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The closure history of the Central American seaway: evidence from isotopes and fossils to models and molecules

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Abstract: The rise of the Panama Isthmus was the last step in the closure of the circumtropical seaways. The closure of the Panama Isthmus had fundamental consequences for global ocean circulation, evolution of the tropical ecosystems and potentially influenced the switch to the modern 'cold house' climate mode. The Atlantic and Pacific marine ecosystems became gradually separated whereas terrestrial organisms suddenly had the means to migrate between North and South America. Combining high-resolution geochemical proxies for the closure history with data on fossil distributions and genetic data provides independent evidence on the closure history. These datasets provide new boundary conditions for Earth System models to simulate the effects of palaeoceanographic change on global climate and allow exploration of hypotheses for the Northern Hemisphere glaciation.

The Miocene was a critical time of palaeoceanographic reorganization during which the oceanic circulation became more similar to that of today. The profound changes in climate and ocean circulation have been linked in part to the final closure of the Tethyan Ocean. There is considerable debate about the respective influence of Central American (Keigwin 1982*b*) and Indonesian seaways (Cane & Molnar 2001) on Neogene climate change. The persistence of entirely different views of the effect and relative importance of a closure of the circumtropical seaways on global circulation reflects in part the considerable uncertainty surrounding the geological evolution of the Central American Seaway (CAS) and the Indonesian Seaway.

This review focuses on the CAS. Its closure and the emergence of the Panama Isthmus in the Miocene to Pliocene stopped the exchange of tropical Atlantic and Pacific water (Fig. 1). This caused the evolution of two different tropical ecosystems. Furthermore, high salinity warm waters of the Caribbean were transported via the Loop Current, Florida Current and Gulf Stream northwards and potentially triggered the switch to the modern 'cold house' climate mode. As an additional consequence, the eastern equatorial Pacific became the locus of upwelling of cold, high CO₂, low-alkalinity, high-nutrient water (Fig. 2). The resulting high productivity and subsequent decay of organic material in the water column caused higher oxygen utilization (Fig. 3) on the Pacific side of the Isthmus in contrast to the Caribbean. Because water vapour is transported from the Caribbean to the Pacific, the Caribbean has an increased surface salinity of around 1‰ relative to the Pacific (Figs 2 and 3). The closure split a

homogeneous plankton community into two vastly different ecosystems (e.g. Jackson *et al.* 1993; Collins *et al.* 1996*b*; Kameo & Sato 2000) while connecting the North and South American terrestrial organisms (Whitmore & Stewart 1965; Marshall *et al.* 1982).

Both palaeontological and geochemical data describing the progressive closure history are available, though not from the same samples or sites, which makes it difficult to constrain the chronology. This review will discuss the current knowledge of the chronology of events and the consequences of the progressive closure for climate and marine/terrestrial ecosystems.

Chronology of events

This review is based on publications over the course of the last 25 years. During this time, the absolute ages for the biostratigraphic framework of these studies have changed, in parts of the record by up to 1 Ma. To facilitate comparisons between records, all biostratigraphic ages were amended to the ATS2004 timescale (Lourens *et al.* 2005).

Today, the Panama Isthmus blocks the flow of Pacific waters into the Atlantic (Fig. 1). During the Miocene, Central America consisted of a complex island-arc archipelago/peninsula (Fig. 4) with several marine corridors/basins: the San Carlos Basin (Northern Costa Rica–southern Nicaragua), the Panama Canal Basin, and the Atrato Basin (northwestern Colombia) (Duque-Caro 1990). There is significant debate about the palaeogeographic shape of the emerging Isthmus, hypothesizing of either a continuous land bridge

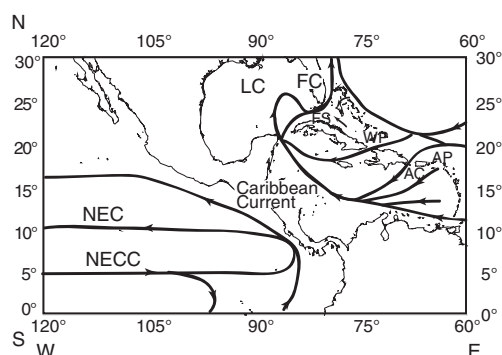


Fig. 1. Modern current systems in the Caribbean and eastern equatorial Pacific. Modified after Tomczak (1994). LC, Loop Current; FC, Florida Current; NEC, North Equatorial Current; NECC, North Equatorial Counter Current; FS, Florida Strait; WP, Windward Passage; AP, Anegada Passage.

with North America or an extensive island-arc system (Fig. 4). Evidence from marine sediments and volcanic records suggests an active volcanic arc during the Miocene consisting of small islands separated by shallow straits (Coates & Obando 1996). In contrast, palaeontological data (Kirby & MacFadden 2005) point towards gene flow with the North American continent and hence support the peninsula hypothesis (see Terrestrial ecosystems, Fig. 4b).

The history of the closure is not unidirectional, since there is evidence for closing and re-establishment of exchange between the Caribbean and the Pacific (Duque-Caro 1990), but step-wise and sequential at different water depths. The deep-sea record points towards gradual shoaling beginning between 15.4 and 14.7 Ma (Keller & Barron 1983) with the final closure around 3 Ma (Keigwin 1982b). Sedimentological evidence (Coates *et al.* 2004) indicates a shallowing of the Central American seaway from bathyal to inner neritic depth from 12.8 to 7.4 Ma. The reliability of the dates for the beginning and end of this process is hampered by two regional unconformities creating sediment gaps from about 15 to 13.5 Ma and 8.3 to 7.4 Ma (Coates *et al.* 2004). At the same time, the neodymium isotopic record in Atlantic and Pacific manganese crust starts to diverge, indicating a gradual establishment of modern circulation patterns (Burton *et al.* 1997). During the middle Miocene, the initial uplift of the Panama sill changed bottom-water circulation and sedimentation in the coastal areas of Central America (Duque-Caro 1990). The earliest time for uplift of the sill to upper middle bathyal depths (1000–500 m) and subsequent blocking of the deep-water

flow through the seaway is suggested for 13.45 to 13.0 Ma for the Atrato Basin (Duque-Caro 1990).

Marine carbon isotope records ($\delta^{13}\text{C}$) of deep-sea benthic foraminifers from Atlantic and Pacific sediments (Fig. 5) have been interpreted to indicate proto-North Atlantic Deep Water (NADW) production starting around 13 Ma (Wright *et al.* 1991), subtly visible in Figure 5. The beginning of NADW production has been linked to a first phase of deep-water blockage in the CAS (Wright *et al.* 1991) but alternatively also to subsidence of the Greenland–Scotland Ridge (Wright & Miller 1996). Intermittent closure of the shallow-water connection was suggested for the 10.71 to 9.36 Ma interval (Roth *et al.* 2000) based on coccolithophorid assemblages (Kameo & Sato 2000). Increasing clay supply from the Amazon to the Atlantic indicates uplift phases in the Andes from 9 to 8 Ma (Dobson *et al.* 1997) and tectonic change in northern South America. At the same time (8.2 to 7.8 Ma), intensive volcanic activity is indicated by ash in deep-sea cores (Ledbetter 1982) and the first significant $\delta^{13}\text{C}$ gradients evolved around 8.3 to 8.5 Ma (Zachos *et al.* 2001). The earliest terrestrial interchange of ‘waif immigrants’ from Northern to South America is dated between 10.1 and 9.1 Ma. The dispersal is assumed to have happened along an island arc system before the establishment of a land bridge (Webb 1985).

Equally, neodymium isotopes in manganese crust show a gradual reduction of exchange between Pacific and northwestern Atlantic waters between 8 and 5 Ma with the largest change between 8 and 7.5 Ma (Frank *et al.* 1999). These data are corroborated by an increase of northern component waters in the Atlantic part of the Southern Ocean between 6.6 and 6 Ma (Billups 2002), indicating invigorated circulation transporting NADW far south. This dataset on the other hand also points to very low export of NADW to the South Atlantic between 8 and 6.6 Ma, which suggested a re-establishment of water exchange between the Caribbean and the Pacific in the latest Miocene. These data cannot be corroborated by faunal data, since most sediments around the seaway are eroded in the Neogene hiatus NH6 ranging from 7.8 to 6.9 Ma (Keller & Barron 1983).

During the last 4 Ma, the amount of clay transported via the Amazon increased a second time (Dobson *et al.* 1997) parallel to the uplift in the Colombian Andes at 4 Ma (Gregory-Wodzicki 2000). A marked reorganization of the surface circulation (Haug & Tiedemann 1998) and ecosystems (Keller *et al.* 1989; Chaisson & Ravelo 2000) started at 4.7 Ma. Comparisons of oxygen isotope records ($\delta^{18}\text{O}$) of planktic, surface-dwelling foraminifers, a proxy for temperature, ice volume and salinity changes, show a

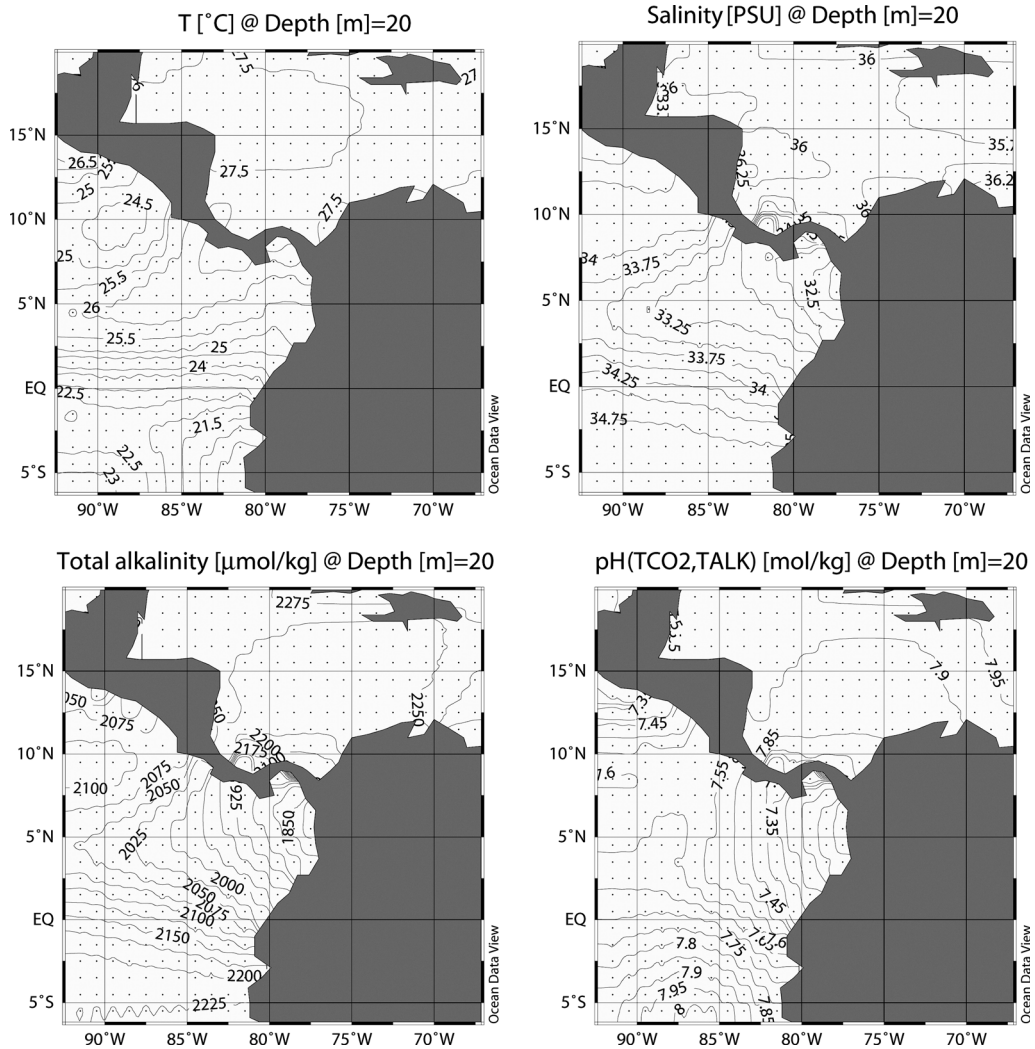


Fig. 2. Temperature, salinity and pH for the Caribbean and eastern equatorial Pacific (from Ocean Data View, Schlitzer (2006)). The modern Caribbean is warmer and more saline than the Pacific. The upwelling of cold and CO₂-rich water is reducing the pH in the Pacific. The black dots indicate the positions of the most important Ocean Drilling Program Sites (from north to south): Site 1000, Site 999, Site 1241, Site 846.

divergence of surface water isotope values starting at 4.7 Ma (Haug *et al.* 2001) indicating a shoaling of the CAS to less than 100 m. A significant sea-level lowstand period starting at 4.6 and lasting until 3.1 Ma (Haug *et al.* 1987) enhanced the shallowing of the Isthmus. Brief reversals of the isotope differential are explained by either short breaching of the Pacific waters into the Caribbean across the still-submerged sill (Haug *et al.* 2001) or by short-lasting re-openings at 3.8 and 3.4–3.3 Ma (Fig. 5) as indicated by reduced ventilation and hence preservation (Haug & Tiedemann

1998). The closure was almost complete at 3.8–3.6 Ma (Coates *et al.* 1992) though a shallow-water connection continued beyond 3.0 Ma (Coates & Obando 1996) most likely until 2.5 Ma though some records even point towards 1.9 Ma as the date for the last breach of the Isthmus (Keller *et al.* 1989). The Great Interchange between North American and South American land mammals indicates the finalization of the land bridge at 2.7 Ma (Webb 1997) when modern elevations in the Colombian Andes were reached (Gregory-Wodzicki 2000).

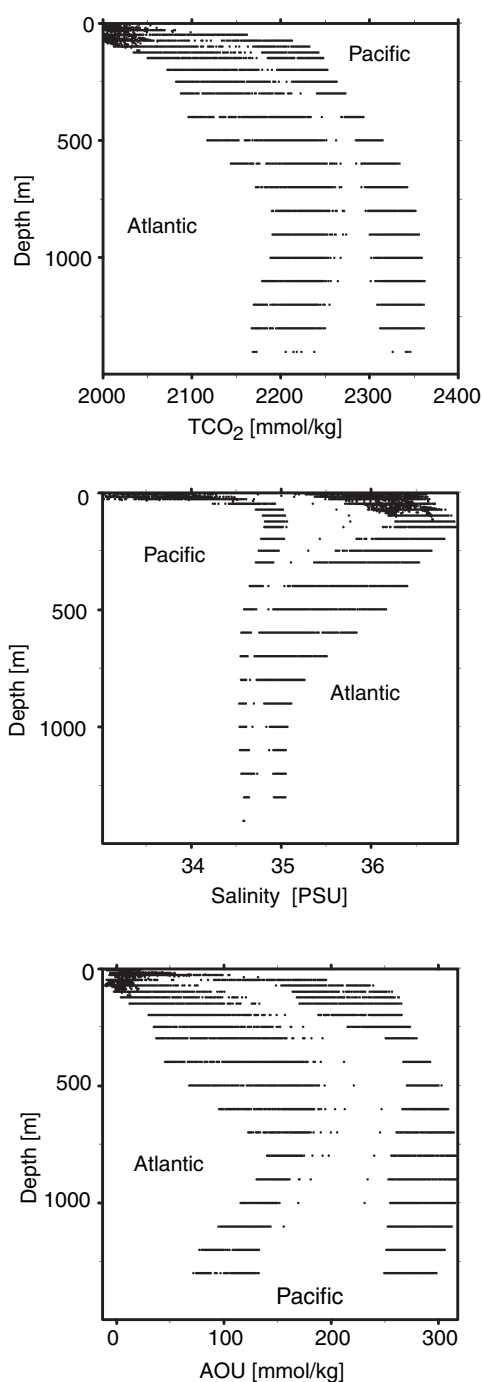


Fig. 3. Water column property profiles from both sides of the Isthmus showing the difference in total CO_2 , salinity and apparent oxygen utilization [AOU] between the modern Atlantic and Pacific throughout the water column (from Ocean Data View, Schlitzer (2006)).

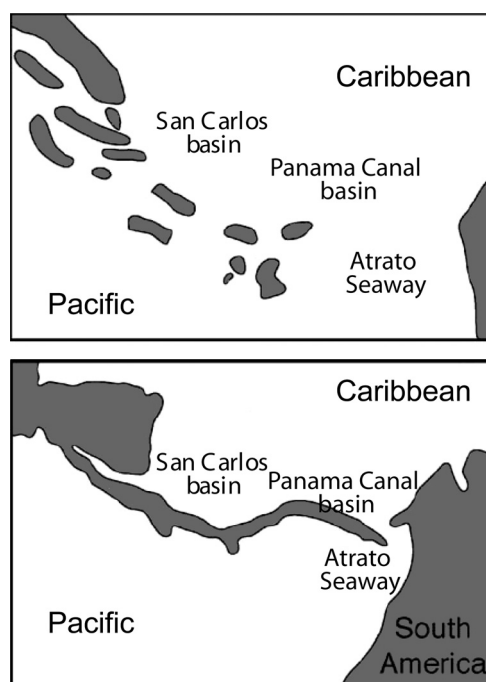


Fig. 4. Two possible palaeogeographic interpretations showing the distribution of land (in grey) in the Central American Seaway during the Middle Miocene: top, the Island model; bottom, the Peninsula model (modified after Kirby & MacFadden 2005).

Consequences of closure

The closure of the CAS changed the boundary conditions of the oceans and created a new state of the oceanic and atmospheric system. The Isthmus blocked the exchange of tropical water masses between the Atlantic and Pacific. The closure of the circumtropical seaways is assumed to have triggered and/or strengthened the North Atlantic Deep Water production, initiated the Caribbean Current, strengthened the Gulf Stream, and, therefore, changed the global distribution of deep-water masses, heat and salinity (Haug & Tiedemann 1998). The intensification of the circulation caused the build-up of sediment drifts in the Caribbean (Anselmetti *et al.* 2000) and later in the North Atlantic (Wold 1994).

Sedimentology

Oxygen-rich, nutrient-poor, northern-sourced deep-water masses (such as NADW) preferentially preserve carbonates, whereas southern-sourced, nutrient-rich, oxygen-poor corrosive water masses (such as the modern Antarctic Intermediate Water,

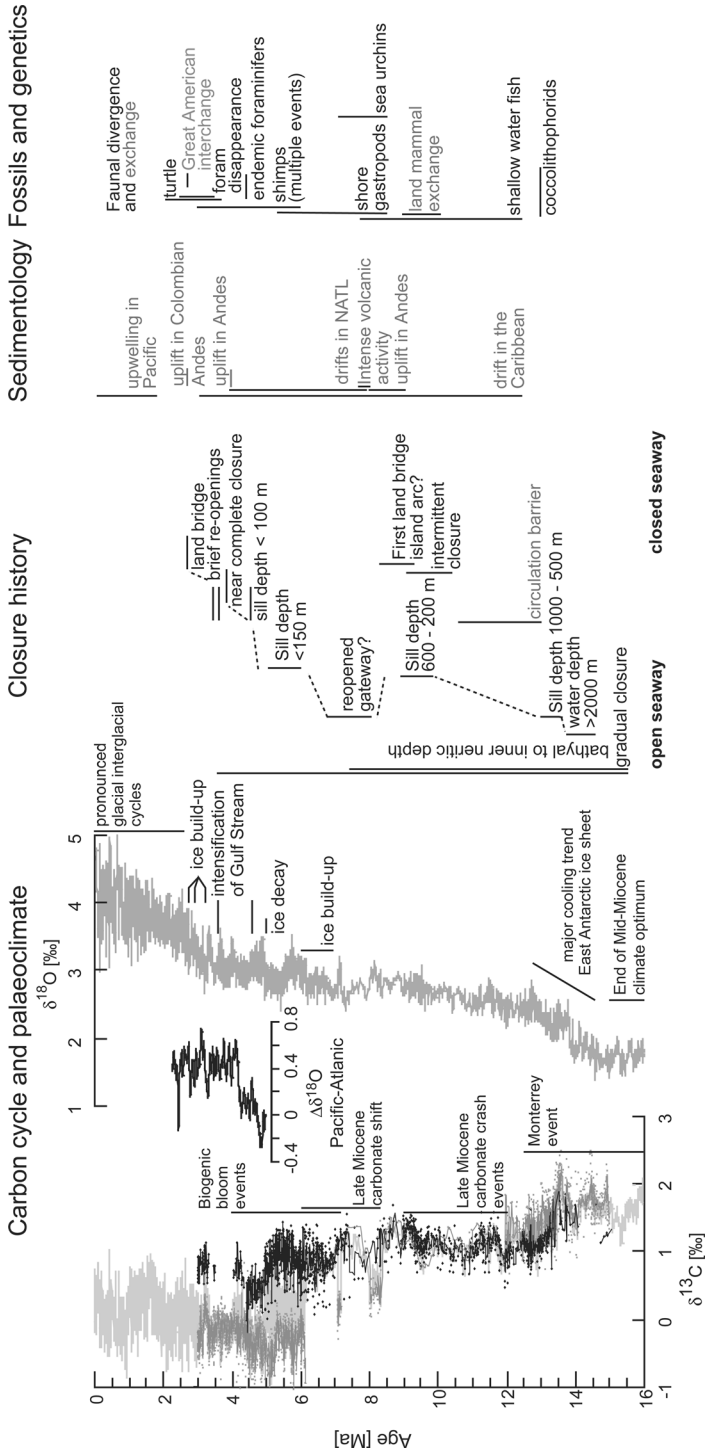


Fig. 5. Overview of the closure history of the Isthmus. Global climate change is exemplified in carbonate [$\delta^{13}\text{C}$] and oxygen isotope [$\delta^{18}\text{O}$] records of benthic foraminiferal carbonate (Zachos *et al.* 2001): major events highlighted. Oxygen isotopes represent changes in ice volume and temperature, whereas carbon isotopes represent changes in water masses and carbonate/carbon deposition history. The development of the salinity contrast between Atlantic and Pacific (Haug *et al.* 2001) is shown as oxygen isotope differentials between planktic foraminifers from both sides of the Isthmus [$\Delta\delta^{18}\text{O}_{\text{Pacific-Atlantic}}$]. The sill depth history is synthesized from the references in the text, as well as sedimentological evidence for events in relationship to the closure history, such as the build-up of drift bodies and tectonic events. The last column represents biological evidence for separation of species on both sides of the Isthmus (terrestrial animals in grey type, marine in black). Gradual changes are indicated with vertical lines, abrupt changes, e.g. separation of ecosystems or sill depth estimates, as horizontal lines. Additional information and references in the text.

AAIW) cause dissolution (Roth *et al.* 2000). The exchange of the corrosive southern water mass against the NADW in the Caribbean related to the re-establishment and intensification of the NADW production (Roth *et al.* 2000) led to better ventilation and carbonate preservation in the Caribbean (Tiedemann & Franz 1997; Haug *et al.* 2001).

The intensification of deep-water flow eroded the Bahamas carbonate platforms (Reijmer *et al.* 2002). The same process led to the erosion of sediments from the continental margins. Their subsequent redeposition led to an increase in the growth rates of sediment drifts, for example the Santaren Drift in the Caribbean from 12.5 Ma onwards (Anselmetti *et al.* 2000) or in the North Atlantic (Feni and Gandar Drift) and Labrador Sea (Eirik Drift) from 7.9 and 3.1 Ma (Wold 1994). The drift deposition at the Santaren Drift is synchronous with the first shallowing of the seaway and the consequent increase in loop current in the Gulf of Mexico which intensified the Gulf Stream and NADW production (Anselmetti *et al.* 2000) whereas the North Atlantic Drift's deposition corresponds to the second closing phase. Three distinct reflectors in seismic profiles of the Bahamas platform at 12.2, 12.6 and 10.8 Ma corroborate the importance of erosion as a result of the current intensification (Anselmetti *et al.* 2000). A prominent erosional surface in the seismic data at 4.2 to 3.3 Ma (Anselmetti *et al.* 2000) indicates a second increase of loop current transport associated with the final closure steps of the CAS.

The exchange a Southern Ocean water mass (AAIW) as the Caribbean deep water with less-corrosive northern component (NADW) water mass at 4.7 Ma led to an increase in deep-water ventilation and carbonate preservation in the Caribbean (Haug & Tiedemann 1998). Similarly, the increased thermohaline circulation amplified the global inter-basin carbonate fractionation, resulting in enhanced preservation in the Atlantic Ocean whereas dissolution prevailed in the Pacific (Haug & Tiedemann 1998).

NADW production

Prior to the late Mid-Miocene, the carbon isotope chemistry of the deep basins was homogeneous because of the lack of low-latitude barriers to deep communication and weak to non-existent NADW production (Fig. 5). The first divergence, though very small, of $\delta^{13}\text{C}$ of deep-sea benthic foraminifers from Atlantic and Pacific sediments can be recognized in the middle Miocene around 13 Ma (Fig. 5). The first significant isotopic differential was established in the late Miocene around 8.3 to 8.5 Ma and the largest step around 6.1 Ma (Delaney 1990; Wright & Miller 1996; King *et al.*

1997). This most significant step in the deep-water divergence is synchronous with the rise of the sill to a water depth of 500–200 m (Fig. 5). This circulation-related basin-to-basin fractionation results in a more than 1.0‰ difference between the deep Pacific and Atlantic (Zachos *et al.* 2001). An increase in NADW production after 4.7 Ma and 4.2 Ma has been documented in the $\delta^{13}\text{C}$ record of benthic foraminifers (Haug *et al.* 2001) and is interpreted to reflect ventilation changes in the North Atlantic (Tiedemann & Franz 1997; Haug & Tiedemann 1998). The similarity of the stepwise changes in deep-water chemistry and planktic foraminifer isotope records suggests a link between the increased salinity contrast and deep-water circulation (Haug *et al.* 2001). During the early to middle Pliocene (4.2 to 3.7 Ma), the production of NADW is considered to have been stronger than modern values (Haug & Tiedemann 1998; Billups 2002).

The necessity of a closure of the CAS for the production of NADW is heavily debated (see section entitled 'Computer models assessing the impact of the closure of the CAS'). Though the onset of NADW production is often related to the closure of the Central American Seaway, some data suggest significant NADW production during the mid-Miocene (Keller & Barron 1983; Delaney 1990; Wright *et al.* 1992).

Surface-water properties

Surface-water properties of the ocean were influenced by the closure of the CAS in two ways: first, the water mass exchange was physically blocked; and secondly, the physicochemical properties of the surface water changed subsequently. The surface-water circulation was altered due to the initiation of the Caribbean Current (Fig. 1) and the strengthening of the Loop Current, Florida Current and Gulf Stream. The global distribution of heat and salinity changed (Haug & Tiedemann 1998), influencing the physical properties of water transported to the Nordic seas and ultimately of NADW (Lear *et al.* 2003).

The restricted exchange of surface-water masses led to the establishment of the modern Atlantic/Pacific salinity contrast. Due to intense evaporation in the Caribbean-freshwater is transported from the tropical Atlantic and Caribbean into the equatorial east Pacific (Broecker & Denton 1989). The high evaporation increases salinity in the Caribbean (Haug *et al.* 2001) and the land bridge or shallow-water strait prohibits the flow of comparatively less-saline waters back into the Caribbean. The divergence of $\delta^{18}\text{O}$ records of planktic foraminifers from both sides of the Isthmus starts at 4.7 Ma (Fig. 5) and is interpreted to reflect the

establishment of the modern Pacific–Caribbean salinity contrast and formation of the Caribbean Warm Pool (Keigwin 1982a; Haug *et al.* 2001). The establishment of the modern salt asymmetry between Atlantic and Pacific is the key driver of the thermohaline circulation pumping heat northwards, which resulted in the Pliocene warm period (Haug *et al.* 2001).

The northward transport of warm waters increased zonal temperature and pressure gradients, changed the trade winds (Billups *et al.* 1999) and shifted the intertropical convergence zone (ICTZ) southwards to its modern position around 4.36 Ma (Cannariato & Ravelo 1997; Chaisson & Ravelo 1997; Billups *et al.* 1999). The southward shift of the ITCZ would have led to an intensification of the North Brazil Current which transports warm and saline water along the northern coast of Brazil towards the Caribbean and further increased the advection of warmer and more saline Caribbean surface waters (Billups *et al.* 1999).

The change in the surface-water structure is visible in the differential $\delta^{18}\text{O}$ ($\Delta\delta^{18}\text{O}$) values between shallow- and intermediate-dwelling planktic foraminifers from three tropical sites (Chaisson & Ravelo 1997, 2000). The record from the eastern equatorial Pacific shows the beginning of upwelling of cold water around 4–5 Ma whereas the western Pacific did not change at all. In the tropical Atlantic, there is also evidence for changes in surface hydrography between 5 and 4 Ma (Chaisson & Ravelo 1997; Billups *et al.* 1999). The east–west hydrographic gradient in the Pacific and its associated faunal provinciality developed between 4.4 and 4.0 Ma (Chaisson & Ravelo 2000). The upwelling of cold nutrient-rich waters in the eastern tropical Pacific changed the depth of the thermocline and shifted the locus of maximum opal accumulation, leading to a decrease in carbonate and opal accumulation around 4.5 Ma (Farrell *et al.* 1995).

The divergence between Pacific and Atlantic oxygen isotope values was not unidirectional, but shows reduced gradients around 3.3 and 2.8 Ma (Fig. 5). The reversals at 3.8 and 3.4–3.3 Ma (Fig. 5) can be best explained by short breaching of the Pacific waters into the Caribbean across the still-submerged sill due to either sea-level change or short-lasting re-openings (Haug *et al.* 2001). They are also visible in the carbonate preservation changes indicating reduced ventilation in the Caribbean (Haug & Tiedemann 1998).

Northern Hemisphere glaciation

The ice build-up in the Northern Hemisphere is the most profound change in the Earth's climate in the Neogene (Shackleton *et al.* 1984). The link between

the closure of the CAS and Northern Hemisphere glaciation (NHG), the build-up of the Laurentide and Scandinavian ice-sheets, is a matter of debate. Hypotheses about the influence of the Panama Isthmus on NHG range from it being the cause for the onset (Berggren & Hollister 1974), a delaying factor due to changes in heat transport (Berger & Wefer 1996), or setting the preconditions of the Northern Hemisphere glaciation (Driscoll & Haug 1998; Haug & Tiedemann 1998).

The earliest evidence for glaciation of the Northern Hemisphere has recently been pushed back to the Eocene (Moran *et al.* 2006). Larger pulses of ice-rafted debris are first recognized in the Mid-Miocene, around 14.4 Ma (Thiede *et al.* 1998). Increasing evidence for ice-sheets, based on $\delta^{18}\text{O}$ records and ice-rafted debris (Lear *et al.* 2003), is linked to the initiation of cold proto-NADW between 7 and 6 Ma during the start of the second closing phase of the CAS. These ice-sheets decayed in the early Pliocene (Lear *et al.* 2003), which has been related to the increased warm-water transport to the north potentially due to the closure of the shallow-water throughflow. Between 3.2 and 2.7 Ma, a gradual change towards the current icehouse conditions is indicated by progressively heavier $\delta^{18}\text{O}$ values during the glacials (Shackleton *et al.* 1984; Tiedemann *et al.* 1994). The first major glaciation happened during MIS 110 at 2.73 Ma (Lisiecki & Raymo 2005). This large increase of ice build-up on the continents must have resulted in a significant sea-level drop and may have led to the final closure of the seaway.

The closure of the CAS has often been linked to the NHG via increased thermohaline circulation (Haug *et al.* 2001). Next to heat, the advection of warm and saline waters to northern high latitudes led to increased moisture supply, which may have increased Siberian runoff and consequently changed the freshwater balance in the Arctic Ocean (Driscoll & Haug 1998; Haug & Tiedemann 1998). The less-saline water could freeze more easily, form sea-ice, increase the Earth's albedo, and isolate the heat of the ocean from the atmosphere (Driscoll & Haug 1998).

Though this scenario is plausible, the increase in heat transport to the North Atlantic would first delay the onset of glaciation in the Northern Hemisphere instead of facilitating it (Berger & Wefer 1996). The c. 1.5 Ma gap between the closure of the seaway and the onset of the glaciation indicates that the closure may have been a pre-condition but not the cause. A second tectonic mechanism related to the NHG is the restriction of the Indonesian Seaway between 4 and 3 Ma and a subsequent reduction in atmospheric heat transport from the tropics to higher northern latitudes in the

Pacific region (Cane & Molnar 2001). The timing of the restriction of the Indonesia throughflow is by far not as certain as the CAS (Hall 2001), making this relationship less convincing.

Regional differences in the timing of cooling imply that global cooling was a gradual process (Ravelo *et al.* 2004) rather than the response to a single threshold or episodic event. Alternative hypotheses for the NHG are plentiful. One scenario relates the climate change to a weathering-induced reduction in the greenhouse gas CO₂ (Crowley & Berner 2001) as a result of Tibetan uplift (Raymo *et al.* 1988). However, this hypothesis is not corroborated by CO₂ proxy data (Kürschner *et al.* 1996; Pearson & Palmer 2000).

Alternatively, long-term reorganization of tropical surface-water conditions has been suggested to have influenced global climate and initiated the change from Pliocene warmth to increased build-up of ice. Wara *et al.* (2005) suggest that the temperature structure of the equatorial Pacific during the warm early to middle Pliocene has been more zonally uniform than today – similar to the modern Pacific in an El Niño state. Modern El Niño events result in a weakening of the easterly trade winds over the equatorial central Pacific (Cane & Molnar 2001), reduced upwelling in the eastern Pacific, a reduction of temperature gradients between the eastern and western Pacific and a reduced low-latitude latent heat transport (Wara *et al.* 2005). The development of a strong Walker circulation and a weakening of the Hadley circulation at *c.* 1.7 Ma coincides with the development of colder interglacials and an increase in the sensitivity of climate to solar forcing (Ravelo *et al.* 2004). In stark contrast, Rickaby & Halloran (2005) give evidence for enhanced thermocline tilt and cold upwelling in the equatorial Pacific which would suggest a prevalence of a La Niña-like state, rather than the proposed persistent warm El Niño-like conditions. Independent evidence is therefore necessary to solve this contradiction.

Another suggestion for the cause of the NHG intensification is changes in Milankovitch cyclicity, such as an increase in obliquity minima (Maslin *et al.* 1998). In contrast, Mudelsee & Raymo (2005) suggest that Milankovitch variability may have influenced Pliocene to Pleistocene climate evolution but was not the trigger.

The ice build-up may have initiated positive-feedback mechanisms such as increased vertical stratification in high latitudes at 2.7 Ma, which in turn would limit CO₂ exchange (Haug *et al.* 1999; Sigman *et al.* 2004). Haug *et al.* (2005) found evidence for increased late summer sea-surface temperatures in the high-latitude Pacific as a response to this increase in stratification while, at the same time, winter sea-surface temperatures cooled. The

warmer summer temperatures are suggested to provide increased moisture transport to northern North America (Haug *et al.* 2005). This scenario would amplify the effects of increased moisture transport in the Atlantic, such as the increase in Siberian runoff and a change to the freshwater balance in the Arctic Ocean reported by the same authors (Driscoll & Haug 1998; Haug & Tiedemann 1998). Causes for and consequences of NHG are discussed in more detail in the paper by Ravelo *et al.* (2007).

Ecosystems and palaeobiogeography

The formation of the Isthmus of Panama facilitated the mixing of terrestrial faunas between the two continents (Webb 1976) while separating the continuous marine province into separate and ecologically distinct Pacific and Caribbean communities (Vermeij & Petuch 1986; Jackson *et al.* 1993). Combining the fossil record with modern molecular data allows dating of some of the splitting events caused by the vicarious living and provides new fascinating evidence for stepwise separation of the marine ecosystems. The phylogenetic relations of species in cosmopolitan genera can point towards barriers for gene flow. Using the molecular clock approach, these divergence times can be dated and provide additional information for the closure history of the CAS.

The palaeogeographic shape of this land connection – either a continuous land bridge with North America or an extensive island-arc system (Fig. 4) – is heavily debated. Evidence from marine sediments and volcanic records suggests an arc during the Miocene consisting of small islands separated by shallow straits (Coates & Obando 1996). Kirby & MacFadden (2005) used body size to determine the palaeogeography of the connection between the Americas. Their work is based on the assumption that the separated population, without exchange and immigration from other populations and the absence of large predators, has effects on body size: the so-called island effect. The island effect leads to gigantism (in small mammals) and dwarfism (in large mammals). Kirby & MacFadden (2005) determined that the body size of land mammals from Central America did not significantly differ from their North America counterparts, which points towards gene flow with the North American continent and hence is evidence for the peninsula hypothesis (Kirby & MacFadden 2005).

Terrestrial ecosystems

The closure of the CAS and the emergence of the Isthmus allowed exchange of terrestrial species

between North and South America in several immigration events. The mammalian fossil record suggests a continuous connection of Panama with North America in the Miocene from 19–16 Ma onwards (MacFadden 2005). The earliest terrestrial interchange of 'waif immigrants' (racoons) from North to South America is dated between 10.1 and 9.1 Ma. The dispersal is assumed to have happened along an island arc system before the establishment of a land bridge (Webb 1985). A similar migration path has been suggested for the New World rats and ground sloths arriving in South America in the early Pliocene (Marshall *et al.* 1982) at a time where the sill depth was less than 100 m.

The biogeographic distribution and the genetic divergence in a group of freshwater and marsh fishes (synbranchid eels) in South and Central America indicated that the South American clade was present in Central America before the final closure of the Isthmus between 7.7 and 12.4 Ma (Perdices *et al.* 2005). This is time-equivalent with the intermittent closure or rather shallow-water connections. These fish are very salinity-tolerant and hence were present before primary freshwater fish could colonize Central America (Perdices *et al.* 2005).

The most significant terrestrial migration, the Great American Interchange around 2.8–2.6 Ma (Lundelius 1987), resulted in exchange of mammals in both directions (Marshall *et al.* 1982) indicating a land bridge connecting North and South America. During the Pleistocene, the exchange became asymmetrical with more North American mammals occurring in South America than *vice versa* (Marshall 1988), which is assumed to be a result of increasing climatic variability rather than a tectonic feature (Webb 1991). The total number of mammalian genera in South America increased markedly as a result of North American immigrants.

Despite the great dispersal potential of seabirds, the Isthmus of Panama is also an effective barrier to gene flow in several pantropical species such as terns (Aulsebrook *et al.* 2000) and boobies (Schreiber *et al.* 2002). These seabirds avoid flying over land (Steeves *et al.* 2003) and hence the 35 km-wide Isthmus, with an interior dominated by steep mountains, provides a barrier which these birds cannot pass. Interestingly, the divergence in masked booby (*Sula dactylatra*) populations is much younger than the closure with a divergence time of c. 640 kyr (Steeves *et al.* 2005) and might be more related to the uplift history of Central America than with the formation of the land bridge.

The history of vegetation shows that the contact between Central America and South America decreased the extent of endemism in both areas (Burnham 1999). Palynoflora lost their distinct differences between North and South America at

c. 4 Ma, though the age is not very well constrained (Graham 1992).

Marine ecosystem

The closure of the circumtropical seaways caused a tectonic constellation which is a novelty in the evolutionary history of all plankton groups and significantly influenced their environment and dispersal possibilities. Speciation in the ocean is hard to determine, mainly because of the dispersal abilities of marine organisms, particularly those species with planktic larvae. Consequently, this distinct geographical event provided classic textbook examples for allopatric speciation (speciation through geographical separation). Different species responded to these changes in a different manner, and thus become separated at different times.

The two ecosystems on both sides of the Isthmus changed profoundly. The closure thus split a homogeneous plankton community into two vastly different ecosystems. Studying the faunal and floral evolution provides a unique opportunity to investigate the effects of changes in temperature, stratification and ocean acidification on ecosystems. Though the evolutionary consequences of the closure of the seaway are well studied, the ecological importance of this unrivalled local case study for climatically induced restructuring of the planktic ecosystem has not yet been exploited.

The closure increased thermohaline circulation (Haug & Tiedemann 1998) and in turn enhanced stratification (Billups *et al.* 1999). This in consequence has changed the density of the surface water, changed the vertical water mass structure and has caused an elevation of the thermocline into the photic zone (Billups *et al.* 1999). Consequently, a distinct planktic foraminiferal faunal difference developed from 7–6.5 Ma between the eastern and western equatorial Pacific (Chaisson & Ravelo 2000). In the eastern Pacific, upwelling of deep water cooled the subsurface waters, increased the temperature gradients in the upper photic zone and hence led to elevated opal deposition (Cortese *et al.* 2004). The higher stratification in the tropics increased the number of available niches in the upper water column (Schmidt *et al.* 2004a). By 4.2 Ma, the closure of the Panamanian Isthmus appears to have facilitated the evolution of unprecedentedly large sizes in planktic foraminifer assemblages (Schmidt *et al.* 2004c) with the largest size in the western tropical Pacific and Atlantic (Schmidt *et al.* 2004b).

The first steps towards closure

Coccolithophore assemblages in deep-sea cores on both sides of the Isthmus were identical from

16.21 to 13.57 Ma (Kameo & Sato 2000). The divergence, starting at 13.57 Ma, led to an increasingly different assemblage with the next step between 10.71 and 9.36 Ma, suggesting an intermittent first closure of this Isthmus. A gradual decrease of the ratio of planktic to benthic foraminifers points towards a shallowing of the seaway by 14.7 and 13.5 Ma (Duque-Caro 1990). The faunal composition of benthic foraminifers and their poor preservation indicates nutrient-rich, oxygen-poor water masses. The benthic fauna in the Atrato Basin indicated a water depth between 500 and 1000 m around 13.45 Ma. By 13.0 to 11.64 Ma, the sill is assumed to have deflected the intermediate water currents and caused a circulation barrier (Duque-Caro 1990). Another shallowing step is indicated by increased abundances of the *Uvigerina*–*Valvulineria* assemblages, pointing towards an upper bathyal depth between 10.4 and 9.9 Ma. Clear differences between Pacific and Caribbean foraminiferal fauna at this time are interpreted as evidence for an interoceanic biogeographic barrier (Duque-Caro 1990) due to intensification of the California Current. Planktic foraminiferal assemblages change towards cool low-diversity faunas (Keller & Barron 1983).

Caribbean reef corals started to diversify rapidly between c. 12 Ma until 8 Ma (Collins *et al.* 1996a). Tropical rocky shore gastropods from both sides of the Isthmus show a high amount of divergence between 8.5 and 5.3 Ma, pointing towards isolation (Collins *et al.* 1996c) which can also be seen in the genetic divergence of sea-urchins between 8.5 and 6.1 Ma (Lessios *et al.* 2001). The similarity between the Pacific and Caribbean benthic foraminiferal assemblages indicates a cessation of the oceanic barrier and a brief re-establishment of the water exchange in the Late Miocene. The shallow-water benthic foraminiferal community in the Caribbean changed from species preferring siliciclastic habitats to a carbonate-associated assemblage around 7.1 Ma exploiting the new reef habitats. The largest change was between 5.3 and 3.5 Ma (Collins *et al.* 1996a). In the latest Miocene and Pliocene, seagrass-associated bryozoans underwent dramatic extinction (Cheetham & Jackson 1996). The diversification of reefs points towards oligotrophic conditions and warm-water temperatures which favour corals and produce carbonate sediments, the new habitats which the benthic foraminifers became adapted to.

The final closure

An increasing abundance of species, today adapted to higher-salinity conditions, in the Caribbean foraminiferal fauna by 4.5 Ma indicates an increase

in salinity (Keller *et al.* 1989). The first appearance of endemic species of planktic foraminifers (*Menardella exilis*) at 4.45 Ma indicates the different evolutionary histories in both ocean basins. Though there is an increase in endemism, diversity starts to decrease around 4.5 Ma (Chaisson & Ravelo 2000). Some species were briefly absent or very rare in one ocean basin but not in the other. For example, *Menardella miocenica*, first appearing at 3.48 Ma, rarely migrated through the Gulf of Panama (Kennett & Srinivasan 1983). *Globorotalia tumida* was absent between 3.7 and 2.1 Ma at Ceara Rise in the western equatorial Atlantic (Chaisson & Pearson 1997) whereas in the western Pacific *G. tumida* showed a marked increase in relative abundance in the Pliocene (Chaisson & Leckie 1993). During the same time interval (3.48 to 2.28 Ma), the pulleniatinids disappeared in the Atlantic (Bolli 1971) whereas they were continuously present in the Pacific (Chaisson & Leckie 1993). By 3 Ma, finely perforate menardellids were dominant in the Atlantic and rare to absent in the Pacific (Kennett & Srinivasan 1983; Chaisson 2003). The occurrences of all these species indicate that the necessary water depth for migration from the Pacific to the Atlantic was not available anymore around 3.7 Ma and definitely by 3.4 Ma. Divergence events in sea-urchins (benthic organisms with planktic larvae) from both sides of the Isthmus, for example, *Diadema mexicanum* from *D. antillarum*, at 3.1 Ma point towards the restriction of larval exchange (Lessios *et al.* 2001).

By 2.5 Ma, permanent divergence of faunal provinces between the Pacific and the Caribbean are interpreted as the closure of the gateway. The further abundance increase of *G. ruber* points towards even higher salinity in the Caribbean (Keller *et al.* 1989) in agreement with changes in nannofossils (Gartner *et al.* 1987) while a reduction in surface dwellers in the Pacific indicates increased upwelling. A decrease in the diversity of Caribbean reef corals starting at 4 Ma (Collins *et al.* 1996a) might be related to the high salinity. The biogeographic migration pattern of planktic species indicates a blocked exchange between the Atlantic and Pacific which forced *Globorotalia truncatulinoides*, for example, to colonize the oceans from the Pacific via the Indic and the Agulhas retroflexion into the Atlantic (Spencer-Cervato & Thierstein 1997). New data (Schmidt submitted) points to an earlier first appearance in the South Atlantic (2.1 Ma) than in the tropical Atlantic and hence corroborates a migration around South Africa.

Caribbean gastropod (*Strombina* group) diversity peaked in the early Pliocene and declined thereafter from 23 to 3 species, whereas eastern Pacific diversity is highest today with 33 species (Jackson *et al.* 1993) indicating the profound ecological

changes in the shallow-water habitats. Shallow-water molluscs, living on the inner shelves, indicate a complete closure by 3.7 Ma (Coates *et al.* 1992). The occurrence of similar pairs of late Pliocene gastropods (2.6 to 1.8 Ma) on both sides of the Isthmus, however, suggests some interchange may still have been possible. The increased separation of the habitats led to disparate histories in gastropod evolution with the Caribbean extinction (1.8–1.6 Ma) being a time of explosive Pacific first appearances (Jackson *et al.* 1993). The extinction did not just affect molluscs but also reef corals throughout the Caribbean. The diversity of Caribbean reef corals decreased dramatically in the Pleistocene (Collins *et al.* 1996a). Marked alteration in the trophic structures in shelf ecosystems since the late Pliocene (2.6–1.8 Ma) led to an increase in reef dwellers and a decrease in suspension feeders in the Caribbean. These food-web changes strongly support the hypothesis that declining nutrient supply had an increasing impact on regional macroecology, culminating in a faunal turnover (Todd *et al.* 2002).

Closure history of nekton

The Panama Isthmus is an important barrier for marine nekton such as turtles and fish (Bowen *et al.* 1997; Lessios *et al.* 2001, 2003). The closing of the seaway led to allopatric separation and consequent divergence. Many sister taxa in the Caribbean and eastern Pacific became isolated during the initial shoaling rather than in final closure (Knowlton *et al.* 1993; Cronin & Dowsett 1996), e.g. the reef fish *Ophioblennius* of about 7 million years ago (Muss *et al.* 2001). The reorganization of Atlantic circulation involved an initial period of high energy in major current systems (Haug & Tiedemann 1998) which some species exploited, e.g. the *Ophioblennius atlanticus* larvae were able to traverse the mid-Atlantic barrier via the Equatorial Undercurrent. Once regularized circulation patterns became established, larvae of *O. atlanticus* were not able to bridge the Amazon–Orinoco or mid-Atlantic barriers anymore (Muss *et al.* 2001).

The genetic divergence between Kemp's ridley sea turtle *Lepidochelys kempi* and the olive ridley turtle *L. olivacea* indicates a restriction of the seaway to a water depth too shallow for these near-shore and inshore organisms to cross between 2.5 and 3.5 Ma. The snapping shrimp genus *Alpheus* shows a staggered separation rather than one event (Knowlton *et al.* 1993). Though some divergences within *Alpheus* are assumed to be synchronous with the final steps of the closure around 3 Ma, several events are significantly earlier (6.1 to 4.4 and 6.3 to 4 Ma). The oldest split in the

genus *Alpheus* is dated for the time interval 9.1 to 6.8 Ma in a species with the adaptation to the relatively deepest habitat in the intertidal zone. This is puzzling though, since the depth of the Atrato Strait (Fig. 2) has been suggested to be at least 150 m (Duque-Caro 1990) which would have allowed larvae to cross from one ocean basin to the other as indicated by the gene flow between several taxa. The smallest trans-isthmian difference in this group is measured in those species that live in mangroves, an environment that was likely to be the last habitat to be separated by the Isthmus (Knowlton & Weight 1998).

Evidence for breaching of the Isthmus

Interestingly, several species point towards gene flow even in the Pleistocene which has been interpreted as evidence for breaching of the Panama Isthmus. Evidence from planktic foraminifers (Cronin & Dowsett 1996) points towards two breaching events during high sea-level stands, the most recent occurring at 2 Ma. Keller *et al.* (1989) also suggested the existence of seawater connections between the Caribbean and eastern Pacific that lasted until 1.8 Ma, based on foraminiferal data. A short-lived breach of the Isthmus would be expected to affect a small number of species, which (because of their ecological attributes or due to pure chance) either re-established genetic connections with their geminates, or replaced the resident population.

Computer models assessing the impact of the closure of the CAS

Computer models were used to identify consequences of the closure of the Panama Isthmus, specifically its influence on the production of North Atlantic Deep Water (NADW) and the glaciation of the Northern Hemisphere. Using the Hamburg Ocean general circulation model (GCM), Maier-Reimer *et al.* (1990) suggested that the closure was the prerequisite for development of the modern thermohaline circulation. Their model suggests that an open seaway would inhibit NADW production. Similarly, Mikolajewicz & Crowley's (1997) model results in severely reduced NADW production when the CAS was partially open due to a flow of relatively fresh Pacific water into the North Atlantic (Mikolajewicz *et al.* 1993). Nisancioglu *et al.* (2003) agree that the shoaling of the CAS had a significant impact on global circulation, but they deduced from their model that significant amounts of NADW formed even though the CAS was open. They calculated that, if the sill depth is larger than 1000 m, most

of the NADW passes as a westward jet through the CAS into the Pacific, greatly reducing NADW transport to the South Atlantic. When the sill depth is shallower than the depth of the NADW outflow, the NADW flow to the Pacific Ocean would be blocked and transport to the South Atlantic increased. Several independent datasets strongly suggest that NADW was formed before the closure of the seaway (e.g. Keller & Barron 1983; Burton *et al.* 1997) and increased in the Miocene (e.g. Delaney 1990) to modern values in the Pliocene (Haug & Tiedemann 1998) and therefore this model is corroborated. Interestingly, Nisancioglu *et al.* (2003) suggest that the similarity of $\delta^{13}\text{C}$ and Cd/Ca data, traditionally interpreted as an indication for the absence of NADW (Delaney 1990; Wright *et al.* 1992), should be interpreted as the presence of the same water mass – young NADW – in the Atlantic and western Pacific. The divergence of the records in the late Miocene indicates the aging of the NADW on its way to the Pacific as a result of the closure of the Isthmus (Nisancioglu *et al.* 2003).

Klocker *et al.* (2005) assessed the importance of the closure of the CAS for the NHG with an intermediate-complexity coupled atmosphere–ocean model. They found that the closure of the Isthmus lead to an increase in sea-surface temperature and salinity in the northern North Atlantic similar to proxy results but not to the predicted increase in snow accumulation in northern latitudes and the initiation of the Northern Hemisphere glaciations (Klocker *et al.* 2005). In contrast, the increased heat transport results in higher temperatures and a retreat of perennial snow cover in line with the arguments of Berger & Wefer (1996). Using the same model, Prange & Schulz (2004) suggested that the closure of the CAS caused an intensification of upwelling of southwest Africa, similar to the sedimentary record (Marlow *et al.* 2000), and an intensified equatorial upwelling system, while the northwest African upwelling around the Canary Islands would be reduced. This change is caused by altered sea-surface temperature patterns influencing atmospheric dynamics and hence wind stress (Prange & Schulz 2004).

Summary and outlook

The Isthmus is the last step in the closure of the circumtropical seaways, resulting in the separate evolution of the Caribbean/Atlantic and the Pacific Ocean. The closure of the Panama Isthmus had fundamental consequences for global ocean circulation, evolution of the tropical ecosystems and potentially the switch to the modern ‘cold house’ climate mode. It influenced global ocean circulation

and climate. Although the connection between NHG and closure of the CAS is plausible, there are ongoing arguments regarding the causal relationship between Panamanian tectonic and climatic and ecological changes (Schmittner *et al.* 2004). Available studies have generated single proxy records, focusing mostly on the last part of the closure history, some of them at large distances from the Isthmus.

The shoaling of the Isthmus started around 14.7 Ma with the first consequences for deep-water flow between 13.5 and 13 Ma when the sill depth was around 1000 to 500 m. This changed bottom-water circulation led to the formation of drift deposits in the Atlantic. Although intermittent closure has been suggested for the time interval from 10.7 to 9.4 Ma, the data can also be explained by an oceanic barrier such as the intensification of the California Current, separating the Pacific from the Caribbean bioprovince. Uplift, as indicated by proxy records of weathering products, combined with active volcanism may have led to an island arc chain which allowed the first terrestrial organisms to migrate between the Americas from 9 to 8 Ma. This increased restriction is also evident from the divergence of bottom water characteristics between the Pacific and Atlantic. The continued shallowing led to genetic isolation of several groups of species and consequently to vicarious speciation. Uncertainty is related to the time between 8 and 6.6 Ma, where several datasets point towards a reopening of the Isthmus whereas others point towards continued restriction. By 6 Ma, the sill depth had decreased to 150 m.

The limitation of surface-water exchange starting at 4.7 Ma resulted in an increase in salinity in the Caribbean, changes in the faunal composition, the origin of endemic planktic species and a profound crisis in Caribbean reef communities. This closing process had two brief reversals at 3.8 and 3.4 Ma. The emergence of a land bridge by 2.8 to 2.6 Ma enabled the Great American Interchange of terrestrial species. The shallow-water connections finally closed at 2.5 Ma, blocking the exchange of shore organisms and influencing the reef communities, resulting in profoundly different faunal provinces. Evidence for potential breaching of the Isthmus at sea-level highstands continues into the early Pleistocene.

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