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A new Late Cretaceous snake from Patagonia: Phylogeny and trends in body size evolution of madtsoiid snakes

Un nouveau serpent du Crétacé supérieur de Patagonie : phylogénie et tendances de l'évolution de la taille des serpents madtsoiidés

Raúl O. Gómez[a,b,*], Fernando F. Garberoglio[c], Guillermo W. Rougier[d]

[a] *CONICET–Departamento de Ciencias Geológicas, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad de Buenos Aires, Pabellón 2, Ciudad Universitaria, 1428 Buenos Aires, Argentina*
[b] *Departamento de Biodiversidad y Biología Experimental, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad de Buenos Aires, Pabellón 2, Ciudad Universitaria, 1428 Buenos Aires, Argentina*
[c] *CONICET–Área de Paleontología, Fundación de Historia Natural Félix de Azara. CEBBAD, Universidad Maimónides, Hidalgo 775, 1405 Buenos Aires, Argentina*
[d] *Department of Anatomical Sciences and Neurobiology, University of Louisville, 511 S. Floyd Street, 40292 Louisville, KY, USA*

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ABSTRACT

Madtsoiids constitute a successful group of extinct snakes widely distributed across Gondwana and the European archipelago during Late Cretaceous times, surviving in reduced numbers to the Pleistocene. They are renowned for including some of the largest snakes that have ever crawled on earth, yet diverse small madtsoiids are also known. Uncovering the evolutionary trends that led these snakes into disparate body sizes has been hampered mainly by the lack of phylogenetic consensus and the paucity of taxa with novel combinations of features. Here we describe a new large madtsoiid snake based on isolated vertebrae from the La Colonia Formation (Maastrichtian–Danian) of Patagonia, Argentina. A comprehensive phylogenetic analysis recovers Madtsoiidae as a basal ophidian lineage and the new snake as sister to a clade of mostly big-to-gigantic taxa, providing insights into early stages and evolutionary trends towards madtsoiid gigantism.

RÉSUMÉ

Les madtsoiidés constituent un groupe réussi de serpents éteints, largement répartis dans le Gondwana et l'archipel européen au cours du Crétacé supérieur, survivant en nombre réduit jusqu'au Pléistocène. Ils sont réputés pour inclure certains des plus grands serpents qui aient jamais rampé sur Terre, mais divers petits madtsoiidés sont également connus. La découverte des tendances évolutives qui ont conduit ces serpents à des tailles de corps disparates a été entravée principalement par le manque de consensus phylogénétique et le manque de taxons dotés de nouvelles combinaisons de caractéristiques. Nous décrivons ici un nouveau grand serpent madtsoiidé sur la base de vertèbres isolées de la formation

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[*] Corresponding author at: Departamento de Ciencias Geológicas, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad de Buenos Aires, Pabellón 2, Ciudad Universitaria, 1428 Buenos Aires, Argentina.
E-mail address: raulorenciogomez@gmail.com (R.O. Gómez).

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t La Colonia (Maastrichtien–Danien) de Patagonie, Argentine. Une analyse phylogénétique complète récupère les Madtsoiidae en tant que lignée basale ophidienne et le nouveau serpent en tant que frère d'un clade de taxons pour la plupart énormes à gigantesques, fournissant un aperçu des débuts et des tendances évolutives vers le gigantisme des madtsoiidés.

1. Introduction

Madtsoiids compose a successful group of extinct snakes with a relatively rich fossil record spanning 100 million years and a widespread distribution across Gondwana and the European archipelago in the Late Cretaceous (reviewed by Rage et al., 2014; Rio and Mannion, 2017; Vasile et al., 2013). Their monophyly and position within snakes have been intensely debated (McDowell, 1987; Rage, 1984, 1998; Rieppel et al., 2002; Scanlon, 2006; Scanlon and Lee, 2000), and even their internal relationships remain uncertain (Rio and Mannion, 2017; Vasile et al., 2013). However, most recent studies support madtsoiids as a clade of basal snakes (Caldwell et al., 2015; Garberoglio et al., 2019a, 2019b; Harrington and Reeder, 2017; Martill et al., 2015; Vasile et al., 2013). Two basal snakes from the Upper Cretaceous of Patagonia might also be related to madtsoiids (Garberoglio et al., 2019a, 2019b): *Dinilysia patagonica* Smith-Woodward, 1901 and *Najash rionegrina* Apesteguía and Zaher, 2006, both well known from crania and postcrania (Caldwell and Albino, 2002; Garberoglio et al., 2019a, 2019b; Scanferla and Bhullar, 2014).

Madtsoiids are renowned for including some of the largest snakes that have ever crawled on earth; large forms are already present in the Latest Cretaceous of India, Madagascar, and Europe (LaDuke et al., 2010; Mohabey et al., 2011; Wilson et al., 2010), becoming truly gigantic worldwide in the Paleogene (Rage et al., 2014; Rio and Mannion, 2017; Simpson, 1933). Diverse small-to-medium-sized madtsoiids are also known over most of the stratigraphic range of the group (Pritchard et al., 2014; Rage, 1996; Scanlon, 1997, 2006; Vasile et al., 2013), which are the only size-class of unambiguous madtsoiids represented to date in the Upper Cretaceous of Patagonia (Albino, 1986, 1994, 2000, 2007; Gómez, 2006, 2011; Gómez and Báez, 2005, 2006; Martinelli and Forasiepi, 2014). Understanding how and when these disparate body sizes have evolved among madtsoiids has been hampered mainly by the lack of resolution and consensus on their phylogeny (Rio and Mannion, 2017; Vasile et al., 2013), but also by the paucity of madtsoiid taxa in general, and particularly, new taxa showing novel character combinations.

Here we describe a large new Late Cretaceous madtsoiid snake from the La Colonia Formation of Patagonia based on isolated vertebrae. We assess the evolutionary relationships of the new and previously known madtsoiids by means of a comprehensive phylogenetic analysis and discuss major trends of body size evolution in Madtsoiidae.

2. Geological and paleontological framework

The fossils described herein come from middle levels of the La Colonia Formation (Pesce, 1979) cropping out on the southeastern slopes of the Somún Curá Massif, Chubut Province, Argentina (Fig. 1A). Particularly, they were exhumed from a small fossil-rich lens at El Uruguayo site (Harper et al., 2018; Rougier et al., 2009a) located on the north-facing slopes of the Mirasol Chico Creek Valley (Fig. 1B). These levels correspond to the second facies association of Pascual et al. (2000), which is the most representative of the unit and consists mostly of massive and laminated claystones and siltstones with scarce intercalated beds of massive, laminated, or cross-bedded sandstones (see stratigraphic sections north of Cerro Bayo in Gasparini et al., 2015: fig. 2). Their depositional environments have alternatively been interpreted as marginal marine, estuaries, tidal flats, lagoons or coastal plains or as more restricted littoral settings including muddy floodplains, marshes or ponds, both influenced by continental freshwater flows and tidal currents from the sea (Ardolino and Delpino, 1987; Cúneo et al., 2014; Gasparini et al., 2015; Page et al., 1999; Pascual et al., 2000). Deposition of these levels occurred during the Late Cretaceous–Paleocene Atlantic transgression (Gasparini et al., 2015; Malumián and Náñez, 2011) that extensively flooded Patagonia with the epeiric Kawas Sea (Casamiquela, 1978; Hugo and Leanza, 2001).

The La Colonia Formation has often been regarded as encompassing, at least, the Campanian–Maastrichtian interval based on microfossils (Ardolino and Franchi, 1996), stratigraphic correlations, and faunal comparisons (Gasparini et al., 2015; Pascual et al., 2000). Noteworthy, Pascual et al. (2000) considered the lower facies association of the La Colonia Formation as equivalent to the Puntudo Chico Formation (Pesce, 1979), a proposal that was, either implicitly or explicitly, followed by many subsequent studies (Gandolfo et al., 2014; Gasparini et al., 2015; O'Gorman et al., 2013; Rougier et al., 2009a; Sterli and de la Fuente, 2011). However, the deposits of the Puntudo Chico Formation (middle-late Campanian–early Maastrichtian) could not be attributed to the La Colonia Formation based on available data (Ardolino *fide* Vera et al., 2019) and should instead been considered as a separate unit underlying the latter in the area (Anselmi et al., 2004; Cúneo et al., 2014; Vera et al., 2019). Furthermore, the uppermost levels of the La Colonia Formation in the Telsen area were regarded as Danian based on palynomorphs (Guler et al., 2014), whereas the mammals from its middle levels at El Uruguayo have been considered slightly younger than those from the Campanian–Maastrichtian Los Alamitos and

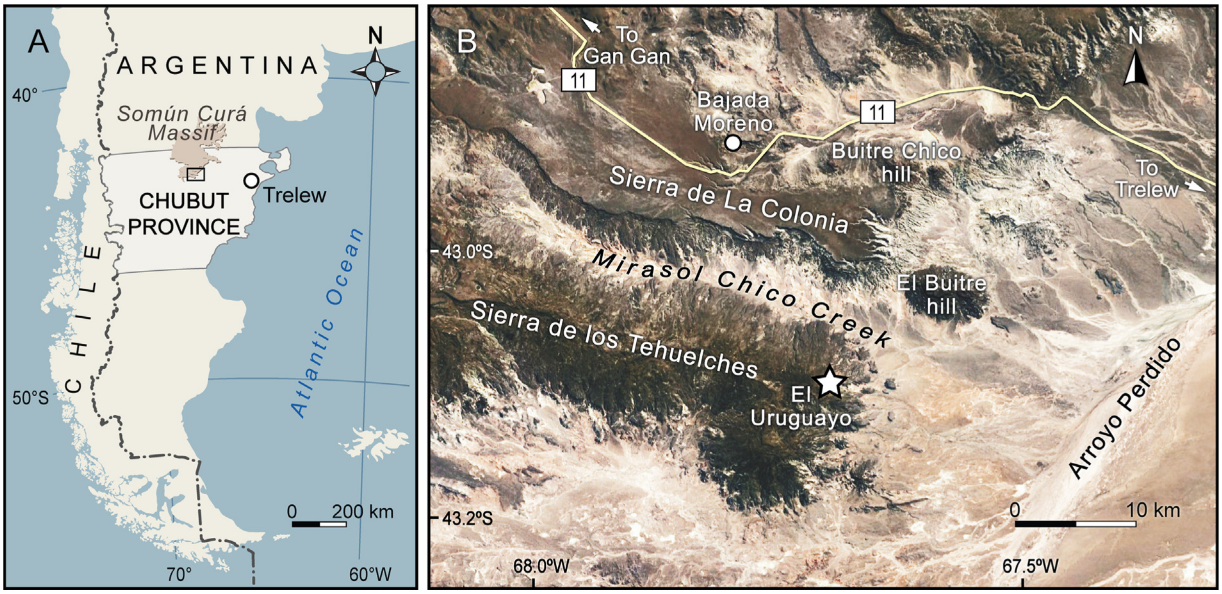

Fig. 1. Locality. **A**. Map of Chubut province, Patagonia, Argentina, showing the area of interest on the southeastern slopes of the Somún Curá Massif. **B**. Detail of the study area and location of El Uruguayo fossil site (white star).

Fig. 1. Localité. **A**. Carte de la province de Chubut, Patagonie, Argentine, montrant la zone d'intérêt sur les versants sud-est du massif du Somún Curá. **B**. Détail de la zone d'étude et de l'emplacement du site fossilifère d'El Uruguayo (étoile blanche).

Allen formations (Rougier et al., 2009a, 2009b). Based on all available evidence, the age of the La Colonia Formation might be considered Maastrichtian–Danian (Anselmi et al., 2004; Page et al., 1999; Vera et al., 2019) and based on the geological framework and associated fauna of the El Uruguayo lens it is most likely that the snake-bearing levels are therefore late Maastrichtian in age (Harper et al., 2018; Rougier et al., 2009a, 2009b).

Abundant fossils of algae, plants, crustaceans, and mostly terrestrial, freshwater or brackish vertebrates indicative of tropical or subtropical wetlands have been recovered to date from the La Colonia Formation from different stratigraphic levels and localities (Cúneo et al., 2014; Gandolfo et al., 2014; Gasparini et al., 2015), although most vertebrate remains come from the middle levels of the unit that crop on the area of Sierra de La Colonia and Sierra de Los Tehuelches (Albino, 2000; Gasparini et al., 2015; Harper et al., 2018; O'Gorman et al., 2013; Rougier et al., 2009a; Sterli and de la Fuente, 2011). At El Uruguayo site, these levels have yielded a rich assemblage of vertebrates including fishes, amphibians, mammals, plesiosaurs, crocodiles, non-avian dinosaurs, enantiornithine birds, turtles, and snakes (Harper et al., 2018; Lawver et al., 2011; Rougier et al., 2009a). Only a few fragmentary snake vertebrae from middle levels of the La Colonia Formation between El Buitre and Buitre Chico hills have been described so far and were ascribed to the small madtsoiid *Alamitophis argentinus*,?Madtsoiidae,?Boidae or Madtsoiidae, and a 'Serpentes *incertae sedis*' (Albino, 2000). *Alamitophis argentinus* as well as other small-to-mid sized madtsoiids have also been reported based on isolated vertebrae from the Campanian–Maastrichtian Los Alamitos and Allen formations of northern Patagonia (Albino, 1986, 1994, 2007; Gómez, 2006; Gómez and Báez, 2005, 2006; Martinelli and Forasiepi, 2014).

3. Materials and methods

3.1. Materials, measurements, and nomenclature

The fossil material object of this contribution has been collected along successive fieldtrips led by one of us (GWR) in collaboration with the Museo Paleontológico Egidio Feruglio to Mesozoic outcrops in northern central Chubut Province (Fig. 1). Fossils are relatively well preserved but show weathering and polished breakage surfaces, particularly in articulation facets, likely due to hydraulic transport prior to deposition (Harper et al., 2018; Varela and Parras, 2013). Measurements were mainly those defined by LaDuke (1991) and Rage (2001) and subsequently used by several authors (Rio and Mannion, 2017; Vasile et al., 2013) and were either taken digitally from photographs or directly on vertebrae with a manual digital caliper (0.01 mm error). Drawings were made with the aid of a Zeiss Stemi SV11 binocular microscope equipped with a camera lucida and photographs were taken with a Nikon D3200 digital camera equipped with a macro lens. The osteological terminology follows that of Rage (1984, 1998, 2001) and LaDuke (1991), with a few additional terms from Scanferla and Canale (2007) and Garberoglio et al. (2019a). The collected fossils are housed at the Museo Paleontológico Egidio Feruglio.

3.2. Phylogenetic analyses

The position of the new taxon from La Colonia Formation as well as the monophyly and internal relationships of Madtsoiidae were tested through a quantitative phylogenetic analysis. For this we used a modified version of the data set of Garberoglio et al. (2019a), which in turn stemmed from that of Caldwell et al. (2015). For the pur-

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pose of this study, we added several additional madtsoiid taxa known mostly or only from vertebrae and vertebral characters based on the data set of Vasile et al. (2013), as later modified by Rio and Mannion (2017). Also, we included the presumably basal snake *Seismophis* from the Upper Cretaceous of Brazil (Hsiou et al., 2014), which is known from *Najash*-like vertebrae (Garberoglio et al., 2019a), and the Cretaceous marine snake *Simoliophis*, also known only from isolated vertebrae (Rage et al., 2016). In total, 18 extant and 36 extinct taxa were scored for 264 osteological characters, of which 52 are of the axial skeleton (Supplementary data).

A maximum parsimony analysis of the complete data set was conducted in TNT Version 1.5-beta (Goloboff et al., 2008). Heuristic searches under equal weights consist of 500 tree replicates obtained by random addition sequence (RAS), searching for new tree topologies with tree bisection and reconnection (TBR), and saving 100 trees per replication and collapsing branches of zero length after tree search. The resulting trees were subjected to a final round of TBR branch swapping and optimal topologies were rooted with *Varanus*. During tree searches, multistate characters based on continuous underlying data or depicting clear morphoclines (Wiens, 2001) were treated as ordered (Supplementary data). Node support was estimated by calculation of the Bremer support (BS) and absolute frequencies under jackknifing, performing 10,000 pseudo-replicates of 10 random sequence additions each followed by TBR swapping, keeping up to 10 trees, with a probability of alteration $P = 0.36$.

3.3. *Body size evolution*

We explored trends in body size evolution among madtsoiids by mapping a proxy of absolute size onto a stratocladogram. As a proxy of size we measured the maximum width of cotyle of middle precloacal vertebrae (Supplementary data). Measurements were either taken digitally from photographs or directly on vertebrae with a manual digital caliper (0.01 mm error). The stratocladogram was derived from one of the optimal trees obtained in the parsimony analysis, including madtsoiids plus a few outgroup taxa. Numerical ages of each extinct taxon were derived from the youngest possible age of the oldest fossil-bearing unit following the current chronostratigraphic framework (Cohen et al., 2013, updated) and internodes were set to a minimum time interval (1 Myr herein), following previous approaches (Gómez and Pérez-Ben, 2019; Marjanović and Laurin, 2008, 2014). Stratocladogram assemblage and character optimization under squared change parsimony were performed in Mesquite Version 3.31 (Maddison and Maddison, 2011).

3.4. *Institutional abbreviations*

MPEF-PV: Vertebrate Paleontological collection, Museo Paleontológico Egidio Feruglio, Trelew, Chubut Province, Argentina; MML-PV: Vertebrate Paleontological collection, Museo Municipal de Lamarque, Lamarque, Río Negro Province, Argentina.

3.5. *Anatomical abbreviations*

ar, Arqual ridge; cd, condyle; cot, cotyle; hk, haemal keel; izc, interzygapophyseal constriction; izr, interzygapophyseal ridge; lf, lateral foramen; lr, lateral ridge; na, neural arch; naf, neural arch foramen; nc, neural canal; ns, neural spine; pcf, paracotylar foramen; pe, posterior embayment; prz, prezygapophysis; pzf, parazygantral foramen; scf, subcentral fossa; scr, subcentral ridge; sy, synapophyses; zp, zygosphene; zt, zygantrum.

4. Systematic Paleontology

Squamata Oppel, 1811
Ophidia Brongniart, 1800 (*sensu* Lee, 1998)
Madtsoiidae (Hoffstetter, 1961) McDowell, 1987
Eomadtsoia gen. nov.

Etymology. From *eos*, Greek for dawn, for the early divergence of a large madtsoiid at the base of a clade of gigantic forms, and *Madtsoia* Simpson, 1933, type genus of Madtsoiidae.

Diagnosis. As for the type and only known species.

Eomadtsoia ragei sp. nov.
Figs. 2 and 3

Etymology. *ragei*, in honor of Jean-Claude Rage for his outstanding work on fossil snakes.

Holotype. MPEF-PV 2378, isolated middle precloacal vertebra (Fig. 2A–E).

Type locality and horizon. The holotype comes from El Uruguayo fossil site (Rougier et al., 2009a), southeastern slopes of the Somún Curá Massif, Chubut Province, Patagonia, Argentina. Second facies association (*sensu* Pascual et al., 2000) of the La Colonia Formation (Maastrichtian–Danian).

Referred specimens. MPEF-PV 641, 2379–2387, several isolated precloacal vertebrae.

Tentatively referred specimens. MPEF-PV 644–649, 2388–2389, fragmentary precloacal vertebrae and fragments of vertebrae.

Geographic and stratigraphic provenance. The referred materials come from El Uruguayo fossil site (Rougier et al., 2009a) or from a nearby locality north of El Buitre hill, southeastern slopes of the Somún Curá Massif, Chubut Province, Patagonia, Argentina. Second facies association (*sensu* Pascual et al., 2000) of the La Colonia Formation (Maastrichtian–Danian).

4.1. *Diagnosis*

Large madtsoiid with wide and short, massively built mid-precloacal vertebrae showing a single parazygantral foramen located in an elliptical shallow depression on each side of the zygantrum and lacking prezygapophyseal processes. *Eomadtsoia* is distinct from all other madtsoiids by the following combination of features (autapomorphies indicated by character and character state numbers): moderately vaulted neural arch shallowly indented posteriorly (215:0) lacking dorsolateral (= parasagittal) ridges (226:0),

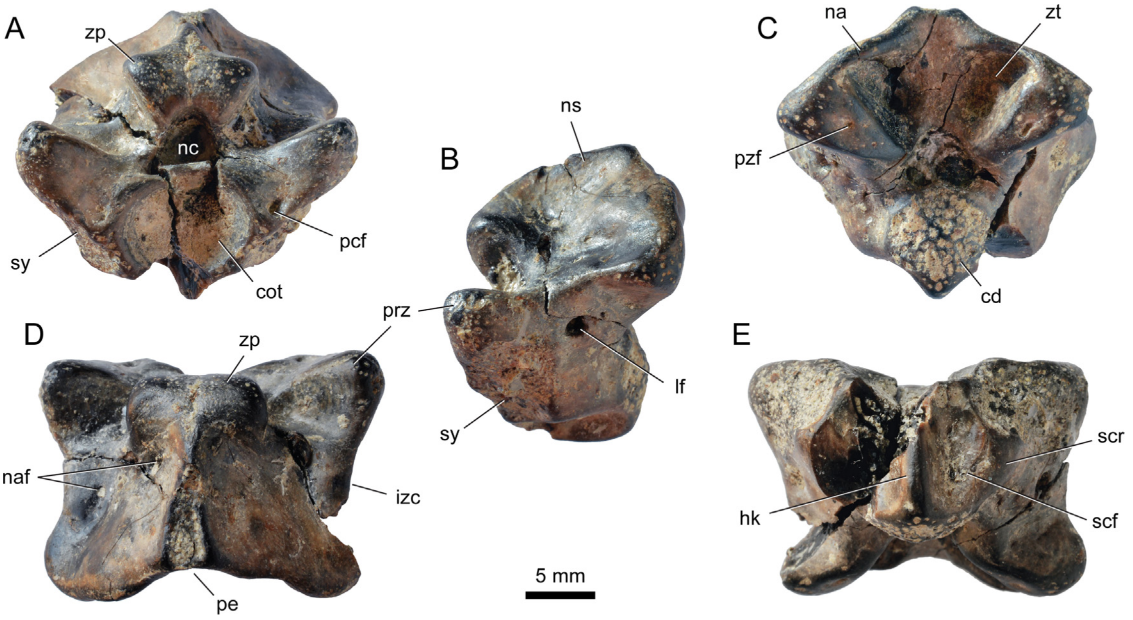

Fig. 2. *Eomadtsoia ragei* gen. et sp. nov. MPEF-PV 2378 (Holotype) in: anterior (**A**), left lateral (**B**), posterior (**C**), dorsal (**D**), and ventral views (**E**). See anatomical abbreviations in Section 3.5.
Fig. 2. *Eomadtsoia ragei* gen. et sp. nov. MPEF-PV 2378 (Holotype) en vues : antérieure (**A**), latérale gauche (**B**), postérieure (**C**), dorsale (**D**) et ventrale (**E**). Voir les abréviations anatomiques en Section 3.5.

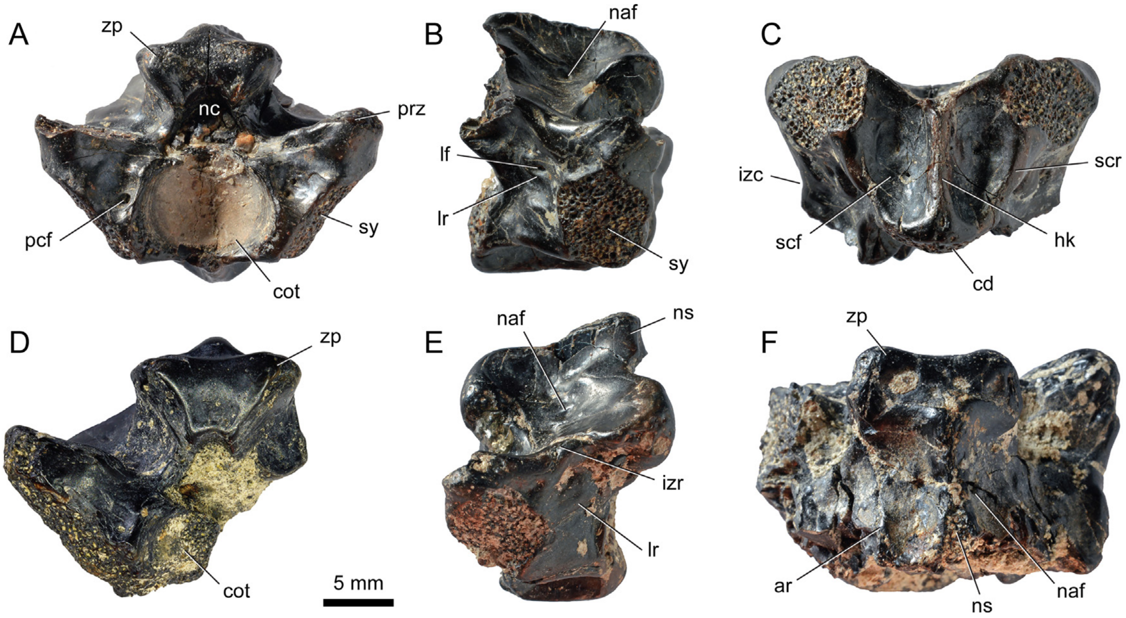

Fig. 3. *Eomadtsoia ragei* gen. et sp. nov. Referred specimens. MPEF-PV 2380 in anterior (**A**), right lateral (**B**), and ventral views (**C**). MPEF-PV 2381 in anterior view (**D**). MPEF-PV 2382 in lateral view (E). MPEF-PV 2383 in dorsal view. All to the same scale. See anatomical abbreviations in Section 3.5.
Fig. 3. *Eomadtsoia ragei* gen. et sp. nov. Spécimens référés. MPEF-PV 2380 en vues : antérieure (**A**), latérale droite (**B**) et ventrale (**C**). MPEF-PV 2381 en vue antérieure (**D**). MPEF-PV 2382 en vue latérale (**E**). MPEF-PV 2383 en vue dorsale. Tous à la même échelle. Voir les abréviations anatomiques en Section 3.5.

pierced by paired small foramina, and bearing a low neural spine (249:2); thick zygosphene nearly as wide as the cotyle; very short and wide triangular centrum in ventral view having clearly laterally convex subcentral ridges; narrow haemal keel clearly demarcated from the centrum by subcentral fossae pierced by small subcentral foramina; large lateral foramina associated with short lateral ridges; at least a large paracotylar foramen on each side of the cotyle; and finally, synapophyses broad and medial to prezygapophyseal lateral edge (221:1).

Eomadtsoia further differs from most other madtsoiids from Patagonia by its markedly larger size. Additionally,

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it differs from the mid-sized *Rionegrophis* (Albino, 1986, 2007; ROG pers. observ. based on MML-PV91–115) by the lower neural spine and the less laterally extended synapophyses. It is easily distinguished from *Madtsoia* by the well-demarcated, narrow and sharp haemal keel and the lack of parasagittal ridges.

4.2. Description

All the vertebrae identified as belonging to *Eomadtsoia* are from the precloacal region. Among the well-preserved vertebrae, MPEF-PV 2383 is one of the largest with a cotylar width of 10.7 mm, but a specimen tentatively referred to *E. ragei* that consists of an isolated zygosphene and portion of the neural arch (MPEF-PV 2388) is noticeably larger than the remaining material, indicating an even larger maximum size for this species.

Anterior view. The cotyle is big and subcircular, slightly wider than high (Fig. 2A). The robust zygosphene is as wide as the cotyle and relatively thick (low width/height ratio). The zygosphene has moderately inclined articular facets (angle between 25–35 degrees from vertical), and an almost straight, horizontal, dorsal margin. The neural canal is relatively small, about half the area of the cotyle, and subtrifoliate in cross section. The prezygapophyses are stout, well projected laterally and moderately inclined, up to 15–20° from horizontal. There is no prezygapophyseal process, though a subtle dorsoventral crest on the prezygapophyseal buttress is present, which extends to the anterodorsal edge of the synapophyses. The synapophyses are heavily weathered and, thus, diapophysis and parapophysis do not differentiate well. It is clear though that the lateral edge of the diapophyses remain clearly medial to the lateral limit of the prezygapophyses, whereas the parapophyses surpass the cotylar margin ventrally. Deep paracotylar foramina, at least one on each side of the cotyle, are located in shallow depressions that are ventrally delimited by blunt short buttresses (Figs. 2A and 3A).

Lateral view. The neural spine is nearly as long as the neural arch, very low along its length, and only slightly slanted posteriorly (Fig. 3B and E). The zygosphenal articular facets are oval in shape. The condyle is eroded in all specimens, but it is clearly posterodorsally oriented and well demarcated from the centrum by a slight precondylar constriction. The synapophyses are broad and dorsoventrally elongated. A thick and oblique lateral ridge is more or less evident among specimens (Figs. 2B, 3B, 3E). The subcentral ridge is almost straight all along its length. The interzygapophyseal ridge is distinct and sigmoid-shaped (Fig. 3E). There is a big lateral foramen of central position, below the above-mentioned lateral ridge. A small lateral ridge or bulge can be present on the lateral wall, below the lateral foramen.

Posterior view. The neural arch is only moderately vaulted (Fig. 2C). The condyle is subcircular. The parazygantral foramina are wide, with a distinct elliptical shape and obliquely oriented, one on each side of the zygantrum, located in small fossae. The zygantral roof is slightly convex ventrally. A pair of zygantral foramina is located on separate deep rounded fossae. The synapophyses are posterolaterally oriented, showing nearly all their articular surface in this view.

Dorsal view. The vertebrae are wider than long with a neural arch only slightly constricted (Fig. 2D). The interzygapophyseal width (minimal neural arch width) is almost the same as the prezygapophyseal width. The prezygapophyseal facets are anterolaterally oriented (angle between 60–80° from the anteroposterior axis) and have a nearly oval outline, although slight posterolateral and anteromedial corners exist. The zygosphenal anterior margin is almost straight, with only a very shallow medial notch. The neural spine is narrow, extending from the back of the anterior margin of the zygosphene, and widens as it extends posteriorly. The neural spine likely has a posterior tubercle based on its terminal widening, but its surface is not well preserved enough to confirm this feature. To both sides of the neural spine, posteriorly to the zygosphenal base, several foramina are present on the neural arch (at least one to each side in all available vertebrae). Posteriorly, the neural arch shows a shallow embayment. The parasagittal ridges are not developed on the neural arch, which in turn is not markedly faceted. Arqual ridges are present on the posterior dorsal margin of the neural arch, anteromedial to the postzygapophyseal lappet (Fig. 3F).

Ventral view. The centrum is very short and subtriangular (Fig. 2E). The subcentral ridges are straight to slightly convex laterally. Much of the synapophyseal articular surface is visible in ventral view. The haemal keel is well developed and demarcated, low and narrow, laterally is delimited by shallow depressions, where small subcentral foramina are located in anterior position. The haemal keel contacts the condylar constriction posteriorly, not reaching the condyle. Posterior processes on the haemal keel are absent.

5. Results and discussion

5.1. Taxonomic comparisons

Among the four snakes that have been previously reported from La Colonia Formation, only one of these, namely the small madtsoiid *Alamitophis argentinus*, was unambiguously referred to family level (Albino, 2000). A single vertebra (MPEF-PV 642) originally reported as a 'Serpentes *incertae sedis*' (Albino, 2000, 2007) is more likely to represent a dolichosaur rather than a snake (Albino, 2011; Scanlon and Hocknull, 2008). The remaining snakes from this unit, formerly reported as a possible madtsoiid and tentatively as a boid or madtsoiid (Albino, 2000), were based on poorly preserved material that precluded a better taxonomic assignment at the time. Now, additional and better preserved snake vertebrae from the La Colonia Formation that show a unique combination of characters justifying the erection of a new taxon, *Eomadtsoia ragei* gen et sp. nov., allow referral of previously known material of uncertain madtsoiids or boids to this same taxon. Therefore, the snake assemblage from La Colonia Formation is restricted to madtsoiids, with *E. ragei* increasing the known diversity of this basal snake radiation.

Among snakes, the overall vertebral configuration of *E. ragei* is only present in the Madtsoiidae and boids, but

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it can be set apart from extinct and extant boids by the presence of distinct parazygantral foramina along with paracotylar foramina, arqual ridges on the neural arch, and the absence of prezygapophyseal processes (Gómez and Báez, 2005; Rage, 1998; Scanlon, 2005). It is readily distinguishable from small-to-mid-sized madtsoiids from the Late Cretaceous of Patagonia and Europe and Paleogene of Australia, namely *Alamitophis*, *Herensugea*, *Nanowana*, *Nidophis*, *Patagoniophis*, *Rionegrophis*, and *Wonambi barriei* (Albino, 1986, 1994, 2007; Rage, 1996; Scanlon, 1997, 2005; Scanlon and Lee, 2000; Vasile et al., 2013), by its conspicuous larger size, along with the wide and short triangular centrum and the distinctly medial position of the synapophyses relative to the lateral edge of the prezygapophyses. *Eomadtsoia* clearly contrasts with the much older *Dinilysia* (Caldwell and Albino, 2002; Scanferla and Canale, 2007), which is the only other Late Cretaceous large snake from Patagonia, in having parazygantral foramina, lower neural spine, and poorly constricted neural arch, among other features.

Noteworthy, the narrow and sharp haemal keel of *Eomadtsoia* contrasts with that of large-to-gigantic madtsoiids, such as species of *Gigantophis*, *Madtsoia*, *Menarana*, and *Platispondylophis*, in which the haemal keel is a somewhat broad and flat process more or less demarcated from the rest of the centrum (Andrews, 1901; LaDuke et al., 2010; Rage, 1996, 1998; Rage et al., 2014; Rio and Mannion, 2017; Smith et al., 2016). In addition, an interzygapophyseal constriction as shallow as that of *E. ragei* is rarely found among large madtsoiids, which generally show a more marked constriction. The lack of parasagittal ridges of *Eomadtsoia* is also uncommon, only resembling *Herensugea* (Rage, 1996) and *Adinophis* (Pritchard et al., 2014) among the surveyed madtsoiids; although some intracolumnar variation cannot be ruled out taken into account what is seen in *Gigantophis* (Rio and Mannion, 2017)

5.2. Phylogenetic analysis

The parsimony analysis yielded 42 most parsimonious trees (MPTs) of 803 steps (consistency index [CI] = 0.400; retention index [RI] = 0.697), the strict consensus of which is relatively well resolved and depicts all madtsoiids in a clade also including the basal snakes *Najash*, *Dinilysia*, and *Seismophis* (Fig. 4). In agreement with recent hypotheses, these snakes lie outside crown-group Serpentes (Caldwell et al., 2015; Garberoglio et al., 2019a, 2019b; Harrington and Reeder, 2017; Martill et al., 2015; Vasile et al., 2013). The monophyly of madtsoiids is here rigorously tested, since we use as outgroup taxa all major groups of extant snakes plus several Mesozoic snakes and the lizard *Varanus* for rooting (Fig. S1), instead of solely the basal snakes *Najash* and *Dinilysia* as in previous similar studies (Rio and Mannion, 2017).

Our results depict *Najash* and *Dinilysia* forming a clade crown-ward to *Seismophis* and all nested within taxa usually considered part of Madtsoiidae, since the poorly known *Herensugea* from the Maastrichtian of Iberia (Rage, 1996) emerges as an early diverging taxon sister to all other snakes in this clade; a position that contrasts with that recovered in previous studies (Rio and Mannion, 2017; Vasile et al., 2013). The isolated vertebrae of *Seismophis* recall in many aspects the vertebrae of *Najash* (Garberoglio et al., 2019a; Hsiou et al., 2014), both from the Cenomanian of South America and, hence, the oldest members of this clade. Interestingly, the vertebral morphology of *Herensugea* is quite unique among madtsoiids, having depressed neural arch with low parasagittal keels, and prezygapophyses and main axis of zygosphenal facets close to horizontal (Rage, 1996), and it would not be surprising if it represented an end-Cretaceous relict of a much earlier snake radiation along with a still unnamed putative madtsoiid from the Cenomanian of North Africa (Rage and Dutheil, 2008).

All these basal snakes from Gondwana and neighboring terrains share the presence of conspicuous parazygantral foramina, which has been considered the clearest synapomorphy of Madtsoiidae by most authors (Albino, 2000; Rage, 1984, 1998; Rio and Mannion, 2017; Scanlon, 2005; Vasile et al., 2013), although they have also been reported as irregularly present in a few other snakes (Holman and Case, 1992; Rage, 1998; Rage et al., 2004). In view of our results depicting *Seismophis*, *Najash*, and *Dinilysia* basal to all madtsoiids other than *Herensugea*, and that the anatomy and relationships of the enigmatic *Herensugea* needs further scrutiny, we opt to not strictly consider the former taxa as part of Madtsoiidae and instead regard the parazygantral foramen as synapomorphic of a more inclusive clade than traditionally acknowledged.

Our results recover all large-bodied madtsoiids as a clade sister to mostly small-sized madtsoiids (Fig. 4), mirroring to some extent previous hypotheses derived from comprehensive analyses of Madtsoiidae (Rio and Mannion, 2017; Vasile et al., 2013). However, our tree topology showing two clades reflecting overall size has not been recovered previously (Vasile et al., 2013: fig. 5A). Large madtsoiids are not members of a single clade either in the analysis of Rio and Mannion (2017: fig. 10B). These size-related groups are here recovered despite the fact that 'body size', in contrast with the previous studies, was not included as a discrete character in our analysis.

Eomadtsoia ragei is here recovered as an early diverging lineage of the clade of large madtsoids, crown-ward to *Sanajeh* and *Rionegrophis* and sister to a poorly resolved clade encompassing snakes in the genera *Gigantophis*, *Madtsoia*, *Menarana*, and *Platyspondylophis* from the Maastrichtian–Eocene interval, as well as the younger *Wonambi* and *Yurlunggur* from Australia (Fig. 4). Interestingly, deeply nested within this clade also appears the small *Adinophis fisaka* (Pritchard et al., 2014), which was previously recovered as more closely related to other small madtsoiids (Rio and Mannion, 2017). None of the madtsoiid genera represented by more than one species have been recovered as monophyletic neither here nor in previous analyses (Rio and Mannion, 2017; Vasile et al., 2013), calling for further revision of the taxonomy of these snakes.

5.3. Body size evolution

Gigantic Madtsoiidae are some of the largest snakes that have ever existed, reaching in some cases 10 m of total length (Head et al., 2009; Rio and Mannion, 2017), but according to our results they evolved from small-to-mid-

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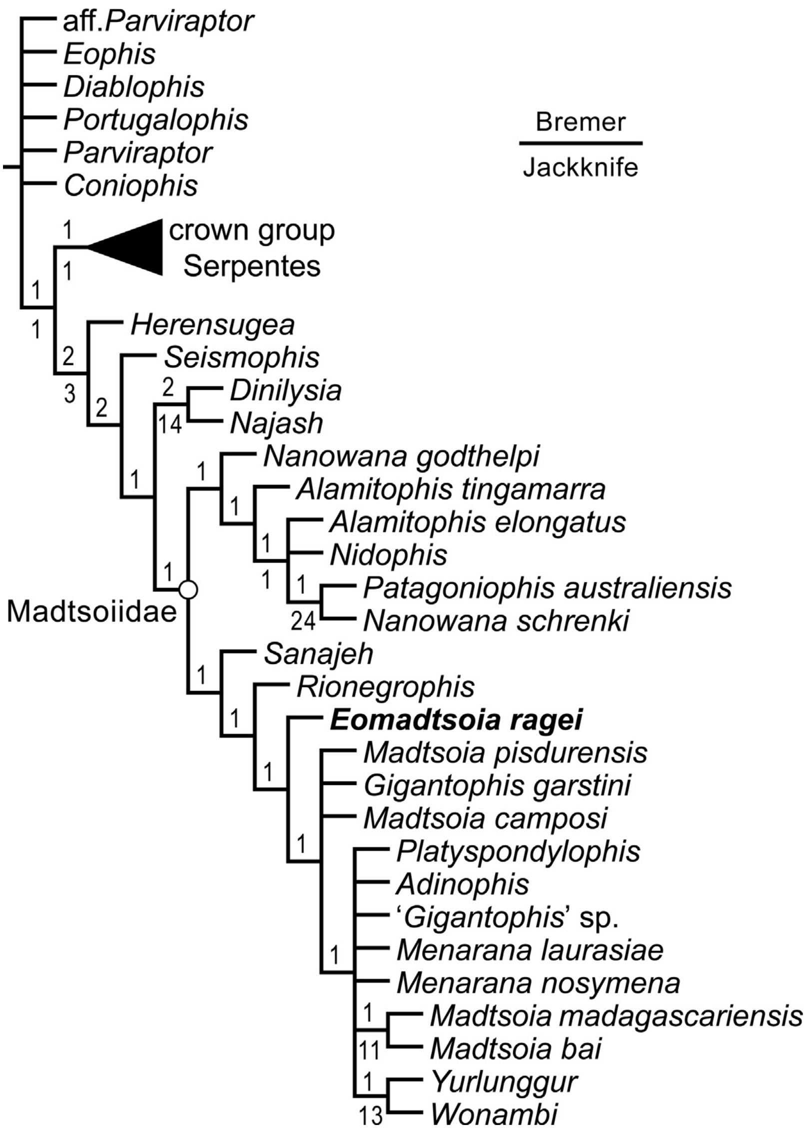

Fig. 4. Phylogenetic relationships of *Eomadtsoia ragei* gen. et sp. nov. (bold) and other madtsoiids. Strict consensus of 42 most parsimonious trees of 803 steps. For simplification, crown-group Serpentes is depicted by a solid triangle (Supplementary data).

Fig. 4. Relations phylogénétiques de *Eomadtsoia ragei* gen. et sp. nov. (gras) et autres madtsoiidés. Consensus strict des 42 arbres les plus parcimonieux de 803 pas. Pour simplifier, le groupe couronne Serpentes est représenté par un triangle plein (voir les données supplémentaires).

sized forms at some point during the Cretaceous (Fig. 5), likely in the Late Cretaceous of Gondwana. Among the closest relatives of true madtsoiids are the relatively small snakes *Seismophis* and *Najash*, but also the much larger *Dinilysia* that might have exceeded 1.8 m in length (Yi and Norell, 2015), suggesting that this early snake radiation was not constrained in size, which is also echoed by the initial split of madtsoiids into sister clades of disparate body size.

Different body-size evolutionary trends characterize these madtsoiid clades. That of small forms, which appear to have radiated to reach a widespread geographic distribution during the Maastrichtian (Vasile et al., 2013), shows relative stasis in body size over time. Into the Cenozoic they remained diverse apparently only in Australia (Scanlon, 1997, 2005), although Paleogene putative madtsoiids scattered across Gondwanan landmasses (Rage, 1991; Rage et al., 2008) might also belong to this group. Conversely, its sister clade shows a general trend of increased body size since the Latest Cretaceous with several independent transitions towards gigantism prior to the K/Pg boundary (Fig. 5). In addition, this subclade exhibits a higher diversity of body sizes with some reversal shifts to a smaller size in *Menarana nosymena* and, more markedly, *Adinophis fisaka*, both from Madagascar (LaDuke et al., 2010; Pritchard et al., 2014).

In the current phylogenetic framework, *Eomadtsoia*, together with *Sanajeh* from the Maastrichtian of India and

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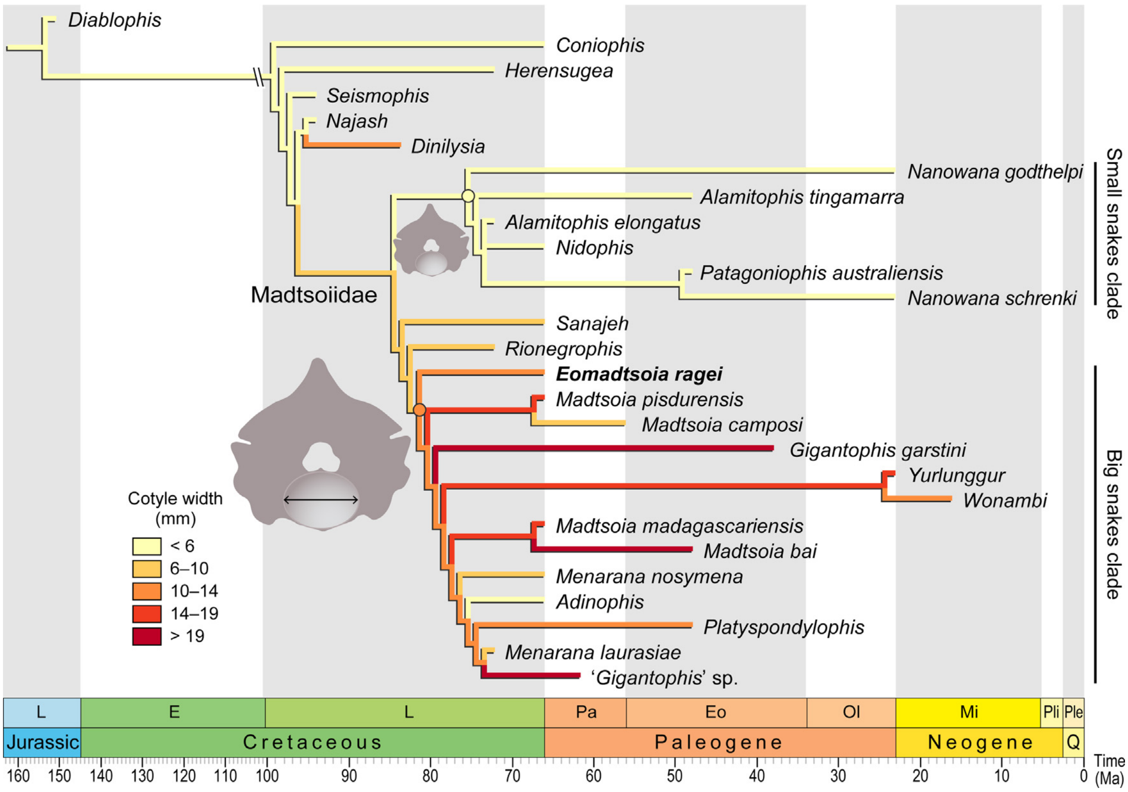

Fig. 5. Evolution of body size in madtsoiid snakes. Squared-change-parsimony optimization of cotyle width on a most parsimonious tree adjusted in time, depicting the ancestral reconstructions for small and large madtsoiids. Diagrams of vertebrae are at natural size.

Fig. 5. Évolution de la taille des serpents madtsoiidés. Optimisation en *squared-change-parsimony* de la largeur du cotyle sur un arbre très parcimonieux ajusté dans le temps, illustrant les reconstructions ancestrales de madtsoiidés de petite et grande taille. Les diagrammes des vertèbres sont à la taille naturelle.

Rionegrophis from the slightly older Los Alamitos and Allen formations of Patagonia (Albino, 1986, 2007; Gómez, 2006), emerge as early diverging mid-to-large madtsoiids with vertebral morphologies and body sizes that could be interpreted as foretelling of the size increase characteristic of the more nested clades. *Eomadstsoia* fits in a morphocline, linking the ancestral madtsoiid conditions with those of large-to-gigantic taxa such as *Madtsoia bai* from the Eocene of Patagonia (Simpson, 1933).

6. Conclusions

Eomadtsoia ragei gen. et sp. nov from the La Colonia Formation (Maastrichtian–Danian) represents the largest madtsoiid snake from the Upper Cretaceous of Patagonia. Given its phylogenetic position sister to a clade that includes the largest forms, the new snake suggests that early stages and evolutionary trends towards madtsoiid gigantism occurred prior to the K/Pg boundary. Further increase of body size following the Cretaceous extinction mirrors trends seen in other groups (but see Apesteguía et al., 2014) such as amphibians (Agnolin, 2012; Gómez et al., 2011), turtles (Bona and de La Fuente, 2005), and archaic mammals (Páez Arango, 2008; Rougier et al., 2009a).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.crpv.2019.09.003.

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