Diversity and Extinction of Tropical American Mollusks and Emergence of the Isthmus of Panama

Jeremy B. C. Jackson,* Peter Jung, Anthony G. Coates, Laurel S. Collins

The gradual closure of the Panamanian seaway and the resulting environmental change stimulated an increase in Caribbean molluscan diversity rather than the mass extinction hypothesized previously on the basis of inadequate data. Upheaval of molluscan faunas did occur suddenly throughout tropical America at the end of the Pliocene as a result of more subtle, unknown causes. There is no necessary correlation between the magnitude of regional shifts in abiotic conditions and the subsequent biological response.

A fundamental question in historical biology is the extent to which biotas are affected by geographic isolation and environmental change (*1, 2*). The Pliocene emergence of the Isthmus of Panama (*3*) and the associated shifts in oceanographic conditions (*4–7*) are widely believed to have caused a mass extinction of tropical American mollusks that was far more severe in the Caribbean than in the eastern Pacific (*8–11*). This inference of differential extinction is based on observations of lower modern diversity in the Caribbean than in the eastern Pacific (*9, 11*); lower fossil diversity in the Caribbean after the early Pliocene than before that time (*8, 10, 11*); and greater numbers of originally widespread fossil taxa that survive today almost exclusively in the eastern Pacific, dubbed paciphiles (*8*), than those that survive only in the Caribbean (*9, 10*). However, all these studies are flawed by sampling bias (*12*) because there are no compendia of late Pliocene to modern Caribbean mollusks comparable to those for modern eastern Pacific (*13*) or older Neogene Caribbean faunas (*14, 15*). Here we provide the first such compilations based on extensive new and revised collections from the isthmian region (*3, 16*).

Our data include the Miocene to modern occurrence of 818 molluscan genera and subgenera from the Caribbean coast of Panama and Costa Rica (Table 1) and 106 species of the *Strombina* group (Gastropoda, Columbellidae) from throughout tropical America (*17*). The total faunal collections facilitate taxonomically consistent measurement of changes in Caribbean molluscan diversity and faunal turnover on the basis of standardized sampling from comparable habitats (*18*) and the relative contribution of paciphiles to the overall pattern. This type of comparison is not yet possible for the eastern Pacific because of the inadequate number of samples from older isthmian faunas (*3*). In contrast, the newly revised (*16*) *Strombina* group (hereafter referred to as strombinids) has been sampled extensively throughout the Caribbean and eastern Pacific well beyond the isthmian region. The strombinids are among the most abundant and diverse paciphile taxa considered to be indicators of Caribbean extinction (*8, 9*). We used strombinids to measure simultaneous changes in species diversity and turnover in both oceans and the timing of isolation of these faunas by the emerging isthmus.

To analyze Caribbean molluscan diversity over time, we grouped our fossil collections into four stratigraphic intervals (Table 1) and plotted cumulative numbers of taxa separately against numbers of specimens for each interval (Fig. 1). Plots of cumulative diversity versus sampling effort are the best way to compare numbers of taxa from different ages or places when sampling is unequal across treatments and most taxa in collections are rare (*12, 19*) (Table 1).

The results show no reduction in Caribbean molluscan diversity since the late Miocene (Fig. 1). To the contrary, diversity increased substantially, with late Miocene collections requiring three to six times as many specimens as the collections for the younger intervals to reach 220 subgenera (*20*). Moreover, the 310 subgenera in our late Miocene collections nearly equal the 317 obtained by Woodring from the Gatun Formation over several decades (*15*), so that our sampling is as representative as the best previous work.

In contrast, it has been reported that the numbers of paciphile subgenera do decrease greatly (Fig. 2A) (*8–10*). Although large and conspicuous (*9*), paciphiles made up only 9% of the subgenera in the late Miocene and were never a major taxonomic component of the Caribbean isthmian fauna. Most of their demise occurred during a brief interval just before the Pliocene-Pleistocene boundary (Fig. 2A). This extinction was part of a major turnover of the entire molluscan fauna, with dramatic increases in rates of both origination and extinction (Fig. 2B). However, extinction rates were more than two times greater for paciphiles than for the fauna as a whole.

Caribbean strombinid diversity peaked at 23 species in the early Pliocene and declined thereafter to 3, whereas eastern Pacific diversity is highest in modern time with 33 species (Fig. 3A). As for Caribbean subgenera, there was a major extinction of strombinid species in both oceans during the brief interval ending at the Pliocene-Pleistocene boundary, but origination was virtually restricted to the eastern Pacific. Thus, the time of Caribbean extinction was one of explosive Pacific origination for this paciphile group, and any difference in modern molluscan diversity between the two oceans (*21, 22*) did not likely result from differential extinction alone.

The disparate histories of strombinids in the Caribbean and eastern Pacific agree with the small proportion of transisthmian species and the substantial interoceanic divergence of strombinid subgenera after the late Miocene (*23*) (Fig. 3A). However, the occurrence of two extremely similar pairs of exclusively late Pliocene to modern strombinid species on opposite sides of the isth-

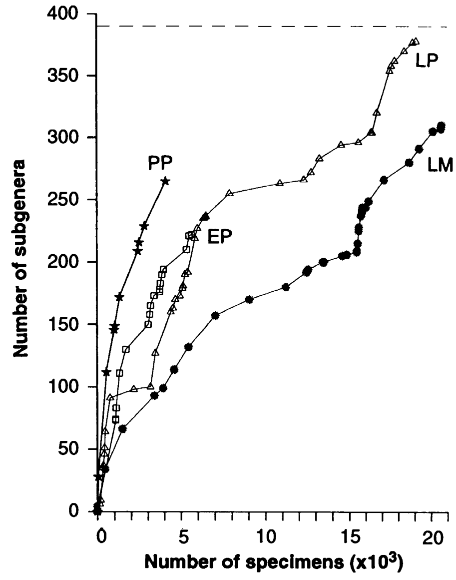

Fig. 1. Cumulative molluscan subgeneric diversity versus numbers of specimens, plotted in sequence of collection for the late Miocene (LM, asterisks), early Pliocene (EP, hollow squares), late Pliocene (LP, hollow triangles), and Pliocene-Pleistocene boundary (PP, stars) [see Table 1 and (*18*) for collection data and localities]. The total modern diversity is indicated by a horizontal dashed line because there are no data on numbers of specimens in collections (*34, 35*).

J. B. C. Jackson and A. G. Coates, Center for Tropical Paleoecology, Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Republic of Panama.
P. Jung, Naturhistorisches Museum, CH-4001, Basel, Switzerland.
L. S. Collins, Museum of Paleontology, University of Michigan, Ann Arbor, MI 48109–1079.

*To whom correspondence should be addressed at Smithsonian Tropical Research Institute, Unit 0948, APO AA 34002–0948, United States.

mus (*24*) suggests that some interchange may still have been possible during the late Pliocene.

Independent stratigraphic and biogeographic evidence demonstrates that shoaling and changes in oceanic circulation occurred at various points along the Panamanian seaway at least 2 million years before the final emergence of the isthmus (*7, 25, 26*). Such conditions should have stimulated speciation by geographic isolation (*2*), a prediction sustained by the increased Pliocene diversity of Caribbean mollusks (Fig. 1), increased originations of benthic foraminifera (*26*), and the chronologically long transisthmian divergence of strombinids (*23, 24*) and the snapping shrimp *Alpheus* (*27*).

The massive turnover of Caribbean isthmian mollusks at the end of the Pliocene (Figs. 2B and 3B) coincides with similar changes in the southeastern United States (*22, 28*) and Venezuela (*29*) and with the more gradual turnover of reef corals throughout the Caribbean (*30, 31*). Thus, the mass extinction first documented for mollusks north of the Caribbean (*28*) occurred in a vastly greater region and affected corals as well as mollusks.

It is tempting to attribute these faunal changes to the direct effects of refrigeration from the onset of Pleistocene glaciation (*28*). However, there was no decline in average winter temperatures since the middle Pliocene in the southern Caribbean and only a 3° to 5°C decrease in Florida and southeastern North America (*32*). In contrast, stable isotope data from venerid bivalves suggest that considerable changes in Caribbean isthmian seasonality took place, possibly in relation to upwelling (*33*). Thus, changes in patterns of upwelling and nutrient distribution may have been a factor in the faunal changes. This connection is evidenced by the persistence of living strombinids and other paciphiles where upwelling occurs along the coast of Venezuela (*9, 10, 16*) and by the apparently coincident onset of upwelling and strombinid radiation in the eastern Pacific (*33*). Whatever the explanation, regional turnover was not a slow and gradual process directly related to the emergence of the isthmus.

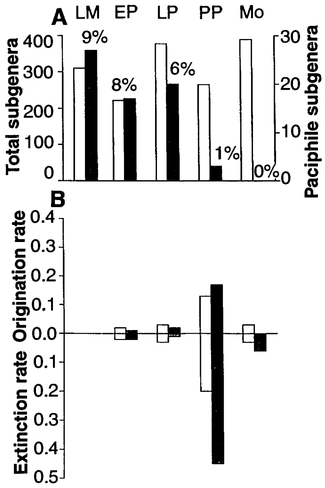

Fig. 2. Temporal changes in Caribbean diversity and turnover rates between successive age intervals for all molluscan subgenera collected versus paciphiles as defined by Woodring (*8*) and Vermeij (*9*). The symbols are as in Fig. 1 (Mo, modern). (**A**) Diversity over time. Percentages are the fraction of paciphile subgenera (solid bars) in the total fauna (open bars). (**B**) Subgeneric origination and extinction rates. The origination rate equals the number of taxa that first appear at time *t* divided by the total taxa at *t*, divided by the time between *t* and *t* − 1 in units of 100,000 years. The extinction rate equals the number of taxa present at *t* − 1 that are absent at *t* and thereafter, divided by the total taxa at *t*, divided by the time between *t* and *t* − 1 in units of 100,000 years. Times between successive intervals *t* and *t* − 1 are between the beginning points for each interval.

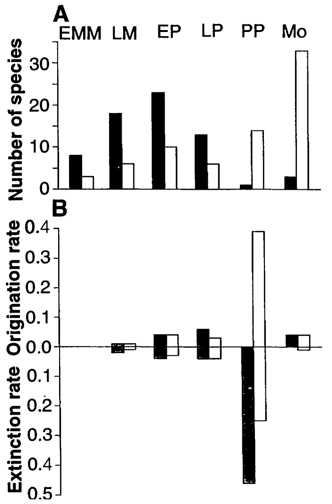

Fig. 3. Temporal changes in diversity and turnover rates for strombinid species on opposite sides of the Isthmus. The symbols are as in Fig. 2 (EMM, early and middle Miocene combined). Solid bars, Caribbean data; open bars, eastern Pacific data. (**A**) Diversity over time. There are four species in common to both oceans from the late Miocene and two species for the early Pliocene (*24*). (**B**) Rates of origination and extinction per species per 100,000 years, calculated as for Fig. 2.

Table 1. Surveys of modern faunas (*34, 35*) and new paleontological collections (*18*) used to determine temporal trends in Caribbean molluscan faunal diversity.

Epoch	Age (Ma)*	Number of collections†	Number of specimens	Number of subgenera‡
Modern	0	4	No data	390
Plio-Pleistocene	1.6 to 1.8	9	4,070	265
Late Pliocene	1.8 to 3.5	42	19,118	378
Early Pliocene	3.5 to 5.2	17	5,629	222
Late Miocene	5.6 to 8.2	33	20,673	310
Total		105	49,490	818

*Intervals reflect stratigraphic distribution of molluscan faunas and available age determinations, in millions of years ago (Ma) (*3, 18*). †A fossil collection comprises all taxa from a single site and stratigraphic horizon collected at one time, including those picked from outcrop surfaces or from one or more washed 10-kg bulk samples. Published data for modern faunas are not consistently broken down by samples, so that a collection comprises all taxa recorded in each study. ‡Most taxa are rare, with over half represented by fewer than ten specimens in fewer than five collections. Descriptive statistics: collections per taxon: median of 2, minimum of 1, maximum of 73, mean of 5.9, SD of 9.3; specimens per taxon: median of 6, minimum of 1, maximum of 4713, mean of 76.9, SD of 290.

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17. All species in (*16*) plus those from our new Caribbean and Pacific isthmian collections (*3*).
18. Fossil collections are from the formations described in (*3*). Age intervals nearly coincide with the time scales of W. A. Berggren, D. V. Kent, J. J. Flynn, J. A. Van Couvering, *Geol. Soc. Am. Bull.* **96**, 1407 (1985) and W. B. Harland *et al.* [*A Geologic Time Scale, 1989* (Cambridge Univ. Press, Cambridge, 1990)]. However, all our Pliocene sections overlap during the interval between 3.5 and 3.6 million years ago (*3*). Therefore, faunas from sections ranging upward from this interval were counted as late Pliocene and those ranging downward from the same interval were counted as early Pliocene. Likewise, age assignments for the Lomas del Mar section overlap with those for the uppermost type Moin Formation by 100,000 years, but the former is unambiguously younger, on the basis of superposition. This relation is the basis for the separation of the Lomas del Mar collections from those of the type Moin and uppermost Escudo de Veraguas Formations. Intervals: approximately 200,000 years before the Pliocene-Pleistocene boundary, Lomas del Mar above the top of the type Moin Formation; late Pliocene, upper Rio Banano Formation type section at La Bomba, upper Escudo de Veraguas Formation, Moin Formation type section, lower Rio Banano Formation at Quitaria, lower Escudo de Veraguas Formation; early Pliocene, Cayo Agua Formation, upper Shark Hole Point Formation; late Miocene, lower Shark Hole Point Formation, Nancy Point Formation, Rio Sandbox section of Uscari Formation, middle and upper Gatun Formation. The environment of deposition was less than 200 m for all formations except the Nancy Point and Uscari Formations [L. S. Collins, *J. Paleontol.*, in press], which contribute little to total late Miocene diversity. Exclusion of these deeper water faunas would only increase the disparity in numbers of subgenera between late Miocene and younger faunas in Fig. 1. Taxa were identified to genus or subgenus by P. Jung, so that names are consistent throughout. Numbers of taxa are total unique genera and subgenera. Except for strombinids, identification to species is impractical pending monographic revisions because most species are undescribed.
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20. By interpolation from Fig. 1 to the nearest 100 specimens: 2500 specimens for the Plio-Pleistocene, 5900 for the late Pliocene, 5500 for the early Pliocene, and 15,600 for the late Miocene. Sampling is inadequate to estimate total diversity during any interval, as shown by the persistently steep slopes of all the curves.
21. The only comparative transisthmian study (*34*) recorded 331 mollusk species from 58 eastern Pacific stations versus 277 species from 105 Caribbean stations, collected with the same equipment. These counts suggest that diversity in the eastern Pacific is twice as large as that in the southwestern Caribbean (*11*), on the assumption of similar abundance of specimens (no data are given). However, mollusks are generally much less abundant in the Caribbean than in the eastern Pacific (*9, 34*), so even this difference in diversity may be due to sampling bias.
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23. The species in common were *Strombina* (*Strombina*) *colinensis, Strombina* (*Strombina*) *lessepsiana, Sincola* (*Sincola*) *chiriquiensis*, and *Sincola* (*Dorsina*) *pigea* in the late Miocene; *Strombina* (*Strombina*) *lessepsiana* and *Sincola* (*Sincola*) *chiriquiensis* in the early Pliocene; and none during any other interval. The subgenera characteristic of different oceans were: *Sincola* (*Sinaxila*), exclusively Caribbean; *Sincola* (*Sincola*), restricted to Caribbean since the late Miocene; *Strombina* (*Recurvina*) and *Cotonopsis* (*Cotonopsis*), restricted to the eastern Pacific except for a single Pliocene species in each.
24. Seven specimens of *Strombina* (*Strombina* ?) aff. *pumilio* from a single locality in the eastern Pacific Rio Corredor section of the Armuelles Formation are most similar to *Strombina* (*Strombina*) *pumilio* from the late Pliocene to modern Venezuela and a single modern specimen from the Gulf of Darien. Five specimens of *Cotonopsis* (*Cotonopsis*) cf. *mendozana* from four localities scattered through the late Pliocene Caribbean Escudo de Veraguas Formation are most similar to *Cotonopsis* (*Cotonopsis*) *mendozana*, known only from the modern eastern Pacific.
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31. Ages of the important sections in Florida, Venezuela, and the Isthmus are not finally resolved (*3, 16*); D. S. Jones *et al.*, *J. Geol.* **99**, 637 (1991); W. D. Allmon, *Palaios*, in press] but are consistent with the hypothesis that massive molluscan turnover throughout the region occurred between 2.0 and 1.5 million years ago. Turnover of reef corals extended through the late Pliocene and early Pleistocene (*30*).
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36. We thank H. Dowsett and L. Bybell for dating the isthmian sections; Y. Ventocilla and K. Muller for preparing the samples; J. Gibson-Smith and W. Gibson-Smith for helping to compile the faunal lists and identify taxa to genus or subgenus; H. Fortunato for helping to analyze the data and preparing the figures; L. Anderson, M. Arosemena, T. Collins, A. Guevara, E. Lombardo, J. Obando, R. Panchaud, A. Velarde, and many others for providing additional assistance; and E. Bermingham, A. Budd, A. Cheetham, E. Leigh, N. Knowlton, and P. Morris for their useful advice. Supported by the National Geographic Society, the National Science Foundation, Kugler Fund of Basel Naturhistorisches Museum, Smithsonian Fellowship Programs, George Washington University, and Smithsonian Tropical Research Institute.

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Diversity of Atlantic Coastal Plain Mollusks Since the Pliocene

Warren D. Allmon,* Gary Rosenberg, Roger W. Portell, Kevin S. Schindler

About 70 percent of tropical western Atlantic mollusk species have become extinct since the Pliocene, which has led to perceptions of a corresponding decline in diversity. However, a compilation of gastropod species from Plio-Pleistocene faunas of the United States Atlantic coastal plain and from Recent western Atlantic faunas indicates that regional diversity has not changed since the Pliocene. Gastropod diversity in the Pliocene Pinecrest Beds in Florida approximates that seen today on either coast of Florida. Gastropod diversity is not demonstrably different in the Recent tropical western Atlantic than in the Recent tropical eastern Pacific. High extinction rates must have been balanced by high origination rates.

The late Cenozoic history of mollusk diversity in the tropical and subtropical western Atlantic has traditionally been viewed as one of a decrease in species richness by a series of extinction episodes, from a Miocene-Pliocene peak to the depauperate fauna of today (*1–4*). In what has been termed a regional mass extinction, 70% of western Atlantic mollusk species are thought to have become extinct since the late Pliocene, whereas only about 30% of eastern Pacific species became extinct over the same interval (*2, 3*). We have compiled lists, in part based on our own new collections, of gastropod species from the Recent and Plio-Pleistocene of the western Atlantic. We have used these data to test whether extinction has led to a substantial decrease in diversity in the region, both in absolute terms and relative to the Recent eastern Pacific fauna.

The fossil database comprises lists of species from three Plio-Pleistocene faunas (Pinecrest, Caloosahatchee, and Bermont)

W. D. Allmon, Paleontological Research Institution, Ithaca, NY 14850.
G. Rosenberg, Malacology Department, Academy of Natural Sciences of Philadelphia, Philadelphia, PA 19103.
R. Portell and K. Schindler, Florida Museum of Natural History, University of Florida, Gainesville, FL 32611.

*To whom correspondence should be addressed.