



EXTANT SQUAMATES IN THE PLEISTOCENE OF NORTHWESTERN ARGENTINA

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ABSTRACT – Squamates are a common component of the present vertebrate communities of Northwestern Argentina, although their fossil record in this region is scarce. In the present contribution, remains of extant genera of squamates from the Pleistocene of Santiago del Estero Province (Argentina) are described. An incomplete hemimandible of the teiid lizard *Tupinambis* and a short section of a vertebral column of the boid snake *Epicrates* are recognized. The presence of *Tupinambis* and *Epicrates* in the Pleistocene of the Termas de Río Hondo coincides with the current distribution of these genera. These records increase the knowledge on the Quaternary herpetofauna of Northwestern Argentina.

Keywords: Squamata, Pleistocene, Argentina, *Tupinambis*, *Epicrates*.

RESUMO – Squamata é um componente comum das comunidades de vertebrados presentes do Noroeste da Argentina, embora o seu registro fóssil nesta região seja escasso. Na presente contribuição são descritos restos de gêneros vivos de Squamata provenientes do Pleistoceno de Província do Santiago del Estero (Argentina). São reconhecidos hemimandíbula incompleta do lagarto Teiidae *Tupinambis* e uma pequena seção de uma coluna vertebral da serpente Boidae *Epicrates*. A presença de *Tupinambis* e *Epicrates* no Pleistoceno da Termas de Río Hondo coincide com a distribuição atual de destes gêneros. Estes registros aumentam com o conhecimento da herpetofauna Quaternária da região do Noroeste da Argentina.

Palavras-chave: Squamata, Pleistoceno, Argentina, *Tupinambis*, *Epicrates*.

INTRODUCTION

The South American Quaternary record of squamates includes mainly specimens of extant families and genera. Iguania, geckonids, teiids, anguids, amphisbaenians, boids, colubrids, viperids, and elapids have been recognized (Albino & Brizuela, 2014). In Argentina, punctuated climatic and environmental changes during the Late Pleistocene resulted in changes in the distributional patterns of some genera (e.g. *Homonota*, *Boa*, *Boiruna*, *Bothrops*, and probably “*Cnemidophorus*”); thus, the present components of the squamate fauna would be already established in the Pleistocene, but changes in the distribution of the taxa would have still taken place (Albino & Brizuela, 2014).

The Northwestern of Argentina (NOA) is a geographic and historical region composed of the provinces of Catamarca, Jujuy, La Rioja, Salta, Santiago del Estero and Tucumán. Although living squamates are common in the NOA (Cei, 1993), the fossil record of the group in this region is scarce (Albino & Brizuela, 2014). Recent archaeological deposits

from Catamarca, Salta and Santiago del Estero have provided remains of *Liolaemus* Wiegmann, 1834 (Albino & Kligmann, 2007), *Tupinambis* Daudin, 1803 (Cione *et al.*, 1979; del Papa *et al.*, 2011; del Papa & Moro, 2014), and *Amphisbaena* Linnaeus, 1758 (Albino & Kligmann, 2009), but the NOA Pleistocene has not contributed with any specimen until the present.

In this paper, remains of extant genera of squamates collected in Pleistocene deposits that outcrop close to the Termas de Río Hondo city, in the Santiago del Estero Province (Figure 1), are described and discussed in the context of the South American fossil record of living squamates.

MATERIAL AND METHODS

Fossil specimens are deposited in the Museo Municipal “Rincón de Athacama”, Termas de Río Hondo, Santiago del Estero, Argentina (MPAT). The material was mechanically prepared to remove sediments. Disarticulation and remotion of the first partial vertebra from the vertebral column section

were necessary to expose the anterior face of one vertebra.

Recently, Harvey *et al.* (2012) performed an extensive study of external anatomical characters of Teiidae and resurrected the genus *Salvator* from the synonymy of *Tupinambis*. Unfortunately, the data sets used by Harvey *et al.* (2012) do not include osteological characters necessary for the evaluation of fragmentary fossil specimens. In addition, a recent molecular-based hypothesis has suggested the retaining of traditional teiid taxonomy (Pyron *et al.*, 2013). Taking into account that the phylogenetic relationships of Teiidae remain insufficiently understood, and that additional taxonomic changes are expected for the future (Pyron *et al.*, 2013), we follow here the traditional phylogeny and taxonomy proposed by Nydam *et al.* (2007), which include character states useful for identification of fossil specimens. Thus, we recognize two subfamilies of crown Teiidae, the Teiinae (*Ameiva*, *Aspidoscelis*, *Cnemidophorus*, *Dicrodon*, *Kentropyx*, *Teius*) and the Tupinambinae (*Callopistes*, *Crocodylurus*, *Dracaena*, *Lumbrerasaurus*, *Paradracaena*, *Tupinambis*), where the genus *Tupinambis* is composed by seven species, two of which are present in Argentina (*T. merianae* and *T. rufescens*).

The systematic scheme for Boidae follows Noonan & Chippindale (2006). The boines of the Neotropical region include the genera *Boa*, *Corallus*, *Epicrates*, and *Eunectes* (Burbrink, 2005; Noonan & Chippindale, 2006). The endemic Neotropical genus *Epicrates* is found in South America,

Central America and the West Indies, and comprises ten species distributed in two monophyletic groups (Burbrink, 2005; Noonan & Chippindale, 2006), without documented vertebral differences. The exclusively continental *E. alvarezii* is the unique species of the genus distributed in Argentina.

The identification of the specimens was based on character states described in the literature and cited below, where comparative analyses were made. Comparative osteological material of extant taxa, deposited in the Herpetological Collection of the Universidad Nacional de Mar del Plata, Osteology Section (UNMDP-O) and Field Museum of Natural History (FMNH), was also used to aid fossil identifications (Appendix 1).

The fossils come from about 10 km east of the Termas de Río Hondo city (27°29'50"S, 64°46'29"W), Río Hondo Department, Santiago del Estero Province, Argentina (Figure 1). The sediments of this area correspond to one of the Pleistocene and/or Holocene units that have been mentioned with different names in the literature, but without an appropriate stratigraphic systematization (Beder, 1928; Battaglia, 1982; Gramajo, 1992; Iriondo, 2010). A general section between the Río Hondo dam and the area of Sotelillo, approximately 20 km long, shows the following sequence: from the regular river level upwards, first appears the Las Cañas Formation, constituted by red and brown silty sandstones, with variable thickness between 6 and 10 m, covered in several places by

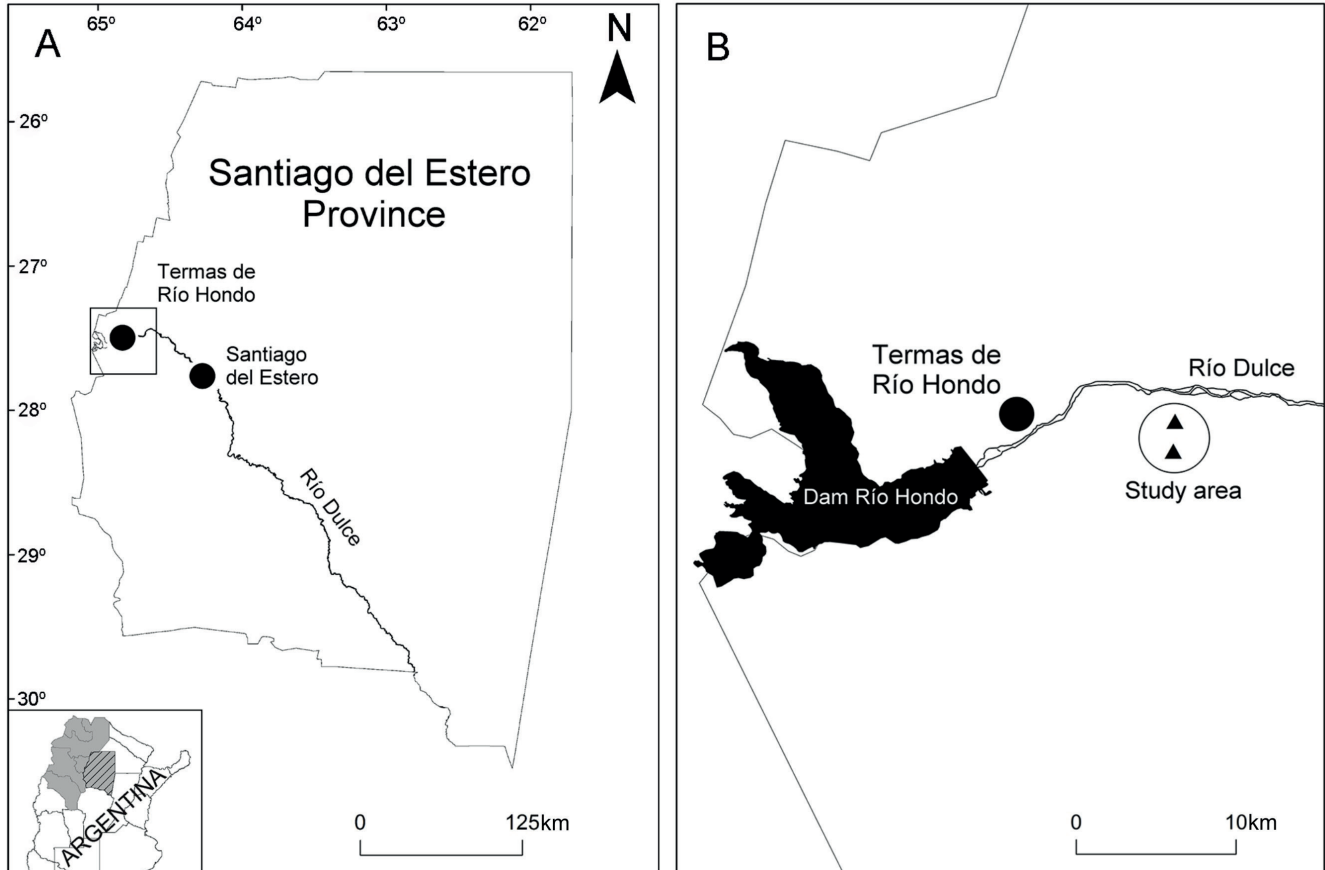


Figure 1. Maps showing the fossil locality. **A.** Santiago del Estero Province (small map with provinces of the NOA in grey, Santiago del Estero Province dashed). **B.** study area.

one or two hardened tuff levels (Battaglia, 1982). This is followed by about 10 m of coarse to medium and fine sands, in part conglomeratic, and grey and beige fine or sandy silts. At the top of this sequence, 78 m of loess covers the whole region. The studied material comes from this loessic level. In the area of the findings, the stratigraphic sequence starts with accumulations of calcareous rolls without exposed base. It continues with two or three meters of power of slightly silty clays and light brown loess. Battaglia (1982) considered these last deposits as being part of the Capellania Formation, which is upper Pleistocene. Recently, Iriondo (2010) defined three Quaternary formations for Santiago del Estero; however, the lithological descriptions of these formations do not coincide with the observed lithology in the studied area. On the contrary, this matches with the lithology described by Battaglia (1982) for the Capellania Formation.

SYSTEMATIC PALEONTOLOGY

SQUAMATA Oppel, 1811
 SCLEROGLOSSA Estes *et al.*, 1988
 SCINCOMORPHA Camp, 1923
 TEIOIDEA Estes *et al.*, 1988
 TEIIDAE Gray, 1827
 TUPINAMBINAE Bonaparte, 1831

Tupinambis Daudin, 1803

Tupinambis sp.
 (Figures 2A–B)

Referred specimen. MPAT 251, distal fragment of a left hemimandible.

Description. The poorly preserved material includes the anterior half of a left dentary and fragments of the articulated splenial. The dentary is preserved from the symphysis to the level of the anterior part of the tenth tooth socket. It is large, tall, and anteriorly lower than posteriorly. In labial view, the dentary is unornamented, and bears four mental foramina. In lingual view, it is possible to infer a Meckel's groove widely open up to the symphysis because the limits of hard sediments that fill the groove are marked. Meckel's groove accommodates the mainly broken splenial, which is included in sedimentary remains. The dentary shows a tall, well-developed subdental shelf. The anterior tip of the dentary ends at the symphyseal surface. Tooth attachment is subpleurodont (*sensu* Zaher & Rieppel, 1999), with extensive deposits of basal cementum and well-developed subdental gutter. In spite of the conservation of only four teeth on the dentary, the dentition is defined as clearly heterodont, with differential morphology along the tooth row. Basal sections of all teeth are almost circular. First, third, fourth and sixth teeth are missing; fifth tooth is scarcely preserved. The anteriormost-preserved tooth is located in the second tooth position; it is conical and unicuspidate. The seventh tooth is complete, with the same morphology but somewhat enlarged and with the sharp apex curved backward. The eighth tooth

is large, robust, and bicuspidate, with a slightly compressed crown where the anterior cusp is tiny and the larger posterior cusp is distally broken. The ninth tooth is similar to the eighth one but the crown is broken.

Comments. In the studied fossil dentary, the presence of a hypertrophied splenial is inferred from the widely open Meckel's groove and the fragmentary remains of this bone. This character, together with the subpleurodont implantation and the deposits (extensive but not extreme) of cementum on the tooth bases, characterizes the Tupinambinae, and specially the genus *Tupinambis* (Presch, 1974; Brizuela & Albino, 2010; pers. obs.). In addition, the robustness and size of the dentary is like in this genus (pers. obs.). A heterodont condition along the tooth row, with conical anterior teeth followed by enlarged bicuspid teeth, bearing a small mesial cusp (Figures 2A–B), is also observed in *Tupinambis* (Presch, 1974; Brizuela & Albino, 2010; Brizuela & Albino, 2012a, 2012b; pers. obs.). Due to the fragmentary conservation of the material, and the absence of clear distinctive tooth morphology among species of *Tupinambis*, a lower level assignation of the fossil is not possible.

SERPENTES Linnaeus, 1758
 ALETHINOPHIDIA Nopcsa, 1923
 MACROSTOMATA Müller, 1831
 BOIDAE Gray, 1825
 BOINAE Gray, 1825

Epicrates Wagler, 1830

Epicrates sp.
 (Figures 3A–F)

Referred specimen. MPAT 252, fragment of a vertebral column.

Description. The material includes 14 articulated and fragmentary vertebrae in a block (Figure 3A), and two incomplete vertebrae in another block. Both blocks were originally part of the same vertebral column section. Some fragmentary ribs remain articulate to the vertebrae. The vertebral section corresponds to a portion of the mid-trunk region, due to the presence of a well-developed haemal keel and high neural spine. The vertebrae are high, short, wide, and relatively small and delicate (Figure 3B). The neural arch is short, clearly vaulted, and its posterior edge is well-notched in the middle (Figure 3F). The neural spine is markedly high, vertical, and anteroposteriorly short (Figure 3D). The zygosphenes are rather thin, wider than the cotyle, and bears an anteriorly projecting median lobe (Figure 3F). The neural canal is comparatively large. The prezygapophyses are slightly inclined above the horizontal plane, and carry a short prezygapophyseal process, not visible in dorsal view. The interzygapophyseal ridge is short and deep. The vertebral centrum is short, anteriorly widened, and with a marked precondylar constriction. The cotyle and condyle are almost round. There are no paracotylar foramina, although a deep depression on each side of the cotyle is evident

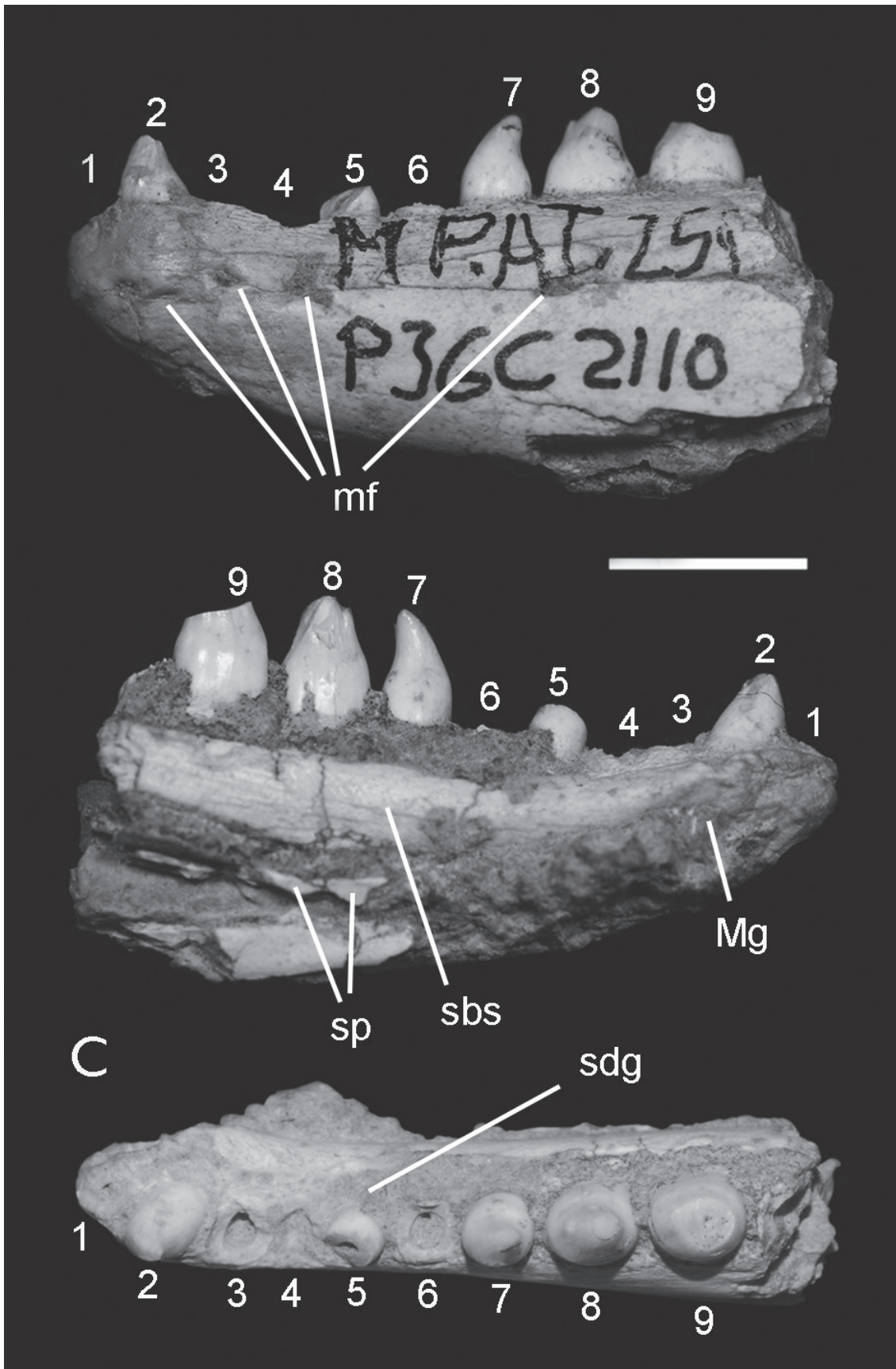


Figure 2. *Tupinambis* sp. MPAT 251, distal fragment of a left hemimandible; **A**, labial view; **B**, lingual view; **C**, occlusal view. Numbers indicate tooth positions along the tooth row. **Abbreviations:** **mf**, mental foramina; **sbs**, subdental shelf; **sdg**, subdental gutter; **sp**, splenial; **Mg**, Meckel's groove (filled by sediments). Scale bar = 5 mm.

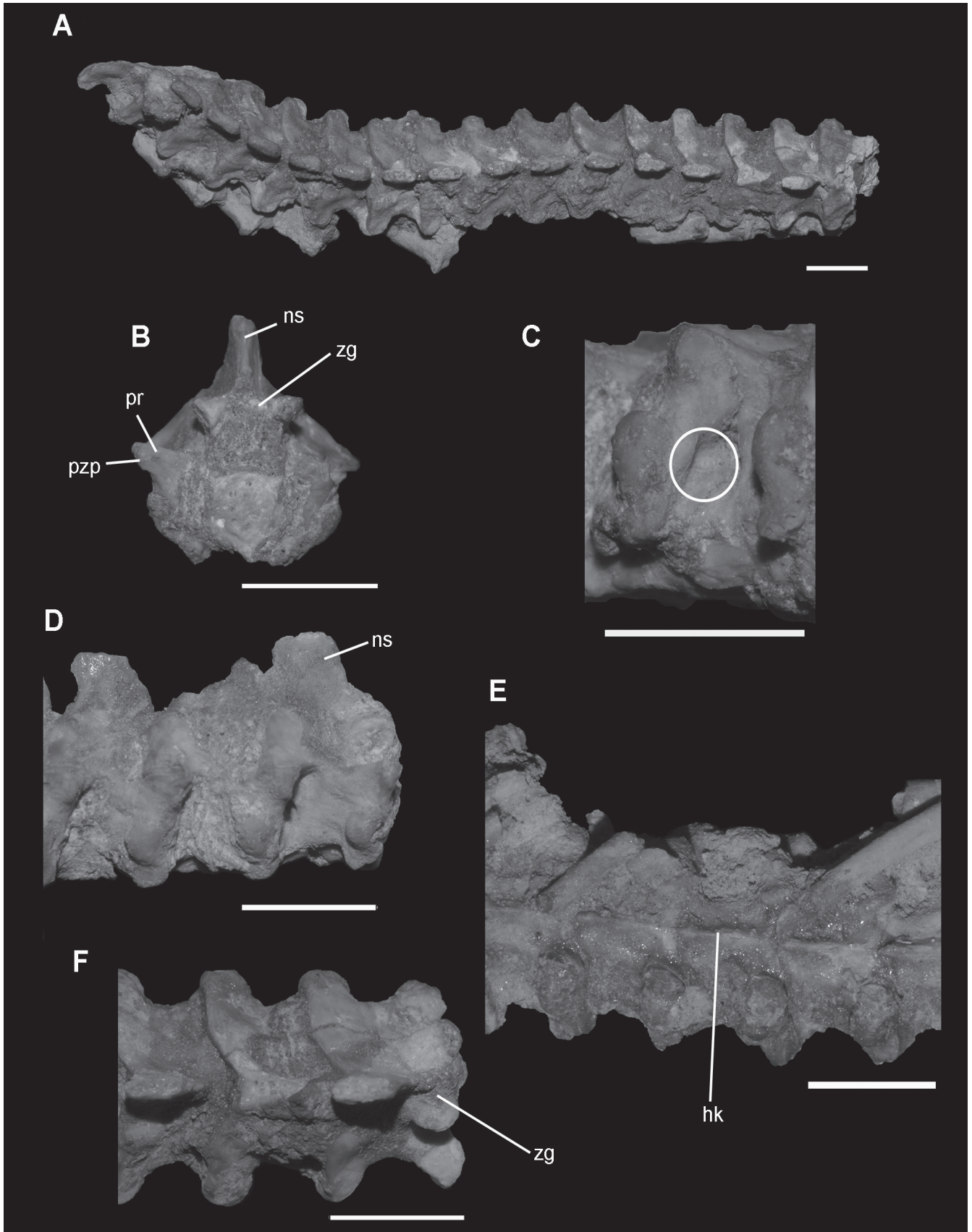


Figure 3. *Epicrates* sp. MPAT 252, fragment of a vertebral column; **A**, articulated vertebrae in dorsal view; **B**, anterior view of the anteriormost vertebra; **C**, lateroanterior view of a vertebra showing the absence of paracotylar foramen (circle); **D**, right lateral view of three vertebrae; **E**, ventral view of four vertebrae; **F**, dorsal view of three vertebrae. **Abbreviations:** **hk**, haemal keel; **ns**, neural spine; **pr**, prezygapophysis; **pzp**, prezygapophyseal process; **zg**, zygosphene. Scale bar = 5mm.

(Figure 3C). The paradiapophyses are robust and inclined lateroventrally, surpassing the ventral edge of the cotyle. Para- and diapophyseal surfaces are distinctive but not divided by a hard constriction. The subcentral ridges are weakly marked. The haemal keel is well developed, thin, and prominent all along the centrum (Figure 3E). Subcentral and lateral foramina are present.

Comments. Neural arch with deep, V-shaped posterior embayment showed by the studied vertebrae is an apomorphy of Macrostromata (Lee & Scanlon, 2002). Among them, the studied material shares with Neotropical boids the following character states: high, short, and wide vertebrae; vaulted neural arch; vertebral centrum shorter than the neural arch width; low inclination of the articular facet of prezygapophyses; short prezygapophyseal process; well-defined precondylar constriction; haemal keel instead hypapophysis; and lateral and subcentral foramina present (Rage, 2001; Lee & Scanlon, 2002; Szyndlar & Rage, 2003; Albino & Carlini, 2008). In comparison with *Boa*, the vertebrae are characterized by the absence of paracotylar foramina, shorter prezygapophyses, and lower neural arch (Kluge, 1991; Albino & Carlini, 2008; Albino, 2011; Onary-Alves *et al.*, 2017). The vertebrae are smaller and more delicate than those of *Boa* and *Eunectes*. This last genus is characterized by a zygosphenes of moderate dorsoventral development, bearing a conspicuous median tubercle anteriorly projected (Hsiou & Albino, 2010; pers. obs.), whereas *Boa* is characterized by a thick zygosphenes with a concave anterior edge (Albino & Carlini, 2008; Albino, 2011). Instead of them, the studied vertebrae have a thinner zygosphenes carrying a wide median lobe as in *Corallus* and *Epicrates* (pers. obs.). The prezygapophyses of *Corallus* are horizontal in anterior view, whereas, in the studied specimen, they are inclined above the horizontal plane as in *Epicrates* (Rage, 2001; Hsiou *et al.*, 2012; pers. obs.). In addition, the neural arch and neural spine are lower in *Corallus* and *Eunectes* than in *Epicrates* and the fossil vertebrae (pers. obs.). Thus, the vertebral morphology is consistent with the presence of a combination of character states recognized as diagnostic for the genus *Epicrates*.

DISCUSSION

Squamates are a common and diverse component of the present herpetological communities of the NOA, among which teiids and boids include the largest reptilian species (Ceï, 1993). In the Santiago del Estero Province, *Tupinambis rufescens* is a widespread teiid lizard whereas boid snakes are represented by the species *Boa constrictor* and *Epicrates alvarezii* (Ceï, 1993; Di Cola *et al.*, 2008).

The specimens studied in the present paper represent the first record of Squamata for the Pleistocene of the NOA. South American fossil remains of Teiidae are known since the Paleogene (Brizuela & Albino, 2016). *Tupinambis* is the best-represented teiid (and even the best-represented lizard) in the paleontological record of Argentina since the early Miocene onwards (Brizuela & Albino, 2004, 2008, 2012a, b; Albino *et al.*, 2006, 2009, 2013). As in the beginning of

the Neogene, *Tupinambis* was widely distributed during the Pleistocene not only in Argentina, but also in Bolivia, Brazil, and Uruguay (Albino & Brizuela, 2014; Hsiou *et al.*, 2016). Nevertheless, unlike the Miocene record of the genus, many of the Pleistocene specimens have not been described and, in some cases, the material is untraceable (Albino & Brizuela, 2014). Specimens of *Tupinambis* have been recognized in some Holocene archaeological sites of the NOA as part of the preserved vertebrate fauna and frequently in relation with its anthropogenic use by the indigenous groups of the Chaco-Santagueña region (Cione *et al.*, 1979; del Papa *et al.*, 2011; del Papa & Moro, 2014). Thus, the partial hemimandible described in the present paper increases the documented Pleistocene record of the genus, which is still scarce in Argentina in comparison to previous and posterior times.

At the moment, remains of extant genera of boids recognized in Argentina are limited to the genus *Boa* known for the lower Eocene, Pliocene and Upper Pleistocene (Albino, 1992, 1993; Albino & Carlini, 2008). Nevertheless, extant boids were also reported in other South-American countries. The lower Eocene, upper Miocene, and Quaternary of Brazil have provided remains of *Boa*, *Corallus*, *Epicrates* and *Eunectes* (Rage, 2001; Camolez & Zaher, 2010; Hsiou & Albino, 2009, 2010; Hsiou *et al.*, 2012, 2013), whereas in the middle Miocene of Colombia and middle-upper Miocene of Venezuela only *Eunectes* (Hoffstetter & Rage, 1977; Hsiou & Albino, 2009, 2010) was identified. Thus, the genus *Epicrates* is reported since probably the late Miocene and early Holocene of Brazil (Hsiou & Albino, 2010; Hsiou *et al.*, 2012), corroborating molecular studies that estimated the origins of the genus in the early Miocene or before (Noonan & Chippindale, 2006). The material of snake described here represents the first paleontological report of *Epicrates* for Argentina and the first Pleistocene specimen assigned to this genus in South America.

As said above, the presence of *Tupinambis* and *Epicrates* in the Pleistocene of Termas de Río Hondo area, in Santiago del Estero Province, coincides with the present day distribution of these taxa. Both strictly Neotropical genera are recognized in South America since the Miocene (Brizuela & Albino, 2004; Hsiou & Albino, 2010), as well as other squamate taxa (Albino & Brizuela, 2014), suggesting that several components of the present South American herpetological communities have already been differentiated as back as the beginning of the Neogene. Taking into account that most of the Pleistocene squamate record from South America corresponds to extant genera and species (Albino & Brizuela, 2014), it is possible to propose that modern squamate communities were completely established at least since the early Pleistocene. Nevertheless, some genera documented in the Pleistocene record of Argentina, such as *Homonota* and *Boa*, and probably “*Cnemidophorus*”, are currently not distributed in the regions of the fossil localities (Albino, 2005; Albino & Carlini, 2008; Agnolin & Jofre, 2011). This indicates that paleoclimatic and paleoenvironmental changes that occurred during the Quaternary could have influenced the squamate distribution, although, so far, there is no evidence

of these chorological modifications for the NOA, given that both *Tupinambis* and *Epicrates* inhabit today the same region than during the Pleistocene.

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Appendix 1. Comparative material.

“*Ameiva*” *ameiva*, UNMdP-O 27; *Boa constrictor*, FMNH 22362, FMNH 211926, FMNH 22353, UNMdPO 44, UNMdP-O45, UNMdP-O 46, UNMdP-O 47, UNMdP-O 49, UNMdP-O 50; “*Cnemidophorus*” *longicauda*, UNMdP-O 81; “*Cnemidophorus*” *serranus*, UNMdP-O 82; “*Cnemidophorus*” *tergolaevigatus*, UNMdP-O 83; “*Cnemidophorus*” *lacertoides*, UNMdP-O 80; *Corallus caninus*, FMNH 223192; *Corallus cookie*, FMNH 212337; *Epicrates cenchrria*, UNMdP-O 42, UNMdP-O 43; *Eunectes murinus*, FMNH 212710; *Eunectes notaeus*, UNMdP-O 48; *Teius suquiensis*, UNMdP-O 84, UNMdP-O 85; *Teius teyou*, UNMdP-O 15, UNMdP-O 16, UNMdP-O 22; *Tupinambis merianae*, UNMdP-O 01 to 13, 17 to 20, UNMdP-O 25, UNMdP-O 32, UNMdP-O 33, UNMdP-O 35; *Tupinambis rufescens*, UNMdP-O 36, UNMdP-O 74.