An enigmatic aquatic snake from the Cenomanian of northern South America

Adriana Albino[1], Jorge Domingo Carrillo-Briceño [2], James M. Neenan [3,4]

[1] CONICET, Departamento de Biología, Universidad Nacional de Mar del Plata, Funes 3250, B7602AYJ Mar del Plata, Argentina.

[2] Paläontologisches Institut und Museum, Universität Zürich, Karl-Schmid-Strasse 4, 8006 Zürich, Switzerland.

[3] Oxford University Museum of Natural History, Parks Road, Oxford OX1 3PW, UK

[4] Department of Earth Sciences, University of Oxford, South Parks Road, Oxford OX1 3AN, UK

Corresponding author:

Adriana Albino[1]

Departamento de Biología, Universidad Nacional de Mar del Plata, Funes 3250, B7602AYJ Mar del Plata, Argentina

E-mail address: aalbino@mdp.edu.ar

Deleted: N

Abstract

We report the first record of a primitive aquatic snake from the Cretaceous of Venezuela and northern South America as a whole. The remains come from the La Luna Formation (La Aguada Member, Cenomanian), Trujillo State of Venezuela, and consist of several vertebrae, which belong to the precloacal region of the vertebral column. Comparisons to extant and extinct snakes show that the remains represent a new taxon, *Lunaophis aquaticus* gen. et sp nov. An aquatic mode of life is supported by the pachyostosis of the vertebrae and ventral position of the ribs, indicating an strongly compressed body. The systematic affiliation of this new taxon is difficult to determine due to the scarcity of fossil material but it would represent a primitive lineage of aquatic snake that exploited tropical marine pelagic environments, as reflected by the depositional conditions of the La Aguada Member.

Deleted: estate, Andes

Deleted: , owing to the

Deleted: being pachyostotic

Deleted: being ventrally-positioned

Deleted: implying

Deleted: extremely

Introduction

Until recently, the oldest record of snakes has been from rocks of the Albian of Algeria (Cuny et al., 1990) and the Albian–Cenomanian of North America (Gardner & Ciffelli, 1999), whereas a supposed snake from the Barremian of Spain (Rage & Richter, 1994) was excluded from the group (Rage & Escuillié, 2003). These records have few phylogenetically informative characters and add little to the knowledge of the early evolution of the group. Nevertheless, new studies on squamate specimens from the Jurassic (Bathonian and Kimmeridgian), which include cranial and postcranial remains of at least four different species from the USA (*Diablophis gilmorei* Caldwell et al., 2015), Portugal (*Portugalophis lignites* Caldwell et al., 2015), and England (*Parviraptor estesi* Caldwell et al., 2015 and *Eophis underwoodi* Caldwell et al., 2015), suggest that snakes have undergone habitat differentiation and evolutionary radiation at least since the mid-Jurassic (Caldwell et al., 2015).

In South America, the oldest snakes are known from the Mesozoic of Brazil and Argentina. The Brazilian taxa consist of the four-limbed snake *Tetrapodophis amplectus* Martill, Tischlinger & Longrich, 2015 from the Early Cretaceous (Aptian), and the small *Seismophis septentrionalis* Hsiou et al., 2014 from the Late Cretaceous (Cenomanian). The fossil record from Argentina comprises several remains of primitive snakes, including the two-limbed *Najash rionegrina* Apesteguía & Zaher, 2006, from the Cenomanian (Apesteguía & Zaher, 2006; Zaher, Apesteguía & Scanferla, 2009; Palci, Caldwell & Albino, 2013), the medium-sized snake *Dinilysia patagonica* Smith-Woodward, 1901, from the Santonian–Campanian (Smith-Woodward, 1901; Estes, Frazzeta & Williams, 1970; Hecht, 1982; Rage & Albino, 1989; Caldwell & Albino, 2002; Caldwell & Calvo, 2008; Zaher & Scanferla, 2012), the small "anilioid" *Australophis anilioides* Gómez, Báez & Rougier, 2008, and diverse taxa of Madtsoiidae from the Campanian–Maastrichtian (Albino, 1986, 1994, 2000,

Deleted: Argelia

Deleted: ,

Deleted: the

Deleted: old snakes

Deleted: contain

Deleted: scarce

Deleted: that

Deleted: had

Deleted: geographic

Deleted: concentrated in

Deleted: Upper

Deleted: of

Deleted: contains

Deleted: the

Deleted: Hoffstetter, 1961,

2007, 2011; Martinelli & Forasiepi, 2004). In this paper we describe a new taxon of aquatic snake based on vertebrae from the Cenomanian La Luna Formation in the Andes of Venezuela. This specimen represents the oldest known record of snakes from northern South America and adds substantial information about the diversity of the group during its early evolution.

Geological setting

The locality where the described specimen was found is in strata of the La Luna Formation (La Aguada Member), exposed in a cement quarry (Cementos Andinos Company), in the Andes of Venezuela, east of Lake Maracaibo, 10 km to the northeast of Monay in the Candelaria Municipality of Trujillo State (Fig. 1).

The Upper Cretaceous La Luna Formation is the most prolific petroleum source rock in western Venezuela and part of eastern Colombia (Zumbergue, 1984; Trivobillard et al., 1991; Zapata et al., 2003), and is characterized by a sequence of marine rocks deposited under anoxic-poorly oxygenated conditions along the passive margin of northern South America during the Cenomanian to Campanian (Zapata et al., 2003). This lithostratigraphic unit was originally named the 'La Luna Limestone' by Garner (1926) in the Quebrada La Luna of the Perijá range (Zulia state, western Venezuela), being formally described as a formation by Hedberg & Sass (1937). The lithology of the La Luna Formation is characterized by alternating black or dark-gray limestones and organic calcareous shales, in which calcareous concretions are abundant (González de Juana, Iturralde de Arocena & Picard, 1980; Trivobillard et al., 1991; Davis, Pratt & Sliter, 1999). Renz (1959) subdivided the La Luna Formation into three members that are exposed in the southeast of the Maracaibo basin in the Lara and Trujillo states: the lower La Aguada Member (~60 m thick of dense, black/dark-gray limestones and black or brown shales), the middle Chejendé Member (~80 m thick of black shales and marls), and the upper Timbetes Member (~90 m thick of laminated

Deleted: work
Deleted: found in rocks
Deleted: of the
Deleted: Northern
Deleted: ,
Deleted: corresponds with rocks
Deleted: and located at
Deleted: town
Deleted: ,
Deleted: upper
Deleted: dysoxic
Deleted: -
Deleted: ,
Deleted: , in
Deleted: where the
Deleted: ,
Deleted: ;
Deleted: ,
Deleted:);
Deleted: ,

limestones and shales) (Fig. 2A). Siliceous and phosphatic horizons characterize the top of the unit, recognizing the Ftanite of Táchira (Coniacian-Santonian) and Tres Esquinas members (upper Campanian), respectively. The Tres Esquinas Member is well exposed in the Cordillera de Mérida and Perijá, whereas the Ftanite of Táchira Member is exposed mainly at the southwest of the Cordillera de Mérida in Táchira state (González de Juana, Iturralde de Arocena & Picard, 1980; de Romero & Galea, 1995; Erlich et al., 2000).

The outcrops of the Aguada Member in the Cementos Andinos quarry (Figs. 2B and 3A, B) present a succession of dense dark-gray limestones of up to ~60-70 cm thick, intercalated with laminated black, dark-gray or brown shales. Molluscs, fish remains, and hard, discoidal or ellipsoidal calcareous concretions are common throughout the section (Fig. 2B), the latter reaching up to 198 cm in diameter (Fig. 3C, D). In the studied section, the strata are inclined almost vertically (Fig. 3A), and its base overlays a fossiliferous dark-gray sandy limestone, which has been recognized in the Andes of Trujillo and Lara as the top of the upper Albian Maraca Formation (González de Juana, Iturralde de Arocena & Picard, 1980). Nevertheless, other authors (Renz, 1968; Erlich et al., 1999) have used the name of La Puya Member to refer to a thin section (< 30 m) at the top of the Peñas Altas Formation in the Andes of Lara and Trujillo. Therefore, the discrepancy between the use of Maraca Formation or La Puya Member for the thin sequence underlying the Aguada Member is still unresolved. A Cenomanian age for the La Aguada Member has been provided by planktonic foraminiferans and ammonites (Renz, 1959).

Materials and methods

The studied specimen is deposited in the Museo de Ciencias Naturales de Caracas, Venezuela (MNCN-1827). The fossil was compared directly with osteological material from a diverse group of present-day squamates in the Colección Herpetológica de la Universidad Nacional de Mar del Plata- Sección Osteología, Argentina (UNMdP-O). Its systematic affinities were

Deleted: Member
Deleted: late
Deleted: , while
Deleted: ,
Deleted: exposed
Deleted: ,
Deleted: characteristic lithology
Deleted: and
Deleted: is overlaying
Deleted: late
Deleted: needs to be
Deleted:
Deleted: included

analyzed taking into account previously published data. Measurements were taken with manual calipers and are in mm.

The specimen was also scanned using micro-computed tomography (μCT) with a Scanco Medical μCT80 machine at the Anthropological Institute, University of Zurich, Switzerland. The specimen was scanned using a voltage of 70 kV and an intensity of 114 μA, resulting in a slice thickness/increment of 18 μm. The resulting slice data were then processed and 3D models created using Avizo 8.

The electronic version of this article in Portable Document Format (PDF) will represent a published work according to the International Commission on Zoological Nomenclature (ICZN), and hence the new names contained in the electronic version are effectively published under that Code from the electronic edition alone. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix http://zoobank.org/. The LSID for this publication is: urn:lsid:zoobank.org:pub:918B6879-8908-488F-876B-EA741DFF627B. The online version of this work is archived and available from the following digital repositories: PeerJ, PubMed Central and CLOCKSS.

Systematic paleontology

Squamata Oppel, 1811

Serpentes Linnaeus, 1758

Lunaophis aquaticus, gen. et sp. nov. urn:lsid:zoobank.org:act:175D3D55-D85A-4013-8D30-563BAB7A4143

Figs. 4–8

Deleted: expressed

Deleted: an energy of

Holotype. MNCN-1827. The type specimen is composed by vertebral remains in a small block of black shale and belong to a single individual. The remains include: an almost complete isolated preclocal vertebra (MNCN-1827-A, Fig. 4), an isolated precloacal vertebra that lacks the left prezygapophysis (MNCN-1827-B, Fig. 5), two isolated and incomplete precloacal vertebrae (MNCN-1827-C, Fig. 6 A-D, and MNCN-1827-D, Fig. 6 E-H), an isolated and partially preserved vertebra probably corresponding to the anterior trunk region (MNCN-1827-E, Fig. 6 I-L), five articulated precloacal vertebrae (MNCN-1827-F, Fig. 7 A-D), and a poorly preserved vertebral fragment (MNCN-1827-G, Fig. 7 E-H).

Type locality and horizon. Cement quarry (Cementos Andinos company), located east of Lake Maracaibo, 10 km northeast of Monay, Trujillo State, Venezuela (Fig. 1). The fossiliferous horizon is a black shale layer ~28 meters above the base of the La Aguada Member of the La Luna Formation (Cenomanian, Renz, 1959, Fig. 2).

Etymology. Lunaophis: snake from La Luna, denotes the origin of the material from rocks corresponding to La Luna Formation; Latin *aquaticus*:water-dwelling,

Diagnosis. NOTE: THIS IS **NOT** AN ACCEPTABLE DIAGNOSIS. A MODERN DIAGNOSIS SHOULD EITHER LIST AUTAPOMORPHIES OR A DIAGNOSTIC COMBINATION OF CHARACTERS. YOUR "DIAGNOSIS" IS AN ABBREVIATED DESCRIPTION. Medium-sized snake with elongate, depressed precloacal vertebrae. All vertebrae with evident pachyostosis. Neural arch longer than vertebral centrum. Neural arch roof depressed, with not notched posterior border. Prominent globes above each postzygapophysis. Longitudinal crests strongly marked at both sides of the neural spine. Neural arch walls are born near the vertebral medium line and diverge ventrally to the subcentral ridges; this morphology causes the neural arch roof to be extended beyond the neural arch walls, resembling prominent shelves at each side of the vertebrae. Interzygapophyseal ridges strongly prominent. Probable differentiation of regions along the

Deleted: that were included

Deleted: block

Deleted: that correspond

Deleted: city

Deleted: corresponds with

Deleted: located

Deleted: from

Deleted:

Deleted: aquatic in Latin

Formatted: Font:Not Bold

Formatted: Font:Not Bold

Formatted: Underline

Deleted:

Deleted: ,

Deleted: and

vertebral column. Neural spine in mid-trunk or posterior vertebrae absent or very low, poorly developed as a long longitudinal crest along the medium line of the neural arch roof. Neural spine in probable anterior vertebrae with tubular form, developed at the most distal part of the neural arch from where it freely slants backwards, and strongly extends posteriorly, significantly surpassing the posterior edge of the neural arch. Zygosphene-zygantral articulation well developed. Zygosphene anteriorly notched. Prezygapophyseal processes absent. Prezygapophyses well inclined above the horizontal plane. Postzygapophyses slightly inclined. Vertebral centrum long and narrow, slightly divergent anteriorly. Subcentral ridges well developed. Cotyle and condyle large and nearly round. Haemal keel defined but scarcely prominent and posteriorly broader. Small paradiapophyses projected beyond the ventral edge of the cotyle, close to each-other, and with articular surfaces facing ventrally. Parapophysis and diapophysis differentiated. Not visible parazygantral, lateral, and subcentral foramina. Paracotylar foramina apparently present.

Formatted: Underline

Description

All vertebrae are characterized by considerable pachyostosis (Fig. 8), which has been interpreted as a method of controlling ballast generally associated with secondarily aquatic tetrapods (Ricqlès & Buffrénil, 2001). In general, the vertebrae are medium-sized RELATIVE TO WHAT? (Table 1), long, wide, and low. They are wider than high (pr-pr or po-po > H), and longer than wide (nal > pr-pr or po-po). Two of the best preserved vertebrae are MNCN-1827-A (Fig. 4) and MNCN-1827-B (Fig. 5). Vertebra B is slightly smaller than vertebra A, but the general aspect and characters are the same except for slight differences. The following comprehensive description is based on these vertebrae.

Deleted: a remarkable hypertrophic thickening that indicates

Deleted:

Deleted: ,

Deleted: little

Deleted: was

In anterior view, the zygosphene is well developed and wider than the cotyle (zgw > ctw); it is thin in the middle and its dorsal edge is almost flat. The articular facets are relatively large and anteriorly oriented. The neural canal is small, with a round outline. The

Deleted: , filled by sediment

prezygapophyses are robust and large; they are borne at the base of the neural canal and slant above the horizontal plane, but do not reach the level of the zygosphenal roof. There are no prezygapophyseal processes. The cotyle is large, scarcely wider than high, nearly circular, and delimited by a well-marked rim. It is partially filled by sediment. There are strong depressions on both sides of the cotyle but the paracotylar foramen is visible only on the right side of vertebra MNCN-1827-A. In specimen MNCN-1827-B there is not a visible paracotylar foramen on the right side and it is broken on the left. The paradiapophyses are positioned ventral to the cotyle, far from the prezygapophyseal surfaces and close to each other; they project ventrally with a short and constricted transverse process separating them from the vertebral centrum. The articular surfaces are small, with clearly distinctive parapophyses and diapophyses facing ventrally and extending beyond the ventral rim of the cotyle.

In posterior view, the neural arch is depressed and forms two globes above each zygantrum as strong convexities, especially on vertebra MNCN-1827-B on both sides and on vertebra MNCN-1827-A on the left. The zygantra are filled by sediment, which also extends over the dorsal condyle. The roof of the neural arch of vertebra B is proportionally less depressed than in specimen A, and the zygantra are better developed. Vertebra A has the left postzygapophysis distally broken whereas in vertebra B the fracture is on the right. The postzygapophyses are large and slightly inclined above the horizontal. There are no parazygantral foramina. The condyle is large and more or less circular. The posterior end of a wide hemal keel is slightly visible ventral to the condyle.

In dorsal view, the neural arch is long and wide, with the posterior edge slightly convex in vertebra A and almost straight in vertebra B. None of the condyle is visible in this view. The interzygapophyseal constriction is concave and well-marked but not especially deep. The articular surfaces of the prezygapophyses are large, oval, longer than wide, and

Deleted: ,
Deleted: ing
Deleted: level
Deleted: showed
Deleted: ly
Deleted: very
Deleted: -
Deleted: through
Deleted: surpassing a lot
Deleted: , but it
Deleted: showed in
Deleted: in
Deleted: developed but
Deleted: roof
Deleted: breaking
Deleted: ,
Deleted: seems to be
Deleted: a
Deleted: seen
Deleted: ly
Deleted: rectilinear
Deleted: seen from
Deleted: profound

anterolaterally oriented. The zygosphene is well developed and notched in the middle. It is partially broken on the left side of specimen A whereas it is complete on vertebra B. Vertebra A does not have any trace of a neural spine, but a low and large neural spine is present at the base of the zygosphene in the vertebra B. It forms a thin and poorly developed crest. Posteriorly, on both sides of the middline, the neural arch forms two well-developed hemispheres over the postzygapophyses. Along the roof of the neural arch, especially in the posterior half, longitudinal crests extend anteroposteriorly on either side of the midline.

In ventral view, the vertebral centrum is long (cl/naw > 1.00) and narrow, slightly wider anteriorly than posteriorly, but not markedly triangular in section. The subcentral ridges are well defined and prominent. The paralymphatic fossae are present. The cotyle is almost not exposed ventrally whereas the condyle is well exposed from this view. The ventral surface of the centrum is concave, with a distinctive but weakly developed hemal keel, which is smooth anteriorly and more defined and wider posteriorly. The short precondylar constriction is marked. There no subcentral foramina. The paradiapophyses are small with articular surfaces well exposed ventrally. The di- and parapophyseal surfaces are distintict and separated by a short and deep constriction.

In lateral view, the vertebrae are long, with significantly depressed neural arch roofs. Anteriorly, the neural arches extend beyond the level of the cotyle due to the anterior projection of the zygosphene. Posteriorly, the neural arch is longer than the vertebral centrum (nal > cl), extending beyond the condyle. The neural arch in the vertebra B is slightly shorter than in specimen A. The neural spine is mostly broken in vertebra B but it would have been long and low, as a thin crest developed from the base of the zygosphene and until the posterior end of the neural arch. Specimen A lacks a neural spine. The zygosphenal surfaces are prominent, oval, longer than wide, and more anteriorly than dorsally oriented. Posteriorly, on either side, the roof of the neural arch forms a convexity as a hemisphere above the

Deleted: ,
Deleted: in
Deleted: in
Deleted: very
Deleted: born
Deleted: at
Deleted: globes
Deleted: All a
Deleted: roof
Deleted: but
Deleted: run
Deleted: , one at each
Deleted: very
Deleted: scarcely
Deleted: a
Deleted: smooth
Deleted: posteriorly
Deleted: strongly
Deleted: clearly
Deleted: ive
Deleted: profound
Deleted: surpass
Deleted: level
Deleted: exceeding
Deleted: level
Deleted: very
Deleted: and prominent
Deleted: at each
Deleted: roof
Deleted: globe

postzygapohyses. As a result, the outline of the neural arch is concave in lateral view. The absence of a neural spine in vertebra A produces a more deeply concave arch in lateral view than in vertebra B. The longitudinal crests and the hemispheres of the arch in specimen A are less well-marked than in B. The prezygapophyses are large, robust, and anterolaterally oriented. The interzygapophyseal crest is well marked and strongly separates the roof from the lateral walls of the neural arch. The distance between the interzygapophyseal crest on either side is much higher than the distance between the lateral walls of the arch where they contact with the roof. This is because the lateral walls are borne near the sagittal axis of the vertebra and diverge dorsoventrally from this point to the subcentral ridges. This structure produces a prominent shelf-like roof of the neural arch on either side between the pre- and postzygapophysis (Fig. 4, H). There are no lateral foramina. The vertebral centrum is long but shorter than the neural arch (nal >cl). The subcentral ridges are strongly marked. The main axis of the condyle is not strongly inclined from the horizontal plane. The precondylar constriction is well defined. The paradiapophyses are low, far from the prezygapophyses, and clearly separated from the centrum by a deep constriction. They are developed at the end of a short projection similar to a transverse process. They are small and ventrally extend beyond the ventral edge of the condyle and subcentral ridges.

Vertebra MNCN-1827-C (Fig. 6 A-D) is approximately the same size as MNCN-1827-B. The zygosphene, left prezygapophysis, and part of the posterior part of the neural arch are not preserved. This vertebra is slightly deformed. The neural arch is slightly higher than in specimen B, whereas the vertebral centrum is relatively shorter and the hemal keel is not defined. There is no neural spine, as in vertebra A.

The vertebra MNCN-1827-D (Fig. 6 E-H) is alsosimilar in size to specimen B. It has lost most of the vertebral centrum, right postzygapophysis, and the zygosphene. In dorsal

Deleted: seems

Deleted: profound

Deleted: globes

Deleted: and

Deleted: of each

Deleted: saggital

Deleted: morphology

Deleted: roof

Deleted: each

Deleted: and

Deleted: condyle has its

Deleted: very

Deleted: very

Deleted: profound

Deleted: surpass

Deleted: a little

Deleted: ,

Deleted: a

Deleted: not

Deleted: of a

view, the posterior edge of the neural arch is strongly convex medially, more than in vertebra A.

Specimen MNCN-1827-E is a poorly preserved vertebra (Fig. 6 I-L). The entire left side as well as the cotyle and zygosphene are missing. This vertebra is also slightly deformed and has deposits of sediment. Its size is similar to that of vertebra B. It also has the same general characters except for the presence of a high neural spine that is developed on the most distal part of the neural arch roof from which it slants backward, beyond the posterior edge of the neural arch. The free portion of the spinecomprises of approximately 63% of the length of the neural arch and thus forms more than half the total length of the vertebra. It has a tubular form and is transversely and anteroposteriorly thin. The vertebra does not have a hypapophysis on the ventral surface of its centrum, as is common on the anterior vertebrae of most snakes. Instead, the most posterior part of the centrum bears a slight prominence not wider than the cotyle, similar to the posterior part of a hemal keel in specimen MNCN-1827-B. Judging based on the presence of a high neural spine, this vertebra is an anterior trunk vertebra.

Specimen MNCN-1827-F includes five tightly articulated vertebrae (Fig. 7 A-D), with the same morphology as vertebra A and without any trace of neural spines. Fragment MNCN-1827-G does not have any distinctive features (Fig. 7 E-H).

Discussion

Comparative osteology

The overall morphology of the vertebrae in *Lunaophis aquaticus* gen. et sp nov. is snake-like and has a combination of characters only present in Serpentes, including well-developed subcentral ridges; well-differentiated diapophyses and parapophyses; and well-developed zygosphene-zygantrum accessory articulations on all known vertebrae (Estes, de Queiroz & Gauthier, 1988). The presence of an anteroposteriorly short and strongly posteriorly inclined

Deleted: All of the
Deleted: ,
Deleted: at
Deleted: where it freely
Deleted: . Thus, the spine is strongly extended posteriorly, surpassing
Deleted: , which extends over the posterior limit of the neural arch,
Deleted: length,
Deleted: ,
Deleted: transversally
Deleted: This
Deleted: the vertebral
Deleted: in
Deleted: in
Deleted: presents
Deleted: a
Deleted: seen
Deleted: by
Deleted: interpreted as
Deleted: At any rate, it is possible to assume some differentiation of the vertebrae along the vertebral column in relation with the development of the neural spine.
Deleted: strongly
Deleted: ,
Deleted: particular morphology
Deleted: ,
Deleted: such as:
Deleted: a marked lateral limitation of the centra (
Deleted:)
Deleted:
Deleted: complex
Deleted: in
Deleted: recorded

neural spine in specimen MNCN-1827-E is reminiscent of the condition in lizards (Estes, de Queiroz & Gauthier, 1988). The anteriorly notched zygosphene and the absence of prezygapophyseal processes are characteristic of some lizards but are also present in some primitive snakes (Hoffstetter & Gasc, 1969).

The vertebrae described here constitute a distinctive taxon that displays a combination of features that distinguishes it from other known fossil and extant snakes. The walls of the neural arch arising from the midline and diverging to the subcentral ridges, the prominent hemispheres on the neural arch above the postzygapophyses, the very long neural arch that posteriorly extends beyond the condyle, and the high and posteriorly extending, tubular spine at least on some vertebrae are all unique to this snake. The hemispheres are developed in the position occupied by the pterapophyses in the aquatic paleophiids and nigerophiids. The depressed neural arches associated with the absence of or greatly reduced neural spines is a feature shared by fossorial snakes such as scolecophidians and anilioids and other burrowing squamates such as amphisbaenians. The presence of this feature contrasts with the ventrally placed paradiapophyses, the medium size of the vertebrae, and the high neural spine shown by vertebra MNCN-1827-E, which argue against possible fossorial habits. In particular, closely spaced paradiapophyses oriented in a ventral position with articular surfaces that face ventrally indicate that the ribs were directed below the vertebral centraand that the body of the snake was likely strongly compressed laterally as an adaptation for swimming. Elongate bodies of snakes are efficient for swimming, but all extant species of sea snakes have evolved paddle-like tails and many have laterally compressed bodies, especially in the pelagic species, which give them an eel-like appearance and increase their locomotory ability in water. The marked and prominent subcentral and interzygapophyseal projections showed by the fossil specimen imply the presence of specialized musculature, perhaps for swimming. Also the strongly marked longitudinal crests on the roof of the neural arch probably served for the

Deleted: form
Deleted: ,
Deleted: found
Deleted: unique
Deleted: , thus justifying the erection of a new taxon
Deleted: walls
Deleted: medial
Deleted: globes
Deleted: extremely
Deleted: surpassing
Deleted: level
Deleted: extended
Deleted: in
Deleted: ,
Deleted: in
Deleted: globes
Deleted: of
Deleted: absent
Deleted: very
Deleted: Scolecophidia
Deleted: Cope, 1864
Deleted: Anilioidea
Deleted: Fitzinger, 1826,
Deleted: Amphisbaenia
Deleted: Gray, 1864
Deleted: character
Deleted: showed
Deleted: contradict
Deleted: completely
Deleted: ,
Deleted: thus
Deleted: some mechanical / muscular role, probably related with locomotion in water
Deleted: ,
Deleted: were

insertion of musculature associated with an aquatic mode of life. A laterally compressed body helped by well-developed muscles makes strong undulations of the vertebral column possible, permitting an efficient propulsion into the water. Thus, the body morphology of *Lunaophis* clearly argues for a highly aquatic mode of life. Finally, the pachyostotic vertebrae would have provided increased ballast.

In the last few years, efforts to understand the origins and evolution of snakes have resulted in several phylogenetic analyses that include vertebral characters. As a consequence, the comparison of vertebral characters in the study of fragmentary fossil vertebrae is an attempt to define their phylogenetic affinities. In this context, the vertebrae described here differ significantly from extant Scolecophidia in having paradiapophyses differentiated into two surfaces (diapophysis and parapophysis), the presence of a precondylar constriction, the absence of a prezygapophyseal process, and the non-oval cotyle and condyle. The former two characters also distinguish *Lunaophis aquaticus* from the extinct *Coniophis precedens* Marsh, 1892, whereas the third character-state contrasts with the condition in *Dinilysia patagonica*, which has a prezygapophyseal process. The same combination of features observed in *Lunaophis aquaticus* is present in primitive, pre-scolecophidian snakes such as aff. *Parviraptor estesi* and *Najash rionegrina*, and at least the two latter features can be verified in *Seismophis septentrionalis*. Similar to these taxa, the posterior border of the neural arch in *Lunaophis aquaticus* is not notched, but it differs significantly in the position of the paradiapophyses below the vertebral centrum and the fact that these face ventrally. In the other species the paradiapophyses face ventrolaterally. Other differences with aff. *Parviraptor estesi* and *Diablophis gilmorei* are the better developed zygosphene, a deeper precondylar constriction, and an apparently non-trifoliate neural canal. A neural spine reduced to a ridge is reminiscent of the condition in *Coniophis precedens* (but it ends in a tuberosity in that species). *Lunaophis aquaticus* also shares with *Coniophis precedens*,

Deleted: to the

Deleted: hard

Deleted: thickened,

Deleted: previously seen only in morphological studies

Deleted: a

Deleted: characters

Deleted: from them

Deleted: compared

Deleted: are strongly lateralized and

Deleted: being better developed

Deleted: more profound

Deleted: in this species

562 *Dinilysia patagonica*, and *Seismophis septentrionalis* the presence of a depressed neural arch.
563 On either side of the neural spine the dorsolateral ridges are present in these snakes, as well
564 as in *Najash rionegrina* and Madtsoiidae. *Lunaophis aquaticus* also differs from *Seismophis*
565 *septentrionalis* in the notched zygosphene and the absence of parazygantral foramina. The
566 vertebral centrum in *Lunaophis aquaticus* differs from other primitive species in not being as
567 markedly wider anteriorly as it is in *Najash rionegrina*, *Dinilysia patagonica*, and *Seismophis*
568 *septentrionalis*. Based on the figures in Caldwell et al. (2015), a centrum that is not much
569 wider anteriorly is present in aff. *Paviraptor estesi* and *Diablophis gilmorei*.

570 Based on these comparisons, *Lunaophis aquaticus* gen. et sp. nov. is probably a pre-
571 scolecophidian snake well-adapted for swimming. In the context of the phylogeny proposed
572 by Martill, Tischlinger & Longrich (2015) it would represent the earliest snake that adopted
573 an aquatic mode of life and then revitalizes the question about the evolving of snakes from
574 burrowing or marine ancestors.

575 *Paleoenvironment and paleoecology*

576 *Lunaophis aquaticus* gen. et sp. nov. represents an aquatic lineage of snakes that exploited
577 marine environments. This is reflected by the depositional conditions of the La Luna
578 Formation, interpreted as a typical marine environment where laminated organic rich
579 intervals suggest a deposition on the mid-shelf to upper continental slope under anoxic or
580 poorly oxygenated conditions (Macellari & De Vries, 1987; Erlich et al., 1999; Bralower &
581 Lorente, 2003; Zapata et al., 2003). The organic matter of the sediments in the La Aguada
582 Member (Trujillo area) is mostly of algal origin (Trivobillard et al., 1991). González de
583 Juana, Iturralde de Arocena & Picard (1980) suggested that the La Aguada Member could be
584 considered as a transitional environment between the shallow waters of the Maraca formation
585 (or La Puya Member according to Renz, 1959, 1968) and the pelagic facies of the La Luna
586 Formation. In contrast with the pelagic and hemipelagic deep water sedimentation suggested

Deleted: is also distinctive of
Deleted: absence
Deleted: because it is
Deleted: According to
Deleted: According to
Deleted: strongly
Deleted: proposed
Deleted: of
Deleted: conquests aquatic environments
Deleted: in
Deleted: -
Deleted: -dysoxic
Deleted: mostly occurs from a marine
Deleted: (algae and dinocysts)
Deleted: ,
Deleted: ,

by Trivobillard et al. (1991) and Erlich et al. (1999), Méndez (1981) suggested that the anoxic conditions of the La Luna Formation during the late Albian-early Cenomanian transgression were not due to water depth but pre-existing anoxic conditions in the slope zone. On basis of benthic and planktonic foraminiferans, Méndez (1981, and references therein) recognized an increase in the submersion of the platform, but probably with depths that did not exceed 50 meters.

The holotype of *Lunaophis aquaticus* gen. et sp nov. is associated with other marine vertebrates (sharks and bony fishes) in the Aguada Member (Cementos Andinos quarry). Bony fish remains are very abundant in the horizon yielding *Lunaophis aquaticus* and adjacent strata (Fig. 2). These remains include isolated and semi-articulated cranial and postcranial elements of *Xiphactinus audax* Leidy, 1870 (Carrillo-Briceño, Alvarado-Ortega & Torres, 2012), ichthyodectiforms, enchodontids and small indeterminate fishes. The chondrichthyans are represented mainly by isolated teeth of at least three species of lamniform sharks although a semi-complete, articulated vertebral column of a lamniform species has also been recovered (all these specimens are currently under study). Benthic invertebrates arescarce in the shales of the Cementos Andinos quarry; however, small indeterminate bivalve molds are common in the limestones. The benthic invertebrate fauna in the La Aguada Member could represent brief periods of better oxygenated conditions on the sea floor or organisms that were tolerant to anoxic environments, as has been suggested for other sections of the La Luna Formation (e.g. Trivobillard et al., 1991). Although anoxic-dysoxic conditions prevailed on the seafloor of the basin (Méndez, 1981; Macellari & De Vries, 1987; Trivobillard et al., 1991; Erlich et al., 1999), the presence of ammonites (Renz, 1959; 1982), reptiles (*Lunaophis aquaticus*), and abundant fishes provides evidence of well-oxygenated surface waters, indicating that the Aguada Member environment was characterized by a stratified water column. In addition, other chondrichthyans, bony fishes,

Deleted: was
Deleted: the
Deleted: ,
Deleted: by
Deleted: deepening
Deleted: specimen
Deleted: also
Deleted: remains of
Deleted: fauna
Deleted: stratum
Deleted: e
Deleted: ,
Deleted: fauna is
Deleted: undetermined
Deleted: are common
Deleted: some short
Deleted: ,
Deleted: these stressed
Deleted: ,
Deleted: could be
Deleted: thus

649 and marine reptiles have also been found throughout the La Luna Formation (Wailer, 1940;
650 Moody & Maisey, 1994; Casas & Moody, 1997; Sánchez-Villagra, Brinkmann & Lozsán
651 2008; Carrillo-Briceño, 2009; 2012).

652 **Conclusion**

653 *Lunaophis aquaticus* gen. et sp. nov. is an early snake that has clear affinities with
654 pre-scolecophidian snakes but is distinguished by a number of characters that make it a new
655 taxon. *Lunaophis aquaticus* represents a primitive aquatic lineage of snakes that exploited
656 tropical marine environments during the Cenomanian and is the oldest known record of the
657 group from northern South America.

Deleted: remain

Deleted: a primitive

Deleted: strong

Deleted: ,

Deleted: s

Deleted: and enigmatic

Deleted: ,

Deleted: the

Deleted: of

658 **Acknowledgments**

659 This project was supported by the PIP-CONICET N° 112-200901-00176 (AA), and Swiss
660 National Science Foundation grants 31003A-149605 (awarded to Marcelo Sánchez- Villagra,
661 Zurich) and P2ZHP3_162102 (JMN). The authors wish to especially thank Lilia Vierma (†),
662 Carlos Torres and Cemento Andino Ca., for their valuable assistance in the field ; to Alfredo
663 Carlini for his substantial assistance in making this collaborative work possible; to Marcelo
664 Sánchez Villagra, Torsten M. Scheyer, and the Evolutionary Morphology and Palaeobiology
665 group at the Palaeontological Institute and Museum at the University of Zurich Switzerland,
666 for generous and important counseling and collaboration; to the Instituo del Patrimonio
667 Cultural de Venezuela for the authorization and collecting permission.

668 **References**

669 Albino, A.M. 1986. Nuevos Boidae Madtsoiinae en el Cretácico tardío de Patagonia
670 (Formación Los Alamitos, Río Negro, Argentina). Actas of the 4th Congreso
671 Argentino de Paleontología y Bioestratigrafía, 2: 15–21.

672 Albino, A.M. 1994. Una nueva serpiente (Reptilia) en el Cretácico Superior de Patagonia,
673 Argentina. Pesquisas, 2: 58–63.

683 Albino, A.M. 2000. New record of snakes from the Cretaceous of Patagonia (Argentina).
684 Geodiversitas, 22: 247–253.
685 Albino, A.M. 2007. Lepidosauria. In: Z. Gasparini, L. Salgado, and R.A., Coria (eds.),
686 Patagonian Mesozoic Reptiles, 87–115. Indiana University Press, Indiana.
687 Albino, A.M. 2011. Evolution of Squamata reptiles in Patagonia based on the fossil record.
688 Biological Journal of the Linnean Society, 103:441–457. doi: 10.1111/j.1095-
689 8312.2011.01691.x
690 Apesteguía, S., and Zaher, H. 2006. A Cretaceous terrestrial snake with robust hindlimbs and
691 a sacrum. Nature, 440:1037–1040. doi:10.1038/nature04413
692 Bralower, T.J., and Lorente, M.A. 2003. Paleogeography and stratigraphy of the La Luna
693 Formation and related Cretaceous anoxic depositional systems. Palaios, 18: 301–304.
694 Caldwell, M.W. and Albino, A.M. 2002. Exceptionally preserved skeletons of the Cretaceous
695 snake *Dinilysia patagonica* Woodward, 1901. Journal of Vertebrate Paleontology, 22:
696 861–866.doi:10.1671/0272-4634(2002)022[0861:EPSOTC]2.0.CO;2
697 Caldwell, M.W. and Calvo, J. 2008. Details of a new skull and articulated cervical column of
698 *Dinilysia patagonica* Woodward, 1901. Journal of Vertebrate Paleontology, 28: 349–
699 362. doi:10.1671/0272-4634(2008)28[349:DOANSA]2.0.CO;2
700 Caldwell, M.W., Nydam, R.L., Palci, A., and Apesteguía, S. 2015. The oldest known snakes
701 from the Middle Jurassic-Lower Cretaceous provide insights on snake evolution.
702 Nature Communications, 6: 5996. doi:10.1038/ncomms6996
703 Carrillo-Briceño J.D. 2009. Presencia del genero *Ptychodus* (Elasmobranchii:
704 Ptychodontiade) en el Cretácico superior de los Andes de Trujillo Venezuela.
705 GEOMINAS, 37 (50): 207–210.

706 Carrillo-Briceño, J.D. 2012. Presencia de *Ptychodus mortoni* (Elasmobranchii:
707 Ptychodontidae) en el Cretácico Superior de Venezuela. Revista Geológica de
708 América Central, 46: 145–150. doi: http://dx.doi.org/10.15517/rgac.v0i46.1837
709 Carrillo-Briceño, J.D., Alvarado-Ortega, J. and Torres, C. 2012. Primer registro de
710 *Xiphactinus* Leidy, 1870, (Teleostei: Ichthyodectiformes) en el Cretácico Superior de
711 América del Sur (Formación La Luna, Venezuela). Revista Brasileira de
712 Paleontología, 15(3):327–335. doi:10.4072/rbp.2012.3.08
713 Casas, J.E and Moody, J.M. 1997. Primera descripción del género *Belenostomus* en la
714 Formación La Luna (Cretácico), Sierra de Perijá, (Pisces: Aspydorhynchidae). Boletín
715 de la Sociedad Venezolana de Geólogos, 22 (1): 51–55.
716 Cope, E.D. 1864. On the characters of the higher groups of Reptilia Squamata and especially
717 of the Diploglossa. Proceedings of the Academy of Natural Sciences of Philadelphia,
718 1864: 224–231.
719 Cuny, G., Jaeger, J.J., Mahboubi, M., and J.C. Rage. 1990. Les plus anciens Serpents
720 (Reptilia, Squamata) connus. Mise au point sur l'âge géologique des Serpentes de la
721 partie moyenne du Crétacé. Comptes rendus des séances de l'Académie des Sciences,
722 Paris, Série II, 311:1267–1272.
723 Davis C., Pratt, l., and Sliter, W. 1999, Factors influencing organic carbon and trace metal
724 accumulation in the Upper Cretaceous La Luna Formation of the western Maracaibo
725 Basin, Venezuela. In: E. Barrera, and C.C. Johnson, (eds.), Evolution of the
726 Cretaceous Ocean-Climate System, 203–231. Geological Society of America Special
727 Paper 332.
728 de Romero, L.M., and Galea, F.A. 1995. Campanian Bolivinoides and microfacies from the
729 La Luna Formation, western Venezuela. Marine Micropaleontology, 26: 385–404.

Deleted: ,

Deleted: ,

732 Erlich, R.N., Macsotay, O., Nederbragt, A.J., and Lorente, M.A. 1999. Palaeoceanography,
733 palaeoecology, and depositional environments of Upper Cretaceous rocks of western
734 Venezuela. Palaeogeography, Palaeoclimatology, Palaeoecology, 153: 203–238.
735 Erlich, R.N., Macsotay, O., Nederbragt, A.J. and Lorente, M.A. 2000. Birth and death of the
736 Late Cretaceous ‘‘La Luna Sea’’, and origin of the Tres Esquinas phosphorites.
737 Journal of South American Earth Sciences, 13: 21–45.
738 Estes, R., Frazzetta, T.H., and Williams, E.E. 1970. Studies on the fossil snake *Dinilysia*
739 *patagonica* Woodward: Part 1. Cranial morphology. Bulletin of the Museum of
740 Comparative Zoology, Harvard University, 140: 25–74.
741 Estes, R., de Queiroz, K. and Gauthier, J. 1988. Phylogenetic relationships within Squamata.
742 In: R. Estes, and G.K. Pregil (eds), Phylogenetic relationships of the lizard families,
743 119–281. Stanford University Press, Stanford, California.
744 Fitzinger L.J. 1826. Neue Classification der Reptilien nach ihren natürlichen
745 Verwandtschaften nebst einer Verwandtschafts-Tafel und einem Verzeichnisse der
746 ReptilienSammlung des K.K. Zoologischen Museum’s zu Wien. J.G. Heubner, Wien.
747 Garner, A.H. 1926. Suggested nomenclatural and correlation on geological formations in
748 Venezuela. American Institute of Mining and Metallurgy Engineers, Transactions,
749 Petroleum Development and Technology in 1925: 677–684.
750 Gardner, J.D. and R.L. Cifelli. 1999. A primitive snake from the Cretaceous of Utah. Special
751 Papers in Palaeontology, 60:87–100.
752 Gómez, R.O., Báez, A.M., and Rougier, G.W. 2008. An anilioid snake from the Upper
753 Cretaceous of northern Patagonia. Cretaceous Research, 29: 481–488.
754 doi:10.1016/j.cretres.2008.01.002
755 González de Juana, C., Iturralde de Arocena, J., and Picard, X. 1980. Geologia de Venezuela
756 y de sus Cuencas Petroliferas. Foninves, Caracas, 1031 pp.

Deleted: Stanford, California,

Deleted: .

Deleted: Natürlichen

Deleted:

Deleted: -

762 Gray, J.E. 1831. Synopsis Reptilium or short descriptions of the species of reptiles. Part I:
763 Cataphracta, tortoises, crocodiles, and enaliosaurians. Treuttel, Wurz & Co., London,
764 85 pp.
765 Hecht, M. 1982. The vertebral morphology of the Cretaceous snake *Dinilysia patagonica*
766 Woodward. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 1982: 523–
767 532.
768 Hedberg, H., and Sass, L. 1937. Synopsis of the geologic formations of the western part of
769 the Maracaibo Basin, Venezuela. Boletín de Geología y Minería, 2-4:71–112.
770 Hoffstetter, R. 1961. Nouveaux restes d'un serpent Boide (*Madtsoia madagascariensis* nov.
771 sp.) dans le Crétacé´ supérieur de Madagascar. Bulletin du Muséum national
772 d'Histoire naturelle, 33: 152–160.
773 Hoffstetter, R., and Gasc, J.P. 1969. Vertebrae and ribs of modern reptiles. In: C. Gans, T.S.
774 Parsons, and A. d'A. Bellairs (eds.), Biology of the Reptilia, vol. 1, 201–310.
775 Academic Press, New York.
776 Hsiou, A.S., Albino, A.M., Medeiros, M.A., and Santos, R.A.B. 2014. The oldest Brazilian
777 snakes from the early Late Cretaceous (Cenomanian). Acta Palaeontologica Polonica,
778 59:635–642. doi: http://dx.doi.org/10.4202/app.2012.0091
779 Leidy, J. 1870. Remarks on ichthyodorulites and on certain fossil mammalians. Proceedings
780 of the American Philosophical Society, 22:12-13.
781 Linnaeus, C. 1758. Systema naturae. Editio Decima, Larentii Salvii, Stockholm, 824 p.
782 Macellari, C.E., and De Vries, T.J. 1987. Late Cretaceous upwelling and anoxic
783 sedimentation in northwestern South America. Palaeogeography, Palaeoclimatology,
784 Palaeoecology, 59: 279–292.
785 Marsh, O.C. 1892. Notice of new reptiles from the Laramie Formation. American Journal of
786 Science, 43:449–453.

Deleted: Jarhbuch

Deleted: Palaöntologie

Deleted: Tenth Edition

790 Martill, D.M., Tischlinger, H., and Longrich, N.R. 2015. A four-legged snake from the Early
791 Cretaceous of Gondwana. Science, 349: 416–419. doi: 10.1126/science.aaa9208
792 Martinelli, A.G. and Forasiepi, A.M. 2004. Late Cretaceous vertebrates from Bajo de Santa
793 Rosa (Allen Formation), Río Negro province, Argentina, with the description of a new
794 sauropod dinosaur (Titanosauridae). Revista del Museo Argentino de Ciencias
795 Naturales Bernardino Rivadavia, 6: 257–305.
796 Méndez, B.J. 1981. La Formación La Luna. Característica de una cuenca anóxica en una
797 plataforma de aguas someras. Proceedings of the 7th Congreso Geológico
798 Venezolano, Barquisimeto, Venezuela, November 12–18, pp. 852–866.
799 Moody, J.M. and Maisey, J.G. 1994. New Cretaceous marine vertebrate assemblages from
800 north-western Venezuela and their significance. Journal of Vertebrate Paleontology 14
801 (1): 1–8. doi:10.1080/02724634.1994.10011534
802 Oppel, M. 1811. Die Ordnungen, Familien und Gattungen der Reptilien als Prodrom einer
803 Naturgeschichte derselben. J. Lindauer, München, 86 p.
804 Palci, A., Caldwell, M.W., and Albino, A.M. 2013. Emended diagnosis and phylogenetic
805 relationships of the Upper Cretaceous fossil snake *Najash rionegrina* Apesteguía and
806 Zaher, 2006. Journal of Vertebrate Paleontology 33: 131–140.
807 Rage, J.-C. and A. Richter. 1994. A snake from the Lower Cretaceous (Barremian) of Spain:
808 The oldest known snake. Neues Jahrbuch für Geologie und Paläontologie,
809 Monatshefte, 9:561–565.
810 Rage, J.-C. and Albino, A.M. 1989. *Dinilysia patagonica* (Reptilia, Serpentes); matériel
811 vertébral additionnel du Crétacé supérieur d'Argentine. eÉtude complémentaire des
812 vertébrés, variations intraspécifiques et intracolumnares. Neues Jahrbuch für Geologie
813 und Paläontologie, Monatshefte 1989: 433–447.

Deleted: München,

Deleted: , Stuttgart

Deleted: E

Deleted: s

Deleted: complementaire

Deleted: vertébres

Deleted: Jarhbuch

Deleted: Pälaontologie

Deleted: e

Deleted: n

824 Rage, J.C. and F. Escuillié. 2003. The Cenomanian: stage of hindlimbed snakes. Carnets de
825 Géologie, 2002:1–11. doi:10.4267/2042/293
826 Renz, O. 1959. Estratigrafía del Cretáceo en Venezuela occidental. Boletín de Geología, 5: 3–
827 48.
828 Renz, O., 1968. Über die Untergattungen *Venezoliceras* Spath und *Laraiceras* n. subgen., der
829 Gattung *Oxytropidoceras* Stieler (Ammonoidea) aus den venezolanischen Anden.
830 Eclogae Geologicae Helvetiae, 61: 615–655.
831 Renz, O. 1982. The Cretaceous ammonites of Venezuela. Maraven, Caracas, 132 p.
832 Ricqlès A. de, Buffrénil V. de (2001). Bone histology, heterochroniesand the return of
833 tetrapods to life in water: where are we? In: J.-M. Mazin V. de Buffrénil, (eds.),
834 Secondary Adaptation of Tetrapods to Life in Water. Verlag Dr. Friedrich Pfeil,
835 München, pp. 289–310.
836 Sánchez-Villagra, M.R., Brinkmann, W., and Lozsán, R. 2008. The Palaeozoic and Mesozoic
837 vertebrate record of Venezuelan overview, summary of previous discoveries and
838 report of a mosasaur from the La Luna Formation (Cretaceous). Paläontologische
839 Zeitschrift, 82:113–124. doi:10.1007/BF02988403
840 Smith-Woodward, A. 1901. On some extinct reptiles from Patagonia of the genera *Miolania*,
841 *Dinilysia*, and *Genyodectes*. Proceedings of the Zoological Society of London 1901:
842 169–184.
843 Tribovillard, N.P., Stephan, J.F., Manivit, H., Reyre, Y., Cotillon, P., and Jautee, E. 1991.
844 Cretaceous black shales of Venezuelan Andes: preliminary results on stratigraphy and
845 paleoenvironmental interpretations. Palaeogeogr, PaIaeocIimatol, Palaeoecol, 81:
846 313–321.
847 Zaher, H. and Scanferla, C.A. 2012. The skull of the Upper Cretaceous snake *Dinilysia*
848 *patagonica* Smith-Woodward, 1901, and its phylogenetic position revisited.

Deleted: Subgen

Formatted: Font:Italic

Deleted: J-M,

Deleted: V de

852 Zoological Journal of the Linnean Society, 164: 194–238. doi: 10.1111/j.1096-
853 3642.2011.00755.x
854 Zaher, H., Apesteguía, S., and Scanferla, C.A. 2009. The anatomy of the upper cretaceous
855 snake *Najash rionegrina* Apesteguía and Zaher, 2006, and the evolution of
856 limblessness in snakes. Zoological Journal of the Linnean Society, 156: 801–826. doi:
857 10.1111/j.1096-3642.2009.00511.x
858 Zapata, E., Padro, V., Madrid, I., Kertznus, V., Truskowski, I., and Lorente, M.A. 2003.
859 Biostratigraphic, sedimentologic, and chemostratigraphic study of the La Luna
860 Formation (Late Turonian-Campanian) in the San Miguel and Las Hernández
861 sections, western Venezuela. Palaios, 18:367-377. doi:10.1669/0883-
862 1351(2003)018<0367:BSACSO>2.0.CO;2