An enigmatic aquatic snake from the Cenomanian of Northern South America

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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 estate, Andes of Venezuela, and consist of several vertebrae, which belong to the precloacal region of the 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, owing to the vertebrae being ~~pachyostotic~~ osteosclerotic and the ribs being ventrally-positioned, implying an extremely compressed body. The systematic affiliation of this new taxon is difficult 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 La Aguada Member.

Introduction

Until recently, the oldest record of snakes has been from rocks of the Albian of Argelia (country) (Cuny et al., 1990), and the Albian–Cenomanian of North America (Gardner & Ciffelli, 1999), whereas the supposed snake from the Barremian of Spain (Rage & Richter, 1994) was excluded from the group (Rage & Escuillié, 2003). These old snake remains contain scarce 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), that 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 had undergone habitat differentiation and geographic radiation at least since the mid-Jurassic (Caldwell et al., 2015).

In South America, the oldest snakes are concentrated in the Mesozoic of Brazil and Argentina. 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 Upper Cretaceous (Cenomanian). The fossil record of Argentina contains several remains of primitive snakes, including the two hind-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 the diverse Madtsoiidae Hoffstetter, 1961, from the Campanian–Maastrichtian (Albino, 1986,

Commenté [A1]: Maybe specify the nature of teh remains to show how limited

Commenté [A2]: Maybe discuss how consistent it is, or not, with molecular phylogenies including estimations of time of snake origin

1994, 2000, 2007, 2011; Martinelli & Forasiepi, 2004). In this work we describe a new taxon of aquatic snake based on vertebrae found in rocks from the Cenomanian of the La Luna Formation in the Andes of Venezuela. This specimen represents the oldest record of snakes from Northern South America, and adds substantial information about the diversity of the group during its early evolution.

Commenté [A3]: Maybe specify that it is one of the richest fauna of early snakes

Geological setting

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

The U~~u~~pper 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-dysoxic conditions along the passive margin of northern South America during the Cenomanian-Campanian (Zapata et al., 2003). This lithostratigraphic unit was originally named the ‘La Luna Limestone’ by Garner (1926), in the Quebrada La Luna, in 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, where the 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 limestones and shales)

Mis en forme : Surlignage

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(Fig. 2A). Siliceous and phosphatic horizons characterize the top of the unit, recognizing the Ftanite of Táchira (Coniacian-Santonian) and Tres Esquinas Member (late Campanian) respectively. The Tres Esquinas Member is well exposed in the Cordillera de Mérida and Perijá, while the Ftanite of Táchira 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 exposed in the Cementos Andinos quarry (Figs. 2B and 3A, B), present a characteristic lithology 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 and ellipsoidal calcareous concretions, reaching up to 198 cm in diameter (Fig. 3C, D), are common through 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 is overlaying a fossiliferous dark-gray sandy limestone, which has been recognized in the Andes of Trujillo and Lara as the top of the late 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 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 still needs to be resolved. A Cenomanian age for the La Aguada Member has been provided by planktonic foraminifera and ammonites (Renz, 1959).

Materials and methods

The studied specimen (MNCN-1827) 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 included in the Colección

Commenté [A5]: You need to choose between Late and Upper throughout the MS

Mis en forme : Surlignage

Herpetológica de la Universidad Nacional de Mar del Plata- Sección Osteología, Argentina (UNMdP-O). Its systematic affinities were analyzed taking into account previously published data. Measurements were taken with manual calipers and are expressed in mm.

Commenté [A6]: Normal – useful sentence??

Commenté [A7]: Maybe specify only in table

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 an energy 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.

Commenté [A8]: Here just specify why you did the scan?? In order to….

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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

Holotype. MNCN-1827. The type specimen is composed by vertebral remains that were included in a small black shale block and that correspond 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).

Commenté [A9]: Maybe justify a bit more – at least consistent in size

Type locality and horizon. Cement quarry (Cementos Andinos company), located east of Lake Maracaibo, 10 km northeast of Monay city, Trujillo State, Venezuela (Fig. 1). The fossiliferous horizon corresponds ~~with~~ to a black shale layer located ~28 meters from 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; *aquaticus*: aquatic in Latin.

Diagnosis. Medium sized, elongate, and 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 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

Commenté [A10]: See comment later

Commenté [A11]: Justify more in the text after 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.

Description

All vertebrae are characterized by a remarkable hypertrophic thickening that indicates pachyostosis (Fig. 8), a ~~method~~ osseous specialization of controlling ballast ((generally)) associated with secondarily aquatic tetrapods (Ricqlès & Buffrénil, 2001). In general, the vertebrae are medium sized (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 little differences. The following comprehensive description was based on these vertebrae.

Commenté [A12]: It seems rather to be osteosclerosis as there does not seem to be a bulging observable morphologically; only an increase in inner compactness, right?? If so only osteosclerosis

Commenté [A13]: Strange to be both long and wide

Commenté [A14]: Parameters not previously described

Commenté [A15]: Say that you call MNCN-1827-B Vertebra B

Commenté [A16]: But you need to say that all diagnostic characters true for all

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 round outline, filled by sediment. The prezygapophyses are robust and large; they are born at the ventral base of the neural canal, and slant above the horizontal plane, but not reaching the zygosphenal roof level. There are no prezygapophyseal processes. The cotyle is large, scarcely wider than high,

Commenté [A17]: Only very slightly, right?

nearly circular, 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 showed 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 and it is broken on the left.))) The paradiapophyses are positioned ventrally to the cotyle, very far from the prezygapophyseal surfaces and close to each-other; they project ventrally through 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 surpassing a lot the ventral rim of the cotyle.

Commenté [A18]: imprecise

Commenté [A19]: confusing term

Commenté [A20]: strongly projecting ventrally beyond

In posterior view, the neural arch is depressed, but it forms two globes above each zygantrum as strong convexities, specially showed in vertebra MNCN-1827-B on both sides and in vertebra MNCN-1827-A on the left. The zygantra are developed but filled by sediment, which also extends over the dorsal condyle. The neural arch roof 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 breaking is on the right. The postzygapophyses are large, slightly inclined above the horizontal. There are no parazygantral foramina. The condyle is large and seems to be circular. The posterior end of a wide haemal keel is ~~slightly~~ seen ventrally to the condyle.

In dorsal view, the neural arch is “”long and wide””, with the posterior edge slightly convex in vertebra A and almost rectilinear in vertebra B. None of the condyle is seen from this view. The interzygapophyseal constriction is concave and well-marked but not especially profound. The articular surfaces of the prezygapophyses are large, oval, longer than wide, and anterolaterally oriented. The zygosphene is well developed, notched in the middle. It is partially broken on the left in specimen A whereas it is complete in vertebra B. Vertebra A does not have any trace of neural spine, but a very low and large neural spine is born at the

Commenté [A21]: useless

Commenté [A22]: but not abruptly

base of the zygosphene in the vertebra B. It forms a thin and poorly developed crest. Posteriorly, at both sides of the middline, the neural arch forms two well-developed globes over the postzygapophyses. All along the neural arch roof, but especially in the posterior half, longitudinal crests run anteroposteriorly, one at each side of the midline.

Commenté [A23]: unclear – label on illustration

In ventral view, the vertebral centrum is long (cl/naw > 1.00) and narrow, slightly wider anteriorly than posterioly, but not markedly triangular in section. The subcentral ridges are well defined and very 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 scarcely developed haemal keel, which is anteriorly smooth and posteriorly more defined and wider. The short precondylar constriction is strongly marked. There is no subcentral foramina. The paradiapophyses are small with articular surfaces well exposed ventrally. The di- and parapophyseal surfaces are clearly distintictive and separated by a short and profound constriction.

Commenté [A24]: refer to fig

Commenté [A25]: label

Commenté [A26]: where?

In lateral view, the vertebrae are long, with significantly depressed neural arch roofs. Anteriorly, the neural arches surpass the cotyle level due to the anterior projection of the zygosphene. Posteriorly, the neural arch is longer than the vertebral centrum (nal > cl), exceeding the condyle level. 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 very low, as a thin and prominent 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, at each side, the neural arch roof forms a convexity as a globe above the postzygapohyses. As a result, the outline of the neural arch seems concave in lateral view. The absence of a neural spine in vertebra A produces a more profound concave arch in lateral view than in vertebra B. The longitudinal crests and the globes of the arch in specimen A are

Commenté [A27]: Already said

Commenté [A28]: Rather antero-laterally, right?

Commenté [A29]: useless

less well-marked than in B. The prezygapophyses are large and robust, 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 of each 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 born near the saggital axis of the vertebra and diverge dorsoventrally from this point to the subcentral ridges. This morphology produces a prominent shelf of the neural arch roof on each side and between 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 condyle has its main axis not strongly inclined from the horizontal plane. The precondylar constriction is very well defined. The paradiapophyses are very low, ~~far from the prezygapophyses~~, and clearly separated from the centrum by a profound constriction. They are developed at the end of a short projection similar to a transverse process. They are small and ventrally surpass the ventral edge of the condyle and subcentral ridges.

Commenté [A30]: already said

Commenté [A31]: just normal; paradiapophyses before the articular facets; avoid transverse processes - confusing

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 higher a little than in specimen B, whereas the vertebral centrum is relatively shorter, and the haemal keel is not defined. There is not neural spine, as in vertebra A.

Commenté [A32]: useful??? Similar for later infos about just preservation or absence of features

The vertebra MNCN-1827-D (Fig. 6 E-H) is also of a similar size to specimen B. It has lost most of the vertebral centrum, right postzygapophysis, and the zygosphene. In dorsal 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). All of the 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 at the most distal part of the neural arch roof from where it freely slants backward. Thus, the spine is strongly extended posteriorly, surpassing the posterior edge of the neural arch. The free portion of the spine, which extends over the posterior limit of the neural arch, comprises of approximately 63% of the neural arch length, and thus forms more than half the total length of the vertebra. It has a tubular form, and is transversally and anteroposteriorly thin. This vertebra does not have a hypapophysis on the ventral surface of the vertebral centrum, as is common in anterior vertebrae of most snakes. Instead, in the most posterior part of the centrum presents a slight prominence not wider than the cotyle, similar to the posterior part of a haemal keel seen in specimen MNCN-1827-B. Judging by the presence of a high neural spine, this vertebra is interpreted as an anterior trunk vertebra. 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.

Commenté [A33]: link to fig

Commenté [A34]: the discussion of the relative position of the vertebrae along the vertebral column is rather poorly justified – it is complicated of course; but if too complicated you can remain very vague, with just x more anterior than y…. However, if you are more sure, please justify more as interesting

Commenté [A35]: base don so few material not perfectly preserved?; interesting; please tell us more

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

Commenté [A36]: ¿?

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, such as: a marked lateral limitation of the centra (well-developed subcentral ridges); differentiated diapophyses and parapophyses; and well developed zygosphene-zygantrum complex in all recorded vertebrae (Estes, de Queiroz & Gauthier, 1988). The presence of an anteroposteriorly short and strongly posteriorly inclined neural spine in specimen MNCN-1827-E is reminiscent of lizards (Estes, de Queiroz & Gauthier, 1988). The anteriorly notched zygosphene and the absence of prezygapophyseal processes are characteristic of lizard forms, but are also found in some primitive snakes (Hoffstetter & Gasc, 1969).

The vertebrae described here constitute a unique taxon that displays a combination of features that distinguishes it from other known fossil and extant snakes, thus justifying the erection of a new taxon. The neural arch walls arising from the medial line and diverging to the subcentral ridges, the prominent globes on the neural arch above the postzygapophyses, the extremely long neural arch posteriorly surpassing the condyle level, and the high and posteriorly extended tubular spine at least in some vertebrae, are all unique in this snake. The globes are developed in the position occupied by the pterapophyses of the aquatic paleophiids and nigerophiids. The depressed neural arches associated with absent or very reduced neural spines is a feature shared by fossorial snakes such as Scolecophidia Cope, 1864 and Anilioidea Fitzinger, 1826, and other burrowing squamates such as Amphisbaenia Gray, 1864. The presence of this character contrasts with the ventrally placed paradiapophyses, the medium size of the vertebrae, and the high neural spine showed by vertebra MNCN-1827-E, which contradict 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 completely below the vertebral centra, and thus 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 some mechanical / muscular role, probably related with locomotion in water. Also, the strongly marked longitudinal crests on the roof of the neural arch were probably for the

Commenté [A37]: Still vague carácter to me

Commenté [A38]: Out of curiosity, could you see base don the virtual sections of what they were made?? Compact, spongious bone??? Would be very interesting to know.

Commenté [A39]: Observed however in some lizards

Commenté [A40]: Gray 1831 in refs - adapt

Commenté [A41]: Add refs about anatomy, not just the systematic ones

Commenté [A42]: Only Pelamis is really pelagic

Commenté [A43]: Without comparative data, the hypothesis seems to come a bit “out of nowhere” insertion of musculature associated to the mode of life. A laterally compressed body helped by hard 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, thickened, pachyostotic vertebrae would have provided increased ballast.

In the last years, efforts to understand the origins and evolution of snakes resulted in several phylogenetic analyses that include vertebral characters previously seen only in morphological studies. 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 a non-oval cotyle and condyle. The former two characters also distinguish *Lunaophis aquaticus* from the extinct *Coniophis precedens* Marsh, 1892, whereas the third 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 characters can be verified in *Seismophis septentrionalis* *(ref)*. Similar to these taxa, the posterior border of the neural arch in *Lunaophis aquaticus* is not notched, but differs significantly from them in the position of the paradiapophyses below the vertebral centrum and the fact that these face ventrally. In the compared species the paradiapophyses are strongly lateralized and face ventrolaterally. Other differences with aff. *Parviraptor estesi* and *Diablophis gilmorei* are the zygosphene being better developed, a more profound precondylar constriction, and an apparently non-trifoliate neural canal. A neural spine reduced to a ridge is reminiscent of *Coniophis precedens* (but in this species it ends in a

Commenté [A44]: Attention, if true pachyostosis, can limit movements between vertebrae; but if only osteosclersois, not the case

Commenté [A45]: You should be able to state on this question base don the virtual sections tuberosity). *Lunaophis aquaticus* also shares with *Coniophis precedens*, *Dinilysia patagonica* and *Seismophis septentrionalis* the presence of a depressed neural arch. On either side of the neural spine the dorsolateral ridges are present in these snakes, as well as in *Najash rionegrina* and Madtsoiidae. *Lunaophis aquaticus* is also distinctive of *Seismophis septentrionalis* in the notched zygosphene and absence of parazygantral foramina. The vertebral centrum in *Lunaophis aquaticus* differs from other primitive species because it is not as markedly wider anteriorly as it is in *Najash rionegrina*, *Dinilysia patagonica* and *Seismophis septentrionalis*. According to the figures in Caldwell et al. (2015), a centrum that is not much wider anteriorly is present in aff. *Paviraptor estesi* and *Diablophis gilmorei*.

According to these comparisons, *Lunaophis aquaticus* gen. et sp. nov. is probably a pre-scolecophidian snake strongly adapted for swimming. In the context of the proposed phylogeny of Martill, Tischlinger & Longrich (2015) it would represent the earliest snake that conquests aquatic environments and then revitalizes the question about the evolving of snakes from burrowing or marine ancestors.

Paleoenvironment and paleoecology

Lunaophis aquaticus gen. et sp. nov. represents an aquatic lineage of snakes that exploited marine environments. This is reflected by the depositional conditions of the La Luna Formation, interpreted as a typical marine environment where laminated organic rich intervals suggest a deposition in the mid-shelf to upper-slope under anoxic-dysoxic conditions (Macellari & De Vries, 1987; Erlich et al., 1999; Bralower & Lorente, 2003; Zapata et al., 2003). The organic matter of the sediments in the La Aguada Member (Trujillo area) mostly occurs from a marine origin (algae and dinocysts) (Trivobillard et al., 1991). González de Juana, Iturralde de Arocena & Picard (1980), suggested that the La Aguada Member could be considered as a transitional environment between the shallow waters of the Maraca formation (or La Puya Member according to Renz, 1959, 1968), and the pelagic facies of the La Luna Formation. In contrast with the pelagic and hemipelagic deep water sedimentation suggested 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 was not due to the depth, but by pre-existing anoxic conditions in the slope zone. On basis of benthic and planktonic foraminifera, Méndez (1981, and references therein) recognized an increase in the deepening of the platform, but probably with depths that did not exceed 50 meters.

The specimen of *Lunaophis aquaticus* gen. et sp nov. is also associated with remains of other marine vertebrate fauna (sharks and bony fishes) in the Aguada Member (Cementos Andinos quarry). Bony fish remains are very abundant in the *Lunaophis aquaticus* stratum 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), ichthyodectiformes, enchodonts 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 invertebrate fauna is scarce in the shales of the Cementos Andinos quarry; however, small undetermined bivalve molds in the limestones are common. The benthic invertebrate fauna in the La Aguada Member could represent some short periods of better oxygenated conditions on the sea floor, or organisms that were tolerant to these stressed anoxic environments, as has been suggested forother 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 could be evidence of well-oxygenated surface waters, thus indicating that the Aguada Member environment was characterized by a stratified water column. In addition, other chondrichthyans, bony fishes and marine reptile remains have also been found throughout the La Luna Formation (Wailer, 1940; Moody & Maisey, 1994; Casas & Moody, 1997; Sánchez-Villagra, Brinkmann & Lozsán 2008; Carrillo-Briceño, 2009; 2012).

Commenté [A46]: Not in ref

+ add anatomical data consistent with aquatic lifestyle + osteosclerosis

Conclusion

Lunaophis aquaticus gen. et sp. nov. is a primitive snake that has strong affinities with pre-scolecophidian snakes, but is distinguished by a number of characters that makes it a new and enigmatic taxon. *Lunaophis aquaticus* represents a primitive aquatic lineage of snakes that exploited tropical marine environments during the Cenomanian, and is the oldest record of the group from the north of South America.

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References

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

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

Albino, A.M. 2000. New record of snakes from the Cretaceous of Patagonia (Argentina). Geodiversitas, 22: 247–253.

Albino, A.M. 2007. Lepidosauria. In: Z. Gasparini, L. Salgado, and R.A., Coria (eds.), Patagonian Mesozoic Reptiles, 87–115. Indiana University Press, Indiana.

Albino, A.M. 2011. Evolution of Squamata reptiles in Patagonia based on the fossil record. Biological Journal of the Linnean Society, 103:441–457. doi: 10.1111/j.1095-8312.2011.01691.x

Apesteguía, S., and Zaher, H. 2006. A Cretaceous terrestrial snake with robust hindlimbs and a sacrum. Nature, 440:1037–1040. doi:10.1038/nature04413

Bralower, T.J., and Lorente, M.A. 2003. Paleogeography and stratigraphy of the La Luna Formation and related Cretaceous anoxic depositional systems. Palaios, 18: 301–304.

Caldwell, M.W. and Albino, A.M. 2002. Exceptionally preserved skeletons of the Cretaceous snake *Dinilysia patagonica* Woodward, 1901. Journal of Vertebrate Paleontology, 22: 861–866.doi:10.1671/0272-4634(2002)022[0861:EPSOTC]2.0.CO;2

Caldwell, M.W. and Calvo, J. 2008. Details of a new skull and articulated cervical column of *Dinilysia patagonica* Woodward, 1901. Journal of Vertebrate Paleontology, 28: 349–362. doi:10.1671/0272-4634(2008)28[349:DOANSA]2.0.CO;2

Caldwell, M.W., Nydam, R.L., Palci, A., and Apesteguía, S. 2015. The oldest known snakes from the Middle Jurassic-Lower Cretaceous provide insights on snake evolution. Nature Communications, 6: 5996. doi:10.1038/ncomms6996

Carrillo-Briceño J.D. 2009. Presencia del genero *Ptychodus* (Elasmobranchii: Ptychodontiade) en el Cretácico superior de los Andes de Trujillo Venezuela. GEOMINAS, 37 (50): 207–210.

Carrillo-Briceño, J.D. 2012. Presencia de *Ptychodus mortoni* (Elasmobranchii: Ptychodontidae) en el Cretácico Superior de Venezuela. Revista Geológica de América Central, 46: 145–150. doi: http://dx.doi.org/10.15517/rgac.v0i46.1837

Carrillo-Briceño, J.D., Alvarado-Ortega, J. and Torres, C. 2012. Primer registro de *Xiphactinus* Leidy, 1870, (Teleostei: Ichthyodectiformes) en el Cretácico Superior de América del Sur (Formación La Luna, Venezuela). Revista Brasilera de Paleontología, 15(3):327–335. doi:10.4072/rbp.2012.3.08

Casas, J.E and Moody, J.M. 1997. Primera descripción del género *Belenostomus* en la Formación La Luna (Cretácico), Sierra de Perijá, (Pisces: Aspydorhynchidae). Boletín de la Sociedad Venezolana de Geólogos, 22 (1): 51–55.

Cope, E.D. 1864. On the characters of the higher groups of Reptilia Squamata and especially of the Diploglossa. Proceedings of the Academy of Natural Sciences of Philadelphia, 1864: 224–231.

Cuny, G., Jaeger, J.J., Mahboubi, M., and J.C. Rage. 1990. Les plus anciens Serpents (Reptilia, Squamata) connus. Mise au point sur l'âge géologique des Serpentes de la partie moyenne du Crétacé. Comptes rendus des séances de l'Académie des Sciences, Paris, Série II, 311:1267–1272.

Davis C., Pratt, l., and Sliter, W. 1999, Factors influencing organic carbon and trace metal accumulation in the Upper Cretaceous La Luna Formation of the western Maracaibo Basin, Venezuela. In: E., Barrera, and C.C., Johnson, (eds.), Evolution of the Cretaceous Ocean-Climate System, 203–231. Geological Society of America Special Paper 332.

de Romero, L.M., and Galea, F.A. 1995. Campanian Bolivinoides and microfacies from the La Luna Formation, western Venezuela. Marine Micropaleontology, 26: 385–404.

Erlich, R.N., Macsotay, O., Nederbragt, A.J., and Lorente, M.A. 1999. Palaeoceanography, palaeoecology, and depositional environments of Upper Cretaceous rocks of western Venezuela. Palaeogeography, Palaeoclimatology, Palaeoecology, 153: 203–238.

Erlich, R.N., Macsotay, O., Nederbragt, A.J. and Lorente, M.A. 2000. Birth and death of the Late Cretaceous ‘‘La Luna Sea’’, and origin of the Tres Esquinas phosphorites. Journal of South American Earth Sciences, 13: 21–45.

Estes, R., Frazzetta, T.H., and Williams, E.E. 1970. Studies on the fossil snake *Dinilysia patagonica* Woodward: Part 1. Cranial morphology. Bulletin of the Museum of Comparative Zoology, 140: 25–74.

Estes, R., de Queiroz, K. and Gauthier, J. 1988. Phylogenetic relationships within Squamata. In: R. Estes, and G.K. Pregil (eds), Phylogenetic relationships of the lizard families, 119–281. Stanford, California, Stanford University Press.

Fitzinger L.J. 1826. Neue Classification der Reptilien nach ihren Natürlichen Verwandtschaften nebst einer Verwandtschafts Tafel und einem Verzeichnisse der Reptilien - Sammlung des K.K. Zoologischen Museum’s zu Wien. J.G. Heubner, Wien.

Garner, A.H. 1926. Suggested nomenclatural and correlation on geological formations in Venezuela. American Institute of Mining and Metallurgy Engineers, Trasactions, Petroleum Development and Technology in 1925: 677–684.

Gardner, J.D. and R.L. Cifelli. 1999. A primitive snake from the Cretaceous of Utah. Special Papers in Palaeontology, 60:87–100.

Gómez, R.O., Báez, A.M., and Rougier, G.W. 2008. An anilioid snake from the Upper Cretaceous of northern Patagonia. Cretaceous Research, 29: 481–488. doi:10.1016/j.cretres.2008.01.002

González de Juana, C., Iturralde de Arocena, J., and Picard, X. 1980. Geologia de Venezuela y de sus Cuencas Petroliferas. Foninves, Caracas, 1031 pp.

Gray, J.E. 1831. Synopsis Reptilium or short descriptions of the species of reptiles. Part I: Cataphracta, tortoises, crocodiles, and enaliosaurians. Treuttel, Wurz & Co., London, 85 pp.

Hecht, M. 1982. The vertebral morphology of the Cretaceous snake *Dinilysia patagonica* Woodward. Neues Jarhbuch für Geologie und Palaöntologie, Monatshefte 1982: 523–532.

Hedberg, H., and Sass, L. 1937. Synopsis of the geologic formations of the western part of the Maracaibo Basin, Venezuela. Boletín de Geología y Minería, 2-4:71–112.

Hoffstetter, R. 1961. Nouveaux restes d'un serpent Boide (*Madtsoia madagascariensis* nov. sp.) dans le Crétacé´ supérieur de Madagascar. Bulletin du Muséum national d'Histoire naturelle, 33: 152–160.

Hoffstetter, R., and Gasc, J.P. 1969. Vertebrae and ribs of modern reptiles. In: C. Gans, T.S. Parsons, and Ad'A. Bellairs (eds.), Biology of the Reptilia, vol. 1, 201–310. Academic Press, New York.

Hsiou, A.S., Albino, A.M., Medeiros, M.A., and Santos, R.A.B. 2014. The oldest Brazilian snakes from the early Late Cretaceous (Cenomanian). Acta Palaeontologica Polonica, 59:635–642. doi: http://dx.doi.org/10.4202/app.2012.0091

Leidy, J. 1870. Remarks on ichthyodorulites and on certain fossil mammalians. Proceedings of the American Philosophical Society, 22:12-13.

Linnaeus, C. 1758. Systema naturae. Tenth Edition, Larentii Salvii, Stockholm, 824 p.

Macellari, C.E., and De Vries, T.J. 1987. Late Cretaceous upwelling and anoxic sedimentation in northwestern South America. Palaeogeography, Palaeoclimatology, Palaeoecology, 59: 279–292.

Marsh, O.C. 1892. Notice of new reptiles from the Laramie Formation. American Journal of Science, 43:449–453.

Martill, D.M., Tischlinger, H., and Longrich, N.R. 2015. A four-legged snake from the Early Cretaceous of Gondwana. Science, 349: 416–419. doi: 10.1126/science.aaa9208

Martinelli, A.G. and Forasiepi, A.M. 2004. Late Cretaceous vertebrates from Bajo de Santa Rosa (Allen Formation), Río Negro province, Argentina, with the description of a new sauropod dinosaur (Titanosauridae). Revista del Museo Argentino de Ciencias Naturales Bernardino Rivadavia, 6: 257–305.

Méndez, B.J. 1981. La Formación La Luna. Característica de una cuenca anóxica en una plataforma de aguas someras. Proceedings of the 7th Congreso Geológico Venezolano, Barquisimeto, Venezuela, November 12–18, pp. 852–866.

Moody, J.M. and Maisey, J.G. 1994. New Cretaceous marine vertebrate assemblages from north-western Venezuela and their significance. Journal of Vertebrate Paleontology 14 (1): 1–8. doi:10.1080/02724634.1994.10011534

Oppel, M. 1811. Die Ordnungen, Familien und Gattungen der Reptilien als Prodrom einer Naturgeschichte derselben. München, J. Lindauer, 86 p.

Palci, A., Caldwell, M.W., and Albino, A.M. 2013. Emended diagnosis and phylogenetic relationships of the Upper Cretaceous fossil snake *Najash rionegrina* Apesteguía and Zaher, 2006. Journal of Vertebrate Paleontology 33: 131–140.

Rage, J.C. and A. Richter. 1994. A snake from the Lower Cretaceous (Barremian) of Spain: The oldest known snake. Neues Jarbuch für Geologie und Paläontologie, Monatshefte, Stuttgart, 9:561–565.

Rage, J.C. and Albino, A.M. 1989. *Dinilysia patagonica* (Reptilia, Serpentes); matériel vertébral additionnel du Crétacé supérieur d’Argentine. Estude complementaire des vertébres,variations intraspécifiques et intracolumnares. Neues Jarhbuch für Geologie und Pälaontologie, Monatseheften 1989: 433–447.

Rage, J.C. and F. Escuillié. 2003. The Cenomanian: stage of hindlimbed snakes. Carnets de Géologie, 2002:1–11. doi:10.4267/2042/293

Renz, O. 1959. Estratigrafía del Cretáceo en Venezuela occidental. Boletín de Geología, 5: 3–48.

Renz, O., 1968. Über die Untergattungen *Venezoliceras* Spath und *Laraiceras* n. Subgen, der Gattung Oxytropidoceras Stieler (Ammonoidea) aus den venezolanischen Anden. Eclogae Geologicae Helvetiae, 61: 615–655.

Renz, O. 1982. The Cretaceous ammonites of Venezuela. Maraven, Caracas, 132 p.

Ricqlès A. de, Buffrénil V. de (2001). Bone histology, heterochroniesand the return of tetrapods to life in water: where are we? In: Mazin J-M, Buffrénil V de, eds. Secondary Adaptation of Tetrapods to Life in Water. Verlag Dr. Friedrich Pfeil, München, pp. 289–310.

Sánchez-Villagra, M.R., Brinkmann, W., and Lozsán, R. 2008. The Palaeozoic and Mesozoic vertebrate record of Venezuelan overview, summary of previous discoveries and report of a mosasaur from the La Luna Formation (Cretaceous). Paläontologische Zeitschrift, 82:113–124. doi:10.1007/BF02988403

Smith-Woodward, A. 1901. On some extinct reptiles from Patagonia of the genera *Miolania*, *Dinilysia*, and *Genyodectes*. Proceedings of the Zoological Society of London 1901: 169–184.

Tribovillard, N.P., Stephan, J.F., Manivit, H., Reyre, Y., Cotillon, P., and Jautee, E. 1991. Cretaceous black shales of Venezuelan Andes: preliminary results on stratigraphy and paleoenvironmental interpretations. Palaeogeogr, PaIaeocIimatol, Palaeoecol, 81: 313–321.

Zaher, H. and Scanferla, C.A. 2012. The skull of the Upper Cretaceous snake *Dinilysia patagonica* Smith-Woodward, 1901, and its phylogenetic position revisited. Zoological Journal of the Linnean Society, 164: 194–238. doi: 10.1111/j.1096-3642.2011.00755.x

Zaher, H., Apesteguía, S., and Scanferla, C.A. 2009. The anatomy of the upper cretaceous snake *Najash rionegrina* Apesteguía and Zaher, 2006, and the evolution of limblessness in snakes. Zoological Journal of the Linnean Society, 156: 801–826. doi: 10.1111/j.1096-3642.2009.00511.x

Zapata, E., Padro, V., Madrid, I., Kertznus, V., Truskowski, I., and Lorente, M.A. 2003. Biostratigraphic, sedimentologic, and chemostratigraphic study of the La Luna Formation (Late Turonian-Campanian) in the San Miguel and Las Hernández sections, western Venezuela. Palaios, 18:367-377. doi:10.1669/0883-1351(2003)018<0367:BSACSO>2.0.CO;2