

PALEOGEOGRAPHY OF THE
CARIBBEAN REGION:
IMPLICATIONS FOR
CENOZOIC BIOGEOGRAPHY

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CONTENTS

Abstract	3
Resumen	4
Resumo	5
Introduction	6
Acknowledgments	8
Abbreviations	9
Statement of Problem and Methods	9
Paleogeography of the Caribbean Region: Evidence and Analysis	18
Early Middle Jurassic to Late Eocene Paleogeography	18
Latest Eocene to Middle Miocene Paleogeography	27
Eocene-Oligocene Transition (35–33 Ma)	27
Late Oligocene (27–25 Ma)	31
Early Middle Miocene (16–14 Ma)	31
Biogeographical Hypotheses and Caribbean Paleogeography	35
Continent-Island Vicariance: Model of Rosen	35
Passive Overwater Dispersal: Model of Hedges and Co-workers	40
Preliminary Issues	40
Sources of Error in Estimating Times of Lineage Origins	43
Passive Transport and Cenozoic Surface-Current Patterns	45
Surface-Current Patterns and Flotsam Dispersal	45
Surface-Current Patterns and Paleogeography	45
Surface-Current Patterns and Proxy Data	48
Other Constraints	50
GAARlandia Landspan and Island–Island Vicariance: Model of MacPhee and Iturralde-Vinent	52
Landspans, Vicariance, and Diversity Scenarios	52
Discussion	56
Conclusions	58
References	59
Appendix 1: Reconstructing Caribbean Paleogeography: An Analytical Guide	72
Yucatan Peninsula	72
Northern Central America, Nicaragua Rise, and Western Jamaica	73
Southern Central America	75
Northwestern South America	75
Aruba/Tobago Belt	75
Greater Antilles	77
Blue Mountains Block	80
Aves Ridge, Lesser Antilles, and Grenada Basin	84
Beata Ridge	87
Cayman Islands and Cayman Ridge	87
Appendix 2: A Plate Tectonic Model of the Caribbean from Latest Eocene to Middle Miocene	87

ABSTRACT

This paper* presents a series of detailed paleogeographical analyses of the Caribbean region, beginning with the opening of the Caribbean basin in the Middle Jurassic and running to the end of the Middle Miocene. Three intervals within the Cenozoic are given special treatment: Eocene–Oligocene transition (35–33 Ma), Late Oligocene (27–25 Ma), and early Middle Miocene (16–14 Ma). While land mammals and other terrestrial vertebrates may have occupied landmasses in the Caribbean basin at any time, according to the interpretation presented here the existing Greater Antillean islands, *as islands*, are no older than Middle Eocene. Earlier islands must have existed, but it is not likely that they remained as such (i.e., as subaerial entities) due to repeated transgressions, subsidence, and (not incidentally) the K/T bolide impact and associated mega-tsunamis. Accordingly, we infer that the on-island lineages forming the existing (i.e., Quaternary) Antillean fauna must all be younger than Middle Eocene. The fossil record, although still very poor, is consistent with the observation that most land mammal lineages entered the Greater Antilles around the Eocene–Oligocene transition.

Western Laurasia (North America) and western Gondwana (South America) were physically connected as continental areas until the mid-Jurassic, ca. 170 Ma. Terrestrial connections between these continental areas since then can only have occurred via landbridges. In the Cretaceous, three major uplift events, recorded as regional unconformities, may have produced intercontinental landbridges involving the Cretaceous Antillean island arc. The Late Campanian/Early Maastrichtian uplift event is the one most likely to have resulted in a landbridge, as it would have been coeval with uplift of the dying Cretaceous arc. However, evidence is too limited for any certainty on this point. The existing landbridge (Panamanian isthmus) was completed in the Pliocene; evidence for a precursor bridge late in the Middle Miocene is ambiguous.

We marshal extensive geological evidence to show that, during the Eocene–Oligocene transition, the developing northern Greater Antilles and northwestern South America were briefly con-

nected by a “landspan” (i.e., a subaerial connection between a continent and one or more off-shelf islands) centered on the emergent Aves Ridge. This structure (Greater Antilles + Aves Ridge) is dubbed GAARlandia. The massive uplift event that apparently permitted these connections was spent by 32 Ma; a general subsidence followed, ending the GAARlandia landspan phase. Thereafter, Caribbean neotectonism resulted in the subdivision of existing land areas.

The GAARlandia hypothesis has great significance for understanding the history of the Antillean biota. Typically, the historical biogeography of the Greater Antilles is discussed in terms of whether the fauna was largely shaped by strict dispersal or strict continent–island vicariance. The GAARlandia hypothesis involves elements of both. Continent–island vicariance *sensu* Rosen appears to be excludable for any time period since the mid-Jurassic. Even if vicariance occurred at that time, its relevance for understanding the origin of the modern Antillean biota is minimal. Hedges and co-workers have strongly espoused over-water dispersal as the major and perhaps only method of vertebrate faunal formation in the Caribbean region. However, surface-current dispersal of propagules is inadequate as an explanation of observed distribution patterns of terrestrial faunas in the Greater Antilles. Even though there is a general tendency for Caribbean surface currents to flow northward with respect to the South American coastline, experimental evidence indicates that the final depositional sites of passively floating objects is highly unpredictable. Crucially, prior to the Pliocene, regional paleoceanography was such that current-flow patterns from major rivers would have delivered South American waifs to the Central American coast, not to the Greater or Lesser Antilles. Since at least three (capromyid rodents, pitheciine primates, and megalonychid sloths) and possibly four (nesophontid insectivores) lineages of Antillean mammals were already on one or more of the Greater Antilles by the Early Miocene, Hedges’ inference as to the primacy of over-water dispersal appears to be at odds with the facts. By contrast, the landspan model is consistent with most aspects of Antillean land-mammal biogeography as currently known; whether it is consistent with the biogeography of other groups remains to be seen.

* Contribution 2 to the series “Origin of the Greater Antillean Land Mammal Fauna.”

RESUMEN

El propósito de este trabajo es presentar una serie de análisis paleogeográficos detallados de la región del Caribe, comenzando con la apertura de la cuenca del Caribe en el Jurásico Medio y extendiéndose hasta el Mioceno Medio. Tres intervalos del Cenozoico reciben un tratamiento especial: la transición Eoceno-Oligoceno (35–33 Ma), el Oligoceno Tardío (27–25 Ma), y el Mioceno Medio temprano (16–14 Ma). Aunque los mamíferos terrestres pudieron haber ocupado masas de tierra en la cuenca del Caribe en cualquier momento de su historia, de acuerdo con la interpretación que se presenta en este trabajo, las actuales Antillas Mayores, *como islas*, son no más antiguas que Eoceno Medio. Islas más antiguas deben haber existido, pero no es probable que ellas hayan permanecido como tales (es decir, como entidades subaéreas) debido a las repetidas transgresiones, subsidencia, y (no incidentalmente) al impacto del límite K/T y el megatsunami asociado al mismo. De acuerdo con esto nosotros inferimos que los linajes insulares que forman la fauna antillana actual (y cuaternaria en general) deben ser más jóvenes que el Eoceno Medio. El registro fósil, a pesar de ser muy pobre aún, es consistente con la observación de que la mayoría de los linajes de mamíferos llegaron a las Antillas Mayores alrededor del límite Eoceno-Oligoceno.

El oeste de Laurasia (América del Norte) y el de Gondwana (América del Sur) estuvieron físicamente conectados como áreas continentales hasta el intervalo Bajociano al Oxfordiano (178–160 Ma) cuando se comenzó a formar la cuenca oceánica del Caribe. Conexiones terrestres entre dichas áreas continentales a partir de entonces sólo pudieron ocurrir mediante puentes naturales de terreno. En el Cretácico tres eventos principales de levantamiento, coincidentes con inconformidades regionales, pudieran haber producido puentes intercontinentales que involucraron al arco de islas volcánicas de las Antillas. El levantamiento ocurrido en el Campaniano tardío a Maastrichtiano temprano es el que tiene las mayores posibilidades de haber producido un puente natural, ya que éste coincidió en el tiempo con la extinción del vulcanismo cretácico. No obstante, la evidencia es muy limitada para tener alguna seguridad sobre este asunto. El puente natural que existe actualmente (itmo de Panamá) se completó en el Plioceno; pero la evidencia para un puente anterior en el Mioceno Medio tardío es ambigua.

Aquí se presenta extensa evidencia geológica para mostrar que, durante la transición entre el Eoceno y el Oligoceno, las tierras antillanas y la porción noroccidental de América del Sur estu-

vieron brevemente conectadas por una “landspan” (proyección de terreno) (es decir, por una conexión subaérea entre un continente y una o más islas situadas fuera del límite de la plataforma continental), conexión que estuvo centrada en la entonces emergida Cresta de Aves. Esta estructura (Crestas de las Antillas Mayores y de Aves) se denominó GAARlandia. El evento de levantamiento masivo que aparentemente permitió esta conexión terminó hace unos 32 millones de años; debido a una subsidencia general que terminó con la fase de “landspan” de GAARlandia. Posteriormente la etapa neotectónica caribeña resultó en la subdivisión de las tierras existentes.

La hipótesis GAARlandia tiene un gran significado para comprender la historia de la biota Antillana. Típicamente, la biogeografía histórica de las Antillas Mayores se discute en términos de si la fauna fue principalmente formada por dispersión estricta o por estricta vicariancia continente-isla. La hipótesis GAARlandia comprende elementos de ambas. Pero la vicariancia continente-isla al estilo de Rosen puede ser excluida para cualquier momento desde el Jurásico Medio. Incluso si la vicariancia hubiese ocurrido en aquella época, su relevancia para comprender el origen de la biota antillana moderna es mínima. Hedges y sus colaboradores han propuesto con énfasis la dispersión por agua como el principal, sino el único, método de formación de la fauna de vertebrados en la región del Caribe. Sin embargo, la dispersión de propágulos mediante las corrientes marinas superficiales es inefectiva para explicar los patrones de distribución actual de la fauna terrestre en las Antillas Mayores. Incluso aunque existe una tendencia general de las corrientes superficiales del Caribe a fluir hacia el norte con respecto a la costa sudamericana, las evidencias experimentales indican que es prácticamente impredecible dónde serán finalmente depositados los objetos flotantes acarreados por dichas corrientes. Al respecto, es crucial el hecho de que, antes del Plioceno, la paleoceanografía regional fue tal que los patrones de corrientes de los ríos sudamericanos debieron acarrear los objetos a la deriva provenientes de América del sur hacia las costas de América Central, o hacia el Pacífico, no hacia las Antillas Mayores. Dado que al menos tres linajes (roedores capromíidos, primates pitecinos y perezosos megaloníchidos) y posiblemente cuatro (insectívoros nesofóntidos) de los mamíferos antillanos se encontraban ya en las Antillas Mayores a comienzos del Mioceno, las inferencias de Hedges respecto al dominio de la

dispersión por agua como el modo de migración de esta fauna está en desacuerdo con los hechos. En contraste, el modelo de “landspan” es consistente con muchos de los aspectos de la biogeografía

histórica de los mamíferos terrestres antillanos tal como se conoce hoy día; aunque si también es consistente con la biogeografía de otros grupos es algo que está aún por definir.

RESUMO

Este trabalho apresenta uma série de análises paleogeográficas detalhadas da região do Caribe, começando com a abertura da bacia do Caribe no Jurássico Médio e seguindo até o fim do Mioceno Médio. Três intervalos do Cenozóico receberam especial atenção: a transição Eoceno-Oligoceno (35–33 Ma), o final do Oligoceno (27–25 Ma) e o início do Mioceno Médio (16–14 Ma). Ainda que mamíferos e outros vertebrados terrestres possam ter ocupado massas de terra na bacia do Caribe em qualquer momento de sua história, segundo o presente estudo, a existência das Grandes Antilhas, como ilhas, não é mais antiga do que o Mioceno Médio. Ilhas mais antigas podem ter existido, no entanto, é pouco provável que tenham permanecido como tais por longos períodos. Assim sendo, inferimos que todas as linhagens que formam a fauna antilhana atual (ou seja, Quaternária) devam ser mais recentes que o Eoceno Médio. O registro fóssil, apesar de ser bastante pobre, é consistente com a observação de que a maioria das linhagens de mamíferos terrestres chegaram às Grandes Antilhas por volta da transição Eoceno-Oligoceno.

O oeste da Laurásia (América do Norte) e o da Gondwana (América do Sul) estiveram fisicamente conectados como áreas continentais até o Jurássico Médio. Três principais eventos de soerguimento no Cretáceo, registrados por inconformidades regionais, podem ter produzido pontes intercontinentais envolvendo o arco de ilhas antilhanas do Cretáceo. O soerguimento ocorrido no Campaniano superior/Maastrichtiano inferior parece ser o mais relacionado com a formação de uma ponte de conexão, uma vez que este coincide com o soerguimento ocorrido durante o desaparecimento do arco do Cretáceo. A conexão atual (istmo do Panamá) completou-se no Plioceno; evidências de uma ponte anterior no fim do Mioceno Médio são ambíguas.

Nós buscamos extensivas evidências geológicas para demonstrar que durante a transição Eoceno-Oligoceno, a parte norte das Grandes Antilhas (então em desenvolvimento) e o noroeste da América do Sul estiveram brevemente conectados por uma “landspan” (i.e., uma conexão sub-aérea

entre um continente e uma ou mais ilhas oceânicas). Esta “landspan” estaria centrada na, então emergente, Cadeia de Aves. Denominou-se esta estrutura (Cadeia das Grandes Antilhas + Cadeia de Aves) como GAARlândia. O soerguimento massivo que aparentemente permitiu estas conexões ocorreu a cerca de 32 milhões de anos, sendo seguido por uma subsidência geral que terminou com a fase de “landspan” da GAARlândia. Posteriormente, o neotectonismo caribenho resultou na subdivisão das terras existentes.

Tradicionalmente, a história biogeográfica das Grandes Antilhas é discutida em termos de formação da fauna estritamente por dispersão ou por vicariância continente-ilha. A hipótese da GAARlândia envolve elementos de ambas as correntes, ainda que os modelos de vicariância continente-ilha sensu Rosen possam ser excluídos para qualquer período desde o Jurássico Médio. Hedges e colaboradores têm veementemente sugerido a dispersão através d'água como o principal, senão o único, meio pelo qual teria ocorrido a formação da fauna de vertebrados do Caribe. Entretanto, a proposta de dispersão de propágulos por correntes marinhas superficiais é inadequada para explicar os padrões de distribuição de fauna terrestre observados nas Grandes Antilhas. Enfatiza-se que, antes do Plioceno, a paleoceanografia da região era tal que o padrão de fluxo de correntes dos principais rios sulamericanos deviam carrear objetos para a costa da América Central e não para as Grandes e Pequenas Antilhas. No mínimo três (roedores capromiídeos, primatas piteciíneos e preguiças megaloníquideas) e talvez quatro (insetívoros nesofondídeos) linhagens de mamíferos antilhanos já ocorriam em uma ou mais ilhas das Grandes Antilhas no início do Mioceno, indicando que as propostas de Hedge quanto a primazia da dispersão aquática da fauna não estão de acordo com os fatos. Neste sentido, o modelo de “landspan” é consistente com a maioria das propostas atualmente aceitas para a biogeografia dos mamíferos terrestres antilhanos. Permanece em aberto se este modelo esta de acordo com as propostas biogeográficas para outros grupos.

It is this independence of biological from geological data that makes the comparison of the two so interesting because it is hard to imagine how congruence between the two could be the result of anything but a causal history in which geology acts as the independent variable providing opportunities for change in the dependent biological world.

— Donn E. Rosen (1985: 637)

INTRODUCTION

During the past century, a number of hypotheses have been offered as partial or complete explanations for the origins of Antillean terrestrial vertebrate faunas.¹ Three mechanisms have been discussed extensively in the literature: (1) dispersal over water barriers (e.g., Matthew, 1918; Darlington, 1938; Woods, 1989; Hedges et al., 1992, 1994; Hedges, 1996a, 1996b); (2) dispersal over short-lived landbridges and landspans² (e.g., Fernandez de Castro, 1884; De La Torre, 1910; Gayet et al., 1992; MacPhee and Iturralde-Vinent, 1994, 1995); and (3) vicariance, i.e., splitting or division of a biota or taxon through the development of a natural barrier (e.g., Rosen, 1975, 1985; Guyer and Savage, 1987; MacPhee and Wyss, 1990). Although these mechanisms are sometimes presented as though they were discrete, mutually exclusive alternatives, depending on the time, place, and taxon under discussion, any or all of them may have been involved in Antillean faunal formation. In fact, to preview the chief conclusion of this paper, it

seems inescapable that all three were involved in the formation of the Antillean land-mammal fauna, although not necessarily in either the manner or the degree envisaged by other authors.

Our present purpose is to present a fresh perspective on the “geography” part of biogeography, as it relates to the Caribbean region, and to examine how this may offer novel insights into historical processes of faunal formation. (For a listing of most of the features and localities mentioned in the text, see figure 1). Although our specific concept of Antillean paleogeographical history differs in various ways from those of other authors (see *Biogeographical Hypotheses and Caribbean Paleogeography*), we have made a particular effort to document and evaluate other views.

It is widely recognized that hypotheses concerning Antillean historical biogeography are critically dependent on specific reconstructions of regional paleogeography, paleoceanography, tectonics, and other bodies of data. However, most discussions of this subject by life scientists have tended to emphasize biological evidence over geological evidence. This bias should not be viewed as being merely reflective of biologists’ understandable preference for their own kinds of data, because several issues are involved.

First, although much of the general geological and tectonic literature is significant for understanding the biogeographical history of the Caribbean region, virtually none of it was written with the needs of biologists in mind. Accordingly, biologists hoping to integrate geological information into their work are faced with the daunting tasks of having to compile evidence from many different sources, judge as best they can the accuracy of age assignments and other primary

¹ There are several current biogeographical definitions of the “Antilles,” “West Indies,” “Caribbean Islands,” “insular Neotropics” and their various subdivisions. In this paper, Greater and Lesser Antilles will have their usual meanings; “Antillean” as an adjective refers to anything having to do with these islands, and is used in preference to “West Indian” (which, as generally used, covers other, non-Antillean islands such as Bahamas). The Caribbean region, which we newly define as a paleogeographical concept, consists (at any stage of its development) of the Caribbean Sea and all of its contents, plus the facing continental margins of North, South, and Central America. Thus the Caribbean region is larger than the Caribbean Plate, although the structures on that plate comprise most of the entities of interest here. It is also larger than “West Indies” as defined by Hedges (1996a, 1996b).

² For definition of “landspan” see section entitled *GAARlandia Landspan and Island–Island Vicariance*.

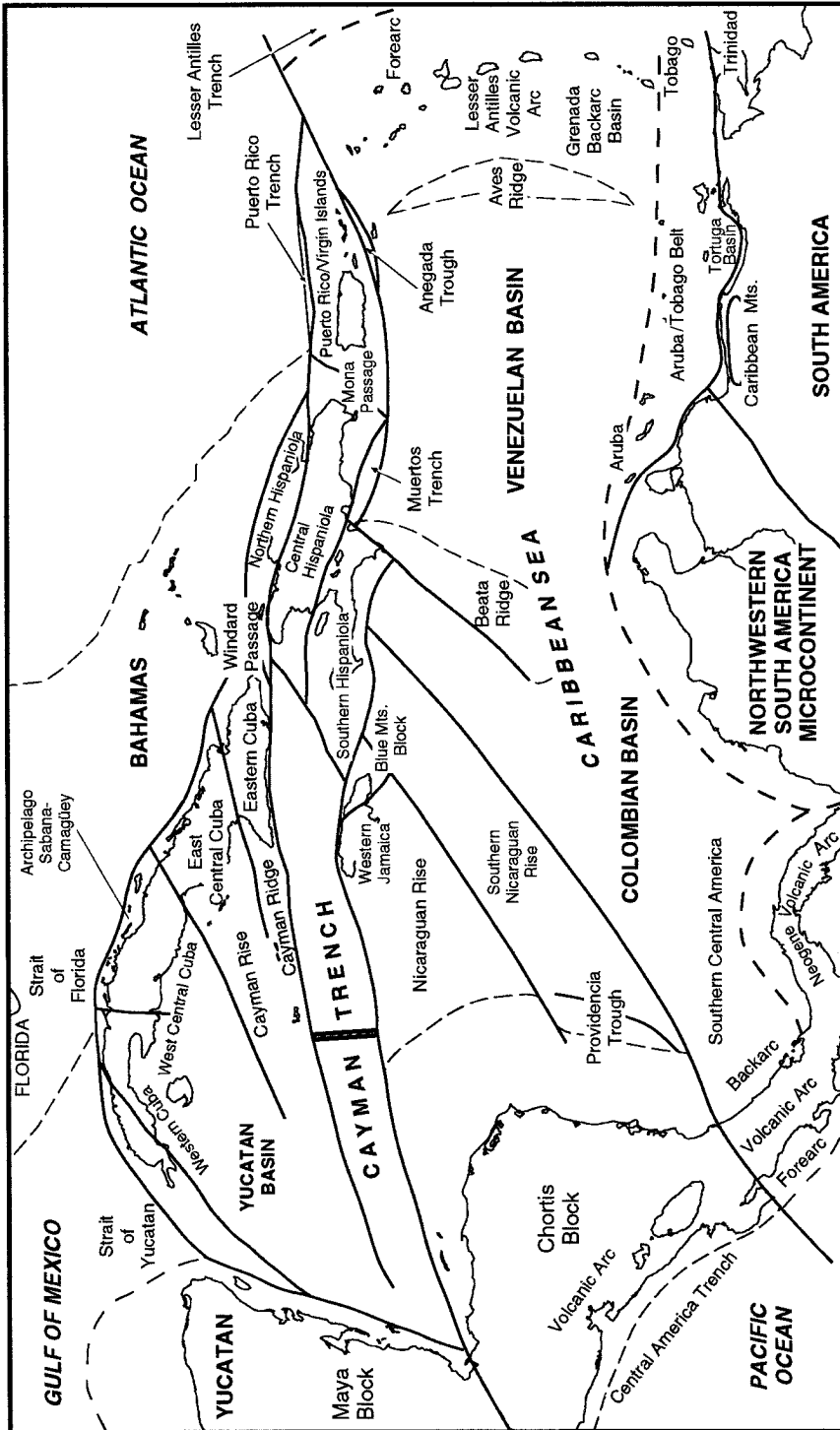


Fig. 1. Reference map of Caribbean region illustrating most of the geographical and geological features referred to in text.

data, and, frankly, recognize when geological theory outstrips fact. Lack of familiarity with the subject matter and the methods of geological argumentation may lead to simple factual errors, or, possibly worse, encourage the uncritical acceptance of insufficiently tested geological scenarios primarily because they appear to support certain biological hypotheses. It is partly for this reason that some authors validly question whether biologists should place themselves in the very vulnerable position of relying on the revealed truths of geologists to explain biogeographical patterns (Henderson, 1991: 61; see also Craw and Weston, 1984). Knowledge, we suggest, is the best antidote to vulnerability.

Second, despite their apparent elegance, plate tectonic models (e.g., Malfait and Dinkelmann, 1972; Duncan and Hargraves, 1984; Leclere and Stephan, 1985; Ross and Scotese, 1988; Donnelly, 1989a; Pindell and Barrett, 1990; Mann et al., 1995; Hay and Wold, 1996; Iturralde-Vinent, 1996a, 1997b) vary widely in their comprehensiveness and testability (Rull and Schubert, 1989; Perfit and Williams, 1989). For example, agreement is still lacking regarding the number and fit of plates and microplates in the Caribbean Region—a basic issue of fact (cf. Donnelly, 1985; Ross and Scotese, 1988; Pindell, 1994; Hay and Wold, 1996). Furthermore, plate tectonic models do not necessarily provide the kinds of information that biologists are most interested in. Typically, such models focus on reconstructing historical positions of specific geologic units commonly denoted as plates, terranes, blocks, volcanic arcs, and ridges (e.g., Malfait and Dinkelmann, 1972; Duncan and Hargrave, 1984; Leclere and Stephan, 1985; Donnelly, 1985; Ross and Scotese, 1988; Pindell and Barrett, 1990; Pindell, 1994; Mann et al., 1995; Hay and Wold, 1996). They are not at all, or are only incidentally, concerned with creating well-constrained paleogeographical maps that portray the physical geography of such units (or parts thereof) through time. (For further discussion of these and other concepts, see *Paleogeography of the Caribbean Region: Evidence and Analysis*.) With the purely tectonic literature as the sole guide, one cannot derive any consistent picture concerning how many times subaerial

land masses existed in the Caribbean, or when or how many times these land masses were connected to nearby continents, or the nature of the relief they exhibited. Thus, Hedges et al. (1992) explored structural relationships among Caribbean land masses and nearby continents on the basis of Pindell and Barrett's (1990) tectonic reconstruction which, in fact, contains no information on such relationships. (The latter authors discuss only the position of geological units, which is not paleogeography as we define it.)

In this paper we offer the first comprehensive paleogeographical and paleoceanographical reconstructions of the Caribbean basin, from latest Eocene to Middle Miocene, an interval selected for reasons explained in detail in succeeding sections. We also briefly review paleogeographical scenarios for Jurassic through Late Eocene time, for the purpose of evaluating evidence for early land connections and island permanency. Reflecting our own interests, we concentrate on the paleogeography of the central part of the Caribbean basin and portions of Central America and northwestern South America. In the main, the biogeographical implications that we have pursued in this investigation are those most closely tied in with geography. Understanding the phylogeny of the Antillean biota is equally important and interesting; however, this topic is reserved for a subsequent paper in this series (MacPhee and Iturralde-Vinent, in prep.).

Because of the large quantity of ancillary documentation required to support a study of this sort, for efficiency in presentation much of the basic geological, paleogeographical, and paleontological information is presented in the form of appendices, tables, and figures. The text summarizes this information in discursive form, but its main function is to discuss problems of interpretation and explanation. Readers wishing to utilize the chief results of our investigations may profitably consult the main text, but those requiring a greater level of detail should refer to the appendices throughout.

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ABBREVIATIONS

AMNH	American Museum of Natural History
ID	immunological distance
Ma	millions of years (ago)
MNHNH	Museo Nacional de Historia Natural, La Habana
NWSA	Northwestern South America (microcontinent or microplate)
Fm	formation

STATEMENT OF PROBLEM AND METHODS

We agree with Hedges (1996b: 166) that the aspect of Caribbean geological history of greatest interest to biogeographers, the relationships of emergent land areas, is unfortunately the one that is most poorly understood. This point is best explored by noting some illustrative examples:

Not all geological maps contain recoverable paleogeographical information.

Eva and MacFarlane's (1985: figs. 4–12) study of carbonate development in Jamaica includes a series of nine illustrations that depict the development of various features (e.g., subaerial land surfaces, subaerial and marine volcanoes, shallow and deep sea) from Paleocene to Pliocene times. However, they are not paleogeographical maps in any literal sense, because all features are shown as evolving within the present-day perimeter of the island, with no attempt to restore folded and faulted rock units to their original relative geographical positions. Because some of Jamaica's basement rocks were strongly folded and faulted during the Middle Eocene and late Neogene (Lewis et al., 1990; Robinson, 1994), any effort to capture paleogeographical reality would require the use of palinspastic methods to reconstruct displacements of blocks along faults and restore original surface areas of deformed formations.

Eva and MacFarlane's (1985) investigation did not require this kind of reconstruction, and they simply portrayed the different geologic units forming the Jamaican basement (ophiolites, metamorphic rocks, Cretaceous/Paleogene island arc suites, and late Campanian to Holocene sedimentary formations) as though they have had the same relative positions and areal dispositions since the Paleocene. The message is that nonpalinspastic reconstructions—by far the most common “paleogeographical” representations in the geological literature (e.g., Khudoley and Meyerhoff, 1971; Maurrasse, 1982; Salvador, 1987; Smith et al., 1994)—may be of negligible value for biogeographical investigations because they are not intended to be paleogeographically accurate. A simplified example of palinspastic reconstruction for the Greater Antilles is illustrated in figures 2 and 3.

Paleogeographical information is difficult to treat in a uniform way.

Just as there is no such thing as a perfect biological classification, there is no such thing as a perfect map. Often, maps are designed to depict only one body of data accurately; thus, even if they are intentionally paleogeographical in nature, they may not show different categories of information with equal degrees of precision. For example, as

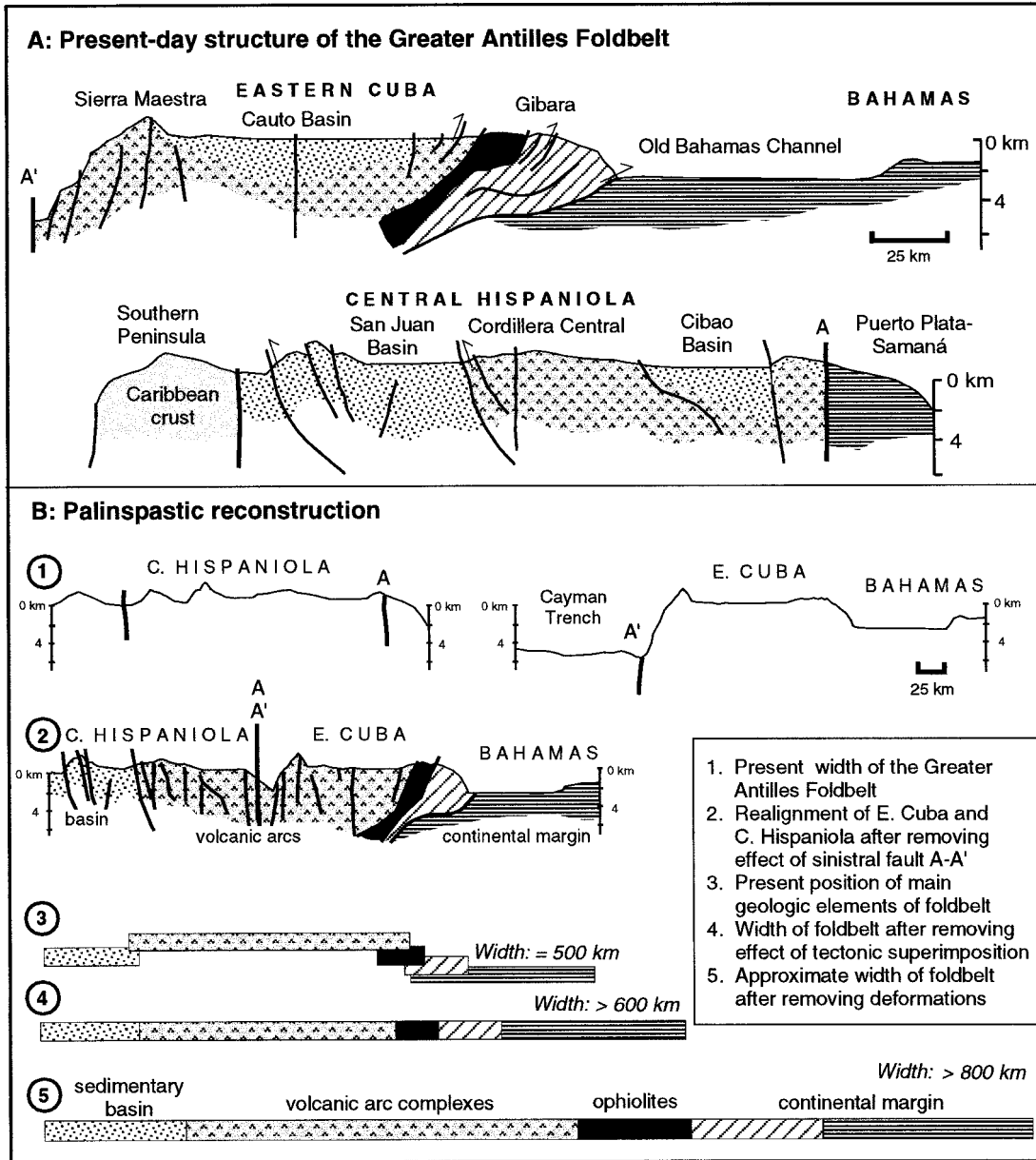


Fig. 2. Simplified palinspastic reconstruction of Greater Antilles Foldbelt along a cross section passing through eastern Cuba and western Hispaniola, to illustrate methodological points. Note that the foldbelt consists of a series of tectonically superimposed units that have been foreshortened by deformation. As a result, the current width of the set of geological units transected by the section amounts to only a fraction of the units' original width (for additional explanation, see text). See figure 3 for location of cross section.

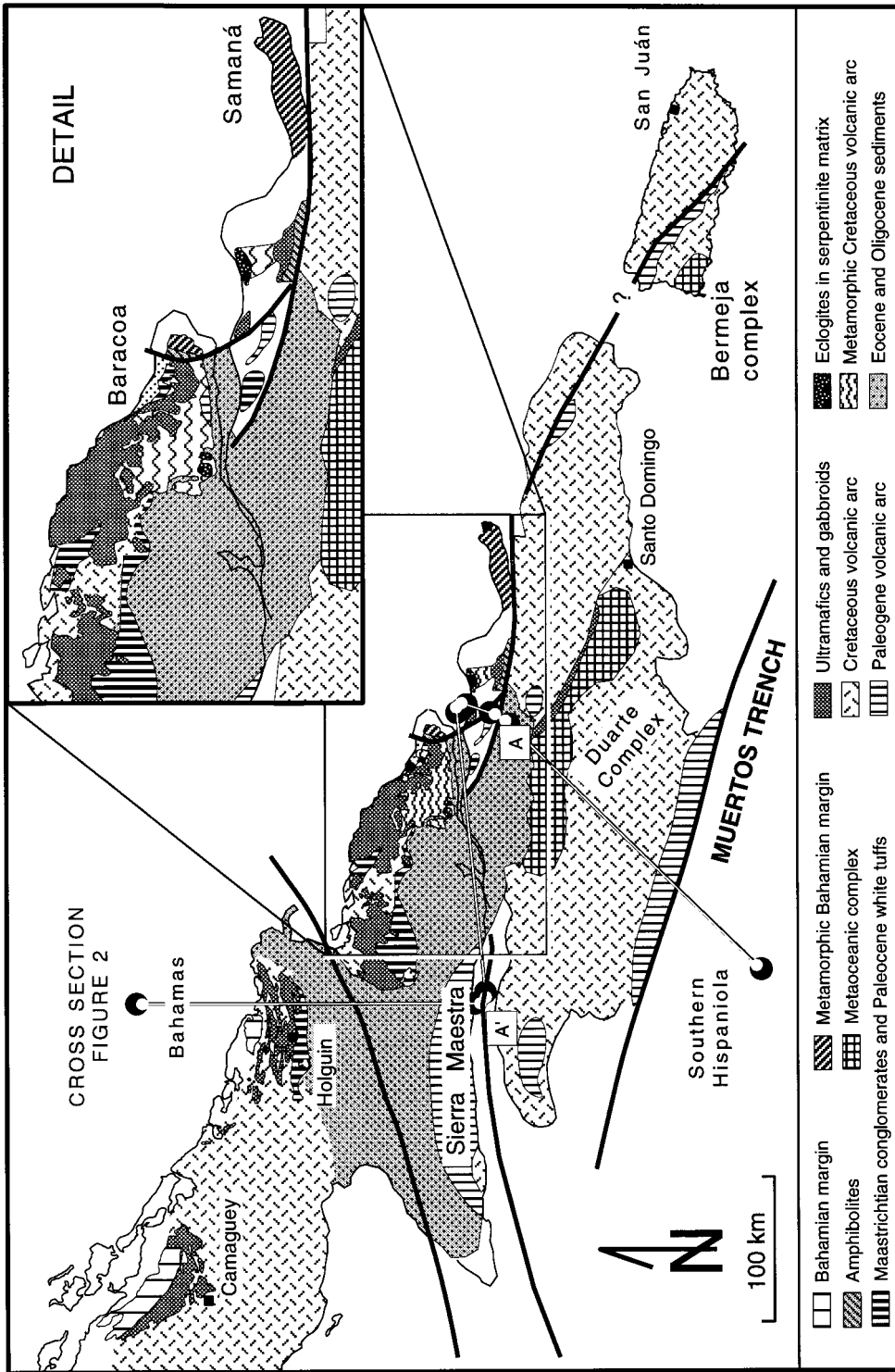


Fig. 3. Palinspastic reconstruction of eastern part of Greater Antilles Foldbelt, for period corresponding to Late Eocene through mid-Oligocene (ca. 37–30 Ma). This framework has been greatly disrupted since the mid-Oligocene by sinistral strike-slip movements and deformations along the northern margin of the Caribbean plate, east of Holguín. A and A' are reference points for cross section depicted in figure 2. (Information compiled from many sources; see appendix 1.)

its title implies, the *Atlas of Mesozoic and Cenozoic Coastlines* (Smith et al., 1994) is concerned with depicting coastline information, on a global scale, for the past 245 Ma. Because its intended scope is the entire planet, regional details are often lost or portrayed inaccurately. As the authors point out, small discrepancies do not affect the big picture, but they do complicate the use of the maps for other purposes. Of interest here is the fact that the Greater Antilles are depicted in their current sizes and positions relative to North America during all relevant time periods. Because the dimensions of the Caribbean Sea have changed over time, the Greater Antilles are forced by the mapping program into positions they could never have occupied. Thus, these islands overlap northern South America at 170 Ma, project east of Trinidad into the South Atlantic (!) at 155 Ma, and finally end up at their present-day position at 80–0 Ma. Furthermore, subaerial exposures on these islands are depicted on Oligocene and later maps, but not on earlier ones. This suggests that land areas did not exist as such prior to the mid-Cenozoic, which is not accurate. Similarly, the Chortis Block is depicted as overlapping southern Central America at 170 Ma, then acting as a bridge between southern Central America and North America at 155 Ma, then coming into contact with the Maya (Yucatan) Block as both were uplifted around 148 Ma, and finally achieving its present-day position with respect to North America by 80–0 Ma. The Yucatan Peninsula is successively depicted as (1) overlapping South America at 170 Ma, (2) uplifted and in contact with northern South America by 155 Ma, and (3) situated near its present-day position with respect to North America in the Tithonian (148 Ma). Although these implied motions can be dismissed as minor artifacts of mapping programs designed to show large segments of the geode, the point is that they seriously conflict with all available models of Caribbean plate tectonics (Malfait and Dinkelman, 1972; Donnelly 1985; Pindell and Barrett, 1990; Pindell, 1994; Mann et al., 1995). Fine-scale interpretation of the paleogeography of small areas is untenable with maps of this sort, although they have been

used for that purpose (e.g., Hedges, 1996a, 1996b).

Island geology and island paleogeography are not isomorphous.

Conventionally, a geographical island is defined by its shoreline (i.e., its subaerial perimeter), although other criteria are of course possible (e.g., –100 m isobath). Shorelines can be affected by rise or fall in sea level, deposition or erosion, and uplift or subsidence of the geological unit that constitutes the islands basement. Shorelines are therefore exceptionally dynamic at virtually all dimensional and temporal scales. Geological units, by contrast, are only indirectly affected by surficial processes such as prograding or degrading shorelines; they reflect a deeper structure, and deep structure is rarely coterminous with conventional geography. The usual objective of geological study is to interpret the history of tectonic elements in terms of their formation, evolution and subsequent transformation into other elements, utilizing the imprints that such processes leave in the rocks themselves. Shoreline reconstruction is therefore a difficult task, because the evidence needed to make paleogeographical reconstructions is almost inevitably destroyed or modified substantially over geologically long periods of time.

Smith et al. (1994) pointed out that coastline reconstruction is additionally complicated by the fact that different datasets, ostensibly for the same interval, may yield quite different paleogeographical results. This can happen when stratigraphic data are collected for specific purposes, such as documenting a general transgression or sealevel drop. For example, reconstructions of Maastrichtian coastlines for the same area may look quite different from one another, depending on what part of the interval and which events individual authors intended to depict.

Another point about island geology versus island paleogeography can be made by reference to Hedges' (1996b) claim that some terrestrial environments in the Caribbean Sea may have been in existence since the end of the Cretaceous. Hedges (1996b: 166) stated that there is "no place in the West Indies that is known by the presence of a continuous

sequence of sediments to have been emergent since the late Cretaceous, although some areas of Cuba, northern Hispaniola, and possibly Puerto Rico, may have been."³ It is unclear what Hedges meant to convey by the phrase "continuous sequence of sediments," since the only conceivable contexts in which unbroken sedimentary accumulations might have occurred throughout the last 65 Ma are deep oceanic basins situated on comparatively ancient sea floor (e.g., eastern Pacific). Furthermore, his paleogeographical observation has significance only if it is additionally inferred that the hypothesized emergent lands of the late Mesozoic and early Cenozoic were incorporated *while still subaerial* into the developing Greater Antilles. We know of no geological evidence that supports this inference; the little evidence that does exist indicates that no terrestrial contexts from these earlier periods survived as such into the Late Eocene (see Paleogeography of the Caribbean Region: Evidence and Analysis).

Tectonic modeling and paleogeographical reconstruction are not the same.

This point can be conveniently illustrated by reference to Pindell's (1994) frequently cited work. As part of a general tectonic reconstruction of the Caribbean region, Pindell (1994: fig. 2.6a–n; see also Pindell and Barrett, 1990) attempted to depict the paleogeographical history of certain physical features (subaerial land, deep and shallow water, volcanic arcs). Although Pindell's model utilizes an extensive database, it contains a few inaccuracies and unverifiable conjectures that have both tectonic and paleogeographical implications. For example, Florida and Bahamas are shown as comprising a single carbonate platform from late Jurassic through Late Miocene, which contradicts recent evidence for their long-term separation (Austin et al., 1988; Droxler et al., 1989; Hine, 1997; Denny et al., 1994; Iturralde-Vinent et al., 1996a). The Nicaragua Rise is drawn as a

shallow-water promontory of the Chortis Block from Middle Eocene to Late Miocene time, contra Sigurdsson et al. (1997) who depict it more correctly as a series of isolated carbonate banks. Cuba is shown as uplifted at 59, 21, and 10 Ma, but as completely submerged at 49 and 35 Ma, in conflict with the data analyzed by Iturralde-Vinent (1969, 1972, 1988a).

Pindell's (1994) maps are particularly problematic in their depiction of island arc connections. North and South America are shown as being completely linked by island arcs in the Valanginian, late Albian, Campanian, Maastrichtian, and Middle Eocene, and as nearly linked in the Barremian, Turonian, and Paleocene. Although these volcanic arcs certainly existed, reconstructing them accurately as paleogeographical entities requires detailed scrutiny of relevant evidence. It is obvious from present-day geography that volcanic arcs may form continuous subaerial entities (e.g., Kamchatka Peninsula, presently sutured to Chukotka; isthmus region of Central America) as well as island chains (e.g., Lesser Antilles, Kuriles). The life-span of an island *qua* island cannot be predicted from first principles: islands at the position of Krakatau and Aldabra, to cite two quite different examples, have appeared and disappeared more than once in the late Quaternary (Stoddart et al., 1971; Nunn, 1994). Without careful appraisal, contradictory conclusions may be reached on the basis of the same evidence. For example, Gayet et al. (1992: fig. 1) argued on the basis of Pindell's model (see Pindell and Barrett, 1990) that "the terrestrial bridge that linked North and South America by latest Cretaceous and Paleocene times probably comprised the Greater Antilles and the Aves Ridge which consisted of a magmatic [arc] submitted to uplift and deformation. . . ." By contrast, Hedges (1996a), also citing Pindell and Barrett (1990), claimed that any possible connection between North and South America via the developing "proto-Antilles" (or "proto-Greater Antilles") was sundered in the Late Cretaceous (70–80 Ma). However, in actuality Pindell and Barrett (1990; see also Pindell, 1994) took no position on the existence of land connections, as this issue was ancillary to the topics they were consid-

³ "West Indies" is defined by Hedges (1996b) to include the Greater and Lesser Antilles, Bahamas, and a number of small islands that lie immediately off the continental shelves of Central and South America. It does not include the southern Netherlands Antilles or Trinidad and Tobago (cf. footnote 1).

ering. In any case, if numerous long-term connections between North and South America had indeed existed (as might be inferred from a literal reading of Pindell's [1994] maps), evidence of this fact would surely have been found in the vertebrate fossil record; but it has not (Gingerich, 1985; Alvarado, 1988; Webb, 1985; see also Biogeographical Hypotheses and Caribbean Paleogeography).

Similar difficulties attend the use of Perfit and Williams' (1989) tectonic reconstructions as paleogeographical evidence. In this useful and incisive paper—in several ways the intellectual precursor of the present monograph—maps were intended to support a critical discussion of Antillean biogeography and paleogeography. However, their reconstructions actually present little in the way of physical geography, as land and sea are the only items discriminated. More problematically, their maps (but not their text) give the impression that most of the Greater Antillean islands originated as such in the late Cretaceous, and merely grew larger as they were tectonically transported to their current relative plate position. In reality, the Greater Antilles in their current guises are relatively young geographical features (see appendix 1; Iturralde-Vinent, 1978, 1982, 1988a, 1994a).

From this brief review it is evident that the recent Caribbean geological literature is not (and was never intended to be) a source of ready-made, easily interpreted paleogeographical maps—that is, maps specifically designed to trace the physical and positional history of particular geographical entities. Appropriate design features for such maps vary with the nature of the entities being traced. In the case of terrestrial environments, which constitute our special concern, reliable paleogeographical maps of the Caribbean region would help to both constrain and enrich discussion of a range of significant inquiries, among which are: (1) When did specific terrestrial environments (“lands”) exist in the Caribbean region, and for how long? (2) Where were these lands geodesically located, at any given time period? (3) What was the nature of physical connections between and among different lands? (4) How long did such connections

last? (5) What were the surface areas of individual lands, and how did their sizes alter over time? As has already been made clear, such questions cannot be answered merely by examining geological maps or tectonic reconstructions.

Our paleogeographical maps provide information on four contexts: high-elevation and low-elevation terrestrial environments (hereafter, “highlands” and “lowlands”), and shallow-water and deep-water marine environments (“shallow marine” and “deep marine”). These environments are distinguished by certain diagnostic features, among which positive or negative elevation relative to ambient sea level is the most significant (see also appendix 1). Although precise measures of elevation are not possible, plausible benchmark estimates can be made within ± 1 order of magnitude. We define highlands as environments that existed at positive elevations greater than ca. 200 m; lowlands were less than 200 m. Although with good faunal evidence it is possible to distinguish marine environments very finely, we reconstruct only two—shallow marine, covering shelf conditions to -100 m; and deep marine, embracing all sea-floor settings deeper than -100 m.

We emphasize that the contact line between terrestrial and marine environments on any given map should be thought of as a median value for coastline position during the interval being depicted. The accuracy of any paleocoastline delimitation is, in any case, a function of sedimentary exposure: in general, paleocoastline positions can be traced more accurately within uplifted areas than in ones that are currently below sea level.

Three quasi-independent parameters were used in map construction: (1) geological constitution, (2) geographical positioning, and (3) physical paleogeography. Geological constitution is the sum of those attributes of a particular geological unit that are defined by its composition, boundaries, and position with respect to other such units in the Caribbean area or elsewhere. A geological unit can be thought of as a time-bounded suite of rocks that were formed by a particular set of geodynamic processes operating at a designated location in the lithosphere. Typical examples of such units might include a specific

section of oceanic or continental crust, a volcanic arc, a set of genetically related sedimentary basins, a foldbelt, or a block-terrane. Each geological unit has its own ontogeny, spanning its origin, evolution, and possible transformation into other units. Units are named for convenience and book-keeping purposes, but the reader should be aware that names do not necessarily imply identity with geographical elements. For example, the Caribbean Mountains of northern South America, which now form an area of high relief, contain fragments of oceanic crust and island arc. Both Beata and Aves are identified as "ridges," but geologically they are quite different. The Beata Ridge is a thick oceanic crustal unit, while the Aves Ridge is part of an extinct volcanic arc (Holcombe et al., 1990). In the Caribbean region, many larger features, such as terranes, blocks, ridges, and arcs, are minutely subdivided by faults. Fault boundaries permit the delimitation of smaller entities that can be considered to have had semi-independent histories since faulting occurred (appendix 1, fig. 1).

Geological units can be superimposed in a single stack (i.e., in the same crustal position), as the following simple example illustrates. A section of early Mesozoic oceanic crust might evolve into a Cretaceous volcanic arc; later, both of these units might be deformed into a series of mountains and basins. The fate of each unit implies a different paleogeographical setting (in this example there are three: ocean floor, volcanic island-arc, and fully terrestrial conditions with complex relief). In this example only the last geologic unit can be said to be "active" or still in its original geomorphological form. The other two units are no longer resolvable as either ocean floor or volcanic arc; they are part of the basement of the last unit.

A more dynamic example would illustrate the point that, over time, segments of the earth's crust can change their relationship, form, and position, thereby affecting paleogeography. Along compressional plate boundaries, for example, oceanic crust and ridges may undergo subduction, thereby losing their original geological and geomorphological character. Similarly, ocean crust or volcanic arc suites overthrusting continental margins along a collisional suture will create

a new stack, one having the distinctive composite nature of a foldbelt (a geological unit in its own right, consisting of several amalgamated "fossil" precursors). Thus a new geography may arise ontogenetically from the old.

In creating reliable paleogeographical maps, it has long been recognized that to determine the successive sizes of a geological unit, the effects of movement and deformation have to be figuratively undone. How "reverse ontogeny" can be understood and worked out in a particular case of interest is illustrated in figure 2. The two cross sections in figure 2A represent the structure of the foldbelt in eastern Cuba and western Hispaniola as seen today. In figure 2B, these cross sections are restored to their relative positions before separation caused by sinistral movements along fault A'-A (steps 1 and 2). This requires the deletion of entities that have been intercalated as the result of movement along A'-A (Cayman Trench and southern and northern Hispaniolan blocks). With these omitted, it can be seen that the two cross sections can be precisely lined up along their volcanic arc sequences (step 2). In step 3, we simplify the present-day relative position and width of the geological units found in the foldbelt (carbonate continental margin, ophiolites, volcanic arcs, and sedimentary basins), depicting them as a series of superimposed bars. In steps 4 and 5 we sequentially remove the effects of overthrusting and shortening due to internal deformation within the units themselves, thereby resolving the original width of the foldbelt. Although this example is schematic, it makes the point that the geography of the present may differ radically from the geography of the past, even for the "same" land mass.

For each geological unit under discussion, positional coordinates in time (in Ma) and space (in degrees of latitude and longitude) are provided in appendix 2. Unit positions were constrained per time-slice using various sources of information, including maximum possible amplitude of strike-slip movements, continuity of geological structures across different block-terrane or arc segments, presence of correlatable rock complexes of known age in two or more distinct units, and

so forth (fig. 3). Plate motions provide another, more general form of constraint (appendix 2).

The third variable used to build paleogeographic maps is physical geography, which we define as information (*indicators*) regarding positive or negative relief of contiguous geological units (or their subcomponents) across time. Relevant information is widely but thinly scattered in the geological literature. For effective use, this information had to be refined in various ways, including reinterpretation of the age of late Tertiary sections according to current paleontological and stratigraphical criteria, reanalysis (if required) of depositional environment, determination of topographic indicators, and so forth.

A *land indicator* provides evidence of the existence of subaerial conditions within a geological unit at a specific time in its ontogeny. However, land indicators have to be interpreted carefully, as some are much better than others. Thus, although unconformities and hiatuses both represent gaps in the geological record, their significance is not the same. An unconformity is a surface that separates two superimposed sets of strata. Unconformities are erosional surfaces and *may* provide clear evidence of land emergence if associated with long-lasting hiatuses (but see below). Although also a gap in the rock record, a hiatus is defined as time not represented by strata (i.e., an interval of nondeposition, erosion, or both). Uplift and nondeposition of sediments during $n1$ Ma can produce a hiatus, but uplift also causes erosion of preexisting rocks, thereby additionally enlarging the gap in the record by $n2$ Ma. The total gap ($n1 + n2$) is therefore produced by erosion as well as nondeposition. Owing to the effects of bottom currents or rising sea floor, hiatuses can also be produced in the absence of subaerial exposure by submarine erosion, nondeposition, or both of these processes. Thus, a hiatus by itself does not imply land emergence, nor does the actual gap (in millions of years) necessarily mirror the time during which the area was uplifted as land.

Usually, indicators other than gaps per se are required in order to reach reliable conclusions about land emergence and coastline

position. These may include (1) sediments deposited in terrestrial environments (e.g., red beds, alluvium), (2) weathering surfaces or weathering products (e.g., paleosols, "coated" pebbles), (3) land-derived sediments in contiguous marine basins (e.g., conglomerates, sandstones), (4) lagoonal deposits representing fresh- or brackish-water near-shore environments, (5) coastal sediments (e.g., beach sands, dunes), and (6) remains of terrestrial organisms preserved in marine sediments (e.g., lignites, terrestrial plants, pollen, spores).

Among *marine indicators*, different rock types and their fossil inclusions are of great value because they are highly correlated with water depth at the time of original deposition. Lack of marine sediments in a particular section may be the result of erosion (within a hiatus), so whether a transgression actually occurred has to be resolved by examining the composition and environment of deposition of rocks in surrounding basins. This is why some geological units are represented as submarine environments in the paleogeographical maps, even though marine rocks of appropriate age are not known within them. For example, although several hiatuses are recorded on the Beata Ridge, unequivocal indicators of subaerial conditions have not been found. Accordingly, we assume that these hiatuses are due to submarine erosion and nondeposition, and portray the ridge as a submarine feature from Late Oligocene to Recent (see fig. 4).

Other phenomena may have paleogeographical significance if they provide insights into specific conditions or occurrences in the past. For present purposes, the most important of these is termination of volcanic activity in island arcs. This phenomenon, usually due to arc-arc, arc-ridge or arc-continental collision (Hamilton, 1988), is known to have a profound effect on uplift. The mechanism of uplift is related to the emplacement of huge intrusive bodies coincidental with arc extinction, causing widespread isostatic adjustment (uplift) along the arc axis (Iturralde-Vinent, 1988a, 1994a). Uplift is then followed by subsidence within a period of only a few million years. Although postmagmatic-phase uplift is well substantiated, its pertinence to Caribbean paleogeography has not

been widely appreciated (but see Early Middle Jurassic to Late Eocene Paleogeography). As discussed here in relation to the arcs associated with the evolution of the Caribbean Plate, termination of arc magmatism in the Aptian, Late Campanian/Early Maastrichtian,

and early Middle Eocene consistently produced substantial uplift followed by deep erosion of the extinct volcanic arc edifices (Iturralde-Vinent, 1988a, 1994a; MacPhee and Iturralde-Vinent, 1994, 1995).

PALEOGEOGRAPHY OF THE CARIBBEAN REGION: EVIDENCE AND ANALYSIS

This section provides an analysis of the several categories of basic geological information presented in the tables, figures, and appendices. Appendices 1 and 2 and tables 1–4 should be consulted throughout for supporting evidence and additional literature not directly referenced in the following paragraphs.

EARLY MIDDLE JURASSIC TO LATE EOCENE PALEOGEOGRAPHY

This long stage in the evolution of the Caribbean region may be considered to have begun with the creation of a basin, the embryonic Caribbean Sea, coincident with the break-up of Pangaea and the separation of Laurasia from Gondwana (fig. 5; table 1). During the late Triassic/middle Jurassic, an epicontinental siliciclastic basin developed between the cratonic areas of South and North America in reaction to the eastward migration of the Tethys (Anderson and Schmidt, 1983; Burke et al., 1984; Bartok, 1993). This epicontinental sea should not be thought of as the Caribbean basin as presently configured, but as a precursor situated within western Pangaea (see Pindell, 1994: fig. 2.6a). Its epicontinental nature is demonstrated conclusively by associated marine invertebrate faunas and sediment composition (Salvador, 1987, 1991; Pszczolkowski, 1987).

The early Caribbean basin began as a narrow seaway between the Pacific and Tethys, probably during the Bajocian/Bathonian (Bartok et al., 1985) as oceanic crust was being formed between western Laurasia (North America) and western Gondwana (South America) (fig. 5; Pindell, 1994: fig. 2.6b, c). The existence of lands closely bordering this seaway is indicated by evidence of coastal-

type vegetation at several localities of ?Early/Middle Jurassic to early Late Jurassic age in Mexico and western Cuba (Areces-Mallea, 1990).

In the North American portion of Laurasia an important marine transgression took place during early to middle Oxfordian time. Volant terrestrial and shallow-water marine vertebrates, indicative of proximate land environments, make an appearance at this time at localities on the Guaniguanico terrane that forms westernmost Cuba (Iturralde-Vinent and Norell, 1996). The occurrence of this Oxfordian faunule in what is now Cuba constitutes an example of “Viking funeral ship” emplacement (McKenna, 1973), because these taxa were extinct before Guaniguanico reached western Cuba long after detaching from the Yucatan borderland early in the Tertiary (Iturralde-Vinent, 1994a, 1996a; Bralower and Iturralde-Vinent, 1997). In the South American portion of Gondwana the paleogeographical context was different, because the main transgression across the northern continental margin took place later, during the Early Cretaceous. With the Oxfordian transgression and widening marine gap between Laurasia (North America) and Gondwana (South America), any possibility of direct, overland dispersal between these continental areas ended (fig. 5).

The developing Caribbean seaway (“Hispanic Corridor” of Bartok et al., 1985) underwent widening from the Middle Jurassic to the Early Cretaceous as a consequence of sea floor spreading (Pindell, 1994: fig. 2.6c, d). Oceanic crust and sediments formed at that time are now represented in part by deformed ophiolite bodies and thrust belts around the margins of the Caribbean region (Guatemala, Greater Antilles, Aruba/Tobago

Belt, Caribbean Mountains, and Colombian–Venezuelan Andes) (Dengo and Case, 1990). Oceanic basalts associated with radiolarian cherts and carbonate rocks of Jurassic through Cretaceous age have been found within these allochthonous crustal bodies (Bartok et al., 1985; Montgomery et al., 1994; Iturralde-Vinent, 1996a). In some places these vulcano-sedimentary rocks constitute segments of a continuous section (e.g., northwestern Cuba, southwestern Puerto Rico), but most frequently they consist of isolated cobble- to boulder-sized bodies within highly deformed belts. Although it cannot be determined from existing information whether the age gaps record actual hiatuses, the absence of any evidence of terrestrial environments in these contexts strongly suggests prevailing deep-water conditions from their origin until their incorporation into the foldbelts fringing the Caribbean region.

Indications of lands or shallow seas (or both) within the confines of the early Caribbean sea are found in rocks of the Cretaceous volcanic arc. As a geological unit, the Cretaceous arc is defined by a particular set of igneous, sedimentary, and metamorphic rocks of Neocomian through late Campanian/early Maastrichtian age (Dengo and Case, 1990; Iturralde-Vinent, 1994a, 1994c, 1996a, 1996b). Today, elements of this arc are widely distributed in the foldbelts found within the Caribbean region (fig. 5). The paleogeographical position of the Cretaceous arc in relation to North and South America remains the subject of debate (see Leclere and Stephan, 1985; Ross and Scotese, 1988; Donnelly, 1989a; Pindell, 1994; Mann et al., 1995; Hay and Wold, 1996; Iturralde-Vinent, 1996a, 1997b).

Shallow marine environments are marked by the occurrence of rudist limestones of different ages, occurring as isolated, lenticular intercalations within marine-deposited volcanic sediments. Although the presence of rudists is not diagnostic of nearby emergent land, it is consistent with the existence of atoll-like islands similar to those seen today on shallowly submerged volcanoes. More substantive indications of land development in the Cretaceous island arc are Neocomian plant remains reported from the Los Ranchos

Fm, a volcanic arc section in Hispaniola (Smiley, MS, cited by Kesler et al., 1991b). This assemblage (including *Gleichenites*, *Zamites*, *Phoenicopsis*, *Yuccites*, *Podozamites*, and other taxa) is thought to have grown in a warm, open, seasonally dry habitat adjacent to the shallow-water marine environment in which the remains were deposited (Kesler et al., 1991b). Other geological indicators of emergence during the evolution of the Cretaceous arc include terrestrially deposited volcanic rocks and several major unconformities occurring within volcanic arc sections, usually in association with hiatuses and basal conglomerates.

Unfortunately, the paleogeographical information content of these indicators is limited and cannot be reliably used to provide a detailed assessment of areal extensiveness and orographic relief in the Cretaceous arc. On the other hand, such information does provide some indication of the temporal succession of environments in specific geological units. In Hispaniola, the Neocomian plant-bearing rocks are overlain by marine limestones of the Albian Rio Husillo Fm (Kesler et al., 1991b; Iturralde-Vinent, 1997a), implying that a transgression obliterated previously existing terrestrial environments. This sequence of events is rather common in the Cretaceous arc sections, and our interpretation is substantiated by two pieces of evidence. First, volcanic and non-volcanic marine rocks drape all of the unconformities recorded in the Cretaceous arc, indicating that hiatuses were succeeded by a new phase of marine deposition (Nagy et al., 1983; Lewis et al., 1991; Rojas et al., 1995; Iturralde-Vinent, 1995, 1997a; Beccaluva et al., 1996). Second, the rudist limestones occur in the form of lenses intercalated within other marine sediments and laterally transitional with isochronous deeper water beds (Rojas et al., 1995). This indicates that any intra-Caribbean land environments existing on the volcanic arc at that time would have been limited in size, and therefore susceptible to rapid obliteration during transgressive phases. We conclude from this that, while land environments certainly existed in the Caribbean Basin during the Cretaceous, they were short-lived, probably winking in and

TABLE 1
**Land and Marine Indicators for Selected Geological Units of Caribbean Region,
 Early Jurassic to Late Eocene (180–37 Ma)**

Geological unit	Current geographical location of the geological unit	Land indicators	Marine indicators
		(1) hiatuses; (2) red beds, alluvia, paleosols, plant and animal fossils; (3) nearshore conglomerates and/or lagoonal sediments	(1) shallow-water environments; (2) deep-water environments; (3) arc/oceanic volcanic activity
1. CONTINENTAL MARGINS AROUND THE CARIBBEAN			
Florida Block	Florida Peninsula	(1) pre-Tithonian, Cenomanian, Danian, Ypresian, mid-Late Eocene: McFarlane and Menes, 1991; Galloway et al., 1991	(1) Tithonian transgression and marine sediments up to Late Eocene: McFarlane and Menes, 1991; Galloway et al., 1991
Bahamas Platform	Bahamas	(2) pre-Oxfordian: Meyerhoff and Hatten, 1974	(1) Oxfordian to Late Eocene (2) channels of Aptian to Late Eocene age: Meyerhoff and Hatten, 1974; Iturralde-Vinent, 1994a; Buffler and Hurst, 1995
Gulf of Mexico Basin	Gulf of Mexico Basin	(1, 3) pre-Oxfordian, late Tithonian, Cenomanian, Turonian–Coniacian, mid-Campanian, latest Maastrichtian, mid-Late Eocene: Salvador, 1991; McFarlane and Menes, 1991; Galloway et al., 1991 (2—red beds) late Triassic to Jurassic (Callovian): Salvador, 1991	(1) Oxfordian to Late Eocene: Salvador, 1991; McFarlane and Menes, 1991; Galloway et al., 1991
Mexican terranes	Southern Mexico	(1) Aptian, early Campanian: Salvador, 1991; McFarlane and Menes, 1991; Galloway et al., 1991 (1, 2, 3) pre-Oxfordian red beds: Michalzik, 1987	(1, 2) Oxfordian transgression and pre-Late Eocene marine sediments: Michalzik, 1987; Salvador, 1991; McFarlane and Menes, 1991; Galloway et al., 1991
Maya Block	Yucatan Peninsula	(1) Aptian-Barremian?: McFarlane and Menes, 1991 (2—red beds) pre-Aptian undifferentiated: López-Ramos, 1975; Salvador, 1991; McFarlane and Menes, 1991	(1) Aptian to Late Eocene carbonates: López-Ramos, 1975; Viniestra, 1981; McFarlane and Menes, 1991; Galloway et al., 1991; Salvador, 1991
Chortis Block	Northern Central America	(1, 2) several levels of late Jurassic, Cretaceous, Paleocene, and Eocene age: Donnelly et al., 1990	(1) several levels of Cretaceous, Paleocene, and Eocene age: Donnelly et al., 1990 (3) Paleocene and Eocene: Donnelly et al., 1990
South American shields, foldbelts, and basins	Northern half of South America	(1) Jurassic–Cretaceous boundary, Campanian–Maastrichtian, Early–Middle Eocene: Lugo and Mann, 1995; Parnaud et al., 1995; Cooper et al., 1995 (1, 2) pre-Cretaceous: Maze, 1984; Lugo and Mann, 1995; Parnaud et al., 1995; Cooper et al., 1995	(1, 2) transgression in early Cretaceous and marine sediments up to Late Eocene: Lugo and Mann, 1995; Parnaud et al., 1995; Cooper et al., 1995 (3) Jurassic and Cenozoic in the Andes: Case et al., 1990

TABLE 1
(Continued)

Geological unit	Current geographical location of the geological unit	Land indicators	Marine indicators
		(1) hiatuses; (2) red beds, alluvia, paleosols, plant and animal fossils; (3) nearshore conglomerates and/or lagoonal sediments	(1) shallow-water environments; (2) deep-water environments; (3) arc/oceanic volcanic activity
Western Cuban allochthonous terranes	Cuba (Guaniguanico, Isla de Juventud, and Escambray)	(1) Campanian–early Maastrichtian, Middle Eocene: Pszczolkowski, 1978; Iturralde-Vinent, 1994a (2, 3) pre-Oxfordian: Pszczolkowski, 1978, 1987; Iturralde-Vinent, 1994a, 1996b	(1) transgression in the Oxfordian; early Tithonian, Cenomanian–Turonian shallow marine (2) since Tithonian: Pszczolkowski, 1978, 1987; Iturralde-Vinent, 1988b, 1994a (3) mid-Jurassic to early Cretaceous rift basalts: Iturralde-Vinent, 1988b, 1996e
2. CRETACEOUS VOLCANIC ARC			
Jamaican arc segment	Western Jamaica	(1) Aptian?, Turonian, Campanian–Maastrichtian: Maurrasse, 1990; Lewis et al., 1990; Robinson, 1994	(1) Aptian, Albian, Santonian, Campanian, Maastrichtian: Maurrasse, 1990; Lewis et al., Draper, 1990; Robinson, 1994 (3—arc) Barremian to Maastrichtian: Montadert et al., 1985; Maurrasse, 1990; Lewis et al., 1990; Robinson, 1994
Greater Antilles Foldbelt	Cuba	(1, 3—conglomerates) mid-Aptian, mid-Albian, Turonian–Coniacian, mid-Campanian, Paleocene, Middle–Late Eocene: Iturralde-Vinent, 1994a, 1996a–1996d; Rojas et al., 1995	(1) late Albian, Santonian, early Campanian, Maastrichtian: Iturralde-Vinent, 1994a, 1996a–1996d; Rojas et al., 1995 (2) Albian, Cenomanian, Santonian: Iturralde-Vinent, 1994a, 1996a–1996d; Rojas et al., 1995 (3—arc and oceanic) Aptian–late Campanian: Iturralde-Vinent, 1994a, 1996a–1996d; Rojas et al., 1995
Greater Antilles Foldbelt	Eastern Jamaica (Blue Mountains)	(1) Campanian–Maastrichtian: Lewis et al., 1990	(1) Barremian, Campanian: Robinson, 1994 (3—oceanic) pre-Barremian?–mid-Albian?, Campanian?–Maastrichtian: Montadert et al., 1985; Robinson, 1994; Iturralde-Vinent, 1995
Greater Antilles Foldbelt	Hispaniola (northern peninsula, Puerto Plata/Samaná, Cordillera Central, Cordillera Oriental)	(1, 3—conglomerates) early Aptian, Santonian?, mid-Campanian–Maastrichtian: Bowin, 1975; Draper et al., 1997; Maurrasse, 1990; Lewis et al., 1990; Mann et al., 1991; Lebrón and Perfit, 1993; Russell and Kesler, 1991; Iturralde-Vinent, 1994b, 1997b (2—plant fossils) Neocomian: Kesler et al., 1991b; Iturralde-Vinent, 1997b	(1—limestone) Albian, Santonian?, Campanian, Maastrichtian, Paleocene: Bowin, 1975; Lebrón and Perfit, 1993; Iturralde-Vinent, 1994b, 1997a (3—arc) Neocomian–Campanian: Bowin, 1975; Maurrasse, 1990; Lewis et al., 1991; Mann et al., 1991; Lebrón and Perfit, 1993; Iturralde-Vinent, 1994b, 1997a; Russell and Kesler, 1991; Kesler et al., 1991a, 1991b

TABLE 1
(Continued)

Geological unit	Current geographical location of the geological unit	Land indicators	Marine indicators
		(1) hiatuses; (2) red beds, alluvia, paleosols, plant and animal fossils; (3) nearshore conglomerates and/or lagoonal sediments	(1) shallow-water environments; (2) deep-water environments; (3) arc/oceanic volcanic activity
Greater Antilles Foldbelt	Puerto Rico/Virgin Islands	(1) Albian, Coniacian–Santonian, mid-Campanian, Maastrichtian: Maurrasse, 1990; Lewis et al., 1990	(1) Aptian?, Albian, Santonian, Campanian, Maastrichtian: Maurrasse, 1990; P. Skelton and H. Santos, personal commun. 1996 (3—arc) Barremian?–Maastrichtian: Maurrasse, 1990; Lewis et al., 1990
Aves–Lesser Antilles arc segment	Aves Ridge		(3—arc) Cretaceous: Nagle, 1972; Bouysse et al., 1985; Pinet et al., 1985
Aves–Lesser Antilles arc segment	Lesser Antilles	(1) Campanian: Maurrasse, 1990	(3—arc) Berriasian?–Maastrichtian: Bouysse et al., 1985; Pinet et al., 1985; Westercamp et al., 1985; Maury et al., 1990
Aruba/Tobago Belt	Aruba to Tobago	(1) Campanian–Maastrichtian: González de Juana et al., 1980; Jackson and Robinson, 1994; Donovan, 1994	(3—oceanic or back arc) early Cretaceous: González de Juana et al., 1980; Jackson and Robinson, 1994; Donovan, 1994 (3—arc) late Cretaceous: González de Juana et al., 1980; Jackson and Robinson, 1994; Donovan, 1994
Caribbean Mountains Foldbelt	Caribbean Mountains	(1) mid-Campanian: Bellizia and Dengo, 1990; Beccaluva et al., 1996	(1) late Campanian, Maastrichtian: Bellizia and Dengo, 1990; Beccaluva et al., 1996 (3—oceanic and back arc) Cretaceous (pre-Campanian): Bellizia and Dengo, 1990; Beccaluva et al., 1996
3. PALEOCENE–EOCENE VOLCANIC ARC			
Nicaragua–Cayman arc segment	Cayman Ridge and Nicaragua Rise		(3—arc) Perfit and Heezen, 1978 (3—back arc) Early to Middle Eocene: Sigurdsson et al., 1997 [Hole 998]
Nicaragua–Cayman arc segment	Western Jamaica	(1) Middle Eocene: Eva and McFarlane, 1985; Robinson, 1994	(1, 2) Eva and McFarlane, 1985; Robinson, 1994
Greater Antilles Foldbelt	Eastern Cuba	(1) Middle Eocene, very local: Iturralde-Vinent, 1976–77	(1) Middle Eocene: Iturralde-Vinent, 1976–77, 1994a, 1996d (2) Paleocene–Late Eocene: Iturralde-Vinent, 1976–77, 1994a, 1996b, 1996d (3—arc, back arc) Paleocene–early Middle Eocene: Iturralde-Vinent, 1976–77, 1994a, 1996

TABLE 1
(Continued)

Geological unit	Current geographical location of the geological unit	Land indicators	Marine indicators
		(1) hiatuses; (2) red beds, alluvia, paleosols, plant and animal fossils; (3) nearshore conglomerates and/or lagoonal sediments	(1) shallow-water environments; (2) deep-water environments; (3) arc/oceanic volcanic activity
Greater Antilles Foldbelt	Eastern Jamaica (Blue Mountains)	(1) Early Paleocene, Middle Eocene: Eva and McFarlane, 1985; Robinson, 1994	(1) Paleocene, Middle–Late Eocene: Eva and McFarlane, 1985; Robinson, 1994 (2) Eocene: Eva and McFarlane, 1985; Robinson, 1994 (3—arc) Paleocene–Early Eocene: Robinson, 1994
Greater Antilles Foldbelt	Hispaniola	(1) Middle Eocene: Butterlin, 1960; Maurrasse, 1982; Draper, 1989; Mann et al., 1991	(1—arc, back arc) Paleocene–Lower Eocene: Butterlin, 1960; Maurrasse, 1982; Draper, 1989; Mann et al., 1991
Greater Antilles Foldbelt	Puerto Rico/Virgin Islands	(1) Middle Eocene: Mattson, 1984; Lewis et al., 1990	(?) Maurrasse, 1990; Mann et al., 1991; Lewis et al., 1990
Aves–Lesser Antilles arc segment	Aves Ridge		(1, 3—arc) Nagle, 1972; Bouysse et al., 1985; Pinet et al., 1985
Aves–Lesser Antilles arc segment	Lesser Antilles		(3—arc) Bouysse et al., 1985; Maury et al., 1990
4. PALEOCENE–EOCENE INACTIVE ARC SEGMENTS (FOLDBELT)			
Western, west-central, and east-central Cuba inactive segment	Western and central Cuba	(1) Paleocene, Middle–Late Eocene: Iturralde-Vinent, 1994a, 1996a	(1, 2) Iturralde-Vinent, 1994a, 1996a
Aruba/Tobago Belt	Aruba to Los Roques and Tobago	(1) Late Paleocene, Middle Eocene, Late Eocene: Jackson and Robinson, 1994	(1) González de Juana et al., 1980; Maurrasse, 1990; Jackson and Robinson, 1994
Aruba/Tobago Belt	Margarita and Trinidad	(1) Middle–Late Eocene locally: Jackson and Donovan, 1994; Algar and Erikson, 1995	(2) Paleocene–latest Eocene: Donovan, 1994; Algar and Erikson, 1995
Cordillera del Caribe thrust belt	Caribbean Mountains	(1) González de Juana et al., 1980	(2) Paleocene–Eocene foreland sediments: González de Juana et al., 1980
5. OCEANIC CRUSTAL SEGMENTS			
Yucatan Basin	Yucatan Deep		(3—oceanic) Maastrichtian?–Eocene?: Rosencrantz, 1990
Cayman Trench	Cayman Trench		(3—oceanic) mid-Eocene–Recent, with Oligocene gap: Rosencrantz, 1990, 1995
Southern Hispaniola Terrane	Hispaniola (Southern [Tiburón] Peninsula)	(1) mid-Campanian, Maastrichtian: Maurrasse, 1990; Lewis et al., 1990; Mann et al., 1991	(3—oceanic) Cenomanian–Campanian: Maurrasse, 1990; Lewis et al., 1990; Mann et al., 1991

TABLE 1
(Continued)

Geological unit	Current geographical location of the geological unit	Land indicators	Marine indicators
		(1) hiatuses; (2) red beds, alluvia, paleosols, plant and animal fossils; (3) nearshore conglomerates and/or lagoonal sediments	(1) shallow-water environments; (2) deep-water environments; (3) arc/oceanic volcanic activity
Beata Ridge	Beata Ridge		(3—oceanic) Cretaceous: Holcombe et al., 1990
Greater Antilles ophiolite thrust belts	Greater Antilles		(3—oceanic) early Jurassic to late Cretaceous: Montgomery et al., 1994; Iturralde-Vinent, 1996a; Dengo and Case, 1990
Colombia and Venezuelan Basins	Colombia and Venezuelan Basins		(3—oceanic) Cretaceous: Holcombe et al., 1990; Case, 1975
Siquisique thrust belt	Venezuela		(3—oceanic) mid-Jurassic: Bartok et al., 1985; Case et al., 1990
Aruba/Tobago Belt	Aruba to Tobago		(3—oceanic) Cretaceous: Jackson and Robinson, 1994
Southern Central American Volcanic Arc	Costa Rica and Panama		(3—oceanic) Jurassic, Cretaceous: Escalante, 1990; Dengo and Case, 1990; Kolarski et al., 1995a, 1995b

out of existence within periods of only a few million years.

A good example of such evanescence can be seen in the section along the Canal Paso Bonito a Cruces, northwest of Sierra de Escambray, Cuba (unpubl. obs.). Here, Cretaceous volcanic breccias and conglomerates are patchily overlain by slope and alluvial sands and gravels which have been weathered to paleosols that exhibit caliches, root casts, and other indications of subaerial exposure. These rocks are in turn succeeded by unweathered, well-bedded tuffs and rare marine limestones. Thus, however long this island may have existed, it did not last *as land* into later epochs.

Tracking the paleoposition (i.e., changes in latitude and longitude through time) of the Cretaceous volcanic arc is another issue of great importance. There appears to be a consensus, at least among authors of the most widely cited plate tectonic models, that this arc originated in the Pacific (Malfait and Dinkelmann, 1972; Burke et al., 1984; Leclere and Stephan, 1985; Pindell and Barrett, 1990; Pindell, 1994), although other interpretations also exist (fig. 5; Turner, 1972;

Donnelly, 1989a; Iturralde-Vinent, 1994a, 1997b). However, whatever its starting position might have been, there is little evidence to support the view that the continents were physically united by the arc. In principle, connection might have occurred during major uplift events recorded in association with various unconformities (between the Neocomian and early Albian, between the Coniacian and Santonian, and in the early Campanian). However, information is lacking concerning whether these erosional surfaces were continuous or synchronous along the trend of the arc (Iturralde-Vinent 1994a, 1996b, 1997b). During the late Campanian and early Maastrichtian (ca. 70–80 Ma) substantial subaerial exposure existed along the Cretaceous arc and adjacent continental margins, as indicated by evidence of deformation, angular unconformities, hiatuses, deep-seated erosion, mountain building, and terrestrial sedimentation (including conglomerate and paleosol development) (Khudoley and Meyerhoff, 1971; Mattson, 1984; Pushcharovski et al., 1989; Maurrasse, 1990; Lewis et al., 1990; Iturralde-Vinent, 1994a, c, 1995, 1996b, 1997b; Beccaluva et al.,

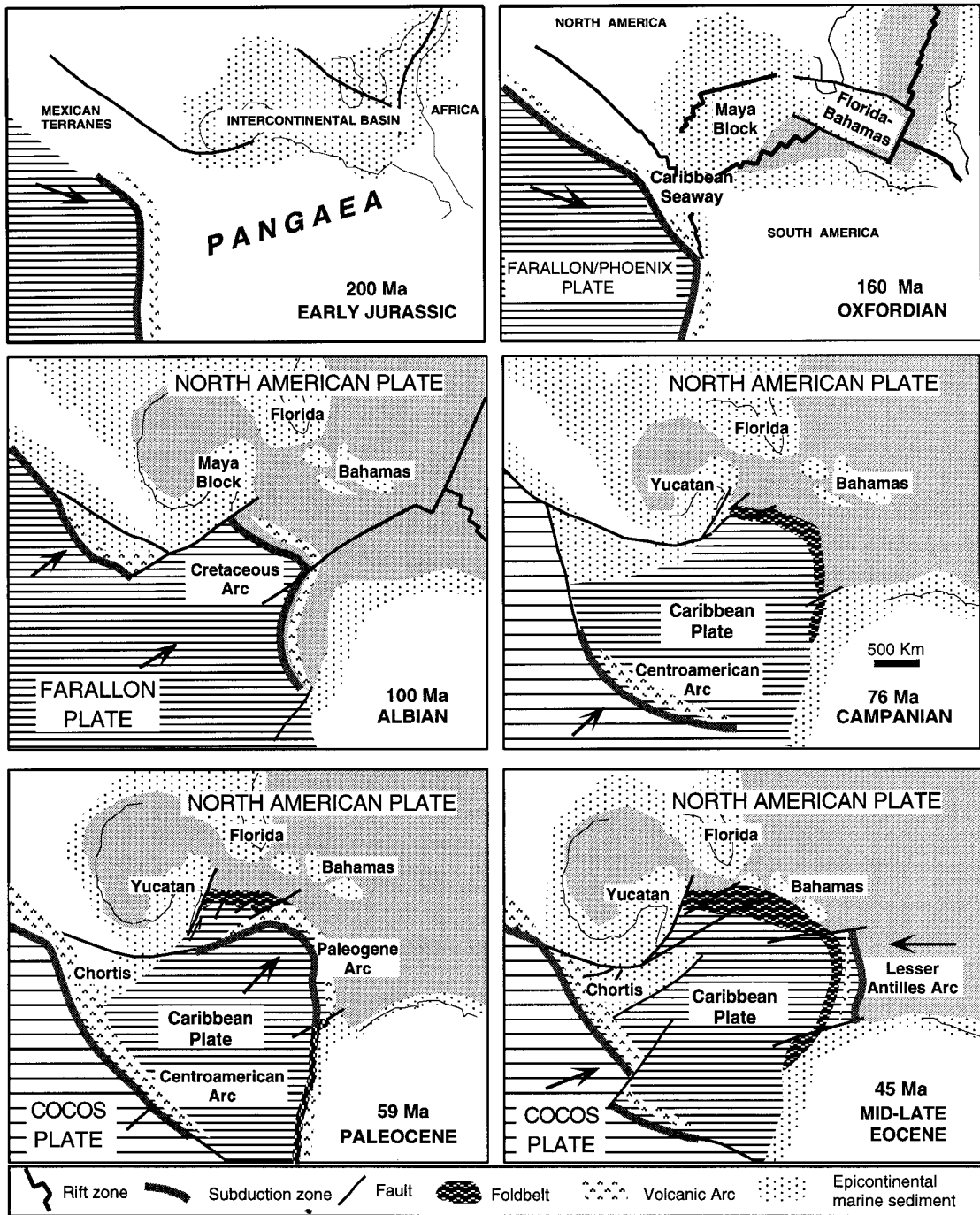


Fig. 5. Plate tectonic model of the Caribbean region for Jurassic through Eocene (after Iturralde-Vinent, 1997b, slightly modified). Maps are designed to display tectonic information; they are not paleogeographically accurate.

1996). At this time magmatic activity terminated along large segments of the volcanic arc, including its western and eastern extremities (i.e., modern central and western Cuba in the north and west, and the Netherlands and Venezuelan Antilles and Caribbean Mountains in the south and east). Cessation of the magmatic phase is coincidental on a wider scale with the Subhercinian orogeny (Schwan, 1980; Leonov and Khain, 1987), an important global tectonic event, and several drops in eustatic sea level (Haq et al., 1987). It is reasonable to infer that if any land connection existed between North and South America in the last part of the Cretaceous, this connection most probably would have occurred during the late Campanian and early Maastrichtian. However, if in fact contact occurred it would have been brief, because transgressive late Maastrichtian marine sediments are recorded in the Cretaceous volcanic arc as well as in North and South America (table 1; appendix 1).

There does not appear to be any reliable evidence of permanent islands or island-continent connections in the Caribbean region during the early part of the Paleogene, although we cannot reject this possibility altogether (see Biogeographical Hypotheses and Caribbean Paleogeography). An unconformity dated to the K/T boundary is known to exist in some parts of the Caribbean sea floor, but uninterrupted sedimentation evidently continued elsewhere in the Caribbean Basin, even within the area of the inactive Cretaceous arc. This unconformity could have been caused by submarine erosion rather than by cessation of deposition if, for example, it was induced by tsunamis triggered by the K/T impactor landing in Chicxulub (Pszczolkowski, 1986; Maurrasse and Sen, 1991) and/or in the Yucatan Basin (Iturralde-Vinent, 1992).

After a period of relative quiescence, volcanic activity began again in the Caribbean region in the Paleocene (Iturralde-Vinent, 1994a, 1997b), as indicated by the occurrence of a set of magmatic, sedimentary, and metamorphic rocks that widely outcrop in the region (eastern Cuba, Jamaica, Hispaniola, Puerto Rico, Virgin Islands, Cayman Ridge, Nicaragua Rise, and Aves Ridge/Lesser Antilles). This resumption of activity ushered in

the formation of the Paleogene volcanic arc. However, magmatism was short-lived in this new arc, effectively ending by the Middle Eocene. Within the Paleogene arc, marine sediments uninterruptedly filled some basins, indicating that land contacts between arc components and the continents were not (or were no longer) in existence (Lewis and Straczek, 1955; Bresznyánszky and Iturralde-Vinent, 1985). Uninterrupted sedimentation from Paleocene through Middle Eocene is recorded in basins located on the Caribbean seafloor (Edgar et al., 1973; Sigurdsson et al., 1997), as well as in foldbelt areas, along the trend of the inactive segments of the Cretaceous arc (e.g., deep marine sediments outcropping through much of La Habana and Matanzas provinces in west central Cuba) (Bronnimann and Rigassi, 1963; Pszczolkowski, 1987; Bresznyánszky and Iturralde-Vinent, 1985; Bralower and Iturralde-Vinent, 1997). Furthermore, a major transgression occurring between the late Early and Middle Eocene produced extensive deposits of shallow- and deep-water marine carbonate rocks on previously positive areas throughout the Caribbean (Lewis and Straczek, 1955; Bronnimann and Rigassi, 1963; Iturralde-Vinent, 1982, 1994a; Holcombe et al., 1990; Lewis et al., 1990; Maurrasse, 1990; Edgar et al., 1973; Sigurdsson et al., 1997). The occurrence of this transgression militates against there having been any considerable exposure of land during the early Middle Eocene.

Another global tectonic event, the Illyrian phase of tectogenesis (Leonov and Khain, 1987), produced a profound modification of the Caribbean tectonic regime between Middle and Late Eocene (fig. 5). Extensive uplift and deformation occurred not only in the Caribbean Basin per se but also in the surrounding continental margins and oceanic domains (Khudoley and Meyerhoff, 1971; González de Juana et al., 1980; Mattson, 1984; Lewis et al., 1990; Iturralde-Vinent 1981, 1994a, 1994b, 1994c, 1996a; Maurrasse, 1990). With reorganization of the geodynamic regime, the relative motion of the Caribbean Plate shifted eastward, and relative motion between the North and South American plates decreased markedly (Pindell, 1994). In concert with these developments, several deformed belts were consolidated and accreted

against continental areas, and magmatic activity shifted to new locations (Central America and Lesser Antilles). The north-western edge of the Caribbean Plate (NW Greater Antilles Belt) collided with the Yucatan and Bahamas margins, while the south-eastern edge (Aruba/Tobago Belt) interacted with the South American margin. Also, beginning in the latest Eocene, new tectonic elements were defined within the Caribbean region. Transverse faulting divided the plate into several microplates and block-terranes, and their subsequent displacement disrupted the original structure (see appendix 2).

In summary, existing data indicate that subaerial entities were formed along the Cretaceous and Paleogene volcanic arcs and nearby continental margins from time to time from the Jurassic into the Eocene. However, there is no evidence that any of these entities lasted for long periods; indeed, none seems to have survived as emergent land into the subsequent interval (latest Eocene to Middle Miocene). Nevertheless, if the Cretaceous arc ever connected North and South America, this most likely occurred during the late Campanian to early Maastrichtian (ca. 70–80 Ma ago), just after extinction of the Cretaceous volcanic arc.

LATEST EOCENE TO MIDDLE MIOCENE PALEOGEOGRAPHY

In this section, three “snapshot” intervals are discussed in detail: Eocene–Oligocene transition (35–33 Ma), Late Oligocene (27–25 Ma), and early Middle Miocene (16–14 Ma). Basic data are presented in appendix 1 (see also figs. 6–8 and tables 2–4). These intervals were chosen in order to contrast periods of maximum and minimum land development. The Eocene–Oligocene transition was a time of general uplift; therefore, the amount of subaerial land in the Caribbean should have been at a maximum. The Late Oligocene was a time of high sea level, and therefore of minimum exposure (and, probably, interconnectedness) of emergent areas in the early Cenozoic. In the early Middle Miocene, further isolation of land areas took place as a consequence of active tectonic disruption of the northern and southern Caribbean Plate boundaries. In the case of the Greater Antilles, this resulted in the subdivi-

vision and separation of block-terranes previously acting as continuous landmasses. This subdivision may have been significant biogeographically if it caused island–island vicariance (as opposed to continent–island vicariance; see Biogeographical Hypotheses and Caribbean Paleogeography).

EOCENE–OLIGOCENE TRANSITION (35–33 Ma)

The transition between the end of the Eocene and the beginning of the Oligocene (zones P16 to P18 of Berggren et al., 1995) coincides with the Pyrenean phase of tectogenesis (Schwan, 1980; Leonov and Khain, 1987), the effects of which are well represented in the Caribbean region (MacPhee and Iturralde-Vinent, 1995). In this phase, general tectonic uplift coincided with a major eustatic sea level drop at ca. 35 Ma (Miller et al., 1996). As a result, subaerial exposure within the Caribbean basin was probably more extensive than at any other time in the Cenozoic, including the late Quaternary. The map in figure 6 reflects this fact (see also table 2). However, it is important to compare this map with other “Oligocene” reconstructions which represent this period as one of overall minimum land exposure (e.g., González de Juana et al., 1980; Gallo-way et al., 1991; Macellari, 1995). The explanation for the difference in treatment lies in the fact that most Oligocene reconstructions depict the paleogeography of the mid-to later Oligocene, by which time the Pyrenean orogenic phase had terminated (see discussion of next map).

Evidence for Pyrenean uplift can be seen in stratigraphic sections as well as submarine dredge samples, drill cores, and seismic lines recovered from many parts of the Caribbean and surrounding continental borderlands (table 2; appendix 1). Stratigraphic sections consistently lack marine sediments of latest Eocene–Early Oligocene age, presenting instead hiatuses, red beds, and other kinds of terrestrial deposits (table 2; appendix 1). In many sedimentary basins located near former topographic highs, latest Eocene/Early Oligocene sediments carry abundant land-derived debris, chiefly very coarse conglomerates (matrix or clast-supported) and sandstones. This type of sedimentary unit is so common that it may usefully be dubbed the

TABLE 2
**Land and Marine Indicators for Selected Geological Units of Caribbean Region,
 Eocene–Oligocene Transition (35–33 Ma, Zones P16–18)**

Geological unit	Current geographical location of the geological unit	Land indicators	Marine indicators
		(1) hiatuses; (2) red beds, alluvia, paleosols, plant and animal fossils; (3) nearshore conglomerates and/or lagoonal sediments	(1) shallow-water environments; (2) deep-water environments; (3) arc/oceanic volcanic activity
Florida Block	Florida Peninsula	(1) Galloway et al., 1991; Hine, 1997; Randazzo and Jones, 1997	(1) Galloway et al., 1991; Hine, 1997, Randazzo and Jones, 1997
Bahamas Platform	Bahamas	(1—local hiatus) Ravenne et al., 1985	(1, 2) Meyerhoff and Hatten, 1974; Buffler and Hurst, 1995
Mexican terranes	Southern Mexico	(1, 3) López Ramos, 1975	(1, 2, 3) López Ramos, 1975
Maya Block	Yucatan Peninsula	(1) Butterlin and Bonet, 1966 (1, 2) López Ramos, 1975	(1, 2) Butterlin and Bonet, 1966; López Ramos, 1975
Chortis Block	Northern Central America	(1, 2) Maurrasse, 1990; Donnelly et al., 1990	(3) Maurrasse, 1990; Donnelly et al., 1990
Nicaragua Block	Nicaragua Rise	(1) Maurrasse, 1990; Holcombe et al., 1990; Sigurdsson et al., 1997 [Hole 1001] (1, 2) Waterford Touche-1, Colombia Berta-1 wells: Holcombe et al., 1990; Maurrasse, 1990; Donnelly et al., 1990	(1) Oligocene rocks dredged from Cayman Trench walls: Perfit and Heezen, 1978 (3) Holcombe et al., 1990
Western Jamaica Block	Western Jamaica	(1) Eocene–Oligocene hiatus of short duration: Eva and McFarlane, 1985; Robinson, 1994; Montadert et al., 1985	(1, 2) Eva and McFarlane, 1985; Robinson, 1994; Montadert et al., 1985
Southern Central American Volcanic Arc	Southern Central America	(3) Escalante, 1990; Kolarsky et al., 1995a	(1, 2, 3) Escalante, 1990; Kolarsky et al., 1995a
Atrato Basin	Northwestern South America	(1) Duque-Caro, 1990	
Northwestern South American foldbelts and basins (NWSA Microcontinent)	Northwestern South America	(1, 2, 3) González de Juana et al., 1980; Balkwill et al., 1995; Macellari, 1995; Lugo and Mann, 1995; Parnaud et al., 1995; Cooper et al., 1995	(1, 2) Orinoco River basin: González de Juana et al., 1980; Cooper et al., 1995; Algar and Erikson, 1995
Cordillera del Caribe Thrust Belt	Caribbean Mountains	(1) González de Juana et al., 1980; Mills, 1994; Macellari, 1995	
Aruba/Tobago Belt	Aruba to Tobago	(1) Hunter, 1978; González de Juana et al., 1980; Jackson and Robinson, 1994; Donovan, 1994; Macellari, 1995	(2) Trinidad: Algar and Erikson, 1995
Greater Antilles Foldbelt (Cuban blocks)	Cuba	(1, 2, 3) Iturralde-Vinent, 1972, 1988a; MacPhee and Iturralde-Vinent, 1995	(1, 2) Iturralde-Vinent, 1972, 1988a; MacPhee and Iturralde-Vinent, 1995
Greater Antilles Foldbelt (Blue Mountains Block)	Eastern Jamaica	(1) Eva and McFarlane, 1985; Montadert et al., 1985; Robinson, 1994	(1) Eva and McFarlane, 1985; Robinson, 1994

TABLE 2
(Continued)

Geological unit	Current geographical location of the geological unit	Land indicators	Marine indicators
		(1) hiatuses; (2) red beds, alluvia, paleosols, plant and animal fossils; (3) nearshore conglomerates and/or lagoonal sediments	(1) shallow-water environments; (2) deep-water environments; (3) arc/oceanic volcanic activity
Greater Antilles Foldbelt (Hispaniolan block-terrane)	Hispaniola	(1, 2, 3) Butterlin, 1960; Maurrasse, 1982; Mann et al., 1991; Iturralde-Vinent and MacPhee, 1996	(1, 2) Butterlin, 1960; Maurrasse, 1982; Mann et al., 1991; Iturralde-Vinent and MacPhee, 1996
Greater Antilles Foldbelt (Puerto Rico/Virgin Islands Block)	Puerto Rico/Virgin Islands	(1, 2, 3) Meyerhoff, 1933; Monroe, 1980; MacPhee and Iturralde-Vinent, 1995 (1) St. Croix: MacLaughlin et al., 1995	(1) Meyerhoff, 1933; Monroe, 1980; MacPhee and Iturralde-Vinent, 1995
Lesser Antilles Volcanic Arc	Lesser Antilles	(1) Westercamp et al., 1985; Maury et al., 1990	(1, 3) Westercamp et al., 1985; Maury et al., 1990
Aves Foldbelt	Aves Ridge	(1, 2, 3) hiatus is inferred; weathering is reported from clasts in the conglomerate: Nagle, 1972; Bock, 1972; Bouysse et al., 1985; Pinet et al., 1985	(1) Saba Bank: Nemeč, 1980; Pinet et al., 1985
Grenada Backarc Basin ^a	Grenada Basin		(1, 2) Bouysse et al., 1985; Pinet et al., 1985; Nemeč, 1980; Bird, 1991; Bird et al., 1993
Beata Block	Beata Ridge	(1) Case, 1975; Mascle et al., 1985; Holcombe et al., 1990; DSDP Hole 151: Maurrasse, 1990	
Cayman Ridge	Cayman Ridge	(1) Perfit and Heezen, 1978; Jones, 1994	(1) Oligocene rocks dredged from Cayman Trench walls: Perfit and Heezen, 1978
Cayman Trench ^b	Cayman Trough	(1) Edgar et al., 1973; Maurrasse, 1990	
Caribbean oceanic crust	Colombia and Venezuela Basins		(2) Edgar et al., 1973; Maurrasse, 1990; Sigurdsson et al., 1997 [Hole 999]
Yucatan Basin and Cayman Rise	Yucatan Basin and Cayman Rise		(1, 2) Inferred from seismic lines: Rosencrantz, 1990 (2) Sigurdsson et al., 1997 [Hole 998]

^a Active at this time (Bouysse et al., 1985; Pinet et al., 1985; Bird, 1991; Bird et al., 1993).

^b Trench not then in existence between Cuba and Hispaniola (Iturralde-Vinent, 1991; Calais et al., 1992).

“Eocene–Oligocene transition conglomerate event.” In places far removed from terrestrial sediment sources, such as basins in the Caribbean sea floor, deep-marine deposition was condensed (i.e., pelagic sedimentation occurred at a low rate). Low sedimentation

rate is in agreement with the combined effects of lowered sea level and restricted seawater circulation (Haq et al., 1987).

The Aves Ridge deserves special mention because it has been proposed as the site of a potential landspan between the Greater An-

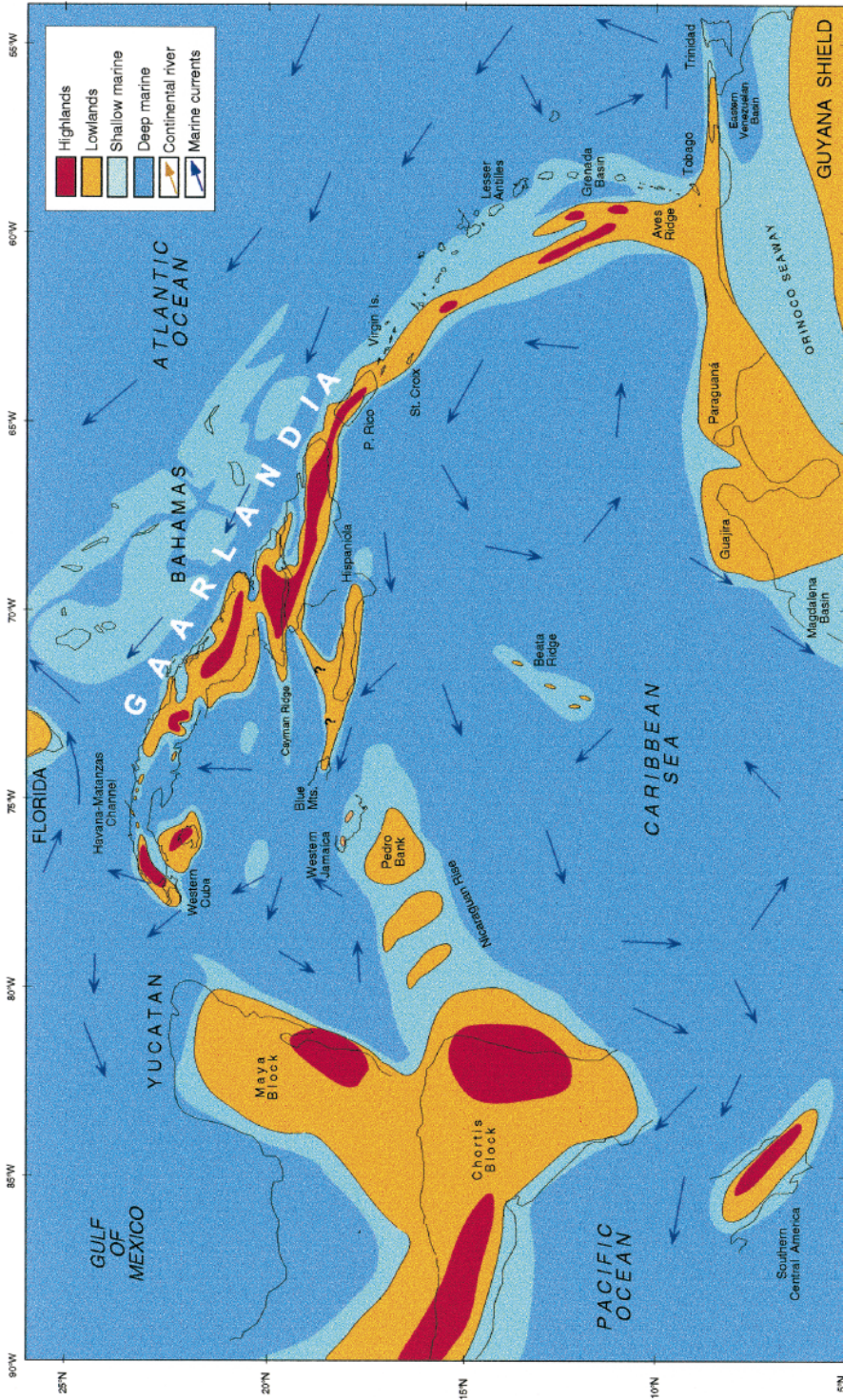


Fig. 6. Paleogeography of Caribbean region as reconstructed for latest Eocene/Early Oligocene (35–33 Ma). The reconstruction is designed to depict conditions obtaining in the Caribbean region during the period of maximum Cenozoic land exposure, occasioned by very low eustatic sealevel and widespread regional uplift (Pyrenean orogenesis). Although subaerial conditions existed along at least part of the Aves Ridge during this period, depicted landspan shorelines and contact point with South America should be regarded as conjectural, as is the illustrated connection between the Southern Hispaniolan and Blue Mountains Blocks (for explanation, see text and appendix 1).

tilles and northern South America (Borhidi, 1985; MacPhee and Iturralde-Vinent, 1994, 1995). This structure—presently almost completely submerged—was originally continuous with the Greater Antilles Ridge and is considered to have constituted a single entity in latest Eocene/Early Oligocene time. We argue that exposure of the ridgecrest created, for a short time ca. 33–35 Ma, a series of large, closely spaced islands or possibly a continuous peninsula stretching from northern South America to the Puerto Rico/Virgin Islands Block (see GAARlandia Landspan and Island–Island Vicariance).

Among the points in the paleogeographical reconstruction that require further refinement and explanation are the close positioning of southwestern Hispaniola and the Blue Mountains Block, as well as inferred permanent exposure of parts of Jamaica as early as 33–35 Ma (see appendix 1). Also noteworthy is the fact that western Cuba would have been separated by deep-water environments (Havana–Matanzas Channel) from central and eastern Cuba at this time.

Other features characteristic of the present Caribbean sea floor that did not exist in Eocene–Oligocene times (and are therefore not depicted) include the Cayman Trench and Anegada Trough, among others (see appendix 1) (Calais et al., 1989, 1992; see discussion by MacPhee and Iturralde-Vinent, 1994, 1995).

LATE OLIGOCENE (27–25 Ma)

The Late Oligocene (zones P21b–P22 of Berggren et al., 1995) was a time of extensive marine invasions, probably due to a combination of tectonic subsidence and high sea level stands (table 3). Marine sediments of this age are common in North and South America and the Greater Antilles (fig. 7). Inundation of terrestrial environments began as early as zone P19 (Berggren et al., 1995) and continued into zone P22. Evidence of Late Oligocene transgression is seen in stratigraphic sections, dredge samples, drill cores, and seismic lines recovered from many parts of the Caribbean region and the Florida Block. Stratigraphic sections consistently record mid-Late Oligocene marine deposits overlying older rocks. In the more distal sed-

imentary basins of the Caribbean sea floor, the rate of sediment accumulation increases at this time and deeper water environments upwardly dominate Oligocene sections. The amount of land-derived debris in such sections is substantially reduced, with fine-grain and biogenic deposits dominating. Nevertheless, heights-of-land remained persistently subaerial along the axis of GAARlandia, as shown by the existence of rocks formed in nonmarine environments, presence of land-derived sediments and plant remains in proximate marine basins, and depositional hiatuses in sections. These results suggest that, in an area such as the Caribbean region, in which vertical motions have been marked, the amount of terrestrial exposure or inundation cannot be simply read out from sea-level curves (e.g., Haq et al., 1987).

EARLY MIDDLE MIOCENE (16–14 Ma)

The early Middle Miocene paleogeography (zones M5–M7 of Berggren et al., 1995) of the Caribbean region shows the effects of disruption of the deformed foldbelt bounding the Caribbean Plate (fig. 1; table 4). The process of Neogene disruption, the tectonic characteristics of which have been extensively investigated (Mann et al., 1990; Pindell and Barrett, 1990; Pindell, 1994; Macellari, 1995), is recorded east of Cuba along the plate's northern boundary, and within the Netherlands and Venezuelan Antilles to Trinidad and Tobago along its southern boundary. Localized extension occurred along both boundaries as grabens, pull-apart basins, and trenches began to form. This, combined with continuing marine transgression, served to further isolate fault-bounded block-terraces from one another along plate boundaries. Examples of extensional features formed or activated at this time in the central Caribbean Basin include the Cayman Trench between Cuba and Hispaniola, the Anegada Trough between the northern Virgin Islands and St. Croix/Aves Ridge, the Puerto Rico Trench (Mann and Burke, 1984; Mann et al., 1990), and the Tortuga Basin (fig. 1). Significantly, extension also took place along the axis of the Nicaragua Rise (Droxler et al., 1989)

Figure 8 shows Puerto Rico and Hispaniola as being connected by a neck of land into the Miocene. The existence of this con-

TABLE 3
**Land and Marine Indicators for Selected Geological Units of Caribbean Region,
 Late Oligocene (27–25 Ma, Zones P21b–22)**

Geological unit	Current geographical location of the geological unit	Land indicators	Marine indicators
		(1) hiatuses; (2) red beds, alluvia, paleosols, plant and animal fossils; (3) nearshore conglomerates and/or lagoonal sediments	(1) shallow-water environments; (2) deep-water environments; (3) arc/oceanic volcanic activity
Florida Block	Florida Peninsula	(1) Galloway et al., 1991; Hine, 1997, Randazzo and Jones, 1997	(1) Galloway et al., 1991; Hine, 1997, Randazzo and Jones, 1997
Bahamas Platform	Bahamas	(1—local hiatus) Ravenne et al., 1985	(1, 2) Meyerhoff and Hatten, 1974; Buffler and Hurst, 1995
Mexican terranes	Southern Mexico	(1, 3) López-Ramos, 1975	(1, 2) López-Ramos, 1975
Maya Block	Yucatan Peninsula	(1) Butterlin and Bonet, 1966 (1, 2) López-Ramos, 1975; Galloway et al., 1991	(1, 2) Butterlin and Bonet, 1966; López-Ramos, 1975
Chortis Block	Northern Central America	(1) Donnelly et al., 1990; Maurrasse, 1990	(1) Donnelly et al., 1990; Maurrasse, 1990
Nicaragua Block	Nicaragua Rise	(1) Holcombe et al., 1990; Sigurdsson et al., 1997 [Hole 1001] (1, 2) Waterford Touche-1, Colombia Berta-1 wells: Holcombe et al., 1990; Maurrasse, 1990; Donnelly et al., 1990	(1) Oligocene rocks dredged from Cayman Trench walls: Perfit and Heezen, 1978
Western Jamaica Block	Western Jamaica	(1) Eva and McFarlane, 1985; Montadert et al., 1985; Robinson, 1994	(1, 2) Eva and McFarlane, 1985; Montadert et al., 1985; Robinson, 1994
Southern Central American Volcanic Arc	Southern Central America	(3) Escalante, 1990; Kolarsky et al., 1995a	(1, 2) Escalante, 1990; Kolarsky et al., 1995a
Atrato Basin	Northwestern South America		(2, 3) Duque Caro, 1990
Northwestern South American foldbelts and basins (NWSA Microcontinent)	Northwestern South America	(1, 2, 3) González de Juana et al., 1980; Balkwill et al., 1995; Macellari, 1995; Lugo and Mann, 1995; Parnaud et al., Cooper et al., 1995	(1, 2) González de Juana et al., 1980; Balkwill et al., 1995; Macellari, 1995; Lugo and Mann, 1995; Parnaud et al., 1995; Cooper et al., 1995
Cordillera del Caribe Thrust Belt	Caribbean Mountains	(1) González de Juana et al., 1980; Macellari, 1995	(1) Interpreted as shallow water regime; patches of Miocene rocks occur in mountains: González de Juana et al., 1980; Mills, 1994; Hoorn et al., 1995
Aruba/Tobago Belt	Aruba to Tobago	(1) Hunter, 1978; González de Juana et al., 1980; Jackson and Robinson, 1994; Donovan, 1994; Macellari, 1995	(1, 2) Algar and Erikson, 1995; González de Juana et al., 1980; Jackson and Robinson, 1994; Donovan, 1994; Macellari, 1995
Greater Antilles Foldbelt (Cuban blocks)	Cuba	(1, 2, 3) Iturralde-Vinent, 1972, 1988a; MacPhee and Iturralde-Vinent, 1995	(1, 2) Iturralde-Vinent, 1972, 1988a; MacPhee and Iturralde-Vinent, 1995

TABLE 3
(Continued)

Geological unit	Current geographical location of the geological unit	Land indicators	Marine indicators
		(1) hiatuses; (2) red beds, alluvia, paleosols, plant and animal fossils; (3) nearshore conglomerates and/or lagoonal sediments	(1) shallow-water environments; (2) deep-water environments; (3) arc/oceanic volcanic activity
Greater Antilles Foldbelt (Blue Mountains Block)	Eastern Jamaica	(1, 3) Eva and McFarlane, 1985; Robinson, 1994; Montadert et al., 1985	(1, 2) Eva and McFarlane, 1985; Robinson, 1994
Greater Antilles Foldbelt (Hispaniolan block-terraces)	Hispaniola	(1, 2, 3) Butterlin, 1960; Maurrasse, 1982; Mann et al., 1991; Iturralde-Vinent, 1991; Iturralde-Vinent and MacPhee, 1996	(1, 2) Butterlin, 1960; Maurrasse, 1982; Mann et al., 1991; Iturralde-Vinent and MacPhee, 1996
Greater Antilles Foldbelt (Puerto Rico/Virgin Islands Block)	Puerto Rico/Virgin Islands	(1, 2, 3) Meyerhoff, 1933; Monroe, 1980; MacPhee and Iturralde-Vinent, 1995 (1) St. Croix: MacLaughlin et al., 1995	(1) Meyerhoff, 1933; Monroe, 1980; MacPhee and Iturralde-Vinent, 1995
Lesser Antilles Volcanic Arc	Lesser Antilles	(1) Westercamp et al., 1985; Maury et al., 1990	(1, 3) Marine and subaerial volcanic activity: Westercamp et al., 1985; Maury et al., 1990
Aves Foldbelt	Aves Ridge	(3) Nagle, 1972; Bock, 1972; Bouysse et al., 1985; Pinet et al., 1985	(1) Nagle, 1972; Bock, 1972; Nemeč, 1980; Bouysse et al., 1985; Pinet et al., 1985
Grenada Backarc Basin ^a	Grenada Basin		(2) Nemeč, 1980; Bouysse et al., 1985; Pinet et al., 1985; Bird et al., 1993
Beata Block	Beata Ridge		(2) Mascle et al., 1985; Holcombe et al., 1990
Cayman Ridge	Cayman Islands and Cayman Ridge		(1) Perfit and Heezen, 1978; Jones, 1994
Cayman Trench ^b	Cayman Trough		
Mona Canyon and Basin ^c	Mona Passage		
Anegada Basin ^d	Anegada Passage		
Caribbean oceanic crust	Colombia and Venezuela Basins	(1) Probably due to submarine erosion and poor core recovery: Edgar et al., 1973; Maurrasse 1990; Sigurdsson et al., 1997	(2) Edgar et al., 1973; Maurrasse, 1990; Sigurdsson et al., 1997 [Hole 999]
Yucatan Basin and Cayman Rise	Yucatan Basin and Cayman Rise		(1, 2) inferred from seismic lines: Rosencrantz, 1990 (2) Sigurdsson et al., 1997 [Hole 998]

^a Active at this time (Bouysse et al., 1985; Pinet et al., 1985; Bird, 1991; Bird et al., 1993).

^b Trench still not present between Cuba and Hispaniola (Iturralde-Vinent, 1988a, 1991; Calais et al., 1992; MacPhee and Iturralde-Vinent, 1995).

^c Not completely opened (Mann et al., 1990; Larue and Ryan, 1990; Pindell and Barrett, 1990).

^d Not yet opened (Masson and Scanlon, 1991; Mann et al., 1990; Larue and Ryan, 1990; Jany et al., 1990).

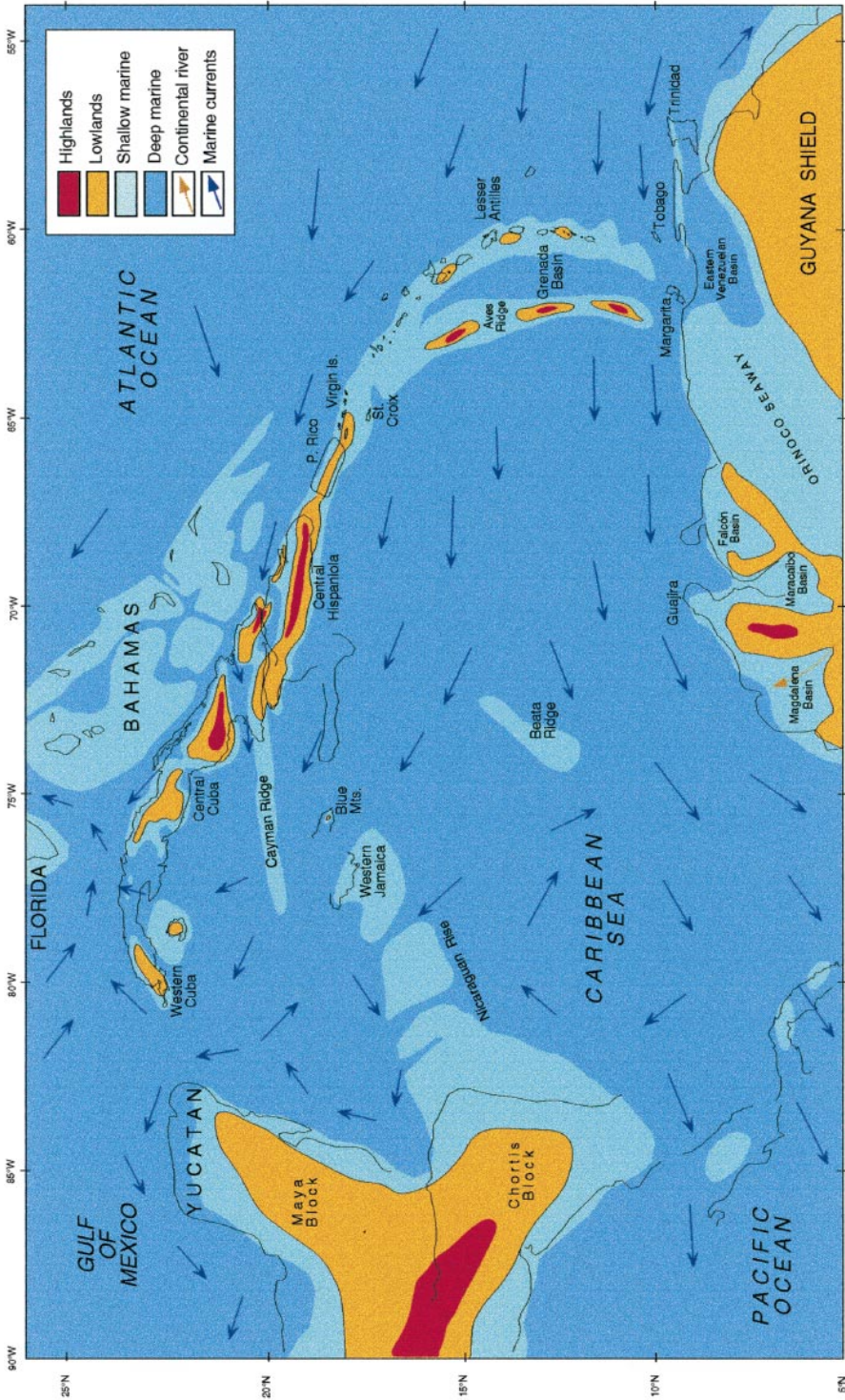


Fig. 7. Paleogeography of Caribbean region as reconstructed for Late Oligocene (27-25 Ma). During this period, general subsidence and higher sealevels greatly diminished land area within the Caribbean Sea, sundering the landspan connection between the Greater Antilles and northwestern South America (for explanation, see text and appendix 1).

nection is indicated, although not proven, by evidence that (1) the formation of the Mona Passage was a neotectonic event (Larue et al., 1990; Jany et al., 1990; Masson and Scanlon, 1991), and (2) the first late Cenozoic marine sediments to onlap eastern Hispaniola and western Puerto Rico were Pleistocene limestones, implying the existence of a barrier of some kind. Additional data from the floor of the Mona Passage would help to clarify the history of this connection.

Comparison of figures 7 and 8 reveals that

the amount of land in the central part of the Caribbean Basin was approximately the same in the Late Oligocene and the early Middle Miocene. However, by the Middle Miocene, block-terraces fringing the Caribbean Plate were already widely separated; many of these would never be reunited again, even during the glaciations (low-stand events) of the late Quaternary. Late in the Middle Miocene, western Cuba finally achieved dryland contact with central Cuba after the disappearance of the Havana–Matanzas Channel.

BIOGEOGRAPHICAL HYPOTHESES AND CARIBBEAN PALEOGEOGRAPHY

This section is not intended as a review of the recent systematically oriented literature on Caribbean biogeography. Such an undertaking, if properly comprehensive, would be a major undertaking unto itself and therefore requires separate treatment (MacPhee and Iturralde-Vinent, in prep.). Our narrower purpose in this paper is to examine specific problems in light of the new paleogeographical reconstructions developed in preceding sections, with an emphasis on “how they did it” as opposed to “who did it.” We pursue this by considering, in turn, three quite different models proposed by Rosen (1975, 1985), Hedges and co-workers (1992, 1994; Hedges, 1996a, 1996b), and MacPhee and Iturralde-Vinent (1994, 1995).

CONTINENT–ISLAND VICARIANCE: MODEL OF ROSEN

Rosen’s (1975, 1985) continent–island vicariance model was the earliest attempt to create a cladistically oriented biogeography of the Caribbean region with an emphasis on vertebrates.⁴ Rosen’s (1975) principal inno-

vation was to wed modern ideas concerning the relationships of whole faunas and areas (see Croizat, 1964; Nelson and Platnick, 1981; Humphries, 1992; Morrone and Crisci, 1995) to the emerging theory of plate tectonics, for one of the world’s most complicated biological and geological regions. Vicariance theory has been critically explored with special reference to Antillean faunas in several recent works (e.g., Guyer and Savage, 1987, 1992; Kluge, 1988, 1989; Page and Lydeard, 1994; Roughgarden, 1995). In the main, however, cladistic biogeographers have not concerned themselves with updating or revising Rosen’s (1975: 453–454) paleogeographical inferences, despite his exhortations that they do so.

In Rosen’s model, the “Antillean archipelago” or “proto-Antilles”—here understood as the Cretaceous and Paleocene–Eocene volcanic arcs, although he did not make this distinction—were assumed to have originated as a series of closely spaced islands on the leading edge of the Caribbean crustal plate in roughly the position occupied by present-day Central America. As these islands were tectonically transported eastward, they interacted with adjacent continental margins in such a manner that they were able to receive the greater part of their biota in essentially one event (Rosen, 1975: fig. 8). As Perfit and Williams (1989) pointed out, although Rosen (1975) described this common-cause event as vicariant in nature, he was ultimately noncommittal as to how immigration actually occurred. (Rosen’s maps

⁴ As a matter of historical record, the first intuitive model of Antillean vicariance was proposed by J. Issac del Corral (1940) in order to explain the origin of the Cuban mammal fauna by Wegenerian “continental drift.” According to this author, before the Late Miocene the Greater Antilles were attached to northern South America (Colombia and Venezuela), whence they received their mammalian fauna. Later on, the islands drifted northward to their current positions. Vandel (1973) used Issac del Corral’s (1940) model to account for the relationship of troglodytic faunas in Cuba and northern South America.

TABLE 4
**Land and Marine Indicators for Selected Geological Units of Caribbean Region,
 Early Middle Miocene (16–14 Ma, Zones M5–7)**

Geological unit	Current geographical location of the geological unit	Land indicators	Marine indicators
		(1) hiatuses; (2) red beds, alluvia, paleosols, plant and animal fossils; (3) nearshore conglomerates and/or lagoonal sediments	(1) shallow-water environments; (2) deep-water environments; (3) arc/oceanic volcanic activity
Florida Block	Florida Peninsula	(1, 3) Galloway et al., 1991; Hine, 1997; Randazzo and Jones, 1997	(1) Galloway et al., 1991; Hine, 1997; Randazzo and Jones, 1997
Bahamas Platform	Bahamas	(1—local hiatus) Ravenne et al., 1985	(1, 2) Meyerhoff and Hatten, 1974; Buffler and Hurst, 1995
Mexican terranes	Southern Mexico	(1, 3) López-Ramos, 1975	(1, 2, 3) López-Ramos, 1975
Maya Block	Yucatan Peninsula	(1) Butterlin and Bonet, 1966 (1, 2) López-Ramos, 1975; Galloway et al., 1991	(1, 2) Butterlin and Bonet, 1966; López-Ramos, 1975; Galloway et al., 1991
Chortis Block	Northern Central America	(1) Maurrasse, 1990; Donnelly et al., 1990	(1, 2, 3) Maurrasse, 1990; Donnelly et al., 1990
Nicaragua Block	Nicaragua Rise		(1) Perfit and Heezen, 1978; Holcombe et al., 1990; Waterford Touche-1, Colombia Berta-1 wells; Holcombe et al., 1990; DSDP 152; Maurrasse, 1990; Donnelly et al., 1990 (2) Sigurdsson et al., 1997 [Holes 1000, 1001]
Western Jamaica Block	Western Jamaica	(1) Eva and McFarlane, 1985; Robinson, 1994; Montadert et al., 1985	(1, 2) Eva and McFarlane, 1985; Montadert et al., 1985; Robinson, 1994
Southern Central American Volcanic Arc	Southern Central America	(3) Escalante, 1990; Kolarsky et al., 1995a	(1, 2, 3) Escalante, 1990; Kolarsky et al., 1995a
Atrato Basin	Northwestern South America		(2, 3) Duque-Caro, 1990
Northwestern South American foldbelts and basins (NWSA Microcontinent)	Northern South America	(1, 3) González de Juana et al., 1980; Balkwill et al., 1995; Macellari, 1995; Lugo and Mann, 1995; Parnaud et al., 1995 (1, 2, 3) Cooper et al., 1995	(1, 2) Orinoco River basin: González de Juana et al., 1980; Cooper et al., 1995; Algar and Erikson, 1995
Cordillera del Caribe Thrust Belt	Caribbean Mountains	(1) González de Juana et al., 1980	(1) Interpreted as shallow water; patches of Miocene rocks occur in mountains: González de Juana et al., 1980; Mills, 1994; Hoorn et al., 1995
Aruba/Tobago Belt	Aruba to Tobago	(1, 3) Hunter, 1978; González de Juana et al., 1980; Jackson and Robinson, 1994; Macellari, 1995; Donovan, 1994	(1, 2) Trinidad: Algar and Erikson, 1995
Greater Antilles Foldbelt (Cuban blocks)	Cuba	(1, 2, 3) Iturralde-Vinent, 1969, 1988a; MacPhee and Iturralde-Vinent, 1994, 1995	(1, 2) Iturralde-Vinent, 1969, 1988a; MacPhee and Iturralde-Vinent, 1995

TABLE 4
(Continued)

Geological unit	Current geographical location of the geological unit	Land indicators	Marine indicators
		(1) hiatuses; (2) red beds, alluvia, paleosols, plant and animal fossils; (3) nearshore conglomerates and/or lagoonal sediments	(1) shallow-water environments; (2) deep-water environments; (3) arc/oceanic volcanic activity
Greater Antilles Foldbelt (Blue Mountains Block)	Eastern Jamaica	(1, 3) Eva and McFarlane, 1985; Montadert et al., 1985; Robinson, 1994	(1, 2) Eva and McFarlane, 1985; Robinson, 1994
Greater Antilles Foldbelt (Hispaniolan block-terraces)	Hispaniola	(1, 2, 3) Butterlin, 1960; Maurrasse, 1982; Mann et al., 1991; Iturralde-Vinent and MacPhee, 1996; Graham, 1990	(1, 2) Butterlin, 1960; Maurrasse, 1982; Mann et al., 1991; Iturralde-Vinent and MacPhee, 1996
Greater Antilles Foldbelt (Puerto Rico/Virgin Islands Block)	Puerto Rico/Virgin Islands	(1, 3) Monroe, 1980; MacPhee and Iturralde-Vinent, 1995	(1) Monroe, 1980; MacPhee and Iturralde-Vinent, 1995 (2) St. Croix: MacLaughlin et al., 1995
Lesser Antilles Volcanic Arc	Lesser Antilles	(1) Westercamp et al., 1985; Maury et al., 1990	(1, 3) Westercamp et al., 1985; Maury et al., 1990
Aves Foldbelt	Aves Ridge		(1, 2) Nagle, 1972; Bock, 1972; Bouysse et al., 1985; Pinet et al., 1985; Saba Bank: Nemeč, 1980; Pinet et al., 1985
Grenada Backarc Basin ^a	Grenada Basin		(1, 2) Bouysse et al., 1985; Pinet et al., 1985; Bird, 1991; Bird et al., 1993
Beata Block	Beata Ridge		(2) Mascle et al., 1985; Holcombe et al., 1990
Cayman Ridge	Cayman Ridge and Cayman Islands		(1) Jones, 1994 (2) Perfit and Heezen, 1978
Cayman Trench ^b	Cayman Trough		(1, 2) Perfit and Heezen, 1978; Iturralde-Vinent, 1988a, 1991; Calais et al., 1992; MacPhee and Iturralde-Vinent, 1995
Mona Basin ^c	Mona Passage		(1, 2) Mann et al., 1990; Larue and Ryan, 1990; Larue et al., 1990
Anegada Basin ^d	Anegada Trough		(1, 2) Mann et al., 1990; Larue and Ryan, 1990; Jany et al., 1990
Caribbean oceanic crust	Colombia and Venezuela Basins	(1) due to submarine erosion and/or poor core recovery: Edgar et al., 1973; Maurrasse, 1990	(2) Edgar et al., 1973; Maurrasse, 1990; Sigurdsson et al., 1997 [Hole 999]
Yucatan Basin and Cayman Rise	Yucatan Basin and Cayman Rise		(1, 2) inferred from seismic lines: Rosencrantz, 1990 (2) Sigurdsson et al., 1997 [Hole 998]

^a Active (see table 3).

^b Open between Cuba and Hispaniola.

^c Open between Puerto Rico and Hispaniola.

^d Open between northern Virgin Islands and St. Croix.

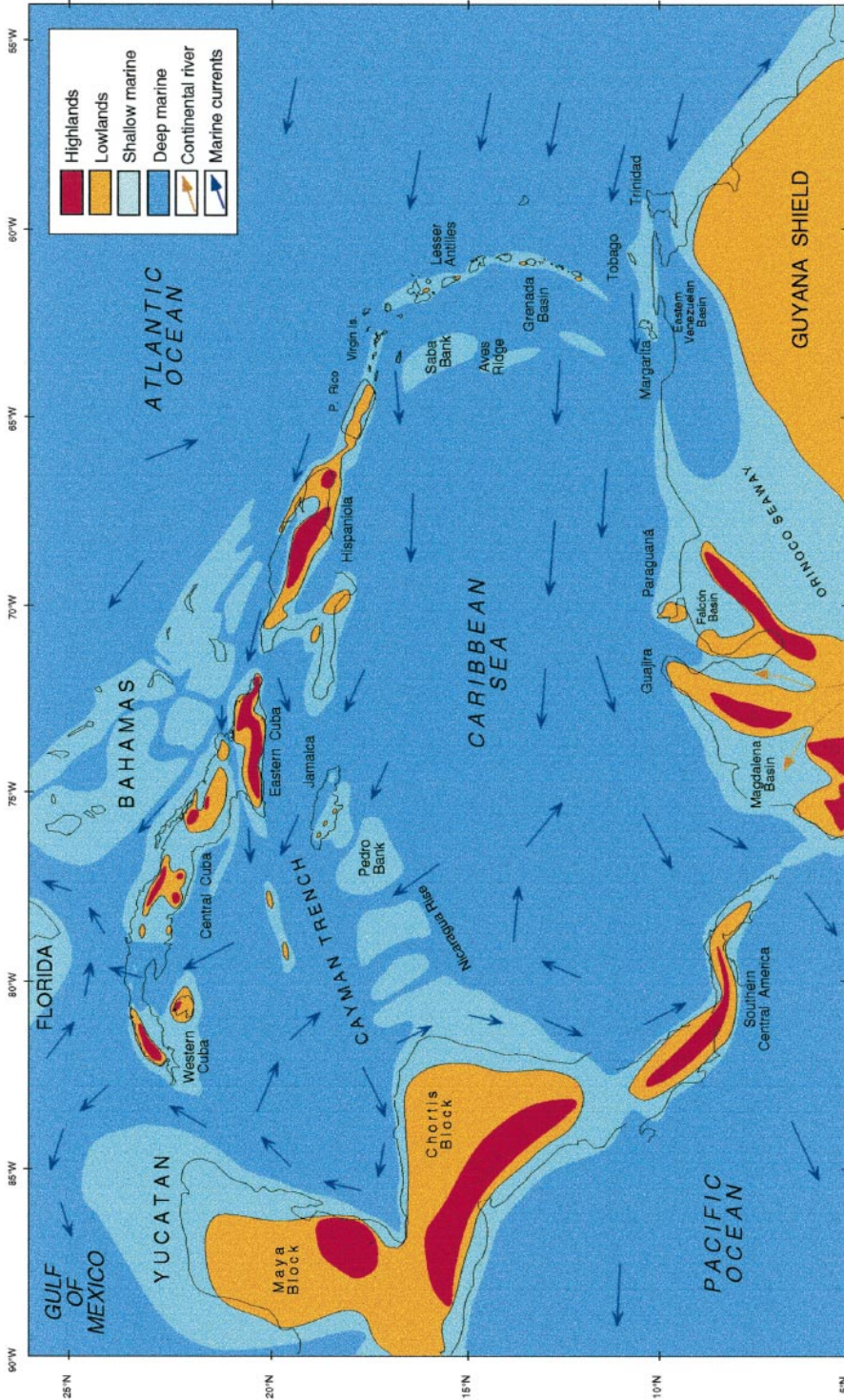


Fig. 8. Paleogeography of Caribbean region as reconstructed for early Middle Miocene (16–14 Ma). Neogene tectonic movements and deformations along the margins of the Caribbean Plate subdivided former structural ridges (Greater Antilles and Aves Ridges), creating isolated tectonic blocks and terranes separated by deep-water gaps (e.g., Cayman Trench, Mona Passage, Aneгада Trough). Southern Central America and South America not in contact across Panamanian region (Duque-Caro, 1990; Kolarsky et al., 1995a, 1995b; for explanation, see text and appendices 1 and 2).

imply that some short-distance, overwater transport would have been required, which of course muddies a primary distinction between vicariance and dispersal.) Subsequent plate motions, Rosen argued, carried the islands and their resident faunas to their current locations. During this postvicariant interval, amounting to all of the Cenozoic, the faunas of the islands were further shaped by extinction, local radiation, and, in a small number of cases, by later overwater dispersals (Rosen, 1975: figs. 9–12). He ended this section of his paper (pp. 453–454) with a list of nine “general remarks” on his “combined vicariant and geophysical model,” remarking that he incorporated “many provisional ideas that urgently need independent testing.”

In assessing Rosen’s (1975) views in light of modern tectonic theory, it should be appreciated that the tectonic model that Rosen utilized—basically that of Malfait and Dinkelmann (1972)—is not very different in its conceptual framework from current models of the evolution of the Caribbean Plate (e.g., Pindell, 1994). Instead, the essential problem lies with Rosen’s *paleogeographical* scenario: he simply assumed an identity relationship between geological units and geographical entities in his discussion of the origin and early history of the “proto-Antilles,” as becomes obvious when his maps are examined (on this point see also Rosen [1985] and comments by Perfit and Williams [1989] and Hedges [1996a]). In short, he viewed the paleoislands which existed in the position of Central America in the Cretaceous as somehow the “same” as the ones in existence today, as the “transposed, original archipelago, the Antilles” (Rosen, 1975: 432; see also Rosen, 1985: 652).

This view of paleogeographical continuity across 80 Ma or more of earth history is fundamentally flawed, because it does not take into consideration the effects of tectonic processes on Antillean biogeography between the late Campanian and Recent (see Iturralde-Vinent, 1982). As noted above, the fold-belt which constitutes the geological basement of the present-day Greater Antilles was created by complex phases of amalgamation and deformation of rock units comprising the Cretaceous and Paleogene arcs, together with associated oceanic crust and continental mar-

gin terranes (Iturralde-Vinent et al., 1996a). As we have emphasized, any islands then existing along the axis of the developing fold-belt would have been intensely modified by thrusting, folding, subsidence, and burial beneath thick tectonic nappes. Therefore, the geography of the “proto-Antilles” (i.e., the Cretaceous and Paleogene volcanic arcs) probably has little or nothing to do with the geography of the existing islands (Iturralde-Vinent, 1982).

This point was also missed by Guyer and Savage (1987, 1992), who in some respects went even further than Rosen did in assuming the permanency of islands. Guyer and Savage (1987: 526) proposed that, with the exception of a very few recent dispersals, the ancestors of the anole faunas of the large islands were emplaced all at once, and diversified there on “the remnants of the once more-or-less continuous land connection (the proto-Greater Antillean block) that originally lay between North and South America during late Cretaceous to early Tertiary.”

Although Rosen (1975) thought that fossil evidence would prove to be of great importance for testing vicariance, at that time the Antillean paleontological record was of little value for testing hypotheses of vicariance because it was almost exclusively Quaternary (MacPhee and Wyss, 1990). In the years since Rosen wrote, the vertebrate fossil record has improved marginally, but not to the extent that it can provide a critical test. As noted by MacPhee and Wyss (1990), a strong test of vicariance would require the discovery of (1) numerous representatives of continental lineages (2) of the same or similar age that are (3) not simply early members of clades represented in the Antillean Quaternary.

As to (1) and (2), the discovery that a rhinocerotoid perissodactyl (*Hyrachyus* sp.) lived on an Early Eocene landmass now incorporated into present-day western Jamaica (Domning et al., 1997) is certainly important because it establishes that Rosen’s mechanism (continent–island vicariance) may indeed occur. However, to date this discovery remains the only fossil-based evidence for Rosen-style vicariance in the Antillean ver-

tebrate record.⁵ However fascinating its discovery may be on other grounds, one Eocene rhinocerotoid from Jamaica is of limited explanatory significance. If this species lived on a terrane that was part of Central America prior to the latter's separation and amalgamation with other terranes represented in modern Jamaica—as is indeed possible, given its substantial age—then it qualifies as a vicariantly emplaced taxon in the very sense that Rosen (1975) intended. There may be more such taxa; the only way to find out is to prospect in the correct contexts on other islands.

Other mammalian fossil discoveries made in recent years include a ?megalonychid sloth femur from an Early Oligocene context in southwestern Puerto Rico (MacPhee and Iturralde-Vinent, 1995), a possible insectivore in Early Miocene Dominican amber (MacPhee and Grimaldi, 1996; see also Iturralde-Vinent and MacPhee, 1996), and various remains attributable to a platyrrhine primate, a capromyid rodent, and another megalonychid from Early Miocene Domo de Zaza, central Cuba (MacPhee and Iturralde-Vinent, 1994, 1995). Although these discoveries significantly extend the insular records of several higher-level mammalian taxa to the early Neogene/late Paleogene, all of them lie within clades that survived into the Antillean Quaternary and are therefore not unambiguously representative of a "continental" faunal aliquot. Reptile fossils have been found in Tertiary contexts on the islands, but few have been adequately published.

PASSIVE OVER-WATER DISPERSAL: MODEL OF HEDGES AND CO-WORKERS

In several recent papers, Blair Hedges and his colleagues (Hedges et al., 1992, 1994; Hedges 1996a, 1996b) have argued that analysis of immunological distances among a variety of reptiles and amphibians reveals that overwater dispersal has been by far the most

important mechanism of faunal formation in the West Indies. A centerpiece of their argument is that "all groups examined had lower estimates of divergence than would be predicted by proto-Antillean vicariance, suggesting an origin by over-water dispersal in mid- to late Cenozoic" (Hedges, 1996a: 97). Although hypotheses other than Rosen-style, mid-Cretaceous vicariance are briefly referenced (e.g., that of MacPhee and Iturralde-Vinent, 1994, 1995), discussion is otherwise essentially bipolar: if classic continent-island vicariance can be rejected, it seems, over-water dispersal must be correct. With respect to historical arguments no such certainty is ever possible, and this is decidedly the case with Antillean vertebrate colonizations. The later papers in the series by Hedges and co-workers introduce minor updates of the albumin data and their interpretation. Graphic representations of times of origin also differ in various, sometimes subtle ways (cf. Hedges et al., 1992: fig. 1; Hedges et al., 1994: fig. 2; Hedges, 1996a: fig. 2).

Page and Lydeard (1994) have comprehensively discussed a number of systematic and interpretative issues raised by Hedges et al. (1992); Hedges et al. (1994) should be consulted for replies to their criticisms. Much of the discussion in these papers is beyond the scope of the present investigation and will not be summarized here. However, other points are clearly pertinent. These may be grouped under three headings: (1) preliminary issues, (2) sources of error in estimating times of lineage origins, and (3) passive transport and Cenozoic surface-current patterns.

PRELIMINARY ISSUES

Hedges' basic database is impressive, but partitioning it in different ways brings out some of the underlying uncertainties and ambiguities in his presentation of the information. Some of these are detailed in the following paragraphs, but others would require a larger investigation than we have the competence to pursue.

(1) *Number of lineages analyzed.* Hedges (1996a: 113) concluded that the "major finding of this analysis is that all but one or two of the 77 independent lineages of amphibians

⁵ Additional, albeit nonvertebrate, fossil evidence for vicariance is provided by the diverse ant fauna recovered from Early Miocene Dominican amber. This fauna has a more continental character than the extant Hispaniolan fauna and includes forms never known to occur on oceanic islands (see commentary by Mayer and Lazell, 1988: 1477).

and reptiles . . . [sampled for] the West Indies apparently originated by dispersal in the Cenozoic.” In fact, age-of-origin estimates are specifically made for only 72 lineages, not 77; we use the corrected figure in computing proportions in subsequent paragraphs. Lineages lacking such estimates are *Hyla heilprini*, *Phyllodactylus wirshingi*, *Mabuya lineolata*, the *Leptotyphlops bilineata* group, and *Geochelone* sp. (described as “unknown” in the text although his table 3 presents an estimate of “0–2?” Ma). Lineages that cannot be dated as to origin cannot contribute to the argument that their emplacement must have been essentially random with respect to time.⁶

(2) *Mixture of morphological and immunodiffusion data.* Although Hedges et al. (1992) presented ID evidence for divergence time for a number of taxa, for many other—more than 40 (56%) in Hedges’ (1996a) most recent analysis—ID data are not provided and morphological divergence is used instead as a proxy measure. Although these latter data are separately analyzed, their value seems to us to be incidental to demonstrating the validity of the main argument (i.e., that Rosen-style vicariance is falsified by the lack of temporal patterning in divergence times as estimated by the ID data). Since there is no linear clock that can be applied to rates of morphological divergence, estimated times of lineage origins can only be expressed in the broadest terms. Thus *Gymnophthalmus pleei*, an endemic Lesser Antillean teiid, is viewed on morphological grounds as a close relative of northern South American *G. lineatus*. Time of origin (by dispersal) is listed as 0–45 Ma, the lower limit being based exclusively on an estimate of the “geologic origin of the Lesser Antilles in the Eocene

(Pindell and Barrett, 1990)” (Hedges, 1996a: 104). An analogous induction is made for the teiid *Cnemidophorus vanzoi* of the Maria Islands (St. Lucia). Origin bandwidths of this magnitude—essentially equivalent to all of the post-Paleocene Cenozoic—could be consistent with practically any biogeographical hypothesis, not just dispersal.

(3) *Taxa are not discriminated in terms of interpretative significance.* Even if it were accepted that the leading cause of faunal formation in the West Indies was overwater dispersal, this phrase as usually understood covers several quite different mechanisms. The majority of lizards, for example, would presumably not be capable of dispersing by long-distance swimming (i.e., self-powered overwater dispersal, unassisted by rafting, palm “boot” transport, or other classically invoked means). By contrast, species of crocodylians (*Crocodylus*) and chelonians (*Geochelone*, some pelomedusids) that are able to tolerate saltwater conditions could have attained their known distributions under their own power, whether their swimming was directed or not. Their propagules could have dispersed by rafting as well, but including taxa that are inherently ambiguous as to probable method of dispersal adds nothing to resolution of the debate. The pertinence of this point becomes obvious when viewed in light of the problems with Hedges’ (1996a) evaluation of surface-current flow in the Caribbean Sea (see below).

(4) *Overrepresentation and ambiguous significance of nonendemics.* The bulk of Hedges’ (1996a) taxon list (37/72 = 51%) consists of lineages that are defined as “non-endemics” (species having populations on the mainland as well as one or more West Indian islands). Hedges assumed that the existence of allopatrically distributed populations of single species is good evidence that some island colonizations occurred so recently that source populations have not differentiated from colonizing ones. From a diversity standpoint, the number of recent (0–2 Ma) lineages is certainly overstated relative to their importance. However, from a mechanism standpoint, if each colonization were an event separate from every other, the rate of dispersal must have been higher in the recent past (assuming that extinctions can be

⁶ Gregory C. Mayer (personal commun.) has called our attention to three errors in enumerated entries in Hedges’ (1996a) table 3: (1) 11, *Crocodylus intermedius*, known from only one or two vagrant individuals, cannot be considered to be established in the West Indies; (2) 26, *Iguana iguana* does not occur on the Cayman Islands; and (3) 41, *Mabuya bistrriata* is presumably a lapsus for *Mabuya mabuya*; *M. bistrriata* is a Brazilian species that is unlikely to be conspecific with anything in the West Indies. Dropping these taxa from the list will also affect the count, but we have not made this correction here.

ignored; see below). Even so, the mechanism of emplacement need not have been always the same. For example, although continent-island vicariance can be excluded from consideration, for very recent introductions determining whether range extensions were due to natural dispersal or to anthropogenic transport cannot be settled merely by observing that the latter is assumed to be less likely. Hedges (1996a: 99) noted that lineages "that clearly are the result of human introduction are mentioned but not treated in the analyses." However, taxa that are ambiguous in this regard, such as *Gonatodes albogularis*, *Hemidactylus haitianus* (= *H. brookii haitianus* of other authors), and *H. mabouia*, are nevertheless included by implication in various statements to the effect that "nearly all," "99%," and "virtually all" lineages originated by natural overwater dispersal. The degree of human involvement in producing some herp distributions will probably never be known except by determining from fossil evidence that the taxon existed in the West Indies well before the earliest presumed date of human arrival (ca. 7000 yrbp; Burney et al., 1994). Currently, however, the paleontological record is of little assistance in this regard as few of the herp taxa listed by Hedges as having a Quaternary origin have independent, associated radiometric dates from sites in the West Indies (cf. Morgan and Woods, 1986; MacPhee et al., 1989). Although it can be argued, trivially, that instances of anthropogenic dispersal still count as dispersals, in a paper designed to test scenarios of faunal formation it is surely problematic to overrepresent such taxa in the database.

(5) *Low number of nonendemic lineages in the Greater Antilles.* According to the data presented by Hedges, the great majority of nonendemic herp lineages live on islands other than the Greater Antilles. Setting aside crocodiles and tortoises, only 6 of 33 Quaternary nonendemic lineages listed by Hedges (1996a) have distributions that include a continental mainland and one or more of the Greater Antilles (*Gonatodes albogularis*, *Hemidactylus haitianus*, *H. mabouia*, *Iguana iguana*, *Mabuya "bistriata"*, and *Nerodia clarki*). Of these, at least three are of questionable pertinence given the ambiguity of

their method of transport to the Greater Antilles (see above). However, in terms of historical biogeography, the real issue is the comparative lack of nonendemic populations in the Greater Antilles in contrast to the Lesser Antilles and islands on the fringe of the Caribbean Sea. How can this pattern be explained?

Not knowing whether the six Greater Antillean herp lineages noted by Hedges were representative of many more that he could have cited, we examined all distributions listed by Schwartz and Henderson (1991) in their exhaustive catalog. In addition to those already discussed, and resolving cases of taxonomic doubtfulness in Hedges' favor, there are only eight other apparent nonendemics (all saurians) whose distribution includes a mainland and one or more of the Greater Antilles (five species of *Anolis* and three of *Sphaerodactylus*). We cannot comment on whether any of these may qualify as additional "independent lineages"; judging from Hedges' comments under individual genera, he seems uncertain as well. However, it seems reasonable to conclude that the number of "Quaternary dispersals" to the Greater Antilles counted according to Hedges' methodology amounts to only a fraction of those that can be enumerated for the other islands, even though the Greater Antilles comprise 90% of the land area in the West Indies. It may be that the herpetofaunas of small islands, with their low endemism, indicate that dispersal is possible; but the faunas of the larger islands, with their very high rates of endemism, show that colonization is hard. But the cays of Cuba do not seem to have gained unusual numbers of nonendemics by comparison to the main island, despite the fact that some of the cays are also close to a continental margin (e.g., Archipelago de Sabana-Camagüey; fig. 1).

(6) *Unknown shaping influence of extinction.* Finally, if, as Hedges' interpretation of his data implies, it were possible for many continental taxa to emit successful propagules during the past 2 Ma, then it should have been possible throughout the Cenozoic. That is, it should have been possible if, at any and all times during the last 65 Ma, the likelihood of passive dispersal was equipotential. Hedges (1996a: 116) addressed this

point indirectly, noting only that, for the West Indies in general, the “large number of [Quaternary] lineages almost certainly is an artifact due to fewer extinctions expected for recent lineages.” Once again, we suggest, fossil evidence will turn out to be critically important for determining whether massive faunal turnovers or taxon cycles occurred on these islands.

SOURCES OF ERROR IN ESTIMATING TIMES OF LINEAGE ORIGINS

Hedges et al. (1992, 1994; see also Hedges, 1996a, 1996b) allowed that their estimations of divergence times for investigated lineages could be subject to three sources of error. The first two are concerned with the interpretation of the immunological data themselves; they concern the effect of differences in reciprocal estimations of IDs between taxa, and interclade variability in rates of albumin evolution. Hedges and co-workers discounted the first on the ground that errors (if any) would not lead to consistent (unidirectional) underestimation of IDs across many groups. In discounting the second, they acknowledged that rate variability exists, but at such a low level (they cite 10–15% as a reptile maximum) that it would have no effect on the kinds of interpretation they pursued in their paper. Their certainty that these potential sources of error affected their conclusions only marginally is open to challenge (Page and Lydeard, 1994), but we are particularly interested in the underpinnings of their third source of potential error. Hedges et al. (1992: 1910–1911) acknowledged that

... the species used here may not be representative of the most recent divergence event between the lineages examined (i.e., a member of the mainland taxon closest to the island taxon examined inadvertently was not used); this type of error always will result in an overestimation of the time of lineage divergence for the taxa from different land masses. If this systematic error could be corrected, some distances reported here could only be lower, further suggesting dispersal as the primary mechanism for vertebrate colonization of the West Indies.

We take this passage to mean that it is not crucial that actual sister taxa (hereafter, “exact sisters”) be used, so long as (by implication) the taxa compared are indeterminate-

ly near relatives. To restate their main points, and assuming the valency of their molecular clock model, we are told that (1) “systematic error” of this kind must always be unidirectional (i.e., will always result in overestimation of time since divergence), and (2) any corrections resulting from the discovery and utilization of exact sisters would only shorten divergence times. We explore the implications of these points by means of simple phylogenetic scenarios superimposed on equally simple biogeographical ones (fig. 9A, B).

In figure 9A, imaginary taxa **A–F** are known to be phylogenetically related in the manner indicated in the small cladogram inset on the lower right. The groups of monophyletic terminal taxa are holophyletic; there are no unknown (undiscovered) taxa above the lowermost node. Taxa **A**, **C**, and **F** are extant (solid stems). Taxa **B**, **D**, and **E** are extinct (outline stems). The main cladogram is superimposed on two landmasses (“Mainland,” “Island”) separated by an expanse of water (suggested by double-headed arrow). The same conventions are followed in figure 9B, except that the distribution of taxa on the landmasses is different.

In figure 9A, one major clade, of which **A**, **B**, and **C** are the terminal taxa, was always resident on Mainland. (The sense of time is toward top of page, as indicated by vertical time line on right.) At a specific point in time, the other major clade, of which **D**, **E**, and **F** are the terminal taxa, came to be isolated on Island. The diagram is purposely ambiguous as to whether the basal split occurred though dispersal or vicariance. All that is assumed is that a barrier separated populations of the last common ancestor of all terminal taxa, interrupting gene flow. Assume now that albumins of **A** and **F** (taxa in boxes outlined in heavy black) are compared within the same analytical framework as the one followed by Hedges et al. (1992) and yield an ID of 100, for the sake of this example. In this case, the geological age of the basal split between the branches ending in **A** and **F**, as estimated by ID (open circle on time line), is for certain the same as the appearance of the stipulated water barrier between populations of the last common ancestor (closed circle). Such a situation, in which ID time, cladogeny, and the event of

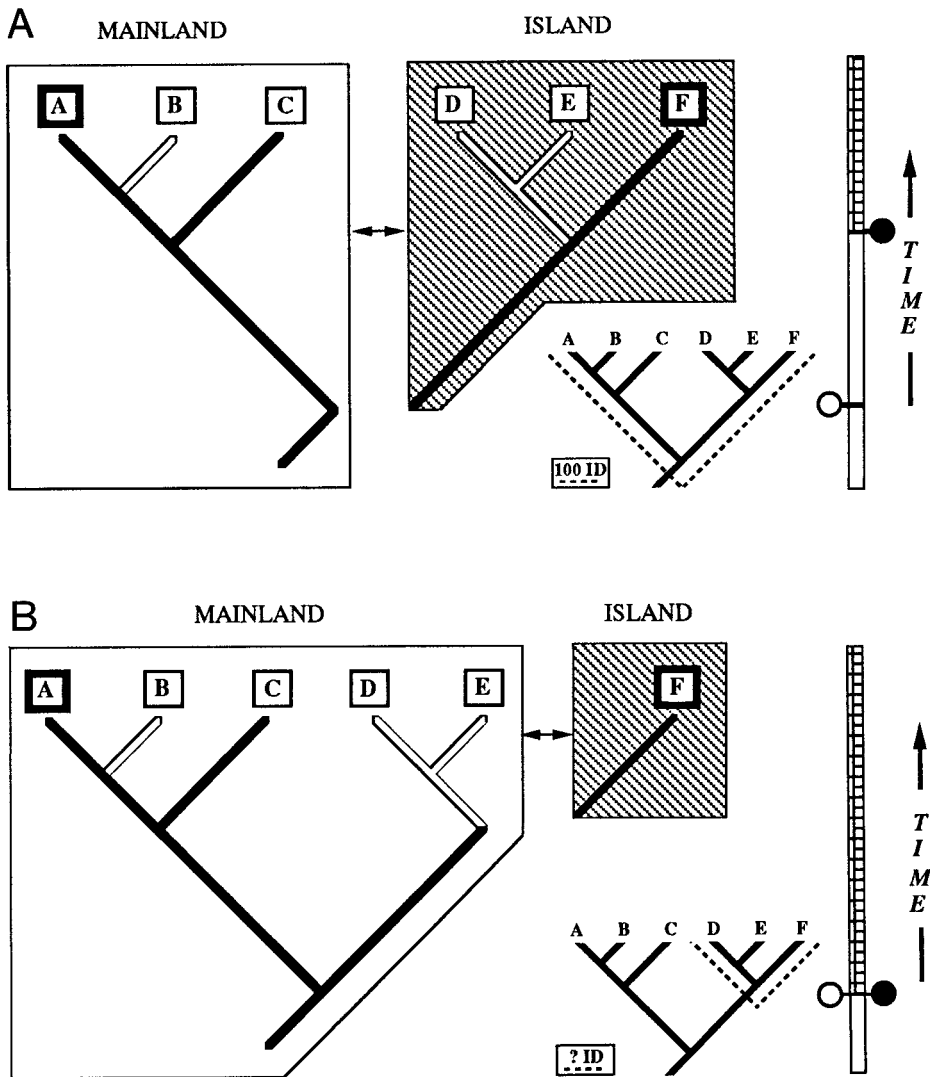


Fig. 9. Splitting lineages vs. splitting lands: Limitations on interpretation (see text).

interest all intersect on the same graph (dashed line on inset cladogram), may be described as one of *congruence*.

In figure 9B, all initial factors are the same, except that extinct taxa D and E were Mainland residents. Only the branch represented by terminal taxon F was isolated on Island. If the extinct taxa were not known, it would be assumed that taxa A and C constitute the sister group of F. Measured ID would still be 100 (between A and F or C and F), but it would not date the appearance

of the barrier between F and its closest exact sister, the clade terminating in taxa D and E (hence “?1D”). The method is blind to later splits (including the one that installed the ancestor of F on Island) because the critical taxa are extinct and cannot therefore be sampled. The result is one of *incongruence*.

In answer to criticisms by Page and Lydeard (1994), Hedges et al. (1994: 48) stated that errors in taxonomic sampling do not matter, because overestimates are always unidirectional, and furthermore “whether the

IDs coincide or not would not affect that conclusion.” However, it actually does matter, because filling a matrix with overestimates can obscure whatever pattern—including any concentration of splits—that may exist within the phylogeny (or sets of compared phylogenies). In their original figure illustrating times of origin (Hedges et al., 1992: fig. 1), for example, the “West Indies–Mainland” row is filled with a flock of ID measurements distributed across the range 55–32 Ma. Some cluster fairly tightly around 28–24 Ma, while others group at approximately 18 and 11 Ma. In a later version of this figure (e.g., Hedges et al., 1994: fig. 2), which includes errors of the estimates, no pattern is evident, and the lack thereof (i.e., apparent randomness) is taken to be evidence for overwater dispersal of relevant taxa/lineages. However, this conclusion is also unjustified, because they do not know (as they acknowledge) whether they are judging distances between exact sisters, i.e., whether congruence obtains. In the context of the present paper, it would be especially important to know if there was a concentration of splits during the earlier part of the Oligocene, when we think paleogeographical conditions were especially favorable for overland colonization (see GAARlandia Landspan and Island–Island Vicariance). And indeed there could be, if the pre-28 Ma splits represent overestimates of just the sort Hedges et al. (1992) deem unimportant.

We take the point that validly identified post-Oligocene splits cannot be explained by either continent–island vicariance or the landspan hypothesis (see below), although some intra-Caribbean splits could be related to island–island vicariance events in the Early and Middle Miocene. Some post-Oligocene lineage origins were probably occasioned by overwater dispersals, although for their identification using Hedges’ methodology, much would depend on whether all of their molecular clocks ticked true all the time. Nevertheless, the timing of splits estimated from albumin divergences cannot be taken as proxies for dating *actual* colonization events unless one knows the true branching sequence of a phylogeny (cf. Hedges et al., 1994: fig. 1).

PASSIVE TRANSPORT AND CENOZOIC SURFACE-CURRENT PATTERNS

SURFACE-CURRENT PATTERNS AND FLOTSAM DISPERSAL: Hedges (1996b: 186) contended that “an overwhelming majority (99%)” of all “independent lineages” of Antillean vertebrates originated from dispersants arriving as passively transported “flotsam,” and that, furthermore, this “dispersal pattern can be explained by the nearly unidirectional current flow [in the Caribbean Sea] from the southeast to the northwest, bringing flotsam from the mouths of South American rivers (e.g., Amazon, Orinoco) to the islands of the West Indies.” Within the Caribbean itself, taxic similarity among nonvolant faunas of different islands is to be explained by subsequent interisland dispersals occurring in the same manner, i.e., passive dispersal by surface currents.

It is critical to note that Hedges’ (1996a, 1996b) argument implicitly requires that the modern surface-current pattern, in which average flow is indeed “almost unidirectionally from southeast to northwest,” obtained for the whole period in which the Antillean fauna was being formed (i.e., virtually the entire Cenozoic according to Hedges’ own analysis). The only causative mechanism for the “almost unidirectional” flow that Hedges (1996a, 1996b) refers to, however, is the Coriolis effect, i.e., the tendency for the trajectories of moving objects on the earth’s surface to be deflected either to the right (northern hemisphere) or the left (southern hemisphere). He gives little attention to the influence of varying paleogeographical configurations of the Caribbean region on current flow. As we show in this section, present evidence supports the conclusion that the existing pattern of surface currents within the Caribbean Sea is characteristic only of the last 4 million years. Before that, other patterns predominated. Some of these, we argue, are incompatible with the history of faunal emplacement in the Caribbean region as envisaged by Hedges (1996a, 1996b).

SURFACE-CURRENT PATTERNS AND PALEOGEOGRAPHY: Figure 10 compares reconstructed patterns of marine surface currents for the Late Eocene–Oligocene (35–32 Ma), Late Oligocene/Middle Miocene (30–14 Ma),

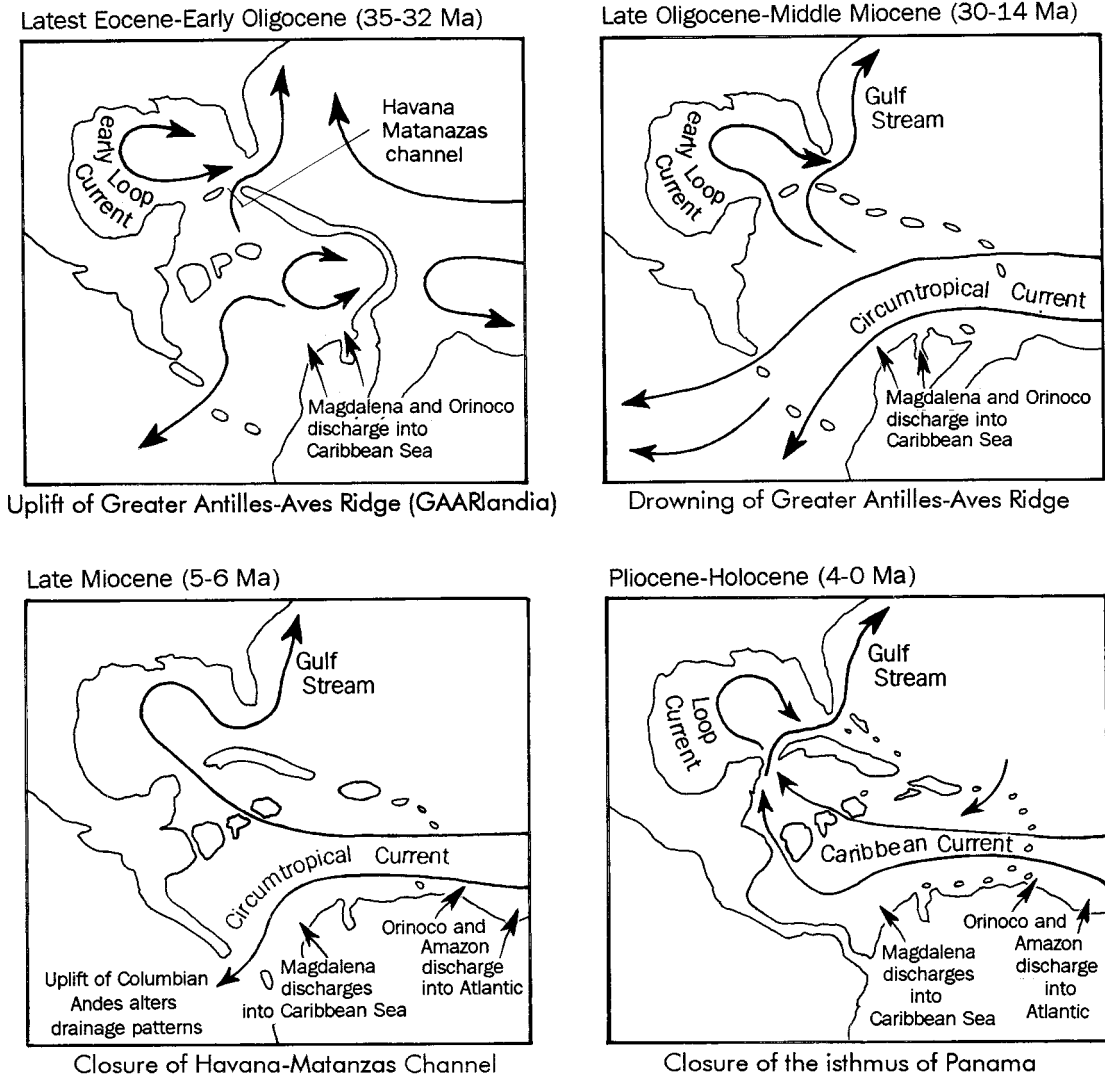


Fig. 10. Paleooceanography of Caribbean region for selected intervals between latest Eocene and Recent, modified from Mullins et al. (1987), Duque-Caro (1990), and Droxler et al. (in press). The purpose of these reconstructions is to depict possible effects of GAARlandia and other features on surface-current patterns during the latter part of the Cenozoic (MacPhee and Iturralde-Vinent, 1995; Iturralde-Vinent et al., 1996a). Since the latest Eocene the course of westward-flowing currents in the mid-Atlantic and Caribbean area has been greatly affected by the appearance and disappearance of various land barriers. Thus, the Circumtropical Current, which originally passed into the western Pacific, was temporarily disrupted in the latest Eocene and Early Oligocene by the emergence of GAARlandia, and was permanently disrupted by the completion of the Isthmus of Panama in the Late Pliocene. This current has played a leading role in mediating climate in the Caribbean region during the Cenozoic. Gulf coast of North America not intended to be paleogeographically accurate.

Late Miocene (6–5 Ma), and Pliocene–Holocene (4–0 Ma) (see also figs. 6–8). These reconstructions, slightly modified from those developed by Mullins et al. (1987), Duque-Caro (1990), and Droxler et al. (1998), attempt to consider the effects of GAARlandia and other recently described paleogeographical features on surface currents (MacPhee and Iturralde-Vinent, 1995; Iturralde-Vinent et al., 1996a).

Latest Eocene to Early Oligocene (35–32 Ma): During this interval, the surface-current pattern in the Caribbean region would have differed radically from patterns that obtained before or after this time. There are two paleogeographical reasons for this: the existence of the Panamanian Seaway, connecting the Caribbean Sea with the Pacific Ocean; and the conformation of GAARlandia, then at its subaerial maximum. The effect of these two features would have been to enhance communication with the Pacific while impeding it with the equatorial Atlantic (Donnelly, 1989b). Connection with the Atlantic would have continued at higher latitudes, via the Yucatan and Havana–Matanzas Channels. However, throughput from the Caribbean Sea to the Atlantic via the Strait of Florida seems to have been rather low (Iturralde-Vinent et al., 1996a). Because of the configuration of land masses, the Gulf Stream would have been fed mostly by the northwesterly current flowing parallel to Bahamas. In South America, the early Magdalena and Orinoco Rivers would have flowed directly into the the Caribbean Sea (Hoorn et al., 1995).

Under such conditions of at least partial isolation, there was probably a very low rate of water circulation across different portions of the Caribbean Sea. Sub-basins such as the Gulf of Mexico may have behaved as large, semi-independent embayments, in which cyclonic circulation patterns dominated, with seasonal changes in direction of flow. These interpretations are supported by two major lines of evidence. Seismostratigraphic studies (Mullins et al., 1987; Denny, 1992; Hine, 1997; Denny et al., 1994) carried out in the southern part of the Strait of Florida indicate that the West Florida ramp was in an aggradational regime from the Late Eocene to the Late Oligocene, with little winnowing and no

evidence of erosional surfaces. Also, the rate of pelagic sedimentation in this period was extremely low. (See description of Holes 998 and 999, Leg 165, by Sigurdsson et al. [1997]; Oligocene sediments are absent in some DSDP cores [Edgar et al., 1973].)

Late Oligocene to Middle Miocene (30–14 Ma): Water circulation patterns were substantially altered by paleogeographical changes during mid-Oligocene/Middle Miocene highstands. The seaways to the Pacific and northern Atlantic persisted, and the Orinoco and Magdalena still drained into the Caribbean Sea (Hoorn et al., 1995). At the beginning of this period, communication between the Pacific and equatorial Atlantic would have been greatly improved following the subsidence and inundation of much of the Aves Ridge, as indicated by the existence of shared foraminiferal assemblages on the Pacific and Caribbean sides of the Panamanian seaway (Duque-Caro, 1990). Warm water derived from the equatorial Atlantic would have been more widely distributed by the Circumtropical Current (Mullins et al., 1987; Droxler et al., 1998), now no longer prevented by southern GAARlandia from fully communicating with the Caribbean Sea. Infusion of warm Atlantic water may have influenced regional climate, as it did elsewhere (Tsuchi, 1993). Within the Caribbean Sea itself, a minor current headed northwest to push warm water through the Havana–Matanzas Channel and Yucatan Channel, thereby contributing to the early Loop surface current in the Gulf of Mexico (Iturralde-Vinent et al., 1996a). However, flow in the early Loop was not as strong as that of the modern system (Mullins et al., 1987; Hine, 1997). These new water masses had a pronounced sedimentological effect in the southern part of the Strait of Florida: the West Florida ramp began to prograde from the east, as illustrated by west-dipping clinofolds.

Later, in the Middle Miocene, rejuvenation of tectonism modified the pattern of water circulation by redistributing the flow carried by the Circumtropical Current (Iturralde-Vinent et al., 1996a). In the Late Miocene, uplift of the Andes drastically altered the fluvial pattern of northern South America, eventually causing the Orinoco to empty into the Atlantic (Hoorn et al., 1995). Foraminiferal

assemblages in sediments of late Middle to Late Miocene age in the Atrato Basin on the Pacific side of Colombia exhibit an overwhelmingly "Californian" aspect (Duque-Caro, 1990), suggesting that at this time there was little throughput from the Caribbean side of the Panamanian seaway. Nevertheless, impairment of circulation across the seaway was evidently short-lived, because Late Miocene to Pliocene rocks in the Atrato basin contain assemblages having a mixed Pacific/Caribbean aspect (Duque-Caro, 1990).

Late Miocene (6–5 Ma): In the Late Miocene (fig. 10), water circulation within the Caribbean Sea may have been diverted to the northwest as a result of (1) reduction in the width of the Panamanian seaway as the isthmus advanced southwards; (2) extension and subsidence of the Nicaragua Rise, which had previously impeded flow into the Yucatan Channel (Mullins et al., 1987; Droxler, 1995); and (3) closure of the Havana–Matanzas Channel, thereby forcing all northwest-bound flow into the Yucatan Channel (Iturralde-Vinent et al., 1996a). The increased volume of water diverted into the Loop Current modified depositional conditions in the Strait of Florida. Erosion took place on the Pourtales Terrace (Gomberg, 1974) and the Miami Terrace (Mullins and Newmann, 1979), and there was a 50% decrease in the rate of sediment accumulation in the southern Strait of Florida (Austin et al., 1988). The modern Loop Current/Gulf Stream circulation was initiated and carbonate deposition changed drastically, becoming a pelagic slope-front-fill system (Mullins et al., 1987).

Pliocene to Holocene (4–0 Ma): The last map in this series illustrates the modern pattern of water circulation (Atlas Nacional de Cuba, 1970; Emery and Uchupi, 1972). This pattern was initiated around the Miocene–Pliocene boundary, following the complete closure of the Panamanian waterway and the termination of the Circumtropical Current. Its successor, the Caribbean Current, is fed directly by the Atlantic equatorial current; surface currents are now mostly directed toward the northwest. Like other changes discussed in this section, this final series of current reorganizations must have had profound effects on terrestrial climates as well (Frakes, 1979).

SURFACE-CURRENT PATTERNS AND PROXY DATA: A current's average vector is not the only influence operating on material passively carried along the sea surface, as experimental data from free-floating objects illustrate. Molinari et al. (1979) and Kinder (1983) employed satellite telemetry to track 23 free-drifting buoys released from stations in the Lesser Antilles (fig. 11A). After wandering widely, often for several months, buoys ended up not only along or near the coasts of Jamaica, Cuba, Hispaniola, Puerto Rico, and several other Caribbean islands, but also those of Central America, Yucatan, and the Gulf of Mexico. The point here is not that the free-floating buoys achieved a certain distribution, but instead that the average gross direction of surface currents provided only the most general guide to the probable movement of any given buoy. Further, the path followed by each buoy was substantially affected by local eddies, deep cyclonic water circulation, storms, and other events (see Molinari et al., 1979; Kinder, 1983; Kinder et al., 1985; Sou et al., 1996). Significantly, such forces generally acted to increase rather than decrease trip length, an important consideration in evaluating the likelihood of successful overwater dispersal for animals that are not physiologically adapted for temporally lengthy sea journeys (such as land mammals).

Brucks' (1971) drift bottle study yielded broadly similar results. Brucks released bottles at various locations off the Windward Islands (southern Lesser Antilles), Gulf of Honduras, and southwestern Caribbean (northern coast of Panama). In the Windward Islands release area, bottle recovery records indicated that surface currents are cyclonic, but with a definite northward trend (instead of a due westward trend as stipulated in previous literature). Bottles came ashore in the northern Windward Islands and a wide variety of other locations (fig. 11B, table 5) distributed throughout the Caribbean Sea and Gulf of Mexico. Of interest is the fact that the greatest number of reports (38% of total) were from Central America; only 15% were from the Greater Antilles (as much as Yucatan alone). Calculated minimum speeds of bottles varied from 0.1 to 2.0 knots, with faster rates of movement in summer and mid-

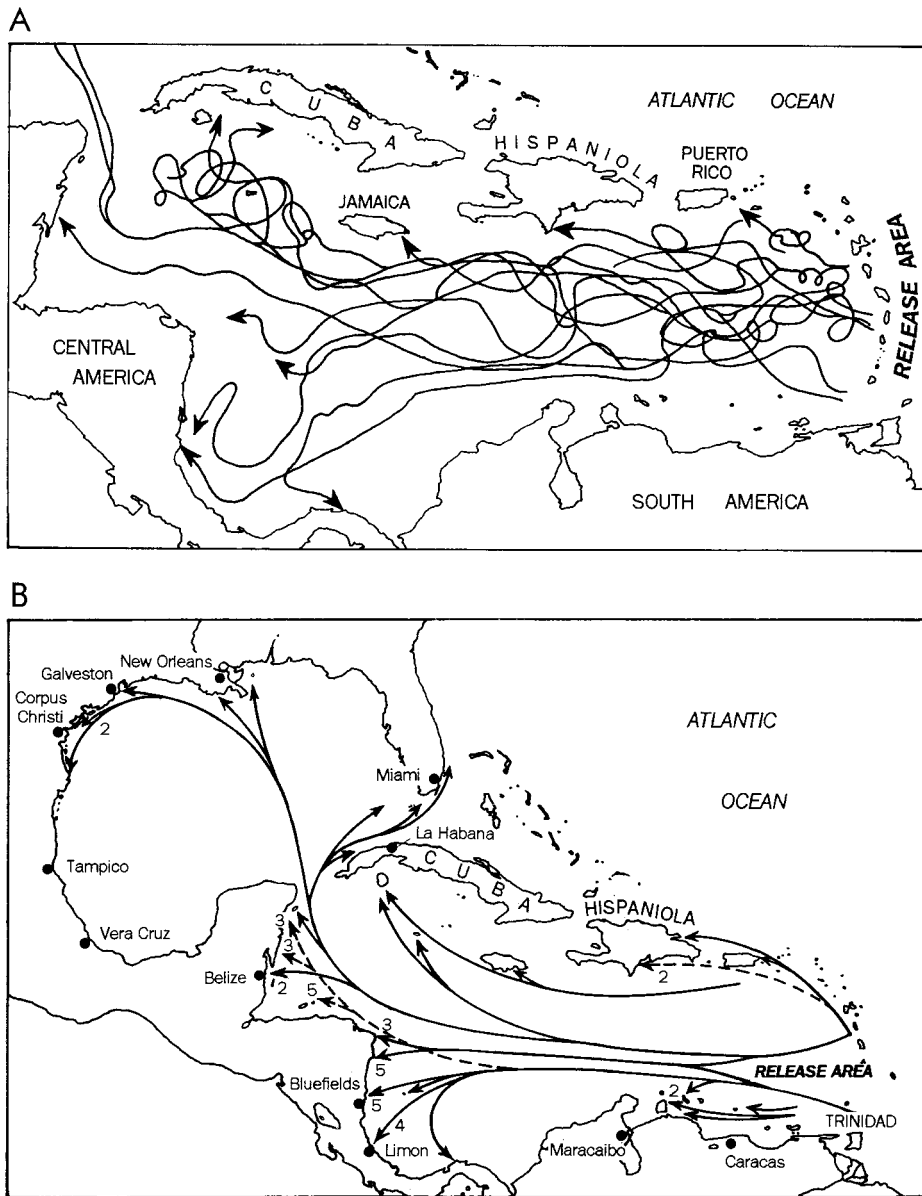


Fig. 11. Surface-current patterns in the Caribbean Sea and nearby waters, as revealed by bouy and drift bottle experiments. **A.** Tracks of bouys released by Molinari et al. (1979) between October 1975 and June 1976 (redrawn from original). Arrows have been added to pinpoint last recorded positions of selected bouys. Results of this experiment demonstrate that "average" marine-current patterns, as routinely depicted on oceanographic maps, fail to capture substantial variance in surface-water movement in the Caribbean Sea. **B.** Surface-current pattern derived from drift bottle experiments conducted by Brucks (1971, modified from original). Bottles were released from sites in the eastern Caribbean. The majority of returned bottles transported to points west of the Lesser Antilles were deposited along the east coast of Central America, Gulf of Mexico, and Florida. Relatively few bottles were returned from the Greater Antilles. These results strongly imply that, given existing surface-current patterns, flotsam emitted from the Orinoco and Amazon Rivers is much more likely to end up in southeastern North America or Central America than in the Greater Antilles.

TABLE 5
**Reported Recoveries of Drift Bottles Released East
 of Windward Islands in February–March 1967^a**

Reporting areas	Number of bottles recovered, by area	Percentage of total recovered
Central America	24	37.5
Yucatan	9	14.5
Florida Peninsula	8	13
Gulf Coast	7	11.2
South America	5	8
Hispaniola	3	4
Puerto Rico	2	3
Isle of Pines	2	3
NW Cuba	1	1
Jamaica	1	1
Total, Greater Antilles	9	14.5
Total, Central America/ Yucatan	33	53

^a Calculated from results presented by Brucks (1971: fig. 3). Total bottles released not recorded, but recovery rate (i.e., reports returned) for entire study was 9.6%.

winter than in spring and fall. These results are in good agreement with work on the dynamic sea-surface topography of the Caribbean Current, which subdivides into a faster-moving southern current and a slower northern one (Duncan et al., 1982).

The relatively slow speed at which passively transported objects move under average conditions in the West Indies is further illustrated by recent work on passively dispersed pelagic larvae (e.g., Roberts, 1997). These investigations indicate that distances actually or potentially travelled by such larvae during one- and two-month “transport envelopes” are relatively small. For example, the two-month envelope for larvae dispersing in the northeastern Caribbean spans only the distance from Anguilla to eastern Puerto Rico. A route crossing the entire Caribbean Sea from southeast to northwest, as envisaged in Hedges’ model, would presumably take much longer. Except under unusual circumstances, therefore, it would appear that modern surface currents in the Caribbean Sea do not flow rapidly enough to ensure the survival of terrestrial amniotes dispersing by rafting (with the possible exception of some reptiles).

This limitation might be overcome by hur-

ricane transport, and there is at least one recent case in which this is the only feasible explanation for a dispersal event. A number of individuals of *Iguana iguana*, a species which does not occur in Anguilla, were conclusively identified on that island in the month following the passage of Hurricane Luis across the northern Lesser Antilles in August, 1995 (Censky et al., 1998). It is probable but not demonstrated that the dispersants came from Guadeloupe or one of the other islands south of Anguilla that support *Iguana iguana*. Although northward transport of propagules by hurricanes might explain some aspects of Lesser Antillean saurian biogeography, modal hurricane tracks may well have differed in previous epochs. Before the completion of the Panamanian isthmus, for example, storm tracks may have been deflected relatively southward by the warm Circumtropical Current flowing into the Pacific. Whether this occurred or not has not been properly modelled, but any southward deflection of high-energy storms would have reduced the chances of successful dispersal to the Greater Antilles.

Tracking studies provide another body of relevant proxy data. Mean sediment concentrations in sea water can be tracked and measured using satellite imagery. In one such study (Richardson, 1996), it was found that water discharged by the Amazon does not always move northwestward into the Lesser Antilles, but is sometimes forced to flow east–southeast. This finding is in agreement with the fact that the North Equatorial Countercurrent carries much of the Amazon’s outflow eastward into the central Atlantic (Richardson, 1996). Interestingly, sediment tracking studies have also shown that outflow from the Orinoco is normally directed to the northwest, where it can be detected as far north as Puerto Rico. By contrast, outflows from the Magdalena and Lake Maracaibo quickly become disorganized after entering the Caribbean Sea: pigment can be traced for only a short distance before becoming diluted (Richardson, 1996: fig. 21-12).

OTHER CONSTRAINTS: Hedges’ (1996a) ID data indicate that two surviving herp lineages (*Eleutherodactylus* and *Cricosaura typica*) could have been established on landmasses in the Caribbean Sea as early as the latest

Cretaceous or early Paleogene (see also Hedges et al., 1992, 1994). In his view, emplacement at this early date could have occurred through either continent–island vicariance or overwater dispersal. However, during the latest Eocene and Early Oligocene, circulation within the Caribbean Sea was limited, and, as discussed above, in any case the patterns then existing would not have uniformly favored the movement of water masses toward the northwest (figs. 6, 10). Further, given the paleoposition of the mouths of the Magdalena and Orinoco, flotsam issuing from these rivers would have been much more likely to end up on the islands that then comprised much of southern Central America and the Nicaraguan Rise than, say, the Cuban/Hispaniolan end of GAARlandia.

The same constraints would have continued into the subsequent period (30–14 Ma) that we have modelled. In our view, it is likely that any natural rafts coming out of large northwestern South American rivers would have been sent into the Pacific (figs. 8, 10; see also Frakes, 1979; Kennett, 1985; Mullins et al., 1987; Droxler et al., 1998). At that time part of the present Amazon Basin was occupied by a large marine embayment (Hoorn et al., 1995). Drainage off the Guyana Shield would have been the only significant source of flotsam directed into the Atlantic; however, from this source any passively transported material would have been as likely to drift toward Africa as the West Indies (cf. Richardson, 1996). Similar conditions would have existed during the subsequent 10 Ma. However, it is necessary to observe that increasing amounts of water would have been directed toward the northwest as Central America grew southward in the Late Miocene. From this it follows that Hedges' (1996a) emplacement scenario would increase in likelihood the closer one comes to the present. The trouble is that, if emplaced by overwater dispersal, the specified "overwhelming majority" of independent insular lineages would have to have originated 4 million years ago or less. Hedges' (1996a) table 3 may be said to underline this very possibility, since no fewer than 55 investigated origins (76% of total) are dated to, or overlap with, the period 4–0 Ma,

which may explain the acknowledged recency of so many relatively undifferentiated South American herps in the southern Lesser Antilles. Yet if these figures were truly representative of the vertebrate fauna as a whole, then it would be necessary to conclude that either (1) the islands had a taxically minuscule vertebrate fauna prior to the Pliocene–Pleistocene, or (2) there was a virtually complete faunal turnover in the latter part of the Neogene. At least for mammals, the first point is flatly contradicted by fossil finds made in the Greater Antilles in the last decade: every major taxon of land mammals known from the Antillean Quaternary now has a minimum origin date of Early Miocene or earlier (MacPhee and Iturralde-Vinent, 1994, 1995; MacPhee and Grimaldi, 1996). The possibility of high faunal turnover, however, is not directly tested by this evidence as no "unexpected" taxa other than *Hyrachyus* in Jamaica have been recovered (see MacPhee and Wyss, 1990). For lizards the data are also unhelpful, inasmuch as recent dispersals (as evaluated by Hedges) have added very little to the faunally rich Greater Antilles, even though there may have been many independent events (G. Mayer, personal commun.).

The proxy data for the effect of surface-current flow as a dispersal agent suggest that, on the basis of existing current patterns, the Orinoco is more likely to release flotsam that finds its way into the central Caribbean Sea than is the Amazon. Whether this pattern was always the rule in earlier times is moot, but it is surely relevant that the Amazon has been an Atlantic coastal river only since the Late Miocene (Hoorn et al., 1995). If rivers acted as potential sources of animal-bearing flotsam in the manner contemplated by Hedges for geologically long periods of time, then it is the basins of northwestern South America, rather than the Amazon itself, that should be under consideration.

A final occasion of lack of fit between Hedges' model and the paleogeographical reconstructions offered here concerns the availability of lands in the Caribbean Sea at purported times of land vertebrate colonization. The data of Hedges and co-workers suggest that 6 to 11 herp lineages originated earlier than the Eocene–Oligocene transition. Although the number of such "early" lineages

is obviously small and therefore does not bear much analysis, the fact that any lineages may go back to the earlier Paleogene conflicts with our view that the islands that now exist in the Caribbean are post-Middle Eocene in origin (Iturralde-Vinent, 1982; MacPhee and Iturralde-Vinent, 1994, 1995). Hedges (1996b: 166) resolved this conflict by stating that “the recent suggestion that there were no permanently subaerial landmasses in the Greater Antilles prior to [the end of the Middle Eocene] is speculative; it can neither be refuted nor supported with current evidence.” We interpret the nature of the current evidence differently, but, notwithstanding that, we pose the following conundrum. If evanescent islands existed in the Caribbean Sea before the Middle Eocene—and it is highly probable that they did—then any resident faunas must have either perished at the time of inundation or subsidence, or they found a means to transfer to newly risen landmasses elsewhere. Hedges (1996a) mentioned the former possibility in relation to the sterilizing effects of giant tsunamis generated by the K/T bolide impact, but speculated that there were, nevertheless, some places where faunal elements could have persisted into the Cenozoic. As we have repeatedly asked in this paper, if such places existed, where were they, and what is their paleogeographical history?

GAARLANDIA LANDSPAN AND
ISLAND-ISLAND VICARIANCE:
MODEL OF MACPHEE AND
ITURRALDE-VINENT

LANDSPANS, VICARIANCE, AND
DIVERSITY SCENARIOS

A “landspan” is here defined as a subaerial connection (whether continuous or punctuated by short water gaps) between a continent and an off-shelf island (or island arc). Although few continuous landspans exist at present (e.g., Kamchatka), during Pleistocene glaciations several significant ones were created during phases of lowered sea level. Among these were the Greater Palawan landspan connecting Bulabac-Palawan-Calamianans with Borneo (and therefore with southeastern Asia; Heaney and Regalado, 1998)

and the Southern Ryukyu landspan extending from Taiwan at least as far as Okinawa (and therefore joining these islands with continental eastern Asia; Ota, 1998). This usage stands in contrast with that favored for “landbridge,” here restricted to mean land linkages between *continental* regions (e.g., DeGeer, Panamanian, Beringian landbridges). It should also be noted that on-shelf (or “continental”) islands are simply extensions of continents that may function as submerged margins, islands, or peninsulas (or often as all three over time), and they are always broadly affected by the same tectonic and isostatic regimes as their mainlands. Off-shelf islands are not by any useful definition extensions of continents, even if they incorporate continental fragments (e.g., Madagascar). Off-shelf islands may be affected by major tectonic events that also affect nearby continents, but they may otherwise evolve quite independently.

We introduce this terminological refinement in order to differentiate between two quite dissimilar contexts in which faunal distributions can be influenced by the appearance of a land connection. In general, transfers from one faunal area to the other across a newly developed land connection will be controlled by a host of factors (i.e., filters) that affect the likelihood that any given species will complete the journey successfully. However, the outstanding feature of landbridges is that they connect areas having continental-scale faunal diversity. At least in theory, the entire diversity of each area is available for interchange (although in practice the actual number of transfers in either direction is usually much less than the theoretical maximum). That flow actually occurs bidirectionally is amply demonstrated by relevant paleontological records (cf. Webb, 1976), even if it occurs predominantly in one direction. Landspans are markedly different because one terminus lacks continental-scale diversity (and, indeed, may initially have no fauna at all). Although in principle any number of continental faunal elements might cross a newly created landspan to colonize an island or island chain, long-term survival after initial colonization will be highly correlated with the availability of appropriate habitat in what are, after all, absolutely small places. In

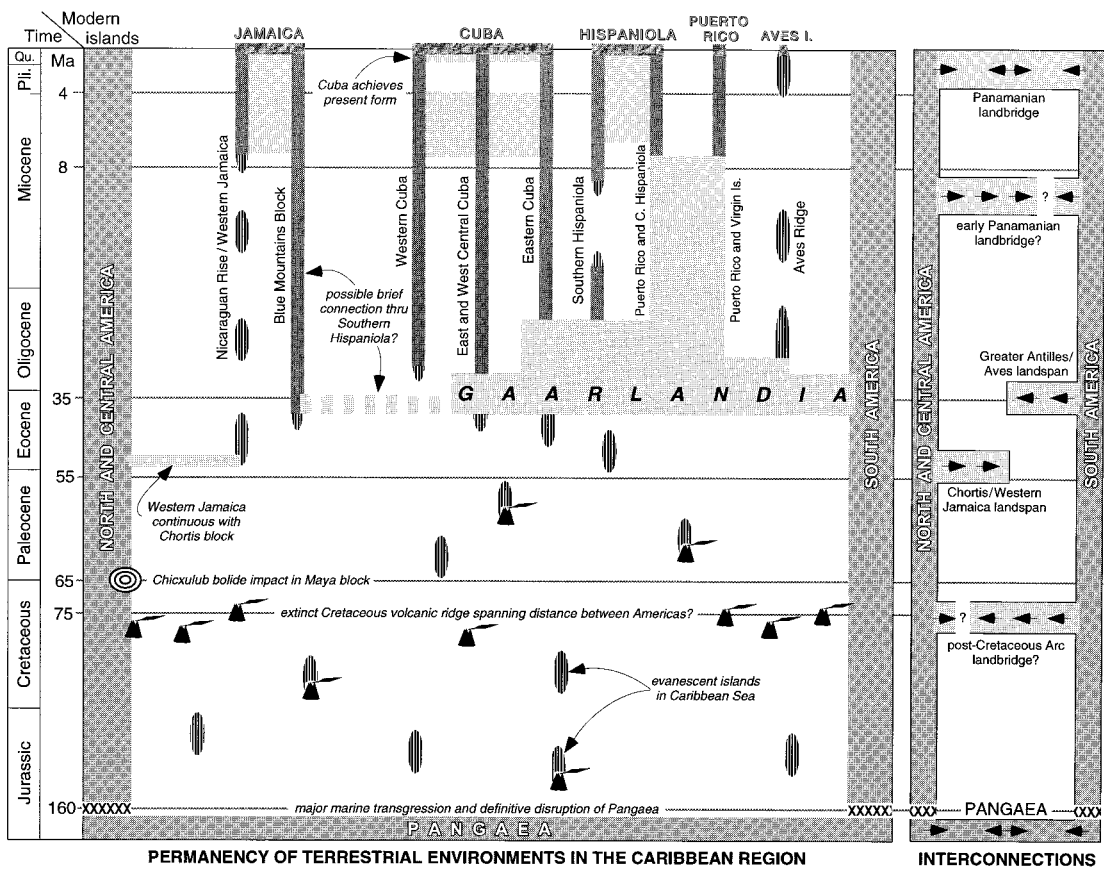


Fig. 12. Schematic paleogeographical scenario for Caribbean region, middle Mesozoic to late Cenozoic, emphasizing permanency of terrestrial environments and fluctuations in land-land connections. Generally speaking, light shading implies temporary lands or connections between landmasses. "Evanescent islands" are purely conjectural, and their number and position are not taken literally. Late Mesozoic and Miocene landbridges between the Americas are not confirmed. Black arrows signify direction of propagule dispersal over land connections, as established by fossil evidence. Thus, dispersal was bidirectional in case of Pliocene-Pleistocene Panamanian landbridge (Great American Biotic Interchange), which permitted exchange between two large continental faunas. By contrast, in case of GAARLANDIA and Chortis/western Jamaica landspans, propagule movement (at least for vertebrates) was necessarily unidirectional, as only the continental terminus possessed a fauna when the landspan was formed. Timing of major tectonic events also indicated. Chronometric scale purposely nonlinear. Interconnections existing at any given time can be easily visualized by placing a ruler horizontally across page.

contrast, continent-sized areas are much more likely to support a great diversity of habitat types, increasing the chances of success of a substantial variety of immigrants.

The two-part landspan/vicariance model of MacPhee and Iturralde-Vinent (1994, 1995, this paper) attempts to infer mechanisms of faunal formation in the Greater Antilles from detailed paleogeographical reconstructions, fossil evidence, and species/area relationships. Central to the hypothesis is the argu-

ment, sustained at length in this paper, that the Cenozoic paleogeography of the Caribbean region strongly favored emplacement over land (as opposed to over water) only once in the past 65 Ma. (Details of Cenozoic connections among lands is schematically presented in figure 12.)

The first component of the model seeks to explain how land mammals might have reached the northern Greater Antilles from northwestern South America by dispersing

across a short-lived landspan during a restricted period in the mid-Cenozoic (ca. 33–35 Ma according to our current estimate). Specifically, it is hypothesized that, during the Eocene-Oligocene transition, the Aves Ridge became subaerial for a short interval, possibly as short as one or two million years. At that time the islands on the northern part of the Greater Antillean Ridge (central and eastern Cuba, north-central Hispaniola, Puerto Rico, Virgin Islands) were in a close-packed array; they either constituted a single, large island, or a series of islands separated by very narrow water gaps. By connecting proximally with the eastern end of the Greater Antilles Ridge and distally with northwestern South American microcontinent, the subaerial Aves Ridge completed the GAARlandia landspan. As in the case of the northern connection, the linkage between GAARlandia and northwestern South America would have existed for only a short time (i.e., between major occurrences of postmagmatic arc uplift in latest Eocene and general subsidence in Oligocene).

The second component seeks to explain how certain distributions of faunal elements might have been produced via island-island vicariance, due to the subdivision of the islands themselves. Mid-Oligocene and Miocene marine transgressions and neotectonics (Mann and Burke, 1984; Mann et al., 1990) substantially affected the disposition and paleogeography of the Greater Antilles Ridge. Several pull-apart basins and related features opened or expanded along the northern Caribbean plate boundary (Cayman Trough, Mona Canyon, Sombrero Basin/Anegada Passage), creating deep-water channels and basins between tectonic units. Paleogeographically, the end result was the gradual subdivision of the subaerial parts of the Greater Antilles Ridge. For example, eastern Cuba and northern Hispaniola, physically connected during the Early Oligocene, were sundered by the expansion of the Windward Passage later in that epoch (Iturralde-Vinent and MacPhee, 1996); by contrast, the connection between central Hispaniola and Puerto Rico probably lasted until late in the Miocene (figs. 6–8, 12). These subdivisions would have divided the ranges of terrestrial faunal elements previously emplaced by dis-

persal. The “orderly,” multi-island distribution of lower level monophyletic units of land mammals (particularly sloths and insectivores) possibly supports this inference of island-island vicariance and ought to be testable cladistically (MacPhee and Iturralde, in prep.; White and MacPhee, in prep.).

This model has major implications for Antillean vertebrate paleontology. As noted earlier, Hedges’ (1996a, 1996b) ID data appear to show that a large proportion of the West Indian herpetofauna originated extremely recently (although much of its *diversity* is due to Tertiary colonizations, as his data also show). By contrast, Rosen’s (1975) and MacPhee and Iturralde-Vinent’s (1994, 1995) models require that the Antillean fauna was formed much earlier (Late Cretaceous or Late Eocene/Early Oligocene, respectively). If the overwater dispersal model is a generally accurate narrative of faunal formation in the West Indies, it follows that the fauna must have formed in an episodic, accretionary manner. Accordingly, one would not expect to find a faunal assemblage that was markedly different or systematically more diverse than the modern one at any point in the past (low diversity scenario). On the other hand, if either Rosen-style vicariance or the landspan hypothesis were correct, it would be expected that diversity would be much greater at the crucial times during which the fauna was being emplaced (high diversity scenario). Figure 13 explores how features of a good paleontological record might be able to help distinguish between high-diversity and low-diversity scenarios.

In the figure, taxa **a–p** (left column) are the initiators or founding species of a series of different imaginary clades. **T1**, **T2**, and **T3** are three different time transects (for the sake of this example, **T1** represents Late Eocene; **T2**, Early Oligocene, **T3**, Pleistocene/Holocene boundary). The cartouches, representing the separate clades, are each portrayed as having a “lifespan” in relation to the time axis.

This example permits models of supposed initial faunal diversity to be compared (see box in upper right for shading conventions). The light gray shading represents possible expectations under the high initial diversity model (taxa = 16). Dark gray represents ex-

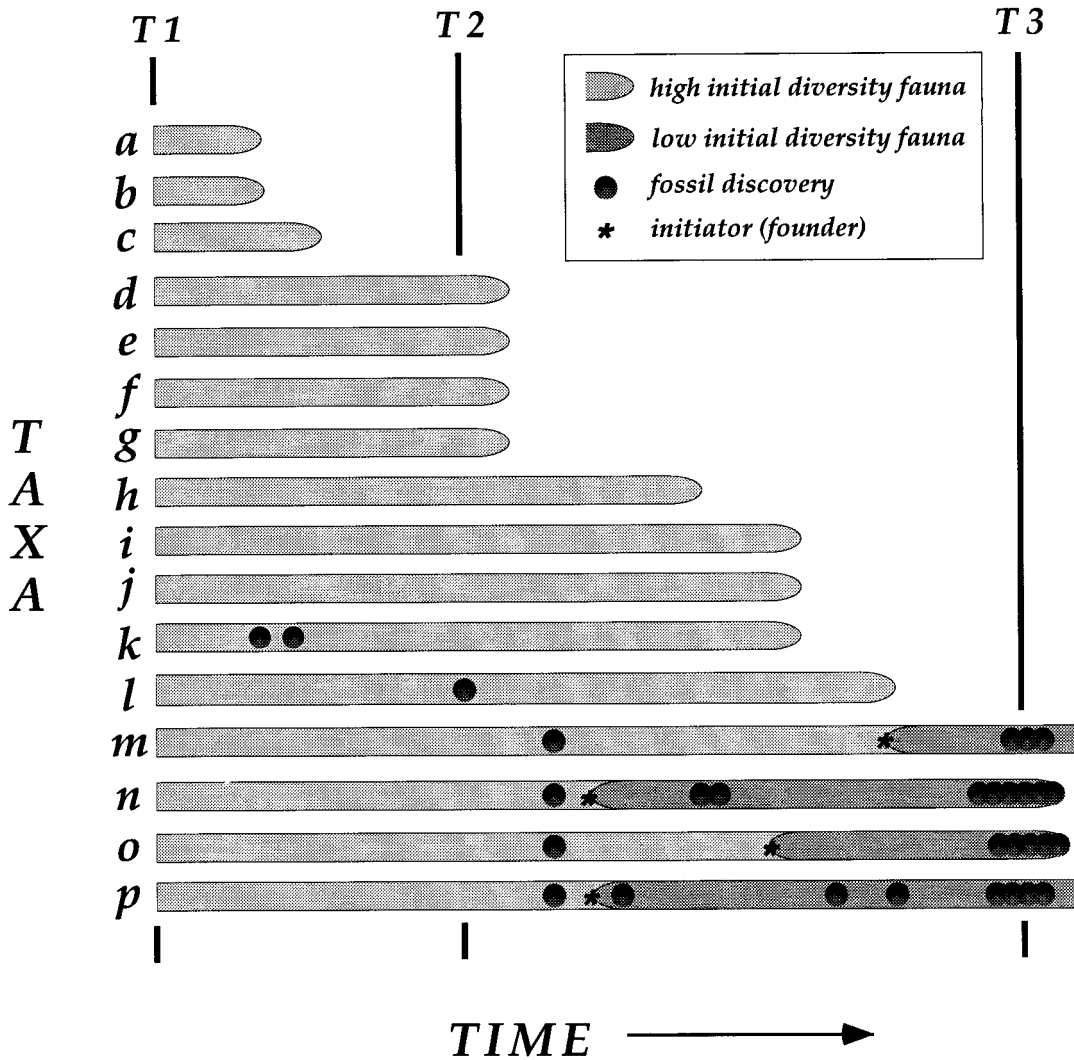


Fig. 13. Speculating on the faunal history of the Greater Antilles: Significance of fossils, “ghosts,” and incomplete evidence (see text).

Expectations under the low initial diversity model (taxa = 4). Gradient-shaded dots represent fossil discoveries; single dots represent isolated finds, numerous dots many finds. To make comparisons realistic, taxa surviving beyond T3 are shown as having very good late Quaternary fossil records (m, n, o, and p; n and o now extinct).

Scenario 1 (high initial diversity, few or no dispersals to augment original composition): At about T1 a fauna of high diversity (taxa a–p, light grey cartouches) is emplaced essentially simultaneously through operation

of some common cause (e.g., vicariance, landspan). (Prior to T1, it is assumed that there was no fauna at all.) Later on, fauna is reduced by extinctions. By time T2, taxa a–c are already extinct; at various times thereafter, taxa d–l also disappear. Taxa m–p survive into the late Quaternary as the much-diminished remnants of a once-diverse fauna.

Scenario 2 (low initial diversity, fauna gradually augmented by new dispersals staggered over a long period): In this example, taxa a–l were never part of the fauna; the entire complement at any time derives from

taxa represented by dark gray cartouches (**m-p**), whose initiators arrive at different times (asterisks). Faunal diversity (by clade) was never more extensive than it was in the Quaternary.

Scenarios 1 and 2 cannot be distinguished merely by inspection of the neontological fauna. However, they can be critically evaluated with fossil evidence. Recovery of substantial numbers of “unexpected” fossils (i.e., evidence of clades not represented in the Quaternary) would tend to favor the high initial diversity model. Failure to find such fossils would imply that the known, latest Cenozoic level of diversity is all there ever was, and that the low initial diversity scenario is correct.

As noted above, recent paleomammalogical discoveries in the northern Greater Antilles (Cuba, Hispaniola, and Puerto Rico) have significantly extended the records of several clades (MacPhee and Iturralde-Vinent, 1994, 1995; MacPhee and Grimaldi, 1996). Nevertheless, all Tertiary taxa recovered to date from these islands appear to be closely related to clades known from the Quaternary, which favors the low initial diversity model. At present any firm conclusion would be premature, as there are as yet no fossil vertebrate sites that date to the crucial period in the Late Eocene when permanent land environments were first established in the northern Greater Antilles. Since the paleogeographical history of Jamaica has been markedly different from that of the other Greater Antilles, it would be equally premature to read anything into the remarkable discovery of *Hyrachyus* on that island (Domning et al., 1997). There may be more such taxa, in Jamaica and elsewhere; the only way to find out is through intensive prospecting.

Specific colonization timetables are always subject to refutation paleontologically, because fossils provide minimum dates of occupation. Thus discovery of an “early” fossil attributable to taxon **m** outside the temporal limits of its cartouche (dark gray shading) is evidence that the colonization time originally inferred for **m** is incorrect. Fossils dating first appearances are also of great significance if they represent numerous clades (whether expected or unexpected) and occur

within a narrow time slice (e.g., first-appearance fossils of taxa **m-p**). Multiple first appearances at a specific time could be evidence of the operation of a common cause. (For specific examples of the use of these criteria in analyzing the Antillean mammalian colonization record, see MacPhee and Iturralde-Vinent, 1995).

DISCUSSION

Most of the topics that require discussion in relation to the geology and paleogeography of the landspan hypothesis have been dealt with at length in earlier sections of this work. Our purpose here is to summarize what we consider to be the outstanding problems with this hypothesis, as a guide to further work.

(1) As noted in earlier sections, we cannot yet offer detailed geological and paleogeographical reconstructions of the Caribbean area during the Mesozoic/early Paleogene, and therefore we are unable to settle whether landspans/landbridges existed in this region before the mid-Cenozoic (but see fig. 12 and point 3 below).

(2) Although geographically a member of the Greater Antilles, Jamaica has had a tectonic history quite different from that of the other islands in the group. The only tectonic unit currently incorporated into Jamaica that might have had some relationship to evolving GAARlandia is the Blue Mountains Block. If, as some evidence indicates, the Blue Mountains Block lay relatively close to the northern Greater Antilles during the Cenozoic, it may have received immigrants directly from GAARlandia, either over water or over a land connection with southern Hispaniola (fig. 12). Collision of Western Jamaica with the Blue Mountains Block—if such an event actually took place—would not have occurred earlier than the Miocene.

(3) In principle, some propagules could have reached Caribbean landmasses from the mainlands either before or after the landspan period, if colonizations occurred by over-water dispersal or continent-island vicariance. However, in our view, earlier colonizations (if they occurred) were ultimately doomed to failure (no permanent landmasses before Late Eocene), and later colonizations

would have become increasingly difficult (owing to the disappearance of landspans and tectonic dismemberment of GAARlandia). Nevertheless, two herp lineages identified by Hedges (1996a, 1996b) may be examples of early emplacement, although there is no fossil evidence relating to these taxa. Jamaican *Hyrachyus* does not constitute a counterexample: perched on its Viking funeral ship, it remains a Central American/North American taxon, despite its allochthonous presence in the Greater Antilles (Domning et al., 1997).

Very late originations, as apparently occurred in the Lesser Antilles among many herp groups (Hedges, 1996a, 1996b) and perhaps some mammals (e.g., sigmodontine radiation of northern Lesser Antilles and Jamaica) cannot be explained by the Greater Antilles landspan model. They are the result of the operation of some other mechanism, evidently natural dispersal (or, in some cases, possibly human transport).

(4) Although island–island vicariance may provide a neat solution for the distributions of several tightly related Quaternary taxa, we cannot account for all cases. For example, the presence of apparently endemic species of capromyid rodents and *Nesophontes* in the Quaternary of the Cayman Islands (Morgan, 1994) cannot currently be explained as a consequence of island–island vicariance, inasmuch as the Cayman Islands are probably very recent geographical entities that are unlikely to have had any land connection with either Cuba or Jamaica during the Eocene–Oligocene transition (figs. 6–8). A very late land connection between the Cayman Islands and Cuba might have occurred during the uplift of the Sierra Maestra during the Plio-Pleistocene, as these mountains are located in the same trend and geological unit as the Caymans (Perfit and Heezen, 1978; Case et al., 1984; Sigurdsson et al., 1997). However, this possibility would require a substantial amount of subsidence during the last 5 Ma, as sea floor depths between Cayman Brac and Cabo Cruz (western end of Sierra Maestra) are in excess of 1000 m (G. Morgan, personal commun.). It may also be noted that colonizations by lineages that were evidently not proximately South American (e.g., solenodontids, with proximate ancestry in North America or possibly the Old World), not well constrained

by this or any other model, will have to be elucidated by additional geological, paleogeographical, and paleontological research.

(5) Detailed paleogeographical reconstructions of the now-submerged Aves Ridge are not currently possible. However, as noted in appendix 1, there is evidence that portions of this ridge must have been subaerially elevated at one time (e.g., regional pattern of post-magmatic phase uplift in the late Paleogene, thin Cenozoic sedimentary cover, presence of Oligocene and Early Miocene land-derived conglomerates on ridge). The critical issue is whether the uplifted, emergent Aves Ridge could have formed a corridor of some sort between the Greater Antilles and northwestern South America. Wells drilled along the ridge's structural highs might provide the late Paleogene record still needed to meaningfully constrain the corridor hypothesis, although it cannot be predicted whether such data will be detailed enough to determine if GAARlandia constituted a *single* subaerial entity at any given time. Transitory water gaps, for example, may have intervened for short periods of time between land masses situated on the Aves Ridge or between segments of the Greater Antilles. Importantly, however, none of them would have had the duration or depth of the Havana–Matanzas Channel between western and central Cuba. Alternatively, faunal elements might have dispersed in a pulsed manner within the confines of a single event, if uplift and subsidence affected different parts of GAARlandia at different times. Episodic movements of this kind, if they occurred, might have increased the chance of extinction of faunal elements unable to transfer to the next landmass on the chain, further diminishing overall diversity.

(6) The degree to which the NWSA microcontinent was physically separated from the rest of the continent by marine barriers has not been fully clarified. From the Eocene–Oligocene transition, the Middle Miocene, and especially during high sea-level stands in the Late Miocene, Pliocene, and Quaternary a large marine embayment in the location of the present-day Orinoco River basin isolated the microcontinent from the Guyana highlands to the east (figs. 2–4; Nuttall, 1990; Webb, 1995; Räsänen et al., 1995; Cooper et al., 1995; Kay and Madden, 1997).

Prior to the rise of the Andes in southern Colombia and Ecuador, the microcontinent may or may not have been bounded by another water gap or lowland to the southwest at the location of the Guayaquil Portal (Domning, 1982; Hoorn et al., 1995; Webb, 1995). Thus, to a greater or lesser degree, the northwestern and eastern parts of the continent were at least partially isolated from one another for long periods of time, until comparatively recently. These points raise an interesting issue. If the northwestern microcontinent was substantially isolated from the rest of South America during the late Paleogene to early Neogene by marine and orogenic barriers, then only that fraction of the South American biota occupying the northwestern corner of the continent would have been in a position to cross over the evanescent landspan into GAARlandia. Unfortunately, we know very little about the faunal composition of northwestern South America at the end of the Paleogene (Marshall, 1985; Kay and Madden, 1997). Nevertheless, the fact that the Antillean fauna has apparently always lacked representatives of many South

American groups that “should” have made the journey (Simpson, 1956) may have something to do with the relative paleogeographical isolation and faunal diversity of the source area as well as the nature and duration of the landspan.

(7) The Late Miocene occurrence of two sloth taxa in North America and the equally early presence of procyonids (*Cyonasua*) and now a ?cuvieronine gomphothere in South America (Webb, 1985; Frailey et al., 1996) may indicate that these continents experienced limited biotic interchange prior to the formation of the (last) Panamanian bridge in the late Neogene. The mechanism that permitted this limited interchange—if that is what it was—is obscure; a possible dryland connection is signalled by the 12.9–11.8 Ma hiatus in the Atrato Basin during the late Middle Miocene (fig. 12; Duque-Caro, 1990), but its existence is unconfirmed. We doubt that the sloths swam the distance, although we note that at least one extinct phyllophage (*Thalassocnus*) is thought to have been highly aquatic (cf. de Muizon and McDonald, 1995).

CONCLUSIONS

(1) *Number of intercontinental landbridges.* The last time that western Laurasia (North America) and western Gondwana (South America) were physically connected as continental areas was during the Middle Jurassic, ca. 170 Ma. Terrestrial connections between these continental areas since then can only have occurred via landbridges. In the Cretaceous, three major uplift events, recorded as regional unconformities, may have produced intercontinental landbridges involving the Cretaceous Greater Antillean island arc. The late Campanian/early Maastrichtian uplift event is the one most likely to have resulted in a landbridge, as it would have been coeval with uplift of the dying Cretaceous arc. However, the evidence is too limited for any certainty on this point.

Whether the Cretaceous island arc was involved in the formation of a late Mesozoic landbridge between North and South America carries no necessary biogeographical implications. As we have stated, it is not un-

likely that there were islands in the Caribbean Sea from the time of its opening in the Jurassic onward. On the other hand, it is very unlikely that any of the early islands continuously remained as such (i.e., as subaerial geographical entities) into later times, due to repeated transgressions, subsidence, and, not incidentally, the K/T bolide impact and associated mega-tsunamis (cf. Hedges et al., 1992).

Since the close of the Mesozoic, any landbridge between North and South America would have to have involved Central America. The existing bridge (Panamanian isthmus) was completed only in the Plio-Pleistocene. Evidence for a precursor bridge late in the Middle Miocene is ambiguous at this time.

(2) *Role of GAARlandia landspan.* There is evidence that northwestern South America was briefly connected during the Eocene–Oligocene transition with large landmasses emergent on the Greater Antilles Ridge and

Aves Ridge. The massive uplift event that apparently permitted these connections was spent by 32 Ma; a general subsidence followed, ending the landspan phase. Thereafter, Caribbean neotectonism resulted in the subdivision of remaining land areas, possibly causing multiple instances of true vicariance among vertebrate species then present.

(3) *Modes of faunal formation in the Greater Antilles*. Currently, there are three main models of faunal formation in the West Indies of interest to vertebrate biogeographers: strict dispersal, strict continent-island vicariance, and one that combines dispersal and vicariance in a two-phase process. This paper reviews recent contributions to theory relevant to each of these major modalities. Continent-island vicariance in the classic sense of Rosen (1975, 1985) appears to be excludable for any period since the mid-Jurassic; even if vicariance occurred at that time, its relevance for understanding the origin of modern Antillean faunas is minimal. Hedges and co-workers (Hedges et al., 1992, 1994; Hedges, 1996a, 1996b) have strongly espoused overwater dispersal as the major and perhaps only method of vertebrate faunal formation in the Caribbean region. Notwithstanding their well-argued case, surface-cur-

rent dispersal of passively transported propagules seems to us to be an ineffective explanation of observed patterns of faunal distribution in the Greater Antilles. Even though a general tendency exists for Caribbean surface currents to flow northward with respect to the South American coastline, experimental evidence indicates that it is highly unpredictable where passively floating objects caught in these currents will be deposited. Prior to the Pliocene, regional paleogeography was such that current-flow patterns from major rivers should have delivered most South American waifs to the Central American coast, not to the Greater or Lesser Antilles. Since at least three (capromyid rodents, pitheciine primates, and megalonychid sloths) and possibly four (solenodontid insectivores) lineages of Antillean mammals were already on one or more of the Greater Antilles by the Early Miocene (MacPhee and Iturralde-Vinent, 1995), Hedges' inference as to the primacy of overwater dispersal appears to be at odds with the facts.

The landspan model is consistent with most aspects of Antillean land-mammal biogeography as now known (MacPhee and Iturralde-Vinent, 1995); whether it is consistent with the biogeography of other groups remains to be seen.

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APPENDIX 1: RECONSTRUCTING CARIBBEAN PALEOGEOGRAPHY: AN ANALYTICAL GUIDE

This appendix presents additional maps, tables, stratigraphic columns, and other information relevant to interpreting the geological history of the Caribbean region and the Late Tertiary paleogeographical reconstructions presented elsewhere in this paper. Information in the appendix is linked to tables 1–4, which analytically summarize relevant geological data and literature. Each table covers a particular temporal interval, organized by geological units (first column). These units, defined in terms of their current location on the geode (second column), are the entities traced on the paleogeographic maps. The third and fourth columns synthesize the evidence available for specific environmental indicators, as preserved in rock-stratigraphic records.

Age of each entity was verified according to

stratigraphic position and fossil context (where applicable) in light of the new chronostratigraphic framework provided by Berggren et al. (1995). Use of this new scale necessitated modification of published time-stratigraphic positions of several formations. Paleoenvironmental interpretations of each unit were assessed using data and interpretations in the literature as well as the results of our own fieldwork.

Yucatan Peninsula

The Yucatan Peninsula (Maya Block or MB; fig. 14) has been part of the North American plate since the late Cretaceous (Marton and Buffler, 1993). Tectonic activity has been largely concentrated in the southwestern part of MB, far from the areas immediately relevant to this study. Nevertheless, there is considerable information on this

unit and its Caribbean borderland (Butterlin and Bonet, 1966; Case, 1975; Lopez-Ramos, 1975; Weidie et al., 1979; Viniestra, 1981; Mascle et al., 1985; see also the paleogeographical maps compiled in papers edited by Salvador, 1991).

Stratigraphic data indicate that MB was probably uplifted from Jurassic through Barremian time (early Cretaceous). The block was covered by shallow seas from late Aptian through Late Eocene, although small islands probably existed on it from time to time (Salvador, 1991; McFarlane and Menes, 1991). Brief emergence of MB may have occurred around 88–90 Ma, as a hiatus has been reported within the Turonian (Lopez Ramos, 1975; Weidie et al., 1979; Viniestra, 1981). This correlates well with a Turonian hiatus represented in rock sequences in the northern Caribbean and Gulf of Mexico (Meyerhoff and Hatton, 1968; Schlager et al., 1984; Pszczolkowski and Flores, 1986; Iturralde-Vinent, 1994a).

Seismic refraction studies of the Chicxulub bolide crater on the NW corner of the Yucatan Peninsula indicate that islands produced by impact debris might have had a brief existence there during the early Paleocene, before they vanished and were covered by younger marine carbonate deposits (Buffler et al., 1995). Unfortunately, there is not enough information available on these structures to offer a plausible reconstruction of their position or duration.

Several geologic units in western and central Cuba (Guaniguanico, Pinos, and Escambray terranes) are allochthonous (Iturralde-Vinent, 1994a, 1994b). These terranes were detached from their original location along the Yucatan borderland (Pszczolkowski, 1987; Rosenkrantz, 1990) between the Late Paleocene and the Middle Eocene, during the formation of the Greater Antilles Fold-belt (fig. 5; Bralower and Iturralde-Vinent, 1997). However, the tectonic processes involved (intense folding, thrust faulting, metamorphism) took place at significant depth, and it is quite improbable that any of these terranes include units from MB that were actually emergent at the time of their incorporation into Cuba.

According to Butterlin and Bonet (1966) and Galloway et al. (1991), parts of MB have been permanently subaerial since Late Eocene. However, latest Eocene to Early Miocene deposits are rare and have been found only in the northern and northwestern parts of the Yucatan Peninsula. In the Oligocene and Miocene, the northeastern section of the peninsula was covered by water, as was the westernmost extremity of Cuba and Isla de la Juventud during the Miocene (Iturralde-Vinent, 1969). Furthermore, data from offshore seismic lines clearly indicate that the Yucatan Channel is an ancient feature that was in existence long be-

fore the Late Eocene (probably since the Maastriichtian; Case, 1975; Mascle et al., 1985; Rosenkrantz, 1990, 1996). Therefore, for most of the Cenozoic, if not longer, the Cuban terranes (wherever they were then stationed) and MB have been separated by a significant water barrier (see also discussion in MacPhee and Iturralde-Vinent, 1995).

Northern Central America, Nicaragua Rise, and Western Jamaica

Geologically, northern Central America (comprising Nicaragua, Honduras, Guatemala, and southern Mexico) consists of a single tectonic terrane, the Chortis Block (CB; fig. 15). In most current plate tectonic models, CB is assumed to have originated off Mexico on the Pacific margin of North America, and to have been rotated into its present position late in the Cenozoic (Malfait and Dinkelmann, 1972; Donnelly et al., 1990). The Monagua–Polochic deformed system, the hinge zone between CB and terranes farther north in Mexico, was particularly active from Middle Eocene through Middle Miocene (Pindell, 1994; Morán-Zenteno et al., 1996). Emplacement of CB is generally correlated with the evolution of the Cayman Trench system (Pindell, 1994; Rosenkrantz, 1995; Morán-Zenteno et al., 1996). Appreciable parts of CB have been uplifted for most of the Cenozoic (Maurrasse, 1990; Donnelly et al., 1990).

Geographically, the Nicaragua Rise (NR) is the prolongation of CB into the Caribbean Sea. Geologically, however, these units are quite different (Holcombe et al., 1990; Donnelly et al., 1990). Stratigraphic data for NR are spotty, but isolated wells, dredge hauls, and seismic stratigraphy are sufficient to create a broad-brush picture. Most importantly, these data confirm that NR and the Western Jamaican Block (WJ) have shared a considerable amount of geological history.

Assuming that the Cretaceous basement of WJ can be correlated with basement rocks of NR (also known to be Cretaceous [Holcombe et al., 1990]), it appears that this terrane (i.e., Western Jamaica and Nicaragua Rise together) was the site of volcanic arc activity in the last part of the Mesozoic, under mostly submarine conditions. Local hiatuses in the Albian and Turonian suggest bouts of temporary uplift of the terrane in the Late Cretaceous (Case, 1975; Mascle et al., 1985; Perfit and Heezen, 1978; Holcombe et al., 1990; Maurrasse, 1990). Although different marine environments dominate the Paleocene and Eocene section (Holcombe et al., 1990; Robinson, 1994), occurrence of at least one terrestrial vertebrate in Early Eocene rocks of WJ indicates the local occurrence of land (Domning et al., 1997). Perhaps, therefore,

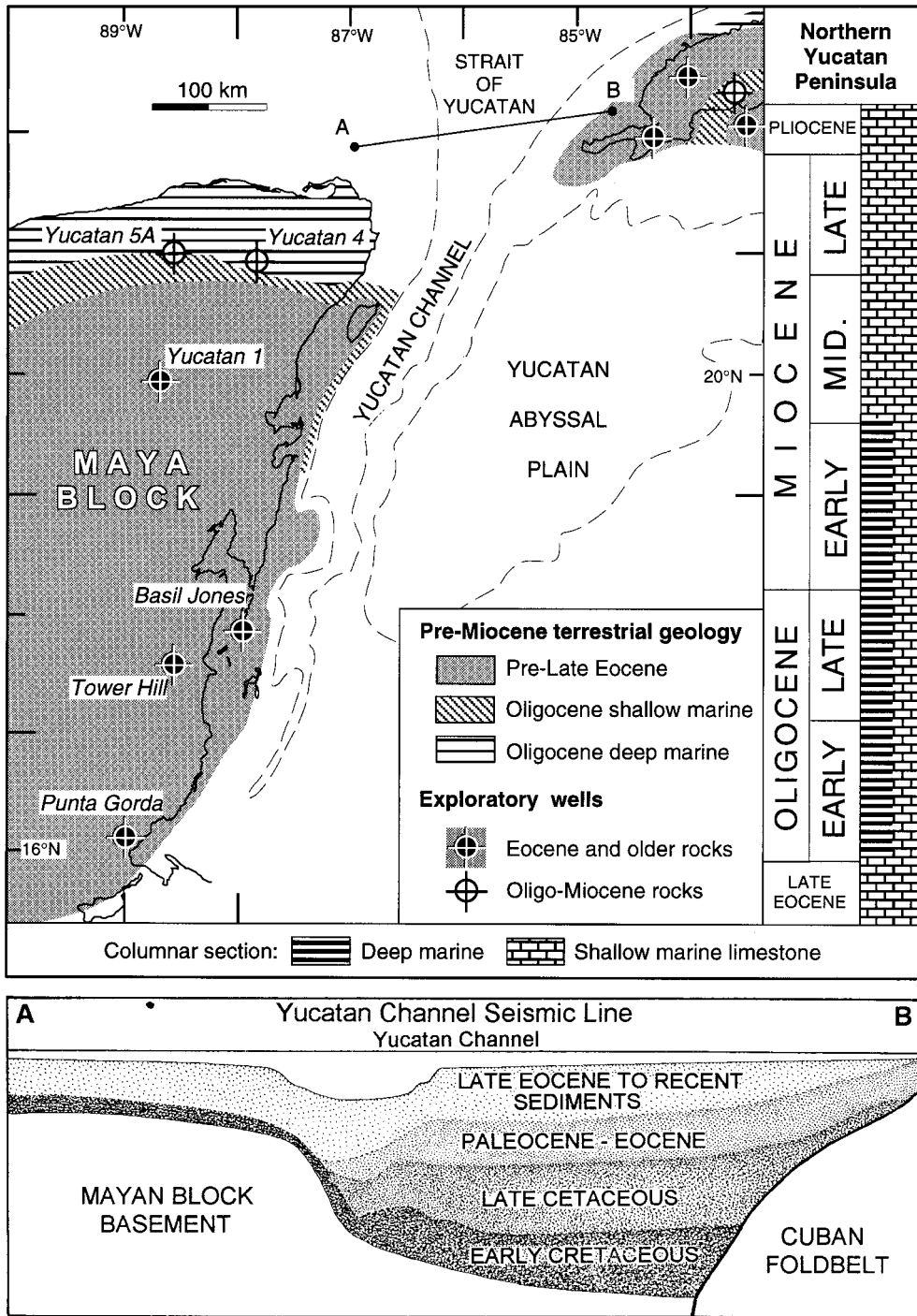


Fig. 14. Yucatan Peninsula (Maya Block): **top left**, Simplified pre-Miocene terrestrial geology; **top right**, late Tertiary stratigraphic columns (compiled from many sources; see appendix 1); **bottom**, cross-section along offshore seismic line (courtesy Institute for Geophysics, University of Texas at Austin). Cenozoic land connections between Maya and Western Cuban Blocks are ruled out by the shape of the section underlying the Yucatan channel and the presence of sedimentary rocks of Mesozoic and Cenozoic age.

CB, NR, and WJ were terrestrially connected to North America for a short time in the Early Eocene. (Eastern Jamaica, comprising the Blue Mountains Block, has had a different and more complex history; see below.) NR was nearly at ambient sealevel during the latest Eocene, and positive areas were partly or completely uplifted during most of the Oligocene. Miocene to Recent marine rocks are found throughout, suggesting that the NR became once again a submarine feature by the Late Miocene.

Two types of late Tertiary sedimentary environments can be defined for WJ (Eva and McFarlane, 1985; Robinson, 1994). One environment is indicated by shallow marine carbonate rocks, resembling those of NR. The other environment is indisputably deep water, suggesting that Jamaica was located at the eastern edge of the Rise. The possible existence of a short-lived hiatus at the base of the shallow-water Oligocene section in WJ (Eva and McFarlane, 1985; Robinson, 1994) correlates well with Oligocene uplift postulated for NR. Final uplift of WJ, to create most of the island as it is known today, probably occurred during the important tectonic deformation that took place during the Middle Miocene (Eva and McFarlane, 1985; Mann et al., 1990, 1995; Robinson, 1994).

Southern Central America

According to data compiled by Escalante (1990) and Kolarsky et al. (1995a, 1995b), Southern Central America (SCA) is underlain by Mesozoic oceanic crustal rocks and late Campanian–Eocene oceanic crust and volcanic arc suites. The Late Eocene to Recent section is summarized in figure 16 (after Escalante, 1990; see also Kolarsky et al., 1995a, 1995b). The Eocene–Oligocene boundary interval (35–33 Ma) is marked by local uplift and deposition of angular, poorly sorted conglomerates, derived from a local source. As elsewhere in the Caribbean region, the Late Oligocene of SCA is transgressive and features marine rocks indicative of shallow- and deep-water environments. An important event occurred late in the Middle Miocene, as elsewhere in the Caribbean region, when strong volcanic activity and general uplift were initiated (see Dengo and Case, 1990; Duque-Caro, 1990). According to Duque-Caro (1990), late in the Middle Miocene, SCA may have been sufficiently uplifted to serve as a connector between Central and South America. The existence of late Neogene deformation and thrust faulting recorded at the hinge zone between Panama and South America (Mann and Kolarsky, 1995) tends to support this inference, although it is far from demonstrated.

Northwestern South America

The geology of this region has been investigated by many authors (fig. 17); key references include González de Juana et al. (1980) Bonini et al. (1984), Duque-Caro (1990), Dengo and Case (1990), and Tankard et al. (1995). The regional geological picture is too complicated for useful summary here, but some general points need to be briefly canvassed for the purposes of this paper. Detailed paleogeographic reconstruction of northwestern South America (NWSA Microcontinent) prior to the latest Eocene is beyond the scope of this report (but see Tankard et al., 1995).

During most of the late Tertiary, the NWSA Microcontinent has moved predominantly eastward with respect to the motion of the rest of South America (González de Juana et al., 1980; Case et al., 1990; Bartok, 1993; Pindell, 1994; Balkwill et al., 1995). Also, this region has been strongly affected by vertical movements since the latest Eocene. Marine sediments corresponding to the P17–18 zones (35–33 Ma) of Berggren et al. (1995) are not known on the microcontinent proper, indicating that most of the area was uplifted during that time (tables 1, 2). However, mid-Oligocene (P19 zone) and younger marine deposits have been found in several basins (González de Juana et al., 1980; Duque-Caro, 1990; Cooper et al., 1995), indicating that uplift was followed fairly rapidly by subsidence or higher sea stands (or both). This must have been accompanied by considerable modification of the pattern of river drainage (Hoorn et al., 1995). The epicontinental seaway that apparently converted northwestern South America into a large island was in existence from the latest Eocene (fig. 17; Cooper et al., 1995; Kay and Madden, 1997).

Aruba/Tobago Belt

The structure and history of the Aruba/Tobago Belt (ATB) has to be considered separately (fig. 18). The basement of these islands consists of Mesozoic oceanic crust and Cretaceous volcanic arc units. Equivalent rocks are also found allochthonously in the Caribbean Mountains, above continental margin sediments, all partially metamorphosed (González de Juana et al., 1980; Beets et al., 1984; Mascle et al., 1985; Jackson and Donovan, 1994). The deformation of ATB took place when the Caribbean Plate interacted with the South American continental margin (Beets et al., 1984; Erikson and Pindell, 1993; Macellari, 1995). Between 35 and 33 Ma this interaction produced general uplift of the Belt (see above), as well as progressive subsidence of local basins along the continental margin (Macellari, 1995; Erikson and Pindell 1993; Stockhert et al., 1995). In Trinidad, sedimentation in deep-water conditions

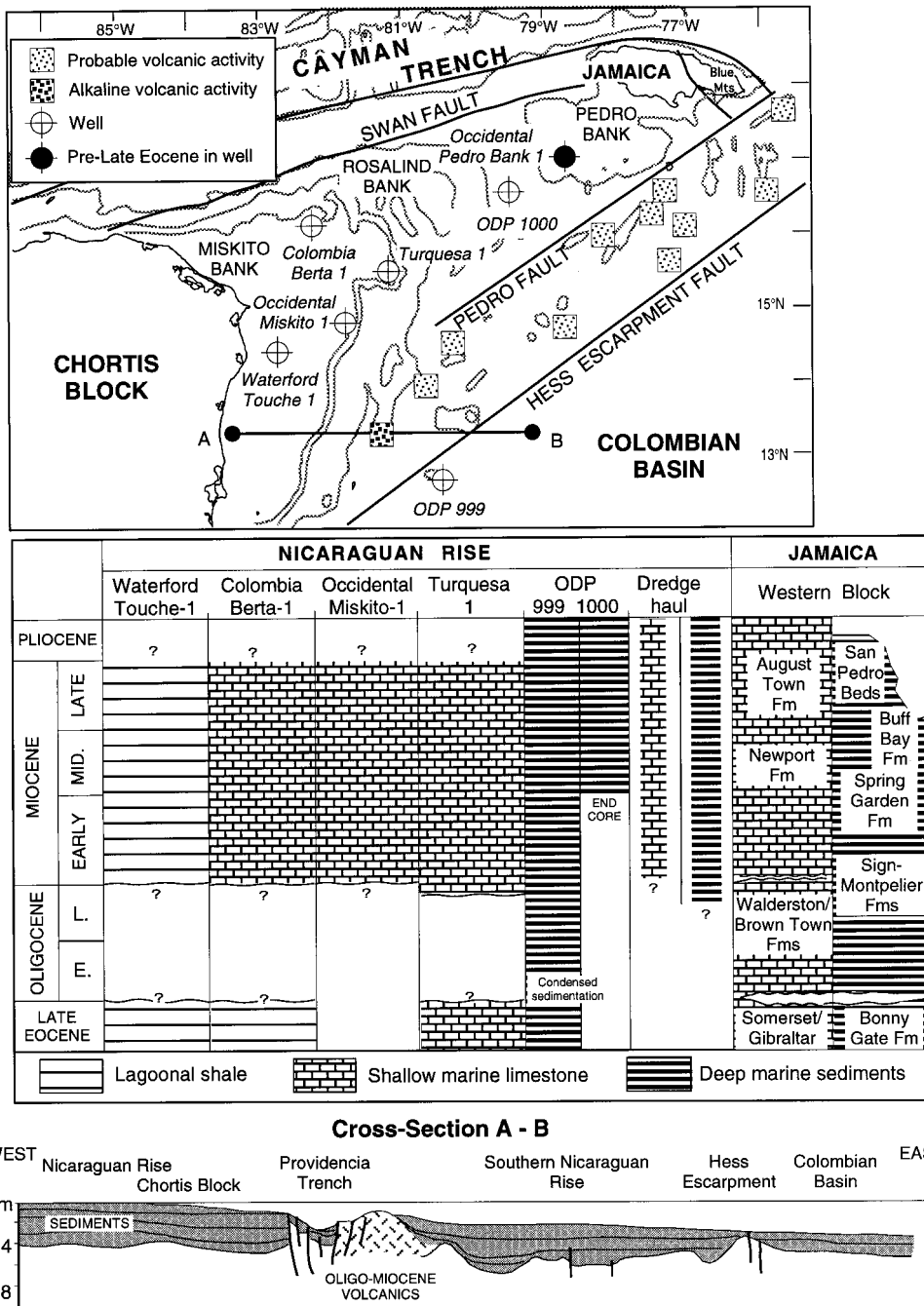


Fig. 15. Chortis/Nicaraguan Rise and Western Jamaican Blocks: **top**, Location map, drilling sites, and important geological features; **middle**, late Tertiary stratigraphic data for Nicaraguan Rise and Western Jamaica (dredge samples from wall of Cayman Trench); **bottom**, simplified cross-section, Nicaraguan Rise to Colombian Basin (compiled from many sources; see appendix 1). Stratigraphic data suggest that Nicaraguan Rise was at or near sealevel in latest Eocene, and remained positive into Early and Middle Oligocene. Off the Rise, Late Oligocene subsidence is indicated by deep-water sediments in ODP 999 hole.

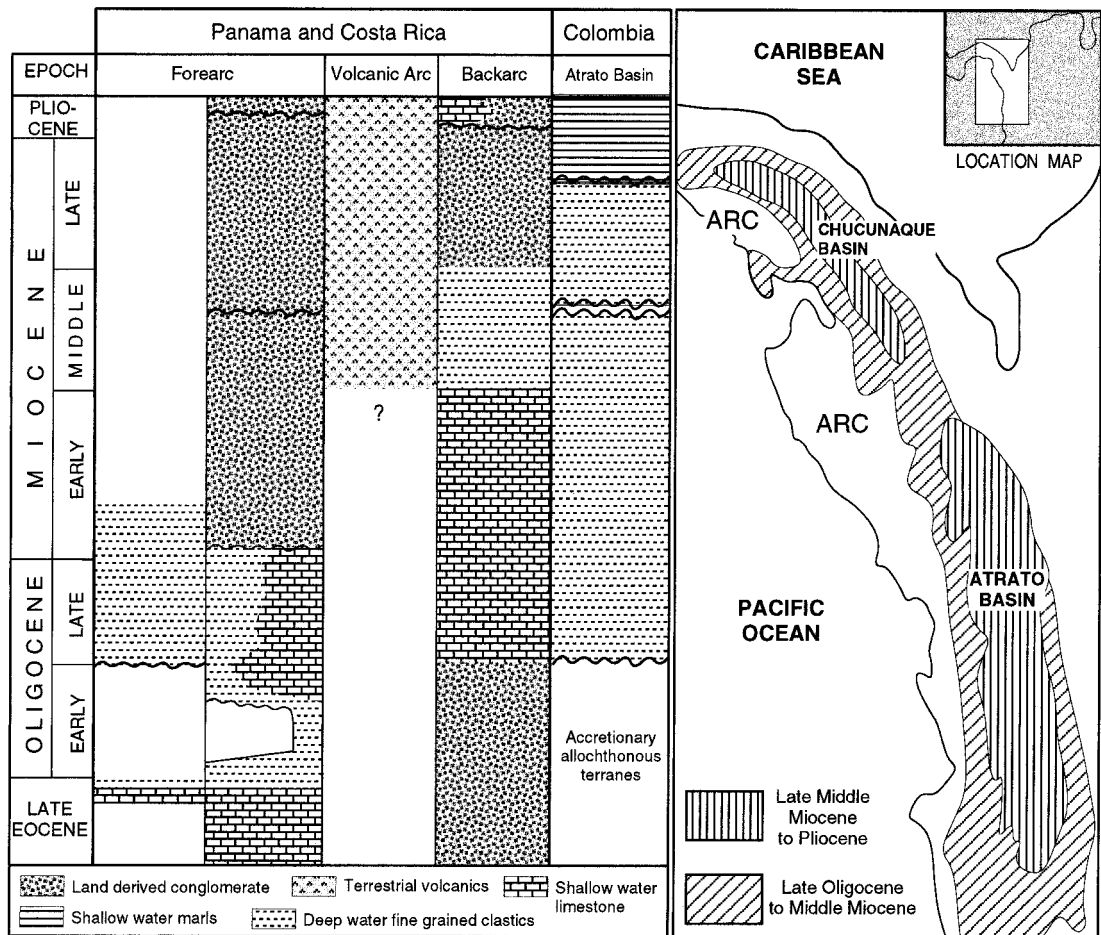


Fig. 16. Southern Central America and northern South America (Atrato Basin area): **right**, Location map, major features, and late Tertiary rocks; **left**, stratigraphic columns (compiled from Escalante, 1990; Duque-Caro, 1990; Kolarsky et al., 1995a, 1995b).

began in the Late Oligocene and persisted until late in the Miocene (Algar and Erikson, 1995). Similarly, in the Orinoco River basin, marine sediments of Eocene to Recent age occur as outcropping or subsurface deposits (González de Juana et al., 1980; Cooper et al., 1995). Stratigraphic sequences in ATB and several basins in the NWSA Microcontinent present a record of the same critical events in late Tertiary geological history that have already been described for other parts of the Caribbean region, such as the 35–33 Ma hiatus and subsequent Oligocene transgression (González de Juana et al., 1980). In some areas, the hiatus seems to have involved long-lasting subaerial exposure, with shorter intervals of marine inundation in the Late Oligocene and the late Early Miocene. For example, this interpretation seems to apply to the exceptional hiatus between the

Late Eocene and Late Miocene seen in sections from Aruba and Margarita. This area is provisionally regarded as the zone in which the inferred land connection between the Aves Ridge and continent was formed during the Eocene–Oligocene transition.

Greater Antilles

The Greater Antilles have been the subject of detailed geological research for most of this century. Key modern sources include Khudoley and Meyerhoff (1971), Dengo and Case (1990), Mann et al. (1991), Donovan and Jackson (1994), and Iturralde-Vinent (1996a). The unusual complexities of this region militate against easy paleogeographical reconstruction, and it is recognized that much more field and laboratory work will have to be undertaken before paleomapping projects will

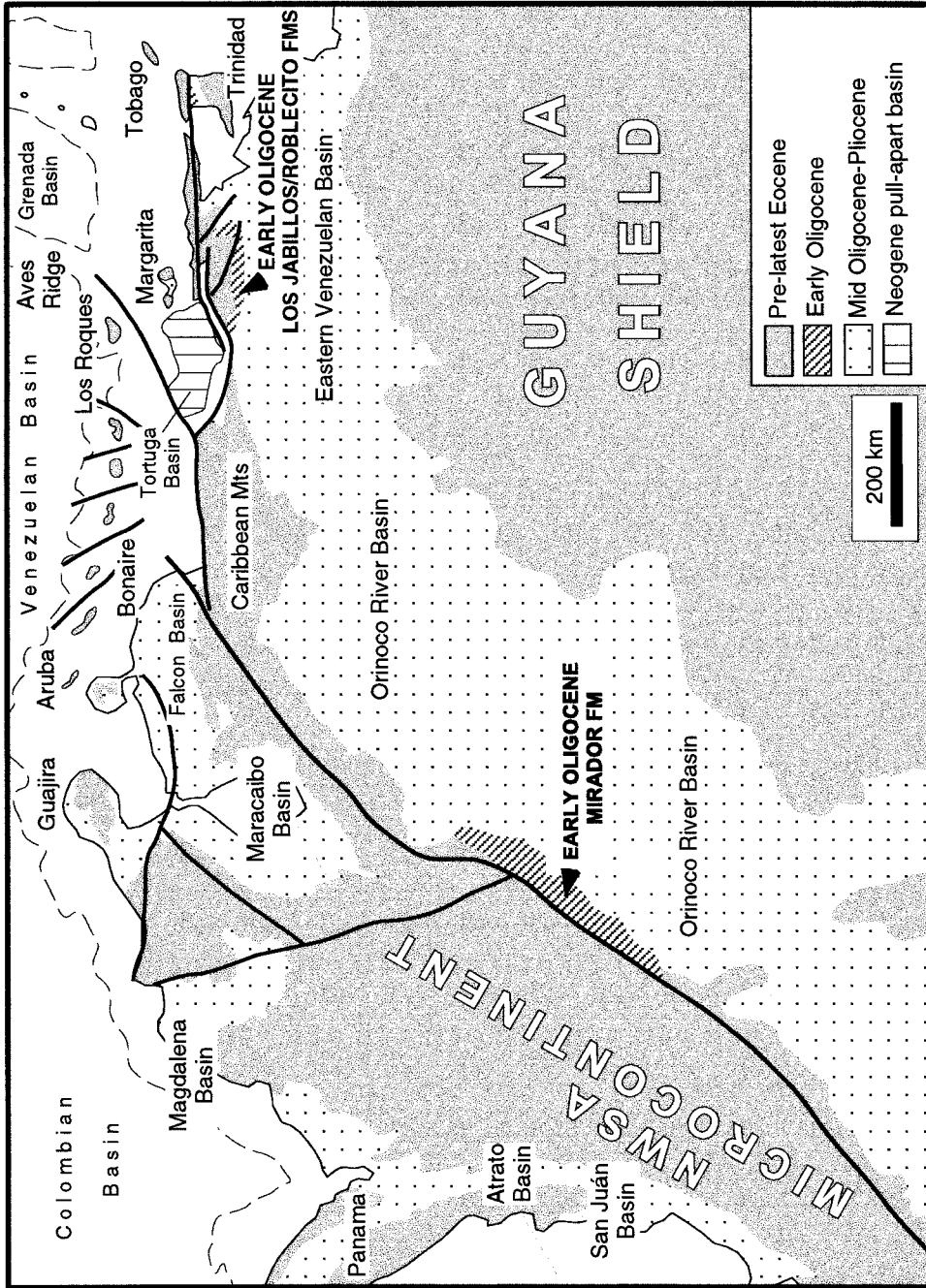


Fig. 17. Northwestern South America: Schematic late Tertiary geological map, showing location of Orinoco and eastern Venezuelan basins separating NWSA Microcontinent from Guyana shield. Note that rocks conforming in age to Eocene-Oligocene boundary are absent throughout, while marine deposits of earliest Oligocene age are restricted to Orinoco and eastern Venezuelan basins (compiled from many sources; see appendix 1).

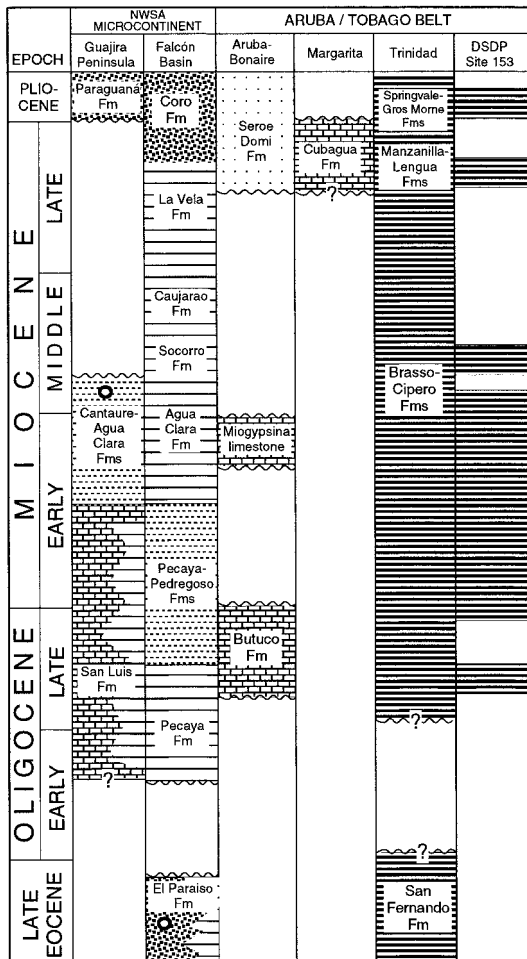


Fig. 18. Late Tertiary stratigraphic columns for selected basins on NWSA Microcontinent (northwestern South America) and Aruba/Tobago Belt (compiled from many sources; appendix 1). Butuco Fm (Aruba-Bonaire) was originally dated as Eocene-Early Oligocene, but age markers are ambiguous and suggest Late Oligocene to Early Miocene age (*Lepidocyclina*, *Heterostegina*, *Pararotalia*, *Antiguastrea cellulosa* [sensu González de Juana et al., 1980]). Lithology as in figure 20A.

achieve the needed level of detail and authoritativeness. However, thanks to recent investigations some headway has been possible (see Paleogeography of the Caribbean Region: Evidence and Analysis).

The basement of the Greater Antilles Foldbelt (GAF) consists of old continental-margin suites, Mesozoic oceanic crustal units, Cretaceous/Paleogene volcanic arcs, and latest Cretaceous to Recent sedimentary basins—all partly metamor-

phosed, deformed, and jumbled together under the pervasive effects of tectonic forces (Fig. 5; Dengo and Case, 1990; Iturralde-Vinent, 1994a). Widely varying opinions concerning the plate tectonic evolution of these elements can be found in the literature (cf. Pindell, 1994; Iturralde-Vinent, 1994a; Hay and Wold, 1996). Most aspects of the tectonic history of GAF prior to the latest Eocene lie outside the special concerns of this paper (but see fig. 5 and main text for background).

From the literature we have compiled stratigraphic data (figs. 19, 20) pertinent to interpreting the post-Eocene paleogeography of the Greater Antilles (Cuba: Bronnimann and Rigassi, 1963; Nagy et al., 1983; Albear and Iturralde-Vinent, 1985; Iturralde-Vinent, 1969, 1972, 1996a, MacPhee and Iturralde-Vinent 1994, 1995; Hispaniola: Butterlin, 1960; Van den Bold, 1981; Eberle et al., 1982; Maurrasse, 1982, 1990; Saunders et al., 1986; García and Harms, 1988; Mann et al., 1991; Heubeck et al., 1991; Toloczyki and Ramírez, 1991; Iturralde-Vinent and MacPhee, 1996; Blue Mountains Block: Robinson, 1965, 1994; Eva and McFarlane, 1985; Maurrasse, 1990; Geddes, 1994; Puerto Rico: Meyerhoff, 1933; Pessagno, 1963; Monroe, 1980; Frost et al., 1983; MacPhee and Iturralde-Vinent, 1995; Virgin Islands: Larue, 1994; MacLaughlin et al., 1995).

Eastward shift of tectonic activity has been a marked trend in the evolution of the Greater Antilles since the end of the Eocene. Thus, in western and central Cuba, vertical movements, with limited sinistral strike-slip faulting, has been the rule since latest Eocene (Iturralde-Vinent, 1978). By contrast, east of the Guacanayabo-Nipe fault in eastern Cuba, sinistral faulting and transpressional tectonics have been dominant. This has resulted in strong deformation and subdivision of GAF into a series of block-terrane correlated with the opening of trenches, grabens, and pull-apart basins (Ladd et al., 1981; Larue et al., 1990; Larue and Ryan, 1990; Jany et al., 1990; MacPhee and Iturralde-Vinent 1995; Mann et al., 1990; Calais et al., 1992). These disrupted block-terrane have to be returned to their original, latest Eocene position in order to reconstruct Greater Antillean paleogeography (figs. 3, 6).

Figure 3 is a palinspastic reconstruction of a critical area in the northern Greater Antilles that encompasses present-day eastern Cuba, northern Hispaniola, and Puerto Rico. Offsets along major strike-slip faults have been calculated for some faults (Iturralde-Vinent, 1981; De Zoeten and Mann, 1991); these figures are used where available. Our reconstruction is based strictly on concordances between identical or strongly correlat-

able geological units (particularly those of Late Eocene age or older), as follows:

(1) ?Neocomian–Campanian Cretaceous volcanic-arc complexes: These rocks outcrop from west-central Cuba across Hispaniola into Puerto Rico and the Virgin Islands.

(2) Maastrichtian massive conglomerates, dominated by ophiolite pebbles and overlain by Paleocene/Early Eocene white tuffaceous rocks: This suite of rocks only outcrops east of Holguín in eastern Cuba and in a small area in northwestern Hispaniola. This suite is of unique importance for correlating terranes (Iturralde-Vinent, 1994b).

(3) Ophiolite trend: Outcropping ophiolites in Cuba follow the same trend as those in Hispaniola, especially when their paleoposition is reconstructed palinspastically.

(4) Distinctive metamorphic rock units: This series consists of four distinctive rock suites—marble and schists of the Bahamas margin complex, amphibolites (metaophiolites), serpentinites with blocks of eclogite, and metamorphosed Cretaceous volcanic arc rocks. This combination of metamorphics outcrops in easternmost Cuba and northwestern Hispaniola (Puerto Plata–Samaná).

(5) Paleogene volcanic arc rocks: Rocks derived from the Paleogene volcanic arc outcrop in eastern Cuba as well as the northern peninsula of Haiti, central Hispaniola, and Puerto Rico.

(6) Latest Eocene/Oligocene sedimentary rocks: Units of this age in the Guantánamo Basin correlate precisely with those found in the the Cibaio-Altamira Basin of Hispaniola (Calais et al. 1992; Iturralde-Vinent and MacPhee, 1996).

The paleoposition of Puerto Rico/Hispaniola is not so well constrained as that of Cuba/Hispaniola, although it is known that the Cretaceous volcanic arc complex outcropping in eastern Hispaniola also forms a large portion of the basement of Puerto Rico. The most important correlatable units are the Duarte complex of Hispaniola and the Bermeja complex of Puerto Rico, which lie in the same trend. Also, outcrops of Paleogene rocks on the eastern side of Hispaniola lie in the same trend as their equivalents in Puerto Rico.

The close match between the main structural fabric and compositional elements of eastern Cuba, Hispaniola, and Puerto Rico/Virgin Islands as illustrated in figure 3 is valid only for the interval between the latest Eocene and the mid-Oligocene (35–30 Ma). Before the latest Eocene, overthrusting and extensive superposition of terranes took place in this area (Meyerhoff and Hatten, 1968; Pardo, 1975), indicating that a different paleogeographic organization prevailed at that time (see main text). Subsequent to the Late Oligocene, movement along several sinistral faults has

strongly disrupted the assemblage of block-terraces (cf. figs. 1–3).

Blue Mountains Block

A possible land connection between the southern peninsula of Hispaniola (SH) and the Blue Mountains Block (BM) of eastern Jamaica is illustrated for the Eocene–Oligocene transition (fig. 6). The evidence for this connection is circumstantial at present, and therefore its inclusion in paleogeographical reconstructions of the Greater Antilles requires some elaboration.

It is generally accepted that Jamaica originated as a single crustal unit in the Cretaceous arc (Pindell, 1994). However, as previously noted, there is evidence that Jamaica is structurally and lithologically divisible into two major terranes, consisting of a large western block (Clarendon and Hanover Blocks of Lewis et al., 1990) and a smaller Blue Mountains Block. These two terranes differ radically in crustal composition, degree of metamorphism, and stratigraphy (including the span of temporally correlated units), as is evident from several recent papers and mapping projects (Geddes, 1994; Montadert et al., 1985; Lewis et al., 1990; Robinson, 1994). It is true that, after the Middle Eocene, resemblances between coeval formations in different parts of Jamaica greatly increase (e.g., Bonnie Gate Fm; Robinson, 1965, 1994). However, lithology by itself has limited correlation value in this case, as compositionally similar formations of late Tertiary age outcrop widely in the Greater Antilles.

According to Pindell's (1994) model of the origin of Jamaica, the island's basement as a whole was originally part of the Cretaceous volcanic arc located on the leading edge of the Caribbean Plate. As the plate moved east during the late Cretaceous, the basement rocks of Jamaica remained attached to northern Central America. It is assumed by necessity that these rocks were carried to their present-day position when the Nicaragua Rise (which originated in the Pacific) was inserted into the Caribbean (Pindell, 1994; fig. 2.6). If this were so, one would expect to find strong similarities between the ophiolitic and Cretaceous-arc suites of western Cuba and Jamaica, since they were located side by side in the original arc (*sensu* Pindell, 1994). Yet there is virtually no similarity between relevant geological sections (cf. Iturralde-Vinent, 1996a, 1996b, 1996c and Robinson, 1994). By contrast, there are evident resemblances in the ophiolitic and metavolcanic sequences of the Eastern Cuban Block and BM, suggesting that these terranes belong to the same geological province (Iturralde-Vinent, 1995). Most importantly, the geological composition of the Mesozoic rocks of

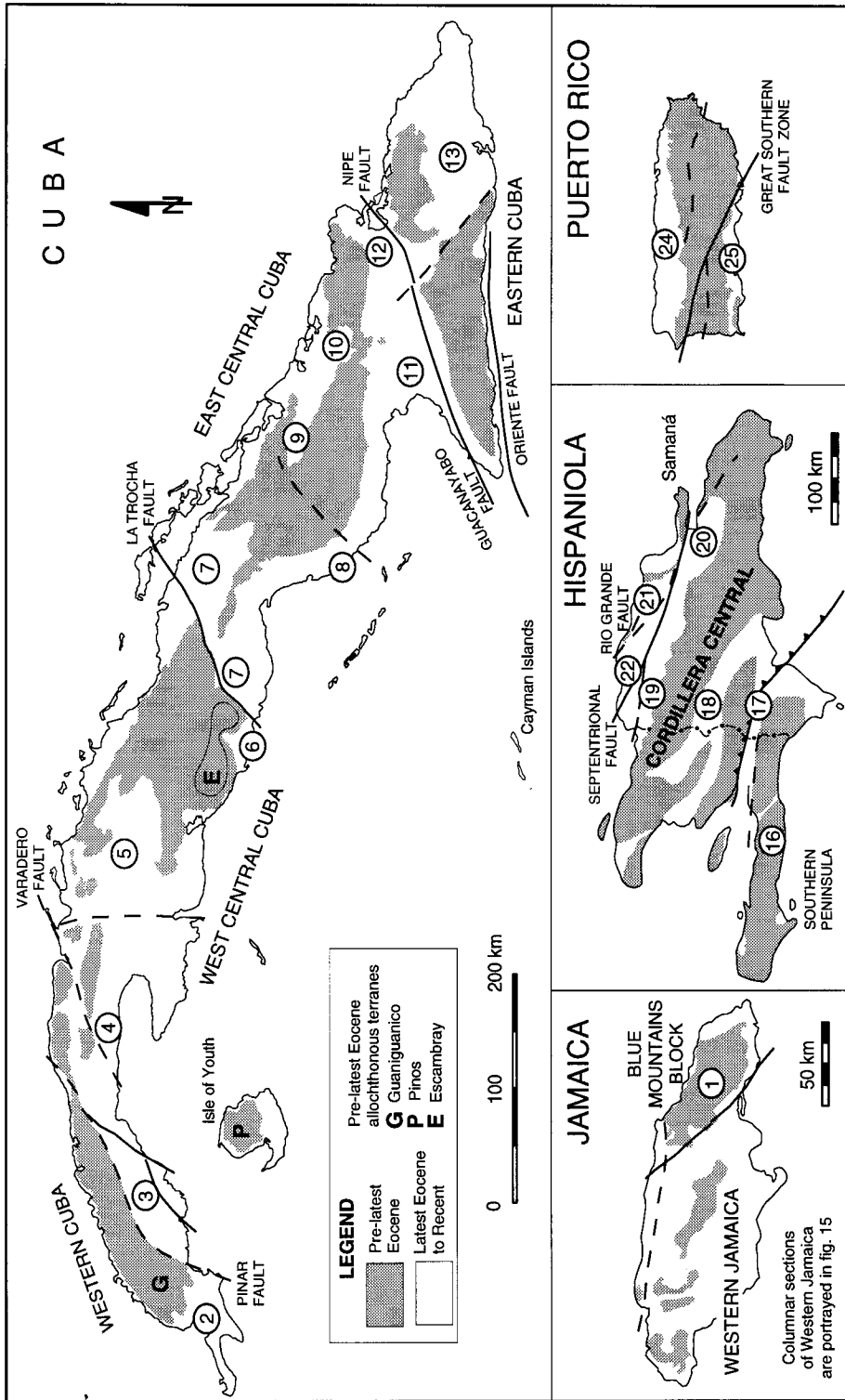


Fig. 19. Greater Antilles: Simplified geological maps showing major terranes and faults active during late Tertiary. Numbers refer to geographical location of late Tertiary stratigraphic columns depicted in figure 20A, B.

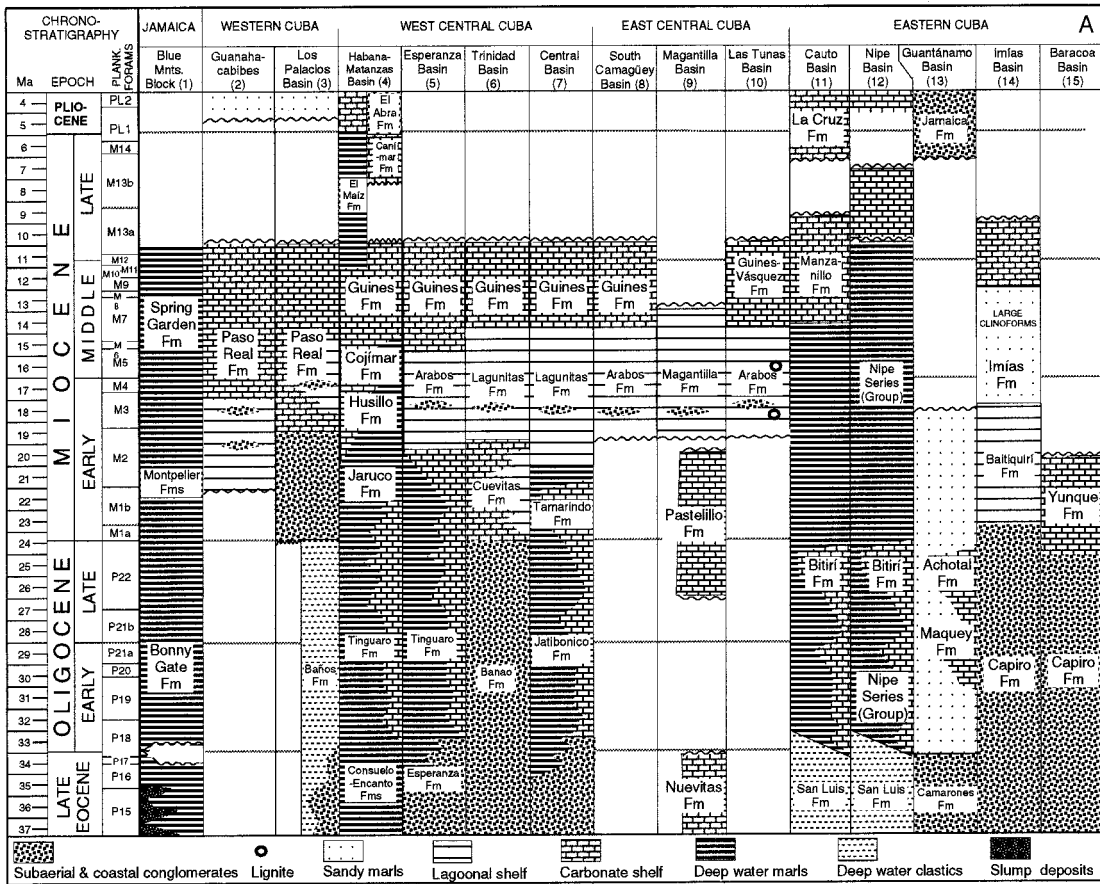


Fig. 20. Greater Antilles: Late Tertiary stratigraphic columns for selected basins: A, Blue Mountains, Cuba (this page); B, Hispaniola, Puerto Rico/Virgin Islands (compiled from many sources; see appendix 1; opposite page).

SH and BM are also remarkably similar. (Cf. descriptions of southern Hispaniola by Butterlin [1960] and Maurrasse [1982] with descriptions of Blue Mountains by Robinson [1994] and Montadert et al. [1985].)

These observations can be made concordant if it is accepted that BM originated as part of the northern Greater Antilles, while WJ evolved from the leading edge of the Nicaragua Rise (sensu Pindell, 1994). In this interpretation, these terranes maintained a separate existence until the Middle Miocene, when they were conjoined during tectonic deformations recorded in the island (Montadert et al. 1985). We acknowledge that this dual-origin hypothesis represents a break with the orthodox view, and that further substantiation is required (see also Stephan et al. 1990: pls. 8–10).

With regard to the possible presence of land on the Blue Mountains unit during the early Tertiary,

one important piece of the puzzle is the identity of the 33–35 Ma hiatus (corresponding to zones P17–18) occurring in BM and SH. In SH, the deep-water *G. ampliapertura* to *G. kugleri* zones of the Jeremie Fm unconformably overlie older rocks (fig. 20B). Rocks deposited in the time-slice corresponding to zones P17–18 have not been reported; this may indicate that SH was uplifted at that time, as were many other terranes in the Caribbean (including blocks having similar oceanic crustal structure, e.g., Beata Ridge).

Likewise, well-dated sediments of 35–33 Ma age have not been recognized in the Blue Mountains either. Eva and McFarlane (1985) identified the Early Oligocene in Jamaica on the basis of an assemblage including *Dictyoconus cookei*, *Archaias angulatus*, and several small species of *Peneroplis*, but these taxa are ambiguous indicators of this age, because *A. angulatus* and *Peneroplis*

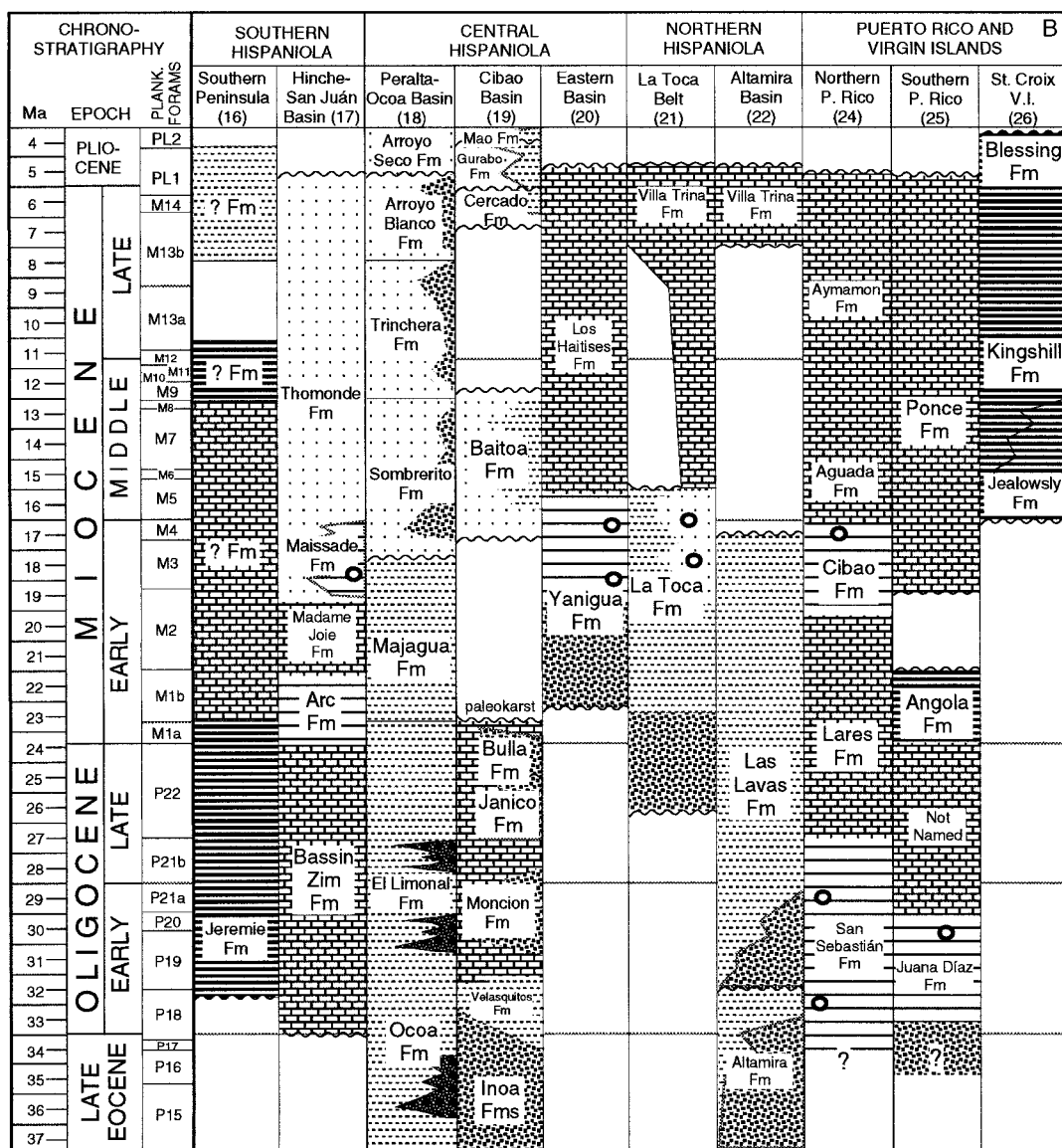


Fig. 20. Continued.

are extant taxa, while *D. cookei* is not restricted to the Oligocene (see Bronnimann and Rigassi, 1963; Albear and Iturralde-Vinent, 1985). Similarly, Robinson (1965, 1994) identified the hemipelagic Bonny Gate Fm from localities surrounding the central Blue Mountains as being Eocene to Late Oligocene in age. However, he does not list fossils consistent with a P17–18 zone allocation (sensu Berggren et al., 1995). In any case, the use of benthic forams as index fossils to date narrow time intervals is problematic, especially in

contexts like the Bonny Gate Fm in which allochthonous biotritus is frequently encountered (Eva and McFarlane, 1985; Robinson, 1965, 1994).

The possibility that uplift occurred within BM and SH 35–33 Ma is underscored by the ubiquitous presence of a hiatus of that precise age in existing positive structures almost everywhere in the Caribbean, including the submarine Beata Ridge. Absence of this hiatus in eastern Jamaica would be completely anomalous.

The nonpalinspastic maps of Eva and McFarlane (1985) indicate the occurrence of land in the Blue Mountains during the Paleocene and Eocene, and, much later, after the Middle Miocene. Although this scenario, involving repeated emergence and submergence of the Blue Mountains, cannot be directly challenged on the basis of the few facts available, we argue that it is more parsimonious to hypothesize that the Blue Mountains have been permanently subaerial since the latest Eocene. This view is consistent with (1) the absence of Eocene and younger rocks from the core of BM; (2) the lithological character of the Bonny Gate Fm, in which the presence of coarse clastic debris (olistostromes, sandstones, silts) in the basal Lloyd member (Maurasse, 1990) indicates the existence of land during the late Paleogene; and (3) the occurrence of shallow-water biotritus throughout the Bonny Gate section (Eva and McFarlane, 1985), suggesting shelf or coastal environments prevailing at the time of deposition. Better evidence of the emergence of the Blue Mountains and the nature of their connection with Hispaniola is sorely needed.

Aves Ridge, Lesser Antilles, and Grenada Basin

In the last three decades, a large amount of geological and geophysical data has been collected concerning the Aves Ridge (AR), Lesser Antilles (LA), and Grenada Basin (GB). For an overview and additional references, the reader is referred to papers by Fox et al. (1971), Bouysse et al. (1985), Pinet et al. (1985), Holcombe et al. (1990), and Maury et al. (1990). Here we concentrate on physical paleogeography.

Cretaceous and Paleogene volcanic and plutonic rocks of island arc affinities occur in AR (Bunce et al., 1970; Fox et al., 1971; Nagle, 1972; Bouysse et al., 1985; Westercamp et al., 1985; Holcombe et al., 1990), as do Mesozoic and Eocene volcanic rocks in LA (fig. 15). This basic compositional similarity suggests that, from Cretaceous through Eocene time, AR and LA were a single entity: the AR-LA Volcanic Arc (Pinet et al., 1985; Bouysse et al., 1985). This arc was presumably linked geologically to the Aruba/Tobago Belt in the south and the eastern Greater Antilles in the north, because all of these landmasses possess a similar Cretaceous volcanic arc-ophiolite basement.

If AR and LA once comprised a single arc, it can be concluded that, at some time in the past, the GB that now separates these two entities did not exist. However, the age of this basin has not been well constrained. Inconclusive seismic evidence suggests that GB is filled by sedimentary rocks of Paleocene(?) to Recent age (Pinet et al., 1985; Bouysse et al., 1985; Bird, 1991), while

dredge hauls from the basin's margins consist of mostly Eocene and younger sedimentary and volcanoclastic rocks (fig. 21).

According to Pindell (1994), GB opened between the Paleocene and Late Eocene, but we postulate a somewhat younger date (Late Eocene or younger) for the following reasons. If GB is interpreted as a back-arc basin, the disjunction of the AR-LA arc into two independent geological units (Aves Ridge remnant arc and Lesser Antilles active arc) would have probably been caused by a local change in the subduction regime (e.g., alteration of angle of dip of lower slab, or migration of position of subduction zone). We hypothesize that this event was correlated with Late Eocene cessation of volcanic activity in AR (and a concomitantly great increase in activity in LA) and increased thickness of Oligocene and younger sediments in GB (see seismic sections in Nemeč [1980] and Pinet et al. [1985]).

Figure 21 depicts islands and other features of the eastern Caribbean as they appear today, together with simplified late Tertiary stratigraphic columns for AR, GB, and LA. The thickness of Tertiary sediments (Pinet et al., 1985) indicates that AR and LA have been positive for most of the Cenozoic. Positive topography is also indicated by the occurrence of shallow-water limestones of Eocene to Lower Miocene age dredged from ridge walls of these features. In addition, Early Oligocene slope deposits have been recovered from cores from Saba Well (Nemeč, 1980); their compositional character suggests that they were derived from some nearby area (presumably AR) that had been block-faulted and significantly uplifted (Pinet et al. 1985).

Calculations by Holcombe and Edgar (1990) establish that, given certain assumptions, before the Miocene most of the topographic highs on AR may have been subaerial, or nearly so, and would have formed a string of emergent lands along a north-south axis. This inference is corroborated by the frequent occurrence of conglomerates in samples dredged from the Ridge (Nagle 1972; Bouysse et al., 1985). These poorly sorted conglomerates contain rounded pebbles and cobbles of andesite, up to 10 cm long and showing altered (weathered?) cortices in a calcareous-tuffaceous matrix. The matrix has yielded large benthic forams and algae, which Bock (1972) identified as Oligocene, Early Miocene, or older (Nagle, 1972).

The existence of these conglomerates strongly implies the existence of subaerial conditions just before and at the time that they were being formed. Observations on the effects of weathering on granular igneous and sedimentary rocks in the Greater Antilles (so-called "big boulder bed" of Bronnimann and Rigassi [1963]; M. A. Iturralde-

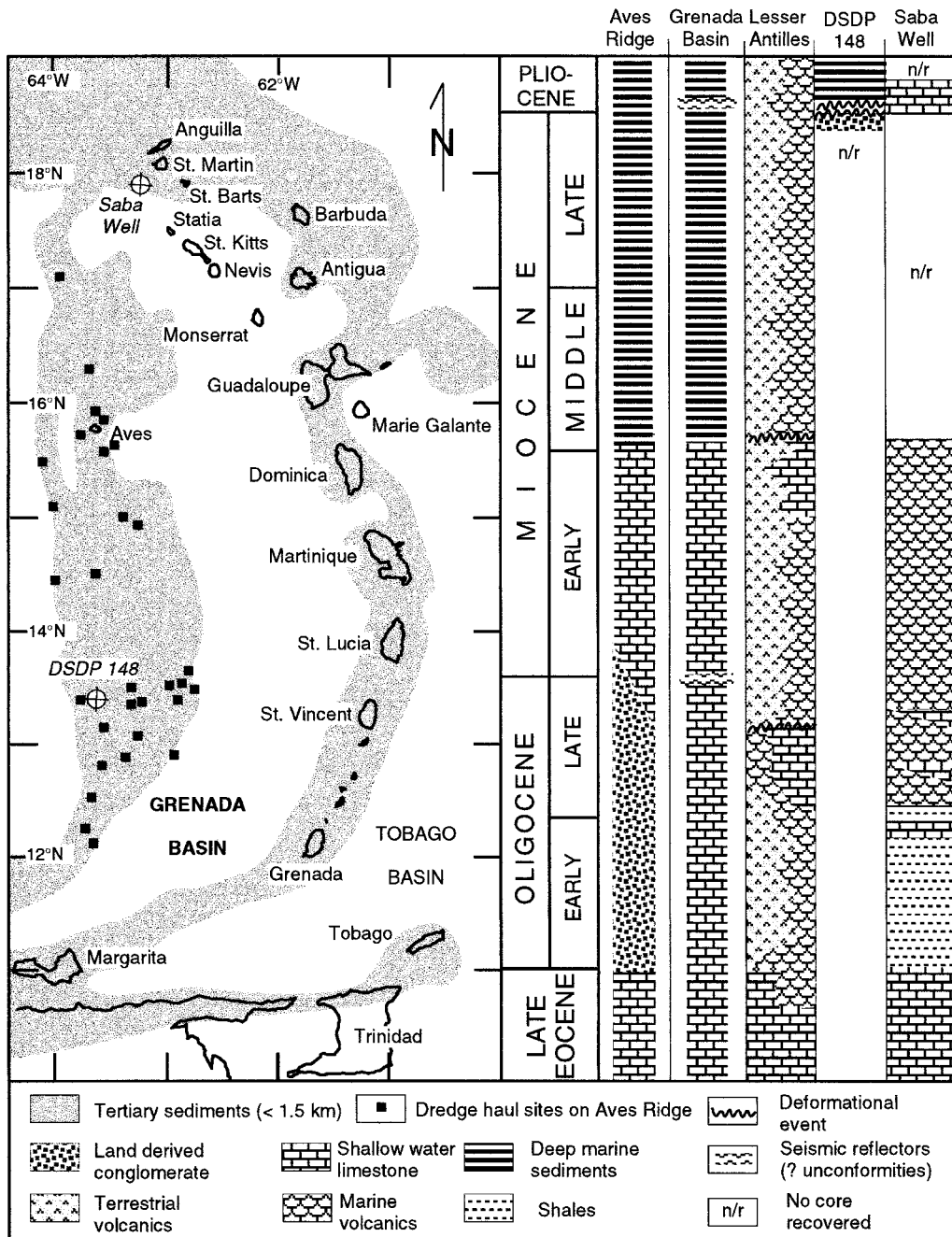


Fig. 21. Aves Ridge, Grenada Basin, and Lesser Antilles: **left**, Present-day topography and thickness of Tertiary sediments; **right**, stratigraphic columns (compiled from many sources; see appendix 1). Aves Ridge and Grenada Basin columns based on combined seismic interpretation and dredge-haul samples. Relative thinness of Paleocene–Oligocene sediments contrasts markedly with thick Miocene–Recent deposits (Holcombe et al., 1990), and is consistent with interpretation that Aves Ridge has been positive for much of the Cenozoic. Existence of terrestrially derived conglomerates establishes that portions of the ridge were subaerial in Oligocene.

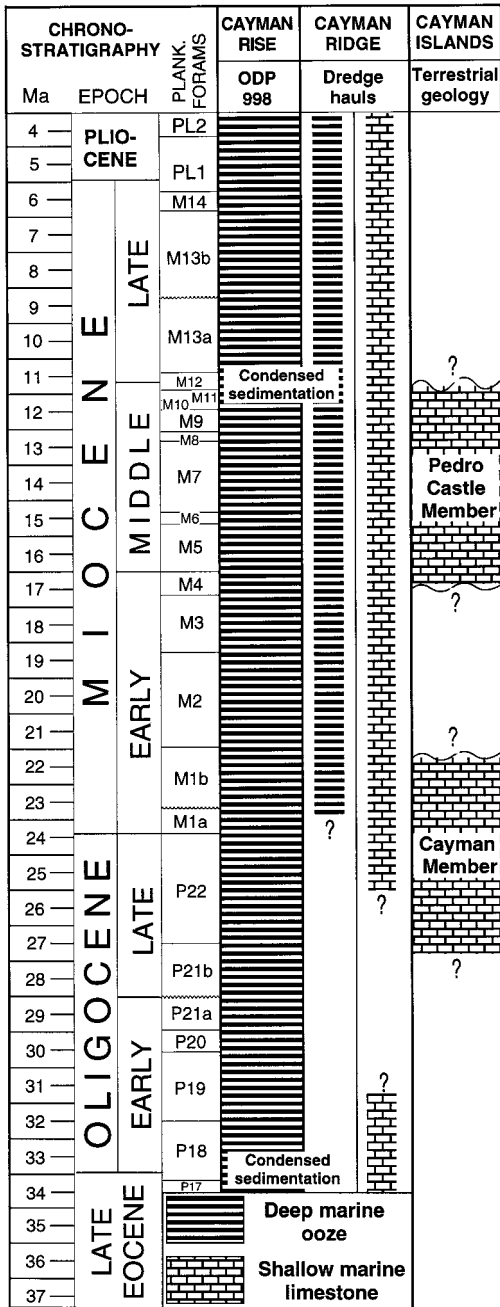


Fig. 22. Cayman Rise, Ridge, and Islands: Late Tertiary stratigraphic columns (compiled from Perfit and Heezen, 1978; Jones, 1994; Sigurdsson et al., 1997). ODP hole 998 drilled on Cayman Rise shows very low sedimentation rates occurred during Eocene–Oligocene transition and late Middle/early Late Miocene. Low rates correlate well with hiatuses and uplift events in Cayman Islands and elsewhere in Caribbean region.

Vinent [unpubl. data] indicate that, under tropical conditions, surface weathering of the cortices of granular rocks causes material to be concentrically lost, eventually resulting in the formation of rounded cobbles. Most rivers in the Greater Antilles are far too short to produce roundedness by abrasion alone, which suggests that conglomerates containing large, rounded cobbles may be diagnostic of highland conditions prevailing at the time of deposition. Incorporation of rounded cobbles into a calcareous matrix is obviously secondary, the result of transport to marine environments. In our view, AR conglomerates are readily correlatable with the Eocene–Oligocene conglomerate event recorded elsewhere in the Greater Antilles and South America (MacPhee and Iturralde-Vinent, 1995).

These facts suggest that AR was a topographic high (Donnelly, 1989b) from the Eocene to the Lower Miocene, and was actually emergent for some indefinite (but probably short) period within the latest Eocene/Early Oligocene, after the termination of arc magmatism and related uplift in the Greater Antilles and Aves Ridge. AR rapidly subsided thereafter, and was already deeply submerged by the Middle Miocene, as indicated by seismic profiles and the occurrence of Middle Miocene and younger deep-water sediments in wells (DSDP 30, hole 148; Edgar et al., 1973) and dredge hauls (Nagle 1972; Bock, 1972; Bouysse et al., 1985).

Structurally, the southern portion of AR–LA is part of the deformed and partly obducted volcanic arc complex that also forms the basement of the Caribbean Mountains and islands along the Aruba/Tobago Belt (González de Juana et al., 1980; Jackson and Robinson, 1994). That the NWSA Microcontinent (Gonzalez de Juana et al., 1980; Balkwill et al., 1995; Parnaud et al., 1995) shares a significant portion of its Cenozoic geological history with the southern AR–LA is also indicated by the fact that they were extensively and coterminously uplifted around the Eocene–Oligocene boundary (35–33 Ma). The possibility that they were physically connected by emergent land during this time is strongly suggested by the absence of marine sediments of this age in northwestern South America, as well as in the Aruba/Tobago Belt and AR–LA arc.

The stratigraphic record of LA (Maury et al., 1990) shows a history of activity in marine as well as subaerial contexts since the Eocene. The presence of late Tertiary marine sedimentary rocks intercalated within volcanic sequences is evidence that the islands have not been permanently uplifted since the Eocene, but have had a complex history involving emergence, subsidence, and migration of topographic highs. In

their present form the majority of them are certainly young (Pliocene to Recent).

Beata Ridge

The geological history of Beata Ridge (BR) has been recently reviewed by Fox et al. (1970), Case (1975), Mascle et al. (1985), Holcombe et al. (1990), and Maurrasse (1990). According to Case (1975) and Holcombe et al. (1990), BR was an undifferentiated part of the Caribbean oceanic crust until the onset of orogenic movements in the Late Cretaceous. Organizationally, BR consists of a set of tectonic blocks (fig. 4, cross section, elevations considerably exaggerated) that have been positive since the end of the Maastrichtian(?). BR was markedly affected by uplift (up to 1000 m) in both Middle Eocene/Oligocene and Middle Miocene time, but there is no direct evidence that it was actually emergent at any stage. In particular, the lack of conglomerates in wells and dredge hauls speaks against the existence of high, dry areas on BR (cf. discussion of Aves Ridge). Hiatuses do occur in the BR section, but none of them shows an unequivocal signature of emergence. For example, the Middle Miocene hiatus observed in cores may be due to an interruption in deposition or to the effects of submarine erosion on BR (Mullins et al., 1987; Iturralde-Vinent et al., 1996a). Beata Island, the only emergent part of the ridge, probably became subaerial in the Quaternary. Therefore, Beata Ridge is of no significance for interpreting the history of land connections in the Caribbean region, as it was evidently never a structural or paleogeographical link between a mainland and the Greater Antilles (Heubeck and Mann, 1991) (figs. 6–8; tables 1–4).

Nevertheless, evidence that BR was subjected

to latest Eocene/Early Oligocene uplift is important, because it establishes that areas composed of thick oceanic crust were affected in the same manner as geological units composed of continental or island-arc crust, underlining the all-embracing character of this event (MacPhee and Iturralde-Vinent, 1995).

Cayman Islands and Cayman Ridge

Because of the small size of outcrops on the Cayman Islands and difficulties in recovering sufficient dredge samples from the walls of the Cayman Trench (CT), information is limited on these units (Perfit and Heezen, 1978). The most recent review of the geology of the Cayman Islands is by Jones (1994); additional topics of interest are covered by Case (1975), Holcombe et al. (1990), and Rosencrantz (1990, 1995).

Stratigraphic columns (fig. 22) indicate that between 35 and 33 Ma the Cayman Ridge was covered by shallow water. Evidence of deeper water environments occurs only in Early Miocene (and later) rocks dredged from the walls of CT, indicating that this is when the trench system began to open (Perfit and Heezen, 1978). On the islands themselves, shallow-water limestones of Oligocene–Miocene and Middle Miocene age have been documented, as has a hiatus within the Early Miocene. These data underline the very recent character of the islands on the Cayman Ridge. However, they do not necessarily preclude the possibility of a recent land connection between the Cayman Islands and eastern Cuba, as both are located along the same structural trend, i.e., the Cayman Ridge (but see point [4] in discussion section under GAARlandia Landspan and Island–Island Vicariance).

APPENDIX 2: A PLATE TECTONIC MODEL OF THE CARIBBEAN FROM LATEST EOCENE TO MIDDLE MIOCENE

Models of the plate tectonic evolution of the Caribbean region tend to agree on the major issues (Malfait and Dinkelmann, 1972; Ross and Scotese, 1988; Pindell and Barrett, 1990; Pindell, 1994), but many details remain uncertain. Most discrepancies among models concern tectonic developments prior to the latest Eocene, although controversy attends several aspects of plate movement in the crucial interval between the end of the Eocene and the Middle Miocene. In order to present new data and interpretations bearing on late Tertiary tectonics, we constructed a tectonic model for the interval 35–14 Ma (see figs. 23–26, table 6). Basic assumptions underlying our reconstruction are presented below and in the caption of figure 23.

1. Crustal plates are deformable

Interactions between plates commonly result in profound deformations of crustal blocks and terranes, not only along plate margins but also within intraplate domains. Typical deformations include crustal shortening and superimposition of units as a consequence of folding and thrust faulting (see figs. 2 and 5) as well as the partial or complete destruction of microplates, blocks, and terranes at subduction zones. These processes operate at all scales, resulting in modification of the size and configuration of individual blocks as well as entire plates. From this it follows that tectonic models that purport to be realistic must take some account of these processes; if not, results will be interpretatively problematic. The recent tectonic model for the Caribbean published by Hay and

TABLE 6
**Computed Finite Poles of Rotation of South America, Caribbean Plate, and Smaller Units
 with Respect to North America, 35 Ma to Recent^a**

	Age	Latitude (°)	Longitude (°)	Angle (°)	Comment
1. <i>South America</i> vs. <i>North America</i>	35	16.3	-53.6	5.92	
	30	15.8	-53.9	5.24	
	25	15.1	-54.1	4.54	
	20	15.6	-53.9	3.93	
	15	13.8	-54.3	2.83	
	10	9.6	-55.3	1.71	
	5	9.0	-54.8	0.85	
	0	0.0	0.0	0.0	Units reach current relative position
2. <i>North America</i> vs. <i>Africa</i>	47.0	75.30	-3.88	15.25	An21 ^b (Mueller et al., 1993)
	33.2	75.37	1.12	10.04	An13 (Mueller et al., 1993)
	19.7	79.57	37.84	5.29	An6 (Klitgord and Schouten, 1986)
	9.8	80.12	50.80	2.52	An5 (Mueller et al., 1993)
	0	0.0	0.0	0.0	Unit reaches current relative position
3. <i>South America</i> vs. <i>Africa</i>	42.5	57.62	-32.07	17.58	An20 (Shaw and Cande, 1990)
	33.1	56.63	-33.91	13.38	An13 (Shaw and Cande, 1990)
	25.8	57.16	-35.34	9.98	An8 (Shaw and Cande, 1990)
	19.0	58.07	-37.42	7.04	An6 (Shaw and Cande, 1990)
	9.7	59.99	-38.89	3.13	An5 (Shaw and Cande, 1990)
	0.0	0.0	0.0	0.0	Unit reaches current relative position
4. <i>Chortis Block/Nicaraguan Rise</i> vs. <i>Maya Block</i>	35	57.15	111.37	4.51	Sinistral motion in the Motagua/Swan fault system
5. <i>Western Cuban Block</i> vs. <i>Maya Block</i>	35	0.0	0.0	0.0	Western Cuban Block N of Pinar fault fixed to Maya Block at latter's present-day position
	0	0.0	0.0	0.0	No further rotation
6. <i>West-Central Cuban Block</i> vs. <i>Maya Block</i>	35	6.68	-72.56	0.86	Between 35 and 25 Ma, Cuban Block slides NE along NE-SW sinistral faults
	25	0.0	0.0	0.0	No important relative motion of blocks
	15	0.0	0.0	0.0	No important relative motion of blocks
7. <i>East-Central Cuban Block</i> vs. <i>Maya Block</i>	35	7.85	-71.10	1.67	Cuban block slides to NE
	15	0.0	0.0	0.0	Low-amplitude sinistral motion along La Trocha fault
	0	0.0	0.0	0.0	Block reaches current relative position
8. <i>Eastern Cuban Block</i> vs. <i>Maya Block</i>	35	6.03	-71.16	2.52	Cuban Block slides NE closer to Bahamas due to movement along Guacanayabo-Nipe sinistral fault
	0	0.0	0.0	0.0	Block reaches current relative position
9. <i>Northern Hispaniolan Block</i> vs. <i>Eastern Cuban Block</i>	35	0.42	-73.38	9.76	Northern and Central Hispaniolan blocks attached to each other
	25	0.42	-73.38	9.76	Sinistral motion begins along Oriente fault, Hispaniolan Block slides E
	15	0.0	0.0	0.0	Northern Hispaniola Block nears current position relative to eastern Cuba
	0	0.0	0.0	0.0	Block reaches current relative position
10. <i>Central Hispaniolan Block</i> vs. <i>Northern Hispaniolan Block</i>	35	19.1	-66.3	-1.28	Hispaniolan blocks fixed between 35 and 15 Ma
	15	19.1	-66.3	-1.28	Northern Hispaniolan Block becomes attached to Bahamas, central Hispaniolan Block slides E
	0	0.0	0.0	0.0	Unit reaches current relative position

TABLE 6
(Continued)

	Age	Latitude (°)	Longitude (°)	Angle (°)	Comment
11. <i>Puerto Rico/Virgin Islands Block vs. Central Hispaniolan Block</i>	35	19.05	-67.94	-43.38	Puerto Rico/Virgin Islands Block fixed to Central Hispaniolan Block
	15	19.05	-67.94	-43.38	Puerto Rico/Virgin Islands Block starts rotation
	0	0.0	0.0	0.0	Unit reaches current relative position
12. <i>Chortis/Nicaraguan Rise/southern Hispaniola vs. Central Hispaniolan Block</i>	35	23.20	-72.20	-9.38	Southern Hispaniolan Block slides NE
	15	0.0	0.0	0.0	Southern Hispaniola collides with and is affixed to Central Hispaniolan Block
	0	0.0	0.0	0.0	Unit reaches current relative position
13. <i>Southern Central America vs. Chortis Block</i>	35	52.90	-124.5	-7.03	Southern Central America located SW of Chortis
	15	52.90	-124.5	-3.73	Southern Central America slides NE due to sinistral movement of Hess Escarpment fault
	0	0.0	0.0	0.0	Unit reaches current relative position
14. <i>Southern Nicaraguan Rise vs. Chortis Block</i>	35	30.00	-95.00	-0.39	Hess Escarpment fault active, associated with alkali volcanism in southern Nicaraguan Rise; general extension in Chortis Block and Nicaraguan Rise
	0	0.0	0.0	0.0	Units reach current relative position
15. <i>Aves Ridge vs. South America</i>	35	5.61	-66.67	22.55	Aves Ridge/Lesser Antilles Arc line up with Caribbean Mountains
	0	0.0	0.0	0.0	Units reach current relative position
16. <i>Lesser Antilles Arc vs. Aves Ridge</i>	35	19.83	-64.79	-4.51	Uneven extension at northern end of Grenada Backarc Basin
	0	0.0	0.0	0.0	Grenada Basin achieves current width
17. <i>Southern part of Lesser Antilles Arc vs. northern part of Lesser Antilles Arc</i>	35	12.05	-61.70	27.96	Lesser Antilles Arc exhibits little curvature
	5	12.05	-61.70	27.96	Lesser Antilles Arc deformed, increases curvature (5-0 Ma)
	0	0.0	0.0	0.0	Lesser Antilles achieve current configuration
18. <i>Tobago Block vs. South America</i>	35	26.80	118.09	-7.60	Tobago Block slides E, ahead of Lesser Antilles Arc
	0	0.0	0.0	0.0	Units reach current relative position
19. <i>Beata Ridge Block vs. Hess Escarpment</i>	35	28.4	-128.1	-3.41	Beata Ridge Block is part of Caribbean ocean crust
	15	28.4	-128.1	-3.41	Ridge starts to slide NE toward Hispaniola
	0	0.0	0.0	0.0	Units reach current relative position
20. <i>NWSA Microplate vs. South America</i>	35	1.5	117.8	-9.50	NWSA Microplate slides NE as South America rotates counterclockwise
	0	0.0	0.0	0.0	Units reach current relative position

^a Column on far left lists geological units (in italics) whose positions are being compared to other such units (e.g., in first entry, position of *South America* is being compared to that of North America). Central columns: **Age**, position at specific time, in millions of years; **Latitude** and **Longitude**, geographical coordinates of pole of rotation; **Angle**, rotation as calculated by the program PLATES. North America includes Maya and Bahama Blocks. The position of South America relative to North America is derived from poles of rotation for South America vs. Africa and North America vs. Africa.

^b Magnetic anomaly number.

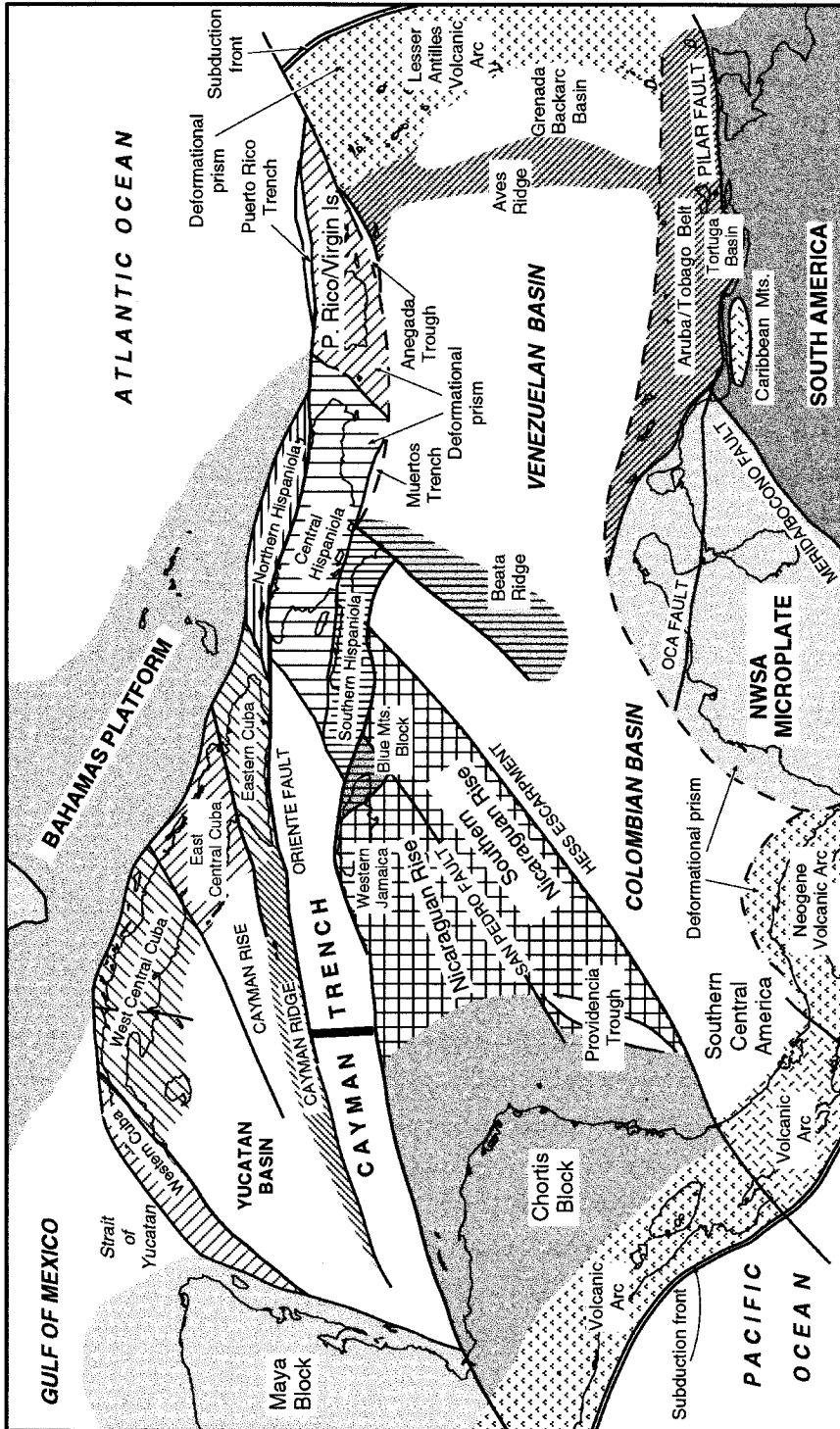


Fig. 23. Caribbean tectonic framework: Current positions of geological units active from latest Eocene to Late Miocene. Units have been palinspastically restored to Late Eocene (~35 Ma) paleopositions using the following four constraints: (1) Cayman Trench system movements sequentially absorbed by Guacanayabo-Nipe and Oriente sinistral faults and local underthrusting within Hispaniola (Mann et al., 1995); (2) Jamaica acts as two distinct terranes, Western Jamaica (originally associated with Nicaraguan Rise) and Blue Mountains (part of Caribbean crust, but structurally related to Eastern Cuban and Southern Hispaniolan Blocks); (3) southern Central America originates southwest of Chortis Block, accounting for sinistral movements associated with alkaline vulcanism along Hess escarpment; and (4) NWSA Microplate acts as part of Caribbean plate for most of late Tertiary, due to activity along Mérida-Boconó dextral fault.

Wold (1996) may be cited as an example of the latter. In their model, tectonic blocks and terranes move, but they do not deform, even after the elapse of many millions of years (Hay and Wold, 1996: figs. 2–7). The resulting lack of realism is evident in the evolution of Hispaniola (our Central and Northern Hispaniolan Blocks, fig. 23). Hispaniola is depicted by these authors as suffering no deformations or alterations from the late Mesozoic onward; to fit within the space available per time slice, it has to be sequentially moved from a position within the Pacific realm (150–130 Ma) to the margin of the Chortis Block (100 Ma), thence to the margin of the Maya Block (67.5 Ma), thence south of western Cuba (58.5 Ma), thence south of eastern Cuba (49.5 Ma), finally ending up east of Cuba at 24.7 Ma (Hay and Wold, 1996: figs. 2–7). Further contortions are introduced by unconstrained rotation of the terrane along its major axis from N–S at 130 Ma to ENE–WSW at 49.5 Ma. These proposed lateral displacements and rotations find no support in the geological composition or structure of central and northern Hispaniola (in addition to main text, see figs. 3 and 5 and appendix 1; Draper, 1989; Mann et al., 1991).

2. Global phases of orogeny have had important implications for Caribbean plate evolution

Many different bouts of orogeny, from regional to global, have affected the Caribbean region and surrounding areas during the past 170 Ma. The most significant of these took place in the late Aptian (120–110 Ma), late Campanian–early Maastrichtian (75–70 Ma), and Middle Eocene (45–40 Ma) and had worldwide effects. In the Caribbean, these effects included (1) modification of the rates of plate movement, (2) rotation of major stress axes, (3) modification of the orientation and extension of volcanic arcs, (4) alteration of arc magmatic geochemistry, and (5) consolidation of foldbelts (fig. 5; Schwan, 1980; Mattson, 1984; Pszczolkowski and Flores, 1986; Iturralde-Vinent, 1994c; Iturralde-Vinent et al., 1996b; Bralower and Iturralde-Vinent, 1997). The orogeny which occurred in the Middle Eocene is especially noteworthy. Correlated with this orogeny were (1) reduction in the relative motion of the North and South American plates (Pindell, 1994: fig. 2.3), (2) reorientation of the Caribbean Plate stress field from mainly NE–SW to dominantly E–W, and (3) formation of numerous microplates, blocks, and terranes along plate margins (Case et al., 1984). Many of the critical geological units discussed in this paper (e.g., various Cuban blocks) were formed after this event, as were many major fault-bounded structures such as the Windward and Mona grabens, Cayman Trench, and the Provi-

dencia and Muertos Troughs. In the Greater Antilles, the Middle Eocene orogeny was associated with cessation of magmatic activity and uplift of volcanic structures formed in the Paleocene though early Middle Eocene. As magmatism ended in the Greater Antilles, it also terminated on the Cayman and Aves Ridges, thereafter shifting permanently to the Lesser Antilles arc (cf. figs. 5 and 6). This orogeny additionally led to deactivation of the Yucatan Basin spreading center and the shifting of ocean crust production to the Cayman center (Rosencrantz, 1990). Due to subsequent movements, crustal segments that were originally part of the foldbelt created by this event are now distributed in a broad circum-Caribbean swath, involving southern Mexico, Greater Antilles, Aves Ridge, Aruba/Tobago Belt, Caribbean Mountains, Columbian/Venezuelan Andes, and Central America (fig. 23).

3. Island arc magmatic activity on the Caribbean plate occurred in discrete stages and was not a continuous process

The most important magmatic events in the history of the Caribbean area were (1) continental margin magmatism (170–110 Ma) in association with the break up of Pangaea (Maze, 1984; Bartok, 1993; Iturralde-Vinent, 1994a), (2) oceanic magmatism (170–110 Ma) related to the formation of the proto-Caribbean oceanic crust between North and South America (Pindell, 1994), (3) eruption of alkaline volcanoes related to intraplate tectonic activity along major faults (Dengo and Case, 1990), and (4) the evolution of the volcanic arcs.

With respect to the last of these phenomena, arc magmatic activity on the Caribbean plate, several discrete stages are evident: (1) ?Neocomian to Aptian (120–110 Ma), (2) Albian to Coniacian–Santonian (100–87 Ma), (3) Santonian to ?early Maastrichtian (87–70 Ma), (4) mid-Paleocene to early Middle Eocene (60–55 Ma), and (5) latest Eocene to Recent (37–0 Ma). Each of these regionally discrete magmatic stages exhibited a specific geological signature marked by structural unconformities due to tectonic deformation and uplift, hiatus formation related to erosion and non-deposition, and deposition of coarse clastic and carbonate sedimentary rocks (see Paleogeography of the Caribbean Region: Evidence and Analysis, Early Middle Jurassic to Late Eocene Paleogeography). This conception of periodic arc magmatism, punctuated by nonvolcanic intervals, contradicts the widely held view originally formulated by Malfait and Dinkelmann (1972), who envisaged a single “Great Arc” continuously developing on the leading edge of the Caribbean plate from the Jurassic onward (see also Burke et

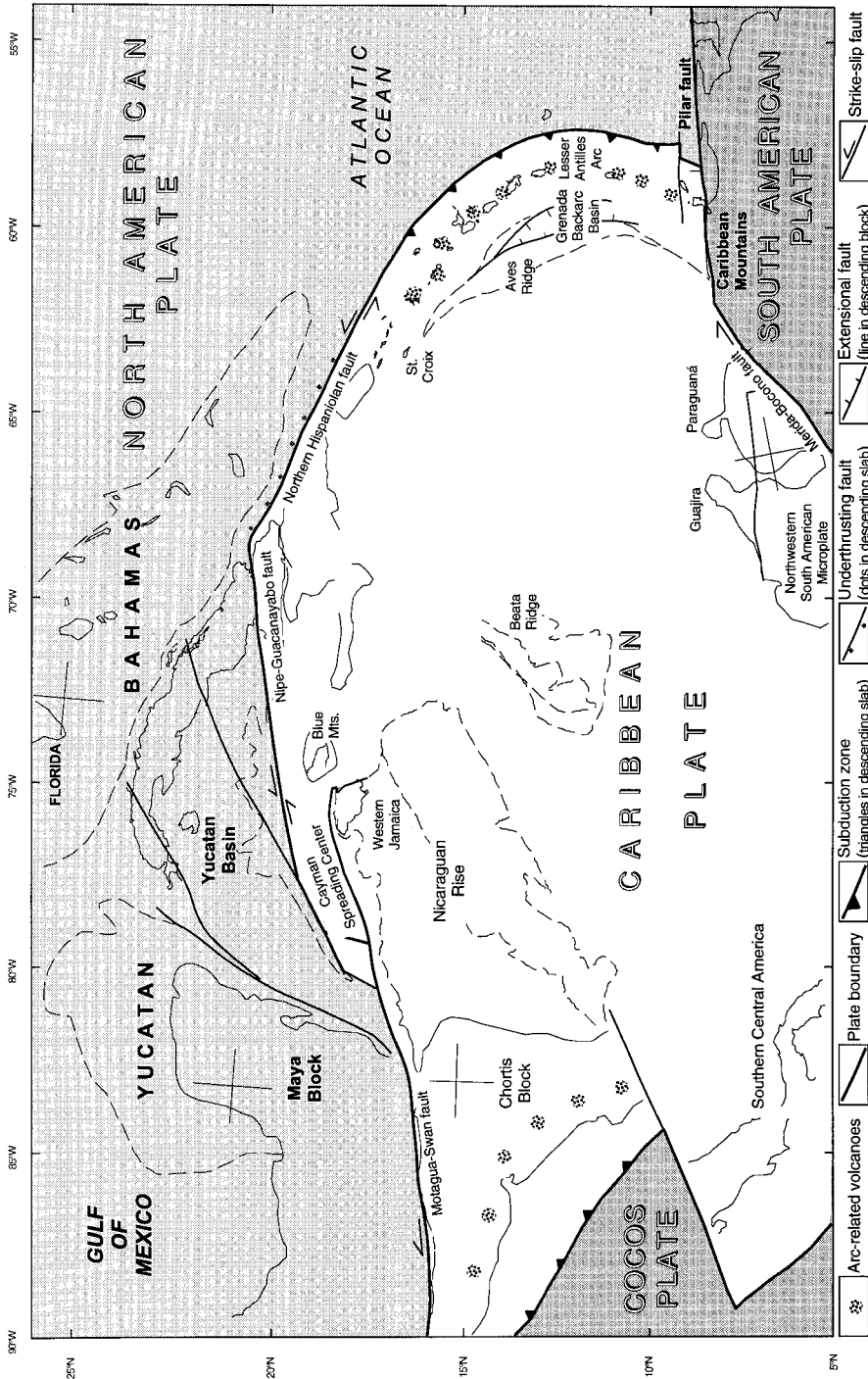


Fig. 24. Plate tectonic reconstruction, Caribbean Region, Eocene-Oligocene transition (35–33 Ma). Figures 24–26 were generated using the program PLATES (Institute for Geophysics, University of Texas at Austin), in which consequences of specific displacements can be investigated over a set interval (here, 35–14 Ma) relative to a fixed master reference unit (here, North American plate; see table 6). Present-day coastlines are used for orientation but do not represent paleogeographical reality. Some structural elements subdivided into smaller units to preserve tectonic accuracy. Contact between North American plate (NOAM) and Caribbean plate (CARIB) occurs along Motagua/Swan/Nipe–Guacanayabo/northern Hispaniolan transform faults, and between Caribbean plate and South American plate (SOAM) along Mérida-Boconó transform fault trend.

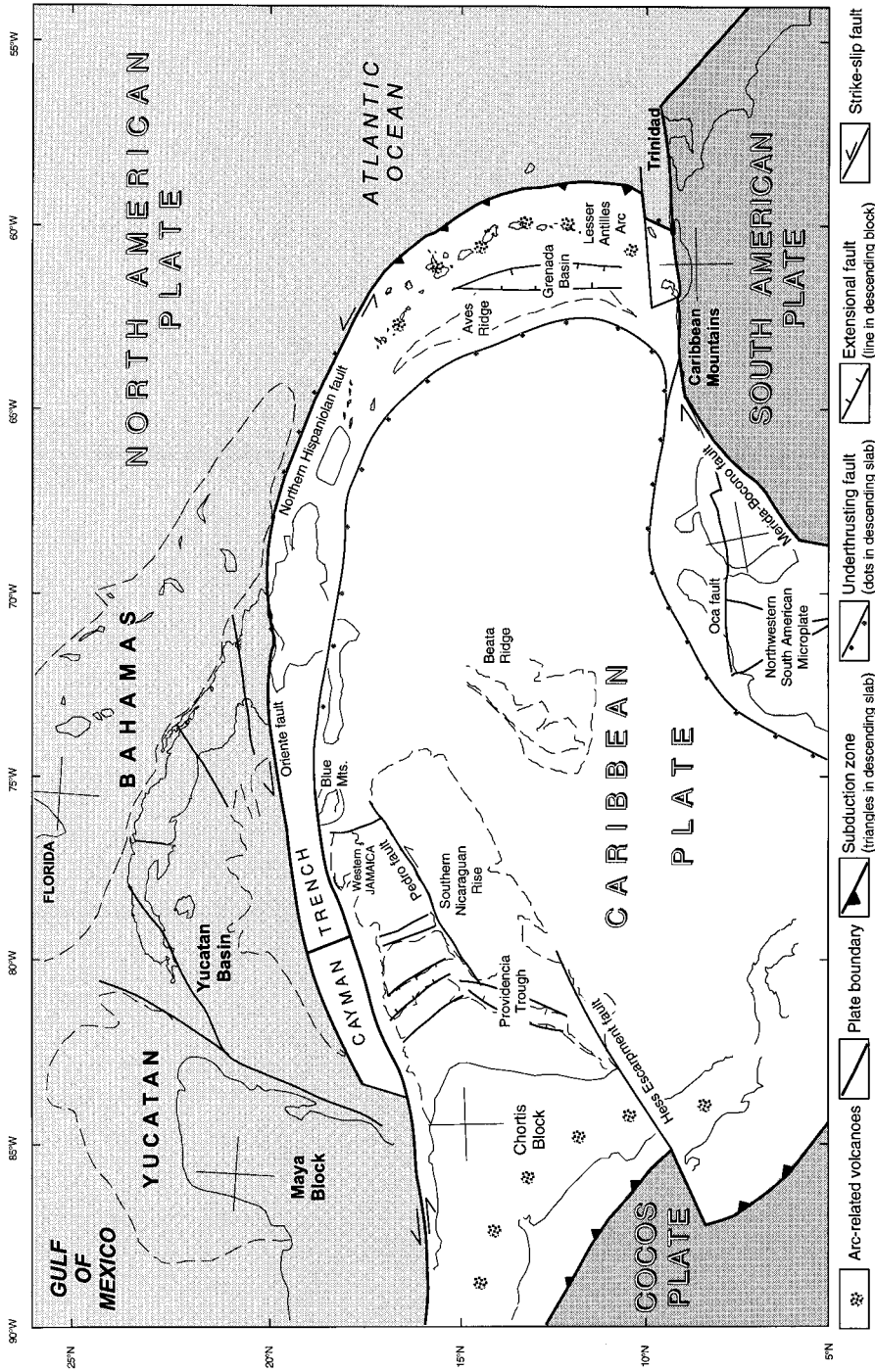


Fig. 25. Plate tectonic reconstruction, Caribbean region, Late Oligocene (27–25 Ma). For abbreviations and other details, see figure 24. In this stage, Cayman Ridge and Eastern Cuban Block became attached to NOAM, and contact with CARIB in eastern Cuba jumped to the Oriente transform fault. CARIB–SOAM contact continued to lie along the trend of Mérida-Boconó transform faults, but Oca–Pilar fault trend became active in association with alkaline volcanic activity. Active plate convergence continued in Lesser Antilles and Pacific Ocean margin of Central America. Hess Escarpment fault trend was active in association with alkaline volcanoes. Strong deformation and accretion took place along plate margins in eastern Caribbean.

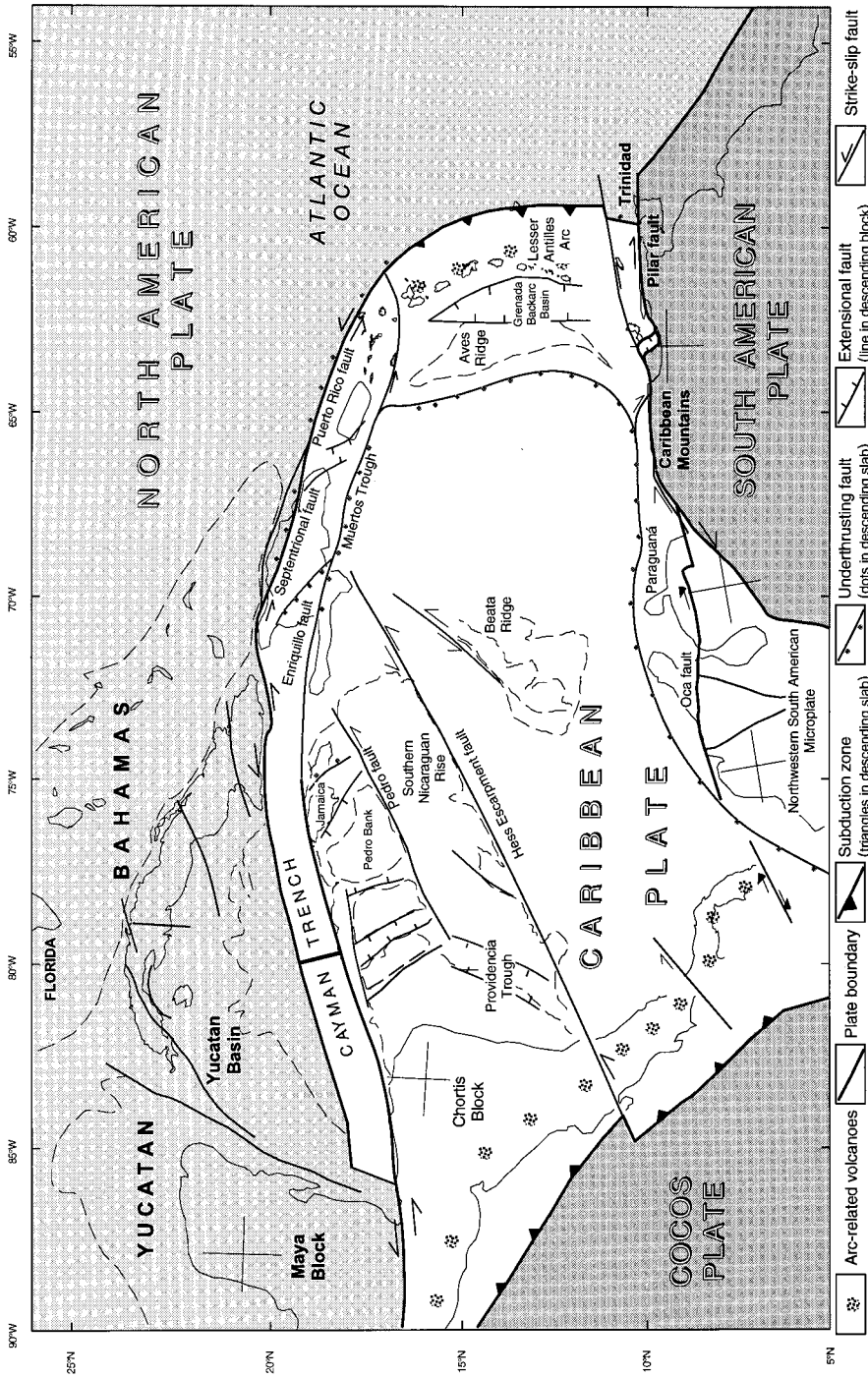


Fig. 26. Plate tectonic reconstruction, Caribbean Region, Middle Miocene (16–14 Ma). For abbreviations, see figure 24. In this reconstruction, Northern Hispaniola Block is now attached to NOAM, and contact with CARIB has jumped to Septentrional fault in Hispaniola. CARIB–SOAM contact is located as before, but Oca–Pilar fault trend was highly active in this period. Active plate convergence continued along Lesser Antilles and Pacific Ocean margin of Central America, with extension of volcanic activity into Panama area. Pedro and Hess Escarpment faults trends were active, producing extension along trend of Chortis/Nicaraguan Rise (for sites of Oligo-Miocene volcanic activity, see fig. 15). At the same time, strong deformation and sediment accretion along underthrusting fronts continued at plate border in eastern Caribbean.

al., 1984; Pindell, 1994). Recent supporters of the continuous-development model include Mann et al. (1995: fig. 36A–C), who argued that the convergent front of the Caribbean Plate was active with subduction deepening to the south from Maastrichtian until Middle Eocene times. However, no magmatic activity subsequent to the late Campanian is recorded in western and central Cuba (Iturralde-Vinent, 1994a), Aruba/Tobago Belt (Hunter, 1978; Jackson and Robinson, 1994), or the Caribbean Mountains (Bonini et al., 1984; Macellari, 1995). Additionally, volcanic arc rocks of mid-Paleocene to early Middle Eocene age in eastern Cuba are structurally unconformable to pre-Maastrichtian Cretaceous arc rocks (fig. 5). The subduction zone of this arc was located to the south and deepened to the north, rather than vice versa (fig. 5; Iturralde-Vinent, 1994a, 1996d; Sigurdsson et al., 1997).

4. Stress fields have rotated eastward within the Caribbean region

Stress-field rotation during the formation and evolution of the Caribbean was first proposed by Iturralde-Vinent (1975). This phenomenon is evident in the present-day N–S orientation of the convergence front (island-arc subduction zone) of the Lesser Antillean and Central American arcs, and in the extension of arc magmatism southward in Central America during the last 25 Ma. It is also evident in the location of post-Eocene transform faults and associated deformations along the northern and southern margins of the Caribbean Plate, and in the sequential shifting of plate

boundaries along major faults (in the north, from Nipe–Guacanayabo to Oriente to Septentrional; in the south, from the Mérida/Boconó suture toward the Oca–Pilar fault; fig. 23–26 and appendix 1).

Migration of volcanic activity and the other phenomena noted above have been interpreted as a consequence of the oblique collision and resulting “escape to the east” (or “escape to the ocean”) of the Caribbean plate as its leading edge progressively collided with the Bahamas platform (e.g., Mann et al., 1995). However, Bralower and Iturralde-Vinent (1997) have rejected this interpretation as it concerns Cuba, on the ground that the Cuba–Bahamas collision is conventionally dated to Early Eocene but arc extinction actually occurred much earlier (15 Ma previously, in the Late Cretaceous; see also Iturralde-Vinent, 1994a, 1994c). Earlier extinction of the Cretaceous arc is also seen in the Caribbean Mountains (Bonini et al., 1984; Macellari, 1995; Beccaluva et al., 1996) and the Aruba/Tobago belt (Jackson and Robinson, 1994), indicating that the Cuban case is not anomalous (fig. 5).

The mechanism of stress-field rotation is not understood. Speculatively, it might be assumed that the phenomenon is driven by the same process that also affects the movement of tectonic plates. From this perspective, tectonic events recorded in the lithosphere may be thought of as a consequence of interactions between individual plates as they accommodate reorientations (rotations) of the deep-seated source (mantle-core) of the stress field.