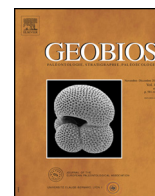




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Original article

# New macrostomatan snake from the Paleogene of northwestern Argentina<sup>☆</sup>

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## ABSTRACT

The lower Eocene Lumbrera Formation in Salta province, northwestern Argentina, outstands for providing snake remains from a non-Patagonian Paleogene site. The material consists of articulated precloacal vertebrae that represent a new medium-sized macrostomatan snake, namely *Amaru scagliai* nov. gen., nov. sp. The vertebral characters of *Amaru scagliai* nov. gen., nov. sp., suggest affinities with advanced clades, which is consistent with the recognition of derived macrostomatans in the early Paleocene of Bolivia and early Eocene of Brazil. The new snake confirms the presence of macrostomatan snakes in South America as early as the Eocene and suggests that the southern continents may have played an unsuspected role in the origin and evolution of advanced macrostomatans during the earliest Cenozoic.

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## 1. Introduction

Most of the Paleogene squamates of Argentina are known from a number of snake vertebrae mainly distributed in Patagonian localities (Simpson, 1933, 1935; Hoffstetter, 1959; Albino, 1987, 1993, 1996, 2011a, 2012; Albino and Brizuela, 2014a). Together with other South American records, they provide useful information about the early distribution of extinct and extant taxa in Gondwana (Albino, 2011a; Albino and Brizuela, 2014b). At least four snake genera are present in Paleogene Patagonian localities: *Madtsoia*, *Chubutophis*, *Waincophis* and probably *Boa*. The Gondwanan *Madtsoia* is present in various Eocene to late Oligocene deposits mostly represented by vertebrae referable to the species *M. bai* (Simpson, 1933, 1935; Hoffstetter, 1959; Albino, 1993, 2011a; Albino and Brizuela, 2014a). A second taxon is the boine *Chubutophis grandis* restricted to the middle-late Eocene (Albino, 1993). Both extinct genera were very large snakes, probably reaching or perhaps surpassing 10 m in length (Hoffstetter, 1959; Albino, 1993, 2011a). Aside from these large snakes, smaller boids have been recorded in Eocene deposits, including probably the oldest record of the extant genus *Boa* (reported as ?*Boa*) and the small extinct species *Waincophis australis* (Albino, 1987, 1993, 2011a; Albino and Carlini, 2008). In addition, unidentified

specimens were documented in other Eocene localities (Albino, 1993, 2011a); in particular, a vertebra from the middle–late Eocene is morphologically related to *Boa* and to the South American Paleogene boines *Titanoboa* and *Chubutophis* (Albino, 2012).

Apart from the above-mentioned Patagonian records, the site Pampa Grande in Salta province, northwest Argentina (Fig. 1), has provided squamatan remains from the Eocene Lumbrera Formation. This represents the first Paleogene report of Squamata from a non-Patagonian site of Argentina, and includes a tupinambine lizard and an undescribed snake (Donadío, 1985; Albino, 1993; Brizuela and Albino, 2016). The last one is formally described for first time in the present paper.

## 2. Material and methods

The Lumbrera Fm. corresponds to the superior unit of the Santa Barbara Subgroup, Salta Group. Based on facies associations, Del Papa (2006) recognized two informal sections in this formation: lower and upper Lumbrera. Contact between them is represented by a discontinuity that separates two sedimentary cycles. Two green levels were recognized within the lower section: the Faja Verde I (inferior) and Faja Verde II (superior) levels (Del Papa, 2006). The material studied here comes from the upper section of the lower Lumbrera Fm., known as Faja Verde, in a canyon between rivers Bordo and Toro, near Pampa Grande, province of Salta, Argentina (Fig. 1). Sedimentological data from the Faja Verde

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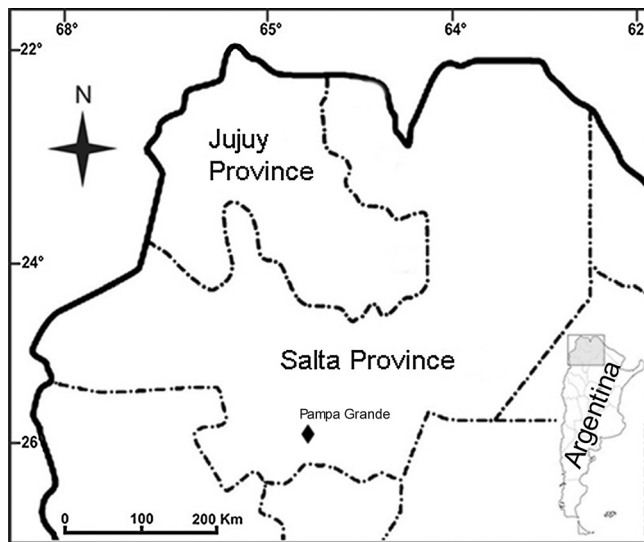


Fig. 1. Location map. The diamond denotes the site of Pampa Grande in Salta province, northwestern Argentina.

section (Del Papa, 2006) support the interpretation of a lake of low energy and freshwater chemistry, surrounded by low relief vegetated areas subject to sporadic flooding.

Traditionally, the Lumbrera Fm. was considered Eocene in age, based only in its mammal association similar to that of the Casamayoran South American Land Mammal Age of Patagonia (Vucetich et al., 2007). Recently, Del Papa et al. (2010) provided strong age evidence by identifying and dating radiometrically a continuous, white, 25 cm-thick layer of crystal tuff near the top of the upper Lumbrera section. The calculated age for this layer is  $39.9 \pm 0.4$  Ma and serves as a minimum age for the end of the formation's deposition. Stratigraphically, this crystal-tuff layer is located 240 m above the fossiliferous level (Del Papa et al., 2010). Thus, sedimentological, paleontological and absolute U/Pb zircon dating studies suggest a late early Eocene age ( $\sim 48.6$  Ma) for the Faja Verde of the Lumbrera Fm. (Malabarba et al., 2014).

The fossil material studied here is deposited in the Museo Municipal de Ciencias Naturales Lorenzo Scaglia, Mar del Plata, Argentina (MMP). It includes thirteen portions of vertebral column, each composed by articulated, incomplete vertebrae. All of these sections were originally associated in the same block in the field, making them likely to come from a single individual. Each section, constituted by one to four fragmentary articulated vertebrae, was denoted by consecutive numbers to identify them in the collection. Table 1 shows available measurements of vertebral centrum length and neural arch width of best-preserved vertebrae.

Macrostromata constitutes the most diverse group of extant snakes, characterized by many unequivocal synapomorphies of the osteology and soft anatomy (Lee and Scanlon, 2002). According to these authors, Macrostromata includes the basal forms Xenopeltidae and Loxocemidae and two more derived subclades: Booidea (including erylinae, pythonines, and boinae) and an advanced clade of snakes including ungaliophiines, bolyeriines, tropidophiines and caenophidians (acrochordids and colubroideans). One of the synapomorphies of Macrostromata is a vertebral character: neural arch with deep, V-shaped posterior embayment (Lee and Scanlon, 2002).

### 3. Systematic paleontology

Squamata Oppel 1811  
Serpentes Linnaeus, 1758  
Alethinophidia Nopsca, 1923

Table 1  
Vertebral measurements (in mm).

Specimen	cl	naw
MMP4660-M-1	9.00	9.64
MMP4660-M-2	8.60	9.56
MMP4660-M-5	8.88	–
MMP4660-M-7	8.36	11.74
MMP4660-M-9	8.70	7.88
MMP4660-M-12	8.54	–
MMP4660-M-13	8.76	–

cl: vertebral centrum length; naw: neural arch width.

Macrostromata Müller, 1831

Genus *Amaru* nov. gen.

**Derivation of the name:** amaru = serpent in Quechua language.

**Type and only known species:** *Amaru scagliai* nov. gen., nov. sp.

**Diagnosis:** As for the type and only known species.

*Amaru scagliai* nov. gen., nov. sp.

Fig. 2

**Derivation of the name:** In honor to Galileo Scaglia for his contribution to the Vertebrate Paleontology of Argentina and collector of the studied specimen.

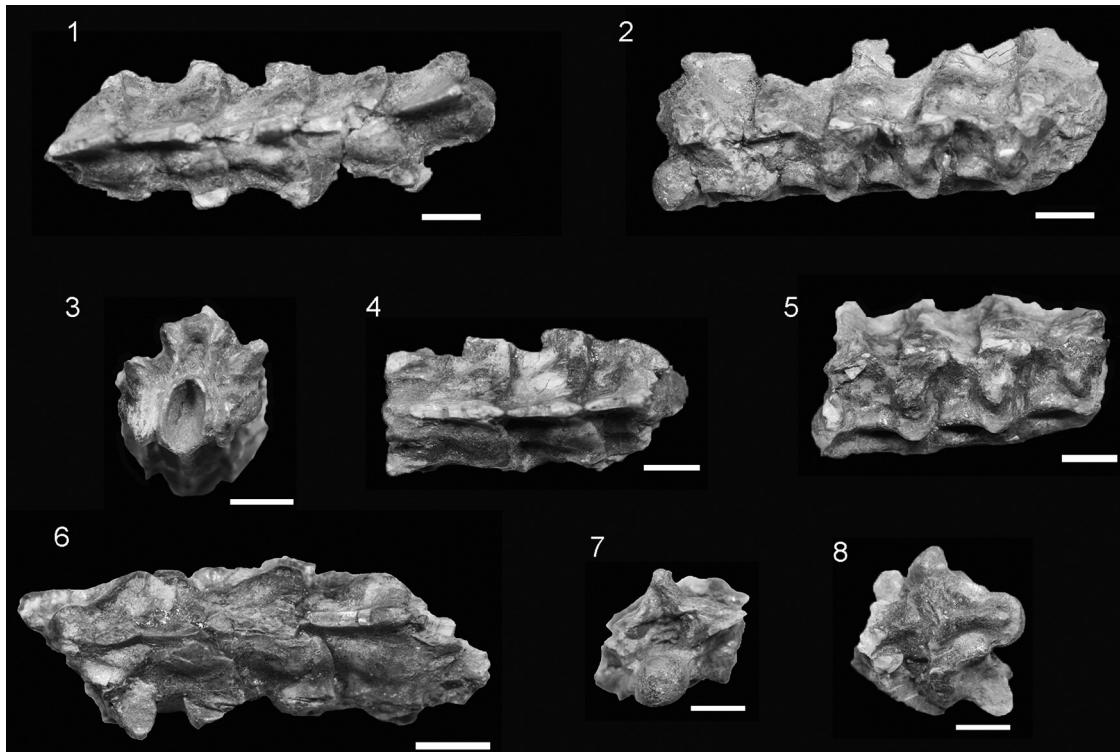
**Holotype:** Thirteen articulated series of precloacal vertebrae (MMP 4660-M).

**Material:** Thirteen portions of the vertebral column, including: four laterally compressed vertebrae and a small fragment of a fifth (MMP4660-M-1; Fig. 2 (1, 2)); three vertebrae with a strong lateral compression (MMP4660-M-2; Fig. 2 (3, 4, 5)); three vertebrae not strongly deformed but twisted and articulated with a fragment of a fourth (MMP4660-M-3; Fig. 2 (6)); two extremely depressed vertebrae articulated with a small fragment of other vertebra (MMP4660-M-4); three right pieces of vertebrae with a strong lateral compression (MMP4660-M-5); two strongly depressed vertebrae (MMP4660-M-6); one slightly depressed vertebra articulated with the posterior face of the preceding vertebra but with exposed posterior surface (MMP4660-M-7; Fig. 2 (7, 8)); two depressed and strongly damaged vertebrae (MMP4660-M-8); two compressed and strongly damaged vertebra (MMP4660-M-9); one extremely compressed vertebra articulated with pieces of the preceding and following vertebrae (MMP4660-M-10); two strongly depressed neural arch roofs (MMP4660-M-11); one depressed and twisted vertebra (MMP4660-M-12); one extremely depressed vertebra (MMP4660-M-13).

**Type locality and horizon:** Pampa Grande, province of Salta, Argentina (Fig. 1); Lumbrera Fm., lower Eocene.

**Diagnosis:** Medium-sized macrostromatan snake characterized by a unique combination of characters: non-depressed neural arch with a notched posterior edge; long and rather low neural spine; zygapophyses inclined; prezygapophyseal process short; zygosphenes wider than the cotyle and showing an anteriorly projected wide tongue; shallow interzygapophyseal constriction; vertebral centrum wide and shorter than the neural arch width; strong and prominent subcentral ridges; paracotylar foramina absent; haemal keel well defined and flanked by deep subcentral grooves; paradiapophyses located far from the articular surfaces of the prezygapophyses and almost reaching the ventral rim of the cotyle; para- and diapophyses well differentiated by a strongly marked constriction between them.

**Description:** All preserved vertebrae have approximately the same size and morphology, suggesting that no different vertebral regions are represented. In general, the vertebrae are poorly preserved and exhibit strong deformations. Some vertebrae are deformed by dorsoventral compression whereas others show lateral compression.



**Fig. 2.** Holotype of *Amaru scagliai* nov. gen., nov. sp. **1, 2.** MMP4660-M-1 in dorsal (1) and right lateral (2) views. **3–5.** MMP4660-M-2 in anterior (3), dorsal (4) and right lateral (5) views. **6.** MMP4660-M-3 in dorsal view. **7, 8.** MMP4660-M-7 in posterior (7) and ventral (8) views. Scale bars: 5 mm.

Vertebrae are heavily built and solidly articulated to each other; thus, most of them show little of the anterior and posterior surfaces. All vertebrae correspond to the preloacal region due to the presence of well-defined haemal keels and absence of haemapophyses, pleurapophyses, or lymphapophyses. The vertebrae are all of moderate size with a slightly variable centrum length, corresponding to a medium-sized snake (Table 1). Vertebrae are robust, short and wide, bearing a short and wide vertebral centrum. The neural arch is wide, vaulted and non-depressed. However, some vertebrae have a strongly depressed and smooth neural arch, presumably due to the strong dorsoventral deformation. The posterior edge of the neural arch is well notched in the middle by a V-shaped indentation. There is no evidence of parazygantral foramina in any vertebrae. The neural spine is thin and long, extending from the zygosphene to the posterior edge of the neural arch. It is well developed but rather low, as long as its basis as apically and well defined laterally. The zygosphene is of moderate dorsoventral thickness and wider than the cotyle. In dorsal view, its anterior edge bears a wide convex tongue anteriorly projected. The neural canal is of moderate size. The prezygapophyses and postzygapophyses are inclined dorsally with respect to the horizontal plane. The interzygapophyseal ridges, that connect pre- and postzygapophysis on each side, are well marked but the constriction is shallow. The prezygapophyseal process is robust and short, slightly evident in dorsal view. The vertebral centrum is shorter than the neural arch width, and broader anteriorly than posteriorly. Subcentral ridges are strongly defined all along the centrum, from the paradiapophyses to the condyle, and separate the ventral surface of the centrum from the lateral surfaces; they diverge anteriorly, producing a subtriangular outline of the ventral surface of the vertebral centrum. The cotyle looks round in slightly deformed vertebrae, higher than wide in laterally compressed vertebrae, and wider than high in dorsoventrally depressed vertebrae. The ventral rim of the cotyle is continuous with the haemal keel and the principal axis of the

condyle is slightly inclined upwards. The paracotylar foramina are absent. The haemal keel is well developed, as wide as the cotyle anteriorly and thinner posteriorly. The haemal keel is flanked by deep subcentral grooves. In some very depressed vertebrae, the haemal keel is wide and flattened, but subcentral grooves are always evident. The paradiapophyses are located far from the articular surfaces of the prezygapophyses and almost reaching the level of the ventral rim of the cotyle. They are composed by a prominent dorsal surface (diapophysis) and a flat ventral surface (parapophysis), both of the same size and with a profound, delineate constriction separating them.

**Remarks:** The neural arch with a deep, V-shaped posterior embayment showed by the studied vertebrae is an apomorphy of Macrostromata (Lee and Scanlon, 2002). Among them, vertebral centrum shorter than the width of the neural arch prevents its inclusion into the Caenophidia, although this character is however present in some species of caenophidians as viperids and *Acrochordus javanicus*. The exclusion of caenophidians is also supported by the absence of paracotylar foramina and the short prezygapophyseal processes. As compared with non-caenophidians, the fossil specimen shows a short prezygapophyseal process different from the prominent process reported in *Xenopeltis* and *Loxocemus* (Lee and Scanlon, 2002). The wide and short vertebral centrum, together with the non-depressed neural arch, distinguish the vertebrae from the “tropicalophiid assemblage” (including tropicalophiines and ungaliophiines) of Lee and Scanlon (2002) which has narrow, elongate vertebral centra and depressed neural arches (Rage, 2008). Bolyeriinae are characterized by possessing developed hypapophyses on all preloacal vertebrae, but the studied specimen has haemal keel instead of hypapophysis. The vertebrae have some characters similar to those present in the Booidea but there are also relevant differences. The shared features with most Booidea are: vertebrae short, high, wide and massively built; no flattened neural arches; neural spine well developed; robust zygosphene; prezygapophyseal process short; and haemal

keels not developed in prominent hypapophyses (Szyndlar and Böhme, 1996; Rage, 2001; Lee and Scanlon, 2002; Szyndlar and Rage, 2003; Albino and Carlini, 2008). The studied vertebrae differ from those of all extant and extinct Booidea in having paradiapophyses differentiated into para- and diapophyseal surfaces with a strongly marked constriction between them, whereas booids have weakly subdivided paradiapophyses. The well-differentiated paradiapophyses are present in caenophidians, as a derived character state, suggesting it is a condition of advanced macrostomatans. In addition, the specimen is characterized by strongly marked, prominent subcentral ridges, which have not been observed in booid vertebrae and, among caenophidians, are exceptionally present in natricines.

Apart from the paradiapophyses and subcentral ridges and in comparison to extant Neotropical booids, the vertebrae differ from those of *Boa* due to the absence of paracotylar foramina, a thinner zygosphenes which bears an anterior projection and the zygapophyses not strongly developed laterally (Albino, 2011b; pers. obs.). The studied vertebrae do not have prezygapophyseal facets horizontal and positioned at the level of the floor of the neural arch as in *Corallus* (Rage, 2001; pers. obs.). Vertebrae of *Epicrates* are taller and bear a significantly higher neural spine, whereas *Eunectes* has vertebrae with thicker zygosphenes and lateralized zygapophyses (pers. obs.).

Among Paleogene South American macrostomatans, the specimen from the Lumbrera Fm. cannot be referred to the Bolivian *Kataria anisodonta* because the size of the studied vertebrae is incompatible with the small size of the skull of this snake. It differs from madtsoiids in general, and from the Patagonian and Brazilian *Madtsoia* in particular, due to the presence of a prezygapophyseal process, absence of parazygantral and paracotylar foramina and paradiapophyses laterally not projected (pers. obs.). The booid *Hectophis austrinus* from the Paleogene of Brazil has deep interzygapophyseal constriction; prezygapophyses strongly produced laterally, neural arch depressed, and presence of paracotylar foramina (Rage, 2001), all conditions different from those of the studied vertebrae. *Waincophis* from Patagonia and Brazil is a booid snake which has depressed vertebrae with paracotylar foramina and moderately to strongly depressed neural arch, differing from the conditions of the Lumbrera's specimen (Albino, 1987; Rage, 2001). *Titanoboa* from Colombia and *Chubutophis* from Patagonia are also booids bearing paracotylar foramina in their vertebra and with a size significantly larger than the studied fossil (Albino, 1993; Head et al., 2009). The Brazilian booid *Itaboraiophis* differs from the studied vertebrae mainly in having a high neural spine, strongly depressed neural arch, haemal keel deeply produced ventrally, presence of a posterodorsal expansion of the diapophyses and dorsal location of the subcentral ridges; whereas *Paulacoutophis* is characterized by neural spines with an anterior border clearly slanting posterodorsally, thin zygosphenes, prezygapophyseal processes slightly projected in dorsal view, paradiapophyses not dorsoventrally elongated, and with the dorsal part of the diapophysis markedly extended posteriorly (Rage, 2008). With respect to the Brazilian *Paraungaliophis*, apart from the mentioned characters that distinguish the studied specimen from all "tropicalophids", the interzygapophyseal and subcentral ridges in the vertebrae from the Lumbrera Fm. are better marked than in this genus, the prezygapophyses are more inclined, the neural spine is long and not restricted to the posterior part of the neural arch, and the paradiapophyses are dorsoventrally developed, not hemispherical (Rage, 2008). A distinctive snake, represented by a single vertebra, was tentatively referred to the Russellophiidae, regarded a basal family of Caenophidia; nevertheless, the specimen from the Lumbrera Fm. does not have the strong vaulting of the neural arch, the peculiar orientation of the zygapophyseal facets (below the horizontal), the relatively small

cotyle and condyle, and the wide and thin zygosphenes, all characters diagnostic of russellophiids present in the Brazilian vertebra (Rage, 2008). Thus, the association of character states of *Amaru scagliai* nov. gen., nov. sp., does not characterize any extant or extinct snake described so far, supporting the erection of the new genus and species.

#### 4. Discussion

With at least one genus of madtsoiid (*Madtsoia*) and three genera of booids (*Boa*, *Chubutophis* and *Waincophis*), the notable diversity of known Paleogene snakes from Patagonia contrasts with the almost absence of lizards during the same period (Albino, 2011a). Previous reports concerning South American Paleogene squamates include a great diversity of lizards and snakes from Brazil and Argentina, few representatives from Bolivia and Peru, a marine palaeopheid snake from Ecuador, and a giant booid from Colombia (Albino and Brizuela, 2014b). Earliest Paleogene records are from Tiupampa in Bolivia (early Paleocene), where a possible iguanian lizard and diverse snakes were recorded (de Muizon et al., 1983; Rage, 1991; Scanferla et al., 2013; Albino and Brizuela, 2014b). Early to middle–late Eocene deposits providing lizard and snake remains are known from Brazil and Patagonia. These deposits are especially rich in snake diversity, including both madtsoiids and booids, among others (Simpson, 1933, 1935; Hoffstetter, 1959; Albino, 1987, 1990, 1996, 2011a, 2012; Rage, 1998, 2001, 2008). Recently, a sample of squamates from the Oligocene of Patagonia provided lizards (an indeterminate Iguanidae and a probable Iguaninae) and madtsoiid snakes (Albino and Brizuela, 2014a). A similar pattern is observed in Patagonian Mesozoic deposits, where snakes are represented by more than six genera whereas continental lizards include only two taxa (Albino, 2011a). However, the rich and diverse lizard fauna of Itaboraí, Brazil (Carvalho, 2001) demonstrates that the principal clades of lizards probably were diversified in South America at least since the early Eocene (Albino, 2011a). Eocene deposits of the Lumbrera Fm. in northwestern Argentina provided an extinct tupinambine lizard, *Lumbrerasaurus scagliai* (Brizuela, 2010; Brizuela and Albino, 2016) and the new macrostomatan snake *Amaru scagliai* nov. gen., nov. sp. (this paper). Thus, they corroborate that lizards were present in the Paleogene of South America as well as snakes. It is not possible to know at present the cause of the difference between the diversity of lizard and snake records in Patagonian and non-patagonian localities.

The new snake *Amaru scagliai* nov. gen., nov. sp., indicates the presence of macrostomatan snakes in South America as early as the early Eocene. The presence of characters suggesting affinities of this snake with advanced clades is consistent with the recognition of a derived macrostomatan in early Paleocene beds of Tiupampa, Bolivia (Scanferla et al., 2013) and a caenophidian in early Eocene deposits of Itaboraí, Brazil (Rage, 2008; Onary et al., 2017). Thus, these findings suggest that southern continents may have played a previously unsuspected role in the origin and evolution of advanced macrostomatans during the earliest Cenozoic, although this clade is also present and diverse in the Paleogene of northern continents.

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