

## TIMING OF THE OCEANOGRAPHIC AND BIOLOGICAL ISOLATION OF THE CARIBBEAN SEA FROM THE TROPICAL EASTERN PACIFIC OCEAN

*Jeremy BC Jackson and Aaron O’Dea*

### ABSTRACT

Geological uplift along the Central American Arc began in the Eocene with extensive development of emergent terrains by the early Miocene. Nevertheless, three independent lines of evidence are consistent with abundant seawater exchange between the oceans until about 4.7–3 Ma. (1) Isotopic and sedimentary data from ocean cores demonstrate that divergence in surface salinity and deep-sea carbonate accumulation between the Caribbean and eastern Pacific did not occur until 4.7–4.2 Ma. Moreover, strong upwelling comparable to the Pacific today persisted in Caribbean shelf environments until 4.5–3.5 Ma. (2) North and South American terrestrial mammals and tropical forest bird faunas remained overwhelmingly isolated until about 3 Ma. Some birds flew across the seaway and numerous small amphibians and plants began mixing millions of years earlier as expected due to their high probability of rafting. The rarity and ambiguity of reported exceptions to these result after a century of intensive sampling strengthen the general pattern. (3) Bathyal foraminifera first separated across the developing Isthmus approximately 13 Ma but numerous mollusks and cheilostomes are known from both oceans until the Middle Pliocene. Some species now restricted to the Pacific persisted in the Caribbean until the Pleistocene, but no species known to have originated after the Early Pliocene occurs in both oceans except for dispersal by shorebirds or human introductions. Molecular clock estimates for the timing of divergence of taxa strongly support these patterns. Isolation of the Caribbean from the Pacific about 3 Ma provides a robust model system for the study of vicariance in the oceans.

The timing of the formation of the Isthmus of Panama and the consequent isolation of the Caribbean Sea from the tropical eastern Pacific (TEP) have long been of fundamental interest to geologists, biologists, and oceanographers (Schuchert 1935, Mayr 1954, Woodring 1966, Lessios 1981, 2008, Stehli and Webb 1985, Vermeij and Petuch 1986, Coates et al. 1992, Jackson et al. 1993, 1996a, Schmidt 2007). The consensus view is that isolation began about 20–25 Ma with the initial development of the Central American island arc with subsequent gradual restriction of the connecting seaways until final closure of the last seaway about 3.5–3 Ma (Coates et al. 2004, Coates and Stallard 2013). This view is strongly supported by a wide variety of paleoceanographic, paleontological, and molecular phylogenetic data. More recently, however, extensive new and detailed geological, geochemical, and geophysical analyses have provided a much more detailed picture of the early formation and uplift of the Central American island arc that resulted in extensive emergent terrains between 25 and 15 Ma (Farris et al. 2011, Montes et al. 2012a,b). This discovery has led to speculation that the oceans were entirely isolated about 15 Ma, >10 Ma earlier than the consensus view.

Reconciliation of these very different perspectives for the timing of isolation of the oceans is complicated by differences in the central questions posed by geologists,

oceanographers, and biologists, the kinds of evidence most relevant to their solution, and the inherent limitations in the different proxies employed to estimate past geographic and environmental conditions. Geologists use the composition of rocks and minerals, the timing and extent of volcanic events, structural and stratigraphic evidence, and geochemical calculations of rates of cooling to determine the timing of the collision among tectonic blocks of North and South America with the neighboring oceanic plates to reconstruct the formation and uplift of the Central American island Arc. However, the inherent incompleteness of the geological rock record precludes paleogeographic reconstruction on the scale of a few tens to hundreds of kilometers that are sufficient for significant oceanographic and marine biological exchange.

Oceanographers use variations in stable isotopes of carbon and oxygen from skeletons, biological proxies, and changes in sediment composition to calculate changes in the properties of ancient seawater and implied rates of restriction of seawater exchange between the oceans. Estimates of changes in paleobathymetry based on assemblages of benthic foraminifera and stratigraphic evidence are used to corroborate the divergence in seawater properties. Proxies for seawater properties are powerful indicators of oceanic conditions on a grand scale of thousands of kilometers. It is not always clear, however, what the proxies are measuring, as in the well-known example of fluctuations in  $\delta^{18}\text{O}$  that reflect both changes in temperature and salinity.

Paleontologists and biologists use the fossil record of the first appearance of terrestrial taxa north and south of the Isthmus, as well as molecular phylogenetic data from extant populations at varying distances from the Isthmus, to estimate when the physical connection between the continents was sufficiently established for the exchange of northern and southern biotas. Occurrences of marine taxa and their morphological and molecular genetic divergences between the oceans provide estimates of the timing and rates of the isolation of Caribbean and TEP biotas and their ecological and evolutionary divergence. Fossils provide direct biogeographic evidence of occurrence but are notoriously patchy in time and space raising problems of missing data. In contrast, molecular phylogenies provide indirect evidence of rates of divergence. The resulting estimates of divergence are hampered, however, by assumptions of static geographical distributions (that source populations were always where we find their descendants today) and low levels of extinction (few missing lineages), neither of which are likely to be true.

Here we address the history of the seaway connection between the TEP and Caribbean with regard to the gradual restriction and ultimate isolation of oceanic and biological exchange between the two oceans. Our emphasis is on paleoceanographic and biological data that pertain directly to the question of marine biological exchange.

#### PALEOCEANOGRAPHIC EVIDENCE

Compelling evidence for divergence in properties of seawater from opposite sides of the developing isthmus, and thus the isolation of the oceans, comes from multiple independent lines of evidence. These include estimates of (1) variations in temperature and salinity based upon stable isotopic fractionation from the skeletons of foraminifera from deep ocean cores (Keigwin 1982a,b, Haug and Tiedemann 1998, Haug et al. 2001), (2) changes in sediment chemistry (L Collins

1996, Collins et al. 1996a, Haug and Tiedemann 1998, O'Dea et al. 2007), (3) seasonal fluctuations in temperature derived from morphological and isotopic variability measured within the skeletons of individual bryozoan colonies and mollusk shells (Teranes et al. 1996, O'Dea and Jackson 2002, O'Dea et al. 2007, Robbins et al. 2012, Tao et al. 2013), and (4) proxies for planktonic productivity based on growth rates of oysters (Kirby and Jackson 2004) and the relative abundance of different taxa of benthic foraminifera (L Collins 1996). In addition, estimates of stratigraphic changes in paleobathymetry based on the occurrence of benthic foraminifera provide a record of the shallowing of seaway connections between the oceans (Duque-Caro 1990, Coates et al. 2004) that can be compared to estimates of changes in seawater conditions.

Keigwin (1982a,b) analyzed interoceanic differences in oxygen isotopes from skeletons of the planktonic foraminifera *Globigerinoides sacculifer* (see Online Appendix for species authorities) from Deep Sea Drilling Project (DSDP) Site 502 in the southwestern Caribbean and Site 503 in the TEP from 6 to 2 Ma (Fig 1). Divergence in values of  $\delta^{18}\text{O}$  between the oceans began approximately 4.2 Ma and persisted thereafter. Keigwin interpreted these results as a signal of rising Caribbean salinity relative to the TEP due to constriction of the isthmian seaway. He also observed increased differences in  $\delta^{13}\text{C}$  from the benthic foraminifera *Cibicidoides* from the same cores at 6 Ma and again at 3 Ma that he interpreted as a signal for decreased deep-water exchange between the oceans. Keigwin concluded that modern circulation patterns within the Caribbean and eastern Pacific were fully established by about 3 Ma.

Others have repeated Keigwin's approach with denser isotopic sampling of different pairs of cores. Haug et al. (2001) analyzed oxygen isotopes in *G. sacculifera* from Ocean Drilling Program (ODP) Site 999 in the southwest Caribbean and Site 851 in the TEP. Values of  $\delta^{18}\text{O}$  began to diverge at approximately 4.7 Ma and reached modern levels equivalent to a difference in salinity between the oceans of approximately 1.5 by 4.2 Ma. Subsequent studies of cores extending from the equatorial Atlantic through the Caribbean to the Florida Straits further support the model of decreased seawater exchange through the Central American Seaway, the concomitant build-up of the salinity contrast between the Atlantic and Pacific, and fundamental reorganization of Caribbean circulation patterns with increased transport of high salinity water into the North Atlantic (Steph et al. 2006).

Haug and Tiedemann (1998) also calculated deep-sea carbonate sand fraction mass accumulation rates at ODP Site 999 and a different TEP core from ODP Site 846. Accumulation rates were near zero in both the Caribbean and TEP up to 4.6 Ma, after which accumulation rates sharply increased in Caribbean samples for reasons the authors attribute to changes in deep ocean circulation consistent with Keigwin's  $\delta^{14}\text{C}$  results. Increased accumulation of Caribbean carbonate is also supported by disproportionate increases in the diversification of carbonate associated benthic foraminifera and reef corals during the Late Miocene (L Collins 1996, Collins et al. 1996a).

Molnar (2008) suggested that differences in salinity do not of themselves require closure of the seaway connection between the oceans that might also be explained by a shift from a permanent El Niño-like state to the modern El Niño-Southern Oscillation (ENSO) state today. However, the hypothesis that the TEP experienced permanent El Niño conditions in the Pliocene (Wara et al. 2005)



Figure 1. Section of tropical America (A) and the Isthmus of Panama (B) with principal locations discussed in the text and approximate position of key Ocean Drilling Program (ODP) and Deep Sea Drilling Program (DSDP) sites.

remains unresolved (see Rickaby and Halloran 2005, Haywood et al. 2007, von der Heydt et al. 2011, Okamura et al. 2013), and the question remains as to what would have caused such a large-scale shift in climatic regimes in the first place?

Independent morphological data for seasonal variations in seawater temperature recorded within the skeletons of bryozoans also support the interpretation of complete seaway closure by about 3.5 Ma (O'Dea et al. 2007). Data are estimates of seasonal ranges in seawater temperature calculated from changes in the surface area of zooids within individual colonies of cupuladriid bryozoans (O'Dea and Okamura 2000a,b). Variation in zooid size in living bryozoans is significantly correlated with the mean annual range in temperature (MART) of the seawater in which the colony grew due to the inverse relationship between zooid size and ambient temperature (references in O'Dea et al. 2012). Adequately replicated measurements of variance in zooid frontal area within colonies provide estimates of MART in seawater within a few degrees centigrade of error (O'Dea and Jackson 2002, O'Dea 2003, Okamura et al. 2011).

Estimates of MART were calculated from 218 colonies from 25 faunal samples of Caribbean fossil cupuladriids ranging in age from 9.0 to 1.4 Ma and 38 Recent

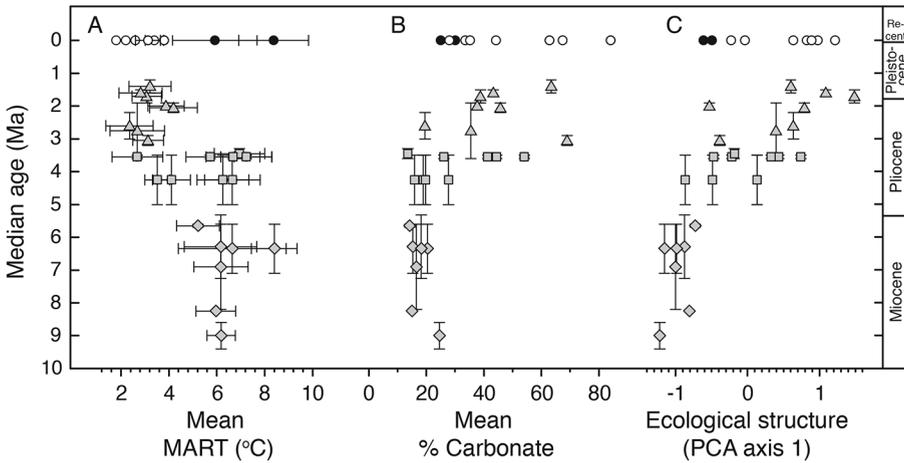


Figure 2. Chronology of environmental and ecological changes in coastal southwestern Caribbean faunules over the last 9 myr. (A) Strength of upwelling revealed from estimates of mean annual range of temperature (MART) calculated by using the zooid size profiling technique on fossil cupuladriid bryozoans. (B) Percent carbonate of  $\leq 2$  mm fraction of coastal sediments. (C) Ecological structure of biotic assemblages estimated by principal components analysis of relative weights of fossil guilds (bivalves, gastropods, corals, bryozoans, fish and echinoid). Horizontal error bars indicate 95% confidence intervals. Vertical error bars indicate maximum and minimum age estimates of faunules. Modified from O’Dea et al. (2007) with permission.

colonies from five Caribbean locations (O’Dea et al. 2007). Sample depths ranged from about 20 to 175 m. Average values of MART decreased by more than half from 6.4 °C (range 5.2–8.7 °C) for samples older than 4.3 Ma to just 3.0 °C (range 1.8–4.2 °C) for samples younger than 3.45 Ma, with intermediate and highly erratic values for samples of intermediate age (mean 5.2 °C, range 2.7–7.2 °C) (Fig. 2A). In contrast, average carbonate content of sediments from the same samples more than doubled from 17.7% for samples older than 4.3 Ma (range 14.3%–24.6%) to 46.7% (range 19.6%–84.2%) for samples younger than 3.5 Ma (Fig. 2B). Seasonal variation in  $\delta^{18}\text{O}$  from closely spaced samples of mollusk shells suggests similar seasonal patterns in temperature (Teranes et al. 1996, Robbins et al. 2012, Tao et al. 2013).

The only mechanism for strong seasonal variations in tropical sea-surface temperature is upwelling that must, therefore, have collapsed along with the reduction in MART in concert with the inferred final closure of the seaway between the oceans approximately 3.5 Ma (O’Dea et al. 2007). Collapse in upwelling implies a similar reduction in planktonic productivity that is further supported by dramatic shifts in the composition of Caribbean benthic communities (Jackson et al. 1993, 1999, Johnson et al. 2007, 2008, O’Dea et al. 2007, Smith and Jackson 2009, Leonard-Pingel et al. 2012) and by sharp reductions in the growth rates of oysters that are suspension feeders on phytoplankton (Kirby and Jackson 2004). Fast growing *Crassostrea cahobasensis* dominated oyster faunas in the Miocene, but was replaced in the Pliocene by slower growing *Crassostrea virginica*. Growth in biomass and shell carbonate in *C. cahobasensis* was 2.5–5 times faster than in *C. virginica*. Further evidence for reduced productivity comes from changes in the composition of benthic foraminiferal paleocommunities from Caribbean ocean

core site 999, most importantly a sharp increase in the abundance of *Nuttalides umbonifera* that is a proxy for oligotrophy (Jain and Collins 2007).

Estimates of paleobathymetry based on assemblages of benthic foraminifera in the pre-Atrato and Atrato Basins of western Colombia (Duque-Caro 1990) are in good agreement with estimates of the timing of constriction and closure of the Panama Seaway based on isotopes and estimates of MART. Water depths >1000–500 m persisted until the end of the Middle Miocene about 13 Ma and shallow water connections >150–100 m only began to be restricted about 7 Ma. However, major changes in current patterns associated with strengthening of the north-south California Current may have effectively severed exchange between the oceans about 13–7 Ma (Duque-Caro 1990). The Atrato marine record ends with the beginning of terrestrial sequence toward the beginning of the Late Pliocene about 3.5 Ma.

A similar scenario exists for all the remaining Neogene sedimentary basins to the west of the Atrato Basin from the Canal Basin in central Panama to the three sedimentary basins of the Chorotega Block comprising most of Costa Rica (Coates and Obando 1996, Coates et al. 2004). In each case, the base of the stratigraphic sequence comprises bathyal sediments as determined by the composition of benthic foraminiferal assemblages, then shallows upwards to shelf depth sediments in the Upper Miocene and Early Pliocene, and ends with marginal marine and terrestrial sediments in the middle to Late Pliocene (Fig. 3).

The most detailed analysis is for the Gatun and overlying Chagres formations along the Caribbean side of the Panama Canal Basin (Collins et al. 1996b). Uppermost Middle Miocene to Upper Miocene Gatun sediments are characterized by shallow water (approximately 25 m) benthic foraminifera and shallow-water mollusks indicating considerable isolation between the oceans. However, the overlying 6 Ma Chagres Formation includes bathyal benthic foraminifera and fish remains of strong Pacific affinity (Collins et al. 1996b, De Gracia 2012). Moreover, the basal Toro Member of the Chagres Formation consists of a cross-laminated sandstone and a shallow-water fauna coquina containing Pacific faunal elements that wedges out to the west with decreasing sediment grain size. This strongly suggests that high-energy currents or tidal waves passed from the Pacific to the Caribbean 6 Ma (Collins et al. 1996b).

In summary, diverse paleoceanographic evidence and the shallowing-upward stratigraphic sequence of bathyal-shelf depths to marginal marine and terrestrial sediments in all of the sedimentary basins of the Chorotega and Choco Blocks consistently corroborate the persistence of bathyal connections between the Caribbean and TEP throughout the Middle Miocene and subsequent gradual shoaling of the remaining seaways to shelf depths of 100–150 m from about 13 to 5 Ma. Subsequent constriction and eventual disappearance of shallow seaways occurred between about 5 to 3 Ma, when values of salinity, temperature, carbonate deposition, and seasonal fluctuations in temperature all strongly diverged.

#### TERRESTRIAL BIOGEOGRAPHIC EVIDENCE

The formation of a dry land connection between the continents triggered rapid intermingling of the long-isolated biotas of North and South America in what stands as one of the most dramatic examples of how regional geological

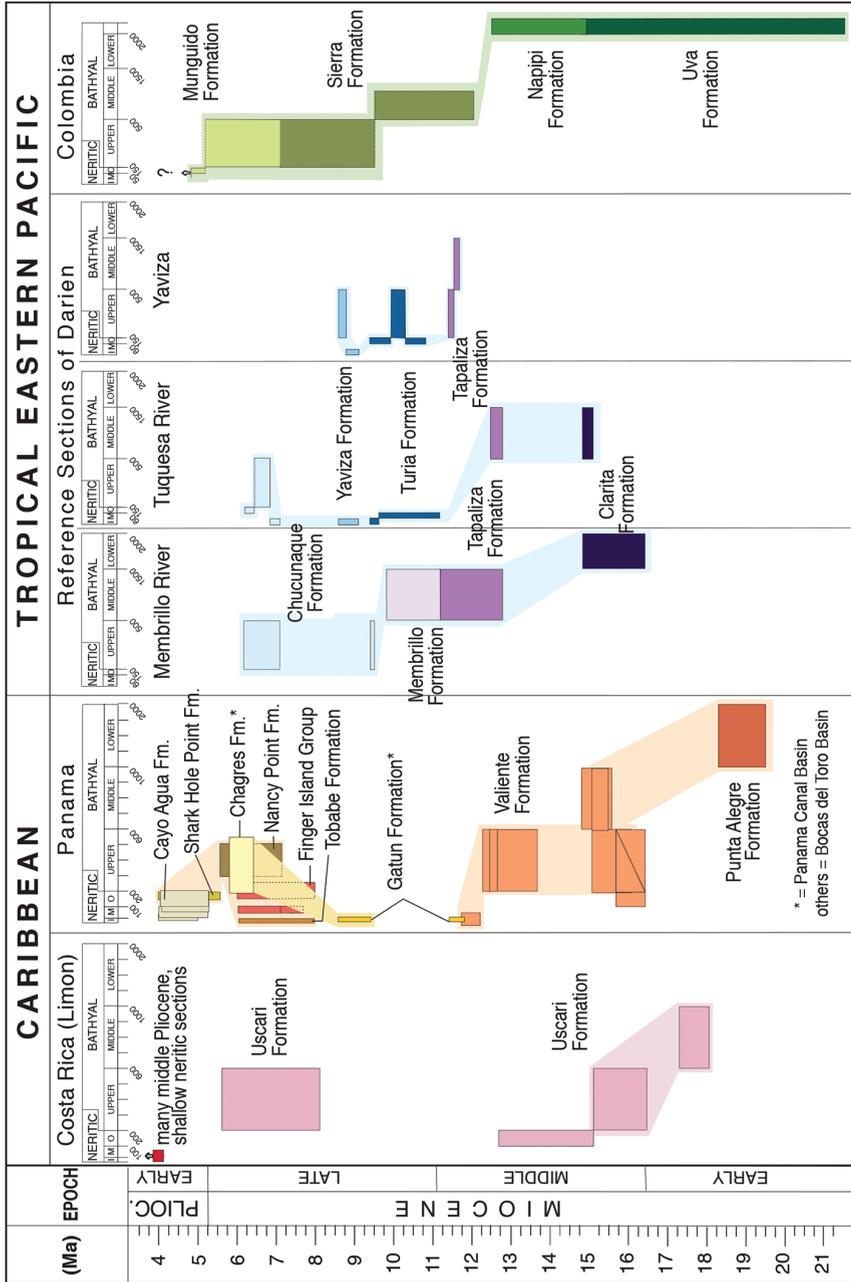


Figure 3. Stratigraphic correlation and paleobathymetric estimates of Neogene formations in Central America and northwestern Colombia. Modified from Coates et al. (2004) with permission.

processes may dramatically alter the composition and distribution of life on earth over continental scales (Stehli and Webb 1985). The overall extent and timing of this Great American Biotic Interchange (GABI) have long been well constrained (Webb 1976, Marshall et al. 1982) and are even more strongly supported by new paleobiological research (MacFadden 2006, Webb 2006, Woodburne et al. 2006, Woodburne 2010, MacFadden et al. 2012). Most of the data are for the fossil occurrences of mammals and other vertebrates from north and south of the Atrato basin in Colombia with more recent contributions from molecular phylogenetic analyses of modern species (Weir et al. 2009, Pinto-Sánchez et al. 2012).

A very few so-called “herald” taxa reached the opposite continent between 7 and 9 Ma, but the overwhelming majority of species failed to make the crossing until about 3.0–2.6 Ma (Webb 2006). This is well after the estimated dates based on paleoceanographic evidence for the final constriction of the shallow-water seaway(s) separating the continents about 3.5 Ma.

Two ground sloths with South American affinities, *Thinobadistes* and *Pliometanastes*, arrived in North America approximately 9 Ma (Tedford et al. 2004). Two other South American sloth genera may have arrived about 4 Ma, although they may have evolved from taxa already in North America (Webb 2006). Moving in the opposite direction, the procyonid (related to modern raccoons) carnivore *Cyanosura* closely related to the North American procyonid *Arctonasua* arrived in northwest Argentina about 7 Ma (Marshall 1985, Flynn and Swisher 1995). Living sloths and raccoons “are particularly adept at floating and swimming, so that they are the most likely groups of land mammals to make water crossings” (Webb 1985, 2006). There are scattered reports that sigmodontine rodents also arrived in South America 6–5 Ma but this is largely discounted due to poor documentation (Webb 2006).

There is a subsequent hiatus of some 5 Ma in the very rich North American mammalian fossil record before the first appearance of several new South American immigrants into central Mexico between 4.6 and 3.1 Ma. These include the armadillo *Plaina*, tank-like edentate *Glyptotherium*, and capybara *Nechoerus* (Miller and Caranza-Castaneda 2001, Flynn et al. 2005, Montellano-Ballasteros and Jimenez-Hidalgo 2006). Then the GABI exploded with the invasion of 21 South American families into southwest North America between 3.04 and 2.58 Ma, and 17 North American families into Argentina 2.7–2.5 Ma (Webb 2006).

The timing of the GABI is all the more remarkable because of the increasingly well-documented occurrence of a diverse, entirely North American mammal fauna in the Early to Middle Miocene (25–14 Ma) Las Cascadas and Cucaracha formations in the Panama Canal Basin (Whitmore and Stewart 1965, Kirby and MacFadden 2005, MacFadden 2006, Kirby et al. 2008, MacFadden et al. 2012). The pace of new discoveries in central Panama is rapidly increasing and the New World tropics may well have been a “cradle of biodiversity” of North American mammals in the Early Miocene (MacFadden et al. 2012). All known Miocene mammals elsewhere in Mesoamerica also show “strict North American affinities” (Ferrusquia-Villfranca 2003).

The fossil record in northern South America is comparatively sparse. However, recent work in the Guajira Peninsula in northeast Colombia has produced a rich Early Miocene to Early Pleistocene fauna of entirely South American affinities and North American migrants are rare throughout the northern South America

region until the Pleistocene (Carrillo et al. 2012). One persistent claim for an earlier Miocene invasion of South America is based on a fauna of proboscideans, tapirs, camelids, and peccaries from Peru underlying an ash deposit dated at 9 Ma (Campbell et al. 2010). The validity of this early date seems highly improbable, however, given the absence of any of these large herbivores from the nearby rich and well-studied Miocene mammalian faunas from Argentina and Bolivia (Webb 2006).

Birds have an extremely poor fossil record compared to mammals so that most of what we know about their migrations north and south of the former seaway is based upon molecular genetic evidence. Weir et al. (2009) analyzed four families of passerines that together comprise about 30% of all New World passerines. Estimated first dates of divergence for generalist species of blackbirds and tanagers (Icteridae and Thraupidae) are about 9–8 Ma. Blackbirds and tanagers also occur on Caribbean islands that, despite considerable disagreement, have not been geologically connected to either the Central or South American mainland for tens of millions of years (Graham 2003, Chackrabarty 2006, Hedges 2006). In contrast, the earliest estimates of divergence for antbirds and woodcreepers (Thamnophilidae and Dendrocolaptidae) that are restricted to tropical forest environments are 4–3 Ma. Forest specialists apparently failed to cross the narrowing seaway until the land connection was complete. These groups have also failed to colonize Caribbean islands. In a similar study, Smith and Klicka (2010) analyzed 135 intraspecific to interfamilial branching events crossing the Isthmus. Diversification between the continents ranged in age from the mid-Miocene to Late Pleistocene, but a remarkable 76% of all the events compiled occurred within the last 4 Ma. Thus, despite being able to fly, the pattern for birds is remarkably similar to that of mammals.

Molecular phylogenetic analyses strongly suggest much earlier divergence across the seaway for numerous frogs, freshwater fishes, and plants that are of uncertain paleogeographic significance because of the absence of a fossil record and the high likelihood of major post-divergence extinction. Moreover, oceanic dispersal is widespread among small animals and plants (de Queiroz 2005). Thus phylogeography is highly inferential based upon modern distributions and in ignorance of where divergence took place.

The túngara frog *Physalaemus pustulosus* first invaded Central America from South America about 6–10 Ma (Weigt et al. 2005). Likewise, at least eight of 11 hypothesized invasions by the South American frog *Pristimantis* into Central America most likely occurred >4 Ma (Pinto-Sánchez et al. 2012). Most remarkably, the very large assemblage of 801 known species of eleutherodactyline frogs have been inferred to have dispersed over water from South America northwards into North America and the Caribbean in the early Cenozoic 47–29 Ma (Heinicke et al. 2007). Eleutherodactylines are notable for breeding out of water and laying their eggs directly on land. Their very early appearance in North America and the Caribbean may reflect dispersal along an early island arc between the continents as the nascent Greater Antilles moved into the Caribbean, dispersal over open water, or both. Rafting of small animals represents an important dispersal mechanism that needs to be taken into account in all such analyses (de Queiroz 2005), as demonstrated by the considerable levels of gene flow amongst *Anolis* lizards across islands in The Bahamas over hundreds of kilometers (Calsbeek and Smith 2003).

The story is even less certain for freshwater fishes because of considerable taxonomic and phylogenetic uncertainties that are only beginning to be analyzed and because many so-called secondary freshwater fishes are tolerant (or may have been tolerant in the past) of a considerable range of salinities. Molecular evidence suggests that invasions of South American stocks into Central America occurred well before 4 Ma, but it is difficult to relate these patterns to the timing of the closure of the seaway because so many of the taxa involved have also colonized Caribbean islands (Bermingham and Martin 1998, Concheiro Pérez et al. 2006) that have long been geologically isolated from either continent (Graham 2003). Likewise, several groups of South American plants that reached Central America >4 Ma are well known to have greater dispersal abilities over water than animals (Cody et al. 2010) and to have colonized Caribbean islands as well as North America (Bacon et al. 2013). Thus, their divergence times based on molecular phylogenies are of little use for establishing the time of the final connection of the continents.

In summary, the terrestrial fossil record for mammals unequivocally supports the existence of a significant barrier between North and South America until 4–3 Ma (Webb 2006), a pattern strongly supported by ecological specialist tropical forest birds (Weir et al. 2009, Smith and Klicka 2010). In contrast, molecular data for lower vertebrates and plants are more complex and indecisive for reasons that are still poorly understood, but almost certainly reflect differences in dispersal ability, the generally underappreciated role of rafting (De Queiroz 2005), and the possible Cretaceous to Paleogene vicariance associated with the movement of the proto–Greater Antilles through the nascent Central American Seaway (Graham 2003, Hedges 2006).

The GABI story for the long isolation of North and South American mammals is also strikingly consistent with everything we know about the recent and fossil distributions of terrestrial vertebrates extending from Southeast Asia through the vast Malay Archipelago island arc to New Guinea and Australia. There, strong biogeographic boundaries have persisted across narrow bathyal gaps of only a few tens to hundreds of kilometers for millions of years (Wallace 1869, Mayr 1944, Simpson 1977). Details vary, but the pattern for mammals is generally well established. Mammals on the large western Indonesian islands of Sumatra, Java, Borneo, and Bali exhibit strong affinities with the continental faunas of Southeast Asia. Just to the east across Wallace's Line, the mammalian fauna on Sulawesi, Lombok, the Lesser Sunda Islands, Timor, and all the other small eastern Indonesian islands exhibits a varying mixture of Asian and Australian elements. The Asian components of this intermediate fauna apparently originated from across the Sunda Sea to the north, and throughout the Quaternary remained virtually isolated from the faunas just to the west across the narrow Makassar and Lombok Straits (van den Bergh et al. 2001). Finally to the east across Lydekker's line, the mammals of New Guinea and Australia are strikingly different descendants of the predominantly marsupial Gondwanan fauna. Yet the distances across the water separating these three great regions are nowhere as great as 200 km.

Narrow seaways are clearly effective barriers to mammalian dispersal, but the existence of North American mammals in central Panama in the Middle Miocene does not require the existence of a peninsula connecting Panama to mainland North America as proposed by Kirby and colleagues (Kirby and MacFadden 2005, Kirby et al. 2008). They based their interpretation on the body size distribution

of fossils from Panama that is similar to that of congeners in mainland North America rather than exhibiting dwarfing as would be expected according to the "island rule" for size distributions of mammals on islands (Van Valen 1973, Lomolino 1985, Kirby and MacFadden 2005). The island rule is generally strongly supported (Lomolino 2005), but remains somewhat controversial because of inconsistent patterns for different taxa (e.g., Schillaci et al. 2009).

Nevertheless, the question remains as to how large an island needs to be for dwarfing to disappear? Data for the tricolored squirrel as a function of island area in Southeast Asia show that the diminishment of body size disappears for islands larger than a few hundred to 1000 km<sup>2</sup> (Heaney 1978). Moreover, body size for insular carnivores is inconsistent with the island rule, although 86% of the data were obtained from islands larger than 2590 km<sup>2</sup> (Meiri et al. 2004, Lomolino 2005). To put this in perspective, the area of the Province of Panama, where the Middle Miocene fossils described by Kirby and MacFadden (2005) are located, is 9633 km<sup>2</sup>. That is nearly four times larger than the area at which the island effects for carnivores virtually disappear (Meiri et al. 2004). Thus, while there is little doubt that the large terrestrial animals that reached central Panama must have arrived there dry-footed, their large size in no way excludes the more likely geological scenario that they arrived there by migration along a highly dynamic landscape of rising and sinking islands along the Central American Island Arc (Coates and Obando 1996), rather than a continuously persistent peninsula stretching all the way to Mexico (Kirby and MacFadden 2005).

#### MARINE BIOGEOGRAPHIC EVIDENCE

The youngest examples of transisthmian species provide the most important marine biological evidence for the final closure of the isthmian seaway. Identification of such occurrences is based on fossil occurrences or inferences on the timing of species divergence from molecular phylogenies (Lessios 2008).

The most complete paleontological data are for bathyal to abyssal benthic foraminifera and neritic to bathyal deposits in the Atrato, Panama Canal, Bocas del Toro, and Limon sedimentary basins (Duque-Caro 1990, L Collins 1996, Collins et al. 1996a,b). The fossil record for Caribbean marine invertebrates is also generally well sampled but the TEP record has large gaps that hamper detailed interoceanic comparison of lineages (Coates et al. 1992, Cheetham et al. 1999, Smith and Jackson 2009). Very few taxa have been investigated using both fossil and molecular data (Marko and Jackson 2001, Marko 2002, Marko and Moran 2009, Jagadeeshan and O'Dea 2012).

Most studies of hypothesized transisthmian evolutionary divergence have focused upon so-called "geminate" species that are morphologically similar presumably sister species that occur on either side of the Isthmus today (T Collins 1996, Lessios 2008). But when fossil data are lacking, it is difficult to know whether the emerging isthmus or some other isolating mechanism was responsible for evolutionary divergence. This is because there is no way of knowing whether the apparent geminates were actually divided by the emerging isthmus or are descendants of species that diverged in one or both oceans due to earlier unrelated events. Without fossils there is also no way to calibrate the molecular clock for calculating divergence times based on data for the specific taxa of interest.

For example, six geminate pairs of arcid bivalves are clearly distinguishable by quantitative morphological techniques (Marko and Jackson 2001). However, both species of one of the pairs, eastern Pacific *Arca mutabilis* and Caribbean *A. imbricata*, were identified using the same quantitative morphological techniques from the Middle Miocene Cantaure Formation in Venezuela as well as younger Caribbean fossil deposits. Moreover, molecular phylogenetic data suggest that divergence between these two species occurred  $63.5 \pm 16.4$  Ma, long before the suggested time of final isolation of the oceans (Marko 2002). Molecular data for three of the other five geminate species pairs also suggest divergence more than 10 Ma, with only two pairs consistent with separation  $>3.5$  Ma. An important caveat, however, is the possibility of cryptic species that are pervasive among marine invertebrates, especially groups that have not been investigated genetically (Jackson and Cheetham 1990, Knowlton 1993). Indeed, Marko and Moran (2009) have shown that at least one of the previously recognized geminate pairs of arcids, *Barbatia (Acar) gradate* and *Barbatia (Acar) domingensis*, is composed of 15 clades. These include four transisthmian lineages of *Acar*, two of which split  $>14$  Ma according to molecular data, and two of which divided about 4–2 Ma. Cryptic species may also be lurking in the other arcid geminate pairs.

Other studies of traditionally defined morphological species of fossil and Recent mollusks suggest exchange between the oceans as recently as about 3 Ma. Beu (2001) reviewed fossil and Recent occurrences of 146 species of tonnoidean gastropods from both sides of the emerging isthmus. He identified numerous putative examples of fossil geminate species pairs extending back to the Miocene and species known as Miocene to Pliocene fossils in the Caribbean that also occur in Pliocene or Pleistocene deposits along the Pacific coast of the Isthmus and in the recent eastern Pacific. Among strombinid gastropods (Jackson et al. 1993, 1996b), Recent *Cotonopsis (Cotonopsis) mendoza* from the TEP is morphologically virtually identical to five specimens of *C. (C.) c. f. mendoza* from the Late Pliocene Caribbean Escudo de Veraguas Formation in Bocas del Toro. Similarly, seven specimens of *Strombina (?Strombina) aff. pumilio* from the Late Pleistocene eastern Pacific Armuelles Formation in the Burica Peninsula are extremely similar to Late Pliocene and Recent Caribbean *S. (S.) pumilio*. Lastly, just two out of 82 Miocene to Recent scallop species from the Caribbean and TEP are common to both oceans between 12.6 to 2.8 Ma (Smith and Jackson 2009).

Molecular and morphologically based phylogenies of fossil and Recent cupuladriid bryozoans provide additional examples of apparently quite recent inter-oceanic exchanges of species (Dick et al. 2003, Herrera et al. 2006, 2008, O'Dea and Jackson 2009, Jagadeeshan and O'Dea 2012). *Cupuladria pacificiensis* and *Cupuladria exfragminis* are common today in the eastern Pacific but also occur as Caribbean fossils, the former from Early Pliocene to Early Pleistocene Caribbean deposits in Panama and Costa Rica, and the latter from the Early Miocene Chipola Formation in Florida and Late Miocene to Late Pliocene deposits in Panama. However, the equivalence of Caribbean fossil *C. exfragminis* and the Recent TEP species remains unresolved. Fossil records and molecular phylogenies of extant cupuladriid species in three clades suggest species divergences in the Late Neogene to Pleistocene (Jagadeeshan and O'Dea 2012), with inferred interoceanic divergences occurring around 7–4 Ma (there are few Neogene fossils from the TEP) and subsequent divergences within the Caribbean occurring later as Caribbean habitats diversified (Jagadeeshan and O'Dea 2012).

Morphologically based phylogenetic analysis of the intensively sampled cheilostome genus *Metrarabdotos* also suggests quite recent speciation across the emerging isthmus (Jackson and Cheetham 1994, Cheetham and Jackson 1996). *Metrarabdotos pacificum* evolved from Caribbean *M. lacrymosum* 2.5 Ma, and its closely related Caribbean sister species *Metrarabdotos unguiculatum* has no fossil record despite extensive sampling, suggesting that it also originated quite recently.

An exceptionally detailed global phylogenetic analysis of rocky intertidal snails in the genus *Echinolittorina* revealed six cases of transisthmian divergence, all considerably >4–3 Ma (Williams and Reid 2004). But there are no fossil data and the authors point out that the apparent geminates are likely to be end points of much earlier divergence unrelated to the emerging isthmus, as shown for species of *Arca* (Marko and Jackson 2001, Marko 2002). However, two additional, solely molecular phylogenetic studies provide especially strong evidence for very recent divergence of species because of the large numbers of species pairs sampled, the exceptional consistency of results, and the strict concordance of different kinds of genetic measures of divergence with the habitats of the species (Knowlton et al. 1993, Knowlton and Weigt 1998, Miura et al. 2010).

Patterns of divergence for allozymes and the COI gene are highly concordant for 15 pairs of snapping shrimp in the genus *Alpheus* (Knowlton and Weigt 1998). Calculations of divergence times based on a molecular clock range from 18 to 3 Ma based on calibration of final closure of the seaway at 3 Ma. These estimates are consistent with molecular clock rates from numerous other well-calibrated molecular studies of divergence. Most importantly, the species pairs with the least, and presumably most recent, genetic divergence occur in marginally marine mangrove environments, whereas species with the greatest, and presumably oldest, genetic divergence are restricted to offshore islands or deeper water environments (Fig. 4). Moreover, aggression among different species within each geminate pair was much less than for species pairs exhibiting stronger genetic divergence (Knowlton et al. 1993). This implies that the isolating mechanisms in species pairs that have been isolated for shorter times have not evolved to be as strong as those for species separated for many more millions of years.

Similar results were obtained for 20 species of coastal marine snails in the genera *Cerithidea* and *Cerithium* (Miura et al. 2010). The authors identified four putative species pairs out of the 20 species. Genetic divergence between geminate pairs varied two-fold with times of divergence based on a molecular clock ranging from 3.1–2.8 to 6.4 Ma. Once again, species pairs with the smallest genetic divergence were from high intertidal and mangrove habitats, whereas those with the highest divergence inhabit low intertidal to subtidal habitats. There is also strong evidence for more recent transisthmian dispersal of one of the geminate pairs by shorebirds (Miura et al. 2011). Eastern Pacific *Cerithideopsis californica* were collected from Santa Barbara to the Gulf of Panama and Caribbean *Cerithideopsis pliculosa* from Texas to Colon, Panama. (These snails were identified as *Cerithidea* by Miura et al. 2010.) Ancestral area analysis combined with molecular dating suggest that dispersal from the eastern Pacific to the Caribbean occurred 750 Ka and a reverse introduction from the Caribbean to the eastern Pacific 72 Ka. Juvenile *Cerithidea* may have been transported on the feathers of wading birds, and adults are known to survive swallowing and subsequent regurgitation by willets days to weeks after feeding (Proctor 1968), which is ample time for transport across the isthmus (Miura et al. 2011).

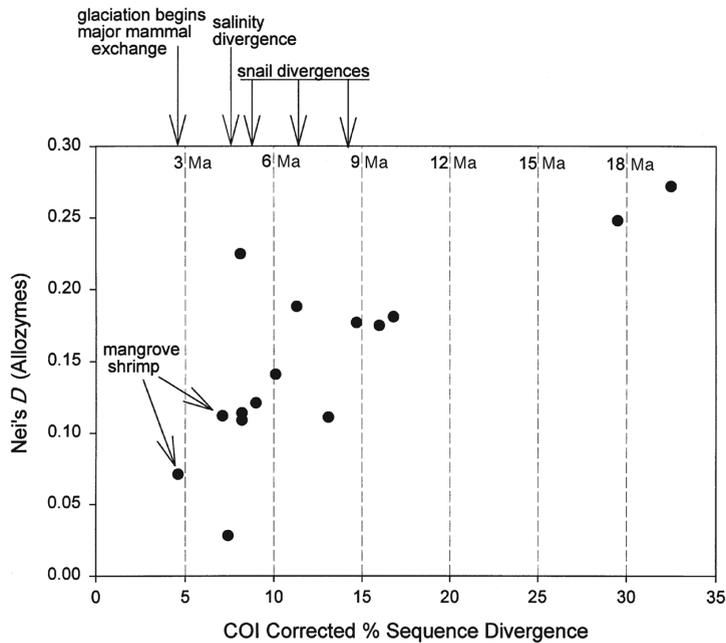


Figure 4. Divergences between 15 pairs of transisthmian snapping shrimp in the genus *Alpheus* as revealed by allozymes and the mitochondrial COI gene. Greatest genetic divergence occurs in species from offshore or deeper water environments while species with minimal genetic divergence inhabit marginally marine mangrove environments. Nei's Genetic Distance ( $D$ ) is the accumulated number of gene substitutions per locus. Modified from Knowlton and Weigt (1998) with permission.

## DISCUSSION

Our analysis shows that paleoceanographic, terrestrial biogeographic, and marine biogeographic data are in striking agreement with the long-established consensus view (Coates and Stallard 2013) regarding the timing of the final isolation of the Caribbean Sea from the TEP approximately 4–3 Ma. Different paleoceanographic proxies demonstrate that seawater properties in the two oceans were virtually identical until 4.7 Ma when they begin to substantially diverge. Numerous examples of exchange of biotas between North and South America occurred 10 Ma or more, but the vast majority of exchanges of mammals, birds, amphibians, and fish occurred about 4 to 2 Ma. This is especially striking for mammals, which have an extensive and well-studied fossil record, and for tropical forest birds that failed to cross the seaway until the continents were connected by dry land. Likewise, numerous lineages of tropical American marine taxa including foraminifera, mollusks, bryozoans, crustaceans, and fishes began to diverge as much as 10–20 Ma, often within the same ocean, but there are also numerous well-documented examples of biological exchange between the oceans as recently as 3 or possibly even 2 Ma. In many cases, these patterns are documented by fossils as well as by molecular phylogenies that are therefore independent of potentially circular assumptions of the time of isolation of the oceans.

So how are we to resolve the apparent disagreement between all these different kinds of oceanographic and biological evidence with the assertion based on geological evidence (Montes et al. 2012a,b) that the barrier between the Caribbean

and tropical eastern Pacific was established ten or more million years before? To some extent the argument is semantic, because in their second paper Montes et al. (2012b) softened their assertion to severing of “the deep water connection” between the oceans. This conclusion is entirely consistent with earlier studies by the Panama Paleontology Project (Coates and Obando 1996, Coates et al. 2004). More fundamentally, however, we believe the disagreement is more apparent than real because geological data cannot possibly resolve paleogeographic landscapes and seaways on the scale of the few 10s of kilometers that can provide for extensive oceanographic exchange (Coates and Stallard 2013).

We need only to examine the geological history and geography of the Malay Archipelago to understand the fundamental oceanographic and biological significance of very small connections between oceans (Coates and Stallard 2013). The Lombok and Ombai Straits and Timor Passage range in depth from 300 to 1450 m and a mere 35 to 160 km in width, dimensions comparable to those reconstructed for the sedimentary basins of the emerging Isthmus of Panama (Coates and Obando 1996, Coates et al. 2004). Yet these three passages accommodate a massive 15 Sverdrups of net throughflow of relatively low salinity water from the Pacific to Indian oceans that is recognizable throughout the entire Indian Ocean basin (Sprintall et al. 2009) and is equivalent to half the flow of the Florida Current just before it joins the Gulf Stream (Larsen and Sanford 1985, Baringer and Larsen 2001). Moreover, patterns of terrestrial and marine biogeography and evolution in the Malay Archipelago exhibit striking parallels with those in tropical America. Numerous mammalian taxa have made their ways east and west across these narrow channels (van den Berg et al. 2001), but the vast majority of Asian and Australian faunas have failed to cross (Wallace 1869, Mayr 1944, Simpson 1977), just as most mammals failed to cross the Central American Seaway between North and South America until 2–3 Ma. Marine taxa also differ widely in their extent of evolutionary divergence through the channels across the Malay Archipelago (Barber et al. 2002, 2006, Nuryanto and Kochzius 2009, Carpenter et al. 2011), just as different taxa have varied widely in their extent of differentiation across the emerging Central American Isthmus.

The validity of the final isolation of the Caribbean from the tropical eastern Pacific about 3 Ma as an example of vicariance in the oceans is strongly supported by the available paleoceanographic and biogeographic evidence.

#### ACKNOWLEDGMENTS

We thank T Coates and N Knowlton for valuable discussions and the entire Panama Paleontology Project team over the past 25 yrs for their innumerable contributions and support. JBCJ was supported by NSF Grant 0921924. AO was supported by the National System of Investigators (SNI) of the National Research Secretariat for Science, Technology, and Innovation of Panama (SENACYT).

#### LITERATURE CITED

- Bacon CD, Mora A, Wagner WL, Jaramillo CA. 2013. Testing geological models of evolution of the Isthmus of Panama in a phylogenetic framework. *B J Linnaean Soc.* 171(1):287–300. <http://dx.doi.org/10.1111/j.1095-8339.2012.01281.x>
- Barber PH, Palumbi SR, Erdmann MV, Moosa MK. 2002. Sharp genetic breaks among populations of *Haptosquilla pulchella* (Stomatopoda) indicate limits to larval transport:

- patterns, causes, and consequences. *Mol Ecol.* 11:659–674. PMID:11972755. <http://dx.doi.org/10.1046/j.1365-294X.2002.01468.x>
- Barber PH, Erdmann MV, Palumbi SR. 2006. Comparative phylogeography of three codistributed stomatopods: origins and timing of regional lineage diversification in the coral triangle. *Evolution.* 60:1825–1830. PMID:17089967.
- Baringer MO, Larsen JC. 2001. Sixteen years of Florida Current transport at 27°N. *Geophys Res Lett.* 28:3179–3182. <http://dx.doi.org/10.1029/2001GL013246>
- Bermingham E, Martin AP. 1998. Comparative mtDNA phylogeography of Neotropical freshwater fishes: testing shared history to infer the evolutionary landscape of lower Central America. *Mol Ecol.* 7:499–517. <http://dx.doi.org/10.1046/j.1365-294x.1998.00358.x>
- Beu AG. 2001. Gradual Miocene to Pleistocene uplift of the Central American Isthmus: Evidence from tropical American tonnoidean gastropods. *J Paleontol.* 75:706–720. [http://dx.doi.org/10.1666/0022-3360\(2001\)075<0706:GMTPUO>2.0.CO;2](http://dx.doi.org/10.1666/0022-3360(2001)075<0706:GMTPUO>2.0.CO;2)
- Calsbeck R, Smith TB. 2003. Ocean currents mediate evolution in island lizards. *Nature.* 426:552–555. PMID:14654839. <http://dx.doi.org/10.1038/nature02143>
- Campbell KE Jr, Prothero DR, Romero-Pittman, Hertel F, Rivera N. 2010. Amazonian magnetostratigraphy: dating the first pulse of the Great American Faunal Interchange. *J S Am Earth Sci.* 29:619–626. <http://dx.doi.org/10.1016/j.jsames.2009.11.007>
- Carpenter KE, Barber PH, Crandall ED, Ablan-Lagman MCA, Ambariyanto, Mahardika GN, Manjaji-Matsumoto BM, Junio-Me-ez MA, Santos MD, Starger CJ, Toha AHA. 2011. Comparative phylogeography of the coral triangle and implications for marine management. *J Mar Biol.* 2011:Article ID 396982.
- Carrillo JD, Vallejo-Pareja MC, Cárdenas AL, Moreno-Bernal JW, Jaramillo C, Jimenez L, Hendy AJW, Jones DS. 2012. The Neotropical fossil record and the Great American Biotic Interchange. *Geol Soc Am, Abstracts with Programs.* 44:163
- Chackrabarty P. 2006. Systematics and historical biogeography of Greater Antillean Cichlidae. *Mol Phylogenet Evol.* 39:619–627. PMID:16495088. <http://dx.doi.org/10.1016/j.ympev.2006.01.014>
- Cheetham AH, Jackson JBC. 1996. Speciation, extinction and the decline of erect growth in Neogene and Quaternary cheilostome bryozoans of tropical America. *In: Jackson JBC, Budd AF, Coates AG, editors. Evolution and environment in tropical America, University of Chicago Press, Chicago.* p. 205–233
- Cheetham AH, Jackson JBC, Sanner J, 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). *Bull Am Paleontol.* 357:159–192.
- Coates AG, Obando JA. 1996. The geologic evolution of the Central American Isthmus. *In: Jackson JBC, Budd AF, Coates AG, editors. Evolution and environment in tropical America. University of Chicago Press, Chicago.* p. 21–56. PMID:8778310
- Coates AG, Collins LS, Aubry M-P, Berggren WA. 2004. The geology of the Darien, Panama, and the late Miocene-Pliocene collision of the Panama arc with northwestern South America. *Geol Soc Am Bull.* 116(11–12):1327–1344. <http://dx.doi.org/10.1130/B25275.1>
- Coates AG, Stallard B. 2013. How old is the Isthmus of Panama? *Bull Mar Sci.* 89:801–813. <http://dx.doi.org/10.5343/bms.2012.1076>
- Coates AG, Jackson JBC, Collins LS, Cronin TM, Dowsett HJ, Bybell LM, Jung P, Obando J. 1992. Closure of the Isthmus of Panama: The near-shore marine record of Costa Rica and western Panama. *Geol Soc Am Bull.* 104:814–828. [http://dx.doi.org/10.1130/0016-7606\(1992\)104<0814:COTIOP>2.3.CO;2](http://dx.doi.org/10.1130/0016-7606(1992)104<0814:COTIOP>2.3.CO;2)
- Cody S, Richardson JE, Rull V, Ellis C, Pennington RT. 2010. The Great American Biotic Interchange revisited. *Ecogeography.* 33:326–332.
- Collins LS. 1996. Environmental changes in Caribbean shallow waters relative to the closure of the Tropical American Seaway. *In: Jackson JBC, Budd AF, Coates AG, editors.*

- Evolution and environment in tropical America. University of Chicago Press, Chicago. p. 130–167.
- Collins LS, Budd AF, Coates AG. 1996a. Earliest evolution associated with closure of the tropical American seaway. *Proc Natl Acad Sci USA*. 93:6069–6072. PMID:11607686. PMCID:PMC39190. <http://dx.doi.org/10.1073/pnas.93.12.6069>
- Collins LS, Coates AG, Berggren WA, Aubry M-P, Zhang J. 1996b. The late Miocene Panama isthmian strait. *Geology*. 24:687–690. [http://dx.doi.org/10.1130/0091-7613\(1996\)024<0687:TLMPIS>2.3.CO;2](http://dx.doi.org/10.1130/0091-7613(1996)024<0687:TLMPIS>2.3.CO;2)
- Collins T. 1996. Molecular comparisons of transisthmian species pairs: rates and patterns of evolution. *In*: Jackson JBC, Budd AF, Coates AG, editors. *Evolution and environment in tropical America*. University of Chicago Press, Chicago. p. 303–334.
- Concheiro Pérez GA, Rican O, Orti G, Bermingham E, Doadiro I, Zardoya R. 2006. Phylogeny and biogeography of 91 species of heroine cichlids (Teleostei: Cichlidae) based on sequences of the cytochrome *b* gene. *Mol Phylogenet Evol*. 43:91–110. PMID:17045493. <http://dx.doi.org/10.1016/j.ympev.2006.08.012>
- De Gracia C. 2012. An exceptional marine fossil fish assemblage reveals a highly productive deep-water environment in the Central American seaway during the Late Miocene. *Geol Soc Am, Abstracts with Programs*. 44:164.
- De Queiroz A. 2005. The resurrection of oceanic dispersal in historical biogeography. *Trends Ecol Evol*. 20:68–73. PMID:16701345. <http://dx.doi.org/10.1016/j.tree.2004.11.006>
- Dick MH, Herrera-Cubilla A, Jackson JBC. 2003. Molecular phylogeny and phylogeography of free-living Bryozoa (Cupuladriidae) from both sides of the Isthmus of Panama. *Mol Phylogenet Evol*. 27:355–371. [http://dx.doi.org/10.1016/S1055-7903\(03\)00025-3](http://dx.doi.org/10.1016/S1055-7903(03)00025-3)
- Duque-Caro H. 1990. Neogene stratigraphy, Paleooceanography, and paleobiogeography in northwest South America and the evolution of the Panama seaway. *Palaeogeogr Palaeoclimatol Palaeoecol*. 77:203–234. [http://dx.doi.org/10.1016/0031-0182\(90\)90178-A](http://dx.doi.org/10.1016/0031-0182(90)90178-A)
- Farris DW, Jaramillo C, Bayona G, Restrepo-Moreno SA, Montes C, Cardona A, Mora A, Speakman RJ, Glascock MD, Valencia V. 2011. Fracturing of the Panamanian Isthmus during initial collision with South America. *Geology*. 37:1007–1010. <http://dx.doi.org/10.1130/G32237.1>
- Ferrusquia-Villfranca I. 2003. Mexico's Middle Miocene mammalian assemblages: an overview. *Bull Am Mus Nat Hist*. 279:321–347. [http://dx.doi.org/10.1206/0003-0090\(2003\)279<0321:C>2.0.CO;2](http://dx.doi.org/10.1206/0003-0090(2003)279<0321:C>2.0.CO;2)
- Flynn JJ, Kowallis BJ, Nu-ez, Carranza-Casta-eda, Miller WE, Swisher CC III, Lindsay E. 2005. Geochronology of the Hemphillian-Blancan aged strata, Guanajuato, Mexico and implications for timing of the Great American Biotic Interchange. *J Geol*. 113:287–307. <http://dx.doi.org/10.1086/428806>
- Flynn JJ, Swisher CC III. 1995. Cenozoic South American land mammal ages: correlation to global geochronologies. *SEPM Special Publication*. 54:317–333.
- Graham A. 2003. Historical phytogeography of the Greater Antilles. *Brittonia*. 55:357–383. [http://dx.doi.org/10.1663/0007-196X\(2003\)055\[0357:HPOTGA\]2.0.CO;2](http://dx.doi.org/10.1663/0007-196X(2003)055[0357:HPOTGA]2.0.CO;2)
- Haug G, Tiedemann R. 1998. Effect of the formation of the Isthmus of Panama on Atlantic Ocean thermohaline circulation. *Nature*. 393:673–676. <http://dx.doi.org/10.1038/31447>
- Haug G, Tiedemann R, Zahn R, Ravelo A. 2001. Role of Panama uplift on oceanic freshwater balance. *Geology*. 29:207–210. [http://dx.doi.org/10.1130/0091-7613\(2001\)029<0207:ROPUOO>2.0.CO;2](http://dx.doi.org/10.1130/0091-7613(2001)029<0207:ROPUOO>2.0.CO;2)
- Haywood AM, Valdes PJ, Peck VL. 2007. A permanent El Niño-like state during the Pliocene? *Paleoceanography*. 22:PA1213. <http://dx.doi.org/10.1029/2006PA001323>
- Heaney LP. 1978. Island area and body size of insular mammals: evidence from the tricolored squirrel (*Callosciurus prevosti*) of Southeast Asia. *Evolution*. 32:9–17. <http://dx.doi.org/10.2307/2407408>

- Hedges SB. 2006. Paleogeography of the Antilles and origin of West Indian terrestrial vertebrates. *Annals Missouri Bot Garden*. 93:231–244. [http://dx.doi.org/10.3417/0026-6493\(2006\)93\[231:POTAAO\]2.0.CO;2](http://dx.doi.org/10.3417/0026-6493(2006)93[231:POTAAO]2.0.CO;2)
- Heinicke MP, Duellman WE, Hedges SB. 2007. Major Caribbean and Central American frog faunas originated by ancient ocean dispersal. *Proc Natl Acad Sci*. 104:10,092–10,097. PMID:17548823. PMCID:PMC1891260. <http://dx.doi.org/10.1073/pnas.0611051104>
- Herrera-Cubilla A, Dick MH, Sanner J, Jackson JBC. 2006. Neogene Cupuladriidae of tropical America. I: taxonomy of Recent Cupuladria from opposite sides of the Isthmus of Panama. *J Paleontol*. 80:245–263. [http://dx.doi.org/10.1666/0022-3360\(2006\)080\[0245:NCOTAI\]2.0.CO;2](http://dx.doi.org/10.1666/0022-3360(2006)080[0245:NCOTAI]2.0.CO;2)
- Herrera-Cubilla A, Dick MH, Sanner J, Jackson JBC. 2008. Neogene Cupuladriidae of tropical America. II: taxonomy of Recent Discoporella from opposite sides of the Isthmus of Panama. *J Paleontol*. 82:279–298. <http://dx.doi.org/10.1666/06-034.1>
- Jackson JBC, Cheatham AH. 1990. Can paleontologists study evolution at the species level? A test using cheilostome Bryozoa. *Science*. 248:579–583. PMID:17791464. <http://dx.doi.org/10.1126/science.248.4955.579>
- Jackson JBC, Cheatham AH. 1994. Phylogeny reconstruction and the tempo and mode of speciation in cheilostome Bryozoa. *Paleobiology*. 20:407–423.
- Jackson JBC, Budd AF, Coates AG, editors. 1996a. *Evolution and environment in tropical America*. University of Chicago Press, Chicago.
- Jackson JBC, Fortunato H, Jung P. 1996b. Paciphilia revisited: transisthmian evolution of the *Strombina* group (Gastropoda: Columbelloidea). *In: Jackson JBC, Budd AF, Coates AG, editors. Evolution and environment in tropical America*. University of Chicago Press, Chicago. p. 234–270.
- Jackson JBC, Jung P, Coates AG, Collins LS. 1993. Diversity and extinction of tropical American mollusks and emergence of the Isthmus of Panama. *Science*. 260:1624–1626. PMID:17810203. <http://dx.doi.org/10.1126/science.260.5114.1624>
- Jackson JBC, Todd JA, Fortunato H, Jung P. 1999. Diversity and assemblages of Neogene Caribbean Mollusca of lower Central America. *Bull Am Paleontol*. 357:193–230.
- Jagadeeshan S, O’Dea A. 2012. Integrating fossils and molecules to study cupuladriid evolution in an emerging Isthmus. *Evol Ecol*. 26:337–355. <http://dx.doi.org/10.1007/s10682-011-9522-6>
- Jain S, Collins LS. 2007. Trends in Caribbean paleoproductivity related to the Neogene closure of the Central American Seaway. *Mar Micropaleontol*. 63:57–74. <http://dx.doi.org/10.1016/j.marmicro.2006.11.003>
- Johnson KG, Todd JA, Jackson JBC. 2007. Coral reef development drives molluscan diversity increase at local scales in the late Neogene and Quaternary of the southwestern Caribbean. *Paleobiology*. 33:24–52. <http://dx.doi.org/10.1666/06022.1>
- Johnson KG, Jackson JBC, Budd AF. 2008. Caribbean reef development was independent of coral diversity over 28 million years. *Science*. 319:1521–1523. PMID:18339937. <http://dx.doi.org/10.1126/science.1152197>
- Keigwin LD. 1982a. Neogene planktonic foraminifera from Deep-Sea Drilling Project sites 502 and 503. *In: Prell WL, Gardner JV, editors. Initial Reports of the Deep-Sea Drilling Project 68*. US Gov Print Office, Washington, DC. p. 269–288.
- Keigwin L. 1982b. Isotopic Paleocyanography of the Caribbean and east Pacific: role of Panama uplift in Late Neogene time. *Science*. 217:350–352. PMID:17791515. <http://dx.doi.org/10.1126/science.217.4557.350>
- Kirby MX, Jackson JBC. 2004. Extinction of a fast-growing oyster and changing ocean circulation in Pliocene tropical America. *Geology*. 32:1025–1028. <http://dx.doi.org/10.1130/G21039.1>
- Kirby MX, MacFadden B. 2005. Was southern Central America an archipelago or a peninsula in the middle Miocene? A test using land-mammal body size. *Palaeogeogr Palaeoclimatol Palaeoecol*. 228:193–203. <http://dx.doi.org/10.1016/j.palaeo.2005.06.002>

- Kirby MX, Jones DS, MacFadden BJ. 2008. Lower Miocene stratigraphy along the Panama Canal and its bearing on the Central American peninsula. *PLoS ONE*. 3:e2791. PMID:18665219. PMCID:PMC2464738. <http://dx.doi.org/10.1371/journal.pone.0002791>
- Knowlton N. 1993. Sibling species in the sea. *Annu Rev Ecol Syst*. 24:189–216. <http://dx.doi.org/10.1146/annurev.es.24.110193.001201>
- Knowlton N, Weigt LA. 1998. New dates and new rates for divergence across the Isthmus of Panama. *Proc Roy Soc B*. 265:2257–2263. PMCID:PMC1689526. <http://dx.doi.org/10.1098/rspb.1998.0568>
- Knowlton N, Weigt LA, Solórzano LA, Mills DK, Bermingham E. 1993. Divergence in proteins, mitochondrial DNA, and reproductive compatibility across the Isthmus of Panama. *Science*. 260:1629–1632. PMID:8503007. <http://dx.doi.org/10.1126/science.8503007>
- Larsen JC, Sanford TB. 1985. Florida Current volume transports from voltage measurements. *Science*. 227:302–304. PMID:17742101. <http://dx.doi.org/10.1126/science.227.4684.302>
- Leonard-Pingel JS, Jackson JBC, O'Dea A. 2012. Changes in bivalve functional and assemblage ecology in response to environmental change in the Caribbean Neogene. *Paleobiology*. 38:509–524. <http://dx.doi.org/10.1666/10050.1>
- Lessios HA. 1981. Divergence in allopatry: molecular and morphological differentiation between sea urchins separated by the Isthmus of Panama. *Evolution*. 35:618–634. <http://dx.doi.org/10.2307/2408235>
- Lessios HA. 2008. The great American schism: divergence of marine organisms after the rise of the Central American Isthmus. *Annu Rev Ecol Syst*. 39:63–91. <http://dx.doi.org/10.1146/annurev.ecolsys.38.091206.095815>
- Lomolino MV. 1985. Body size of mammals on islands: the island rule re-examined. *Am Nat*. 125:310–316. <http://dx.doi.org/10.1086/284343>
- Lomolino MV. 2005. Body size evolution in insular vertebrates: generality of the island rule. *J biogeogr*. 32:1683–1699. <http://dx.doi.org/10.1111/j.1365-2699.2005.01314.x>
- MacFadden BJ. 2006. Extinct mammalian biodiversity of the ancient New World tropics. *Trends Ecol Evol*. 21:157–165. PMID:16701492. <http://dx.doi.org/10.1016/j.tree.2005.12.003>
- MacFadden BJ, Foster DA, Rincon AF, Morgan GS, Jaramillo C. 2012. The New World tropics as a cradle of biodiversity during the Early Miocene: calibration of the Centenario fauna from Panama. *Geol Soc Am, Abstracts with Programs*. 44:163.
- Marko PB. 2002. Fossil calibration of molecular clocks and the divergence times of geminate species pairs separated by the Isthmus of Panama. *Mol Biol Evol*. 19:2005–2021. PMID:12411609. <http://dx.doi.org/10.1093/oxfordjournals.molbev.a004024>
- Marko PB, Jackson JBC. 2001. Patterns of morphological diversity among and within arcid bivalve species pairs separated by the Isthmus of Panama. *J Paleontol*. 75:590–606. [http://dx.doi.org/10.1666/0022-3360\(2001\)075<0590:POMDAA>2.0.CO;2](http://dx.doi.org/10.1666/0022-3360(2001)075<0590:POMDAA>2.0.CO;2)
- Marko PB, Moran AL. 2009. Out of sight, out of mind: high cryptic diversity obscures the identities and histories of geminate species in the marine bivalve subgenus *Acar*. *J Biogeogr*. 36:1861–1880. <http://dx.doi.org/10.1111/j.1365-2699.2009.02114.x>
- Marshall LG. 1985. Geochronology and land-mammal biochronology of the transamerican faunal interchange. *In: Stehli FG, Webb SD, editors. The Great American Biotic Interchange*. Plenum Press, New York. p. 49–85. [http://dx.doi.org/10.1007/978-1-4684-9181-4\\_3](http://dx.doi.org/10.1007/978-1-4684-9181-4_3)
- Marshall LG, Webb SD, Sepkoski JJ, Raup DM. 1982. Mammalian evolution and the Great American Interchange. *Science*. 215:1351–1357. PMID:17753000. <http://dx.doi.org/10.1126/science.215.4538.1351>
- Mayr E. 1944. Wallace's Line in the light of recent zoogeographic studies. *Quart Rev Biol*. 19:1–14. <http://dx.doi.org/10.1086/394684>
- Mayr E. 1954. Geographic speciation in tropical echinoids. *Evolution*. 8:1–18. <http://dx.doi.org/10.2307/2405661>
- Meiri S, Dayan T, Simberloff D. 2004. Carnivores, biases and Bergmann's rule. *Biol J Linnean Soc*. 81:579–588. <http://dx.doi.org/10.1111/j.1095-8312.2004.00310.x>

- Miller WE, Caranza-Castaneda O. 2001. Late Cenozoic mammals from the basins of central Mexico. *Boll Soc Paleontol Ital.* 40:235–242.
- Miura O, Torchin ME, Bermingham E. 2010. Molecular phylogenetics reveals differential divergence of coastal snails separated by the Isthmus of Panama. *Mol Phylogenet Evol.* 56:40–48. PMID:20399869. <http://dx.doi.org/10.1016/j.ympev.2010.04.012>
- Miura O, Torchin ME, Bermingham E, Jacobs DK, Hechinger RF. 2011. Flying shells: historical dispersal of marine shells across Central America. *Proc Roy Soc B.* 279:1061–1067. PMID:21920976. PMCid:PMC3267146. <http://dx.doi.org/10.1098/rspb.2011.1599>
- Molnar P. 2008. Closing of the Central American seaway and the Ice Age: a critical review. *Paleoceanography.* 23(2). <http://dx.doi.org/10.1029/2007PA001574>
- Montellano-Ballasteros M, Jimenez-Hidalgo E. 2006. Mexican fossil mammals, who, where and when. *In:* Vega F, et al., editors. *Studies on Mexican paleontology.* Springer, Dordrecht. [http://dx.doi.org/10.1007/1-4020-3985-9\\_12](http://dx.doi.org/10.1007/1-4020-3985-9_12)
- Montes C, Cardona A, McFadden R, Morón SE, Silva CA, Restrepo-Moreno S, Ramírez DA, Hoyos N, Wilson J, Farris D, Bayona GA, Jaramillo CA, Valencia V, Bryan J, Flores JA. 2012a. Evidence for middle Eocene and younger land emergence in central Panama: implications for Isthmus closure. *Geol Soc Am Bull.* 124:780–799. <http://dx.doi.org/10.1130/B30528.1>
- Montes C, Bayona A, Cardona A, Buchs DM, Silva CA, Morón S, Hoyos N, Ramírez DA, Jaramillo CA, Valencia V. 2012b. Arc-continent collision and orocline formation: closing of the Central American seaway. *J Geophys Res.* 117:B04105. <http://dx.doi.org/10.1029/2011JB008959>
- Nuryanto A, Kochzius M. 2009. Highly restricted gene flow and deep evolutionary lineages in the giant clam *Tridacna maxima*. *Coral Reefs.* 28:607–619. <http://dx.doi.org/10.1007/s00338-009-0483-y>
- O’Dea A. 2003. Seasonality and variation in zooid size in Panamanian encrusting bryozoans. *J Mar Biol Assoc UK.* 83:1107–1108. <http://dx.doi.org/10.1017/S0025315403008348h>
- O’Dea A, Jackson J. 2002. Bryozoan growth mirrors contrasting seasonal regimes across the Isthmus of Panama. *Palaeogeogr Palaeoclimatol Palaeoecol.* 185:77–94. [http://dx.doi.org/10.1016/S0031-0182\(02\)00278-X](http://dx.doi.org/10.1016/S0031-0182(02)00278-X)
- O’Dea A, Jackson J. 2009. Environmental change drove macroevolution in cupuladriid bryozoans. *Proc Roy Soc B-Biol Sci.* 276:3629–3634. PMID:19640882. PMCid:PMC2817302. <http://dx.doi.org/10.1098/rspb.2009.0844>
- O’Dea A, Okamura B. 2000a. Intracolony variation in zooid size in cheilostome bryozoans as a new technique for investigating palaeoseasonality. *Palaeogeogr Palaeoclimatol Palaeoecol.* 162:319–332. [http://dx.doi.org/10.1016/S0031-0182\(00\)00136-X](http://dx.doi.org/10.1016/S0031-0182(00)00136-X)
- O’Dea A, Okamura B. 2000b. Cheilostome bryozoans as indicators of seasonality in the Neogene epicontinental seas of Western Europe. *In:* Cubilla AH, Jackson JBC, editors. *Proceedings of the 11th International Bryozoology Association Conference, Smithsonian Tropical Research Institute, Balboa, Republic of Panama.* p. 316–320.
- O’Dea A, Jackson J, Fortunato H, Smith J, D’Croz L, Johnson K, Todd J. 2007. Environmental change preceded Caribbean extinction by 2 million years. *Proc Natl Acad Sci USA.* 104(13):5501–5506. PMID:17369359. PMCid:PMC1838446. <http://dx.doi.org/10.1073/pnas.0610947104>
- O’Dea A, Jackson J, Taylor P, Rodriguez E. 2008. Modes of reproduction in recent and fossil cupuladriid bryozoans. *Palaeontology.* 51:847–864. <http://dx.doi.org/10.1111/j.1475-4983.2008.00790.x>
- O’Dea A, Hoyos N, Rodríguez E, De Gracia B, De Gracia C. 2012. History of upwelling in the tropical eastern Pacific and the paleogeography of the Isthmus of Panama. *Palaeogeogr Palaeoclimatol Palaeoecol.* 348–349:59–66. <http://dx.doi.org/10.1016/j.palaeo.2012.06.007>

- Okamura B, O'Dea A, Knowles T. 2011. Bryozoan modular growth and the retrospective analysis of environments. *Mar Ecol Prog Ser.* 430:133–146. <http://dx.doi.org/10.3354/meps08965>
- Okamura B, O'Dea A, Taylor PD, Taylor A. 2013. A new bryozoan assemblage-based proxy reveals ENSO variability in the Pliocene. *Bull Mar Sci.* 89:857–876. <http://dx.doi.org/10.5343/bms.2012.1041>
- Pinto-Sánchez NR, Ibáñez, Madrián, Sanjur OI, Bermingham E, Crawford AJ. 2012. The Great American Biotic Interchange in frogs: multiple and early colonization of Central America by the South American genus *Pristimantis* (Anura: Craugastoridae). *Mol Phylogenet Evol.* 62:954–972. PMID:22178362. <http://dx.doi.org/10.1016/j.ympev.2011.11.022>
- Proctor V. 1968. Long-distance dispersal of seeds by retention in digestive tract of birds. *Science.* 160:321–322. PMID:4230509. <http://dx.doi.org/10.1126/science.160.3825.321>
- Rickaby REM, Halloran P. 2005. Cool La Niña during the warmth of the Pliocene? *Science.* 307:1948–1952. PMID:15790852. <http://dx.doi.org/10.1126/science.1104666>
- Robbins JA, Tao K, Grossman EL, O'Dea A. 2012. Exploring the delayed overturn in Caribbean fauna using gastropod stable-isotope profiles to quantify seasonal upwelling and freshening of coastal waters. *Geol Soc Am, Abstracts with Programs.* 44.
- Schillaci MA, Meijaard E, Clark T. 2009. The effect of island area on body size in a primate species from the Sunda Shelf Islands. *J Biogeogr.* 36:362–371. <http://dx.doi.org/10.1111/j.1365-2699.2008.01984.x>
- Schmidt DN. 2007. The closure history of the Central American seaway: evidence from isotopes and fossils to models and molecules. *In: Williams M, Haywood AM, Gregory FJ, Schmidt DN, editors. Deep-time perspectives on climate change: marrying the signal from computer models and biological proxies. The Micropaleontological Society, Special Publications. The Geological Society, London.* p. 429–444. PMID:17568788.
- Schuchert C. 1935. *Historical geology of the Antillean-Caribbean region.* New York: John Wiley and Sons, Inc.—London, Chapman & Hall, Ltd.
- Simpson GG. 1977. Too many lines: the limits of the oriental and Australian zoogeographic regions. *Proc Am Philosoph Soc.* 121:107–120.
- Smith JT, Jackson JBC. 2009. Ecology of extreme faunal turnover of tropical American scallops. *Paleobiology.* 35:77–93. <http://dx.doi.org/10.1666/07054.1>
- Smith BT, Klicka J. 2010. The profound influence of the Late Pliocene Panamanian uplift on the exchange, diversification, and distribution of New World birds. *Ecogeography.* 33:333–342.
- Sprintall J, Wijffels S, Molcard R, Jaya I. 2009. Direct estimates of the Indonesian Throughflow entering the Indian Ocean: 2004–2006. *J Geophys Res-Oceans.* 114.
- Stehli FG, Webb SD, editors. 1985. *The Great American Biotic Interchange.* Plenum Press, New York. <http://dx.doi.org/10.1007/978-1-4684-9181-4>
- Steph S, Tiedemann R, Prange M, Groeneveld J, Nürnberg, Reuning L, Schulz M, Haug GH. 2006. Changes in Caribbean surface hydrography during the Pliocene shoaling of the Central American Seaway. *Paleoceanography.* 21:PA4221. <http://dx.doi.org/10.1029/2004PA001092>
- Tao K, Grossman E, Robbins J, O'Dea A. 2013. Quantifying upwelling and freshening in nearshore tropical environments using stable isotopes in modern tropical American mollusks. *Bull Mar Sci.* 89:815–835. <http://dx.doi.org/10.5343/bms.2012.1065>
- Tedford RH, Albright II LB, Barnosky A, Ferrusquía-Villafranca I, Hunt Jr RM, Storer JE, Swisher III CC, Voorhies MR, Webb SD, Whistler DP. 2004. Mammalian biochronology of the Arikarean through Hemphillian interval (late Oligocene through early Pliocene epochs). *In: Woodburne MO, editor. Late Cretaceous and Cenozoic mammals of North America.* Columbia University Press, New York. p. 169–231.
- Teranes JL, Geary DH, Bemis BE. 1996. The Oxygen Isotopic Record of Seasonality in Neogene Bivalves from the Central American Isthmus. *In: Jackson JBC, Budd AF, Coates*

- AG, editors. Evolution and environment in tropical America. The University of Chicago Press, Chicago. p. 105–129.
- Van der Bergh GD, de Vos J, Sondaar PY. 2001. The Late Quaternary palaeogeography of mammal evolution in the Indonesian Archipelago. *Palaeogeogr Palaeoclimatol Palaeoecol.* 171:385–408. [http://dx.doi.org/10.1016/S0031-0182\(01\)00255-3](http://dx.doi.org/10.1016/S0031-0182(01)00255-3)
- Van Valen L. 1973. A new evolutionary law. *Evol Theory.* 1:1–33.
- Vermeij GJ, Petuch EJ. 1986. Differential extinction in tropical American molluscs: endemism, architecture, and the Panama land bridge. *Malacologia.* 27:29–41.
- Wallace AR. 1869. *The Malay archipelago*. Mac-millan and Co., London. PMCid:PMC2260842.
- von der Heydt AS, Nnafie A, Dijkstra HA. 2011. Cold tongue/warm pool and ENSO dynamics in the Pliocene. *Clim Past Disc.* 7:997–1027. <http://dx.doi.org/10.5194/cpd-7-997-2011>
- Wara MW, Ravelo AC, Delaney ML. 2005. Permanent El Niño-like conditions during the Pliocene warm period. *Science.* 309:758–761. PMID:15976271. <http://dx.doi.org/10.1126/science.1112596>
- Webb SD. 1976. Mammalian faunal dynamics of the Great American Interchange. *Paleobiology.* 2:216–234.
- Webb SD. 1985. Late Cenozoic mammal dispersal between the Americas. *In: Stehli FG, Webb SD, editors. The Great American Biotic Interchange.* Plenum Press, New York. p. 357–386. [http://dx.doi.org/10.1007/978-1-4684-9181-4\\_14](http://dx.doi.org/10.1007/978-1-4684-9181-4_14)
- Webb SD. 2006. The Great American Biotic Interchange: patterns and processes. *Annals Missouri Bot Garden.* 93:245–257. [http://dx.doi.org/10.3417/0026-6493\(2006\)93\[245:TG ABIP\]2.0.CO;2](http://dx.doi.org/10.3417/0026-6493(2006)93[245:TG ABIP]2.0.CO;2)
- Weigt LA, Crawford AJ, Rand AS, Ryan MJ. 2005. Biogeography of the túngara frog, *Physalaemus pustulosus*: a molecular perspective. *Mol Ecol.* 14:3857–3876. PMID:16202101. <http://dx.doi.org/10.1111/j.1365-294X.2005.02707.x>
- Weir JT, Bermingham E, Schluter D. 2009. The Great American Biotic Interchange in birds. *Proc Natl Acad Sci USA.* 106:21737–21742. PMID:19996168. PMCid:PMC2799814. <http://dx.doi.org/10.1073/pnas.0903811106>
- Whitmore Jr FC, Stewart RH. 1965. Miocene mammals and Central American seaways. *Science.* 148:180–185. PMID:17780078. <http://dx.doi.org/10.1126/science.148.3667.180>
- Williams ST, Reid DG. 2004. Speciation and diversity on tropical rocky shores: a global phylogeny of snails of the Genus *Echinolittorina*. *Evolution.* 58:2227–2251. PMID:15562687.
- Woodburne MO. 2010. The Great American Biotic Interchange: dispersals, tectonics, climate change and holding pens. *J Mamm Evol.* 17:245–264. PMID:21125025. PMCid:PMC2987556. <http://dx.doi.org/10.1007/s10914-010-9144-8>
- Woodburne MO, Cione AL, Tonni EP. 2006. Central American provincialism and the Great American Biotic Interchange. *In: Carranza-Casta-eda O, Lindsay EH, editors. Advances in Late Tertiary vertebrate paleontology in Mexico and the Great American Biotic Interchange.* Universidad Nacional Autónoma de México, Instituto de Geología and Centro de Geociencias Publicación Especial 4. p. 73–101.
- Woodring WP. 1966. The Panama land bridge as a sea barrier. *Proc Am Philosoph Soc.* 110:425–433.

DATE SUBMITTED: 7 December, 2012.

DATE ACCEPTED: 14 June, 2013.

AVAILABLE ONLINE: 10 October, 2013.

ADDRESSES: (JBCJ) *Smithsonian Tropical Research Institute, PO Box 0843-03092, Panama City, Panama; Scripps Institution of Oceanography, La Jolla, California 92093-0244.* PRESENT ADDRESS: *Department of Paleobiology, Smithsonian Institution, PO Box 30172, MRC 121, Washington, DC 20013-7012.* (AO) *Smithsonian Tropical Research Institute, PO Box 0843-03092, Panama City, Panama.* CORRESPONDING AUTHOR: (JBCJ) Telephone: (858) 518-7613, Email: <[jeremybcjackson@gmail.com](mailto:jeremybcjackson@gmail.com)>.