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## Evolution of the Isthmus of Panama: Biological, Paleoceanographic and Paleoclimatological Implications

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### Abstract

The rise of the Isthmus of Panama was the product of small-scale geological processes that, nonetheless, had worldwide repercussions. The building of the Panamanian landscape can be summarized in four phases: (i) the emergence of a large, late Eocene island across central Panama and the Azuero Peninsula; (ii) the early Miocene large-scale generation of terrestrial landscapes in Central America, which connected central Panama with North America; (iii) the full closure of the Central American Seaway (CAS) at 10 Ma, which interrupted the exchange of deep waters between the Caribbean and the Pacific, and generated most of the landscape across the Isthmus (exchange of shallow waters continued until 3.5 Ma, albeit intermittently); and (iv) the persistence of a terrestrial landscape across the Isthmus over the past 3.5 My. Four major events have been linked to the rise of the Isthmus: (i) the onset of thermohaline circulation (TCH); (ii) the onset of northern hemisphere glaciation (NHG); (iii) the birth of the Caribbean Sea; and (iv) the Great American Biotic Interchange (GABI). The available evidence indicates a strong link between the closure of the CAS and the onset of Atlantic meridional overturning circulation (AMOC, a precursor of THC), but at 10.0 rather than 3.5 Ma, as had been assumed. There is no evidence of a connection between the full emergence of the Isthmus at 3.5 Ma and the onset of the NHG. There is, however, strong evidence that the full emergence of the Isthmus at 3.5 Ma changed the oceanography of the Caribbean Sea to its modern conditions, although the role of other variables influencing Pleistocene Caribbean Sea conditions, including the changes in the Pleistocene climate and the cessation of the freshwater flow of several South American rivers into the Caribbean, still needs to be evaluated. The GABI is more complex than is often assumed, and it seems that variables other than a continuous terrestrial Isthmus have controlled the direction, timing and speed of migrations in both directions.

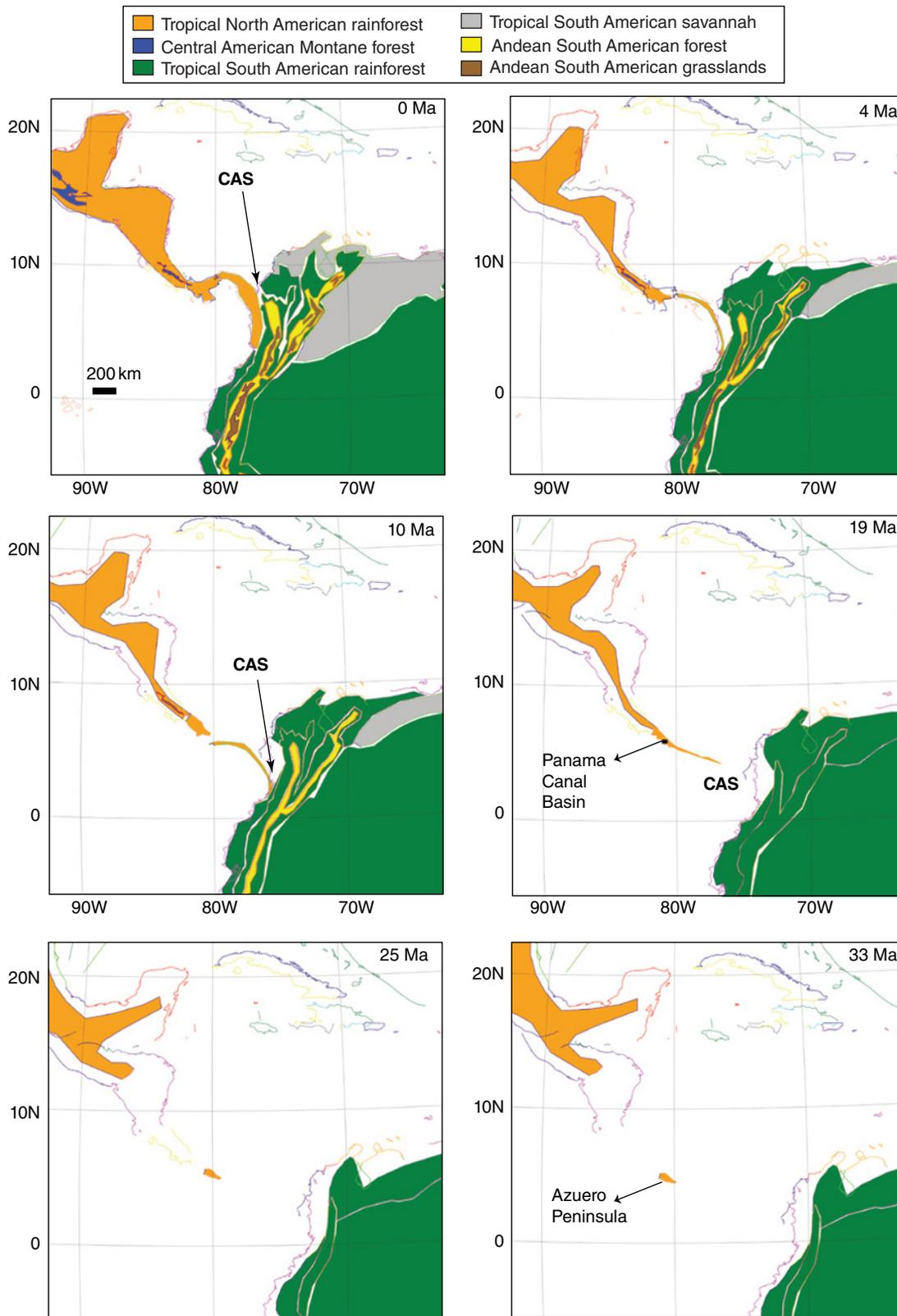
**Keywords:** *biogeography, phylogeny, oceanography, biological invasion, biome, neotropics*

### 22.1 Introduction

Southern Caribbean geology is a very complex product of three colliding tectonic plates and their interactions since the Late Cretaceous (e.g., Wadge & Burke 1983; Adamek et al. 1988; Mann & Corrigan 1990; Pindell & Barret 1990; Kolarsky et al. 1995; Mann & Kolarsky 1995; Coates et al. 2004; Rockwell et al. 2010; Montes et al. 2012a; Barat et al. 2014). These geological processes drive both the generation and the movement of terrestrial landmasses, which in turn control the distribution, migration and, ultimately, the evolution of terrestrial biotas. One of most interesting geological events in the southern Caribbean has been the rise of the Isthmus of Panama, also simply called the Isthmus. Even though the

geological build-up of Panama occurred over a small spatial scale, it produced major paleoceanographic, climatic, biogeographic and evolutionary changes that have attracted the attention of researchers for a long time.

Over 2000 publications (compiled in Bacon et al. 2015a) have cited an age of 4.2–3.5 Ma for the rise of the Isthmus. This range was derived from a number of geological (Coates et al. 1992, 2003, 2004, 2005; Coates & Obando 1996) and paleoceanographic (Haug & Tiedemann 1998; Haug et al. 2001) studies. Four major events have been linked to the rise to the Isthmus: (i) the onset of thermohaline circulation (THC); (ii) the onset of northern hemisphere glaciation (NHG); (iii) the formation of the Caribbean Sea; and (iv) the onset of the Great American Biotic



**Figure 22.1** Terrestrial biome reconstruction for the past 36 Myr of the Isthmus of Panama. The reconstruction is an orthographic projection based on the plate tectonic model of GPlates 1.5.0, using the plate reconstruction of Seton et al. (2012). Terrestrial biomes include the tropical rainforest from South America, the tropical rainforest of North America (corresponding to the Central American rainforest), the Central American montane forests (forest >2000 m elevation), the Andean South American forest (forest >2000 m elevation) and the Andean South American grasslands (grasslands above the tree line in the Andes of South America). The first development of terrestrial landscape occurred during the late Eocene, as an island spanning from the present site of central Panama to

Interchange (GABI). Some of these links have been heavily criticized, however (Molnar 2008).

In late 2007, Panama started an 8-year construction effort to expand the Panama Canal, during which numerous new outcrops were exposed, providing an unparalleled opportunity for additional studies on the timing and dynamics of the Isthmus' formation. This set of new data has revised our understanding of the rise of the Isthmus and its consequences, which will be explored in this chapter.

## 22.2 A Brief History of the Isthmus Landscape Construction

The Isthmus is predominantly the product of three events of arc magmatism build-up on the trailing edge of the Caribbean Plate during the late Cretaceous–Cenozoic, together with the successive accretion of Pacific-born sea-mounts. These arcs are deformed by collisions with both the South American Plate and oceanic plateaus (e.g., Wadge & Burke 1983; Mann & Corrigan 1990; Coates et al. 2004; Rockwell et al. 2010; Buchs et al. 2011; Wegner et al. 2011; Montes et al. 2012a,b).

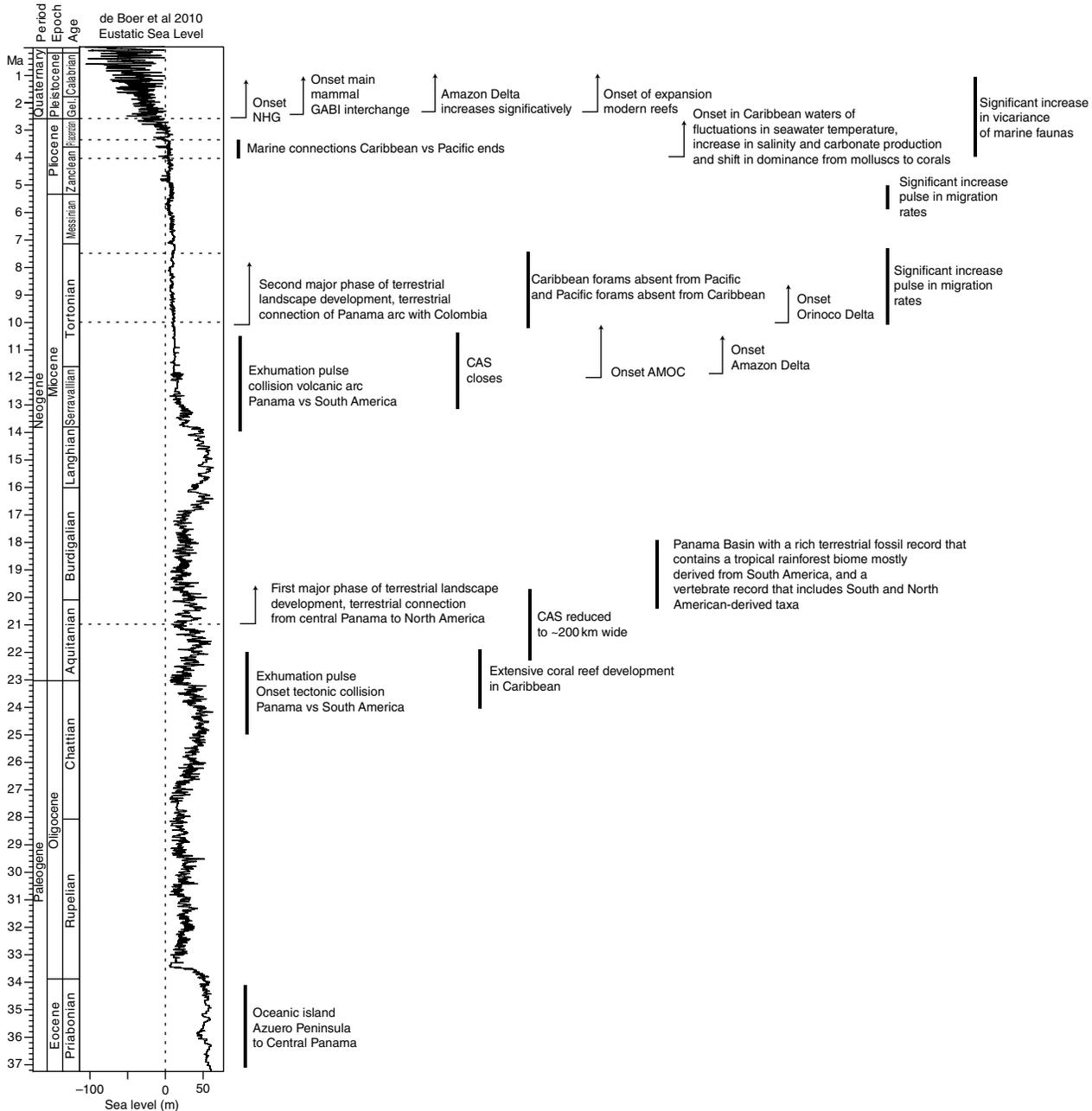
During the early–middle Eocene (50–43 Ma) (Montes et al. 2012b; Ramirez et al. 2016), a large exhumation pulse occurred, which was probably the result of the accretion of intraplate Pacific volcanoes to the southern boundary of the Caribbean plate (Buchs et al. 2011). This accretion generated the first terrestrial land in Panama during the late Eocene: a large island that extended from the present-day Azuero Peninsula to central Panama (Figures 22.1 and 22.2). There are extensive fossil wood remains in the Tonosi Formation of the Azuero Peninsula, dated as late Eocene (Baumgartner-Mora et al. 2008), that include large *Arecaceae* and *Humiriaceae* trees (Stern & Eyde 1963), as well as fruits and seeds of *Arecaceae*, *Vitaceae*, *Humiriaceae*, *Anacardiaceae* and *Lamiales* (Herrera et al. 2012b). The landscape extended into central Panama, where deposits of the late Eocene

Gatuncillo Formations have yielded a rich palynoflora that indicates a tropical rainforest biome (Graham 1984, 1985, 1994).

A second major phase of terrestrial landscape development along the Isthmus occurred during the early Miocene (~21 Ma), probably derived from an extensive exhumation pulse during the late Oligocene–early Miocene (25–22 Ma) produced by the onset of the tectonic collision between South America and Panama (Farris et al. 2011). There are several deposits in central Panama, including the Cascadas, Cucarachas and Pedro Miguel formations, that indicate the presence of a terrestrial landscape since ~21 Ma (Figures 22.1 and 22.2) (Montes et al. 2012a,b). The North American-derived mammal fauna of the Cascadas and Cucaracha formations indicates a continuous landscape from central Panama to North America across Central America (Kirby & MacFadden 2005; MacFadden 2006b, 2009; Kirby et al. 2008; MacFadden et al. 2010, 2014) made up of biomes that were dominated by tropical rainforest (Jaramillo et al. 2014). The width of the Central American Seaway (CAS) at this time has been estimated at ~200 km (Montes et al. 2012b).

A third major phase occurred during the late Miocene (~12–10 Ma) (Figures 22.1 and 22.2). There was an extensive exhumation pulse during the late–middle Miocene to the late Miocene (15–10 Ma) (Coates et al. 2004; Montes et al. 2012b). This pulse was produced by the collision of the Panamanian Volcanic Arc with South America, which resulted in the closure of the CAS (Montes et al. 2015). The widespread effects of this collision can be clearly seen in north-eastern Colombia (Vargas & Mann 2013). It was also concomitant with the onset of subduction in Costa Rica and eastern Panama of the oceanic crust that originally formed above the Galápagos mantle plume, resulting in the production of new continental crust and widespread exhumation in Central America (Gazel et al. 2015). This drastic change in the configuration of the Panamanian landscape has also been recognized by previous studies (Duque 1990; Duque-Caro 1990a,b; Coates et al. 1992, 2003, 2004). Most of the landscape was dominated by a tropical

**Figure 22.1** (Continued) the Azuero Peninsula. A second major build-up of the terrestrial landscape occurred during the early Miocene. A third occurred during the late Miocene. The Central American Seaway (CAS; defined as the ocean gap along the tectonic boundary between the South American plate and the Panama microplate) was closed by 10 Ma. From 10.0 to 3.5 Ma, there were intermittent Caribbean–Pacific connections through pathways other than the CAS. At 3.5 Ma, there was a complete closure of the Isthmus. A movie of the GPlates landscape reconstruction can be found in online Appendix 22.1 ([www.wiley.com/go/hoorn/mountains,climateandbiodiversity](http://www.wiley.com/go/hoorn/mountains,climateandbiodiversity)). *Source:* Terrestrial biomes adapted from Jaramillo & Cardenas (2013), the exhumation evolution of the Isthmus of Panama from the Montes models (Farris et al. 2011; Montes et al. 2012a,b, 2015), the terrestrial plant fossil record of the region from Stern & Eyde (1963), Jaramillo et al. (2006, 2014), Herrera et al. (2010, 2012a,b, 2014a,b), Jaramillo & Cardenas (2013) and Rodriguez-Reyes et al. (2014), and the terrestrial vertebrate record from (Whitmore & Stewart 1965; Slaughter 1981; MacFadden & Higgins 2004; MacFadden 2006a,b, 2009, 2010; Cadena et al. 2012; Head et al. 2012; MacFadden et al. 2012; Rincon et al. 2012, 2013; Hastings et al. 2013). See also Plate 35 in color plate section.



**Figure 22.2** Summary of the main events discussed in the text. *Source:* Adapted from Walker et al. (2012) and de Boer et al. (2010).

rainforest biome (Jaramillo et al. 2014), and there is no evidence of extensive savannahs.

From 10.0 to 3.5 Ma, the Caribbean Sea and Pacific Ocean were still connected by shallow water through other passages than the CAS (Figures 22.1 and 22.2) (Coates et al. 2004), although these connections were intermittent, as seen in the 10.0–7.5 Ma interval when Caribbean foraminifera faunas are absent from Pacific deposits in the Atrato Basin (Duque-Caro 1990b) and Pacific faunas are mostly absent from Caribbean

deposits (Collins et al. 1996). The evolution of Tonnoid gastropods also indicates intermittent marine connections during this interval (Beu 2001). Most of the landscape was dominated by a tropical rainforest biome (Jaramillo et al. 2014).

All marine connections between the Caribbean and Pacific finally ended in the interval between 4.2 and 3.5 Ma (Haug & Tiedemann 1998), and since 3.5 Ma there has been a continuous terrestrial landscape across the Isthmus of Panama (Figures 22.1 and 22.2).

## 22.3 Thermohaline Circulation

Numerous paleoclimatic and paleoceanographic studies have addressed the implications of the rise of the Isthmus, from both modeling and empirical perspectives. More than 24 different modeling exercises have explored the consequences of the rise (Maier-Raimer et al. 1990; Mikolajewicz et al. 1993; Mikolajewicz & Crowley 1997; Murdock et al. 1997; Nisancioglu et al. 2003; Nof & van Gorder 2003; Prange & Schulz 2004; van der Heydt & Dijkstra 2005, 2006; Klocker et al. 2005; Schneider & Schmittner 2006; Steph et al. 2006a,b, 2010; Lunt et al. 2008a,b; Vizcaíno et al. 2010; Butzin et al. 2011; Zhang et al. 2012; Fedorov et al. 2013, 2015; Fyke et al. 2015; Brierley & Fedorov 2016), most of which are summarized in Sepulchre et al. (2014). Although models differ in the assumed width and depth of the CAS, almost all of them produce similar results. Once the CAS is closed, the salinity of the Atlantic Ocean increases and Atlantic Meridional Overturning Circulation (AMOC) is greatly enhanced. Sepulchre et al. (2014) found that the CAS depth is critical for paleoceanographic purposes. Once the flow of deep and intermediate waters (>200–500 m depth) of the Pacific Ocean into the Caribbean is interrupted, AMOC is enhanced. Additional reduction of shallow water flow across the Isthmus does not greatly affect Atlantic Ocean circulation.

Empirical evidence indicates that AMOC is much older than 3.5 Ma, and that it has become significantly stronger since the late Miocene, 12–10 Ma (Poore et al. 2006). Bell et al. (2015) showed that the North Atlantic Deep Water, a key component of AMOC, was vigorous prior to 4.7 Ma, and that during the 4.2–3.5 Ma interval there were no major changes in its strength. Therefore, the modeling/empirical results contradict the assumption of a 3.5 Ma closure of the CAS.

New geological results indicate that the CAS started to close by the late–middle Miocene (~14 Ma), and was fully closed by the late Miocene (10 Ma) (Figures 22.1 and 22.2) (Montes et al. 2012a, 2015). This full closure of the CAS (as it is defined here; see Glossary) has been previously recognized (Coates et al. 2004). The closure ceased most of the flow of deep and intermediate waters from the Pacific into the Caribbean along the CAS, as registered by the neodymium record of the Caribbean (Sepulchre et al. 2014). This 12–10 Ma major uplift of the Isthmus has also been previously recognized, in multiple studies (Bandy & Casey 1973; McDougall 1985; Duque-Caro 1990b; McNeill et al. 2000; Harmon 2005). Exchange of shallow waters continued across the Isthmus along pathways other than the CAS until complete closure at 3.5 Ma, but this exchange was not sufficient to alter AMOC significantly.

This new geological evidence allows for the reconciliation of the empirical evidence of the link between AMOC and the closure of the CAS, as most modeling exercises have predicted – not at 3.5 Ma, as has been traditionally accepted, but rather at 12–10 Ma.

## 22.4 Northern Hemisphere Glaciation

It has been argued that the closure of the CAS at 4.2–3.5 Ma resulted in the onset of NHG at 2.7 Ma (Haug & Tiedemann 1998; Haug et al. 2004). However, this hypothesis has been heavily criticized based on both the empirical data available and climate modeling (Molnar 2008; Fedorov et al. 2013). Some models indicate that closing the CAS does not have a significant effect either on Arctic ice volume (Vizcaíno et al. 2010) or on any of the major climatic changes that occurred at the end of the Pliocene, 2.7 Ma (Fedorov et al. 2013, 2015; Brierley & Fedorov 2016). The climate of the last 2.7 My (Quaternary) is characterized by the combination of four major elements, including a steep temperature gradient from the tropical zone to the poles, a temperature gradient from the western to the eastern equatorial Pacific, fluctuating CO<sub>2</sub> levels reaching below 200 ppm and permanent ice caps on both poles (Fedorov et al. 2013). The coincidence of these four features at ~2.7 Ma represents a major shift in Earth's climate, the causes of which are still a major unresolved question and the object of intensive research (Fedorov et al. 2015). It seems, however, that neither the closure of the CAS at 12–10 Ma nor the full closure of the Isthmus at 4.2–3.5 Ma had a major influence in the onset of NHG or the climate of the Quaternary.

## 22.5 The Caribbean Sea

The modern Caribbean Sea is characterized by high salinities, warm waters experiencing low temperature seasonality, low productivity and extensive reef development, in contrast to the western Pacific of Panama, which is characterized by low salinities, interannual and seasonal variations in temperature, high productivity and relatively low reef development (O'Dea et al. 2007). Abundant empirical evidence indicates that several changes occurred in the Caribbean during the 4.2–3.5 Ma interval, including a decrease in the fluctuations of Caribbean seawater temperature, an increase in salinity, an increase in carbonate production, a shift in dominance in benthic ecosystems from molluscs to reef corals and a more pronounced difference in taxonomic composition

between shallow marine faunas from the Caribbean versus the Pacific Ocean (Keigwin 1982; Coates et al. 1992, 2003, 2004, 2005; Collins et al. 1996; Haug & Tiedemann 1998; Collins & Coates 1999; McNeill et al. 2000; Haug et al. 2001; Kirby & Jackson 2004; Steph et al. 2006b; Jain & Collins 2007; O’Dea et al. 2007; Groeneveld et al. 2008; Jackson & O’Dea 2013). All of these changes have been interpreted as indicating the final closure of the Isthmus and the cessation of shallow-water exchange between the Pacific and Caribbean water masses. This interpretation has not been challenged by any of the more recent studies on the geology of the Isthmus (Farris et al. 2011; Montes et al. 2012a,b, 2015), although a recent paleoceanographic study has proposed that the differences in the Caribbean versus eastern tropical Pacific salinity could be consistent with the transition from permanent El Niño-like conditions of the early Pliocene to La Niña-like modern conditions (Mestas-Nuñez & Molnar 2014).

However, two additional variables that could affect the climate and ocean of the Caribbean region still need to be investigated. The first is the reorganization of South American fluvial drainages, a byproduct of the Andean uplift. Modern freshwater fluvial discharge into the southern Caribbean is  $\sim 700 \text{ km}^3/\text{y}$  (Restrepo et al. 2014), equivalent to about 16% of the Orinoco ( $830 \text{ km}^3/\text{y}$ ) and Amazon ( $3420 \text{ km}^3/\text{y}$ ) fluvial discharges combined. During the Miocene, however, most of the tropical South American drainages flowed into the southern Caribbean. Following the rise of the Andes, rivers shifted into their present configuration (Hoorn 1994; Hoorn et al. 1995, 2010a,b). The formation of the Amazon delta had two main stages: 9.4–2.4 Ma, when sedimentation rates were relatively low (0.05–0.30 m/ka), and 2.4 Ma to modern times, when sedimentation rates have been very high (1.22 m/ka) (Figueiredo et al. 2009; Hoorn et al. 2017). The Orinoco (or proto-Orinoco) delta, located in western Venezuela and eastern Colombia, drained into the southern Caribbean. At  $\sim 10$  Ma, it shifted to its modern delta, which drains into the Atlantic (Diaz de Gamero 1996). What were the consequences in the southern Caribbean Sea of this reduction of freshwater discharge? Preliminary studies indicate that the Caribbean Colombia Basin would have had a lower salinity before the shifting of South America’s major drainages into the Atlantic (P. Sepulchre, pers. comm.).

The second variable that needs to be investigated is the extensive coral reef development across the Caribbean during the late Oligocene, 24–22 Ma (e.g., Johnson 2008; Johnson et al. 2009). At this time, the CAS was deep and  $\sim 200$  km wide (Farris et al. 2011; Montes et al. 2012b). Why did reefs develop in the Caribbean if there was massive water exchange across the CAS between the Pacific and Caribbean? Why didn’t they develop there during the late Miocene ( $\sim 10.0$ – $7.5$  Ma), when there was a temporary disconnection between Caribbean and Pacific

waters (Duque-Caro 1990b; Collins et al. 1996)? This suggests that there are factors other than the rise of the Isthmus, such as slope and upwelling intensity, that controlled the development of reefs in the Caribbean (e.g., van der Heydt & Dijkstra 2005; Maier et al. 2007; Klaus et al. 2011). Indeed, modern reefs have developed extensively only since the onset of the NHG, as the sharp drops in sea level produced a change of low-angle ramps into steep-dipping shelf margins, thereby shifting coral growth toward shallower environments conducive to the large, fast-growing species that dominate reefs worldwide today (Budd & Johnson 1999; Klaus et al. 2012; Renema et al. 2016).

## 22.6 The Great American Biotic Interchange

The rise of the Isthmus is one of the major biogeographical events of the Cenozoic – a massive experiment in biological invasions – and as such it has been the focus of intensive research over many decades. It is a vicariant event from a marine perspective, as two oceans that were formerly connected – the Pacific and the Caribbean – became separated; however, it is a migration event from a terrestrial perspective, as lands formerly separated – South America and Central/North America – became connected.

Hundreds of biogeographic and phylogenetic studies have used 3.5 Ma as the a priori date for this event (Bacon et al. 2015a), although several genetic studies of taxa with low dispersal capabilities have reported evidence of earlier exchanges, including of bees (Roubik & Camargo 2011), tree frogs (Pinto-Sanchez et al. 2012), salamanders (Elmer et al. 2013), freshwater *Poecilia* fishes (Alda et al. 2013) and *Amazilia* hummingbirds (Ornelas et al. 2014). Is 3.5 Ma a safe assumption? We have explored this question by examining the DNA record of extant taxa and the fossil record. A meta-analysis of the molecular phylogenetic data of 426 taxa across many clades, both terrestrial and marine, indicates a large increase in the rate of migrations/vicariance events at around 10 Ma (Figure 22.2). The analysis shows four significant migration rate shifts, at 41.1 (46.2–35.9), 23.7 (26.2–19.9), 8.7 (10.0–7.2) and 5.2 (6.0–5.1) Ma (Bacon et al. 2015a). The latter two dates represent drastic rate increases, and all predate the inferred migration at 3.5 Ma. Even restricting the analysis to marine vicariance, there is a significant pulse at  $\sim 9$  Ma (Bacon et al. 2015b); this predates a rate increase at 2.06 (4.3–1.0) Ma (Bacon et al. 2015a) that is indeed associated with the final closure of the Isthmus at 3.5 Ma. The overall results indicate that the GABI occurred over a much longer time period than previously proposed, that it comprised several distinct migrational pulses and that the onset of significant migration was at  $\sim 10$  Ma.

The fossil record indicates a similar pattern to that shown by the molecular analysis. The early Miocene plant record (20–18 Ma) from Panama (Jaramillo et al. 2014; Rodriguez-Reyes et al. 2014) is dominated by South American-derived lineages and indicates an earlier crossing of the CAS by many South American plant families (e.g., Humiriaceae, Annonaceae, Euphorbiaceae), implying that plants were one of the first groups crossing the CAS (Cody et al. 2010). These results derived from the plant fossil record were also suggested by Graham in his multiple studies of Panamanian floras (Graham 1988a,b, 1991, 1992, 1999, 2010, 2011). Other recent studies of fossils have found earlier migrations (~19 Ma) of vertebrates from South America into central Panama across the CAS, including turtles (Cadena et al. 2012), snakes (Head et al. 2012) and crocodiles (Hastings et al. 2013; Scheyer et al. 2013).

Most of what has been written about the GABI in the paleontological literature is derived from the mammal record (e.g., Woodburne 2010). Consequently, the mammal-derived GABI has been accepted as the *de facto* pattern for all other organisms, even though mammals represent only a small fraction (~0.02%) of the high biodiversity of the Americas (1418 mammal species, versus more than half a million plants, invertebrates and other vertebrates). There are two major ideas about the GABI that are ingrained in the literature, both scientific and popular: first, the onset was due to the closure of the Isthmus, and second, the North American lineages replaced most of the South American lineages in South America.

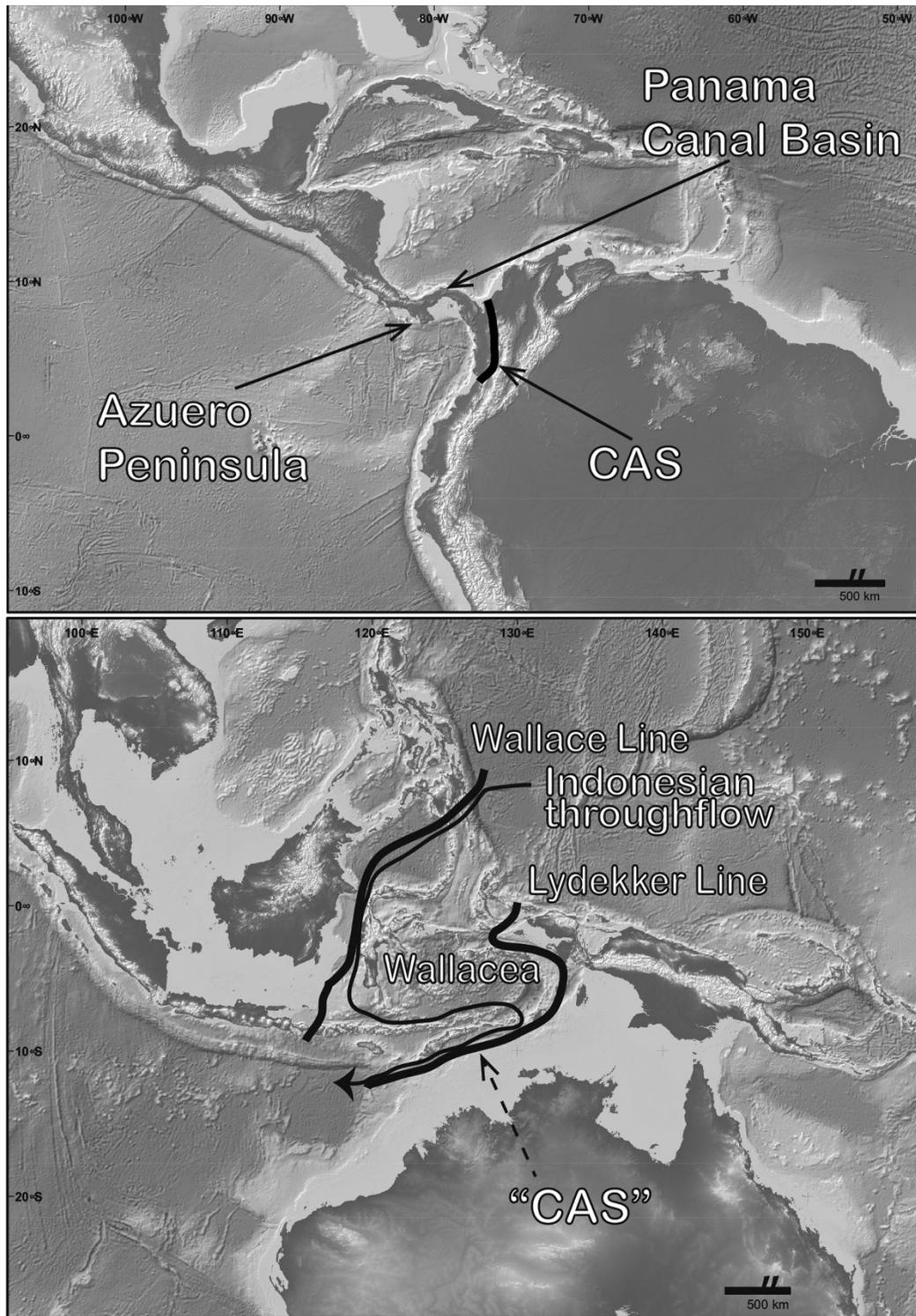
Let us discuss the first idea first: the closure driving the GABI. Both the fossil and genetic records show that mammal exchange started at 10 Ma and accelerated greatly at ~2.5 Ma (Webb 1976, 2006; Woodburne 2010; Forasiepi et al. 2014; Leite et al. 2014; Bacon et al. 2015a; Carrillo et al. 2015), rather than at 3.5 Ma. This difference in timing between the final closure of the Isthmus and the onset of the massive GABI mammal migrations has been used to suggest that other factors than a land connection were major drivers of the GABI acceleration: mainly habitat change due to the onset of the NHG and concomitant reductions in precipitation across the Americas (Webb 1976, 1978, 2006; Molnar 2008; Smith et al. 2012; Leigh et al. 2014; Bacon et al. 2016), and lower sea levels during glacial intervals (Woodburne 2010). Recent new findings in Guajira, northern Colombia, of late Pliocene age (~2.7 Ma) – the closest paleontological site in time and space to the Isthmus of Panama – indicate that most vertebrate faunas, including mammals, are still strongly dominated by South American clades (Forasiepi et al. 2014; Jaramillo et al. 2015; Moreno et al. 2015; Suarez et al. 2016), suggesting that the GABI acceleration occurred during the Pleistocene in tropical South America, rather than during the late

Pliocene. These new localities support the hypothesis that factors other than the final closure of the Isthmus accelerated the GABI among mammals.

The second major idea – the replacement of South American lineages by North American ones – involves two different hypotheses. The first is that North American taxa had a competitive advantage over South American fauna and therefore, when they migrated into South America, they displaced the South American taxa (Simpson 1983). The second suggests that major habitat changes drove many South American lineages to extinction prior to the arrival of North American lineages (Vrba 1992). These contrasting hypotheses are difficult to test using the fossil record, as that would require fine stratigraphic resolution and a large spatial distribution of the sampling. Nevertheless, the few studies addressing the point indicate that at least when comparing carnivorans (North American-derived) with Sparassodonta (South American-derived), factors other than competitive displacement caused the extinction of the latter (Prevosti et al. 2013).

It is interesting to see how the proportion of South American- versus North American-derived taxa in the fossil mammal fauna of Panama compares with that of the extant fauna. The early Miocene (20–18 Ma) mammal record of central Panama includes a wide variety of groups, including horses, camels, peccaries, bear-dogs, anthracotheriums, rhinocerotids, geomyoid rodents, dogs, oreodonts and protoceratids (Whitmore & Stewart 1965; Slaughter 1981; MacFadden & Higgins 2004; MacFadden 2006a,b, 2009; MacFadden et al. 2010, 2012; Rincon et al. 2012, 2013), all of which are derived from North American lineages. In contrast, only two are South American-derived taxa (a bat and a monkey: Bloch et al. 2016), representing 5% of the early Miocene assemblage (from a total of 40 fossil taxa). In the extant mammal assemblage of Panama, however, 57% (118 of 208 species) are South American-derived lineages. Therefore, from a Panamanian perspective (i.e., looking from the southern tip of North America), the prevalent direction of mammal migration was south to north, rather than the traditional view of north to south (57% of modern taxa in Panama are South American, versus 5% during the Miocene).

Coates & Stallard (2013) compared the Caribbean region during the Neogene with the modern Indonesian–Australia tectonic configuration. Because the collision of Australia with Indonesia has not fully closed the marine gap between them, the geographic situation could be thought of as an analog to the Isthmus of Panama ~11 Ma, when the CAS was still open (Coates & Stallard 2013). The CAS would be analogous to the Timor Trough–Ceram Sea: the deep strait that follows the southern tectonic boundary of Wallacea (Figure 22.3) (Hall 1998). The Timor Trough is about 100 km wide (Figure 22.1) – similar to the CAS at 16–15 Ma (Montes et al. 2012a). This tectonic contact point also demarks a biogeographic boundary called



**Figure 22.3** Topographic map illustrating Indo-Australia versus the Caribbean and Isthmus of Panama (Amante & Eakins 2009). Both maps are at the same scale. The region between Wallace and Lydekker's Line is called Wallacea, and corresponds to a complex plate boundary between the Indo-Australian plate to the south and the Eurasian Plate to the north (Hall 1998). The Central American Seaway (CAS) corresponds to the Uramita suture on the western Cordillera of Colombia (Montes et al. 2015), and it is an analog to the Timor Trough, the deep strait that follows the southern boundary of Wallacea, which also corresponds to Lydekker's Line. Most ocean water flow through the region (Indonesian throughflow) goes via the Timor Trough (Godfrey 1996), but it is small enough that there is already a distinctive difference between the Indian Ocean and the western equatorial Pacific (Cane & Molnar 2001). Note that Wallacea is ~1000 km wide – as wide as half of Central America from Panama to Nicaragua. Wallacea is a biogeographical region of transition between Australian and Asian biotas (Lohman et al. 2011), and has several mammal lineages derived from Australia that have been able to cross Lydekker's Line.

Lydekker's Line (Lohman et al. 2011). Most of the water output into the Indian Ocean, the "Indonesian through-flow," arrives through the Timor Trough (Godfrey 1996). As Coates & Stallard (2013) point out, the modern setting of Indonesia–Australia provides a valid analog to the Panamanian configuration just prior to the closure of the CAS at 12–11 Ma.

The comparison provides several insights. (i) Even though the Timor Trough has not been fully closed and the waters of the Pacific and Indian oceans are still connected by the Indonesian throughflow, the total output is not sufficient to prevent an oceanographic distinction between the Indian and Pacific oceans. In other words, a complete collision and a fully formed land bridge between Australia and Indonesia are not necessary to produce an oceanographic effect on the Pacific and Indian oceans. Such a "closing" of the Indonesian seaway has been proposed as one of the causes for major climatic changes around 4–3 Ma (Cane & Molnar 2001). This comparison underscores the major effects that closing the CAS 10 Ma would have had on the Atlantic–Pacific connection as it has been discussed in this chapter, relative to the minor effect produced by the final closure of the Isthmus 3.5 Ma. (ii) The Wallace Line is located ~1000 km west of Lydekker's Line (Lohman et al. 2011). Wallacea, the region in between, represents a transition zone of faunas and floras derived from both Asia and Australia (Lohman et al. 2011). This transition region is equivalent in area to half of Central America, from Panama to Nicaragua, and consists of many islands that have not been connected recently by dry land to either of the large continental masses. However, in this zone there are several mammal lineages with an Australian affinity that are east of the Timor Trough and have been able to reach the islands of eastern Wallacea by crossing sea passages. Why, then, was there not an active mammal migration between Panama and South America until 2.7 Ma? This question raises the possibility that factors other than continuous land across the Isthmus drove mammal migration during the GABI.

## 22.7 Unresolved Questions

The rise of the Isthmus is probably one of the best cases in which the interactions among geology, climate and biota can be observed. In spite of the intensive research in the region, several questions remain:

- 1) There were sloths, South American capromyid rodents and primates in Cuba during the early Miocene (MacPhee et al. 2003). Why, then, were there primates in Panama in the early Miocene, but no sloths or South American rodents? One hypothesis is that a continuous terrestrial bridge or a continuous chain of islands (known as GAARlandia) connected

the Antilles with South America during the Oligocene (Iturralde-Vinent & MacPhee 1999); in other words, Cuba was more connected to South America than Panama during the Oligocene/early Miocene. This hypothesis is still highly controversial (e.g., Graham 2003; Hedges 2006).

- 2) What controls the rate of migration across the Isthmus? Why were mammals so delayed in migrating in either direction compared to other groups?
- 3) What were the roles of biomes and sea-level change over the past 2.7 My in the migration process? It has been argued that migration was facilitated by a massive expansion of savannahs in both Central and South America. Were there extensive savannahs during the glacial intervals in Central America?
- 4) It has been assumed that the extensive development of reefs across the Caribbean was due to the final closure of the Isthmus. If that is the case, why were Caribbean reefs widespread during the late Oligocene (Johnson et al. 2009) if the CAS was a wide and deep marine strait connecting the Atlantic and Pacific oceans at this time? Why didn't reef development occur during the late Miocene (~10.0–7.5 Ma) when there was a separation of Caribbean and Pacific waters (Duque-Caro 1990b; Collins et al. 1996)? Perhaps Caribbean reef development is driven by other factors than the closure of the Isthmus, such as tectonism through the generation of new suitable habitats for reef development.
- 5) How did the closure of the Isthmus affect the position and migration of the Intertropical Convergence Zone (ITZC)? Novel research on the ITZC suggests that a strong AMOC pushed it north of the equator (Schneider et al. 2014).
- 6) What effect, if any, did the closure of the Isthmus have on the shallowing of the thermocline of the eastern equatorial Pacific?

Answering these questions will require intercontinental comparisons and additional fieldwork. The continent–continent collision of Asia with Australia is an excellent analog for the Panamanian arc–South America collision during the late Miocene (Coates & Stallard 2013). We could learn about the process and mechanism of migration by comparing the two events across multiples clades, both terrestrial and marine. It is also imperative to find many more late Miocene and Pliocene terrestrial deposits in eastern Colombia, Panama and Costa Rica. There is a large gap of information during this time period that is probably critical to understanding the GABI and the role of the Isthmus in mass migration. Several geological formations in eastern and western Costa Rica, eastern Panama and eastern Colombia have great potential to fill this void.

The geological building of the terrestrial landscape that represents the Isthmus of Panama developed across a very small geographical area, but nonetheless it

produced changes on a global scale. There is no better example of the relationship between biological evolution and the development of landforms.

Recently O’Dea et al. (2016) proposed that findings regarding a Miocene closure of CAS are unsupported and provided a new age for the formation of the Isthmus at 2.8 Ma. Both conclusions have been rejected (Jaramillo et al. 2017; Molnar 2017).

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