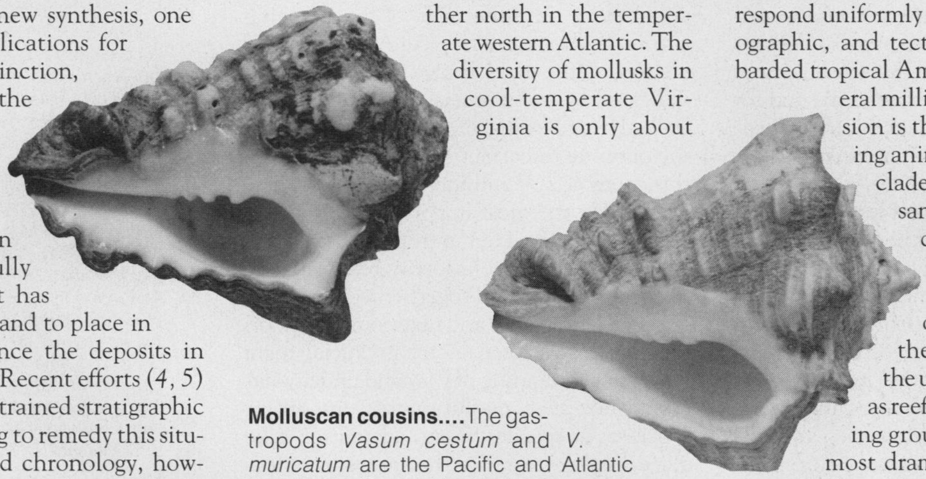
PERSPECTIVE

The Biological History of a Seaway

Geerat J. Vermeij

Once upon a time there was a seaway connecting the Atlantic and Pacific oceans in what is now Central America. As great blocks of crust were being squeezed and shifted by the Earth's tectonic engine, an isthmus slowly took shape and finally emerged as a land bridge between North and South America about 3 million years ago. Pacific and Atlantic populations of marine species became isolated by this barrier and began to go their independent, evolutionary ways. At the same time, extinctions impoverished the once rich fauna of the western Atlantic. For years this was the accepted chronology of events in marine tropical America, but three papers (*1–3*), beginning on page 1624 of this issue, are helping to forge a new synthesis, one that has profound implications for the understanding of extinction, species formation, and the history of diversity.



Molluscan cousins.... The gastropods *Vasum cestum* and *V. muricatum* are the Pacific and Atlantic members of a species pair whose ancestor existed before final closure of the Central American Seaway.

Tropical America presents historians with daunting methodological challenges. There is an abundance of beautifully preserved fossils, but it has proved difficult to date and to place in proper temporal sequence the deposits in which they were found. Recent efforts (*4, 5*) to construct a well-constrained stratigraphic framework are beginning to remedy this situation. Even with a good chronology, however, the fossil record cannot be read literally. Differences in sampling intensity in the various fossil deposits introduce all sorts of artifacts that must be eliminated if patterns of extinction and evolution are to be distinguished from statistical noise.

Building on their geological studies (*4*), Jackson *et al.* (*1*) have carried out an ambitious sampling program in order to reconstruct the history of diversity on the Caribbean coast of Central America. They eliminated sampling artifacts by assessing the number of subgenera present during each of four time intervals at common sampling intensities. Earlier work (*6*) had led to the conclusion that episodes of extinction beginning about 3.2 million years ago caused diversity in Atlantic tropical America to plummet. The new compilation (*1*), however, indicates that the extinctions began later, about 2.4 million years ago, and that they were fully compensated for by speciation (the formation of species through the branching of lineages) and by the invasion of species from elsewhere. In fact, diversity may have risen more or less continuously from 8 million years ago to the present. The situation in Florida is similar. Allmon *et al.* (*2*) show that, although extinction wiped out many species beginning about 2.4 million years ago, most of the losses were made up by speciation and invasion, so that overall diversity has remained roughly constant over the last 4 million years.

One very intriguing puzzle that emerged from these compilations is that evolution largely or completely replaced the losses in the tropical belt but not further north in the temperate western Atlantic. The diversity of mollusks in cool-temperate Virginia is only about 40% of what it was during Pliocene time (*2, 6, 7*). Perhaps even more interesting is the observation that the fauna of the temperate northwestern Atlantic has recouped some of its losses more by invasion, especially from Europe and the North Pacific, than by speciation, whereas the tropical faunas, although affected by immigrants from the coasts of West Africa and even the Indian Ocean, have been enriched mostly by speciation within surviving groups. The idea that the tropics are especially favorable to speciation is not new—in fact, it has been invoked to explain the high diversity of species in the equatorial belt—but no convincing explanation for this pattern has yet come to light.

Another approach is to chart diversity through time in particular clades (evolutionary branches) at the species level. By inferring ancestor-descendant and sister-group relationships among all living and fossil species of the group in question and by incorporating stratigraphic and biogeographic data for each species, one can reconstruct a tree in which instances of speciation, evolution without branching, invasion, and extinction can be counted and placed in temporal sequence. Evolutionary trees thus provide another means of filling in missing data.

The number of studies sufficient for the construction of such trees is remarkably small. Those that are available indicate a wide variety of evolutionary patterns. Ostracode crustaceans (*8*) and many mollusks (*9*) conform to the general pattern of evolutionary pruning followed by extensive branching (speciation) in the Atlantic; but others, including mollusks (*10*) and large barnacles (*11*), show patterns in which speciation was concentrated largely in the eastern Pacific or was not frequent anywhere in tropical America. It is too early to draw firm conclusions about why not all groups behaved in the same way evolutionarily.

However, different clades clearly did not respond uniformly to the biological, oceanographic, and tectonic changes that bombarded tropical America during the last several million years (*12*). My impression is that large suspension-feeding animals, as well as molluscan clades living in shallow water sand and mud habitats, underwent particularly dramatic diversification in the eastern Pacific and only modest speciation in the western Atlantic after the uplift of the isthmus, whereas reef-dwelling and rock-dwelling groups recouped their losses most dramatically in the Atlantic.

Ecology obviously plays a crucial role and, although its effects cannot be detected in compilations of entire faunas, must be taken into account if further progress is to be made in our understanding of the history of diversity and the factors that affect speciation.

Besides offering an exceptionally rich fossil record, tropical America also provides an unparalleled opportunity for the study of evolution at the molecular level. Final closure of the Central American seaway caused Pacific and Atlantic populations of once continuously distributed species to become separated and to go their own way. The date of this event, about 3 million years ago, has been widely used for the calibration of rates of molecular evolution. The new work by Knowlton *et al.* (*3*) on species pairs of snapping shrimps shows that such calibration must be applied with caution.

Pacific and Atlantic populations, it seems, did not all become separated at the same time. Three independent measures of evolutionary divergence based on behavior, metabolic enzymes, and mitochondrial DNA se-

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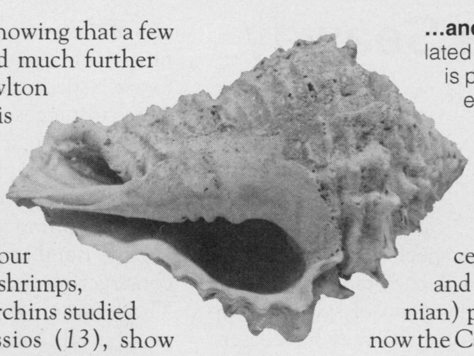
The author is in the Department of Geology and the Center for Population Biology, University of California, Davis, CA 95616.

quences are consistent in showing that a few species pairs have diverged much further than have the others. Knowlton and colleagues interpret this to mean that some pairs were separated as early as 12.5 million years ago, when the seaway was in the early stages of uplift. Four of seven pairs of snapping shrimps, and all three pairs of sea urchins studied by Bermingham and Lessios (*13*), show similar rates of mitochondrial DNA divergence, indicating a separation about 3 million years ago.



...and relative. The related *Hystrivasum locklini* is part of an Atlantic lineage that became extinct about 1.7 million years ago.

Why should separation have been earlier for some species pairs than for others? Once again, ecology seems to play a significant but little studied role. Knowlton *et al.* (*3*) propose that species unable to tolerate inshore conditions such as turbidity would be isolated early by an emerging land bridge, whereas species pairs adapted to environments such as mud flats and mangrove swamps could remain in interoceanic genetic contact until the final imposition of the barrier. Ecology may also account for the highly variable rates of evolution at the level of proteins and for the many external forms that have been documented for species pairs of mollusks, sea urchins, and fishes (*3*, *12–14*).

There are some important lessons in these findings. Barriers need not be fully formed in order to effectively separate populations genetically. This should come as no surprise to biogeographers. In pre-isthmian tropical America, many clades were confined to the Atlantic and never extended into the eastern Pacific despite the absence of an obvious barrier to dispersal (*9*). Moreover, tropical America was divided into a northern (Caloosahatchian) biogeographic province centered on Florida and a southern (Gatunian) province in what is now the Caribbean Basin and the eastern Pacific (*15*). The nature of the barrier between these provinces remains obscure, but there was nothing as impenetrable as a land bridge.

The time of final imposition of a barrier that is obvious to humans may therefore be an insensitive and potentially misleading point for the calibration of rates of evolution. Perhaps the disintegration of a barrier is more reliable. The first appearance of invaders across a crumbling barrier is less ambiguous than is the last genetic contact between populations on either side of an emerging barrier. In the case of tropical America, completion of the land bridge is perhaps best indicated by the dispersal of mammals that walked from North to South America and in the opposite direction. Marshall (*16*) places this event at 2.92 million years ago.

Possibly the most important facet of the work being carried out in tropical America is the emphasis on evolutionary renewal. The historical framework, together with the species-level molecular and taxonomic work on the living and fossil biota, is crucial for a better understanding of how and under what conditions such evolutionarily important processes as speciation and adaptation take place. Ecology as well as the nature and effectiveness of barriers will figure prominently in this new synthesis. Tropical America will continue to be perhaps the finest laboratory in which to answer the big questions about what controls biological diversity.

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