

## BOIRUNA CF. *B. MACULATA* (OPHIDIA: COLUBROIDES) FROM THE EARLY TO MIDDLE PLEISTOCENE OF ARGENTINA, AND THE EFFECTS OF PLEISTOCENE EXTINCTIONS ON SOUTH AMERICAN REPTILES

CARLOS A. SCANFERLA<sup>1,3</sup>, FEDERICO AGNOLIN<sup>1</sup> AND DAMIÁN VOGLINO<sup>2</sup>

<sup>1</sup>Laboratorio de Anatomía Comparada y Evolución de los Vertebrados, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Av. Angel Gallardo 470 (1405), Capital Federal, Argentina. E-mail: agustin\_scanferla@yahoo.com.ar; fedeagnolin@yahoo.com.ar

<sup>2</sup>Fundación Oga, Guardias Nacionales N° 19 (2900), San Nicolás, Buenos Aires, Argentina. E-mail: dvooglino@fundacionoga.org.ar

<sup>3</sup>Corresponding Author.

**ABSTRACT.** A new specimen referable to *Boiruna* cf. *B. maculata* from a Lower-Mid Pleistocene locality in Ramallo, Buenos Aires, Argentina is described, representing the first fossil record of this genus. This specimen is referred to this living genus on the basis of the following features: robust supratemporal bone very wide at mid-length; subcentral process of the basioccipital with three well-developed subequal projections forming a wide, flat, posteriorly indented surface; lymphatic fossae of trunk vertebrae wide and deep, with well developed subcentral ridges; and third cloacal vertebra with anteroposteriorly extended neural spine, amongst others. This record is outside the current geographical range of the species of this genus, indicating warmer environmental conditions at the end of the Ensenadan age in Buenos Aires province. As in other continents, the South American fossil Pleistocene record indicates that Pleistocene extinctions affected mainly (and perhaps only) large reptiles.

**KEYWORDS.** *Boiruna maculate*, Pleistocene, South America, Reptiles, Extinction.

### INTRODUCTION

The pseudoboine snakes presumably represent a suprageneric monophyletic group of xenodontine colubrids exclusive to the Neotropical realm. This group is composed of several taxa, including the genera *Boiruna* Zaher and *Clelia* Fitzinger, both widely distributed in Argentina (Giraudó, 2001; Scott *et al.*, 2006).

In spite of its relevance in the extant South American herpetofauna, the fossil record of the tribe Pseudoboini is scarce and biased, as is the case for other South American Neogene snakes. This record is limited to Upper Pleistocene-Holocene *Clelia rustica* from the Cueva Tixi archaeological site (Albino, 1999) and specimens assigned to the genus *Clelia* from the Lower-Middle Pleistocene of Buenos Aires province (Scanferla, 2006). However, during several field trips to Pleistocene outcrops at the Paraná River near the locality of Ramallo (Buenos Aires province; Fig. 1), a partially articulated and nearly complete skeleton of a large pseudoboine colubrid was collected.

The aim of the present paper is to identify, describe, and discuss this new specimen, referable to the genus *Boiruna*. Additionally, several new reptilian records from numerous localities are briefly discussed in order to analyze the Pleistocene extinction and related phenomena throughout the South American continent.

### MATERIALS AND METHODS

Dry skeletal specimens of several South American colubroid species were used for comparative purposes (*see* Appendix 1). Anatomical terminology follows Auffenberg (1963), Cundall (1981), and Hoffstetter and Gasc (1968). Qualitative osteological characters, especially crests and processes, may vary along ontogeny (Kluge, 1991) and therefore only the largest specimens available were used in the analysis.

### RESULTS

#### Stratigraphy and chronology

The stratigraphic profile of the fossiliferous locality (Fig. 2) was established at the Paraná River cliffs (Voglino and Pardiñas, 2005). It is approximately 15 m thick and composed of massive siltstones intercalated with cross-bedded sandy siltstones with clay intraclast. The fossil specimen reported here was found in unit US7 of Voglino and Pardiñas (2005). A conspicuous paleosol occurs at the base of the profile; this was indicated by Nabel (1993) as the boundary between the Brunhes-Matuyama (0.78 MY) magnetostratigraphic zones. Thus the fossiliferous level corresponds to the Brunhes paleomagnetic chron.

This level has also yielded megamammal skeletons (*e.g.* *Scelidotherium leptcephalum*, *Sclerocalypus*

sp., *Pampatherium typum*, *Eutatus seguini*), indeterminate tayassuids, and rheid birds. Below level US7, extant caviomorph rodent genera associated with arid and sandy environments (e.g. *Ctenomys* sp., *Microcavia* sp., *Dolichotis* sp.; Voglino and Pardiñas, 2005) have been recovered. The presence of *Theriodictis platensis* and *Scelidodon* sp. in this unit (US8) indicates an Upper Ensenadan age (*Mesotherium cristatum* biozone *sensu* Cione and Tonni, 2005; see Prevosti and Palmqvist, 2001), between 0.78 and 0.5 MY (Cione and Tonni, 2005). This biostratigraphic information agrees with the above-mentioned magnetostratigraphic data that indicate level US7 as the boundary between Bonaerian and Ensenadan ages.

### Systematic paleontology

Serpentes Linnaeus, 1758

Alethinophidia Nopcsa, 1923

Colubroides Zaher *et al.*, 2009

Pseudoboini Bailey, 1967

*Boiruna* Zaher, 1996

*Boiruna* cf. *B. maculata* (Boulenger, 1896)

*Referred material*: MLP (Museo de La Plata) 94-XII-10-1, basioccipital, left supratemporal, parietal, right maxilla with seven preserved teeth, four anterior trunk vertebrae, 40 mid and posterior trunk vertebrae, third cloacal vertebra, two anterior post-cloacal vertebrae, and several ribs (Figs. 3, 4).

*Locality*: Cliffs on the right margin of the Paraná River, Northern Buenos Aires province, Ramallo district (33°28'47"S, 59°59'45"W).

### DESCRIPTION

In this section we compare the new fossil material with other Pseudoboini and several colubrids (see Appendix 1). Given the lack of osteological diagnoses for most South American colubrids, our description is focused on qualitative characters that may be useful to assign the specimen to different taxonomic categories.

### Skull

The anterior portion of the maxilla (Fig. 3A) is dorsoventrally tall (maximum height 2.5 mm), a

feature also present in other Pseudoboini (e.g. *Clelia*, *Phimophis*), but absent in other South American xenodontines, such as *Philodryas* and *Liophis*. The palatine process is well developed and is subrectangular in outline, as in *Clelia rustica* and *Phimophis vittatus*, and different from the reduced subtriangular condition in other xenodontine genera (e.g. *Philodryas*, *Liophis*). Furthermore, the dorsal margin of the anterior portion of the maxilla is continuous with the palatine process in *Clelia*, whereas it is clearly separated by a notch in *Boiruna maculata* (Fig. 3B), *B. sertaneja* and MLP 94-XII-10-1. The ectopterygoid process of the maxilla is markedly directed ventrally in MLP 94-XII-10-1 and *Boiruna maculata* and forms a vertical articular facet for the ectopterygoid that is wider than in *Clelia rustica* and *Phimophis vittatus*. *Boiruna maculata* and MLP 94-XII-10-1 present a laterally directed process at the posterior end of the labial margin of the maxilla, above the alveolar

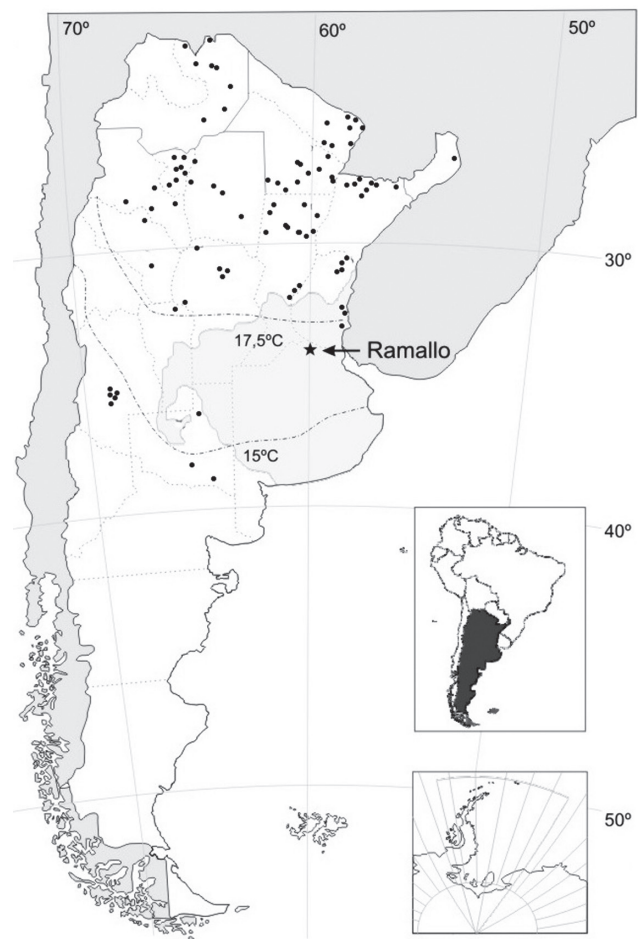


FIGURE 1. Location of Ramallo city, in northeastern Buenos Aires Province, Argentina. Points indicate current locations of *Boiruna maculata* (from Scott *et al.*, 2006).

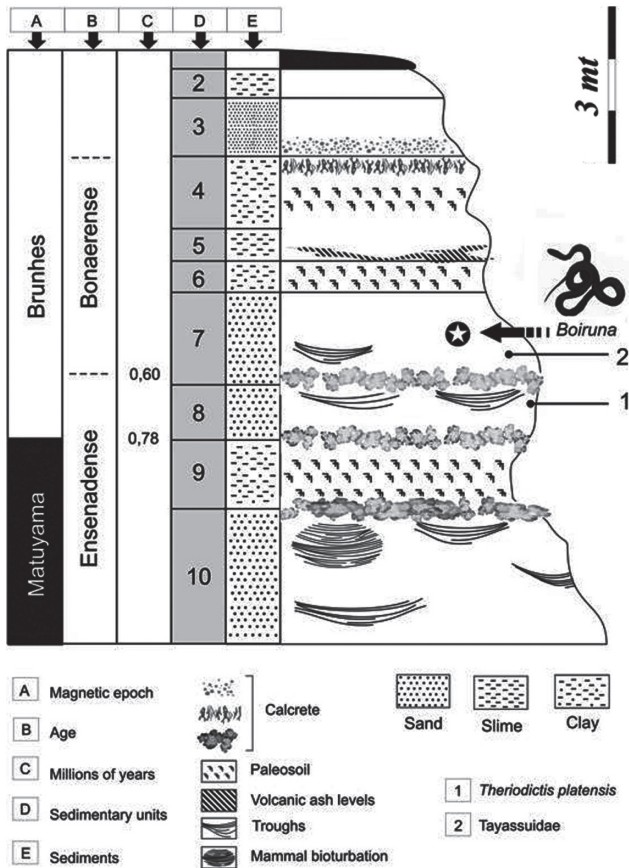


FIGURE 2. Sedimentological profile at the Paraná River in Ramallo city.

margin, which is absent in *Clelia rustica* and *Phimophis vittatus*. This process is located at the alveolar margin in *Philodryas*.

The fanged tooth is located at the posterior end of the maxilla and has a lateral groove as in other xenodontines including *Boiruna*.

The parietal of MLP 94-XII-10-1 (Fig. 3C) is dorsally flat, with strong, well developed parietal crests that contact each other at the posterior margin, as in *Boiruna* (in contrast, both crests converge at the supraoccipital in *Phimophis vittatus*). The frontoparietal suture is concave. The postorbital process is more laterally directed than in *Clelia rustica* and *Phimophis vittatus*. Participation of the parietal in the orbital fenestra is usually reduced in Pseudoboini because of the large dorsoventral extension of the frontoparietal suture, which is even more developed in MLP 94-XII-10-1 and *Boiruna maculata* (Fig. 3D). On the other hand, participation of the parietal in the orbital fenestra is greater in most xenodontines (e.g. *Liophis*, *Waglerophis*, *Lystrophis*).

The basioccipital bone (Fig. 3E) bears large subcentral and lateral processes. The subcentral process

is formed by three caudoventrally oriented projections as in *Boiruna maculata*. This morphology differs clearly from that of *Clelia rustica* or *Phimophis vittatus*, in which these projections are poorly developed. In other xenodontines the subcentral process is formed by a single (e.g. *Philodryas patagoniensis*) or two (e.g. *Philodryas mattogrossensis*, *Liophis miliaris*) projections, which are less developed than in *Boiruna maculata* (Fig. 2F) and MLP 94-XII-10-1.

The supratemporal (length 12.4 mm) shows a well defined articulation with the cephalic condyle of the quadrate and the anterior end articulates widely with the parietal (Fig. 3G). The middle portion of the supratemporal is laterally expanded (maximum width 3.5 mm), a feature also present in living specimens of *Boiruna maculata* (Fig. 3H). This expansion is absent in most xenodontines such as *Philodryas*, *Liophis*, and other pseudoboines (i.e. *Clelia rustica*), in which the supratemporal shows subparallel medial and lateral borders.

#### Vertebrae and ribs

The trunk vertebrae are similar to those of *Clelia rustica* and *Phimophis vittatus*. MLP 94-XII-10-1 (Figs. 4A-C) resembles *Boiruna maculata* in the greater anteroposterior development of the neural spines (4.9 mm at the base, in mid-trunk vertebra) compared to *Clelia rustica*. In MLP 94-XII-10-1 the anterior and posterior dorsal projections of the neural spines are reduced, in contrast with specimens of *Boiruna maculata*. The centra (width 4.5 mm in a mid-trunk vertebra) are transversely wider than in *Clelia rustica* and *Phimophis vittatus*. These centra have well-developed subcentral lymphatic fossae that begin anterior to the level of the precondylar constriction as in *Boiruna maculata*. The lymphatic fossae are laterally well-delimited by deep subcentral ridges, a feature also present in adult specimens of *Boiruna maculata*; whereas in subadults the fossae are shallower and the subcentral ridges are poorly developed. However, in adult specimens of *Clelia rustica* and *Phimophis vittatus* this feature is never as developed as in MLP 94-XII-10-1 and *Boiruna maculata*. The prezygapophyseal processes are robust and have a truncated tip as in Pseudoboini. However, these processes are narrower in MLP 94-XII-10-1 than in *Boiruna maculata*.

The preserved anterior trunk vertebrae (number 30-35 approximately) have well-developed hypapophyses. The bases of the hypapophyses of MLP

94-XII-10-1 are anteroposteriorly less extended than in *Boiruna maculata*.

In MLP 94-XII-10-1 only the third cloacal vertebra is preserved (Figs. 4D-E). The neural spine is low and extended anteroposteriorly as in *Boiruna maculata*, but different from the condition in *Clelia rustica* and *Phimophis vittatus*, in which this spine

is anteroposteriorly short (basal length 3.1 mm). The fossil specimen differs from extant specimens of *Boiruna maculata* in having more robust prezygopophyseal processes and a posteriorly wider ventral keel. Additionally, the fossil resembles *Boiruna*, rather than *Phimophis* and *Clelia*, in having reduced hemapophyses.

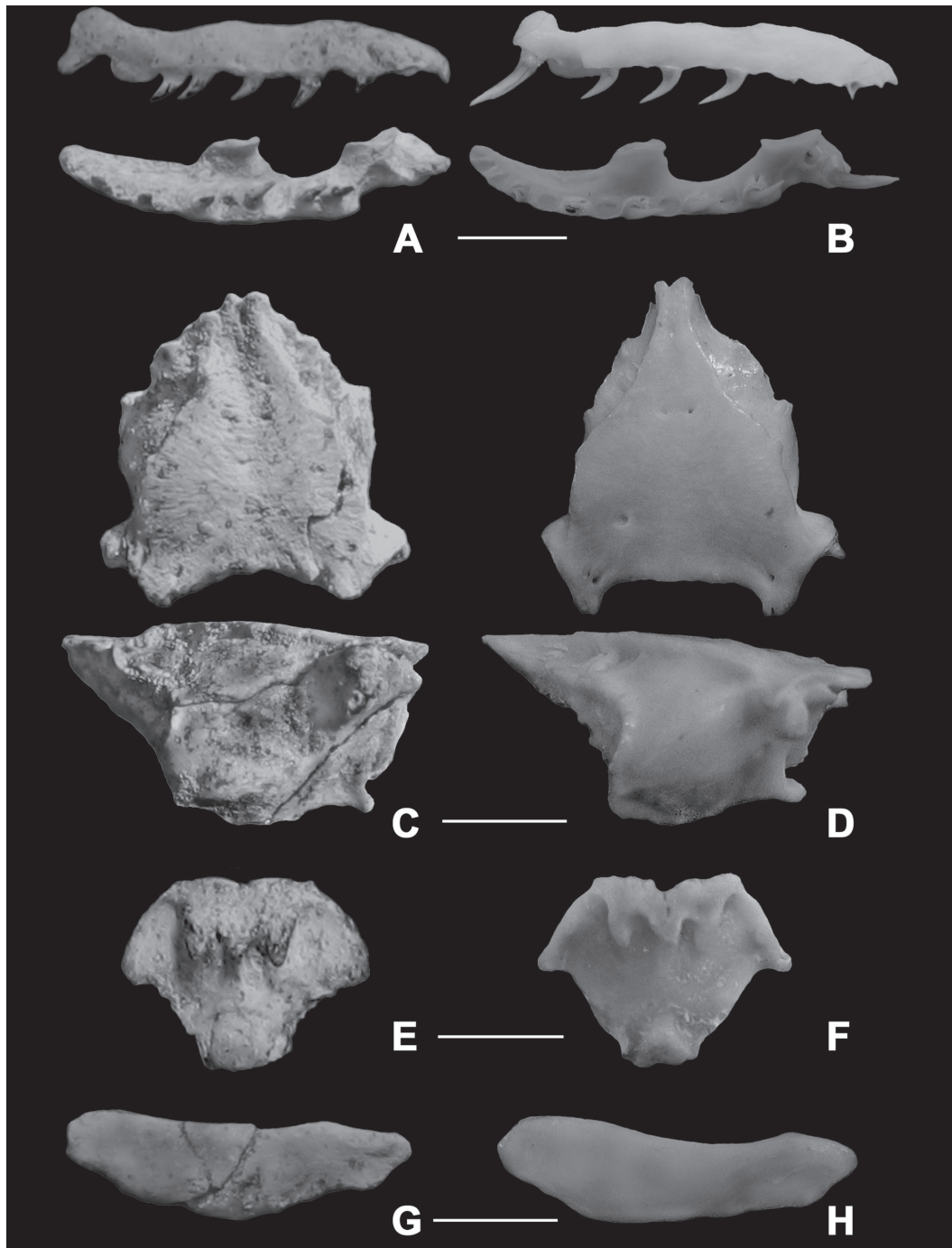


FIGURE 3. Cranial bones of the specimen assigned to *Boiruna* cf. *B. maculata* (MLP 94-XII-10-1; A,C,E,G) and an extant specimen of *Boiruna maculata* (MACN 40006; B,D,F,H): A, B, right maxilla; C, D, parietal; E, F, basioccipital; G, H, left suprtemporal. Scale bar 5 mm.

The first two anterior postcloacal vertebrae are preserved (Fig. 4F). As in *Boiruna*, the hemapophyses of MLP 94-XII-10-1 are less developed than in *Clelia* and other xenodontines (*e.g.* *Philodryas*). The neural spines are lower than in *Clelia*, a feature shared by the fossil specimen (height 2.4 mm) and *Boiruna maculata*. In *Clelia rustica* the neural spines of postcloacal vertebrae are anteroposteriorly narrower than in MLP 94-XII-10-1 (basal length 3.2 mm), *Boiruna maculata* and *Phimophis vittatus*.

Several ribs were found articulated with the preserved vertebrae. These ribs present the typical snake morphology, with a well developed tuberculiform process and a concave tubercular facet, separated from the nearly flat capitular facet.

#### DISCUSSION

The fossil specimen described here is referred to Pseudoboini on the basis of: 1) anterior portion of the maxilla dorsoventrally tall, 2) palatine process of the maxilla with subrectangular outline, 3) segment of maxilla anterior to the palatine process anteroposteriorly short, 4) parietal participation in orbital fenestra reduced, 5) trunk vertebrae dorsoventrally tall, and 6) robust, distally truncated and laterally oriented prezygapophyseal processes on trunk vertebrae.

Furthermore, MLP 94-XII-10-1 is referred to the genus *Boiruna* on the basis of the following traits: 1) supratemporal bone robust and very wide at mid length, 2) subcentral process of basioccipital with three well developed subequal projections that form a wide, flat, caudally indented surface, 3) posterolabial process of maxilla located at the alveolar margin, 4) ectopterygoid process of maxilla with dorsoventrally extended articular surface for the medial process of the ectopterygoid, 5) lymphatic fossae of trunk vertebrae wide and deep, with well developed subcentral ridges, 6) third cloacal vertebra with anteroposteriorly extended neural spine, 7) hemapophyses of cloacal vertebrae reduced. Regrettably, it is impossible to distinguish both *B. maculata* and *B. sertaneja* on the basis of skeletal morphology. In this way, we prefer to assign the specimen MLP 94-XII-10-1 as *Boiruna cf. B. maculata*, until more complete fossil material comes to light and more osteological comparisons between these two species can be carried out.

A common morphological pattern in South American colubrids (and probably all living colubrids) is the homogeneity of vertebral morphology. However, some features are taxonomically useful and diagnostic, at least at generic level (Szyndlar, 1984; Scanferla *et al.*, 2005). In this respect, MLP 94-XII-10-1 differs in some traits from the recent individuals of the *Boiruna maculata* sample studied in this paper.

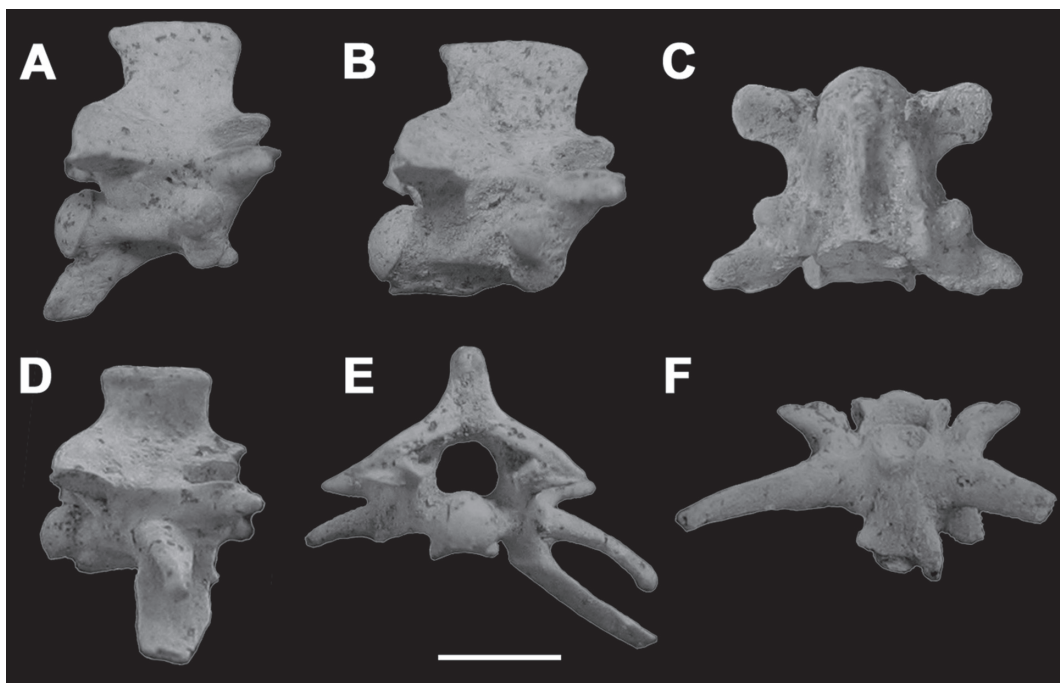


FIGURE 4. *Boiruna cf. B. maculata* MLP 94-XII-10-1 A, anterior trunk vertebra; B, C, mid-trunk vertebra; D, E, cloacal vertebra; F, post-cloacal vertebra. Scale bar 5 mm.

These traits of the Pleistocene specimen (*e.g.* more robust prezygapophyseal processes, haemapophyses of postcloacal vertebrae) are tentatively interpreted here as individual variation, until more information about intraspecific osteological variation of both extinct and extant specimens of this species becomes available.

Voglino and Pardiñas (2005) inferred xerophilous scrub vegetation and a warmer paleoclimate for the level where MLP 94-XII-10-1 was found based on the presence of tayassuid pigs, necrofagous dipterans from the family Calliphoridae, and bones with traces left by dermestid coleopterans, among other evidence. In addition, MLP 94-XII-10-1 was found in association with several megamammals (*Glyptodon*, *Scelidotherium*, etc.) that probably inhabited open environments (*see* Alberdi *et al.*, 1995).

Living species of the genus *Boiruna* inhabit open areas and warm environments across Brazil, Uruguay, Paraguay, and Argentina (Zaher, 1996; Scott *et al.*, 2006). In the latter country only *B. maculata* is present; its geographical range includes North Argentinian provinces (Entre Ríos, Santa Fe, Córdoba, La Pampa, San Luis and Mendoza; Fig. 1). Extant *B. maculata* is absent from the Buenos Aires province; its distribution is restricted to warmer ecoregions of Central Argentina (Espinal and Monte ecoregions; Giraudó, 2001; Scott *et al.*, 2006). Thus, the present record in the Buenos Aires province supports the climatic inferences stated by Voglino and Pardiñas (2005) for the northern part of this province during the Latest Ensenadan age.

#### The south american reptile fauna during the pleistocene extinctions

The Pleistocene extinction events are phenomena recorded world-wide (Martin and Klein, 1984). In South America, current knowledge of these events is restricted mainly to large mammals (*e.g.* Litopterna, Notoungulata, large-sized Xenarthra; Cione *et al.*, 2003) and birds (Tambussi *et al.*, 1993). The effects of these events upon South American continental reptilian faunas are almost unknown, mainly because of the poorly known Pleistocene reptilian fossil record (Báez and Gasparini, 1979; Albino, 1996). However, despite this incomplete fossil record, the present record of *Boiruna cf. B. maculata*, together with other personal observations and recently published data, invites an initial evaluation of the effects of the Pleistocene extinctions on the South American reptilian faunas.

The chelonian fossil record has yielded several remains of living taxa that are at present widely distributed in most South American countries. The exception are the extinct giant species of the tortoise genus *Chelonoidis* recovered from Argentina, Bolivia, Peru, Brazil, Uruguay, and Ecuador (*see* Hoffstetter, 1970; De la Fuente, 1988; 1999; Broin, 1990; Noriega *et al.*, 2000; Agnolin, 2004), which disappeared suddenly at the end of the Pleistocene.

The crocodylians are represented by records of the extant species *Caiman latirostris* from Northwestern Argentina (which was found together with Late Pleistocene megamammals; Patterson, 1936), and from the Late Pleistocene locality in Rio Grande do Norte, Brazil (Marinho *et al.*, 2005).

The lizard fossil record comprises living genera and species. Iguanians are represented by the liolaemid *Liolaemus* from Buenos Aires province, Argentina (Bonaerian age, Middle Pleistocene; MLP 04-VII-1-150; Late Pleistocene-Holocene; Albino, 2005), the tropidurid *Tropidurus* from Minas Gerais state, Brazil (Latest Pleistocene; Camolez, 2006), the leiosaurid *Leiosaurus belli* from Mendoza, Argentina (Late Pleistocene; Van Devender, 1977), and the iguanid *Iguana* from Ecuador (Late Pleistocene; Hoffstetter, 1970). Teiid lizards are represented by *Tupinambis* from the Pleistocene of Argentina and Brazil (Albino, 1996; Camolez, 2006; de la Fuente, 1999), *Dicrodon* sp. from Ecuador (Late Pleistocene; Hoffstetter, 1970), *Cnemidophorus* from Argentina (Late Pleistocene-Holocene; Albino, 2005), and *Ameiva* from Brazil (Late Pleistocene; Estes, 1983; Camolez, 2006). Gekkotan fossil representatives correspond to the genus *Homonota* from the Late Pleistocene-Holocene of Argentina (Albino, 2005). The record of amphisbaenians is restricted to the living genera *Leposternon* from the Pleistocene of Bolivia (Hoffstetter, 1968), and *Amphisbaena* from the Pleistocene of Argentina and Brazil; the latter genus is represented by two extinct species (*A. braestrupi* and *A. laurenti*; Gans and Montero, 1998), and two living species (*A. heterozonata* and *A. bolivica*; Scanferla *et al.*, 2006; whereas *Amphisbaena marelli* [Torres and Montero, 1998] is possibly synonymous with *A. bolivica*; R. Montero, *pers. comm.*).

The fossil remains of snakes also correspond to living taxa. Boids are represented by *Boa constrictor* from the Late Pleistocene of Argentina (Albino and Carlini, 2008) and *Corallus cf. C. hortulanus* from the Late Pleistocene of Brazil (Camolez, 2006). The colubrid record includes *Synophis* aff. *S. bicolor* from the Late Pleistocene of Colombia (Porta, 1965).

Several extant snake genera have been recorded from the Lower-Middle Pleistocene of Argentina, including the pseudoboines *Clelia* sp. and *Boiruna* cf. *B. maculata* (Scanferla, 2006; this paper), the xenodontini *Lystrophis* (Scanferla *et al.*, 2005), as well as an isolated vertebra of the genus *Philodryas* (MLP 04-IX-2-1) from the same locality and horizon where the specimen here described was collected. Moreover, the colubrid genera *Philodryas* and *Clelia* have been documented from the Upper Pleistocene-Holocene of Southern Buenos Aires province, Argentina (Albino, 1999). Viperids are represented by the genus *Bothrops* from the Lower-Middle Pleistocene of Argentina (Scanferla and Nenda, 2005) and the Upper Pleistocene of Brazil and Argentina (Albino, 1999; Camolez, 2006).

Accordingly, most of the Pleistocene reptile record from South America corresponds to living genera and species, and the available evidence suggests that modern reptile communities were well-established at least since the Lower Pleistocene, which resembles the patterns documented on other continents (Szyndlar, 1981; 1984; Meylan, 1982; 1995; Holman, 1998; 2000; Delfino and Bailon, 2000). Thus, the paucity of fossil South American species recorded is here interpreted as the result of background extinctions (following Raup and Sepkoski, 1986), suggesting that the Pleistocene extinction events affected mainly the large tortoises. Hence, the fossil record indicates only chorological changes, similar to those observed in some living mammalian and avian species (Tonni *et al.*, 1999; Tambussi *et al.* 1993; Tonni and Noriega, 1998). For example, some species that occur in the fossil record of Buenos Aires province, such as *Boiruna* cf. *B. maculata* and several lizards from the southernmost coastal region (Albino, 2005), are currently distributed in other regions. Resumen

Se describe un nuevo espécimen asignado a *Boiruna* cf. *B. maculata* proveniente del Pleistoceno Inferior-Medio de la localidad de Ramallo, Buenos Aires, Argentina, representando el primer registro fósil para el género. Este espécimen es referido a *Boiruna* en base a los siguientes caracteres: hueso supratemporal robusto y ancho en la parte media; proceso subcentral del basioccipital con tres proyecciones subiguales bien desarrolladas conformando una amplia y plana superficie posterior dentada; fosas linfáticas de las vértebras troncales medias amplias y profundas, con crestas subcentrales bien desarrolladas; y tercera vértebra cloacal con espina neural anteroposteriormente extendida, entre otros caracteres. Este registro se encuentra por fuera de la distribución geográfica actual

del género, indicando condiciones ambientales más cálidas a fines de la edad Ensenadense en la provincia de Buenos Aires. Como en otros continentes, el registro fósil de reptiles del Pleistoceno Sudamericano indica que las extinciones Pleistocénicas reconocidas a través de mamíferos y aves afectaron principalmente (y quizá únicamente) a los reptiles de gran tamaño.

#### ACKNOWLEDGMENTS

We thank Marcelo Reguero and Lucas Pomi (MLP), Julián Faivovich and Santiago Nenda (MACN), and Hussam Zaher (MZSP) for permission to study the collections under their care. Lucas Pomi, Fernando Novas, Francisco Prevosti, and Martín Ezcurra reviewed an early draft of the manuscript. Finally, we deeply appreciate the English corrections made by Anjan Bhullar.

#### LITERATURE CITED

- AGNOLIN, F. L. 2004. Comentarios sobre las tortugas Testudinidae (Reptilia, Chelonii) del Pleistoceno de Argentina. *Studia Geologica Salmanticensia*, 40:91-101.
- ALBERDI, M. T., G. LEONE, AND E. P. TONNI. 1995. Evolución geológica y climática de la región pampeana durante los último 5 millones de años; CSIC Monografías 12, Madrid, 526 pp.
- ALBINO, A. M. 1996. The South American fossil Squamata (Reptilia: Lepidosauria). *Müncher Geowissenschaften Abhandlungen*, 30:185-202.
- ALBINO, A. M. 1999. Serpientes del sitio arqueológico Cueva Tixi Pleistoceno tardío-Holoceno), provincia de Buenos Aires, Argentina. *Ameghiniana*, 36:269-273.
- ALBINO, A. M. 2005. A Late Quaternary lizard assemblage from the Southern pampean region of Argentina. *Journal of Vertebrate Paleontology*, 25:185-191.
- 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 (1):82-88.
- AUFFENBERG, W. 1963. The Fossil Snakes of Florida. *Tulane Studies in Zoology*, 10:131-216.
- BÁEZ, A. AND Z. GASPARINI. 1979. The South American herpetofauna: An evaluation of the fossil record. *Monographs Museum of Natural History (University of Kansas)*, 7:29-54.
- BROIN, F. 1990. Fossil turtles from Bolivia. *Revista Técnica de Yacimientos Petrolíferos Fiscales Bolivianos*, 12:509-527.
- CAMOLEZ, T. 2006. Levantamento, identificação e descrição da fauna de Squamata do Quaternário brasileiro (Lepidosauria). Ms. Dissertation, University of São Paulo, Brazil, 212 pp.
- CIONE, A. L. AND E. P. TONNI. 2005. Bioestratigrafía basada en mamíferos del Cenozoico Superior de la provincia de Buenos Aires, Argentina. *Relatorio del XVI Congreso Geológico Argentino, La Plata, Capítulo XI:183-200.*
- CIONE, A. L., E. P. TONNI, AND L. SOIBELZON. 2003. The Broken Zig-Zag: Late Cenozoic large mammals and tortoise extinction in South America. *Revista Museo Argentino de Ciencias Naturales*, 5:1-19.
- CUNDALL, D. 1981. Cranial osteology of the colubrid snake *Opheodrys*. *Copeia*, 1981:353-371.

- DE LA FUENTE, M. 1988. Las tortugas Chelidae (Pleurodira) y Testudinidae (Cryptodira) del Cenozoico argentino. Unpubl. Ph. D. Thesis, Universidad Nacional de La Plata, Argentina.
- DE LA FUENTE, M. 1999. A review of the Pleistocene reptiles of Argentina: Taxonomic and palaeoenvironmental considerations. *Quaternary of South America and Antarctic Peninsula*, 12:109-136.
- DELFINO, M. AND S. BAILON. 2000. Early Pleistocene herpetofauna from Cava Dell'Erba and Cava Pirro (Apulia, Southern Italy). *Herpetological Journal*, 10:95-110.
- DEVENDER, T. VAN. 1977. Observations on the argentine iguanid lizard *Leiosaurus belli*, Duméril and Bibron (Reptilia, Lacertilia, Iguanidae). *Journal of Herpetology*, 2:238-241.
- ESTES, R. 1983. The fossil record and early distribution of lizards. In A. Rhodin and K. Miyata (eds.), *Studies in Herpetology and Evolutionary Biology. Essays in honour of Ernest Edward Williams*, pp. 365-398. Harvard University Press, Cambridge.
- GANS, C. AND R. MONTERO. 1998. Two new fossil amphisbaenids (Reptilia: Squamata) from the Pleistocene of Lagoa Santa (Minas Gerais, Brazil). *Steenstrupia*, 24:9-22.
- GIRAUDO, A. R. 2001. Serpientes de la Selva Paranaense y del Chaco Húmedo. L.O.L.A., Buenos Aires, Argentina.
- HOFFSTETTER, R. 1968. Ñupua, un gisement de vertébrés Pleistocènes dans le chaco Bolivien. *Bulletin du Muséum National d'Histoire Naturelle*, 40:823-836.
- HOFFSTETTER, R. 1970. Vertebrados Cenozoicos de Ecuador. Congreso Latinoamericano de Zoología, Caracas, Actas, 4:955-970.
- HOFFSTETTER, R. AND J-P. GASC. 1968. Vertebrae and Ribs of Modern Reptiles. In C. Gans and T. Parsons (eds.), *Biology of the Reptilia*, pp. 258-490. Academic Press, New York.
- HOLMAN, J. A. 1998. Pleistocene Amphibians and Reptiles in Britain and Europe. *Oxford Monographs of Geology and Geophysics* 38, Oxford Univ. Press, New York.
- HOLMAN, 2000. *Fossil Snakes of North America*. Indiana University Press, Bloomington and Indianapolis.
- KLUGE, A. G. 1991. Boine snake phylogeny and research cycles. *Miscellaneous publications of the Museum of Zoology, Michigan University*, 178:1-58
- MARINHO, T. S., K. O. PORPINO, AND M. F. SANTOS. 2005. Ocorrência de *Caiman latirostris* Daudin, 1802 (Crocodylia: Alligatoridae) no Quaternário do Rio Grande do Norte, Brasil. II Congreso Latinoamericano de Paleontología de Vertebrados, Museu Nacional do Rio de Janeiro, Boletim de resumos.
- MARTIN, P. S. AND R. G. KLEIN. 1984. *Quaternary Extinctions. A Prehistoric Revolution*. The University of Arizona press, Tucson, 892 pp.
- MEYLAN, P. A. 1982. The Squamate reptiles of the Inglis IA fauna (Irvingtonian: Citrus County, Florida). *Bulletin of the Florida Museum of Natural History*, 37:273-297.
- MEYLAN, P. A. 1995. Pleistocene amphibians and reptiles from the Leisey Shell Pit, Hillsborough County, Florida. *Bulletin of the Florida State Museum (Biological sciences)*, 27:1-85.
- NABEL, P. 1993. The Brunhes-Matuyama boundary in Pleistocene sediments of Buenos Aires province, Argentina. *Quaternary International*, 17:79-85.
- NORIEGA, J. I., A. S. MANZANO, M. S. DE LA FUENTE, AND E. P. TONNI. 2000. Un Testudinidae gigante (Chelonii: Cryptodira) del Pleistoceno de la Provincia de Corrientes, Argentina. *Ameghiniana*, 37:321-326.
- PATTERSON, B. 1936. *Caiman latirostris* from the Pleistocene of Argentina, and a summary of South American Cenozoic Crocodylia. *Herpetologica*, 1:43-51.
- PORTA, J. 1965. Nota preliminar sobre la fauna de vertebrados hallada en Curiti (Departamento de Santander, Colombia). *Boletín de Geología*, 19:112-115.
- PREVOSTI, F. AND P. PALMQVIST. 2001. Análisis ecomorfológico del cánido hipercarnívoro *Theriodictis platensis* Mercerat (Mammalia, Carnívora), basado en un nuevo ejemplar del Pleistoceno de Argentina. *Ameghiniana*, 38:375-384.
- RAUP, D. M. AND J. J. SEPKOSKI. 1986. Periodic extinction of families and genera. *Science*, 231:833-836.
- SCANFERLA, C. A. 2006. The oldest record of *Clelia* (Serpentes-Colubridae) in South America. *Comptes Rendus Palevol*, 5:721-724.
- SCANFERLA, C. A. AND S. J. NENDA. 2005. El registro más antiguo del género *Bothrops* (Serpentes, Viperidae), proveniente del Pleistoceno inferior a medio de Argentina. *Revista del Museo Argentino de Ciencias Naturales*, 7:177-181.
- SCANFERLA, C. A., M. CENIZO, AND M. DE LOS REYES. 2005. Sobre el primer registro fósil del género *Lystrophis* Cope, 1885 (Serpentes-Colubridae-Xenodontinae). *Studia Geologica Salmanticensia*, 41:93-101.
- SCANFERLA, C. A., R. MONTERO, AND F. L. AGNOLÍN. 2006. The first fossil record of *Amphisbaena heterozonata* from the Late Pleistocene of Buenos Aires province, Argentina. *South American Journal of Herpetology*, 1:138-142.
- SCOTT, N. J., JR., A. R. GIRAUDO, G. SCROCCHI, A. L. AQUINO, P. CACCIALI, AND M. MOTTE. 2006. The genera *Boiruna* and *Clelia* (Serpentes: Pseudoboini) in Paraguay and Argentina. *Papéis Avulsos de Zoologia*, 46:77-105.
- SZYNDLAR, Z. 1981. Early Pleistocene reptile fauna from Kozi Grzbiet in the Holy Cross Mts. *Acta Geologica Polonica*, 31:81-101.
- SZYNDLAR, Z. 1984. Fossil snakes from Poland. *Acta Zoologica Cracoviensia*, 28:1-156.
- TAMBUSSI, C. P., J. I. NORIEGA, AND E. P. TONNI. 1993. Late Cenozoic birds of Buenos Aires Province: An attempt to document quantitative faunal changes. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 101:117-129.
- TONNI, E. P. AND J. I. NORIEGA. 1998. Los Cóndores (Ciconiiformes, Vulturidae) de la Región Pampeana de la Argentina durante el Cenozoico tardío: Distribución, interacciones y extinciones. *Ameghiniana*, 35:141-150.
- TONNI, E. P., A. L. CIONE, AND A. FIGINI. 1999. Predominance of arid climates indicated by mammals in the Pampas of Argentina during the Late Pleistocene and Holocene. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 147:257-281.
- TORRES, S. AND R. MONTERO. 1998. *Leiosaurus marellii* Rusconi 1937 is a South American amphisbaenid. *Journal of Herpetology*, 32:602-604.
- VOGLINO, D. AND U. F. J. PARDIÑAS. 2005. Roedores sigmodontinos (Mammalia: Rodentia: Cricetidae) y otros micromamíferos pleistocénicos del norte de la provincia de Buenos Aires (Argentina): reconstrucción paleoambiental para el Ensenadense cuspidal. *Ameghiniana*, 42:143-158.
- ZAHER, H. 1996. A new genus and species of Pseudoboine snake, with a revision of the genus *Clelia* (Serpentes, Xenodontinae). *Bolletino Museo Regionale di Scienze Naturali di Torino*, 14:289-337.



## NOTE ADDED IN PROOF

Recently, Hsiou (2007) described a new species of teiid lizard, *Tupinambis uruguaiensis*, from the Late Pleistocene of Rio Grande do Sul State, Brazil. Following this author, *T. uruguaiensis* is distinguished from other species of the genus *Tupinambis* on the basis of three characters of the lower jaw: 1) articular bone with ventral margin deeply concave; 2) angular process rounded and large, and projecting ventrally and posteriorly beyond the adjacent limits; 3) lateral surface of the articular bone is lateroventrally directed, with a highly protuberant adductor crest.

We question the validity of *T. uruguaiensis* for the following reasons: the concave ventral edge of the articular bone is also present in some specimens of *T. merianae*; the prominence of the angular process seems to represent a by product of the deeply concave ventral edge of the articular bone (in fact, this process in the fossil specimen exhibits the same morphology as in extant specimens of *T. merianae* and *T. rufescens*); the condition of a highly protuberant adductor crest might be due to an artifact of preservation since the dentary and all postdentary bones present strongly cracked and distorted surfaces (Hsiou, 2007, figs. 4A and 5A).

More thorough comparative analyses with extant species are needed, in order to establish the taxonomic status of *T. uruguaiensis*.

HSIOU, A. S. 2007. A new Teiidae species (Squamata, Scincomorpha) from the Late Pleistocene of Rio Grande do Sul State, Brazil. *Revista Brasileira de Paleontologia*, 10:181-194.

## APPENDIX 1

Material used in this study: MZUSP (Universidade de Sao Paulo, Museu de Zoologia), MLP (Museo de La Plata), MACN (Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”)

†*Amphisbaena heterozonata* (MLP 04-IX-1-1); †*Liolaemus* sp. (MLP 04-VII-1-150); *Boiruna maculata*, MACN 40006 (Juárez, Formosa), MACN 40007 (no locality); *Boiruna sertaneja*, MZUSP 7031 (no locality), *Clelia rustica*, MACN 40004 (La Plata, Buenos Aires), *Phimophis vittatus*, MACN 40005 (no locality); *Helicops leopardinus*, MACN 40014 (Resistencia, Chaco); *Liophis miliaris*, MACN 40013 (Colonia Pellegrini, Corrientes); *L. anomalus* MACN 40012 (Oliden, Buenos Aires); *L. poecilogyrus* MACN 40011 (Oliden, Buenos Aires), †*Lystrophis* sp. (MLP 94-XII-5-1); *Lystrophis dorbignyi* MACN 40009 (La Plata, Buenos Aires); *Mastigodryas bifossatus* MACN 40017 (no locality); *Oxyrhopus rhombifer* MACN 40010 (Entre Ríos, Argentina); †*Philodryas* sp. (MLP 04-IX-2-1), *Philodryas patagoniensis* MACN 40008 (Colonia Pellegrini, Corrientes); *P. mattogrossensis*, MACN 33420 (no locality); *Thamnodynastes hypoconia* MACN 40016 (Ibicuí, Entre Ríos); *Waglerophis merremi* MACN 40015 (Tucumán, Argentina); †*Bothrops* sp., MLP 89-XII-7-1; *Bothrops alternatus*, MACN 40018 (Sierra de la Ventana, Buenos Aires).