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# FIRST SNAKE RECORD FROM THE SARMIENTO FORMATION AT LA GRAN HONDONADA (CHUBUT PROVINCE, ARGENTINA)

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**Abstract**. The described indeterminate boid snake was collected in rocks belonging to the Sarmiento Formation and exposed at La Gran Hondonada (Chubut Province, Argentina). This is the first snake record for the mid–late Eocene Mustersan South American land-mammal age. The specimen proves that medium- to large-sized boids inhabited the Patagonian region during most of the Palaeogene, suggesting climatic conditions warmer than those established at the beginning of the Neogene.

**Key words.** Boidae. Eocene. Palaeogene. South America. Argentina.

**Resumen**. PRIMER REGISTRO DE SERPIENTES EN LA FORMACION SARMIENTO, GRAN HONDONADA (PROVINCIA DE CHUBUT, ARGENTINA). El boideo indeterminado descripto en este trabajo fue hallado en sedimentitas de la Formación Sarmiento aflorantes en la localidad La Gran Hondonada (Provincia del Chubut, Argentina). Éste es el primer registro de serpientes para la Edad mamífero Mustersense (Eoceno medio–tardío). El espécimen evidencia que boideos de mediano a gran tamaño habitaron en la región patagónica durante la mayor parte del Paleógeno, sugiriendo condiciones climáticas más cálidas que aquellas desarrolladas a partir del Neógeno.

**Palabras clave.** Boidae. Eoceno. Paleógeno. América del Sur. Argentina.

SNAKES are known to have lived in South America since the Late Cretaceous, showing a relatively high diversity that became higher still during the Cenozoic (Albino, 1996a, 2007). The biochronological sequence of South American Land Mammal ages (SALMAs) published by Gelfo *et al.* (2009) provides an updated scheme for the record of early Cenozoic snakes. Deposits from the early Paleocene (Tiupampan SALMA) to middle–late Eocene (Casamayoran SALMA) yielded significant snake remains (Simpson, 1933, 1935; Hoffstetter, 1959; Rage, 1981, 1991, 1998, 2001; Albino, 1987, 1990, 1993, 1996a; Head *et al.*, 2009). Formal descriptions of snake material coming from rocks older than the Miocene (Colhuehuapian SALMA) are still wanting (Simpson, 1933; Simpson *et al.*, 1962; Albino, 1989, 1996a). The single exception is a marine palaeopheid specimen from the late Eocene of Ecuador (Hoffstetter, 1958). Rocks of the Sarmiento Formation at La Gran Hondonada (Chubut Province) contain a rich mammal assemblage referable to the Mustersan SALMA (Cladera *et al.*, 2004), which is considered middle–late Eocene in age (Bond and Deschamps, 2010; Ré *et al.*, 2010). Vertebrates found in this site include a snake that represents the sole South American record for this time interval. The purpose of this paper is to describe this single snake vertebra and to discuss its significance.

## MATERIALS AND METHODS

Most morphological studies (Underwood, 1976; Underwood and Stimson, 1990; Kluge, 1991, 1993a,b) led to recognizing the Boidae consisting of three subfamilies, *i.e.*, Boinae (Neotropics, Madagascar, Pacific Islands), Pythoninae (Australasia to Africa), and Erycinae (western North America, Africa, southeast Europe, southwest Asia, and India). Nevertheless, modern molecular analyses suggest that Boidae is not monophyletic, and its current division into three subfamilies would not reflect evolutionary history accurately (Burbrink, 2005; Noonan and Chippindale, 2006). Also, recent phylogenetic analyses indicate that Boinae in the sense of Kluge (1991) is not a monophyletic group (Vences *et al.,* 2001; Burbrink, 2005; Noonan and Chippindale, 2006), although the Neotropical boines, including *Boa* Linnaeus 1758, *Corallus* Daudin 1803, *Epicrates* Wagler 1830, and *Eunectes* Wagler ,1830, are a well supported clade (see also Rivera *et al.*, 2009). Because of the strong morphological homoplasy suggested by these molecular phylogenies, and considering that fossil snakes are limited to vertebral elements which are especially poor in polarizable characters, the identification of fossil boids is difficult. In spite of this, Neotropical boines can be characterized by a combination of character states whose co-occurrence is unique to this group (Rage, 2001). These characters were used to identify the fossil vertebra described in this paper. Osteological specimens of extant taxa at UNMdP-O and FMNH were used for comparisons.

The geographic location of La Gran Hondonada is figured in Cladera *et al.* (2004: fig. 1). Although no isotopic data is available from the locality, the Mustersan SALMA is well represented at Gran Barranca (also in Chubut Province, Argentina) by assemblages from both the Rosado and Lower Puesto Almendra members; these units have been dated between 39 and 36.5 Ma (Bond and Deschamps, 2010). Taking into account that the boundary between the middle and late Eocene is at 37.2. Ma (Gradstein *et al.,* 2004), the Mustersan SALMA is assignable to the middle–late Eocene.

***Anatomical abbreviations.*** Anatomical abbreviations used are **cl,** centrum length; **coh**, condyle height; **cow**, condyle width; **cth**, cotyle height; **ctw**, cotyle width; **naw**, neural arch width; **prl**, prezygapophyseal facet length; **prw**, prezygapophyseal facet width; **zh**, zygosphene height; **zw**, zygosphene width.

***Institutional abbreviations.*** **FMNH**, Field Museum of Natural History, New York, USA; **MPEF-PV**, Museo Paleontológico Egidio Feruglio, Trelew, Argentina; **UNMdP-O**, Herpetological Collection - Osteological Section, Universidad Nacional de Mar del Plata, Mar del Plata, Argentina.

## SYSTEMATIC PALAEONTOLOGY

Order Serpentes Linnaeus, 1758

Suborder Alethinophidia Nopcsa, 1923

Family Boidae Gray, 1825

Subfamily Boinae Gray, 1825

Genus and species indet.

**Figure 1**

***Referred material***. MPEF-PV1039, a fragmentary precloacal vertebra.

***Locality and age***. La Gran Hondonada (44°20′49″S–69°46′57″W), Tehuelches Department, Chubut Province, Argentina; Sarmiento Formation, Mustersan SALMA (middle–late Eocene).

***Description.*** The specimen is a robust medium-sized precloacal vertebra, wide and short (see measurements). The right prezygapophysis, most of the neural spine, and both postzygapophyseal surfaces are missing. It is massive, strongly built, and non-depressed. The vertebral centrum is shorter than the width of the neural arch (cl/naw<1). In anterior view, the zygosphene is robust, very thick, narrower than the cotyle (zw/ctw<1), with a straight dorsal roof and a narrow basis. The articular facets of the zygosphene are oval, with the major axis well inclined upward. The cotyle is large, wider than high (ctw/cth>1). A small paracotylar foramen opens in a deep dorsolateral depression on each side of the cotyle. The neural canal is very small and triangular in section. The prezygapophysis is well inclined above the horizontal plane but its lateral margin does not reach the level of the zygosphene roof. It bears a short and blunt prezygapophyseal process that does not project beyond the articular facet. The paradiapophyses are damaged, not projected laterally. In posterior view, the neural arch is high and vaulted. The zygantra are large and deep. There are no parazygantral foramina. The condyle is wider than high (cow/coh>1). In dorsal view, the zygosphene shows a slightly concave anterior edge. The neural spine would have been probably well developed, short and thick, with the anterior edge thinner than the posterior end. The median posterior border of the neural arch is deeply notched. The prezygapophyseal facet is large, subtriangular, longer than wide (prl/prw>1), with the major axis anterolaterally oriented. In ventral view, the centrum is short and not strongly widened forward. The ventral surface is delimited by distinct subcentral ridges, slightly widened anteriorly. The haemal keel is well developed, rather thin but not very prominent. It finishes anteriorly to the well-defined precondylar constriction. Moderate subcentral foramina are present on the anterior half of the ventral surface, one on each side of the haemal keel. In lateral view, the interzygapophyseal ridge is short and strongly marked. A moderate lateral foramen is present on both sides. The paradiapophyses are large, massive, wider dorsally (diapophyseal area) than ventrally (parapophyseal area). The major axis of the condyle is slightly inclined above the horizontal.

The available measurements are the following (in mm.): cl= 10,32; coh= 5,38; cow= 6,66; cth= 6,10; ctw= 7,44; naw= 13,30; prl= 6,00; prw= 4,42; zh= 3,84; zw= 6,52.

***Comparisons***. The size and morphology of the vertebra is typical of those belonging to extant surface snakes, excluding all aquatic and fossorial taxa. Among basal terrestrial snakes, the deeply notched posterior margin of the neural arch differs from the straight margin found in *Dinilysia* Smith-Woodward, 1901, whereas presence of prezygapophyseal process, lack of parazygantral foramina, and synapophyses not laterally projected exclude the vertebra from the Madtsoiidae. Neural arch with deep, V-shaped posterior embayment is an apomorphy of Macrostomata (Lee and Scanlon, 2002). Vertebral centrum shorter than the width of the neural arch prevents its inclusion among the most advanced snakes. Within basal macrostomatans, vertebrae of the family Boidae are

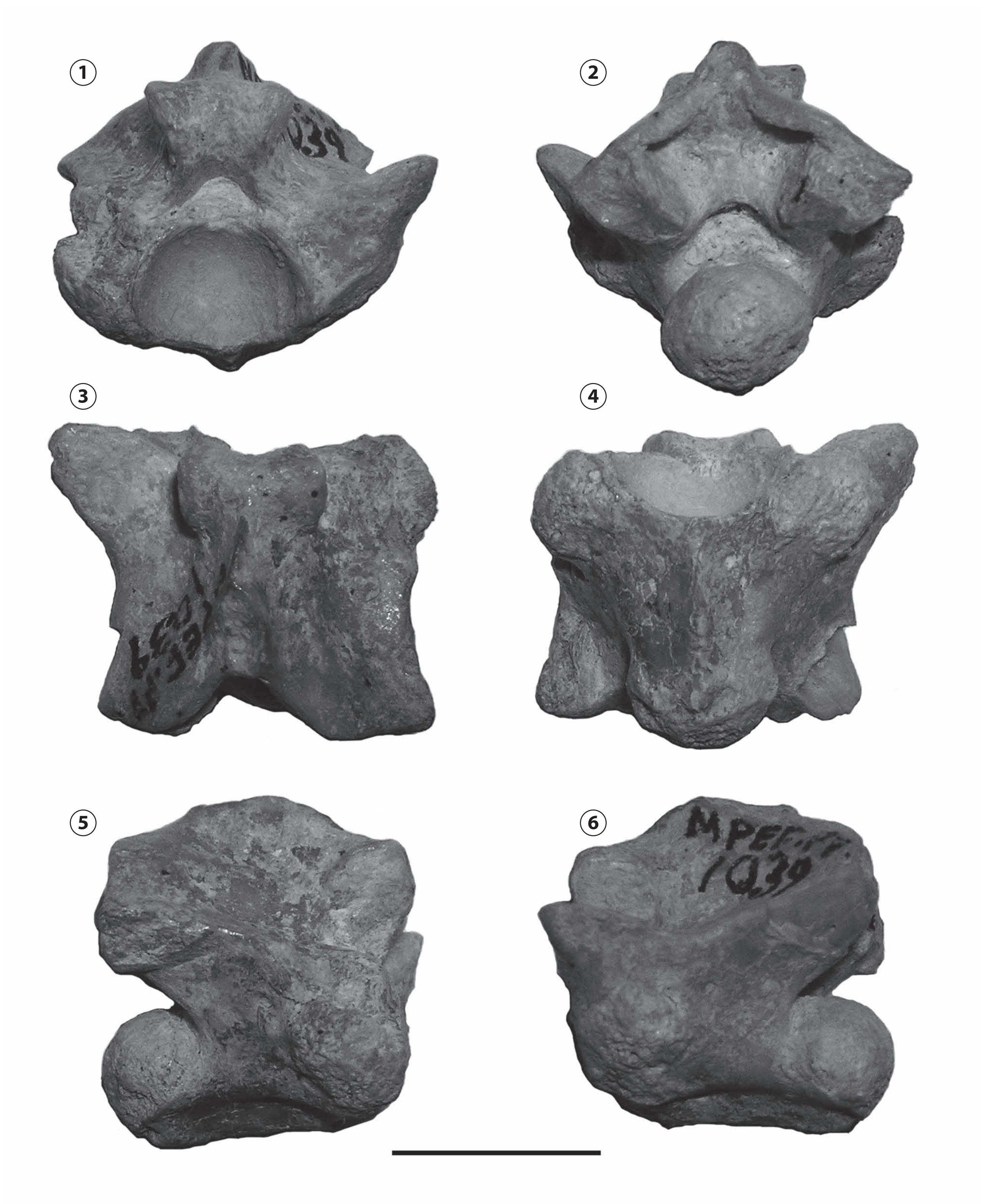

**Figure 1.** Mid-trunk vertebra (MPEF-PV 1039) in anterior; **1**, posterior; **2**, dorsal; **3**, ventral; **4**, right lateral; **5** and left lateral; **6**, views/ *vértebra troncal mediana (MPEF-PV 1039) en vistas anterior*; ***1***, *posterior*; ***2***, *dorsal*; ***3***, *ventral*; ***4***, *lateral derecha*; ***5*** *y lateral izquierda* ; ***6***. Scale/ *escala* = 10 mm.

easily differentiated by the following combination of character states, also observed in the studied vertebra: vertebrae short, wide, and massively built; non-depressed neural arches; prezygapophyseal process short; paradiapophyses weakly subdivided into para- and diapophyseal surfaces; spine-like hypapophyses lacking on mid- and posterior trunk vertebrae, replaced by haemal keels (Szyndlar and Böhme, 1996; Rage, 2001). Trunk vertebrae of Erycinae are distinguished from those of other boids because the neural arches are not high and vaulted, which contrasts with the studied specimen. Presence of paracotylar foramina, zygapophyses well inclined above the horizontal, zygosphene without a vertical median ridge, and absence of small parazygantral foramina clearly argue against an assignment to Pythoninae (Scanlon and Mackness, 2001). Thus, the vertebra shows a combination of character states that only occurs in mid- and posterior precloacal vertebrae of boines. Among extant boines, paracotylar foramina are present in *Candoia* Gray, 1842, two species of *Corallus*, and *Boa* (Kluge, 1991; Albino and Carlini, 2008; Albino, 2011). *Candoia* is distinguished from the studied specimen and from all Neotropical taxa because it has well developed hypapophyses all along the trunk (Kluge, 1991). The openings of the paracotylar foramina are especially large in *Corallus* (Kluge, 1991), contrasting with the small ones in *Boa* and the fossil specimen. In addition, the general size of precloacal vertebrae of *Corallus* is smaller than the size observed in *Boa* and the fossil vertebra. The fossil specimen shows a strongly thickened zygosphene, with no trace of an anterior protuberance or tubercle, also resembling the state found only in *Boa* (Albino and Carlini, 2008; Albino, 2011). Confronting the fossil specimen with mid- and posterior precloacal vertebrae of *Boa*, the former has a high neural arch, a thick zygosphene, a non prominent prezygapophyseal process, and a thin haemal keel, as in vertebrae of the middle part of the trunk (Albino, 2011). However, the vertebra from La Gran Hondonada has the articular facets of the prezygapophyses shorter than those in mid-trunk vertebrae of *Boa*, and they are antero-laterally oriented, contrasting with the more laterally developed prezygapophyses of mid-trunk vertebrae of this genus (Albino, 2011). Also, the vertebral centrum is not clearly widened anteriorly, comparatively longer and narrower than the centra of the available comparative mid-trunk vertebrae of *Boa* (see Albino and Carlini, 2008; Albino, 2011). Because all these characters vary throughout the vertebral spine and the limits between mid- and posterior trunk vertebrae are not rigorous, they cannot be used *per se* to assume a taxon different from *Boa.* Nevertheless, in spite of the similarities with *Boa*, the fossil specimen differs significantly from all living Neotropical boines –including *Boa*– in the zygosphene narrower than the cotyle. This alone prevents an assignation to *Boa*. This last character –together with the concave anterior border of the zygosphene in dorsal view and the presence of paracotylar foramina– appears in the extinct *Chubutophis* Albino, 1993, and *Titanoboa* Head *et al.,* 2009, although the size of the studied vertebra is much smaller than in these two boine genera. Thus, the studied vertebra shows strong similarities with the extant *Boa*, but especially, with the extinct *Chubutophis* and *Titanoboa*. Because of the fragmentary preservation of the vertebra (that does not permit the description of all vertebral structures) and the lack of additional material to describe the intracolumnar and ontogenetic variation, a new taxon is not proposed at the moment.

## DISCUSSION

Although the record of boids in the Cretaceous of South America is still doubtful (Albino, 1996a, 2000, 2007), they were usually present in Paleogene deposits of Argentina, Bolivia, Brazil, and Colombia (Albino, 1987, 1990, 1993, 1996a; Rage, 1991, 2001; Head *et al.*, 2009). The long gap between the Casamayoran (middle–late Eocene) and the Colhuehuapian (early Miocene) SALMAs is not well documented by snakes and all remains come from non-patagonian regions (Hoffstetter, 1958; Simpson *et al.*, 1962; Albino, 1989, 1996a). A possible exception is a single vertebral centrum from the Deseadan SALMA (Oligocene) mentioned by Simpson (1933, p. 10), but it has never been described nor illustrated. The boid specimen described herein constitutes the first record of snakes for the Mustersan SALMA (middle–late Eocene), contributing to the knowledge of the South American snake distribution during the Paleogene. The strong similarities between this specimen and other South American Paleogene boines (*Chubutophis* and *Titanoboa*) indicate close relationships among these snakes. This, together with the records of indeterminate boines in Paleogene rocks of Brazil, Bolivia and Argentina suggests a diversification of Neotropical boines earlier than previously supposed merely on the basis of the extant fauna (Noonan and Chippindale, 2005).

The described boids from the South American Paleogene include small (*Waincophis australis* Albino, 1987, *Hechtophis austrinus* Rage, 2001), as well as very large extinct taxa (*Chubutophis grandis* Albino, 1993, *Titanoboa cerrejonensis* Head *et al.,* 2009). However, medium- to large-sized snakes are the most common. They are *Waincophis pressulus* Rage, 2001, *W. cameratus* Rage, 2001, *Corallus priscus* Rage, 2001, a probable *Boa*, and some indeterminate specimens (Rage, 2001; Albino and Carlini, 2008). The fossil vertebra from La Gran Hondonada has a size observed in vertebral specimens of extant *Boa* measuring two meters long (Albino, 2011). It corroborates the great body-size diversity of boids in South America during the Paleogene and the high number of medium- to large-sized snakes that inhabited the Patagonian region, as noted (Albino, 1993).

The past distribution of boids in Patagonia contrasts with their present distribution, which ranges as far south as northern Mendoza and San Luis provinces, in Argentina (*Boa constrictor* Linnaeus, 1758; Waller and Micucci, 1993; Giraudo and Scrocchi, 2002). The present southernmost distribution of boids in South America is around 34°S, showing that extant medium- to large-sized boids live in regions with average annual temperatures above 16.5–17°C and rainfall regime of more than 250 mm annually. The taphonomy of the fossil mammalian fauna at La Gran Hondonada locality indicates that the vertebrate assemblage would have lived near fluvial waterbodies surrounded by arboreal vegetation and open environments dominated by gramineous covers (Cladera *et al.*, 2004). This proposed paleoenvironment agrees with the presence of medium- to large-sized boids in this paleontological site as well as with the temperatures around 20°C suggested by Andreis (1972) for the Sarmiento Formation. The specimen described here evidences that medium- to large-sized boids survived in the Patagonian region at least up to the Mustersan SALMA (middle–late Eocene). In contrast, early Miocene boids coming from Patagonian localities are all small-sized (Albino, 1996b). Taking into account that snakes of colder regions are almost all small-sized (Parker and Grandison, 1977), the presence of smaller boids in the Patagonian Neogene with respect to those from earlier periods might be related in general terms with a temperature drop. This is supported by the known changes in mean global annual temperatures reported for this period (Zachos *et al.*, 2001).

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