Tertiary evolution of Caribbean vegetation in the context of geologic and nearshore marine events

Alan Graham

Graham A 1996. Tertiary evolution of Caribbean vegetation in the context of geologic and nearshore marine events. *Palaeobotanist* **45** : 109-116.

Estimates of SST (sea surface temperature) during the Cenozoic are complicated by uncertainty as to the presence, extent, and effect of glaciers in the Paleogene, and by an emerging re-evaluation of the accuracy of foraminifera to precisely record changes in equatorial ocean water temperatures in the Neogene, especially at the last glacial maximum (18,000 yrs B.P.). If Paleogene marine temperatures were as warm as at present, Early Tertiary floras deposited at the ocean-continent interface should record vegetation comparable in ecological import to that of the present. The middle(?) to Late Eocene Gatuncillo flora from Panama (9° N latitude) is similar to the modern vegetation along the north (Atlantic) coast of southern Central America. This argues for the presence of limited glaciers, probably on Antarctica, to account for the increasing ^{18}O in the marine waters. Assuming that any cooling of low latitude SSTs in the late-glacial extended into early glacial times, at least to some extent, Neogene floras should reflect these cooler conditions. The Middle Pliocene (N20; 4-5 Ma) Paraje Solo palynoflora from coastal southeastern Mexico (~18° N latitude) suggests a MAT (mean annual temperature) at least 2°-3°C cooler than at present. The cause (s) likely involved continued decline in CO_2 concentration, threshold changes in ocean water circulation, upwelling, deposition just prior to closure of the Isthmus of Panama (~3.5-2.5 Ma) which strengthened poleward transport of ocean heat, and also orbitally-induced global lowering of temperatures. The temperature change suggested by the Middle Pliocene Paraje Solo palynoflora is about mid-way between the calculated ~5° C cooling by 18,000 yrs B.P., based on the $^{18}O/^{16}O$ ratios and strontium evidence from Barbados corals, and the CLIMAP (Climate Long-range Investigation and Mapping Program) estimate of stable equatorial SST about as warm as at present.

Key-words—Palaeopalynology, Neotropics, Palaeotemperature, Tertiary.

Alan Graham, Department of Biological Sciences, Kent State University, Kent, Ohio 44242, U.S.A.

साराँश

भूवैज्ञानिक एवं तटीय समुद्री घटनाओं के सन्दर्भ में कैरीबियन वनस्पति का तृतीयक कल्प में विकास

एलॅन ग्राहम

पश्चनूतन कल्प में ग्लेशियरों की उपस्थिति आदि के कारण नूतनजीवी काल में समुद्र की सतह का तापक्रम अन्वेषित करना काफी कठिन कार्य है। अगर पश्चनूतन काल में भी समुद्र का तापक्रम आज की ही तरह गर्म होता तो आज की ही भाँति तृतीयक वनस्पतिजात समुद्री महाद्वीप में परिरक्षित होता। पनामा से मध्य से अनंतिम आदिनूतन गेटनसिलो वनस्पतिजात दक्षिणी केन्द्रीय अमेरिका के उत्तर तट के साथ-साथ विद्यमान वर्तमान वनस्पति के ही समान है। इससे यह विदित होता है कि अन्टार्कटिका पर सीमित ग्लेशियर विद्यमान थे जिसके कारण समुद्री पानी में आक्सीजन 18 की मात्रा में वृद्धि हुई है। इन परिवर्तनों के समय कार्बन डाईऑक्साइड की सांद्रता में कमी, समुद्री पानी के बहाव आदि के कारण समुद्री गर्मी ध्रुवों की तरफ स्थानान्तरित हो गई।

INFORMATION from the study of paleovegetation is being used as validation data for sensitivity tests and long-term modeling of paleoclimates. This is necessary because until the models can accurately reflect known past climates (hindcast), little confidence can be placed in their predictions of future conditions. Two aspects of modeling Cenozoic paleoclimates have proven particularly troublesome. First, there has been uncertainty about tropical marine SSTs during the Eocene. One method for determining paleotemperatures is based on the ratio of $^{18}O/^{16}O$ in the shells of marine invertebrates, which varies with the temperature of the ambient water—more ^{18}O is taken up as the water cools. Temperature values are assigned to the ratios by callibration with laboratory standards. A complication is that the equilibrium of the oxygen isotopes also varies with ice volume. The lighter ^{16}O differentially evaporates from the ocean surface, but during non-glacial times it is returned by precipitation, runoff, and ground water seepage. A nearly uniform distribution of the isotopes is maintained among the various marine basins by ocean water circulation. In the absence of glaciers a change in the ratio can be attributed to temperature. In glacial times, however, much of the ^{16}O-rich water is stored in the cryosphere and the relative proportion of ^{18}O increases in the ambient water. If there is agreement about the presence of glaciers, compensation can be made in assigning temperature values to the ratios. At the last glacial-interglacial interval the amplitude was ~1.7%, and an estimated ~0.4% has been attributed to cooling and 1.3% to ice-volume effect (Shackleton & Duplessy, 1986). If there is uncertainty, and there is for the Paleogene, this allows a wide range in the estimate of SST. For tropical regions during the Eocene this range is from ~28° C (about the same as at present) assuming the presence of some ice, to ~18°-20° C (or 8°- 10° C cooler than at present) assuming ice-free conditions. Evidence is accumulating for small, temporary glaciers on Antarctica in the middle to Late Eocene, favouring an interpretation of warm equatorial climates. This is consistent with other emerging paleontological data (Adams *et al.*, 1990). A data base is also accumulating for terrestrial paleovegetation deposited in tropical coastal environments, including the middle(?) to Late Eocene Gatuncillo flora of Panama (~9° N latitude; Graham, 1985).

A second problem in modeling global paleoclimates has been establishing the temperature history of equatorial regions during recent glacial times. The initial effort to reconstruct this history was CLIMAP (climate Long-Range Investigation and Mapping Program, 1976, 1981) based, in part, on the temperature requirements of various planktic groups (primarily foraminifers along with coccolithophores, diatoms and radiolarians). One conclusion was that while the rest of the world cooled by ~5° C at the last glacial maximum (18,000 yrs B.P.), the lower latitudes remained about the same. This has complicated understanding both the record and the mechanism of long-term temperature fluctuations because when models adequately account for cooling at the poles, they also predict a similar cooling for the tropics (Rind & Peteet, 1985). Also, pollen records suggest a cooling of ~6°-8° C in the highlands of Colombia (van der Hammen & González, 1960; Hooghiemstra, 1984, 1989; Hooghiemstra & Sarmiento, 1991) that extended into the lowlands (~4°-6° C; Absy, 1979, 1982; Absy & van der Hammen, 1976; Colinvaux, pers. comm., 1995).

The possibility that foraminifera in the CLIMAP study may be able to adjust to temperature changes and, therefore, not faithfully record temperature variations, is raised by a study of corals from Barbados (~13° N latitude; Guilderson *et al.*, 1994). The isotopes $^{18}O/^{16}O$ in the calcium carbonate walls suggest a cooling of ~5° C at 19 ka. An independent check was made by measuring the strontium in the carbonate. Strontium replaces the chemically similar calcium at a rate dependent on the water temperature, and thermal ionization mass spectrometry allows accurate measurement of the amounts of strontium present. Temperature values were similar to those obtained from the oxygen isotope ratios. These techniques also have potential sources of error (Anderson & Webb, 1994), and establishing precise SST in the tropics during the Neogene requires further investigation.

Although the studies noted above are concerned with climates at the last glacial maximum, the results should apply generally throughout recent glacial history when conditions were similar, or fluctuated within approximately comparable ranges. Glaciers became a more widespread and sustained feature of Antarctica beginning in the Oligocene, as marked by a sharp drop in sea level at ~30 Ma (Haq *et al.*, 1987; Vail & Hardenbol, 1979). Further cooling occurred in the middle Miocene, initiating Arctic glaciations, and this trend intensified in the middle to Late Pliocene when ice volume reached about one-half to two-thirds that of the Quaternary glaciations (Crowley & North, 1991, p. 203; Curry & Miller, 1989; Raymo *et* *al.*, 1989, 1992; Repenning & Brouwers, 1992). The Greenland ice sheet was already forming at ~3.2 Ma (millions of years ago; Leg 105 Shipboard Scientific Party, 1986).

A series of Tertiary palynofloras are preserved in coastal lignites, clays and silts from the Gulf/Caribbean region (for their geographic and stratigraphic distribution, see Graham, 1992a, 1993a, 1994b). This data base has been used to address various aspects of neotropical paleoenvironments and biogeography—e.g., paleoaltitudes; timing of the closure of the isthmian land bridge; marine water temperature during the Eocene; and the history of various lineages (Leguminosae, Compositae) and vegetation types (mangrove, tropical dry forest; Graham, 1989, 1992a, b, 1994a, 1995, in press; Graham & Dilcher, in press). One of these floras is from the Middle Pliocene Paraje Solo Formation of southeastern Veracruz, Mexico. It was deposited in a coastal setting and was both influenced by, and reflected environmental conditions in the adjacent marine environment. The flora provides an opportunity for testing the hypotheses of warm versus cool low latitude SST during the early stages of polar glaciation. For both the middle(?) to Late Eocene Gatuncillo assemblage, and the Middle Pliocene Paraje Solo flora, paleoenvironments presently must be reconstructed via the modern analog method from pollen and spore data; there are no macrofossil floras known from the region sufficient to make independent assessments based on leaf physiognomy. Thus, there is some latitude in the estimates of paleotemperature, and conservative values are presented pending further data.

MATERIAL AND METHODS

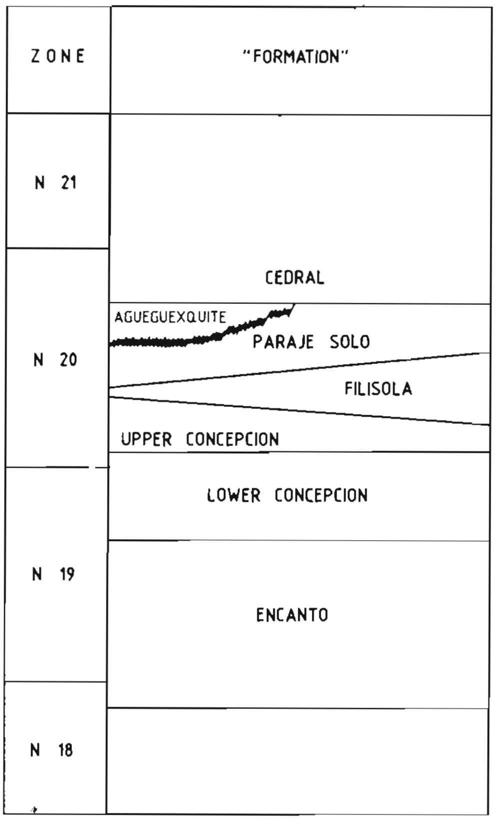
Processing procedures and other methods for studying palynomorphs from the Late Eocene Gatuncillo and the Middle Pliocene Paraje Solo lignites and associated clays, siltstones, and fine-grained sandstones have been described previously (Graham, 1976, 1985). The samples were processed by standard palynological techniques (Gray, 1965), involving HCl for removal of carbonates, HF for removal of silicates, and HNO_3 for oxidation of lignins and other organic debris. Identification of the palynomorphs was through comparisons with a modern reference collection of ~24,000 slides, with strongest representation of neotropical species. Fifteen samples were collected from the Gatuncillo Formation near Alcalde Diaz, 87 palynomorph types were recovered, and 47 were identified. A collection of 55 samples was made from the Paraje Solo Formation at 6 localities along the Ferrcarril del Sureste (sites 1, 2, 3) and from roadcuts along Mexico 180 (sites 4, 5, 6) near Coatzacoalcos in southeastern Veracruz, Mexico, One hundred and twenty four palynomorph taxa were recovered, and 106 were identified.

DISCUSSION

The Gatuncillo flora— The Gatuncillo flora has been discussed previously with regards to the oxygen isotope paleotemperature record (Graham, 1994a), and will be only briefly summarized here. The most important results relevant to the present discussion are the distribution of modern communities most similar to the paleocommunities, and the ecological conditions (especially temperature) under which the individual components currently grow. The taxa represented by fossil palynomorphs sort into three principal paleocommunities— tropical wet, tropical moist, and premontane wet forests. None of the modern analog assemblages extend latitudinally into temperate environments or range altitudinally into cool montane habitats. The most similar modern communities are found along the north (Atlantic) coast of Central America, including a zone between Gatun Lake and Piña, immediately adjacent to the collecting site. Thus, at the level of vegetation type the implied paleoenvironments of the Gatuncillo assemblage are comparable to those of the present in the region—MAT 28° C, with a mean annual minimum of 21.1°C. Among individual taxa, all of the principal components grow primarily or only in frostfree climates. These include *Ceratopteris* (15%), *Pelliceria* (11%), *Rhizophora* (10%), *Crudia* (3.5%), *Combretum/Terminalia* (3%), *Lisianthus* (2.5%), *Euqenia/Myrcia* (1%), *Pteris* (0.5%), and *Ficus* (0.5%). For example, the northernmost distribution of *Rhizophora mangle* in North America is to central peninsula Florida, and it is clearly associated with a SST minimum of 27° C. Thus, the most numerous individual components of the Gatuncillo flora also indicate that paleotemperatures along the coast were not significantly different from those of the present.

This would mean that any increase in the $^{18}O/^{16}O$ ratio was due, at least in part, to early glaciation and not exclusively to colder waters. This is consistent with recent paleontological studies and with evidence for local and temporary late Middle Eocene glaciers on Antarctica (Adams *et al.*, 1990).

The Paraje Solo Flora—In southeastern Mexico the picture from the Middle Pliocene Paraje Solo Formation is quite different. The sequence of sediments is typical for paralic (marine coastal) and paludal (swamp) environments where cycles of autochthonous lignite, clay, silt, fine-grained and progressively coarser sandstones are deposited with changes in relative sea level. Palynomorphs were recovered from all but the coarser sandstones. The exposures range from ~0.6 to ~6 m thick, and sampling intervals were ~15 cm, but varied to include all sediment types at each exposure. Deposition is typically rapid in these tropical coastal *Rhizophora* (mangrove) environments. Although there is some variation in palynomorph content between sites, mostly with regards to *Rhizophora* pollen (Graham, 1976, table 1), for purposes of comparing modern versus paleocommunities and climates, the assemblage is considered as a unit.



Text-figure 1—Stratigraphic position of the Paraje Solo Formation in relation to other in the Isthmian Salt Basin of southeastern Mexico (from a Machain-Castillo, 1985).

The Paraje Solo Formation is underlain by the Upper Conception Formation, and is overlain and partly contemporaneous with the Agueguexquite Formation (Text-figure 1). The latter contains a diverse ostracode fauna typical of the N20 marine zone (Machain-Castillo, 1985). Calcareous nannofossil and planktic foraminifera indicate that "the Agueguexquite Formation must be considered to be of Middle Pliocene age, and it probably belongs just above the precise middle of Zone N20" (Akers, 1979; Akers & Koeppel, 1973). Thus, the Paraje Solo assemblage represents the vegetation and coastal environments at ~4-3 Ma. The question is whether it reflects SSTs similar to those of the present, or cooler than at present and consistent with the emerging coral data from Barbados.

Modern vegetation— The study site is located at the junction of the southern Sierra Madre Oriental and the eastern terminus of the Transvolcanic Belt near Coatzacoalcos, Veracruz, Mexico. The region includes the highest peaks in Mexico-Pico de Orizaba (5650 m), Popocatepetl (5450 m), and Ixtaccihuatl (5280 m). The Sierra Madre Oriental began contributing sediments to the Veracruz Basin in the Late Cretaceous/Paleocene (Helu *et al.*, 1977), while the Transvolcanic Belt was uplifted in the Early Tertiary, with major elevations attained in the Late Miocene, Pliocene, and Pleistocene (de Cserna, 1989; Demant, 1978; Ferrusquia-Villafranca, 1993; Nixon, 1982; Thorpe, 1977). Thus, a diversity of habitats has been available throughout the Neogene. The coast is fringed with mangroves (manglar; *Laguncularia*, *Rhizophora*), bordered immediately inland by the lowland tropical rain forest (selva alta perennifolia). The latter is a multi-dominant community of *Bernoulia*, *Brosimum*, *Calophyllum*, *Dialium*, *Ficus*, *Inga*, *Lonchocarpus*, *Nectandra*, *Pouteria*, *Pseudolmedia* and others (Gómez-Pompa, 1973; Wendt, 1993). In the lower montane zone there is a gradational series of forests (selvas) defined by height and degree of deciduousness which correlate with increasing altitude and dryness. At an elevation of ~1000-2000 m there are woods (bosques) composed of *Pinus* (pine), *Quercus* (oak; bosque de pino y encino) and *Liquidambar* (sweetgum; bosque caducifolio). Near timberline, other species of *Pinus* are mixed with *Abies religiosa* (fir; bosque de oyamel), and this community extends to an alpine tundra (paramo).

The Pliocene vegetation—The identified palynomorphs are listed in Table 1, and these have been arranged into paleocommunities according to the modern associations recognized by Gomez-Pompa (1973; table 2). Mangrove vegetation is represented by abundant *Rhizophora*, reaching 96 per cent at one locality, and by *Laguncularia*. Although the tropical rain forest appears well-represented by the numerous taxa listed in Table 2, it is noteworthy that all of these presently range through several communities and none are the characteristic or defining members of the rain forest. The rain forest was poorly developed to absent as shown by the absence of pollen from all of the dominants. Pollen of *Pinus*, *Liquidambar*, and *Quercus* was found, which documents the presence of the mid-altitude bosque de pino y encino and bosque caducifolio. *Abies* pollen as also recovered from a high-altitude bosque de oyamel. Today *Abies* typically grows at elevations above 2400 m and it does not now occur in the vicinity of the Paraje Solo locality. In addition, *Picea* (spruce) pollen was present. These are well-preserved unfragmented grains and show no effect of long-distant transport or redeposition. *Picea* in Mexico now grows only at high elevations in the mountains to the north, fully 1000 km removed from the depositional site.

Tabel 1— Palynomorphs identified from the Paraje Solo Formation, southeastern Veracruz state, Mexico. Listing is from the revised composition (Graham, 1993b) of the original study (Graham, 1976). Numbers in parentheses are the highest percentages encountered among the 6 sites; no number means percentage was less than 0.5%

- Psilotaceae
  - *Psilotum* (7%)
- Lycopodiaceae
  - *Lycopodium*
- Selaginellaceae
  - *Selaginella*(1%)
  - Cyatheaceae
  - *Alsophila*
  - *Cyathea*
  - *Cnemidaria* (*Hemitelia*) (4%)
  - *Sphaeropteris/Trichipteris*
- Dryopteridaceae
  - *Lomariopsis* (2%)
- Gleicheniaceae
  - *Dicranopteris*
- Polypodiaceae (other monolete fern spores) (48%)
- Pteridaceae
  - *Ceratopteris* (2%)
  - *Pteris*
- Pinacae
  - *Abies*
  - *Picea* (1%)
  - *Pinus* (1%)
- Podocarpaceae
  - *Podocarpus* (2%)
- Araceae
  - *Spathiphyllum* (1%)
- Cyperaceae
- Dioscoreaceae
  - *Rajania* (7%)
- Gramineae (45%)
- Liliaceae
  - *Smilax* (2%)
- Palmae
  - cf. *Astrocaryum*
  - cf. *Attalea* (6%)
  - cf. *Brahea* (6%)
  - cf. *Chamaedorea* (2%)
  - cf. *Maximiliana* type
- Acanthaceae
  - *Bravisia* (1%)
  - *Justicia* (1%)
- Amaranthaceae
  - *Irisene*
- Amaranthaceae/Chenopodiaceae
- Anacardiaceae
  - *Comocladia* (1%)
- Aquifoliaceae
  - *Ilex* (1%)
- Betulaceae
  - *Alnus*
- Boraginaceae
  - *Tournefortia*
- Burseraceae
  - *Bursera* (4%)
  - *Protium* (5%)
- Chloranthaceae
  - *Hedyosmum* (2%)
- Combretaceae
  - *Combretum/Terminalia* (25%)
  - *Laguncularia* (56%)
- Compositae (27%)
- Dichapetalaceae
  - *Dichapetalum*
- Euphorbiaceae
  - *Alchornea* (4%)
  - cf. *Bernaridia*
  - cf. *Sapium* (3%)
  - cf. *Stillingia*
  - cf. *Tetrorchidium* (1%)
  - cf. *Tithymalus* (1%)
- Fagaceae
  - *Quercus* (34%)

- Flacourtiaceae
  - *Casearia* (1%)
  - *Laetia*
- Guttiferae
  - *Symphonia*
- Hamamelidaceae
  - *Liguidambar*
- Juglandaceae
  - *Juglans*
  - *Alfaroa/Oreomunnea* (13%)
- Lecythidaceae
  - *Gustavia*
- Leguminosae
  - *Acacia* (1%)
  - *Desmanthus* (1%)
  - *Mimosa*
- Lentibulariaceae
  - *Utricularia* (1%)
- Loranthaceae
  - *Struthanthus* (8%)
- Lythraceae
  - *Cuphea*
- Malpighiaceae
  - cf.*Malpighia* (6%)
  - cf.*Mezia* (?) type (1%)
  - cf.*Hiraea*
- Malvaceae
  - *Hampea/Hibiscus* (2%)
- Meliaceae
  - *Cedrela* (2%)
  - *Guarea*
- Myricaceae
  - *Myrica* (4%)
- Myrtaceae
  - *Eugenia/Myrcia* (16%)
- Onagraceae
  - *Ludwigia* (2%)
- Passifloraceae
  - *Passiflora* (1%)
- Polygalaceae
- cf. *Securidaca*
  - cf. *Bredemeyera* (1%)
- Polygonaceae
  - *Coccoloba* (9%)
- Ranunculaceae
  - *Thalictrum* (1%)
- Rhizophoraceae
  - *Rhizophora* (96%)
- Rubiaceae
  - cf. *Alibertia* (1%)
  - *Borreria*
  - *Faramea* (2%)
  - *Terebrania* (1%)
- Salicaceae
  - *Populus*
- Sapindaceae
  - *Allophylus*
  - *Cupania*
  - *Matayba (1%)*
  - *Meliosma* (1%)
  - cf. *Paullinia* (1%)
  - *Serjania* (1%)
- Serculiaceae
  - *Buettneria*
- Theaceae
  - *Cleyera*
- Thymelaeaceae
  - *Daphnopsis* (1%)
- Tiliaceae
  - *Mortoniodendron*
- Ulmaceae
  - *Celtis* (3%)
  - *Ulmus* (1%)

Table 2—Paleocommunities of the Paraje Solo assemblage. Genera are placed according to their typical occurrence (s) and may range through several vegetation types

Needle-leaved and scale-leaved forest (including pine and pineoak forests):

Abies, *Picea*, *Pinus*, *Alchornea*, *Alnus*, *Quercus*, cf. *Sapium*, *Coccoloba*, *Smilax*, cf. *Stillingia* (*Cyathea*, *Liquidambar* and *Myrica* occasionally occur in a typically low-altitude forests).

Broad-leaved (oak) forest:

Alchornea, *Coccoloba*, *Quercus*, cf. *Sapium*

Deciduous (oak-*Liquidambar*) forest:

Psilotum, *Lycopodium*, *Sphaeropteris/Trichipteris*, *Selaginella*, *Alsophila*, *Cyathea*, *Pinus*, *Podocarpus*, *Alchornea*, *Alnus*, cf. *Chamaedorea*, *Cleyera*, *Dichapetalum*, *Alfaroa/ Oreomunnea*, *Eugenia*, *Guarea*, *Hampea*, *Hedyosmum*, *Ilex*, *Iresine*, *Juglans*, *Justicia*, *Liquidambar*, *Meliosma*, *Myrica*, *Populus*, *Quercus*, *Struthanthus*, *Tournefortia*, *Ulmus*

High evergreen selva:

Lycopodium, *Sphaeropteris/Trichiptris*, *Podocarpus*, *Alchornea*, *Allophyllus*, cf. *Astrocaryum*, *Bursera*, *Casearia*, *Cedrela*, cf. *Chamaedorea*, *Cupania*, *Faramea*, *Guarea*, *Gustavia*, *Hampea*, *Hibiscus*, cf. *Hiraea*, *Iresine*, *Matayba*, *Mortoniodendron*, *Myrcia*, cf. *Paullinia*, cf. *Sapium*, *Spathiphyllum*, *Symphonia*, *Terminalia*, cf. *Tetrorchidium*

High semi-evergreen selva:
Lycopodium, *Selaginella*, *Cyathea*, *Alchornea*, cf. *Bernardia*, *Bursera*, *Casearia*, *Cedrela*, cf. *Chamaedorea*, *Cupania*, *Daphnopsis*, *Faramea*, *Hampeo*, *Hibiscus*, *Ilex*, *Iresine*, cf. *Paullinia*, *Protium*, *Quercus*, *Rajania*, cf. *Sapium*, *Securidaca*, *Spathiphyllum*, cf. *Tetrorchidium*, *Ulmus*

Low deciduous selva:
cf. *Acacia*., cf. *Brahea*, *Bursera*, *Casearia*., *Celtis*, *Combretum*, *Cupania*, *Daphnopsis*, *Eugenia*, *Ilex*, cf. *Sapium*, *Comocladia*

Swamp/Aquatic vegetation
Ceratopteris, *Bravaisia*, *Ludwigia*, *Utricularia*

Mangrove swamp
Hibiscus, *Laguncularia*, *Ludwigia*, *Mimosa* (*M. pigra* type), *Rhizophora*, cf. *Sapium*

The cause for the differences between the Paraje Solo and the modern vegetation is undoubted complex and multi-faceted. Sea levels were an estimated 35 m higher along the Atlantic coast of the U.S.A. during the mid-Pliocene (Dowsett & Cronin, 1990; Krantz, 1991), and extended further inland than at any time since the Eocene (Cronin, 1991). This would have certainly restricted habitats available for the lowland tropical rain forest, but it would not account for the presence of *Picea* or the representation of upland to highland elements in the fossil flora. The explanation must include some lowering of temperatures which would contribute to the absence or poor development of the rain forest, the downward shift in ecotones bringing the upland and highland communities into closer depositional range of the accumulating coastal sediments, and the presence of *Picea*. The extent of this lowering can only be approximated, based on the present ecological requirements and altitudinal distribution of the modern genera and communities. The estimate is a minimum of 2-3° C lower than the present interglacial MAT (Graham, 1989). The MAT at Coatzacoalcos now is 25.3° C (annual range 22°-27° C), so the maximum mid-Pliocene MAT along the ocean margin at ~18° N latitude is estimated at ~23°C. Although the sensitivity of the method is not precise, the vegetation change alone reflects parameters different in the Middle Pliocene compared with the present interglacial. The ostracode assemblages in adjacent formations were discussed with reference to paleodepths rather than paleotemperatures (Machain-Castillo, 1985).

To the extent that these data are relevant to tropical Atlantic Ocean water temperatures, they are difficult to reconcile with proposed near-constant values throughout the Neogene. SST which had already declined by a minimum of ~2°-3° C in the mid-Pliocene are more consistent with the calculated 5° C cooling during the various glacial maxima, as at 18,000 B.P. A question still open is the relative importance of ocean circulation, coastal upwelling, closure of the Isthmus of Panama with greater poleward transport of heat beginning ~3.5 Ma (Willard *et al.*, 1993), and Milankovitch variations in determining temperatures at the ocean-continent interface. Sea levels higher by ~35 m, at least along the Atlantic coast of the United States, would argue for climates warmer than at present and support the view of a Middle Pliocene warm interval. Local cooling, as along the coast of southeastern Mexico would be ascribed to changes in ocean circulation and to upwelling.

However, the probability that all the differences between the fossil and modern vegetation can be ascribed to ocean circulation upwelling, and closure of the Isthmus is unlikely. These conditions have generally prevailed after ~3.4 Ma and they do not presently allow for the presence of *Picea*, or for upland and highland communities in the lowlands. This suggests that MAT was in fact lower that at present. The apparent difference between the sea level and paleotemperature record, based on the Paraje Solo flora, may be due to lag time between temperature change, glaciation, and the response of terrestrial vegetation.

The data from the Late Eocene Gatuncillo flora of Panama supports the emerging view of warm equatorial waters and some continental ice during parts of the Paleogene, while results from the Paraje Solo study are consistent with independent evidence for cooling equatorial waters during the Neogene. If these conclusions are sustained by future studies, fossil lowland tropical floras can be assumed to reflect SST trends in the nearshore marine realm. This provides one more approach for assessing models of the long-term history of ocean paleoenvironments.

ACKNOWLEDGEMENTS

The author gratefully acknowledges comments on the manuscript by Tom Cronin and Thomas P. Guilderson, and the review by C.M. Clapperton. Research was supported by NSF grant DEB-9206743.

REFERENCES

Absy ML 1979. A palynological study of Holocene sediments in the Amazon Basin. *Thesis*, Univ. Amsterdam, The Netherlands.

Absy ML 1982. Quaternary palynological studies in the Amazon Basin. *In* Prance GT (Editor)—*Biological diversification in the tropics*: 67-73. Columbia Univ. Press, N.Y.

Absy ML & van der Hammen T 1976. Some palaeoecological data from Rondônia, southern part of the Amazon Basin. *Acta amazonica* **6**: 293-299.

Adams CG, Lee DE & Rosen BR 1990. Conflicting isotopic and biotic evidence for tropical sea-surface temperatures during the Tertiary. *Palaeogeogr. Palaeoclimat. Palaeoecol.* **77**: 289-313.

Akers WH 1979. Planktic foraminifera and calcareous nannoplankton biostratigraphy of the Neogene of Mexico. *Tulane Studies Geol. Paleontol.* **15**: 1-31.

Akers WH & Koeppel PE 1973. Age of some Neogene formations, Atlantic coastal plains, United States and Mexico. *Proc. Symposium on Calcareous Nannofossils Gulf Coast Sect. Soc. Econ,. Poaleontologists Mineralogists*: 80-93.

Anderson DM & Webb RS 1994. Ice-age tropics revisited. *Nature* **367**: 23-24.

CLIMAP Project Members 1976. The surface of the ice-age earth. *Science* **191**: 1131-1137.

CLIMAP Project Members 1981. Seasonal reconstruction of the earth's surface at the last glacial maximum. *Geol. Soc. Am. Map Chart* Ser. MC-36.

Cronin TM 1991. Pliocene shallow water paleoceanography of the North Atlantic Ocean based on marine ostracodes. *In*: Cronin TM & Dowsett HJ (Editors)—*Pliocene climates*. *Quaternary Science Rev.* **10**: 175-188.

Crowley TJ & North GR 1991. *Paleoclimatology*. Oxford University Press, Oxford.

Curry WB & Miller KG 1989. Oxygen and carbon isotopic variation in Pliocene benthic foraminifera of the equatorial Atlantic. *In*: Ruddiman WF *et al.* (Editors) *Ocean drilling program scientific results* **108**: 157-166.

de Cserna A 1989. An outline of the geology of Mexico. *In*: Bally AW & Palmer AR (Editors)— *The geology of North America, an overview*: 233-264. Geol. Soc. Amer., Boulder Co.

Demant A 1978. Caracteristicas del Eje Neóvolcanico Transmexicano y sus problemas de interpretacion. *Revista* Inst. *Geol., Univ. Nacl. Auto. Mex.* **2**; 172-187.

Dowsett HJ & Cronin TM 1990. High eustatic sea level during the middle Pliocene: evidence from the southeastern U.S. Atlantic Coastal Plain. *Geology* **18**: 435-438.

Ferrusquia-Villafranca I 1993. Geology of Mexico: a Synthesis. *In*: Ramamoorthy TP, Bye R, Lot A & Fa J (Editors)— *Biological diversity of Mexico, origins and distribution* : 3-107. Oxford Univ. Press, Oxford.

Gomez-Pompa A 1973. Ecology of the vegetation of Veracruz. *In*: Graham A (Editor)— Vegetation and vegetational history of Northern Latin America: 73-148. Elsevier Scientific Publ. Co., Amsterdam.

Graham A 1976. Studies in neotropical paleobotany. II. The Miocene communities of Veracruz, Mexico. *Ann. Miss. bot. Gdn* **63**: 787-842.

Graham A 1985. Studies in neotropical paleobotany. IV. The Eocene communities of Panama. *Ann. Miss. bot. Gdn* **72**: 504-534.

Graham A 1989. Late Tertiary paleoaltitudes and vegetational zonation in Mexico and Central America. *Acta bot. Neerl.* **38**:417-424.

Graham A 1992A. Utilization of the isthmian land bridge during the Cenozoic— paleobotanical evidence for timing, and the selective influence of altitudes and climate. *Rev. Palaeobot. Palynol.* **72**: 119-128.

Graham A 1992b. The current status of the legume fossil record in the Caribbean region. *In*: Herendeen PS & Dilcher DL (Editors)— *Advances in Legume Systematics* Part 4. *The Fossil record* : 161-167. Royal Botanic Gardens, Kew.

Graham A 1993a. 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* Wright RM & Robinson E (Editors)— *Biostratigraphy of Jamaica. Geol. Soc. Amer. Mem.* **182**: 443-461.

Graham A 1993b. Historical factors and biological diversity in Mexico. *In* Ramamoorthy TP, Bye R, Lot A, & Fa J (Editors)— *Biological diversity of Mexico, origins and distribution*: 109-127. Oxford Univ. Press, Oxford.

Graham A 1994a. Neotropical Eocene coastal floras and $^{18}O/^{16}O$- estimated warmer vs. cooler equatorial waters. *Amer. J. Bot.* **81**: 301-306.

Graham A 1994b. Neogene palynofloras and terrestrial paleoenvironments in northern Latin America. *In*: Thompson RS (Editor)— *Pliocene terrestrial environments and data/model comparisons*: 23-40. U.S. Geol. Surv. Open-File Report 94-23.

Graham A 1995. Diversification of Gulf Caribbean mangrove communities through Cenozoic time. *Biltropica* **27**: 20-27.

Graham A. A contribution to the geologic history of the Compositae. *R. bot. Gdn Kew* (in press).

Graham A & Dilcher DL. The Cenozoic record of the tropical dry forest in northern Latin America and the southern United States. *In*: Mooney HA & Bullock SH (Editors)— *The tropical dry forest*. Cambridge Univ. Press, Cambridge. (in press).

Gray J (Coordinator) 1965. Palynological techniques. *In*: Kummel B & Raup D (Editor)— *Handbook of paleontological techniques*: 471-706. W. H. Freeman & Co., San Francisco.

Guilderson T, Fairbanks R & Rubenstone J 1994. Tropical temperature variations since 20,000 years ago: modulating interhemispheric climate change. *Science* **263**: 663-665.

Haq BU, Hardenbol J & Vail PR 1987. Chronology of fluctuating sea levels since the Triassic. *Science* **235**: 1156-1157.

Helu PC, Verdugo V & Barcens R 1977. Origin and distribution of Tertiary conglomerates, Veracruz Basin, Mexico. *Am. Assoc. Petrol. Geol. Bull.* **61**: 207-226.

Hooghiemstra H 1984. Vegetational and climatic history of the High Plain of Bogota, Colombia: a continuous record of the last 3.5 million years. *Diss. Bot.* **79**: 1-368.

Hooghiemstra H 1989. Quaternary and Upper-Pliocene glaciations and forest development in the tropical Andes: evidence from a long high-resolution pollen record from the sedimentary basin of Bogota, Colombia. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **72**: 11-26.

Hooghiemstra H & Sarmiento G 1991. Long continental pollen record from a tropical intermontane basin: late Pliocene and Pleistocene history from a 540-meter core. *Episodes* **14**: 107-115.

Krantz DE 1991. A chronology of Pliocene sea-level fluctuations: The U.S. middle Atlantic coastal plain record. *In*: Cronin TM & Dowsett HJ (Editors)— *Pliocene climates Quaternary Sci. Rev.* **10**: 163-174.

Leg 105 Shipboard Scientific Party 1986. High-latitude palaeoceanography. *Nature* **230**: 17-18.

Machain-Castillo ML 1985. Ostracode biostratigraphy and paleoecology of the Pliocene of the Isthmian salt basin, Veracruz, Mexico. *Tulane Studies Geol. Paleontol.* **19**: 123-139.

Nixon GT 1982. The relationship between Quaternary volcanism in central Mexico and the seismicity and structure of subducted ocean lithosphere. *Bull.geol. Soc. Am.* **93**: 514-523.

Raymo ME, Hodell D & Jansen E 1992. Response of deep water circulation to initiation of northern hemisphere glaciations (3-2 Ma). *Paleoceanography* **7**: 645-672.

Raymo ME, Ruddiman WF, Backman J , Clement BM & Martinson DG 1989. Late Pliocene variation in northern hemisphere ice sheets and North Atlantic Deep Water circulation. *Paleoceanography* **4**: 413-446.

Repenning CA & Brouwers EM 1992. Late Pliocene-early Pleistocene ecologic changes in the Arctic borderland. *U.S. geol. Surv. Bull.* **2036**:37.

Rind D & Peteet D 1985. Terrestrial conditions at the last glacial maximum and CLIMAP sea-surface temperature estimates: are they consistent? *Quaternary Res.* **24**: 1-22.

Shackleton NJ & Duplessy J-C 1986. Temperature changes in ocean deep waters during the late Pleistocene. *Abstract, 2nd Internat. Conf. Paleoceanography, Woods Hole, MA*.

Thorpe RS 1977. Tectonic significance of alkaline volcanism in eastern Mexico. *Tectonophysics* **40**: T19-T26.

Vail PR & Hardenbol J 1979. Sea-level changes during the Tertiary. *Oceanus* **22**: 71-79.

van der Hammen T & Gonzalez E 1960. Upper Pleistocene and Holocene climate and vegetation of the 'Sabana de Bogota' (Colombia, South America). *Leidse geol. Meded.* **25**: 261-315.

Wendt T 1993. Composition, floristic affinities, and origins of the canopy tree flora of the Mexican Atlantic slope rain forests. *In*: Ramamoorthy TP, Bye R, Lot A, & Fa J (Editors)— *Biological diversity of Mexico, origins and distribution*: 595-680. Oxford Univ. Press, Oxford.

Willard DA, Cronin TM, Ishman SE & Litwin RJ 1993. Terrestrial and marine records of climatic and environmental changes during the Pliocene in subtropical Florida. *Geology* **21**: 679-682.