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VERTEBRATE PALEONTOLOGY IN CENTRAL AMERICA: 30 YEARS OF PROGRESS

PALEONTOLOGÍA DE VERTEBRADOS EN AMÉRICA CENTRAL: 30 AÑOS DE PROGRESO

Spencer G. Lucas

New Mexico Museum of Natural History and Science, 1801 Mountain Road N. W., Albuquerque, New Mexico 87104 USA
spencer.lucas@state.nm.us

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ABSTRACT: Vertebrate paleontology began in Central America in 1858 with the first published records, but the last 30 years have seen remarkable advances. These advances range from new localities, to new taxa to new analyses of diverse data. Central American vertebrate fossils represent all of the major taxonomic groups of vertebrates—fishes, amphibians, reptiles (especially turtles), birds and mammals (mostly xenarthrans, carnivores and ungulates)—but coverage is very uneven, with many groups (especially small vertebrates) poorly represented. The vertebrate fossils of Central America have long played an important role in understanding the great American biotic interchange. New data and analyses identify a Miocene Central American peninsula that extended from Guatemala to Panama, and suggest the possibility of a Central American province of vertebrate endemism and evolution. The Central American record of vertebrate fossils needs augmentation, especially of microvertebrate fossils, and a more detailed chronological framework to enhance our current understanding of vertebrate evolution and biogeography in the New World.
Keywords: Central America, vertebrate paleontology, great American biotic interchange, Central American peninsula, Central American province.

RESUMEN: La paleontología de vertebrados inició en América Central en 1858 con los primeros registros publicados; sin embargo, en los últimos 30 años se han visto avances notables. Estos avances varían desde nuevas localidades, nuevos taxones, a nuevos análisis de datos diversos. Los fósiles de vertebrados de América Central representan todos los grupos taxonómicos principales de vertebrados—peces, anfibios, reptiles (tortugas en particular), aves y mamíferos (mayormente xenartros, carnívoros y ungulados)—pero la cobertura es muy irregular con muchos grupos (especialmente los vertebrados pequeños) pobremente representados. Los fósiles de vertebrados de América Central han jugado un papel importante en la comprensión del gran intercambio biótico americano. Nuevos datos y análisis identifican una

península Mioceno Centroamericano que se extendía desde Guatemala a Panamá y sugieren la posibilidad de una provincia Centroamericana de endemismo de vertebrados y evolución. El registro centroamerico de fósiles de vertebrados requiere aumento, especialmente de los fósiles microvertebrados, así como un marco cronológico más detallado para mejorar nuestra comprensión actual de la evolución de los vertebrados y biogeografía en el Nuevo Mundo.
Palabras clave: América Central, paleontología de vertebrados, gran intercambio biótico américano, Península de América Central, provincia centroamericana.

INTRODUCTION

Vertebrate paleontology began in Central America in 1858, with the first scientific report of vertebrate fossils from Honduras (Lucas et al., 2011). The next 130 years witnessed the discovery and study of fossil vertebrates from all of the countries of Central America (Fig. 1), most of it in a very haphazard and unsystematic way. This record of fossil vertebrates is concentrated in sedimentary rocks of late Cenozoic (Miocene-Pleistocene) age. Perhaps Webb (1985), who masterfully reviewed the "great American interchange" (migration of vertebrates between North and South America after closure of the Panamanian isthmus), best summarized most of what we had learned 30 years ago from this fossil record by identifying Central America as a pathway for vertebrate dispersal during the late Cenozoic, but not an important center of vertebrate evolution. Nevertheless, much has been learned since Webb's article, and the last 30 years of vertebrate paleontology in Central America have continued to unearth an important fossil record that has great bearing on questions of vertebrate evolution and biogeography in the New World.

HISTORICAL PERSPECTIVE

I divide the history of vertebrate paleontology in Central America into three phases: earliest discoveries (1858-1930), a developing record (1930-1980) and a vertebrate paleontological renaissance of discovery and study (1980-present).

Earliest discoveries

During the 1800s, fossil vertebrates were discovered in Honduras, Nicaragua and Panama and published on by LeConte (1858), Squier (1858), Leidy (1859, 1870, 1886) and Blake (1862), among others. In the early 1900s, they were discovered in Costa Rica (Alfaro, 1911; Alvarado, 1986, 1989, 1994). Discoveries in Guatemala, El Salvador and Belize came later (Osborn, 1929; Ibarra, 1980; Czaplewski et al., 2003; Cisneros, 2008). The early discoveries were made mostly by travelers, military men or naturalists who shipped their fossils to the United States, where North American paleontologists studied them and published the results. This produced a spotty record of (mostly) Pleistocene large mammals that drew little interest from vertebrate paleontologists.

A developing record

The record of Central American fossil vertebrates advanced greatly during the 20th Century. This is largely because a few geologists and paleontologists decided to search in Central America for vertebrate fossils to develop a better record. And, interest in the late Cenozoic interchange of vertebrates between North and South America identified the Central American vertebrate fossil record as biogeographically significant.

Furthermore, in 1930, a turning point in the history of Central American vertebrate paleontology appeared in the form of Alfonso Segura Paragua (1913-2003) (Fig. 2), the first native

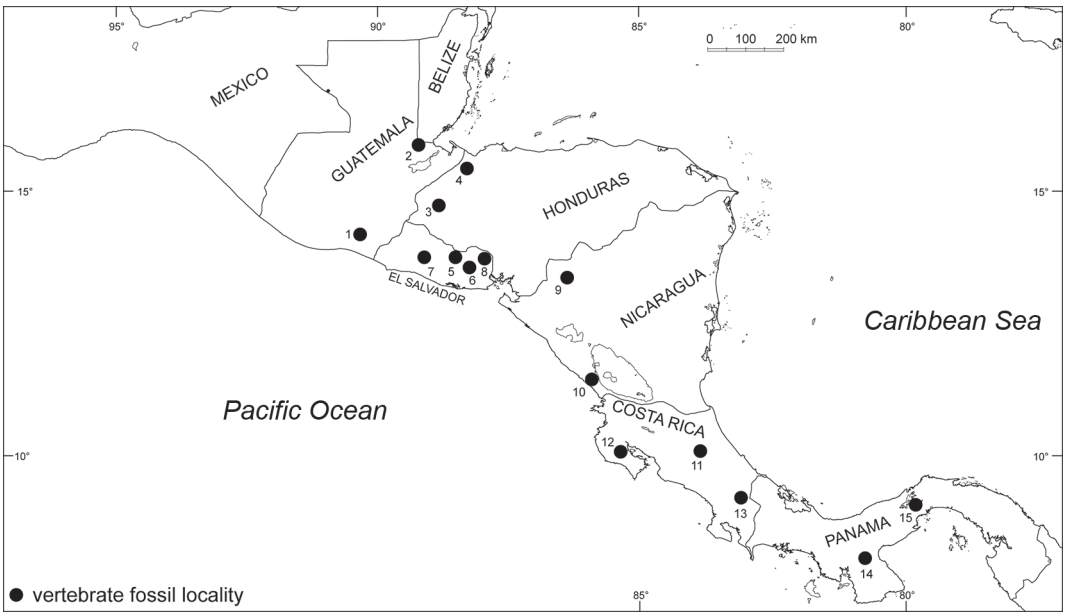

Fig. 1: Map of Central Ameriac showing some principal vertebrate fossil localities. Loclities are: 1 = Estanzuela (Pleistocene), 2 = Rio Carboneras (Miocene), 3 = Gracias (Miocene), 4 = Yeroconte (Pleistocene), 5 = Barranca del Sisimico (Pleistocene), 6 = El Hormiguero (Pleistocene), 7 = Tomayate (Pleistocene), 8 = Corinto (Miocene), 9 =El Bosque (Pleistocene), 10 = El Palmar (Pleistocene), 11 = Bajo Barrantes (Pleistocene), 12 = Peninsula de Nicoya (Pleistocene), 13 = San Gerardo de Limoncito (Miocene), 14 = Azuero Peninsula (Pleistocene), 15 = Canal Zone (Miocene).

Costa Rican geologist and Central America's first native vertebrate paleontologist (Alvarado, 1989, 1994). Segura actually spent time in the United States working at the Smithsonian Institution in Washington, D. C., and this included collecting vertebrate fossils with Smithsonian vertebrate paleontology curator Charles W. Gilmore (1874-1945). Segura described various Costa Rican vertebrate fossils, including important discoveries on the Nicoya Peninsula and the Bajo Barrantes locality, one of the most diverse vertebrate fossil sites in Central America and still the subject of ongoing research (Segura, 1938, 1941, 1942, 1944, 1963) (Fig. 1).

The other countries of Central America, however, relied on foreign (mostly North American) expertise in vertebrate paleontology. Thus, Stirton and Gealey (1949) presented the first attempt to summarize the vertebrate paleontology of an entire Central American country (El Salvador), including the first report on the important locality of El Hormiguero (Fig. 1).

The rich patron of vertebrate paleontology of the American Museum of Natural History (AMNH) in New York, Childs Frick (1883-1965), sent AMNH fossil collector John Blick to Honduras in 1929, and he discovered Miocene mammals, including gomphothere proboscidean fossils near Tapasunas (Frick, 1933).

Both a 1937-1938 paleontological expedition of the University of Chicago (USA) and a later expedition of the Field Museum of Natural History (also Chicago, USA) in 1941-42 collected vertebrate fossils in Honduras (Olson and McGrew, 1941; McGrew, 1942; Lucas, 2008). Their collections from the Gracias Formation of late Miocene (Hemphillian) age produced what was long Central America's most diverse Miocene vertebrate fauna (Fig. 1).

In 1950-1951, a Smithsonian expedition lead by vertebrate paleontology curator Charles Gazin (1904-1996) collected giant ground sloths (*Eremotherium*) and other late Pleistocene mammals in the Azuero Peninsula of Panama (Gazin, 1957; Anonymous, 1958; Lucas, 2014). In 1962, Smithsonian vertebrate paleontologist Frank Whitmore (1917-2012) also collected Miocene vertebrate fossils in the Panama Canal Zone (Whitmore and Stewart, 1965; MacFadden, 2006).

In the late 1960s and 1970s, David Webb (Florida State Museum) and Steven Perrigo (U. S. Peace Corps) collected Miocene and Pleistocene fossil vertebrates in El Salvador and Honduras (Webb, 1976; Webb and Perrigo, 1984, 1985). Thus, by the 1980s, a diverse record of fossil vertebrates was known from Central America, especially from Honduras, El Salvador, Costa Rica and Panama.

Fig. 2: Alfonso Segura Paragua (1913-2003), Costa Rica's first geologist and Central America's first vertebrate paleontologist. Photograph courtesy of Guillermo Alvarado.

A vertebrate paleontological rennassiance

During the last 30-35 years, we have learned much more about the vertebrate paleontology of Central America than was learned in the preceding century. Indeed, most of what we know about the Central American record of fossil vertebrates has been published during the last 30 years. These advances range from new localities to new taxa to new analyses of diverse data. Particularly significant have been up-to-date reviews of the vertebrate paleontology of various countries, including El Salvador, Nicaragua and Costa Rica (Lucas et al., 1997, 2007, 2008; Cisneros, 2008).

This advance owes much to local geologists and vertebrate paleontologists working in Costa Rica (Guillermo Alvarado, Cesar Laurito, Ana Valerio) and El Salvador (Juan Carlos Cisneros) as well as to continued efforts by various North American paleontologists, especially in Guatemala (e.g., Mead et al., 2012) and Nicaragua (Lucas et al., 2008), and the ongoing efforts of a University of Florida lead team working in Panama (e.g., Pimiento et al., 2010, 2013; Uhen et al., 2011; Cadena et al., 2012; Rincon et al., 2013). Currently, our knowledge of the vertebrate fossil record of Central America is growing at a rapid rate.

CENTRAL AMERICA'S FOSSIL VERTEBRATES

Fishes

A few records of fossils of freshwater bony fishes are available from Central America, such as from the Miocene Gracias Formation in Honduras and the Pleistocene of El Salvador and Costa Rica (Webb and Perigo, 1984; Alvarado, 1994). However, the Central American record of fossil fishes is mostly of selachians—sharks and their allies. These marine cartilaginous fishes (Chondrichthyes) are best known from the Miocene of Costa Rica and Panama (e. g., Gillette,

1984; Laurito, 1999; Laurito and Valerio, 2008a; Pimiento et al., 2010, 2013). These ichthyofaunas are from Caribbean coastal regions and are assemblages of mixed biogeographic affinity—Pacific and Caribbean—that accumulated prior to closure of the Central American seaway.

Amphibians, reptiles and birds

Fossils amphibians, reptiles and birds are little documented and relatively little studied from Central America, though recent work is changing that. There are very few amphibian records, such as that of a frog (*Rana*) from the Miocene of Honduras (Webbb and Perrigo, 1984). Turtles are best known, with a particularly interesting turtle in the guise of *Geochelone costarricensis* from the "Oligo-Miocene" or "Eocene" of Peralta de Limón in Costa Rica (Fig. 3). Segura (1944) first described this tortoise, which is considered an early immigrant from North America (Auffenberg, 1971; Coto and Acuña, 1986). Various other fossil turtle records from Central America include Miocene records of *Rhinoclemmys* and *Geochelone* from Honduras, *Apalone* and others from the Miocene of Costa Rica and Pleistocene *Rhinoclemmys*, *Hesperotestudo* (=*Geochelone*), *Kinosternon* and emydids from El Salvador (e. g., Webb and Perrigo, 1984; Acuña-Mesén and Laurito-Mora, 1996; Laurito et al., 2005; Cisneros, 2005). Panama has recently yielded a late Eocene-Miocene turtle record dominated by taxa with North American affinities (Cadena et al., 2012).

Miocene and/or Pleistocene records of *Crocodylus* are documented from Guatemala, El Salvador and Costa Rica (Mook, 1959; Mead et al., 2006). *Gavialosuchus* has also been reported from the Miocene of Costa Rica (Laurito and Valerio, 2008b). Recently named new taxa of crocodylians from Panama, *Culebrasuchus* and *Centenariosuchus*, are early caimanines of South American affinity that evidently crossed seawater to reach Panama (Hastings et al., 2013).

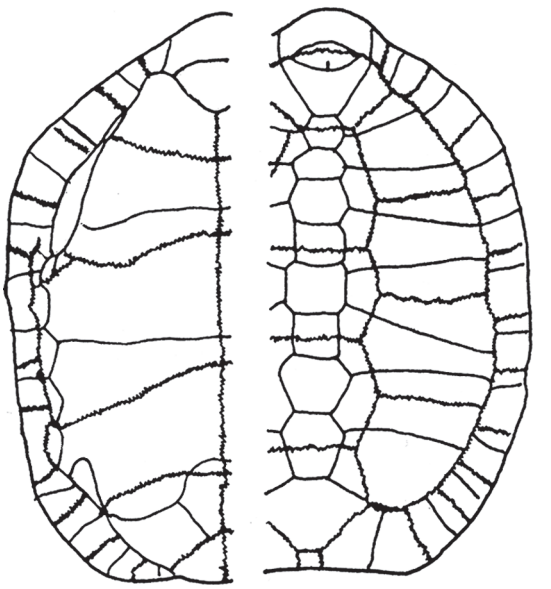

Fig. 3: Outline drawing of the shell (plastron on left, carapace on right) of Geochelone costarricensis (after Coto and Acuña, 1986).

Central America's only dinosaur fossil was discovered in 1971 and published by Horne (1994). This is an ornithopod femur (Fig. 4), likely of a hadrosaur, from the lower red beds (Cretaceous, probably Cenomanian) of the Valle de Angeles Group in Honduras (Horne et al., 1990). The locality has been interpreted as part of a suspect terrane that was close to southwestern Mexico during the Cretaceous (Horne et al., 1990), which makes paleobiogeographic sense, as the dinosaur has North American affinities.

Very few fossil birds have been reported from Central America. The few records are mostly of Pleistocene ducks (e.g., Gazin, 1957; Cisneros, 2005, 2011).

Mammals

Most of Central America's vertebrate fossils are of mammals, and they have received the most intense study. Edentates are the most diverse group and are armadillos, glyptodonts and an array of sloths. These are all taxa of South American

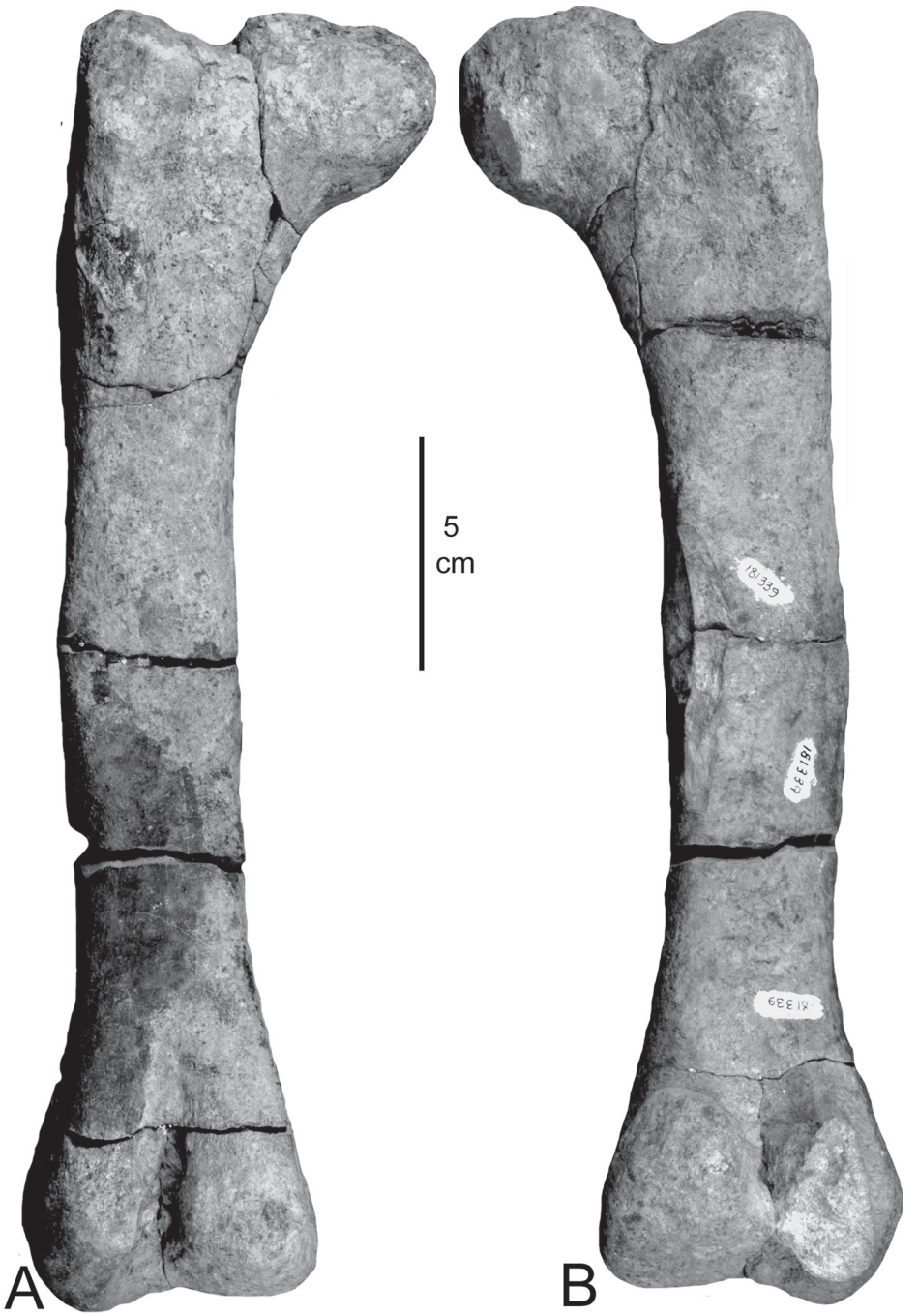

Fig. 4: Right femur of a Cretaceous ornithopod dinosaur from Honduras in anterior (A) and posterior (B) views. Specimen is in the National Museum of Natural History, Smithsonian Institution, Washington, D. C., USA, catalogued as USNM 181339. Photographs courtesy of Michael Brett-Surman.

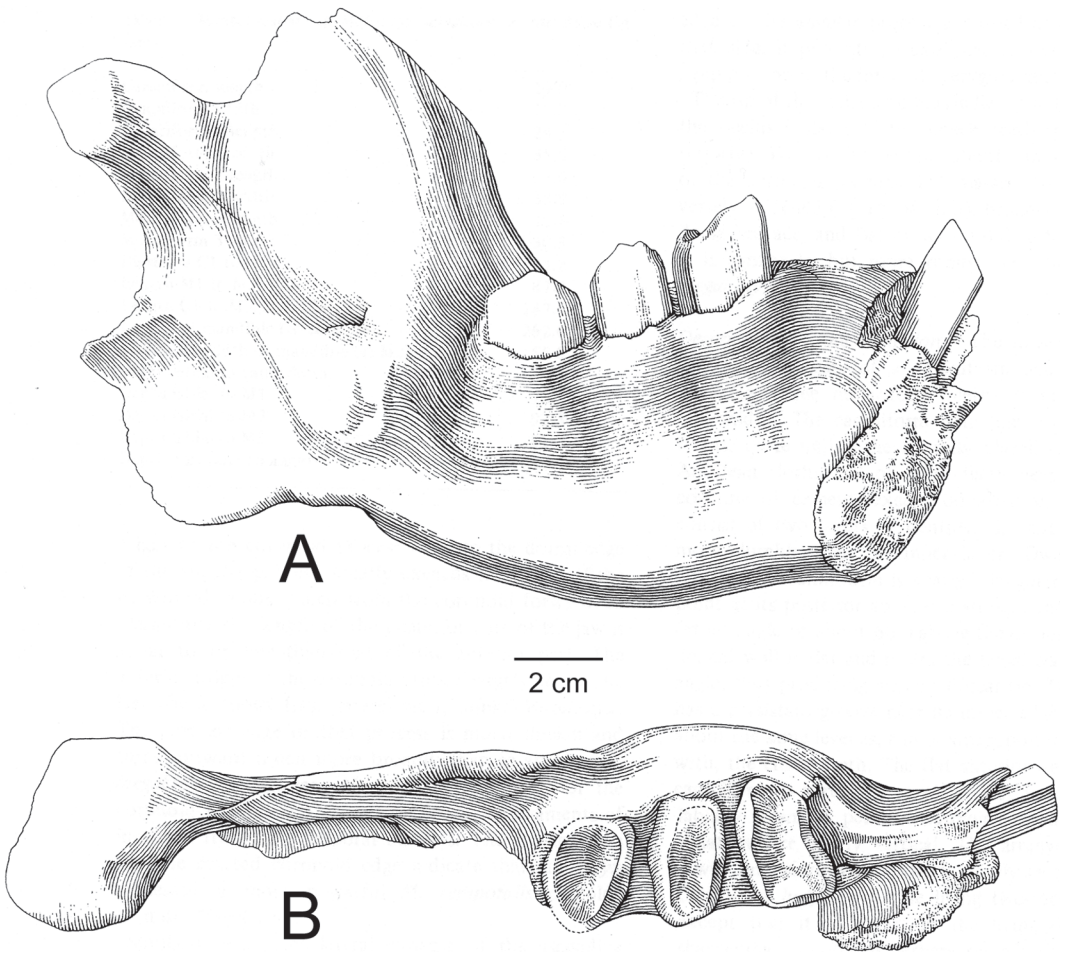

Fig. 5: Holotype left dentary of Meizonyx salvadorensis, a ground sloth endemic to the Pleistocene of El Salvador, in medial (A) and occlusal (B) views. After Webb and Perrigo (1985).

origin, and include both giant ground sloths (megalonychids and megatheriids) plus smaller mylodontid ground sloths. Two ground sloth taxa named from the Pleistocene of the Barranca del Sisimico in El Salvador are endemic to Central America (Webb and Perrigo, 1985) (Fig. 5).

Small mammals are greatly under-represented in the Central American vertebrate fossil record, primarily due to collecting bias. Among rodents, only the relatively large capybaras (Hydrochoeridae) are well known, and rabbit (lagomorph) records are sparse. Only a few fossil bats have been reported (Webb and Perrigo, 1984; Czaplewski et al., 2003).

Fossil carnivores from Central America are all taxa of North American origin. These are mostly cats, saber-tooths, dogs, bears and raccoons. They are found in both Miocene and Pleistocene assemblages but are neither particularly diverse or abundant as fossils (e.g. Olson and McGrew, 1941; Webb and Perrigo, 1984; MacFadden, 1986; Cisneros, 2005, 2011). One

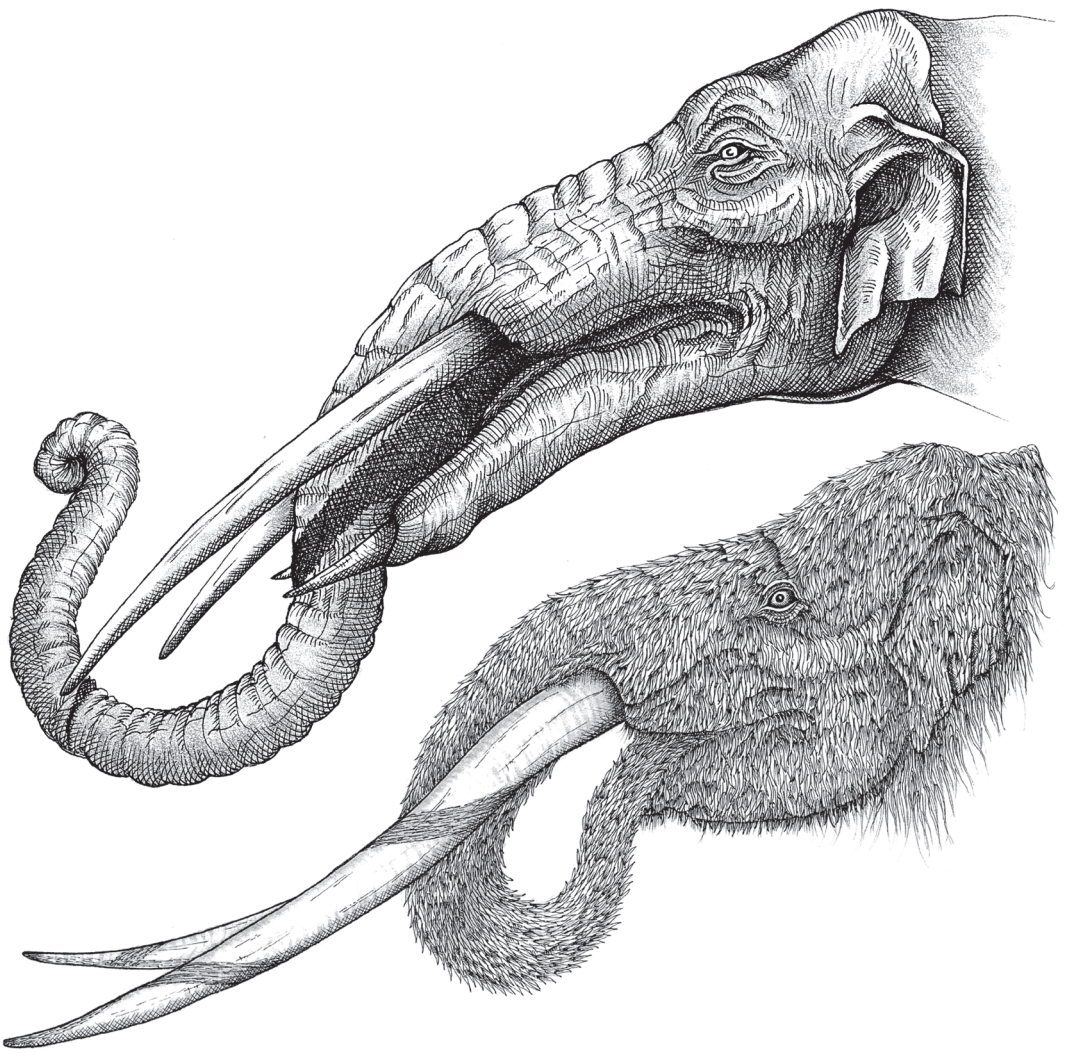

Fig. 6: Restoration of the heads of two Central American gomphotheres, Gomphotherium (above) and Cuvieronius (below). Artwork by Pedro Toledo.

interesting record is of the coyote *Canis latrans*, from Costa Rica, the southernmost Pleistocene record of a coyote (Lucas et al., 1997).

Ungulate mammals known from Central American fossils are notoungulates, proboscideans, perissodactyls and artiodactyls. Only the notoungulates are of South American origin and mostly pertain to a single genus *Mixotoxodon*, which looks like it was endemic to northern South America and Central America (between latitudes 15oS and 18oN) (e.g., Van Frank, 1957; Laurito, 1993; Lucas et al., 1997, 2007; Rincón, 2011).

The proboscidean fossils of Central America represent three distinct groups of North American origin (Lucas and Alvarado, 2010a, b). Oldest are the gomphotheres, which arrived in Central America about 10 Ma in the form of *Gomphotherium* (Fig. 6). Its descendant, *Cuvieronius* (Fig. 6), arose in North America and arrived in Central America about 3 Ma, and then travelled on to Argentina and Chile (Lucas, 2013). There is a single record of the American mastodon, *Mammut americanum*, in Honduras, a late Pleistocene arrival from the North (Lucas and

Alvarado, 1991). Mammoths, early Pleistocene arrivals, are found in most of the Central American countries and attest to the presence of some savanna grasslands in the rainshadows of the volcanoes (Cisneros, 2005; Lucas et al., 2008; Lucas and Alvarado, 2010a).

Central American fossil perissodactyls are a few records of tapirs and rhinoceroses and many more of horses. The rhinos are aceratheres from the Miocene of Honduras and Panama. The horses range from Miocene hipparionines to Pleistocene records of "true horses" (*Equus*). Particularly significant has been recent description of an extensive assemblage of fossil horses from the late Miocene (Hemphillian) of Costa Rica (Laurito and Valerio, 2010). Also note that *Pliohippus hondurensis* from the Miocene of Honduras is a species endemic to Central America.

Artiodactyls known from Central American fossils are oreodonts, anthracotheres, peccaries, camels, gelocids, deer and bison. These are split between Miocene and Pleistocene records but are not particularly abundant or diverse at any locality (e.g., Webb and Perrigo, 1984; Lucas et al., 1997, 2008; Cisneros, 2005, 2008; Rincon et al., 2013; Lucas, 2014). Perhaps most interesting are fossil records of *Bison*, which in North America indicates the beginning of Rancholabrean time (~ 250 kyr), so its Central American records are thought to be younger than that datum. Bison footprints at the famous human footprint site at Acahualinca in Nicaragua may be as young as 2100 years BP (Lockley et al., 2007, 2008, 2009; Schminke et al., 2009), and together with archaeological/ethnological evidence suggest a much later survival of Bison in Central America than many have posited, as young as 150 A.D. (Alvarado et al., 2008).

Marine mammals live today in the Caribbean and Pacific basins, and must have lived in the seaways that covered Central America during parts of its Cenozoic history. Yet, only recently have fossils of marine mammals been reported from Central America, notably a baleen whale (balenopterid mysticete) from the Pliocene of Nicaragua, a toothed whale (squalodontid odontocete) from the Miocene of Costa Rica and cetacean and sirenian fossils from the Panamanian Miocene (Lucas et al., 2009; Laurito et al, 2011; Uhen et al., 2011).

CHRONOLOGY AND CORRELATION

One of the great challenges to vertebrate paleontology in Central America is to place the fossil vertebrate localities in a precise temporal framework. At a coarse scale of resolution, many can be assigned to North American land-mammal "ages," which generally resolve their age within a couple of million years or less (Fig. 7). Thus, localities of Hemingfordian/Barstovian, Hemphillian, Irvingtonian and Rancholabrean age are well known in Central America (Fig. 8). However, greater temporal precision is needed, particularly for the vast majority of so-called "Pleistocene" sites. This precision can be achieved not just with more detailed biostratigraphy, but also with the help of radioisotopic ages and magnetostratigraphy, where applicable. This is one of the real frontiers of Central American vertebrate paleontology, one that when fully crossed will greatly enhance our understanding of what the Central American vertebrate fossil record has to teach us about vertebrate evolution.

PALEOBIOGEOGRAPHY

Central America's role in land-vertebrate dispersal between North and South America has been discussed at length. Simpson (1965) well represented the first synthesis--in stabilist terms he saw Central America as a land bridge or island chain rising and falling at various times during the Cenozoic. Simpson envisioned three vertebrate migrations across Central America: Late Cretaceous/Paleocene, Eocene/Oligocene and Pliocene-Recent.

However, in the light of plate tectonic reconstructions (e.g., Pindell and Kennan, 2009), we can say with some certainty that Central America played little or no role in the two oldest disperals—Late Cretaceous/Paleocene and Eocene/Oligocene—because of its isolation as an island arc. The most likely north-south pathway for land vertebrate dispersal at those times was across an Antillean arc that connected the southeastern United States to Venezuela (e. g., Alvarado, 1994; Lucas and Alvarado, 1994). The

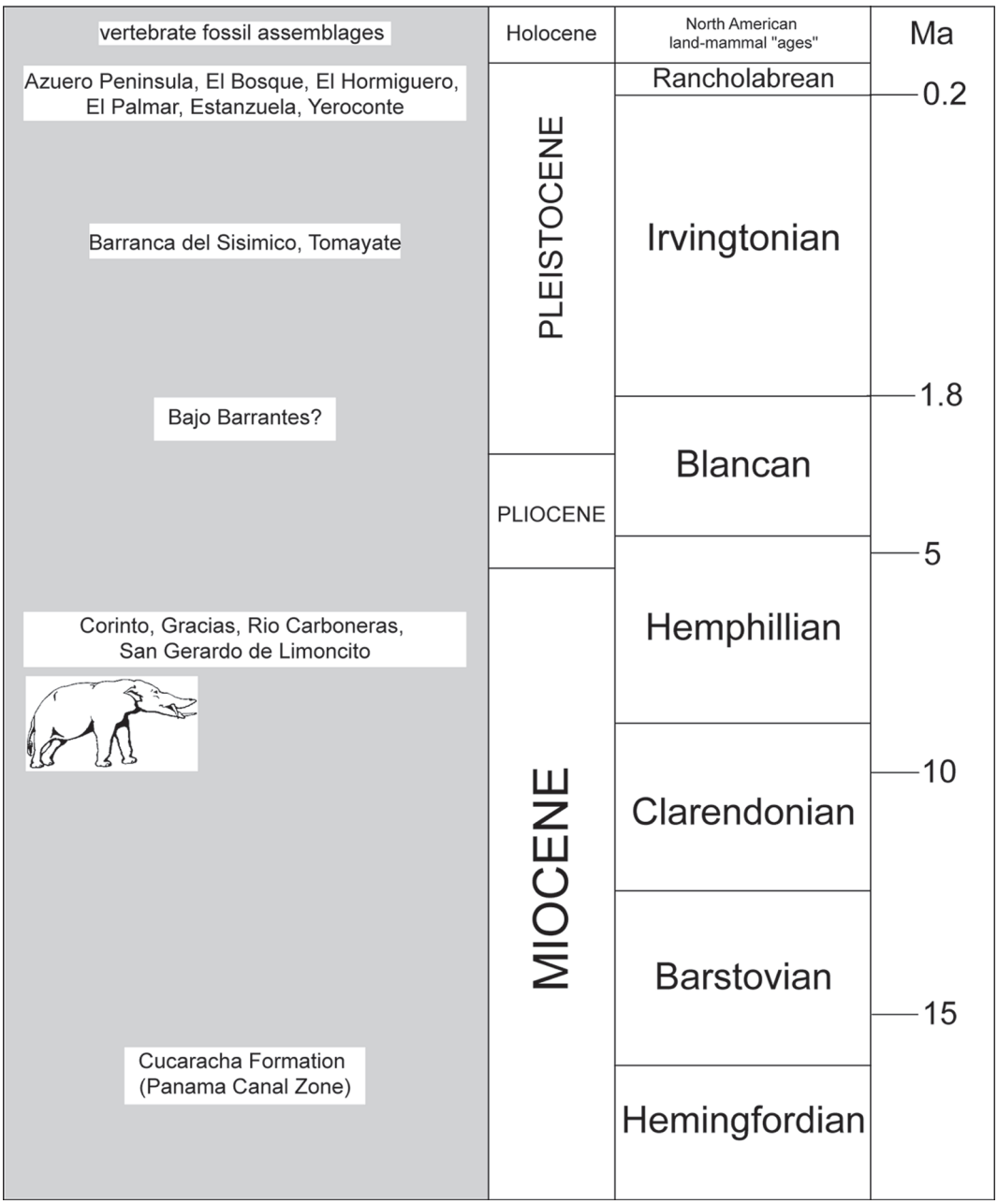

Fig. 7: Chronology and correlation of some of the principal Central American vertebrate fossil localities.

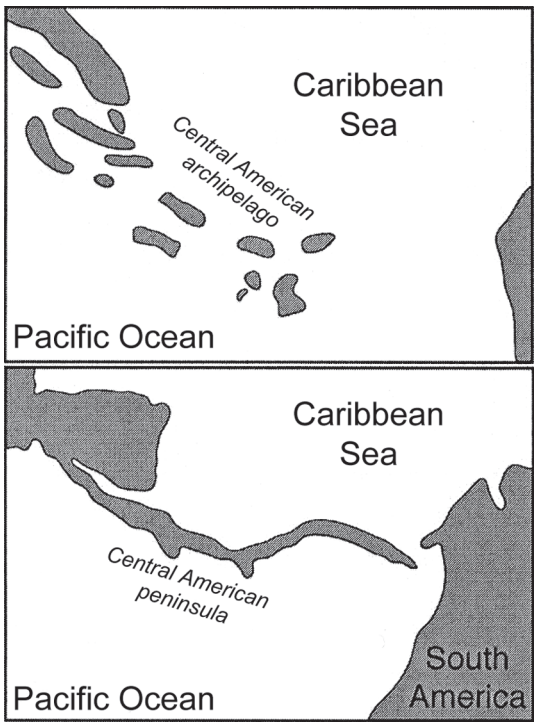

Fig. 8: Two reconstructions of Central America during the Miocene, as an archipelago (above) and as a peninsula (below). After Kirby and MacFadden (2005).

Cretaceous ornithopod dinosaur from Honduras does not contradict this assertion, as it is from a suspect terrane evidently attached to or close to North America, so it is present in Honduras on a "beached Viking funeral ship."

Simpson was not aware of some land vertebrate dispersal during the late Miocene, which brought two genera of ground sloths to North America and large procyonids (raccoons) to South America. These mammals have long been envisioned as island hoppers who crossed Central America when it was an island archipelago with short water gaps (Webb, 1985) (Fig. 8)

During the late Cenozoic, about 3 Ma, Central America became an isthmus that connects North and South America. This connection separated the Atlantic (Caribbean) and Pacific marine ecosystems, and it allowed land plants and animals to readily move between North and South America, the great American biotic interchange (GABI), one of the most significant biotic events in earth history. As mentioned earlier, Central America has long been envisioned as a "passive" part of the GABI, little more than a pathway between the two New World continents.

Vertebrate paleontology strongly suggests that Central America became a peninsula of North America in the Miocene, as land vertebrates of North American affinitiy are known from Miocene fossils from Guatemala to Panama (e.g., Kirby and MacFadden, 2005; Kirby et al., 2008). This Central American peninsula (Fig. 8) clearly became connected to South America circa 3 Ma, at about the beginning of the newly defined base of the Pleistocene.

Perhaps the most significant recent idea that has grown out of increased knowledge of Central American fossil vertebrates is that of a late Cenozoic Central American province of vertebrate evolution, developed by Woodburne (2010; also see Woodburne et al., 2006). An important role of this province may have been as a "holding pen" that delayed dispersals between North and South America. However, a complete evaluation of this important idea requires better age data and broad-based taxonomic and phylogenetic analyses. Thus, for example, Woodburne et al. (2006) pointed to rhynchothere proboscideans as a group likely to have originated in an endemic Central American province, but subsequent taxonomic/phylogenetic evaluation of rhynchotheres suggests a North American origin is more likely (Lucas and Morgan, 2008; Lucas and Alvarado, 2010a; Lucas, 2013).

PROSPECTUS

This review indicates the ongoing rapid growth of our knowledge of the Central American record of fossil vertebrates. We need to continue to augment that record, which remains uneven and incomplete in many ways. What is now being done in Panama, by University of Florida paleontologists and their collaborators, is a good model to follow. They are intensively collecting Miocene strata exposed in the remodelling of the Panama Canal, especially with the use of screenwashing techniques to recover small vertebrate fossils. Most vertebrate diversity (and, in many habitats, biomass) is in small vertebrates, and these are the vertebrate animals we know the least about from Central America's fossil record—many kinds of fishes, amphibians, reptiles such as lizards and snakes, birds and mammals (especially insectivores, bats, rodents and lagoromophs) await discovery through microvertebrate fossil collecting.

We also need much better age control of the Central American vertebrate fossil record. This means we must integrate radioisotopic ages with biostratigraphy, and magnetostratigraphy may be of help in some deposits as well. Currently, most Central American vertebrate fossil records can only be imprecisely assigned a "Pleistocene" age. An augmented record with better age constraints is the way forward in Central American vertebrate paleontology, a pathway that will increase our understanding of the evolutionary and biogeographic significance of one of the world's most intriguing fossil records.

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