

Commentary

The Concepts of Deep-Time Floras and Paleobotanical Hot-Spots

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ABSTRACT. Increased attention is being given to the preservation of paleontological sites, collections, and other archival resources that record stages in the history of the Earth's biota. The success of these efforts will be enhanced with greater recognition that the extant biota and its immediate past stages are part of a continuum (e.g., deep-time floras). An expected consequence of this view would be to bring identification of the fossil representatives under closer scrutiny by specialists in the extant lineages. Improvement in the quality and reliability of the paleontological database benefits the use of the information both in its biological applications (e.g., historical biogeography, calibration of molecular clocks, construction of area cladograms) and in geological investigations (e.g., paleoenvironmental reconstructions). Inherent in the increasing recognition of time as important in these considerations is continued access to the remarkably few fossil-bearing sites, especially in tropical America, that have provided virtually all of the existing museum specimens used in investigations for anchoring lineages in time and place. The destruction of these sites before additional collections can be made, and before they can be studied by modern methods of identification and interpretation, is an impediment to understanding the modern biota much like the destruction of sites with high concentrations of extant endemic taxa (hotspots). The relatively rare sites providing archival material for revealing the history of the Earth's vegetation should be relocated, studied more collaboratively by paleobotanists and taxonomists, and preserved. Preliminary efforts are underway to conserve three collection sites (San Sebastian flora, Puerto Rico; Sanchez flora, Dominican Republic; Yumari flora, Cuba), and to develop a project whereby paleobotanists and taxonomists will work collaboratively to establish a reliable database of fossil material.

Changes in terminology reflect the modifications, innovations, trends, and subtle shifts in emphasis that are taking place in a discipline. New dimensions in biodiversity research are reflected by recent introduction of the term biocomplexity (Dybas 2001; Michener et al. 2001), while phylogeography (Avise 2000) captures efforts to integrate biologically meaningful taxonomies with distributions to reveal patterns of geographic affinities and to suggest possible routes and means of dispersion.

There is also an increasing awareness of the importance of time in understanding the modern biota—how it got that way, and where it may be heading in response to human impact and natural fluctuations in climate and the physical environment. The calibration of molecular clocks and the temporal anchoring of events in constructing area cladograms are examples of the need to integrate geologic time with biological occurrences. This re-emerging view of the modern biota and lineages as projecting back in time, and whose modern condition is a product of events and processes that have impacted them during that history, is reflected in the phrase 'deep time'. It was initially introduced by McPhee (1981) to emphasize the vast amount of time involved in Earth history, and has been used to provide perspective to the evolution of biological taxa and communities (Erwin and Wing 2000), proselytizing the value of cladistics in revealing that history (Gee 2000), and synthesizing the fields of biogeography and paleobiology into an approach for studying aspects of plate tectonics, global change, dispersal, and vicariance (Lieberman 2000).

An extension of the concept is deep-time floras—a view that the extant and the ~Late Cretaceous/Cenozoic fossil floras of a region are part of a continuum, and that understanding the origin, present status, functioning, conservation, restoration, and future of the extant systems is improved by access to information on their history. This access is provided by fossil floras, which in their rarity and vulnerability qualify as paleobotanical hot spots much as centers of endemism do in the modern biota. A view of the modern and ancient vegetation as parts of a continuum is what is meant by deep-time floras, and the fossil assemblages that preserve the record of their development through ~Late Cretaceous/Cenozoic time is what is meant by paleobotanical hot spots. There are two consequences to the concepts.

One is the need for fuller and more direct involvement of taxonomic specialists in the identification of fossil material (Graham 1962). Most paleobotanists consult authorities in extant plant groups for leads or confirmation in the identification and paleoecological implications of the specimens, and taxonomists frequently examine fossil material ascribed to their group. Even so, the identification of fossils is left primarily in the hands of the paleobotanist, and the borrowing, examination, or annotation of fossil material by taxonomists is not a routine part of revisions. A paleobotanical study of Cenozoic material may involve efforts to establish the biological affinities of ascomycete reproductive structures, followed by consideration of the ecological parameters of Asian gymnosperms, and then estimating the biogeographic implications of hun-

dreds of unrelated angiosperm taxa. The quality and confidence in the paleobotanical database would be improved considerably if the vast number of specimens in museum collections that have been identified by paleobotanists also were examined by specialists in the extant group. This is particularly true of tropical material collected in the early 1900s, and frequently cited in the taxonomic and biogeographic literature, but which has not been re-examined in nearly 100 years. The acceptance of these identifications for placing a lineage at a particular location at a given time, or for establishing 'the oldest known occurrence' for calibrating the molecular clock, imparts a very tentative aspect to the subsequent conclusions. An often-cited example that demonstrated the need to improve the quality of the database was the fossil *Carya bendirei*. The leaf was described as "four different species of *Salix*, two species of *Carya*, *Rhus*, and *Prunus*, and as *Magnolia*, *Cassia*, *Celastrus*, *Aesculus*, *Hicoria*, *Juglans*, *Ptelea*, *Quercus*, and *Arbutus*" (Graham 1972, p 8). An example from the tropics is the occurrence of the fossil fruit *Juglans linki* Brown (1946) from the late Miocene or early Pliocene of Punta Gorda, Ecuador. If the identification and age are correct, it would place *Juglans* in South America ahead of any other northern temperate element (Graham 1999), and prior to full closure of the Isthmian land bridge (Graham 1992). There is no inherent reason why a trip to US to study herbarium material, for example, should not include a visit to the adjacent Paleobiology Division to look at fossil specimens attributed to the same group. The examination of these and other specimens by specialists would enhance confidence in the database, and in its reliability for a wide variety of biological, geological, and paleoecological applications. A project of the type envisioned is presently in the planning stages and involves the family Rubiaceae. Conventional bibliographies and electronic global databases include reports of a wide variety of fossil pollen, leaves, fruits, and seeds attributed to the family from the Cretaceous to the Recent. The pollen reported by paleopalynologists will be examined by specialists in the modern pollen morphology of the family, and identifications of leaf and other fossil material will be evaluated by taxonomic specialists in extant Rubiaceae. The goal is to produce a fossil record as definitive and reliable as possible for interpreting the origin, radiation, and diversification of the family.

A second consequence of the concepts of deep-time floras and paleobotanical hot spots is an enhanced appreciation of the fossil archives. Considerable effort and attention has been devoted to the study and preservation of the extant biota, and now it is becoming more widely recognized that comparable efforts must be devoted to preserving the documentation of how it

came into existence (Alverson and Eakin 2001; Koenig 2001; Stokstad 2001).

The preservation of past stages in the development of the modern flora has precedent in such localities as the Petrified Forest National Park, Arizona (<http://www.nps.gov>), and the Florissant Fossil Beds National Monument, Colorado (<http://nps.gov>). The consequence of delay in protecting sites is evident at the former Fossil Cycad National Monument in the Black Hills of South Dakota (<http://www.nps.gov>). It was set up in 1922 to preserve a unique concentration of Mesozoic gymnospermous plants, but these have all been collected and the site is no longer in operation. One problem in preserving paleontological archives is that while protecting extensive field assemblages of popular and spectacular fossil organisms located in impressively scenic surroundings is comparatively easy, the protection of those that may be of great scientific importance but less dramatically displayed is more difficult.

With reference to the Caribbean region, there are a limited number of fossil plant localities that indicate the vegetation at that time and place, and collectively these paleobotanical hot spots reveal stages in the evolution of lineages, communities, and environments through Cenozoic time. Among information not evident from analysis of the modern vegetation is that 1) *Pelliceria*, now confined to southern Central America and northern South America, and *Nypa*, an Old World mangrove palm, were widespread in the Caribbean region during the warm periods of the early Cenozoic (Graham 1995), 2) *Picea*, with a current southern distribution to the mountains of northern Mexico, was repeatedly present as far south as Veracruz, Mexico and into Guatemala during the cold intervals of the late Cenozoic (Graham 1998, 1999), and 3) genera presently confined to the temperate forests of eastern Asia, and previously known from the Tertiary fossil record of the New World only as far south as the western United States, are now being reported from the late Tertiary of southeastern Mexico (Magallón-Puebla and Cevallos-Ferriz 1994).

Within the Greater Antilles there are a few sites (usually one) on each island that preserve representatives of the former vegetation and provide clues to the origin and subsequent history of the extant flora and the environmental fluctuations that conditioned that history. For example, Berry (1922) studied a Late Tertiary flora from the Dominican Republic "near the pier at Sanchez, District of Samana, cut in clay, fossil plants collected April 1, 1919." Neither the site nor the specimens have been examined since Berry's original study; it is the only megafossil flora known for the entire country, and reports include several lineages presently under taxonomic study—Combretaceae (*Bucida*), Leguminosae (*Inga*, *Pithecolobium*, *Sophora*), Melastoma-

taceae (*Melastomites*), Myrtaceae (*Calyptanthus*), Nyc-taginaceae (*Pisonia*), Rubiaceae (*Guettarda*), Sapinda-ceae (*Sapindus*), and Sapotaceae (*Bumelia*). It is not known whether the site still exists, if additional collec-tions would add new megafossil taxa, provide the first material for palynological studies, or if timely efforts made now would preserve the site from destruction.

The principal Cenozoic fossil floras of the Greater Antilles are listed in Appendix 1, together with the pertinent literature and the genera reported for each assemblage. It would be worthwhile, especially for res-ident scientists and students seeking research projects of moderate cost, to determine if these localities are still available for collecting and study, and if so, to ini-tiate new studies using modern approaches of identi-fication and interpretation. Each site is a part of the island's biological heritage; collectively they tell the story of the origin and development of its natural plant resources, and they should be preserved.

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APPENDIX 1

Deep-time flora sites and paleobotanical hot spots in the Greater Antilles.

CUBA

Locality: "It comes from Abra del Yumurí in the province of Matanzas, a locality which has frequently been visited by geologists since it was first described by J. W. Spencer in 1895."

Reference: Berry (1939).

Deep-time flora (original identifications; genera only): *Gleichenia*, *Heliconia*, *Palmae*, *Pseudolmedia*, *Pisonia*, *Capparis*, *Inga*, *Pithecolobium*, *Caesalpinia*, *Cassia*, *Sophora*, *Dalbergia*, *Fagara*, *Simaruba*, *Trichilia*, *Swietenia*, *Drypetes*, *Metopium*, *Celastrus*, *Dodonaea*, *Sapindus*, *Reynosa*, *Zizyphus*, *Eugenia*, *Myrcia*, *Laguncularia*, *Bumelia*, *Mimosa*, *Calophyllum*, *Rheedia*, *Exostema*, *Bignonia*.

Locality: "Included in the paleobotanical material from Cuba gotten together by the late Arthur Hollick and turned over to me by the New York Botanical Garden are two lots from the Pleistocene which are of especial interest."

The first of these was collected by Barnum Brown in 1911 and came from the celebrated hot spring of Chapapote at Baños de Ciego Montero in Santa Clara province and found in association with a Pleistocene mammal fauna."

Reference: Berry (1934).

Deep-time flora: *Pinus*, *Juniperus*, *Minusops*, *Conocarpus*, *Chrysobalanus*, *Spondias*.

Additional note: Palynofloras derived from well cores or road/stream-side exposures are not as susceptible to destruction as surface outcrops, and unprocessed original samples, processed residues, and duplicate slides often remain. However, the sites may be covered over through development, and they should remain accessible if possible.

Locality: "The palynomorphs were from a core ~30 cm long from the Saramaguacán Formation in the Sierra de Maraguán in east-central Cuba (Provincia de Camagüey) and Sibanicú."

Reference: Graham et al. (2000).

Deep-time flora: Most specimens had to be named by an artificial system because of the age of the flora. Included were monolete and trilete fern spores, and possible affinities are *Acrostichum*, cf. *Pteris*, *Palmae*, *Cruidia*, *Eugenia*/*Myrcia* type, *Bombacaceae*, *Symplocos*, *Gramineae*, *Moraceae*, *Bursera*, and *Celtis*.

HAITI

Locality: Most of the specimens were from a locality designated W 185 F (station 7544), just north of the Cul-de-Sac—Enriquillo Basin: "Departemente de l'Ouest, cut along road from Mirebalais to Las Cahobas, on north of ravine at foot of mountain on north side of gap. W. P. Woodring, collector, January 8, 1921."

Reference: Berry (1923).

Deep-time flora: *Chara*, *Gymnogramme*, *Mespilodaphne*, *Pisonia*, *Guet-tarda*, *Bumelia*, *Chrysophyllum*, *Mimusops*.

Additional note: A small piece of rock matrix from one of Berry's specimens was removed with permission of the Smithsonian Institution and processed for plant microfossils.

Reference: Graham (1990).

Deep-time flora: *Alsophila*, *Pteris*, cf. *Antrophyum*, *Pinus*, *Palmae*, *Hydrophila*, *Chenopodiaceae*/*Amaranthaceae*, *Compositae*, *Alchornea*, *Alfaroa*/*Oreomunnea*, *Oryctanthus*, *Malpighiaceae*, and *Allophylus*.

DOMINICAN REPUBLIC

Locality: "The fourth locality, No. 8684 (D.C. 4) has furnished most

of the determinable forms. This is a yellow sandy clay exposed in a cut near the pier at Sanchez."

"8684 (D.C. 4). District of Samaná, cut in clay near pier at Sanchez, eastward-dipping beds, fossil plants and few mollusks. D. D. Condit and C. W. Cooke, collectors. April 1, 1919."

Reference: Berry (1922).

Deep-time flora: *Poacites*, *Pisonia*, *Inga*, *Pithecolobium*, *Sophora*, *Sap-indus*, *Calyptanthus*, *Bucida*, *Melastomites*, *Bumelia*, *Guet-tardia*.

Additional note: If it has not already been undertaken, it is obvious that the famed amber sites or selected specimens should be preserved.

Reference: Poinar and Poinar (1999).

PUERTO RICO

Locality: "Collazo River, near (or "at") base of second falls below Carretera bridge; Lares-San Sebastian road bridge."

Reference: Hollick (1928).

Deep-time flora: *Chondrites*, *Hemitelia*, *Isoetes*, *Zamia*, *Acrodiclidium*, *Aniba*, *Annona*, *Apocynophyllum*, *Aspidosperma*, *Bactris*, *Cassia*, *Chrysophyllum*, *Coccoloba*, *Combretum*, *Copaiva*, *Cynometra*, *Dipholis*, *Echites*, *Echitonium*, *Eugenia*, *Ficus*, *Guarea*, *Guet-tardia*, *Hancornia*, *Hufelandia*, *Icacorea*, *Inga*, *Iriarteia*, *Juglans*, *Lonchocarpus*, *Malvocarpus*, *Manicaria*, *Melicocca*, *Misanteca*, *Musophyllum*, *Myrcia*, *Myrsine*, *Oreodaphne*, *Palmacites*, *Palmocarpus*, *Palmophyllum*, *Pithecellobium*, *Plumeria*, *Protorhipis*, *Psidium*, *Ramulus*, *Rhizophora*, *Sap-indus*, *Sapota*, *Sideroxylon*, *Sophora*, *Stylogyne*, *Trichilia*, *Zizyphus*.

Additional note: A palynoflora was recovered from the same locality as above:

Reference: Graham and Jarzen (1969).

Deep-time flora: *Lycopodium*, *Selaginella*, *Cyathea*, *Hemitelia*, *Jamesonia*, *Pteris*, *Podocarpus*, *Abutilon*, *Acacia*, *Aetanthus*, *Alchornea*, *Bernoullia*, *Bombax*, *Brunellia*, *Bursera*, *Casearia*, *Catostemma*, *Chrysophyllum*, *Corynostylis*, *Dendropanax*, *Engelhardia*, *Eugenia*, *Fagus*, *Faramea*, *Guarea*, *Hauya*, *Ilex*, *Jacaranda*, *Liquidambar*, *Marcgravia*, *Merremia*, *Myrcia*, *Norantea*, *Nyssa*, *Oxalis*, *Palmae*, *Pelliciera*, *Pleodendron*, *Rauwolfia*, *Rhizophora*, *Salix*, *Tecoma*, *Tetrorchidium*, *Tournefortia*, *Zanthoxylum*, monolete fern spores, trilete fern spores.

JAMAICA

Palynoflora only (see Additional note, Cuba)

Reference: Graham (1993).

Deep-time flora: Most specimens had to be named by an artificial system because of the age of the flora. Included were those similar to *Acrostichum*, *Pelliciera*, *Palmae*, *Bombacaceae*, *Sapindaceae*, *Onagraceae*, and *Mauritia*.