ECOLOGY

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 often occurs along tectonic boundaries, and both modeling and empirical data indicate that the blockage of deep and intermediate waters (>200- to 500-m depth) across the Isthmus affects global oceanography at least as much as the blockage of shallow waters (*6*).

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 m^3 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.* [table S2 in the study 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 [marine] divergences…to imply a common geological cause." Here, we used the data presented in O'Dea *et al.* [table S3 in the study by 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

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Table 1. Annotated table S2 of O'Dea *et al.* (*1*).

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 Diabásico (dolerite)	34.0		K/Ar	3.27	−76.62	Cretaceous ages
4	Santa Marta batholith (granodiorite)	34.2	1.6	Ar/Ar Kfs	11.24	−74.02	Cooling age
5	Dibulla Gneiss (anorthosite)	35.0	3.0	Ar/Ar Hb	10.74	−74.08	Metamorphic age
6	Cocha Río Téllez Migmatitic Complex (gneissic granodiorite)	35.0	0.4	Ar/Ar Hb	0.81	−77.33	Metamorphic age
7	Santa Marta schist (amphibolic schist)	36.2	5.1	K/Ar Hb	11.28	−74.15	Metamorphic age
8	Paja Fm. (mineralized vein)	36.4	0.1	Ar/Ar Ms	5.64	−74.14	Vein, unrelated to magmatism
9	Cocha Río 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	1.7	Ar/Ar	1.98	−77.15	Unreported rock type
12	Paja Fm. (mineralized vein)	37.3	0.1	Ar/Ar wr	5.64	−74.14	Vein, unrelated to magmatism
13	Socorro stock (granodiorite)	37.8	1.7	K/Ar Bt	10.79	−74.03	Cooling age
14	Santa Marta batholith (granodiorite)	38.7	0.6	Ar/Ar Kfs	11.24	−74.02	Cooling age
15	Santa Marta schist Fm. Concha (phyllite)	38.7	3.4	K/Ar wr	11.31	−74.13	Metamorphic age
16	Acandí batholith (quartz diorite)	38.9	3.0	K/Ar Ser	8.53	−77.42	Cooling age, west of suture
17	Timbiquí Fm. (andesite)	38.9	4.3	K/Ar	2.29	−77.65	West of suture
18	Rio Napi intrusives (Hb diorite)	39.0	2.0	K/Ar	2.49	−77.48	Cooling age, west of suture
19	Grupo Diabásico (dolerite)	39.0		K/Ar	3.27	−76.62	Cretaceous ages
20	Grupo Diabásico	39.7	3.5	Ar/Ar Hb	1.33	−77.46	Cretaceous ages
21	Grupo Diabásico (lava)	40.0	2.0	K/Ar wr	12.23	−71.69	Cretaceous ages
22	Piedrancha batholith (granodiorite)	40.5	3.0	K/Ar Bt	1.23	−77.73	Cooling age
23	Cocha Río Téllez Migmatitic Complex (gneissic granodiorite)	40.0	0.5	Ar/Ar Hb	0.81	−77.33	Metamorphic age
24	Grupo Diabásico (dolerite)	40.0		K/Ar	3.27	−76.62	Cretaceous ages
25	Santa Marta batholith (granodiorite)	40.2	1.4	Ar/Ar Kfs	11.28	−73.90	Cooling age
26	Santa Marta batholith (granodiorite)	40.2	1.5	Ar/Ar Kfs	11.28	−73.90	Cooling age
27	Santa Marta batholith (granodiorite)	40.4	0.3	Ar/Ar Kfs	11.28	−73.90	Cooling age
28	Santa Marta schist, Cinto Fm. (phyllite)	40.9	4.7	K/Ar wr	11.25	−74.18	Metamorphic age
29	Nudillales stock (quartz monzonite)	41.0	3.0	K/Ar wr	7.04	−76.32	Cooling age, west of suture
30	Timbiquí Fm. (andesite)	41.0	1.0	K/Ar	2.20	−77.68	West of suture
31	Los Cholos–Napi River pluton (Hb-bearing quartz diorite)	41.0	4.0	K/Ar	2.46	−77.50	Cooling age, west of suture
32	Basalt	41.4	8.6	Ar/Ar Pl	6.02	−76.26	West of suture
33	Llanitos latiandesite	41.5	1.8	K/Ar wr	7.07	−76.41	West of suture
34	Timbiquí Fm. (andesite)	41.7	1.2	K/Ar	2.40	−77.57	West of suture
35	Santa Marta batholith (granodiorite)	41.8	0.8	Ar/Ar Kfs	11.27	−74.09	Cooling age
36	Patía 29-Ra-002	41.9	0.7	Ar/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	1.7	K/Ar Bt	10.99	−74.14	Metamorphic age
40	Mandé batholith (porphyritic dacite)	42.7	0.9	K/Ar Ser	6.70	−76.50	West of suture
41	Pórfido Pantanos (porphyritic dacite)	42.7	0.9	K/Ar Bt	6.42	−76.30	West of suture
42	Río Napi intrusives (Hb-bearing gabbro)	43.0	0.4	K/Ar	2.53	−77.45	Cooling age, west of suture
43	Basalt	43.1	0.4	Ar/Ar Pl	6.02	−76.26	West of suture
44	Santa Marta batholith (granodiorite)	43.6	0.5	Ar/Ar Kfs	11.27	−74.09	Cooling age
45	Buriticá andesite (andesite, porphyritic diorite)	43.8	4.3	K/Ar wr	6.70	−75.91	Cooling age
46	Santa Marta batholith (granodiorite)	43.9	0.5	Ar/Ar Bt	11.28	−73.90	Cooling age
47	Santa Marta batholith (granodiorite)	44.0	0.8	Ar/Ar Bt	11.28	−73.90	Cooling age
48	Río Napi intrusives (Hb-bearing tonalite)	44.0	4.0	K/Ar	2.49	−77.49	Cooling age, west of suture
49	Timbiquí Fm. (andesite)	44.0	1.0	K/Ar	2.18	−77.70	West of suture
50	Santa Marta schist (amphibolic schist)	44.1	2.7	K/Ar Hb	11.22	−73.89	Metamorphic age
51	Santa Marta batholith (quartz diorite)	44.1	1.6	K/Ar Bt	11.29	−73.97	Cooling age
52	Mandé batholith (tonalite)	44.6	0.9	U/Pb Zr	6.73	−76.52	West of suture
53	Los Azules (ophiolite sequence + pillow lavas)	44.7	6.0	K/Ar wr	1.90	−77.00	Cretaceous ages
54	Mandé batholith (tonalite)	44.8	1.0	Ar/Ar Hb	6.81	−76.59	Cooling age, west of suture
55	Sevilla Complex (schist)	44.8	0.4	Ar/Ar Bt	11.26	−73.62	Metamorphic age
56	Mandé batholith (tonalite)	45.3	1.2	U/Pb Zr	6.72	−76.52	West of suture
57	Grupo Diabásico (lava)	46.0	3.0	K/Ar wr	3.51	−76.53	Cretaceous ages
58	Santa Marta batholith (granodiorite)	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	8.1	Ar/Ar Hb	3.82	−76.60	Cooling age
63	Grupo Diabásico (dolerite)	47.0		K/Ar	3.27	−76.62	Cretaceous ages
64	Mandé batholith (tonalite)	47.1	2.5	K/Ar Hb	NA	NA	No coordinates
65	Santa Marta schist (amphibolic schist)	47.4	2.4	K/Ar Hb	11.12	−74.05	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	Balsitas pluton (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	Acandí batholith (tonalite)	48.1	1.0	K/Ar Hb	8.20	−77.24	Cooling age, west of suture
72	Acandí batholith (tonalite)	48.1	1.0	K/Ar Ser	8.46	−77.36	Cooling age, west of suture
73	Acandí batholith (tonalite)	48.1	2.0	K/Ar Ser	8.20	−77.24	Cooling age, 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	4.8	K/Ar	2.29	−77.64	West of suture
77	Buriticá 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	9.8	K (R)	1.60	−77.40	Cretaceous ages
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 Pl	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	Santa Marta batholith (granodiorite-tonalite)	50.6	1.7	U/Pb Zr	11.31	−73.94	Not Panamanian signal
87	Santa Marta batholith (granodiorite)	50.7	0.9	Ar/Ar Hb	11.27	−74.09	Cooling age
88	Santa Cecilia–La Equis Complex (porphyritic basalt)	50.7	2.0	Ar/Ar glass	6.74	−76.39	West of suture
89	Timbiquí Fm. (andesite)	50.7	2.0	K/Ar	2.18	−77.70	West of suture
90	Plutón de Buriticá (tonalite, quartz diorite)	50.8	1.5	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 (amphibolic 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	3.3	Ar/Ar Hb	4.38	−75.72	Metamorphic age
96	Gabbronorite	51.7	3.9	Ar/Ar wr	6.58	−76.59	Cooling age, west of suture
97	Santa Marta batholith (aplite dike)	52.3	0.7	U/Pb Zr	11.14	−74.12	Not Panamanian signal
98	Gabbronorite	52.7	3.2	Ar/Ar wr	6.58	−76.59	Cooling age, west of suture
99	El Hatillo stock (quartzodiorite)	53.0	1.8	K/Ar Bt	5.19	−75.00	Cooling age
100	Río Napi intrusives (Hb-bearing tonalite)	53.0	5.0	K/Ar	2.52	−77.43	Cooling age
101	Grupo Diabásico (pillow lava)	53.2	4.6	K/Ar wr	1.60	−77.40	Cretaceous ages
102	Santa Marta batholith (aplite dike)	53.3	1.0	U/Pb Zr	11.24	−74.06	Not Panamanian signal
103	Timbiquí Fm. (andesite)	53.4	3.0	K/Ar	2.19	−77.71	West of suture
104	Gabbronorite	53.6	2.9	Ar/Ar wr	6.58	−76.59	Cooling age, west of suture
105	Gneis de Dibulla (anorthosite)	53.8	0.7	Ar/Ar Bt	10.74	−74.08	Metamorphic age
106	Sevilla Complex	53.9	0.5	Ar/Ar Bt	11.26	−73.62	Unreported rock type
107	Plutón Tucurinquita (granodiorite)	54.0	2.2	K/Ar Bt	10.68	−74.08	Cooling age
108	Sevilla Complex (schist)	54.1	0.7	Ar/Ar Bt	11.26	−73.62	Metamorphic age
109	Gneis de Dibulla (anorthosite)	54.3	1.9	Ar/Ar Hb	10.74	−74.08	Metamorphic age
110	Esquistos de Santa Marta Rodadero Fm. (amphibolite)	54.3	2.7	K/Ar Hb	11.20	−74.21	Metamorphic age
111	Esquistos de Jambaló (glaucophane blue schist)	54.5	1.6	Ar/Ar Pg	2.77	−76.33	Metamorphic age
112	Gneis de Dibulla (anorthosite)	54.5	0.8	Ar/Ar Bt	10.74	−74.08	Metamorphic age

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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 (aplite 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	1.3	K/Ar Hb	7.05	−76.75	Cooling age, west of suture
118	Florencia stock (quartz diorite)	54.9	1.9	K/Ar Bt	5.53	−75.05	Cooling age
119	Florencia stock (quartz diorite)	54.9	1.9	K/Ar Bt	5.37	−75.01	Cooling age
120	Santa Bárbara batholith (diorite)	55.0	1.0	K/Ar Bt	3.37	−76.13	Cooling age
121	Santa Cecilia–La Equis Complex (porphyritic basalt)	55.1	1.5	Ar/Ar	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	Sonsón batholith (leucogranite)	55.8	1.0	U/Pb Zr	5.66	−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	11.21	−74.24	Not Panamanian signal
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	K/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 Gelogic 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 age in biotite (records #47 and #46), and 40 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 basalts. 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 knowledge of the rock type dated, 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.

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 any given marine sister taxa found on either side of the Isthmus split 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 (*Mellita 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 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*).

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.

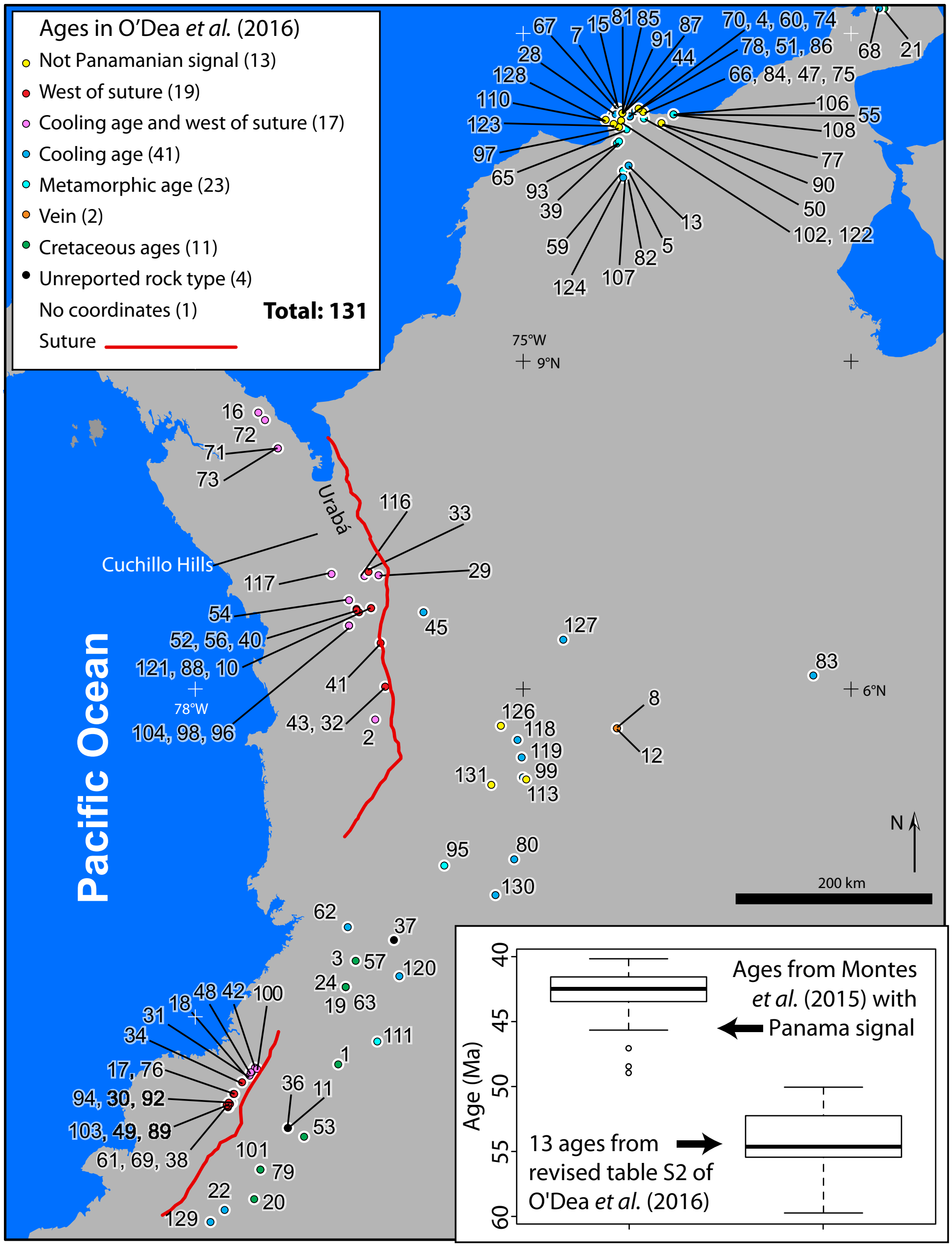

Fig. 1. Data from O'Dea *et al.* [table S2 plotted and categorized (*1*)]. Colored circles show that none of the 131 localities listed in that publication could be sources for the Panamanian signal in middle Miocene sediments reported by Montes *et al.* (*2*). Location of suture after Duque-Caro (*16*) 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*).

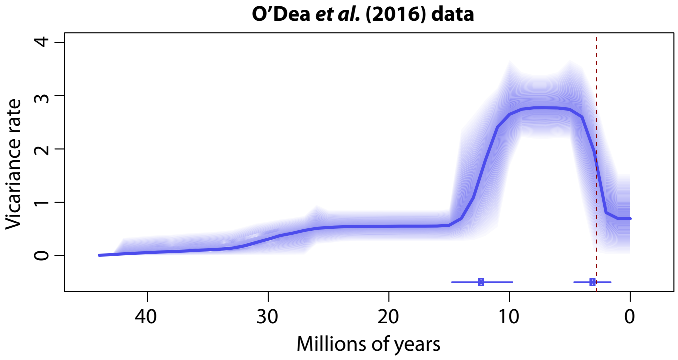

Fig. 2. Data from O'Dea *et al.* [table S3 analyzed and plotted (*1*)]. Rate through time plot showing the tempo of vicariance events (estimated number of events per million year) in marine organisms inferred from the data presented in table S3 of O'Dea *et al*. (*1*). Shaded area shows the 95% confidence interval (95% CI) around the rate estimates based on 1000 replicated analyses, in which the ages of the vicariance events were resampled from the age intervals presented in O'Dea *et al*. (*1*). Two statistically significant shifts in vicariance rate are detected, at 12 Ma (95% CI: 14.77 to 9.76 Ma) and 3.01 Ma (95% CI: 4.65 to 1.61 Ma). The red dashed line shows the new, 2.8-Ma date for the formation of the Isthmus of Panama proposed by O'Dea *et al*. (*1*).

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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Acknowledgments: We thank P. Molnar. **Funding:** C.J. was funded by the Smithsonian Institution and the NSF (OISE/EAR/DRL 0966884). A.A. and C.D.B. were funded by the Swedish Research Council (B0569601), the European Research Council (331024; Framework Programme 2007 to 2013), and a Wallenberg Academy Fellowship. D.S. was funded by the Swedish Research Council (2015-04748). **Author contributions:** C.J. and C.D.B. wrote the paper with contributions from all the other authors. D.S. analyzed the molecular data, and C.M. and A.C. reviewed the geological data. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** All data needed to evaluate the conclusions in the paper are present in the paper and/or table S1. Additional data related to this paper may be requested from the authors.

Submitted 21 September 2016
Accepted 25 April 2017
Published 14 June 2017
10.1126/sciadv.1602321

Citation: C. Jaramillo, C. Montes, A. Cardona, D. Silvestro, A. Antonelli, C. D. Bacon, Comment (1) on “Formation of the Isthmus of Panama” by O’Dea *et al. Sci. Adv.* **3**, e1602321 (2017).

Science Advances

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Sci Adv **3** (6), e1602321.
DOI: 10.1126/sciadv.1602321