

BIOGEOGRAPHIC EFFECTS OF THE CLOSING CENTRAL AMERICAN SEAWAY ON BENTHIC FORAMINIFERA OF VENEZUELA

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ABSTRACT

Studies of the effects of the Central American Seaway's closure on microfossil taxa and stable isotopes of foraminifera previously addressed the timing of emplacement of the Caribbean–tropical eastern Pacific sill, changes in marine nutrients, evolutionary and paleobiogeographic events associated with closure, and rates of uplift in Central America. However, there have been no quantitative studies of the transisthmian divergence of whole biotas. Here we assess biogeographic effects of the closing Central American Seaway by comparing middle Miocene to Pliocene, neritic benthic foraminiferal assemblages from Falcón State, Venezuela, to those of coeval deposits with similar paleoenvironments from Panama, Costa Rica, and Ecuador. Benthic foraminiferal assemblages from the Urumaco, Codore, Caujarao, and La Vela formations of Venezuela's central coast were compared to other Caribbean and tropical eastern Pacific assemblages with Simpson's, Dice, and Jaccard similarity coefficients. Results of the Simpson's Coefficient indicate that the Caribbean inner neritic faunas of Venezuela, Costa Rica, and Panama became significantly more similar from the late Miocene to Pliocene, as mixing with Pacific waters was reduced and modern oceanic conditions of the Caribbean Sea were established.

Twenty million years ago, according to all paleoceanographic evidence, the Central American Seaway connected Caribbean and tropical eastern Pacific waters. Over the next 15 My, the movement of tectonic plates and uplift caused shoaling of the seaway to depths that restricted deepwater flow between the tropical Atlantic and Pacific until complete emergence of Central America approximately 4 Ma. Paleontological research on evolution and biogeographic changes resulting from seaway closure has focused on shallow-water invertebrate and protist fossils in land-based deposits, and deepsea or open-ocean, surface-water protists preserved in deepsea cores. Here we briefly review the physical cutoff of Caribbean from tropical Pacific waters and the microfossil response, then quantitatively compare whole tropical American benthic foraminiferal assemblages through the late Miocene and Pliocene.

UPLIFT OF THE ISTHMUS OF PANAMA AND PALEOCEANOGRAPHIC CHANGES

The southern Central American arc on the southwestern edge of the oceanic Caribbean plate has been moving generally eastward since at least 65 Ma, to finally collide with continental South America. Coates et al. (2004) used the regional, land-based microfossil record of paleobathymetry and regional unconformities of southern Central America and northwestern South America to put the time of their collision at approximately 15–13 Ma, within the range of all estimates other than Farris et al. (2011), who suggested 20 Ma. After initial collision, marine basins from

northwestern Colombia to southeastern Costa Rica generally shallowed to neritic depths. A regional unconformity suggests collision was completed by approximately 7 Ma (Duque-Caro 1990, Collins et al. 1995, 1996b, Coates et al. 2003, 2004), although there were localized uplift events such as that caused by the subduction of the Cocos Ridge beneath Central America (Collins et al. 1995).

The progressive closure of the Central American Seaway and resulting oceanographic changes have been studied primarily with proxies of physical oceanography and general circulation models. As of 8 Ma, a reduction of eastward-flowing Pacific bottom water into the tropical Atlantic was indicated by low Nd and high Pb radioisotopes at North Atlantic sites (Frank et al. 1999, Reynolds et al. 1999). Throughout the late Miocene, the Caribbean was poorly ventilated, as seen from amounts of foraminifer shells and $\delta^{13}\text{C}$ (Bickert et al. 2004). About 8 Ma mesotrophic conditions with little ventilation of bottom waters and low current velocity were indicated by benthic foraminiferal proxies (Jain and Collins 2007). Between 8 and 7 Ma, nutrient-rich bottom waters flowing into the Atlantic were reduced, based on diverging Caribbean–eastern Pacific $\delta^{13}\text{C}$ values (Billups 2002, Spezzaferri et al. 2002). By about 6 Ma, benthic foraminiferal faunas show that bottom-water masses on either side of the isthmian deep-water sill had diverged, because Antarctic Deep Water was replaced in the Caribbean by North Atlantic Deep Water and in the Pacific by Pacific Deep Water (McDougall 1996).

Seaway closure decreased Atlantic primary productivity and reduced the inflow of high-nutrient, subsurface Pacific water, according to a climate-ocean model of differing sill depths and vertical diffusivity (Schneider and Schmittner 2006). For the eastern equatorial Pacific, the same model predicted increasing productivity, agreeing with foraminiferal $\delta^{13}\text{C}$ gradients that suggested an increase in surface-water nutrient concentrations during the last 5 My (Cannariato and Ravelo 1997). Foraminiferal proxies show decreased paleoproductivity after about 4 Ma (Bornmalm et al. 1999, Jain and Collins 2007, Jain et al. 2007). About 3 Ma, Caribbean surface waters became oligotrophic and the thermocline/nutricline deepened, based on calcareous nanofossil assemblages (Kameo 2002).

Most paleoceanographic proxies agree that the Central American Seaway closed completely about 4 Ma (although Pleistocene sea-level rises may have breached the isthmus; Keller et al. 1989). Whereas recent lithologic studies of the Central American volcanic arc proposed seaway closure by 15 Ma (Farris et al. 2011, Montes et al. 2012), their direct evidence is for the geological collision of elements of the Isthmus of Panama rather than the vertical changes in land vs sea that directly caused seaway closure (Coates and Stallard 2013). Studies of foraminiferal $\delta^{18}\text{O}$ in deepsea cores indicated that the modern Caribbean–eastern Pacific salinity contrast of 2 began to develop around 4.5 Ma (Keigwin 1982a, Haug et al. 2001) as a result of higher evaporation in the Caribbean and reduced mixing with the Pacific. Although Molnar (2008) suggested that an early Pliocene change from a permanent El Niño-like state to the modern El Niño–Southern Oscillation state could also explain trans-isthmian divergence in $\delta^{18}\text{O}$, the proposed changeover has not been explained. In any case, after accounting for changing salinities, $\delta^{18}\text{O}$ also reflects North Atlantic surface warming as shown by Mg/Ca ratios that indicated an increase of 2 °C in the central Caribbean at about 4.5 Ma (Groeneveld et al. 2008).

EFFECTS OF CHANGES IN SEAWAY DEPTH ON MICROFOSSILS

During the Paleogene, the gap between Central America and South America was bordered by a shallow carbonate platform extending north to central Panama (Cole 1952, 1957). In the early Eocene, bathyal to abyssal facies existed in present central to eastern Panama, as indicated by mollusks (Woodring 1970), foraminifera, and radiolarians (Bandy 1970, Bandy and Casey 1973). Other deeper, bathyal facies of southern Central America (Collins 2007) possibly resulted from local basin subsidence or down-dropped grabens. By late-early to early-middle Miocene, the southern Central American volcanic arc became more emergent, with foraminiferal faunas that shallowed from lower-middle bathyal to outer neritic depths (Collins et al. 1995, Coates et al. 2004), but a lower bathyal-abyssal seaway in eastern Panama–southwest Colombia still existed as indicated by benthic foraminifera (Duque-Caro 1990). Late-middle to early-late Miocene foraminifera of the Gatun Formation (Cushman 1918, Collins et al. 1996b), central Panama, were inner-middle neritic, indicating a closed Panama Canal strait. However, bathyal foraminifera of the overlying Chagres Formation suggest re-opening of the strait about 6 Ma (Collins et al. 1996b).

Microfossil paleobiogeography agrees with the early-middle Miocene history of Central American Seaway depths. In the early Miocene, radiolarian taxa that had been distributed across the tropical Pacific and Atlantic gradually declined to virtual disappearance while their Pacific counterparts remained (Maurrasse 1979). Early-middle Miocene, bathyal benthic foraminiferal faunas of Venezuela and Ecuador were very similar with a broad tropical distribution (Cushman 1929, Hasson and Fischer 1986, Whittaker 1988), although Duque-Caro (1990) noted that Caribbean and Pacific faunas of Colombia were different. By middle Pliocene, Ecuador foraminifera had “much closer affinities” to those of California than the Caribbean, resulting from a Caribbean-Pacific barrier by this time (Hasson and Fischer 1986).

The late Miocene was a time of great evolutionary and paleogeographic change in Caribbean-tropical eastern Pacific microfossils. Origination in common, shallow-water benthic foraminifera of southern Central America increased in the late Miocene (Collins et al. 1996a). Late Miocene outer neritic foraminiferal faunas of coastal Ecuador had less similarity with the Caribbean than did shallower, middle neritic faunas of the same formation, possibly reflecting development of tropical Pacific-Caribbean endemism with the rising sill (Collins 2006). In the deep eastern equatorial Pacific, amounts of middle Miocene, transported neritic species with Caribbean affinities decreased in the late Miocene (McDougall 1985). The diversity of deepsea Caribbean foraminifera peaked around 8 Ma during high paleoproductivity and declined thereafter (Jain et al. 2007), although the diversity of shallow-water taxa of southern Central America has increased until today (Buzas et al. 2002).

Complete closure of the Central American Seaway about 4 Ma apparently had less effect on benthic microfossil evolution than did late Miocene events (Collins et al. 1996a). The occurrence in both the tropical Atlantic and eastern Pacific of the planktic foraminifera *Globorotalia pertenuis* Beard, 1969 and *Globorotalia mioenica* Palmer, 1945 (Keigwin 1982b) that originated about 3.5 Ma confirms surface-water exchange across the isthmus. Also occurring in planktic foraminifera at about 3.5 Ma are discordant patterns between the Atlantic and Indo-Pacific oceans in the coiling direction of *Pulleniatina* (Saito 1976), and an abrupt increase in the average

number of supplementary apertures in the *Sphaeroidinella* lineage (Kucera 1998); both events are ascribed to complete seaway closure.

THE PRESENT STUDY

Microfossils are well suited to the study of paleobiogeographic change through time because they are generally well preserved from shallowest to deepest marine settings for a comprehensive regional study, and easily sampled in quantities sufficient for statistical analysis. In comparing the similarity of faunas to ascertain paleobiogeographic differences across regions through time, we compare assemblages from comparable paleoenvironments to exclude the possibility of differences due to depositional settings alone.

This study of the similarities between Venezuelan benthic foraminiferal assemblages and those of Caribbean Panama–Costa Rica and Ecuador is the first to use similarity indices to compare directly whole paleocommunities across Central America through the time of the closure of the Central American Seaway. Neritic assemblages collected from formations and members of the Falcón Basin, Venezuela (Smith 2008, Smith et al. 2010), were compared to previously studied assemblages of late middle Miocene to Pliocene deposits of the Panama Canal and Bocas del Toro basins of Caribbean Panama, Limón Basin of Caribbean Costa Rica, Chucunaque Basin of Pacific Panama, and Manabí and Borbón basins of coastal Ecuador.

We test three hypotheses: (1) Late Miocene, neritic faunas of Venezuela became more similar to those of other Caribbean sites than to those from the Pacific, as constriction of the Central American Seaway increased. (2) The rise of the isthmus in the late Miocene resulted in the biogeographic divergence of deep neritic biotas, followed by successively shallower faunas. (3) The gradual separation of Caribbean and tropical eastern Pacific waters and faunas resulted in an increase in homogeneity within the Caribbean as mixing with Pacific waters decreased.

METHODS

One-hundred-and-twenty-one samples were collected from outcrops along the Urumaco River and several small, ephemeral creeks in Falcón State, Venezuela, for paleoenvironmental analysis and paleobiogeographic comparison of foraminiferal assemblages with those of Panama, Costa Rica and Ecuador. The localities, stratigraphy, paleoenvironments, sample preparation, and distribution of foraminiferal taxa among Venezuelan samples were described by Smith (2008) and Smith et al. (2010). The lithology, biostratigraphy, and foraminifera of the formations of Panama, Costa Rica, and Ecuador were described by Whittaker (1988), Coates et al. (1992, 2003, 2004), Collins (1993, 2006), and Collins et al. (1995, 1996b). All foraminifera were taxonomically standardized.

SELECTION OF ASSEMBLAGES FROM COMPARABLE PALEOENVIRONMENTS

Nineteen foraminiferal assemblages from Venezuela were selected for paleobiogeographic study on the basis of the abundance and preservation of the fossils, their ages, and their paleoenvironments. Of the 121 samples, 102 were barren of microfossils or contained poorly preserved, unidentifiable species. Samples with common to abundant foraminifera with minimal recrystallization, quartz overgrowths, or replacement, and from sections restricted to the middle Miocene–middle Pliocene and inner-outer neritic depths, were chosen for comparison with assemblages of Panama and Costa Rica. The 19 assemblages were distributed across formations and ages as follows: two from the lowermost (middle Miocene) Urumaco

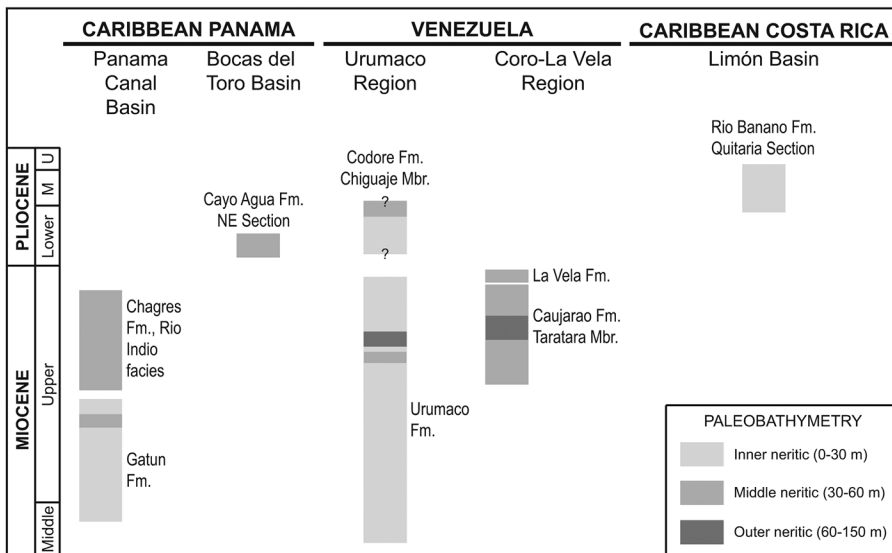


Figure 1. Formations and paleobathymetries of Venezuela, Caribbean Panama, and Caribbean Costa Rica to demonstrate the paleobiogeographic comparisons that are possible for the ages and paleoenvironments of the studied sections.

Formation, nine from the lower-upper (late Miocene) Urumaco Formation, three from the early-middle Pliocene Chiguaje Member of the Codore Formation, three from the lower, middle, and upper parts (late Miocene) of the Taratara Member of the Caujarao Formation, and two from the lowermost (late Miocene) La Vela Formation (Smith et al. 2010).

For foraminifera of the southwestern Caribbean (Fig. 1, Table 1), inner neritic assemblages of the middle Miocene lower Gatun Formation of Panama were compared to inner neritic assemblages of the basal unit of the Urumaco Formation. The middle and upper Gatun Formation of late Miocene age has both inner and middle neritic assemblages that were compared with those of the same paleobathymetry from the Urumaco, Caujarao, and La Vela formations. Middle neritic assemblages of the Rio Indio facies of the late Miocene Chagres Formation of Panama were compared to middle-shelf assemblages of the Urumaco, Caujarao, and La Vela formations. Outer neritic assemblages of the late Miocene Caujarao Formation were not compared with the Caribbean formations mentioned, as no outer shelf assemblages from Caribbean Panama or Costa Rica were available for analysis. From the Pliocene, middle neritic assemblages of the northeast section of the Cayo Agua Formation of Caribbean Costa Rica and the Chiguaje Member of the Codore Formation were compared.

Formations comparable in paleoenvironment to the Venezuela collections from the tropical eastern Pacific (Fig. 2, Table 1) are confined to the late Miocene; assemblages prepared from the middle Miocene and Pliocene are from different paleoenvironments, usually deeper paleobathymetries. From Ecuador, inner and middle neritic assemblages of the Punta Ballena section of the Jama Formation, and middle and outer neritic assemblages of the Punta Verde and Rio Santiago sections of the Angostura Formation, were compared with those from the Urumaco, Caujarao, and La Vela formations. Outer neritic assemblages from the Punta Pajonal section of the Bahia Formation and Rio Santiago section of the lower Onzole Formation were compared with outer neritic assemblages from the Urumaco and Caujarao formations.

STATISTICAL ANALYSES

Similarity Coefficients.—To quantify the similarity between each pair of assemblages, the Simpson, Dice, and Jaccard coefficients were calculated. The Simpson Coefficient (Simpson

Table 1. Paleobiogeographic comparisons of Caribbean and Pacific benthic foraminiferal assemblages. Site numbers in rightmost columns are from the Panama Paleontology Project (PPP; Collins and Coates 1999). Venezuelan localities and stratigraphy described in detail by Smith et al. (2010).

Age	Paleobathym. (neritic)	Venezuela			Caribbean	Pacific
		Site no.	Formation	Section	Formation and PPP site numbers	Formation and PPP site numbers
Early-middle Pliocene	Middle	LC461	Codore	Chiguaje	Cayo Agua Fm NE: 59, 60, 61, 62	
	Inner	LC464	Codore	Chiguaje	Rio Banano Fm Quitaria	
	Inner	LC465	Codore	Chiguaje	Section: 679, 680, 681, 682, 683	
Late Miocene	Outer	PPP2972	Urumaco	Middle		Angostura Fm Punta Verde: 3321, 3325
	Outer	LC453	Caujarao	M. Taratara		L. Onzole Fm Rio Santiago: 3307, 3312, 3314
						Bahia Fm Punta Pajonal: 3577, 3579, 3581
						Chucunaque Fm Rio Tuquesa: 888
	Middle	LC460	La Vela	Basal	Chagres Fm Rio Indio: 24, 26, 1645	Angostura Fm Rio Santiago: 3297, 3302, 3304
	Middle	LC458	La Vela	Basal	Upper Gatun Fm: 17, 28	Jama Fm Punta Ballena: 3564
	Middle	LC456	Caujarao	U. Taratara		Favio Alfaro: 3583
	Middle	LC446	Caujarao	L. Taratara		
	Middle	PPP2974	Urumaco	Middle		
	Inner	PPP2977	Urumaco	Upper	Upper Gatun Fm: 20, 27, 160, 1660	Tuira Fm Rio Tupisa: 1633, 1634
	Inner	LC489	Urumaco	Upper	Middle Gatun Fm: 18, 34	Yaviza Fm Rio Tupisa: 1144
	Inner	LC487	Urumaco	Middle		Jama Fm Punta Ballena: 3559
	Inner	LC483	Urumaco	Middle		
	Inner	LC440	Urumaco	Lower		
	Inner	LC439	Urumaco	Lower		
Inner	LC437	Urumaco	Lower			
Middle Miocene	Inner	LC493	Urumaco	Basal	Lower Gatun Fm: 6, 14, 15, 16, 35, 1037, 1038, 1040	
	Inner	LC492	Urumaco	Basal		

1943), one of the simplest indices for bioassociational studies, is calculated by C/N_1 , where N_1 equals the number of taxa in the formation with the smaller number of species, and C equals the number of taxa in common between the two formations. Dice's index (Dice 1945) is expressed as $2C/(N_1 + N_2)$, where N_2 equals the number of species in the region with the higher diversity. Jaccard's Coefficient of similarity (Jaccard 1912) is represented by $C/(N_1 + N_2 - C)$. Because equivalent quantities are considered in each of these coefficients they are functionally related. However, each provides a distinct assessment of the relationship between faunas. The coefficients are often expressed as percentage similarity.

Because the Dice and Jaccard coefficients take into account the number of species, they are sensitive to large discrepancies in the diversity of two faunas, and the resulting effect on values may even produce the opposite similarity trend than expected or observed (Fallaw 1979). The Simpson measure was devised to minimize this effect, as only the number of species in the fauna with the smaller amount of taxa is used. Simpson's measure is particularly useful for paleontological collections where poor preservation can have a large negative effect on the species present in an assemblage. In our comparisons, even with the well-preserved faunas, there can be large differences in diversities that may reflect original values rather than localized preservation. For example, benthic foraminiferal diversities of Caribbean Panama and Costa Rica are almost always higher than those from the Falcón Basin, which tend to be more equal with the lower-diversity Pacific assemblages (Online Appendix 1). We present all

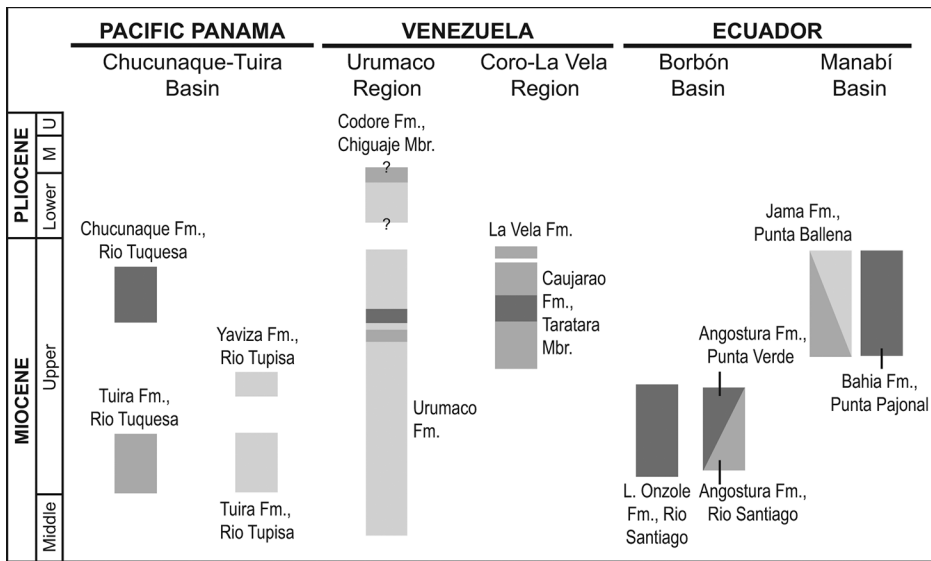


Figure 2. Formations and paleobathymetries of Pacific Panama and Ecuador. One sample from the late Miocene Favio Alfaro beds of the Manabí Basin, Ecuador, used in the present study, is not included. Venezuela formations are included to show the paleobiogeographic comparisons that are possible with Pacific units of the same paleoenvironments and ages.

three biogeographic coefficients to more fully explore the comparisons, although we focus on Simpson's coefficient.

Analysis of Variance.—To determine the statistical significance of differences in the mean similarity of assemblages, analysis of variance (ANOVA) tests were performed. Goodall (1973) determined sampling characteristics of these measures and their bias under statistical testing, whereas Morey and Agresti (1984) provided the adjustments for chance agreement. For all data sets, a Levene's test of the homogeneity of variance (Green and Salkind 2003) was insignificant.

The variation in the similarity between assemblages (response variable) can be "explained" by the effects of differing regions, environments, or time (i.e., classification variables or factors). For each comparison, the generalized linear model (GLM) predicts the mean response, and the difference between the actual and predicted response as residual error. We used the method of least squares in which ANOVA models fit parameters to minimize the sum of squares of residual errors. The variance of the random error, σ^2 , is estimated by the mean squared error, MSE or s^2 (Wilkinson 1989). If the resulting P -values of the ANOVA were significant at the $P \leq 0.05$ test level, a Bonferroni correction was applied for post-hoc testing. SYSTAT and SPSS statistical software packages were used in all calculations.

RESULTS

The Simpson, Dice, and Jaccard coefficients were calculated for 168 pairwise comparisons of assemblages from Venezuela to Panama, Caribbean Costa Rica, and Ecuador (Online Appendix 1, Table 2), and the values were plotted (Online Appendix 2A,B). When the number of species in the paired assemblages was approximately equivalent (e.g., $N_1 = 40$ and $N_2 = 50$), the three coefficients were comparable, especially the Simpson and Dice values (Online Appendix 2A). However, when they

Table 2. Mean Simpson (S), Dice (D), and Jaccard (J) coefficients of similarity for benthic foraminiferal assemblages*.

Age	Paleobathym. (neritic)	Venezuela vs Caribbean Panama/Costa Rica			Venezuela vs Pacific Panama			Venezuela vs Ecuador		
		S	D	J	S	D	J	S	D	J
Early-middle Pliocene	Middle	0.26	0.18	0.10						
	Inner	0.58	0.10	0.05						
Late Miocene	Outer				0.27	0.19	0.11	0.25	0.18	0.10
	Middle	0.26	0.23	0.13				0.28	0.23	0.13
	Inner	0.42	0.18	0.10	0.40	0.25	0.14	0.32	0.18	0.10
Middle Miocene	Inner	0.33	0.18	0.10						

* Shading = no assemblages from comparable depositional settings

differed greatly (e.g., $N_1 = 10$ and $N_2 = 110$), the Dice and Jaccard coefficients produced relatively low similarity values as compared to Simpson's (Online Appendix 2B).

In comparing the indices, the Dice and Jaccard indices agree well as is expected (Online Appendix 2) since these are equivalent indices, one based upon the harmonic mean and one upon the proportional data (Hayek 1994). The mean Dice and Jaccard values tend to display no change in similarity, or the opposite trend of the Simpson values (Table 2). Where Simpson's shows a decrease in similarity of inner neritic faunas across regions during the late Miocene, the Dice and Jaccard values reveal no change in similarity when comparing Venezuela and Caribbean Panama, and Venezuela and Ecuador (Dice = 18%; Jaccard = 10%), and an increase in faunal similarity with Pacific Panama (Dice = 25%; Jaccard = 14%). Although the Simpson values for Venezuela vs Ecuador decrease from inner to middle and then outer neritic environments during the late Miocene, the Dice and Jaccard coefficients have the same values for both inner and outer paleodepths (Dice = 18%; Jaccard = 10%), and an increase of faunal similarity between middle neritic biotas (Dice = 23%; Jaccard = 13%).

The Dice and Jaccard coefficients produce another opposite trend from Simpson's when comparing assemblages within the Caribbean. Where Simpson's values show an increase in similarity of Caribbean inner neritic assemblages from the middle Miocene to Pliocene, the Dice and Jaccard coefficients show no change during the Miocene (Dice = 18%; Jaccard = 10%), and a decrease in inner neritic Caribbean faunal similarity during the Pliocene (Dice = 10%; Jaccard = 5%). The similarity of middle neritic assemblages also decreases when examining the mean Dice and Jaccard values from the late Miocene (Dice = 23%; Jaccard = 13%) to Pliocene (Dice = 18%; Jaccard = 10%). According to these coefficients (Table 2), the late Miocene, middle neritic faunas of Venezuela are as similar to those of Caribbean Panama as to faunas of Ecuador (Dice = 23%; Jaccard = 10%).

Three trends can be seen in the mean Simpson Coefficient values (Table 2, Fig. 3). The first is a small decrease in faunal similarity with distance from Venezuela of inner neritic assemblages during the late Miocene (Fig. 3A). Venezuelan assemblages show a 42% similarity with the other Caribbean assemblages, a 40% similarity with Pacific Panama, and a 32% similarity with Ecuador assemblages. The second trend is a decrease in faunal similarity with water depth, where inner neritic assemblages are more similar than the middle or outer neritic assemblages of the same age. This is particularly noticeable when examining the mean Simpson values for Venezuela and Ecuador during the late Miocene; outer neritic assemblages are 25% similar, middle

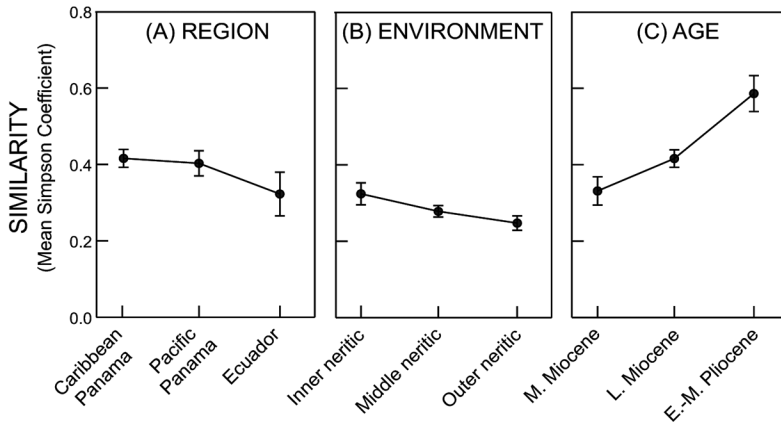


Figure 3. Least squares means for similarity (A) with Venezuela across other regions, (B) across paleoenvironments of Venezuela and Ecuador, and (C) across ages of inner neritic faunas of Venezuela and Caribbean Panama/Caribbean Costa Rica.

neritic assemblages are 28% similar, and inner neritic assemblages are 32% similar (Table 2, Fig. 3B). Thirdly, inner neritic assemblages of the Caribbean show an increase in homogeneity (Table 2, Fig. 3C) from the middle Miocene (33%), to the late Miocene (42%), and then to the Pliocene (58%).

There are several unexpected trends (Table 2). The mean Simpson Coefficient stays constant (26%) for the Caribbean middle neritic assemblages from the late Miocene to Pliocene. There is also a slightly greater similarity of late Miocene, middle neritic faunas across regions than within the Caribbean: the mean similarity of Venezuela and Caribbean Panama is 26%, and the mean similarity of Venezuela and Ecuador is 28%.

Because Simpson's Coefficient is not overwhelmed by the large differences between N_1 and N_2 sometimes present in this study, we focus on that coefficient in testing the significance of changes in mean similarity. Analyses of variance were performed across regions, environments and time (Table 3, Fig. 3). The difference in mean similarity of Upper Miocene assemblages across regions (Fig. 3A) was not significant ($P = 0.340$). Likewise, the similarity of Venezuela and Ecuador assemblages across environments (Fig. 3B) was not significantly different ($P = 0.085$). However, the third trend of increasing similarity of Caribbean inner neritic environments from the middle Miocene to early-middle Pliocene (Fig. 3C) was significant ($P < 0.001$). To examine differences in the mean similarity of each unit of time, a Bonferroni post-hoc test was applied (Table 4). The Bonferroni-adjusted hypothesis-driven results show

Table 3. Analysis of variance of similarity, Simpson's Coefficient, P -values for significance testing of differences across regions, paleoenvironments, and times.

Similarity analysis	Significance
Similarity across region [†]	0.340
Similarity across environment [‡]	0.085
Similarity through time ^{††}	<0.001

[†] Upper Miocene inner neritic comparisons of Venezuela, Caribbean and Pacific Panama, and Ecuador

[‡] Upper Miocene inner, middle and outer neritic comparisons of Venezuela and Ecuador

^{††} Miocene and Pliocene inner neritic comparisons of Venezuela and Caribbean Panama and Costa Rica

Table 4. Analysis of variance of similarity through time, Bonferroni post-hoc test, *P*-values (right column) for significance testing.

(A) Time	(B) Time	Mean difference (A – B)	Standard error	Significance
1 [†]	2 [‡]	-0.084	0.0434	0.1360
	3 ^{††}	-0.252*	0.0596	0.0001
2	1	0.084	0.0434	0.1360
	3	-0.168*	0.0520	0.0050
3	1	-0.252*	0.0596	0.0001
	2	-0.168*	0.0520	0.0050

[†] Mean Simpson's Coefficient for Venezuela vs Caribbean Panama, middle Miocene inner neritic samples

[‡] Mean Simpson's Coefficient for Venezuela vs Caribbean Panama, late Miocene inner neritic samples

^{††} Mean Simpson's Coefficient for Venezuela vs Caribbean Costa Rica, early-middle Pliocene inner neritic samples

* Pairs of means that differ significantly

that the difference in the mean similarity of Caribbean inner neritic faunas from the middle to late Miocene is not significant ($P = 0.136$). However, there were significant differences in the mean similarity of Caribbean inner neritic faunas from the middle Miocene to early-middle Pliocene ($P < 0.001$), and from late Miocene to early-middle Pliocene ($P = 0.005$). Thus, mean Simpson Coefficients indicate that inner neritic faunas of the southwestern Caribbean (Venezuela, Costa Rica, and Panama) became more similar from the Miocene to the Pliocene.

DISCUSSION

As the Dice and Jaccard coefficients reveal similar trends that are often opposite to the trends illustrated by Simpson's Coefficient, one might conclude that their results should be given more consideration. However, when comparing faunas of very different diversities, the Dice and Jaccard values are strongly influenced by taking into account both faunal sizes (Online Appendix 2A,B). When the diversity of the assemblages is fairly equal, the coefficients tend to correlate with one another, but greatly unequal diversities may give uninformative results. For example, trends in Simpson's vs Dice/Jaccard for lower Miocene, middle-neritic assemblages of Venezuela, and Ecuador are fairly similar, but they are very different for early-middle Pliocene, inner-neritic assemblages of Venezuela, and Costa Rica (Online Appendix 2B) because of the large disparity in numbers of species between the two groups. Because the Simpson Coefficient was devised to minimize this effect, below we mainly discuss those results.

Values of the Simpson Coefficient are generally consistent with what one might expect of assemblages from two epochs (Miocene–Pliocene) and a single tropical region, with relatively moderate ranges from 0.09 to 0.91 and most in the 0.20–0.39 range (Online Appendix 1). In comparison, Jurassic dinoflagellate cysts of Bulgaria are 100% similar to distant England, but 0% similar to nearby Greece (Palliani and Riding 2003), and modern and Cretaceous bivalves across the North Atlantic and eastern Pacific are 1%–94 % similar (Schmachtenberg 2008). Both of these other studies included more dissimilarity than ours, consistent with their larger geographic ranges and separate ocean basins. As might be expected, Miocene subtropical ostracodes off southwest Africa, from a single epoch and region, have less range in similarity, 24%–38% (Dingle et al. 2001).

Although the late Miocene, neritic Caribbean assemblages were more similar to each other than to those from the Pacific, the differences between Caribbean and Pacific assemblages were not significant (Hypothesis 1), demonstrating that shallow-water environments and their faunas were still relatively similar during late Miocene constriction of the Central American Seaway. Collins et al. (1996b) showed that benthic foraminifera of the late-middle to early-late Miocene Gatun Formation of Caribbean Panama were strongly cosmopolitan, with 78% of species found in both Caribbean and tropical eastern Pacific Neogene sediments. Yet Gatunian species had a stronger Caribbean than Pacific affinity because 21% of them have not been found either living or as fossils in the Pacific. Apparently, some divergence in tropical Atlantic and Pacific deep inner neritic to shallow middle neritic faunas had occurred by the late Miocene, but not enough to significantly affect our biogeographic indices.

We reasoned (Hypothesis 2) that deeper faunas may have been affected first by the progressive rise from the ocean bottom of the sill that severed the connection between Caribbean and tropical eastern Pacific faunas. McDougall (1996) found that bottom-water masses on either side of the isthmus had diverged by about 6 Ma, based on benthic foraminiferal faunas. Collins (2006) showed that deeper, outer neritic faunas of the late Miocene Angostura Formation of Ecuador were less similar with Caribbean Panama and Costa Rica than the shallower, middle neritic faunas from the same formation, possibly reflecting a progressive divergence from deeper to shallower faunas as the isthmian sill rose. In the present study, late Miocene, inner neritic assemblages of Venezuela and Ecuador were more similar than middle and outer neritic faunas, which might at first appear to support this hypothesis, but their mean similarities did not differ significantly. Paleobathymetric studies of the Central American isthmus summarized by Collins in Coates et al. (2004) show that in the latter part of the late Miocene, tropical Atlantic and Pacific waters mixed to upper bathyal depths in the major isthmian straits including northern Costa Rica, northwestern Panama, far eastern Panama, and northwestern Colombia. Thus, our results agree with mixing within neritic depths across the isthmian sill during the late Miocene.

There are two unexpected trends (Table 2), both in middle neritic faunas: the slightly (2%) greater similarity of late Miocene faunas between Venezuela and Ecuador than between Venezuela and Panama, and the same similarity of Venezuela and Caribbean Panama from the late Miocene to Pliocene. In both cases, the differences are minimal, and the same is true for the Dice and Jaccard coefficients between regions. In the Caribbean, the constancy from the late Miocene to Pliocene suggests that divergence at these depths, about 30–100 m, had already taken place so that a middle neritic Caribbean fauna had already become established in the late Miocene. The regional differences could be due to the similarity of a stronger siliciclastic influence in Venezuela and Ecuador than in Caribbean Panama; on the other hand, a 2% difference is slight. The trends in the middle neritic faunas will be tested in the future with comparisons between Caribbean Central America and Ecuador, and between late Miocene to Pliocene middle neritic faunas of Panama and Costa Rica.

Finally, the results are consistent with our Hypothesis 3 that Caribbean inner neritic faunas became more similar from Miocene to Pliocene time, as mixing with Pacific waters and faunas became reduced. The average longevity of Caribbean benthic foraminiferal species (Collins 1996) and warm temperate northeastern Atlantic taxa (Culver et al. 1987) is approximately 20 My; thus, the observed patterns are

unlikely due to macroevolutionary shifts in faunal assemblages caused by speciation and extinction, but instead resulted from decreasing migration of taxa through the Central American Seaway, as well as paleoceanographic changes. The increase in faunal similarity within the Caribbean can be attributed to both the geographic isolation of the Caribbean and tropical eastern Pacific marine biotas, and changes in Caribbean temperature and sedimentation patterns as the isthmus rose and severed the connection between tropical waters of the two oceans. Future studies will incorporate additional samples from the tropical eastern Pacific to test the prediction of a progressive differentiation of the transisthmian tropical faunas through time.

In conclusion, we found Simpson's Coefficient to be more useful than the Dice and Jaccard indices for analyzing biogeographic trends across all assemblages, because Simpson's is less affected by large disparities in the total number of species. Inner neritic benthic foraminifera faunas of Venezuela, Panama, and Ecuador were still relatively similar during late Miocene restriction of the Central American Seaway. When comparing inner, middle, and outer neritic assemblages of the late Miocene of Venezuela to those of Ecuador, no significant differences in similarity were found, suggesting that the seaway was not yet restricted enough to cause significant divergence of neritic assemblages of the Caribbean and tropical eastern Pacific. As the Central American Seaway constricted and closed in the late Miocene to early Pliocene, which progressively changed circulation and cut off the influence of the tropical eastern Pacific, Caribbean inner neritic faunas of Venezuela and southern Central America increased in their similarity.

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LITERATURE CITED

- Bandy OL. 1970. Upper Cretaceous–Cenozoic paleobathymetric cycles, eastern Panama and northern Colombia. *Trans Gulf Coast Assoc Geol Socs.* 20:181–193.
- Bandy OL, Casey RE. 1973. Reflector horizons and paleobathymetric history, eastern Panama. *Amer Assoc Petrol Geologists Bull.* 49(4):4433–4444.
- Bickert T, Haug GH, Tiedemann R. 2004. Late Neogene benthic stable isotope record of Ocean Drilling Program Site 999: implications for Caribbean paleoceanography, organic carbon burial, and the Messinian salinity crisis. *Paleoceanography.* 19:PA1023. <http://dx.doi.org/10.1029/2002PA000799>
- Billups K. 2002. Late Miocene through early Pliocene deep water circulation and climate change viewed from the sub-Antarctic South Atlantic. *Palaeogeogr Palaeoclimatol Palaeoecol.* 185:287–307. [http://dx.doi.org/10.1016/S0031-0182\(02\)00340-1](http://dx.doi.org/10.1016/S0031-0182(02)00340-1)
- Bornmalm L, Widmark JGV, Malmgren BA. 1999. Changes in circulation and trophic levels in the Pliocene Caribbean Sea; evidence from benthic foraminifer accumulation rates. *J Foraminiferal Res.* 29:209–221.

- Buzas MA, Collins LS, Culver SJ. 2002. Latitudinal difference in biodiversity caused by higher tropical rate of increase. *Proc Natl Acad Sci.* 99:7841–7843. PMID:12060730. PMCID:PMC122981. <http://dx.doi.org/10.1073/pnas.122241499>
- Cannariato KG, Ravelo AC. 1997. Pliocene-Pleistocene evolution of eastern tropical pacific surface water circulation and thermocline depth. *Paleoceanography.* 12:805–820. <http://dx.doi.org/10.1029/97PA02514>
- Coates AG, Aubry M-P, Berggren WA, Collins LS. 2003. Early Neogene history of the Central American arc from Bocas del Toro, western Panama. *Geol Soc Amer Bull.* 115:271–287. [http://dx.doi.org/10.1130/0016-7606\(2003\)115<0271:ENHOTC>2.0.CO;2](http://dx.doi.org/10.1130/0016-7606(2003)115<0271:ENHOTC>2.0.CO;2)
- 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 Amer Bull.* 116:1327–1344. <http://dx.doi.org/10.1130/B25275.1>
- Coates AG, Jackson JB, Collins LS, Cronin TM, Dowsett HJ, Bybell L, Jung P, Obando JA. 1992. Closure of the Isthmus of Panama: the near-shore marine record of western Panama and Costa Rica. *Geol Soc Amer 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)
- Coates AG, Stallard RE. 2013. How old is the Isthmus of Panama? *Bull Mar Sci.* 89:801–813. <http://dx.doi.org/10.5343/bms.2012.1076>
- Cole WS. 1952. Eocene and Oligocene Larger Foraminifera from the Panama Canal Zone and Vicinity. *US Geol Surv Prof Pap.* 244. 41 p.
- Cole WS. 1957. Late oligocene larger foraminifera from Barro Colorado Island, Panama Canala Zone. *Bulls Amer Paleontol.* 37(163):313–338.
- Collins LS. 1993. Neogene paleoenvironments of the Bocas del Toro Basin, Panama. *J Paleontol.* 67:699–710.
- Collins LS. 1996. Environmental changes in Caribbean shallow waters relative to the closing Tropical American Seaway. *In: Jackson JBC, Budd A, Coates AG, editors. Evolution and environment in tropical America.* University of Chicago Pr., Chicago, Ill. p. 130–167.
- Collins LS. 2006. Divergence of late Miocene Caribbean and tropical eastern pacific shallow-water benthic foraminifera: *Anuario Inst Geosciencias.* 29:530.
- Collins LS. 2007. Chapter 18. Micropaleontology of Central America. *In: Bundschuh J, Alvarado GE, editors. Central America—geology, hazards and resources.* Taylor and Francis, Leiden, The Netherlands. 2:1–17. <http://dx.doi.org/10.1201/9780203947043.ch18>
- Collins LS, Budd AF, Coates AG. 1996b. Earliest evolution associated with closure of the tropical American seaway. *Proc Natl Acad Sci.* 93:6069–6072. PMID:11607686. PMCID:PMC39190. <http://dx.doi.org/10.1073/pnas.93.12.6069>
- Collins LS, Coates AG. 1999. A Paleobiotic Survey of Caribbean Faunas from the Neogene of the Isthmus of Panama. *Bull Am Paleontol.* 357:91–107.
- Collins LS, Coates AG, Berggren WA, Aubry M-P, Zhang J. 1996a. 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 LS, Coates AG, Jackson JBC, Obando JA. 1995. Timing and rates of emergence of the Limón and Bocas del Toro basins: Caribbean effects of Cocos Ridge subduction? *In: Mann P, editor. Geologic and tectonic development of the Caribbean Plate Boundary in southern Central America.* *Geol Soc Amer Spec Pap.* 295:263–289. <http://dx.doi.org/10.1130/SPE295-p263>
- Culver SJ, Buzas MA, Collins LS. 1987. On the value of taxonomic standardization in evolutionary studies. *Paleobiology.* 13:169–176.
- Cushman JA. 1918. The smaller fossil foraminifera of the Panama Canal Zone. *US Natl Mus Bull.* 103:45–87, pl. 19–33.
- Cushman JA. 1929. A late Tertiary fauna of Venezuela and other related regions. *Contr Cushman Lab Foraminiferal Res.* 5:76–107.
- Dice LR. 1945. Measures of the amount of ecologic association between species. *Ecology.* 26:297–302. <http://dx.doi.org/10.2307/1932409>

- Dingle RV, McMillan IK, Majoran S, Bisset L. 2001. Palaeo-oceanographical implications of Early-Middle Miocene subtropical faunas from the continental shelf of the SE Atlantic Ocean. *Palaeogeogr Palaeoclimatol Palaeoecol.* 173:43–60. [http://dx.doi.org/10.1016/S0031-0182\(01\)00312-1](http://dx.doi.org/10.1016/S0031-0182(01)00312-1)
- Duque-Caro H. 1990. Neogene stratigraphy, paleoenvironment and paleobiology in north-west 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)
- Fallaw WC. 1979. A test of the Simpson coefficient and other binary coefficients of faunal similarity. *J Paleontol.* 53:1029–1034.
- 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.* 39:1007–1010. <http://dx.doi.org/10.1130/G32237.1>
- Frank M, Reynolds BC, O-Nions RK. 1999. Nd and Pb isotopes in Atlantic and Pacific water masses before and after closure of the Panama gateway. *Geology.* 27:1147–1150. [http://dx.doi.org/10.1130/0091-7613\(1999\)027<1147:NAPIIA>2.3.CO;2](http://dx.doi.org/10.1130/0091-7613(1999)027<1147:NAPIIA>2.3.CO;2)
- Goodall DW, 1973. Sample similarity and species correlation. *In:* Whittaker RH, editor. *Handbook of vegetation sciences Part V: ordinations and classifications.* Dr W Junk BV Publ, The Hague, Netherlands. p. 106–156.
- Green SB, Salkind, NJ. 2003. *Using SPSS for Windows and Macintosh: analyzing and understanding data*, 3rd ed. Pearson Education, Inc., Upper Saddle River, New Jersey. 443 p.
- Groeneveld J, Nürnberg D, Tiedemann R, Reichert GJ, Steph S, Reuning L, Crudele D, Mason P. 2008. Foraminiferal Mg/Ca increase in the Caribbean during the Pliocene: western Atlantic Warm Pool formation, salinity influence, or diagenetic overprint? *Geochem Geophys Geosyst.* 9:Q01P23. 21 p. <http://dx.doi.org/10.1029/2006GC001564>
- Hasson PE, Fischer AG. 1986. Observations on the Neogene of northwestern Ecuador. *Micropaleontology.* 32:2–42. <http://dx.doi.org/10.2307/1485698>
- Haug GH, Tiedemann R, Zahn R, Ravelo AC. 2001. Role of Panama uplift on oceanic freshwater balance. *Geology.* 29:207–210. [http://dx.doi.org/10.1130/0091-7613\(2001\)029<0207:ROP UOO>2.0.CO;2](http://dx.doi.org/10.1130/0091-7613(2001)029<0207:ROP UOO>2.0.CO;2)
- Hayek LC. 1994. Analysis of amphibian biodiversity data. *In:* Measuring and monitoring biological diversity: standard methods for amphibians. Heyer WR, Donnelly MA, McDiarmid RW, Hayek LC, Foster MS, editors. Smithsonian Institution Press Washington DC. p. 207–269.
- Jaccard P. 1912. The distribution of the flora in the alpine zone. *New Phytol.* 11:37–50. <http://dx.doi.org/10.1111/j.1469-8137.1912.tb05611.x>
- 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>
- Jain S, Collins LS, Hayek L-A. 2007. Relationship of benthic foraminiferal diversity to paleoproductivity in the Neogene Caribbean. *Palaeogeogr Palaeoclimatol Palaeoecol.* 255:223–245. <http://dx.doi.org/10.1016/j.palaeo.2007.05.017>
- Kameo K. 2002. Late Pliocene Caribbean surface water dynamics and climatic changes based on calcareous nannofossil records. *Palaeogeogr Palaeoclimatol Palaeoecol.* 179:211–226. [http://dx.doi.org/10.1016/S0031-0182\(01\)00432-1](http://dx.doi.org/10.1016/S0031-0182(01)00432-1)
- Keigwin L. 1982a. Isotopic paleo-oceanography 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>
- Keigwin L. 1982b. Stable isotope stratigraphy and paleoceanography of sites 502 and 503. *Init Repts Deep Sea Drilling Proj.* 68:445–453. <http://dx.doi.org/10.2973/dsdp.proc.68.119.1982>
- Keller G, Zenker CE, Stone SM. 1989. Late Neogene history of the Pacific-Caribbean gateway. *J S Amer Earth Sci.* 2:73–108. [http://dx.doi.org/10.1016/0895-9811\(89\)90028-X](http://dx.doi.org/10.1016/0895-9811(89)90028-X)

- Kucera M. 1998. Biochronology of the mid-Pliocene *Sphaeroidinella* event. *Mar Micropaleontol.* 35:1–16. [http://dx.doi.org/10.1016/S0377-8398\(98\)00016-4](http://dx.doi.org/10.1016/S0377-8398(98)00016-4)
- Maurrasse FJ-MR. 1979. Cenozoic radiolarian paleobiogeography: implications concerning plate tectonics and climatic cycles. *Palaeogeogr Palaeoclimatol Palaeoecol.* 26:253–289. [http://dx.doi.org/10.1016/0031-0182\(79\)90151-2](http://dx.doi.org/10.1016/0031-0182(79)90151-2)
- McDougall K. 1985. Miocene to Pleistocene benthic foraminifers and paleoceanography of the Middle America Slope, Deep Sea Drilling Project Leg 84. *Init Repts Deep Sea Drilling Proj.* 84:363–418. <http://dx.doi.org/10.2973/dsdp.proc.84.109.1985>
- McDougall K. 1996. Benthic foraminiferal response to the emergence of the Isthmus of Panama and coincident paleoceanographic changes. *Mar Micropaleontol.* 28:133–169. [http://dx.doi.org/10.1016/0377-8398\(95\)00081-X](http://dx.doi.org/10.1016/0377-8398(95)00081-X)
- Molnar P. 2008. Closing of the Central American Seaway and the Ice Age: a critical review. *Paleoceanography.* 23:PA2201. <http://dx.doi.org/10.1029/2007PA001574>
- Montes C, Cardona A, McFadden R, Moron SE, Silva CA, Restrepo-Moreno S, Ramirez DA, Hoyos N, Wilson J, Farris D, et al. 2012. 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>
- Morey L, Agresti A. 1984. The measurement of classification agreement: an adjustment to the statistics for chance agreement. *Educ Psych Measurement.* 44:33–37. <http://dx.doi.org/10.1177/0013164484441003>
- Palliani RB, Riding JB. 2003. Biostratigraphy, provincialism and evolution of European Early Jurassic (Pliensbachian to Early Toarcian) dinoflagellate cysts. *Palynology.* 27:179–214. <http://dx.doi.org/10.2113/27.1.179>
- Reynolds BC, Frank M, O’Nions RK. 1999. Nd- and Pb-isotope time series from Atlantic ferromanganese crusts: implications for changes in provenance and paleocirculation over the last 8 My. *Earth Planet Sci Lett.* 173:381–396. [http://dx.doi.org/10.1016/S0012-821X\(99\)00243-5](http://dx.doi.org/10.1016/S0012-821X(99)00243-5)
- Saito T. 1976. Geologic significance of coiling direction in the planktonic foraminifer *Pulleniatina*. *Geol.* 4:305–309. [http://dx.doi.org/10.1130/0091-7613\(1976\)4<305:GSOCDI>2.0.CO;2](http://dx.doi.org/10.1130/0091-7613(1976)4<305:GSOCDI>2.0.CO;2)
- Schmachtenberg WF. 2008. Resolution and limitations of faunal similarity indices of biogeographic data for testing predicted paleogeographic reconstructions and estimating intercontinental distances: a test case of modern and Cretaceous bivalves. *Palaeogeogr Palaeoclimatol Palaeoecol.* 265:255–261. <http://dx.doi.org/10.1016/j.palaeo.2008.05.010>
- Schneider B, Schmittner A. 2006. Simulating the impact of the Panamanian seaway closure on ocean circulation, marine productivity and nutrient cycling. *Earth Planet Sci Lett.* 246:367–380. <http://dx.doi.org/10.1016/j.epsl.2006.04.028>
- Simpson GG. 1943. Mammals and the nature of continents. *Amer J Sci.* 241:1–31. <http://dx.doi.org/10.2475/ajs.241.1.1>
- Smith CJ. 2008. Biogeographic comparisons of Neogene benthic foraminifera of Venezuela, Costa Rica, Panama and Ecuador. MS Thesis, Florida International University, Miami. 87 p.
- Smith CJ, Collins LS, Jaramillo C, Quiroz LI. 2010. Marine paleoenvironments of Miocene-Pliocene formations of north-central Falcón state, Venezuela. *J Foraminiferal Res.* 40:266–282. <http://dx.doi.org/10.2113/gsjfr.40.3.266>
- Spezzaferri S, McKenzie JA, Isern A. 2002. Linking the oxygen isotope record of late Neogene eustasy to sequence stratigraphic patterns along the Bahamas Margin: Results from a paleoceanographic study of ODP Leg 166, Site 1006 sediments. *Mar Geol.* 185:95–120. [http://dx.doi.org/10.1016/S0025-3227\(01\)00292-4](http://dx.doi.org/10.1016/S0025-3227(01)00292-4)
- Whittaker JE. 1988. Benthic Cenozoic foraminifera from Ecuador. British Museum (Natural History), London. 194 p.
- Wilkinson L. 1989. SYSTAT: the system for statistics. SYSTAT, Inc., Evanston, Illinois. 882 p.
- Woodring WP. 1970. Geology and paleontology of Canal Zone and adjoining parts of Panama. Description of Tertiary mollusks (Gastropods: Eulimidae, Marginellidae to Helminthoglyptidae). *US Geol Surv Prof Pap.* 306-D:299–326.

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