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Boid snake fossils from the Neogene of Southern Costa Rica

Serpientes boídos fósiles del Neógeno del sur de Costa Rica

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ABSTRACT: Three dorsal vertebrae of boid snakes from the Upper Miocene deposits of southern Costa Rica are documented and tentatively assigned to *Boa constrictor*. These fossils represent the first described snake remains from Costa Rica and their earliest record from Central America north of Panama. Their presence supports the possibility of bidirectional snake dispersal between South and North America during the Late Miocene.
Keywords: Costa Rica; San Vito; Miocene; *Boa*; immigration.

RESUMEN: Se documentan tres vértebras dorsales de serpientes boídos procedentes de depósitos del Mioceno Superior en el sur de Costa Rica, las cuales se asignan tentativamente a *Boa constrictor*. Estos fósiles representan los primeros restos de serpientes descritos en Costa Rica y el registro más antiguo en América Central al norte de Panamá. Su presencia respalda la posibilidad de una dispersión bidireccional de serpientes entre América del Sur y América del Norte durante el Mioceno Superior.
Palabras clave: Costa Rica; San Vito; Mioceno; *Boa*; inmigración

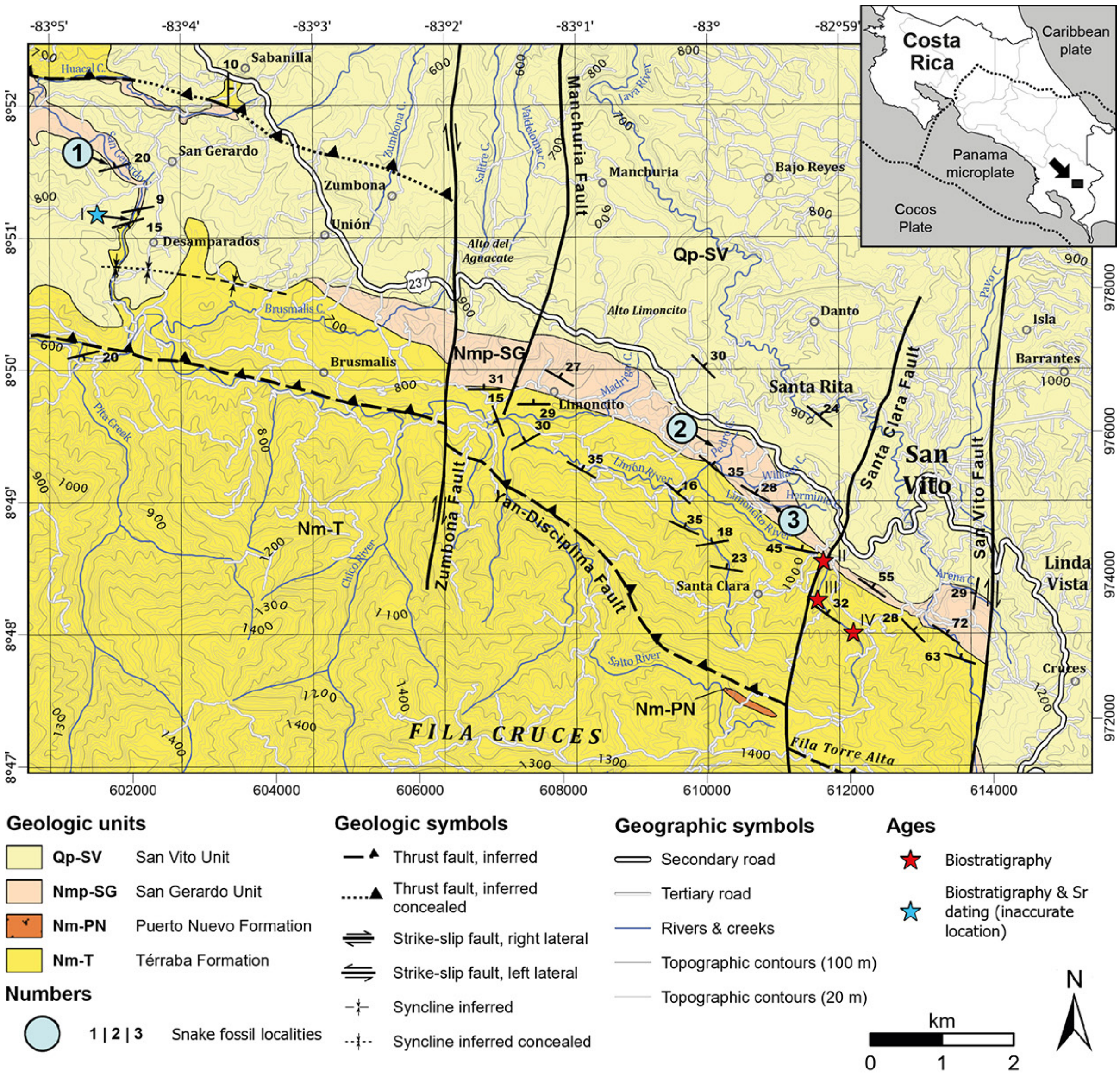
Introduction

The vertebrate fossil record of Central America is largely dominated by late Cenozoic (Miocene-Pleistocene) fossil mammals, yet, in contrast, the fossil record of lower vertebrates such as amphibians and reptiles, and that of birds is much less well-known (Lucas, 2014). Among reptile fossils, most records pertain to the turtles (Auffenberg, 1971; Webb & Perrigo, 1984; Coto & Acuña, 1986; Acuña & Laurito, 1996; Cisneros, 2005; Laurito et al., 2005; Cadena et al., 2012; Weems et al., 2025), and crocodilians (Mook, 1959; Mead et al., 2006; Laurito & Valerio, 2008b; Hastings et al., 2013; Lucas et al., 2022). Fossil snakes are exceptionally rare, with only a single documented record from the Miocene of Panama (Head et al., 2012). Additionally, an undocumented boid fossil from the San Gerardo de Limoncito area, in southern Costa Rica, is mentioned in the Palmar Sur Finca 6 Museum exhibits. Here, we document *Boa constrictor* fossils from Late Miocene deposits of southern Costa Rica. These remains represent the first fossil snake formally described from Costa Rica and from Central America north of Panama. Their presence supports the possibility of bidirectional dispersal of snakes between South and North America during the Late Miocene, thus traversing Central America.

Geological context

The snake fossils documented here come from three localities in southern Costa Rica near San Vito de Coto Brus (Fig. 1). The first locality, informally named San Gerardo Creek, is a well-known fossil-bearing site situated about 12 km northwest of San Vito, west of the eponymous village (e.g., Laurito et al., 2005; Mead et al., 2006; Valerio & Laurito, 2008, 2020). The second locality, locally known as Pedro Creek, and the third, Herminio Creek, are small tributaries of the Limoncito River, located 2.8 and 2.3 km west of San Vito, respectively. These latter two localities are currently under exploration, but fossil remains from them have already revealed at least five different kinds of Neogene turtles (Weems et al., 2025).

The deposits at Pedro and Herminio creeks largely consist of fossil remains clearly redeposited into recent alluvial sediments eroded from the San Gerardo unit. This unit, previously referred to as the Río Boquilla unit (Laurito & Valerio, 2005) or Curré Formation (e.g., Laurito et al., 2005; Laurito & Valerio, 2008a), lies unconformably over the currently defined Térraba Formation (Fig. 2) [referred to as possible Middle Miocene Curré Formation in Laurito & Valerio, (2008a) and subsequent contributions]. For a detailed explanation of why these two units should be distinguished, see Weems et al. (2025). The San Gerardo unit is primarily composed of intercalated claystone, sandstone, and conglomerate layers. At Pedro Creek, the lowest observed deposits are of shallow marine origin, whereas the overlying beds reflect significant fluvial-alluvial input in a transitional to fully continental deltaic environment (Fig. 3). Some of these beds contain abundant, as-yet not identified fossils, together with remains of *Boa constrictor* and turtles such as *Apalone*, *Dermatemys*, *Hesperotestudo*, and *Pseudemys* (Weems et al., 2025).



#	Series	Stage	NALMA / Plank. zone	Ma	Fossils	Method
I	Mio-Pliocene	Tortonian-Zanclean	Hemphillian (Hh1-Hh4)		Vertebrate	Biostratigraphy
I	Miocene	Messinian (terminal)	Hemphillian (Hh3)	5.8	Oyster	$^{87}Sr/^{86}Sr$ dating
II	Miocene	Langhian (basal)	M6		Plankt. foram.	Biostratigraphy
III	Miocene	Langhian (basal)	M6		Plankt. foram.	Biostratigraphy
IV	Miocene	Burdigalian (top)-Langhian (basal)	M5a-M6		Plankt. foram.	Biostratigraphy

Figure 1: Location and geologic map of the studied area in southern Costa Rica. The snake fossil localities discussed in this paper are: 1 = San Gerardo Creek; 2 = Pedro Creek; 3 = Herminio Creek. Abbreviations on the geologic map and table: C. = Creek; Plank. zone = planktonic foraminifera biozones; Plankt. foram. = planktonic foraminifera. Age determinations are based on the following sources: I = unnamed creek southwest of San Gerardo (Laurito & Valerio, 2010, 2012a, 2012b, 2016; Valerio, 2010; Valerio & Laurito, 2012, 2014, 2020; Rincón et al., 2020; Valerio, Laurito, McDonald, & Rincón, 2022). Field observations point to an inaccurate stratigraphic position given for these ages, falling into the Lower Miocene deposits of

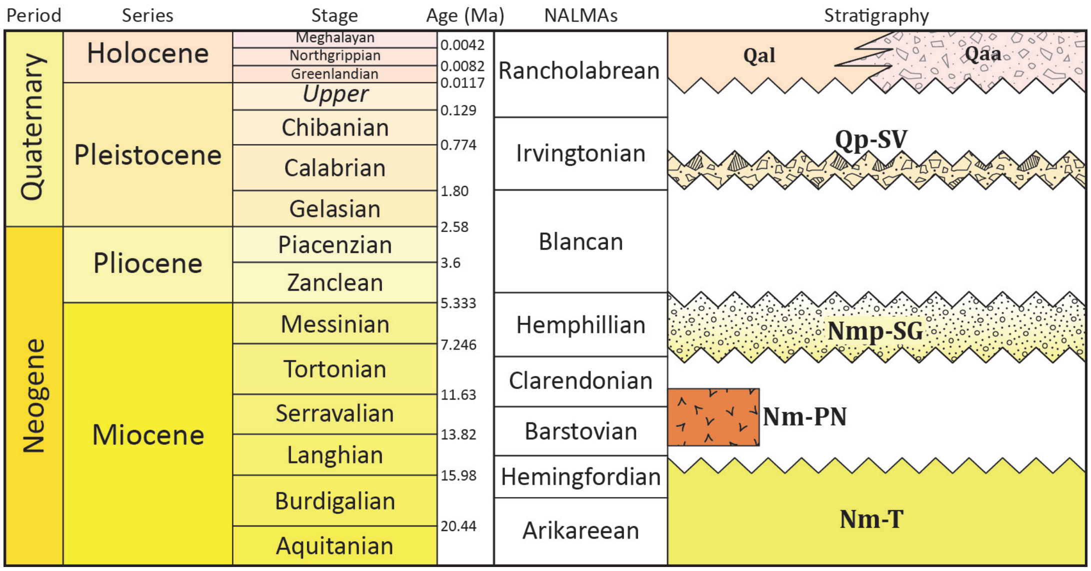


Figure 2: Chart illustrating the geologic timescale, the North American land-mammal "ages" (NALMAs), and the regional stratigraphy of San Vito. Snake fossil localities are primarily derived from the Hemphillian-aged San Gerardo unit (Nmp-SG), while most discoveries have been reworked into Holocene alluvial deposits (Qal). Other abbreviations are: Qaa (Quaternary alluvial fan), Qp-SV (Quaternary Pleistocene San Vito unit), Nm-PN (Neogene Miocene Puerto Nuevo Formation) and Nm-T (Neogene Miocene Térraba Formation).

In general, the San Gerardo unit yields mostly fossil bones of Upper Miocene (Hemphillian North American land-mammal "age") mammals, such as *Gomphotherium*, *Dinohippus* and *Protohippus*. An age of late Hemphillian (Hh3), or Messinian, approximately 5.80 Ma ± 0.60/0.80 Ma, has been determined based on the $^{87}Sr/^{86}Sr$ ratio from an oyster shell (Rincón et al., 2020). However, field research at San Gerardo Creek and nearby localities (Pedro, William and Herminio creeks) has identified a few mammal fossils that could potentially be younger (Pliocene or Pleistocene), although these remains require further study and assessment. Consequently, the *Boa constrictor* fossils presented here are tentatively considered of Hemphillian age, while a possible younger age cannot be ruled out at this time.

Description

Fossils numbered CF 6616 and CF 6653 are curated in the San Vito branch of the paleontological collection of the Central American School of Geology (Escuela Centroamericana de Geología – ECG).

the Térraba Formation; II–IV = Upstream section of the Limoncito River, south of San Vito (Yuan, 1984). Yuan's (1984) age determinations were revised using the chart by Wade et al., (2011) and two online foraminiferal catalogs: "Cenozoic Planktonic Foraminifera" (https://www.mikrotax.org/), and the "World Register of Marine Species (WoRMS)" (https://www.marinespecies.org/). Updated concurrent acrozones were generated using the free software MicroStratiRange, developed by the Institute for Research in Stratigraphy of the University of Caldas (https://microstratirange-iies.site/). Geographic coordinates are provided in the international WGS84 grid (left and top) and the national CRTM05 grid (right and bottom).

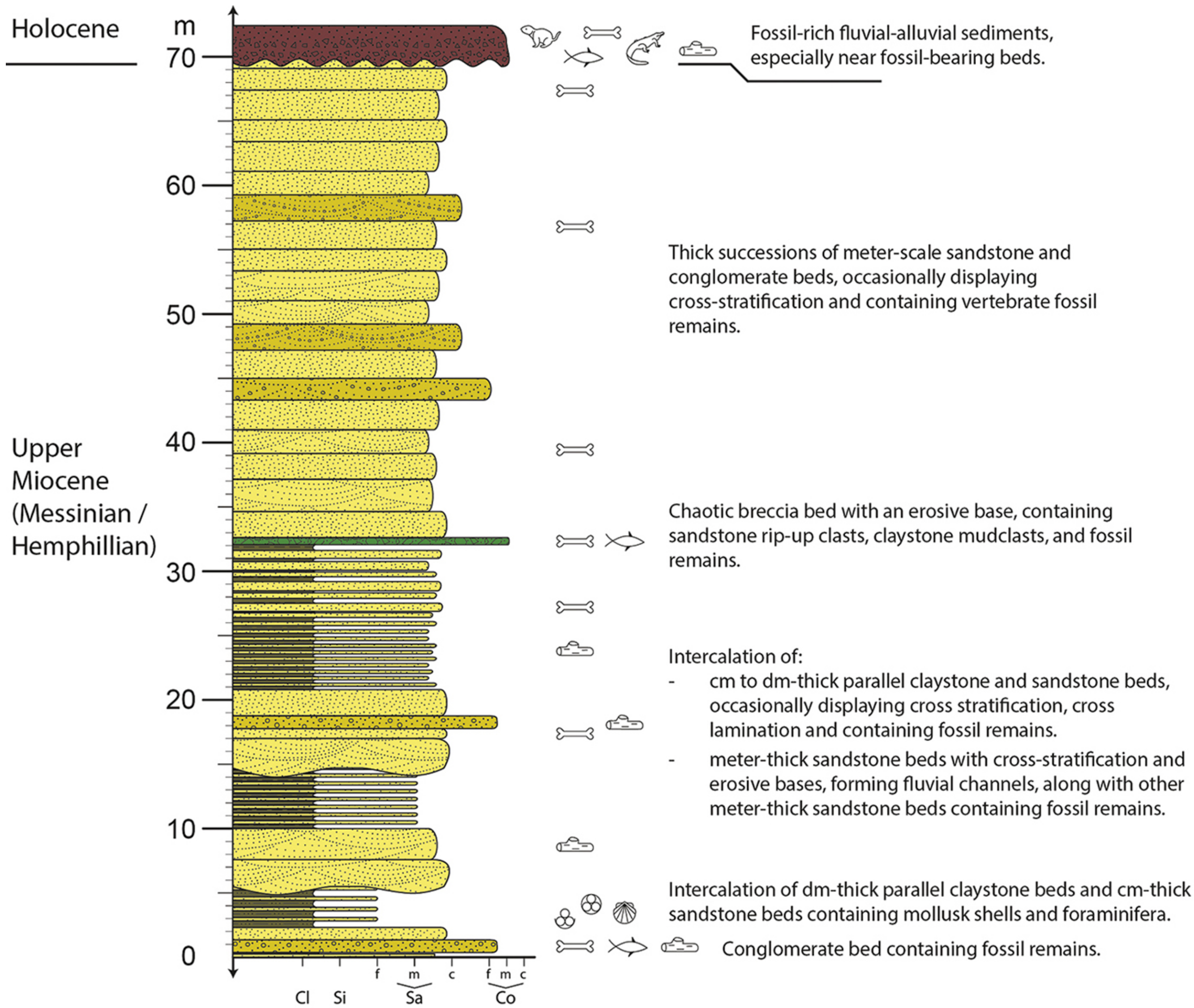


Figure 3. Stratigraphic column at Pedro Creek, showing at least seven documented fossiliferous beds. Note that the fossil remains, including the probable *Boa constrictor* vertebra, were mostly recovered from Holocene alluvial sediment deposits.

The specimen MNCR CFM 2032 belongs to the collection of the Costa Rican National Museum (Museo Nacional de Costa Rica – MNCR). Both CF vertebrae are mostly complete, except for their broken neural spines. The MNCR vertebra is less well-preserved, with a partially missing neural spine, abraded transverse processes, and rock matrix covering part of the bone, notably filling the neural canal. Due to its poor preservation, it is not illustrated. The presence of synapophyses and ventral (haemal) keels confirms that all three vertebrae are from the anterior region of the pre-cloacal (trunk) vertebral column (cf. Head et al., 2012).

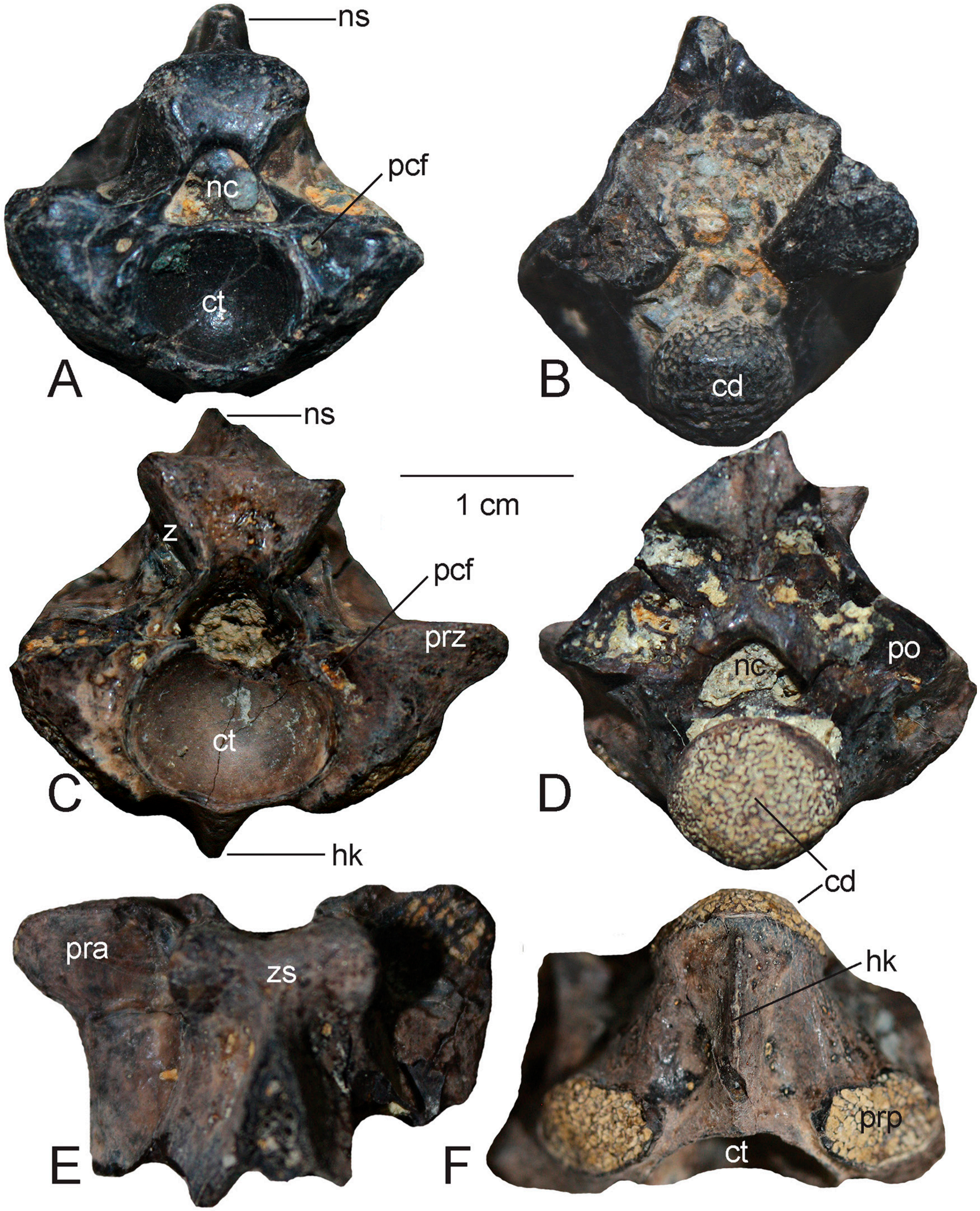


Fig. 4: Dorsal vertebrae of *Boa constrictor* from the Upper Miocene of southern Costa Rica. A–B: CF 6616 in anterior (A) and posterior (B) views. C–F: CF 6653 in anterior (C), posterior (D), dorsal (E), and ventral (F) views. Abbreviations: cd = condyle, ct = cotyle, hk = haemal keel, nc = neural canal, ns = neural spine, pa = parapophysis, pcf = paracotylar foramen, po = postzygapophysis, pra = prezygapophyseal articular facet, prp = prezygapophseal accessory process, prz = prezygapophysis, z = zygantrum.

These vertebrae share an identical morphology, allowing them to be assigned to a single taxon (Fig. 4). They are wider than long, with a large and elaborate neural arch and associated zygapophyses. The vertebrae are procoelous, featuring a cup-like cotyle (anterior articular surface) that appears semicircular in anterior view, being slightly wider than tall. The neural canal is slightly narrower and has a subtriangular cross section in anterior view. Relatively large paracotylar fossae flank the cotyle dorsolaterally and contain distinct paracotylar foramina along their dorsomedial margins. The prezygapophyses are nearly horizontal, projecting laterally from a level slightly dorsal to the cotyle. Consequently, the postzygapophyseal facets are long, wide, and inclined slightly above the horizontal plane. The prezygapophyses exhibit oval articular facets.

The zygosphene is tall and slightly narrower than the cotyle in anterior view. Its articular facets are elevated, slightly convex laterally, and oriented at a high angle. The base of the neural spine originates from the posterodorsal margin of the zygosphene, with its base displaying a posterior concavity. The interzygopophyseal ridge is broad and continuous, extending from the posterior margin of the prezygapophysis to the anterior margin of the postzygapophysis.

Each vertebra is triangular in ventral view, with a concave ventral margin between large synapophyseal bases. The lateral margins of the centrum extend from the synapophyses to the condyle. A sharp haemal keel runs ventrally from the cotyle to the condyle, defining two prominent paralymphatic fossae on either side. The measurements of each vertebra are shown in table 1.

Identification

The identification of *Boa constrictor* is based on a combination of vertebral features, including a straight, posteromedially angled interzygapophyseal ridge, well-developed paracotylar foramina within deep fossae, a relatively tall neural spine, and a tall, thickened zygosphene (e.g., Albino & Carlini, 2008; Albino, 2011; Head et al., 2012; Pyron et al., 2014; Onary-Alves et al, 2017; Bochaton & Bailon, 2018). As noted by Head et al. (2012), none of these characters are uniquely diagnostic of *Boa* when considered individually or in partial combination. However, the simultaneous occurrence of all these features are distinctive just to the genus *Boa* compared to other known boids (see the other boid genera listed in Pyron et al., 2014, Table 1). *Boa* is a monospecific genus, and the San Vito specimens are consistent with the extant of *Boa constrictor*, supporting their tentative assignment to this species, pending the discovery of more complete material.

Paleobiogeography

Fossil and molecular evidence suggests that boid snakes originated in South America during the Paleogene (see review by Head et al., 2012). The oldest record of boids in North America dates back to the Early Miocene of Florida (e.g., Auffenberg, 1963), while Miocene boid fossils have been documented in South America from Colombia and Argentina (Albino & Brizuela, 2014). The only previously published Central American boid fossils are vertebrae from the Lower Miocene (~ 19 Ma) of Panama (Head et al., 2012). By at least the Late Miocene, boids had reached southern Costa Rica.

Table 1

Measurements, in millimeters, of the centrum length, cotyle width and condyle width for each of the three vertebrae of *Boa constrictor*.

Catalog number	Centrum length (mm)	Cotyle width (mm)	Condyle width (mm)
CF 6616	16.1	8.5	8.5
CF 6653	14.1	10.3	9.7
MNCR CFM 2032	-	7.5	7.8

However, the exact route by which boids reached Costa Rica remains uncertain. The North American Miocene boid record has been used to propose a dispersal route from South to North America via the Antilles (Albino, 2011). In contrast, the Miocene *Boa* fossils from Costa Rica support the suggestion by Head et al. (2012) that there may have been bidirectional (north-south) dispersal, with Central American boids indicating immigration from either South or North America.

Given that snakes are capable of crossing water due to their morphology and metabolism, the Central American distribution of boids does not necessarily correlate with the timing of closure of the Central American seaway, which linked Panama to northern South America (e.g., Kirby & MacFadden, 2005; Montes et al., 2015; O'Dea et al., 2016). Thus, boids immigrating to Costa Rica from South America across a seaway is as possible as their dispersal from North America across land. While boid snakes had dispersed into Central America by the Miocene, additional, well-dated fossil evidence will be necessary to determine their precise origin.

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