

PALEOBOTANY OF PUERTO RICO From Arthur Hollick's (1928) Scientific Survey Paper to the Present^a

ALAN GRAHAM

*Department of Biological Sciences
Kent State University
Kent, Ohio 44242*

CHARLES ARTHUR HOLLICK (FIG. 1) was born on February 6, 1857 at New Brighton, Staten Island, New York. He graduated from the Columbia College (now Columbia University) School of Mines in 1879 with a Bachelor of Philosophy degree, concentrating in geology and paleontology. He lists his profession as an engineer, and his first position was as Superintendent of the Mexican Mine, Mariposa County, California. He soon returned to New York (in 1881) as a sanitary engineer and as a member of the City of New York Board of Health (1883–1893). His responsibilities were to insure that new buildings were free of harmful odors, gases, and discharge. On his inspection list there were a number of prominent landmarks then under construction, including Madison Square Garden. In 1897 he received a doctorate degree from Columbian (now George Washington) University. Other posts included membership on the New York State Board of Education (1907–1910), Director of the Board of Education of New York City (1907–1910); tutor and Fellow in geology (1890–1900), curator of fossil botany (1900–1913), and Honorary Curator (1914–1921) at Columbia College. He also served as Assistant Curator (1901–1913) and paleobotanist (1921–1933) at the New York Botanical Garden, and geologist for the United States Geological Survey intermittently throughout his career. It is interesting that the only instruction in botany that he and his lifelong friend Nathaniel Lord Britton ever received was one lecture a week during one term by John Strong Newberry; "There was no laboratory work of any kind and we were left entirely to our own devices . . ." (Hollick,¹ p. 29). His interest in geology and botany derived from his training and work as a mining engineer, and from his participation in the Torrey Botanical Club:

I shall never forget the first meeting I attended. I felt that I was under indictment for the crime of being a young man. There were no young botanists in those days. Many of those whose acquaintance I made at these early meetings were as

^a Research for this paper was supported by NSF Grant DEB-9206743.



FIGURE 1 (Charles) Arthur Hollick. Photograph provided by the New York Botanical Garden.

old as I am now and others were older, and that was forty years ago. I recall particularly Alphonso Wood . . . and several others. No woman had yet been elected to membership in the Club. Any such innovation would have been unthinkable at the time. We brought specimens to the meetings, discussed them, helped each other to identify them, described how, when and where they were collected, and then arranged informally for a field-meeting—perhaps for more than one—before the next meeting of the Club. If I remember correctly the dues were one or two dollars a year. Subscription to the *Bulletin* was a dollar. The money in the treasury was mostly spent for refreshments, and after each meeting we had a pleasant sociable time, drinking coffee and eating cakes and sandwiches and occasionally fruit when in season.

Attending meetings in those days was not so easy as it is now—I mean for out-of-town members. I lived at Port Richmond on Staten Island. The last boat to the island was at 9 P.M. I used to take the midnight train on the Central Railroad of New Jersey at Liberty Street, get off at Bergen Point Station, walk three quarters of a mile to the shore of the Kill van Kull, wake up a man who lived

in a little shanty there, and hire him to ferry me over to Staten Island in a rowboat, arriving home about 1:30 A.M. Sometimes, in winter, the trip was not a comfortable one; but I do not recall that I ever thought of it a hardship, and, to the best of my recollection, I think I merely regarded it all as a matter of course.

Hollick died on March 11, 1933 at the age of 76. A list of his 280 publications and reports is included in an account of his life by Howe² (see also Andrews,³ pp. 226–229). Jeffrey⁴ described him as a singularly lovable man, physically almost tireless, and an indefatigable collector.

THE MACROFOSSIL RECORD

The publication of Hollick's⁵ paper on Tertiary plants from near Lares/San Sebastian provided the first extensive information on the ancient plant communities of Puerto Rico. It was also an early contribution to paleobotanical studies in the Antilles region generally, being preceded only by Berry's^{6,7} reports on 13 fossil plant taxa from the Dominican Republic and nine species from the Republic of Haiti. The San Sebastian flora consisted of 88 recognized taxa, and still stands as the largest Tertiary plant macrofossil assemblage known for all of Latin America. Considering the current interest in tropical biology and geology, and the critical role of the Caribbean region in unraveling the biogeographic and plate tectonic relationships between the Americas, it is singular that the flora has not been studied since Hollick's time.

Earlier, Hodge^{8,9} mentioned some Cenozoic (presumably Cretaceous) leaves from the Coano-Guayama region which E. W. Berry and F. H. Knowlton identified as *Nelsonia* (a cycad), *Protohipis* (fern), an unidentified fern, and a 'dicot.' Later Hollick tried to examine the specimens, but Berry and Knowlton recalled little about them and they could not be located. Hodge⁹ described a coralline alga, *Lithothamnion* (= *Lithothamnium*) from the Coano-Guayama material. Hubbard¹⁰ made a small collection of mostly poorly preserved plant fossils from the Lares Limestone along the Guajataca River just north of Lares from which Hollick¹¹ identified *Coccoloba*(?) sp., *Anona* (= *Annona*) *saraviana* Berry?, and *Aniba portoricensis*. Sr. Adriano Gonzales of Arecibo also collected from recent (post-Pliocene) sediments along the Guajataca River, and Hollick¹² identified *Juglans archaеоantillana* from that site. A second locality sampled by Hubbard was along the Collazo River at the base of the second falls below the Carretera bridge. Hollick¹¹ identified 20 species from this collection. Don Narciso Rabell, a resident of San Sebastian, also collected a large number of specimens from the Collazo River locality that were sent to Hollick for study. In 1926 N. L. Britton visited the site with W. D. Nobel of San Juan. They confirmed the presence of abundant, well-preserved fossils, and Britton suggested that Hollick come to Puerto Rico and begin a detailed investigation of the material. Although several small florules were found, Hollick's station A (the same as Hubbard's Collazo River locality) at the second falls below the Carretera Bridge proved to be the most productive. A brief account was provided by Britton¹³ prior to Hollick's⁵ summary paper. The plant macrofossils listed by Hollick⁵ from the San Sebastian Formation is presented in TABLE 1.

TABLE 1 Plant Macrofossils from the Middle Oligocene San Sebastian Formation, Puerto Rico (from Hollick⁵)

Algae	Leguminosae
<i>Chondrites dictyotoides</i>	Caesalpinioideae
Pteridophyta	<i>Cassia</i> (?) <i>dubiosa</i>
<i>Isoetes</i> (?) <i>incerta</i>	<i>C. evidens</i>
<i>Hemitelia brannerii</i>	<i>C. imitativa</i>
Gymnospermae	<i>C. imparilis</i>
Cycadales	<i>C. ordinaria</i>
<i>Zamia collazoensis</i>	<i>C. puryearensis</i>
<i>Z. noblei</i>	<i>C. visibilis</i>
Angiospermae	<i>Copaiva oligocenica</i>
Monocotyledonae	<i>Cynometra rabellii</i>
Musaceae	Mimosoideae
<i>Musophyllum</i> sp.	<i>Inga curta</i>
Palmae	<i>I. pseudinsignis</i>
<i>Bactis pseudocuesco</i>	<i>I. pseudonobilis</i>
<i>Iriarteia collazoensis</i>	<i>I. pseudospuria</i>
<i>Manicaria portoricensis</i>	<i>I. sp.</i>
<i>Palmocarpon acrocomioides</i>	<i>Pitbecellobium</i> (?) <i>imperfectum</i>
<i>P. cetera</i>	<i>P. pseudotrapeziefolium</i>
<i>P. exemplare</i>	<i>P. vexativum</i>
<i>P. opinabile</i>	Papilionoideae
<i>P. rabellii</i>	<i>Lonchocarpus praelatifolius</i>
<i>Palmacites alius</i>	<i>Sophora</i> (?) <i>suspecta</i>
<i>P. conformis</i>	Malvaceae
<i>P. sparsistriatus</i>	<i>Malvocarpon clarum</i>
<i>Palmophyllum</i> sp.	Meliaceae
Dicotyledonae	<i>Guarea opinabilis</i>
Annonaceae	<i>Trichilia evidens</i>
<i>Annona cetera</i>	<i>T. pseudobarkerii</i>
<i>A. pseudoglabra</i>	<i>T. pseudobirta</i>
Apocynaceae	<i>T. spatulata</i>
<i>Apocynophyllum pseudo-</i>	Moraceae
<i>willughbya</i>	<i>Ficus hyphodroma</i>
<i>A. wilcoxense</i> (?)	<i>F. schimperii</i>
<i>Aspidosperma collazoensis</i>	<i>F. vexativus</i>
<i>Echites pseudostellaris</i>	<i>F. sp.</i>
<i>Echitonium</i> (?) sp.	Myrsinaceae
<i>Hancornia minor</i>	<i>Myrsine pseudoferruginea</i>
<i>H. pseudopubescens</i>	<i>Icacorea prisca</i>
<i>Plumiera evidens</i>	<i>I. (?) sp.</i>
Combretaceae	<i>Stylogyne</i> (?) <i>fragmenta</i>
<i>Combretum pseudojacquinii</i>	Myrtaceae
Lauraceae	<i>Eugenia comparabilis</i>
<i>Acroclididium pseudo-</i>	<i>E. pseudaeuruginea</i>
<i>salicifolium</i>	<i>Myrcia denuntiata</i>
<i>A. pseudocanelo</i>	<i>M. eugenoides</i>
<i>Aniba collazoensis</i>	<i>Psidium dissimile</i>
<i>Hufelandia portoricensis</i>	<i>P. (?) sp.</i>
<i>Misanteca dubiosa</i>	Rhamnaceae
<i>Oreodaphne mississippiensis</i> (?)	<i>Zizyphus pseudochloroxylon</i>

(continued)

TABLE 1 (continued)

Angiospermae	<i>S. gracilentus</i>
Dicotyledonae (continued)	<i>S. pseudomarginatus</i>
Rhizophoraceae	Sapotaceae
<i>Rhizophora</i> (?) <i>doctrinalis</i>	<i>Chrysophyllum comparabile</i>
Rubiaceae	<i>C. pseudargenteum</i>
<i>Guettarda intercalaris</i>	<i>Dipholia pseudoleiantha</i>
Sapindaceae	<i>Sapota agnitionalis</i>
<i>Melicocca immutata</i>	<i>Sideroxylon aequale</i>
<i>M. sp.</i>	Undetermined relationship
<i>Sapindus brittonii</i>	<i>Ramulus</i> (?)

THE TERTIARY PLANT MICROFOSSIL RECORD

My own interest was initially drawn to tropical American vegetational history during doctoral studies at the University of Michigan by the seemingly anomalous occurrence of *Oreopanax* in the otherwise temperate Miocene Succor Creek flora of southeastern Oregon. Also, during a course in biogeography by W. S. Benninghoff, a guest lecture on tropical botany by Rogers McVaugh described the high biodiversity of tropical communities. In another lecture, by Warren Wagner on plant speciation, we were told that habitat disturbance and environmental instability were conducive to the generation of novel genotypes. At about this time I was reading in Richard's,¹⁴ *The Tropical Rain Forest*, that in regions where the rain forest is the climax vegetation, "similar vegetation has extended uninterruptedly since a very remote geological period" (p. 14); in Ashton¹⁵ that the complexity of the Malayan rain forest could be explained in terms of the seasonal and geological stability of the climate, the great stability of tropical ecosystems in geological time, and that they probably have remained under a uniform climate since the Cretaceous; and in Corner¹⁶ that the Amazon forests must have extended in modern dress since Eocene times. I recall that it seemed incongruous that if environmental instability favored speciation, and if the tropics had more species than anywhere else on earth, that tropical communities and climates should be ancient and stable. A survey of the literature revealed virtually no recent information on Cenozoic tropical floras, and there was little basis for reconstructing any aspect of their Tertiary history.

At the time, it seemed unlikely I would pursue the subject further because after I had completed the Sucker Creek study,^{17,18} Ralph Chaney and Harry MacGinitie, during a visit I made to Berkeley in 1961, suggested my next project should be on the Latah flora. Also, while at Florissant, Colorado with my dissertation advisor, Chester A. Arnold, and Richard A. Scott in 1960, Estella Leopold prophetically counseled that work on tropical fossil floras would be fascinating, but tedious and difficult. Before a decision could be made, Arnold received a call in 1963 from Elso Barghoorn at Harvard who was looking for a post-doctoral student to work on some Miocene pollen-bearing material from Panama. A doctoral student, Alexandra Bartlett, was studying the Quaternary section of a core retrieved from Gatun Lake by the Panama

Canal Commission. Inadvertently, they had taken samples from a part of the core that extended into the underlying Miocene, and these contained fossil palynomorphs.

Among the deterrents to developing the Panama study into a long-term project were the unpredictability of obtaining researchable material from tropical deposits, together with the expense and logistic difficulties of organizing field work in distant localities. This difficulty was partially overcome by developing a research plan that focused initially on a palynological study of lignites. These sediments frequently contain fossil pollen and spores, and, since they are economically important as a low-cost source of fuel, their age and location is usually better known than for economically less important deposits. About 60% of our collections have yielded fossil palynomorphs, and they now include associated rock types (siltstones, claystones) that reduce the influence of lithology on the composition of the assemblages. Seventeen Tertiary plant microfossil floras from the Gulf/Caribbean region have been studied or are under investigation in our laboratory. Although material from the Mio-Pliocene Gatun Formation was collected first,¹⁹⁻²¹ the initial publication from the project, "Studies in Neotropical Paleobotany," was on the middle Oligocene San Sebastian Formation of Puerto Rico.²² The material was from the same site along the Collazo River sampled by Hubbard, Britton, Hollick, and others earlier in the century. In the initial visit there in July/August, 1965 with David Jarzen, the major lens of lignite described in the old publications could not be located. In a later visit (February, 1967) with Shirley A. Graham and Othmar Tobisch, the creek was dry, and the lignites were found exposed on the escarpment face which is obscured when water is flowing over the falls. The principal reasons for beginning the project with the Puerto Rican material were access to information on the modern vegetation of the Antilles from Richard A. Howard (Harvard University), on the geology of Puerto Rico from R. P. Briggs (U.S. Geological Survey, San Juan), and on the associated macrofossil flora from Hollick's⁵ study. A list of the microfossils from the San Sebastian Formation is presented in TABLE 2.

CURRENT STATUS AND FUTURE RESEARCH

Fundamental changes have taken place in paleobotanical methodologies, and in our concepts of Caribbean geology and paleobiology since Hollick's time. The early paleobotanists compared macroscopic features of the fossils with those of extant species to make identifications, and then used the present ecological parameters of the existing species to reconstruct paleoenvironments (modern analog method). The study of plant macrofossils now includes cleared leaf collections, and light and scanning electron microscopy of leaf surfaces, stomata, and venation. As expected, many identifications in the older literature have proven incorrect upon reexamination of the specimens using modern methodologies, and this will likely be true of Hollick's determinations of the San Sebastian specimens. His frustrations in working with this difficult material, and the tendency of the early paleobotanists to name fragmentary and poorly preserved material, is perhaps reflected by use of

TABLE 2 Plant Microfossils from the Middle Oligocene San Sebastian Formation, Puerto Rico (based on Graham and Jarzen²²)

Pteridophyta	Flacourtiaceae
<i>Lycopodium</i> (A, B)	<i>Casearia</i>
<i>Selaginella</i>	Hamamelidaceae
<i>Cyathea</i>	<i>Liquidambar</i>
<i>Hemitelia</i> (<i>Cnemidaria</i>)*	Juglandaceae
<i>Jamesonia</i> (<i>Eriosorus</i>)	<i>Engelbardia</i> (now <i>Alfaroa</i> / <i>Oreomunnea</i>)
<i>Pteris</i> (A, B, C)	Leguminosae
Gymnospermae	Mimosoideae
<i>Podocarpus</i>	<i>Acacia</i> (omitted from original list)
Angiospermae	Loranthaceae
Dicotyledonae	<i>Aetanthus</i>
Annonaceae	Malvaceae
<i>Annona</i> (new report)*	<i>Abutilon</i>
Apocynaceae	Marcgraviaceae
<i>Rauwolfia</i>	<i>Marcgravia</i>
Aquifoliaceae	Meliaceae
<i>Ilex</i>	<i>Guarea</i> *
Araliaceae	Myrtaceae
<i>Dendropanax</i>	<i>Eugenia</i> *
Bignoniaceae	<i>Myrcia</i> * (listed as <i>Myrica</i> in original list)
<i>Jacaranda</i>	Nyssaceae
<i>Tecoma</i>	<i>Nyssa</i>
Bombacaceae	Onagraceae
<i>Bombax</i>	<i>Hauya</i>
Boraginaceae	Oxalidaceae
<i>Tournefortia</i>	<i>Oxalis</i>
Brunelliaceae	Rhizophoraceae
<i>Brunellia</i>	<i>Rhizophora</i> *
Burseraceae	Rubiaceae
<i>Bursera</i>	<i>Faramea</i>
Canellaceae	Rutaceae
<i>Pleodendron</i>	<i>Zanthoxylum</i>
Convolvulaceae	Sapotaceae
<i>Merremia</i>	<i>Chrysophyllum</i> *
Euphorbiaceae	Theaceae
<i>Alchornea</i>	<i>Pelliceria</i>
Fagaceae	Violaceae
<i>Fagus</i>	<i>Corynostylis</i>

* Designates genera also represented by macrofossils.

"pseudo-" (or variants) in 19 names (some from previous descriptions or from other authors), sp. for 8, ? for 10, and the epithets *dubiosa*, *fragmenta*, *incerta*, *imperfectum*, *suspecta*, and *vexativus*.

The bases for interpretation of fossil floras have also changed fundamentally. At the turn of the century, the modern analog method was the only approach available from paleobotanical evidence for estimating climates, paleo-physiography, and pathways of migration. Now observations are made on leaf size, texture, and margins (leaf physiognomy) because these have been found

to correlate generally with climate. The data can be treated by multivariate statistics through computer programs (e.g., CLAMP²³), further enhancing the accuracy and consistency of paleoenvironmental reconstructions. In the first quarter of this century permanence of continents and ocean basins was the accepted dogma; paleotemperature analysis, sea-level curves, radiometric dating, and pollen/spore analysis (paleopalynology) had not been developed; and the Milankovitch variations were unknown, as were the effects of CO₂ concentration on global temperatures and the climatic implications of regional features such as the Barbados coral terraces.^{24,25} Both determinations and interpretations were affected by the relatively limited collections of modern plants then available for comparison. For example, in 1925, plant collections in the United States National Herbarium were about 1/4 those of the present (~1,223,000 vs. 4,500,000 specimens; Harvey, personal communication, 1990), with far fewer representatives of tropical species, and this was generally true of all North American herbaria consulted by Hollick, Berry, and others in making their determinations.

Today, information provided by ancillary disciplines constitutes a valuable and, indeed, an essential context for interpreting fossil floras (FIG. 2). Today, we know that at the beginning of the middle Eocene (~45 Ma) there began a global lowering of temperatures from early Eocene maxima that intensified during the Eocene/Oligocene and earliest Oligocene (~32 Ma). This decline correlates with a major drop in sea level designated on the Haq et al.²⁶ sea-level curve as Tejas A4.5, and presumably marks the beginning of extensive glaciation on Antarctica. It was at about this time that the San Sebastian flora was being deposited. The island arc including Puerto Rico was transported from a more westerly position and by the Eocene had collided with the Bahama Platform. As a result, substantial elevations were present by the middle Oligocene. With the availability of mid- to high altitudes during a period of generally cooling temperatures, it is not surprising to find a substantial upland temperate and upland tropical element in the San Sebastian plant microfossil flora (*Podocarpus*, FIG. 5; *Alfaroa/Oreomunnea*, FIG. 8). More tropical to warm-temperate elements were present at lower elevations (*Hemitelia/Cnemidaria*; *Pteris*; *Acacia*, FIG. 3; *Alchornea*, FIG. 7; *Bursera*, FIG. 6), and a mangrove community of *Pelliceria* (FIG. 4) and *Rhizophora* (FIG. 9) fringed the coast. These identifications and reconstructions are generally consistent with those from 16 other fossil palynofloras now known from the region, including the Miocene Artibonite assemblage from Haiti²⁷ and the middle Eocene Chapelton flora from Jamaica.²⁸

Some of the limitations described for the study of the San Sebastian plant macrofossils in 1928, also apply to that of the microfossils published in 1969. Much of the context information described above was unknown, or in early stages of development and debate; no other Caribbean Tertiary pollen and spore floras were available; and the modern reference collection used for identification of the microfossils numbered ~6,500 slides, with mostly temperate coverage, compared to the present ~25,000 slides with greater emphasis on tropical species. A revision of the San Sebastian plant microfossil assemblage

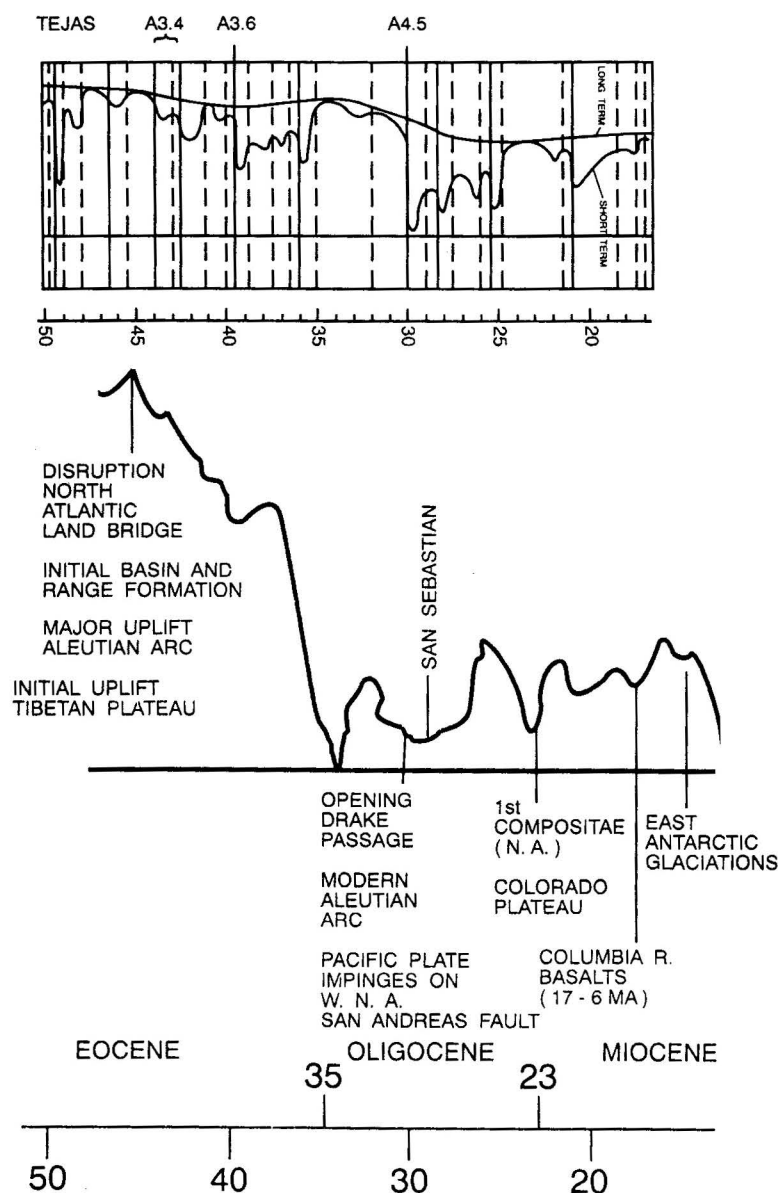
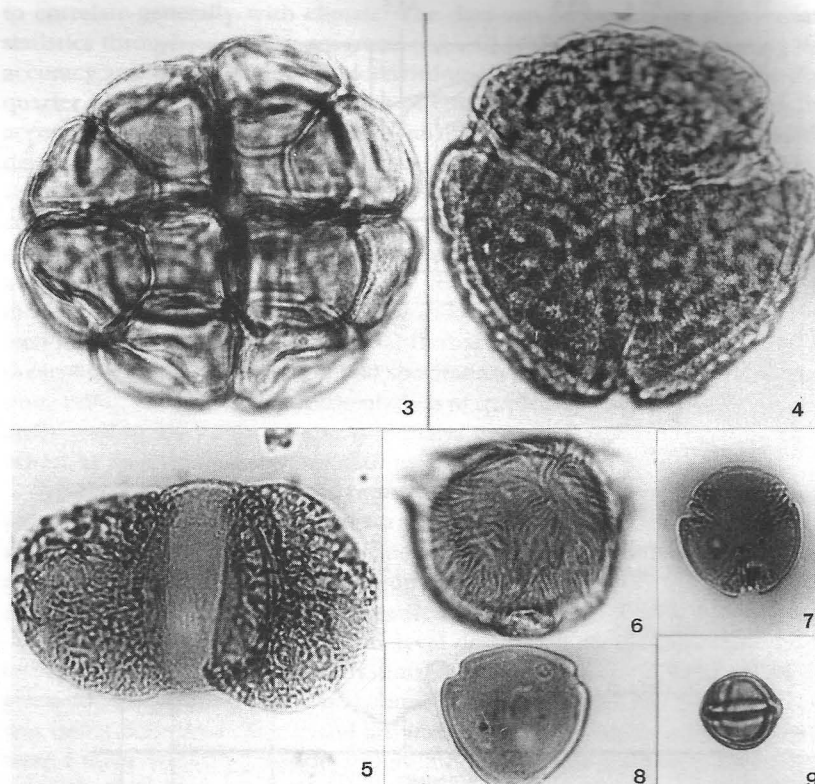


FIGURE 2 Environmental context information for the middle Oligocene San Sebastian flora. Upper diagram is the global sea level curve (Haq et al.²⁶), and lower diagram is the benthic paleotemperature curve (Miller et al.³⁰), with scales adjusted for comparison. Note the drop in sea level and lower temperature values corresponding approximately in time to the deposition of the San Sebastian assemblage.



FIGURES 3-9 Palynomorphs from the San Sebastian Formation. 3. *Acacia* (72 μ). 4. *Pelliceria* (75 μ). 5. *Podocarpus* (68 μ length). 6. *Bursera* (29 μ). 7. *Alchornea* (20 μ). 8. *Engelhardia* (now *Alfaroa/Oreomunnea*, 27 μ). 9. *Rhizophora* (14 μ).

is underway to update interpretations and to expand and refine identifications (e.g., *Annona* can now be added to the species list; *Engelhardia* is *Alfaroa/Oreomunnea*; the pollen of *Eugenia* and *Myrcia* is no longer considered distinguishable²⁹).

Future activities should focus on additional collections and re-examination of the San Sebastian macrofossil assemblage using modern methodologies, with attention devoted, for the first time, to retrieving the small seeds that are likely present in the lignite blocks; revising the plant microfossil flora; obtaining radiometric dates on the San Sebastian material; and interpreting paleoenvironments within the context of new ancillary information available on global paleotemperatures, sea-level changes, and tectonic movements of and within the Caribbean plate. When completed, these data will constitute a further step in understanding the complex biotic and geologic history of the Antilles that essentially began with publication of the New York Academy of Sciences *Scientific Survey of Porto Rico and the Virgin Islands*.

ACKNOWLEDGMENTS

The author gratefully acknowledges information on Arthur Hollick provided by Anne Rumsey, Reference Librarian (NY), and Anita L. Karg, Archivist (Hunt Institute for Botanical Documentation), and the manuscript review by Steven R. Manchester.

REFERENCES

- 1 HOLLICK, A. "Torrey Botanical Club Reminiscences." *Memoirs of the Torrey Botanical Club* 17: 29-30, 1918.
- 2 HOWE, M. A. Arthur Hollick, February 6, 1857-March 11, 1933. *Bulletin of the Torrey Botanical Club* 60: 537-553, 1933.
- 3 ANDREWS, H. N. *The Fossil Hunters, In Search of Ancient Plants*. Ithaca, NY: Cornell University Press, 1980.
- 4 JEFFREY, E. C. Arthur Hollick, 1857-1933. *Science* 77: 440-441, 1933.
- 5 HOLLICK, A. "Paleobotany of Porto Rico," in *Scientific Survey of Porto Rico and the Virgin Islands*, vol. VII, pt. 3: 177-393. New York: New York Academy of Sciences, 1928.
- 6 BERRY, E. W. "Tertiary fossil plants from the Dominican Republic." *Proceedings of the U.S. National Museum* 59: 117-127, 1921.
- 7 BERRY, E. W. "Tertiary Fossil Plants from the Republic of Haiti." *Proceedings of the U.S. National Museum* 62: 10 pp., 1923.
- 8 HODGE, E. T. "Geology of the Coamo-Guayama Region, Porto Rico [Secretary's abstract]." *Annals of the New York Academy of Sciences* 27: 277-278, 1917.
- 9 HODGE, E. T. "Geology of the Coamo-Guayama District," in *Scientific Survey of Porto Rico and the Virgin Islands*, vol. I, pt. 2: 111-228. New York: New York Academy of Sciences, 1920.
- 10 HUBBARD, B. "The Geology of the Lares District, Porto Rico," in *Scientific Survey of Porto Rico and the Virgin Islands*, vol. II, pt. 1: 1-115. New York: New York Academy of Sciences, 1923.
- 11 HOLLICK, A. "A Review of the Fossil Flora of the West Indies, with Descriptions of New Species." *Bulletin of the New York Botanical Garden* 12: 259-323, 1924.
- 12 HOLLICK, A. "Fossil Walnuts and Lignite from Porto Rico." *Journal of the New York Botanical Garden* 27: 223-227, 1926.
- 13 BRITTON, N. L. "Further Botanical Investigations in Porto Rico." *Journal of the New York Botanical Garden* 27: 97-102, 1926.
- 14 RICHARDS, P. W. *The Tropical Rain Forest*. Cambridge: Cambridge University Press, 1964.
- 15 ASHTON, P. S. "Speciation among Tropical Forest Trees: Some Deductions in the Light of Recent Evidence," in *Speciation in Tropical Environments*, edited by R. H. Lowe-McConnell. New York: Academic Press, pp. 155-196, 1969.
- 16 CORNER, E. J. H. "The Evolution of Tropical Forest," in *Evolution as a Process*, edited by J. Huxley, A. C. Hardy, and E. B. Ford. London: Allen & Unwin, pp. 34-46, 1958.
- 17 GRAHAM, A. "Systematic Revision of the Sucker Creek and Trout Creek Miocene Floras of Southeastern Oregon." *American Journal of Botany* 50: 921-936, 1963.
- 18 GRAHAM, A. "The Sucker Creek and Trout Creek Miocene Floras of Southeastern Oregon." *Kent State University Research Bulletin* IX: 1-147, 1965.
- 19 GRAHAM, A. "Studies in neotropical paleobotany. VIII. The Pliocene Communities of Panama—Introduction and Ferns, Gymnosperms, Angiosperms (Monocots). *Annals of the Missouri Botanical Garden* 78: 190-200, 1991.
- 20 GRAHAM, A. "Studies in Neotropical Paleobotany. IX. The Pliocene Communities of Panama—Angiosperms (Dicots). *Annals of the Missouri Botanical Garden* 78: 201-223, 1991.
- 21 GRAHAM, A. "Studies in Neotropical Paleobotany. X. The Pliocene Communities of Panama—Composition, Numerical Representations, and Paleocommunity Paleo-

- environmental Reconstructions. *Annals of the Missouri Botanical Garden* 78: 465-475, 1991.
- 22 GRAHAM, A. and D. M. JARZEN. "Studies in Neotropical Paleobotany. I. The Oligocene Communities of Puerto Rico." *Annals of the Missouri Botanical Garden* 56: 308-357, 1969.
- 23 WOLFE, J. A. "Estimates of Pliocene Precipitation and Temperature Based on Multivariate Analysis of Leaf Physiognomy." U.S. Geological Survey Open-File Report 90-94: 39-42, 1990.
- 24 BROECKER, W. S., D. L. THURBER, J. GODDARD, TEH-LUNG KU, R. K. MATTHEWS, and K. J. MESOLELLA. "Milankovitch Hypothesis Supported by Precise Dating of Coral Reefs and Deep-sea Sediments." *Science* 159: 297-300, 1968.
- 25 MESOLELLA, K. J., R. K. MATTHEWS, W. S. BROECKER, and D. L. THURBER. "The Astronomical Theory of Climatic Change: Barbados Data." *Journal of Geology* 77: 250-274, 1969.
- 26 HAQ, B. U., J. HARDENBOL, and P. R. VAIL. "Geochronology of Fluctuating Sea Levels since the Triassic." *Science* 235: 1156-1166, 1987.
- 27 GRAHAM, A. "A Late Tertiary Microfossil Flora from the Republic of Haiti." *American Journal of Botany* 77: 911-926, 1990.
- 28 GRAHAM, A. "Contribution toward a Tertiary Palynostratigraphy for Jamaica—the Status of Tertiary Paleobotanical Studies in Northern Latin America and Preliminary Analysis of the Guys Hill Member (Chapelton Formation, Middle Eocene) of Jamaica," in *Biostratigraphy of Jamaica*, edited by R. M. Wright and E. Robinson. Geological Society of America, Memoir 182, 1993.
- 29 GRAHAM, A. "Morfología del polen de *Eugenia/Myrcia* (Myrtaceae) y *Combretum/Terminalia* (Combretaceae) en relación a su alcance estratigráfico en el Terciario del Caribe." *Biotica* 5: 5-14, 1980.
- 30 MILLER, K. G., R. G. FAIRBANKS, and G. S. MOUNTAIN. "Tertiary Oxygen Isotope Synthesis, Sea Level History, and Continental Margin Erosion." *Paleoceanography* 2: 1-19, 1987.