

FOSSIL EVIDENCE FOR EARLIEST NEOGENE AMERICAN FAUNAL INTERCHANGE: *BOA* (SERPENTES, BOINAE) FROM THE EARLY MIOCENE OF PANAMA

JASON J. HEAD,^{*1} ALDO F. RINCON,^{2,3} CATALINA SUAREZ,² CAMILO MONTES,² and CARLOS JARAMILLO²

¹Department of Earth and Atmospheric Sciences, University of Nebraska–Lincoln, and University of Nebraska State Museum, Lincoln, Nebraska 68502, U.S.A., jhead2@unl.edu;

²Smithsonian Tropical Research Institute, Box 0843-03092, Balboa, Ancon Republic of Panama;

³Florida Museum of Natural History, Gainesville, Florida 32611, U.S.A.

ABSTRACT—Isolated precloacal vertebrae from the early to middle Miocene Gaillard Cut of Panama represent the first Central American fossil record of the extant boine snake *Boa* and constrain dispersal of the genus into Central America from South America as no younger than approximately 19.3 Ma. *Boa* from the Las Cascadas fossil assemblage and the Centenario Fauna represent the oldest record of terrestrial southern vertebrate immigration into Central America, and demonstrate American interchange by the earliest Neogene. Interchange of snakes precedes contiguous terrestrial connection between Central and South America by approximately 17 Ma, necessitating dispersal across an approximately 100 km wide marine strait. The biogeographic history of snakes across the Neotropics is distinct from the mammalian record, and indicates a more complicated assembly of New World vertebrate faunas than previously recognized.

INTRODUCTION

Episodes of faunal interchange between North and South America during the Neogene have been heavily studied for mammals and constrained by the origin of dispersal routes through the tectonic evolution of southern Central America from the late Miocene to Pleistocene (MacFadden, 2006a; Webb, 2006; Woodburne, 2010). The Great American Biotic Interchange (GABI) was the largest event, consisting of four major episodes between 2.6 and 0.13 Ma following the final uplift of the Panamanian isthmus and closure of the Central American Seaway (Woodburne, 2010), with older records of first occurrences of mammal immigrants in both North and South America indicating more diffuse interchange beginning by at least 9 Ma (Campbell et al., 2000, 2010; Webb, 2006). Older mammalian records indicate faunal provinciality during the middle Miocene, including the absence of South American taxa from southernmost Central America (MacFadden, 2006b; MacFadden et al., 2010), suggesting that the Cretaceous–Paleogene biogeographic isolation of South America persisted until the early Neogene.

Patterns of interchange and assembly of American reptile faunas are much more poorly constrained (e.g., Estes and Baez, 1985; Vanzolini and Heyer, 1985), despite high species richness among Neotropical taxa (Reed, 2003). Biogeographic analyses are primarily ahistorical inferences based on molecular phylogenies and geographic distributions of extant taxa (Cadle and Greene, 1993; Wüster et al., 2005), and the fossil record of reptiles from Central America is poorly sampled relative to coeval records from North and South America (e.g., Albino, 1996a; Holman, 2000; Hsiou and Albino, 2009, 2010). As a result, any discoveries of northern Neotropical reptile fossils from the Neogene are significant to constraining their biogeographic histories.

Here we describe the first records of *Boa* from the early and middle Miocene of Panama, and discuss their implications for understanding the tempo and mode of biogeographic interchange

between Central and South America, as well as constraining rates of molecular sequence divergence within the genus.

Geologic Context

The fossils were collected in the Las Cascadas and Cucaracha formations of the Gaillard Cut (Culebra Cut) in the Panama Canal Basin, a Cenozoic depositional basin located between 8.9°N and 9.2°N in the central region of the Republic of Panama (Fig. 1). From youngest to oldest, the Gaillard Cut section includes the Pedro Miguel, Cucaracha, Culebra, and Las Cascadas formations. The Pedro Miguel Formation is terrestrial and consists principally of basalt flows, tuff, and interbeds of paleosol and fine-grained sediment (Woodring and Thompson, 1949; Kirby et al., 2008; Montes et al., 2012). The Cucaracha Formation is also predominately terrestrial, consisting of paleosols, lithic arenites, and conglomerates (Montes et al., 2012). The Culebra Formation is shallow marine, and together these formations are thought to represent a fluvial-deltaic coastal plain that likely included mangrove swamps in the near-shore areas (Kirby et al., 2008; Moron et al., 2008; Strong et al., 2008; Montes et al., 2012) and tropical forests (Herrera et al., 2010; Graham, 1988a, 1988b).

Specimens from the Cucaracha Formation were found in terrestrial facies within a variably thick (~20–85 m) section of predominantly terrestrial volcanoclastic sediments, lignite, and paleosols (Fig. 1). Fossils of *Boa* were found in the upper part of the Cucaracha Formation at two localities, Cartagena Hill and Hodges Hill (Fig. 1). The snake vertebrae were found as pebble-sized clasts within laterally discontinuous lenses at Cartagena Hill, and laterally extensive thick beds (>1 m) of clast-supported, indurated, volcanoclastic pebble conglomerates at Hodges Hill. These conglomerates are interbedded with olive-gray claystones exhibiting variable degrees of paleosol development based on the presence (or absence) of mottling, rhizoconcretions, and slickensides. We suggest that these conglomerates were deposited as fluvial channel deposits, that the claystone beds formed in an associated floodplain environment (Retallack and Kirby, 2007; Kirby et al., 2008; Moron et al., 2008;

*Corresponding author.

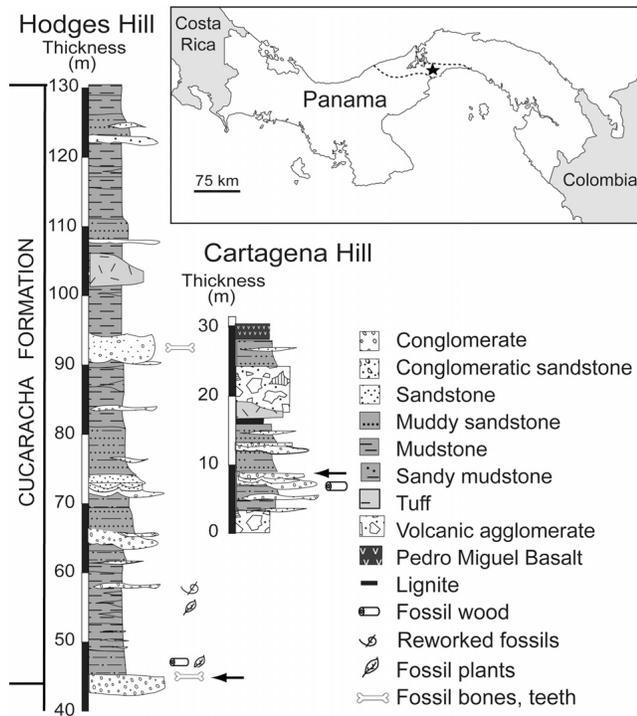


FIGURE 1. Geology of Panamanian *Boa* localities. Inset, map view of Republic of Panama showing position of the Centenario Fauna (star) within the Panama Canal Basin (dashed lines). Position of *Boa* localities in local stratigraphic sections at Hodges Hill (after MacFadden et al., 2010) and Cartagena Hill within the Cucaracha Formation are represented by arrows.

Strong et al., 2008, MacFadden et al., 2010; Montes et al., 2012), and that the snake fossils likely were transported short distances into the fluvial-deltaic environment as clasts.

The oldest fossil-bearing formation in the Gaillard Cut, the Las Cascadas Formation, consists predominately of volcanoclastics, including welded agglomerates and tuffs, capped by fossiliferous fluvial conglomerates and shallow marine limestones (Montes et al., in press). The lower part of the overlying Culebra Formation has been dated using strontium ($\text{Sr}^{87}/\text{Sr}^{86}$) chemostratigraphy on corals and calcareous shells and magmatic U/Pb, with age ranges from 20.62 ± 0.58 to 23.07 ± 0.53 Ma (Kirby et al., 2008) and 19.3 ± 0.4 Ma (Montes et al., 2012), and the underlying Bas Obispo Formation has been dated as 25.37 ± 0.13 Ma based on $\text{Ar}^{40}/\text{Ar}^{39}$ ages calculated for andesitic water-saturated arc lavas (Farris et al., 2011; Rooney et al., 2011). Based on these ages, the Las Cascadas Formation spans the Late Oligocene to Early Miocene (<25 Ma to $>19.3 \pm 0.4$ Ma). The Las Cascadas specimens of *Boa* were recovered from a conglomeratic and tuffaceous interval located in the upper part of the formation, which crops out in the northern part of the Gaillard Cut (Kirby et al., 2008; Rincon et al., 2012; Montes et al., 2012).

Institutional Abbreviation—UF, Vertebrate Paleontology Collection, Florida Museum of Natural History, University of Florida, Gainesville, Florida, U.S.A.

SYSTEMATIC PALEONTOLOGY

SERPENTES Linnaeus, 1758
ALETHINOPHIDIA Nopsca, 1923
BOIDAE Gray, 1825

BOINAE Gray, 1825
BOA Linnaeus, 1758
BOA cf. *B. CONSTRICTOR* Linnaeus, 1758
(Fig. 2)

Referred Specimens—UF 255000, incomplete preloacal vertebra from the Las Cascadas Formation; UF 237882, UF 237883, UF 245521, incomplete preloacal vertebrae from the upper part of the Cucaracha Formation.

Localities and Horizon—Lirio Norte (site key YPA-024 in UF Vertebrate Paleontology Collection), upper part of the Las Cascadas Formation, early Miocene (Rincon et al., 2012); Cartagena Hill (site key YPA-031 in UF Vertebrate Paleontology Collection) and Hodges Hill (site key YPA-026 in UF Vertebrate Paleontology Collection), Cucaracha Formation, middle Miocene (MacFadden, et al., 2010), Panama.

Description—All specimens are incomplete elements from the preloacal vertebral column, as indicated by the presence of synapophyses and hemal keels. UF 255000 is from the anterior preloacal region, as evidenced by the presence of an incomplete but prominent hypapophyses. Distal processes of all specimens are worn or abraded, consistent with hydrodynamic transport. UF 237882 and 237883 are the largest recovered vertebrae and appear to represent somatically mature individuals based on the relative proportions of the neural canal, apophyses, and cotyle (Albino, 2011). Intracolumnar variation in size, shape, and changes in vertebral numbers with body size in snakes limit body size estimation from vertebral size without quantitatively determining the position of isolated vertebrae (e.g., Polly and Head, 2004; Head and Polly, 2007; Head et al., 2009), but the size of the largest elements are consistent with vertebrae from the approximate middle of the preloacal column of an animal with a snout-vent length of 1.5–2.0 m. Anatomical terminology follows Head (2005).

In anterior view (Fig. 2A.1, B.1), the cotyle is subcircular and slightly wider than tall. The ventral margins of the cotyle are flattened and anteromedially angled toward the anterior margin of the hemal keel. The hemal keel is deep and visible in anterior view. Large, deep paracotylar fossae are present at the dorsolateral margins of the cotyle. Prominent paracotylar foramina are present within the median margins of the fossae. The fossae are positioned at a level between the midline height and dorsal margin of the cotyle, as in extant *B. constrictor*.

The prezygapophyses are low-slung and diverge from the body of the element at a level just dorsal to the cotyle, with wide and long postzygapophyseal articular facets oriented slightly above horizontal. Lateral to the articular facets, the abraded margins of the prezygapophyses include the bases of small, narrow accessory processes. The ventrolateral margins of the prezygapophyses consist of wide synapophyses. The extent of synapophyseal differentiation into discrete para- and diapophyseal articular surfaces is not well preserved in any specimen. The neural canal is subtriangular with a widely concave ventral margin. The canal is narrower than the cotyle, and is capped by a tall, similarly narrow zygosphen. The zygosphen has a broadly concave dorsal margin, and its thickness is consistent with *Boa* among boines (Albino and Carlini, 2008). The zygosphenal articular facets of the zygosphen are steep and high-angled. The anterior margin of the neural spine arises from the posterodorsal margin of the zygosphen. The spine is tall with parallel lateral margins anteriorly and is concave posteriorly where it contacts the dorsal extent of the neural arch.

In dorsal view (Fig. 2A.2, B.2), both specimens are wider than long. The anterior margin of the zygosphen is concave and the zygantral articular facets are laterally convex. The articular facets of the prezygapophyses are approximately triangular, with transverse anterior margins. The facets have narrow lateral margins and widen medially toward the midline of the elements. Posterior

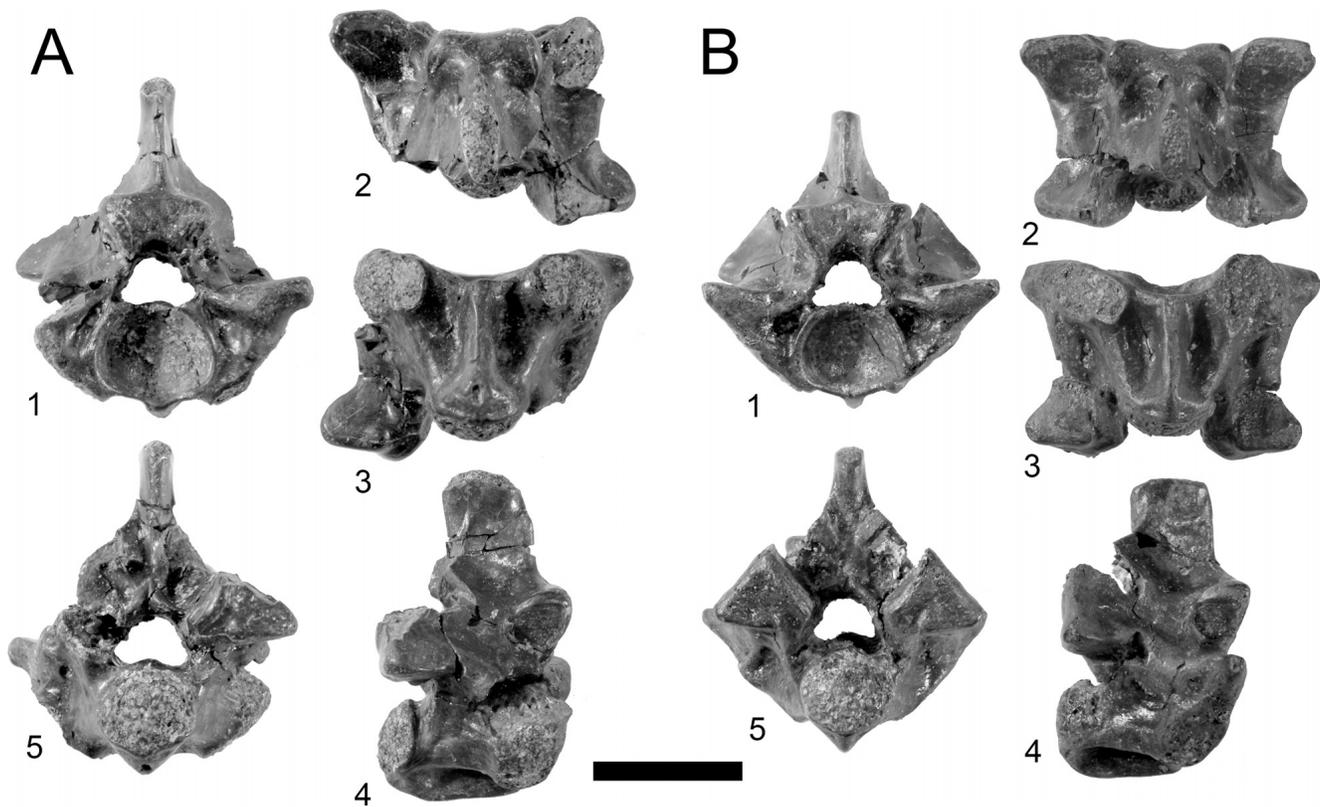


FIGURE 2. *Boa* cf. *B. constrictor* preclacal vertebrae. (A) UF 237883 and (B) UF 237882 in anterior (1), dorsal (2), ventral (3), right lateral (4), and posterior (5) views. Scale bar equals 1 cm.

to the prezygapophyses, the interzygapophyseal ridge is broad and spans the posterior margin of the prezygapophysis and the anterior margin of the postzygapophysis. The ridge has straight, posteromedially angled lateral margins as in large-bodied boids (e.g., Head, 2005; Head et al., 2006; Albino and Carlini, 2008).

The lateral extent of the neural arch widens from the zygosphene to the posterior border of the element where it flares laterally to cap the postzygapophyses, forming a steep, anteromedially angled margin. The preserved posterior margin of the neural arch in UF 237883 (Fig. 2B.2) includes a deep posteromedian notch. The postzygapophyses correspond in triangular shape to the prezygapophyses, but do not extend as far laterally. The neural spine is ovoid and elongate in cross-section, originating anteriorly as a thin blade at the base of the zygosphene and terminating posteriorly at the posteromedian notch of the neural arch.

In ventral view (Fig. 2A.3, B.3), the centrum is triangular. The anterior margin consists of the concave ventral margin of the cotyle positioned between broad synapophyseal bases consisting of broad dorsolateral diapophyseal and narrower ventromedial parapophyseal surfaces. The lateral margins are composed of prominent, posteromedially angled ridges that extend from the synapophyses to the condyle and define deep paralympathic fossae on the ventral surface of the centrum. Medially, a tall hemal keel extends from the cotyle to the condyle. The keel forms the medial margins of the fossae and is capped by a thin crest along its length. The condyle is approximately circular and only partially visible ventrally. Dorsal to the centrum, the ventral surface of the interzygapophyseal ridge possesses a deep medial excavation. The prezygapophyseal articular facet of the postzygapophyses is flattened, broad, and well defined from the rest of the process.

In lateral view (Fig. 2A.4, B.4), the elements are narrow. The zygosphene articular facets are ovoid and anterodorsally angled. The spinous process is tall, with equal anterior and posterior margins, and is angled only slightly posteriorly. The dorsal margin of the process is badly eroded in UF 237883, but the complete process in UF 237882 includes a flat top to the spine. The prezygapophysis is anterodorsally angled and the preserved bases of the accessory processes are approximately circular in cross-section. The interzygapophyseal ridge extends posteriorly from the prezygapophysis, and is strongly angled dorsally. A broad, deep fossa excavates the lateral margin of the centrum, extending onto the ventral margin of the ridge. The postzygapophysis is approximately horizontal. The posterior margin of the neural arch is vertical to the level of the zygosphene, at which point it slopes anteriorly and contacts the lateral surface of the spinous process just beneath its dorsal margin. Ventrally, the hemal keel has a straight margin that is slightly posteroventrally angled. The lateral ridges of the centrum decrease in height posteriorly and terminate posteriorly at the lateral surface of the condyle, exposing the sides of the hemal keel. The condyle is well defined relative to the body of the centrum, and is slightly angled anterodorsally.

In posterior view (Fig. 2A.5, B.5), the condyle is circular. The hemal keel is triangular and the lateral ridges of the centrum are slightly concave toward their contact with the synapophyses. The posterior surface of the prezygapophysis is excavated by the same fossa that occurs on the lateral surface of the centrum and the ventral surface of the interzygapophyseal ridge. The preserved portions of the lateral margin of the neural arch in both specimens indicate that it was vaulted and triangular. The posterior surface of the arch is broad, extending from the postzygapophyses to the tall, ventromedially angled articular

facets of the zygantrum. The roof of the zygantrum is broken in both specimens, revealing deep parazygantral fossae and foramina at the base of the neural spine.

DISCUSSION

Taxonomic Identification

Taxonomic identification of the Panamanian specimens as *Boa* partially follows Albino and Carlini (2008). All specimens preserved the character combination of a straight, posteromedially angled interzygapophyseal ridge, well-developed paracotylar foramina within deep fossae, tall neural spine, and tall, thickened zygosphenes. None of these characters in isolation or partial combination is uniquely apomorphic for *Boa*, but the occurrence of all characters is unique to the genus relative to all other known boids. *Boa* is monotypic, and the Gaillard Cut specimens compare favorably with extant *B. constrictor*. However, we cannot determine if the materials described here represent individuals nested within extant *B. constrictor* subspecies populations, and we refrain from making a species assignment.

Timing of Dispersal and Interchange

Boa from the early to middle Miocene of Panama is the oldest unambiguous Neogene record of a South American vertebrate taxon in Central America and represents a temporal range extension of initial American interchange by least 9.8 Ma (Fig. 3) between the youngest age estimate of the upper Las Cascadas Formation (~19.3 Ma) and the maximum age of *Amahuacatherium peruvium*, the oldest North American mammal immigrant into South America at 9.5 Ma (Campbell et al., 2010). *Boa* is considered to be South American in origin, based on Gondwanan vicariance models of boine biogeography (e.g., Burbrink, 2005; Noonan and Chippindale, 2006a, 2006b), which necessitates an initial South American endemicity of Neotropical taxa with subsequent dispersal into Central America and the Caribbean. Molecular divergence timings for *Boa* are estimated to be between 48 and 70 Ma, whereas first occurrences of its sister taxon *Titanoboa* (Head et al., 2009) constrains divergence of *Boa* to no younger than 60–58 Ma (Fig. 3). The oldest record of *Boa* is from the late Eocene (Barrancan ~41.6–39.0 Ma; Ré et al., 2010) of Gran Barranca, Argentina (Albino, 1993), indicating a 13.6–31-million-year unrecovered history of the genus in South America, and 25–39 million years between divergence estimates and the oldest Central American record from the Centenario Fauna (Fig. 3).

The range of divergence estimates for *Boa* is coeval with an interval of terrestrial isolation of the South American landmass from the north preceding assembly of southern Central America (Donnelly, 1985), and Cretaceous–Paleogene South American herpetofaunas do not include members of unambiguously Laurasian clades (e.g., Albino, 1993, 1996a, 2000; Rage, 1998, 2001). The absence of either a terrestrial connection between South and Central America or evidence of Late Cretaceous–Paleogene herpetofaunal interchange suggests that the Neogene would be the earliest opportunity for interchange and that the Gaillard Cut record may approximate the initial dispersal of *Boa* out of South America.

The tectonic arrangement of southern Central America during the early Miocene constrains the mode of dispersal for immigrant snakes. Southern Central America consisted of the Chortis Block to the north bordered to the southeast by the Chortega Block, a volcanic arc derived from the western border of the Caribbean Plate. Initial docking of the southern limb of the Central American forearc with northern Colombia occurred between 23 and 25 Ma and included regional exhumation of the Panamanian peninsula (Farris et al., 2011; Montes et al., 2012). Formation of contiguous terrestrial dispersal conduits between

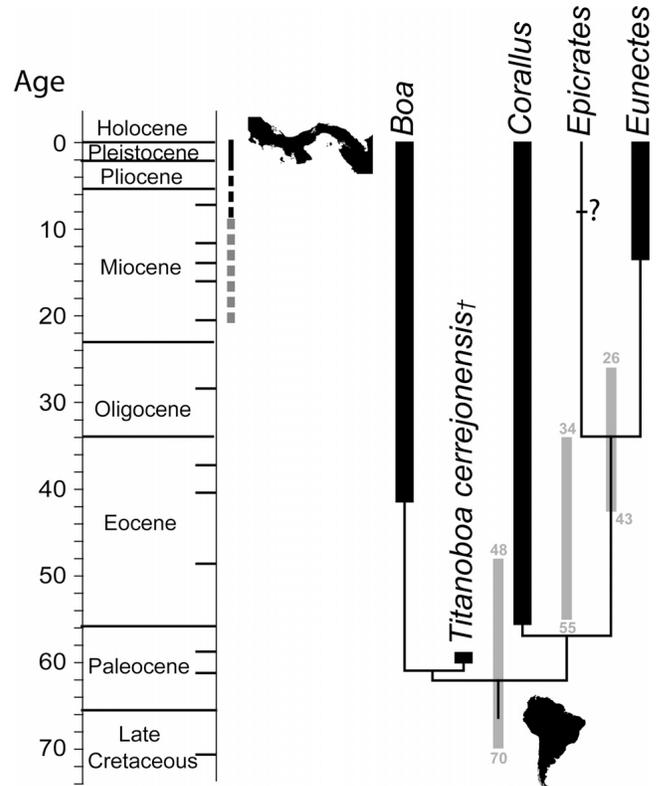


FIGURE 3. Temporally calibrated phylogeny of Neotropical boines based on fossil first-occurrence and molecular-divergence estimates. Tree topology is based on molecular analyses indicating a South American origin of the clade (Burbrink, 2005); thin gray lines and numbers represent the range of molecular divergence timing estimates for boine clades (Noonan and Chippindale, 2006a). The first occurrence of *Corallus* exceeds the oldest molecular divergence estimate for (*Corallus* + (*Epicrates* + *Eunectes*)). Thick black lines indicate stratigraphic records. Map view symbol of Panama and dashed-to-solid vertical line represent evolution of Panamanian Isthmus and intervals of terrestrial interchange between Central and South America. Gray dashed lines represent temporal range extension of interchange based on Panamanian record of *Boa*. First-occurrence data are as follows: *Boa*, Sarmiento Formation Albino (1993), Barrancan, ~41.6–39.0 Ma (Ré et al., 2010); *Titanoboa*, Cerrejón Formation, Colombia, Head et al. (2009), 58–60 Ma (Jaramillo et al., 2007); *Corallus*, São José de Itaboraí, Brazil (Rage, 2001), early Eocene (Gelfo et al., 2009); Huayquerian, 9–6.5 Ma (Latrubesse et al., 2010); *Eunectes* Villavieja Formation, Colombia, Laventan, 13.8–12.0 Ma (Hoffstetter and Rage, 1977). Question mark refers to first occurrence of “aff. *Epicrates*,” Solimões Formation, Brazil (Hsiou and Albino, 2010).

Central and South America did not begin until the final uplift of the Chortega block in the Pliocene, and the two landmasses were separated during the Miocene by the Central American Seaway (Woodburne, 2010), a shallow marine strait in excess of 100 km wide (Coates and Obando, 1996; Coates et al., 2004; Farris et al., 2011; Montes et al., 2012). Within the Chortega forearc system, terrestrial continuity is poorly constrained, with geologic and vertebrate fossil evidence supporting a continuous peninsula (Kirby and MacFadden, 2005; Montes et al., 2012) or archipelago island chain (Coates et al., 2004). Persistence of marine barriers during the early Miocene required interchange through over-water dispersal across the >100-km Central American Seaway. The lower metabolic energy requirements of ectothermic snakes may have allowed for greater success traversing marine dispersal routes than for mammals (e.g., Censky et al., 1998; Stankiewicz et al., 2006) prior to terrestrial connection. Tests of this

hypothesis would include discovery of additional South American immigrant components in the Gaillard Cut herpetofauna.

Additional Neogene snake records suggest a complex American biogeographic history. *Boa constrictor* has been reported from the early Miocene (early Hemingfordian, ~18.5 Ma) of southern North America, based on a record from the Thomas Farm fauna of Florida (Vanzolini, 1952; Auffenberg, 1963, after Kluge, 1988). Colubroids have been recovered from the early Miocene (Colhuehuapian South American Land Mammal Age, 21–17.5 Ma) Trelew Member of the Sarmiento Formation, Argentina (Albino, 1996b), and the middle Miocene (Laventan, 13.8–12.0 Ma) La Venta Fauna of Colombia (Hoffstetter and Rage, 1977; Hecht and LaDuke, 1997). The record of *B. constrictor* has been considered to represent northward immigration through an Antillean conduit (Albino, 2011), and the taxonomic ambiguity of the colubroid records prohibits determination of Central American or Caribbean immigration route into South America. The presence of *Boa* in the early Miocene of Panama suggests that Central America would be an available route for colubroid immigration into South America, and an alternate route into southern North America instead of (or in addition to) the Caribbean.

Patterns of first occurrence in the Neogene snake record indicate asynchronous dispersal timings. New World viperids are Asian immigrants with first occurrence in North America during the early Miocene (Holman, 2000). Conversely, the oldest record of viperids in South America is late Miocene (Huayquerian, 9.0–6.8 Ma) (Albino, 2006), younger than both the colubroid and *Boa* records, but roughly concurrent with the oldest records of mammalian interchange (Campbell et al., 2010).

The Gaillard Cut record of *Boa* has implications for molecular divergence timing estimates within the genus. Hynková et al. (2009) recovered two clades within *Boa* consisting of a monophyletic Central American *B. c. imperator* subspecies and monophyletic South American *B. c. constrictor* based on mitochondrial cytochrome b sequences. They additionally proposed a Pliocene (<3.5 Ma) divergence of Central American from South American subspecies based on low mitochondrial sequence divergence, and suggested that late Panamanian uplift was required to allow dispersal concurrent with GABI into Central America. Presence of *Boa* in both the Las Cascadas and Cucaracha formations indicates establishment of the genus in Central America by the early Miocene, and if the fossil distribution of *Boa* represents the establishment of modern subspecies, then molecular divergence rates miscalculate divergence timings by ~15.8 million years. Conversely, if molecular rates are accurate, then the absence of older divergences among extant subspecies indicates that either gene flow was uninterrupted between Central and South America, despite the persistence of the Central American Seaway, or the Miocene fossil record is derived from past *Boa* populations outside of the extant mitochondrial genome. Earliest Neogene dispersal into Central America indicates that Panamanian uplift does not explain the recent molecular divergence estimates. Instead, the distribution of *B. c. imperator* includes Ecuador west of the Andes and the estimated divergence timing in extant subspecies is consistent with Andean uplift as a barrier to gene flow, a pattern similar to that of mammalian species (e.g., Larsen et al., 2010).

At a minimum, establishment of components of modern Neotropical snake faunas across the Americas by the early Miocene indicates that the prey resource partitioning observed among tropical extant snakes (Luiselli, 2006) was achieved prior to the assembly of modern mammalian faunas, that access to new mammalian prey types was not a driver of snake immigration (contra Hynková et al., 2009), and that terrestrial migration corridors were not requisite for inter-American dispersal in snakes.

CONCLUSIONS

Boa from the Gaillard Cut of Panama represents the oldest South American immigrant during the Neogene. The antiquity of Central American *Boa* does not support hypotheses of recent subspecific divergence based on Pliocene Panamanian dispersal routes, and presence on either side of the Central American Seaway by at least 19.3 Ma indicates overwater dispersal. Bidirectional immigration of snakes between the Americas precedes episodes of mammalian interchange and represents a distinct biogeographic pattern than may be characteristic of herpetofaunas in general during the early Neogene.

ACKNOWLEDGMENTS

This research was made possible through the collaboration and funding of the Autoridad del Canal de Panama (ACP), the Mark Tupper Fellowship, Ricardo Perez S.A., the National Science Foundation grants EAR 0824299 and OISE 0966884, and the National Geographic Society. We thank the paleontology/geology team at Smithsonian Tropical Research Institution and UF for help with fieldwork. Support for collection and curation of fossils was provided by US NSF grants OISE 0638538 and EAR 0642528 and University of Florida 2007 Research Opportunity Fund to B. J. MacFadden, PI/PD. J.J.H. was supported by a NSERC Discovery Grant.

LITERATURE CITED

- Albino, A. M. 1993. Snakes from the Paleocene and Eocene of Patagonia (Argentina): paleoecology and coevolution with mammals. *Historical Biology* 7:51–69.
- Albino, A. M. 1996a. The South American fossil Squamata (Reptilia: Lepidosauria); pp. 185–202 in G. Arratia (ed.), *Contributions of Southern South American to Vertebrate Paleontology*. *Münchner Geowissenschaftliche Abhandlungen, Reihe A, Geologie und Paläontologie* 30.
- Albino, A. M. 1996b. Snakes from the Miocene of Patagonia (Argentina) part II: the Colubroidea. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 300:353–360.
- Albino, A. M. 2000. New record of snakes from the Cretaceous of Patagonia (Argentina). *Geodiversitas* 22:247–253.
- Albino, A. M. 2006. Snakes from the Cerro Azul Formation (upper Miocene), Central Argentina, with a review of fossil viperids from South America. *Journal of Vertebrate Paleontology* 26:581–587.
- Albino, A. M. 2011. Morfología vertebral de *Boa constrictor* (Serpentes: Boidae) y la validez del género Mioceno *Pseudoepicrates* Auffenberg, 1923. *Ameghiniana* 48:53–62.
- Albino, A. M., and A. A. Carlini. 2008. First record of *Boa constrictor* (Serpentes, Boidae) in the Quaternary of South America. *Journal of Herpetology* 42:82–88.
- Auffenberg, W. 1963. The fossil snakes of Florida. *Tulane Studies in Zoology* 10:131–216.
- Burbrink, F. T. 2005. Inferring the phylogenetic position of *Boa constrictor* among the Boinae. *Molecular Phylogenetics and Evolution* 34:167–180.
- Cadle, J. E., and H. W. Greene. 1993. Phylogenetic patterns, biogeography, and the ecological structures of Neotropical snake assemblages; pp. 281–293 in R. E. Ricklefs and D. Schleter (eds.), *Species Diversity in Ecological Communities: Historical and Geographical Approaches*. University of Chicago Press, Chicago, Illinois.
- Campbell, K. E., Jr., C. D. Frailey, and L. Romero-Pittman. 2000. The late Miocene gomphothere *Amahuacatherium peruvium* (Proboscidea: Gomphotheriidae) from Amazonian Peru: implications for the Great American Faunal Interchange. *Boletín-Instituto Geológico Minero y Metalúrgico, Serie D, Estudios Regionales* 23:1–152.
- Campbell, K. E., Jr., D. R. Prothero, L. Romero-Pittman, F. Hertel, and N. Rivera. 2010. Amazonian magnetostratigraphy: dating the first pulse of the Great American Faunal Interchange. *Journal of South American Earth Sciences* 26:619–626.
- Censky, E. J., K. Hodge, and J. Dudley. 1998. Over-water dispersal of lizards due to hurricanes. *Nature* 395:556.

- Coates, A. G., and J. A. Obando. 1996. The geologic evolution of the Central American Isthmus; pp. 21–56 in J. B. C. Jackson, A. F. Budd, and A. G. Coates (eds.), *Evolution and Environment in Tropical America*. University of Chicago Press, Chicago, Illinois.
- Coates, A. G., L. S. Collins, M.-P. Aubry, and W. A. Berggren. 2004. The geology of the Darien, Panama, and the late Miocene-Pliocene collision of the Panama arc with northwestern South America. *Geological Society of American Bulletin* 116:1327–1344.
- Donnelly, T. W. 1985. Mesozoic and Cenozoic plate evolution of the Caribbean region; pp. 89–121 in F. G. Stheli and S. D. Webb (eds.), *The Great American Interchange*. Plenum Press, New York.
- Estes, R., and A. M. Báez. 1985. Herpetofaunas of North and South America during the Late Cretaceous and Cenozoic: evidence for interchange?; pp. 139–197 in F. G. Stheli and S. D. Webb (eds.), *The Great American Interchange*. Plenum Press, New York.
- Farris, D. W., C. Jaramillo, G. Bayona, S. A. Restrepo-Moreno, C. Montes, A. Cardona, A. Mora, R. J. Speakman, M. D. Glascock, and V. Valencia. 2011. Fracturing of the Panamanian Isthmus during initial collision with South America. *Geology* 39:1007–1010.
- Gelfo, J. N., F. J. Goin, M. O. Woodburne, and C. de Muizon. 2009. Biochronological relationships of the earliest South American Paleogene mammalian faunas. *Palaeontology* 52:251–269.
- Graham, A. 1988a. Studies in Neotropical paleobotany. V. The lower Miocene communities of Panama—the Culebra Formation. *Annals of the Missouri Botanical Garden* 75:1440–1466.
- Graham, A. 1988b. Studies in Neotropical paleobotany. VI. The lower Miocene Communities of Panama—the Cucaracha Formation. *Annals of the Missouri Botanical Garden* 75:1467–1479.
- Gray, J. E. 1825. A synopsis of the genera of Reptiles and Amphibia, with a description of some new species. *Annals of Philosophy, series 2* 10:193–217.
- Head, J. J. 2005. Snakes of the Siwalik Group (Miocene of Pakistan): systematics and relationship to environmental change. *Palaeontologia Electronica* 8(1):16A.
- Head, J. J., and P. D. Polly. 2007. Dissociation of somatic maturity from segmentation drives gigantism in snakes. *Biology Letters* 3:296–298.
- Head, J. J., M. R. Sánchez-Villagra, and O. Aguilera. 2006. Fossil snakes from the Neogene of Venezuela (Falcón State). *Journal of Systematic Palaeontology* 4:233–240.
- Head, J. J., J. I. Bloch, A. K. Hastings, J. R. Bourque, E. A. Cadena, F. A. Herrera, P. D. Polly, and C. A. Jaramillo. 2009. Giant boid snake from the Paleocene neotropics reveals hotter past equatorial temperatures. *Nature* 457:715–717.
- Hecht, M. K., and T. C. LaDuke. 1997. Limbless tetrapods; pp. 95–99 in R. F. Kay, R. H. Madden, R. L. Cifelli, and J. J. Flynn (eds.), *Vertebrate Paleontology in the Neotropics—The Miocene Fauna of La Venta, Colombia*. Smithsonian Institution Press, Washington, D.C.
- Herrera, F., S. Manchester, C. Jaramillo, B. MacFadden, and S. Silva. 2010. Phylogeographic history and phylogeny of the Humiriaceae. *International Journal of Plant Sciences* 171:392–408.
- Hoffstetter, R., and J.-C. Rage. 1977. Le gisement de vertébrés miocènes de La Venta (Colombie) et sa faune de serpents. *Annales de Paléontologie (Vertébrés)* 63:161–190.
- Holman, J. A. 2000. *The Fossil Snakes of North America*. Indiana University Press, Bloomington and Indianapolis, Indiana, 376 pp.
- Hsiou, A. S., and A. M. Albino. 2009. Presence of the genus *Eunectes* (Serpentes, Boidae) in the Neogene of Southwestern Amazonia, Brazil. *Journal of Herpetology* 43:612–619.
- Hsiou, A. S., and A. M. Albino. 2010. New snake remains from the Miocene of northern South America. *Herpetological Journal* 20:249–259.
- Hynková, I., Z. Starostová, and D. Frynta. 2009. Mitochondrial DNA variation reveals recent evolutionary history of main *Boa constrictor* clades. *Zoological Science* 26:623–631.
- Jaramillo, C., A. Pardo-Trujillo, M. Rueda, G. J. Harrington, G. Bayona, V. Torres, and G. Mora. 2007. The Palynology of the Cerrejón Formation (upper Paleocene) of northern Colombia. *Palynology* 31:153–189.
- Kirby, M. X., and B. J. MacFadden. 2005. Was Central America an archipelago or a peninsula in the middle Miocene? A text using land-mammal body size. *Palaeogeography, Palaeoclimatology, Palaeoecology* 228:193–202.
- Kirby, M. X., D. S. Jones, and B. J. MacFadden. 2008. Lower Miocene stratigraphy along the Panama Canal and its bearing on the Central American peninsula. *PLoS ONE* 3:e2791.
- Kluge, A. G. 1988. Relationships of the Cenozoic boine snakes *Paraeoplicrates* and *Pseudoeoplicrates*. *Journal of Vertebrate Paleontology* 8:229–230.
- Larsen, P. A., M. R. Marchán-Rivadeneira, and R. J. Baker. 2010. Natural hybridization generates mammalian lineage with species characteristics. *Proceedings of the National Academy of Sciences of the United States of America* 107:11447–11452.
- Latrubesse, E. M., M. Cozzuol, S. A. F. da Silva-Caminha, C. A. Rigsby, M. L. Apsy, and C. Jaramillo. 2010. The Late Miocene paleogeography of the Amazon Basin and the evolution of the Amazon River system. *Earth-Science Reviews* 99:99–124.
- Linnaeus, C. von. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Two volumes. Tenth edition. Laurentii Salvii, Holmiae, 1384 pp.
- Luiselli, L. 2006. Resource partitioning and interspecific competition in snakes: the search for general geographical and guild patterns. *Oikos* 114:193–211.
- MacFadden, B. J. 2006a. Extinct mammalian biodiversity of the ancient New World tropics. *Trends in Ecology and Evolution* 21:157–165.
- MacFadden, B. J. 2006b. North American Miocene land mammals from Panama. *Journal of Vertebrate Paleontology* 26:720–734.
- MacFadden, B. J., M. Kirby, A. Rincon, C. Montes, S. Moron, N. Strong, and C. Jaramillo. 2010. Extinct peccary “*Cynorca*” *occidentale* (Tayassuidae) from the Miocene of Panama and correlations to North America. *Journal of Paleontology* 84:288–298.
- Montes, C., A. Cardona, R. R. McFadden, S. E. Morón, C. A. Silva, S. Restrepo-Moreno, D. A. Ramirez, N. Hoyos, D. Farris, G. A. Bayona, C. A. Jaramillo, V. Valencia, J. Bryan, and J. A. Flores. 2012. Evidence for middle Eocene and younger land emergence in Central Panama: implications for isthmus closure. *Geological Society of America Bulletin*. 124:780–799.
- Moron, S., C. Montes, A. Cardona, C. Jaramillo, and G. Bayona. 2008. Clay mineralogy constraining the middle Miocene climatic optimum in Panama. *Geological Society of America, Abstracts with Programs* 40:484.
- Noonan, B. P., and P. T. Chippindale. 2006a. Dispersal and vicariance: the complex evolutionary history of boid snakes. *Molecular Phylogenetics and Evolution* 40:347–358.
- Noonan, B. P., and P. T. Chippindale. 2006b. Vicariant origin of Malagasy reptiles supports a Late Cretaceous Antarctic land-bridge. *The American Naturalist* 168:730–741.
- Nopsca, F. 1923. *Eidolosaurus* und *Pachyophis*, Zwei neue Neocom-Reptilien. *Palaeontographica* 55:97–154.
- Polly, P. D., and J. J. Head. 2004. Maximum-likelihood identification of fossils: taxonomic identification of Quaternary marmots (Rodentia, Mammalia) and identification of vertebral position in the pipe snake *Cylindrophis* (Serpentes, Reptilia); pp. 197–222 in A. M. T. Elewa (ed.), *Morphometrics: Applications in Biology and Paleontology*. Springer-Verlag, New York.
- Rage, J.-C. 1998. Fossil snakes from the Paleocene of São José de Itaboraí, Brazil. Part I. Madtsoiidae, Aniliidae. *Palaeovertebrata* 27:109–144.
- Rage, J.-C. 2001. Fossil snakes from the Paleocene of São José de Itaboraí, Brazil. Part II. Boidae. *Palaeovertebrata* 30:111–150.
- Ré, R. H., E. S. Bellosi, M. Heizler, J. F. Vilas, R. H. Madden, A. A. Carlini, R. F. Kay, and M. G. Vucetich. 2010. A geochronology for the Sarmiento Formation at Gran Barranca; pp. 46–58 in R. H. Madden, A. A. Carlini, M. G. Vucetich, and R. F. Kay (eds.), *The Paleontology of Gran Barranca*. Cambridge University Press, New York.
- Reed, R. N. 2003. Interspecific patterns of species richness, geographic range size, and body size among New World venomous snakes. *Ecography* 26:107–117.
- Retallack, G. J., and M. X. Kirby. 2007. Middle Miocene global change and paleogeography of Panama. *Palaios* 22:667–669.
- Rincon, A. F., J. I. Bloch, B. J. MacFadden, S. Suarez, and C. A. Jaramillo. 2012. New floridatragulines (Mammalia, Camelidae) from the early Miocene Las Cascadas Formation, Panama. *Journal of Vertebrate Paleontology* 32:456–472.
- Rooney, T. O., P. Franceschi, and C. M. Hall. 2011. Water-saturated magmas in the Panama Canal region: a precursor to adakite-like magma generation? *Contributions to Mineralogy and Petrology* 161:373–388.
- Stankiewicz, J., C. Thiart, J. C. Masters, and M. J. de Wit. 2006. Did lemurs have sweepstake tickets? An exploration of Simpson’s model

- for the colonization of Madagascar by mammals. *Journal of Biogeography* 33:221–235.
- Strong, N., D. Farris, A. Cardona, C. Monte, and C. Jaramillo. 2008. Evolution of fluvial drainage networks evolving in response to an emerging Cenozoic Panama Cordillera. *EOS Transactions AGU* (89)53, Fall Meeting Supplement, Abstract T33–2098.
- Vanzolini, P. E. 1952. Fossil snakes and lizards from the lower Miocene of Florida. *Journal of Paleontology* 26:452–457.
- Vanzolini, P. E., and W. R. Heyer. 1985. The American herpetofauna and the interchange; pp. 475–488 in F. G. Stehli and S. D. Webb (eds.), *The Great American Interchange*. Plenum Press, New York.
- Webb, S. D. 2006. The Great American Biotic Interchange: patterns and processes. *Annals of the Missouri Botanical Garden* 93: 245–257.
- Woodburne, M. W. 2010. The great American biotic interchange: dispersals, tectonics, climate, sea level and holding pens. *Journal of Mammalian Evolution* 17:245–264.
- Woodring, W. P., and T. F. Thompson. 1949. Tertiary formations of Panama Canal Zone and adjoining parts of Panama. *Bulletin of the American Association of Petroleum Geologists* 33:223–247.
- Wüster, W., J. E. Ferguson, J. A. Quijada-Mascareñas, C. E. Pook, M. Da Graca Salomão, and R. S. Thorpe. 2005. Tracing an invasion: landbridges, refugia, and the phylogeography of the Neotropical rattlesnake (Serpentes: Viperidae: *Crotallus durissus*). *Molecular Ecology* 14:1095–1108.

Submitted February 5, 2012; revisions received April 24, 2012; accepted May 2, 2012.

Handling editor: Paul Barrett.