

## The Central American land bridge: evolution at work

**H. Fortunato**

*Center for Tropical Palaeoecology and Archaeology, Smithsonian Tropical Research Institute, Balboa, Republic of Panama*

The Neogene of tropical America was a time of revolutionary change both at community and species levels. The Panama gateway region has been widely used to document and model patterns of evolution in a well-constrained geologic setup. The changes brought about by the slow closure of the gateway were dramatic to say the least and led to the formation of two strikingly different realms, the Caribbean Sea and the eastern Pacific Ocean. Whereas the eastern Pacific has a strong tidal regime, high planktonic biomass, primary productivity and intense predation levels, the Caribbean became oligotrophic, with increased surface water temperature, salinity and carbonate deposition, as well as extensive reef and shallow-water seagrass communities. These changes were accompanied by the increased isolation and divergence of species across the developing barrier and shifts in diversity due to differential extinction and origination rates. The study of past and present day communities and their relationships in such a well documented setup can be used for a better understanding of the relation between adaptation, selection and changing environmental parameters. This paper reviews results documenting the events that shaped the shallow water marine biota during the last 15 million years during the gradual rise of the Central American land bridge. These data show how important it is to know the context in which they first evolved to properly understand modern species ecology and adaptation.

*Shallow-water benthic communities, speciation, extinction, environmental change*

### INTRODUCTION

Central America is a good example of the drama brought about by the fundamental forces at work on earth. This is one of the most complicated regions in the world, both in its geological structure and in the variety of its expression. The same complexity can be observed in the evolutio-

nary history of its biota. Several key events shaped the tropical American biota during the last ten million years. The gradual formation of the Central American Isthmus lead to different oceanographic conditions and marine systems on both sides of the barrier connecting the northern and

southern terrestrial biotas with dramatic consequences. The development of the barrier changed the global oceanic circulation, strengthening the Gulf Stream and eventually triggering the northern hemisphere's glaciation. Ultimately, both events lead to a series of extinction and speciation events that changed the tropical American marine life about two million years ago (Vermeij 1987; Collins et al. 1999; Allmon et al. 1993; Allmon 2001; Todd et al. 2002). On land, human groups migrating across Central America at the end of the last glacial period lead most probably to the extinction of most of the large vertebrate species and the subsequent vegetation changes (Webb and Rancy 1996; Webb 1997; Cooke 1997). While there are substantial data concerning the interchange of land animals and plants much less attention has been given to the events that occurred in the shallow coastal waters. The few existing studies concentrated on the

description of a few faunas (Olsson 1922, 1942; Woodring 1925, 1957-1982; Weisborg 1929; Rutsch 1942; Jung 1965, 1969, 1971), but little data concerning environmental and ecosystem changes were available. This situation was due partially to the poor documentation concerning the chronology and stratigraphic framework of the above mentioned events, thus not contributing much to the understanding of the complex interdependence of evolution and environments.

This paper intends to review results from several studies carried out in the region documenting the events that shaped the shallow water marine biota of the once continuous tropical sea as the gradual rise of the Central American land bridge took place during the last 15 million years. These results show how the knowledge of the context in which they first evolved is important for the understanding of modern species ecology and adaptation.

## THE FORMATION OF THE LAND BRIDGE: BRIDGE AND BARRIER

The formation of the Central American Isthmus was a very complex and long process that took several million years to complete. The Central American volcanic arc began forming during the late Cretaceous and continued throughout the Cenozoic as a result of the subduction of the Farallon and later the Cocos and Nazca plates under the Caribbean plate. Continuous Cenozoic volcanic activity at the margin of the continen-

tal Chortis plate (where today lie Nicaragua and Costa Rica) developed the arc in the north (Coates and Obando 1996; Coates et al. 1992). On the other hand, in the western part (near the Panama fracture zone and the Cocos ridge) the volcanism was much higher during the late Miocene but mostly absent afterwards until the Pleistocene (Coates and Obando 1996; Coates et al. 1992). It was also mostly absent to

the east of the Gatun fault zone where a marine valley at least 2,000 meters deep existed until the end of the middle Miocene connecting the Canal basin and the Western Cordillera of northwestern South America (Coates and Obando 1996; Coates et al. 1992).

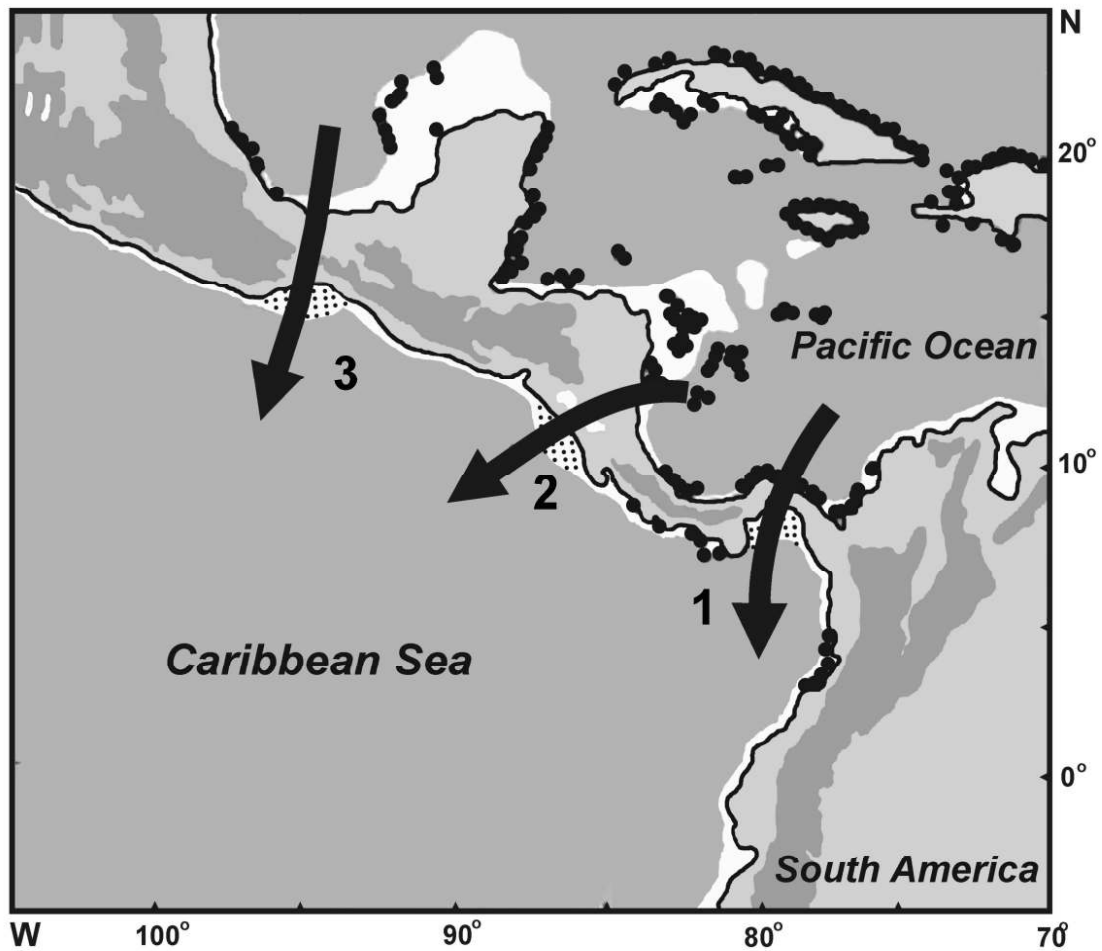
During the middle Miocene the eastern end of the Central American arc collided with the South American plate, bending the Central American plate which acquired its typical "S" shape. Due to the thickness of the Caribbean crust, the suture moves starting the rise of the San Blas-Darien massif and the constriction of the circulation between the Caribbean and the Pacific. This starts the development of an archipelago and the gradual isolation of the sedimentary basins (Coates and Obando 1996; Coates et al. 1992). The last connections between the would be Caribbean and Pacific oceans were probably located between the northwesternmost continental margin of the South American plate in the south, and the southern margin of the continental Chortis block, close to today's Costa Rica-Nicaragua border. Another connection was along the Gatun fault zone. One of the last corridors to close connected the Tempisque, San Carlos and northern Limon basins. Foraminifera distributions indicate that some degree of connectivity was still present as late as 3.1 million years (Collins 1996; Collins et al. 1996).

The formation of the Central American Isthmus was one of the most influential events in the last 15 million years of earth history. The

new barrier changed the climate and oceanographic conditions in both sides, dividing the once continuous ocean into two ecologically different realms providing at the same time, a land bridge for the terrestrial faunas to cross and mix (Fig. 1; Coates 1997).

One of the best-known consequences of the closure of the Panama gateway and the formation of a land bridge between South and North America was the mass migration of animals and plants through the tropics and into the temperate latitudes on both sides (see Stehli and Webb 1985 for examples). The so-called "Great American Biotic Interchange" (Stehli and Webb 1985) started at the very late Miocene and was in itself a truly revolution. Indeed, the deep-water expansion to the east of the Gatun fault zone constituted an absolute barrier to land life, effectively isolating both continents until then.

This migration is believed to have occurred in successive waves. Although by about 8 million years ago, a few island-hopping swimming animals such as raccoons and sloths were probably able to migrate between north and south America using the developing island chain, this was not a major break-through and no other examples appear until much later (Webb and Rancy 1996; Webb 1997). It is only about 3 million years ago that vast numbers of emigrants appear abundant and clearly on both sides of the barrier giving evidence of the existence of a continuous land bridge providing a land route for over a dozen of families and several dozen genera to pass in both directions



**Figure 1** Map of Central America showing the major environmental characteristics of both coasts. Arrows indicate the pass through the mountains for the trade winds. White patches represent the continental platform. Dark circles represent coral reef areas. Stippled areas are zones of upwelling in the eastern Pacific coast: 1- Bay of Panama; 2- Gulf of Papagayo (Costa Rica and El Salvador); 3- Gulf of Tehuantepec (Mexico). (Coates 1997, modified)

(Stehli and Webb 1985). Many of the emigrants from both sides were grazers living in large herds (like horses and llamas from North America, and toxodons and ground sloths from the south). These herds ranging throughout Central America had a heavy impact on the landscape, similar to what grazers have today in African savannahs. They were fol-

lowed suit by carnivores: at least 6 families of North American carnivores spread all through the southern continent with catastrophic impact in native grazers that had never before encountered such efficient hunters (Simpson 1980; Webb and Rancy 1996; Webb 1997).

Fossil evidence shows that this interchange was fast and reached

stability by the early Pleistocene. One of the last comings was the opossum that reached Florida only about 1 million years ago (Webb and Rancy 1996; Webb 1997). This wave of migratory forms at the onset of the land-bridge, was followed by a second phase, ecologically very different from the first one. This time, most of the immigrants came from the Amazon basin and stopped around the area of Veracruz (Mexico). They included mainly birds (toucans, parrots), butterflies, pacas and several species of monkeys. This second wave is the main responsible for the shift of the actual Central American fauna from North American temperate to South American tropical, leading to its inclusion in the Neotropical realm. Recent Central American fauna also bears the consequences of the late Pleistocene extinctions of the large mammals attributed usually to both heavy hunting by human migrations and abrupt climatic changes during the Holocene (Webb and Rancy 1996; Webb 1997; Cooke 1997).

But if changes in the continent were notable, then changes in the seas were dramatic to say the least. Separation of the two oceans stopped the strong westward flow from the Atlantic to the Pacific giving birth to the Gulf Stream. As a result, the warm water from the Tropical Atlantic moves upwards and warms the eastern coast of North America and Western Europe, resulting in precipitation increase and the intensification of the northern hemisphere's glaciation (Coates 1997). This also exemplifies how sensitive global

climate is to geographical changes related to continents and oceans.

The coastlines of Central America show their very different geological origins (Fig. 1). The Caribbean coast is broadly sinuous, forming the western boundary of a semi-isolated sea and an extensive continental platform, with submarine banks that may extend all the way to Jamaica and Cuba which are less than a thousand kilometers away (Jackson and D'Croz 1999). On the other hand, the eastern Pacific coast is pretty much straight and wide open, the platform deepens suddenly and the closest lands are located over 10,000 km to the west. The continental shelf is narrow and closely bounded by the Middle America trench.

Geologic and geographic differences are mirrored in both the oceanographic and biological parameters. The Caribbean coast is part of the extensive western Caribbean system of reef corals, mangroves, and sea grasses that stretches over much the coastline. Under the influence of the warm southern Caribbean current, it is much warmer and saltier, with very little annual variation in spite of heavy rains during most of the year (Jackson and D'Croz 1999). Nutrient levels are low in general, although parts of the Venezuelan and Colombian coast have a weak upwelling (Keigwin 1982). This dramatic drop in primary productivity happened about 3 million years ago, as documented by the fossil record of mollusks, the disappearing of microfossils and sediments rich in phosphates, and fluctuations in oxygen isotopes (Keigwin 1982; Teranes et al. 1996).

On the other hand, the eastern Pacific is extremely vulnerable to periodic disturbances in water movement, atmospheric pressure, and sea surface temperatures (Jackson and D'Croz 1999 and references therein). The resulting El Niño (ENSO) occurs periodically and can greatly vary in intensity (Soon-II An and Bin Wang 2000). The eastern Pacific is affected by the Equatorial Counter current, bounded by the North and South Equatorial currents, flowing to the west and fed by the California and Peru currents. Seasonal and oceanographic fluctuations are quite stronger especially in areas where the gaps in the Central American cordillera allow the trade winds to drive the surface water out to sea, replacing it with deeper, colder water, much denser and rich in nutrients as it happens in the Bay of Panama and the Gulfs of Papagayo and Tehuantepec. Daily tidal range is large and can reach 6 meters or more, following a regular semidiurnal and lunar cycle, and surface seawater temperatures (SSTs) may drop by more than 10 degrees in a few days and can be as low as 15 degrees centigrade during the upwelling season (D'Croz and Robertson 1997; D'Croz and O'Dea 2007).

The ratio of oxygen isotopes in modern shells from the eastern Pacific shows clearly this cycle of warmer wet season followed by colder, dry upwelling season, whereas data from the Caribbean show no temperature variation (Terranes et al. 1996). These differences can also be followed in the fossil record. Indeed, while 0.8-1.9 million years old shells

show the above mentioned contrast, strongly suggesting that the isthmus was already formed by then, shells older than 3 million years show similar profiles for both oceans, indicating less seasonality on the Pacific side and suggesting that the isthmus was still shallow enough to allow cold surface Pacific water to be replaced with warm Caribbean surface water (Terranes et al. 1996).

Due to its uniqueness and relatively recent history, the Central American gateway has been used to document patterns of evolution in a well constrained geologic setup and to study geographic isolation, connectivity and how environmental changes affect life on earth. The closure was not a single event and its biological effects, especially on marine life, stretched probably over time as oceanic circulation, salinity, temperature, habitats, etc. modified over and over. As the archipelago developed, physical heterogeneity would have provided major opportunities for speciation and extinction events. This heterogeneity decreased with the conversion of the archipelago into a sub-continuous barrier. The differences between the marine systems became more clearly defined and stable as the isthmus closed definitively about 2.8 million years ago and both oceans became isolated (Coates 1997). However, the rising land bridge became a barrier probably much earlier, with deep water organisms being the first ones to be affected. Such effects were specific for different taxa depending of their ecological and evolutionary histories.

## CHANGES IN BIODIVERSITY: MECHANISMS AND PROCESSES

Marine sediments deposited in marginal basins and on the marine shelves flanking the volcano chain contain rich deposits of marine fossils which can be used to reconstruct the closure of the gateway. These rich fossil outcrops were first noted and described at the beginning of the 20th century (Woodring 1957-1982) and have been key in many studies of biodiversity, rates of speciation and extinction, degrees of phylogenetic relationships, trends in morphological change, etc.

Neogene mollusks of tropical America are a good example of a group that has been extensively sampled during the last century. Unfortunately, and in spite of several detailed monographs describing faunas ranging from Trinidad through Ecuador and Florida (Olsson 1922, 1942; Woodring 1925, 1957-1982; Weisborg 1929; Rutsch 1942; Jung 1965, 1969, 1971), most studies had a very limited sampling design or none at all. Mostly, they recorded only common taxa and dealt with Miocene and early Pliocene ages and much less with younger faunas. All this led to serious erroneous interpretations of patterns and trends in mollusk diversity in space and time in this region such as the supposed dramatic decline in mollusk diversity in the Western Atlantic during the Pliocene as a result of oceanographic changes driven by the rise of the Panama land bridge and the northern glaciation. Indeed, recent extensive sampling of late Pliocene and Pleis-

tocene faunas shows that diversity did not decrease, but probably even increased towards the Recent (Jackson et al. 1999). Studies show that the progressive isolation of the two oceans as the barrier formed caused major changes in primary productivity that correlate with faunal origination and extinction. Results show that this dramatic re-structuring of the shallow water biota about 2 million years ago was specific in tempo and mode for each taxonomic group (for examples see papers in Jackson et al. 1996; Collins and Coates 1999).

Rates of extinction and origination of mollusk taxa increased enormously towards the end of the Pliocene with an extinction peak at about 2-4 million years ago, whereas origination is pretty much constant throughout the Pliocene (Jackson et al. 1999). However, extinction/origination rates compensated each other in such a way that no net decrease of total biodiversity was observed. This apparent stability in mollusk diversity in the southern Caribbean during the last 10 million years was also noticed in Florida during the Pliocene through the Recent (Allmon 2001; Allmon et al. 1993). But the patterns were different for both gastropods and bivalves. Indeed, in spite of the fact that common gastropods are much more eurytopic than bivalves, 42% of gastropods went extinct during the extinction peak but only 14% of bivalve taxa were affected. Moreover, several mollusk groups did not recover at all from the abrupt decline

at the end of the Pliocene, the so-called paciphile taxa (Jackson et al. 1996, 1999).

Likewise mollusks, corals underwent a serious trend of extinction during this time. Eleven genera of Caribbean reef corals became extinct during the late Pliocene, almost as many as during the previous 20 million years. Only one coral genus originated during the last 3 million years, versus 21 new genera before that. While extinctions of coral genera were mostly confined to the late Pliocene, first appearances were spread over the Miocene. The same trend is observed at species level: most originations occur during the early-late Miocene, and the late Pliocene, while extinctions follow the generic pattern. Changes were also qualitative. Indeed, while *Acropora* Oken, 1815 dominates modern faunas, except in the eastern Pacific where *Pocillopora* Lamarck, 1816 is

the dominant genus since the Miocene. Specific to corals is the earlier start of their originations, the fact that these were spread over a longer period, and the almost absence of recovery after the mass extinction (only 1/3 of the over 100 Miocene species are still alive). As a result, the Caribbean reef fauna is much poorer, and includes Indo-Pacific as well as Caribbean elements (Budd and Johnson 1999).

Nevertheless, some taxa show an extreme stasis and constancy over time. For example, common species of benthic foraminifera hardly changed throughout the Neogene (Collins 1996; Collins et al. 1999). The same can be noticed in cheilostome Bryozoa, with encrusting forms predominantly surviving into the Recent, whereas arborescent forms, and the ones associated with subtidal seagrasses became differentially extinct (Cheetham et al. 1999).

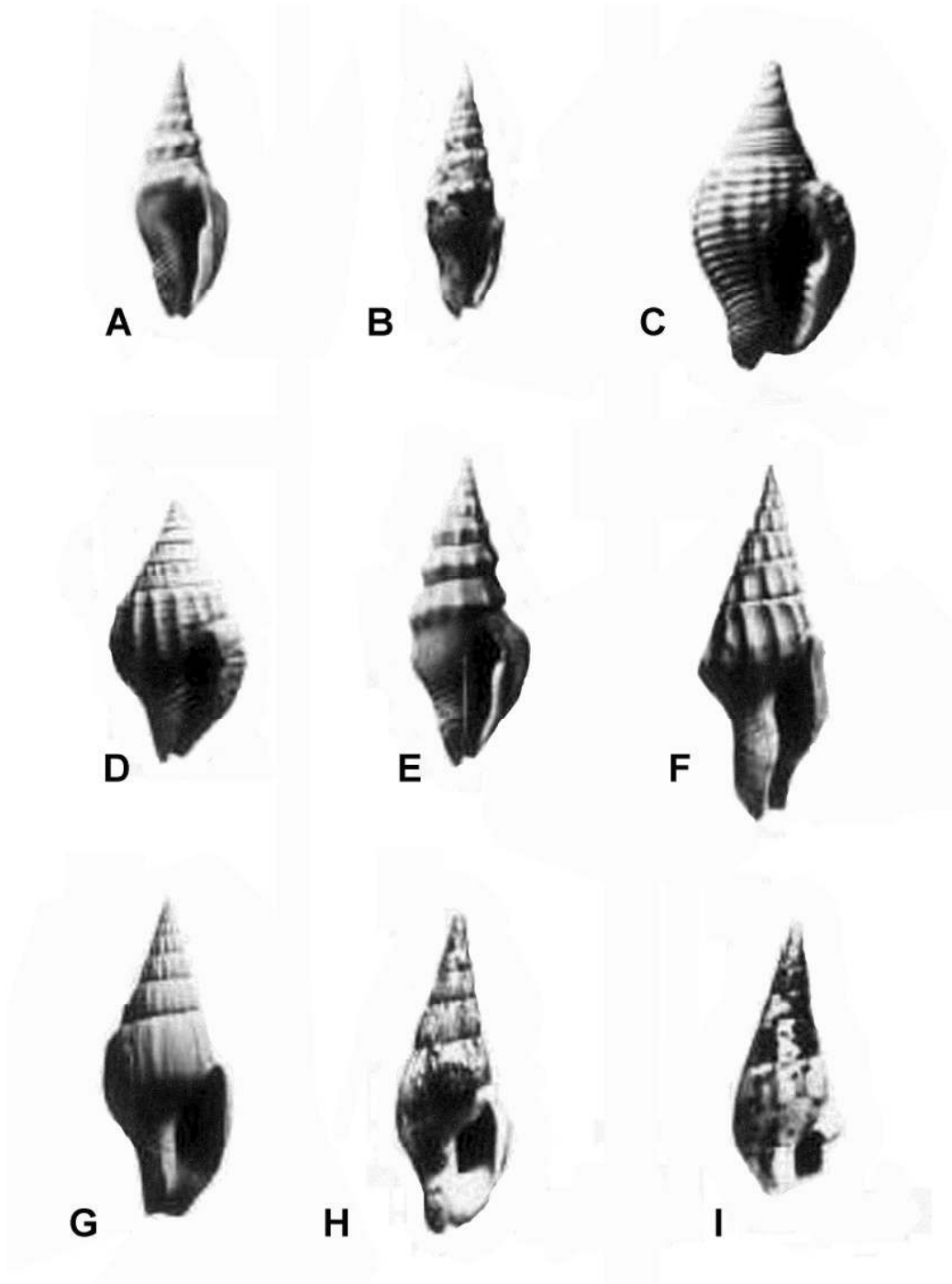
## THE ECOLOGY OF EXTINCTION: BIOGEOGRAPHY, LIFE HISTORIES AND FEEDING MECHANISMS

One of the most intriguing and interesting issues in evolutionary biology are triggers for speciation in the ocean. What are the barriers that lead to geographic isolation and speciation in the sea? Of course, there is no doubt that strong geographical barriers can effectively divide marine populations and lead to the formation of reproductively isolated species. But are these strong barriers really a requirement, or even a common event, for the speciation

process to happen?

Snails of the *Strombina*-group sensu Jung (1989) have been used to quantify the amount of speciation that took place in only one ocean versus that occurring across the developing land barrier (Fortunato 1998). These are small, buccinacean gastropods (Fig. 2) that have inhabited the shallow waters of Tropical America during the last 25 million years. They have been extremely well collected thus being a good





**Figure 2** Species of the *Strombina*-group: (A) *Strombina (Strombina) lanceolata* (Sowerby, 1832), x1; (B) *Strombina (Spiralta) maculosa* (Sowerby, 1832), x1,5; (C) *Strombina (Lirastrombina) pulcherrima* (Sowerby, 1832), x2; (D) *Strombina (Arayina) arayana* Gibson-Smith, 1974, x2; (E) *Strombina (Recurvina) recurva* (Sowerby, 1832), x1,5; (f) *Strombina (Costangula) angularis* (Sowerby, 1832), x1,5; (G) *Cotonopsis (Cotonopsis) panacostaricensis* Olsson 1942, x1,5; (H) *Cotonopsis (Turrina) turrita* (Sowerby, 1832), x1,5; (I) *Clavistrombina clavulus* (Sowerby, 1834), x2.

model to study origination and extinction processes in the context of the closing isthmus.

The group seems to have originated in the Caribbean most probably around the developing archipelago and radiates within the Caribbean Sea (Fortunato 1998). Two pulses of speciation can be documented in its evolutionary history, one before 5 million years ago, and the second afterwards. Almost 67% of all speciation events taking place during the first pulse were related to species living in the forming island arc and only 13% of events occur within one ocean. However, during the second pulse, the pattern is completely reversed: over 65% of speciation events occur within one ocean and only 9% can be attributed to the forming barrier. The percentages of events that can be attributed to the forming barrier are very similar in both pulses: about 20% before 5 million years and a little over 24% after that. About 2 million years ago there was a sudden geographic shift in diversity from the Caribbean to the eastern Pacific (Jackson et al. 1996; Fortunato 1998). This is the famous turn-over event documented for mollusks, corals, bryozoans and several other groups which was the result of the reversal in the speciation/extinction rates during a relatively short time and led to a complete re-build of the Caribbean invertebrate, and possible vertebrate, marine fauna (Allmon et al. 1993; Budd and Johnson 1999; Jackson et al. 1999).

It is commonly thought that environmental changes can act as major

triggers for differentiation leading to life histories shifts (Hellberg 1998). The mode of larval development is commonly associated with dispersal ability, geographic range and longevity of a wide variety of marine benthic invertebrates, as well as rates of extinction and speciation events. With adult stages generally sessile or sedentary, and larvae with different ontogenies spending varying amounts of time developing and presumably dispersing in the plankton, the variation in larval dispersal capability among species can be enormous. While the larvae of some species spend many weeks in the plankton and can be found thousands of kilometers offshore, the larvae of other species will settle side by side with their parents (Jablonski 1986; Jablonski and Lutz 1980; 1983).

Gastropods provide a good system to infer developmental modes for both living and fossil species. Adult shells retain a record of early developmental stages, the so-called protoconch, the size of which reflects the egg size and, consequently, contains information about the presence or absence of a yolky food supply during development. The later is considered to be directly related to dispersal ability. Two types of development can be found in marine gastropods: planktotrophic, with a free swimming and actively feeding larva and usually associated with large dispersal capacity and greater temporal and geographical range of the species; and non-planktotrophic (including direct developers, brooders and lecithotrophic species) where

a larva is either absent or non-feeding until the metamorphosis and recruitment. This type is often associated with endemism, restricted geographical dispersal, low gene flow and, consequently, higher extinction and speciation rates (Jablonski 1986; Jablonski and Lutz 1980, 1983).

Species of the *Strombina*-group show a general increase in the proportion of non-planktotrophs over time. The first species were apparently entirely planktotrophic, but by the early Pliocene non-planktotrophic species represent already 40%. The proportion of non-planktotrophs continued towards the recent where they represent more than half of the living species. Although this increase towards non-planktotrophy happens in both oceans, it is qualitatively different: whereas in the eastern Pacific lecithotrophic taxa constitute 40% of the total, direct development dominates in the Caribbean where two of the three extant species have direct development and the third one is strongly inferred to have also direct development (Fortunato 2002, 2004).

This trend towards loss of planktotrophy with the increase in environmental instability can be followed in whole faunas. Indeed, a survey of modes of development in recent gastropods in both oceans shows that, while over 70% of Caribbean taxa are non-planktotrophs, eastern Pacific taxa show a higher tendency towards planktotrophy (Fortunato 2004).

The trend towards the loss or reduced planktotrophy in the Carib-

bean is observed in many other unrelated groups of marine organisms. Indeed, echinoderm geminate species separated by the Panama barrier, show a tendency towards larger egg sizes in the Caribbean species. Similarly, mean ovicell size in bryozoans are significantly larger in the Caribbean. Likewise, of 19 Caribbean species of corals, 12 are brooders, whereas in the eastern Pacific only two out of 24 species are brooders (Lessios 1990; Richmond and Hunter 1990; Jackson and Cubilla 2000).

Patterns of larval development in recent species reflect probably regional differences in productivity for reasons that are still poorly understood. But regardless of the mechanism, the shift toward non-planktotrophic development in the Caribbean and planktotrophic in the eastern Pacific agrees well with the apparent shift in oceanographic conditions (Fortunato 2004).

The tremendous diversity found in feeding and life habits of mollusks is another parameter that can be used to see how different ecologies answer changing environmental conditions thus helping to understand the mechanisms that led to the heightened pulse of extinction observed at the Plio-Pleistocene boundary in the Caribbean fauna.

From the Miocene throughout the Plio-Pleistocene-Recent abundance of carnivorous gastropod genera and subgenera as well as suspension feeding bivalves show a highly significant decrease without significant differences in taxic diversity (Todd et al. 2002). Indeed, while predatory

gastropods' abundance declined from 63% in the Miocene to about 36% during the late Pliocene through the Recent, with more than 3/4 of this decrease happening during the last 5 million years, no reduction in diversity was noted. On the contrary, there was even a slight increase of the number of taxa during the Pliocene and Recent. Similarly, filter feeders's abundance drops by 20% during the same period, with most of it occurring during the last 5 million years. Once again, there is no drop in taxic diversity (Todd et al. 2002).

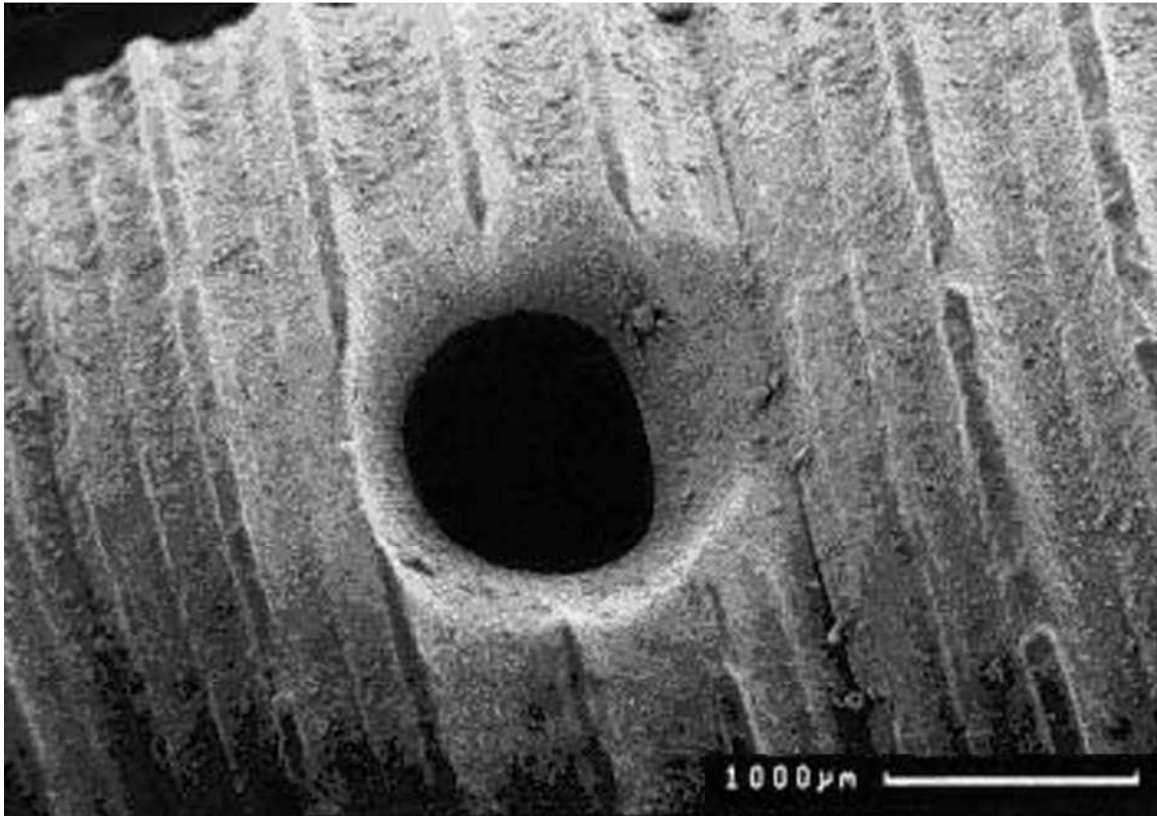
At the same time, a temporal significant increase in all types of deposit feeders and micro carnivores typical of rubble, shell debris and sponge substrates, is observed. This increase, constant from the early Pliocene through the recent, is simultaneous with a gradual replacement of taxa common in cool, nutrient rich waters, by epifaunally cemented or embedded suspension feeding taxa common today in southern Caribbean reef habitats. The whole trend suggesting that productivity decline was indeed a major factor in the turnover in the western Atlantic during the Plio-Pleistocene rise of the Central American barrier (Todd et al. 2002).

The ability to infer patterns from the fossil record relies heavily on the possibility of following those same patterns on recent data, thus allowing the extrapolation of conclusions about past processes. Predation by way of drilling on mollusk shells (Fig. 3) is one of those processes that can be recognized in past assemblages and quantified, allowing us to make

predictions about paleoecological patterns and evolutionary trends such as predator/prey systems, co-evolution and escalation in a time scale.

Drilling intensities in modern eastern Pacific assemblages are almost twice as high as in similar environments in the Caribbean coast. Although the most active predator is the same in both regions (i.e. naticids) only in the eastern Pacific drilling frequency correlates with the abundance of predators. Predation intensity highly correlates with the frequency of preferred prey (turrids and turritelids) in both coasts, but not with general prey abundance (some groups are very abundant but have low drilling intensities) (Fortunato 2007).

Snapping shrimps of the genus *Alpheus* Fabricius, 1798 provide one of the best examples of how the closure of the Panama gateway affected the evolutionary history of the shallow marine fauna (Knowlton 1998). The extent of divergence of seven geminate pairs was measured by molecular differences in proteins and DNA and by the amount of aggression in experimental combats. The study shows that isolation of these pairs did not occur at the same time. The four most similar pairs probably separated about 3 million years ago when the last marine connections were cut. Assuming constant rates of divergence, the most dissimilar pairs must have separated more than 7 million years ago, when the oceans were still connected by shallow seaways. Most interesting, this pattern correlates closely with



**Figure 3** Borehole made by a naticid snail in a turrillid snail shell, Gatun Formation, Panama.

the ecology of the studied taxa: the four most closely related pairs occur in the mid intertidal zone along the mainland, which was probably the last habitats to be isolated by the

closure of the isthmus, while the most divergent pairs inhabit deeper water, offshore habitats, which presumably became isolated earlier (Knowlton 1998).

## CONCLUSIONS

An important question remains: what triggered the profound community re-structuring observed during the establishment of the barrier? All available data suggest that productivity decline was probably the major factor responsible for the faunal turnover that happened in the Western Atlantic during the Plio-Pleistocene rise of the Central Amer-

ican barrier. The slowly diversification and expansion over the last three million years of coral reefs and the development of shallow water seagrass communities with their characteristic fauna of deposit feeders agrees with a profound decline in planktonic primary productivity and the increase in water temperatures predicted by the oceanographic

changes brought about by the rise of the Panama land bridge (Jackson et al. 1999; Budd and Johnson 1999; Todd et al. 2002). High rates of origination and extinction towards the end of the Pliocene were also documented for the mollusk faunas of Florida, followed by much lower rates of evolution thereafter (Stanley 1986; Allmon 2001). Vermeij (1987) points to a decline in predatory organisms and predation intensities in general in the Caribbean region after the Plio-

Pleistocene boundary.

In conclusion, we can assume that the asynchronous dynamics of the turnover shown by different taxa suggest a long period of regional escalation and community reorganization. The changes in the post-isthmian Caribbean region were so profound and are so well documented that it can be used today as a case study to provide a baseline to study the effects of environmental changes in whole communities.

*I am grateful to Dr. Roberto Bruno and Dr. Mirella Martinez who reviewed the manuscript. This work was supported by the German Research Foundation (DFG) Mercator visiting professorship to Dr. Helena Fortunato.*

## REFERENCES

- Allmon, W. D. (2001): Nutrients, temperature, disturbance and evolution: a model for the Late Cenozoic marine record of the western Atlantic. *Palaeogeogr. Palaeoclimat. Palaeoecol.* 166, 9-26.
- Allmon, W. D., Rosenberg, G., Portell, R. W., Schindler, K. S. (1993): Diversity of Pliocene to Recent Atlantic coastal plain mollusks. *Science* 260, 1626-1628.
- Budd, A.F., Johnson, K. G. (1999): Origination preceding extinction during Late Cenozoic turnover of Caribbean reefs. *Paleobiol.* 25, 188-200.
- Cheetham, A. H., Jackson, J. B. C., JoAnn, S., Ventocilla, Y. (1999): Neogene cheilostome Bryozoa of tropical America: Comparison and contrast between the Central American isthmus (Panama, Costa Rica) and the North-Central Caribbean (Dominican Republic). In: Collins, L. S., Coates, A. G. (Eds.), *A Paleobiotic survey of Caribbean faunas from the Neogene of the Isthmus of Panama*. *Bull. Am. Paleon.* 357, 159-192.
- Coates, A. G. (1997): The forging of Central America. In: Coates, A. G. (Ed.), *Central America: A natural and cultural history*, 1-37, Yale University Press, New Haven.
- Coates, A. G., Obando, J. A. (1996): The geologic evolution of the Central American Isthmus. In: Jackson, J. B. C., Budd, A. F., Coates, A. G. (Eds.), *Evolution and Environment in Tropical America*, 21-56, University of Chicago Press, Chicago.
- Coates, A. G., Jackson, J. B. C., Collins, L. S., Cronin, T. M., Dowsett, H. J., Bybell, L. M., Jung, P., Obando, J. (1992): Closure of the Isthmus of Panama: the near-shore marine record of Costa Rica and Western Panama. *GSA Bull.* 104, 814-828.
- Collins, L. S. (1996): Environmental changes in Caribbean shallow waters relative to the closing of the tropical American seaway. In: Jackson, J. B. C., Budd, A. F., Coates, A. G. (Eds.), *Evolution and Environment in Tropical*

- America, 130-167, University of Chicago Press, Chicago.
- Collins, L. S., Coates, A. G. (1999): A Paleobiotic Survey of Caribbean Faunas from the Neogene of the Isthmus of Panama. *Bull. Am. Paleon.* 357, 1-351.
- Collins, L. S., Budd, A. F., Coates, A. G. (1996): Earliest evolution associated with closure of the Tropical American Seaway. *Proc. Nat. Acad. Sci. USA* 93, 6069-6072.
- Collins, L. S., Aguilera, O., Borne, P. F., Cairns, D. (1999): A paleoenvironmental analysis of the Neogene of Caribbean Panama and Costa Rica using several phyla. *Bull. Am. Paleon.* 357, 81-87.
- Cooke, R. (1997): The native peoples of Central America during Precolumbian and Colonial times. In: Coates, A.G. (Ed.), *Central America, a natural and cultural history*, 137-176, Yale University Press, New Haven.
- D'Croz, L., O'Dea, A. (2007): Variability in upwelling along the Pacific shelf of Panama and implications for the distribution of nutrients and chlorophyll. *Estuar. Coast. Shelf. Sci.* 73, 325-340.
- D'Croz, L., Robertson, D. R. (1997): Coastal oceanographic conditions affecting coral reefs on both sides of the Isthmus of Panama. *Proceedings of the eight International Coral Reef Symposium 2*, 2053-2058.
- Fortunato, H. (1998): Reconciling observed patterns of temporal occurrence with cladistic hypotheses of phylogenetic relationship. *Am. Mal. Bull.* 4, 2, 191-200.
- Fortunato, H. (2002): Reproduction and larval development of the *Strombina*-group (Buccinoidea: Columbelloidea) and related gastropods: testing the use of the larval shell for inference of development in fossil species. *Boll. Malacol.* 4, 111-126.
- Fortunato, H. (2004): Reproductive strategies in gastropods across the Panama seaway. *Invert. Reprod. Devel.* 46, 139-148.
- Fortunato, H. (2007): Naticid gastropod predation in the Gatun Formation (late Middle Miocene), Panama: preliminary assessment. *Paläont. Zeitschr.* 81, 356-364.
- Hellberg, M. E. (1998): Sympatric sea-shells along the sea's shore: the geography of speciation in the marine gastropod *Tegula*. *Evolution* 52, 1311-1324.
- Jackson, J. B. C., D'Croz, L. (1999): The Ocean Divided. In: Coates, A. G. (Ed.), *Central America: A natural and cultural history*, 38-71, Yale University Press, New Haven.
- Jackson, J. B. C., Herrera Cubilla, A. (2000): Adaptation and constraints as determinants of zooid and ovicell size among encrusting ascophoran cheilostome Bryozoa from opposite sides of the Isthmus of Panama. In: Herrera Cubilla, A., Jackson, J. B. C. (Eds.), *Proceedings 11<sup>th</sup> International Bryozoology Association Conference 249-258*, Smithsonian Tropical Research Institute, Panama.
- Jackson, J. B. C., Budd, A. F., Coates, A. G. (1996): Evolution and environment in tropical America. University of Chicago Press, Chicago.
- Jackson, J. B. C., Jung, P., Fortunato, H. (1996): Paciphilia revisited: transisthmian evolution of the *Strombina*-group (Gastropoda: Columbelloidea). In: Jackson, J. B. C., Budd, A. F., Coates, A. G. (Eds.), *Evolution and Environment in Tropical America*, 234-270, University of Chicago Press, Chicago.
- Jackson, J. B. C., Todd, J. A., Fortunato, H., Jung, P. (1999): Diversity and assemblages of Neogene Caribbean Mollusca of lower Central America. In: Collins, L. S., Coates, A. G. (Eds.), *A Paleobiotic survey of Caribbean faunas from the Neogene of the Isthmus of Panama*. *Bull. Am. Paleon.* 357, 193-230, Paleontological Research Institution, New York.
- Jablonski, D. (1986): Larval ecology and macroevolution in marine invertebrates. *Bull. Mar. Sci.* 9, 565-587.

- Jablonski, D., Lutz, R. D.* (1980): Molluscan larval shell morphology. Ecology and paleontological implications. In: Rhoads, D., Lutz, R. D. (Eds.), Skeletal growth of aquatic organisms, 323-377, Plenum Press, New York.
- Jablonski, D., Lutz, R. D.* (1983): Larval ecology of marine benthic invertebrates: Paleobiological implications. *Biol. Rev.* 58: 21-89.
- Jung, P.* (1965): Miocene Mollusca from the Paraguana Peninsula, Venezuela. *Bull. Amer. Paleon.* 49, 223, 385-652.
- Jung, P.* (1969): Miocene and Pliocene mollusks from Trinidad. *Bull. Amer. Paleon.* 55, 247, 289-657.
- Jung, P.* (1971): Fossil mollusks from Carriacou, West Indies. *Bull. Amer. Paleon.* 61, 269, 147-262.
- Jung, P.* (1989): Revision of the *Strombina*-Group (Gastropoda: Columbellidae), Fossil and Living. *Schweiz. paläont. Abh.* 111, 1-298.
- Keigwin, L. D.* (1982): Isotopic paleoceanography of the Caribbean and east Pacific: role of the Panama uplift in late Neogene time. *Science* 217, 350-353.
- Knowlton, N.* (1998): New dates and new rates for divergence across the Isthmus of Panama. *Proc. Roy. Soc. London B* 265, 2257-2263.
- Lessios, H. A.* (1990): Adaptation and phylogeny as determinants of egg size in echinoderms from the two sides of the Isthmus of Panama. *Am. Nat.* 135, 1-13.
- Olsson, A. A.* (1922): The Miocene of northern Costa Rica, with notes on its general stratigraphic relations 1. *Bull. Am. Paleon.* 9, 39, 1-168.
- Olsson, A. A.* (1942): Tertiary and Quaternary fossils from the Burrica Peninsula of Panama and Costa Rica. *Bull. Am. Paleon.* 27, 106, 153-259.
- Richmond, R. H., Hunter, C. L.* (1990): Reproduction and recruitment of corals: comparisons among the Caribbean, the tropical Pacific and the Red Sea. *Mar. Ecol. Prog. Ser.* 60, 185-203.
- Rutsch, R. F.* (1942): Die Mollusken der Springvale-Schichten (Obermiocaen) von Trinidad (Britisch-West-Indien). *Verh. Nat. Ges. Basel* 54, 96-182.
- Simpson, G. G.* (1980): Splendid isolation: The curious history of South American mammals. Yale University Press, New Haven.
- Soon-Il An, Bin Wang* (2000): Interdecadal Change of the Structure of the ENSO Mode and Its Impact on the ENSO Frequency. *J. Clim.* 13, 2044-2055.
- Stanley, S. M.* (1986): Anatomy of a regional mass extinction: Pliocene-Pleistocene decimation of the Western Atlantic bivalve fauna. *Palaios* 1, 17-36.
- Stehli, F., Webb, S.* (1985): The great American biotic interchange. Plenum Press, New York.
- Teranes, L., Geary, D. H., Bemis, B. E.* (1996): The oxygen isotope record of seasonality in Neogene bivalves from the Central American Isthmus. In: Jackson, J. B. C., Budd, A. F., Coates, A. G. (Eds.), *Evolution and Environment in Tropical America* 105-120, University of Chicago Press, Chicago.
- Todd, J. A., Jackson, J. B. C., Johnson, K. G., Fortunato, H., Heitz, A., Alvarez, M., Jung, P.* (2002): The ecology of extinction: molluscan feeding and faunal turnover in the Caribbean Neogene. *Proc. Roy. Soc. London B* 269, 571-577.
- Vermeij, G. J.* (1987): *Evolution and Escalation. An ecological history of life.* University Press, Princeton.
- Webb, D. S.* (1997): The great American faunal interchange. In: Coates, A. G. (Ed.), *Central America, a natural and cultural history*, 97-122, Yale University Press, New Haven.
- Webb, D. S., Rancy, A.* (1996): Late Cenozoic evolution of the Neotropical mammal Fauna. In: Jackson, J. B. C., Budd, A. F., Coates, A. G. (Eds.), *Evolution and Environment in Tropical America*, 335-358, University of Chicago Press, Chicago.
- Weisbord, N. E.* (1929): Miocene Mollus-



- ca of northern Colombia. Bull. Amer. Paleon. 14, 54, 1-57.
- Woodring, W. P. (1925): Miocene mollusks from Bowden, Jamaica; part 1, pelecypods and scaphopods. Carnegie Institution of Washington, Publ. 366, 1-222.
- Woodring, W. P. (1957-1982): Geology and paleontology of the Canal zone and adjoining parts of Panama. U. S. Geological Survey Professional Paper 306 (A-F), 1-759.
- 

*Dr. Helena Fortunato (fortunatomh@hotmail.com)  
Institut für Geowissenschaften der Christian-Albrecht-Universität  
Ludewig-Meyn-Strasse 10, D-24118 Kiel*