollen-spore analysis of marine cores provides an opportunity to determine the history of plant communities at a single locality through a much longer period of time. However, critical ecological interpretation of marine cores will require a better understanding of marine basins as pollen traps than we have at present (*33*).

*Miocene pollen floras.* The Miocene floras of the Columbia Plateau of east central Oregon represent a mixed deciduous forest of needle-leaved conifers (especially Taxodiaceae) and broad-leaved hardwoods, such as typify summer-wet climates in the Northern Hemisphere. Although some of the genera (*Ailanthus, Alangium, Cedrus, Cephalotaxus, Cercidiphyllum, Glyptostrobus, Keteleeria, Metasequoia, Pterocarya,* and *Zelkova*) are no longer native to North America, Chaney (*34*) states that, "with the East American element dominant in the fossil flora, both in number of species and in number of specimens included in them, it is apparent that we may best reconstruct the physiognomy of Mascall vegetation by a survey of the modern forests of eastern United States and Canada."

What does the pollen record reveal? Our comparison will be based on pollen counts (*18*) from three mid-Miocene localities—Mascall, Blue Mountains, and Stinking Water—on the Columbia Plateau (Fig. 3). Some common Miocene pollen types are illustrated in Fig. 4. Mascall megafossils, known to the paleobotanist since 1870, include 46 genera and 68 species (*34*). Study of associated fossil pollen has added several families and genera to this flora. Leaves or fruits of some of these additional genera have been found in fossil localities adjacent to the Mascall. With the exception of the perplexing *Ephedra,* the genera and families discovered through their pollen record, such as *Cedrus, Corylus, Juglans, Pachysandra, Tilia, Tsuga,* and members of the Compositae, Gramineae, Onagraceae, and Ericaceae, would be expected on ecological grounds.

It is interesting to compare the relative abundance of leaf specimens with that of their respective pollen types. In the Mascall, *Taxodium* comprised 34 percent of the leaves collected, *Quercus* 27 percent, and *Carya* 11 percent (34). In the pollen record, *Taxodium* is not identified as a genus, but the percentage for the category which should include it—the Taxodiaceae plus Cupressaceae plus Taxaceae (TCT)—varied from about 6 to 40 percent. The percentage for oak pollen was between 4 and 24 at these same localities, and percentages for *Carya* pollen ranged from 2 to 10 (see Fig. 3).

A similar comparison can be made for the Blue Mountains (see Table 1) and Stinking Water floras, equivalent in age to the Mascall (*34*). Chaney has interpreted the Stinking Water megaflora as indicating well-drained conditions, relatively dry in comparison to those of the Mascall swamp flora. This interpretation is based on abundant remains of *Quercus* (57.4 percent of the megafossils), some of whose living equivalents are woodland species, "common in the rather dry western foothills of the Sierra Nevada," and on *Glyptostrobus,* replacing the swamp-inhabiting *Taxodium* (*34*). The pollen count yielded the following percentages: *Quercus,* 21.8; TCT, 22.5; *Ulmus,* 6.5; *Pinus,* 6.2; and *Alnus,* 5.7. Eighteen

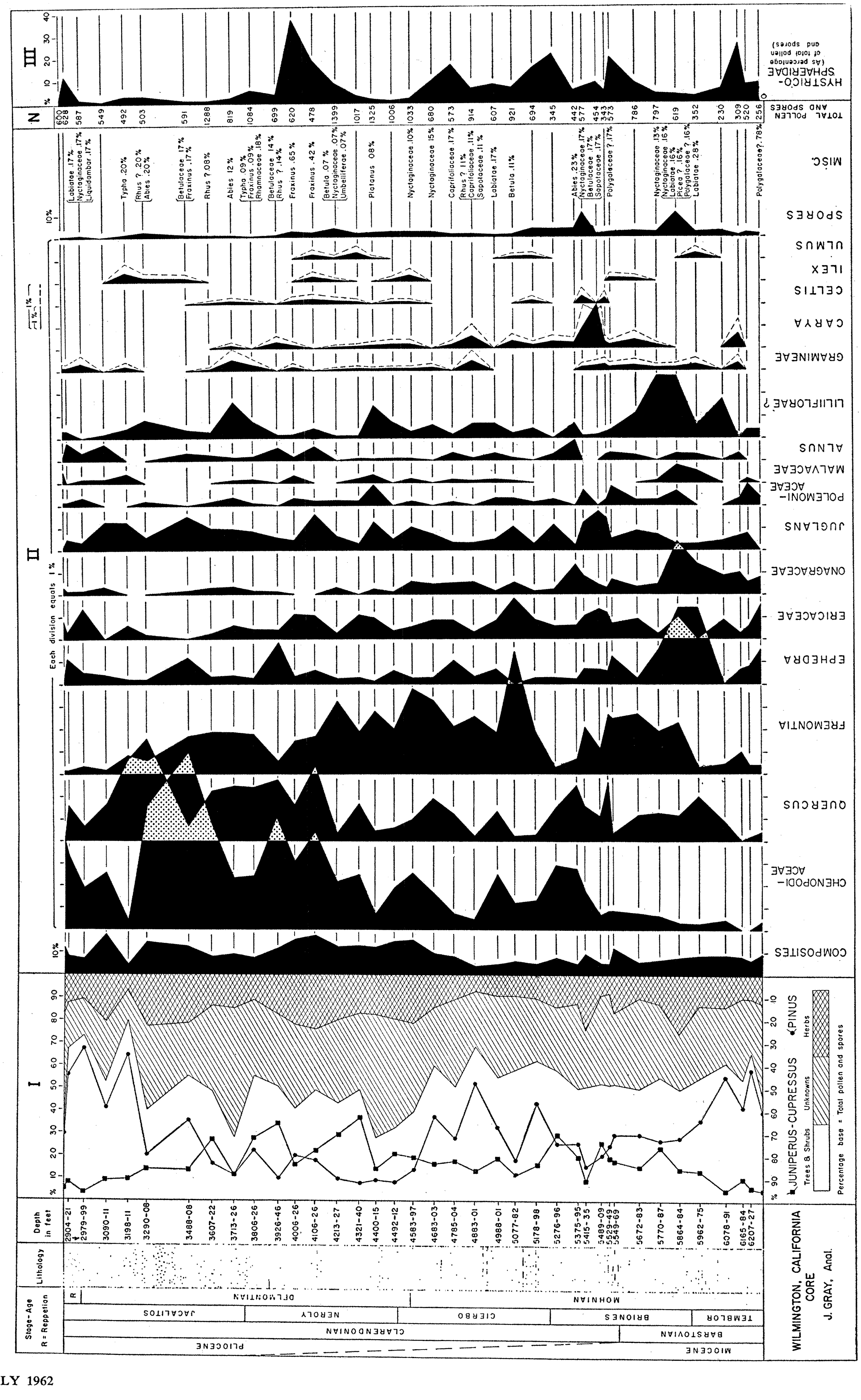

Fig. 2. Pollen profile of a marine Mio-Pliocene core from the Los Angeles basin.

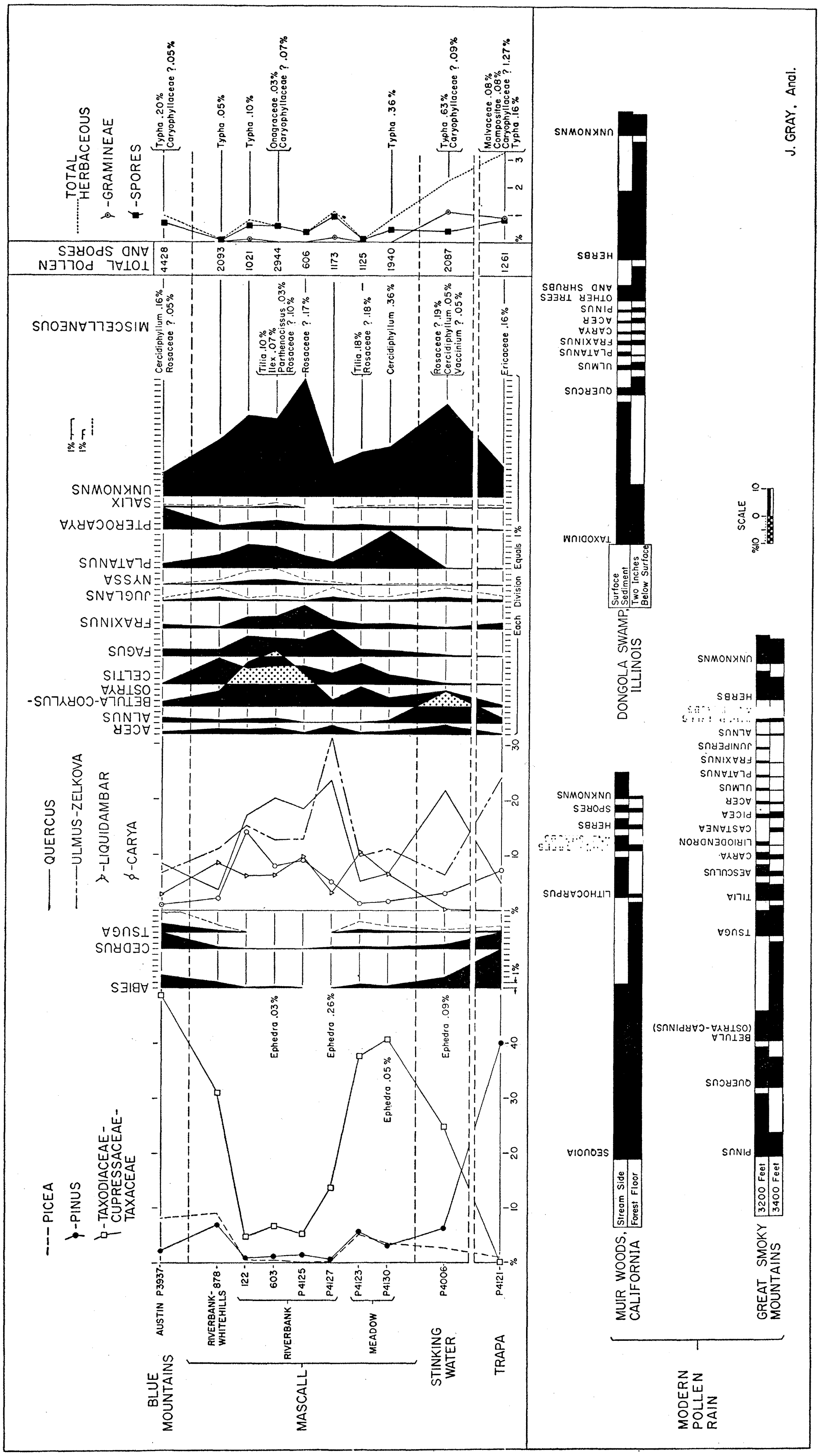

Fig. 3. (Top) Pollen spectra from four Miocene localities in the Columbia Plateau. (Bottom) The modern pollen rain in three forests of Arcto-Tertiary derivation.

pollen types, constituting 47 percent of the total flora, represent mainly trees not found in the megaflora. Although several of these trees are represented by only a few grains, some of the 18 types occur in sufficient abundance to make long-distance wind transport unlikely. In contrast to what one might infer from the leaf evidence alone, the pollen analysis suggests a forest flora more mesic than Chaney's semi-xeric oak woodland.

The microfossil record extends our knowledge of the fossil floras by adding genera not previously discovered and by providing an independent estimate, based on pollen count, of the relative abundance of the dominant trees in the Miocene community. Furthermore, the palynologist can at once distinguish certain genera from others—such as *Betula* from *Alnus* and *Juglans* from *Pterocarya*—in cases where it is difficult to make this distinction on leaf evidence alone. Paleoecology benefits from consideration of both megafossil and microfossil evidence.

To compare Miocene and modern pollen rains, pollen rain samples of three different forests thought to be segregates of Arcto-Tertiary origin are shown in Table 1 and Fig. 3. The areas studied include Muir Woods, California (redwood forest), Dongola Swamp, Illinois (*Taxodium*-hardwood swamp), and the Great Smoky Mountains, Tennessee (mixed mesophytic broad-leaved forest), the latter at two different elevations, 960 and 1020 meters (3200 and 3400 feet). In the sample from evergreen redwood forest at Muir Woods there is a high frequency of TCT, in this case *Sequoia,* and of *Lithocarpus* and *Alnus* (not shown in the sample in Fig. 3). The rest of the pollen rain bears little resemblance to the Miocene microfloras.

A much closer approximation to the fossil flora can be obtained at Dongola Swamp. The present pollen rain includes *Taxodium, Fraxinus, Acer, Ulmus, Liquidambar, Nyssa,* and *Quercus,* seven of the pollen types found frequently in the Miocene deposits. The Great Smoky Mountain pollen samples most closely resemble the fossil microflora in generic composition. On the other hand, the pollen percentages are dissimilar; the Great Smoky Mountain samples have very little *Taxodium* or other component of the TCT group and a great abundance of betulaceous and pine pollen (Fig. 3). One might expect to find a pollen rain closely resembling that of mid-Miocene Oregon

Table 1. Frequency of occurrence (in percent) of pollen and plant megafossils (leaves and other structures) in Middle Miocene sediments of Oregon, as compared to the frequencies of pollen in contemporary sediments from western and eastern North America.

| Group or genus | Middle Miocene sediments (Blue Mountains, Ore.) | | Contemporary sediments | | | |
|---|---|---|---|---|---|---|
| | Micro-flora (*N*, 4428) | Mega-flora* (*N*, 573) | Muir Woods, Calif. (Stream sediments) (*N*, 303) | Dongola Swamp, Ill. (Swamp muck) (*N*, 1110) | Great Smoky Mts., Tenn. (Moss polsters) | |
| | | | | | 3200 ft (*N*, 1280) | 3400 ft (*N*, 1000) |
| TCT† | 47.8 | 7.5 (IV) | 63.7 | 21.6 | 0.6 | |
| *Quercus* | 8.6 | 31.4 (I) | 0.3 | 6.5 | 14.9 | 11.1 |
| *Picea* | 8.1 | 0.9 (XIV) | | | 1.3 | 2.1 |
| *Ulmus-Zelkova* | 6.8 | | | 2.8 | 0.9 | 0.2 |
| *Pterocarya* | 3.9 | | | | | |
| *Liquidambar* | 3.0 | .5 (XVI) | | 0.5 | .1 | .1 |
| *Cedrus* | 2.9 | | | | | |
| *Abies* | 2.3 | .4 (XIX) | | | .1 | .1 |
| *Pinus* | 2.3 | 4.7 (VII) | .3 | 1.4 | 22.9 | 8.6 |
| *Tsuga* | 1.5 | 1.1 (XIII) | | | 9.4 | 11.5 |
| *Fagus* | 1.2 | 17.3 (II) | | | 0.1 | 0.1 |
| *Carya* | 1.1 | | | 1.1 | 2.5 | 1.7 |
| *Alnus* | 1.0 | 4.5 (VIII) | 1.0 | | 0.5 | 0.5 |

* Roman numerals show the relative order of abundance. † TCT represents Taxodiaceae plus Cupressaceae plus Taxaceae, three gymnosperm families whose pollen is not readily distinguished in routine analysis. In Muir Woods TCT is probably the pollen of Sequoia; in Dongola, the pollen of *Taxodium*.

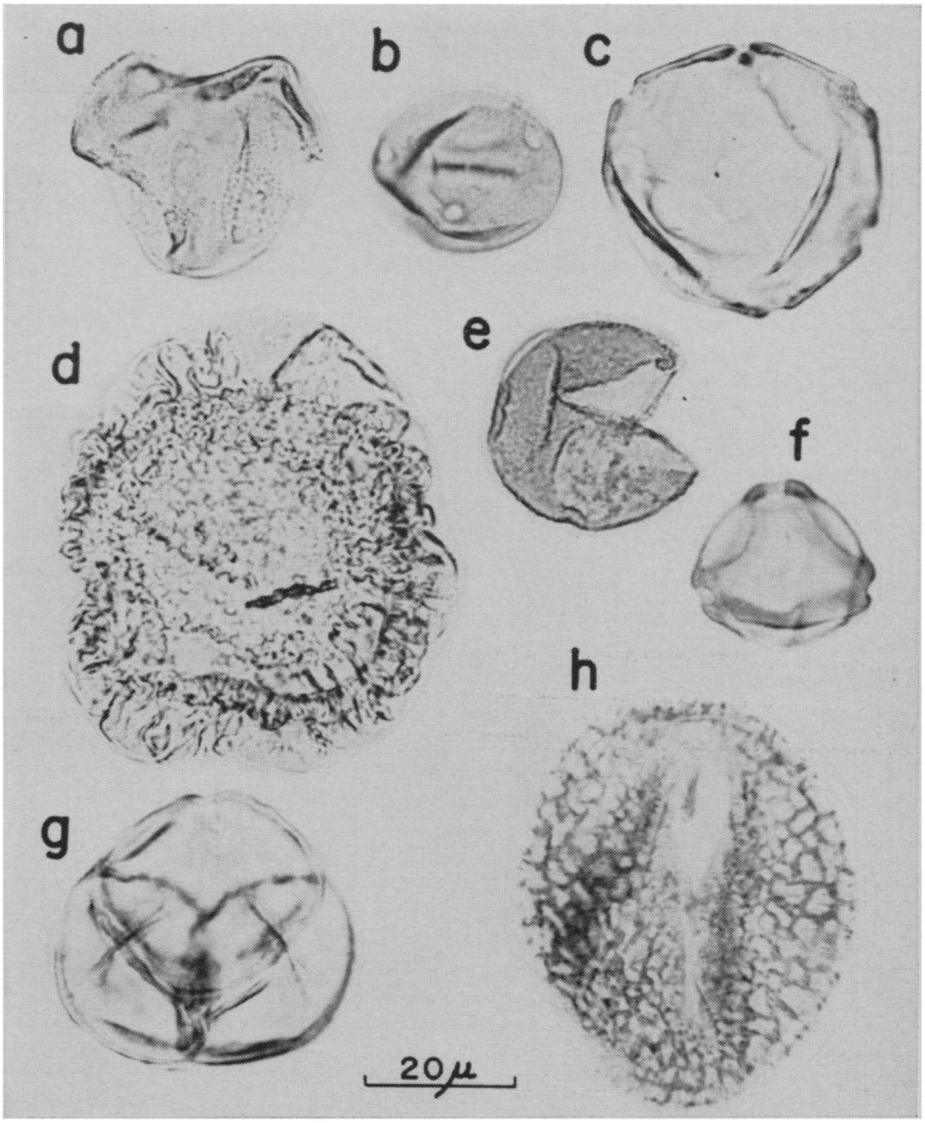

Fig. 4. Some Miocene pollen grains from the Columbia Plateau: *a, Cercidiphyllum; b, Celtis; c, Pterocarya; d, Tsuga; e,* TCT (Taxodiaceae or Cupressaceae or Taxaceae); *f, Alnus* with three pores; *g,* Ericaceae; *h,* unknown.

on certain parts of the Atlantic Coastal Plain. There, between the *Pinus-Quercus-Carya* woods of the uplands and the *Taxodium-Nyssa-Pinus* swamp forest of the bottomlands, occur occasional mesophytic mixed hardwoods of *Fagus, Carya, Quercus, Liquidambar, Ulmus,* and *Betulaceae* (*35*), all of which are important plants in the mid-Miocene pollen record.

## Pleistocene Events in the Arid Southwest

In the pollen record of northern Europe, the first or Donau glaciation is seen in the disappearance of *Sciadopitys, Liquidambar, Nyssa, Sequoia* type, and *Taxodium* type and in the entry of subarctic plant communities (*36*). A few warm temperate Tertiary trees returned during the first interglacial age (*Pterocarya, Carya, Tsuga*), to be obliterated finally by the second advance of ice (*12*). Drastic Pleistocene plant extinctions are not evident in the North American Southwest. Pliocene and early Pleistocene genera known from Arizona and New Mexico are also present in the late Pleistocene (*37*).

The survival of Pliocene genera might lead to the notion that arid America escaped serious climatic change during the glacial periods, or that, "glacial and inter-glacial periods were less clearly marked in the West and Southwest than they were in the North and Northeast" (*3*). What do recent pollen studies reveal regarding the glacial-age climate of the Southwest?

At Rampart Cave, in the lower Grand Canyon, Upper Sonoran sagebrush (*Artemisia*), with juniper, preceded postglacial Lower Sonoran vegetation (*27*); in the San Augustin Plains, boreal forest with spruce occupied what is presently grassland and juniper-pinyon woodland (*38*); in the Mohave Desert at Searles Lake there was an invasion of coniferous woodland (*39*); in the Chuska Mountains of northwestern New Mexico, subalpine vegetation preceded the present open yellow pine forest (*40*). On the Llano Estacado, or Staked Plain of Texas and New Mexico, the pollen record suggests invasion by yellow pine trees, as pluvial-age diagrams show a pine-pollen content of over 90 percent, with small amounts of spruce.

At Croton Springs on the west shore of the Willcox Playa of southern Arizona, late Pleistocene sediments contain high percentages of pine, along with small percentages of spruce, fir, and Douglas fir (*41*) (Fig. 5). As we emphasized in our introduction, critical comparison of the fossil abundance with the modern pollen rain is essential in arid areas. In livestock tanks and soil surfaces in the desert grassland immediately adjacent to the Willcox Playa we found a pine-pollen content of 0.5 to 12 percent (Fig. 5). In soil samples at higher elevations within pine forest and woodland we found much higher percentages (Fig. 1). Under montane coniferous forest, mainly of *Pinus ponderosa* in the Catalina Mountains, surface samples of the soil at elevations of 2160, 2370, and 2350 meters yielded pine-pollen percentages similar to those for fossil samples from the Willcox Playa 90 kilometers to the east (Fig. 5). The similarity in pollen rain points toward a former forest environment in the arid Willcox basin comparable to the yellow pine parkland and forest now found at elevations 900 to 1200 meters above the basin.

Three early-Pleistocene pollen counts from cores collected near Safford, Ari-

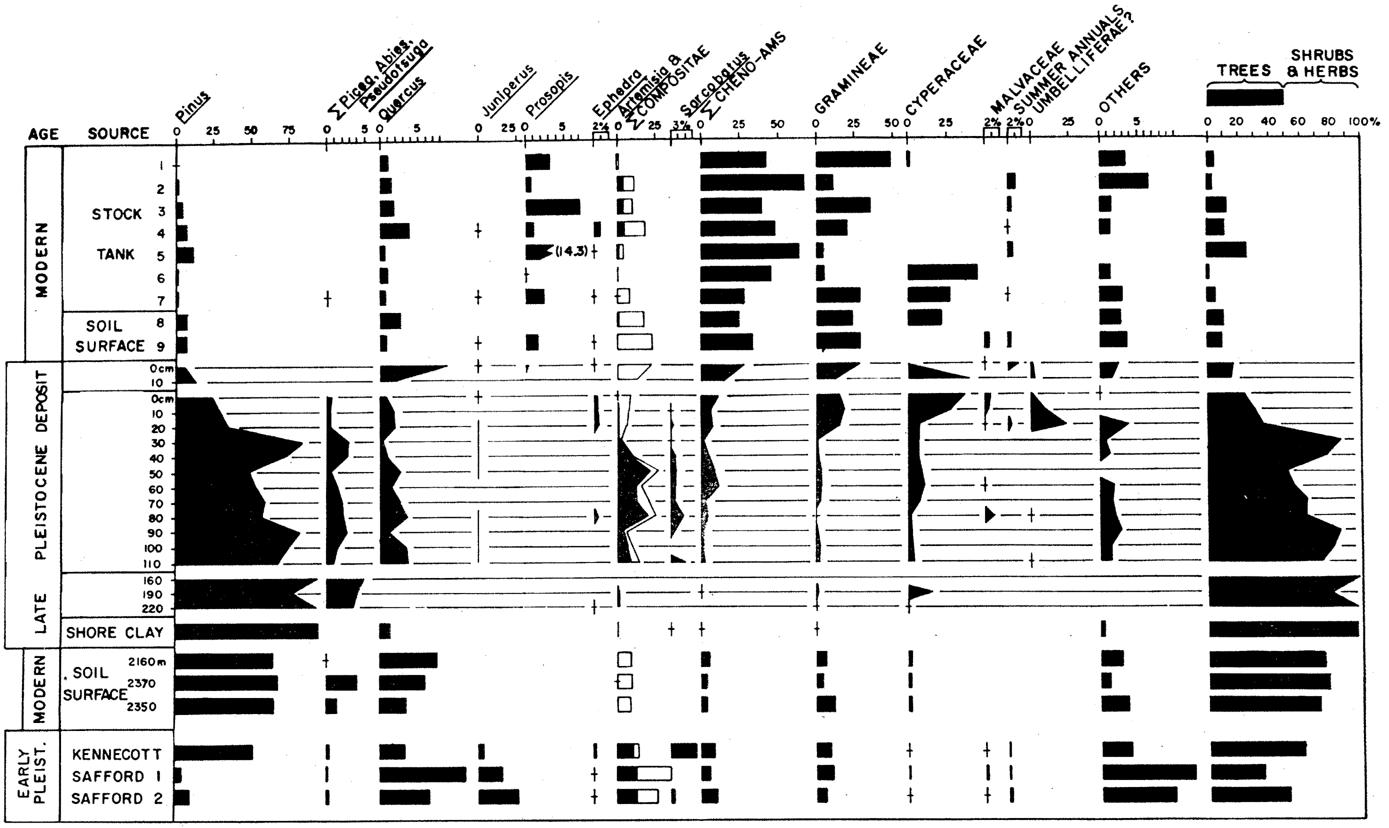

Fig. 5. Spectra of Pleistocene and modern pollen from southern Arizona. (Top) Nine modern samples from the vicinity of the Willcox Playa; (middle) diagrams of late Pleistocene pluvial pollen from the same locality and of three modern samples from a forest of yellow pine and Douglas fir 900 to 1200 meters above the Willcox Playa. (Bottom) Three spectra of early Pleistocene pollen fom the vicinity of Safford, 75 kilometers north of the playa. "Cheno-ams" signifies the Chenopodiaceae plus *Amaranthus*; within the "Compositae" curve *Artemisia* is shown in solid black.

zona (elevation, 900 meters) are shown in Fig. 5 (bottom) (*42*). The Kennecott core had the largest amount of pine pollen (53 percent), with occasional *Picea, Abies,* and *Ulmus.* Modern pollen samples collected near Safford contain mainly Compositae and Chenopodiaceae, with a pine-pollen content of 1.4 to 3.0 percent. Using Fig. 1 as an approximate guide to the relationship between pine-pollen production and regional vegetation, we interpret the Kennecott pollen count as indicating a time when the upper part of the Sonoran Desert was occupied by woodland of pine, oak, juniper, and sagebrush.

To summarize, the pluvial pollen record of the Southwest is vastly different from the postpluvial (postglacial) pollen record. The drastic changes found in the fossil pollen record show that the arid Southwest did not escape profound climatic and vegetational change during glacial times.

## Conclusions

As a source of pollen and spores, the paleoecologist may utilize marine, lacustrine, alluvial, aeolian, cave, and cultural deposits, in addition to the lignites and peats of early 20th-century investigations. The variety of pollen-bearing sediments is much greater than generally imagined. Ecologists should realize that it is impossible to identify most species and even many genera by pollen and spores alone. Qualitative inventories of microfloras are useful, but the use of percentage data offers greater promise in the study of vegetation history. For proper interpretation of fossil pollen percentages, a detailed study of both species composition and the pollen rain of natural plant communities is essential.

To illustrate the relationship between plant ecology and fossil microfloras we have presented our findings in three Cenozoic deposits. A 960-meter core from the Los Angeles Basin revealed changes in pine-pollen content and a relatively high content of herb and shrub pollen. Pollen samples from lacustrine, leaf-bearing Miocene outcrops of the Columbia Plateau, Oregon, included several genera not known as megafossils. The pollen counts provided an independent estimate of ancient forest composition, readily compared with the pollen rain of existing forests. The results modify but do not seriously alter Chaney's interpretation of a mixed deciduous forest with both needle-leaved and broad-leaved species, quite similar to the mixed mesophytic forest communities to be found today on parts of the Atlantic coastal plain in the southeastern United States.

Pollen analysis is effective in documenting Pleistocene conditions far beyond the continental ice sheets in regions thought by some authors to have escaped the influence of glacial climatic change. Pluvial lake beds in western North America contain a pollen record revealing major changes in Pleistocene vegetation zones. These changes were comparable in magnitude to those known from the fossil record at higher latitudes near the glacial boundary (*43*).

### References and Notes

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16. *Ephedra* is a green-stemmed, shrubby gymnosperm with vestigial leaves. In North America the genus is confined to arid areas from sea level to elevations of 2700 to 3000 meters. *Ephedra* occurs throughout the Sonoran and Chihuahuan deserts, in the desert grassland, in sagebrush of the Great Basin, in pinyon-juniper woodland of the southern Rocky Mountains, and in xeric open woodland of the highest, driest desert mountains of eastern California, where *E. viridis* grows on southwestern exposures adjacent to limber pine and bristlecone pine [the latter observation is from C. W. Ferguson (personal communication)]. The Old World distribution is remarkable: in Kashmir *Ephedra* reaches 5450 meters, the greatest elevation of any gymnosperm in the world [G. L. Webster, *Ecology* **42**, 589 (1961)]. *Ephedra* produces pollen in small amounts for a gymnosperm. The large, prolate, polyplicate pollen grain is distinctive.
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43. We acknowledge the support of the National Science Foundation (grants G 10692 and G 11344) and of the Rockefeller Arid Lands Program of the University of Arizona. We are grateful for the comments of R. W. Chaney, L. M. Cranwell, F. R. Fosberg, G. O. W. Kremp, J. E. Mosimann, P. B. Sears, and W. Smith. This article is contribution No. 52 of the program in Geochronology, University of Arizona.