



General Palaeontology, Systematics and Evolution (Vertebrate Palaeontology)

A new species of *Gaimanophis* (Serpentes, Boidae) from the Miocene of northwestern Argentina with remarks on the Neogene boids of South America



Une nouvelle espèce de Gaimanophis (Serpentes, Boidae) du Miocène du Nord-Ouest de l'Argentine et remarques sur les boïdés du Néogène d'Amérique du Sud

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ARTICLE INFO

Article history:

Received 10 August 2016

Accepted after revision 14 November 2016

Available online 12 January 2017

Handled by Lars vanden Hoek Ostende

Keywords:

Argentina

Boidae

Gaimanophis

Miocene

Snakes

Mots clés :

Argentine

Boidae

Gaimanophis

Miocène

Serpents

ABSTRACT

Gaimanophis is an extinct boid genus represented so far by a single species (*Gaimanophis tenuis*) known by isolated vertebrae from the early Miocene of Patagonia. In this paper, a new species of *Gaimanophis* is described from the India Muerta Formation (late Miocene) of Tucumán province (Argentina). *Gaimanophis powelli* sp. nov. distinguishes itself from *G. tenuis* mainly in its larger size, prezygapophyses less slanting, neural spine shorter dorsally than ventrally, and zygosphen straight bearing an anteriorly protruding tongue. This record indicates a wider temporal and geographical distribution of the genus from the early Miocene of Patagonia to the late Miocene of northwestern Argentina. The recognition of a new species of boid in South America increases the known diversity of this group. Although boids have inhabited in this territory since the Paleocene, fossils belonging to the group only show a glimpse of the real past diversity in the continent.

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R É S U M É

Gaimanophis est un genre de Boïdé éteint, représenté jusqu'à présent par une unique espèce (*Gaimanophis tenuis*) reconnue par des vertèbres isolées, dans le Miocène inférieur de Patagonie. Dans cet article, une nouvelle espèce de *Gaimanophis*, provenant de la formation India Muerta (Miocène supérieur) de la province de Tucumán (Argentine), est décrite. *Gaimanophis powelli* sp. nov. se distingue principalement de *G. tenuis* par sa plus grande taille, des prézygapophyses moins inclinées, une épine neurale plus courte dorsalement que ventralement, un zygosphène droit portant antérieurement une langue saillante. Le registre indique une plus large répartition géographique et temporelle du genre, depuis le Miocène inférieur de Patagonie jusqu'au Miocène supérieur du Nord-Ouest de l'Argentine. La reconnaissance d'une nouvelle espèce de boïdé en Amérique du Sud augmente la

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<http://dx.doi.org/10.1016/j.crpv.2016.11.007>

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diversité connue de ce groupe. Bien que les boïdés aient habité ce territoire depuis le Paléocène, les fossiles appartenant à ce groupe permettent seulement d'entrevoir la réelle diversité passée sur ce continent.

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1. Introduction

Snakes are usually present in Neogene deposits of South America, but compared to the records from other continents, the richness and diversity of South American fossil snakes are relatively poor. Among boids, extant (*Eunectes*, *Epicrates*) and extinct genera (*Waincophis*, *Gaimanophis*) have been recognized in Miocene formations of Argentina, Colombia, Brazil and Venezuela (Albino and Brizuela, 2014). *Gaimanophis* is a genus of uncertain affinities, represented, up to now, by a single species (*Gaimanophis tenuis*) known from isolated vertebrae from the early Miocene of Patagonia (Albino, 1996). Recently, new vertebrate discoveries in Miocene deposits of northwestern Argentina (Tucumán province) provided a small vertebra of snake from the India Muerta Formation (late Miocene). In the present paper, a new species of *Gaimanophis* is described based on this specimen, and comments about the Neogene record of boids in South America is given.

2. Geological setting

The studied vertebra was collected from sediments belonging to the India Muerta Formation exposed at the intersection between Ruta Nacional 9 and access to Dique El Cadillal (also known as Celestino Gelsi), north of the city of San Miguel de Tucumán, Tucumán Province, northwestern Argentina (Fig. 1).

The India Muerta Formation (Choromoro Group) is represented by discontinuous outcrops scattered in the vicinities of Dique El Cadillal. The lithology of this unit is characterized by grey, coarse- to fine-grained sandstones, either massive or with cross-bedding, and brownish siltstones (both massive and bioturbated) representing a fluvial system of meandering rivers (Bossi et al., 1998).

The fossil record of the India Muerta Formation includes remains of Crocodylia, Testudines, and various mammals (Babot and Ortiz, 2008; García López and Babot, 2015). The associated mammalian fauna was assigned to the late Miocene Huayquerian South American Land Mammal Age (SALMA) (Bossi et al., 1998).

3. Materials and methods

The fossil specimen is deposited in the PVL. Comparative skeletons of extant snakes at UNMDP-O and fossil specimens belonging to the MACN and MLP collections were used to assist with fossil identifications. Measurements were taken using a digital caliper and they are in millimeters.

Institutional abbreviations are: MACN: Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”,

Colección Nacional de Paleovertebrados, Ciudad Autónoma de Buenos Aires, Argentina; MLP: Museo de La Plata, División Paleontología de Vertebrados, La Plata, Argentina; PVL: Fundación Miguel Lillo, Colección Paleontología Vertebrados, San Miguel de Tucumán, Argentina; UNMDP-O: Universidad Nacional de Mar del Plata, Colección Herpetológica, Sección Osteología, Mar del Plata, Argentina.

Anatomical abbreviations are: cl: centrum length; cth: cotyle height; ctw: cotyle width; H: vertebra height; naw: neural arch width at interzygapophyseal constriction; pr-po: distance between anterior edge of prezygapophysis and posterior edge of postzygapophysis of the same side; pr-pr: distance between outer edges of prezygapophyses; zgh: zygosphene height.

4. Systematic paleontology

Serpentes Linnaeus, 1758

Alethinophidia Nopcsa, 1923

Macrostromata Müller, 1831

Boidae Gray, 1825

Gaimanophis Albino, 1996

Type species. *Gaimanophis tenuis* Albino, 1996

Gaimanophis powelli sp. nov.

Fig. 2

Etymology. In honor to my colleague and friend Jaime Powell (†), collector of the studied specimen, for his contribution to the vertebrate paleontology of Argentina.

Holotype. PVL 6547, isolated mid-trunk vertebra.

Type locality and horizon. National Route 9 (26° 39' 31" S, 65° 14' 00" W), at the access to Dique El Cadillal (Celestino Gelsi), Tafi Viejo Department, north to the city of San Miguel de Tucumán, Tucumán Province, Northwestern Argentina (Fig. 1). India Muerta Formation. Huayquerian SALMA, late Miocene.

Diagnosis. Small boid snake of the genus *Gaimanophis* differentiated from *G. tenuis* in the larger size, the prezygapophyses less slanting, the neural spine shorter dorsally than ventrally, and the zygosphene straight bearing an anteriorly protruding tongue.

Measurements. cl = 5.60; cth = 3.60; ctw = 3.84; H = 8.46; naw = 7.90; pr-pr = 10.80; pr-po = 7.76; zgh = 0.80.

5. Description

The specimen is a nearly complete mid-trunk vertebra, lacking the right postzygapophysis, most of the right zygantrum, part of the posterior edge of the neural arch and left zygosphene. The vertebra is rather eroded, with the condyle and paradiapophyses badly conserved. It is

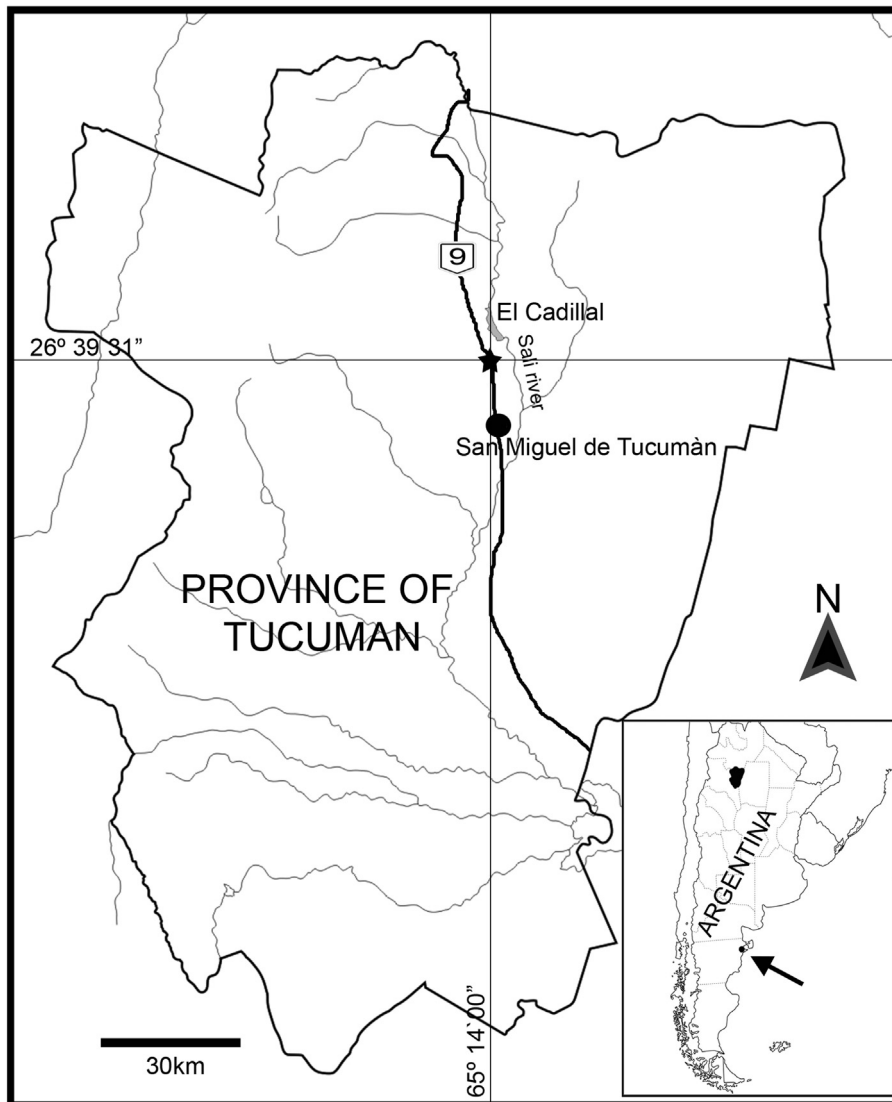


Fig. 1. Map showing the geographic location of the site (star) near Dique El Cadillal (Tucumán province, Argentina). The arrow in the small map shows the locality that yielded *Gaimanophis tenuis*.

Fig. 1. Localisation géographique du site (étoile) près de Dique El Cadillal (Tucumán province, Argentina). La flèche dans la petite carte montre la localité qui a fourni *Gaimanophis tenuis*.

small, robust, wide, low and short, with the vertebral centrum shorter than the neural arch width ($cl < naw$). In anterior view, the zygosphene is well developed, dorsoventrally thin, straight and presumably wider than the cotyle. It has a small articulate surface conserved on the right side and a thin tongue protruding anteriorly. The prezygapophyses are small, emerging above the level of the neural canal floor, and scarcely inclined on the horizontal plane. Each prezygapophysis is separate from the neural canal by a short, deep notch. The distance between prezygapophyses surpasses greatly the height and length of the vertebra ($pr-pr > H > pr-po$); thus, the vertebra looks notably widened. The prezygapophyseal process is small, short, and robust. The neural canal is subtriangular, rather large, wide, high, and bearing only a ventral longitudinal

crest. The cotyle is rather large, wider than high ($ctw > cth$), with a thin border. The ventral edge of the cotyle is broken. There are not paracotylar foramina. The paradiapophyses are rather small, low, not projected laterally; they do not reach the level of the ventral edge of the cotyle and have surfaces ventrolaterally oriented.

In posterior view, the neural arch is depressed and wide. The left zygantrum is deep, containing a well-developed articulate surface. Dorsally, the zygantrum is broken. The left postzygapophysis is rather small and scarcely slanting on the horizontal plane. The neural canal looks subtriangular. The condyle is extremely eroded, slightly wider than high.

In lateral view, the vertebra is higher than long, with the vertebral centrum clearly shorter than the neural

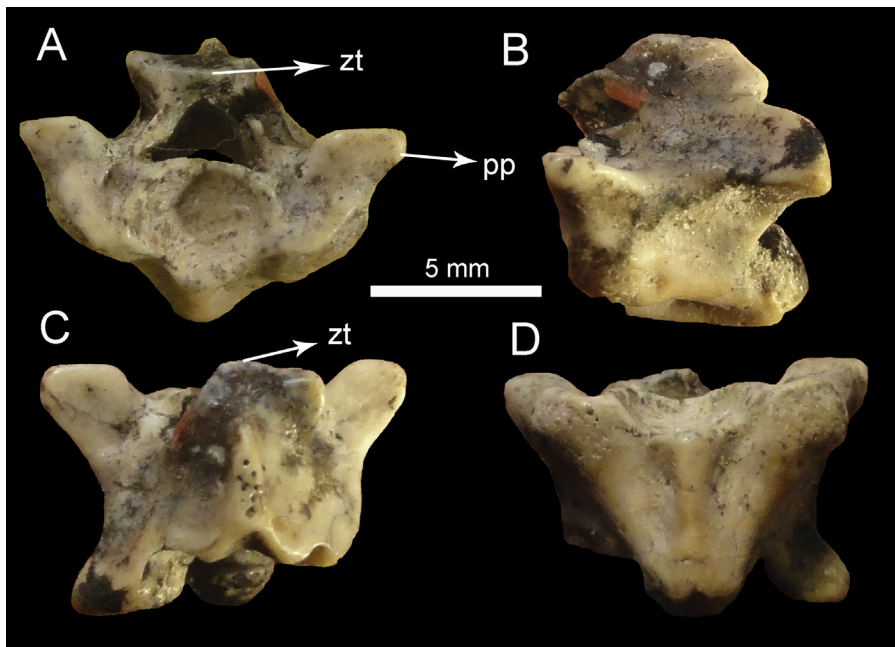


Fig. 2. *Gaimanophis powelli* sp. nov., holotype, PVL 6547, precloacal vertebra, in anterior (A), lateral (B), dorsal (C) and ventral (D) views; pp: prezygapophysial process; zt: tongue of the zygosphene.

Fig. 2. *Gaimanophis powelli* sp. nov., holotype, PVL 6547, vertèbre pré-cloacale, vues antérieure (A), latérale (B), dorsale (C) et ventrale (D) ; pp : processus prézygapophysaire ; zt : langue du zygosphène.

arch ($H > pr-po > cl$). The neural arch is depressed. The neural spine is low and its basis is long. It has anterior and posterior edges slightly converging in a dorsal border; thus, the base of the spine is longer than the dorsal rim. Dorsally, the spine is somewhat eroded and broken, but its anterior edge is complete revealing its slight tallness. The articulate surface of the zygosphene is small, oval, and anterodorsally oriented. The interzygapophysial crest is long, sinuous, and marked. Lateral foramina are present at each side. The subcentral ridges are moderately defined, anteroposteriorly developed along a straight line. Ventrally, the haemal keel surpasses the level of these ridges. The paradiapophyses are not well developed dorsoventrally, far from the prezygapophysial surfaces and rather downwards oriented, exposing much of their articulate surfaces ventrally. Although the paradiapophyses are eroded, there is no evidence of strong differentiation into di- and parapophysial surfaces. The condyle axis is slightly inclined on the horizontal.

In dorsal view, the vertebra is short, wide, with the neural arch wider than long ($pr-pr > pr-po$). The interzygapophysial constriction is well defined at the middle, but moderately deep and anteroposteriorly short. Although the posterior border of the neural arch is partially broken, it is possible to note the presence of a strong and deep medial notch. The zygosphene has the anterior edge convex, forming a flat tongue, protruding anteriorly. The basis of the neural spine is long but the dorsal border is short, thinner anteriorly than posteriorly. The prezygapophyses are small, with short and narrow surfaces anterolaterally projected. The prezygapophysial processes are hidden in dorsal view.

In ventral view, the vertebral centrum is short and wide, especially in its anterior part due to a strong divergence

of the moderately defined subcentral ridges. The paradiapophysial surfaces are small, clearly visible in ventral view. The left postzygapophysis has a small articulate surface, which is subtriangular and posterolaterally projected. The cotyle is ventrally visible because of the broken ventral border. The haemal keel is wide and moderately protruding. Its anterior part is widened, but does not reach the width of the cotyle. Posteriorly, it is thinner and finishes as a smooth and not well-defined keel, not reaching the condyle. The subcentral channels are not deep. The subcentral foramina are opened on the anterior part of the centrum.

6. Discussion

The described vertebra is attributed to the extinct genus *Gaimanophis* based on the presence of a combination of characters present in the holotype of *G. tenuis*, which is the type species of the genus and the single species described up to now (Albino, 1996). These features are: small size; vertebra clearly wider than longer; neural arch depressed; low, thin and long neural spine; zygosphene thin, wider than the cotyle; rather large and subtriangular neural canal; prezygapophyses arising dorsally from the level of the neural canal floor and slightly inclined above the horizontal plane; short and thick prezygapophysial process; vertebral centrum short and anteriorly notoriously widened; cotyle and condyle wider than high; absence of paracotylar foramina; and paradiapophyses small, not surpassing the ventral edge of the cotyle. The haemal keel of the known vertebrae of the type species of *Gaimanophis* varies according to the position in the column. It is clearly prominent and distinctive as a short hypopapophysis, or

poorly developed and wide (Albino, 1996). The haemal keel of the studied specimen is defined but not protruding, smooth and rather wide anteriorly but thinner posteriorly. It probably corresponds to a vertebra of an intermediate position in the column, between vertebrae with short hyopapophysis and vertebrae with wide and flat keel.

In conclusion, most characters support the assignation of this vertebra to *Gaimanophis*. Nevertheless, some features between the Patagonian and northwestern specimens are different. The morphology of the zygosphenes with an anterior tongue and straight in the middle part, as well as the neural spine shorter dorsally than ventrally, are distinctive characteristics of the studied vertebra, differing from the vertebrae assigned to *G. tenuis* in Albino (1996). Moreover, all of the vertebrae referred to *G. tenuis* are smaller and the prezygapophyses are more inclined than in the new specimen. Thus, the vertebra from India Muerta Formation is referred to a new species of the genus, *Gaimanophis powelli* sp. nov.

Based on the Patagonian specimens of the genus, Albino (1996) tentatively assigned *Gaimanophis* to the Erycinae, a group presently absent in South America. The small size, absence of paracotylar foramina, depressed neural arch, and low neural spine are all characters found in this group. However, the erycines are characterized by the presence of caudal vertebrae with additional apophyses (Szyndlar and Rage, 2003), although it was demonstrated that snakes with erycine-like trunk vertebrae could possess caudal vertebrae without additional apophyses (Szyndlar and Böhme, 1996). Unfortunately, caudal vertebrae of *Gaimanophis* are unknown, so the assignation of this genus to Erycinae is not well supported.

Although absent from the Mesozoic, boid snakes are present in South America since the Paleocene (Albino and Brizuela, 2014). Until some years ago the Paleogene boid record came only from Argentina and Brazil, with few remains from Bolivia (Albino, 1987, 1990, 1992, 1993, 2011, 2012; de Muizon et al., 1983; Rage, 1991, 2001), whereas the Neogene provided remains from Argentina and Colombia (Albino, 1992, 1996; Albino et al., 2013; Hecht and LaDuke, 1997; Hoffstetter and Rage, 1977).

The Paleocene and Eocene climates were characterized by quite warm and tropical conditions extended north and south towards the poles. In this scenery, Paleogene boids were relatively diverse in South America. The Patagonian Paleogene boid fauna included small (*Waincophis*), medium-sized (*Boa*) and large forms (*Chubutophis*), but only small genera (*Waincophis*, *Gaimanophis*) persisted into the Miocene. The absence of large snakes in the Patagonian Miocene with respect to those from earlier periods would have been related to decreased temperatures, which is consistent with known changes in mean global annual temperatures reported for this epoch (Albino, 2012; Albino and Brizuela, 2014). Nevertheless, the climatic conditions in the Patagonian region during the Miocene would have been yet temperate enough to permit the presence of small boids at latitudes around 44°S, where they do not exist today (Albino and Brizuela, 2014). There are no records of post-Miocene boids from Patagonia, but during the latest Miocene and Pliocene some boids still lived outside their present range (Albino, 1992; Albino and Carlini,

2008; Albino et al., 2013). In addition, the genus *Boa* inhabited the Mesopotamian region of Argentina during the Late Pleistocene, but changes in the Paraná and Uruguay Rivers would have caused its extinction from this region (Albino and Carlini, 2008). No other fossil boid has been reported for Argentina, except for the new species of *Gaimanophis* from the northwestern region described in this paper.

With respect to the Brazilian Paleogene boids, Rage (2001) recognized some extinct genera (*Waincophis presulus*, *W. cameratus*, *Hechtophis austrinus*) as well as the oldest record of the extant *Corallus* (*Corallus priscus*). During the latest years, the record of fossil boids from Brazil has been enlarged with the description of remains collected from Neogene sediments outcrops in southwestern Brazilian Amazonia, including the extinct *Waincophis* and the earliest presence of the extant genera *Eunectes* and probably *Epicrates* (Hsiou and Albino, 2009, 2010). Furthermore, the fossil record of boids from Colombia, which was limited to the extant *Eunectes* from the Miocene (Hoffstetter and Rage, 1977), has been increased with the description of a very large boid from the Paleogene (*Titanoboa cerrejonensis*, Head et al., 2009). The latest years also provided records of boid snakes from the late Miocene of Venezuela, which include the extant genus *Eunectes* (Head et al., 2006; Hsiou and Albino, 2010).

7. Conclusions

The identification of a new species of the extinct boid *Gaimanophis* in the Dique El Cadillal increases the diversity of the genus into two species. Besides, it indicates a wider temporal and geographical distribution of the genus than the previously known. At present, *Gaimanophis* extends from the early Miocene of Patagonia (*G. tenuis* in Chubut province, Albino, 1996, indicated by an arrow in Fig. 1) to the late Miocene of northwestern Argentina (*G. powelli* in Tucumán province, this work).

Boids are currently slightly diverse in South America, containing five genera (*Boa*, *Corallus*, *Epicrates* and *Eunectes*) with 17 species distributed in tropical and subtropical environments from Colombia and Venezuela to Argentina, north to 34°S. Known since the Paleocene, fossils belonging to this group do not appear to be representative of the real past diversity in the continent. This would be in part consequence of the lack of enough studies focused on Cenozoic snakes of South America. Nevertheless, the most recent discoveries in Argentina, Brazil, Colombia and Venezuela demonstrate the importance of focusing future prospectations for fossil snakes in the Neogene of little explored regions. In this sense, the recognition of a new species of boid in the late Miocene of northwestern Argentina increases the known diversity of this group in this territory.

Acknowledgements

The author wishes to especially thank the paleontologist Jaime Powell (†) for the loan of the studied specimen under his care and for his sincere friendship during more than three decades. Jean Claude Rage and an anonymous

reviewer provided valuable comments to increase the clarity of the manuscript. The associate editor Lars van den Hoek Ostende contributed with language improvements of the manuscript. This is a contribution to the project PIP CONICET 112-201501-00065 (2015–2017).

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