Comment (1) on “Formation of the Isthmus of Panama” by O’Dea et al.

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A review and reanalysis of geological, molecular, and paleontological data led O’Dea et al. (1) to propose (i) that reports by Montes et al. (2) and Bacon et al. (3) regarding a middle Miocene closure of the Central American Seaway (CAS) are unsupported, and (ii) a new age of the formation of the Isthmus at 2.8 million years ago (Ma). Here, we reject both of these conclusions.

THE CAS

An unambiguous definition of the CAS is critical to any discussion regarding the Isthmus of Panama, yet O’Dea et al. (1) failed to provide one. O’Dea et al. (1) appear to suggest that the CAS is any body of water connecting the Caribbean with the Pacific Ocean. In contrast, papers from our research group (2–6) have explicitly restricted the term CAS to the “oceanic seaway along the tectonic boundary of the South American plate and the Panamanian microplate” (3). Although our definition was ignored and/or misrepresented by O’Dea et al. (1), this is the definition that we maintain here when referring to the CAS. This definition is far more than a semantic issue because deepwater flow is the definition that we maintain here when referring to the CAS. This collection of ages ignores hundreds of published magmatic and detrital ages [for example, (2, 9, 10–15)]. Among the 131 ages presented by O’Dea et al. (1), 118 ages cannot be considered as valid ages for a possible source rock derived from South America (Table 1). They include 41 K/Ar and Ar/Ar dates that record magmatic cooling rather than crystallization and therefore could not have affected the ages of zircons, 36 from rocks that are west of the suture and therefore belong to the Panama Block (16, 17), 23 are K/Ar and Ar/Ar ages in metamorphic rocks that record reheating and cooling due to intrusives older than 50 Ma (18), 11 ages reported as Eocene correspond to Cretaceous ocean floor sequence basalts (19, 20), 4 are of an unreported rock type, 2 date veins in Cretaceous rocks, and 1 lacks geographic coordinates (Table 1 and Fig. 1). The remaining 13 ages of table S2 of O’Dea et al. (2) that did date South American source rocks are significantly older than the middle Eocene Panamanian signal reported in Montes et al. (2) (t test, P < 0.001, df = 19.8; Fig. 1). In summary, the arguments O’Dea et al. (1) used to dismiss Montes et al. (2) are not supported by the data presented or available in the literature.

Montes et al. (2015)

O’Dea et al. (1) dismiss the geological data presented in Montes et al. (2) using two main lines of argument. First, O’Dea et al. (1) state that “sediments of the Atrato Basin were connected with the Urabá Basin entirely unaffected by the Cuchillo Hills.” Their statement is based on modeling of seismic and gravimetric data by Garzon-Varon (7), which lacks empirical evidence of age and accumulation environments of strata in the Urabá Basin. O’Dea et al. (1) do not present any additional evidence to support their interpretation that sediments of the southern Urabá Basin are early Pliocene in age and accumulated in marine environments with Pacific connections. The Atrato hydrographic basin is characterized by high rainfall (averaging 4944 mm/year) and high water discharge (2740 m³ s⁻¹) (8). Therefore, it is equally possible that sediments observed in the seismic lines of Garzon-Varon (7) are fluvial deposits of the Atrato River. Furthermore, the geological interpretation of the cross section [Figure 8.2 in the study by Garzon-Varon (7)] shows sedimentary cover being disrupted by the Cuchillo Hills rather than being “entirely unaffected,” as O’Dea et al. (1) suggest.

Second, O’Dea et al. (1) state that “the true extent of Eocene zircons in the region [South American Block] categorically negates the assertions of Montes [that middle Eocene zircons found in Miocene sediments in the South American Block are derived from the Panama Block].” To support this statement, O’Dea et al. (1) present 131 ages of possible South American sources [table S2 in the study by O’Dea et al. (1)] and conclude that the zircons reported in Montes et al. (2) could also be derived from the South American Block. This collection of ages ignores hundreds of published magmatic and detrital ages [for example, (2, 9, 10–15)]. Among the 131 ages presented by O’Dea et al. (1), 118 ages cannot be considered as valid ages for a possible source rock derived from South America (Table 1). They include 41 K/Ar and Ar/Ar dates that record magmatic cooling rather than crystallization and therefore could not have affected the ages of zircons, 36 from rocks that are west of the suture and therefore belong to the Panama Block (16, 17), 23 are K/Ar and Ar/Ar ages in metamorphic rocks that record reheating and cooling due to intrusives older than 50 Ma (18), 11 ages reported as Eocene correspond to Cretaceous ocean floor sequence basalts (19, 20), 4 are of an unreported rock type, 2 date veins in Cretaceous rocks, and 1 lacks geographic coordinates (Table 1 and Fig. 1). The remaining 13 ages of table S2 of O’Dea et al. (2) that did date South American source rocks are significantly older than the middle Eocene Panamanian signal reported in Montes et al. (2) (t test, P < 0.001, df = 19.8; Fig. 1). In summary, the arguments O’Dea et al. (1) used to dismiss Montes et al. (2) are not supported by the data presented or available in the literature.

Bacon et al. (2015 A, B)

The goal of the study by Bacon et al. (3) was to test the assumption that “no vicariant date [3.5 Ma] is better dated than the Isthmus” (21). O’Dea et al. (1) dismiss the molecular results using analysis derived from a single gene presented by Bacon et al. (3, 22). They further indicate disagreement with the use of a universal rate of mitochondrial DNA (mtDNA) divergence and point out that several published data sets had not been included in the study [despite the fact that the latter has already been addressed (22)]. To circumvent these issues, O’Dea et al. (1) compiled data to examine a “corresponding concentration of [mature] divergences...to imply a common geological cause.” Here, we used the data presented in O’Dea et al. (1) to explicitly examine the temporal distribution of vicariance events using a nonhomogeneous Poisson process to infer statistical significance of rate shifts [table S1 and Fig. 2; following Supporting Information 1.6 from the study by Bacon et al. (3)]. Both our results and those shown by O’Dea et al. (Fig. 3) (1) fully support the conclusions of Bacon et al. (3, 22), showing two rate shifts of vicariance, one increase at 12 Ma (14.77 to 9.76 Ma) and another decrease at 3.01 Ma (4.65 to 1.61 Ma). These results propose a scenario of ongoing divergence of geminate species over several million years as a function
| Record # | Lithology | Age (Ma) | Error (Ma) | Method | Latitude | Longitude | Comment* |
|----------|-----------|----------|------------|--------|----------|-----------|----------|
| 1        | Dacite    | 33.9     | 0.7        | K/Ar wr | 2.56     | –76.69    | Cretaceous ages |
| 2        | Mandé batholith (granodiorite) | 34.0 | K/Ar Bt | 5.72 | –76.35 | Cooling age, west of suture |
| 3        | Grupo Diábásico (dolerite)     | 34.0 | K/Ar      | 3.27   | –76.62   | Cretaceous ages |
| 4        | Santa Marta batholith (granodiorite) | 34.2 | Ar/Ar Kfs | 11.24 | –74.02 | Cooling age |
| 5        | Hibulla Gneiss (anorthosite)   | 35.0 | 3.0       | Ar/Ar  | 10.74    | –74.08    | Metamorphic age |
| 6        | Cocha Rio Téllez Migmatitic Complex (gneissic granodiorite) | 35.0 | 0.4       | Ar/Ar Hb | 0.81 | –77.33 | Metamorphic age |
| 7        | Santa Marta schist (amphibolite schist) | 36.2 | K/Ar Hb | 11.28 | –74.15 | Metamorphic age |
| 8        | Paja Fm. (mineralized vein)     | 36.4 | K/Ar Ms   | 5.64   | –74.14   | Unrelated to magnetism |
| 9        | Cocha Rio Téllez Migmatitic Complex (gneissic granodiorite) | 36.4 | 0.6       | Ar/Ar Hb | 0.81 | –77.33 | Metamorphic age |
| 10       | Santa Cecilia–La Equis Complex (porphyritic basalt) | 36.7 | 11.5      | Ar/Ar  | 6.74     | –76.39    | West of suture |
| 11       | Patía 29-Ra-002                  | 37.1 | K/Ar Hb   | 1.98   | –77.15   | Unreported rock type |
| 12       | Socorro stock (granodiorite)     | 37.8 | K/Ar Bt   | 10.79  | –74.03   | Cooling age |
| 13       | Santa Marta schist (granodiorite) | 38.7 | K/Ar Bt   | 11.24  | –74.02   | Cooling age |
| 14       | Acandi batholith (quartz diorite) | 38.9 | 3.0       | K/Ar Ser | 8.53 | –77.42 | Cooling age, west of suture |
| 15       | Timbiquí Fm. (andesite)          | 38.9 | 4.3       | K/Ar   | 2.29     | –77.65    | West of suture |
| 16       | Rio Napi intrusives (Hb diorite) | 39.0 | 2.0       | K/Ar    | 2.49     | –77.48    | Cooling age, west of suture |
| 17       | Grupo Diábásico (dolerite)      | 39.0 | K/Ar      | 3.27   | –76.62   | Cretaceous ages |
| 18       | Paja Fm. (graniandesite vein)    | 39.0 | 3.5       | Ar/Ar Hb | 1.33 | –77.46 | Cretaceous ages |
| 19       | Piedranca batholith (granodiorite) | 40.5 | 3.0       | K/Ar Bt | 1.23 | –77.73 | Cooling age |
| 20       | Cocha Rio Téllez Migmatitic Complex (granodiorite) | 40.0 | 0.5       | Ar/Ar Hb | 0.81 | –77.33 | Metamorphic age |
| 21       | Grupo Diábásico (dolerite)      | 40.0 | K/Ar      | 3.27   | –76.62   | Cretaceous ages |
| 22       | Santa Marta batholith (granodiorite) | 40.2 | 1.3       | Ar/Ar Kfs | 11.28 | –73.90 | Cooling age |
| 23       | Santa Marta batholith (granodiorite) | 40.2 | 1.5       | Ar/Ar Kfs | 11.28 | –73.90 | Cooling age |
| 24       | Santa Marta batholith (granodiorite) | 40.4 | 0.3       | Ar/Ar Kfs | 11.28 | –73.90 | Cooling age |
| 25       | Santa Marta batholith (granodiorite) | 40.4 | 1.1       | K/Ar wr | 11.25 | –74.18 | Metamorphic age |
| 26       | Santa Marta batholith (granodiorite) | 40.5 | 3.0       | K/Ar wr | 7.04 | –76.32 | Cooling age, west of suture |
| 27       | Nudillales stock (quartz monzonite) | 41.0 | 3.6       | K/Ar    | 2.20     | –77.68    | West of suture |
| 28       | Los Cholos–Napi River pluton (Hb-bearing quartz diorite) | 41.0 | 4.0       | K/Ar    | 2.46     | –77.50    | Cooling age, west of suture |
| 29       | Basalt    | 41.4 | 8.6       | Ar/Ar Pl | 6.02 | –76.26 | West of suture |
| 30       | Llanitos latiandesite             | 41.5 | 1.8       | K/Ar wr | 7.07     | –76.41    | West of suture |
| 31       | Timbiquí Fm. (andesite)          | 41.7 | 1.2       | K/Ar    | 2.40     | –77.57    | West of suture |
| 32       | Santa Marta batholith (granodiorite) | 41.8 | 0.8       | Ar/Ar Kfs | 11.27 | –74.09 | Cooling age |
| 33       | Patía 29-Ra-002                  | 41.9 | K/Ar      | 1.98   | –77.15   | Unreported rock type |

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| Record # | Lithology | Age (Ma) | Error (Ma) | Method | Latitude | Longitude | Comment* |
|----------|-----------|----------|------------|--------|----------|-----------|----------|
| 37       | Amaime Fm. | 42.0     | 13.0       | Ar/Ar wr | 3.70     | −76.18    | Unreported rock type |
| 38       | Balsitas pluton (andesite dike) | 42.6 | 1.3 | K/Ar | 2.17 | −77.70 | West of suture |
| 39       | Santa Marta schist (biotite schist) | 42.6 | 1.2 | K/Ar Bt | 0.99 | −74.14 | |
| 40       | Mandé batholith (porphyritic dacite) | 42.7 | 0.9 | K/Ar Ser | 6.70 | −76.50 | West of suture |
| 41       | Rio Napi intrusives (Hb-bearing gabbro) | 43.0 | 0.4 | K/Ar | 2.53 | −77.45 | Cooling age, west of suture |
| 42       | Basalt | 43.1 | 0.4 | Ar/Ar Pl | 6.02 | −76.26 | West of suture |
| 43       | Santa Marta batholith (granodiorite) | 43.6 | 0.5 | Ar/Ar Kfs | 11.27 | −74.09 | Cooling age |
| 44       | Bunticá andesite (andesite, porphyritic diorite) | 43.8 | 4.3 | K/Ar wr | 6.70 | −75.91 | Cooling age |
| 45       | Santa Marta batholith (granodiorite) | 43.9 | 0.3 | Ar/Ar Bt | 11.28 | −73.90 | Cooling age |
| 46       | Mandé batholith (porphyritic dacite) | 43.9 | 0.3 | K/Ar Bt | 11.28 | −73.90 | Cooling age |
| 47       | Rio Napi intrusives (Hb-bearing gabbro) | 44.0 | 2.4 | K/Ar Bt | 11.28 | −73.90 | Cooling age |
| 48       | Timbiquí Fm. (andesite) | 44.0 | 0.9 | K/Ar | 11.25 | −73.90 | Cooling age |
| 49       | Santa Marta schist (amphibolic schist) | 44.1 | 2.7 | K/Ar Hb | 11.2 | −73.89 | Metamorphic age |
| 50       | Santa Marta batholith (quartz diorite) | 44.1 | 1.6 | K/Ar Bt | 11.29 | −73.97 | Cooling age |
| 51       | Mandé batholith (tonalite) | 44.6 | 0.9 | U/Pb Zr | 6.73 | −76.52 | West of suture |
| 52       | Los Azules (ophiolite sequence + pillow lavas) | 44.7 | 6.0 | K/Ar wr | 1.90 | −77.00 | Cretaceous ages |
| 53       | Mandé batholith (tonalite) | 44.8 | 1.0 | Ar/Ar Hb | 6.81 | −76.59 | Cooling age, west of suture |
| 54       | Santa Marta batholith (granodiorite) | 44.8 | 1.0 | Ar/Ar Bt | 11.26 | −73.62 | Metamorphic age |
| 55       | Timbiquí Fm. (andesite, dike) | 44.8 | 0.4 | K/Ar | 2.18 | −77.70 | West of suture |
| 56       | Santa Marta batholith (granodiorite) | 45.3 | 1.2 | U/Pb Zr | 6.72 | −76.52 | West of suture |
| 57       | Dibulla Gneiss (anorthosite) | 46.1 | 0.9 | K/Ar Bt | 6.72 | −76.52 | West of suture |
| 58       | Mandé batholith (tonalite) | 46.0 | 0.4 | Ar/Ar Bt | 11.24 | −74.02 | Cooling age |
| 59       | Dibulla Gneiss (anorthosite) | 46.1 | 1.4 | Ar/Ar Hb | 10.74 | −74.08 | Metamorphic age |
| 60       | Santa Marta batholith (granodiorite) | 46.3 | 0.7 | Ar/Ar Bt | 11.24 | −74.02 | Cooling age |
| 61       | Timbiquí Fm. (dike, andesite) | 46.7 | 2.0 | K/Ar | 2.18 | −77.70 | West of suture |
| 62       | Sabaletas stock (gabbro, diorite) | 46.9 | 3.5 | K/Ar | 2.18 | −77.70 | West of suture |
| 63       | Dibulla Gneiss (anorthosite) | 46.1 | 0.8 | K/Ar Bt | 6.72 | −76.52 | West of suture |
| 64       | Mandé batholith (tonalite) | 47.1 | 2.5 | K/Ar Hb | NA | NA | No coordinates |
| 65       | Dibulla Gneiss (anorthosite) | 46.1 | 1.4 | Ar/Ar Hb | 10.74 | −74.08 | Metamorphic age |
| 66       | Santa Marta batholith (granodiorite) | 47.8 | 0.6 | Ar/Ar Hb | 11.28 | −73.90 | Cooling age |
| 67       | Esquistos de Santa Marta (pegmatite) | 47.8 | 1.9 | K/Ar Ms | 11.26 | −74.15 | Cooling age |
| 68       | Parashi stock (quartzodiorite) | 48.0 | 4.0 | K/Ar Hb | 12.23 | −71.74 | Cooling age |
| 69       | Mandé batholith (tonalite) | 48.0 | 1.0 | K/Ar | 2.17 | −77.69 | Cooling age |
| 70       | Santa Marta batholith (granodiorite) | 48.0 | 0.8 | Ar/Ar Hb | 11.24 | −74.02 | Cooling age |
| 71       | Mandé batholith (tonalite) | 48.0 | 1.0 | K/Ar Bt | 6.72 | −76.52 | West of suture |
| 72       | Mandé batholith (tonalite) | 48.1 | 1.0 | K/Ar Ser | 8.46 | −77.36 | Cooling age, west of suture |
| 73       | Mandé batholith (tonalite) | 48.1 | 1.0 | K/Ar Bt | 6.72 | −76.52 | West of suture |
| 74       | Santa Marta batholith (granodiorite) | 48.3 | 0.8 | Ar/Ar Hb | 11.24 | −74.02 | Cooling age |

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| Record # | Lithology | Age (Ma) | Error (Ma) | Method | Latitude | Longitude | Comment* |
|----------|-----------|----------|------------|--------|----------|-----------|----------|
| 75       | Santa Marta batholith (granodiorite) | 48.3 | 0.9 | Ar/Ar Hb | 11.28 | −73.90 | Cooling age |
| 76       | Timbiquí Fm. (porphyritic andesite) | 48.4 | 4.6 | K/Ar | 2.29 | −77.64 | West of suture |
| 77       | Burtitá pluton (quartzodiorite) | 48.4 | 1.8 | K/Ar Bt | 11.17 | −73.73 | Cooling age |
| 78       | Santa Marta batholith (quartzodiorite) | 48.8 | 1.7 | K/Ar Hb | 11.29 | −73.97 | Cooling age |
| 79       | Grupo Diabásico (pillow lava) | 49.4 | 0.8 | K/Ar | 4.44 | −75.08 | Cooling age |
| 80       | El Bosque batholith (granodiorite) | 49.1 | 1.7 | K/Ar Bt | 4.44 | −75.08 | Cooling age |
| 81       | Santa Marta batholith (granodiorite) | 49.5 | 0.8 | Ar/Ar Bt | 11.27 | −74.09 | Cooling age |
| 82       | Gneis de Dibulla (anorthosite) | 49.8 | 1.1 | Ar/Ar Bt | 10.74 | −74.08 | Metamorphic age |
| 83       | Gabro de Rodrigo (Hb-Px-bearing gabbro) | 49.9 | 0.2 | Ar/Ar | 6.12 | −72.34 | Cooling age |
| 84       | Santa Marta batholith (granodiorite-tonalite) | 50.1 | 0.8 | U/Pb Zr | 11.28 | −73.90 | Not Panamanian signal |
| 85       | Santa Marta batholith (granodiorite) | 50.4 | 1.1 | Ar/Ar Hb | 11.27 | −74.09 | Cooling age |
| 86       | Gneis de Dibulla (anorthosite) | 50.6 | 1.5 | U/Pb Zr | 11.18 | −73.73 | Not Panamanian signal |
| 87       | Santa Marta batholith (granodiorite-tonalite) | 50.7 | 0.9 | K/Ar Hb | 11.27 | −74.09 | Cooling age |
| 88       | Santa Cecilia-La Equis Complex (garnet-bearing amphibolite) | 51.0 | 3.6 | K/Ar Hb | 11.20 | −74.21 | Metamorphic age |
| 89       | Timbiquí Fm. (andesite) | 51.0 | 2.0 | K/Ar | 2.18 | −77.70 | West of suture |
| 90       | Plutón de Burtitá (garnet-talcite quartz diorite) | 51.0 | 1.2 | U/Pb Zr | 11.18 | −73.73 | Not Panamanian signal |
| 91       | Santa Marta batholith (granodiorite) | 50.9 | 0.8 | Ar/Ar Bt | 11.27 | −74.09 | Cooling age |
| 92       | Plutón El Salto (pegmatite) | 51.0 | 1.0 | K/Ar | 2.21 | −77.66 | Cooling age |
| 93       | Esquistos de Santa Marta (amphibolitic schist) | 51.0 | 3.6 | K/Ar Hb | 11.01 | −74.12 | Metamorphic age |
| 94       | Timbiquí Fm. (porphyritic andesite) | 51.5 | 1.5 | K/Ar | 2.21 | −77.69 | West of suture |
| 95       | Arquía Complex (garnet-bearing amphibolite) | 51.6 | 3.1 | Ar/Ar Hb | 4.38 | −75.72 | Metamorphic age |
| 96       | Gabbronite | 51.7 | 3.9 | Ar/Ar wr | 6.58 | −76.59 | Cooling age, west of suture |
| 97       | Gabbronite | 52.7 | 3.2 | Ar/Ar wr | 6.58 | −76.59 | Cooling age, west of suture |
| 98       | Gabbronite | 52.3 | 0.7 | U/Pb Zr | 11.14 | −74.12 | Not Panamanian signal |
| 99       | Rio Napi intrusives (Hb-bearing tonalite) | 53.0 | 5.0 | K/Ar | 2.52 | −77.43 | Cooling age |
| 100      | Grupo Diabásico (pillow lava) | 53.2 | 4.6 | K/Ar wr | 1.60 | −77.40 | Cretaceous ages |
| 101      | Santa Marta batholith (aplite dikes) | 53.3 | 1.0 | U/Pb Zr | 11.24 | −74.06 | Not Panamanian signal |
| 102      | Timbiquí Fm. (andesite) | 53.4 | 3.0 | K/Ar | 2.19 | −77.71 | West of suture |
| 103      | El Hatillo stock (quartzodiorite) | 52.3 | 0.7 | U/Pb Zr | 11.24 | −74.06 | Not Panamanian signal |
| 104      | Gneis de Dibulla (anorthosite) | 53.8 | 0.7 | Ar/Ar Bt | 10.74 | −74.08 | Metamorphic age |
| 105      | Sevilla Complex | 53.9 | 0.5 | Ar/Ar Bt | 11.26 | −73.62 | Unreported rock type |
| 106      | Plutón Tucurinquita (granodiorite) | 54.0 | 2.2 | K/Ar Bt | 10.68 | −74.04 | Cooling age |
| 107      | Sevilla Complex (schist) | 54.1 | 0.7 | Ar/Ar Bt | 11.26 | −73.62 | Metamorphic age |
| 108      | Esquistos de Santa Marta Rodadero Fm. (amphibolite) | 54.3 | 2.7 | K/Ar Hb | 11.20 | −74.21 | Metamorphic age |
| 109      | Gneis de Dibulla (anorthosite) | 54.3 | 1.9 | Ar/Ar Hb | 10.74 | −74.08 | Metamorphic age |
| 110      | Esquistos de Jambuló (glaucophane bluish schist) | 54.3 | 1.7 | Ar/Ar | 2.71 | −76.43 | Metamorphic age |
| 111      | Gneis de Dibulla (anorthosite) | 54.5 | 0.8 | Ar/Ar Bt | 10.74 | −74.08 | Metamorphic age |

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of Isthmus formation. This corroboration of results clearly shows that any issues with mtDNA calibration do not affect the conclusions presented by Bacon et al. (3, 22).

Bacon et al. (3, 22) demonstrated that several pulses of terrestrial migration and marine vicariance occurred in the Neogene, rather than a single, time-limited event at 3.5 Ma. Can we therefore assume, a priori, that mammal migration and marine vicariance occurred in the Neogene, rather than a single, time-limited event at 3.5 Ma? The answer given by Bacon et al. (3, 22) based on 424 data points from molecular phylogenies across multiple taxonomic groups and ecological forms, and further supported by the smaller data set (38 data points) in Figure 4 of O’Dea et al. (1), is no.

NEW AGE FOR THE FORMATION OF THE Isthmus OF PANAMA

O’Dea et al. (1) propose a new age for the formation of the Isthmus of Panama at 2.8 Ma. This new hypothesis is based on the (i) "end of surface water exchange at 2.76 Ma based on marine plankton assemblages and surface ocean salinity contrast" (Figure 3 in the study by O’Dea et al. 1), (ii) absence of gene flow between shallow marine animal populations after ~3.2 Ma [Figure 4 in the study by O’Dea et al. (1)], and (iii) acceleration of the dispersal rate of terrestrial mammals at ~2.7 Ma [Figure 5 and table S2 in the study by O’Dea et al. (1)]. An examination of each of these points indicates that there is insufficient support for their hypothesis.

First, O’Dea et al. (1) discuss how salinity and carbonate accumulation rates diverge at 4.2 Ma, but there is no significant change at 2.8 Ma [Figure 3 in the study by O’Dea et al. (1)]. Second, Figure 3 of O’Dea et al. (1) provides no evidence of "marine plankton assemblages" splitting between Caribbean and Pacific waters at 2.8 Ma. Third, the youngest divergence time estimated from the molecular data set (Melitta quinquiesperforata; table S3 in the study by O’Dea et al.) has a mean age of 3.21 Ma with a 95% credible interval of 3.91 to 2.51 Ma and therefore does not define a precise split at 2.8 Ma, as O’Dea et al. (1) conclude. Fourth, although O’Dea et al. (1) show an increase in terrestrial

| Record # | Lithology | Age (Ma) | Error (Ma) | Method | Latitude | Longitude | Comment* |
|----------|-----------|----------|------------|--------|----------|-----------|----------|
| 113      | El Hatillo stock (quartz diorite) | 54.6     | 0.7        | U/Pb Zr | 5.17     | −74.97    | Not Panamanian signal |
| 114      | Santa Marta batholith (plutonic dike) | 54.7     | 0.7        | U/Pb Zr | 11.27    | −74.09    | Not Panamanian signal |
| 115      | Gneis de Dibulla (anorthosite) | 54.7     | 4.0        | Ar/Ar Hb | 10.74 | −74.08    | Metamorphic age |
| 116      | Pórfido de Murindó (porphyry tonalite) | 54.7     | 1.3        | K/Ar Bt | 7.03 | −76.45    | Cooling age, west of suture |
| 117      | Mandé batholith (tonalite) | 54.7     | 1.2        | K/Ar Bt | 7.05 | −76.72    | Cooling age, west of suture |
| 118      | Florencia stock (quartz diorite) | 54.9     | 1.9        | K/Ar Bt | 5.33 | −75.05    | Cooling age |
| 119      | Florencia stock (quartz diorite) | 54.9     | 1.9        | K/Ar Bt | 3.37 | −76.13    | Cooling age |
| 120      | Santa Bárbara batholith (diorite) | 55.0     | 1.0        | K/Ar Bt | 3.37 | −75.05    | Cooling age |
| 121      | Santa Cecilia-La Equis Complex (porphyritic basalt) | 55.1     | 1.5        | Ar/Ar Bt | 6.74 | −76.39    | Cooling age, west of suture |
| 122      | Santa Marta batholith (granodiorite-tonalite) | 55.1     | 1.1        | U/Pb Zr | 11.20 | −74.10    | Not Panamanian signal |
| 123      | Santa Marta batholith (granodiorite-tonalite) | 55.3     | 0.6        | U/Pb Zr | 11.17 | −74.17    | Not Panamanian signal |
| 124      | Gneis de Dibulla (anorthosite) | 55.4     | 0.7        | Ar/Ar Bt | 10.74 | −74.08    | Metamorphic age |
| 125      | Santa Marta batholith (granodiorite-tonalite) | 55.5     | 0.3        | U/Pb Zr | 11.27 | −74.09    | Not Panamanian signal |
| 126      | Sonson batholith (leucogranite) | 55.8     | 1.0        | U/Pb Zr | 6.66 | −75.20    | Not Panamanian signal |
| 127      | Dike (andesite-dacite) | 55.9     | 2.0        | K/Ar Ser | 6.45 | −74.63    | Cooling age |
| 128      | Santa Marta batholith (dike) | 55.9     | 0.3        | U/Pb Zr | 11.27 | −74.24    | Cooling age |
| 129      | Piedrancha batholith (microdiorite) | 57.7     | 3.0        | K/Ar Bt | 1.12 | −77.86    | Cooling age |
| 130      | Pórfido Rio Manso (quartz diorite porphyry) | 58.0     | 10.0       | Ar/Ar Hb | 4.11 | −75.25    | Cooling age |
| 131      | Manizales stock | 59.8     | 0.7        | U/Pb Zr | 5.12 | −75.29    | Not Panamanian signal |

*Comments: 1) Not Panamanian signal: These ages, although representing South American rocks, are significantly older than the middle Eocene signal. See text and Fig. 1. 2) West of suture: Rocks that are located west of the Uramita suture and therefore belong to the Panama-Choco block or oceanic terranes west of the South American realm. The suture was defined by Duque-Caro (16), and its corresponding trace in the Geological Map of Colombia is to the south (17). See Fig. 1. 3) Cooling age: Ages indicate cooling, not magmatism. For instance, table S2 of O’Dea et al. reports several ages for a single site of Santa Marta batholith including a U/Pb in zircon of 50.1 ± 0.7 Ma (record #84), as well as Ar/Ar ages of 48 to 47 Ma in hornblende (records #75 and #66), 44 to 43 Ma in biotite (records #47 and #46), and 50 Ma in K-feldspar (records #25 to #27). This succession shows the gradual cooling of the batholith. By the time the Ar/Ar system closed in K-feldspar at 40 Ma, zircons in the same pluton were already 10 million years old. Thus, detritus derived from this body will therefore yield zircons in the 50-Ma range rather than the 40-Ma range as O’Dea wrongly assumed. 4) Metamorphic age: These ages reflect metamorphic cooling or reheating events unrelated to magmatism. These metamorphic rocks are intruded by plutonic rocks older than 50 Ma (18), therefore being older. 5) Vein unrelated to magmatism: These ages date veins in Cretaceous rocks associated to deformation, not magmatism. 6) Cretaceous ages: These Eocene ages had been previously dismissed by (19), because they were obtained in Cretaceous ocean floor sequence basals. These Eocene ages are therefore unreliable and most likely related to heating and cooling by the thermal effects of well-dated Cretaceous and Miocene intrusions (34). 7) Unreported rock type: Without sample coordinates, it is impossible to assess the meaning of the age. 8) No coordinates: Without sample coordinates, it is impossible to assess the meaning of the age.
mammal migration at ~2.7 Ma [Figure 5 and table S2 in the study by O’Dea et al. (1)], this age does not necessarily reflect formation of a terrestrial land bridge. From an analysis of 1411 migrating mammal fossil records [versus 68 in O’Dea et al. (1)] of 35 families and 124 genera, Bacon et al. (23) had already obtained a similar result. Alternative hypotheses have been proposed to explain this acceleration in mammal migration. These include habitat and environmental changes due to the onset of the Northern Hemisphere glaciation and concomitant reductions in precipitation across the Americas (23–30) and lower sea levels during glacial periods (31, 32).

**Fig. 1.** Data from O’Dea et al. (2016) [table S2 plotted and categorized (1)]. Colored circles show that none of the 131 localities listed in that publication could be sources for the Panamanian signal in middle Miocene sediments reported by Montes et al. (2). Location of suture after Duque-Caro (16) mapped onto a geological map of Colombia (17). One hundred eighteen of those ages do not represent valid ages for a possible source rock derived from South America. Inset shows that 13 ages that do date South American source rocks are significantly older ($t$ test, $P < 0.001$, df = 19.8) than the middle Eocene Panamanian signal reported in Montes et al. (2).

**TRANSMOGRIFICATION**

O’Dea et al. (1) published several statements that are incorrect and mislead readers. “If, on the other hand, one assumes that the Panama Arc permanently blocked all genetic exchange from 23 to 13 Ma (Montes et al. 2015)” misrepresents the data, results, and interpretation presented in Montes et al. (2). That publication and additional papers from our research groups (4–6, 22) have indicated that since the final closure of CAS ~10 to 15 Ma until 4.2 to 3.5 Ma, the Caribbean Sea and Pacific Ocean were still connected by shallow water, albeit intermittently, through other passages than CAS.
CONCLUSIONS

The rise of the Isthmus of Panama is a fascinating event in Cenozoic history that has attracted worldwide attention, mostly because it has been linked to four major events in the history of Earth: the onset of the Thermohaline Circulation, the onset of Northern Hemisphere glaciation, the birth of the Caribbean Sea, and the Great American Biotic Interchange (4). Some of these links have been criticized or dismissed (for example, (4, 25, 33)) and are still far from being resolved. Unfortunately, O’Dea et al. (1), rather than providing a clear synthesis on the issue, have added more confusion. Further fieldwork and new data generation are needed to fully understand the implication of the rise of the Isthmus of Panama.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/3/6/e1602321/DC1

table S1. Molecular results from O’Dea et al. (1) used as input for the migration rate through time (MRTT) and the MRTT results from model testing.

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