16. P. Jung, *Palaeontol. Schweiz. Abh.* **111**, 1 (1989).
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.
19. H. L. Sanders, *Am. Nat.* **102**, 243 (1968); J. C. Tipper, *Paleobiology* **4**, 423 (1979); A. E. Magurran, *Ecological Diversity and its Measurement* (Croom Helm, London, 1988).
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.
22. W. D. Allmon, R. Portell, G. Rosenberg, and K. Schindler [*Paleontol. Soc. Spec. Publ. 6* (1992), p. 4; W. D. Allmon, G. Rosenberg, R. Portell, K. Schindler, *Science* **260**, 1626 (1993)] made a new compilation of described shelled gastropods from Florida to northeastern Brazil. Their list contains 2643 species, compared with 2475 species from the same latitudinal range in the eastern Pacific.
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.
25. A. Coates, J. Obando, H. Gonzalez, *Paleontol. Soc. Spec. Publ. 6* (1992), p. 62.
26. L. S. Collins, *ibid.*, p. 67.
27. N. Knowlton, L. A. Weigt, L. A. Solórzano, D. K. Mills, E. Bermingham, *Science* **260**, 1629 (1993).
28. S. M. Stanley and L. D. Campbell, *Nature* **293**, 457 (1981); S. M. Stanley, *Palaios* **1**, 17 (1986).
29. J. Gibson-Smith and W. Gibson-Smith, *Geos* **24**, 11 (1979).
30. A. F. Budd, T. A. Stemann, K. G. Johnson, *Paleontol. Soc. Spec. Publ. 6* (1992), p. 43.
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*).
32. H. J. Dowsett and R. Z. Poore, *Quat. Sci. Rev.* **10**, 189 (1991); H. J. Dowsett *et al.*, *Science* **258**, 1133 (1992).
33. D. H. Geary, T. A. Brieske, B. E. Bemis, *Palaios* **7**, 77 (1992); D. H. Geary *et al.*, *Paleontol. Soc. Spec. Publ. 6* (1992), p. 108.
34. F. M. Bayer, G. L. Voss, C. R. Robins, *Bioenvironmental and Radiological Safety Studies Atlantic-Pacific Interoceanic Canal. Report on the Marine Fauna and Benthic Shelf-Slope Communities of the Isthmian Region* (University of Miami, Miami, FL, 1970).
35. A. A. Olsson and T. L. McGinty, *Bull. Am. Paleontol.* **39**, 1 (1958); G. E. Radwin, *Trans. San Diego Soc. Nat. Hist.* **15**, 229 (1969); M. Arrunategui and J. B. C. Jackson, unpublished data.
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.

15 January 1993; accepted 26 April 1993

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.

at two localities in southern Florida (*5–7*). We concentrated on the Pliocene Pinecrest fauna because it is the oldest and is therefore critical to understanding patterns of diversity in the region (*8*). Data for molluscan diversity in the Pliocene of the Atlantic coastal plain north of Florida were taken from previously published sources (*9–11*) (Table 1). The Recent database was compiled from the published literature (*12*); it includes all described shelled marine species of gastropods known to occur between Cape Hatteras, North Carolina, and Rio de Janeiro (35°N to 23°S, including Bermuda).

Our results give a tally of 460 species of gastropods >5 mm in maximum adult dimension in the Pliocene Pinecrest Beds (Table 1). Of these species, 173 (38%) are known to occur in the overlying Caloosahatchee Formation (Table 2). Of the 500 total gastropod species reported from the Pinecrest, only 150 survive today, a number that reflects an extinction rate of 70%. About 95% of the extant Pinecrest species are known to occur in depths <30 m in the Recent fauna (*12*). In addition, independent paleoenvironmental evidence suggests that the Pinecrest Beds were deposited in depths ≤30 m (*13*). Therefore, we used 30 m as the cutoff point in making comparisons between Recent and Pinecrest diversity.

To obtain an estimate of diversity representing all size ranges, we added to the 460 species >5 mm a proportion of species with maximum observed size ≤5 mm that corresponds to the proportion present in the Recent Florida shallow-water fauna (22%) (Table 3). We thus obtained a total of about 590 species of gastropods. About 211 bivalve species have been reported in the Pinecrest after intensive recent study (*3*), giving a total for bivalves and gastropods of 801 (*14*).

Pinecrest bivalve diversity can be used to estimate expected gastropod diversity. There are 320 species of bivalves known to occur in water depths <30 m in Florida [compiled from Florida references in (*12*)]. Thus, the gastropod:bivalve ratio is 2.58:1 for the Recent Florida fauna (827:320). Applying this ratio to the 211 Pinecrest bivalves, we expect a total of 544 Pinecrest gastropods. We consider our estimate of 590 Pinecrest gastropods reliable because it is within 8% of the number expected on the basis of diversity of bivalves.

Our estimates of diversity of Pinecrest gastropods are comparable to our estimates for the Recent shallow water gastropod fauna of Florida (*12*) (Fig. 1). The count of 460 fossil species >5 mm is about 7% higher than the 429 species in this size range now living in western Florida; the estimate of 590 Pinecrest species of all sizes is only 8% greater than the 545 living species documented in western Florida. Similarly, numbers for the living fauna of eastern Florida are approximately 4% greater than those for the Pinecrest fauna. Thus, although the Pinecrest fauna is about 70% extinct, it is not possible to demonstrate that Recent diversity in Florida has declined as a result of Pliocene or subsequent extinctions.

The molluscan fauna of the Pinecrest has been estimated to contain as many as 1200 species. This number exceeds that of the Recent fauna of Florida by as much as three times (*2, 15, 16*) and approximates Recent diversity of the entire Caribbean region (*2*). Estimates such as these have created the impression of a tremendous diversity for the fossil beds of Florida, while underestimating Recent diversity there, which is ≥1147 species. Although further work may reveal that the Pinecrest contains considerably more species than we have been able to document, species are still being discovered in the Recent fauna of Florida, through both range extensions and new species (*17*). Therefore, we expect that additions to the fossil fauna will be approximately balanced by additions to the Recent.

Diversity in the Pinecrest also does not differ substantially from that reported in the overlying Caloosahatchee Formation (Table 2), which has a documented fauna of 386 species of gastropods >5 mm in maximum size. This number is about 16% fewer than the 460 Pinecrest species, a difference comparable to the 12% difference today between counts for the east and west coasts of Florida (Table 3). Documented diversity is considerably lower in the Bermont than in the underlying Caloosahatchee. The Bermont beds, however, were not recognized as containing a distinct fauna until the 1960s (*8*) and so have been undersampled relative to the longer known Pinecrest and Caloosahatchee faunas. Not surprisingly, recent studies indicate that the Bermont contains a considerable number of undescribed or unreported species [for example, (*18*)].

Comparison of diversities over time is difficult because the Recent fauna has been sampled better geographically than have the fossil faunas, whereas the latter are much better sampled temporally. The count of 333 species that we report for the Pinecrest at Sarasota (Table 1) is an overestimate of local diversity in that it includes many discrete beds, each of which may

Table 1. Diversity of gastropods in Plio-Pleistocene stratigraphic units of the Atlantic coastal plain.

Unit	Locality	Total species	Species >5 mm	Data source
Bermont	Belle Glade	261	225	*7*
Bermont	Leisey	95	86	*30**
Bermont	Total	304	259	*7, 30**
James City	Total	99	99	*10*
Waccamaw	Total	213	200	*9*
Caloosahatchee	Sarasota†	42	40	*
Caloosahatchee	Total	495	386	*9*
Chowan River	Total	113	113	*10*
Bear Bluff	Total	22	22	*10*
Duplin	North Carolina	211	195	*9*
Duplin	South Carolina	216	198	*9*
Jackson Bluff	Total	170	144	*9*
Yorktown	North Carolina	117	101	*9*
Yorktown	Virginia	293	275	*9*
Pinecrest	Sarasota‡	333	333	*31**
Pinecrest	Total	500	460	*9, 31**

*Florida Museum of Natural History collections. †Unit 1, APAC Quarry (*13*). ‡Units 10 to 2, APAC Quarry (*13*).

Table 2. Molluscan origination and extinction for selected Plio-Pleistocene units of the Atlantic coastal plain. See (*8*) for stratigraphic relations. The calculations are based only on species >5 mm (Table 1). YDJP, putative synoptic time slice of late Pliocene age comprised of the Yorktown, Duplin, Jackson Bluff, and Pinecrest units; CB, Chowan River and Bear Bluff formations; JWC, James City, Waccamaw, and Caloosahatchee formations. The gastropod data are from Table 1; bivalve data, indicated by the abbreviation b, are from (*3*).

Unit	Number of species			Apparent extinction (%)	Apparent origination (%)
	Older unit	Younger unit	Shared		
Pinecrest-Caloosahatchee	460	386	173	62.4	55.2
Pinecrest-Caloosahatchee (b)	211	150	110	47.9	26.7
YDJP-CB	600	100	53	91.1	47.0
CB-JWC	100	462	75	25.0	83.8

reflect an average of diversity over time (13). The diversity of a single horizon may be considerably lower than 300 species. Two studies of restricted local shallow molluscan faunas in Florida reported 181 and 155 species of gastropods, respectively (19). Thus, local diversity may not have changed significantly in Florida since the Pliocene. Confirmation of this hypothesis would require quantitative sampling in Recent sites and fossil horizons that represent comparable environments.

There is thus no evidence that molluscan diversity has changed appreciably in Florida from the late Pliocene to the Recent: the Pinecrest, Caloosahatchee, and Recent faunas do not differ substantially in number of species. The late Neogene regional mass extinction recognized in the western Atlantic (2, 3), and best represented in strata exposed in southern Florida (3), must therefore have been a phenomenon of not only high extinction but also high origination. During the time of this extinction, origination rates exceeding 50% occurred not only in Florida but also farther north along the Atlantic coastal plain (Table 2). Further research is needed to parse these originations into components of speciation, immigration, and lineage transformation. Nevertheless, the regional mass extinction in Florida may be an example of the often observed linkage between speciation and extinction (20) and may be similar in this respect to other regional episodes of extinction in the geological record (21). Similar patterns have been documented for gastropods in the late Neogene record of the southern Caribbean, where there was also substantial origination with no decline in diversity during this time (22).

Even at the level of faunal province, we see no evidence for an overall decline in

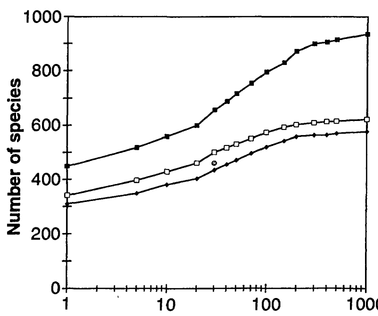

Fig. 1. Cumulative number of species by depth for Recent Floridian gastropods >5 mm in maximum size. Each species is counted from its minimum known depth in the western Atlantic. The circle representing total Pinecrest diversity (Table 1) is placed at 30 m, on the basis of independent paleoenvironmental data (13). Symbols: filled squares, all Florida; open squares, East Florida; and diamonds, West Florida.

Table 3. Species diversity of Recent shelled gastropods in Florida. The size and depth ranges are those covered by analysis of Pinecrest and Caloosahatchee fossil assemblages (<30 m depth and >5 mm in maximum adult dimension). The counts for western (W.) and eastern (E.) Florida do not include tallies for the Florida Keys.

Region	Total species	Species <30 m	Species <30 m and >5 mm (%)
Florida	1171	827	645 (78.0)
W. Florida	710	545	429 (78.7)
E. Florida	778	617	490 (79.4)

diversity in the western Atlantic. The Recent fauna of the tropical western Atlantic has traditionally been viewed as less diverse than that of the tropical eastern Pacific (1–4), having declined from approximate parity before the uplift of the Central American Isthmus to a depauperate condition at present. However, our data show that the western Atlantic has almost 7% more species of shelled gastropods than in the comparable latitudinal range of the tropical eastern Pacific (31°N to 6°S) (23) (2643 versus 2475); the Gulf of Mexico and Caribbean alone (30°N to 8°N) contain 2362 species (12). The tropical fauna of the western Atlantic is therefore not demonstrably less diverse than that of the eastern Pacific. If it has suffered more extinction than has the eastern Pacific, then it has also seen more origination.

Western Atlantic faunal history farther north may have been different. In North Carolina and Virginia, diversity has declined since the Pliocene. Virginia has about 100 Recent shallow water gastropod species >5 mm in maximum size, and North Carolina has about 230 such species (12), whereas the Pliocene Yorktown Formation of Virginia has 275 species in this size range (Table 1). The reason for this difference may be different climatic histories north and south of Cape Hatteras (24). Virginia and North Carolina north of Cape Hatteras have temperate Recent faunas, and climatic cooling may have caused the loss of diversity since the Pliocene (2, 3, 25). South of Cape Hatteras, however, large degrees of Neogene extinction cannot be attributed to climatic cooling alone.

Our results suggest that any environmental change associated with Plio-Pleistocene faunal change produced not only high rates of extinction but also high rates of origination (26). Other mechanisms may have been present in this system, such as changes in sea level (25, 27) or, more probably, changes in productivity caused by variations in oceanic circulation associated with closure of the Central American Isthmus, the onset of Northern Hemisphere glaciation (28), or both. These mechanisms could also be used to explain a simultaneous increase in molluscan originations and extinctions in the late Pliocene.

REFERENCES AND NOTES

1. A. A. Olsson, *Mollusks of the Tropical Eastern Pacific, Particularly from the Southern Half of the Panamic-Pacific Faunal Province: Panamic-Pacific Pelecypoda* (Paleontological Research Institution, Ithaca, NY, 1961); W. P. Woodring, *Proc. Am. Philos. Soc.* **110**, 425 (1966); G. J. Vermeij, *Biogeography and Adaptation* (Harvard Univ. Press, Cambridge, MA, 1978); *Science* **253**, 1099 (1991).
2. S. M. Stanley and L. D. Campbell, *Nature* **293**, 457 (1981).
3. S. M. Stanley, *Palaios* **1**, 17 (1986).
4. A. M. Keen, *Sea Shells of Tropical West America* (Stanford Univ. Press, Stanford, CA, ed. 2, 1971).
5. To construct these lists, we identified every gastropod >5 mm in maximum dimension from stratigraphically collected bulk samples, found in the Pinecrest Beds and Caloosahatchee Formation exposed in two quarries in Sarasota County and in the Bermont Formation exposed in a quarry in Hillsborough County. Specimens <5 mm were excluded because of the difficulty of sorting and identifying mollusks of this size range. The Pinecrest Beds [units 10 to 2 of Petuch (16)], were sampled at APAC Quarry and Quality Aggregates Quarry, northern Sarasota County, Florida. The Caloosahatchee Formation [unit 1 of Petuch (16)] was sampled at APAC Quarry [see (13) for site description]. The Bermont Formation was sampled at Leisey Shell Pit, Hillsborough County, Florida [see S. D. Webb *et al.*, *Quat. Res.* **32**, 96 (1989) for site description]. Taxa that we could identify only to genus level (some probably undescribed) were included in the tallies. Specimens from these collections are housed in the Florida Museum of Natural History (FLMNH).
6. We supplemented data from the bulk samples by reference to earlier species lists for the Pinecrest [(16); E. J. Petuch, *J. Coastal Res.* **2**, 391 (1986); *ibid.* **3**, 189 (1987); *W. H. Dall Paleontol. Res. Center Spec. Publ. 1* (1991); J. J. Tripp, *Ann. Carnegie Mus.* **57**, 259 (1988); E. H. Vokes, *Tulane Stud. Geol. Paleontol.* **23**, 1 (1990); *ibid.* **25**, 1 (1992); (9)] and for the Caloosahatchee (9).
7. We supplemented bulk sample data from the Bermont with that of S. E. Hoerle [*Tulane Stud. Geol. Paleontol.* **8**, 56 (1970)]. We updated Hoerle's species count on the basis of nomenclatural changes since 1970 and our comparison with newer collections at FLMNH.
8. Stratigraphic terminology in the Florida Plio-Pleistocene is unclear. Most units have been defined faunally rather than lithostratigraphically and thus properly should not be referred to as formations. See W. G. Lyons, *Bull. Fla. Mus. Nat. Hist.* **35**, 131 (1991) and T. M. Scott and W. D. Allmon, Eds., "The Plio-Pleistocene stratigraphy and paleontology of southern Florida," *Fl. Geol. Surv. Spec. Pub. 36* (1992), p. 1. Some aspects of correlation between Plio-Pleistocene units in Florida and those of the Atlantic coastal plain are disputed. We have used the relations presented by J. E. Hazel [*Smithsonian Contrib. Paleobiol.* **53**, 81 (1983)] and in (13, 25).
9. L. D Campbell, S. Campbell, D Colquhoun, J. Ernissee, *S.C. Geol. Notes* **19**, 51 (1975). We used data from this publication as given, assuming synonymies to be correct.
10. L. W. Ward and B. W. Blackwelder, *Smithson. Contrib. Paleobiol.* **61**, 113 (1987) (James City Formation); L. W. Ward and N. L. Gilinsky, *Va. Mus. Nat. Hist. Mem.*, in press (Chowan River and Bear Bluff formations).
11. To make these data comparable to our sample data, we determined a maximum adult size of each species from the collection at FLMNH or from the literature. Comparisons among the faunas were car-

ried out on the basis of only those species known to reach sizes >5 mm in any linear dimension.
12. G. Rosenberg, *Am. Malacol. Bull.*, in press. More than 1000 publications on western Atlantic mollusks were consulted in the compilation of this data base.
13. W. D. Allmon, *Palaios* **8**, 183 (1993).
14. We estimate that the total shelled molluscan fauna of the Pinecrest is about 1050 species. We obtained this number by taking the estimated 801 Pinecrest gastropods and bivalves and adding 20% for species yet to be discovered and 5% for two less diverse classes, the chitons and scaphopods (*29*). This number is the same as a widely cited estimate for the Pinecrest (*9*), which listed 300 species, including 170 gastropods, and gave a total of about 1000 species.
15. A. A. Olsson, in *Miami Geological Society Fieldtrip Guidebook*, R. D. Perkins, compiler (Miami, FL 1968), p. 75.
16. E. J. Petuch, *Proc. Acad. Nat. Sci. Philadelphia* **134**, 12 (1982).
17. In 1977, the Florida fauna was tallied at 1085 gastropods and bivalves (*29*); here we have tallied 1147 (827 gastropods and 320 bivalves), an increase of almost 6%.
18. E. J. Petuch, *Neogene History of Tropical American Mollusks* (Coastal Education and Research Foundation, Charlottesville, VA, 1988).
19. J. K. Reed and P. M. Mikkelsen, *Bull. Mar. Sci.* **40**, 99 (1987); W. G. Lyons, *Fla. Mar. Res. Inst. Publ. 47* (1989).
20. S. M. Stanley, in *Causes of Evolution, a Paleontological Perspective*, R. M. Ross and W. D. Allmon, Eds. (Univ. of Chicago Press, Chicago, 1990), pp. 103–127.
21. K. W. Flessa *et al.*, in *Patterns and Processes in the History of Life*, D. M. Raup and D. Jablonski, Eds. (Springer-Verlag, Berlin, 1986) pp. 232–257.
22. J B. C. Jackson, P. Jung, A. G. Coates, L. S. Collins, *Science* **260**, 1624 (1993).
23. Eastern Pacific data from (*4*) as revised by C. Skoglund, *Festivus* (suppl.) **24**, 1 (1992).
24. T. M. Cronin, *Quat. Sci. Rev.* **10**, 175 (1991).
25. L. W. Ward, R. H. Bailey, J. G. Carter, in *The Geology of the Carolinas*, J. W. Horton and V. A. Zullo, Eds. (Univ. of Tennessee Press, Knoxville, 1991), pp. 274–289.
26. S. M. Stanley, *Paleobiology* **12**, 89 (1986); W. D. Allmon, *Oxford Surv. Evol. Biol.* **8**, 219 (1992).
27 B. W. Blackwelder, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **34**, 87 (1981); T. M. Cronin, *Geol. Soc. Am. Bull.* **92**, 812 (1981); H. J. Dowsett and T. M. Cronin, *Geology* **18**, 435 (1990).
28. W. D. Allmon, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **92**, 41 (1992), and references therein.
29. D. Nicol, *Nautilus* **91**, 4 (1977).
30. R. W. Portell, K. S. Schindler, G. M. Morgan, in "The Plio-Pleistocene stratigraphy and paleontology of southern Florida," T. M. Scott and W. D. Allmon, Eds., *Fla. Geol. Surv. Spec. Publ. 36* (1992), pp. 181–194.
31. R. W. Portell, K. S. Schindler, D. S. Jones, *Tulane Stud. Geol. Paleontol.*, in press.
32. We thank A. Collazos, K. Ketcher, and S. Schellenberg for assistance in data analysis and T. Cronin, J. Jackson, D. Jones, and L. Ward for comments on earlier drafts. This paper is University of Florida Contribution to Paleontology no. 415.

19 January 1993; accepted 23 April 1993

Divergence in Proteins, Mitochondrial DNA, and Reproductive Compatibility Across the Isthmus of Panama

Nancy Knowlton,* Lee A. Weigt, Luis Aníbal Solórzano, DeEtta K. Mills,† Eldredge Bermingham

It is widely believed that gene flow connected many shallow water populations of the Caribbean and eastern Pacific until the Panama seaway closed 3.0 to 3.5 million years ago. Measurements of biochemical and reproductive divergence for seven closely related, transisthmian pairs of snapping shrimps (*Alpheus*) indicate, however, that isolation was staggered rather than simultaneous. The four least divergent pairs provide the best estimate for rates of molecular divergence and speciation. Ecological, genetic, and geological data suggest that gene flow was disrupted for the remaining three pairs by environmental change several million years before the land barrier was complete.

Geographic isolation is thought to permit divergence and speciation by disruption of gene flow (*1*). Pairs of marine sister taxa separated by the Isthmus of Panama are ideal for studying these processes (*2–5*) because isolation of the Caribbean and the eastern Pacific is well dated and relatively recent (*6, 7*). This geological framework has prompted study of transisthmian sister taxa to test the accuracy of molecular clocks and to estimate the timing of other evolutionary events (*3, 4, 8*). It has been difficult to interpret inconsistencies and estimate possible phylogenetic differences in divergence rates (*9*), however, because of the limited number of taxa and characters studied. To address these problems, we investigated divergence in allozymes, mitochondrial DNA (mtDNA), and reproductive compatibility for seven shallow water transisthmian pairs of sister taxa in the snapping shrimp genus *Alpheus*.

Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Republic of Panama.

*To whom correspondence should be addressed. Alternate mailing address: Smithsonian Tropical Research Institute, Unit 0948, APO AA 34002–0948, United States.
†Present address: Route 2, Box 538, Joshua, TX 76058.

We used the taxonomic literature to identify transisthmian pairs that were specifically and unambiguously described as each other's closest relatives on the basis of morphological criteria (*10*). Collections along the two coasts and adjacent islands of central Panama at depths less than 5 m revealed unrecognized sibling species in addition to these pairs (*11*). In total, we examined 17 taxa (Table 1): two unambiguous pairs (P4-C4, P5-C5), three triplets (P3-C3, P3-C3′; P6-C6, P6′-C6; P7-C7, P7′-C7), and one quartet (P1-C1, P1-C2, P2-C1, P2-C2). We used shared anatomical and color pattern character states (*12*) to posit relations within the triplets and quartet. The result was seven morphologically defined transisthmian sister species pairs (bold in Tables 1 and 2).

For each taxon, we characterized allozymes by using conventional starch gel electrophoresis (*13*) and sequenced a segment of the mtDNA cytochrome oxidase I (COI) gene (*14*). Aggressive behavior was used as an estimate of behavioral components of reproductive compatibility (*15*) because snapping shrimp attack heterospecific individuals and all conspecifics except potential mates (*16*). We calculated genetic divergence between transisthmian pairs using Nei's D for allozymes and Kimura's corrected percent sequence divergence for mtDNA (*17*). We estimated divergence in behavioral compatibility by standardizing measures of tolerance and intolerance for transisthmian pairs against values observed in intraoceanic, conspecific control matings (*15*).

These three measures of divergence consistently support assignments of transisthmian sister species pairs on the basis of morphology and color pattern. Within the

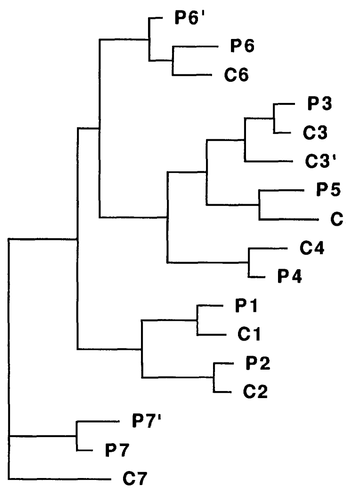

Fig. 1. Single most parsimonious phylogenetic tree constructed on the basis of mtDNA sequences with PAUP (*18*). Transitions were given one-quarter the weight of transversions (based on the fourfold greater abundance of transitions than transversions in our data), and trees were rooted by the P7-P7′-C7 clade. Taxon codes are as in Table 1.