Quaternary glaciation and the Great American Biotic Interchange

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ABSTRACT

Recent geological studies demonstrate that the Isthmus of Panama emerged some 10 m.y. earlier than previously assumed. Although absent today in Panama, Central American savanna environments likely developed in connection with the onset of Northern Hemisphere glaciations. As is widely recognized, most of the mammals crossing the isthmus since 2.5 Ma lived in savannas. Could climate-induced vegetational changes across Panama explain the delayed migration of mammals, rather than terrestrial connectivity? We investigate the congruence between cross-continental mammal migration and climate change through analysis of fossil data and molecular phylogenies. Evidence from fossil findings shows that the vast majority of mammals crossed between South and North America after ca. 3 Ma. By contrast, dated mammal phylogenies suggest that migration events started somewhat earlier, ca. 4–3 Ma, but allowing for biases toward greater ages of molecular than geologic dating and uncertainties in the former, we consider this age range not to be significantly earlier than 3 Ma. We conclude that savanna-like environments developed in response to the vast Laurentide ice sheet at the first Quaternary glaciation triggered the initiation of the Great American Biotic Interchange in mammals.

INTRODUCTION

Two virtually simultaneous events occurred at the end of the Pliocene Epoch, ca. 2.5 Ma: the onset of recurring ice sheets covering North America and Fennoscandia (e.g., Haug et al., 1999; Jansen and Sjøholm, 1991; Shackleton et al., 1984) and the intensification of an interchange of mammals across the Isthmus of Panama between North and South America (Fig. 1A)—the Great American Biotic Interchange (GABI) (e.g., Simpson, 1980; Stehli and Webb, 1985). The simultaneity of the mammal exchange and the onset of Quaternary glaciations gave rise to the contention that the emergence of the isthmus was necessary for both the GABI and the onset of ice ages.

Essentially all vertebrate paleontologists who have presented evidence for the GABI (e.g., Cione et al., 2015; Marshall, 1985; Marshall et al., 1979, 1982; Webb, 1978, 1985, 1991, 2006; Woodburne, 2010) recognize that this logic is incomplete: although a land bridge is necessary for the GABI, its existence is not sufficient for the GABI to have occurred. Environmental conditions must have been different when mammals crossed (Fig. 1B). During the Last Glacial Maximum, the climate in Panama was more arid than today, with environments in at least some regions resembling those of savannas (e.g., Leyden, 1984; Piperno, 2006; Piperno and Jones, 2003). In addition, during glacial times, sea levels dropped ~100 m, increasing the width of emergent Panama and creating a wider savanna

corridor that would have further aided the GABI (e.g., Gartner et al., 1987; Savin and Douglas, 1985). Moreover, the "vast majority" (Webb, 1985, p. 378) or "overwhelming majority" (Jackson and O'Dea, 2013, p. 786) of the GABI participants have been assumed to be savanna-adapted mammals (e.g., Leigh et al., 2014; Marshall, 1985; Stehli and Webb, 1985; Webb, 1978, 1991, 2006; Woodburne, 2010).
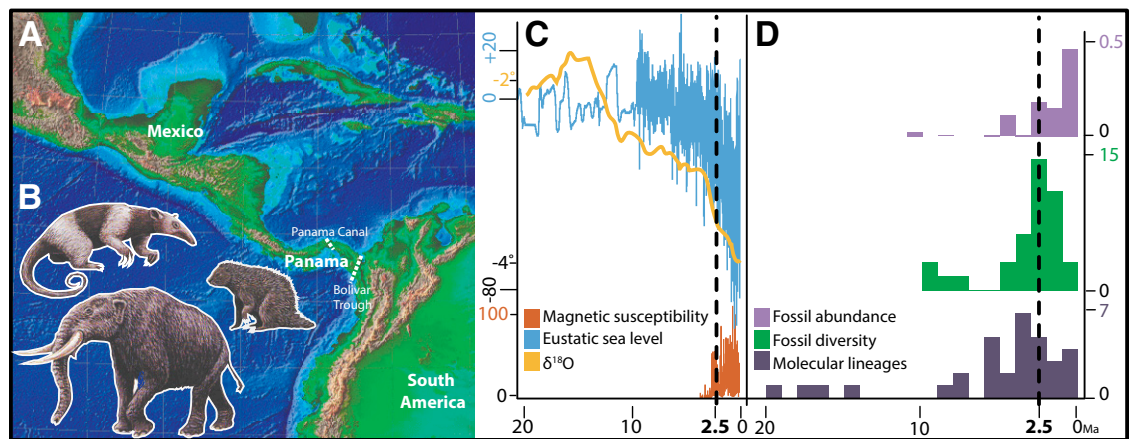
Because both geological (e.g., Montes et al., 2012a, 2012b, 2015) and biological (e.g., Bacon et al., 2015a, 2015b) evidence suggest that the isthmus had emerged long before 3 Ma, another mechanism needs to be sought for explaining the GABI in mammals. Our purpose here is to revisit the hypothesis put forth by the vertebrate paleontologists that ice-age climates triggered the GABI (e.g., Cione et al., 2015; Marshall, 1985; Marshall et al., 1979, 1982; Molnar, 2008; Webb, 1978, 1985, 1991, 2006; Woodburne, 2010).

THE LATE CENOZOIC ICE AGES

The date of the first Northern Hemisphere glaciation remains controversial, for a brief ~1‰ increase in $\delta^{18}O$ of benthic foraminifera at ca. 3.3 Ma (Lisiecki and Raymo, 2005) corresponds to a drop in sea level of ~50 m (Miller et al., 2005) and may suggest a small precursory ice sheet. Regardless of when ice first accumulated over Canada, since ca. 2.5 Ma, ice sheets have waxed and waned over Canada and Fennoscandia some 50 times (e.g., Lisiecki and Raymo, 2005). The five largest ice advances, which reached hundreds of kilometers south of the most recent one, include the first at ca. 2.5 Ma (Balco and Rovey, 2010). Large ice sheets increase albedo and consequently cool the Northern Hemisphere. That cooling then increases the north-to-south gradient in sea-surface temperatures, which in turn induces a southward displacement of the Inter-Tropical Convergence Zone (ITCZ), where localized precipitation occurs (e.g., Chiang et al., 2003). Moreover, General Circulation Model (GCM) runs of climate suggest that in periods when the North Atlantic is covered by ice, in Heinrich events during glacial times, such cooling and southward displacements of the ITCZ are yet greater (Chiang and Bitz, 2005). Southward displacements of the ITCZ during glacial times suppress summer rainfall in the tropics north of the equator, causing aridification and facilitating expansion of savanna habitats. Paleoclimatic proxies from the Cariaco Basin, in Venezuela at approximately the same latitude as Panama, show dry climate associated with southerly displacements of the ITCZ in glacial periods (Peterson et al., 2000) and the Younger Dryas (Haug et al., 2001). Thus, both GCM runs and observations connect aridification of the tropics with wide expanses of Northern Hemisphere ice cover.

Despite the incomplete stratigraphic record for Panama, evidence has accumulated to show that environments in much of Central America were

Figure 1. Ice ages and their influence on Great American Biotic Interchange. A: Map of Isthmus of Panama region. B: Representative mammal species that migrated across Americas (top: anteater; below: elephant-like gomphothere; right: fossil porcupine) (credit: Wikimedia Commons, commons.wikimedia.org). C: Correspondence amongst independent data sets supporting drying environment at 2.5 Ma, shown by δ18O from benthic foraminifera (Zachos et al., 2008), a proxy for global temperature, smoothed with Gaussian window of 200 k.y.; eustatic sea level (Miller et al., 2005); and magnetic susceptibility, a proxy for ice-rafted debris and for Northern Hemisphere glaciation (Lawrence et al., 2013). D: Mammal migration estimated from both fossil and molecular data, plotted based on occurrence data binned by million-year intervals and calculated for abundance (standardized proportion of occurrences) and diversity (number of species). Dashed line at 2.5 Ma reflects onset of ice ages.

4–6 °C cooler and more arid during at least portions of the last glacial period and the early stages of deglaciation, including during the Younger Dryas, than today (e.g., Bush and Colinvaux, 1990; Bush et al., 1992; Hodell et al., 2008; Escobar et al., 2012; Leyden et al., 1993; Piperno et al., 1990). Ironically, in some regions, like Lake Petén Itzá, in Guatemala ~10° north of Panama, the 23–18 ka period of the Last Glacial Maximum was moist, but during most of the last glacial period and its deglacial period, both a smaller lake and geochemical proxies suggest climates drier than those of today (Hodell et al., 2008; Escobar et al., 2012). Some have explicitly noted "savanna" habitats (e.g., Leyden, 1984; Piperno, 2006; Piperno and Jones, 2003), although others (e.g., Bush and Colinvaux, 1990; Jaramillo et al., 2014) have questioned their existence. We recognize that savannas and tropical dry forests thrive in similar climates, with soil type determining their relative dominance (e.g., Pennington et al., 2000). In any case, these lines of evidence suggest that by ca. 2.5 Ma and during glacial periods, tropical forests withdrew and were complemented by arid habitats suitable for savanna-dwelling species (Fig. 1C). Such arid conditions may have prevailed briefly at ca. 3.3 Ma, when camelids reached South America (Cione et al., 2007; Woodburne, 2010), and presumably recurred successively with subsequent ice ages.

THE GEOLOGICAL SETTING

The Isthmus of Panama today is narrow and at low elevation, with <65 km separating the Pacific Ocean from the Caribbean Sea (Fig. 1A). Fossil evidence from identical species recovered from central Panama along the canal area and in North America suggests that North America was connected to central Panama by the early to middle Miocene (Cadena et al., 2012; Kirby and MacFadden, 2005; Kirby et al., 2008; MacFadden, 2006, 2009; MacFadden and Higgins, 2004; MacFadden et al., 2010; Rincon et al., 2012; Whitmore and Stewart, 1965). Although periodic flooding of low-elevation areas between Panama and North America could have temporarily severed a land bridge (e.g., Coates et al., 2004), the final and more permanent barrier separating North and South America was often assumed to lie east of the canal zone of Panama (e.g., Marshall, 1979, 1988; Marshall et al., 1982; Stehli and Webb, 1985; Webb, 1976, 2006).

Emergent terrain in eastern Panama has been present since late Eocene–Oligocene times (Montes et al., 2012a). These conditions are unlikely to have changed significantly in the past ~3 m.y., because once fluvial exchange was established between the Panama arc and South America at ca. 15–13 Ma, any deep passages were above sea level (Montes et al., 2015). The incompleteness of the record also permits shallow passages between the Pacific Ocean and the Caribbean Sea not just in Panama but

also farther west (e.g., Coates et al., 2004), but we are unaware of any evidence of a deep (>200 m), wide (>400 km), longstanding passage.

THE FOSSIL RECORD OF THE GREAT AMERICAN BIOTIC INTERCHANGE

An abrupt increase in mammal lineages and individuals crossing from North to South and South to North America began at ca. 2.5 Ma (e.g., Cione et al., 2015; Leigh et al., 2014; Marshall, 1985; Marshall et al., 1982; Webb, 1991, 2006; Woodburne, 2010). Webb (2006) listed 17 families that crossed from North to South America and 18 families of terrestrial mammals from South to North America. Two key facts characterize these animals. First, most do not swim well, and hence a land bridge seems necessary. Second, as noted above, most of these animals were adapted to savanna ecosystems.

Clearly some animals crossed from one continent to the other before 3 Ma (Fig. 1D). The most commonly cited cases based on fossil data, referred to as "heralds" by Webb (1976), include three genera of ground sloths, *Megalonyx*, *Pliometanastes*, and *Thinobastides*, that moved from South to North America at 9.5–9 Ma (Marshall et al., 1979), and the procyonid (related to modern raccoons) carnivore *Cyonasua* that crossed to South America at ca. 7 Ma (e.g., Marshall, 1985, 1988; Marshall et al., 1979; Webb, 1978, 1985; Woodburne, 2010). As Webb (2006, p. 247) noted explicitly, "living sloths and raccoons are particularly adept at floating and swimming" which may explain the interchanges of their predecessors (e.g., Jackson and O'Dea, 2013; Marshall et al., 1979; Webb, 1978, 1985).

ANALYSIS OF THE MAMMAL FOSSIL RECORD

Bacon et al. (2015a) (see Table DR2 in the GSA Data Repository[1]) showed that, based on fossil data, mammal migration over the Isthmus of Panama region occurred primarily after 3–2 Ma. Here, we excluded non-migrant taxa and compiled new migrant data from recent publications. We excluded some Peruvian fossils (e.g., Campbell et al., 2010), whose ages are debated. The vetted data set comprises 1411 fossil records from

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[1]GSA Data Repository item 2016122, Appendix DR1 (abundance of mammal fossil occurrences found that migrated across the Isthmus of Panama through time), Appendix DR2 (number of mammal families that migrated across the Isthmus of Panama), Appendix DR3 (summary table of calculations to estimate the proportion of immigrants within 1 million year time intervals), Appendix DR4 (compilation of dated molecular phylogenies of American mammal clades that include at least one migrant population or species), is available online at www.geosociety.org/pubs/ft2016.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.

35 families and 124 genera of migrating mammals (Appendix DR1 in the Data Repository). We plotted fossil occurrences in million-year time intervals, standardized by the total number of sites, using the conservative measure of maximum age for each occurrence, resulting in a bar plot showing the proportion of the total number of occurrences found in each time interval (Fig. 1D).

To compare the abundance of the GABI mammals with an estimate of the diversity of these mammals, we compiled a list of families from Webb (2006) (Appendix DR2). Woodburne (2010) reported dates for many of these, but for some, Webb (2006) merely stated that these families migrated during the late Pliocene, by which he clearly meant either 2.7 Ma (Webb, 2006) or 2.5 Ma (Webb, 1991), so we coded these as occurring at 2.6 ± 0.1 Ma (Fig. 1D).

We found an overall increase in mammal migration across the Isthmus of Panama region starting after 3 Ma (Fig. 1D). Prior to 3 Ma, both GABI mammal fossils and fossil localities are relatively scarce, which could cause bias (Carrillo et al., 2015). Despite this, after 3 Ma, the proportion of occurrences per million years rose to nearly 20% and reached nearly 50% after 1 Ma (Appendix DR3). Although low levels of interchange were detected as early as 9 Ma, 26 of the 35 total families listed by Webb (2006), and perhaps more with allowance for errors in dating, did not cross between continents before ca. 2.5 Ma.

THE MOLECULAR RECORD OF THE INTERCHANGE

Molecular data have shed light on temporal and spatial patterns of the GABI (Bacon et al., 2015a and 2015b; Cody et al., 2010; Pinto-Sánchez et al., 2012; Weir et al., 2009), but few studies have explicitly examined the impact of the environment on dispersal (e.g., Bacon et al., 2013; Smith et al., 2012). To test whether molecular-based dates are concordant with the fossil data analyzed here, we further compiled phylogenetic data from mammals involved in the GABI following the criteria of Bacon et al. (2015a). We excluded studies that directly or indirectly incorporated any assumption of the timing of the closure of the isthmus for the calibration of phylogenies. The data set included 33 dated dispersal events across the Isthmus of Panama (Appendix DR4). Based on simulations, Bacon et al. (2015b) showed that results from cross-taxonomic analyses are generally robust to considerable amounts of potential error in molecular data, such as ascertainment bias in taxonomic sampling, variation in molecular clock calibration methods, and topological and branch length estimates.

We found that most mammal migrations fall within 4–3 Ma (Fig. 1D). The fact that molecular-based estimates are older than those based on fossils should be expected, because divergence times inferred strictly from genetic data are commonly older than the divergence of morphologically recognizable and reproductively isolated species (e.g., Arbogast et al., 2002). Furthermore, neither fossils nor molecular data can readily distinguish fine-scale temporal differences (e.g., between 4 and 2.5 Ma). Thus, while the mean and variation of colonization times for fossil data are both lower and younger than for molecular-based estimates, we find that these data sources are broadly consistent in the reconstruction of the GABI. Importantly, both data sets converge on an event that is not temporally linked to the establishment of a terrestrial connection between North and South America, but took place millions of years later.

CONCLUSIONS

Because the emergence of the Isthmus of Panama occurred at ca. 15–13 Ma (Montes et al., 2015), another mechanism must be invoked to explain the mammal interchange after ca. 2.5 Ma. We conclude that climatic and environmental changes alone, without changes in geological configurations of land, are the most likely trigger for the GABI in mammals. Specifically, the ice-age climates converted enough of tropical Central America into recurring dry environments, that savanna-dwelling mammals—the majority of those that participated in the GABI—no longer needed to traverse dense rainforests and could disperse between continents.

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