Lower Miocene floras and biogeography of Central America

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Abstract — Four palynofloras of lower Miocene age have been studied from southern Central America. These are from the Uscari Sequence of southeastern Costa Rica and the Culebra, Cucaracha and La Boca Formations of central Panama. They reveal a generally low- to moderate-altitude vegetation (at or below about 1,200–1,500 m), lack of extensive dry to arid habitats (including savannahs), a composition (and climate) similar to that in existing lowland habitats in the region, and a flora with distinct Central and North American affinities. These features are consistent with emerging models of Gulf/Caribbean Cenozoic biogeography based on other, independent lines of enquiry showing the region to consist of low-lying volcanic islands, palaeotemperatures near present values (as opposed to the sharp lowering at the end of the Miocene), and isolation of the North and South American biota until approximately 3.0 Ma.

INTRODUCTION

A PRINCIPAL difficulty in obtaining an overall picture of Tertiary vegetation in the Gulf/Caribbean region has been the lack of adequate and reliable palaeobotanical data. Until recently there have been neither enough floras of the same age from different localities to give a regional view of the vegetation nor enough floras of sequential age from any single region to reflect changes in vegetation and environments through time. For example, the San Sebastian flora of Puerto Rico (Graham and Jarzen, 1969) is still the only one of middle to late Oligocene age published for all of Latin America. Similarly, the middle(?) to late Eocene Gatuncillo flora of Panama (Graham, 1985) is the only one of lower Tertiary age known for Mexico, Central America and the Antilles. There is a general recognition that tropical biotas are not only important in themselves but also central to an understanding of the origin and Cenozoic evolution of temperate floras and faunas, and several early models were proposed to explain their environmental and migratory history (e.g., stability of the rain forest and rain-forest environments). A review of the literature reveals, however, an almost complete lack of factual information upon which these models could have been based. Some early works were available (Berry, 1918, 1921a, b, 1923a, b; Hollick, 1928), but identification of many of these megafossils has proved so unreliable (Dilcher and Dolph, 1970; Dilcher and Mehrotra, 1969; Jones and Dilcher, 1980; see discussion in: Graham,

1987b) that the results were actually misleading rather than helpful. For this reason, a series of four lower Miocene floras from Costa Rica and adjacent Panama are of special interest (Fig. 1).

Recently, a number of important summaries have been published, based on a variety of approaches and representing independent lines of enquiry. These include palaeotemperature curves from DSDP cores (Savin, 1977; Savin and Douglas, 1985; Savin *et al.,* 1975), sea-level curves (Haq *et al.,* 1987; Vail and Hardenbol, 1979; Vail *et al.,* 1977), plate tectonic reconstructions (Dengo, 1973; Malfait and Dinkelman, 1972; and others), and study of marine invertebrates (Jones and Hasson, 1985) and terrestrial faunas (Marshall, 1985; Webb, 1985a, b). The plate tectonic data have been used as a framework for analysing zoogeographic patterns in Jamaica (Buskirk, 1985) and as a basis for a cladistic approach to Caribbean biogeography (Rosen, 1985). These studies are valuable in providing a context within which the meagre palaeobotanical data can be assessed and in setting parameters for interpretation.

THE USCARI SEQUENCE

PLANT MICROFOSSILS from this sequence were obtained from the outer matrix of a small collection of megafossils made by Woodring in 1917 and sent to E.W. Berry (1921a) for study. The specimens are at present in the col-
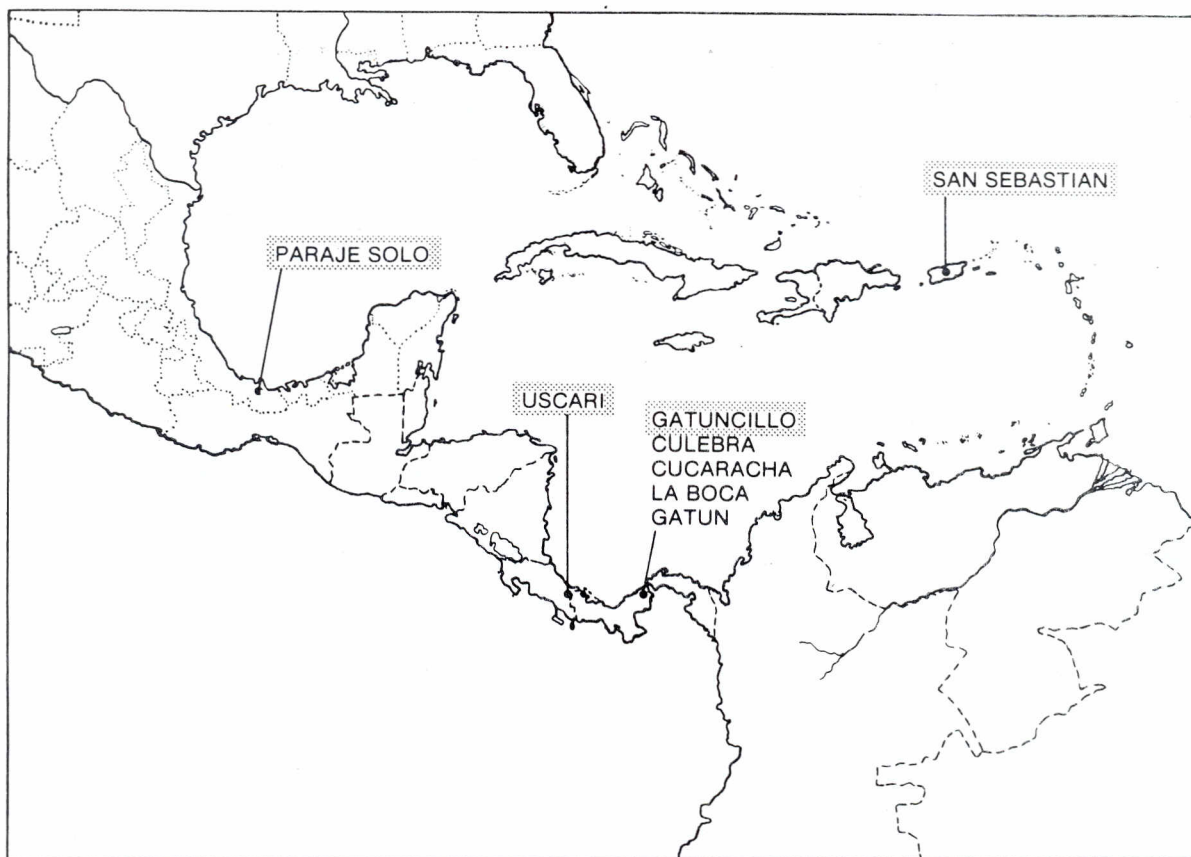
Figure 1. Location map for Tertiary microfossil floras in the Gulf/Caribbean region. Stippling indicates the study is complete (data for the Culebra and Cucaracha Formations are in press: Graham, 1988a, b). Gatuncillo — middle(?) to upper Oligocene; Uscari, Culebra, Cucaracha and La Boca — lower Miocene; Paraje Solo — upper Miocene; Gatun — Mio-Pliocene (possibly middle Pliocene: Vokes, personal communication, 1988).

lections of the Smithsonian Institution. The locality is in the Talamanca Valley in southeastern Costa Rica, near the Panamanian border. The geology of the area is poorly known, but current estimates are that the Uscari Sequence is probably early Miocene in age (Cooke *et al.,* 1943). Twenty-five taxa are recognized from the Uscari material.

THE CULEBRA FORMATION

THE CULEBRA Formation of central Panama consists of calcareous sandstones and siltstones with interbedded lenses of coalified lignite and lignitic shales. It was deposited near shore in an estuarine environment, and the lignites contain plant microfossils of fair preservation and diversity. In 1958 a well was drilled in front of Gold Hill, on the west side of the Canal (Hole No. GH-9; latitude 9° 02′ N, longitude 79° 38′ W). Fifty-seven samples were taken from along the core; 21 yielded palynomorphs and

11 were selected for study. Forty-one taxa are recognized from the Culebra material.

THE CUCARACHA FORMATION

THE CUCARACHA samples were obtained from outcrops on the southwestern side of the Cucaracha Reach section of the Gaillard Cut between Canal Stationings 1983 and 2010 (latitude 9° 01′ N, longitude 79° 38′ W). The section is composed mostly of bentonitic clay shales, tuffaceous siltstones, and sandstones with discontinuous lenses of lignite. Seven samples contained palynomorphs and 19 taxa have been identified.

THE LA BOCA FORMATION

THIS FORMATION also consists of typical near-shore, estuarine sediments, including mudstones, siltstones,

Table 1. Plant microfossils from lower Miocene formations in the Gulf/Caribbean region (Costa Rica and Panama).

	Usc.	Cul.	Cuc.	L.B.
Fungi				
Microthyrium type	●			
Bryophyta				
Phaeoceros	●			
Muscae	●			
Lycopsida				
Lycopodium	●	●	●	●
Selaginella	●	●	●	●
Filicineae				
cf. *Antrophyum*		●	●	●
Ceratopteris		●		
Cnemidaria	●			
Cyathea		●	●	●
Danaea		●		
cf. *Hymenophyllum*	●			
Lophosoria	●			
Lygodium		●		
Pityrogramma	●			
Pteris	●	●	●	●
Other monolete fern spores	●	●	●	●
Other trilete fern spores	●	●	●	●
Gymnospermae				
Podocarpus	●			
Angiospermae				
Acacia		●		
Alchornea	●	●	●	●
Allophyllus		●		
cf. *Banisteriopsis*	●			
Bombacaeae	●			
Casearia		●		

	Usc.	Cul.	Cuc.	L.B.
(Angiospermae, *cont.*)				
Cheno/Am		●		
Combretum/Terminalia		●		
Compositae	●	●	●	
Crudia			●	
Cryosophia type		●	●	●
Cupania		●		
Desmoncus type		●		
Dioscorea/Rajania		●		
cf. *Doliocarpus*		●		
Engelhardia (/*Alfaroa*)			●	
Ericaceae	●			
Eugenia/Myrcia	●	●	●	
cf. *Glycydendrum*	●			
Gramineae		●		●
cf. *Guazuma*		●		
Hampea/Hibiscus		●		●
cf. *Hiraea*	●			
Ilex	●	●	●	●
Lisianthus	●			
Malpighiaceae		●		●
Manicaria type		●	●	●
Matayba		●		
Melastomataceae	●			●
Pelliceria				●
Rhizophora	●	●	●	●
cf. *Rourea*		●		
Sabicea		●		
Sapium		●	●	
Sideroxylon		●		
Synechanthus type		●	●	●
Tetrorchidium		●	●	●
Utricularia				●

● = present

Table 2. Plant palaeocommunities from the lower Miocene of the Gulf/Caribbean region (Costa Rica and Panama).

Placement is according to the principal or most common occurrence(s), and most range through more than one community. Genera occurring in virtually all communities, or where placement is uncertain, are not included (e.g., the ascomycete fungus *Microthyrium*). Also omitted are taxa identified only to family or higher taxonomic groups (Muscae, Other monolete fern spores, Bombacaceae, etc.).

Floating or submerged fresh-water aquatic communities
>   *Ceratopteris, Utricularia*

Mangrove swamp
>   *Pelliceria, Rhizophora, Hibiscus, Sapium*

Tropical moist forest
>   *Lycopodium, Selaginella,* cf. *Antrophyum, Cyathea, Danaea, Lygodium, Pteris, Cryosophia* type, *Desmoncus* type, *Manicaria* type, *Synechanthus* type, *Acacia, Alchornea, Allphylus, Casearia, Combretum, Crudia, Cupania, Dioscorea,* cf. *Doliocarpus, Eugenia, Hampea, Matayba, Myrcia,* cf. *Rourea, Sabicea, Sapium, Terminalia, Tetrorchidium*

Tropical wet forest
>   *Phaeoceros, Lycopodium, Selaginella,* cf. *Antrophyum, Cnemideria, Danaea, Lygodium, Pteris, Cryosophia* type, *Desmoncus* type, *Manicaria* type, *Alchornea, Allophyllus,* cf. *Banisteriopsis, Casearia, Combretum, Crudia, Cupania, Dioscorea, Eugenia,* cf. *Gylydendrum, Hampea,* cf. *Hiraea, Matayba, Myrcia, Terminalia, Tetrorchidium*

Premontane wet forest
>   *Lycopodium, Selaginella,* cf. *Anthophyum, Cyathea, Danaea, Lygodium, Pteris, Cryosophia* type, *Manicaria* type, *Synechanthus* type, *Alchornea, Allophyllus, Casearia, Combretum, Crudia, Cupania, Dioscorea,* cf. *Doliocarpus, Eugenia,* cf. *Guazuma, Matayba,* cf. *Rourea, Sabicea, Sapium, Terminalia, Tetrorchidium*

Premontane moist forest
>   cf. *Antrophyum, Lygodium, Allphylus, Combretum, Dioscorea, Eugenia,* cf. *Guazuma, Hampea, Ilex, Matayba,* cf. *Rourea, Terminalia*

Lower montane moist forest
>   *Lycopodium, Selaginella, Cyathea,* cf. *Hymenophyllum, Lophosoria, Pityrogramma, Pteris, Manicaria* type, *Podocarpus, Engelhardia, Lisianthius*

Tropical dry forest
>   *Lygodium, Allophylus, Casearia, Combretum,* cf. *Guazuma, Matayba,* cf. *Rourea*

Lower montane wet forest
>   *Lycopodium, Selaginella, Cyathea, Pteris, Manicaria* type, *Sapium*

Montane moist forest
>   cf. *Hymenophyllum, Lophosoria, Pityrogramma, Podocarpus, Engelhardia, Lisianthius*

Premontane rain forest
>   *Synechanthus* type, *Alchornea, Casearia, Hampea*

Premontane dry forest
>   *Casearia, Combretum, Eugenia,* cf. *Guazuma*

Lower montane rain forest, montane wet, and montane rain forest

sandstones, lignitic shales, tuffs, and, in the lower part, coralliferous limestone. Bathyl siltstones cap the section, and fragments of marine invertebrate shells occur scattered throughout the sequence. Palynomorphs from the La Boca Formation are currently under study, and 22 taxa have been identified.

The Culebra, Cucaracha and La Boca Formations of Panama are considered sequential in age, with the Culebra being oldest and the La Boca youngest; all are regarded as lower Miocene (see discussion in: Graham *et al.*, 1985). The age of the Uscari Formation of Costa Rica is more problematical, but is likely lower Miocene — although it cannot be correlated at present with any one of the Panama formations.

THE PALAEOCOMMUNITIES

BASED ON earlier published results from the late Miocene Paraje Solo Formation of Veracruz, Mexico (Graham, 1976), the middle(?) to late Eocene Gatuncillo Formation of Panama (Graham, 1985), and especially on data from the several other sources noted previously, some concepts have been formulated concerning the physiography, vegetation, and climate of southern Central America during the Tertiary. These new floras from Central America are of interest, therefore, for two reasons. First, they give us our first insight into the lower Miocene vegetation of the Gulf/Caribbean region and the physical and climatic conditions under which it existed. Second, from a more theoretical viewpoint, they allow an assessment of current concepts derived from increasing, but still limited, palaeobotanical data. If we have reached a point of predictability in anticipating the kinds of palaeocommunities and palaeoenvironments present at a point in time for a given locality, this suggests previous studies and interpretations are generally sound and justifies integration of the data into developing models of Gulf/Caribbean geologic history and biogeography.

The following four assumptions or expectations about the new floras were based on collective results from the various other studies previously noted. From plate tectonic data the environment was certainly insular and probably relatively low-lying. Although there were oscillations in uplift and subsidence, the trend has been toward increasingly higher altitudes, with the highest elevations of most recent origin. The consequence of such a physiography for vegetation is *(a)* the expectation of low- to moderate-altitude forests and *(b)* little evidence of extensive dry habitats. From global palaeotemperature curves (Savin, 1977; Savin and Douglas, 1985; Savin *et al.*, 1975), it is evident that the lower Miocene was a time of warm temperatures, in contrast to the sharp lowering at the end

of the Miocene. Thus, *(c)* the vegetation should be similar in composition and ecology to the modern tropical lowland plant communities occupying southern Central America at present. Finally, if the palaeobotanical data are consistent with accepted palaeophysiographic reconstructions and with evidence from terrestrial faunas (Marshall, 1985; Webb, 1985a, b; Whitmore and Stewart, 1965), marine invertebrates (Jones and Hasson, 1985), and phytogeographic patterns (Raven and Axelrod, 1974), *(d)* the fossil floras should have Central and North American affinities. The South American influence would become evident only after the closing of the isthmus in late Pliocene/Pleistocene times (*c.* 3.0 Ma).

Table 1 lists fossil pollen and spores currently identified from lower Miocene deposits in Costa Rica and Panama. In fact, the list represents all lower Miocene plants recently reported for northern Latin America. As noted earlier, study of the Uscari (Graham, 1987a), Culebra (Graham, 1988a), and Cucaracha (Graham, 1988b) material is complete, but data from the La Boca Formation have not been published previously. In Table 2, these genera are arranged into palaeocommunities based on the principal occurrence(s) of the modern analogues.

Altitudes
Coastal communities and forests of lower altitudes are prominent, not only in terms of number of genera but also in the presence of characteristic or defining elements for these vegetation types. This is in contrast to higher-altitude communities, which are represented primarily by wide-ranging genera that extend through several communities. The coastal mangrove is defined by *Rhizophora*, and by *Pelliceria* in more localized areas (Pacific Costa Rica to Colombia — Graham, 1977; Jiménez, 1984), and these are both present in the fossil floras, as well as genera with species that extend into the mangrove vegetation (*Hibiscus, Sapium*). The tropical moist forest (29 genera), tropical wet forest (27 genera), and premontane wet forest (26 genera) are well documented, while all remaining palaeocommunities are represented by 12 or fewer genera. Of special interest in terms of altitude is the presence of *Podocarpus* pollen in the Uscari Sequence of Costa Rica and of *Engelhardia* in the La Boca Formation of Panama (it was absent from the Culebra and rare in the Cucaracha Formations of Panama). These are primarily temperate to warm-temperate genera that grow in upland habitats in Latin America. The pollen is distinctive, and both are common in their respective palaeofloras. These two genera present the best evidence to date for moderate altitudes in southern Central America during the lower Miocene. It should be noted, however, that both exist as common components of the vegetation (as opposed to more isolated individual occurrences) at altitudes as low

as 1,200–1,500 m. It is interesting that one (*Podocarpus*) occurs in a palaeoflora closest to more continuous and diverse landscapes to the north (Graham, 1988c), and the other (*Engelhardia*) occurs in the youngest of the three lower Miocene floras from Panama. The latter has been reported from the Maestrichtian of the Gulf coast and interior USA, as well as from the Paleocene of South Carolina (see summary in: Muller, 1981, pp. 29-30). Both are known from the Oligo-Miocene Simojovel Group of Chiapas, Mexico (Langenheim *et al.*, 1967). Since neither *Podocarpus* nor *Engelhardia* were recovered from the middle(?) to late Eocene Gatuncillo Formation of Panama (Graham, 1985), it is possible that they (and their moderate-altitude habitats) first appear to any extent in southern Central America during the global cooling trend evident in the late Miocene. In light of the very limited palaeobotanical information noted previously, however, such patterns are only speculative and must be reviewed as more data become available. For the present, all known components of lower Miocene vegetation in southern Central America can be accommodated in habitats at or below 1,200–1,500 m.

Dry to arid habitats

Drier vegetation is represented in southern Central America by the tropical dry forest (a low semi-deciduous forest) and savannahs (the premontane dry forest is not recorded for Costa Rica by Hartshorn, 1983). The forest localities are usually only marginally dry, however, and are often surrounded by moist transition vegetation. Their extent is commonly physiographically or edaphically controlled or, in the case of savannahs, influenced by anthropogenic factors. In the Costa Rican tropical dry forest, mimosoid and caesalpinoid legumes are the conspicuous canopy trees, with bromeliads as common epiphytes (Hartshorn, 1983). None of these are represented in the lower Miocene floras currently known from Costa Rica and Panama. Most *Acacia* are more typical of moist forest types in this region. Also, none of the genera listed in Table 2 for the tropical dry forest or the premontane dry forest are restricted to or even typical of these communities. They are wide-ranging general found in several vegetation types. Virtually none of the genera listed by Porter (1973) for the drier communities of Panama (thorn forest, deciduous seasonal forest) occur in the fossil floras. Grass pollen is currently known from the Culebra and La Boca Formations, but in very low percentages (two or three grains only). As noted previously, there is not a sufficient number of fossil floras from a wide enough variety of sediment types to definitely exclude dry to arid communities and savannahs from the early Miocene vegetation of southern Central America. The available evidence suggests, however, that if they were present they were not

extensive, and this assessment is consistent with the palaeophysiographic character of the landscape (viz. low-lying and insular).

Composition and ecology

Of the 50 genera listed in Table 1, 48 or 49 currently occur in the modern vegetation of southern Central America. The exceptions are cf. *Glycydendrum*, also reported from the Quaternary of Panama (Bartlett and Barghoorn, 1973), and possibly *Crudia*, currently known only from South America. Of the 12 communities listed in Table 2, all are part of the modern vegetation. The possibility of bias towards local vegetation in the pollen and spore reference collection used for identification of the microfossils is limited by the extensive scope of the collection. Sampling of herbarium material from various parts of the neotropics, as well as a nearly world-wide exchange programme, has reduced the likelihood of bias towards existing Panamanian/Costa Rican plant communities. Thus, a consistent feature of lower Miocene floras from southern Central America is their close similarity to local and regional vegetation. The extent, location, and to some degree the composition of the lower Miocene vegetation may differ somewhat from the modern communities, but the general nature of the modern and fossil vegetation is very similar. The exceptions are absence or poor representation tationtationtationtationtationtationtationof communities of higher altitude, dry to arid habitats, and savannahs.

Affinities

Plate tectonic models for the Gulf/Caribbean region show North and South America separated from the end of the Cretaceous until about 3.0 Ma. Fossil mammalian faunas from southern Central America show the expected North American affinities (e.g., Whitmore and Stewart, 1965; their material is also from the Cucaracha Formation and from the same site as the palaeobotanical samples). Comparison of the taxa represented in the lower Miocene floras of Costa Rica and Panama with the list of families presented by Raven and Axelrod (1974) having South American versus North American affinities shows an overwhelming relationship with the North American flora. Only genera widely distributed throughout tropical regions of the world (e.g., *Rhizophora*) are common to the modern and lower Miocene floras. This is the expected pattern of affinities, but the Uscari, Culebra, Cucaracha, and La Boca floras provide its first documentation.

It is apparent from these preliminary data on fossil floras from the Gulf/Caribbean region that the general outline of Tertiary vegetational history is becoming clearer. All lower Miocene floras studied to date are consistent in

reflecting a relatively low-lying insular landscape, little evidence of dry to arid habitats (including savannahs), a close relationship to the modern vegetation of the region, and decidedly North American affinities. Periodic assessment of these interpretations and refinement of details will continue as current studies on the Tertiary vegetation of northern Latin America are completed.

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