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Late tertiary paleoaltitudes and vegetational zonation in Mexico and Central America

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SUMMARY

During the middle Pliocene seven principal arborescent plant communities occupied the zone between sea level and the highest elevations of the eastern Transvolcanic Belt—manglar (mangrove swamps; *Rhizophora*), bosque caducifolio (deciduous or *Quercus*/*Liquidambar* woods), bosque de encino (oak woods; *Quercus*, both lowland tropical and upland temperate types), bosque de pino (pine woods; *Pinus*), bosque de pino y encino, and bosque de oyamel (high-altitude *Abies*/*Pinus* woods). The presence of *Picea*, now confined in Mexico to the northern mountains 1000 km distant from the fossil locality in south-eastern Veracruz state, and the poor representation of the selva alta perennifolia (tropical rain forest) suggest cooler mean annual temperatures estimated at 2–3°C below the present. A downward shift in ecotones of about 500–1000 m is suggested, with a maximum altitude in the region of about 2500 m (the present maximum is 5650 m; present altitudinal range of *Abies* in eastern Mexico is 2400–3600 m). In southern Central America (Costa Rica, Panama) all modern anologues of taxa recently reported from late Eocene and early Miocene palynofloras can be accommodated in a zone between sea level and 1200–1500 m (current maximum elevations *c.* 3500–4000 m). Tertiary temperature fluctuations were muted by the insular environment of proto-Central America, and altitudinal shifts in ecotones are not evident in the fossil floras.

Key-words: Central America, Mexico, paleoaltitudes, palynology, tertiary.

INTRODUCTION

The classical studies of van der Hammen and his associates (van der Hammen, 1961; 1962; 1963; 1964) on Cenozoic climatic changes and plant community zonation in northern South America provide a valuable context for interpreting vegetational history in adjacent regions. The area encompassed by the Gulf of Mexico–Caribbean Basins and surrounding lands (northern Latin America; Fig. 1) include, however, two separate paleophysiographic provinces with different tectonic, climatic, and biotic histories. The area of southern Mexico, and northern South America, have provided continental environments with significant physiographic relief throughout the mid- to late Tertiary, while the intervening area of southern Central America consisted of low-lying volcanic

This paper is dedicated to Professor Dr T. van der Hammen on the occasion of his 65th birthday.

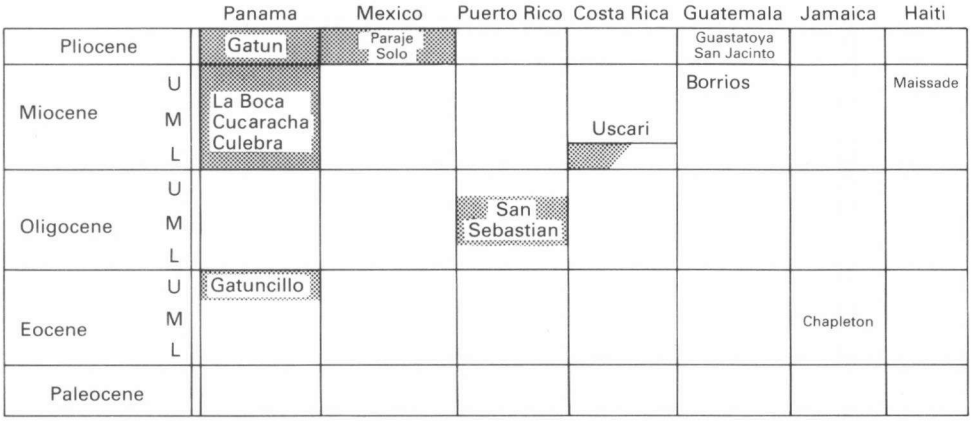

Fig. 1. Age and locality for Gulf/Caribbean Tertiary microfossil floras as part of the project, 'Studies in Neotropical Paleobotany'. (▒) Indicates the study is complete (Gatun flora in preparation).

islands and peninsulas. These differences influenced the impact of climatic change and consequent altitudinal shifts in vegetation within the two subregions of northern Latin America.

CENOZOIC PALEOPHYSIOGRAPHIC HISTORY

The Cordillera of western North America constitute a structural unit consisting of the Rocky Mountains of Canada and the USA, which branches in New Mexico to form the western Sierra Madre Occidental and the eastern Sierra Madre Oriental of Mexico (Bird, 1988). Deformation features associated with this system indicate it underwent principal uplift and development in the Paleocene and Eocene (Sutter, 1984), with tectonism diminishing in the middle and late Tertiary. The mountain chain marks the position of an older subduction zone, and to a lesser extent, is influenced by more recent overriding and compression against the east Pacific rise to the west. The system is truncated in south Central Mexico by the east–west trending Transvolcanic Belt, which includes the youngest and the highest peaks in northern Latin America (Pico de Orizaba, 5650 m; Popocatepetl, 5450 m; Ixtaccihuatl, 5280 m; Nevada de Toluca, 4560 m). Uplift began in the mid- to late Tertiary, with principal uplift in the late Miocene and Pliocene, and continuing to the present (Thorpe, 1977; Dermat, 1978; Nixon, 1982).

In Central America the mountains are primarily north–south trending cordillera centrals, and are also of mid-Tertiary and later age, but lower in elevation: Guatemala–Volcan Tajumulco, 4220 m; Costa Rica–Cerro Chirripo, 3820 m, Volcan Irazu, 3432 m; Panama–Volcan Baru, 3475 m. They have resulted from subduction along the middle American trench, and from compression forces acting on the Caribbean plate by movements of North and South America.

PRESENT-DAY ZONATION OF THE PLANT COMMUNITIES

The principal area of Mexico for which there is good eco-floristic data (Gómez-Pompa, 1973; Rzedowski, 1978; Puig & Bracho, 1987) and Tertiary paleobotanical information (Langenheim *et al.* 1967; Graham, 1976; Fig. 1) is east Central Mexico, particularly in the state of Veracruz. Twenty-two plant communities are recognized (Gómez-Pompa, 1973),

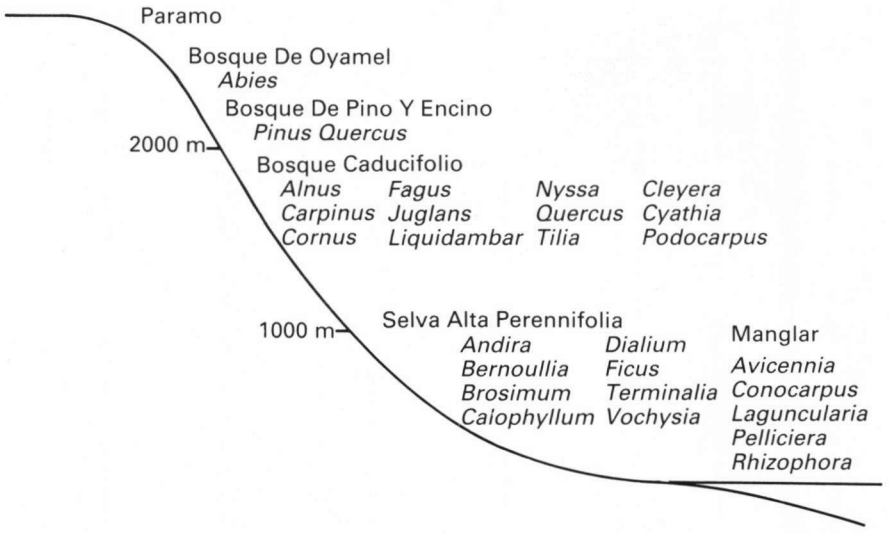

Fig. 2. Idealized transect from sea-level to higher elevations of the Transvolcanic Belt, Veracruz, Mexico, Generic names represent taxa identified from the middle Pliocene Paraje Solo microfossil flora near Coatzacoalcos, and are arranged by the principal or common occurrence of their modern analogues.

most of which can be represented in a generalized transect from sea-level up the eastern escarpment of the Mexican Plateau (eastern Sierra Madre Oriental/Transvolcanic Belt; Fig. 2). At several places the coast is fringed by mangroves (manglar; *Avicennia, Conocarpus, Laguncularia, Rhizophora*), including such associates as the ferns *Acrostichum* and *Hibiscus*, both with species tolerant of brackish water. Also present in the low-lying areas, but generally beyond the influence of marine or brackish waters, is coastal dune vegetation (principally grasses, *Andropogon, Eragrostis, Spartina, Uniola*; composites, *Bidens, Iva, Palafoxia*; and sedges, *Cyperus, Fimbristylis*), aquatic and floating communities (*Ceratopteris; Pachria, Utricularia*), and reed (*Typha*) and broad-leaved (*Thalia*; popal) fresh-water swamps which also frequently include various ferns and palms. On adjacent slopes is the selva alta perennifolia (tropical rain forest; *Bernoulia, Brosimum, Calophyllum, Dialium, Pseudolmedia*) which, in progressively drier habitats, grades into shorter forest types with increasing deciduousness (e.g. selva alta sub-perennifolia, selva mediana sub-perennifolia, selva baja sub-perennifolia, selva baja caducifolia). At elevations of about 1000 m the bosque caducifolio or deciduous forest begins, containing over 50 genera of trees and shrubs disjunct from the temperate eastern deciduous forest of the USA (*Acer, Alnus, Cornus, Fagus, Juglans, Platanus, Quercus, Tilia, Ulmus*), as well as more tropical elements (*Cyathea, Podocarpus, Alfaroa/oreomunnea, Clethra*). This forest type continues up to elevations of about 1200–1500 m, where various combinations of *Quercus* (encino) and *Pinus* (pino) occur; the bosque de pino y encino is the most widespread vegetation type in Mexico. At about 2800 m the mid-altitude pines are replaced by such high-altitude species as *P. montezumae* and *P. hartwegii*, and at the junction with the alpine tundra (paramo) are mixed with *Abies* (oyamel; Fig. 3).

A similar idealized transect through southern Central America (e.g. from Limon on the Caribbean coast to the Cerro de la Muerte, 3491 m, Cordillera de Talamanca, Costa Rica; Fig. 4) reveals a somewhat less extensive and complex biota because of reduced physiographical diversity, although in richness of species the flora of Costa Rica (51 100 km^2),

Fig. 3. Bosque de oyamel (*Pinus*/*Abies* forest) at volcan Popocatepetl, eastern Transvolcanic Belt, Mexico. Both genera are represented in the Paraje Solo assemblage; the understory grass is *Muhlenbergia*, a recent introduction, spreading as a consequence of overgrazing.

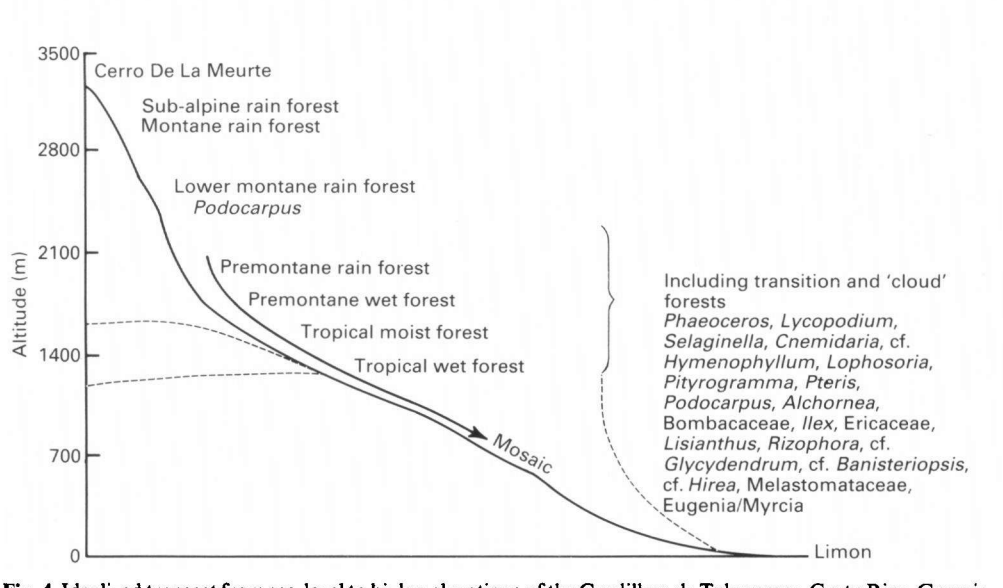

Fig. 4. Idealized transect from sea-level to higher elevations of the Cordillera de Talamanca, Costa Rica. Generic names represent taxa identified from the lower Micocene Uscari sequence flora in south-eastern Costa Rica, and arranged by the principal or common occurrence of their modern analogues; many genera range through more than one vegetation type. (– –) Represents estimated range for maximum altitudes during the lower Miocene, based on the present altitudinal occurrences of the modern genera.

with an estimated 8000 species, compares closely with the 7700 species in Veracruz (62 820 km^2).

Fig. 5. *Quercus*, with numerous bromeliad epiphytes, at Cerro de la Muerte in the high Cordillera de Talamanca, Costa Rica, montane rain forest life zone. The grass *Swallenchloa* is common as an understory ground cover.

Hartshorn (1983) recognizes 12 life zones for Costa Rica, and seven of these are encountered in a Limon-Cerro de la Muerte transect. In the lowlands, from sea-level to about 2000 m, is a mosaic of premontane wet forest, tropical moist forest (the most extensive of the Costa Rican communities, with the palm *Scheelea rostrata* common, and including mangrove swamps of *Rhizophora*, with *Pelliceria* on the Pacific coast), and the tropical wet forest, which is the most species-rich vegetation type in Costa Rica. The premontane rain forest occurs on the Atlantic slope of the Cordillera de Talamanca. At elevations between about 2000 and 3000 m is the lower montane rain forest with *Podocarpus* and *Quercus*, supporting bromeliads and other epiphytes, as the conspicuous elements of this life zone. The montane rain forest (Fig. 5) is generally found at elevations around 3000 m in the high Talamanca with the dwarf bamboo [*Swallenchloa (Chusquea) subtessellata* (Hitch.) McClure] common in the understory (Fig. 5). At the highest elevations, on restricted and isolated peaks (e.g. Chirripo, east of San Isidro), is the sub-alpine rain paramo.

Several of the mid-altitude communities and transition vegetation are often collectively referred to as cloud forests, but these are different in composition from the temperate cloud forest (bosque caducifolio) described for Veracruz. The northern temperate genera characteristic of that flora (*Abies, Pinus, Acer, Platanus, Ulmus*, etc.) mostly filter out in the region between Chiapas, Mexico and Bluefields in south-eastern Nicaragua (the southernmost distribution of *Pinus*, for example). Four genera (*Alnus, Ilex, Myrica, Quercus*) continue through Costa Rica to South America, with *Alnus* first appearing in northern South America *c.* 2 Ma and *Quercus c.* 900 ka (van der Hammen, 1978); *Liquidambar* does

occur in Costa Rica, but mostly as isolated trees rather than in *Quercus/Liquidambar* forests as found in Veracruz.

TERTIARY CLIMATIC CHANGES AND VEGETATION ZONES

The Tertiary Period opened with some of the warmest climates of Phanerozoic time. These conditions persisted until the late Eocene when the temperature dropped significantly, followed by a more gradual cooling until the middle Miocene when the temperature again fell dramatically. The middle (?) to late Eocene Gatuncillo microfossil flora of Panama (Graham, 1985), the lower Miocene Culebra, Cucaracha, and La Boca floras of Panama (Graham, 1988a,b, 1989a,b) and Uscari flora of Costa Rica (Graham, 1987a,b), and the middle Pliocene Paraje Solo flora of Mexico (Graham, 1976; Fig. 1) record the effects of these changes on vegetation zones in different parts of northern Latin America.

The impact of the cooling trend beginning in the middle Miocene is clearly evident in the middle Pliocene Paraje Solo flora from Veracruz. *Picea*, which currently only occurs in Mexico in the mountains 1000 km to the north, is present in the Paraje Solo assemblage. Also well-represented is the mid-altitude bosque caducifolio (deciduous forest), and higher altitude bosque de pino y encino (pine/oak forests), and the even higher altitude bosque de oyamel (pine/fir forests; Fig. 3), suggesting lower ecotones, bringing these upland forests into closer proximity to the coastal depositional basin for the Paraje Solo sediments. Lower temperatures are also consistent with the poor representation of the lowland tropical rain forest. It is estimated that a 2–3°C lowering of annual mean temperature (compared to present values), with a concomitant downward shift of ecotones by about 500–1000 m, would account for the differences between the modern and fossil vegetation. These values may be compared with estimates of a 2·5°C lowering for the late-glacial/early post-glacial (12 ka) of Panama (Bartlett & Barghoorn, 1973), 4·5°C for the Amazon lowlands at 33 ka (Liu & Colinvaux, 1985), and the 8°C lowering on the much higher altitude high plain of Colombia (van der Hamman & González, 1960).

In contrast, the late Eocene global temperature drop appeared to have little effect on the Gatuncillo flora from Panama. The microfossil assemblage is very similar to the modern vegetation along the Atlantic lowlands. The lower Miocene Culebra, Cucaracha, La Boca, and Uscari floras are also similar in composition to modern lowland communities. One factor accounting for the differences between the southern Mexico and southern Central American histories is the difference in paleophysiography between the two regions (Graham, 1989b). The Paraje Solo flora was deposited under continental conditions in a region with considerable physiographic relief. Thus the effects of a generally lowering temperature would be enhanced on vegetation already stressed along altitudinal gradients. Throughout the Tertiary the area of present-day southern Central America consisted of isolated volcanic islands and peninsulas. Analysis of the Uscari flora from Costa Rica, as well as the lower Miocene floras from Panama, reveals little evidence for high altitudes in the region; all taxa recognized from the floras can be accommodated in a zone between sea-level and about 1200–1500 m (Fig. 4). Thus the southern Central American floras were deposited under insular conditions in a region of moderate physiographic relief where the effects of a global cooling trend would be buffered by the surrounding ocean waters.

The importance of insular versus continental conditions, and moderate versus extensive physiographic relief, in the interpretation of Gulf/Caribbean Tertiary floras is further illustrated by the studies of van der Hammen and associates (van der Hammen &

González, 1960) in adjacent northern South America. Extensive highlands have existed in the Andres since at least Miocene times and the floras were deposited under continental conditions, comparable to the physical environment at the Paraje Solo locality. The late Cenozoic climatic fluctuations had a major effect on the zonal distribution of the communities, with treeline estimated to have been lower by about 1300 m in the high glacial stages of the Würm. Between these two regions is a zone where the Tertiary floras were deposited in estuaries along the margin of low-lying volcanic islands. The stabilizing effect of these physical conditions is clearly reflected in the composition of the microfossil assemblages, and are relevant to generalizations on Tertiary paleoclimatic changes and biotic response in the Gulf/Caribbean region.

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