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Evolution

Earliest evolution associated with closure of the Tropical American Seaway

(Caribbean/diversity/speciation/corals/foraminifera)

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ABSTRACT **Oceanographic changes caused by the emerging Central American isthmus, which completely severed connections between the Caribbean Sea and tropical Pacific Ocean about 3.5 million years ago, began to stimulate evolution of Caribbean reef corals and benthic foraminifera in the Late Miocene. At that time, first appearances of benthic foraminifera increased, especially those species strongly associated with carbonate-rich substrata; reef corals diversified dramatically; and the carbonate content of southern Caribbean deep-sea sediments increased. We suggest that the changes in marine environments caused by the constricting seaway and resulting in increasing carbonate content of sediments induced accelerated origination in reef corals and carbonate-associated benthic foraminifera.**

When did closure of the Tropical American Seaway (Fig. 1), which connected the Caribbean Sea and eastern Pacific Ocean until ≈3.5 million years ago (Ma) (1, 2), begin to affect the evolution of marine invertebrates? In this paper, we present new paleobiotic surveys of collections of Late Paleogene to Recent benthic foraminifera and reef corals of the Caribbean region that indicate accelerated evolution and diversification in Late Miocene time. We also examine ecologic trends in originating species of benthic foraminifera to infer environmental changes for shallow Caribbean waters.

Several previous studies indicate that evolutionary divergence between Caribbean and eastern Pacific faunas occurred by Early Pliocene time, before the middle Pliocene closure of the Tropical American Seaway. Substantial evolutionary change is known to have occurred in Caribbean mollusks (6) by the Early Pliocene, but the lack of older, precisely dated molluscan collections has prevented determination of the initiation of this change. Similarly, divergence between Caribbean and Pacific species of the *Strombina* gastropod group caused by seaway closure also occurred by Early Pliocene time (7, 8). The mollusk patterns are in accord with evidence that indicates changes in Late Miocene southern Caribbean oceanic conditions due to advanced seaway constriction (9–12) that caused weakening of westward circulation and increasing carbonate deposition (13). However, these paleoceanographic patterns contrast with evidence for an open, unrestricted surface-water connection (2, 9) that would have allowed free mixing of Caribbean and eastern Pacific shallow waters at that time.

To investigate the earlier, pre-Pliocene record of evolutionary change in the Caribbean region, we compiled Late Paleogene to Recent Caribbean-wide occurrences of benthic foraminifera and reef corals, both of which are sensitive environmental indicators (14, 15). Benthic foraminifera are abundant, diverse, shell-bearing protists that have species distributions strongly controlled by water and sediment conditions (14). Reef corals are usually restricted to shallow (commonly <50 m deep) tropical waters with limited sediment, freshwater, and nutrient influx (15).

The benthic foraminiferal data set consists of first and last occurrences in the Caribbean region of species common to Neogene sediments of southern Central America (1, 16, 17), where Caribbean and Pacific waters were last connected. Fig. 2 shows that the largest increase in originations in the last 40 m.y. started ≈6 Ma and lasted until ≈3.5 Ma. Table 1 lists first Caribbean occurrences of the species, 69% of which are comparably dated in the Caribbean region outside of southern Central America. Few originations subsequent to 3.5 Ma were recorded, despite our extensive sampling of the 3.6–1.6 Ma interval (1).

Caribbean reef corals also show accelerated evolution in Late Miocene time. New geologic range compilations of genera and species indicate increased Late Miocene diversity due to increased origination (19) (Fig. 3). Because both generic and species richness increased, accelerated evolution was broadly based across taxa. Diversification was greatest in free-living corals commonly associated with seagrass flats and in foliaceous agariciid corals common on the deeper forereef (19).

These Late Miocene evolutionary trends were concurrent with oceanographic changes caused by the closing seaway (9–12), including a progressive increase to present levels in the carbonate content of southern Caribbean deep-sea sediments 7.5–3.8 Ma (20, 21). Because continental shelves bypass a large proportion of sediment to deeper accumulation sites (22), deep-sea sediments can track shallower trends. Based on depositional rates determined from deep-sea cores, a weakening of strong, westward circulation in the Middle to Late Miocene eastern Caribbean and later Miocene to Early Pliocene southwestern Caribbean has been attributed to increasing seaway constriction (10, 11). Carbonate dissolution in deep-sea cores was insignificant (20), so carbonate content increased in response to decreasing input of noncarbonate material (perhaps from changing current patterns due to seaway closure) and/or increased biogenic carbonate production (11, 20, 21). The Miocene record of southern Caribbean shallow waters is poorly known, but diverse carbonate foraminiferal facies, largely absent in Late Miocene deposits such as the Gatun Formation, Panama (16, 23), characterize Early Pliocene sediments of southern Central America to South America (17, 24, 25).

We examined the correspondence between evolutionary patterns and increasing carbonate content by looking for this ecologic trend in neritic (approximately <200 m deep) species of common Caribbean benthic foraminifera of southern Central America that originated between 15 and 1.6 Ma. Deeper water taxa were excluded because Pliocene sediments from deeper, bathyal waters were inadequately sampled (1, 16). Neritic species were classified by their preferred habitats (14) as primarily associated with shoal to reef carbonate sediments, or siliciclastically associated to generalistic (i.e., abundant in

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Abbreviation: Ma, millions of years ago.

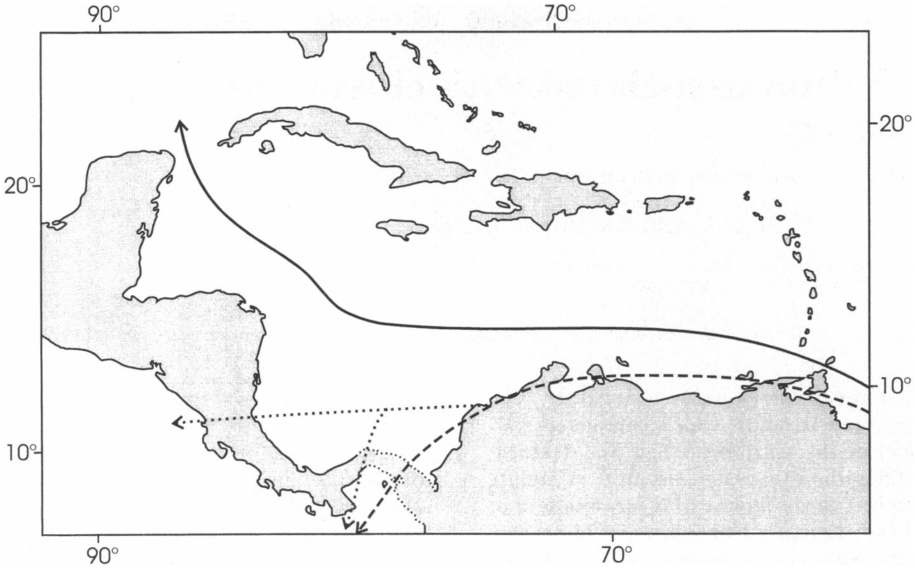

FIG. 1. Past and present surface circulation in the Caribbean region. Solid arrow, present Caribbean current; dashed arrow, main Late Miocene current; dotted arrows, probable Late Miocene straits (3). Eastern Panama Isthmus (dotted outline) was probably the last main Caribbean–eastern Pacific connection, since North American, late Arikareean age (4) land mammals had migrated as far south as central Panama by ≈20 Ma (5).

both carbonates and siliciclastics). The ecologic distribution of neritic species first appearing 3.5–6 Ma (Fig. 2, *Inset*) shows proportionately few carbonate-associated taxa first appearing 15–7.1 Ma, relatively more originating 7.1–5.3 Ma (44%), and a majority (86%) first occurring 5.3–3.5 Ma. A χ^2 test of homogeneity yields a reasonable probability ($P < 0.100$) that proportions of carbonate-associated species are significantly different between these three intervals. This suggests that an increasing proportion of carbonate-associated species originated in the southern Caribbean Sea starting in Late Miocene time.

A Late Miocene expansion of carbonate-rich areas in the Caribbean may have been caused by decreased coastal upwelling and the cutoff of Pacific waters due to advanced seaway constriction. Weakening southern Caribbean flow (10, 11) probably resulted in less coastal upwelling (26), which would be expected to reduce nutrients, productivity, and turbidity in neritic waters. Reef corals, which are primary producers of carbonate sediments (27), thrive in clear, oligotrophic waters. Both decreased upwelling and the cutoff of inflowing colder, Pacific waters would have increased shallow-water tempera-

Table 1. Benthic foraminifera with regional first occurrences 6–3.5 Ma

Species	Regional fossil occurrences other than SCA* samples	Other first occurrences with dates overlapping SCA* dates
Bigenerina irregularis	×	Gurabo Fm., Dominican Republic
Biloculinella eburnea		
Bulimina aculeata	×	Buff Bay deposits, Jamaica
Bulimina marginata	×	Gurabo Fm., Dominican Republic
Cassidulina minuta	×	
Cassidulina norcrossi australis	×	U. Trinchera Fm., Dominican Republic
Cymbaloporetta atlantica	×	Gurabo Fm., Dominican Republic
Eponides turgidus		
Fursenkoina complanata	×	Buff Bay deposits, Jamaica
Lagena ornata	×	Choctawhatchee (*Arca* zn.), Florida
Miliolinella californica		
Neoconorbina parkerae	×	
Nodobaculariella cassis	×	
Pararotalia magdalenensis	×	Jama Fm., Ecuador
Planulina foveolata	×	Buff Bay deposits, Jamaica
Quinqueloculina compta	×	Tubara Fm., Colombia
Rosalina floridana	×	Choctawhatchee (*Arca* zn.), Florida
Rotalia garveyensis	×	Encanto deposits, Mexico
Rotorbinella umbonata	×	
Seabrookia earlandii	×	Marga de Las Hernández, Venezuela
Sorites marginalis	×	Cercado Fm., Dominican Republic
Spiroplectammina floridana	×	Choctawhatchee (*Ecphora* zn.), Florida
Stetsonia minuta	×	
Textularia foliacea occidentalis	×	Choctawhatchee (*Cancellaria*. zn.), Florida
Textularia panamensis	×	Pozón Fm., Venezuela
Textularia schencki	×	Trinchera Fm. (?), Dominican Republic

*SCA, southern Central America = Panama and Costa Rica samples (1).

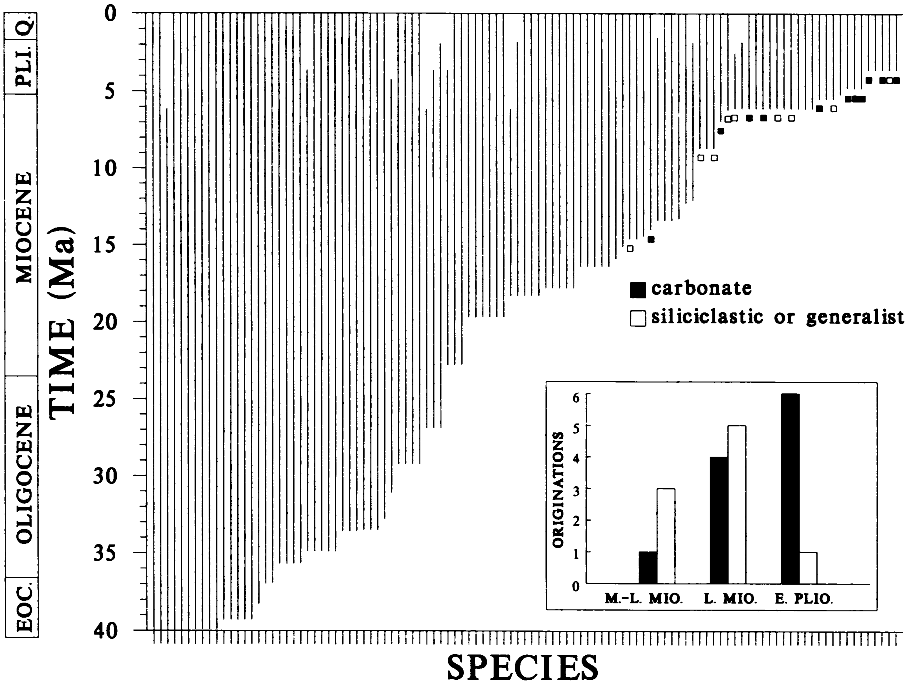

FIG. 2. Caribbean time ranges (vertical lines) of 107 benthic foraminiferal species common to 10 to 1.7 million-year-old, upper bathyal to neritic ($<$300-m water depth) sediments of southern Central America (1). Taxa included have $>$1% abundance in $>$1 of 83 sediment samples prepared using methods of Collins (16). Panama formations are Cayo Agua, Escudo de Veraguas, Shark Hole Point, Nancy Point, and Gatun. Costa Rica formations are Rio Banano, Moin, and uppermost Uscari [= post-Uscari beds (1)]. The six ranges at far left start before 40 Ma. This compilation primarily records originations; no extinctions could occur before $\approx$10 Ma (species used are those common in sediments $<$10 m.y. old), and $\approx$90% of species are extant. Taxonomic names were standardized with major Caribbean-Gulf of Mexico collections. Many (76%) of oldest and youngest specimens were examined; for the others, figures were sufficiently diagnostic. Range lines use midpoints of latest published biochronologic ages for stratigraphic units. To supplement the Caribbean data set, which is biased toward older and deeper or younger and shallower deposits, collections from older, shallower Gulf Coast strata between Florida and Mexico were included. Gulf Coast collections are mostly pre-Late Miocene, when latitudinal oceanographic gradients were less steep (18), the Antilles less emergent, and Caribbean-Gulf of Mexico faunal mixing presumably greater than present high levels. Ranges of neritic taxa originating 15–0 Ma are marked with squares and categorized as primarily carbonate-associated, or siliciclastic-associated, to generalistic. (*Inset*) Facies associations of originating neritic taxa summed for Middle to Late Miocene, 15–7 Ma; Late Miocene microfossil zone N17, 7.1–5.3 Ma; and Early Pliocene, 5.3–3.4 Ma. Late Pliocene and Quaternary intervals lack first occurrences and are excluded. Note increasing proportions of carbonate-associated taxa.

tures (13). Warmer temperatures promote growth of corals and other calcareous organisms and generally correlate with greater nearshore carbonate abundance (28). A general circulation model (29) shows less Caribbean heat flux with an unconstricted isthmus, possibly due to a cooler Caribbean, and further suggests that seaway constriction caused oceanographic changes as early as 7 Ma. Decreasing surface-water δ^{18}O values in the southwestern Caribbean occurred between 8 and 5 Ma, which contrasts with increasing eastern Pacific values (2) and agrees with the hypothesis of increasing Caribbean temperatures.

Taken together, the diversification of reef corals and the disproportionate increase in originations of carbonate-associated benthic foraminiferal species indicate a Late Miocene expansion of Caribbean carbonate-related taxa that may correspond to increasing carbonate deposition. We speculate that corals diversified and expanded their ecologic distribution because marine conditions became more favorable for coral reef growth. Increased coral reef distribution may have resulted in greater carbonate production by corals, which is quantitatively significant on a global scale (26). An increase in carbonate substrata, in turn, may have induced the origination of carbonate-associated organisms such as benthic foraminifera by creating more habitat space for diversification.

Regardless of cause, the paleontologic record of Caribbean corals and benthic foraminifera demonstrates that great evolutionary changes in the marine invertebrate fauna occurred in Late Miocene time, 3–5 m.y. before middle Pliocene closure of the Tropical American Seaway (2). This early diversification established the modern Caribbean benthic foraminiferal fauna and a basic Caribbean coral fauna, parts of which subsequently experienced extinction and origination (6, 19) possibly asso-

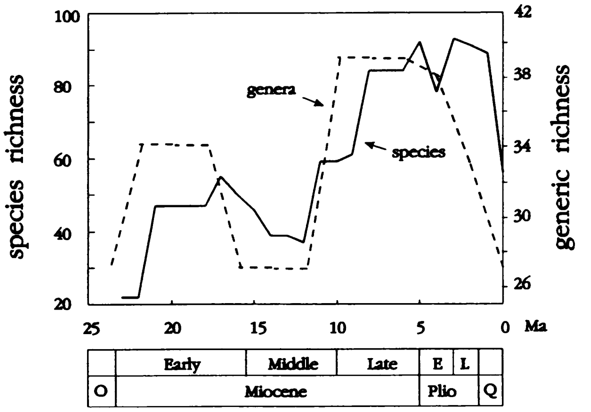

FIG. 3. Diversification of species and genera of Caribbean reef corals (15), derived through analysis of 175 Early Miocene to Recent species. The compilation is based on occurrences in (*i*) Neogene sequences in the Dominican Republic and Costa Rica, (*ii*) Late Miocene to Recent Bahamas platform cores, (*iii*) faunal lists for 21 fossil sites scattered across the Caribbean region, and (*iv*) a list of Recent taxa along the north coast of Jamaica. Richness (numbers of taxa present within an interval) is calculated using an interval duration of 1 m.y. for species and 2 m.y. for genera. Points are plotted at the young end of each interval. Origination and extinction are per taxon rates, weighted relative to locality duration and standardized to standing diversity within intervals. Note Late Miocene rise in richness.

ciated with complete seaway closure and northern hemisphere glaciation.

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