Miocene Pollen and Spore Flora of Eniwetok Atoll, Marshall Islands

GEOLOGICAL SURVEY PROFESSIONAL PAPER 260-II

U.S. DEPARTMENT OF THE INTERIOR
March 3, 1849

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By ESTELLA B. LEOPOLD

BIKINI AND NEARBY ATOLLS, MARSHALL ISLANDS

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A Miocene pollen and spore flora representing
raised island, intertidal, and beach-ridge
environments is described from depths of
670 to 2,500 feet beneath Eniwetok Atoll

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CONTENTS

Systematic descriptions—Continued

Angiospermae—Continued

Dicotyledonae—Continued

ILLUSTRATIONS

[Plates follow index]

TABLES

BIKINI AND NEARBY ATOLLS, MARSHALL ISLANDS

MIOCENE POLLEN AND SPORE FLORA OF ENIWETOK ATOLL, MARSHALL ISLANDS

By Estella B. Leopold

ABSTRACT

Drill-hole sediments from depths of 670 to 2,500 feet beneath Eniwetok contain zones in which pollen, spores, and colonial blue-green algae are very abundant. The Miocene age of these sediments is established by the contained Foraminifera. Sparse pollen at 4,528–4,553 feet is of Eocene age based on associated Foraminifera.

Fifty-seven kinds of plants are represented in the Miocene flora, and these are mainly dicotyledons, but also present are remains of blue-green algae, pteridophytes, and monocots. Seventeen angiosperm genera were identified, and these can be grouped as follows. Four are native to Eniwetok today: *Pandanus, Pisonia, Tournefortia,* and *Cordia.* Six now grow in the southern Marshalls, but are not native to Eniwetok: *Sonneratia, Rhizophora, Bruguiera, Lumnitzera, Morinda, Randia.* Five grow in western or central (but not eastern) Micronesia today: *Acalypha, Ceriops, Terminalia, Avicennia, Ixora.* One other genus, *Gardenia,* occurs in Borneo or New Guinea but is unknown in Micronesia. In addition, *Thespesia* of the Malvaceae was identified, but the Miocene fossils do not show an affinity with an existing Micronesian strand species, *T. populnea;* instead they are related to a Malayan species, *T. lampas,* an upland form with a unique pollen morphology.

On a subgeneric basis, 80 percent of the Miocene flora now has relatives in the Western Caroline Islands, and the bulk of these relatives also grow in Indo-Malaya. This preponderance suggests that the primary affinity of the Miocene flora of Eniwetok is with the present flora of western Micronesia.

From the present habitats of taxa which are related to the Miocene forms, the following Miocene environments can be inferred for Eniwetok.

1. Mangrove swamps in intertidal zones: typified by very abundant *Rhizophora* pollen, and occasional pollen of *Sonneratia, Lumnitzera, Ceriops, Avicennia.*
2. Beach-ridge environments typified by strand genera such as *Morinda, Pandanus, Terminalia,* and *Cordia.*
3. Mangrove depressions on beach ridges, based on presence of *Bruguiera.*
4. Raised island habitats including upland forest, in which soils are not saline: based on identification of *Ixora, Acalypha, Thespesia* cf. *T. lampas, Randia* and *Gardenia.*
5. Intertidal beach rock, based on presence of large numbers of blue-green algae.

Of these, only environments 2 and 5 exist today on Eniwetok.

Samples of modern mud from atolls of Micronesia contain very little, if any, pollen; but muds from lagoons and harbors of larger islands contain abundant pollen. From the preparation of modern mud samples from various Micronesian islands, I have come to these conclusions:

1. If the island or atoll has a land area smaller than 5 square miles and has a maximum elevation below 20 feet, pollen rain is negligible, and pollen usually can not be found in sediments except in muds of thickly vegetated swamps. Large numbers of blue-green algae are present in many lagoon muds.
2. If the island is larger or considerably higher, pollen rain is apparently more substantial, for near-shore marine muds contain several hundred or more pollen per gram of sediment. If mangrove communities are present locally, pollen density may range from 1,000 to 35,000 per gram of sediment (dry weight). Blue-green algae are occasional.

In the Miocene sediments in which blue-green algae are numerous, pollen abundance ranges from 0 to 1,000 per gram in sediments. In the zones in which *Rhizophora* pollen was especially abundant, pollen frequency went as high as 100,000 per gram of sediment—higher than my modern comparative material from Micronesia.

Considering the high abundance of Miocene pollen in the sediments of several zones, I conclude that the pollen is of local (not transported) origin and that the pollen rain was probably more substantial in the Miocene than now, suggesting either a more dense vegetation on the same land area or an increased land area. The presence of high-island forms in the plant assemblage corroborates evidence from fossil land snails that at times during the Miocene, Eniwetok was a raised limestone island that stood well above the sea and supported upland forest communities.

Drill holes at Eniwetok and Bikini reveal about 4,000 feet of carbonate sediments underlain by volcanic basalt. The sedimentary section, which has been studied in great detail by Schlanger (1963) and his associates, is mainly composed of coral and shallow-water sediments. Three deeply weathered zones, which show leaching and solution cavities and which contain no pollen and have unconformities at their tops, indicate at least three periods of prolonged emergence of Bikini and Eniwetok—one between the late Eocene and the Miocene, one during the Miocene, and one in the post-Miocene interval. The evidence from lithology and fossils indicates that Eniwetok, Bikini, and probably the other Marshall Islands, are cylinders of coral slowly building on a sinking volcanic neck or guyot; subsidence has occurred in Eocene and younger time, and there were three major periods of emergence during which the coral rocks were weathered subaerially.

From my analyses of Miocene pollen floras of Fiji and Guam, I note that some forms in both floras record spectacular cases of former wide ranges.

At Guam, Miocene pollen of *Anacolosa* (Olacaceae) and probable *Wikstroemia* (Thymeliaceae) are both Indo-Malayan, and I find no records that they grow in Micronesia today. Other plants identified from the Miocene of Guam connote strandline vegetation (*Rhizophora*, *Pisonia*, *Pandanus*, *Combretum* or *Terminalia*), and one high-island form (*Ixora*) was found; these genera probably grow at Guam today.

At Fiji, Miocene pollen assemblages include *Sonneratia*, which now grows as far east as the Southern Marshalls and New Guinea, and Anonaceae, cf. *Miliusa;* the family Anonaceae is apparently absent from Fiji today. Other Miocene forms from Fiji include strand plants (*Rhizophora*, *Morinda*, cf. *Timonius*, *Terminalia* or *Combretum*, Palmae) and various ferns.

A Miocene pollen flora from Palau seems to be largely composed of native genera. A Miocene pollen flora from Midway subsurface samples is now under study, but it is too early to state results.

Late Cenozoic floras of the north temperate zones show a general loss in forms, or impoverishment of the great floristic diversity characteristic of the Miocene. This change is usually associated with a late Cenozoic deterioration of climate. For example, in the northwestern coastal United States, from two-thirds to one-half of the plant genera have disappeared from the regional flora since the Miocene, and the flora has changed in aspect from warm temperate to cool temperate.

At Eniwetok, 78 percent of the Miocene plant genera no longer grow on the atoll, and 66 percent do not grow any longer in the Marshall Islands. In spite of the similarity of these percentages with those of the coastal United States, the nature of the Eniwetok floral change does not suggest that it is caused by climate alone. The evidence from Eniwetok and Bikini overwhelmingly indicates that relative subsidence and emergence of the atolls have been extremely limiting factors. Tectonic factors probably controlled the availability of fresh-water environments, the total amount of land available to plants, the height of atoll ridges, and therefore the vulnerability of lagoon plants to typhoons; lastly, tectonic factors probably controlled the height of the island above sea level, which would probably affect the total amount of rainfall received.

INTRODUCTION

The purpose of this investigation was to identify and describe pollen, spores, and algae from drill-hole sediments of Miocene age on Eniwetok Atoll, and to determine thereby the nature of plant life and environment on that atoll during the Miocene.

Two deep holes were drilled to basement rock under Eniwetok in 1952 (Ladd and others, 1953) to determine the nature and depth of the sedimentary rocks beneath the atoll. The operation was supported by the Armed Forces Special Weapons Project and carried out for the Atomic Energy Commission and the Los Alamos Scientific Laboratory in cooperation with the Office of Naval Research and the U.S. Geological Survey. The middle and upper middle parts of the 4,000 feet of sedimentary rock above the igneous-rock foundation were found to be of Miocene age, according to contained Foraminifera (Cole, 1957; Todd and Low, 1960), and the present study is mainly concerned with these Miocene sediments. Pollen from selected drill-hole sediments from Bikini Atoll is also described.

I attempted pollen analysis of a few Eniwetok Miocene samples in 1957. The discovery of abundant fossil pollen in drill hole F–1 at depth 810–860 feet, as mentioned by Ladd and Tracey (1957, p. 218) and by Ladd (1958, p. 194), indicated that a detailed palynological study should be made.

In this study the Miocene pollen and spore forms from Eniwetok are compared on generic and subgeneric levels with living forms from Micronesia. Identification on these taxonomic levels, which are most often the feasible limits of plant identification based on palynological evidence alone, provides a picture of the general type of vegetation that inhabited the atoll during the Miocene. The generic list of plants also gives some indication of the habitats that existed in the area.

Because information on the number of fossil pollen grains per gram of Miocene sediment might be worth comparing with pollen density in Recent sediments from the atoll area, the fossil samples were prepared by measured aliquots. For comparison, collections of Recent lagoon muds from Micronesia were obtained from several workers, and these were prepared by the same aliquot method. Tallies of pollen are extrapolated to number of grains per gram of sediment wherever possible.

For floristic comparison with the Miocene pollen assemblage of Eniwetok, collections of probable Miocene age from Fiji, Guam, and the Palau Islands were obtained from several field geologists and analyzed for fossil pollen and spores. I refer to these collections in this report. The general results of this study were summarized earlier (Leopold, 1963).

Because the pollen and spores are of a relatively young age, and because the primary objective here is to compare them with living material, the following taxonomic procedure seems appropriate. Where possible, the forms are identified to the nearest living plant group, and similarities to pollen of living species are cited with the indication "cf." (compare to). Where no family affinity is certain, the forms are indicated by arbitrary code numbers following the system suggested by Tschudy (1957). If a family assignment cannot be made, morphological comparisons with genera are cited as type, for example, "*Brucea* type." No formal species names for fossil pollen or spores are proposed in this report.

AREA

The fossil materials described here were obtained from drill holes on Eniwetok and Bikini Atolls in the northern Marshall Islands. These islands are 200 miles apart and lie in easternmost Micronesia. (See figs. 332, 338.)

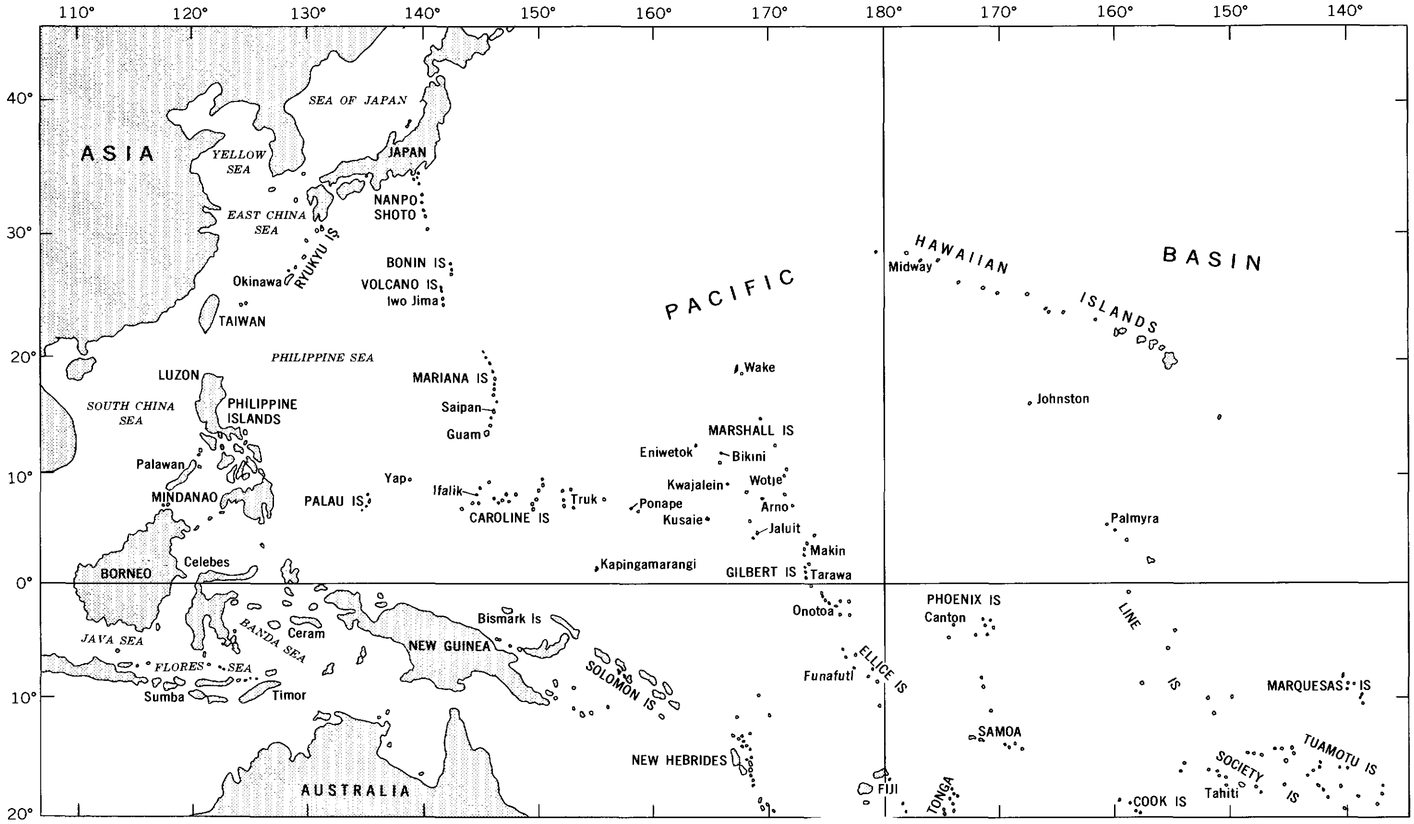

FIGURE 332.—Western Pacific region, showing location of Eniwetok and the Marshall Islands. Micronesia proper includes the Pacific islands east of the Philippines and north of the equator (map modified from Tracey and others, 1964).

Miocene pollen from outcrops on Guam, the Palau Islands, and Fiji were also examined for comparison with the Marshall Islands fossil flora. Guam is in the Mariana Islands group, about 1,200 miles west of Eniwetok (fig. 332). The Palau Islands and Fiji lie 1,800 miles west and 1,300 miles southeast of Eniwetok, respectively. Ponape, from which modern pollen samples were obtained for comparison, lies 450 miles southwest of Eniwetok (fig. 332).

MARSHALL ISLANDS DRILL HOLES

The location of the three drill holes on Eniwetok Atoll that are discussed in the present report is shown in figure 335; these are drill holes F-1 on Elugelab, K-1B on Engebi, and E-1 on Parry Island. The drilling operations on Eniwetok and the lithology of the cores and cuttings obtained were described in detail by Ladd and Schlanger (1960) and Schlanger (1963). The holes on Bikini that were drilled in 1947 were described by Emery, Tracey, and Ladd (1954).

ACKNOWLEDGMENTS

Cores and cuttings from drill holes for this study were made available to me by Harry S. Ladd, whose helpful advice and aid throughout this project are most gratefully acknowledged. For botanical guidance in making ecologic interpretations of the material and for providing me with up-to-date unpublished data on Micronesian plant distribution, I am very grateful to F. R. Fosberg of the National Research Council.

Identification of the fossil pollen material depended on the availability of appropriate modern pollen collections from herbarium material of Micronesia. Selected herbarium sheets for such collections were made available through the courtesy of the U.S. National Herbarium. With the permission of Dr. J. R. Swallen, Head Curator, U.S. National Herbarium, and Dr. A. C. Smith, then Director of the U.S. Museum of Natural History, I assembled material from about 600 plant species, including about 540 genera from the modern flora of Micronesia.

Recent sediments used for comparison include field collections by P. E. Cloud, Jr., from Onotoa, Gilbert Islands; by F. R. Fosberg and E. D. McKee from Jaluit; by J. I. Tracey, Jr., from Ifalik; by K. O. Emery from Bikini; and by Sam Riesenberg from Ponape.

Helen Pakiser, Imogene Doher, and Anne Davis assisted in the laboratory preparation of the pollen materials.

GEOLOGIC RELATIONS

The structure of the reef at Eniwetok Atoll is better understood than that of most Pacific atolls because of information obtained from the two deep drill holes (F-1 and E-1) that reached the basalt under the reef (Ladd and others, 1953; Ladd and Schlanger, 1960). Darwin's (1897) premise that an atoll reef is the product of upward and outward growth of a coral mass on a sinking island has been proved by the lithologic and paleontologic evidence obtained from the deep holes on Eniwetok Atoll. An interesting summary of Darwin's reasoning in relation to present subsurface evidence from this and other parts of Micronesia was presented by Ladd (1961, p. 710–711). Much of the detailed paleontologic evidence from these drill holes was described by various authors in previous chapters of Professional Paper 260.

LITHOLOGIC TYPES AND AGES

Lithologic information from Eniwetok deep drill holes indicates that the atoll reef is at least 4,630 feet in greatest thickness and that it rests on a somewhat irregular basalt surface. The thickness of the reef rock beneath Bikini is not yet known. A sedimentary profile of the drill holes on Eniwetok and Bikini by Schlanger (1963) is shown in general outline in figure 333; this profile is based on a detailed study of the subsurface sediments using X-ray and chemical methods. Rocks penetrated in the five drill holes are classified by Schlanger (1963) and Macdonald (1963) as comprising five types.

1. Aragonitic limestone, unlithified. These sediments typically contain perfectly preserved mollusks, and some of the shells retain their original color patterns. Unaltered layers of aragonite presumably were not emergent, or at least not for a time long enough to permit alteration to calcite.
2. Calcitic limestone, with solution features, usually leached and lithified. In some levels the limestone contains prominent molds of coral and mollusks, and coarsely crystalline calcite fills the cavities. This sediment type was probably derived from primary aragonitic limestone by subaerial weathering during emergence.
3. Dolomitic limestone, well lithified, and containing calcite but no aragonite. Schlanger (1963) proposed that the dolomitization in these sediments may have followed the conversion of primary aragonite to calcite by solution and reprecipitation.
4. Partly recrystallized and leached limestones. These contain a mixture of calcite and aragonite matrix and altered and unaltered fossils of coral and mollusks; the sediments are poorly lithified. Schlanger (1963) interpreted these limestones as being intermediate between aragonitic and calcitic, probably derived from aragonitic limestone by incomplete subaerial weathering.
5. Basement basalt, somewhat altered by epigene solutions that formed carbonate veins in the upper layers. This alteration may have occurred when the top of the basalt was close to sea level, and part or all of the overlying limestone was well above sea level (Macdonald, 1963, p. 1047).

The distribution of these rock types in the five drill holes permits a correlation of beds that is well substantiated by the fossil evidence. Four clear unconformities (fig. 333) have been identified in the sedimentary section; these are solution unconformities and present a rather sharp interface between a lower leached calcite sediment and an overlying primary aragonite. Three of the four unconformities coincide with faunal breaks (Schlanger, 1963).

The primary basis for age determination within the Eniwetok section is a study of diagnostic larger Foraminifera by Cole (1957) and of smaller Foraminifera by Todd and Low (1960). Cole reported that Recent, Pleistocene, and Pliocene larger Foraminifera occur from the surface to a depth of 615 feet, and below this he recognized several zones of Miocene age. Eocene sediments occur from a depth of 2,900 feet to the bottom of the holes, according to Cole (1957) and Todd and Low (1960). However, Todd and Low drew the upper boundary of the Miocene at a depth of about 500 feet instead of about 615 feet; they also suggested that the lowest 600 feet of what Cole considered Miocene may be Oligocene on the basis of smaller Foraminifera. Cole (1957) and Todd and Low (1960) seem to agree that there is as yet no certainty that Oligocene sediments are present.

LITHOLOGIC SEQUENCE

From the top downward, the section (fig. 333) may be summarized as follows.

The upper 70–100 feet in all four drill holes is unaltered aragonitic limestone, and below it is 150–200 feet of partly recrystallized and leached limestones; Schlanger (1963) suggested that a poorly developed unconformity exists at the top of the leached beds in each hole. Isotope dates on the sediments above that unconformity are from <12,000 to 13,000 years, whereas immediately below, the range of dates is from 38,000 to 280,000 years B.P. (Sackett and Potratz, 1963, p. 1060). Sediments from these depth intervals were not examined for pollen.

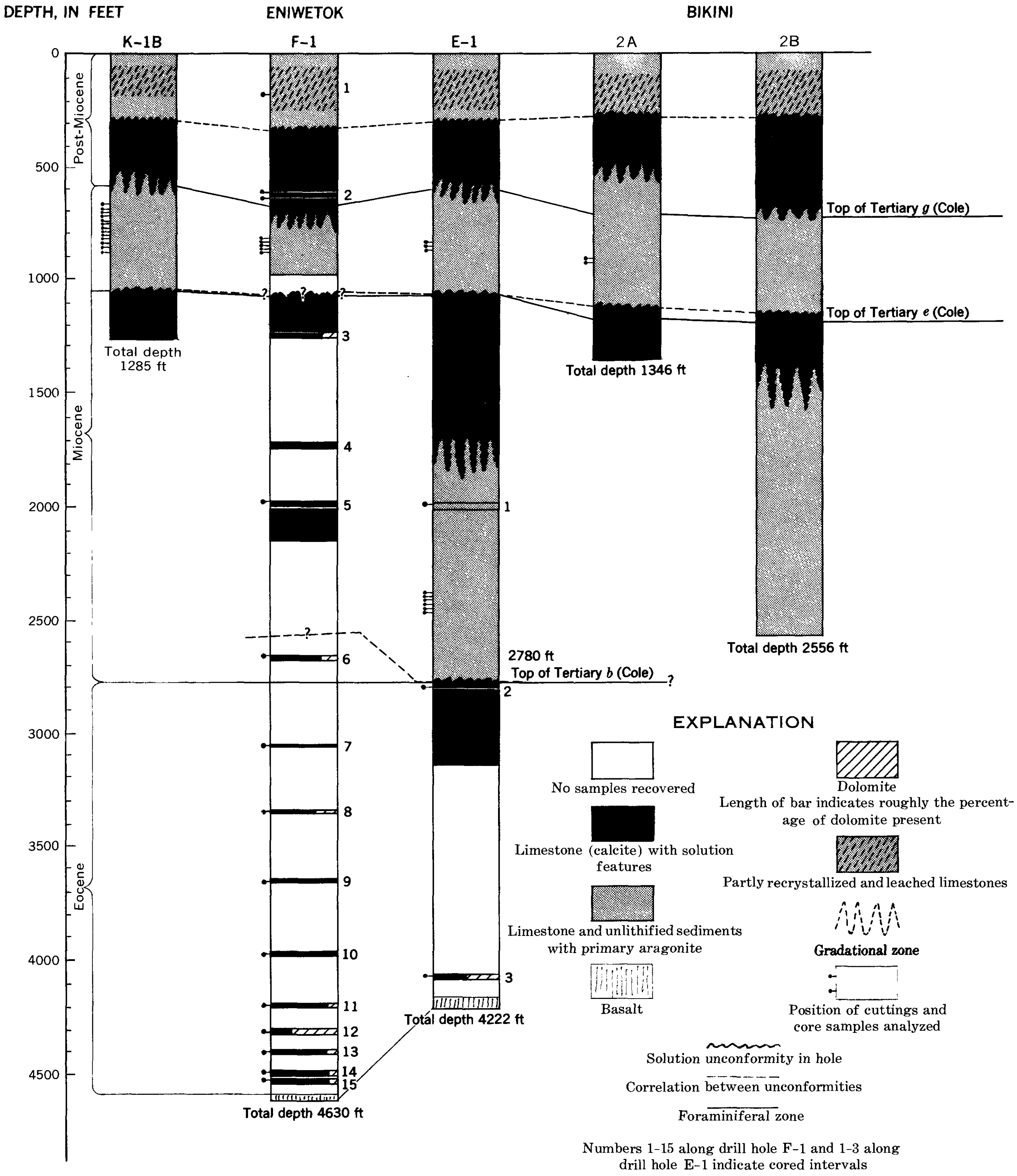

Figure 333.—Drill-hole sections showing weathered and unweathered limestone zones beneath Eniwetok and Bikini Atolls. The basalts underlying Eniwetok are shown (modified from Schlanger, 1963, fig. 308).

At a depth of about 300 feet a very well developed unconformity exists where the partly leached sediments at Bikini and the primary aragonite beds at Eniwetok overlie calcitic limestone that shows solution features. This calcitic limestone is 300–400 feet thick. In contrast to the sharp contact at 300 feet, there is a gradational contact between the calcitic limestone and the unconsolidated aragonite beds below. Schlanger interpreted the calcite beds as a zone that had weathered under subaerial conditions. These sediments are of post-Miocene age, as indicated by larger Foraminifera (Cole, 1957), and some may be of Pleistocene age (Ladd, 1958). Samples from this interval were not studied for pollen. Beneath the weathered zone to a depth of about 1,000 feet are primary aragonite beds rich in fossil corals, shallow-water mollusks (Ladd, 1958), and, at some levels, pollen. Larger and smaller Foraminifera indicate a Miocene age for this interval (Cole, 1957; Todd and Low, 1960) (fig. 333.) This zone, designated as Tertiary *g* by Cole (1957), is considered as late Miocene in age by Ladd (1958).

At a depth of 1,000 feet another sharp unconformity occurs at the top of a thick (300–800 ft) cemented calcite unit and represents another weathered zone. The calcite beds overlie (with a gradational contact) a very thick (about 1,000 ft) aragonite zone, which contains well-preserved remains of shallow-water Foraminifera, pelecypods, and corals. The lithology in this interval in drill hole F–1 is poorly known. On the basis of larger Foraminifera from the various holes, this entire interval between 1,000 and 2,800 feet is of Miocene age (Tertiary *e* of Cole, 1957). However, smaller Foraminifera (Todd and Low, 1960) in the lower 600 feet of this zone suggest an early Oligocene age (Tertiary zone *c*). Ladd (1958) considers Tertiary *e* to be early Miocene in age. The aragonite beds between 2,003 and 2,510 feet are rich in Chroococcalean algae and contain some pollen.

A fourth solution unconformity marking the top of a thick calcite unit at the 2,780-foot level is well defined in drill hole E–1. Here Eocene calcite sediments (Cole's Tertiary zone *b*) are overlain by Miocene aragonitic lime muds, and according to Cole (1957) this unconformity is the position of a sharp faunal break. Schlanger (1963, p. 996) concluded that the coincidence of this sedimentary unconformity with the faunal break indicates a post-Eocene emergence and erosional removal of Oligocene sediments before the first Miocene submergence of Eniwetok. Only spotty core runs of sediments at a depth below the 500-foot-thick Eocene calcite zone of hole E–1 are available, and most of these are from hole F–1; all are Eocene cemented dolomitic limestones that contain shallow-water Foraminifera, corals, pelecypods, and calcareous algae. A few pollen grains were found in the lowest core run, only 100 feet above the basement basalt.

In summary, the three deeply weathered zones indicate at least three periods of prolonged emergence of Bikini and Eniwetok atolls—one after the late Eocene and before the Miocene, one during the Miocene, and one in the post-Miocene interval. The weakly developed unconformity at a depth of 300 feet suggests a brief emergence in the late Quaternary earlier than 12,000 years ago.

PALEOECOLOGY

The ecology and paleoecology of sediments inferred from studies of Foraminifera, algae, corals, and mollusks have been discussed in detail by several authors (Tracey and others, 1948; Ladd and others, 1950; Cloud, 1952; Emery and others, 1954; Forman and Schlanger, 1957) and so will be only briefly summarized here.

Paleoecological interpretations for Eniwetok and Bikini are shown in the stratigraphic diagram (fig. 334).

The sediments of the post-Miocene (younger than Tertiary *g*, fig. 334) are thought to represent lagoonal deposits, except for those at 140–300 feet in hole E–1, which are probably of reef-wall or reef-knoll origin.

The entire Miocene section is considered to be a shallow-water lagoonal deposit with the exception of certain zones below 1,750 feet in all drill holes; these zones probably represent a reef-wall environment in F–1 and a lagoonal, fore-reef, and (or) open-shoal environment in E–1, 2A, and 2B. Abundant remains of the alga *Lithophyllum* suggest a deeper water environment for parts of these zones.

The Eocene sediments in F–1, as far as they are known, seem to represent a fore-reef outer slope environment, and in the lower 300 feet shallow-water Foraminifera (*Peneroplis triloculina*, *Ornatanomolina*, and *Asterigerina* zones, fig. 334) are present. These Foraminifera are also present at the top of the Eocene section in E–1, where other evidence suggests a near-reef environment; Todd and Low (1960) concluded that the basal parts of the F–1 section are probably synchronous with the upper 700 feet of the E–1 Eocene section. Thus, the lower parts of the Eocene section in E–1 have no counterpart in F–1, and the unconformity at 2,780 feet in hole E–1 is greater than the unconformity in F–1 (fig. 333). The only Eocene sediments recovered from the bottom of hole E–1 (at depths 4,078–4,100 ft) suggest shallow lagoonal and reef-wall environments (fig. 334).

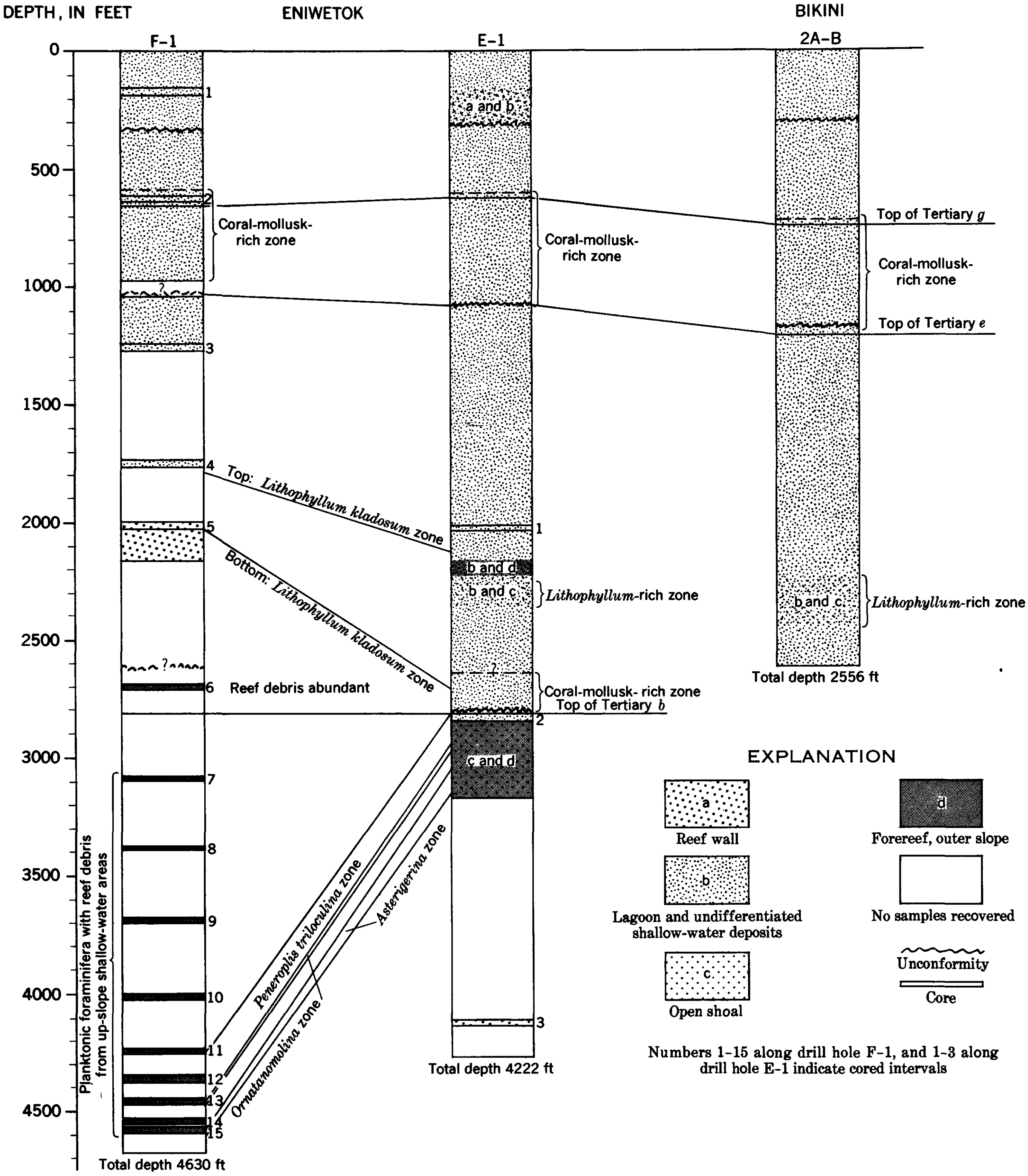

FIGURE 334.—Paleoecology logs of drill holes E-1 and F-1 on Eniwetok and drill holes 2A and 2B on Bikini. From Schlanger (1963).

In summary, the combined evidence suggests that the greater part of the sedimentary section was deposited in relatively shallow water. Since Eocene time, at least three periods of prolonged emergence have occurred, during which the marine and lagoonal sediments underwent severe subaerial weathering.

PALEOBOTANY OF THE OCEANIC PACIFIC ISLANDS

By F. R. Fosberg

Paleobotanical work on Cenozoic material from the oceanic islands of the Pacific has been so rudimentary as to be almost nonexistent. Fossil calcareous algae from various Micronesian islands (including Guam, Saipan, Tinian, Rota, Palau, Bikini, and Eniwetok) were studied by J. H. Johnson, who published detailed and well-illustrated reports on algae from the Bikini drill holes (1954) and from the Eniwetok drill holes (1961). Mention was made of algal remains and also of carbonaceous material in the preliminary report on the Eniwetok core (Ladd and others, 1953). E. B. Leopold (in McKee and others, 1959) reported dinoflagellate cysts and rare pollen in Recent sediments from the lagoon of Kapingamarangi Atoll, Caroline Islands.

Lignite beds exist on Rapa in the Austral Group and on Babelthuap in the Palaus. Some fossils from the Babelthuap occurence were mentioned by Tayama (1939) and by Sato (1941), and material was collected there by P. E. Cloud, Jr., Gilbert Corwin, and P. Q. Elmquist; a cursory pollen study of these is reported in the present work (p. 1163). Attempts have been made to isolate from the Rapa lignite beds plant material collected by F. R. Fosberg in 1934, but no identifiable remains were found until recently, when Cranwell (1962, 1964) found scattered pollen in this and in Rapa material collected by the St. George expedition. The only positive identification of higher plant pollen from the material was *Coprosma* of the Rubiaceae; this genus now is represented by an endemic species (*C. rapensis*) on the island.

Boureau (1953) reported on certain fossil woods from the Mesozoic of New Caledonia. In Hawaii, tree molds and impressions of *Sadleria* ferns in lava are shown to tourists at Hawaii National Park and are described and illustrated in popular literature for tourists. The only scientific report on such impressions is a short paper by Palmer (1947) describing impressions of fronds of *Cibotium chamissoi* in recent lava in Kilauea Iki Crater, Hawaii. On Oahu a fossil flora preserved in volcanic tuff or ash at Salt Lake Crater was found and briefly described by Lyon (1930), but again no scientific report was published. More material of this kind has been collected recently, and both collections are now in the laboratory of C. N. Lamoureus. Selling (1947) published an extensive report on pollen from cores taken in Hawaiian postglacial bogs. More recently some fossil wood from Guam was examined by E. S. Barghoorn (in Tracey and others, 1964, p. A32). Mention of plant fossils from the northern Marianas may be quoted in translation from Tayama (1952, p. 46): "the tuff forming the surface of Alamagen and Guguan volcanoes contains fossilized plants such as coconut and screwpine leaves." Fosberg and Corwin (1958) reported a fossil flora from the tuffs on Pagan Island that was extensive enough to provide some basis for paleoecological speculation.

Fossil pollen records of mangrove vegetation in the Tertiary of Borneo were summarized by Muller (1964). Muller's own work indicates that the palm genus *Nypa* and probable *Brownlowia* (Tiliaceae) go back locally at least through the Eocene. He reported *Rhizophora*-type pollen from Oligocene and younger sediments, and *Sonneratia* cf. *caseolaris* from lower Miocene and younger sediments. His earliest records of *Sonneratia* cf. *alba* are from uppermost Miocene to Recent, and of *Avicennia* type from middle Miocene to Recent.

PRESENT ENVIRONMENT AND FLORA OF ENIWETOK

Eniwetok Atoll lies in the northern and drier section of the Marshall Islands, at lat. 11°30′ N., long. 162°14′ E. It is oval shaped, elongate toward the northwest, and 27 miles in greatest diameter. The forested larger islands all lie along the east flank of the atoll, whereas reefs and very small islets compose the west flank (fig. 335). The reefs of the atoll are well developed and have several shallow passages on their south margin and one deep passage on the southeast extending from the lagoon to the sea.

The sea-depth contours diagramed in figure 336 shows a pronounced platform of basalt at a depth of 500–800 fathoms (3,000–4,800 ft). Its axis trends northwest and it measures 52 by 28 miles. Below a depth of 800 fathoms its flanks slope steeply. Hess (1946) suggested that this platform is an old guyot surface planed by wave action before subsidence, when the Marshall Islands were more highly elevated.

Eniwetok has a total of 39 islets, of which some of the larger are Parry, Engebi, and Runit. Most of the larger islands are on the eastern, or windward, side of the atoll.

Bikini Atoll, from which a few plant fossils were obtained, lies about 200 miles east of Eniwetok. The ocean between Eniwetok and Bikini is up to 13,000 feet deep.

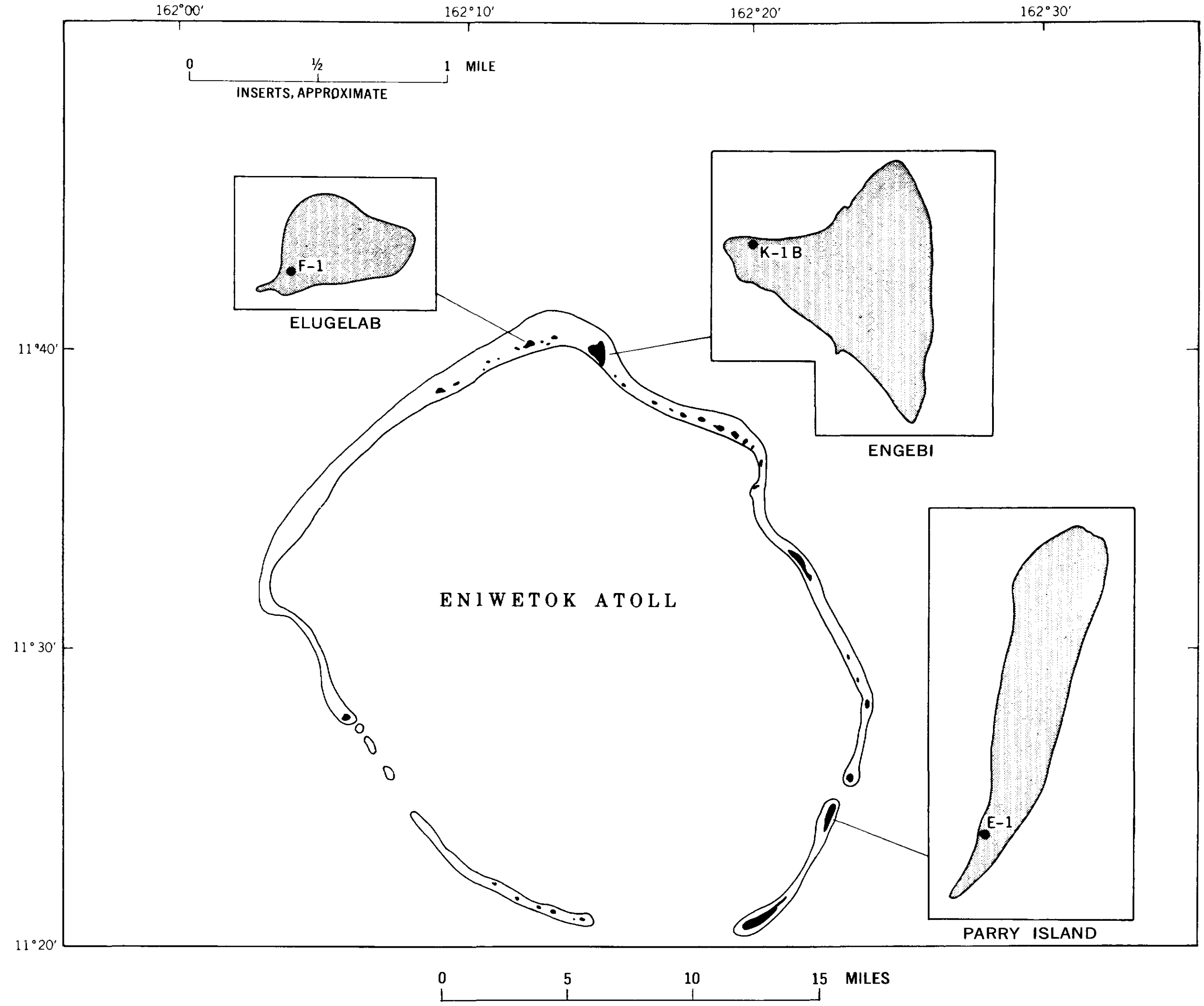

FIGURE 335.—Map of Eniwetok Atoll, showing location of drill holes F–1, K–1B, and E–1.

Bikini Atoll is also oval shaped and has a northwest-trending axis; most of its larger islands are also on the eastern, or windward, side (fig. 337).

The current drift in the northern Marshalls is westward in the path of the North Equatorial Current; an equatorial countercurrent flows eastward through the southern Marshalls, and the boundary between these currents is known to shift during the seasons. There is no large island group between the northern Marshalls and the American mainland along the path of the North Equatorial Current. There is, therefore, no significant source of flora nearby or up current (east).

The Marshall Islands lie in the trade wind belt, and prevailing winds blow from the east or northeast. As a result of these constant winds, there are clear vegetational differences between the windward and leeward islands, and even between the windward and leeward sides of single islands (Fosberg, 1956). From June to September, calms or weak variable winds may occur. Storms and, rarely, typhoons usually come from the south.

The climate of the Marshall Islands is characterized by rather uniform temperatures and by southward-increasing precipitation (Fosberg, 1956). In the north, Eniwetok receives a mean annual rainfall of 50 inches, whereas farther south Ujelang receives 77 inches and Kwajalein 96 inches. The months during which the rainfall gradient is most obvious are December through February, when the southern Marshalls receive roughly three times more rain than the northern Marshalls. Variation in annual and monthly rainfall is very great; the annual rainfall on Eniwetok ranged from 48 to 83 inches within a 3-year period (years not specified; Fosberg, 1956).

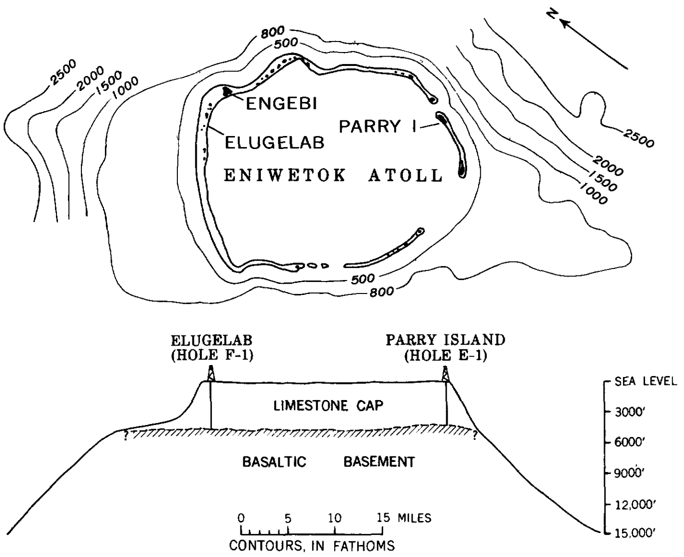

FIGURE 336.—Generalized depth chart and section of Eniwetok Atoll. From Ladd and Schlanger (1960, fig. 285).

Corresponding to the north-south rainfall gradient in the Marshalls is a proportionate trend in luxuriance of vegetation. Fosberg (1956, p. 187) divided the vegetation of the northern Marshalls into four east-west belts (fig. 338).

Vegetation zone 1—the northernmost—comprises the Taongi Atoll and Wake Island. In the aridity of this belt, the coconuts do not thrive, and the vascular flora is very poor in species (nine native species). The atoll vegetation is sparse, and there is much open ground.

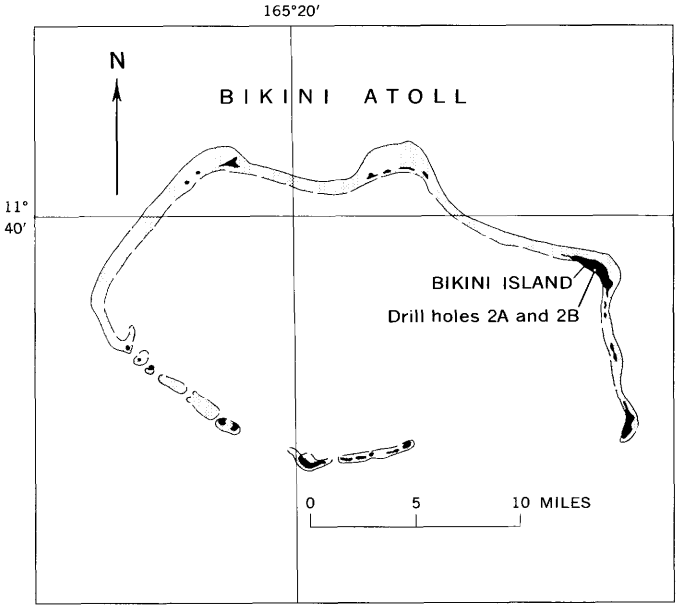

FIGURE 337.—Map of Bikini Atoll, showing location of drill holes 2A and 2B.

Only one atoll, Bikar, is in vegetation zone 2. Though coconut trees grow there, they fail to produce normal nuts in dry years; consequently the environment is considered to be marginal for that species. As in vegetation zone 1, the flora is very small; according to Fosberg (1956), only eight species of native vascular plants are known from Bikar but pure *Pisonia* forest with closed canopy occurs, which gives the atoll a more luxuriant aspect than on the islands of zone 1.

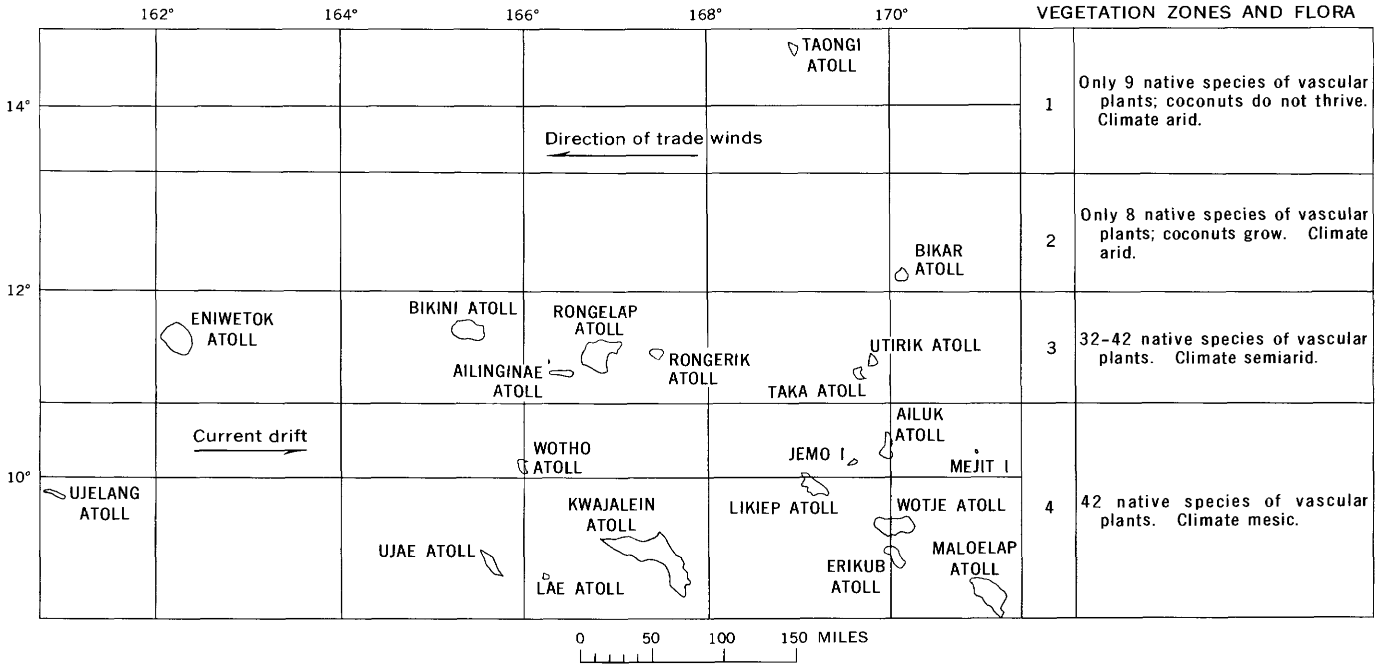

FIGURE 338.—Map of northern Marshall Islands, showing vegetation zones. From Fosberg (1955b).

The third vegetation zone described by Fosberg includes seven atolls that lie along an east-west line at lat 11°30′ N., from Eniwetok and Bikini on the west to Utirik on the east. These atolls have larger floras and, as compared with those farther north, include more types of forest, such as _Pisonia_, _Cordia_, and _Pemphis_, as well as mixed forest. Eniwetok has a flora of 32 indigenous species, according to F. R. Fosberg (oral commun., 1963), and Bikini has about 28 native species (Fosberg, 1956).

In Fosberg's fourth, and southernmost, vegetation zone are 10 atolls, including the largest one in the northern Marshalls, Kwajalein. These atolls have a more luxuriant aspect; their diverse vegetation includes all those types present on the more northern atolls and a few others, such as pure forests of _Ochrosia_. Fosberg listed 42 indigenous vascular species for this zone.

The existing vascular flora of Eniwetok totals 95 species or minor taxa, according to St. John (1960, p. 314), but many are not indigenous; 27 are adventive weeds, 26 are cultivated plants, including both food crops and ornamentals, and seven are species known only from seeds drifted up on the beaches. Of the 42 native species or minor taxa listed by St. John, four are endemic to Eniwetok and belong to the genus _Pandanus_. F. R. Fosberg (oral commun., 1963), however, suggested that these four and four others are merely forms of the species _Pandanus tectorius_. St. John's (1960) enumeration of this flora, which is a summary of his own and earlier collecting by others on the atoll, is given below as modified by F. R. Fosberg (oral commun., 1963); taxa which St. John or Fosberg considered native to Eniwetok are marked with an asterisk; these include 29 vascular genera and 32 species.

- Polypodiaceae
  - *_Polypodium scolopendria_ Burm. f. (fern)
- Pandanaceae
  - *_Pandanus tectorius_ Soland. (screw pine)
- Gramineae
  - _Cenchrus brownii_ R. & S. (grass)
  - _C. echinatus_ L. (grass)
  - _Chloris inflata_ Link. (grass)
  - _Cynodon dactylon_ (L.) Pers. (grass)
  - _Dactyloctenium aegyptium_ (L.) Aschers. & Schweinf. (grass)
  - *_Digitaria pruriens_ (Trin.) Buese. (grass)
  - _Eleusine indica_ (L.) Gaertn. (grass)
  - _Eragrostis amabilis_ (L.) Wight & Arn. (grass)
  - *_Lepturus repens_ (Forst. f.) Rr. Br. var. _repens_, var. *_occidentalis_ Fosberg, and var. *_septentrionalis_ Fosberg. (grass)
  - _Setaria verticillata_ (L.) Beauv. (grass)
  - _Sorghum bicolor_ (L.) Moench. var. _technicum_ (Koern.) Jav. (sorghum)
  - *_Thuarea involuta_ (Forst. f.) R. & S. (grass)
  - _Tricachne insularis_ (L.) Nees. (grass)
  - _Tricholaena rosea_ (Willd.) Hitchc. (grass)
  - _Zea mays_ L. (corn)
- Cyperaceae
  - _Cyperus odoratus_ L. (sedge)
  - _Cyperus javanicus_ Houtt. (sedge)
  - *_Fimbristylis atollensis_ St. John (sedge)
- Palmae
  - _Cocos nucifera_ (coco palm)
- Liliaceae
  - _Allium cepa_ L. (?) (onion)
- Amaryllidaceae
  - _Crinum asiaticum_ L. (?) (spider lily)
- Taccaceae
  - _Tacca leontopetaloides_ (L.) Ktze.
- Urticaceae
  - *_Fleurya ruderalis_ (Forst. f.) Gaud.
- Olacaceae
  - *_Ximenia americana_ L.
- Amaranthaceae
  - _Achyranthes aspera_ L.
  - *_A. velutina_ H. & A.
  - _Amaranthus dubius_ Mart. (pigweed)
  - _A. viridus_ L.
- Nyctaginaceae
  - *_Boerhavia repens_ L.
  - *_B. tetrandra_ Forst. f.
  - _Mirabilis jalapa_ L.
  - *_Pisonia grandis_ R. Br.
- Portulacaceae
  - *_Portulaca lutea_ Solander.
  - _P. oleracea_ L.
  - *_P. samoensis_ v. Poelln.
- Lauraceae
  - *_Cassytha filiformis_ L.
- Cruciferae
  - _Brassica oleracea_ L. _capitata_ (cabbage)
  - _B. pekinensis_ (Lour.) Rupr.
  - _Raphanus sativus_ L. (radish)
  - _Caesalpinia bonduc_ (L.) Roxb.
- Leguminoseae
  - *_Canavalia microcarpa_ (DC.) Piper
  - _Phaseolus vulgaris_ L. (bean)
  - *_Vigna marina_ (Burm.) Merr.
- Zygophyllaceae
  - *_Tribulus cistoides_ L.
- Surianaceae
  - *_Suriana maritima_ L.
- Euphorbiaceae
  - *_Euphorbia chamissonis_ (Klotsch & Garcke) Boiss.
  - _E. hirta_ L.
  - _E. thymifolia_ L.
  - _Phyllanthus amarus_ Schum. & Thonn.
  - _Ricinus communis_ L. (casterbean)
- Tiliaceae
  - *_Triumfetta procumbens_ Forst. f.
- Malvaceae
  - _Malvastrum coromandelianum_ (L.) Garcke
  - *_Sida fallax_ Walp.
- Caricaceae
  - _Carica papaya_ L. (papaya)
- Lythraceae
  - *_Pemphis acidula_ J. R. & G.
- Rhizophoraceae
  - _Rhizophora mangle_ L. (mangrove)

Combretaceae
    *_Terminalia samoensis_ Rechinger
Apocynaceae
    *_Ochrosia oppositifolia_ (Lam.) K. Schum.
Convolvulaceae
    *_Ipomoea pes-caprae_ (L.) Sweet ssp. _brasiliensis_ (L.) v. Ooststr.
    I. purpurea (L.) Roth.
    *_I. tuba_ (Schlecht.) G. Don.
Boraginaceae
    *_Cordia subcordata_ Lam.
    *_Tournefortia argentea_ L.
Solanaceae
    Nicotiana glauca Graham
    Physalis angulata L.
    Solanum lycopersicum L.
Rubiaceae
    *_Guettarda speciosa_ L.
    Morinda citrifolia L.
Cucurbitaceae
    Citrullus vulgaris Schrad. (watermelon)
    Cucumis melo L. (cantaloupe)
    Cucurbita maxima Duch. (squash)
Goodeniaceae
    *_Scaevola taccada_ (Gaertn.) Roxb.
Compositae
    Conyza bonariensis L.
    Lactuca sativa L. (lettuce)
    Pluchea indica (L.) Less.
    P. ordorata (L.) Cass.
    Veronia cinerea (L.) Less.
    *_Wedelia biflora_ (L.) DC.
    Zinnia elegans Jacq. (?) (zinnia)

Eniwetok Atoll has a land area above high tide of only about 2.5 square miles, and, thus, the habitats and area capable of supporting vascular plants are limited. St. John (1960, p. 314) described the only habitats as including "outer beaches of coral rock or coral gravel, inner beaches of coral sand, small coral sand dunes, coral gravel flats, and coral sand flats." Today there are no fresh ponds or central hollow depressions in the middle of the islets, nor is there any dark topsoil. The present vegetation on the large islands is reduced to a few sickly coconut trees and a small number of weedy plants, the original vegetation having been almost completely destroyed during World War II (Fosberg, 1956) and subsequent bomb testing.

The highest elevation above mean sea level at Eniwetok is about 12 feet. Ground water in existing wells on Eniwetok contains 88–300 ppm chloride (Fosberg, 1956).

Bikini has a land area above high tide of about 2.4 square miles. As on Eniwetok, the greater part of the original vegetation has been destroyed by man, and only on the small islets can relics of the original flora be observed. Fosberg (1956) and Taylor (1950) concluded that the original flora of Bikini was much like that of Eniwetok, but two genera, _Tribulus_ and _Euphorbia_, native to Eniwetok have not been found on Bikini. _Tribulus_ is doubtfully native to Bikini, and _Euphorbia_ was presumably present but not found (F. R. Fosberg, written commun., 1964).

METHODS OF STUDY

The collection of cuttings from drill holes and methods of estimating depth intervals for the cuttings were described by Ladd and Schlanger (1960, p. 867). The chips of cuttings, though somewhat soft when wet, are too large to have been derived from the drilling mud. The samples were washed before preparation, to reduce the possibility of contamination. The surfaces of core samples were chipped clean before preparation.

TREATMENT OF FOSSIL SAMPLES

All dry-sediment fractions used for pollen analysis were weighed and the volumes of sediment were estimated before preparation. Only very small pieces of cuttings were available for analysis and, with two exceptions, less than 1 gram of sediment per cutting sample was used. (See list of cuttings used, table 1.) Core materials were not limited as to sample size, and 13–33 grams of each sample were used (table 1).

Methods of sediment preparation employed in this study are similar to those I used with Kapingamarangi sediments (McKee, Chronic, and Leopold, 1959, p. 539). The technique involved dissolving a measured dry weight of sediment in a 10-percent HCl solution and counting pollen, spores, and algae in a measured fraction of the suspended organic residues. To accomplish this, slides were prepared from aliquot fractions of the total organic residues, and the exact area of the slide examined for each tally was noted. Tallies were then multiplied by constants according to the fractions observed, and the number of pollen and spore grains and (or) algal colonies per gram was extrapolated (tables 1, 3) The calculated number of palynomorphs per gram of sediment (table 1) should be considered only a general indication of pollen density.

Tallies of pollen and spores included more than 200 specimens where adequate material was available; counts of less than 200 grains included all the pollen and spores that could be found in the preparation.

After a first aliquot slide was made, the remaining materials of each sample were acetylated for 2 minutes in a boiling-water bath (Faegri and Iversen, 1964, p. 71), and a second slide was made. In certain algae-rich sediments, such as sample D1200–9 at depths of 2,490–2,500 feet in drill hole E–1, a second acetylation was done for an additional 2 minutes and a third slide made. As would be expected, prolonged acetylation definitely

TABLE 1.—*Calculated number of pollen, spores, and Chroococcalean algal colonies per gram of sediment, Eniwetok and Bikini drill holes*

[Samples are cuttings, except those marked by asterisk (*). which are from cores]

Depth (ft)	Sample		Pollen and spores	Algal colonies	
	Number	Dry weight (grams)		Less than 12 cells	More than 12 cells
Drill hole F-1 (Eniwetok)					
Post-Miocene:					
170-191	F-1-1-2*	28	---	---	---
600-625	2-1*	32	---	---	---
Miocene:					
670-680	D1215-A	.17	35,605	---	---
810-820	B	2.17	8,300	---	---
820-830	C	.15	4,650	---	---
830-840	D	.17	102,000	---	---
840-850	E	1.09	12,600	---	---
850-860	F	.17	3,295	---	---
1,232-1,248	F-1-3-3*	33	---	---	---
1,718-1,740	4-19*	28	---	---	---
1,978-2,003	5-6*	28	---	---	---
2,662-2,687	6-10*	24	---	---	---
Eocene:					
3,054-3,055	F-1-7-7*	25	---	---	---
3,350-3,353	8-1*	24	---	---	---
3,655-3,665	9-4*	21	---	---	---
3,963-3,988	10-1*	17	---	---	---
4,197-4,222	11-33*	24	---	---	---
4,316-4,341	12-13*	30	---	---	---
4,406-4,431	13-2*	23	---	---	---
4,500-4,525	14-28*	24	---	---	---
4,528-4,553	15-12*	13	2	6	25
Drill hole E-1 (Eniwetok)					
Miocene:					
850-860	D1200-1	0.02	21,200	150	---
870-880	2	.20	545	85,250	2,090
880-890	3	.25	36	128	---
2,003-2,028	E-1-1-8*	23	---	---	---
2,440-2,450	D1200-4	.33	72	10,618	1,100
2,450-2,460	5	.60	169	6,580	539
2,460-2,470	6	.23	960	2,160	640
2,470-2,480	7A	.31	180	10,440	1,080
2,480-2,490	8	.23	120	5,460	650
2,490-2,500	9	.04	12	5,630	525
2,500-2,510	10B	.73	8	222	82
Eocene:					
2,802-2,808	E-1-2-9*	27	---	---	---
4,078-4,100	3-17	26	---	---	---
Drill hole K-1B (Eniwetok)					
Miocene:					
694.8-705.3	D1381-1	0.4	---	---	---
726.3-736.8	2	.5	---	---	---
736.8-747.3	3	.17	---	---	---
747.3-757.8	4	.16	---	---	---
799.8-810.3	5	.16	75	---	---
810.3-820.8	6	.15	---	---	---
820.8-831.3	7	.16	---	---	---
841.8-852.3	8	.50	---	---	---
852.3-862.8	9	.20	15	---	---
862.8-873.3	10	.22	14	---	---
873.3-833.8	11	.08	25	---	---
883.8-894.3	12	.18	6	---	---
894.3-904.8	13	.33	---	---	---
Drill hole 2A (Bikini)					
Miocene:					
929-935.5	D1416-1	2.1	1	---	---
935.5-946.0	2	2.0	2	---	---

reduced the amount of Chroococcalean algae in the material, making it possible to observe more pollen per slide. However, tallies on which the calculated number of algal colonies and pollen and spores per gram of sediment was based were carried out on the first, unacetylated, aliquot slide to simplify calculations for the pollen and not modify the real number of algae present. The first acetylation tended to break up the large colonies of algae present, so that a tally of this material yielded a higher number of smaller colonies than did the first unacetylated slide. The second acetylation actually tended to destroy the algal cells, and thus the ratio of algae to pollen and spore grains was lower in the third slide than in the first and second slides.

Mounting medium was glycerine jelly for about half the slides; polyvinyl alcohol was used for the remaining material; all fossil materials were stained with Safranin O. Visibility of the palynomorph structures is good in many of the glycerine jelly slides and poor in most of the material mounted in polyvinyl alcohol.

Location of the figured specimens on the microscope slides are given as coordinates in the plate descriptions. Though the coordinates refer to the mechanical stage readings on a Zeiss photomicroscope in the U.S. Geological Survey pollen laboratory in Denver, the specimens can be relocated on another microscope by calculating the distances from the center of a standard 1×3 inch slide. On our photomicroscope, the position of that center is 108.2 (horizontal axis) × 12.4 (vertical axis), and the coordinates increase toward the left and upward on the slide; coordinate readings cited here pertain when the slide label is placed on the left of the stage.

Slide designations begin with the USGS paleobotany locality number prefixed with a "D" for the Denver laboratory, and following a hyphen is the sample designation (a letter or a number) if one has been assigned; the last number which is in parentheses is the slide number. Slides of the fossil material described here are stored at the USGS pollen laboratory in Denver, Colo. Preparations from core samples carry the original core numbers assigned by Ladd and Schlanger (1960).

REFERENCE COLLECTION OF RECENT POLLEN

Pollen collections representing nearly all the higher plant genera listed in Kanehira's (1933) "Flora Micronesia" were obtained from sheets in the U.S. National Herbarium and consisted of 600 species in about 500 genera. Pollen of each species was prepared by acetylation. Two sets of photographs at × 1000 were made; one set of pictures was organized taxonomically and the other was classified according to pollen morphology. The morphological file was used as a key revealing possible affinities of the fossil pollen to guide the selection of reference material for detailed comparisons.

As a supplement to the modern pollen collection from Micronesia just described, I used a modern pollen collection of about 3,000 selected species of woody plants from Eastern Asia and the United States in the U.S. Geological Survey pollen laboratory in Denver. The photographic key to this collection was useful in checking the range of morphological variations within particular genera or families.

Modern pollen preparations are referred to here by their accession number which begin with "P"

COMPOSITION AND RELATIONSHIP OF FOSSIL FLORA TO RECENT FLORA

The following systematic list summarizes the relationships of the Miocene pollen, spore, and organic algal remains. Forms are identified to family and living genus, where possible. For some forms no affinity with living plants can be cited, nor can several unknown but distinctly different pollen or spore forms be recognized under a single morphological category or form species. For convenience in referring to these unknown forms, they have been given morphological code designations according to the system suggested by Tschudy (1967), which consists of three parts. The first part indicates aperture type and number, for example, C_3 (tricolpate), Tl (trilete), M (monolete), and P_3 (triporate); the system is adapted from J. Troell-Smith (in Faegri and Iversen, 1964). The second part describes the sculpture of the grain: sm, smooth; r, rough or psilate; rt, reticulate; p, projections larger than 1 micron; and st, striate. The third part represents an accession number for the particular species in the combined aperture and sculpture category.

Systematic list of Miocene plant microfossils from Eniwetok

- Algae, Chroococcales:
  - Chroococcaceae:
    - *Gloeothece* type
    - *Gomphosphaeria* type
    - *Gloeocapsa* type
    - *Coelosphaerium* type
    - *Aphanocapsa* type
- Algae or Protista, Hystrichosphaeridae:
  - *Pterospermopsis* cf. *P. ginginensis* Deflandre & Cookson
  - *Micrhystridium tenuissimum* Deflandre
  - Cysts, undet.
- Spores of Pteridophyta:
  - ?Polypodiaceae:
    - M–sm(1)
    - Tl–sm(2)
  - ?Hymenophyllaceae:
    - *Trichomanes* type, Tl–p(2)
  - ?Pteridaceae:
    - Tl–r(3)
- Pollen of Monocotyledonae:
  - Pandanaceae:
    - *Pandanus*
- Monocotyledenous pollen of uncertain family affinity:
  - ?Palmae:
    - *Livistona* type
    - C_1–sm(2), monosulcate
- Pollen of Dicotyledonae:
  - Nyctaginaceae:
    - *Pisonia* cf. *P. grandis* R. Br.
  - Euphorbiaceae:
    - *Acalypha*
  - Malvaceae:
    - *Thespesia* cf. *T. lampas* (Cav.) Dalz.

Systematic list of Miocene plant microfossils from Eniwetok—Continued

- Pollen of Dicotyledonae—Continued
  - Sonneratiaceae:
    - *Sonneratia* cf. *S. alba* J. Sm.
  - Rhizophoraceae:
    - *Rhizophora* cf. *R. apiculata* Bl.
    - *Rhizophora* cf. *R. mucronata* Lam.
    - *Rhizophora* sp.
    - *Bruguiera* cf. *B. gymnorhiza* (L.) Merr.
    - *Ceriops* cf. *C. tagal* (Perr.) C. B. Rob.
  - Combretaceae:
    - *Terminalia* cf. *T. catappa* L.
    - cf. *Combretum*
    - *Lumnitzera* cf. *L. littorea* (Jack.) Voight
  - Myrtaceae:
    - cf. *Eugenia*
  - Boraginaceae:
    - *Tournefortia* cf. *T. argentea* L.
    - *Cordia* cf. *C. subcordata* Lam.
  - Verbenaceae:
    - *Avicennia* cf. *A. marina* Forsk.
  - Rubiaceae:
    - *Ixora* cf. *I casei* Hance
    - *Gardenia* cf. *G. grievei* Horne
    - *Randia* cf. *R. cochinchinensis* (Lour.) Merr.
    - cf. *Guettarda*
    - cf. *Timonius*
    - *Morinda* cf. *M. citrifolia* L.
    - cf. *Mussaenda*
    - cf. *Scyphiphora*
- Dicotyledonous pollen of uncertain family affinity:
  - Colpates:
    - C_3–r(1), ?Verbenaceae, *Callicarpa* type
    - C_3–sm(3), ?Gesneriaceae, *Cyrtandra* type
    - C_3 undet.
    - C_4–r(1), ?Callitrichaceae, *Callitriche* type
    - C_4 and C_5 undet.
  - Porates:
    - P_3–sm(3)
    - P_3 undet.
    - P_2–sm(1), ?Moraceae, *Malaisia* type
    - P_4–p(1), ?Simarubaceae, *Picrodendron* type
    - $P\infty$–(1)
  - Colporates:
    - C_3P_3–sm(10), C_3P_8–sm(8), ?Elaeocarpaceae, *Elaeocarpus* type
    - C_3P_3–sm (9)
    - C_3P_3–sm(7), ?Rhizophoraceae, *Gynotroches* type
    - C_3P_3–r(11), ?Leguminoseae, *Sophora* type
    - C_3P_3–r(9), ?Hippocrateaceae, *Salacia* type
    - C_3P_3–st(1), ?Simarubaceae, *Brucea* type
    - C_3P_3–r(10)
    - C_5P_5–r(1), ?Rubiaceae, *Coprosma* type

FLORISTIC COMPOSITION

The Miocene flora of Eniwetok includes 56 kinds of plants; of these, five are algae, four are pteridophytes, three are monocotyledons, and 44 are dicotyledons. Seventeen angiosperm genera are definitely identified, including one monocot and 16 dicot genera. One algal, one monocot, and 10 dicot families are recognized. Twenty-four pollen types are definitely assignable to dicot families, but only one monocot and five algal types can be identified to living family.

The flora is overwhelmingly dicotyledonous and all identified genera are trees or shrubs. Rubiaceae is the best represented family, with four genera and eight pollen types; next best represented are Rhizophoraceae with three genera and six pollen types; Combretaceae, with two genera and three pollen types; and Boraginaceae, with two genera and two pollen types.

Numerically, Rhizophoraceae (*Rhizophora*) pollen grains vastly outnumber pollen or spores of all other groups. The only other pollen form that was at all abundant in the tallies (table 5) was that referred to *Elaeocarpus* type (code species C_3P_3-sm(10)). More abundant than pollen and spores of vascular plants in drill hole E-1 were the remains of Chroococcalean algae, which numbered 5,000–10,000 colonies per gram of sediment. Relative abundance of plant materials is discussed on p. 1152.

The Pteridophyta are poorly represented in the flora; only four spore types were found. The form having the widest stratigraphic occurrence was a simple monolete smooth spore (M-sm(1), pl. 305, figs. 1, 2) that very probably represents a member (or members) of the Polypodiaceae. This fossil is unlike the spores of *Polypodium scolopendria*, which is the only Polypodiaceae now known to grow on Eniwetok.

Of the three monocot pollen types found, only *Pandanus* pollen was identified (pl. 305, figs. 16, 18, 19). *Pandanus*, known as screw pine, now grows on Eniwetok and is distributed throughout the Indo-Pacific region, where it occupies many habitats from coastal to montane.

Fossil *Pisonia* pollen of the *P. grandis* R. Br. type (pl. 306, figs. 1, 5) was compared with modern collections of *P. grandis* R. Br. and *P. umbellifera* (Forst.) Seem., which were the only two species of the genus listed by Kanehira (1933) as present in Micronesia. Pollen of these two species is easily distinguished, and only *P. grandis* seems to be represented now on Eniwetok as a coastal forest tree; it is common at low elevations on South Pacific islands.

The *Sophora*-type pollen (pl. 306, figs. 6–8) was compared with two collections of *S. tomentosa* L. and one of *S. secundiflora*. Its resemblance to *S. tomentosa* L. is striking, but because the morphology involved is not particularly unusual among dicot pollen types there is no certainty as to either the family or the generic affinity. Of 60 other leguminous genera considered, *Sophora* is the only form similar to the fossil. The genus grows on many Pacific islands today; the species *S. tomentosa* L. was recorded in the northern Marshalls at three localities by Fosberg (1955a, p. 12), who suspects that the plant is native to those islands. He observed that the plant is a common pantropical strand species.

A single fossil specimen of *Acalypha* (pl. 306, figs. 9, 10) is extremely similar to a modern collection from Ponape at an elevation of 400 feet which was identified as *Acalypha* sp. by S. F. Glassman. In comparing the fossil with modern pollen of five other *Acalypha* species (only one of these was from Micronesia), it was evident that there is considerable pollen morphological variation within the genus. The fossil is somewhat larger than the modern pollen of *Acalypha*, but otherwise it is almost identical with the Glassman collection. *Acalypha* was not reported from the present Eniwetok flora by St. John (1960), but it grows on Arno Atoll and in the northern Marshalls, where it was introduced (Fosberg, 1955a). It is common throughout Malaysia, New Guinea, Melanesia, west through Polynesia to the Austral Islands, in the high islands of the Carolines, and on low Kayangel Atoll in the Palaus (F. R. Fosberg, oral commun., 1965).

Probable *Callitriche* pollen was unexpected in this flora; the genus is generally characterized as a cosmopolitan fresh-water annual in the temperate and tropical zones, but no record of the genus, fossil or living, is known from Micronesia. A living species in New Guinea was reported by Merrill and Perry (1941); many species occur in New Zealand and Australia, some of which may tolerate brackish water, since they are reported from harbors and barrier reef islands.

Salacia-type pollen (pl. 306, figs. 12, 13), of which two specimens were found at Eniwetok, is probably a member of the family Hippocrateaceae. The family does not now grow on Eniwetok, but Kanehira (1933) reported *Salacia* and *Hippocratea* (referred to *Loesneriella* by A. C. Smith) from Yap and the Palau Islands, and a third genus, *Salacicratea*, with an endemic species, in the Palaus; these plants are described as climbing shrubs. I have compared the fossils with material of the first two but not with that of the third. Van Campo and Hallé (1959), in describing the range of pollen morphology in the family Hippocrateaceae, indicated that many intermediate morphological pollen types occur within the family. For lack of enough comparative material, the fossils here reported are only tentatively assigned to *Salacia*.

Pollen assigned to *Thespesia* (pl. 306, figs. 22–24) includes only two specimens, and both resemble the Indo-Malayan species *T. lampas* (Cav.) Dalz rather than *T. populnea* (Linn.) Soland. ex Corr. The latter species is the only member of the genus now known in Micronesia. *Thespesia populnea* was described by Kanehira (1933) as being of broad paleotropical distribution in coastal forests. *Thespesia* is not represented in the living Eniwetok flora, according to St. John (1960), but another malvaceous genus, *Sida*, now grows on the atoll and is considered native there.

Modern pollen of the genus *Sonneratia* (pl. 307, figs. 7–11, 22–24) has a unique morphology among angiosperm pollen types. The fossil material assigned to this genus (pl. 307, figs. 1–6, 12–21) varies greatly in size and in degree of folding and may represent more than one species. The fossils compare well with two collections of modern *S. alba* J. Smith pollen. Five species of the genus exist, according to Mahabale and Deshpande (1957, p. 52), and, except for *S. alba*, which grows in Micronesia as far east as the southern Marshalls, are of Indo-Malayan distribution (fig. 339). On Arno Atoll, about 5° south of Eniwetok, *S. alba* grows in association with *Lumnitzera* in mangrove depressions in the central higher parts of the atoll (Anderson, 1951). *Sonneratia* also grows on Jaluit, according to F. R. Fosberg (written commun., 1964).

Modern distribution of the genus *Sonneratia* is shown in figure 339, in which the localities of individual herbarium collections are indicated. The known fossil occurrences (fig. 339) include one recorded in southern India—fossil wood thought to be of Eocene or late Tertiary age (Ramanujam, 1957). A fruit from the Deccan flora (Eocene or younger Tertiary) (Sahni, 1943; Mahabale and Deshpande, 1957) and a flower from the Deccan flora (Shukla, 1944) may be related to *Sonneratia* also. Fossil pollen occurrences shown in figure 339 include not only those on Eniwetok but also those on Fiji (p. 1163–1164), Borneo (Muller, 1964), and Palau India.

Rhizophoraceae pollen (pl. 308), which is so abundant in the Miocene sediments, is of five types: two primary *Rhizophora* types (cf. *R. apiculata* Bl. and cf. *R. mucronata* Lam.) and *Bruguiera*, *Ceriops*, and cf. *Gynotroches*. Modern comparative material includes pollen of *R. mucronata* (three collections), *R. apiculata* (two collections), a hybrid of *R. mucronata* × *R. apiculata* (one collection), *R. mangle* L. (one collection), *B. gymnorhiza* (L.) Merr. (three collections), *Ceriops tagal* (Perr.) C. B. Rob. (two collections), and *G. axillaris* Bl. (one collection). These collections include all the living genera of the family and all the Micronesian species reported by Kanehira (1933). Fossil material that compares favorably with *R. apiculata* is the most frequent pollen type (pl. 308, figs. 1–8), but fossil *R. mucronata* types are represented (pl. 308, figs. 20, 21, 26, 27). Also present are some forms (pl. 308, figs. 20, 21, 26) which are identical with the modern hybrid material of *R. mucronata* × *R. apiculata*. Kanehira (1933, p. 212) reported that *R. mucronata* and *R. apiculata* are widely distributed in the paleotropical zone and often occur together; he noted their presence on Ponape and Yap. *R. apiculata* is reported on Kusai but is not known from the Marshall Islands. *R. mucronata* now

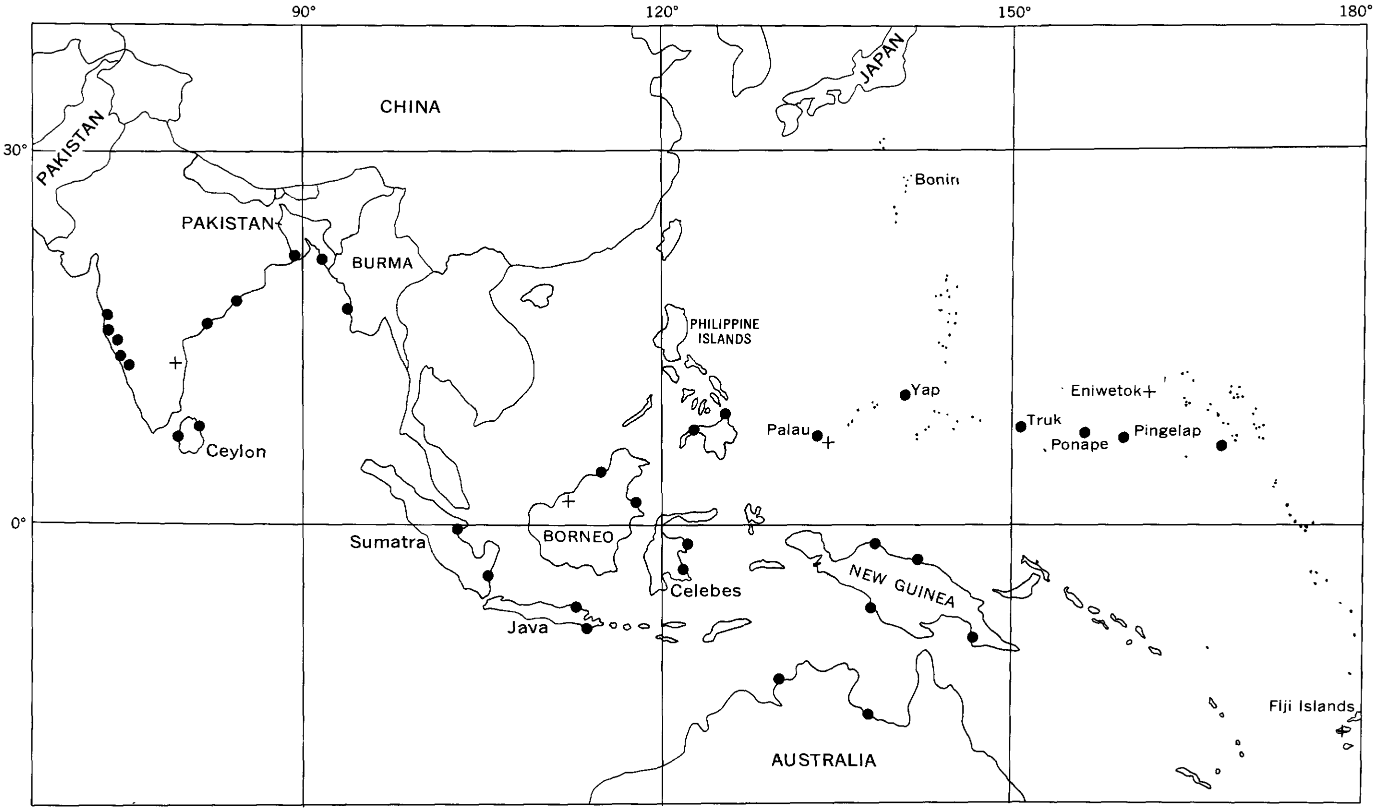

FIGURE 339.—Distribution of modern and fossil *Sonneratia*. Circles, modern distribution (Mahabale and Deshpande, 1957). Crosses, Tertiary occurrences. Fossil wood in southern India is of Eocene or younger Tertiary age (Ramanujam, 1957); pollen from Borneo is Miocene and Pliocene (Muller, 1964), and pollen from Fiji (p. 1164) and from Eniwetok (p. 1168) is Miocene.

ranges eastward into the southern Marshalls (Fosberg, 1960). *R. mangle*, now of New World and eastern Pacific distribution, was reported by St. John (1960) to have been planted on Eniwetok in 1954; it is therefore exotic to the atoll. None of the fossil forms resemble the modern pollen of *R. mangle* (pl. 308, figs. 36, 37).

Fossil pollen assignable to *Bruguiera* (pl. 308, figs. 31, 32, 40) occurs infrequently in the Miocene sediments, though some of the forms tallied as *Elaeocarpus* type (table 8) may be weathered specimens of *Bruguiera*. The genus is Indo-Pacific; it now grows in the mangrove depressions on the higher parts of the southern Marshall Islands and on Lae, Utirik, Ailuk, and Bikini in the northern Marshalls (Fosberg, 1947, 1960).

Fossil pollen of *Ceriops* is comparable with *C. tagal* (pl. 308, figs. 41–43), which is the only species of that genus now in Micronesia. However, comparisons with *C. roxburghiana* Arn. of India and Malaya were not made, so subgeneric affinities are not clear. *C. tagal* is Indo-Malayan and ranges eastward as far as the western Carolines.

A few fossil pollen are similar to the genus *Gynotroches* (pl. 308, figs. 44, 45), but the genus is not identified with certainty in this flora.

All the living relatives of the identified Rhizophoraceae are trees occupying swamp habitats in the intertidal coastal zones or in mangrove depressions (Fosberg, 1947). *Gynotroches*, however, is an upland tree.

Of the Combretaceae forms represented in the Eniwetok flora, *Lumnitzera* pollen is the most abundant (pl. 309, figs. 22–26); the fossils are identical with the pollen of *L. littorea* (Jack.) Voigt, and are quite different from the pollen of *L. racemosa* Willd. (pl. 309, fig. 40). *L. littorea* is the only species of the genus now in Micronesia; it is a small- to medium-size tree that grows in association with *Rhizophora* in mangrove swamps in the Indo-Malayan area, but in the southern Marshalls it grows with *Bruguiera* and *Sonneratia* in mangrove depressions.

At least two other types of Combretaceae pollen were found in the Miocene flora; *Terminalia* cf. *T. catappa* L. (pl. 309, figs. 1–5) and a probable *Combretum* type (pl. 309, figs. 6, 7). *T. samoensis*, which now grows on Eniwetok, does not compare favorably with the fossil *Terminalia* pollen. *T. catappa* is a large tree in the coastal forests of the Caroline and Mariana Islands, and it is introduced in the Marshall Islands (Fosberg, 1956, p. 288).

The family Myrtaceae, which is certainly represented by the fossil pollen shown on plate 310, figures 1 and 2, is not now represented in the Eniwetok vegetation. Unfortunately, only one fossil pollen grain assignable to that family has been found in the Miocene sediments. Determination of Myrtaceae genera on the basis of pollen type is not a very good procedure because of the large number of similar pollen types in the family; for this reason comparisons with living genera made on the basis of pollen are arbitrary. In Micronesia, one would expect *Eugenia* and *Decaspermum;* of these the fossil in question is somewhat like *Eugenia*, although no good matching species could be found, but it is more like pollen of *Rhodamnia* (pl. 310, fig. 3). *Eugenia* is of worldwide distribution, and many endemic species inhabit Micronesia.

Tournefortia pollen of the *T. argentea* L. type (pl. 310, figs. 4, 5) occurs occasionally in the fossil flora; *T. argentea* is a small tree of the coastal forests and sandy beaches of Micronesia, and it now grows on Eniwetok Atoll.

Pollen assignable to *Cordia* cf. *C. subcordata* Lam. was found at two levels in hole F–1. This tree, which now grows on Eniwetok, is a highly variable widely distributed Indo-Pacific and Micronesian species.

Fossil *Avicennia* pollen in the flora (pl. 310, fig. 10) is extremely similar to that of *A. marina* Forsk., but is unlike that of *A. nitida*. *A. marina* grows in mangrove swamps in China, Indo-Malaya, the Palaus, and as far east as Guam. According to F. R. Fosberg (written commun., 1964), it does not grow in the Marshall Islands today.

The Rubiaceae pollen types in this flora are many and varied. Fossil *Morinda* pollen (pl. 311, figs. 1, 2, 9, 10) compares especially well with that of *M. citrifolia* var. *bracteata*, Roxb., which ranges from India to the Ryukyus and occurs on Amboina in the Moluccas. The fossil pollen compares fairly well with *M. citrifolia* L., which now grows on Eniwetok but may not be native there; Fosberg (1956) thought the species might have been introduced by aborigines.

Pollen that is suggestive of *Mussaenda frondosa* L. is present in the Miocene flora (pl. 311, figs. 3, 4), as are forms that are similar to *Scyphiphora hydrophyllacea* Gaertn. (pl. 34, figs. 15, 16). Both species occur in central and western Micronesia today.

Miocene *Randia* pollen from Eniwetok is sparse, but several specimens have been found. They are very similar to pollen of the modern *R. cochinchinensis* (Lour.) Merr. of the Carolines and Marianas except that they are somewhat larger (pl. 310, figs. 31, 32). *R. cochinchinensis* is a small tree of the coastal forests; the genus *Randia* is not found in the living flora of Eniwetok, but *R. graeffi* (equals *cochinchinensis*) was collected on Arno Atoll by Anderson (1951).

Pollen assigned to *Ixora* (pl. 310, figs. 13–15) was compared with that of only one living species (*I. casei* Hance), but they are a close match, and the morphology of *Ixora* is apparently unique among genera of the Rubiaceae. The genus includes several shrub and forest tree species endemic to the Caroline Islands. One occurrence of *Ixora casei* in the Marshall Islands (Likiep Atoll) was noted by Fosberg (1955a, p. 20), who termed the species an introduced plant but thought it might be native to the southern Marshalls.

Pollen that probably represents the genus *Timonius* (pl. 310, figs. 21–23) is found at several levels in the Miocene section. The pollen of a Central American species of *Guettarda*, *G. macrosperma* Donnel Smith, is rather similar to that of *Timonius*; the similarity suggests that these two genera perhaps cannot be distinguished morphologically. Actually, the pollen of the only Micronesian *Guettarda* species (*G. speciosa* L.) is competely different from that of the *Timonius* species considered here. *Timonius*-type fossil material is compared with modern *Timonius* and *Guettarda* pollen on plate 310. *Timonius* is a common genus in the Carolines and Marianas but is an upland form. An atoll species, *T. polygamus* Robinson, occurs in Polynesia (F.R. Fosberg, written commun., 1964).

A single specimen of *Gardenia* pollen was found in the Eniwetok Miocene flora (pl. 310, figs. 16, 17). Its discovery was unexpected because the genus is known as an upland or montane form; it occurs in Malaysia, Borneo, Fiji, the Ryukyus, Polynesia, and Hawaii, but I could find no record for the genus in Micronesia. The pollen morphology of *Gardenia* is unusual in Rubiaceae, because it is one of the few genera of this family in which the pollen tetrads do not break apart upon anthesis. The other Gardenieae of which this is also characteristic are of Asiatic or Caribbean distribution. The present record cannot be explained by laboratory or field contamination. One might suppose that this specimen could have reached Eniwetok lagoon during the Miocene by means of long-distance transport by wind, except that it is a relatively heavy large grain. *Gardenia* may have grown on islands nearer Eniwetok than it does today.

Of the 21 pollen types of undetermined family affinity listed on page 1146, 12 are described under "Systematic Descriptions" (p. 1165).

MODERN DISTRIBUTION OF MIOCENE GENERA

Generically, the Miocene Eniwetok flora can be classified into broad geographic elements according to their total ranges; geographic groups are according to Glassman (1957). On this basis, the fossil flora can be classified as follows:

Group 1. Micronesian or Pacific island genera: None found.

Group 2. Indo-Pacific genera (occurring in Indonesia or southeast Asia and on islands of the Pacific and Indian Oceans) and paleotropical genera: 29 percent.
- *Lumnitzera*
- *Sonneratia*
- *Bruguiera*
- *Pandanus*
- *Ceriops*

Group 3. Pantropical genera: 71 percent.
- *Ixora*
- *Tournefortia*
- *Morinda*
- *Gardenia*
- *Randia*
- *Terminalia*
- *Rhizophora*
- *Thespesia*
- *Cordia*
- *Acalypha*
- *Pisonia*
- *Avicennia*

Group 4. Cosmopolitan genera: None found.

The prevalence (71 percent) of pantropical genera in the Miocene flora is also characteristic of the modern genera of Eniwetok flora (48 percent pantropical genera). Indo-Pacific and paleotropical genera, which comprise 29 percent of the Miocene flora, represent 31 percent of the modern flora. Cosmopolitan genera which as a group were lacking in the fossil flora comprise 21 percent of the modern Eniwetok flora.

Only four of the identified fossil genera are native to Eniwetok today; these are *Pandanus*, *Pisonia*, *Cordia*, and *Tournefortia*. The relation between the generic composition of the Micronesian fossil and modern floras is discussed in the context of other late Tertiary floras on pages 1163–1165.

DISTRIBUTION OF SIMILAR LIVING SPECIES

Even though the preponderance of fossil genera has pantropical distribution, the modern affinities of the fossil flora may be Indo-Pacific. Almost all species affinities suggested in the systematic descriptions are Indo-Pacific in distribution; however, this specific relationship, probable as it may be, cannot be categorically established for all the fossils belonging to pantropical genera for two reasons: (1) the geographic scope of the modern reference material was, for several species, not wide enough to establish an Indo-Pacific affinity versus some other, or (2) the pollen morphological differences between the species of a genus were not great enough (as they are, for example, in *Pandanus*) to permit subgeneric determinations.

An evaluation of fossil affinities by geographic divisions, including fossils identified on a subgeneric level where that was possible, is as follows (an asterisk marks genera which have all their species in the same geographic province):

Group 1. Micronesian or Pacific island species: None identified.

Group 2. Indo-Pacific elements: 56 percent.
Pisonia cf. _P. grandis_
Sonneratia cf. _S. alba_
Rhizophora cf. _R. apiculata_
Rhizophora cf. _R. mucronata_
*_Bruguiera_ sp.
*_Ceriops_ sp.
Lumnitzera cf. _L. littorea_
Tournefortia cf. _T. argentea_
Morinda cf. _M. citrifolia_
Thespesia cf. _T. lampas_

Group 3. Pantropical elements: 44 percent.
Pandanus sp.
Acalypha sp.
Terminalia sp.
Cordia
Avicennia
Ixora
Gardenia
Randia

Group 4. Cosmopolitan elements: None identified.

Whereas the affinity of the fossil flora is primarily paleotropical (Indo-Pacific), the affinity of the modern flora at Eniwetok (here classified) is about evenly split among Micronesian, paleotropical, and pantropical species (those for which comparative fossils have been found are marked with an asterisk):

Group 1. Micronesian and Pacific island species: 31 percent.
Lepturus repens
Fimbristylis atollensis
Achryanthes velutina
Portulaca lutea
P. samoensis
Boerhavia tetrandra
Euphorbia chamissonis
Terminalia samoensis
Ochrosia oppositifolia
Sida fallax

Group 2. Paleotropical or Indo-Pacific species: 38 percent.
Polypodium scolopendria
*_Pandanus tectorius_
Pemphis acidula
*_Cordia subcordata_
*_Tournefortia argentea_
Fleurya ruderalis
*_Pisonia grandis_
Canavalia microcarpa
Triumfetta procumbens
Wedelia biflora
Thuarea involuta
Scaevola taccada

Group 3. _Pantropical species_: 28 percent.
Ximenia americana
Boerhavia repens
Cassytha filiformis
Vigna marina
Tribulus cistoides
Suriana maritima
Ipomoea pes-caprae
Guettarda speciosa
Ipomoea tuba

Group 4. Cosmopolitan species: 3 percent.
Digitaria pruriens

In comparison with the affinities of the living indigenous plant species of Eniwetok, the plants with which the fossils have affinities are of the following distribution types (figures are percentages of the identified floras):

Present distribution	*Fossil taxa*	*Modern species*
Pacific island or Micronesian	None certain	31
Paleotropical (Indo-Pacific)	56	38
Pantropical	44	28
Cosmopolitan	None certain	3

These figures indicate that the Miocene taxa which now either grow mainly west and south of Eniwetok or are paleotropical were partly replaced by taxa which are Pacific island forms today. The composition of the vegetation of Eniwetok clearly was altered significantly during the late Cenozoic, and because consideration of these floral changes will perhaps aid in understanding environmental changes on the island during that time, these floral changes are considered in detail here.

Table 2 and the foregoing lists show that more than half the identified Miocene flora now occur in the Indo-Malayan area; some species range as far west as Africa (paleotropical distribution) and some eastward into Micronesia. The ranges of two plants to which the fossils are related have retreated westward at least 20° longitude since the Miocene; these are *Ceriops*, which is not now found east of the western Carolines, and *Thespesia lampas*, not now found east of New Guinea in the South Pacific (table 2). *Gardenia* has several endemic species in Hawaii, longitude 40° E. of Eniwetok, and also grows in Fiji, Tahiti, and New Guinea. Its fossil occurrence at Eniwetok suggests that in the mid-Pacific its range has retreated southward about 1,300 miles since Miocene time.

Four other taxa to which the fossils are related—*Acalypha*, *Rhizophora apiculata*, *Ixora casei*, and *Avicennia marina*—now occur in Micronesia as far east as the Mariana Islands and the eastern Carolines, 400 miles southwest and 1,000 miles west of Eniwetok, respectively. (*Acalypha* also occurs on Fiji.) Five others range from Indo-Malaya eastward into the southern Marshalls; these are *Terminalia catappa*, *Lumnitzera littorea*, *Rhizophora mucronata*, *Randia cochinchinensis*, and *Sonneratia alba*. Two taxa, *Bruguiera gymnorhiza* and *Morinda citrifolia*, now range from Indo-Malaya eastward to the southern Marshalls, but they are not indigenous to Eniwetok today. Four others have the same general range but, in addition, are native to Eniwetok today: *Pandanus* sp., *Pisonia grandis*, *Tournefortia argentea*, and *Cordia subcordata*.

TABLE 2.—*Distribution of living taxa (native occurrences only) with which Eniwetok fossils show affinity*

[Localities listed from west to east; question mark indicates either questionable occurrence or occurrence but questionably native]

Taxa (17 genera, 18 species)	Continental eastern Asia	Indo-Malaya and Borneo	New Guinea, Philippine Islands	Micronesia						Fiji	Hawaiian Islands
				Western Caroline Islands	Mariana Islands	Eastern Caroline Islands	Southern Marshall Islands	Northern Marshall Islands	Eniwetok Atoll		
Acalypha sp	----	X	X	X	----	X	----	----	----	X	----
Avicennia marina	X	X	X	X	X	----	----	----	----	----	----
Bruguiera gymnorhiza	----	X	X	X	X	X	X	X	----	X	----
Ceriops tagal	----	X	X	X	----	----	----	----	----	----	----
Cordia subcordata	X	X	X	X	X	X	X	X	X	X	X
Gardenia sp	X	X	X	----	----	----	----	----	----	X	X
Ixora casei	----	----	----	X	----	X	?	----	----	----	----
Lumnitzera littorea	----	X	X	X	X	X	X	----	----	----	----
Morinda citrifolia	X	X	X	X	X	X	X	?	----	X	X
Pandanus sp	X	X	X	X	X	X	X	X	X	X	X
Pisonia grandis	----	X	X	X	X	X	X	X	X	?	----
Randia cochinchinensis	X	X	?	X	X	X	X	----	----	----	----
Rhizophora apiculata	X	X	X	X	X	X	----	----	----	----	----
R. mucronata	X	X	X	X	X	X	X	----	----	X	----
Sonneratia alba	----	X	X	X	----	X	X	----	----	----	----
Terminalia catappa	----	X	X	X	?	X	?	----	----	----	----
Thespesia lampas	X	X	X	----	----	----	----	----	----	----	----
Tournefortia argentea	----	X	X	X	X	X	X	X	X	X	----
Total	9	17	16	16	11	14	10	5	4	8	4

Table 2 shows that 16 out of 18, or 89 percent, of the present relatives of the Miocene flora now grow in the western Carolines, and that most of these taxa also occur in Indo-Malaya. Moreover, the enormous diversity of the Indo-Malayan and New Guinea-Borneo modern floras is not at all suggested by the relatively sparse Miocene flora of Eniwetok. Therefore, it is reasonable to conclude that the primary affinity of the fossil flora is with the present flora of the western Carolines rather than with flora on larger land areas farther west.

ABUNDANCE OF FOSSIL POLLEN AND SPORES IN ENIWETOK SEDIMENTS

In this report the abundance of plant fossils is expressed in two ways: absolute number of fossils per gram of dry sediment, and relative number, expressed as a percentage, of the total pollen and spores tallied. When the area of the aliquot slide used for a tally has been noted, the tally can be used to calculate the approximate number of specimens per gram of sediment (p. 1144). Calculations for the Eniwetok sediments are summarized in table 1, and are shown on a semilogarithmic graph in figures 340 and 341. Table 4 indicates relative abundance of the identified fossil pollen and spores in tallies, and figure 342 shows this abundance graphed as a pollen histogram.

Hole E–1.—Small amounts of pollen and large amounts of Chroococcalean algae per gram of sediment occur at depths 2,000–2,500 feet (table 1 and fig. 340). Pollen density is very great (about 21,000 grains per gram) in the highest interval sampled, at 850–860 feet; algae are present in this pollen-rich sample but are not abundant.

Hole F–1.—No algae were found except in the sample from the lowest interval; this sample is of Eocene age, and was taken 100 feet above the basement basalt (table 1 and fig. 341). A total of 24 (about 2 per gram) waxy pollen grains was found in this sample, but none could be identified with living genera. Peak concentrations of pollen and spores occur at two levels in drill hole F–1; the astonishing calculated density of 102,000 pollen grains per gram of sediment was determined for the sample taken at depths 830–840 feet, and 35,000 pollen grains per gram for the sample at 670–680 feet.

SOME ASPECTS OF MODERN POLLEN RAIN IN EASTERN MICRONESIA

To compare the abundance of pollen and Chroococcalean algae in fossil sediments with that in modern sediments, 32 modern lagoonal and marine sediments from eastern Micronesia were analyzed. Table 3, which shows the results for the modern samples, indicates that only five of the 32 samples contained pollen, and that only three contained remains of Chroococcalean algae. I was unable to find any pollen in the atoll lagoonal sediments of Eniwetok, Bikini, or Jaluit in the Marshalls, or in Onotoa lagoon, Gilbert Islands. However, in the Caroline Islands rare pollen was found in lagoonal muds of Kapingamarangi and in a taro-swamp mud on Ifalik. It will be noted that the only significant amounts of pollen (more than 500 grains per gram of sediment) were found in three lagoonal samples from Ponape.

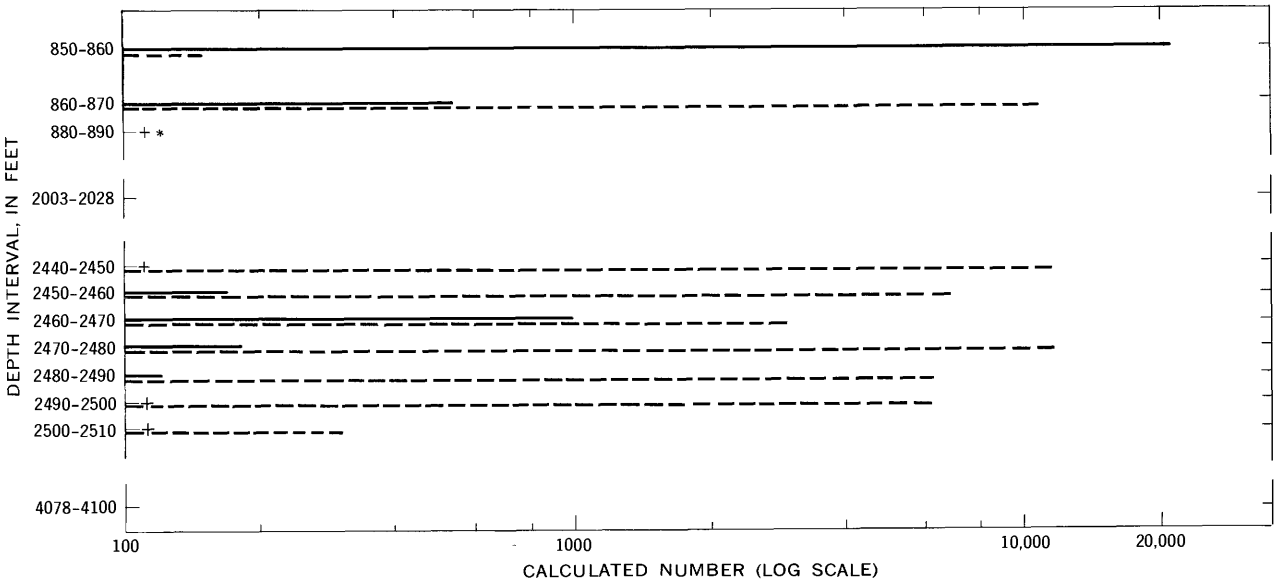

Figure 340.—Calculated number of pollen and spores (solid lines) and colonial algae (dashed lines) per gram of sediment in drill hole E–1. +, Pollen or spores present but less than 100 per gram. *, Colonial algae present but less than 100 per gram.

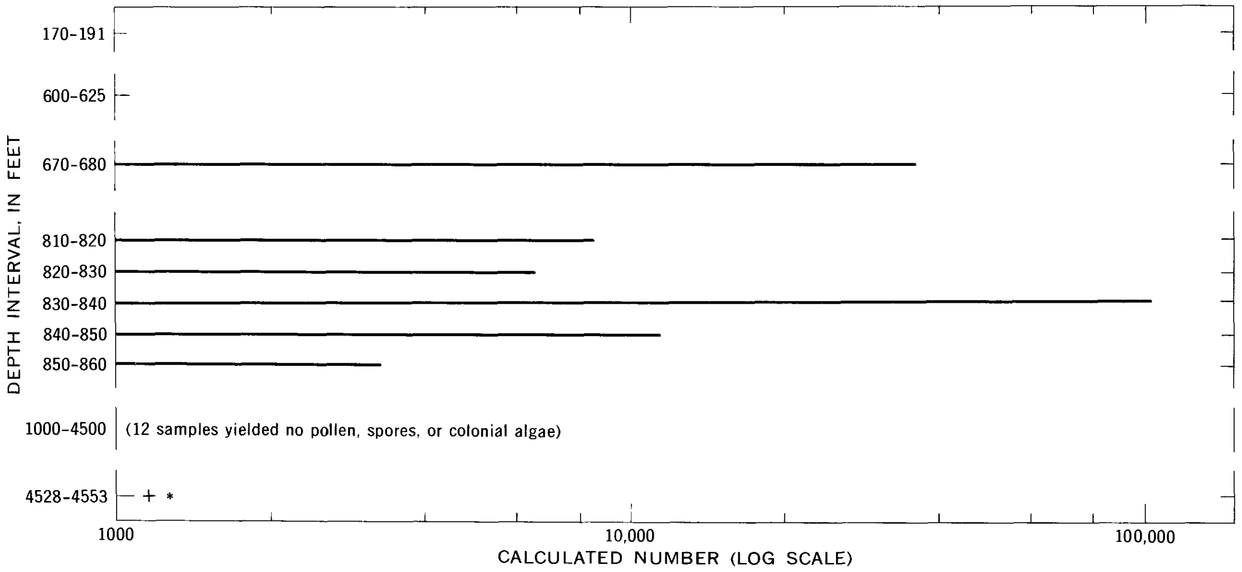

Figure 341.—Calculated number of pollen and spores and colonial algae per gram of sediment in drill hole F–1. +, Pollen or spores present but less than 1,000 per gram. *, Colonial algae present but less than 1,000 per gram.

If the modern pollen data listed in table 3 are arranged by localities according to size of land area, an interesting relation is suggested. On the atolls and islands having a land area of less than 4 square miles and a maximum elevation of less than 20 feet (Eniwetok, Bikini, Jaluit, Onotoa, Kapingamarangi, and Ifalik) no pollen is present in 23 lagoonal or swamp sediments and rare pollen is present in five samples. In contrast, lagoonal sediments from the large high island of Ponape (90 sq mi of land area, and 2,595 ft maximum elevation) contain abundant pollen—about 34,000 pollen and spores per gram of sediment (four samples).

Even though in the present study the sampling of modern sediments is limited (32 samples from seven islands or atolls), a strong indication of an all-or-nothing situation is apparent; the contrast between the scarcity or lack of pollen in random samples from atolls or small islands and the abundance of pollen in samples from a large high island is extreme. The data strongly indicate that the size and, probably, height of the vegetated land area are important limiting factors for maximum pollen density in the lagoonal sediments of eastern Micronesia. Though there is no direct evidence, as from modern pollen traps, in that part of the world to establish the volume of annual pollen rain at different

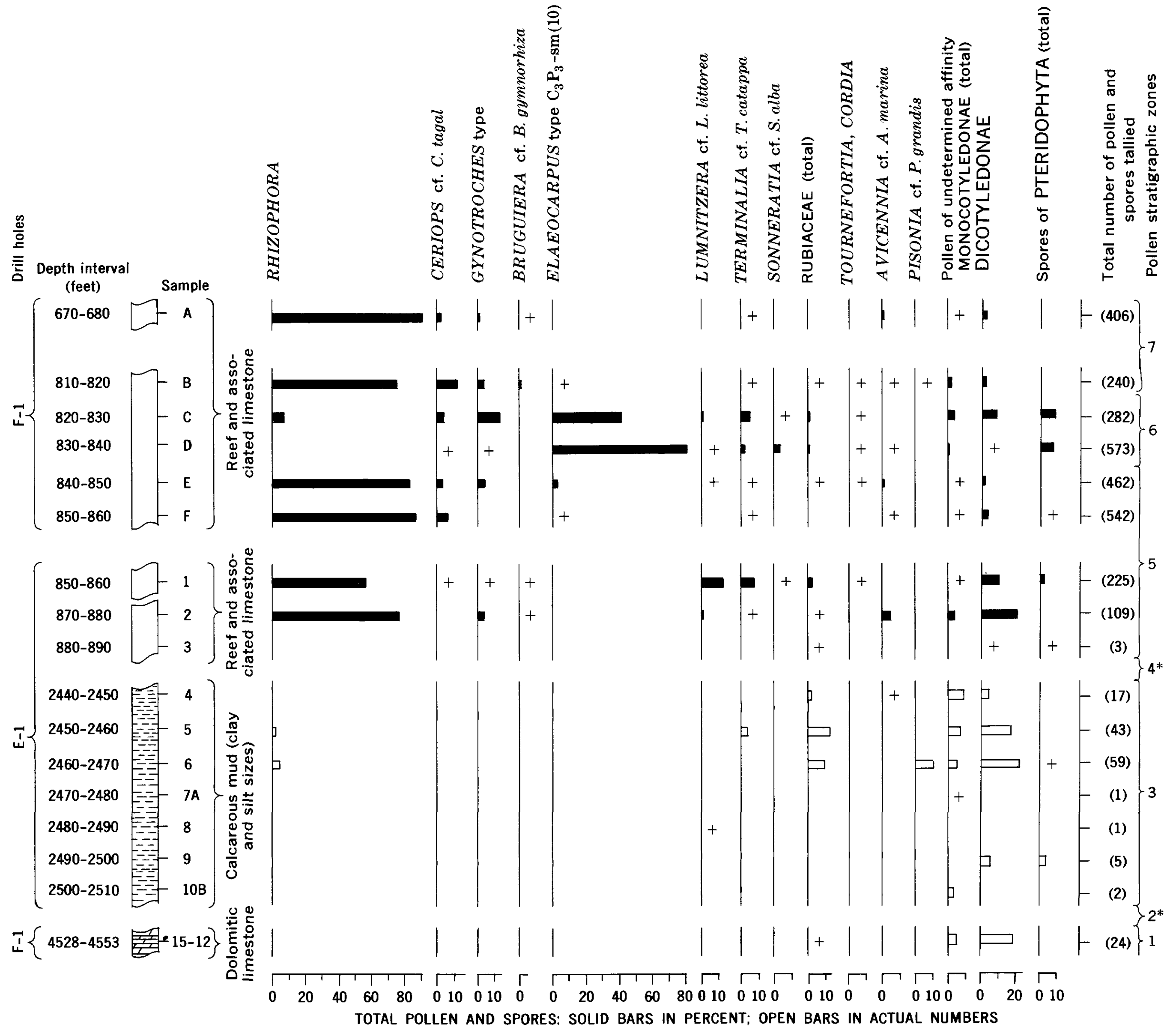

FIGURE 342.—Pollen diagram showing percentages (solid bars) of total pollen and spores in Eniwetok drill holes E–1 and F–1; in lower part of section where less than 100 grains were found per sample, results are shown as actual numbers of grains (open bars). +, Percentages of less than 1 or occurrences not included in tally. Samples from drill hole F–1 are assigned USGS paleobotany loc. D1215, and those from drill hole E–1, USGS paleobotany loc. D1200. *, barren zone.

sites, evidence from the modern lagoonal sediments indicates that pollen rain is relatively sparse on atolls and prolific on high larger islands.

Factors other than the abundance of plants should be considered in discussing abundance of pollen in atoll sediments; distance from source plants, nature of water currents, depth of water at the deposition site, and texture of the sediments are a few. In a modern pollen study at Kapingamarangi, I found that occasional pollen is present in shoreline and shallow-water sediments and in very deep water sediments (E. B. Leopold, in McKee and others, 1959) and that pollen is more abundant in finer grained sediments, as at Ponape (table 4). Another important factor affecting pollen density is probably the location of land along the reef rim of atolls in relation to dominant wind direction. At Eniwetok, Bikini, and Kapingamarangi, the bulk of land above mean sea level is on the windward side of the atoll, so that local pollen has a reasonable possibility of falling into the lagoon. If the vegetation were mainly on the lee side of the atoll, however, pollen might be even more infrequent in lagoonal sediments.

TABLE 3.—*Calculated number of pollen and spores and Chroococcalean algal colonies in modern sediments from eastern Micronesia*

[All sediments are lagoonal except sample D1655, which was taken from seaward slope]

Locality	Total land area (sq mi)	Elevation (ft)	Sample: Type of collection area	Sample: Number	Sample: Dry weight (grams)	Sample: Depth below mean sea level (ft)	Pollen and spores: Per tally	Pollen and spores: Per gram	Algal colonies: Per tally	Algal colonies: Per gram
Marshall Islands:										
Eniwetok	≈2. 5	≈12	Lagoon	Emory 165	9	9				
			do	Fosberg 1	10	10				
			do	Fosberg 2	10	10				
Bikini	≈2. 4	≈12	do	D1654	20	8–10				
			Pacific Ocean, northwest of Bikini.	D1655	20	3, 400				
Jaluit	≈. 4	≈12	Lagoon	McKee 494–496, 498.	14–20	6–14				
Gilbert Islands:										
Onotoa	≈1	≈12	do	D1657	20	5			151	4, 200
			do	D1658	20	0			43	1, 600
			do	51–S–7, D1659–D1661.	20	0–19				
			do	D1662	20	0			15	320
Caroline Islands:										
Kapingamarangi	≈1	≈12	do	D1141–1 through –11.	2	0–240		0–200		
Ifalik	≈. 6	≈18	Taro swamp	IF–9	8. 5	0	140	214		
Ponape	90	2, 595	Metalanim Harbor area.	D3248	5	4	225	34, 640		
			do	D3249	5	4	550	1, 180		
			do	D3250	5	4	430	1, 475		
			do	D3251	5	4	325	392		

TABLE 4.—*Percentage composition and absolute numbers of pollen and spores per gram in modern sediments from Metalanim Harbor area, Ponape, Caroline Islands*

[Water depth, −4 ft mean sea level; asterisk (*), forms found as Miocene fossils on Eniwetok. Actual numbers shown in parentheses]

Type of sediment	Black organic silt	Brown organic sand and silt	Brown organic carbonate sand and silt	Gray carbonate sand
Distance from mangrove stands (ft)	20	100	300	360
USGS paleobotany loc	D3248	D3249	D3250	D3251
Rhizophoraceae:				
cf. *Rhizophora*	9. 6			
*Rhizophora**	46. 5	41. 4	46. 0	24. 4
cf. *Bruguiera*		7. 8		
Sonneratiaceae:				
Sonneratia cf. *S. alba**	16. 0	20. 2	23. 8	14. 1
Combretaceae:				
cf. *Lumnitzera**	. 8			
Proteaceae?	. 8			
Malvaceae:				
Sida fallax	1. 6	. 6		
cf. Rosaceae	. 8			
cf. Annonaceae	. 8			
cf. Polypodiaceae:				
Phegopteris type				. 7
Verrucate monolete	5. 6	6. 1	11. 3	20. 8
Smooth monlete*	4. 8	5. 6	11. 0	23. 0
Verrucate trilete				3. 0
Smooth trilete			. 4	4. 4
cf. Palmae	. 8	1. 7	. 4	. 7
Taccaceae:				
cf. *Tacca*	. 8	2. 2	1. 1	2. 2
Pandanaceae:				
Pandanus sp.*		. 6		
Rubiaceae:				
Guettarda speciosa		. 6	. 4	
Other		. 6		
Gramineae			. 4	1. 5
Leguminoseae:				
Caesalpinia cf. *C. jayabo*			. 4	
Ulmaceae:				
Trema				. 7
Undetermined dicots	10. 4	11. 7	4. 1	3. 0
Undetermined monocots	. 8		. 8	1. 5
Total	100. 1	99. 1	100. 1	100. 1
Total pollen and spores tallied for percentages	(125)	(179)	(265)	(135)
Calculated pollen and spores per gram of sediment	(34, 640)	(1, 180)	(1, 475)	(392)
Based on counts of	(100)	(472)	(163)	(190)

NOTE.—2 Foraminifera per 125 pollen and spores were found in D3248, and 2 per 135 pollen and spores in D3251; one dinoflagellate cyst was seen in D3249.

Distance from source vegetation was shown by Muller (1957) to be an important factor in determining major differences in pollen abundance. He established that, in the Gulf of Paria, Venezuela, a great abundance of pollen (more than 2,000 to 10,000 pollen and spores per gram of sediment) is found within a few miles of land, whereas at greater distances from the coast, progressively less pollen is found and that amount seems to have been controlled by water currents. He found the greatest abundance of pollen (100,000 pollen and spores per gram of sediment) in a continental (back swamp) environment where source plants were only a short distance away and where deposition rates were probably slow.

Productivity of source plants also should be considered as a controlling factor. Mangroves of the Rhizophoraceae characteristically are higher pollen producers than are other types of strand vegetation, such as *Pandanus* and *Pisonia*. Modern sediment samples (D3248–D3250) from Ponape collected from 18 to 300 feet from mangrove stands contain about 50 percent mangrove pollen and the sediments are rich in pollen; but one sample (D3251) taken 360 feet away contains only about 25 percent mangrove pollen (table 4), and total pollen frequency is much lower. Muller (1957) found, however, that the mangrove pollen represents as much as 70 percent of the pollen assemblage at sampling points about 50 miles from land, though at that distance the pollen grains were fewer than 500 per gram of sediment. In the Gulf of Paria the combination of dominance of mangrove pollen in the assemblage and high pollen density in the sediments is found only between 1 and 5 miles from the shoreline.

Both Muller's and my own modern pollen data suggest that mangrove pollen can mask the abundance of pollen from inland vegetation types. At Ponape (table 4) and in the Gulf of Paria, pollen of the rich vegetation of inland environments and nonmangrove strand vegetation is poorly represented in nearshore marine environments.

The mere presence of mangroves on an atoll does not guarantee that mangrove pollen will be readily found in lagoonal sediments. A small patch of mangroves now grows on the atoll of Onotoa, Gilbert Islands; yet mangrove pollen was not found in any of the seven samples of Onotoa lagoonal sediments. Mangroves now grow on Jaluit, but mangrove pollen was not found in the four samples from that lagoon (table 3).

In summary, the abundance of fossil pollen and spores in the Miocene sediments under Eniwetok, ranging from 100 to 100,000 per gram of sediment, is in complete contrast to their apparent scarcity in modern lagoonal sediments of eastern Micronesia. The abundance of fossil pollen in certain of the Miocene sediments of Eniwetok is comparable with the abundance of modern pollen in shallow-water lagoonal sediments from Ponape in the Caroline Islands; the predominance of mangrove pollen in both is a second feature in common. Data secured by the comparative study of modern and fossil pollen for this report indicate that the pollen-rich Miocene sediments were deposited in an environment not far from dense stands of vegetation; the vegetated land area on Eniwetok was probably larger in Miocene time than at present.

FLORAL SEQUENCE IN DRILL HOLES

Tallies of pollen and spores in samples from drill holes F–1 and E–1 are shown in table 5. These results are presented in graph form in figure 342, which is drawn as a composite section incorporating data from both holes. A sampling overlap occurs in the two holes at 850–860 feet.

The deepest interval, recognized stratigraphically in this study as zone 1, is in drill hole F–1 at 4,528–4,553 feet, sample 15–12. In 13 grams of Eocene sediment, 24 angiosperm pollen grains, or about two per gram, were found. In addition, Chroococcalean algal colonies numbering about 25 per gram of sediment were seen. These were the only fossils found within the Eocene part of the section, although about nine sampling levels of Eocene core runs were examined. The contained pollen is not identifiable in terms of living genera (table 5, sample 15–12); but because some grains can be assigned to Rubiaceae, one can be sure that pollen of land plants is present. This occurrence of land-plant remains is of great interest because of its stratigraphic position about 77–102 feet above the basement basalt. The lithology of this zone is firm dolomitic and calcitic limestone. These sediments are at the base of Cole's (1957) Tertiary zone *b* (Eocene).

The second zone, at 2,662–4,525 feet in drill hole F–1, may be defined as a barren interval in terms of pollen, spores, or Chroococcalean algae. Samples from nine core intervals (table 1) were found to be devoid of these fossils. The interval includes mainly the sediments of Eocene (Tertiary *b*) age but also the lowest part of the Miocene sediments. The lithology of this zone is lithified calcite and dolomite of clay and silt sizes.

The third zone, from 2,440 to 2,510 feet in drill hole E–1, may be termed the "Chroococcalean algal zone" because it is characterized by high frequencies of Chroococcalean algae, numbering from about 200 to 10,000 colonies per gram of sediment. Pollen is present in small to moderate amounts (up to 1,000 grains per gram of sediment) in every sampling level. The pollen is mainly that of *Pisonia*, Rubiaceae, and an undetermined monocot, but *Callitriche* type and cf. *Coprosma* are also present. The zone represents lower Miocene sediments at the base of Cole's Tertiary *e* (Ladd, 1958), Lithology is soft unaltered aragonitic mud.

The fourth zone is barren, and no organic remains were found. It is represented by only four samples: from drill hole E–1, a core from 2,003–2,028 feet, and from drill hole F–1, three cores from the interval 1,232–2,003 feet. The lithology of the core in both holes E–1 and F–1 is recrystallized calcitic limestone; age is early Miocene (Tertiary zone *e* of Cole, 1957; Ladd, 1958).

The fifth zone is a richly polleniferous interval represented in both drill holes E–1 and F–1; *Rhizophora* pollen is the dominant form. Because another zone, the seventh, is also dominated by *Rhizophora* pollen, I refer to the fifth as the lower *Rhizophora* zone.

TABLE 5.—*Percent total pollen and spores tallied in sediments from drill holes F–1 and E–1, Eniwetok*

[Numbers in parentheses are actual number of grains observed; + indicates occurrence but not encountered in tally]

Drill hole	F-1	E-1										F-1					
USGS paleobotany loc.	D1215	D1200										D1215					
Sample No.	15-12	10B	9	8	7A	6	5	4	3	2	1	F	E	D	C	B	A
Depth (ft)	4,528–4,553	2,500–2,510	2,490–2,500	2,480–2,490	2,470–2,480	2,460–2,470	2,450–2,460	2,440–2,450	880–890	870–880	850–860	850–860	840–850	830–840	820–830	810–820	670–680
Palynological zones [1]	Zone 1	Zone 3							Zone 5					Zone 6		Zone 7	
Spores of Pteridophyta:																	
?Polypodiaceae:																	
M–sm(1)			(3)			(1)					2.2	0.4		2.1	6.4		
Tl–sm(2)									(1)					1.4	2.5		
?Pteridaceae:																	
Tl–r(3)														3.8			
?Hymenophyllaceae:																	
Trichomanes type, Tl–p(2)														+			
Pollen of Monocotyledonae:																	
Pandanaceae:																	
Pandanus										0.9	.4			.3	1.1	0.8	
Monocotyledonous pollen of uncertain family affinity:																	
?Palmae:																	
Livistona type, C_1–sm(1)		(2)					(7)	(2)		1.8					1.1	+	0.5
C_1–sm(2)					(1)	(1)		(2)				.2		.7	.4		
C_1 and Inaperturate undet.	(6)					(4)		(6)				.2	0.2		1.8		
Pollen of Dicotyledonae:																	
Nyctaginaceae:																	
Pisonia cf. *P. grandis*						(12)											
Euphorbiaceae:																	
Acalypha													.2				
Malvaceae:																	
Thespesia cf. *T. lampas*													+				+
Sonneratiaceae:																	
Sonneratia cf. *S. alba*											.4			2.9	.4		
Rhizophoraceae:																	
Rhizophora cf. *R. apiculata*						(1)	(1)			30.2	21.2	51.8	60.7		.7	54.6	57.8
Rhizophora cf. *R. mucronata*						(1)				31.2	32.0	5.3	.7			.8	1.7
Rhizophora sp.						(3)	(1)			6.4	4.8	30.6	22.8		6.4	21.3	20.9
cf. *Rhizophora*																.8	9.3
Bruguiera cf. *B. gymnorhiza*										.9	.9					1.7	.2
Ceriops cf. *C. tagal*											.4	6.5	3.1	.3	4.6	12.5	2.5
Combretaceae:																	
Terminalia cf. *T. catappa*							(3)			.9	7.1	.2	.7	1.9	5.0	.4	.7
cf. *Combretum*											.4						+
Lumnitzera cf. *L. littorea*				(1)						1.8	14.6		.2	.2	1.8		
Myrtaceae:																	
cf. *Eugenia*														.2			
Boraginaceae:																	
Tournefortia cf. *T. argentea*											.9			.2	.4		
Cordia cf. *C. subcordata*													.2			+	
Verbenaceae:																	
Avicennia cf. *A. marina*								(1)		5.5		.2	1.1	.2		.4	1.2
Rubiaceae:																	
Ixora cf. *I. casei*														+	.7		
Gardenia cf. *G. grievei*															.4		
Morinda cf. *M. citrifolia*						(1)	(3)			.9	1.3		+	.7		+	
cf. *Guettarda*							(2)							.5	.4		
cf. *Timonius*						(8)	(6)		(1)					+			
Randia cf. *R. cochinchinensis*											.9					+	
cf. *Scyphiphora*						(1)	(1)	(2)						+			
cf. *Mussaenda frondosa*	(1)						(1)				+						

See footnote at end of table.

TABLE 5.—*Percent total pollen and spores tallied in sediments from drill holes F-1 and E-1, Eniwetok*—Continued

[Numbers in parentheses are actual number of grains observed; + indicates occurrence but not encountered in tally]

Drill hole	F-1	E-1										F-1					
USGS paleobotany loc.	D1215	D1200										D1215					
Sample No.	15-12	10B	9	8	7A	6	5	4	3	2	1	F	E	D	C	B	A
Depth (ft)	4,528-4,553	2,500-2,510	2,490-2,500	2,480-2,490	2,470-2,480	2,460-2,470	2,450-2,460	2,440-2,450	880-890	870-880	850-860	850-860	840-850	830-840	820-830	810-820	670-680
Palynological zones [1]	Zone 1	Zone 3							Zone 5					Zone 6		Zone 7	
Dicotyledonous pollen of uncertain family affinity:																	
?Moraceae:																	
Malaisia type, P_2-sm(1)								(3)									
?Leguminoseae:																	
Sophora type, C_3P_3-r(11)										.9							
?Simarubaceae:																	
Brucea type, C_3P_3-st(1)												.2					
Picrodendron type, P_4-p(1)															.4		
?Callitrichaceae:																	
Callitriche type, C_4-r(1)						(1)	(1)										.2
?Hippocrateaceae:																	
Salacia type, C_3P_3-r(9)														+			
?Elaeocarpaceae:																	
Elaeocarpus type, C_3P_3-sm(10), C_3P_8-sm(8)												.9	4.5	83.3	41.1	.8	
?Rhizophoraceae:																	
Gynotroches type, C_3P_3-sm(7)										3.7	.4		4.7	.7	14.6	4.2	1.2
?Verbenaceae:																	
Callicarpa type, C_3-r(1)								(1)		5.5						+	+
?Gesneriaceae:																	
Cyrtandra type, C_3-sm(3)						(3)	(3)										
?Rubiaceae:																	
Coprosma type, C_5P_5-r(1)						(4)	(1)										
C_3 undet.	(11)		(1)				(1)			1.4		1.1	.4	.3	.4		2.2
C_4, C_5 undet.						(2)	(2)				+		+				
P_3 undet.	(4)		(1)			(9)	(8)		(1)		4.4	.4		.2	.4		.2
$P\infty$-r(1)										1.8							
C_3P_3-sm(9)															.4		
C_3P_3-r(10)											2.6		+		.7		
C_3P_3 undet.	(2)					(7)	(2)			6.5	5.2	1.8			6.7	2.5	1.5
Total number of pollen and spores tallied	(24)	(2)	(5)	(1)	(1)	(59)	(43)	(17)	(3)	(109)	(225)	(542)	(462)	(573)	(282)	(240)	(406)

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[1] Palynological zones 2 and 4 defined as barren intervals are omitted here.

In drill hole E–1, the fifth zone is at 850–880 feet, and abundant pollen occurs at two intervals (850–860 and 870–880 ft). (Pollen is present between depths of 880 and 890 ft, but only three grains were found.) Pollen grains in the two rich intervals are about 500 and 21,000 per gram, respectively, and algal colonies are as numerous as 85,000 per gram of sediment. In the lower level sampled, *Rhizophora* pollen is associated with small amounts of *Avicennia*, *Lumnitzera*, *Terminalia* and Rubiaceae pollen; undetermined pollen constitutes 20 percent of the sample. In the upper level, *Rhizophora* is associated with *Lumnitzera*, *Terminalia*, *Sonneratia*, and *Avicennia*.

In drill hole F–1, the fifth zone is at 840–860 feet, and samples were taken from two levels. Pollen abundance at the two levels is about 3,000 and 13,000 grains per gram of sediment, and algae are absent. Dominant *Rhizophora* is accompanied by 5 percent *Ceriops*. *Randia*, *Morinda*, *Avicennia*, *Tournefortia*, *Cordia*, *Bruguiera*, cf. *Gynotroches*, *Sonneratia*, and cf. *Sophora* are also present. The lithology of the zone is unaltered soft aragonitic mud, which includes Miocene sediments of Cole's (1957) Tertiary *f* and *g* (late Miocene, Ladd, 1958).

The sixth zone, at 820–840 feet in drill hole F–1, is dominated at the two sampling levels by *Elaeocarpus* type pollen, accompanied by fern spores (about 7 percent of pollen count). In the lower level sampled, cf. *Elaeocarpus* is especially frequent (about 83 percent of pollen count). Here is the only zone in which *Sonneratia* pollen represents more than 1 percent of the count. In the upper level, *Ceriops*, cf. *Gynotroches*, and *Terminalia* are present in small percentages. Cf. *Salacia*, cf. *Eugenia*, *Gardenia*, and *Ixora* occur only in this zone. Cf. *Guettarda*, *Morinda*, *Avicennia*, *Tournefortia*, and *Lumnitzera* are also present. The lithology is soft aragonitic mud containing small flakes of carbonaceous material. These sediments belong to the lower part of Cole's (1957) Tertiary *g* or youngest Miocene zone.

In the seventh zone, a polleniferous zone, *Rhizophora* dominates again; the zone is therefore termed the "upper *Rhizophora* zone." Samples were taken at two levels in drill hole F–1 at 810–820 feet and 670–680 feet. A small amount of *Ceriops* pollen is present; *Thespesia*, *Callitriche* type, *Bruguiera*, *Gynotroches* type, *Cordia*, *Terminalia*, *Morinda*, *Randia*, and *Pandanus* are all present. The sediments are soft aragonitic mud and represent the upper part of the Tertiary *g* of Code (1957) or the youngest Miocene.

In zone eight (drill hole F–1, at 170–190 ft. and 600–625 ft.) two samples of cores were barren. The lithology of the sediments is calcitic reef limestone, which is post-Miocene in age.

A summary of the data concerning the eight zones and the number of fossils per gram of sediment, follows:

Age (Cole, 1957)	*Zone*	*Depth*	*Maximum density of palynomorphs per gram of sediment*		*Zone description*
			Pollen	*Colonial algae*	
Post-Miocene	8	170–625			Barren.
Late Miocene, Tertiary *g*	7	670–820	40,000		Upper *Rhizophora* zone.
Late Miocene, Tertiary *g*	6	820–840	100,000		*Sonneratia* zone.
Late Miocene, Tertiary *f*, *g*	5	840–880	10,000	10,000	Lower *Rhizophora* zone.
Early Miocene, Tertiary *e*	4	1,232–2,028			Barren.
Early Miocene, Tertiary *e*	3	2,440–2,510	1,000	10,000	Chroococcalean algal zone.
Eocene to Miocene, Tertiary *e*, *b*.	2	2,662–4,525			Barren.
Eocene, Tertiary *b*	1	4,528–4,553	2	25	Eocene pollen zone.

ECOLOGICAL RELATIONS

The present habitats of the species and genera with which the fossil forms have affinity are given under "Systematic Descriptions" (p. 1165) and are summarized in table 6. Also listed in the table are the habits of these plants: seven are mangrove swamp; four are strand and coastal forest or thicket; three are coastal forest or thicket; two are coastal forest to upland forest; two are upland forest only. Evidence from identification of pollen indicates that certainly two if not three of the habitats existed on Eniwetok during Miocene time. A discussion of the inferred plant associations follows.

MANGROVE SWAMP FORMS

None of the seven mangrove swamp forms to which the Miocene pollen are related now grow on Eniwetok Atoll. Estimation of the probable community structure requires comparisons with mangrove swamps elsewhere in Micronesia.

Though most of the mangrove forms identified here can be found in association in mangrove swamps in the Palau Islands and in Malaya, a few of the forms are known in the southern Marshalls in a unique mangrove habitat, described by Fosberg (1947, 1949) as mangrove depressions. In the middle of atoll islets in the southern Marshalls, he observed depressions in which *Bruguiera*, *Sonneratia*, *Lumnitzera*, and even *Rhizophora mucronata* grow. On the atoll ridges, salinity of the ground water is much lower than that of soils closer to the shoreline (Fosberg, 1956). The water in mangrove depressions, especially where *Bruguiera* grows, is of surprisingly low salinity; Hatheway (1953) found chlorine concentrations of only 15 ppm (parts per million), or only about 0.1 percent of that in local sea water, in a *Bruguiera* swamp on Arno Atoll, and in water from a

TABLE 6.—*Habits and habitats of living taxa with which Miocene fossils of Eniwetok show affinity*

Taxa	Habit	Habitat	Number of species of the genus now growing in Micronesia [1]
Acalypha sp	Shrub	Coastal forest to upland forest, but not strand	2
Avicennia marina	Tree	Mangrove swamp	1
Bruguiera gymnorhiza	do	Mangrove swamp and mangrove depression	1
Ceriops tagal	do	Mangrove swamp	1
Cordia subcordata	do	Coastal forest and strand	2
Gardenia sp	Shrub	Upland forest, not strand	0
Ixora casei	do	Coastal forest or thicket	3
Lumnitzera littorea	Tree	Mangrove swamp and mangrove depression	1
Morinda citrifolia	Shrub	Strand and coastal forest or thicket	5
Pandanus sp	Tree	Coastal forest or thicket	5
Pisonia grandis	do	do	2
Randia cochinchinensis	do	Coastal forest to low-hill forest, but not strand	2
Rhizophora apiculata	do	Mangrove swamp	2
R. mucronata	do	do	2
Sonneratia alba	do	Mangrove swamp and mangrove depression	1
Terminalia catappa	do	Strand and coastal forest or thicket	4
Thespesia lampas	do	Upland forest, not strand	1
Tournefortia argentea	do	Strand and coastal forest or thicket	1

[1] Kanehira (1933); F. R. Fosberg (written commun., 1964).

Lumnitzera swamp he found 640 ppm chloride, or about 3 percent of that in local sea water. Species of *Bruguiera* also grow in tidal-inlet mangrove swamp in Malaya (Richards, 1952). Thus, it is clear that *Bruguiera* can tolerate a wide range of salinity.

Fosberg (1949) described mangrove depressions as typically having *Bruguiera* or *Lumnitzera* growing on the lagoon side of swales and *Rhizophora* (presumably *R. mucronata*) or *Sonneratia* growing on the seaward margin of depressions. He stated, however, that *Bruguiera* and *Lumnitzera* usually occur in separate depressions and that each may be associated with *Sonneratia.*

As mangrove-depression ground water appears to be nearly fresh, this may have been an environment in which *Callitriche* could have grown at Eniwetok. *Callitriche* type pollen is found in the upper *Rhizophora* and the Chroococcalean zones.

Hatheway (1953) distinguished between the firm-bottomed depressions with no outlet and the softer mud-bottomed mangrove swamps along lagoon margins. He indicated that *Rhizophora* and *Sonneratia* can grow in both environments, whereas *Bruguiera* is rarely found in open lagoonal environment.

The presence of fossil *Bruguiera* pollen suggests that an atoll mangrove-depression environment probably existed on Eniwetok in Miocene time. *Rhizophora* probably grew along the margins of Eniwetok lagoons near tidal passes, and *Sonneratia* may have been associated with both *Bruguiera* and *Sonneratia.*

The mangrove forms *Ceriops* and *Avicennia* are not known to grow in the mangrove communities in the Marshall Islands today; they do, however, belong to the so-called Indo-Malayan mangrove vegetation. On Ponape, which is the east limit of their present geographic range, *Avicennia* and *Ceriops* are associated with *Lumnitzera littorea*, *Nypa*, *Rhizophora apiculata*, *R. mucronata*, *Scyphiphora hydrophyllacea*, *Sonneratia alba*, and *Xylocarpus granatum* (Kanehira, 1933, p. 36). This vegetation grows in Kilonia Harbor at Ponape but occupies a relatively small area there.

With the exception of *Xylocarpus*, forms comparable to the taxa just mentioned are identified in the Miocene flora. Kanehira (1933, p. 213) observed that mangrove associations require intertidal mud in somewhat protected coastal indentations. Because the mangrove taxa are dominant in the Miocene flora and because their remains are so numerous at both drill-hole sites, we can suppose that conditions appropriate for mangrove-swamp development existed on two sides of Eniwetok lagoon during Miocene time—in the vicinities of Parry Island and Elugelab Island.

PISONIA FOREST

Pure stands of *Pisonia* are among the most widely distributed types of atoll forests and in historical time may have covered the greatest area of any pure tree stands in the Marshalls (Wiens, 1962, p. 395). But pure *Pisonia* stands have been practically eliminated by man from larger atolls and are now largely replaced by coconut plantations (Fosberg, 1956). Hatheway (1953, p. 61) indicated that *Pisonia grandis* tends to grow in groves as large as 10 acres. Anderson (1951) described *Pisonia* on Arno Atoll as associated with *Tournefortia* and *Cordia* just above high-tide level on seaward beaches, and other authors have indicated that *Pisonia* most commonly grows in this environment today in the Marshalls.

Pisonia pollen makes two appearances in the drill holes. In the Chroococcalean algal zone, at 2,460 and 2,470 feet, *Pisonia* pollen is the dominant type, although only 12 grains of it were found; it appears at only one other level in the drill holes, at 810–820 feet in the upper *Rhizophora* zone. Associated with *Pisonia* in the Chroococcalean zone are rare pollen of *Rhizophora*, *Callitriche* type, and some unidentified dicot forms. It seems likely that *Pisonia* grew near the deposition site (Parry Island) at that time.

The occurrence of *Callitriche* type pollen in the same level as *Pisonia* pollen raises a question concerning a possible fresh-water environment at Eniwetok. Of interest here is Fosberg's (1955b) observation of fresh-water ostracodes growing in an old hollow trunk of *Pisonia* on Bikar; the water in the *Pisonia* trunk was fresh. However, it seems unlikely that on a mid-Pacific atoll such an isolated environment could persist over a long period of time. Because the ostracode anomaly indicates that fresh-water animal forms can grow on atolls today, it seems possible that fresh-water plant forms could too. A few fresh-water plants occur in the present flora of coral atolls, and include *Lemna*, sedges, grasses, and many fresh-water algae (F. R. Fosberg, written commun., 1964).

The occurrence of a fresh-water planorbid snail (*Gyraulus*) and a brackish-water neritid (*Neritilia*) in sediments of Bikini drill hole 2B at depths below 1,700 feet provides strong evidence that fresh-water environments did exist on Bikini during Miocene time (Ladd, 1965). Occurrence of fossil endodont land snails like those that now live in forests of high islands also strongly indicates that Bikini and probably Eniwetok were raised limestone islands at times during the early and late Miocene and Pleistocene(?) (Ladd, 1958). Apparently there was fresh and brackish water on the elevated Marshall Islands.

CHROOCOCCALEAN ALGAL ASSEMBLAGES

Fosberg (1956) described an association of microscopic blue-green algae as growing on beach rock, elevated reef rock, boulders, cobbles, and pebbles that are scattered on reef flats just above high-tide level. He stated that a crust of bluish-gray to blackish algae literally covers every type of exposed sedimentary material in this particular zone above high tide on coral atolls, and that the same crust grows equally well on noncoralline limestone in the tropical region.

Fosberg (1956, p. 210) observed that algal crusts of the same color form in areas of bare coral sand. These algae have a gelatinous consistency when wet, and sand grains are embedded in them. He pointed out that these algae "contribute in a very important way to stabilizing the sand and to initiating soil formation. It is probable that at least some of the species of algae are capable of nitrogen fixation. In any event, the development of such crusts often represents the initial stage in establishment of vegetation on coral sand."

At Bikini, Taylor (1950, p. 103) identified three filamentous Myxophyceae algae and the gelatinous colonial *Gloeocapsa*, a Chroococcalean alga, as the chief constituents of the sand crust.

At Eniwetok, Dawson (1957, p. 125–126) collected two kinds of Chroococcalean algae and described three others collected by other workers. He found the colonial form *Anacystis dimidiata* (Kutzing) Drouet and Daily (equals *Gloeocapsa turgida* (Kutz.) Hollerbach) growing as "scum on lagoon rocks" on Igurin Island. He collected another colonial form, *Coccochloris stagnina* Sprengel, on the seaward flats of Bokanjoio Island and in the lagoon and listed and figured several other blue-green algae from Eniwetok.

Dawson's figured specimens of *Gomphosphaeria aponina* Kutzing from Eniwetok closely resemble my specimens identified as *Gomphosphaeria* type (pl. 304, fig. 3). His illustrations of *Anacystis* (=*Gloeocapsa turgida*) are very similar to my *Gloeocapsa* type (pl. 304, fig. 5).

Modern sediments from the lagoon margin of Onotoa Atoll, Gilbert Islands, were found to contain as many as 4,200 Chroococcalean algal colonies per gram, which were mainly of the *Clorogloea* and *Placoma* types (pl. 304, figs. 9–13).

The crustlike material from Eniwetok drill hole E–1 (at 2,490–2,510 ft), sectioned by microtome and figured on plate 304, figure 19, is a cross section of a probable algal crust similar to the one described by Fosberg (1956). Although the morphology of the algal cells could not be discerned in the sectioned material, it follows Fosberg's description of brittle flat flakes that curl when dry. The crust material sectioned here was mainly organic. Upon laboratory maceration, the crusts were found to be composed almost entirely of Chroococcalean colonies of the *Gloeocapsa* type; no pollen or spores were present.

There is little doubt that the Chroococcalean zone is a deposit related to the algae-encrusted sand or reef-rock flats described by Fosberg (1956). Whether the environment was lagoonal or seaward reef cannot be determined from the present material; however, the large number of blue-green algae in the sediments of the Chroococcalean zone in drill hole E–1 indicates that the sedimentary surface was not far from sea level during that depositional interval. It should be stressed that these algae are light-dependent forms that cannot tolerate water of great depth.

MIXED ATOLL FOREST VERSUS FOREST ON RAISED CORAL LIMESTONE

The primary difference between plant environments on atolls and those on raised coral limestone islands may be related to the comparative frequency of halophytic and mesophytic environments. "Strand vegetation, in general of course, indicates salinity" (Fosberg, 1960, p. 20). In the interior of atoll islands the substantial number of plants that do not normally grow on strand lines is, according to Fosberg (1947), chiefly a reflection of differences in salinity of atoll soils. This differentiation of vegetation even on low atolls displays a trend toward mesophytic forest on the higher parts of the atoll.

The vegetation on elevated limestone is a modified strand type (Fosberg, 1960, p. 21), and boundaries between this and the atoll type of forest are difficult to delimit. Many of the atoll forest trees also occur on elevated limestone, and these include, from the Eniwetok flora, *Morinda citrifolia*, *Pisonia grandis*, *Randia*, *Ixora*, and *Pandanus*. Certain forest forms, such as *Thespesia lampas* and *Gardenia*, found on elevated limestone are never found on strand lines or on atolls.

During Miocene time, atoll-islet environments in which the atoll type of mesophytic forest could grow were certainly present at Eniwetok; *Pisonia*, *Pandanus*, *Tournefortia*, and perhaps *Eugenia* probably comprised that vegetation. Also, a raised-limestone environment where *Thespesia lampas* and *Gardenia* could grow was probably present.

LONG-DISTANCE TRANSPORT HYPOTHESIS

Because only a few pollen specimens represent the nonatoll forms (*Gardenia* and *Thespesia* cf. *T. lampas*), one could assume that during Miocene time the pollen reached the site by wind transport from an upwind source. Long-distance transport by wind has been shown to be the source for a small percentage of the post glacial pollen flora of Tristan da Cunha (Hafsten, 1960). The inferred and only possible source was about 1,000 miles away; the transported pollen, however, belongs to groups that are high pollen producers and are wind pollinated.

The source for the Eniwetok material probably would have been from the west, for centers of distribution for the two taxa are west of the Marshalls today. A long-distance-transport hypothesis requires consideration of two influential factors:

1. Wind direction. The trade winds now extant in the northern Marshalls emanate from the east and the northeast. The exceptions are either weak winds or winds from the south bringing storms. A shift in basic wind patterns to account for a western source for the pollen types involved seems unlikely.
2. Pollen characteristics in relation to long-distance transport. Both *Thespesia* and *Gardenia* have relatively large, heavy (thick walled) pollen; their respective families, which probably are insect pollinated, are in general poorly represented in the fossil pollen record even when member taxa are growing locally. Hence pollen of these genera are not likely candidates for long-distance transport by wind.

The assumption that favorable environments for these plants existed on Eniwetok during the Miocene seems reasonable. The ample evidence from fossil endodont land snails (Ladd, 1958) and the presence of extensive leached zones in the subsurface (Schlanger, 1963) suggests that Eniwetok was in fact a raised limestone island capable of supporting forests during long periods of Miocene and later time.

SUMMARY OF ENVIRONMENTAL CONDITIONS

A chronological description of the inferred environments on Eniwetok, as indicated by fossil pollen and spores from the drill holes, may be summarized as follows:

Zone 1 (4,553–4,528 ft).—Low densities of Chroococcalean algae and pollen of land plants indicate that these Eocene (Tertiary *b*) sediments now only about 100 feet above basement rock and 4,500 below sea level were near sea level when they were deposited.

Zone 2 (4,525–2,662 ft).—No plant fossil evidence. Pollen, if present after deposition, may have been oxidized during the period(s) of emergence in Eocene or Oligocene time.

Zone 3 (2,510–2,440 ft).—The great abundance of Chroococcalean algae and small amounts of pollen present in this depth interval in drill hole E-1 indicate that these early Miocene (Tertiary *e*) deposits accumulated at or very near sea level. The palynological evidence corroborates the conclusion based on calcareous algae and Foraminifera that the sediments of this zone were deposited in shallow water and suggests that the environment was either lagoonal or seaward reef flat.

The association of *Pisonia* pollen with pollen of *Rhizophora* in the upper part of this zone indicates that a beach-ridge environment and tidal passes where *Rhizophora* could grow were not far from the area of drill hole E-1. The presence of probable *Callitriche* pollen near the top of this zone suggests that fresh-water environments were available on the island at this time.

Zone 4 (2,028–1,232 ft).—No pollen found at Eniwetok. Petrographic evidence indicates a major period of uplift and leaching at the end of this early Miocene interval. In this zone at Bikini, fresh- or brackish-water mollusks were found (Ladd, 1965) and occurrence of endodont land snails suggests a high-island forest environment (Ladd, 1958). Also at Bikini, in drill hole 2A, *Pandanus* and ?Palmae pollens suggest that strand plants grew on the island at this time.

Zone 5 (*890–850 ft*).—The great abundance of both Chroococcalean algae and pollen in the lower *Rhizophora* zone (in drill hole F–1 and above a depth of 880 ft in E–1) indicates that the deposition sites were very close to sea level during late Miocene. The abundance of *Rhizophora* pollen suggests that the environment was lagoonal rather than seaward reef—a conclusion supported by other fossil evidence. The presence of *Bruguiera* pollen suggests that mangrove depressions may have existed on the atoll at this time. Strand plant elements of the beach-ridge environment, *Morinda*, *Pandanus*, *Terminalia*, and *Cordia*, are present. Coastal and upland forest forms that do not grow on strand lines are present also and include *Acalypha*, *Thespesia* cf. *T. lampas*, and *Randia*.

Zone 6 (*840–820 ft*).—*Sonneratia* zone. Because the dominant pollen form, cf. *Elaeocarpus*, is not identified with certainty this zone is difficult to interpret. Maximum pollen densities are greatly in excess of those now found in eastern Micronesian atoll lagoons; hence, the vegetation probably was far more luxuriant and occupied a larger land area then than now. The presence of *Sonneratia*, *Lumnitzera*, *Ceriops*, and *Avicennia* indicates that the mangrove communities were rich in species. Coastal forest forms (*Ixora*) and upland forest forms (*Gardenia*) were also present. High-island land snails in drill hole K–1B indicate that Eniwetok stood well above the sea during this part of the late Miocene (Ladd, 1958).

Zone 7 (*820–670 ft*).—Upper *Rhizophora* zone. Mangrove communities continued to occupy Eniwetok at the end of the late Miocene and were locally dominated by *Rhizophora*. Mangrove depressions probably existed on the beach ridges (supposition based on the presence of *Bruguiera*), and *Callitriche*-type pollen suggests that fresh-water environments may have occurred locally on the island at that time. Atoll forest forms are scarce in the highest fertile sample, at 670 feet, and mangrove forms comprise almost the entire count. Coastal and upland forest forms (*Thespesia* cf. *T. lampas*, *Ixora*, and *Randia*) are present.

Zone 8 (*625–170 ft*).—The two samples of post-Miocene sediments, as far as they have been examined, are barren of plant fossils. High-island land snails of probable Pleistocene age from this zone were found at Bikini (447–453 ft; Ladd, 1958).

In summary, the abundance and kinds of pollens, spores, and colonial algae strongly support the theory that part of the Eocene and much of the Miocene sediments beneath Eniwetok were deposited near sea level. Evidence from vascular plants also supports the conclusion based on the presence of land snails (Ladd, 1958) that a coastal and upland forest grew on Eniwetok during parts of the Miocene; the soils of that forest could not have been saline.

RELATION OF ENIWETOK MIOCENE FLORA TO OTHER FOSSIL FLORAS, AND PALEOGEOGRAPHIC IMPLICATIONS

The Eniwetok Miocene flora has been compared with several pollen collections from Miocene(?) localities in Micronesia and Polynesia: Guam, Fiji, the Palaus, and Bikini. Correlation of Miocene sediments from these islands is discussed by Cloud (1953). Pollen from an undated Tertiary lignite of Rapa (Austral Islands) reported by Cranwell (1962, 1964) was compared with the pollen considered in this study as well.

Pollen from the Tertiary lignite of Rapa has little in common with the Miocene pollen flora of Eniwetok. Cranwell reported identifications of *Coprosma*, Myrtaceae, Liliaceae, Taccaceae, Piperaceae?, and Sapindaceae. Of these, *Coprosma*, a high-island member of the Rubiaceae, is tentatively identified in the Miocene of Eniwetok (pl. 311, fig. 37); unidentified members of the Myrtaceae are found in both floras. The other pollen identified from the Rapa material were not found in Eniwetok sediments.

The Miocene Airai Clay (Tayama, 1939) of the Palau Islands (USGS paleobotany locs. D1182, D1186, D1317, D1647, D1648, D1649, D1650, and D1626) contains a rich flora of almost 100 pollen and spore forms that is very different from the flora at Eniwetok. Present in the Airai Clay but absent from Eniwetok are a very distinctive palm, *Lycopodium* cf. *L. phlegmaria*, and *Pteris*, *Schizaea*?, *Spathyphyllum*, Rubiaceae undet., Nyctaginaceae cf. *Abronia*, Sterculiaceae cf. *Kleinhovia*, *Sida* cf. *S. fallax*, Sapotaceae cf. *Northiopsis*. Myrtaceae, Anacardiaceae cf. *Campnosperma*, and cf. *Semecarpus*, among other forms. In common with the Eniwetok flora are *Avicennia*, *Terminalia*, *Timonius* or *Guettarda*, *Pandanus*, *Rhizophora*, *Sonneratia*, and *Combretum*?. The present flora of Palau is, of course, very much more diverse than that of Eniwetok; also, because Palau is close to the continent, it shows a strong relation to the present flora of Malaysia. The Palau Miocene flora includes strand-line plants (*Terminalia*, *Pandanus*), mangrove forms (*Rhizophora*, *Sonneratia*), and probably high-island forms (cf. *Campnosperma* and others). The relation of this fossil flora to the Malayan flora of today cannot be defined from the present cursory study, but the Miocene flora from Palau is both larger and more complex than the one described from Eniwetok.

A Miocene sample of the Suva Series, Viti Levu, Fiji (USGS paleobotany loc. D1417), contains pollen and spores of cf. *Casuarina*, Schizaeaceae, Polypodiaceae cf. *Botrychium*, *Morinda* cf. *M. citrifolia*, and several unidentified fern spores. Another Miocene sample from the Suva Series (USGS paleobotany loc. D3277), Nasoranga Creek, Viti Levu, Fiji, contains the following forms:

	Number of grains in tally
Sonneratia cf. *S. alba*	37
Rhizophora	21
cf. *Bruguiera*	1
?Palmae	2
Terminalia or *Combretum*	2
Anonaceae, *Miliusa* type	16
cf. *Timonius*	1
Pteris	2
Cyathea type	5
Polypodiaceae types	16
Humata or *Davallia* type	4
Vaginularia type	5
?Amaranthaceae	1
Undetermined dicotyledons	23
Undetermined fern spores	1
Total	137

These results are mentioned by Ladd (1965), who described a fresh-water snail from the same Miocene rocks.

Of the plants identified, *Sonneratia* represents the most remarkable extension of range in the Miocene; the nearest modern occurrence of this Indo-Pacific genus is at Ponape in the southern Marshall Islands, 1,300 miles northwest of Fiji, and in New Guinea, about 2,100 miles west of Fiji. The fossil *Miliusa* type of Anonaceae is of interest because the family is not known to occur on Fiji today, although it is represented by several genera in Burma and Java. *Rhizophora* and *Timonius*, and probably *Pteris*, now grow on Fiji.

Samples of the Miocene Talisay Member of the Alifan Limestone on Guam (USGS paleobotany locs. D1653, D1652) yield the following assemblage: *Pandanus*, *Anacolosa*, Thymeliaceae cf. *Wikestroemia*, *Rhizophora* (pl. 308, figs. 63–65), *?Pisonia*, *Combretum* or *Terminalia*, *Ixora* cf. *I. casei*, and *Phegopteris* or *Lastrea*. The genera *Anacolosa* of the Olacaceae and *Wikestroemia* are Indo-Malayan; I could find no record of their occurrence in Micronesia today. *Ixora*, which also was found in the Miocene of Eniwetok is represented by three species in Micronesia, *I. triantha* being very common on Guam. The other pollen forms in the Guam flora represent mangrove and strand plants that occur in the Miocene of Eniwetok. *Phegopteris* and *Lastrea* are polypodiaceous ferns closely related to *Thelypteris* (Copeland, 1947, p. 136). Their spores are distinct from those of many other species of Polypodiaceae (95 species were checked). These genera now grow on Ponape and probably elsewhere in Micronesia; both are pantropical.

Only about five pollen grains were found in two Bikini drill-hole samples (Miocene) (USGS palebotany loc. D1416), and only *Pandanus* pollen could be identified. Palm pollen of the *Livistona* type was seen.

In summary, high-island plants were identified from Miocene or probable Miocene sediments from Guam, Fiji, Palau, and Eniwetok. Mangroves and associated forms were also found at Guam, Fiji, the Palaus, and Eniwetok. Strand plants were identified at these localities as well as at Bikini. These data indicate that certain of the strand plants now widespread in Micronesia (*Pandanus*, *Tournefortia*, *Morinda*, *Cordia*, *Pisonia*) were equally widespread there in the Miocene. Mangroves and their associates (*Sonneratia*, *Rhizophora*, *Lumnitzera*, and *Avicennia*) ranged much farther southeast and northeast than they do now. Indo-Malayan upland forms such as *Anacolosa* and *Thespesia* cf. *T. lampas*, and Indo-Malayan and Fijian forms, such as *Gardenia*, had greatly extended ranges during the Miocene, occurring at Guam or Eniwetok. These plants probably occupied high islands in Micronesia during the Miocene. Coastal forest forms (*Acalypha*, *Randia*, and *Ixora*) grew somewhat east and north of their present Indo-Pacific ranges.

The plant evidence discussed here indicates that the present high islands of the Palaus, Fiji, and Guam were also high islands in Miocene time. Because their floras were enriched by Indo-Malayan forms, it is likely that more intermediate islands than now exist provided stepping stones that allowed the extension of Indo-Malayan plant ranges into north-central and southeastern Micronesia.

Climatic change, particularly decrease in annual rainfall, may have been a factor in the disappearance of several Miocene taxa from Eniwetok. As has been pointed out (p. 1142), the existing north-south gradient in rainfall in the Marshall Islands group is reflected by a north-south gradient in diversity of the modern flora—a trend which seems somewhat independent of islet size. During an unusually dry season in 1951 in the northern Marshalls, *Pisonia*, *Cordia*, and *Terminalia* were partially defoliated in some places (Fosberg, 1953). Short-term climatic fluctuations apparently affect the luxuriance of some species on atolls, and longer term shifts might eliminate more sensitive taxa.

The amount of precipitation is not solely a result of climate, but it is partly dependent upon land height above the sea. Hosakawa (1950) observed that in the same trade-wind belt in the equatorial zone, Kusaie, which has about the same land area as Truk but is 1.6 times higher, receives 1.8 times more rain in the average year. If, for purposes of discussion, the Miocene climate of Eniwetok had been the same as it is now, Eniwetok would have received slightly more rainfall during the end of Tertiary *g* and *e* time (of Cole, 1957) than now, because the presence of fossil land snails and certain plants have established that the atoll had a greater elevation then. Increases in precipitation that probably resulted from Eniwetok's higher elevation during periods of emergence were probably temporary because submergence followed emergence.

In evaluating the possible effects of overall climatic change on the late Cenozoic vegetation of Eniwetok, one should bear in mind that at least four of the Miocene plant taxa now absent from the atoll are raised limestone island forms (table 6) that cannot tolerate saline soils. The relative availability of mesophytic environments on Eniwetok thus has been an important limiting factor in the survival of the raised-island flora. In view of the obviously important tectonic history of the northern Marshalls, it is reasonable to assume that relative rates of submergence and emergence controlled the overall availability of land environments and, hence, the impoverishment of the flora.

Possibly at times during the post-Miocene, Eniwetok was completely submerged, and the present flora may be the result of recolonization of the atoll by strand and atoll forms. The present Eniwetok flora is primarily of southwestern Pacific distribution, and no outposts of the Micronesian flora now occur east of the Marshall Islands; hence, it does not seem reasonable to assume that the last recolonization came from eastern sources (for example, by means of the easterly trade winds and ocean currents). However, the present storm patterns from the south may have prevailed in Pliocene and Pleistocene time and could have served to transport seeds or fruits to Eniwetok from Kusaie or Ponape, about 400 miles south and 400 miles southwest of the atoll, respectively.

Modern mangrove communities at lagoon margins seem to require quiet tidal embayments. The height of the atoll islets perhaps in part controls the vulnerability of atoll lagoons to typhoon damage, and if so, the relative relief on atolls may affect the diversity of mangrove associations. The local extinction of mangroves from Eniwetok may have been aided by typhoon damage during a time when subsidence provided low relief.

In summary, the post-Miocene elimination of the high-island and atoll forest forms from the Eniwetok flora may have been primarily the result of subsidence; the effects of secular climatic change on floristic impoverishment may have been incidental during the late Cenozoic.

SYSTEMATIC DESCRIPTIONS

ANGIOSPERMAE
MONOCOTYLEDONAE
PANDANACEAE

PANDANUS Rumph. ex. L.

Plate 305, figures 16, 18, 19

Pollen monoporate; 14–17 μ at equator, and 21–23 μ in polar dimension. Wall of one layer, 1 μ thick at proximal pole and thinning to distal pole where pore is situated. Pore circular, 4–5 μ in diameter, and simple, with no marginal thickenings. Spinules on outer surface 0.75–1 μ in length and distributed 2–3 μ apart.

Comparative material.—Fossil *Pandanus* pollen was compared with modern pollen of *P. tectorius* Sol. (pl. 305, fig. 17) and *P. kafu* Martelli. There is little morphologic difference between these modern *Pandanus* collections. Other authors (Selling, 1947, p. 340; Cranwell, 1953, p. 31) have found that pollen morphology is quite uniform within the genus.

Fossil occurrence.—In Eniwetok drill hole E–1 at 850–880 feet and in drill hole F–1 at 810–840 feet, rare (about 1 percent total pollen and spores). Bikini (US GS paleobotany loc. D1416–2), in drill hole 2A, core 2A–36–2, at depths 929–935.5 feet, one specimen. Guam, Miocene Talisay Member of the Alifan Limestone (USGS paleobotany loc. D1653), one specimen. Palau Miocene Airai Clay (USGS paleobotany loc. D1186), several specimens.

Present distribution.—The genus *Pandanus* has wide distribution in the South Pacific, and many endemic species occur in Micronesia. The genus ranges from Hawaii and the Henderson Islands to Africa. Eight species are thought to be native to Eniwetok, according to St. John (1960), but F. R. Fosberg (written commun., 1964) considered all specimens to belong to *P. tectorius.*

Ecology.—Fosberg (1955a, p. 3) stated that in the northern Marshalls *Pandanus* species grow in mixed forest stands. On Arno Atoll in the Marshalls *Pandanus* grows on the wetter shores of the lagoon along with *Terminalia samoensis* Rech.

?PALMAE
LIVISTONA R. Brown
Livistona type

Plate 305, figure 20

Pollen monosulcate; 27–29 μ at equator, and 13–15 μ in polar dimension. Wall 1 μ thick in proximal hemisphere, thinning toward sulcus. Sulcus passing through distal pole and extending to equator. Margins of sulcus inrolled toward cell lumen. Wall surface appears smooth except under oil, and then very finely granulate or shagreenate. Not apparent whether wall is two layered, even under oil.

Comparative material.—This form was compared with a wide range of monocotyledonous groups and with *Cycas* in the Gymnospermae. Though *Cycas* grows in Micronesia today, the boatlike shape of *Cycas* pollen is unlike the shape of the fossil material. The sulcus of *Cycas* pollen does not ordinarily reach the poles, whereas sulci of the fossils pass through the polar area. Many members of the Palmae have monosulcate pollen, and in some the pollen wall is nearly smooth, as in *Ptychosperma* and *Erythaea*. Pollen of the genus *Livistona* (pl. 305, fig. 19) is of the same average size and wall thickness as the fossil material and has a very similar shape in the contracted grains but a clear granular sculpture. The fossil material compares favorably with pollen of palm genera such as *Livistona;* however, this is not a positive identification even on the family level.

Fossil occurrence.—Code species C_1–sm (1) in Eniwetok drill hole E–1 at various depths between 870 and 2,510 feet and in drill hole F–1 at 670–830 feet, rare (less than 2 percent of total pollen and spores). Bikini (USGS paleobotany loc. D1416–2), core 2A–37–15, at 935.5–946, one specimen.

Present distribution.—Palms are not now indigenous to the northern Marshalls. *Livistona* now occurs on the Bonin and Ryukyu Islands and from Formosa to Australia.

DICOTYLEDONAE
NYCTAGINACEAE
PISONIA L.
cf. P. grandis R. Brown

Plate 306, figures 1, 5

Pollen tricolplate, subprolate; 34–44 μ in polar dimension and 26–35 μ in equatorial diameter. Colpae extending four-fifths of way from equator to poles; colpal margos well defined, and about 1 μ in width. Wall characteristically folded inward to lumen under colpi; hence, what appear to be margos on plate 306, figure 1, are partly folds where wall bends inward into lumen. Sculpture scabrate. Wall 1.5 μ thick; ektexine thicker than endexine.

Comparative material.—Comparative material includes *Pisonia grandis* (pl. 306, figs. 2–4), *Ceodes umbellifera* (Forst.) Seem., and six other Nyctaginaceous genera. According to Erdtman (1952, p. 285), the genus *Ceodes*, which is closely related to *Pisonia*, has "minute spinules" on the scabrate pollen wall. Selling (1947, p. 99) stated that these features are probably minute projections that might be interpreted as vestiges of true spines, which are a common feature in this family. My *Ceodes* material displays small projections among the smaller scabrae that seem to confirm Selling's interpretation. *Pisonia grandis* either lacks these "spinule" projections, or they are small and hard to see. Pollen of both genera have simple colpi that are not folded inward to the lumen in fresh uncontracted material. *Pisonia grandis* pollen is mainly contracted and infolded after acetylation; only about half the *Ceodes* pollen grains contracted after acetylation. *Ceodes* pollen, which has 6–12 rugate colpi, tends to contract along three parallel latitudinal lines, and closely resembles *Pisonia* pollen in the contracted state; however, *Ceodes* pollen is nearly isodiametric in shape, whereas *Pisonia* is subprolate. Selling's (1947, pl. 2, figs. 39, 40) figures of *Rockia* pollen indicate that it is closely related to *Pisonia*, though its wall is tectate according to Erdtman (1952, p. 285).

The fossil specimens are identified as contracted grains of *Pisonia;* they display what seem to be well-developed margos along the colpi but are simple folds marking the place where the wall bends inward to the lumen.

Fossil occurrence.—In two samples only, at 2,460–2,470 feet in drill hole E–1, 12 specimens; and at 810–820 feet in drill hole F–1, one specimen. Miocene Talisay member of the Alifan Limestone, Guam (USGS palebotany loc. D1653), one specimen.

Present distribution.—*Pisonia grandis* is widespread in Micronesia: Moluccas, northwestern Australia, the Pacific islands, and east to the Palmyra Islands and Tuamota Archipelago; it is absent from Bonin Islands. The genus is also Indo-Malayan and American.

Ecology.—*Pisonia grandis* is a tall tree with a large crown. It grows in mixed stands (commonly in pure stands) on atoll ridges and dunes; on Arno Atoll it grows on the seaward slope on the windward islets but does not grow on the leeward islets (Anderson, 1951, p. 3). Fosberg (1955b) described a phosphatic hardpan under humus as a soil characteristic of a *Pisonia* forest floor.

EUPHORBIACEAE

ACALYPHA L.

Plate 306, figures 9, 10

Pollen triporate; single specimen found measures 25 by 26 μ in polar view. Pollen circular to somewhat intersemiangular in polar view; pores appear to be circular in outline and are from 2.5 to 3 μ in diameter. Pore rim protrudes very slightly relative to overall shape of cell. Endexine thickens as a costa under pore lip; as seen in cross section, thickening is wedge shaped, whereas ektexine is same thickness at all points on equator. Two wall layers are fused at pore lip to form simple pore margin. Wall is 0.8 μ thick at equator in interpore area and 1.5 μ thick at pore lip. Sculpture under high dry lens appears scabrate; however, analysis under different focal levels with an oil lens reveals that connected muri and poorly defined probably shallow lumina form vague microreticulate pattern. Lumina are about 0.8 μ in width and muri between them are about the same thickness.

Comparative material.—Six collections, including five species of *Acalypha*, were examined for this identification: *A. alopecuroides* Jacq., *A. californica* Benth., *A. grandis* L., *A. leptopoda* Muell., *A. lindheimeri* Muell., and a specimen identified only as *Acalypha* sp. (pl. 306, figs. 11, 17–19) collected from Ponape by Glassman. These pollen collections all show costae under the pores as just described for the fossil and have from three to five pores, but in most of them the pollen walls are smooth. Only the collection from Ponape has sculpture and cell shape comparable with those of the fossil. The average size of the *Acalypha* sp. pollen from Ponape is 19 μ, with a maximum dimension of 22 μ (in polar view). The fossil is 30 percent larger than specimens from this modern collection; however, the great similarity in morphology and structural details makes *Acalypha* a certain generic determination for the fossil.

Fossil occurrence.—In drill hole F–1 at 840–850 feet, one specimen.

Present distribution.—Three Micronesian species of *Acalypha* were recorded by Kanehira (1933); two are pantropic (*A. hispida* Burm. f.; *A. indica* L.), and F. R. Fosberg (written commun., 1963) thought that these were introduced in Micronesia; and one is Malayan and Micronesian (*A. grandis*). Others, *A. godseffiana* Mast. and *A. hispida* Burm. f., grow on Likiep, and *A. wilkesiana* M. A. grows on Ailuk Atoll, but all are considered to be introduced (Fosberg, 1955a). Merrill (1929) listed another species, *A. caturus* Blume, as a shrublike tree on forested ridges in Borneo.

Ecology.—The genus includes about 400 species, all tropical; most are woody, but some are herbaceous. The habitats of the Micronesian forms include secondary scrub and forest margins on Truk and upland thickets on atolls near Palau.

MALVACEAE

THESPESIA Soland.

cf. T. lampas (Cav.) Dalz. ex. Dalz. and Gibs.

Plate 306, figures 22, 23

Peri-brevicolporate; suboblate; one specimen measures 65 by 53 μ without including projections; a second broken one is at least 65 μ in one dimension. Colpi slitlike, measuring 6–9 by 1–2 μ. Pores internal, oval, about 4 by 6 μ. Five apertures; four of these appear to be in one plane but colpi are not parallel to each other; fifth is in separate plane. Rim of endopore marked with endexinal thickening.

Wall thickness ranges from 2 μ in the areas between the sculpture projections to 5 μ at the base of the projections. Endexine is 1–1.2 μ thick except on the margins of endopore, where it swells to 2.5 μ. Ektexine ranges from 1 μ thick in the areas between sculptural projections to 4 μ thick immediately at the base of the projections. Ektexine is composed of vertical unbranched collumellae about 0.5 μ thick fused into a closed tectum. Small rounded projections appear to protrude above the tectum, so that the sculptural topography is scabrate. The major wall projections are baculae and clavae 6–8 μ long and 2–2.5 μ wide; they are slightly thicker at the base and tip than in the middle. These are curled and bent; none seem to stand erect on the pollen wall. About nine projections occur on each hemisphere.

Comparative material.—The fossil was compared with herbarium collections of eight genera and 16 species of Malvaceae and with figures and descriptions of 10 other Malvaceous genera, including 19 species. Comparisons were made with five species of *Thespesia.* Also considered were *Ipomaea* of the Convolvulaceae, *Eriolaena* and *Dombeya* of the Sterculiaceae, and *Montezuma*, *Hampea*, and *Matisia* of the Bombacaceae; these have pollen similar to the pattern of the Malvaceae. Among these, however, only *Thespesia lampas* and *T. peckelii* have pollen comparable to this fossil.

Thespesia lampas (Cav.) Dalz. ex Dalz & Gibs. pollen (pl. 306, fig. 26), of which two collections were observed, has heteromorphic projections in some specimens; some grains have only straight spines, but some are heteromorphic having spines, clavae, and baculae. The projections are moderately crowded (about 12 per hemisphere), usually have swollen bases, and are in many cases bent or curved. Though the fossil does not possess spines, the clavae and baculae of the fossil closely resemble the comparable projections in *T. lampas* pollen.

Thespesia peekelii (Ulbr.) Borss. (equals *Cephalohibiscus peekelii* Ulbr.) has projections which are clavae and baculae, with somewhat swollen bases, and which are sometimes bent or curved and occasionally branched. The projections are more crowded than those of the fossils but their resemblance to those of the fossils is striking.

The apertures of *Thespesia peekelii* and *T. lampas* are four to six brevicolpori, some of which are arranged in a single plane and some not. In some modern grains the apertures appear to be narrow slits, but in most the endopores are clearly evident. The microstructure of the wall in the fossils is similar to that in both of these modern species, except the fossils lack the spines which are the dominant projection type in *T. lampas.*

Pollen of *Thespesia patellifera* Borss., *T. multibracteata* Borss., and *T. fissicalyx* Borss. have sharp spines or echinae and so do not resemble the fossils. *T. populnea* (L.) Soland., the common pantropical strand species, has sharp or blunt spines that are sometimes branched and are usually crowded (from 12 to 30 per hemisphere), but it has no baculae or clavae. In summary, *Thespesia lampas* and *T. peekelii* are the only species thus far found in the Malvaceae which have baculae, clavae, and the structure comparable with those of the fossils.

Fossil occurrence.—In drill hole F–1 one specimen at 670–680 feet and a broken specimen at 840–850 feet.

Present distribution.—*T. lampas* occurs in the tropics of India, Burma, China, Malaya, Philippines, the Celebes, Java, and Borneo. I cannot find records of it in Micronesia. The genus contains some 18 species, all tropical, and occurs in Africa, the Caribbean area, and Asia. *T. peekelii* occurs in New Guinea, New Britain, and the Solomons. *T. populnea* Soland. ex. Correa, which the fossil does not resemble, is the only Micronesian species of this genus and is widespread in Micronesia, as well as in Southeast Asia. The genus does not now occur on Eniwetok but does grow on Kwajalein Atoll where it is planted (Fosberg, 1955a).

Ecology.—*T. lampas* is a lowland forest tree. *T. peekelii* is an upland forest tall tree (occurs at 3,250 ft elevation in New Guinea). *T. populnea* is a medium-sized tree that occasionally occurs in the coastal forests of Micronesia. Fosberg (1960, p. 45) observed *T. populnea* growing with *Bruguiera* in a mangrove swamp and with *Pisonia* in the strand zone on Saipan.

SONNERATIACEAE

SONNERATIA L. f.

cf. S. alba J. Smith

Plate 307, figures 1–6, 12–21

Pollen triporate; prolate in equatorial view, ranging from 38 by 24 to 53 by 33 μ in size. No polar views were available. Canted equatorial views suggest circular outline in polar view, with pores protruding. Pore margins granular; pores round from 3 to 4 μ in diameter. Meridional endexinous thickenings in the interpore area have 2–3 meridional thin areas as bands between pores, and these areas resemble colpi, though all do not coincide with the pores. One of these inward folds is shown in optical section on plate 307, figure 1. The linear thickenings seem to form structural axes for folding, and usually there are at least two well-developed wall folds between each pair of pores, as shown on plate 307, figures 2–4. The wall folds sometimes pull the pore margo inward so that only part of it protrudes. These pores seem to be partly hidden behind the folds, as on plate 307, figures 12–21. Sculpture is scabrate or lacking at the poles, and coarsely scabrate or verrucate at the equator. Wall ranges from 1.5 to 3 μ in thickness. The endexine is smooth except for surface of endexinal thickenings, which appears granular on the underside (pl. 307, fig. 1). Ektexine is strikingly different in polar and equatorial areas: at the poles it is composed of crowded vertical elements which are fused in a tectum that sometimes has small scabrate projections as surface sculpture, but at the equator the ektexine is reduced to simple verrucae (or scabrae in some individuals) and does not form a tectum.

The unique morphology of this pollen seems to be restricted to the genus *Sonneratia* of the Sonneratiaceae. The only other modern pollen known to me that seems comparable is that of *Santalum* of the Santalaceae. Cookson and Pike (1954, pl. 2, figs. 67–70, 72) figured early Tertiary pollen of the *Santalum* type under the name *Santalumidites* Cookson and Pike (p. 209), and in addition they figured one grain (pl. 2, fig. 71) from the Pliocene of New Guinea which I believe should be assigned to the living genus *Sonneratia*, not to *Santalumidites.* Miocene and younger occurrences of *Sonneratia* pollen are reported from Borneo by Muller (1964), who distinguishes between *S. caseolaris* (L.) Engl. pollen in Miocene beds and *S. alba* pollen which first appears there in Pliocene beds.

Though Erdtman (1952, p. 413) indicated that the pollen of *Sonneratia* is very similar to the pollen of *Diplusodon*, a Brazilian genus of the Lythraceae, the meridional thickenings are absent from *Diplusodon.*

Comparative material.—The fossils were compared with pollen of *Sonneratia alba* J. Smith, some specimens of which are figured on plate 307 (figs. 7–11, 22–24). The three medidional thickenings in the interpore area are clearly shown on figure 9; this specimen apparently represents a turgid grain that has undergone no folding. Figures 10 and 11 show that folding is not always bilaterally symmetrical in *Sonneratia,* and similar deviations are found in the fossil material (pl. 307, fig. 19).

Because the fossils range in polar dimension from about 25 to 54 μ and show some variation in sculpture pattern, it is possible that two different species are represented in the Eniwetok material. Lacking a variety of comparative material, however, I have chosen to treat them as one form in the present study.

Fossil occurrence.—In drill hole E-1 at 850-860 feet, rare. In drill hole F-1 at 820-840 feet, rare (maximum 3 percent of pollen and spore tally). Miocene Airai Clay, Palau (USGS paleobotany loc. D1626), several specimens. In Suva Series, Viti Levu, Fiji, Miocene sample (USGS paleobotany loc. D1417), several specimens. A similar form from Pliocene of Borneo was reported by Muller (1964).

Present distribution.—The genus has six species of Indo-Malayan distribution; of these, the only species now known from Micronesia is *S. alba*. It grows in the Carolines and in the southern Marshalls on Arno and Jaluit Atolls (Mahabale and Deshpande, 1957). The present distribution of the genus is shown in figure 339.

Ecology.—On Arno Atoll, *S. alba* inhabits saline mangrove swamp depressions, where it is associated with *Bruguiera* and *Lumnitzera* (Anderson, 1951).

RHIZOPHORACEAE
RHIZOPHORA L.

The fossil material of *Rhizophora* seems to represent two basic types of morphology: pollen with strongly developed costae and a tendency toward a somewhat prolate shape (pl. 308, figs. 7, 8), and pollen with weak costae and a spherical shape (pl. 308, figs. 20, 21, 26, 27). The latter are referred to as cf. *R. mucronata* and the former as cf. *R. apiculata*. Other distinctive forms (pl. 308, figs. 46-48) which are referred to *Rhizophora* have a long prolate shape and rather well developed costae under the colpi and under the equator; these are referred to *Rhizophora* sp.

cf. R. apiculata Bl.

Plate 308, figures 1-8, 19

Pollen tricolporate; spherical to prolate spherical, ranging from 17 by 16 to 18 by 17 μ in size. Polar views show *Rhizophora* sp. to be circular, mostly with colpi open. From an equatorial view, colpi have parallel margins and are long, extending three-fourths of the distance to the poles. Costae along the equator are very clear in both equatorial and polar views. They are composed of endexine and are as much as 2 μ wide in the pore area, as can be seen by their outlines in plane view on plate 308, figures 1-5. In a canted specimen (pl. 308, fig. 7, 8), the costae appear to be very thin (about 1 μ) in the intercolpal area and very thick (about 3 μ) in the colpus area. In polar view their outlines may be represented by the characteristic dark circle 1.5-2 μ wide within the inside circumference of the equatorial belt (pl. 308, fig. 17), but in this view the true thickness of the equatorial costae is probably distorted by the curvature of the wall. Grains in polar view were not assigned to subgeneric taxa, but the dark inner circle formed by these costal thickenings is a characteristic that permits the assignment of these grains to *Rhizophora*. The pores may be defined as the area of intersection of the equatorial costae with the colpus margins and range from about 2 by 3 to 3 by 3 μ in size.

Costae that underlie the colpal margins are rounded and wedge shaped in optical section, and they are thickest (as much as 2 μ) just beneath the pore rim, where the total wall thickness is about 3 μ.

Sculpture is lacking. Wall layers are of about equal thickness at the poles, but endexine is thicker than ektexine at the equator and along the furrows. Total wall thickness ranges from 1.5 to 3 μ.

Canted polar and equatorial views may be seen in the clump of *Rhizophora* pollen shown on plate 308, figure 19. Clumps of this type, which are common in the Eniwetok material, are probably young pollen grains from *Rhizophora* anthers that fell into the lagoon before anthesis. Though some plants that are high pollen producers occasionally release clumps of pollen grains, according to Rempe (1937, p. 103), this occurrence is extremely rare. Clumps of pollen from a high pollen-producing plant such as *Rhizophora* may be construed as representing the contents of a young anther, and probably the parent plant was near the site of deposition.

Comparative material.—Collections for comparative purposes include the following species: *Rhizophora mucronata* Lam. (four collections), *R. apiculata* (one collection), and *R. mangle* L. (two collections). Material of *R. apiculata* appears to have a somewhat more prolate shape and better developed costae than that of *R. mucronata* Lam. *R. mangle* (pl. 308, figs. 36, 37) differs from both in having a far more prolate shape and more strongly developed costae along the colpi but weak equatorial costae. In addition, it is considerably larger than pollen of *R. apiculata* or *R. mucronata*.

The fossil material resembles *R. apiculata* in having strongly developed costae at the furrows and the equator but is more nearly spherical in shape.

Fossil occurrence.—In drill hole E-1 at 2,450-2,470 feet, two specimens found, and at 850-880 feet, common (as much as 30 percent of the pollen count). In drill hole F-1 at 840-860 feet, dominant (as much as 60 percent of the pollen count), and at 670-830 feet, rare to dominant (0.7 to about 58 percent). Talisay member of Alifan Limestone (Miocene), Guam (USGS paleobotany loc. D1653, D1652), many specimens. Airai Clay (Miocene), Palau (USGS paleobotany loc. D1626), many specimens. Suva Series, Viti Levu, Fiji (Miocene sample; USGS paleobotany loc. D3277), 21 specimens.

Present distribution.—*Rhizophora* is pantropical. *R. apiculata* is Indo-Malayan and occurs in the Philippines, Melanesia, and Polynesia; in Micronesia it occurs in the Carolines as far east as Kusaie. *R. mangle*, a South American species, is introduced on Eniwetok (St. John, 1960).

Ecology.—*R. apiculata* grows in association with *R. mucronata* in salt-water mudflats, where tidal channels flood the flats at high tide (Fosberg, 1960). The mudflats where these species grow are generally at exactly mean sea level.

cf. R. mucronata Lam.

Plate 308, figures 20, 21, 26, 27

Pollen tricolporate; spherical to prolate spheroidal; ranging from 18 by 18 to 20 by 18 μ in size. In equatorial view, colpi are uniformly 1 μ wide when closed (pl. 308, fig. 26) and as much as 2 μ wide when open (pl. 308, figs. 20, 21). Colpi are long, extending three-fourths or more of distance from equator to pole. Costae along equator are less well developed than those in *R.* cf. *apiculata* and often are not well defined between pores (pl. 308, figs. 20, 21). Maximum wall thickness in colpus area is about 1.5 μ, including both wall layers. Equatorial costae are thin to absent in interfurrow area. Specimens presenting polar views were not identified to subgeneric level, but all those assigned to *Rhizophora* displayed a discernible equatorial thickening; some were exceptionally thick (pl. 308, fig. 17).

Sculpture is lacking except at poles; ektexine at poles in many grains shows columellae or tiny clavae with heads crowded together, giving an apparent roughness to sculpture (pl. 308, figs. 20, 26). Wall layers are of about equal thickness in many parts of grain; total wall thickness ranges from 1 to 1.5 μ.

Comparative material.—Collections used for comparative purposes are the same as those listed for *Rhizophora* cf. *R. apiculata* (p. 1169). The fossil material resembles *R. mucronata* in having poorly developed costae, both equatorial and colpal. The polar wall structure that provides a rough sculpture in that area of some fossil grains is a feature not found in modern *R. mucronata* material, however. A somewhat rough sculpture is seen on some *Rhizophora mangle* grains (pl. 308, fig. 36), but it does not seem to be limited to the polar areas, indicating that the fossil material may represent either a modern species not included in the comparative material studied here or an extinct species.

Fossil occurrence.—In drill hole E-1 at 2,460-2,470 feet, one specimen found, and at 850-880 feet, common (about 31 percent of count). In drill hole F-1, at 840-860 feet, rare (less than 6 percent of count), and at 670-820 feet, rare (less than 2 percent of count).

Present distribution.—Present distribution is the same as that for *R. apiculata* except that this species ranges farther eastward into the southern Marshalls (Fosberg, 1960).

Ecology.—Same as that for *R. apiculata.*

RHIZOPHORACEAE

BRUGUIERA Lam.

cf. B. gymnorhiza (L.) Merrill

Plate 308, figures 31, 32, 40

Pollen tricolporate; prolate spherical; ranging from 16 by 16 to 18 by 17 μ in size. Specimens presenting polar views could not be assigned to *Bruguiera* with certainty. Colpi observed are all closed, and have parallel margins. Endexinal costae well developed immediately under colpus margins and, when viewed from above, appear as a thin dark line in the position of a margo. (Note center furrow, pl. 308, fig. 32.) Viewed at an angle or in optical section, these costae appear very prominent indeed and are about 1 μ thick. (See left and right furrows, pl. 308, fig. 32.) Costae are discontinuous across the equator, as they are absent under the pores. The pores are slitlike, their longest dimension is in the plane of the equator, and they are about 1.5 by 3.5 μ in maximum size. True equatorial costae do not seem to be present in this form; however, there is a thinning of the endexine in the equatorial area on each side of each pore, perhaps representing a reduced equatorial girdle. Sculpture is lacking. Wall layers are of equal thickness and have a maximum total thickness of 2 μ.

Comparative material.—Comparative material includes three collections of *Bruguiera gymnorhiza.* The fossil material is similar to modern *B. gymnorhiza* in all respects. It differs from pollen of *Rhizophora* as it lacks equatorial costae and from *Ceriops* as it is larger and has a more prolate shape.

Fossil occurrence.—In drill hole E-1, at 850-880 feet, less than 1 percent. In drill hole F-1, 670-820 feet, less than 2 percent. Suva Series, Viti Levu, Fiji (Miocene sample; USGS paleobotany loc. D3277), one specimen.

Present distribution.—The genus is Indo-Pacific. *B. gymnorhiza* grows in Indo-Malaya, New Guinea, the Marianas, the Carolines, and the Marshall Islands. In the southern Marshalls it is present on many of the atolls; in the northern Marshalls it has been found on

Lae, Likiep, Utirik, and Ailuk, and a few specimens are reported from Bikini (Fosberg, 1960). It is probably not limited to these atolls but merely has not been collected on the others. However, it has most likely been spread by the Marshallese, who used it, according to F. R. Fosberg (written commun., 1964).

Ecology.—Bruguiera can grow farther inland and in fresher water than either *Sonneratia* or *Rhizophora.* In the Marshalls it occupies mangrove depressions on the higher parts of the atoll islands (Fosberg, 1947, 1960).

CERIOPS Arnott

cf. C. tagal (Perr.) C. B. Rob.

Plate 308, figures 41–43

Pollen tricolporate; spherical to prolate spherical; ranging from 13 by 13 to 12 by 13 μ in size. Colpi vague, extending one-half to three-fourths of the distance from equator to pole. Pores elongated along equatorial plane, with dimensions of about 2 by 4 μ, their poleward margins very slightly thickened by endexine. Endexinous costae line the inner margins of colpi resulting in maximum wall thickness of 2 μ under poleward margins of pore. Equatorial costae not evident. Sculpture lacking. Wall layers of equal thickness in intercolpal areas, and average wall thickness of about 1 μ.

Comparative material.—Includes three collections of *Ceriops tagal* pollen.

Fossil occurrence.—In drill hole E–1 at 850–860 feet, less than 1 percent. In drill hole F–1, at 670–860 feet, as much as 13 percent.

Present distribution.—One species, *Ceriops tagal*, occurs in India, Malaya, the Palaus, and on Yap.

Ecology.—Ceriops tagal is a small tree growing in mangrove swamps. In Borneo, Merrill (1929, p. 214) observed the species growing "on saline soil"; he stated that in India and Malaysia it grows "along the seashore and tidal streams."

COMBRETACEAE

TERMINALIA L.

cf. T. catappa L.

Plate 309, figures 1–5

Pollen tricolporate, with three distinct pseudocolpi in intercolpal areas; prolate; ranging from 18 to 19 μ in equatorial diameter and from 19 to 23 μ in polar dimension. Colpi extending about two-thirds of distance from equator to pole. Pore not evident from polar view, but as seen from above in equatorial view is rectangular with rounded corners and 4 by 5 μ in maximum size; its long axis lies along equator. At its intersection with equator, pore is extended as two thin straight line slits. *Terminalia* and *Combretum* may be distinguished in equatorial view by this feature: *Combretum* lacks the slits and usually has less distinct, often rounded or figure-eight-shaped pores. Because some *Terminalia* grains do not show a distinct pore, not all equatorially oriented specimens of the two genera can be distinguished.

Wall thickest, 1.5 μ, at costae near the colpus margins; farther toward colpus opening, wall thins to membranous margin which sometimes lies flat with surface of grain and often projects slightly outward (pl. 309, fig. 1). Margin rarely folds inward in cf. *T. catappa;* where it does, grain appears to have six colpi, for the colpi resemble pseudocolpi that lie between them (pl. 309, figs. 3, 4).

Sculpture is lacking or granulate under oil. Wall is clearly two layered and simple, outer layer thinner than inner at most points.

Comparative material.—Comparative material includes four collections of *Terminalia catappa* pollen, two collections of *Terminalia samoensis* Rech., and one collection of *Terminalia hayesii* Pittier. Also considered were four species of *Combretum* (listed p. 1172), *Conocarpus erectus* L., two species of *Lumnitzera* (listed p. 1172), *Laguncularia racemosa* (L.) Gaertn. f., *Buchenavia capitata* (Vahl.) Eichler, and *Caliopteris floribunda* Lambert.

Fossil occurrence.—In drill hole E–1 at 2,450–2,460 feet, three specimens, and at 850–880 feet, less than 7 percent. In drill hole F–1, occurs in every sample between 670 and 860 feet, and represents as much as 5 percent. Airai Clay (Miocene), Palau (USGS paleobotany loc. D1186), two specimens.

Present distribution.—The genus is pantropical; *T. samoensis* occurs on Eniwetok today, as well as on most of the Marshall Islands south of Eniwetok. *T. catappa* is planted on Likiep in the northern Marshalls (Fosberg, 1956, p. 288); elsewhere in Micronesia it grows in the western and eastern Carolines and the Marianas where it may be indigenous (Kanehira, 1933). Degener and Gillaspy (1955), who observed *T. catappa* on Canton Island, stated that it is native to the Old World and is planted on Canton Island. Kanehira (1933) reported that it also grows in the Ryukyus and Bonins and on Formosa.

Ecology.—*T. catappa* is a large tree of the coastal forests (Kanehira, 1933). Taylor (1950, p. 192) reported that *T. samoensis* on Eniwetok and Bikini is "most characteristic of the area just behind the beach or shore rocks. * * * This species ordinarily occurs as scattered individuals and seldom dominates the vegetation, though it is common on the lagoon shore of * * * Elugelab Island."

COMBRETUM L.

cf. Combretum

Plate 309, figures 6, 7

Pollen tricolporate, with three distinct pseudocolpi between the true apertures; spheroidal prolate to prolate; from about 19 by 22 to 19 by 25 μ in size. Colpi long, extending about two-thirds of distance from equator to pole. Only equatorial views available. Pores indistinct rounded or figure-8 shaped, usually transected or partly bisected by margo of colpus (pl. 309, figs. 6, 7).

Wall thickness probably greatest at costae on colpus margin (about 3 μ), and it is about 2 μ at other parts of grain. Wall thins at pseudocolpi and typically bends inward at these points, so that grains appear to have six colpi. Outer wall layer thinner than inner. Sculpture lacking, or granulate under oil.

Comparative material.— One collection each of *Combretum decandrum*, *C. farinosum* H. B. & K., *C. tetralophum* Clarke, and *C. squamosum* Roxb. were considered. The fossil grains are similar to *C. tetralophum* and *C. squamosum* and resemble certain grains of *Terminalia catappa.*

Fossil occurrence.—In drill hole E–1 at 850–860 feet, and F–1 at 670–680 feet, less than 1 percent. Suva Series, Viti Levu, Fiji (Miocene sample; USGS paleobotany loc. D3277), two specimens. Talisay Member of Alifan Limestone (Miocene), Guam (USGS paleobotany loc. D1653), one specimen. Airai Clay (Miocene), Palau (USGS paleobotany loc. D1626), three specimens.

Present distribution.—The genus *Combretum* does not grow in the northern Marshalls, but it does occur in the western Carolines, Africa, Indo-Malaya, and Borneo.

Ecology.—*C. tetralophum* is a woody vine, occurring in "wayside" thickets in coastal areas of the Palau Islands (Kanehira, 1933).

LUMNITZERA Willd.

cf. L. littorea (Jack.) Voight.

Plate 309, figures 22–26, 32–36

Tricolporate, with strongly developed pseudocolpi between apertures; spheroidal prolate to prolate; 29–32 μ in equatorial dimension and 30–31 μ in polar length. Colpal margins bend inward on most grains. Costal thickenings are present; these, in addition to inward-folding margins of colpi, give grain the appearance of having very thick margos. Wall also bends inward at pseudocolpi, so that grain appears to have six colpi. Pore represented as a slit or break in costae under furrow. As seen from above, pore is slit along equator, as much as 8 μ long and 2 μ wide (pl. 309, figs. 32, 33).

Sculpture lacking except in polar region, which has distinctive canallike grooves on surface. Grooves are dichotomizing (pl. 309, fig. 22) and threadlike and appear on several fossil grains.

Wall of two simple layers, outer layer thinner than inner. (See pl. 309, fig. 36.) Wall averages 3 μ in thickness and is 4 μ at costal thickenings.

Comparative material.—Pollens of both living species of *Lumnitzera*, including two collections of *Lumnitzera racemosa* Willd. and one of *L. littorea*, were examined. *L. racemosa* pollen is characterized by a reticulate sculpture (pl. 309, fig. 40), but sculpture is lacking or canaliculate in *L. littorea.* The pollen of this genus seems to be somewhat larger than that of the other Combretaceous genera considered here (listed, p. 1171). In my estimation, the fossil *Lumnitzera* pollen in the Eniwetok material is identical with that of *Lumnitzera littorea*, and is unlike that of *L. racemosa.* Except for the Miocene age of the material, the fossils could probably be assigned to *L. littorea.*

Fossil occurrence.—In drill hole E–1 at 2,480–2,490 feet, one specimen, and at 850–880 feet, as much as 15 percent of count. In drill hole F–1 at 805–820 feet, less than 2 percent of count.

Present distribution.—One species in Micronesia, *L. littorea*, is also in Indo-Malaya, Australia, and the Pacific islands. Fosberg (1956) indicated that the genus is absent from the northern Marshalls. Anderson (1951) reported *L. littorea* on Arno Atoll. It is also on Jaluit and Ailinglaplap (F. R. Fosberg, written commun., 1964).

Ecology.—On Arno Atoll, *L. littorea* occurs in saline swamps on the higher parts of the islands, where it is associated with *Bruguiera* and *Sonneratia.*

MYRTACEAE

EUGENIA L.

cf. Eugenia

Plate 310, figures 1, 2

Brevicolporate; only two specimens, both oriented in polar view; pores internal, colpi intruding, semiangular in shape; 15 μ in equatorial dimension; polar axis probably much shorter than 15 μ. Colpi very short, about 2 μ in total length and about 0.5 μ in greatest width. Brevicolpori subtended by pronounced local endexinous thickenings of about 1.5 μ that have flat surface on underside of colpus. Sculpture minutely rough under direct light and appears lacking under phase lighting. In interfurrow area, wall thickness 1 μ. Two wall layers not distinct except under furrow, where inner layer thicker than outer.

Comparative material.—Pollen of the following Myrtaceae forms was examined: three species of *Eugenia* (*E. capuli* (S. & C.) Berg., *E. lineata* DC., and *E. antiquae* Riley), *Eucalyptus incrassata* Labill., *E. globulus* Labill., *Decaspermum fruiticosum* Forst., *D. raymondii* Diels, *Myrtella benningseniana* (Volkens) Diels, *Rhodamnia trinervia* (Sm.) Bl., *Psidium guajava* L., and *P. guineense* Sw. Pike (1956) figured and described modern pollen of a large number of southwest Pacific Myrtaceae, including about 30 genera of the family. The fossil form certainly belongs to the family Myrtaceae for, like the pattern in that family, it has a breviaxial brevicolporate form, a subtriangular equatorial shape, and thickenings under the furrow. It is similar to pollen of the genera *Chamaelaucium* and *Rhodamnia*. The fossils do not seem to belong to the Micronesian species of myrtaceous genera that one might expect here, such as *Eugenia*, *Decaspermum*, or *Myrtella*. As far as I know, pollen of these genera all typically have rather long colpi. I have not seen a wide selection of *Eugenia* species, and it is possible that the fossils belong to one of the many species of that genus now in the South Pacific. However, from what I have seen of this family, the fossils compare well with pollen of *Rhodamnia*, a Malaysian genus (pl. 310, fig. 3).

Fossil occurrence.—In drill hole F–1 at 830–840 feet, two specimens.

Present distribution.—*Eugenia* has a worldwide distribution in the temperate and subtropical zones; it has many endemic species in central and western Micronesia. Members of the family Myrtaceae are now absent from the Marshall Islands.

Ecology.—*Eugenia* species are known from both coral atoll and highland forest environments in the Carolines. On atolls, *Eugenia* grows in mixed forest on the higher parts of the islands (Fosberg, 1960, p. 19).

BORAGINACEAE
TOURNEFORTIA L.
cf. T. argentea L.

Plate 310, figures 4, 5

Tricolporate; prolate; 12–15 μ in equatorial dimension, and 20–22 μ in polar length. (Only specimens presenting equatorial views were identifiable.) Colpi extending about two-thirds of distance to pole, subtended by costae. Pseudocolpi occur between true colpi; both colpi and pseudocolpi margins tend to fold inward toward cell lumen, so that this form is similar to the pollen forms in Combretaceae. Pore is not clearly defined and appears to be merely an interruption in colpus margin and costae. Pore is an area of thin wall about 2 μ long in the plane of equator and 1 μ wide in polar dimension. In profile, pore area is bulging; colpus margin bends at pore and follows straight line from pore to polar area.

Sculpture is lacking. Wall thickness about 1.3 μ in polar area and about 2 μ under colpi. Outer wall layer seems thicker than inner.

Comparative material.—One collection of *Tournefortia argentea* was examined (pl. 310, figs. 6–9). *Heliotropium* pollen was considered because it has pseudocolpi. Combretaceae forms are similar, but none of the ones examined had such long axes and small size as *T. argentea*. This form may be hard to find in polar view, for its preferred orientation is equatorial because of its long prolate shape. In polar view, *T. argentea* closely resembles *Combretum*.

Fossil occurrence.—In drill hole E–1 at 850–860 feet, less than 1 percent of count. In drill hole F–1 at 820–840 feet, less than 1 percent.

Present distribution.—The species *T. argentea* is paleotropical and is widespread in Micronesia; it grows on Eniwetok today.

Ecology.—Anderson (1951) described *T. argentea* on Arno Atoll as growing on drier lagoon shores with *Sophora* and *Cordia*. Fosberg (1960) stated that these three forms grow along the beach above high tide level. Pure stands of *T. argentea* are occasionally found (Fosberg, 1960, p. 19). *T. argentea* is generally found in all atoll environments except dense mature forests and is one of the commonest Micronesian plants (F. R. Fosberg, written commun., 1964).

BORAGINACEAE
CORDIA L.
cf. C. subcordata Lam.

Tricolpate spheroidal (two specimens found, only polar view available); 44 μ in equatorial diameter. Apertures are thin places in wall where ektexine absent; in single specimen found, apertures of ill-defined shape and size but seem to be restricted to equatorial area. Sculpture irregularly clavate, heads of some clavae joining to form vermiculate pattern. Endexine of uniform thickness (about 1 μ), and ektexine has an irregular thickness ranging from 1 to 2 μ.

Comparative material.—Three collections of *Cordia subcordata* were each different from the other, and only Fosberg's collection 33784 from the Marshall Islands was similar to the fossil. Pollen of the Cordioidae do not seem to resemble pollen types in other sections of the family (Erdtman, 1952, p. 78). Selling (1947) reported that *C. subcordata* has large grains (43 by 40 μ) with minutely reticulate sculpture; one of our *C. subcordata* pollen preparations from Tonga resembles his description. *Cordia* is a large, complex, and variable genus that has not yet been thoroughly worked out taxonomically. Even so, it is surprising that in one species there is such diversity in pollen sculpture.

Fossil occurrence.—In drill hole F–1 at 840–850 feet, one specimen, and at 810–820 feet, one specimen.

Present distribution.—*C. subcordata* is pantropical. In the Marshalls it is absent from the driest, most northern atolls but occurs on Eniwetok and those Marshall atolls farther south.

Ecology.—On atolls, *C. subcordata* occurs in brushy strips of mixed forest just inside the beach along with *Tournefortia*, *Sophora*, *Pisonia*, *Terminalia samoensis*, and *Guettarda*.

VERBENACEAE
AVICENNIA L.
cf. A. marina Forsk.

Plate 310, figure 10

Tricolpate; spheroidal; 27–28 μ in equatorial diameter (only polar view seen). Colpi long, extending three-fourths of distance from equator to pole. No pore visible.

Sculpture reticulate, with muri and lumina each about 0.7 μ wide. Inner wall of even thickness, 0.8 μ. Outer wall 1.2 μ thick in intercolpal area and thins abruptly at colpus margin; ektexine is composed of small clavae with heads joined in an open tectum.

Comparative material.—Comparative material includes *Avicennia marina* var. *rumphiana* (Hall f.) Balsh. (pl. 310, figs. 11, 12), *A. resinifera* Forst. f., and *A. nitida* Jacq. *A. nitida* has pollen that is very similar to the fossil, but wall-thinning at the edge of the colpus is not as pronounced as in *A. marina*. *A. resinifera* has a coarser reticulum than the fossil. Several other genera of Verbenaceae were examined, but none compared well with the fossil.

Fossil occurrence.—In drill hole E–1 at 2,440–2,450 feet, one specimen, and at 870–880 feet, 5.5 percent. In drill hole F–1 at 830–860 feet, less than 2 percent, and at 670–820 feet, less than 2 percent. Airai Clay (Miocene), Palau (USGS paleobotany loc. D1626), about 10 specimens. Upper Miocene and younger beds of Borneo (Muller, 1964).

Present distribution.—*A. marina* occurs in India, Malaya, south China, and in the Pacific islands eastward as far as the Mariana Islands.

Ecology.—*A. marina* is a mangrove forest tree; in the Palaus it is rare but is more common farther west.

RUBIACEAE
IXORA L.
cf. I. casei Hance

Plate 310, figures 13–15

Tricolporate; all three Eniwetok specimens found present polar views. One specimen (pl. 310, figs. 13–15) is 25 μ in greatest equatorial dimension; other two measure only 18–19 μ, but three are identical in all other respects. Spheroidal shape, pore margins protruding slightly. Colpi very long, extending seven-eights of distance to pole. Colpi gape but are subtended with thin membrane of endexine; colpal margins very distinct but not thickened externally. Colpal margins have small endexinous thickenings where they intersect pore, and at these points wall protrudes slightly. Pores 1.5 μ wide along equatorial axis and probably round. (See pore at upper left corner of pl. 310, figs. 13–15.)

Sculpture finely reticulate and centers of lumina about 0.75 μ apart. Polar areas of one specimen marked by two small veinlike canals as viewed under phase lighting. Wall 1.5 μ thick in midintercolpal area and thins slightly toward furrow and then thickens at pore margin to 1.5 μ. Wall is two layered, endexine somewhat thicker than ektexine in intercolpal area.

Comparative material.—The comparative materials used were *Ixora casei*, three collections, and *I. volkensii* Hosakawa (=*I. casei*). Pollen of some 24 Rubiaceae genera of Old World and Micronesian distribution were examined. Of these, only the Malayan, Melanesian, and Micronesian genus *Gynochthodes* has the same general pollen morphology as *Ixora*, but its pollen is larger and has coarser reticulation. Among the three collections of modern *Ixora casei* pollen, one was large, 22–28 μ in equatorial diameter, and two were smaller, 18–28 μ. The three fossil *Ixora* pollen grains fall within that size range and are referred to cf. *I. casei*.

Fossil occurrence.—In drill hole F–1 at 820–840 feet, three specimens. At Guam (USGS paleobotany loc. D1652) in the Talisay Member of the Alifan Limestone of Miocene age, one specimen.

Present distribution.—*Ixora* has three endemic species in Micronesia. *Ixora* sp. (probably *I. casei*, according to F. R. Fosberg, written commun., 1964) was reported from Arno Atoll by Anderson (1951), but is not known in the northern Marshalls.

Ecology.—*Ixora* is a shrub in the coastal forests of the Palaus (Kanehira, 1933; F. R. Fosberg, written commun., 1964).

GARDENIA Ellis

cf. G. grievei Horne

Plate 310, figures 16, 17

Pollen in tetrads; each cell triporate. Single tetrad found is torn and flattened, 35 by 54 μ in size. Individual cells 25 by 30, 20 by 31, 30 by 32, and 30 by 30 μ in equatorial diameter. Polar axes cannot be measured, but cells seem to be oblate and short axial. Pores are round, as much as 3 μ in size. Endexine thickening immediately under pore rim makes total wall thickness from 3 to 3.5 μ at that point; wall at interpore area only 0.8–1 μ thick. Ektexine thicker than endexine. As seen from above, pore rim thickening is 1.5 μ wide. Scabrate sculpture.

Comparative material.—Of the entire Micronesian modern pollen collection prepared for this study, only seven genera have pollen in tetrads: *Gardenia*, *Hydrostachys*, *Alocasia*, *Cyathodes* (equals *Styphelia*), *Codiaeum*, *Nepenthes*, and *Drosera*. Of these, only *Gardenia* resembles the fossil. Of the monad forms with triporate pollen of rough sculpture and thickened pores, only *Guettarda speciosa* L. is much like the individual cells of the fossil tetrad, but not only is its pollen about twice as large as that of *Gardenia grievei*, its sculpture is very rough, or gemmate. No tetrads were present in the modern *Guettarda speciosa* collections I examined.

Gardenia grievei pollen is very similar in size, sculpture, and aperture morphology to the fossil. There is little question in my mind that the fossil represents pollen of that genus.

Fossil occurrence.—In drill hole F–1 at 820–830 feet, one specimen.

Present distribution.—*Gardenia* is not known from Micronesia. Seven species of *Gardenia* were reported from Borneo by Merrill (1929). Takeda (1957) reported one species from the Ryukyu Islands. The genus has about 80 paleotropical species, ranging from Africa, Indo-Malaya, and Thailand to the Philippines, Fiji, and Tahiti; several endemic species occur in the Hawaiian Islands.

Ecology.—*Gardenia* is either a tree or a shrub; most species are upland forest forms and are not found growing close to sea level in halophytic environments.

MORINDA L.

cf. M. citrifolia L.

Plate 311, figures 1, 2, 9, 10

Pollen tricolporate and 35–39 μ in equatorial diameter. Equatorial views not found, but grain appears oblate, short axial. Colpi extend two-thirds of distance to pole. Colpi margins distinct, unornamented, and gape (from 1 to 3 μ) at pore to reveal a wedge-shaped membrane of endexine. Pore margins thickened on underside by endexine where intersected by colpi margins. Ektexine thins slightly at pore margin and arches upward over endexine thickening, so that pore edge protrudes. From polar view, pore appears circular and is of same width as colpi at equator. Endexine 0.8 μ thick; ektexine 1.2 μ thick, composed of clavae with partly fused heads. Sculpture an even reticulum with lumina about 1 μ in diameter and muri about 0.3 μ in width.

Comparative material.—Comparative material includes *Morinda umbellata* L. and three collections of *M. citrifolia*. Certain other Rubiaceae genera have pollen of this general form but of vastly different sizes. (See *Scyphiphora*, pl. 311, figs. 15, 16; *Mussaenda*, pl. 311, figs. 7, 8.)

Fossil occurrence.—In drill hole E–1 at 2,450–2,470 feet, four specimens, and at 850–880 feet, less than 2 percent. In drill hole F–1 at 830–850 feet and 810–820 feet, less than 1 percent. Suva Series, Viti Levu, Fiji (Miocene sample; USGS paleobotany loc. D1417), two specimens.

Present distribution.—*Morinda citrifolia* occurs from India to Polynesia; it is present on Eniwetok and all the larger northern Marshall Islands, but Fosberg (1956, p. 285) thought that it was introduced by man in this area.

Ecology.—Fosberg described *M. citrifolia* as growing either on atolls inland from the beach line with *Tournefortia*, *Cordia*, *Pisonia*, and *Pandanus* or along passages between islets, usually in shade.

Of the fruit of this species, Kanehira (1933, p. 365) said: "Fruit a multiple drupe about the size of a hen's egg, (seeds) hollow inside, buoyant, retaining germinating power for a long time, and can therefore be distributed by ocean currents." Because the root of this species is used by natives as a dye for loincloths (Kanehira, 1933, p. 365), its present distribution might have been aided by man.

GUETTARDA L.

cf. Guettarda

Plate 310, figures 29, 30

Pollen triaperturate, probably porate. Equatorial outline circular, and cell probably oblate. Equatorial diameter from 28 to 30 μ. Apertures are represented only by parting of ektexine; nature of aperture in many specimens obscured by sculpture elements. The aperture areas free of ektexine for equatorial distance of 1–2 μ and appear isodiametric. Sculpture uniformly and coarsely reticulate. Ektexine composed of clavae 2 μ in length, their heads partly joined in an open tectum. Endexine barely visible through ektexine but seems to be about 1 μ thick and without accessory thickenings.

Comparative material.—Comparative material includes *Guettarda odorata* Lam. (pl. 310, figs. 35, 36), *G. macrosperma* J. D. Smith (pl. 310, figs. 37, 38), and two collections of *G. speciosa* L. Pollen of *G. macrosperma* has a reticulum similar to that of the fossil form, but its pore has wall thickenings that are not evident in the fossil. *G. odorata* has a wall structure like that of the fossil form but is slightly larger in size; the fossil cannot be assigned to this genus with certainty because the morphology of *Guettarda* pollen intergrades with that of *Timonius*. The fossils are definitely not comparable to *G. speciosa* pollen because that species has scabrate triporate pollen.

Fossil occurrence.—In drill hole E–1 at 2,450–2,460 feet, two specimens. In drill hole F–1 at 820–840 feet, less than 1 percent.

Present distribution.—The species which compare favorably with the fossil material (*G. macrosperma* of Costa Rica, *G. odorata* of Panama) are not represented in Micronesia today. The Micronesian strand species, *Guettarda speciosa*, is not similar to the fossil.

Ecology.—*G. macrosperma* and *G. odorata* are upland forest forms.

TIMONIUS Rumph.

cf. Timonius

Plate 310, figures 21–23

Pollen triaperturate, probably porate; equatorial outline circular. Cell short axial, probably oblate. Equatorial diameter ranges from 27 to 30 μ. Apertures represented only by a parting of ektexine; nature of apertures hidden by thick ektexine reticulum near them. Aperture areas seem free of ektexine for an equatorial distance of only 2 μ and appear isodiametric. Sculpture medium to coarsely reticulate. Ektexine composed of clavae from 1.5 to 2 μ in length, with heads joined in an open tectum and in a reticulate pattern that grades toward a finer pattern at the poles (pl. 310, figs. 21, 22). Endexine, barely visible through the ektexine, appears to have a uniform thickness of about 1 μ.

Comparative material.—Comparative material includes *Timonius corymbosus* Val. and *Timonius affinis* A. Gray. The pollens of 24 Rubiaceae genera were considered in the course of this study, and of these only *Guettarda* and *Timonius* were similar to the fossils. The New World species *Guettarda odorata* (pl. 310, figs. 35, 36) and *G. macrosperma* Donnell Smith (pl. 310, figs. 37, 38) have pollen rather similar to that of the fossil but are distinguished by their coarser reticulate sculpture. *Timonius corymbosus* pollen is rather like that of *G. macrosperma*, but *T. affinis* pollen (pl. 310, figs. 26–28) is very close indeed to the fossil form.

Fossil occurrence.—In drill hole E–1 at 2,450–2,470 feet, 14 specimens, and at 880–890 feet, one specimen. In drill hole F–1 at 830–840 feet, less than 1 percent. Airai Clay (Miocene), Palau (USGS paleobotany loc. D1186), one specimen. Suva Series (Miocene), Viti Levu, Fiji (USGS paleobotany loc. D3277), one specimen.

Present distribution.—The genus is of Indo-Malayan distribution; it also occurs in Melanesia and Polynesia, and in Micronesia eastward as far as the eastern Carolines. *T. affinis*, which the fossils especially resemble, occurs on Fiji. The genus shows a high degree of endemism in the Palau Islands, where it has eight species.

Ecology.—Of the eight species in the Palaus, all are shrubs, and only one is definitely known to grow on coral soil; seven are forest forms.

RANDIA Houst. ex. L.

cf. R. cochinchinensis (Lour.) Merr.

Plate 310, figures 31, 32

Pollen 4-pored; oblate; single specimen is 22 by 25 μ in size. Pores distributed randomly on cell; pores 4.5 μ in diameter, round; borders thickened only on underside by wedge-shaped endexinous thickening. As seen from above, pore margins very distinct. Sculpture microreticulate, with centers of lumina only 0.8 μ apart. Ektexine composed of small clavae 0.8–1 μ in length, with heads fused in an open tectum. Endexine about 0.8 μ thick except under pores, where 1–1.5 μ thick.

Comparative material.—Comparative material includes *Randia cochinchinensis*, three collections, and *Randia carolinensis* Val. Four-pored pollen is apparently uncommon, not only in the family Rubiaceae, but in the genus *Randia*. Erdtman (1952, p. 386) indicated that among 120 Rubiaceae genera, none typically are four or five pored. In discussing pollens of about 12 species of *Randia* he said that these are triporate, polycolpate, or polycolporate. However, in the three collections of *R. cochinchinensis* pollen I noted that although the pollen is predominantly three pored, a few four-pored pollens occur in each. The similarity of the fossil pollen morphology to that of *Randia cochinchinensis* is unmistakable, though there is a slight difference in size; *R. cochinchinensis* is 18–22 μ in greatest diameter, and the fossil is 25 μ. A second specimen may be assignable to *Randia*, but it seems to have small colpi passing through the pores. The second is figured on plate 311, figure 20.

Fossil occurrence.—In drill hole E–1 at 850–860 feet, one specimen.

Present distribution.— *Randia* has a pantropical distribution. Two species are recorded in Micronesia, *R. cochinchinensis* from the western Carolines, Marianas, and southern Marshalls (Arno Atoll), and *R. carolinensis* from the Carolines.

Ecology.—*R. cochinchinensis* is a small tree abundant in the coastal forests, on the plains, and in the foothills of every island in western Micronesia (Kanehira, 1933); it grows in forests on Arno Atoll, according to F. R. Fosberg (written commun., 1964).

SCYPHIPHORA Gaertn. f.

cf. Scyphiphora

Plate 311, figures 13, 14

Tricolporate; 25–26 μ in equatorial dimension; four specimens seen; apparently breviaxial. Colpi extending three-fourths of distance to poles. Pores indicated by costal thickenings at equator but not seen clearly in this specimen. Wall protruding slightly at pore rims. Sculpture uniformly reticulate, with centers of lumina 1 μ apart. Wall 1.7 μ thick at intercolpus areas and 2.5 μ thick at pore rim. Ektexine thicker than endexine and composed of small bacculae elements with heads fused into an open reticulum.

Comparative material.—One collection of *Scyphiphora hydrophyllacea* Gaertn.

Fossil occurrence.—In drill hole F–1 at 830–840 feet, one specimen. In drill hole E–1 at 2,440–2,470 feet, four specimens.

Present distribution.—*Scyphiphora hydrophyllacea* is paleotropical and occurs as far east in Micronesia as Yap in the western Carolines. It seems to be absent from Ponape (Glassman, 1957) and from the Marshalls.

Ecology.—A small tree or shrub and mangrove swamp associate.

DICOTYLEDONOS POLLEN OF UNCERTAIN FAMILY AFFINITY

?MORACEAE
MALAISIA Blanco

Malaisia type

Plate 311, figure 18

Diporate; 16 by 13 μ in size; oblate. Pores round, about 1.5 μ in diameter, spaced opposite each other. Sculpture lacking or very slightly granulate. Wall simple, two layered, about 0.7 μ thick.

Comparative material.—One collection of *Malaisia tortuosa* Blanco has pollen that is nearly identical with this fossil, but *Morus* and *Trema* (Ulmaceae) have pollen that is closely similar. Lacking more comparative material, I feel that neither the family nor the genus can be ascertained at this time.

Fossil occurrence.—Code species P_2–sm(1); in drill hole E–1 at 2,440–2,450 feet, three specimens.

Present distribution.—*Malaisia scandens* is paleotropical; *M. tortuosa* occurs on New Caledonia.

Ecology.—*M. scandens* is a woody creeper occurring at the foot of mountains and at the edge of forests and clearings on Saipan (Kanehira, 1933).

?LEGUMINOSEAE
SOPHORA L.

Sophora type

Plate 306, figures 6–8

Tricolporate; single specimen found measures 12 μ in equatorial diameter and about 11 μ in polar dimension. Spheroidal or oblate spheroidal. Colpi long, extending almost to pole, with narrow margos, 0.5 μ wide. Pores circular, 4 μ in diameter. Sculpture finely reticulate, with lumina and muri each about 0.5 μ in width.

Comparative material.—The fossil grain was compared with *Sophora tomentosa* L. and *Sophora secundiflora* Lag. Mature pollen of *S. tomentosa* (pl. 306, figs. 14–16) is similar to the fossil because of its large pore (6 by 7 μ), overall similarity in length of colpi, small margos, size of grain, and microreticulate sculpture; however, the outline of the grain in polar view is not similar to that of the fossil. *S. tomentosa* has a somewhat triangular rounded shape in polar view, whereas the fossil is rounded but somewhat folded inward at the pore in a pattern termed "fossaperturate" by Erdtman (1952, p. 13).

Fossil occurrence.—Code species C_3P_3–r(11); at 870–880 feet in drill hole E–1, one specimen.

Present distribution.—Genus presently occurs in Japan, Polynesia, Melanesia, and east to eastern Caroline Islands; *Sophora tomentosa* occurs at Arno, Ujelang, Ujae, and Likiep Atolls in the Marshall Islands but is not known on Eniwetok. It is a pantropical strand plant.

Ecology.—*S. tomentosa* grows along lagoon sides of islets just in back of beaches (Fosberg, 1955a, p. 12). On Arno Atoll, Anderson (1951) observed the species on the drier lagoon shores in association with *Scaevola*, *Suriana*, *Pemphis*, *Tournefortia*, and *Cordia*.

?SIMARUBACEAE
BRUCEA J. S. Miller

Brucea type

Plate 311, figure 31

Tricolporate; prolate in equatorial view. Single specimen 26 by 30 μ in size. Colpi extending three-fourths of distance to poles. Colpus margins folding inward, forming what appear to be narrow margos. Pores internal, 3–4 μ along equatorial plane and 1–3 μ along polar axis, size depending on state of contraction of the furrow. Sculpture finely striate; sculptural elements consist of clavae or baculae in optical section. Ektexine about 1.5 μ thick; endexine 0.5 μ thick.

Comparative material.—The single specimen was compared with pollen of the same general structure in the Anacardiaceae, Rutaceae, Rosaceae, and Simarubaceae. Though comparative material for *Brucea* was not available for this study, the fossil seems to closely resemble that genus as described and figured by Erdtman (1952, p. 407). The family assignment to Simarubaceae must be considered tentative.

Fossil occurrence.—Code species C_3P_3–st(1); single specimen in drill hole F–1 at 850–860 feet.

Present distribution.—The genus has one species in Micronesia, *B. Javanica* (L.) Merr. (Kanehira, 1933), which also occurs in India, Australia, and Malaya, and it is planted on Ponape.

Ecology.—Unknown to me.

?SIMARUBACEAE

PICRODENDRON Planch.

Picrodendron type

Plate 311, figure 19

Pollen with four apertures, stephanoporate. Only specimen is 35 by 33 μ in equatorial view; even though specimen is split, its shape is clearly oblate spheroidal. Apertures oval to circular, range from 2 to 2.5 μ in diameter, and have a rough outline. Pores are subtended by thickenings, presumably of the endexine, although no aperture can be seen in optical section. Sculpture is echinate, and conical spines are about 0.5 μ across at base and about as wide as long. The two layers of cell wall are of about equal thickness, and the total wall is 1 μ thick in interpore area. The wall is about 1.5 μ thick at the pore margin, as shown at extreme right on plate 311, figure 19. Wall sculpture between spines seems lacking, but because this specimen is mounted in polyvinyl alcohol, visibility is not good even under oil immersion lens or phase lighting.

Comparative material.—This fossil was compared with groups which are characteristically three to five stephanoporate or brevicolporate, including Campanulaceae (Section Campanuloideae), and Curcurbitaceae. The characteristics of the fossil seem best matched by the pollen of a morphologically isolated genus of the Simarubaceae, *Picrodendron.* Pollen of *P. baccatum* (L.) Krug & Urban is nearly identical with the fossil form except that it has a greater wall thickness. However, because neither this genus nor closely related forms are now known from the Micronesian area and because critical comparison of the pore structures is not possible here, the identification even to family must be considered tentative. More modern collections in the family Simarubaceae should be studied to assure the assignment suggested here, but of the 24 genera of Simarubaceae whose pollen was described by Erdtman (1952) none except *Picrodendron* has pollen of this fossil type.

Fossil occurrence.—Code species P_4–p(1); in drill hole F–1 at 820–830 feet, one specimen.

Present distribution.—*Picrodendron* is a genus of the West Indies.

?CALLITRICHACEAE

CALLITRICHE L.

Callitriche type

Plate 311, figure 24

Pollen tricolpate or quadricolpate; when tricolpate, shape is circular, and when quadricolpate, rectangular; in both, colpi are open. Equatorial views are not available in fossil material. Colpi extend halfway from equator to poles and have a vague outline. The sculpture under high dry lens appears merely scabrate, but under oil immersion lens it is very clearly reticulate. The sculpture is coarser on the poles, and there the lumina are about 1 μ wide and about 1 μ apart. The cell wall is composed of two distinct layers of equal thickness, the outer wall being composed of the fused verrucate elements of the reticulum. The endexine and ektexine extend to the furrow edge together and without thickening. The wall is about 0.8 μ thick.

Comparative material.—*C. christensenii* Christoph. was used for comparison; the fossils match well with *Callitriche* pollen described and figured by several authors (Moar, 1960; Hafsten, 1960).

Fossil occurrence.—Code species C_4–r(1). In drill hole E–1 at 2,450–2,470 feet two specimens. In drill hole F–1, at 670–680 feet, one specimen.

Present distribution.—The genus is cosmopolitan except for Pacific islands. No records are known for *Callitriche* in Micronesia. One species, *C. papuana* Merrill and Perry (1941), is recorded from New Guinea.

Ecology.—*Callitriche* is a delicate plant whose stems usually are supported by water but sometimes are prostrate on mud or on moist soil. Many species are freshwater forms, as is *C. papuana* of New Guinea. *C. muelleri* Sond. has been collected from numerous harbors and reef islands between lats 17° and 41° S. by Mason (1959); precise local ecology was not documented by Mason, but the occurrence of this species on Great Barrier Island suggests a somewhat brackish soil environment.

?HIPPOCRATEACEAE

SALACIA L.

Salacia type

Plate 306, figures 12, 13

Tricolporate; single specimen found is 18 by 19.5 μ in polar view. Circular to somewhat intersubangular in polar view with colpi intruding. No equatorial view available. Colpi and narrow margos extend three-fourths of distance to poles. In polar view, specimen has narrow pores only 1 μ wide. Wall 2.5–3 μ thick at equator in intercolpal area, both component layers thinning toward colpi. Wall protrudes slightly at furrow edge and then ektexine bends inward at furrow lip. Endexine appears to thicken immediately under colpus margins and may either form internal costae or represent an endexinous membrance subtending colpus itself. (See lowermost colpus, pl. 306, fig. 13). Sculpture microreticulate with lumina about 1 μ apart.

Comparative material.—This specimen was compared with modern pollen of *Salacia princides* DC. (pl. 306, figs. 20, 21) and (*Hippocratea macrantha* Koeth. The detailed pollen descriptions of 14 genera and 46 species of Hippocrateaceae by Van Campo and Hallé (1959) provided information on the range of pollen morphology in this family. Their work makes it clear that the nature of the structure under the furrow is a critical feature in assigning pollen to the Hippocrateaceae, though Erdtman (1952, p. 205) did not mention nor figure it in *Salacia.* Because the exact nature of that structure is not clear in my fossil specimen, a definite assignment cannot be made. A species of *Salacia* that appears to have a pollen morphology closely resembling that of the fossil specimen, but of which comparative material was not available for this study, is *S. zenkeri* Loesener. Van Campo and Hallé (1959, description for their pl. 46) indicated that the equatorial size of *S. zenkeri* is 19–20 μ and that it is finely reticulate. Pollen of that species seems to resemble closely the fossil described here, but because of its present African distribution it seems unlikely that *S. zenkeri* is related to this Pacific fossil.

Fossil occurrence.—Code species C_3P_3–r(9); in drill hole F–1 at 830–840 feet, one specimen.

Present distribution and ecology.—*Salacia* has one known species in Micronesia, *S. naumannii* Engl., which is a small twinning shrub of low-elevation thickets in New Guinea and in the western Carolines (Kanehira, 1933, p. 196). Merrill (1929) described *Salacia korthalsiana* Mig. as a liana in dense forests in Java.

?ELAEOCARPACEAE

ELAEOCARPUS Burm. ex. L.

Elaeocarpus type

Plate 311, figures 25–27

Tricolporate; oblate; 9–11 μ in equatorial dimension. Colpi gaping and protruding at equator and extending two-thirds of distance to poles. Pores evident as pouting areas at equator, where colpus margins bend so as to appear angular in equatorial view. Pores 1 μ in dimension. Sculpture lacking, and wall two layered, about 0.8 μ thick.

Comparative material.—Comparative material includes *Elaeocarpus carolinensis* Koidz., *E. graeffei* Seem., *E. joga* Merrill, and *E. polystachyus* Wall. Pollen of these species are difficult to distinguish, and the fossil form is very similar to pollen of all these taxa. Small tricolporate smooth pollen of this very ordinary pattern is found in *Gynotroches* (Rhizophoraceae), *Tarenna* (Rubiaceae), and in other unrelated genera; hence, a family and genus assignment cannot be made with certainty.

Fossil occurrence.—C_3P_3–sm(10), polar view; C_3P_3–sm(8), equatorial view; in drill hole F–1 at 840–860 feet, less than 3 percent of total pollen and spores, at 820–840 feet, common to dominant, 40–80 percent of total pollen and spores, and at 810–820 feet, less than 1 percent.

Present distribution.—*Elaeocarpus* is pantropical and has six species in the western Carolines. It is not now found in easternmost Micronesia but has one species in the Marianas and several on Ponape.

Ecology.—*Elaeocarpus* is one of the largest trees on Ponape and grows scattered in forests at low elevation, according to Kanehira (1933).

?RHIZOPHORACEAE

GYNOTROCHES Blume

Gynotroches type

Plate 308, figures 44, 45

Tricolporate; prolate; 12.5 by 8.5 μ in size. Colpi extending about two-thirds of distance from equator to pole. Polar view (pl. 5, fig. 45) shows that colpi margins are rolled inward toward the cell lumen and appear as internal thickenings. Pores are areas of thin endexine elongated along equatorial plane or of poorly defined equatorial extent and are about 2 μ wide along polar axis. Inrolled colpus margin (or possibly internal costae under colpus) attenuated greatly at equator in pore area. Sculpture lacking, and wall about 1 μ thick in noncolpus areas. Wall simple, of two equally thick structureless layers.

Comparative material.—The comparative material is one collection of *Gynotroches axillaris* Bl. pollen (pl. 308, figs. 53–55). The fossil pollen is slightly larger than *Gynotroches* pollen, and though the gross morphology of the fossil is of a somewhat generalized tricolporate type so as to make certain identification difficult, the fossil bears a striking resemblance to pollen of *Gynotroches.*

Fossil occurrence.—Code species C_3P_3–sm(7); in drill hole E–1 at 850–880 feet, less than 3 percent. In drill hole F–1 at 670–850 feet, as much as 15 percent.

Present distribution.—One species, *Gynotroches axillaris*, occurs in Micronesia (Kanehira, 1933). It is Indo-Malayan, Polynesian, Melanesian, and Philippine in distribution and occurs in the eastern Carolines on Ponape.

Ecology.—Gynotroches axillaris occurs in forest stands, both lowland and highland, on Ponape and is a medium-sized tree.

?VERBENACEAE
CALLICARPA L.

Callicarpa type

Plate 311, figures 22, 23

Tricolpate; oblate; 21 μ in equatorial dimension. Colpi reaching two-thirds of distance to poles. Colpus margins have no accessory thickenings, and no evidence of pores. Colpi gaping at equator; endexinous membranes extend from ektexine to form membranous colpus margins. Sculpture microreticulate, with lumina centers about 1 μ apart. Wall 1.5–2 μ thick, with ektexine thicker than endexine. Reticulum composed of bacculae with heads fused.

Comparative material.—Comparative material includes *Callicarpa acuminata* H.B.K., and *C. cana* L. The fossils are very similar to the pollen of *C. acuminata.* More modern comparative collections from Pacific species must be seen, however, before a generic determination can be made.

Fossil occurrence.—Code species C_3–r(1); in drill hole E–1 at 2,440–2,450 feet, one specimen, and at 870–880 feet, six specimens. In drill hole F–1, at 810–820 feet, one specimen, and at 670–680 feet, one specimen.

Present distribution.—Callicarpa is pantropical; in Micronesia, Kanehira (1933) recorded one species of Malayan Archipelago distribution and two endemic to the western Carolines.

Ecology.—Kanehira's species are shrubs in mixed and open forest.

?GESNERIACEAE
CYRTANDRA Forst.

Cyrtandra type

Plate 311, figure 21

Tricolpate; subprolate; 23 by 31 μ in size. Colpi almost reaching poles; margins turning inward toward cell lumen. Specimens are compressed, showing infolding on two lateral colpi. No clear evidence of pores, which are vaguely defined in *Cyrtandra* pollen. Wall 1.5 μ thick, and made up of two layers of equal thickness. Sculpture lacking or minutely granulate.

Comparative material.—One collection of *Cyrtandra urvillei* C. B. Clarke, which has pollen much smaller (12 by 18 μ) than the fossil type, was used for comparison. Selling (1947, pl. 40) figured pollen of *Cyrtandra lysiosepala* (A. Gray) C. B. Clarke, which is very similar in morphology to the fossils and almost as large; his material averages 26 by 20 μ in size, is up to 29 μ long. There is, I think, a fair indication that this fossil belongs to the genus *Cyrtandra,* but more modern comparative material would be needed to be certain.

Fossil occurrence.—Code species C_3–sm(3); in drill hole E–1 at 2,450–2,470 feet, six specimens.

Present distribution.—Cyrtandra is a paleotropical genus with a high degree of endemism (250 species of this genus are known). Kanehira (1933) recorded four endemic species for the Palau Islands; there are also one or two on Kusaie.

Ecology.—Cyrtandra species are shrubs or vines in the Palaus. All four species mentioned by Kanehira are highland wet forest forms, but at least one grows on limestone (F. R. Fosberg, written commun., 1964).

?RUBIACEAE
COPROSMA Forst.

Coprosma type

Plate 311, figure 37

Pentacolporate; spherical; 32 μ in equatorial diameter; single specimen seen. Colpi reaching halfway to pole, and gaping at equator; margins simple and unadorned. Pores 5 by 7 μ in size, with long axis along equator; poleward margins thickened slightly by endexine. Sculpture lacking or minutely granulate. Wall two layered and about 1 μ thick.

Comparative material.—This fossil was compared with Sapotaceae genera that have four- to six-colporate pollen; the fossil is unlike members of that family because of its spheroidal shape, thin wall, gaping furrows, and lack of costae or margos. The fossil resembles Selling's (1947, pl. 48, especially figs. 758, 762) figured pollen of *Coprosma* of the Rubiaceae. Modern pollen of *C. ernodeoides* A. Gray and a collection of *Coprosma* sp. from New Guinea were on hand for direct comparison. *Coprosma* pollen is typically tricolporate, whereas pollen of *C. ernodeoides* A. Gray is either tricolporate or tetracolporate; other species are occasionally tetracolporate, according to Selling (1947, p. 315). Apparently the polycolporate condition is a tendency in pollen of this genus. The great similarity in shape, size, wall thickness, and aperture structure between the fossil and Selling's *Coprosma* and my own *Coprosma* sp. material indicates that the fossil may belong to this or a closely related genus.

Fossil occurrence.—Code species C_5P_5–r(1); in drill hole E–1 at depths 2,450–2,470 feet, five specimens. Cranwell (1962, 1964) reported Neogene(?) pollen of this genus from Rapa, Austral Islands.

Present distribution.—Coprosma is an Antarctic and Austral-Pacific genus, not now known in Micronesia (Croizat, 1952, p. p. 101).

Ecology.—The habit is shrubby; the habitat is not known to me.

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INDEX

[Italic page numbers indicate major references]

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PLATES 304–311

PLATE 304

FIGURES 1–8. Chroococcales, Algae, Miocene of Eniwetok, × 800.
 1. *Gloeothece* type, D1200–9(2), 97.5 × 9.4.
 2. *Gloeothece* type, D1200–9(2), 98.1 × 3.7.
 3. *Gomphosphaeria* type D1200–7A(2), 88.3 × 8.5.
 4. *Aphanothece* type, D1200–9(2), 100.8 × 5.5.
 5. *Gloeocapsa* type, D1200–10B(2), 103 × 7.2.
 6. *Gloeothece* type, D1200–10B(2), 111.5 × 7.
 7. *Coelosphaerium* type, D1200–9(2), 100.4 × 3.
 8. *Chroococcus* type, D1200–7A, 78.4 × 16.6.
9–13. Chroococcales, Recent algae from lagoon margin, Onotoa Atoll, Gilbert Islands, × 800.
 9. *Clorogloea* type, D1657(1), 97.3 × 14.6.
 10. *Clorogloea* type, D1657(1), 78.5 × 9.5.
 11. *Clorogloea* type, endospore D1657(1), 90 × 15.4.
 12. *Placoma* type, D1657(1), 92.4 × 15.1.
 13. *Placoma* type, D1657(1), 81.1 × 19.4.
14–18. Algal cysts and Hystrichosphaeridae, Miocene of Eniwetok.
 14. *Pterospermopsis* cf. *P. ginginensis* Deflandre & Cookson, D1215–A(1), 16.1 × 89.5, × 600.
 15. Cyst, undet., D1200–2(2), 108.2 × 10, × 800.
 16. Cyst, undet., D1200–2(2), 106.6 × 10, × 800.
 17. *Micrhystridium tenuissimum* Deflandre, D1215–C (2), 93×5.3,×600.
 18. *Aphanocapsa* type, D1200–9(2), 104 × 13.1, × 600.
19. Microtome thin section, transverse section of laminae of lignitic fragment, Miocene of Eniwetok, D1200–4 (B–4), 117.2 × 19.4, × 248. Colonies of *Gloeothece* and *Gloeocapsa* types total about 11,000 per gram of sediment at this sample level; however, their structures could not be discovered from these microtome sections.

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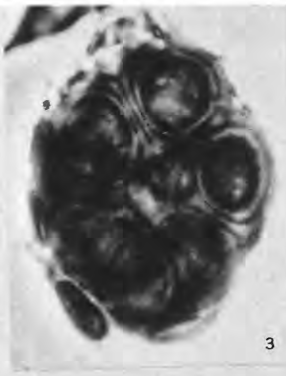

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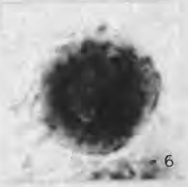

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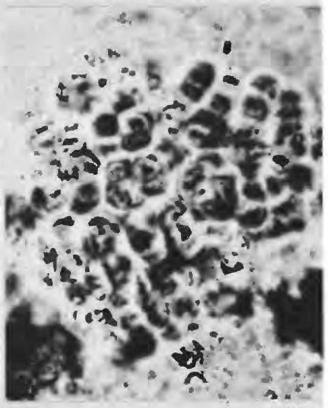

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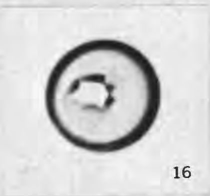

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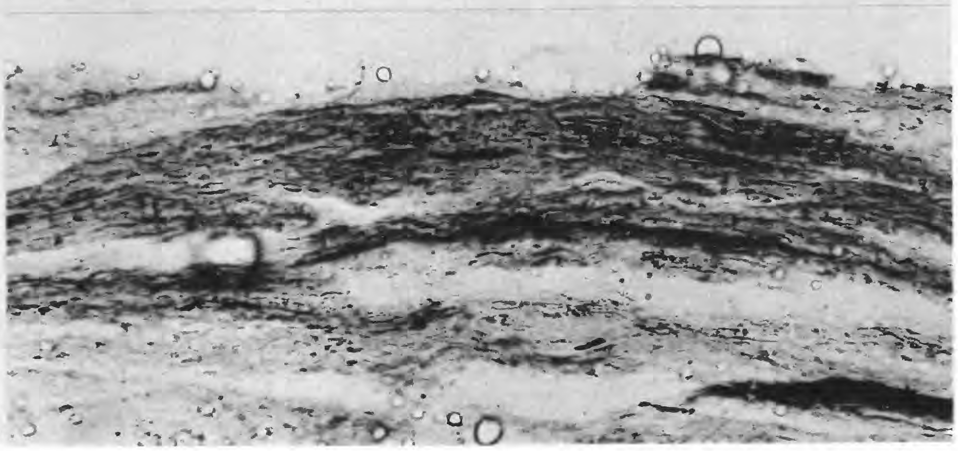


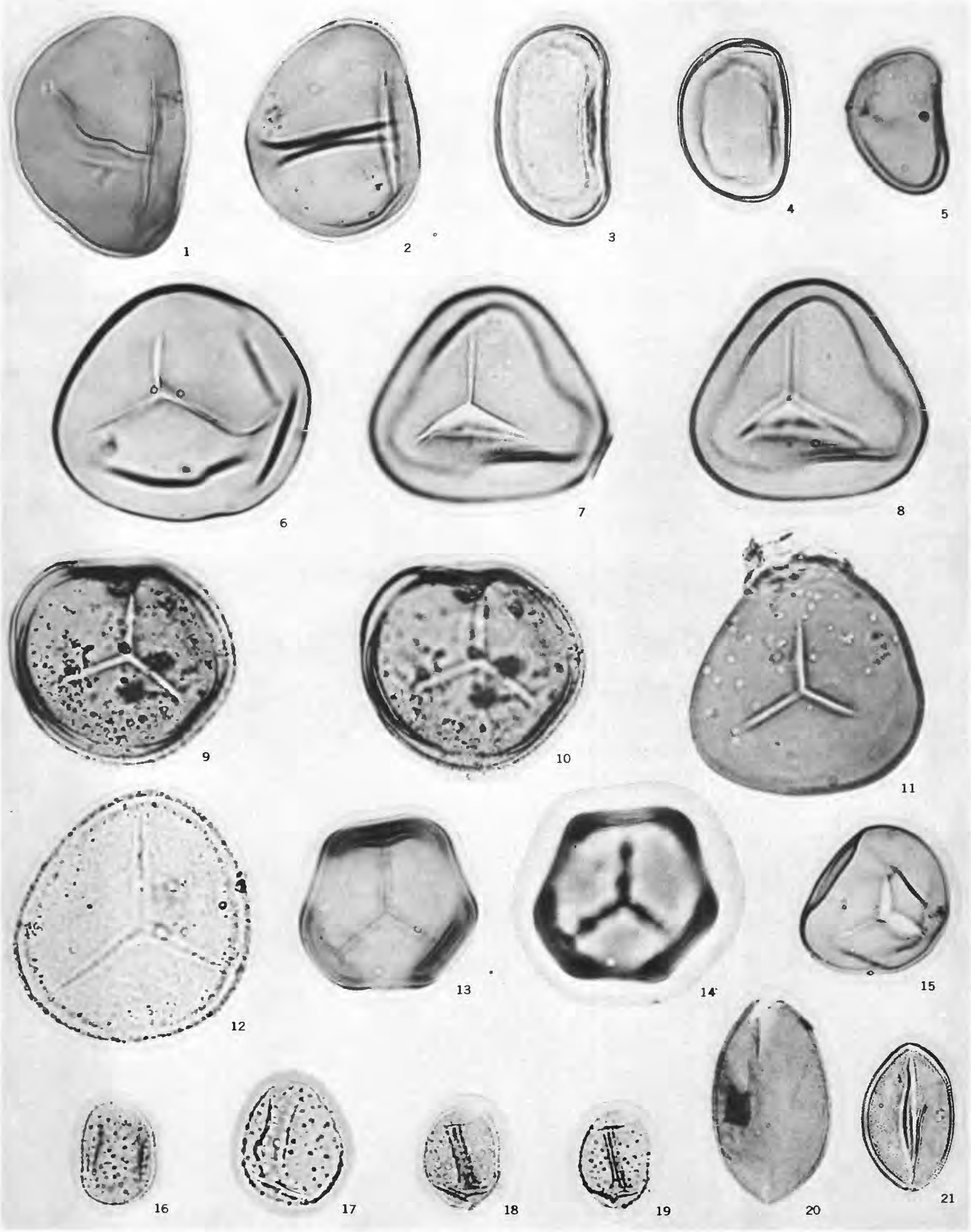
19

MIOCENE ALGAE AND MARINE CYSTS FROM ENIWETOK
AND RECENT ALGAE FROM THE GILBERT ISLANDS

PLATE 305

[All magnifications × 800]

- FIGURES 1, 2, 5. Fossil spores of the Polypodiaceae type, code species M–sm(1).
  - 1. D1215–C(2), 81 × 15.
  - 2. D1215–C(2), 93.9 × 4.1.
  - 5. D1215–D(3), 82.5 × 11.7.
- 3, 4. Modern spores of Polypodiaceae and Aspidiaceae.
  - 3. *Goniophlebium ponapense* Copeland p1584, Ponape, Glassman colln. 2378.
  - 4. *Cyclosorus goggilodus* (L.) Link p1578, Ponape, Glassman colln. 2446.
- 6–8. Fossil spores, Polypodiaceae type, code species Tl–sm(2).
  - 6. D1215–D(3), 104.8 × 13.
  - 7, 8. D1215–D(3), 12.6 × 100.9.
- 9, 10. Fossil spore, Hymenophyllaceae type, cf. *Trichomanes*, code species Tl–p(2). D1215–D(6), 88.4 × 16.2.
- 11. Fossil spore, D1215–C(2), 102.7 × 13.3.
- 12. Modern spore, *Trichomanes javanicum* Blume p1422B, Yap Island, Wong colln. 371.
- 13–15. Fossil spore, Pteridaceae types.
  - 13, 14. D1215–D(3), 100.3 × 13.5 (cf. *Dennstaedtia*).
  - 15. D1215–D(3), 100.7 × 7.8.
- 16, 18, 19. Fossil pollen, *Pandanus* sp. (p. 1165).
  - 16. D1215–B(3), 96.5 × 12.6.
  - 18, 19. D1215–B(3), 85.7 × 10.
- 17. Modern pollen, *Pandanus tectorius* Sol. p1224, Hawaii, W. H. Elder colln.
- 20. Fossil, *Livistona* type, (p. 1166).
  - D1215–B(3), 15.5 × 86.8.
- 21. Modern, *Livistona chinensis* var. *subglobosa* (Mart.) Becc., p441, Okinawa, Reid Moran colln. 5058.

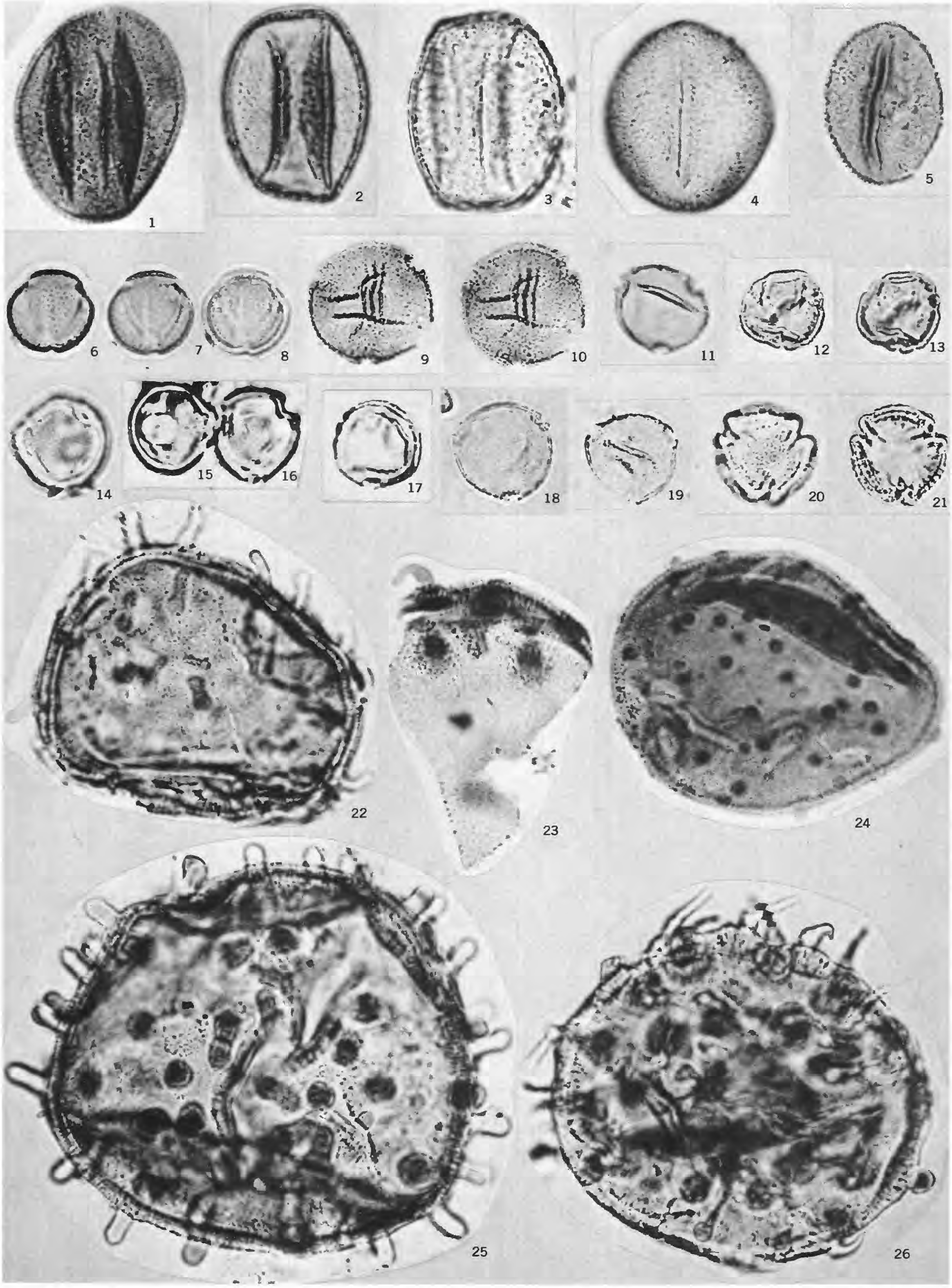


MIOCENE FERN SPORES AND MONOCOTYLEDONOUS POLLEN OF ENIWETOK AND SELECTED MODERN COUNTERPARTS

PLATE 306

[All magnifications × 800]

- FIGURES 1–5. Pollen of Nyctaginaceae (p. 1166).
  - 1. Fossil, *Pisonia* cf. *P. grandis.* D1200-6(1), 96.5 × 12.5.
  - 2–4. Modern, *Pisonia grandis* R. Br. p1731, Marshall Islands, Fosberg colln. 34263.
  - 5. Fossil, *Pisonia* cf. *P. grandis.* D1215–B(3), 6.4 × 104.
- 6–8, 14–16. Pollen of ?Leguminoseae (p. 1177).
  - 6–8. Fossil, *Sophora* type, D1200–2(2), 101.4 × 8.
  - 14–16. Modern, *Sophora tomentosa* L. p1767, Tonga, Yuncker colln. 15865.
- 9–11, 17–19. Pollen of Euphorbiaceae (p. 1167).
  - 9, 10. Fossil, *Acalypha,* D1215–E(2), 19.2 × 81.4.
  - 11, 17–19. Modern, *Acalypha* sp.; p1536, Ponape, Glassman colln. 2916.
- 12, 13, 20, 21. Pollen of ?Hippocrateaceae (p. 1178).
  - 12, 13. Fossil *Salacia* type, D1215–D(7), 71.4 × 16.9.
  - 20, 21. Modern *Salacia princides* DC. p1803, N. Borneo, A. Villamil colln. 286.
- 22–26. Pollen of Malvaceae (p. 1167).
  - 22, 23. Fossil *Thespesia* cf. *T. lampas.* D1215–A(1), 12.7 × 96.2, D1215–E(1), 85.8 × 15.8.
  - 24. Fossil Malvaceae, undet., D1215–E(1), 85.8 × 15.8.
  - 25. Modern *Thespesia peekelii* (Ulbr.) Borss., p3183, New Guinea, P. J. Darbyshire colln. 174.
  - 26. Modern *Thespesia lampas* Dalz. ex Dalz. & Gibs., p2031, Lacchrwale, Mohammad colln.

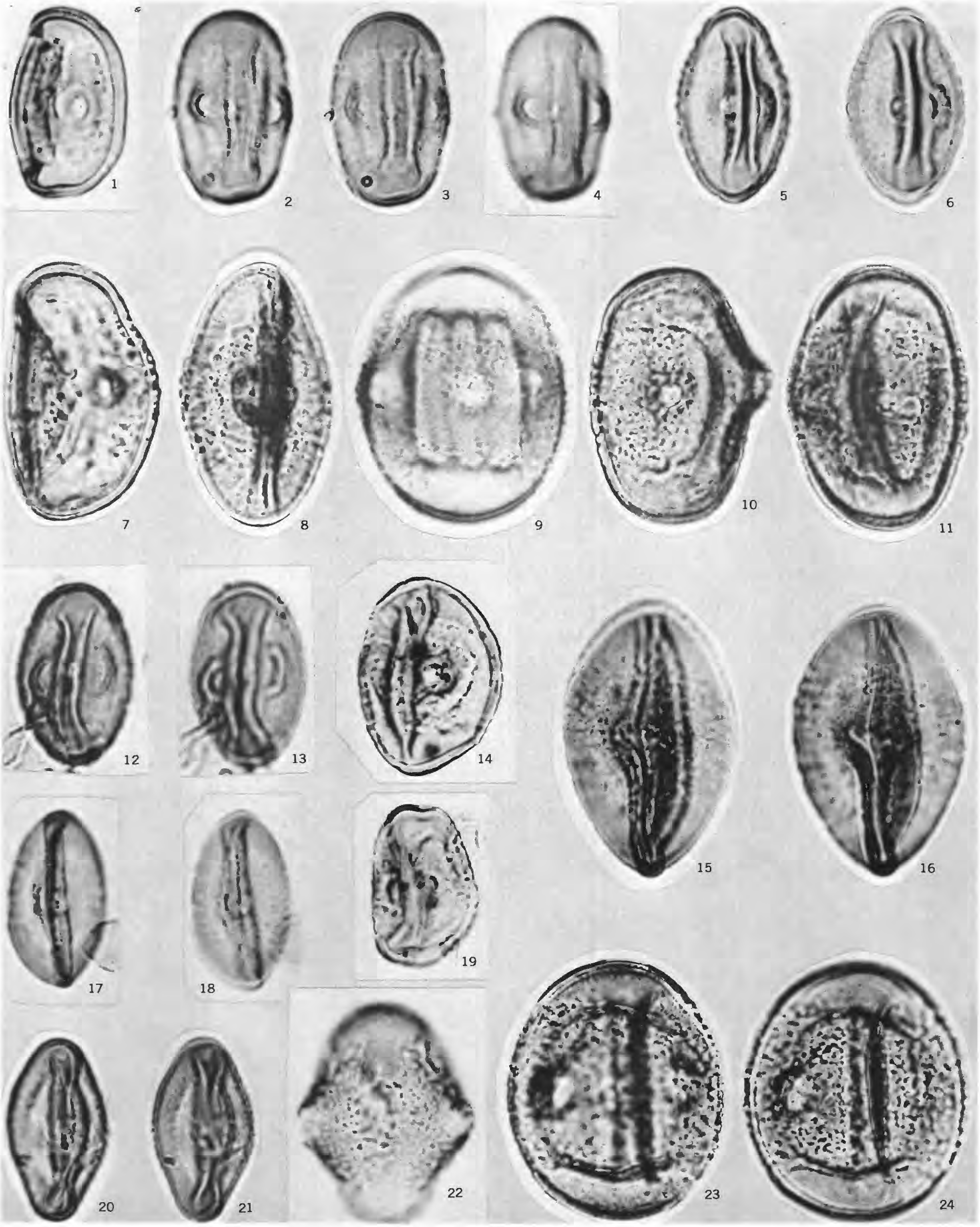


MIOCENE DICOTYLEDONOUS POLLEN OF ENIWETOK AND THEIR MODERN COUNTERPARTS, NYCTAGINACEAE, ?LEGUMINOSEAE, EUPHORBIACEAE, ?HIPPOCRATEACEAE, MALVACEAE

PLATE 307

[All magnifications × 800]

FIGURES 1–6, 12–21. Fossil pollen, *Sonneratia* cf. *S. alba* J. Sm. (p. 1168). Equatorial views.
1. D1215–D(4), 106 × 19.7.
2–4. D1215–D(3), 11.5 × 85, high, middle, and low focus.
5, 6. D1215–D(3), 92.9 × 16.7, high, and middle focus.
12, 13. D1215–D(3), 96.8 × 14.9, high and middle focus.
14. D1215–D(7), 71.7 × 13.5.
15, 16. D1215–D(2), 89.7 × 18.6, high and middle focus.
17, 18. D1215–D(3), 94.8 × 12.9.
19. D1215–D(4), 110.5 × 18.5.
20, 21. D1215–D(3), 99.4 × 14.8.
7–11, 22–24. Modern pollen, *Sonneratia alba* J. Sm.; equatorial views, p1984, Kusaie, H. F. Moore colln. 76.



MIOCENE SONNERATIACEAE POLLEN OF ENIWETOK AND MODERN COMPARATIVE MATERIAL

PLATE 308

[All magnifications × 800]

FIGURES 1–8, 19. Fossil pollen, *Rhizophora* cf. *R. apiculata* Bl., equatorial views (p. 1169).

  1, 2. D1200–2(2), 107.4×8, middle and high focus.

  3. D1200–2(2), 75.3×9.

  4, 5. D1215–A(1), 91×13, high and middle focus.

  6. D1215–A(1), 90.7×13.3.

  7, 8. D1200–2(2), 98.8×19, high and middle focus.

  19. D1215–A(1), 92.8×14.6, clump of nine grains.

9–16, 22, 23. Modern pollen, *Rhizophora apiculata* Bl., p1996, Sumatra, Liitzeharm colln. 5201.

  9–16. Equatorial views.

  22, 23. Polar views.

17, 18. Fossil pollen, *Rhizophora* sp., polar views.

  17. D1215–A(1), 100.5×11.8.

  18. D1215–B(3), 116×16.6.

20, 21, 26, 27. Fossil pollen, *Rhizophora* cf. *R. mucronata* Lam., equatorial views (p. 1170).

  20, 21. D1215–A(1), 100.9×8.1.

  26. D1200–1(1), 91.6×5.1, note polar columellae in wall.

  27. D1215–A(1), 88×8.7.

24, 25, 33–35. Modern pollen, *Rhizophora mucronata* Lam., equatorial views, p1989, New Caledonia, McKee colln. 2073.

28–30. Fossil pollen, *Rhizophora* sp.

  28. D1215–A(1), 105.9×9.1, equatorial view.

  29. D1215–A(1), 90.1×9.2, equatorial view.

  30. D1215–E(2), 93.5×6.1, polar view.

31, 32, 40. Fossil pollen, *Bruguiera* cf. *B. gymnorhiza* (L.) Merr. (p. 1170).

  31, 32. D1215–B(4), 94.6×13.3. Compare with figs. 38, 39.

  40. D1215–B(3), 85.7×10. Compare with fig. 49.

36, 37. Modern pollen *Rhizophora mangle* L., equatorial and polar views, p1292, Venezuela, R. H. Tschudy colln. 293.

38, 39, 49. Modern pollen, *Bruguiera gymnorhiza* (L.) Merr., equatorial views, p1560, Ifalik, Abbott and Bates colln. 27

41–43. Fossil pollen, *Ceriops* cf. *C. tagal* (Perr.) C. B. Rob. (p. 1171). Compare with figs. 50–52.

  41. D1215–B(3), 91×15, equatorial view.

  42. D1215–A(1), 86×11, equatorial view.

  43. D1215–A(1), 91.5×11.3, polar view.

44, 45. Fossil pollen, ?Rhizophoraceae, *Gynotroches* type. (p. 1179). Compare with figs. 53–55.

  44. D1215–D(3), 95.1×15.5, equatorial view.

  45. D1215–A(1), 104.5×19.7, polar view.

46–48. Fossil pollen, *Rhizophora* sp.

  46, 47. D1215–A(1), 91.4×18.5.

  48. D1200–1(4), 97×8.2.

50–52. Modern pollen, *Ceriops tagal* (Perr.) C. B. Rob., two equatorial views, one polar view, p1986, Wilhelmsland, K. Weinland colln., USNH 795002.

53–55. Modern pollen, *Gynotroches axillaris* Bl., p1455, Ponape, Glassman colln. 2550.

56–65. Fossil pollen, cf. *Rhizophora.*

  56. D1215–B(3), 100.1×14.8, polar view.

  57. D1215–B(4), 104.2×9.9, equatorial view.

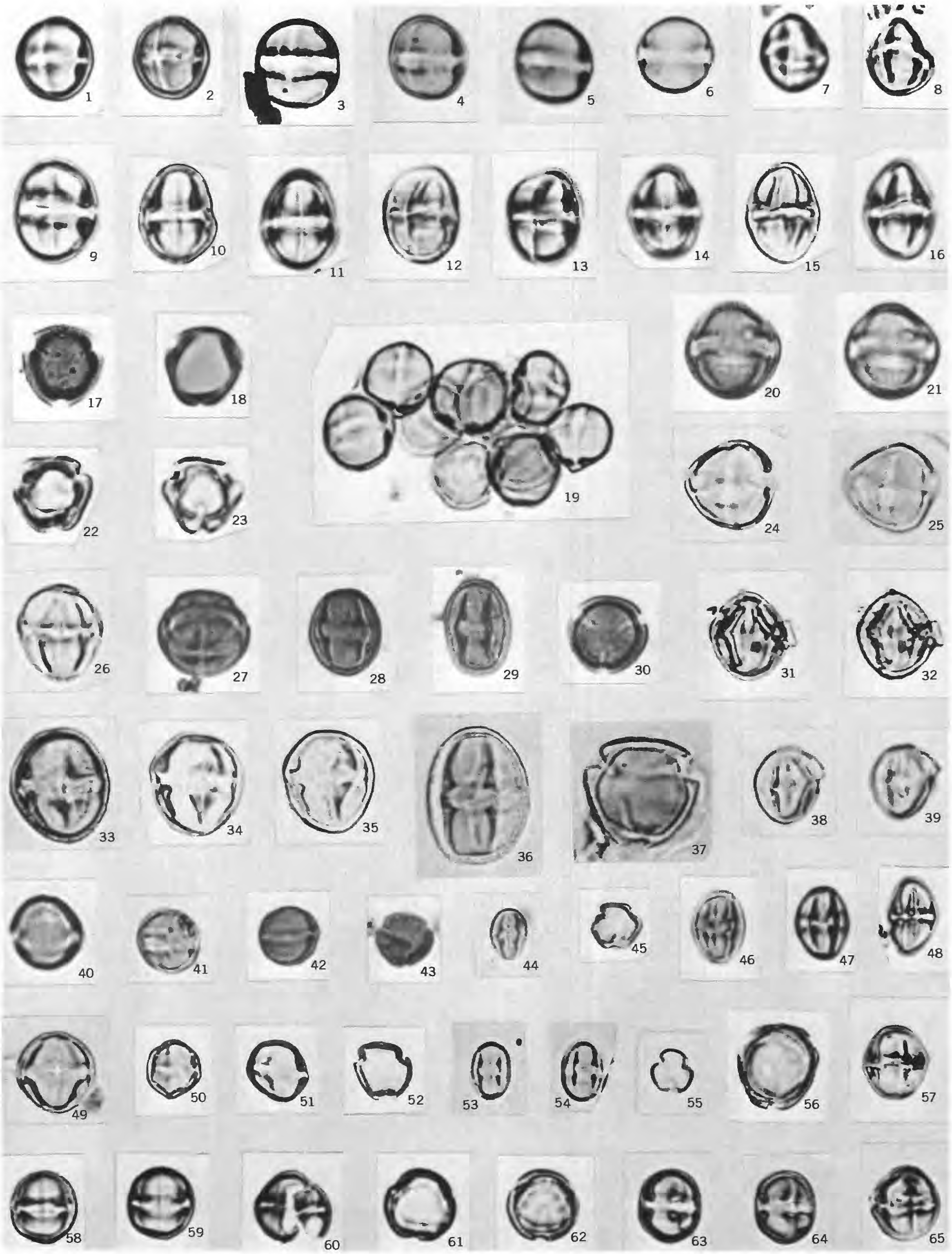
  58, 59. D1200–2(2), 99×19.3, high and medium focus.

  60. D1200–2(2), 100×18.1, broken along two colpae.

  61, 62. D1200–2(2), 89.5×9, canted polar view.

  63, 64. D1652(1), 100.5×14.2 (Guam, Miocene).

  65. D1652(1), 84.8×17 (Guam, Miocene).

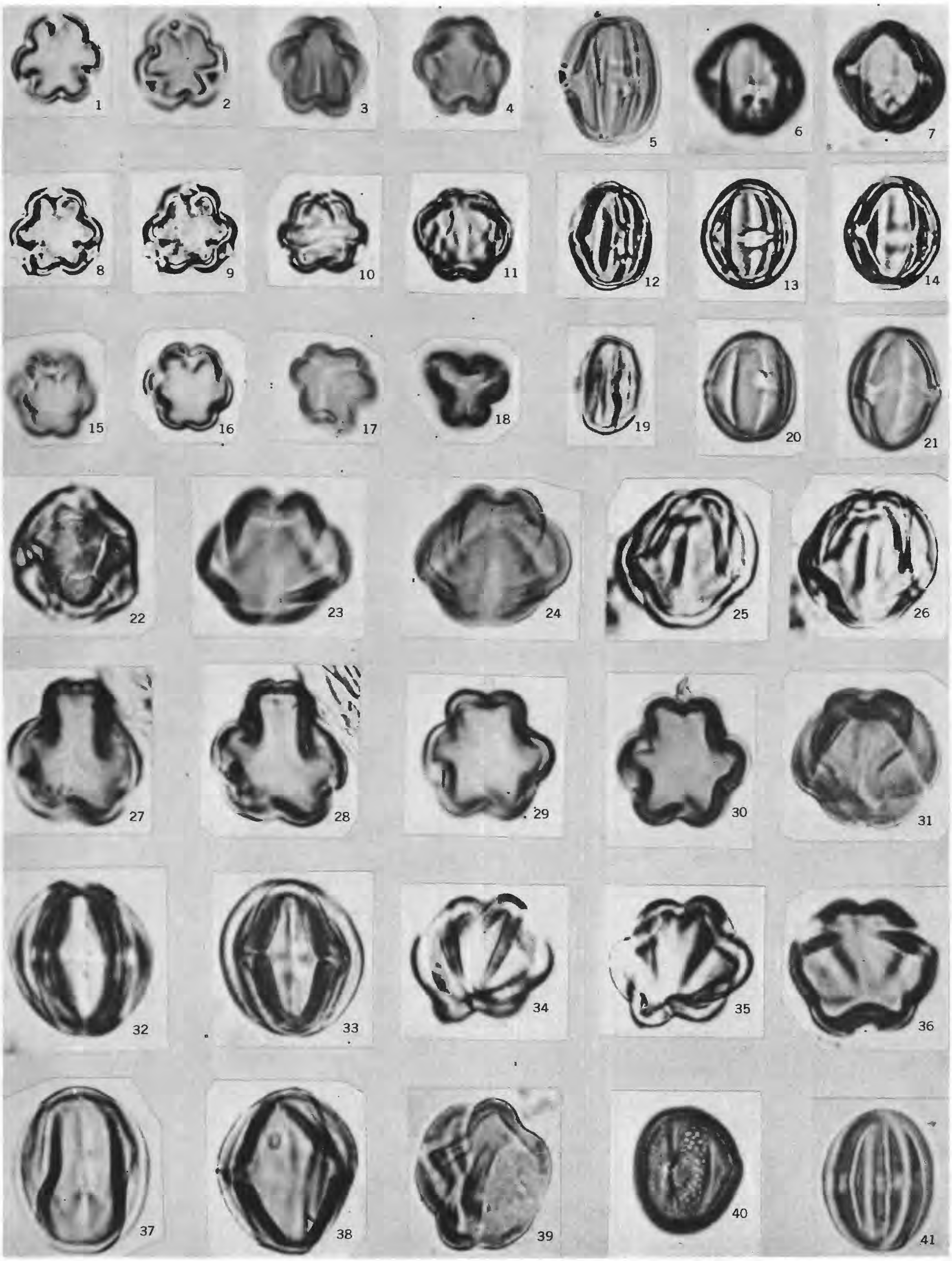


MIOCENE RHIZOPHORACEAE POLLEN OF ENIWETOK AND GUAM AND MODERN COMPARATIVE MATERIAL

PLATE 309

[All magnifications × 800]

FIGURES 1–5. Fossil pollen, *Terminalia* cf. *T. catappa* (p. 1171).
1, 2. D1215–D(3), 83×10.5, polar view.
3, 4. D1215–D(3), 102×10, polar view.
5. D1215–D(3), 86.7×16. 9, equatorial view.
6, 7. Fossil pollen, cf. *Combretum*. D1215A, 11.8×85 (p. 1172).
8–14. Modern pollen, *Terminalia catappa* L., p2046, Guam, Anderson colln. 191.
8–10. Polar views.
11. Canted polar view (more typical than true polar view because of prolate shape).
12–14. Equatorial views.
15, 16, 19, 21. Modern pollen, *Combretum tetralophum* Clarke, p1846, Borneo, Foxworthy colln. 9.
15, 16. Polar views.
19, 21. Equatorial views.
17, 18, 20. Modern pollen, *Combretum squamosum* Roxb., p1847, Sumatra, Toroes colln. 3951.
17, 18. Polar views.
20. Equatorial view.
22–26. Fossil pollen, *Lumnitzera* cf. *L. littorea* (Jack.) Voight. (p.1172).
22. D1200–1(2), 104.3×7.5, polar view. Compare with fig. 27.
23, 24. D1215–C(1), 102×17, canted grain, high and middle focus.
25, 26. D1200–1(1), 99.7 × 17.5, equatorial view, high and middle focus.
27–31, 37–39. Modern pollen, *Lumnitzera littorea* (Jack.) Voight, p1469, Ponape, Glassman colln. 2452.
27–30. Polar views in high and middle focus; note veinlike areas of ektexine thinning.
31, 39. Canted polar view.
37, 38. Equatorial view, high and middle focus.
32–36. Fossil pollen, *Lumnitzera* cf. *L. littorea* (p. 1172).
32, 33. D1200–1(2), 96.8×8.
34, 35. D1200–1(2), 102.4×1.8.
36. D1200–1(2), 96.7×3.7.
40. Modern pollen, *Lumnitzera racemosa* Willd., p2032, Philippines, McGregor colln. 1718, equatorial view.
41. Fossil pollen, cf. *Lumnitzera*. D1215–D(2), 99.3×14.5.



MIOCENE COMBRETACEAE POLLEN OF ENIWETOK AND MODERN COMPARATIVE MATERIAL

PLATE 310

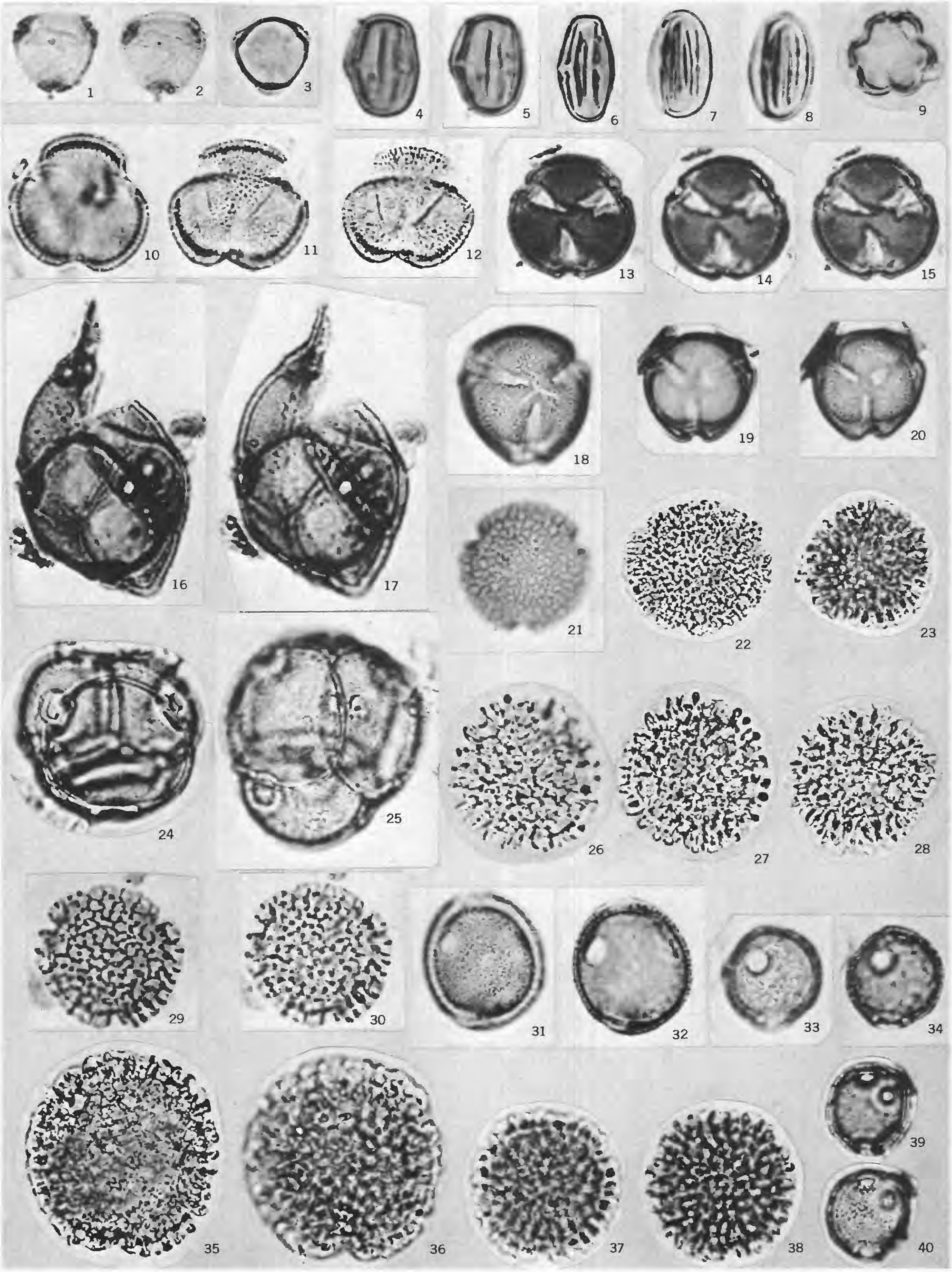
[All magnifications × 800]

FIGURES 1–3. Pollen of Myrtaceae (p. 1172).
- 1, 2. Fossil, cf. *Eugenia*. D1215–D(3), 96.7×16.0.
- 3. Modern, *Rhodamnia trinervia* (Sm.) Blume, p566, China, F. C. How colln. 71052.

4–9. Pollen of Boraginaceae (p. 1173).
- 4, 5. Fossil, *Tournefortia* cf. *T. argentea* L. D1215–C(2), 89.3×15.5, equatorial view, high and middle focus.
- 6–9. Modern, *Tournefortia argentea* L., p1914, Marshall Islands, Fosberg colln. 33643. Three equatorial views, high and middle focus; one polar view at middle focus.

10–12. Pollen of Verbenaceae (p. 1174).
- 10. Fossil, *Avicennia* cf. *A. marina*, Forsk. D1215–B(3), 87.2×14.8, middle focus.
- 11, 12. Modern, *Avicennia marina* var. *rumphiana* (Hall. f.) Balsh., p1995, Philippines, Ferraris and Stadt Miller colln. 20800, high and middle focus.

13–40. Pollen of Rubiaceae (p. 1174).
- 13–15. Fossil, *Ixora* cf. *I. casei* Hance. D1215–C(2), 105.8×15, high, middle and low focus. Compare with figs. 18–20 (p. 1174).
- 16, 17. Fossil, *Gardenia* cf. *G. grievei* Horne (p. 1175). D1215–C(2), 80×14. Tetrad with one broken cell, high and middle focus. Compare with figs. 24, 25.
- 18–20. Modern, *Ixora casei* Hance, p2043, Caroline Islands, Hosaka colln. 3207, polar views.
- 21, 22. Fossil, cf. *Timonius* (p. 1176). D1215–D(3), 103×8.9, high and middle focus. Compare with figs. 26, 27.
- 23. Fossil cf. *Timonius* (p. 1176). D1215–D(4), 84.1×16.5. Compare with fig. 28.
- 24, 25. Modern, *Gardenia grievei* Horne, p1930, Fiji, A. C. Smith colln. 6694.
- 26–28. Modern, *Timonius affinis* A. Gray, p1896, Fiji, A. C. Smith colln. 4159.
- 29, 30. Fossil, cf. *Guettarda* (p. 1175). D1200–5(1), 94.5×16.4. Compare with figs. 35–38.
- 31, 32. Fossil, *Randia* cf. *R. cochinchinensis* (Lour.) Merr. (p. 1176). D1215–B(3), 101.1×12.4; probably four pores. Compare with figs. 33, 34, 39, 40.
- 33, 34. Modern, *Randia cochinchinensis* (Lour.) Merr., p2037, Guam, Hosaka colln. 3051, equatorial view showing three pores, high and middle focus.
- 35, 36. Modern, *Guettarda odorata* (Jacq.) Lam., p2035, Panama, Erlanson colln. 155.
- 37, 38. Modern *Guettarda macrosperma*, p1062, Costa Rica, Paul H. Allen colln. 5642.
- 39, 40. Modern, *Randia cochinchinensis* (Lour.) Merr., p2038, Saipan, Fosberg colln. 25222.

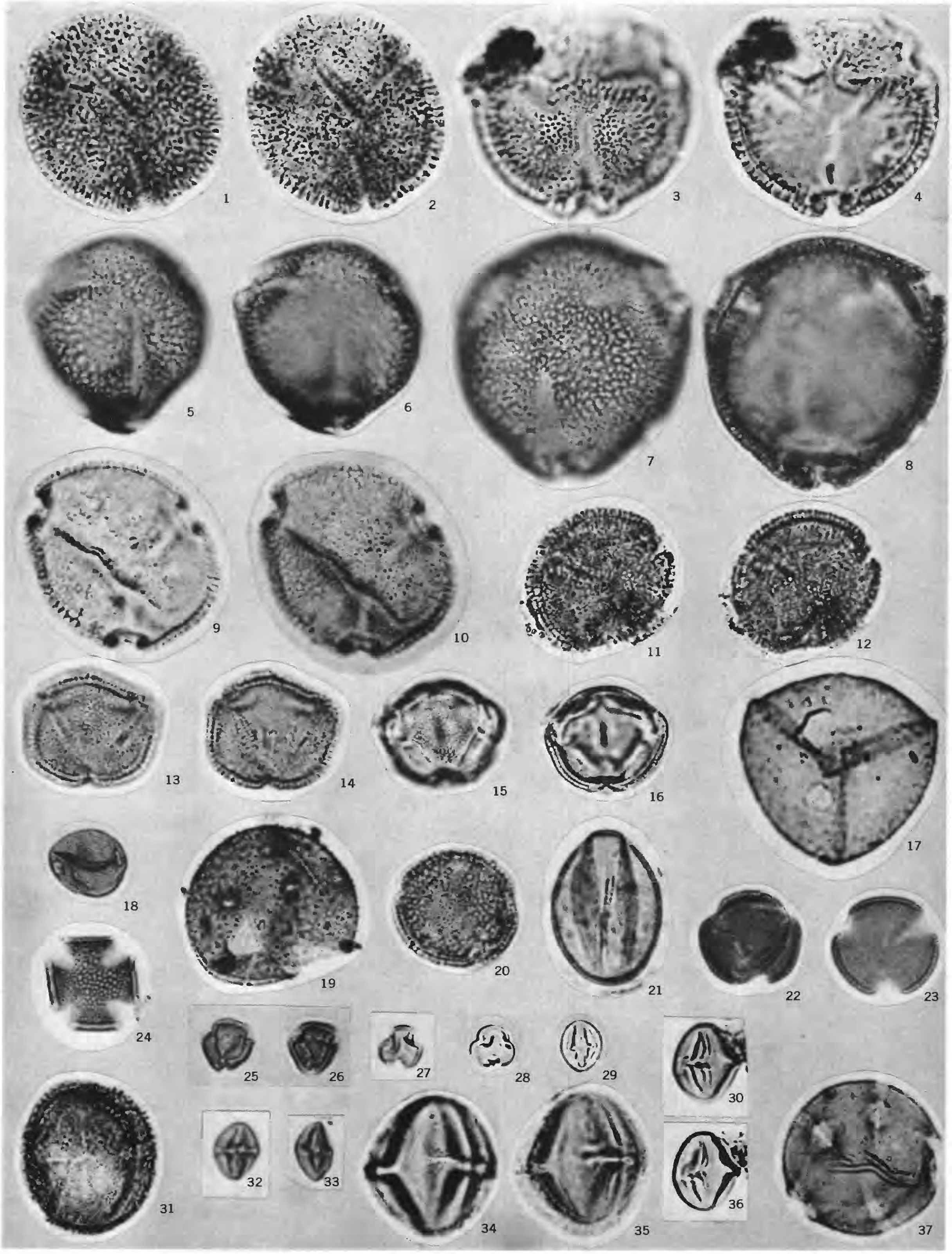


MIOCENE DICOTYLEDONOUS POLLEN OF ENIWETOK AND THEIR MODERN COUNTERPARTS, MYRTACEAE, BORAGINACEAE, VERBENACEAE, RUBIACEAE

PLATE 311

[All magnifications × 800]

FIGURES 1–16. Pollen of Rubiaceae, polar views in high and middle focus.
1, 2. Fossil, *Morinda* cf. *M. citrifolia* L. (p. 1175). D1200–1(1), 91.8×8.6.
3, 4. Fossil, cf. *Mussaenda*, D1200–1(2), 98.1×12.1.
5, 6. Modern, *Morinda citrifolia* L., p1893, Amboina, C. B. Robinson colln. 155.
7, 8. Modern, *Mussaenda frondosa* L., p2039, Palau, Fosberg colln. 32132.
9, 10. Fossil, *Morinda* cf. *M. citrifolia* L. (p. 1175). D1215–D(2), 88.6×16.7.
11, 12. Fossil, Rubiaceae undet., D1215–D(7), 75.9×21.2.
13, 14. Fossil, cf. *Scyphiphora* (p. 1177). D1215–D(3), 102.8×16.1.
15, 16. Modern, *Scyphiphora hydrophyllacea* Gaertn., p1895, Australia, Hoagland colln. 4378.
17. Undetermined spore, code species Tl–sm(5); D1200–3(1), 89.7×17.
18–27, 30–37. Dicotyledonous pollen; family assignment uncertain (p. 1177).
18. Code species P$_2$–sm(1); ?Moraceae, *Malaisia* type (p. 1177). D1200–4(2), 93.9×6.6; diporate with smooth wall.
19. Code species P$_4$–p(1); ?Simarubaceae, *Picrodendron* type (p. 1178). D1215–C(2), 97.8×15.9.
20. Code species P$_4$–r(1); ?Rubiaceae, *Randia* type. D1200–2(2), 95.7×14.4; pentaporate with infrabacculate wall.
21. Code species C$_3$–sm(3); ?Gesneriaceae, *Cyrtandra* type (p. 1180). D1200–6(1), 107.6×6.1; tricolpate with psilate wall.
22, 23. Code species C$_3$–r(1); ?Verbenaceae, *Callicarpa*, type (p. 1180). D1215–A(1), 89.8×11, and D1215–E(2), 96.1×10.1; tricolpate with reticulate sculpture.
24. Code species C$_4$–r(1); ?Callitrichaceae, *Callitriche* type (p. 1178). D1215–A(1), 104.9×15.8; tetracolpate scabrate sculpture.
25–27. Code species C$_3$P$_3$–sm(10); ?Elaeocarpaceae, *Elaeocarpus*, type, polar view (p. 1179). 27, D1215–A(1), 104.5 ×19.7; and 25, 26, D1215–D(3), 80.1×10.2. Compare with figs. 28, 29.
30, 36. Code species C$_3$P$_3$–sm(9), D1215–C(2), 95×15.9; tricolporate, with smooth wall.
31. Code species C$_3$P$_3$–st(1), ?Simarubaceae, *Brucea* type (p. 1177). D1215–F(1), 98×16.9; tricolporate with striatoid reticulate sculpture.
32, 33. Code species C$_3$P$_3$–sm(8) ?Elaeocarpaceae, *Elaeocarpus* type, equatorial view (p. 1179). D1215–D(3), 90×15.
34, 35. Code species C$_3$P$_3$–r(10), D1200–1(1), 94.4×6.9; tricolporate with scabrate wall.
37. Code species C$_5$P$_5$–r(1); ?Rubiaceae, *Coprosma* type (p. 1180). D1200–6(1), 87.4×16.3; pentacolporate with granulate wall.
28, 29. Modern, *Elaeocarpus joga* Merr., p. 1813, Guam, Robert Rodin colln. 804.



MIOCENE DICOTYLEDONOUS POLLEN OF ENIWETOK AND THEIR MODERN COUNTERPARTS, RUBIACEAE AND UNDETERMINED POLLEN TYPES