

## First Record of *Boa constrictor* (Serpentes, Boidae) in the Quaternary of South America

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**ABSTRACT.**—Vertebral remains assignable to the extant snake *Boa constrictor*, found in the Toropí Formation (Late Pleistocene, Lujanian age) at Arroyo Toropí, northeastern Argentina, are here described. These remains represent the first snake record from the Lujanian age and determine the minimum age for the species as 50–35 ka BP. *Boa* is presently absent in northeastern Argentina. Interruption of the continuity between the Mesopotamian and Brazilian faunas, including disappearance of *Boa* from Mesopotamia (northeastern Argentina), occurred subsequent to the Late Pleistocene and might be explained by changes in the Paraná and Uruguay Rivers. In addition, previous taxonomic referral of fossils to ?*Boa* is revised, with the conclusion that the specimen from the Early Eocene is tentatively referred to this genus, whereas that from the Pliocene is an indeterminate Boinae.

Burbrink (2005) analyzed the relationships among extant Boinae and obtained a phylogeny with two main sister groups, one including *Candoia* (Eastern Pacific), *Sanzinia*, and *Acrantophis* (Malagasy region); and another one including the boines of the Neotropical region, *Boa*, *Corallus*, *Epicrates*, and *Eunectes*. *Boa constrictor*, the single species of the genus, is a 2–4 m long snake distributed from northern Mexico to Argentina (Waller and Micucci, 1993). Among all boines, *B. constrictor* is the least specialized, with terrestrial or subarctic habits, and exploiting a wide variety of environments, from tropical woodlands, savannas, and deserts to cultivated grasslands (Parker and Grandison, 1977; Henderson et al., 1995). Within the species, 10 subspecies are considered valid (Uetz and Hallermann, 2007), among which *Boa constrictor occidentalis* is the only one living in Argentina, in addition to southern Bolivia and western Paraguay (Langhammer, 1983; Waller and Micucci, 1993; Henderson et al., 1995). It occupies environments of the semiarid “Chaco” biome in the Argentine provinces of Catamarca, Córdoba, Chaco, Formosa, Jujuy, La Rioja, Mendoza, Salta, San Juan, San Luis, Santa Fé, Santiago del Estero, and Tucumán (Giraudo and Scrochi, 2002).

Recently, vertebral remains of *B. constrictor* have been found in Quaternary sediments near the sources from the Arroyo Toropí (28°36'S, 59°02'W), 10 km south from Bella Vista, Bella Vista Department, Corrientes Province, Argentina (Fig. 1). The fossil-bearing level of the

remains studied here belongs to the Toropí Formation described by Herbst and Álvarez (1977) for the upper level of the calcrete. The age of this formation, based on the fossil content, was controversial, but it has always been referred to the Pleistocene (see Herbst and Santa Cruz, 1999; Iriondo, 1996; Scillato Yané et al., 1998; Carlini et al., 2004). More recently, the Toropí Formation has been referred to the latest Pleistocene on the basis of OSL (Optic Stimulated Luminescence) dating that yielded ages between 50 ka and 35 ka BP; that is, Lujanian sst. (Tonni et al., 2005), which matches the chronological data inferred through the faunal content in recent reviews (Carlini et al. 2004; Tonni et al. 2005).

The main goal of this paper is to describe the snake remains of the Toropí Formation found at the source of the Arroyo Toropí, to discuss their significance, and to make a revision of the previous assignments of fossils from the Early Eocene and Pliocene of Argentina to the genus *Boa* (Albino, 1992, 1993).

### MATERIALS AND METHODS

Most of the remains from the Toropí Formation are extremely fragmentary. They belong to anterior, middle, and posterior trunk vertebrae; cloacal and caudal vertebrae have not been conserved. The remains include zygosphenes, vertebral centra, isolated pre- and postzygapophyses, and halves of vertebrae. Among the best-preserved remains, there is an almost complete anterior trunk vertebra (Fig. 2A–E) and a midtrunk vertebra (Fig. 2F–J), on which the comparative descriptions were based. Ad-

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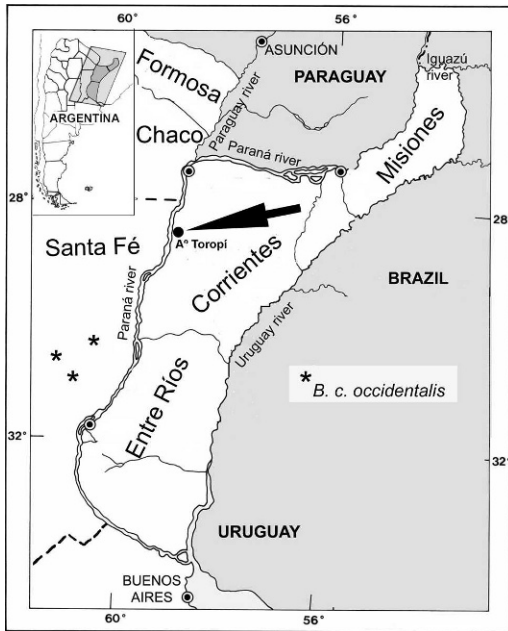


FIG. 1. Location map of the paleontological site.

ditional material does not show significant variation with respect to these vertebrae. Because all vertebral remains were closely associated in an area of 0.5 m<sup>2</sup> and the vertebral morphology shows a great homogeneity, we assume they belong to a single individual. Skeletons of extant boas were used for comparisons (Table 1). The systematic arrangement follows Lee and Scanlon (2002).

Institutional abbreviations are FMNH, Field Museum of Natural History, USA; HAA, private Herpetological collection of Adriana Albino; MACN-Pv, Colección Nacional de Paleovertebrados, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires; MLP, Museo de La Plata, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata; PZ-Ctes, Paleozoología Corrientes, Facultad de Ciencias Exactas y Naturales y Agrimensura, Universidad Nacional del Nordeste, Corrientes.

Systematic Paleontology  
 Serpentes Linnaeus, 1758  
 Alethinophidia Nopcsa, 1923  
 Macrostromata Müller, 1831  
 Booidea Gray, 1825  
 Boinae Gray, 1825  
*Boa* Linnaeus, 1758  
*Boa constrictor* Linnaeus, 1758

#### Figure 2

*Referred Specimens.*—PZ-Ctes 7351, 87 associated fragmentary trunk vertebrae.

*Comparative Description.*—The anterior trunk vertebra (PZ-Ctes 7351-1) lacks the distal end of the hypapophysis, both paradiapophyses and the condyle (Fig. 2A–E). The midtrunk vertebra (PZ-Ctes 7351-2) has not preserved most of the neural spine, the right prezygapophysis and both paradiapophyses (Fig. 2F–J). The specimens share with the Boinae the following combination of characters (Fig. 2): strongly built, high, short, and wide vertebrae; high neural arch and neural spine; posterior margin of the neural arch strongly notched; thick zygosphenes; low inclination of the articular facet of the prezygapophysis (less than 15°); short prezygapophysial process; vertebral centrum shorter than the neural arch width ( $cl/naw < 1$ ); well-defined precondylar constriction; haemal keel in midtrunk vertebrae; and lateral, subcentral, and paracotylar foramina present (Rage, 2001; Lee and Scanlon, 2002; Szyndlar and Rage, 2003). The anterior vertebrae are slightly smaller than the middle ones; they have a higher neural arch, thinner zygosphenes, and shorter and almost horizontal pre- and postzygapophyses (Table 1; Fig. 2). In addition, the anterior trunk vertebrae have a long hypapophysis on the ventral surface of the centrum (Fig. 2B,C), whereas in the midtrunk vertebrae, there is a well-developed, thin haemal keel (Fig. 2H,J). The absence of hypapophysis in midtrunk vertebrae distinguishes the fossil specimens from the derived condition seen in *Candoia*, in which the hypapophysis is well developed in the vertebrae all along the trunk (Underwood, 1967; Kluge, 1991; Lee and Scanlon, 2002; pers. obs.). According to Kluge (1991), the presence of a paracotylar foramen at both sides of the cotyle is a derived character state within the boines, shared by *Acrantophis*, *Sanzinia*, *Boa*, and some species of *Corallus*. The two first genera have paracotylar foramina only in a few vertebrae and irregularly along the vertebral column (Kluge, 1991; Rage, 2001), unlike in *Boa*, *Corallus annulatus*, and *Corallus cropanii*, in which it is always present (Kluge, 1991; pers. obs.). In the fossil remains of Arroyo Toropí, the paracotylar foramen is regularly present along the column, as it is seen in all vertebral fragments in which the cotyle has been preserved. The opening of the foramen is especially large in the species of *Corallus* (Kluge, 1991), unlike in *Boa* and the fossils of Arroyo Toropí in which this foramen is small (Figs. 2A,F).

In addition, the vertebrae of *B. constrictor* and the fossil specimens are distinct from those of the other Neotropical boines by having a very thick zygosphenes (>30% of the width, Table 1), with concave anterior surface and an anterior margin notched in dorsal view (Figs. 2D,I). The

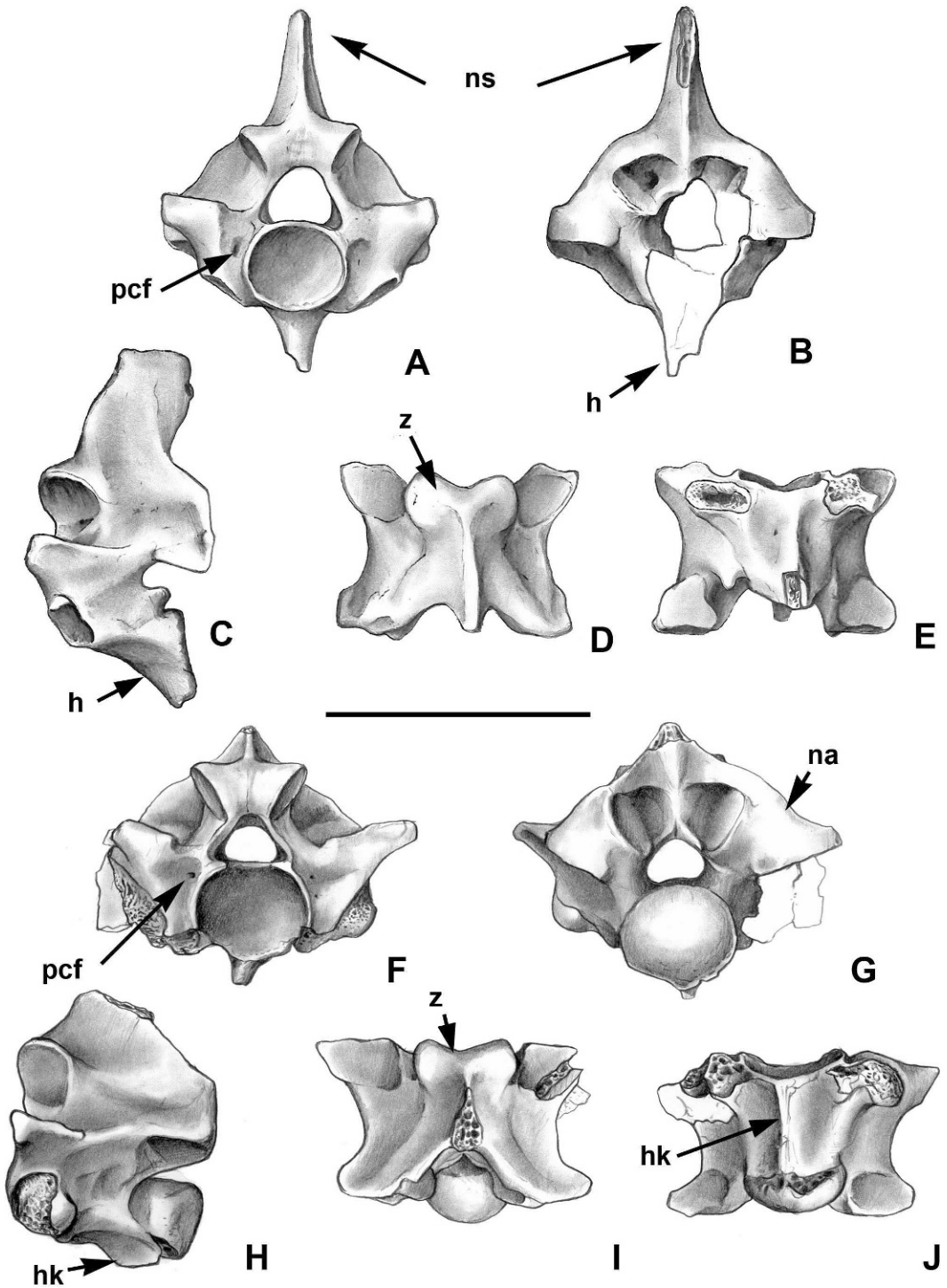


FIG. 2. Vertebrae of *Boa constrictor* from the paleontological site. (A-E) anterior trunk vertebra (PZ-Ctes 7351-1); (F-J) midtrunk vertebra (PZ-Ctes 7351-2). Anterior (A and F), posterior (B and G), lateral (C and H), dorsal (D and I), and ventral (E and J) views; na, neural arch; ns, neural spine; h, hypapophysis; hk, haemal keel; pcf, paracotylar foramen; z, zygosphenes. Scale bar equals 2 cm.

TABLE 1. Comparative measurements of anterior (Ant) and midtrunk vertebrae (Mid) of the fossil specimens from Arroyo Toropí and modern Neotropical boas. Nonavailable data are marked with a dash.

Species	Collection number	% zh/zw		% cl/naw	prl/prw	
		Ant	Mid	Mid	Ant	Mid
Fossil specimens	PZ-Ctes 7351	42	44	61	1.51	1.87
<i>B. c. occidentalis</i>	HAA 13	42	43	65	1.39	2.12
<i>B. c. occidentalis</i>	HAA 14	35	40	58	1.44	1.90
<i>B. c. occidentalis</i>	HAA 15	36	37	64	1.61	2.12
<i>B. c. occidentalis</i>	HAA 16	37	39	64	1.30	1.91
<i>B. c. occidentalis</i>	HAA 19	34	35	62	1.56	2.04
<i>B. c. occidentalis</i>	HAA 25	33	33	61	1.34	2.00
<i>B. c. occidentalis</i>	FMNH 211926	32	38	62	1.27	2.00
<i>B. c. occidentalis</i>	FMNH 22353	30	35	65	1.39	2.00
<i>Eunectes notaeus</i>	HAA 18	29	29	77	1.46	1.59
<i>Eunectes murinus</i>	FMNH 212710	27	29	70	1.69	1.87
<i>Epicrates cenchria</i>	HAA 1	16	21	80	1.51	1.41
<i>Epicrates cenchria</i>	HAA 6	15	19	96	1.72	1.37
<i>Corallus cookii</i>	FMNH 212337	-	14	68	-	1.42
<i>Corallus caninus</i>	FMNH 223192	-	25	70	-	1.45

centrum of the midtrunk vertebrae is also shorter ( $\leq 65\%$  of the neural arch width, Table 1), and the prezygapophysial articular facets are longer (around twice their width, Table 1) and more laterally oriented than in the remaining compared species. The studied vertebrae and those of *Boa* also share, although not exclusively, a large size, elevated and vaulted neural arch in posterior view and high neural spine (Fig. 2). Consequently, the material from Arroyo Toropí is assigned to *B. constrictor* because no difference could be seen with the comparative material of this species.

The variation between anterior and midtrunk vertebrae described for the fossil specimens is also observed in the Recent skeletons of *B. constrictor* (Table 1). The best-preserved midtrunk vertebra (Fig. 2F-J) is approximately equal in size as a vertebra of the same region of an adult specimen 205 cm long when living.

*Measurements (in millimeters).*—Anterior trunk vertebra: cth (cotyle height) = 5.30; ctw (cotyle width) = 5.66; naw (neural arch width at interzygapophysial constriction) = 12.86; nch (neural canal height) = 3.00; ncw (neural canal width) = 4.68; po-po (distance between postzygapophyses) = 16.72; pr-po (distance between pre- and postzygapophysis of the same side) = 11.48; pr-pr (distance between prezygapophyses) = 16.48; prl (prezygapophysial length) = 5.26; prw (prezygapophysial width) = 3.48; zh (zygosphene height) = 3.12; zw (zygosphene width) = 7.46. Midtrunk vertebra: cl (centrum length) = 10.68; coh (condyle height) = 7.00; cow (condyle width) = 7.64; cth = 7.28; ctw = 8.24; naw = 17.36; nch = 7.28; ncw = 5.30; prl = 7.48; prw = 4.00; zh = 3.64; zw = 8.24.

## DISCUSSION

Fossil specimens referred to *?Boa* sp., were reported for the Early Eocene of Gran Barranca, Chubut Province (Albino, 1993) and for the Pliocene of Monte Hermoso, Buenos Aires Province (Albino, 1992), both in Argentina. With respect to the former, the poor preservation of the single vertebra (MACN-Pv 10875) prevents comparison of some characters, which according to this study are typical of *Boa* (notched dorsal margin and concave anterior surface of the zygosphene, length of the prezygapophyses almost twice the width). Noteworthy, as in this genus, the paracotylar foramina are present and the zygosphene would have been very thick (Albino, 1993; Fig. 3). The well-defined, thick haemal keel and the slight depression of the neural arch, as well as the length of the centrum (cl/naw = 73%) match with the posterior trunk vertebrae of *Boa* (Albino, 1993); hence, a tentative assignment to this genus is supported. Concerning the vertebra from the Pliocene of Monte Hermoso (MLP 87-II-25-1), which has also paracotylar foramen, it differs strongly from midtrunk vertebrae of *Boa* in the greater length of the centrum (cl/naw = 88%), the short prezygapophyses, the moderately thick zygosphene (zh/zw = 21%), and the thick haemal keel. Although these characters are variable in *Boa* along the trunk vertebrae, and a posterior vertebra could share these features, it is noteworthy that the neural spine is clearly high as in the midtrunk vertebrae and contrary to the posterior vertebrae of *Boa* in which it is lower, suggesting this specimen belongs to a different taxon. In addition, the prezygapophyses are almost hor-



FIG. 3. Approximate area of distribution of *Boa constrictor occidentalis*, *Boa constrictor amarali*, and *Boa constrictor constrictor*.

izional, set at a high level, and the anterior margin of the zygosphenon is rather straight, but because it is incompletely preserved, this cannot be seen clearly. Consequently, the affinity of this vertebra with those of *Boa* is dubious, and we consider it as an indeterminate *Boinae*.

According to Rage (2001), the lineages of modern boines would have originated early in the Tertiary or in the Late Cretaceous. Phylogenetic information suggests that *Boa* is the most basal extant lineage among Neotropical boines (Burbrink, 2005). The recognition of the genus *Corallus* in the Middle Paleocene of Brazil (Rage, 2001) and the confirmation of the presence of a probable *Boa* in the Early Eocene of Argentina (Albino, 1993; this study) suggest that the cladogenesis that originated the genus *Boa* would have occurred at least at the beginning of the Tertiary.

Boines were much more widely distributed during most of the Cenozoic than today, even reaching the Patagonian region in the Early Tertiary (Albino, 1993, 1996). At present, they do not surpass the latitude of 34°S. Their northward retraction would have been caused by climatic-environmental changes that affected most of southern South America during the Tertiary, restricting the distribution of the sub-

tropical herpetofauna (Albino, 1996). The Pliocene record in the southern Buenos Aires Province (Albino, 1992) suggests that, by the end of the Tertiary, the boines still inhabited regions where they are not found today.

The specimens of *B. constrictor* reported in this paper for Lujanian levels (Late Pleistocene) of Argentina represent the first snake record of this age and determine the minimum age for this species. These fossils are out of the range of the modern distribution of the species, because it is not found today in the Mesopotamian region of Argentina (provinces of Entre Ríos, Corrientes, and Misiones, Figs. 1, 3; Giraudo and Scrochi, 2002). The nearest populations of *B. constrictor* with respect to the fossiliferous locality are those of the provinces of Chaco, Formosa, and Santa Fé (9 de Julio, Garay and La Capital Departments), located west of the Paraná River (Bosisio and Trucco, 2002; Giraudo and Scrochi, 2002). The isolated population of *B. constrictor* reported for northwestern Uruguay, east of the Paraná and Uruguay Rivers and approximately 2° south of the fossiliferous locality of Arroyo Toropí (according to the distribution map of Henderson et al., 1995) has not been confirmed and appears to be erroneous (T. Waller, pers. comm.).

The paleoclimatic interpretation, based on the mammal fauna recovered in the same sediments of the studied snake material, suggests that the model inferred for the Pampean region, central-northern Argentina, Paraguay, and southern Bolivia does not apply to the Mesopotamian region, because in the Chaco-Pampean plains the regime was still colder and more arid by these times (Tonni and Figini, 1999). At least during a large part of the Pleistocene, the Mesopotamian region would have had a more humid and warmer climate, with a marked influence of Brazilian fauna that would have continued even during the last interglacial (Scillato-Yané et al., 2002; Carlini et al., 2004). Paleoclimatic differences implied by the vertebrate fauna have been supported by evidence from other sources, especially sedimentological ones (Iriando and García, 1993). Taking into account the notable Brazilian relationships of the associated mammal paleofauna in Arroyo Toropí, probably, the boas that inhabited the Mesopotamian region during the deposition of the Toropí Formation would have been genetically related to the Brazilian populations of *B. constrictor*. Two subspecies of *B. constrictor* inhabit Brazilian environments, *Boa constrictor constrictor* and *Boa constrictor amarali* (Fig. 3). The former is the most widely distributed in South America, including the whole Amazonian, Orinoquia and Guyana regions up to Rio de Janeiro (Brazil) by the Atlantic coast. *Boa*

*constrictor amarali* is geographically intermediate between *B. c. constrictor* and *B. constrictor occidentalis* and is found in northeast Paraguay ("cerrado" and high basins of the Paraná and Paraguay Rivers), east of Bolivia, and southeast and southwest Brazil (out of the Atlantic slope; Price and Russo, 1991; Waller and Micucci, 1993; Giraud, 2001). The hydric regime of the Paraná and Paraguay Rivers in the most humid periods of the Pleistocene could have caused the interruption of the continuous distribution of *B. constrictor* favoring the differentiation of a subspecies better adapted to the arid habitats of the western regions (*B. c. occidentalis*). This hypothesis is supported by the fact that living specimens at the east of the Paraguay River, in Paraguay and bordering areas of Brazil (in ecotonal environments of the "cerrado"), are populations of *B. constrictor amarali*, whereas at the same latitude but on the western margin of the Paraguay River (dry "Chaco" biome) the specimens are typical of *B. c. occidentalis* (Waller and Micucci, 1993). These authors proposed that the eastern "Chaco," where none of these forms occur, would act as a geographical barrier.

The break between the Mesopotamian and the Brazilian fauna subsequent to the Late Pleistocene, which occurred as a consequence of the changes in the main rivers that delimit this region (Paraná and Uruguay, Fig. 1), would have established the insularity conditions of Mesopotamia, leading to the extinction of some Brazilian elements. The disappearance of *B. constrictor* from this area may be attributed to this isolation.

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