LETTER

Appearance of an early closure of the Isthmus of Panama is the product of biased inclusion of data in the metaanalysis

In their PNAS article "Biological evidence supports an early and complex emergence of the Isthmus of Panama," Bacon et al. (1) use data from molecular comparisons of terrestrial and marine organisms taken from the literature to estimate dates of rate shifts in migration. One of their conclusions is that "events separating marine organisms in the Atlantic and Pacific oceans [occurred] at ca. 23 and 7 Ma" (1). The authors base this conclusion on two kinds of molecular dating: (*i*) 31 dates from phylogenies with evolutionary rates calibrated from fossils at one or more nodes, and (*ii*) 52 dates from mitochondrial divergence between sister species on either side of the Isthmus taken from the review by Lessios (2) (note: complete data are available from the Dryad Digital Repository). For the latter, divergence was converted to time by assuming a mitochondrial DNA divergence rate of 2% per million years. Unfortunately, Bacon et al.'s (1) metaanalysis of separations of marine organisms contains unexplained omissions of data and mistakes. Nine of the fossil calibrated divergence values are wrong, and three are omitted (though present in publications used to derive other dates). Thirty-eight comparisons from Lessios (2) are excluded. Criteria for inclusion of data are not stated but, judging from the estimated dates, only data from Cytochrome *c* oxidase subunit 1 were taken into account, even though Lessios (2) presents data for multiple mitochondrial genes. This selectivity in the marine dataset of Bacon et al. (1) is hard to explain, because the terrestrial data come from various genes, and because eight comparisons of Cytochrome *c* oxidase subunit 1 of marine species are among those excluded.

The omission of 50 comparisons has caused a definite skew in the distributions of marine separations toward older dates, because 34 of the missing data points produce estimated dates younger than 7 Ma when the 2% per million year calibration is applied. Bacon et al. (1) simulate error in the estimation of dates, but this procedure does not address bias because of data exclusion. When all available data are included, 62 splitting events are estimated as having occurred 1–5 Ma, 29 as having occurred 6–10 Ma, but only 3 events as having occurred 19–23 Ma. Thus, the conclusion that there was a peak of separations at ca.7 Ma is justified, but the evidence is scant for similar occurrences at 23 Ma, and thus for the claim for an early emergence of the Isthmus. The lack of mention of the peak at >5 Ma in the conclusion of Bacon et al. (1) is puzzling, because a clear signal of it exists even in the biased set of data that they used. Figure 1D of Bacon et al. (1) identifies a rate shift at 2 Ma, significant by their analysis and reported in the results, but (despite the preponderance of data supporting it) ignored in their conclusions and their abstract.

The most recent time at which marine organisms maintained genetic contact between the Atlantic and Pacific oceans is important for biogeographic and paleoceanographic reconstructions, calibrations of molecular evolution, and studies of speciation. It deserves to be based on careful inclusion of available data and objective reporting of results.

Harilaos A. Lessios[1]

Smithsonian Tropical Research Institute, Box 0843-03092 Balboa, Panama

1 Bacon CD, et al. (2015) Biological evidence supports an early and complex emergence of the Isthmus of Panama. *Proc Natl Acad Sci USA* 112(19):6110–6115.

2 Lessios HA (2008) The Great American Schism: Divergence of marine organisms after the rise of the Central American Isthmus. *Annu Rev Ecol Evol Syst* 39(1):63–91.

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Data deposition: The data reported in this paper have been deposited in the Dryad Digital Repository, datadryad.org (doi:10.5061/dryad.b29k1).

[1]Email: Lessiosh@post.harvard.edu.