

# The Great American Biotic Interchange: Dispersals, Tectonics, Climate, Sea Level and Holding Pens

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**Abstract** The biotic and geologic dynamics of the Great American Biotic Interchange are reviewed and revised. Information on the Marine Isotope Stage chronology, sea level changes as well as Pliocene and Pleistocene vegetation changes in Central and northern South America add to a discussion of the role of climate in facilitating trans-isthmian exchanges. Trans-isthmian land mammal exchanges during the Pleistocene glacial intervals appear to have been promoted by the development of diverse non-tropical ecologies.

**Keywords** Great American Biotic Interchange · Central America · Biogeography · Pleistocene ice ages

## Introduction

The Great American Biotic Interchange (Stehli and Webb 1985) refers to the exchange of land mammals that represents the strongest biogeographic link between North and South America ever achieved (Simpson 1950, 1953; Webb 1976, 1985; Marshall et al. 1982; Woodburne et al. 2006; Morgan 2008).

Woodburne et al. (2006) summarized aspects of Central American and Mexican faunas in this context. In addition to contributing to the mammalian range extensions of which the Great American Biotic Interchange (GABI) is comprised, these regions also served as a source of cladogenesis on one

hand, and a holding pen for certain taxa, on the other. Webb and Rancy (1996) evaluated centers of endemism for Neotropical mammal faunas of the late Cenozoic. Webb (1991) proposed that Great American Biotic Interchange (GABI) dispersals were aided by the development of Northern Hemisphere glaciations that promoted the development of savanna-like ecologies in Central America, in contrast to their generally tropical character, and thereby permitted savanna-adapted mammals to cross between North and South America. The formulation of a succession of astronomically-calibrated oxygen isotope curves, summarized in Lisecki and Raymo (2005) has provided a detailed chronology of oceanic temperature changes during the past 5 Ma. Sosdian and Rosenthal (2009) offered a detailed scale of sea level changes during the past 3.2 Ma, and Bartoli et al. (2005) presented a valuable analysis of the final closure of the Isthmus of Panama. Papers by Graham and Dilcher (1998) and others, including Piperno (2006), Andreissen et al. (1993), and Bush et al. (2004), aid in the discussion of Pliocene and Pleistocene vegetation and climatic patterns in Central and northern South America.

The purpose of the present paper is to integrate the above and pursue the roles played by tectonics, climate, sea level, and holding pens in facilitating or otherwise affecting the exchange of land vertebrates across the Panamanian isthmus during GABI. Figure 1 shows the districts and faunal sites discussed in the text.

## Abbreviations and definitions

CAS	Central American Seaway; Bartoli et al. (2005).
Central America	The region encompassed between the southern border of Panama and the Isthmus of Tehuantepec, Mexico (Fig. 1).

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Endemic	a taxon that either phylogenetically originates in, or is introduced to, but in any case subsequently remains restricted to, the area indicated.	MIS	Marine isotope scale, astronomically calibrated (Lisecki and Raymo 2005).
GABI	Great American Biotic Interchange. GABI began about 2.6 Ma (see text).	m.y.	Segment of geologic time 1 million years in duration or the age of an event (e.g., 10 million years ago) without reference to a point or a set of points on the radioisotopic time scale.
GP	Glacial pulse corresponding to a MIS in Fig. 7 that represents a strong departure from the general pattern during a time of stable or lowering of mean sea level as indicated by the heavy black line thereupon. This is noted as <i>GP</i> in Fig. 4 opposite MIS stages numbered in <i>italic boldface</i> in both Figs. 4 and 7.	NALMA	North American Land Mammal Age (Woodburne 2004).
GPTS	Geomagnetic Polarity Time Scale (after Lourens et al. 2004).	Neogene Period	The content of the Neogene System/Period and the base of the Pleistocene Series/Epoch at 1.81 Ma follows Lourens et al. (2004), contra Gibbaard et al. (2010).
holding pen	this refers to situations in which a taxon occurs earlier in a given location, only to be found later on in an adjacent area. As discussed below and by Flynn et al. (2005), a number of taxa have an earlier record in deposits of the Guanajuato region of central Mexico (G; Fig. 1) relative to their first occurrence in the United States. In that case, the Mexican record is considered as having been a holding pen with respect to the later occurrence. All references in the text to Flynn et al. (2005) refer to this record in Guanajuato.	NHG	Northern Hemisphere glaciation, which began at about 3.6 Ma, but exhibited its first glacial event at about 3.3 Ma (Mudelsee and Raymo 2005).
		North America	The North American continent north of Central America (Fig. 1).
		PCO	Pliocene climatic optimum (Dowsett et al. 1994), where temperatures rose about 6°C (Lawrence et al. 2009) during an interval from 3.25–3.05 Ma. (Mudelsee and Raymo 2005).
		SALMA	South American Land Mammal Age (see text).
		South America	The South American continent from the northern border of Colombia with Panama (Fig. 1).
IRD	Ice-rafted debris, in the context of indicating episodes of Northern Hemisphere Glaciation (NHG) (Bartoli et al. 2005) and other significant glacial events (Lawrence et al. 2009).		
ky	Kiloyear, a segment of geologic time 1,000 years in duration or the age of an event (e.g., 200,000 years ago) without reference to a point or a set of points on the radioisotopic time scale.		
Local Fauna	This (also abbreviated L.F.) is an aggregate of fossil vertebrates that have a limited distribution in time and space, derived from a number of closely grouped localities in a limited geographic area. See Tedford (1970). A local fauna could be based on taxa from as single locality.		
Ma	Megannum. One million years in the radioisotopic time scale (e.g., 10 Ma refers to the 10 million year point on that time scale).		

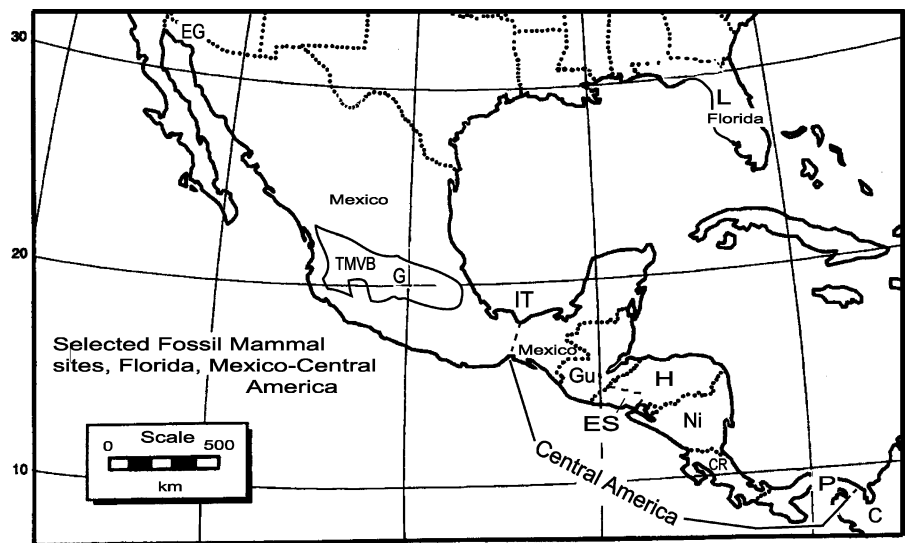
### Tectonic background

The traditional viewpoint has been that GABI signaled the development of an overland corridor across the Panamanian region, and that this transpired about 3.0 Ma (e.g., Marshall et al. 1979, 1982 and references cited therein). It also was recognized that there had been a limited exchange of taxa in both directions prior to this time, and presumably prior to the development of a well-defined ‘land bridge’, with the precursors being designated variably as ‘heralds’ (Webb 1976, 1985, 2006) or New Island Hoppers, with the latter appellation indicating the method of dispersal (Simpson 1950).

The geologic and tectonic reconstructions of Coates et al. (2004) indicate that the Panamanian region contained a series of islands as early as 6 Ma (Fig. 2), with the formerly through-going Central American Seaway (CAS) being largely interrupted by an evolving volcanic arc as early as about 12 Ma, as the southwestern margin of the Caribbean Plate collided with the South American continent.

**Fig. 1** Map of Florida, Mexico, and Central America showing fossil localities and other areas discussed in the text.

EG=El Golfo, Mexico; ES=El Salvador; G=Guajuato, Mexico; Gu=Guatemala; H=Honduras; IT=Isthmus of Tehuantepec; L=Leisey Bone Bed, Florida; Ni=Nicaragua; P=Panama; TMVB=Transmexican Volcanic Belt.

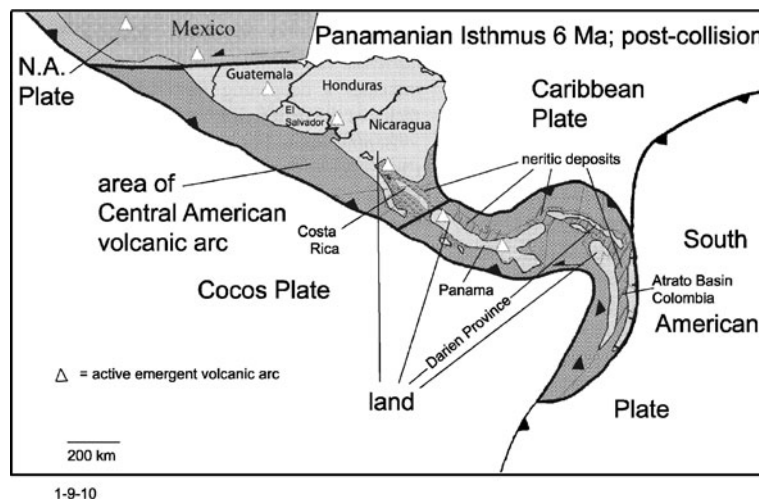


Tectonic highlights include a widespread unconformity at about 8.6–7.1 Ma that reflects complete docking and widespread uplift of the Central American Isthmus (including Panama). This apparently fostered the 7.3 Ma entry of the Procyonidae to South America (Fig. 3).

From Costa Rica to Colombia (Fig. 2), marine deposits reflect shallow marine (neritic) conditions adjacent to emergent lands between about 7.1–4.0 Ma (and 4.8 Ma in Colombia; 4.0 Ma in Costa Rica) subsequent to which the region was further strongly uplifted, including the final emergence of the Panamanian district. In this context (including a brief increase of marine flooding about 6 Ma; Coates et al. 2004), overall conditions reflected increased shallowing of the CAS until about 2.8 Ma (Bartoli et al.

2005), after which time the isthmian region apparently was dry land.

From the evidence in Fig. 3 and the following discussion of the dispersal pattern (Fig. 4) it appears that land mammals began to extend their ranges across Central America soon after the initial tectonic closure from about 12 Ma. Whereas the first sloths arrived in North America at about 9 Ma, that is only a minimum age regarding their actual crossing of the isthmian region, and whether they were present in Central America prior to their occurrence in continental North America remains to be determined. In fact, the degree to which Central America acted as a holding pen for any trans-isthmian dispersal remains an open question, considered further below.



**Fig. 2** Reconstruction of the geologic setting of the Central American volcanic arc region at 6 Ma, after Coates et al. (2004: fig. 8c). The Central American volcanic arc is still active (open triangles) subsequent to a major plate collision between 8.6–7.1 Ma. The presence of numerous islands as well as emergent land in Mexico,

Guatemala, Honduras, Nicaragua, and Colombia sets the stage for the Great American Biotic Interchange well prior to the final closure of the Central American Seaway, perhaps as late as 2.8 Ma. Neritic conditions dominated near island segments prior to a brief bathyal incursion.

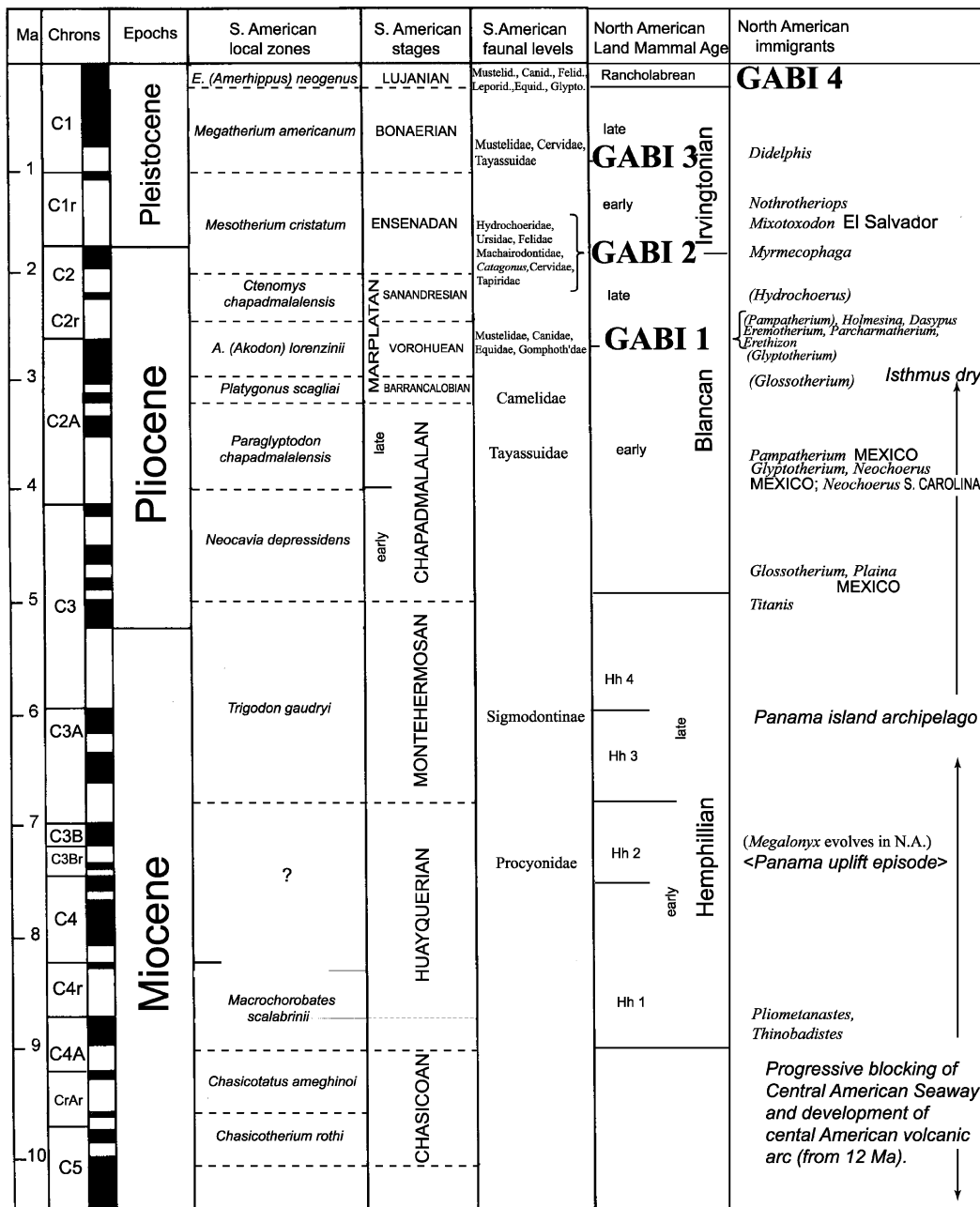
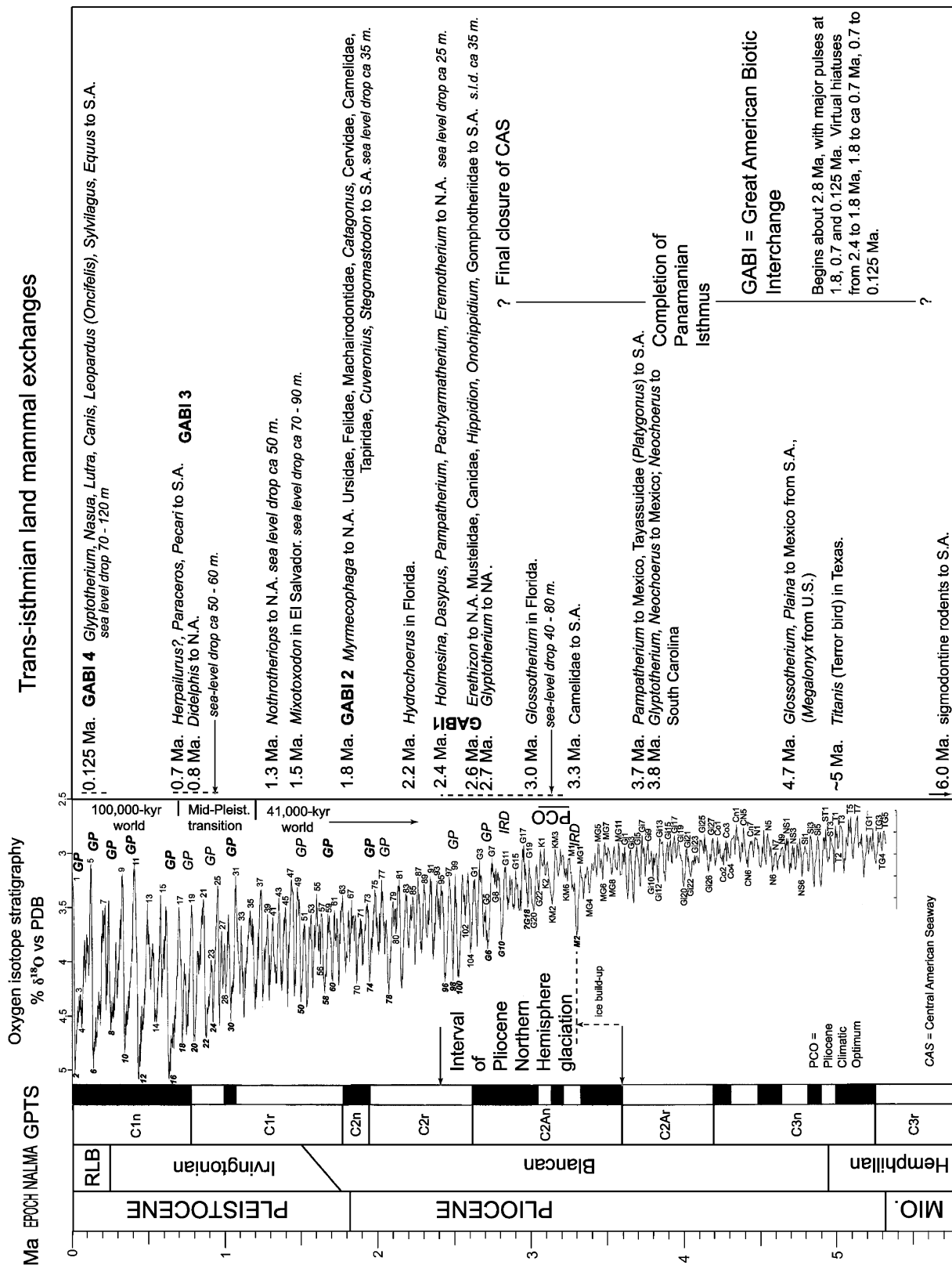


Fig. 3 General chronology of North and South American dispersal episodes, after Cione et al. (2007). Dispersal taxa to North and South America modified according to the text.

**Dispersal pattern**

This is updated and revised from Woodburne et al. (2006) and Cione et al. (2007), and other cited references. The discussion recognizes the fact that the South American record still is being developed in areas north of Argentina. Fig. 3 shows the overall chronology of the mammal-bearing units in North and South America, with a summary of the faunal exchanges detailed more fully in Fig. 4. The information also is outlined in Table 1, which additionally shows some of the South American taxa that were endemic

results of the immigrations. The pattern shown in Fig. 4 indicates that the main pulse of the interchange began about 2.6 Ma, but there had been a number of more limited dispersals prior to that time. The earliest of these (Fig. 3) is represented by the sloths *Thinobadistes* and *Pliomatanastes* found in faunas of early Hemphillian age (ca 8.5–9 Ma) in North America (Morgan 2008), derived from South American mylodontid and megalonychid ancestors, respectively. This is comparable to Webb (1976), modified to reflect the origin of *Megalonyx* from *Pliomatanastes* at about 7 Ma (Fig. 3 and McDonald and Naples 2008). In the



**Fig. 4** Chronology of late Miocene through Pleistocene trans-isthmian land mammal exchanges with respect to oxygen isotope stratigraphy. Chronologic framework (Ma, Epoch, GPTS, NALMA, Oxygen isotope stratigraphy) follows Lisiecki and Raymo (2005). Interval of Pliocene Northern Hemisphere glaciation, PCO, and ice build-up, after Mudelsee and Raymo (2005). IRD=ice rafted debris

after Bartoli et al. (2005). GP=glacial pulse, interpreted from sea level lowstands of Fig. 7. MIS stages such as **100** (boldface) indicate those in Fig. 7 considered to reflect lowstands due to strong pulses in glaciation. Chronology and list of mammalian taxa as in text. Sigmodontine rodent as per text. Completion of Panamanian Isthmus after Coates et al. (2004), and Bartoli et al (2005).

overall context, in which more taxa dispersed southward at the height of GABI (see below), the fact that the first elements of the interchange were from South America is noteworthy. This part of the pattern also is consistent with most newcomers to North America being, in fact, xenarthrans.

The first dispersal southward was accomplished by a procyonid carnivoran, reflected by *\*Cyonasua* (\*=endemic South American taxon that reflects a dispersal), at about 7.3 Ma (Procyonidae, Fig. 3; also Cione et al. 2007). This was followed by sigmodontine rodents at about 6 Ma. Verzi and Montalvo (2008) proposed that mustelid carnivorans also entered South America at about this time, but that chronology and identification have been questioned by Prevosti and Pardiñas (2009). Lindsay (2008) indicated that sigmodontine rodents (cricetids, contra murids in Webb 2006 and other papers) were well developed by the Clarendonian NALMA (ca 12 Ma) in North America. Forasiepi et al. (2007) pointed out that the late Huayquerian record of *Cyonasua* may have coincided with the last occurrence of metatherian borhyaenids and that there was effectively no direct competition between large terrestrial marsupial carnivores and the placental taxa that arrived in the early part of GABI.

The next exchanges (Figs. 3 and 4) took place at about 5.0–4.7 Ma, with the Terror Bird (*Titanis*) in Texas (ca 5 Ma; MacFadden et al. 2007) and two South American xenarthrans (the pampatheriid *Plaina*; and the mylodontid *Glossotherium*) in Guanajuato, Mexico (G; Fig. 1). Flynn et al. (2005) noted that *Glossotherium* is recorded in the early Blancan (4.7–4.8 Ma) in Mexico, but significantly later in the United States, where it persists to the Irvingtonian (McDonald and Naples 2008). Tomida (1987) documented *Glossotherium* in Arizona at about 3.0 Ma (Bell et al. 2004), an example of the Mexican holding pen (Figs. 3 and 4). *Glossotherium* is considered to have originated in South America (McDonald and Naples 2008, contra Webb 2006). Reguero et al. (2007) recorded the presence of *Plaina* in South American deposits of Montehermosan age (Fig. 3), possibly 5–7 Ma, and Flynn et al. (2005) indicated that the genus is known from the Guanajuato deposits about 4.7–4.8 m.y. old. *Megalonyx* is also known from Mexico at this time interval (McDonald and Naples 2008), which is the oldest record of the genus south of the United States.

At about 3.1–3.9 Ma, the glyptodont *Glyptotherium* and the hydrochoerid rodent *Nechoerus* are recorded in Guanajuato, Mexico (Flynn et al. 2005). On Table 1 *Nechoerus* is noted from the Ensenadan NALMA, at about 1.8 Ma. Whether this indicates that the genus arose in Central America and dispersed later to South America remains to be determined (Woodburne et al. 2006:97). *Glyptotherium* persisted at least until about 2.7 Ma, when it

entered North America, possibly released from a holding pen. The original dispersal episode was followed at about 3.7 Ma, as the pampatheriid xenarthran *Pampatherium* entered Mexico (Woodburne et al. 2006: 95 L) and Tayassuidae (artiodactyl peccaries) are recorded in the late Chapadmalalan SALMA in South America (Cione et al. 2007). Shortly after, at about 3.1 Ma, the peccary, *Platygonus scagliai*, is recorded in Argentina. Unless reflecting a second immigration, this species apparently descended from a Chapadmalalan precursor, which must have been an un-named species of that genus (see also Prevosti et al. 2006, and references cited therein). *Platygonus* is shown at about 3.7 Ma in South America on Table 1. Wright (1998) indicated that *Platygonus* is known from early late Hemphillian faunas in North America (Hh3, Fig. 3), at about 7 Ma. The former use of the hog-nosed skunk *Conepatus* (e.g., Webb 1985) as a Chapadmalalan immigrant has been discounted by Cione et al. (2007).

Also at about 3.8 Ma, the typically wet-temperate to tropical-adapted South American hydrochoerid rodent *Nechoerus* is recorded in South Carolina (Sanders 2002), as well as in Mexico. *Nechoerus* persisted in Florida (Macaspah Shell Pit; Bell et al. 2004) and Arizona (111 Ranch L.F., Morgan 2005) at about 2.6 Ma, and survived on into the Rancholabrean in coastal localities of the southeastern United States (Morgan 2008).

At about 3.3 Ma, the North American camelid artiodactyl group is represented by the South American genus *\*Lama* (Camelidae; Barrancalobian SALMA, Fig. 3; Cione and Tonni 1995, 2005; Cione et al. 2007). As discussed further below, the record of this savanna-adapted genus occurs within the early development of prominent Northern Hemisphere glaciation.

At 3.0 Ma, the South American mylodontid xenarthran *Glossotherium* is found in Arizona and Florida (Bell et al. 2004), derived from its older Mexican record (above).

GABI began in earnest (**GABI 1**, Figs. 3 and 4) at about 2.6–2.4 Ma, with the first major dispersal of both North American and South America taxa. This is comparable to the time of final closure of the CAS (Bartoli et al. 2005) but, as discussed below, climate change was a key factor without which such a strong interchange would not have taken place. In general, the taxa discussed here resemble those typically having been involved in the interchange by Webb (1985) and Marshall et al. (1984) at about 2.5 Ma, and as discussed by Cione et al. (2007). Regarding the South American record, Cione and Tonni (1995) and Cione et al. (2007) pointed out that the interchanges took place as a number of pulses, as did North American entrants as well, as indicated here. As noted in Figs. 3 and 4, *Glyptotherium* arrived in North America at about 2.7 Ma, but this is not considered part of GABI 1 due to its previous presence in Mexico (ca 3.8 Ma).

Reguero et al. (2007) recorded the first occurrence of the porcupine *Erethizon* in South America at about 2.6 Ma, essentially coeval with its dispersal to North America. Until this update, Flynn (2008) as well as (Webb 1985, 2006, and other papers) indicated *Erethizon* had been introduced to North America, even though that genus or a close relative still had been unknown in South America. Flynn (2008) included in *Erethizon* the North American fossil species referred to *\*Coendu* by White (1970) that ranged from the late Blancan to Irvingtonian, the earliest record of which is the ca 2.6 Ma Wolf Ranch L.F. of Arizona (see also Harrison 1978; Albright 1999). *\*Coendu* remains an endemic South and Central American porcupine that is found today no farther north than Honduras (Flynn 2008).

As clarified by Cione et al. (2007), a large number of taxa dispersed to South America at this time, including a mustelid carnivoran (*\*Galictis*; Table 1), a canid carnivoran (*\*Dusicyon*—also known as *\*Pseudalopex*; Prevosti 2006), and equid perissodactyls (*\*Hippidion*, *\*Onohippidium*; both genera have an earlier record in North America, but subsequently are indigenous to South America). López et al. (2001) add a ?gomphotheriid proboscidean. The South American elements of this dispersal are thus reflected in the Vorohuean record of the Canidae, Equidae, Mustelidae, and Gomphotheriidae in Fig. 3.

Beginning about 2.4 Ma, the pampatheriid xenarthran *Pampatherium* entered the United States from Mexico (a laggard from a 3.7 Ma holding pen; Morgan and Hulbert 1995; Flynn et al. 2005) along with its through-moving relative *Holmesina*, a dasypodid armadillo (*Dasypus*), a glyptodontid (*Pachyarmatherium*), and a megatheriid sloth (*Eremotherium*) (Bell et al. 2004; Morgan 2005). On Figs. 3 and 4, this is the last interval assigned to GABI 1.

As indicated in Fig. 4, four families of xenarthrans—Dasypodidae (*Dasypus*), Pampatheriidae (*Holmesina*), Glyptodontidae (*Pachyarmatherium*), and Megatheriidae (*Eremotherium*)—and an erethizontid rodent dispersed to North America during GABI 1, with previously dispersed elements of the Pampatheriidae (*Pampatherium*) and Glyptodontidae (*Glyptotherium*) having been released from Mexico. This compares with four non-xenarthran placental families having entered South America (Mustelidae, Canidae, Equidae, and Gomphotheriidae). In that the southward contingent included two families of carnivorans as well as advanced herbivores, it can be argued that the diversity of that group is greater than the northward dispersants, as discussed further below.

An apparent gap in dispersals from 2.4 to 1.8 Ma seems to have been a tropical holding pattern for hydrochoerid rodents. *Hydrochoerus* is present in Florida at about 2.2 Ma in presumably wet conditions and might have been lingering in local sites in the Isthmian region in any case.

At approximately 1.8 Ma South America witnessed a strong dispersal pulse (GABI 2, Figs. 3 and 4) from North America. This pulse is represented in South America by the Ursidae (*\*Arctotherium*), the felid cats *Felis*, *Puma* and *Panthera*, the saber-toothed cat *Smilodon*, the peccary *Catagonus*, the camels *\*Palaeolama* and *\*Hemiauchenia*, Cervidae (endemic representatives being the marsh deer *\*Epiuryceros* and the South American deer *\*Antifer*; Table 1), the tapir *Tapirus*, and the gomphotheriid proboscideans *Stegomastodon* and *Cuvieronius*. All of these taxa have first South American appearances in the Ensenadan SALMA (bracket, Fig. 3, and Tonni et al. 1992; Cione and Tonni 1995, 2005; MacFadden 2000; Pomi and Prevosti 2005; Soibelzon et al. 2005). In that context, *\*Palaeolama* and *\*Hemiauchenia* are considered endemic South American taxa subsequent to their dispersal from their congeners in North America (Honey et al. 1998; Woodburne et al. 2006). This episode also records the presence of the USA endemic mylodontid *Paramylodon* in Florida (Morgan 2005), and the South American vermilinguan immigrant *Myrmecophaga* (Morgan 2008), known from the El Golfo L.F. of Sonora, Mexico (North America) at about 1.6–1.8 Ma (Shaw and McDonald 1987). McDonald and Naples (2008) indicated that *Paramylodon* descended from the North American taxon *Glossotherium chapadmalense*.

Single-taxon dispersals took place at 1.5 and 1.3 Ma. *Mixotoxodon* is recorded from the early Pleistocene Barranca del Sisimico Local Fauna of El Salvador, along with *Pteronotus* (bat), *Cuvieronius* (gomphotheriid proboscidean), *Eremotherium* (megatheriid sloth), and *Megalonyx* and *Meizonyx* (megalonychid sloths). The 1.5 Ma age is an approximation, but Webb and Perrigo (1984) considered this the earliest occurrence of *Mixotoxodon* in Central America. The record of *Megalonyx* may represent the oldest and southern-most occurrence of that genus south of Mexico. The other taxa in the Barranca del Sisimico L.F. were not involved in immigrations at this time.

The dispersal at 1.3 Ma is represented by the megatheriid *Nothrotheriops* from the Leisey Shell Pit, Florida. Bell et al. (2004) considered the genus to be present in the Vallecito Creek L.F. of California, dated at about 2.1 Ma, but Morgan (2005) revised that record to the endemic *Megalonyx*. Morgan (2005) is followed here for the age of the Leisey Shell Pit.

At about 0.8 Ma (~0.8–1.0 Ma) the marsupial *Didelphis* entered North America (Fyllan Cave; Bell et al. 2004; Morgan 2008), likely coincident with a dispersal at about 0.7 Ma to South America by the jaguarundi *\*Herpailurus*, the cervid *\*Paraceros*, and the peccary *\*Pecari*, taxa known from faunas of Bonaerian age (Mustelidae, Cervidae, and Tayassuidae, Fig. 3 and Cione and Tonni 2005; Prevosti 2006; Cione et al. 2007). This interval is dubbed

**GABI 3** (Figs. 3 and 4) in representing a bi-polar exchange of at least four taxa.

Finally, at about, or subsequent to, 0.125 Ma, a major dispersal (**GABI 4**, Figs. 3 and 4) to South America is recorded by the glyptodontid xenarthran *Glyptotherium*, the coati *Nasua*, the river otter *Lutra*, the canid *Canis*, the ocelot *Leopardus (Oncifelis)*, the sylvilagine rabbit *Sylvilagus*, and the equid *Equus*: a relatively diverse if not balanced assemblage of Lujanian age (Mustelidae, Canidae, Felidae, Leporidae, Equidae, and Glyptodontidae, Fig. 3 and Tonni et al. 1985; Cione and Tonni 1995, 2005; Prevosti 2006; Carlini et al. 2008). Hulbert and Pratt (1998) record *Leopardus* from about coeval deposits in Georgia. Prevosti and Rincón (2007) also record the entry of *Urocyon* (gray fox) to northern South America at about 25 ka.

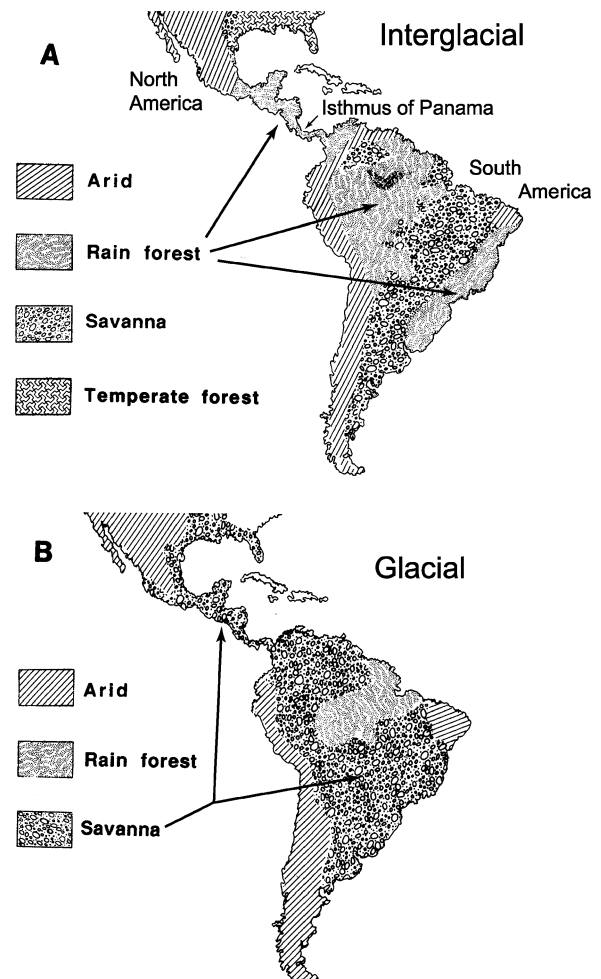
In summary, the GABI can be considered as a series of pulses, possibly reflecting the impact of glacial conditions in the Northern Hemisphere (see below). A major exchange (**GABI 1**) from 2.6 to 2.4 Ma resulted in a porcupine and variety of xenarthrans coming to North America, a group of carnivorans and equids and a gomphotheriid proboscidean to South America. The just antecedent dispersal of a camelid to South America at about 3.3 Ma likely records the earliest glacially-coeval southward dispersal of North American savanna-adapted mammals, but is not considered part of GABI 1 as defined above.

A dispersal gap from about 2.4–1.8 Ma saw limited northward ingress of a hydrochoerid rodent, possibly representing an earlier presence in an isthmian tropical holding pen.

Renewed dispersal at about 1.8 Ma (**GABI 2**) entailed a diversity of carnivorans, artiodactyls, a perissodactyl, and two proboscideans to South America, and a myrmecophagid xenarthran to the north.

Another gap from about 1.7–0.7 Ma saw limited dispersal to Central America by a toxodont at 1.5 Ma and by a megatheriid sloth to North America at 1.3 Ma. **GABI 3** recognizes a bi-polar exchange of an opossum at 0.8 Ma northward and a carnivoran and two artiodactyls at 0.7 Ma to the south. The last major dispersal, **GABI 4**, at about 0.125 Ma reflected a diversity of carnivorans, a sylvilagine rabbit, the equid *Equus*, and a glyptodont xenarthran having dispersed to South America.

The above indicates that, overall, somewhat more mammalian genera dispersed southward (32) than northward (17, excluding the bird, *Titanis*), with that pattern being most sharply evident in GABI 2, 3, and 4. As indicated above, the phyletic diversity was always greater in the southern contingent, with the northern comprised mostly of xenarthrans, a minor contribution of an erethizontid rodent, two hydrochoerid rodents, and a marsupial.



**Fig. 5** Distribution of Pleistocene landscape types in North and South America. After Webb (1991: fig. 3). **a.** Interglacial (present-day) conditions result in rainforest habitats dominating the isthmian region, as well as in the Orinoco and Amazon basins of South America. In this situation, arid or savanna habitats of North America are completely separated from South American counterparts. **b.** Northern Hemisphere glacial conditions result in the preponderance of savanna and other open landscapes that allowed the extensive population of South America by North American taxa during the Great American Biotic Interchange. Note the many apparently close correlations between multi-taxon dispersal events and glacial pulses (GP) in Fig. 4.

### Climate

Under the above tectonic interpretation, elements of the isthmian land bridge were physically present well before the major GABI dispersals transpired, and in this context the climatic stimulus invoked by Webb (1991) is even more appropriate as identifying the major dispersal instigator. Regardless of the presence of a pathway composed at least of a series of islands, major overland dispersal of terrestrial mammalian taxa apparently did not take place until the climate was conducive to support the temperate-adapted taxa that experienced the changes in their respective home ranges. It seems strongly credible that climate was the



primary control for the initiation (2.6–2.4 Ma; GABI 1, Figs. 3 and 4) and subsequent development of the Great American Biotic Interchange.

As indicated in Fig. 5, a glacially driven climate would have resulted in the development of savanna-like conditions in the isthmian region in contrast to the tropical rainforests of Pleistocene interglacial (and present-day) settings that would have presented (and now does present) a major ecologic barrier regardless of it being a dry-land route. The ecologic adaptations and diversity of the dispersing taxa witnessed throughout the GABI episodes are largely consistent with their having occupied a savanna environment (Webb 1991), although the floral pattern likely was not as generalized as suggested in Fig. 5b (see below). Implicit in this scenario is the thesis that pre-GABI climates in Central America were essentially tropical (Graham and Dilcher 1998) even though differently constructed than at present. In contrast, the dispersals during this earlier interval lack a similarly-focused mechanism, and are perhaps more difficult to interpret.

The data in Figs. 3 and 4 indicate that in the pre-GABI interval, from about 9 Ma to 3 Ma, South America contributed five genera in three families of xenarthrans Mylodontidae and Megatheriidae (9 Ma), Pampatheriidae and Mylodontidae (4.7 Ma), and Pampatheriidae (3.7 Ma), plus one genus of hydrochoerid rodent (3.8 Ma). This compares with a similar number of genera (4) passing southward: a procyonid carnivoran (7.3 Ma), a sigmodontine rodent (6.0 Ma), a peccary (3.7 Ma), and a camel (3.3 Ma). Typically, the northward contingent was composed mostly of xenarthrans, whereas the southward group was more diverse, and even picked up a few apparently savanna-adapted genera toward the end of the interval (*Platygonus*, Camelidae) at, or slightly prior to, the

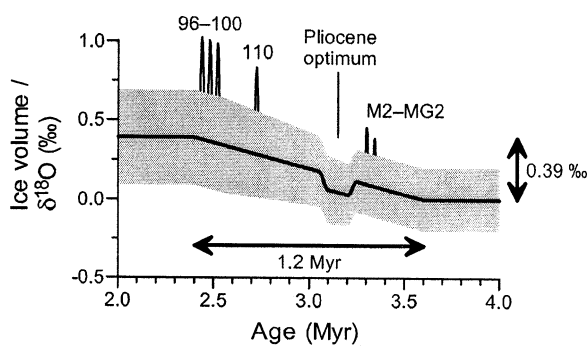
Pliocene Climatic Optimum (3.25–3.05 Ma; Mudelsee and Raymo 2005).

This interval definitely preceded both the beginning of the main episodes of the Great American Biotic Interchange and Northern Hemisphere glaciation. Whereas the general trend in global climate shows a cooling after the Mid-Miocene Climatic Optimum at about 15 Ma (Zachos et al. 2001), significant pulses of NHG did not take place until about 3.3 Ma (Fig. 6 and Mudelsee and Raymo 2005). Under those conditions it is most plausible that the isthmian region supported a tropical ecosystem, at least until about 2.7 Ma, when the major episodes of NHG began in earnest.

In that context, Webb (1976) suggests that *Thinobadistes* and *Pliometanastes* likely swam across minor stretches of ocean in their northward dispersal adventures. Based on McDonald (2005) and McDonald and Naples (2008), it appears that virtually all of the xenarthrans that crossed the Panamanian isthmus to reach North America were somewhat smaller than their contemporaries and also, of the other members of their respective families, were generalists in habit and ecology rather than specialists. It also appears that the digestive system (no caecum) used by some of these xenarthrans—in contrast to many contemporary artiodactyls and other ungulates—allowed them (except for *Myrmecophaga* and insectivorous dasypodids) to utilize food types comparable to those of non-ruminant artiodactyls and that, hence, they were not in direct competition with either ruminant artiodactyls or proboscideans. This adaptation apparently was heightened by the low metabolic rate for xenarthrans in comparison with other mammals, and in contrast with non-ruminant peccaries and camels.

Thus, the North American xenarthran immigrants apparently succeeded by accessing ecologies not occupied by other herbivores. This is consistent with the fact that, with the exception of *Eremotherium*—which retained a mainly southeastern coastal distribution in the United States—other xenarthrans became widely distributed across the continent in a variety of habitats (McDonald and Naples 2008). It thus is perhaps not surprising that xenarthrans fared so successfully in trans-isthmian dispersals. It also appears instructive that the only non-xenarthran immigrants to North America were omnivorous marsupials, a porcupine, and aquatic (and probably tropically adapted) hydrochoerid rodents. It seems reasonable to suggest that these northward dispersants were ecologically gregarious.

The coincidence between tectonic uplift in Central America and the southward dispersal of *Cyonasua* at about 7.3 Ma has been noted above. Although not closely related to the living coati (*Nasua*), *Cyonasua* is a member of its sister-group. Both appear to be omnivorous, rather than dietarily specialized, and likely shared forested habitats (Baskin 1998; Koepfli et al. 2007). *Arctonasua*, the purported sister-taxon to *Cyonasua* (Baskin 1982, 1998),



**Fig. 6** Schematic portrayal of NHG climatic transition in the Pliocene after Mudelsee and Raymo (2005). NHG began about 3.6 m.y. with increase in ice volume (solid line); increase was 0.39‰ ( $\delta^{18}\text{O}$  equivalent). Shaded band shows  $\delta^{18}\text{O}$  fluctuation relative to the ice volume trend. The warm deviation from 3.25–3.0 Ma represents the Pliocene Climate Optimum. M2–MG2 (3.2 m.y.), 110 (2.7 m.y.), 96–100 (2.4–2.5 m.y.) are oxygen isotope cycles showing glacial pulses. Ages are in m.y. rather than Ma to reflect astronomically-based chronology.

is found in deposits of late Barstovian through late Hemphillian age in North America with all but *A. floridana*, chiefly represented in the Great Plains (Texas, Oklahoma, Nebraska) states. *A. floridana* is of late Clarendonian age, from the Love Bone Bed of Florida, ca 9.5 Ma (Tedford et al. 2004), and *A. eurybates* is represented in the late Hemphillian, Upper Bone Valley L. F. of Florida, ca 5.5 Ma. These records suggest that species of this genus were capable of living in moist, humid conditions that likely were similar to those exploited by *Cyonasua* regardless of whether this genus was phylogenetically close to either *A. floridana* or *A. eurybates*. Note, however, that these species bracket the age of the dispersal of *Cyonasua*. Webb (2006) recounts the aquatic expertise of raccoons (and living sloths).

In this general context the ca 6.0 Ma dispersal of a sigmodontine rodent to South America was considered sufficiently remarkable climatically that Verzi and Montalvo (2008) chose to align this record with a cool spike in the MIS chronology. The associated mammalian fauna includes a diversity of marsupials, xenarthrans, litopterns, and hystricomorph rodents considered to have lived in relatively cool, arid, and open conditions in southern, in contrast to more tropical settings of northern, South America. Whereas this interpretation is highly interesting, the actual age of the faunas considered by Verzi and Montalvo (2008) has been questioned and discounted by Prevosti and Pardiñas (2009), so whether the cooler climates envisioned by Verzi and Montalvo (2008) can be applied to the basic sigmodontine immigration in Central America remains to be seen. Whether or not comparably cooler and drier conditions were present in Central America at the 4.7, 3.7, and 3.3 Ma dispersal events (Fig. 4) also remains to be ascertained, but the southward dispersal of a peccary at 3.7 Ma and a camel at about 3.3–3.1 Ma is perhaps suggestive of at least drier environments. This peccary is well represented in continental deposits of Hemphillian and Blancan age in the North American Great Plains region (Wright 1998) and savanna-like ecologies (Prothero 1998; Janis et al. 1998; Mio-Pliocene Chronofauna), and appears to have been the earliest savanna-adapted element to have traversed the isthmus to South America. Whereas the northward dispersals of *Pampatherium* and *Glyptotherium* might be ascribed to the adventurous dispersal capabilities of xenarthrans, the 3.8 Ma entry of *Neochoceros* to Mexico (and South Carolina) certainly carries connotations of at least local humidity, as well, reflective of a diversity of habitats.

Webb (1991) noted that prior to the advent of Northern Hemisphere glaciation, faunal exchanges between North and South America had been relatively balanced numerically, if not necessarily ecologically. This is consistent with

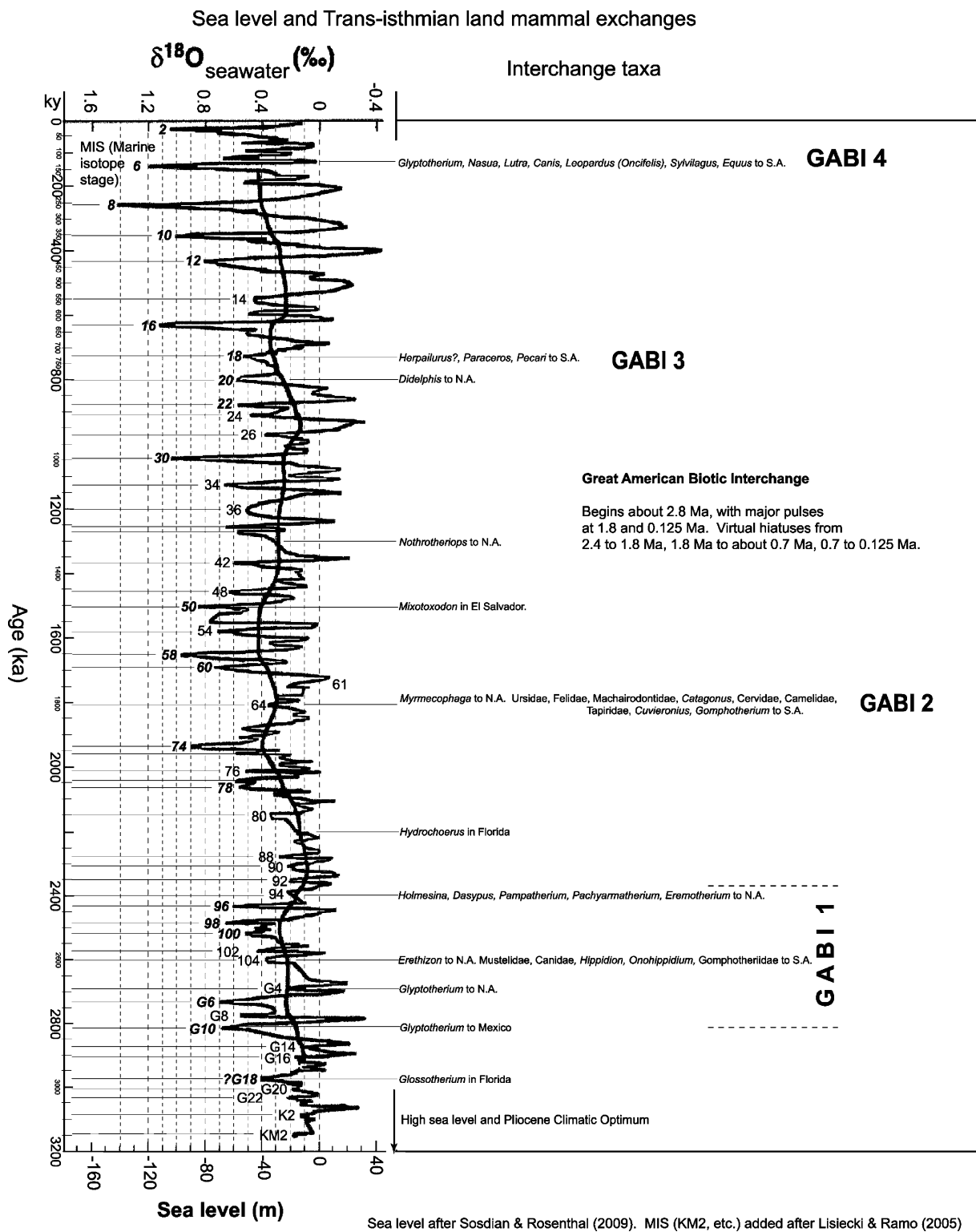
the numbers of taxa discussed above, with four genera in as many families having dispersed southward from the Huayquerian to Barrancalobian SALMAs, in comparison to six genera in four families going northward (Fig. 3) during an equivalent interval.

Similarly, about the same number of genera moved southward (five) as northward (five) in GABI 1, from 2.6–2.4 Ma, distributed among a mustelid, a canid, two equids and a gomphotheriid moving southward, and a porcupine, an armadillo, a pampatheriid, a glyptodontid, and a megatheriid xenarthran going north. Of those moving northward at 2.4 Ma, the still living *Dasypus* now inhabits warm-temperate to subtropical districts in the Gulf and Atlantic Coastal plains and formerly occurred as far north as Iowa in the Pleistocene (Morgan 2008). Overall, the GABI 1 interval appears to include mostly savanna- (or at least non-tropical) adapted taxa. As indicated on Fig. 4, this interval coincides with the first episode of Northern Hemisphere glaciation after the Pliocene Climatic Optimum, with major pulses at 3.3, 2.7 and 2.5 Ma (also Figs. 6 and 7).

The sole hydrochoerid immigrant to Florida at 2.2 Ma likely reflects the presence of humid, and potentially tropical, conditions in Central America with the family having been present there at least by 3.8 Ma (the family is present as early as the Chasicuan SALMA in South America; Fig. 3 and Cione et al. 2000). As summarized by Morgan (2008) *Hydrochoerus* persists into the late Pleistocene of wet temperate to tropical North America (South Carolina, Florida) as well as Honduras and Mexico, but is not found at the present time north of southern Panama.

GABI 2 at 1.8 Ma shows the pattern typical of Webb (1991), with a much greater number (11) and diversity of taxa moving southward than the reverse (one xenarthran), and the presence of numerous glacial pulses at about this time (Fig. 4) is consistent with his proposal that the dispersals reflected episodes of Northern Hemisphere glaciation. The pattern in Fig. 4 suggests (along with Zachos et al. 2001) continued climatic cooling between the intervals described as GABI 1 and GABI 2, which apparently resulted in a much stronger development of savanna-like conditions at that time (see discussion of Central American plants below). This seems to be reflected in the strong ecologic diversity displayed by the southern contingent of GABI 2.

If the pattern in GABI 1 is consistent with the exchange of taxa being coeval with major Northern Hemisphere glaciation, that of GABI 2 would appear to be even more so, based on the strength of its southward contingent and depending on the actual age of the 1.8 Ma dispersal relative to the major glacial pulses (GP) shown on Fig. 4. A similar suggestion can be made



**Fig. 7** Chronology of sea level changes during the past 3.2 Ma. After Sosdian and Rosenthal (2009), with MIS units after Lisiecki and Ramo (2005), and vertebrate exchanges added.

relative to GABI 3, with a number of glacial pulses from MIS 16 to MIS 20. GABI 4 is a strong example of the pattern espoused by Webb (1991), with a virtual absence of northward dispersants versus a strong diversity of

savanna-adapted taxa moving southward. The interval beginning with GABI 2 and continuing through GABI 4 is unusual in not having witnessed northward incursions of tropical taxa perhaps attesting to overall cooler

conditions regardless of any potential interglacial influence during the NHG. The 1.5 Ma immigration of *Mixotoxodon* as far north as El Salvador appears to reflect South American savanna affinities.

Regarding the NHG, Bartoli et al. (2005) consider the beginning of severe Northern Hemisphere glaciation to have been aided by the final closure of the Central American Seaway (CAS), with the effect that Pacific Ocean waters no longer advected into the Atlantic Ocean. Bartoli et al. (2005) proposed that closure of the CAS was virtually complete by 2.8 Ma; they noted that ice-rafted debris (*IRD* in Fig. 4), generally considered to reflect major continental glaciation, is recorded as early as 2.82 Ma, and pointed out that a major expansion in global ice volume occurred during an interval from 2.93–2.82 Ma (MIS G16-G10; Fig. 4). Under these scenarios, the climatic as well as CAS closure factors were in place prior to the apparent beginning of the GABI.

This is compatible with conclusions of Mudelsee and Raymo (2005), who portray a gradual build-up in ice volume from 4.0 to 2.0 Ma (Fig. 6), with the NHG pulses beginning at about 3.6 m.y., and the first glacial event (MIS M2 and MG2) recorded at about 3.3 m.y. Stage M2 apparently reflects a stronger glaciation than stage MG2, has a stronger  $\delta^{18}\text{O}$  excursion (Fig. 4) and a strong *IRD* record, as well.

In distinct contrast, the Pliocene Climatic Optimum from about 3.25–3.05 m.y. saw a rise in sea level and deglaciation. Cronin and Dowsett (1991) indicated that at 3.1 Ma, the Atlantic coast shoreline was  $35 \pm 18$  m higher than at present (also Fig. 7). This secular reversal, however, is part of an overall pattern of gradual cooling of the Northern Hemisphere. Mudelsee and Raymo (2005) indicated that further glaciations occurred at 2.7 m.y. (compatible with the second NHG and strong *IRD* pulse of Bartoli et al. 2005), and also at 2.4–2.5 m.y., with strong oxygen isotope excursions shown at MIS 100–96 (Fig. 4). Figure 7 indicates that sea level lowstands ranging from about 50 m–75 m occurred at MIS 100–96 as well, indicated here as a glacial pulse (*GP*) on Fig. 4. In summary, the Mudelsee and Raymo (2005) compilation indicates that not only was the onset of Northern Hemisphere glaciation part of a gradual process, but also that the shallowing of the CAS had been underway for several millions of years (also Coates et al. 2004), and was unlikely to have been the root cause of the NHG. Lawrence et al. (2009) concurred with the gradual development of NHG and demonstrated the prominence of *IRDs* in the glacial record subsequent to about 2.7 Ma. It also seems clear from Lawrence et al. (2009: Fig. 2) that their *IRD* record closely parallels the intervals labeled as *GP* on Fig. 4 of the present article.

## Sea level

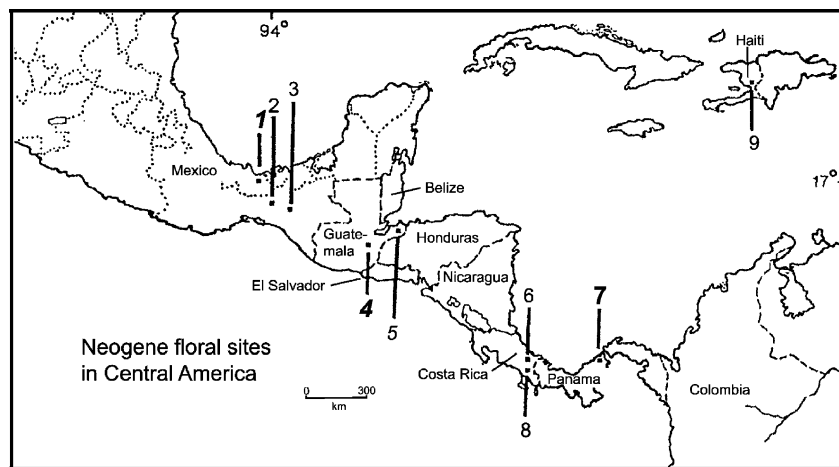
Figure 7 shows sea level curves interpreted by Sosdian and Rosenthal (2009), with MIS units added from Lisecki and Raymo (2005) and times of trans-isthmian land mammal exchange from Fig. 4. It is recognized that the correlation of the terrestrial mammals is less precise and thus less accurate than the MIS chronology. Still, the ages of the land mammal events were developed independently of any consideration of the MIS or sea level scales, so the apparent alignment of many of those events with strong MIS excursions or drops in sea level is at least compatible with the thesis of Webb (1991) that trans-isthmian dispersals that involved mammals having an affinity with savanna-like environments most likely transpired during times of Northern Hemisphere glaciations (Fig. 5). It is possible that at least some of the pre-GABI dispersals were aided by cooler, if not glacially-associated, conditions with respect to their impact on vegetation patterns.

The pattern in Fig. 7 suggests that, subject to strong departures in some cases, mean sea level fluctuated within a range of –10 to –40 m during the past 3.2 Ma, with an eventual drop toward the present. It appears that significant episodes of mean lowstand occurred at about 2.5, 1.9, 1.6, 0.7, and 0.1 Ma. The coincidence in timing between these ages and those of the dispersals shown on those figures is striking, even after the Isthmus of Panama is considered to have been closed. It is tempting to suggest that increased development of coastal plain settings during lowstand intervals contributed to the successful overland dispersals, in addition to general climatic influence. This is discussed further below.

## Plants and ecologies

Plant megafossils apparently are not well represented in Central America (and Mexico). Graham (1998) and a series of publications (Graham and Dilcher, 1998; Graham 1999, 2010; Burnham and Graham 1999) provided seminal studies and discussions regarding the Neogene pollen and spores from this region. Even though the records reported upon are derived from lowland swamps and comparable settings, the discussions also provide insight on the plant community composition at higher elevations. Central America is presently typified by its tropical rain forest (Fig. 5), but many plant communities of Miocene, Pliocene, and Pleistocene ages have different compositions, as discussed below. A major factor as regards GABI is the virtual absence of any fossil record of early Pleistocene floras. Therefore, the following begins with a Pliocene background for an interpretation of what was a likely floral

**Fig. 8** Location of Neogene floras of Central America. After Graham and Dilcher (1998: fig. 30).



Pliocene: **Paraje Solo** (1); *Herreria* (5), Rio Banano (6)  
 Mio-Pliocene: Artibonite (9), **Gatun** (7), **Padre Miguel** (4)  
 Mid Miocene: Ixtapa (2), Mendez (3)  
 Early Miocene: Cucaracha, Culebra, La Bocha (7), Uscari (8), La Quinta (3)  
**bold** = northern temperate elements; *italic* = no lowland temperate rainforest (also 1 and 4).  
 Sites affiliated with diverse topography are (1), (4) and (7, Gatun). Other sites record lowland/lignite associations.

and environmental scenario during the Pleistocene, discussed subsequently.

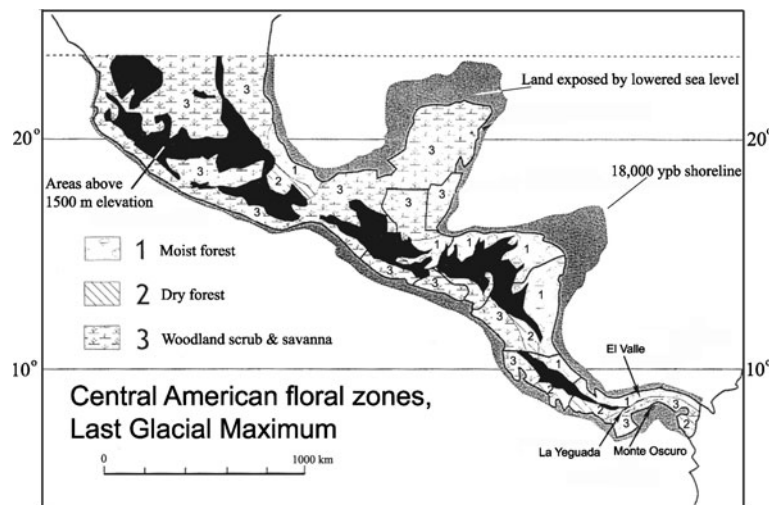
Graham and Dilcher (1998) surveyed a number of Neogene plant communities from Central America, and indicated that the region supported a tropical rain forest during the Miocene and into the Pliocene. These conditions began to change about in the Pliocene. The coastal Paraje Solo flora, SE Veracruz, Mexico (Fig. 8) shows evidence of at least local cooling (presence of *Picea*) and lowering of ecotones, perhaps due to the effects of local upwelling in the adjacent ocean (Graham 1973, 1976; Akers 1979). In any case the rainforest association was disrupted in this area at about 4–5 Ma (the palynoflora is associated with strata that yield Plantkic Foraminiferal Zone N19; chronology follows Lourens et al. 2004). Farther south, in inland Guatemala, the Padre Miguel flora at about 7 Ma contains a sedge marsh association with grasses and composites along with a pike-oak temperate forest (*Alfaroa-Oreomunnea*, *Juglans*, *Ulmus*) and possibly a cool-temperate forest (*Picea*, *Pinus*, *Quercus*) in upland settings. Another Guatemalan plant community in its southeastern coast, the Herreria flora, about 3.1 Ma (Fig. 8), reflects a mangrove setting and surrounding swampy conditions. Individually and collectively these plant communities contrast with the others shown on Fig. 8 in diverging from the otherwise typical lowland rainforest of the region, and suggest a distinct level of diversity. In that the region had achieved nearly its present elevation and topography by about this time, it is plausible that the current eastern moist versus a western drier distinction also was manifested, at least in the Panamanian district.

Another aspect of floral change is shown by the first occurrence of northern temperate elements in these Central

American settings. Graham and Dilcher (1998) indicated that the Paraje Solo flora (ca 4–5 Ma) records the appearance of *Abies*, *Picea*, *Pinus*, *Alnus*, *Celtis*, *Juglans*, *Liquidambar*, *Myrica*, *Populus*, *Quercus* and *Ulmus*, whereas the Padre Miguel flora, farther south and older (about 7 Ma), contains even earlier records of *Picea*, *Pinus*, *Juglans*, *Quercus*, and *Ulmus*. In fact, the approximately coeval Gatun flora of Panama records an even more distant record of *Ulmus*.

From these examples, it appears that the typical Neogene lowland tropical rainforest of Central America underwent certain degrees of alteration toward the end of the Miocene and possible cooling or drying as suggested by the incursion of temperate elements and potentially compatible with the late Pliocene land mammal dispersals discussed above. A more coherent pattern is shown at the nearly opposite end of the Neogene/Quaternary interval, as summarized by Piperno (2006), with inferences that this pattern also was manifested in earlier parts of the Pleistocene.

Currently, the Central American lowlands are humid areas. Figure 9, however, shows a reconstruction of the vegetation between 20,000 and 10,500 ybp, including the time of the Last Glacial Maximum (LGM; 18,000 ypb). By this time Central America had achieved its full tectonic uplift (Piperno 2006). Note especially on the Caribbean side the increased coastal area afforded by maximum lowering of sea level. Such then-exposed areas mostly lie adjacent to the thorn woodland, low scrub, and wooded savanna vegetation (type 3 on Fig. 9) but, also in Honduras and Nicaragua, adjacent to forests that were significantly drier than at present, but still moist enough to support that type of forest (type 1 on Fig. 9). These floral associations



**Fig. 9** Reconstruction of distribution of lowland Neotropical forest associations at the Last Glacial Maximum (18,000 ybp). After Piperno (2006: fig. 1). Gray areas indicate land exposed by lowered Pleistocene sea level during maximum glacial advance. Black areas are elevations above 1,500 m. 1. Largely unbroken moist forest, often with a mixture of present-day high-elevation and lowland forest elements. In some areas montane forest elements (*Podocarpus*, *Quercus*, *Alnus*, *Ilex*) were conspicuous. Annual precipitation less

than at present, but sufficient to support a forest. 2. Forest containing drier elements than typical of the present. High-elevation forest elements occur in moister areas of the zone. 3. Mostly undifferentiated thorn woodland, low scrub, and wooded savanna vegetation. Some regions (such as Guatemala) with temperate elements (*Juniperus*). Areas that presently receive >2000 mm annual rainfall may still have supported a drier forest, as in 2. River- and stream-side locations supported a forest.

reflected climates that were significantly drier and cooler than at present, with surface temperatures  $4^{\circ}\text{C}$ – $7^{\circ}\text{C}$  lower than now, and forest canopies possibly more open than at present due to lower levels of atmospheric  $\text{CO}_2$  (Piperno 2006). Rainfall was less, possibly by 30%–50%.

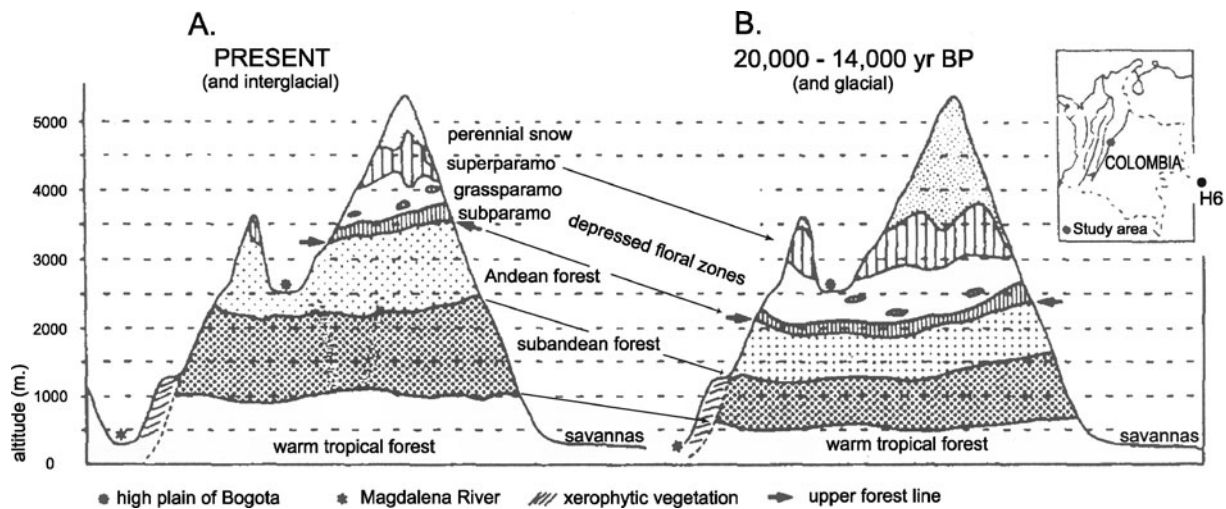
The general conditions shown on Fig. 9 persisted until about 10,500 yrs ago, which indicates that the modern lowland tropical forest of Central America did not develop until after that time (also Leyden 1984). Piperno (2006) noted that even today, the flora of western (Pacific) coastal Panama is a deciduous tropical forest living under fairly dry conditions, which, in the above late Pleistocene reconstruction, was the thorn woodland, low scrub, and wooded savanna association (type 3, Fig. 1), and consisted of many grasses, sedges, and herbaceous plants, along with the archetypal savanna indicator shrub or small tree, *Curatella americana*. The grasses (short and tall) used the  $\text{C}_4$  photosynthetic pathway, indicative of a dry and open landscape. Palms adapted to dry land habitats also were present. Modern deciduous trees were present only sparingly, likely along watercourses. Rainfall was reduced by 35%. Piperno (2006) suggested that much of the Panamanian land bridge at this time likely was a dry open habitat, but perhaps not exactly a savanna.

Middle-elevation Panamanian late Pleistocene sites (such as La Yeguada, El Valle, Fig. 9) then as now occur at 500–650 m. The Pleistocene vegetation was composed of a forest with trees that nowadays live at 1500 m, but at that time had descended downslope by 800–1200 m,

compatible with the dry climate indicated by enclosing sediments (illite clays), as compared to the present 3–4 m annual precipitation.

Piperno (2006) characterized the Pleistocene lowland Neotropical climate as being substantially drier and cooler than at present, as a result of a peculiar combination of low temperature, low precipitation, and low atmospheric  $\text{CO}_2$ . Areas having what is now arboreal forest vegetation supported herbaceous types instead. Some upland areas still would have been moist enough to support  $\text{C}_3$  plants, but in general drier-adapted  $\text{C}_4$  grasses prevailed. In situations where the present forest exists in high rainfall zones, the late Pleistocene flora was a savanna/thorny scrub association. The modern flora thus is not analogous to that of the late Pleistocene, and the latter flora contained associations of taxa not presently found together. Forest elements now found at elevations at or above 1500 m descended to much lower elevations (ca 800–1200 m) in the late Pleistocene.

Piperno (2006) noted that, on average, glacial periods last four to five times longer than interglacials, so during the past ca 2 m.y., plants and animals of Central America spent over 80% of their time in, and must have been adapted to, the above-summarized climatic conditions. The modern closed-canopy forests apparently represent those typical of the short-term interglacial floral associations, whereas those of the more prevalent glacial conditions are not like modern floras, and contain combinations of species not presently found together. In that sense, the glacial floras



**Fig. 10** Schematic representation of present-day **a** and last glacial **b** altitudinal distribution of the zonal vegetation belts in the Colombian Eastern Cordillera. After Andreissen et al. (1993: fig. 6). H6 in inset map=Hill of Six Lakes, Brazil (Bush et al. 2004).

are not analogous to those of the present. As indicated by Bush et al. (2004) for Brazil, the pre-modern Pleistocene floras there contain associations of elements not found together today, and also represent ‘non-analog’ forests. This appears to be comparable to the situation in Central America and, overall, the general patterns are similar. In this context it seems reasonable to project deeper into the early Pleistocene the environmental setting and composition of the late Pleistocene floras of the region, with implications for similar climatic conditions during those older times.

It thus appears that, at the very least, conditions amenable to the dispersal of non tropical-adapted land mammals must have predominated in the Pleistocene of Central America, as well as Amazonia (i.e., Andreissen et al. 1993; below). The increased area of at least dry and open, if not completely savanna-type, environments along coastal Central America during times of decreased sea level must have played a part in facilitating GABI dispersals across the region. Whereas the early Pleistocene record of the strong onset of cooler, glacial conditions seen at Bogotá, Colombia (Andreissen et al. 1993), is not yet recorded in Central America, the Colombian record validates the above proposed projection of late Pleistocene conditions into the earlier part of the epoch, which must have affected Central America, as well.

Andreissen et al. (1993) summarized the palynology and climatic implications of extensive cores drilled in the vicinity of Bogotá, Colombia (Fig. 10) at an elevation of about 2500 m. In contrast to the record in much of Amazonia, as well as Central America, the sequence in the cores, Funza I and Funza II, extends nearly continuously from the Pliocene through the Pleistocene, and records the climatic and tectonic conditions that were in

effect during that interval. Funza I core is 357 m deep, Funza II, 586 m deep.

The interval between 541 and 586 m in Funza II has few pollen grains, but in the interval between 465 and 540 m palynofloras show high arboreal percentages and a warmer climate than subsequent parts of the core. The open character of the Andean forest is indicated by high percentages of arboreal taxa (*Ilex*, *Rapanea*, *Myrica*, *Eugenia*, plus the shrub *Borreria*, and high maxima of Graminae).

At 465 m in Funza II (and 357 m in Funza I) pollen indicate that conditions became much colder, and the Bogotá basin became alternately covered with Andean forest and open paramo (basically high country tundra) vegetation. The age of this level is estimated at 2.7 Ma, near an ash at horizon 506 m dated at  $2.7 \pm 0.63$  Ma. The climatic conditions recorded here represent the beginning of global glacial influence in this part of Colombia, and was accompanied by the onset of mountain glaciation around Bogotá. Interestingly, the onset of glaciation here fits well with the later part of NHG and onset of GABI I, as discussed above.

The interval between 320 and 357 m (Funza I) or 320–465 m (Funza II) yields alternate indications of cold and warm climates considered to reflect major pulses of glaciation in the vicinity of Bogotá. At 233 m in both Funza cores, the palynofloral record indicates that climatic oscillations became longer and of greater amplitude. The upper 233 m in these cores is interpreted as reflecting ten major climatic cycles, apparently beginning with MIS 23 at about 0.9 Ma (Lisecki and Raymo 2005) and extending to MIS 3 at about 0.05 Ma (50 ka). During these cold episodes, the forest line shifted between about 3400 and 1800 m (arrows on Fig. 10), to follow a decrease of mean annual temperature from  $15^{\circ}\text{C}$  to about  $6^{\circ}\text{C}$ .

Based on the taxonomy of the units, Andreissen et al. (1993) arranged the succession into biozones. In Biozone I, which ranges in age from about 5.0 Ma to about 4.2 Ma, the plant community consists of lower elevation tropical vegetation. *Hedyosmum*, a northern taxon, dispersed into the region at this time.

Biozone II ranges in age from about 4.2 Ma to 3.2 Ma, and reflects the presence of tropical to sub-Andean vegetation at relatively low elevations. The floras previously characteristic of the lowlands were replaced by those from intermediate altitudes. Floras indicate a lower tropical to lower sub-Andean forest belt, between ca 1,000 and 1,500 m, as at present (Fig. 10a). *Hedyosmum* is present, but *Myrica* still absent.

Biozone III, of 3.2–2.5 Ma is represented by an upper sub-Andean vegetation, and continues to reflect communities characteristic of intermediate altitudes. *Myrica* disperses into the region. Note that, as discussed above, the Paraje Solo flora (ca 4–5 Ma) of Mexico contains the first record of *Myrica* in Central America (also as summarized in Graham 1999).

Biozone IV ranges from about 2.5 Ma to 1.2 Ma. In the lower part, plants of Andean type predominate, but in the upper part of the section these alternate with paramo vegetation, and show a consistently high representation of *Borreria*. The Biozone IV flora is of high-altitude type, and its upper part begins to show the alternating vegetation types reflective of cool and warmer climates and Pleistocene glaciations.

Biozones V–VII range from 1.2 Ma to 0.2 Ma, and contain vegetation that alternates between cool and warm climates considered to be related to major Quaternary climatic changes. *Alnus* disperses at beginning of biozone VI, *Quercus* at beginning of biozone VII. Biozone V begins at about 1.2 Ma, Biozone VI at ca 0.8 Ma, and Biozone VII at about 0.2 Ma. Note that the Padre Miguel flora of Guatemala contains the first Central American record of *Quercus* at about 7 Ma (discussed above).

Tectonic activity in the region is related to Andean uplift (Andreissen et al. 1993). The sediments associated with Biozone I reflect ongoing uplift, and the presence of tropical lowland forests with extensive stands of *Mauritia*. Biozone II reflects the final Andean uplift in this region.

As indicated above, *Myrica* dispersed into the region in Biozone III, prior to Pleistocene glaciations, but *Alnus* still is absent. The associated plants reflect an upper sub-Andean forest, which would have a modern elevation of about 2,200 m (Fig. 10a). By the early part of Biozone IV (ca 2.5–1.8 Ma), the Bogotá area (black dot in valley, Fig. 10a, b) supported an Andean forest belt that would occur at a modern elevation of about 2,600 m (Fig. 10a). Beginning with the later part of Biozone IV and on into biozones V–VII, the Pleistocene changes in climatic

conditions resulted in downward altitudinal shifts of vegetation belts along the Cordillera. Paramo vegetation dominated during glacial conditions in the Bogotá district. As at present (Fig. 10a), Andean forests returned to this area during interglacial intervals. Mountain glaciers were present in the glacial times. *Quercus* entered the record in Biozone VII, likely at 200,000 yrs.

In summary, the Colombian succession records the presence of an open Andean forest that lived under a warm climate at the elevation of Bogotá in the late Pliocene. In the Pleistocene the situation changed markedly in which plants of high-altitude character descended several hundred kilometers to co-exist with lowland elements under much cooler conditions, with mean annual temperatures near 6°C in contrast to the current 14°C. The cool versus warmer pattern is manifested throughout the Pleistocene in these cores and provides empirical demonstration of the older, as well as late, Pleistocene age of such changes. The Colombian record gives credence to the above supposition that late Pleistocene floral configurations in Central America may be projected into earlier times.

Bush et al. (2004) reported on a pollen succession derived from cores drilled in the Hill of Six Lakes district at an elevation of about 300 m in the Amazon Plain of northwestern Brazil (H6 on inset map of Fig. 10). The site thus represents conditions that occurred at lowland settings in this part of Amazonia. A record developed from three drilled cores extends to about 140,000 yrs and records at least two major glacial cycles.

The results indicate the Hill of Six Lakes region supported a mesic lowland forest that became infiltrated with montane elements during the last two glacial cycles, as a result of major climatic cooling. The arrival and departure of these montane elements occurred in the context of a stable backdrop of a lowland forest. The pollen in the cores indicate that upland elements descended into the lowland environment, with the amount of descent being 800–900 m relative to the modern upland setting. The development of these glacially-timed non-analog mixed lowland and montane communities was in response to the periodic cooling of mean annual temperatures by 5–6 °C. It appears that the indigenous lowland flora was able to withstand the temperature changes that drove the montane taxa to lower elevations.

From the examples cited here, it appears that Pleistocene cooling from Central America to Amazonia was on the order of 9°C to 6°C, respectively, and was the greatest cause of environmental and floral change, regardless of the potential effects of diminished levels of CO<sub>2</sub> or rainfall. The effect in Brazil was to periodically lower the elevation at which montane forests existed into those areas where lowland mesic forests already were present, and which remained under the new circumstances. This pattern, over



the past 140,000 yrs in the Hill of Six Lakes, Brazil, is comparable to that seen in the temporally more extensive record in the Bogotá plain of Colombia (Andreissen et al. 1993). If these comparisons are used as a model, it suggests that the late Pleistocene floral configurations reconstructed in Central America by Piperno (2006) also can be extended to glacial conditions earlier in the Pleistocene of that region.

An interesting aspect of Fig. 10 is the location of savanna floras in the low, coastal regions of Colombia, comparable to their setting in Central America (Fig. 9). Floral changes in Central America include the emergence of a broader coastal region at times of lowered sea level that nominally would be expected to support savanna-like ecologies, based on those that are reconstructed as lying adjacent to the coast at that time. Graham and Dilcher (1998) consider it unlikely that any given floral association formed a through-going avenue across the whole of Central America during the Pleistocene. Still, it appears that an expanded coastal environment during the 80% of the Pleistocene occupied by glacial conditions would have supplied at least one of the avenues in support of GABI dispersals.

### Holding pens and dispersal times

Flynn et al. (2005) demonstrated numerous cases in which taxa considered to be part of the GABI phenomenon occurred earlier in Guanajuato, Mexico, than in the United States, and Woodburne et al. (2006) reviewed this in the context of other instances that demonstrate or suggest the strong role played by the Mexican-Central American region as a center of cladogenesis for diverse mammalian groups in the Neogene. In the present report, the holding-pen aspect of this situation has been emphasized. The pattern mostly involves various xenarthrans moving northward, and results in an apparent embargo on border crossing that lasted as long as 1.7 m.y. (*Glossotherium*) to 1.3 m.y. (*Pampatherium*) and 1.1 m.y. (*Glyptotherium*). It may turn out that *Nechoerus* entered South America at about 1.8 Ma, well after its earlier presence in Central America is suggested by a 3.8 Ma record in Mexico and South Carolina. Examples of this order of magnitude, for which there is no obvious physical, geologic, or biologic cause, raise the question of the fidelity of the paleontological record, also voiced by Verzi and Montalvo (2008), as to the actual age of dispersals when found at their eventual endpoints (see also Dispersal Lag; Woodburne and Swisher 1995). In this regard it is encouraging that the Neogene fossil mammal record for Central America is improving (Cisneros 2008; Lucas 2008; Lucas et al. 2008), which may further aid in addressing the question of the times when mammals actually transgressed the Panamanian Isthmus.

Campbell et al. (2000, 2001, 2010) have described gomphotheriid fossils identified as *Amahuacatherium peruvianum* from deposits in the Cerro Colorado region of Peru, and have discussed stratigraphic, radioisotopic and paleomagnetic data that collectively form the basis for assigning an age of somewhat greater than 9 Ma to these remains. If accurate, this would place the entry of gomphotheriid proboscideans in South America substantially earlier than their currently understood record of about 1.8 Ma (above). In those papers Campbell et al. also assert that at least one species of peccary and a camel co-occur with *Amahuacatherium*, in which case that would also pre-date significantly the otherwise known first occurrences of these taxa in South America, 3.7 and 3.4 Ma, respectively.

The above hypotheses include a geological perspective that favors a fairly simple and regionally more or less uniform Neogene stratigraphy of western Amazonia. That proposal is challenged to a large degree by papers of Latrubesse et al. (2007, 2010) that address evidence suggesting a more complicated, terrace complex series of stratigraphic relations for Neogene deposits across western Amazonia. It is possible that the beds that overlie *Amahuacatherium* at Cerro Colorado are not as old as conventionally thought, which also might elevate the age of *Amahuacatherium*, itself.

Whereas the a number of the diverse demonstrations and interpretations presented by Campbell et al. (2000, 2001, 2010) have merit, it still is not clear how a proposed 9+ Ma record of gomphotheriids, peccaries, and camels in Peru can be reconciled with their essential absence for 6+ m.y. in the fossil mammal record of all of South America. The *Amahuacatherium* situation remains unresolved.

### Summary

Whereas closure of the Central American Seaway at about 2.8 Ma set the stage for major episodes of trans-isthmian land mammal exchanges, the well-known intervals of prior dispersals are compatible with the dynamic tectonic activity that affected the region from at least 9 Ma. Apparently those dispersals took place under generally tropical conditions in Central America, but the climate potentially was modified somewhat just before and after the Pliocene Climatic Optimum (3.25–3.05 Ma) and perhaps at about 6.0 Ma, as well, when nominally savanna-adapted taxa dispersed southward (3.7 Ma, Tayassuidae; 3.3 Ma, Camelidae).

The first significant episode of faunal exchange is recognized as GABI 1 (2.6–2.4 Ma) concurrent with the initiation of major Northern Hemisphere glaciation. Then, as well as earlier and later, most northward-moving taxa were xenarthrans, with hydrochoerid and porcupine rodents being another conspicuous contingent. Eventually (GABI 2)

more taxa dispersed southward than the reverse, but up to about 1.8 Ma, the average count for either direction was about equal. In all cases the southward contingent was phylogenetically more diverse and tended to include taxa of clear savanna-like ecologies. On the other hand, the northward dispersants typically included forms that exhibited a wide range of ecological diversity (xenarthrans, porcupines, and, in GABI 3, opossums). GABI 3 represents a relatively minor episode, but is so identified on the basis of involving at least four genera in a bi-polar pattern. GABI 4, at nearly the end of the Pleistocene, shows a singularly one-way, and quite diverse, southward dispersal.

It seems that the four GABI episodes correspond at least generally to times of sea level lowering and it is tempting to suggest that expanded coastal regions contributed to dispersal in addition to a role played by climatic cooling during glacial episodes with concomitant floral changes in Central and northern South America.

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