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Review article

Reworked marine pythonomorph (Reptilia, Squamata) remains in Late Pleistocene cave deposits in central Spain

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ABSTRACT

Three sites at the Calvero de la Higuera complex (Camino Cave, Navalmaíllo Rock Shelter, and Buena Pinta Cave), near the village of Pinilla del Valle (Madrid, Spain), are known for their record of Neanderthals and other Late Pleistocene mammals. Occasionally, they also yield much more ancient reworked remains, which come from the Upper Cretaceous dolomites and carbonatic sandstones in which these caves and shelters are developed. These are mostly teeth of sharks and rays and vertebrae and teeth of bony fishes, but several reptile vertebrae and teeth have also been found. These reptile remains, which we describe here, likely belong to the pythonomorph incertae sedis *Carentonosaurus* cf. *mineaui*. This taxon is known from several outcrops in the southwest of France but is rare on the Iberian Peninsula; indeed, only a few remains possibly related to the genus have been found (in the Cabaña Formation, Asturias, Spain). The pythonomorph remains discussed here are the first fossils of marine reptiles from the Madrid region. Should the assignment to *Carentonosaurus* be confirmed, the teeth would provide novel data on the characteristics of this rather poorly known taxon, and might help clarify its phylogenetic relationship within Pythonomorpha.

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Abbreviations:

Institutional Abbreviations—**MAR**, Museo Arqueológico Regional de la Comunidad de Madrid, Alcalá de Henares, Madrid; **MNCN**, Museo Nacional de Ciencias Naturales, Madrid, Madrid; **MNHN**, Muséum National d'Histore Naturelle.

Anatomical Abbreviations—**cd**, condyle; **ct**, cotyle; **er**, epidiapophyseal ridge; **ir**, interzygapophyseal ridge; **lf**, lateral foramen; **nc**, neural canal; **ns**, neural spine; **pcf**, paracotylar foramen; **pd**, paradiapophysis; **prf**, prezygapophyseal facet; **prz**, prezygapophysis; **ptf**, postzygapophyseal facet; **ptz**, postzygapophysis; **pzf**, parazygosphenal foramen; **sb**, subcentral border; **sbf**, subcentral foramen; **zs**, zygosphene; **zt**, zygantrum.

1. Introduction

The early Late Cretaceous was a key period in the evolution of the reptile order Squamata, as shown by the spectacular radiation recorded in marine sediments, especially those along the edge of the Tethys Sea and in the Western Interior Seaway of North America (Bardet et al., 2008a). Three groups stand out among marine squamates: the mosasauroids, the hindlimbed snakes (belonging to Ophidia) and the non-ophidian Ophidiomorpha (here referred to as stem ophidians; Bardet et al., 2008a; Houssaye, 2013). While the plesiopedal and plesiopelvic mosasauroids (with terrestrial-like limbs and pelvis, previously known as 'aigialosaurs'; Bell and

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Polcyn, 2005; Caldwell and Palci, 2007), the hindlimbed snakes and the stem ophidians adapted over a short period (Cenomanian–Turonian) to life in shallow water largely along the shores of the Mediterranean Tethys (Bardet et al., 2008a), hydropedal mosasauroids (i.e., with paddles and no sacrum, the traditional 'mosasaurs'; Bell and Polcyn, 2005) became large nektonic predators with a worldwide distribution by the end of the Cretaceous (Russell, 1967; DeBraga and Carroll, 1993; Bardet et al., 2008a).

In the Cretaceous deposits of the Iberian Peninsula, the hydropedal mosasauroid record is rich. Teeth are the remains most commonly found, and these allow identification to the genus and even species level (Bardet et al., 2008b). Many specimens have been described from the north coast of Portugal (Sauvage, 1897–1898; Crespo, 2002), the Basque–Cantabrian Basin (Bardet et al., 1997, 2006, 2012a; Corral et al., 2011), Burgos (Bardet et al., 1997, 1999) and Alicante (Bardet et al., 2012b). In contrast, remains of basal mosasauroids and ophidiomorphs are rare. The La Cabaña Formation in Asturias, in the north of the Iberian Peninsula, has yielded various cranial and post-cranial remains that have been assigned to the pythonomorph incertae sedis *Carentonosaurus* sp., a vertebra that has been tentatively assigned to the stem ophidian indet. *Coniasaurus* sp., and another small vertebra from the hindlimbed snake *Simoliophis* (Vullo et al., 2009). Remains of the last have also been unearthed in Portugal (Jonet, 1981; Rage, 1984; Bardet et al., 2008b). At the Lo Hueco site in Cuenca (central Spain), vertebrae belonging to a terrestrial or freshwater amphibious pythonomorph have also been found (Houssaye et al., 2013a).

The present work describes new fossils, the vertebrae and teeth of a marine pythonomorph found at the karstic Calvero de la Higuera complex in Madrid (Spain), and justify their systematic assignment to *Carentonosaurus* cf. *mineaui*. The difficulties surrounding the taxonomic assignment of some teeth, and in determining their dental position, are discussed.

1.1. Geological context

The sites of the Calvero de la Higuera complex, located near the village of Pinilla del Valle in the northwest of the Madrid region, lie in the upper western part of the Lozoya Valley, in the southwest of the Guadarrama Mountains (Fig. 1). These mountains, which run NE–SW and have a general pop-up structure, form part of Spain's Sistema Central range (Warburton and Álvarez, 1989; De Vicente et al., 2007).

The Lozoya Valley is a tectonic pop-down basin that formed mainly during the Alpine Orogeny (De Vicente et al., 2011). At the bottom of this basin, mesozoic sediments of Late Cretaceous age outcrop as cuestas (locally known as calveros) (Alférez et al., 1982; Pérez-González et al., 2010). The deepest sediments are Utrillas facies (Turonian–Coniacian) formed mainly of sands, gravels and clays associated with a fluvial system (ITGE, 1991; Pérez-González et al., 2010). Over these lie intercalations of marls and thick deposits of dolomite laid down on a marine platform at the time of the maximum extension of the Cretaceous transgression (late Cenomanian-early Turonian) and slightly later (ITGE, 1991; Gil and García, 1996). This platform was probably associated with the interior sea of the Iberian Basin, which was generated by the communication (along what is now the Iberian Cordillera) of the Eastern Tethys and the Atlantic domain between the Iberian and Ebro Massifs (Segura et al., 2008; Gil et al., 2010).

During the Quaternary, the carbonate materials of the Upper Cretaceous series became karstified. This process led to the formation of a series of endo- and exokarstic structures including the rock shelters and cavities that now make up the archaeopalaeontological complex of Calvero de la Higuera. The origin of this karstic system probably goes back to the start of the Early Pleistocene, while its infilling sediment was laid down from the Middle Pleistocene to the present (Pérez-González et al., 2010).

The recovered reptile remains (found alongside the teeth of sharks, rays and bony fish) come from the Camino Cave, Buena Pinta Cave and the Navalmaíllo Rock Shelter sites. These moderately large cavities (longest axis 10–50 m) are all karstic in origin, and within dolomites and sandstones with dolomitic cement from the Late Cretaceous (Pérez-González et al., 2010). According to the geological map (ITGE, 1991), these materials are of Santonian age, as deduced from their correlation with others of similar lithological characteristics that outcrop on the northern margin of the Sistema

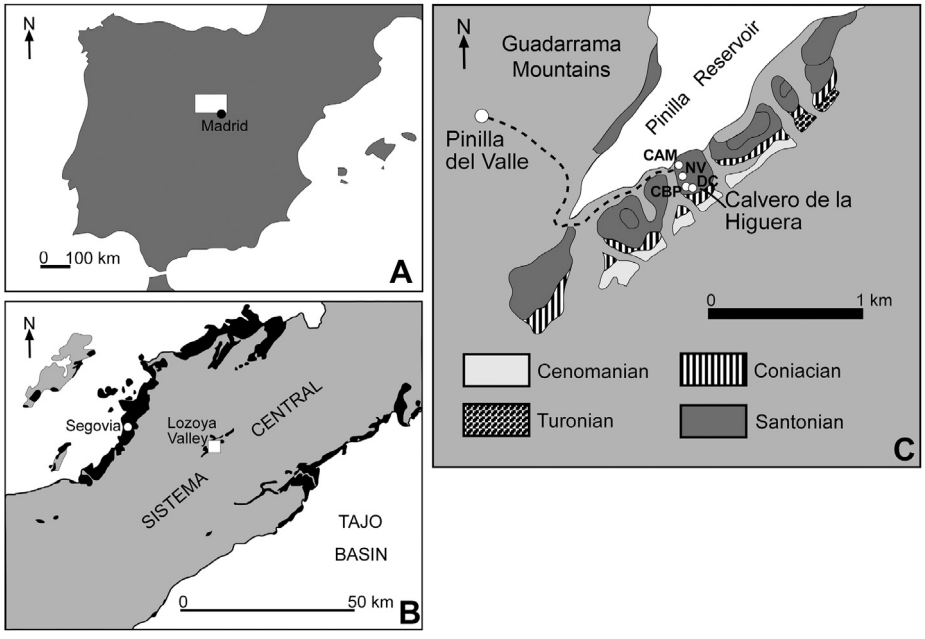


Fig. 1. Location of the Calvero de la Higuera complex. **A**, in the Iberian Peninsula; **B**, within the Sistema Central range (black, cretaceous outcrops; grey, palaeozoic materials) (modified after Gil et al., 2010); **C**, within the Lozoya Valley (modified after ITGE, 1991). **Abbreviations**: **CAM**, Camino Cave; **CBP**, Buena Pinta Cave; **DC**, Des-Cubierta Cave; **NV**, Navalmaíllo Rock Shelter. Geographic coordinates of these sites are: 3°48′ 32″ W – 40° 55′ 25″ N.

Central range (Alonso, 1981). These cavities have been excavated over the same stratigraphic interval (some 15–m–thick) of the aforementioned dolomitic units. After their formation, the cavities became filled with sediments, in which two main facies can be discerned. The first corresponds to fluvial sediment and is composed of gravel with pebbles formed from gneisses and quartz sandstones. The second, which represents autochthonous deposits from the karst system, is formed of silts and clays with abundant dolomitic clasts. These autochthonous deposits formed during the degradation of the cavities; this led to an accumulation of rock fragments from the walls and ceiling mixed with mudflows. The fluvial facies are usually very poor in vertebrate fossils, while the autochthonous facies contain large accumulations of Late Pleistocene amphibian, reptile, bird and mammal remains. The origin of these accumulations lies in the use of these caves and rock shelters by hyaenas (*Crocuta crocuta*) and Neanderthals (*Homo neanderthalensis*) (Arsuaga et al., 2010, 2012; Huguet et al., 2010) after the river stopped flowing through them.

Remains of Cretaceous vertebrates are also found in the autochthonous facies of each site, mixed in with those from the Late Pleistocene. Their concentration in Late Pleistocene deposits may have occurred via gravitational accumulation. As the walls and ceilings of the caves and rock shelters were dissolved by the water filtering through the carbonate massif, the phosphatic vertebrate fossils they contained would have resisted dissolution and fallen from the rocks that once contained them, accumulating inside these cavities.

2. Material and methods

The material studied comprises 26 specimens, 10 vertebrae and 16 teeth, all deposited at the MAR (Alcalá de Henares, Madrid). These pieces correspond to accessions MAR 1981/3/5–MAR 2011/13/1, collected during the 1981–2011 excavations of the Camino Cave, the Navalmaíllo Rock Shelter, and the Buena Pinta Cave sites. The specimen of *Varanus salvator* used as comparative material (MNCN 13818) was loaned from the collections of Museo Nacional de Ciencias Naturales (Madrid, Spain).

2.1. Teeth

The teeth were examined under an Olympus© SZX12 binocular microscope equipped with an Olympus© DP71 digital camera. All measurements recorded using these images were made with Cell^A© software. Images were also made using a Fei Quanta 200 scanning electron microscope (SEM) at the Microscopy Service of the MNCN, Madrid. This was equipped with an environmental camera usable under vacuum conditions; the examined remains therefore required no metal coating. Solid state, backscattered electron and large field detectors were used in the production of these SEM images.

We have used the dental nomenclature of Heckert (2004) to describe the orientation of the teeth, although with slight modifications (Fig. 2): the term anterior was replaced by mesial, for the convex margin towards the front of the skull; the term posterior was replaced by distal, for the concave margin towards the back of the skull. Both terms were only used for the teeth assigned as marginal teeth (see Section 4.1. Teeth). The term apical was used for the upper part of the crown, and basal for the lower part of the crown. Tooth measurements (see Table 1) were taken according to Sankey et al. (2002) also with slight modifications, as shown in Fig. 3. The angles that describe the position of the morphological elements in the crown of the teeth (see Section 4.1. Teeth) were taken in all cases from the mesial end of the perimeter of the crown and always clockwise.

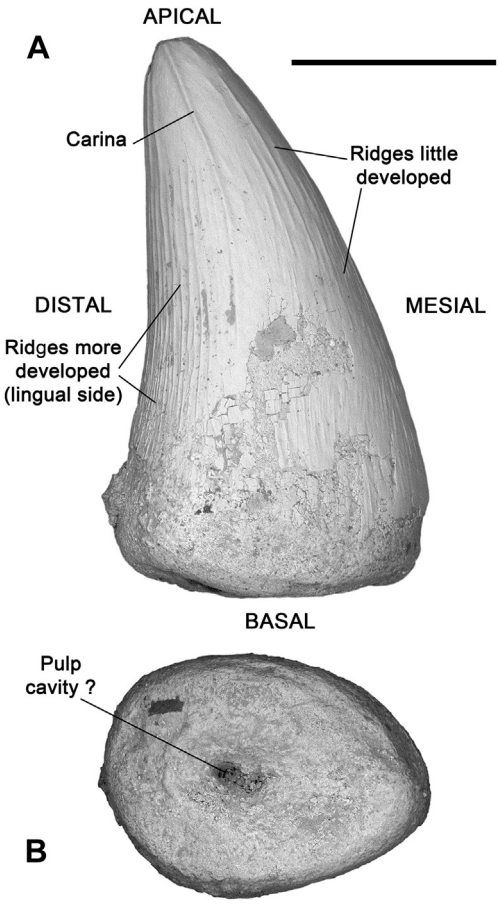


Fig. 2. Structures seen in teeth (MAR 2005/34/11). **A**, labial view; **B**, basal view. Terms mesial and distal are only used to describe marginal teeth. Scale bar equals 2 mm. SEM photographies: Microscopy Department/ MNCN.

2.2. Vertebrae

The vertebrae were examined using an Olympus© SZX9 binocular microscope, and measured using a Mitutoyo electronic calliper. The approximate positions of the vertebrae within the spinal column were determined via comparisons with extant and extinct lizards and snakes (Romer, 1956; Hoffstetter and Gasc, 1969; Estes et al., 1988; Houssaye et al., 2011). Whenever the degree of

Table 1
Measurements taken on teeth of *Carentonosaurus* cf. *mineaui*. Measures in mm.

Specimen	A	B	C	D
MAR 1981/3/5		9.53		
MAR 2004/20/7		4.81		1.77
MAR 2004/20/5		5.52		2.60
MAR 2004/20/6				
MAR 2005/34/8		8.18	0.51	
MAR 2005/34/11	3.60	6.02	0.21	2.65
MAR 2003/35/4		4.93		
MAR 2004/20/10	2.30	4.56	0.10	1.69
MAR 2006/37/4		6.21		
MAR 2006/37/3		5.85	0.22	
MAR 2006/37/2	3.95	6.21	0.46	3.25
MAR 2006/37/1		4.07		
MAR 2007/29/5		5.80		2.79
MAR 2008/29/1	3.79	6.11		2.86
MAR 2008/29/2		5.50		
MAR 2006/37/5	1.36	2.64		1.46
Average:	3	5.73	0.3	2.38

A, B, C and D are the dimensions shown in Fig. 3.

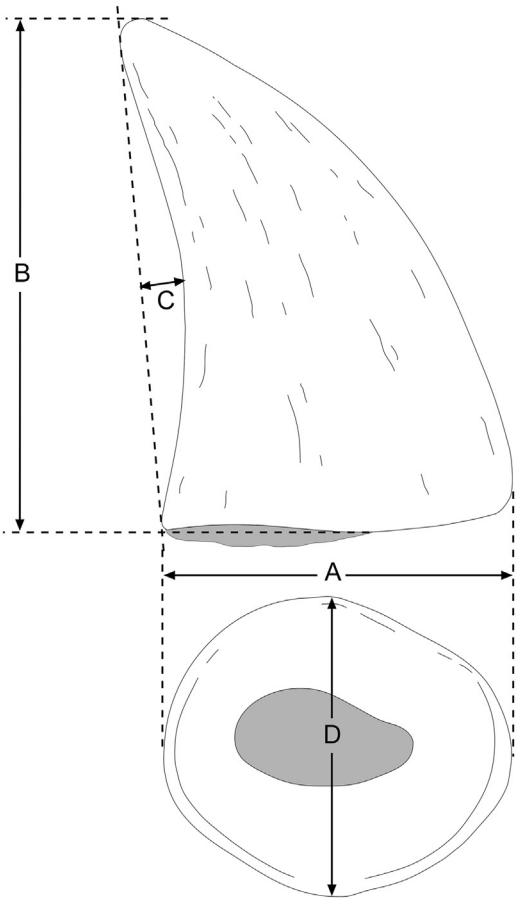


Fig. 3. Measurements of the studied teeth. **A**, antero-posterior basal length; **B**, greatest height, from crown tip to base; **C**, curvature, the greatest perpendicular distance from posterior border to the line from tooth tip to base; **D**, cross-sectional thickness. Modified after Sankey et al. (2002).

preservation was sufficient, the standard measurements used to describe vertebrae were taken from the corresponding viewpoints, as suggested by Rage and Néraudeau (2004) and Houssaye et al. (2013b) to which new measurements were added (Fig. 4, Table 2).

3. Systematic palaeontology

Class: Reptilia Linnaeus, 1758
Order: Squamata Oppel, 1811
(unranked): Pythonomorpha Cope, 1869
Genus *Carentonosaurus* Rage and Néraudeau, 2004
Carentonosaurus cf. *mineaui*
Newly referred material (see Tables 1 and 2 for details).
Description. The teeth (Figs. 5–7) have slender, curved and approximately conical crowns; moderately widened at the base of the crown, with an elliptical base and in basal view a degree of lateral compression can be seen. Generally they have two small carinae without denticles or serrations. The base normally shows a cavity (discussed below) (Fig. 2B). Along the edge of its base, specimen MAR 2004/20/5 (Fig. 6E) shows marked radial furrows reminiscent of the basal striations on the plicidentine of extant varanids (Kearney and Rieppel, 2006), although they could be artefacts of reworking.

Some teeth show no ornamentation, while others have ridges partially or entirely covering the crown. Three ridge variations are seen: those following an irregular, longitudinal path (MAR 2005/34/11, MAR 2003/35/4, MAR 2006/37/3, MAR 2008/29/1); those approximately equidistant running longitudinally in a more uniform manner (MAR 2007/29/5, MAR 2004/20/10, MAR 2006/37/4, MAR 2008/29/2, MAR 2006/37/5, MAR 2006/37/2); and those converging with the carinae (MAR 2004/20/5).

Of the 10 vertebrae examined (Figs. 8–9), one was identified as an anterior dorsal vertebra (MAR 2011/13/1), four as mid-posterior dorsal vertebrae (MAR 2005/34/9, MAR 2005/34/12, MAR 2007/29/3 and MAR 2003/35/2), and one as a posterior dorsal vertebra (MAR 2007/29/4). Four were too incomplete for them to be adequately assigned a position.

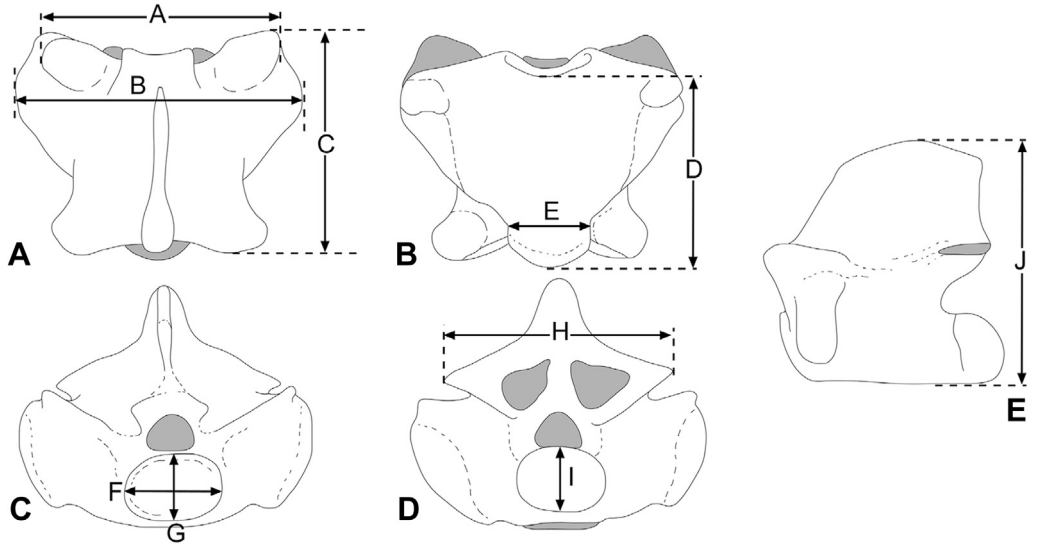


Fig. 4. Measurements made on the vertebrae. **A**, dorsal view: (A) distance between the prezygapophyseal facets, (B) distance between the paradiapophyses, and (C) length of the neural arch; **B**, ventral view: (D) length of the centrum, and (E) horizontal diameter of the condyle; **C**, cranial view: (F) width of the cotyle, and (G) height of the cotyle; **D**, caudal view: (H) distance between the postzygapophyses, and (I) height of the condyle; **E**, lateral view: (J) vertical distance between the highest preserved dorsal point of the neural spine to the line on which lowest point of the centrum falls. Modified after Rage and Néraudeau (2004).

Table 2
Measurements on vertebrae of *Carentonosaurus* cf. *mineaui*. found during the campaigns of 2003–2011. Data from bibliography: 1 = Carroll and DeBraga (1992); 2 = Polcyn et al. (1999); 3 = Lee and Scanlon (2002); 4 = Houssaye (2010); 5 = Rage and Néraudeau (2004); 6 = Nopcsa (1923). Measures in mm.

Specimen	A	B	C	D	E	F	G	H	I	J
MAR 2003/35/2	10.36[a]		12.46	10.44	4.70			8.73	3.30	11.08
MAR 2005/34/10										10.34
MAR 2005/34/9	15.54[a]	17.01	16.67	13.47	6.66	5.82[a]	3.78	12.74	3.40	13.32
MAR 2007/29/2										
MAR 2004/20/11				5.47[a]	4.95[a]	4.53[a]	1.98[a]		2.58[a]	
MAR 2004/20/9										
MAR 2005/34/12	8.72	9.87	9.60	8.14	3.86[a]	3.95	1.83	7.08	2.59	8.04
MAR 2007/29/4	11.51	14.23	12.40			5.62		9.16		10.25
MAR 2007/29/3	10.60[a]			11.25[a]	4.85		2.96[a]		2.77[a]	
MAR 2011/13/1	7.44	9.33	8.72	6.77	4.06	3.23	1.65[a]		2.10	7.93
Average:	10.69	12.61	11.97	9.26	4.85	4.63	2.44	9.43	2.79	10.16
Plesiopelvic Mosasauroidea										
[b]*Aigialosaurus bucchichi*[1]				20						
[b]*Aigialosaurus dalmaticus*[1]				19						
[b]*Carsosaurus marchesettii*[1]				28						
[b]*Haasiasaurus gittelmani*[2]				21						
[b]*Komensaurus carrolli*[1]				25						
Pythonomorpha incertae sedis										
[b]*Mesoleptos zendrinii*[3] (Vertebrae N° 8–13)		27.33		22.58						
[b]Pythonomorph indet[4].				12.4						
Carentonosaurus mineaui[5] (Holotype MNHN, IMD 21)	11.7	14.1		9.3	4.3					
Stem ophidians										
[b]*Adriosaurus*[4]				3.3–4.4						
[b]*Acteosaurus*[4]				5.3						
[b]*Eidolosaurus trauthi*[6] (Vertebrae N° 13–27)		5.0–7.0		5						
[b]*Pontosaurus lesinensis*[4]				9.7						

[a] Approximate measurement. A–J are the dimensions shown in Fig. 4.
[b] Average dorsal vertebra.

In dorsal view, the paradiapophyses project laterally beyond the prezygapophyses (much further in the most posterior vertebra). The postzygapophyses, however, do not project much laterally (Fig. 10A). The width of the anterior region of the vertebra is, therefore, greater than its posterior region, with a mediolateral constriction of the neural arch (Fig. 10A). The prezygapophyseal facets are ovoid, large and markedly inclined to the horizontal. Despite the poor preservation of the neural spine, it appears to be long, rectangular in profile and running nearly the entire length of the neural arch, almost reaching the zygosphene (which is usually poorly preserved). The neural spine has a wide posterior border (Fig. 10A). Parazygosphenal foramina are seen in MAR 2005/34/9 and MAR 2007/29/3 (Fig. 11).

In ventral view, the anterior region of the centrum is wider than its posterior region; the resulting subtriangular shape is well defined by the subcentral borders (Fig. 10B). The centrum of the most posterior vertebra is longer and narrower (Fig. 9N). All these vertebrae, except the most posterior one, show a non-pathological bone thickening known as pachyostosis. This is visible externally as a posterolateral thickening of the subcentral borders anterior to the condyle (Houssaye et al., 2008) (Fig. 10B). It is quite difficult to determine with the naked eye whether the neural arches show pachyostosis. The postzygapophyseal facets are ovoid and smaller than the prezygapophyseal facets; they are directed ventrolaterally and orientated posteriorly. The centrum is slightly transversely convex, but flat along the mid-sagittal plane. Subcentral foramina are visible on the ventral surfaces (Fig. 10B). There is no precondylar constriction. The cotyle is partially visible since it is slightly inclined in an anteroventral fashion.

In anterior view, the vertebrae are strongly depressed. The neural canal is small and subtriangular. The width of the cotyle is greater than that of the zygosphene. The latter is poorly preserved in MAR 2005/34/9 and MAR 2011/13/1; only its convex morphology can be made out. The paradiapophyses are faintly projected laterally, almost level with the prezygapophyses (Fig. 10C). Except in MAR 2011/13/1, the ventral part of the paradiapophyses is situated above the ventral edge of the cotyle. The cotyle, like the condyle, is wider than it is tall. The paracotylar foramina are clearly visible on both sides of vertebra MAR 2011/13/1 (Fig. 10C).

In posterior view, the zygantrum appears as two fossae with no articular facets (Fig. 10D); the zygantral foramina are clearly observable in some vertebrae (MAR 2005/34/12 and MAR 2003/35/2, and in the right fossa of MAR 2005/34/9 and MAR 2011/13/1).

In lateral view, the neural arch slopes anteriorly. Although the height of the neural spine is unknown, it appears to have been quite tall. Behind the zygosphene the anterior edge of the neural spine ascends rapidly with a pronounced slope directed posterodorsally at first and later more horizontally. The caudal edge is slightly to moderately inclined posteriorly (Fig. 10E). The paradiapophyses are dorsoventrally tall. In the most posterior dorsal vertebra, the paradiapophyses are dorsoventrally shorter, widened, and inclined posteriorly. The condyle is convex (a feature of procoelic vertebrae) and slightly inclined posterodorsally; the axis of the cotyle-condyle system is slightly oblique (Fig. 10E).

The epidiapophyseal ridges project posterolaterally, while the interzygapophyseal ridges are projected anterolaterally, without reaching the postzygapophyses and prezygapophyses respectively. Both are subparallel to the horizontal plane of the vertebrae and are not connected (Fig. 10E). In the most posterior dorsal vertebra (MAR 2007/29/4), the epidiapophyseal and interzygapophyseal ridges project slightly laterally, and in dorsal view describe a posterolaterally directed concavity (Fig. 9M). Lateral foramina can be seen.

4. Results

The teeth and the vertebrae show signs of irregular corrosion and/or abrasion on their surfaces. It is probably the result of both the action of plant roots growing through the sediments in very recent times (Huguet et al., 2010), and of the reworking of the fossils.

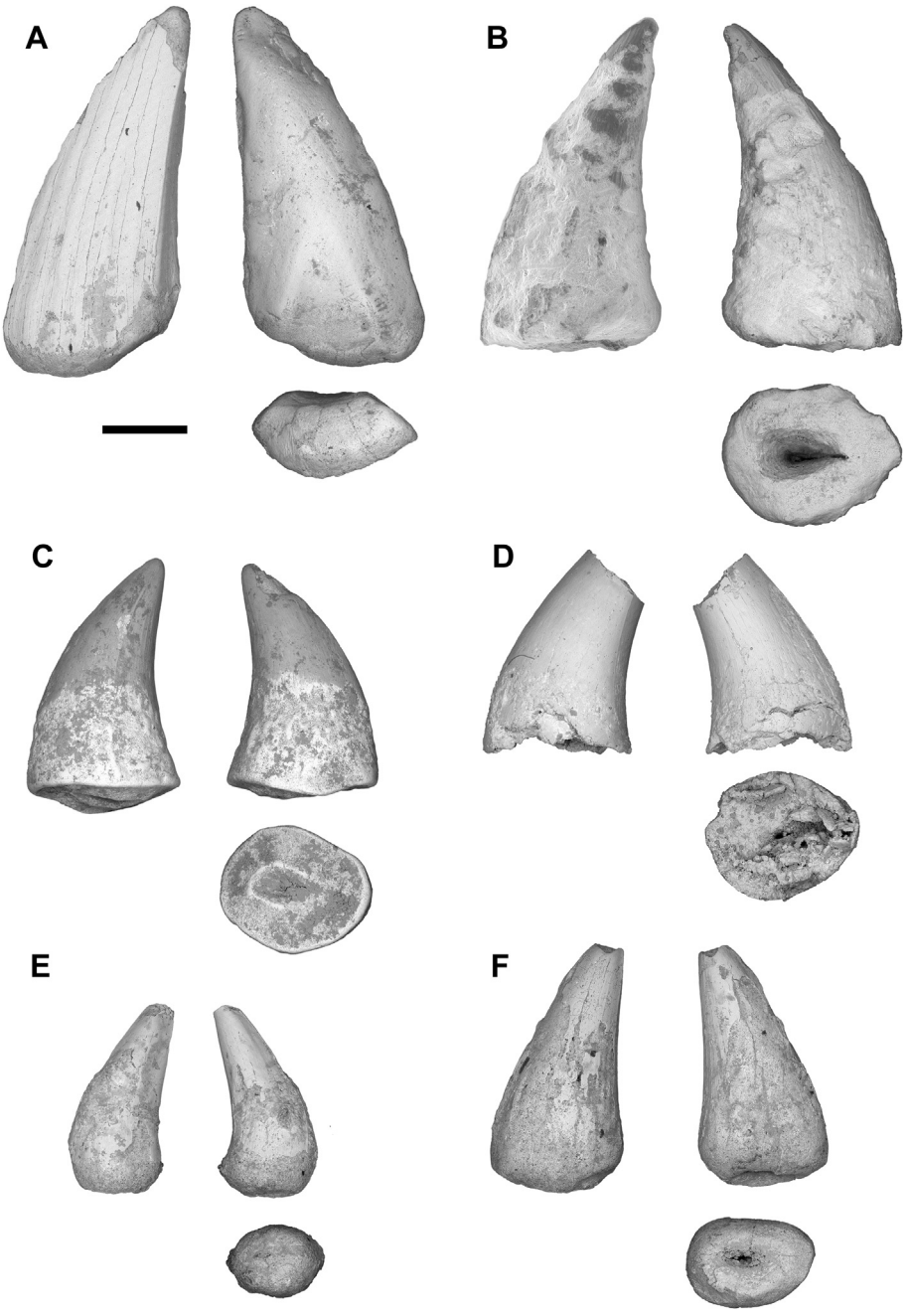


Fig. 5. Isolated teeth. **A**, MAR 1981/3/5; **B**, MAR 2005/34/8 (left view, made with LFD detector); **C**, MAR 2006/37/2; **D**, MAR 2004/20/6; **E**, MAR 2003/35/4; **F**, MAR 2006/37/4. In **A, B** (left and right = lateral views; below right = basal view); in **C**, **D**, **E**, **F** (left = labial; right = lingual view; below right = basal view [top side = lingual, bottom side = labial]). Scale bar equals 2 mm. SEM photographies: Microscopy Department/MNCN.

4.1. Teeth

The correct orientation of the teeth was established by comparison with other, extant taxa such as *Varanus salvator*. A large number of the teeth studied in this paper have an ellipsoidal basal section, the main axis coincident with the plane of maximal curvature of the crown (Fig. 2). These teeth have been taken as marginal. In marginal teeth, the concave side in lateral view is the distal side and the primary carina marks the mesial side. The tooth apex is slightly curved towards what has been interpreted as the lingual side. On this side, ornamentation is usually better preserved than on the labial side, on which a secondary carina is observed. The secondary carina shows a higher variability in its position. An equidimensional basal outline has been observed on a single specimen that together with its smaller size indicates it is probably a pterygoid tooth.

Five angular variables (see Table 3) were established according to the position of the carinae and the ornamentation of the crown enamel (Fig. 12). In most specimens the primary carina is found on the mesial part of the crown in a position that varies within 5°–30° clockwise. The secondary carina is more variable in its position, ranging from 135° to 270° clockwise.

4.1.1. Ornamentation of the enamel

In those teeth in which the ornamentation on the enamel is preserved, its appearance is highly variable. Some teeth have smooth crowns (MAR 2004/20/7 and MAR 2006/37/1) while other

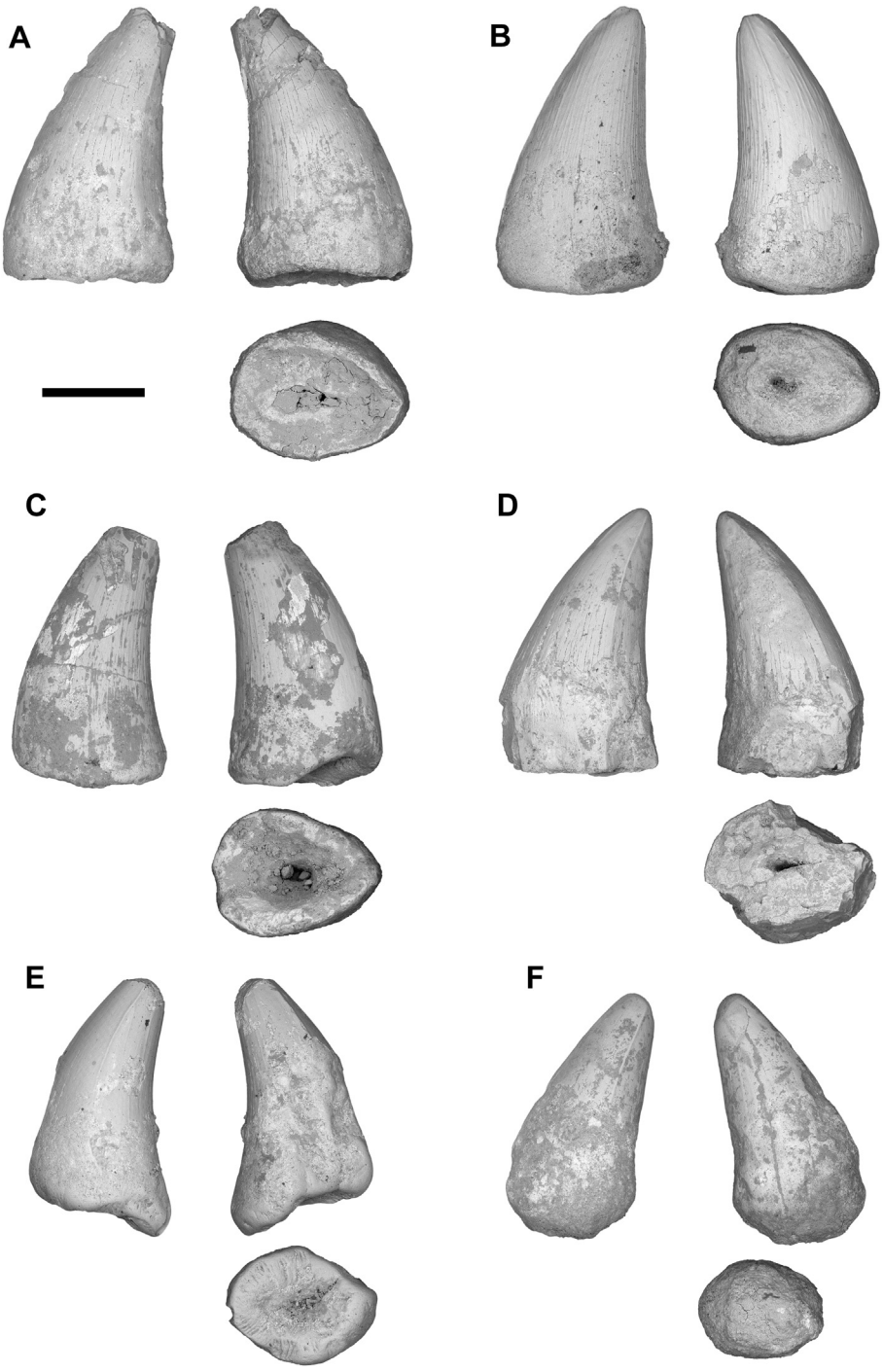


Fig. 6. Isolated teeth. **A**, MAR 2008/29/1; **B**, MAR 2005/34/11; **C**, MAR 2007/29/5; **D**, MAR 2006/37/3; **E**, MAR 2004/20/5; **F**, MAR 2008/29/2. In **A**, **D**, **E**, **F** (left = labial view; right = lingual view; lower right = basal view [top side = lingual, bottom side = labial]); in **B**, **C** (left = lingual view; right = labial view; below right = basal view [top side = labial, bottom side = lingual). Scale bar equals 2 mm. SEM photographies: Microscopy Department/MNCN.

teeth are almost entirely covered by ridges (MAR 2005/34/11). Most commonly, the ornamentation consists of ridges found on the lingual and distal surfaces of the tooth on the area between both carinae. Four morphotypes were established from these variables (Fig. 12A–D; Table 3):

Morphotype A. This is represented by several teeth in which the position of primary carina varies from 0° to 30° and the secondary carina from 190° to 270°. Ridges cover the lingual and distal surfaces between the two carinae, covering the surface of the tooth from 5° to 270° (see Table 3).

Morphotype B. This is found in several teeth in which the primary carina is situated at 0° while the secondary carina varies its position from 135° to 170°. Ridges extend over practically the whole surface of the tooth.

Morphotype C. This is represented by single tooth in which the primary carina stands at 45° and the secondary carina at 315°. Ridges cover the entire surface between the carinae.

Morphotype D. This is represented by a single tooth, which has two corners (squares in Fig. 12D) in the perimeter of the crown, marking the edge of a flat area on the opposite position to the single

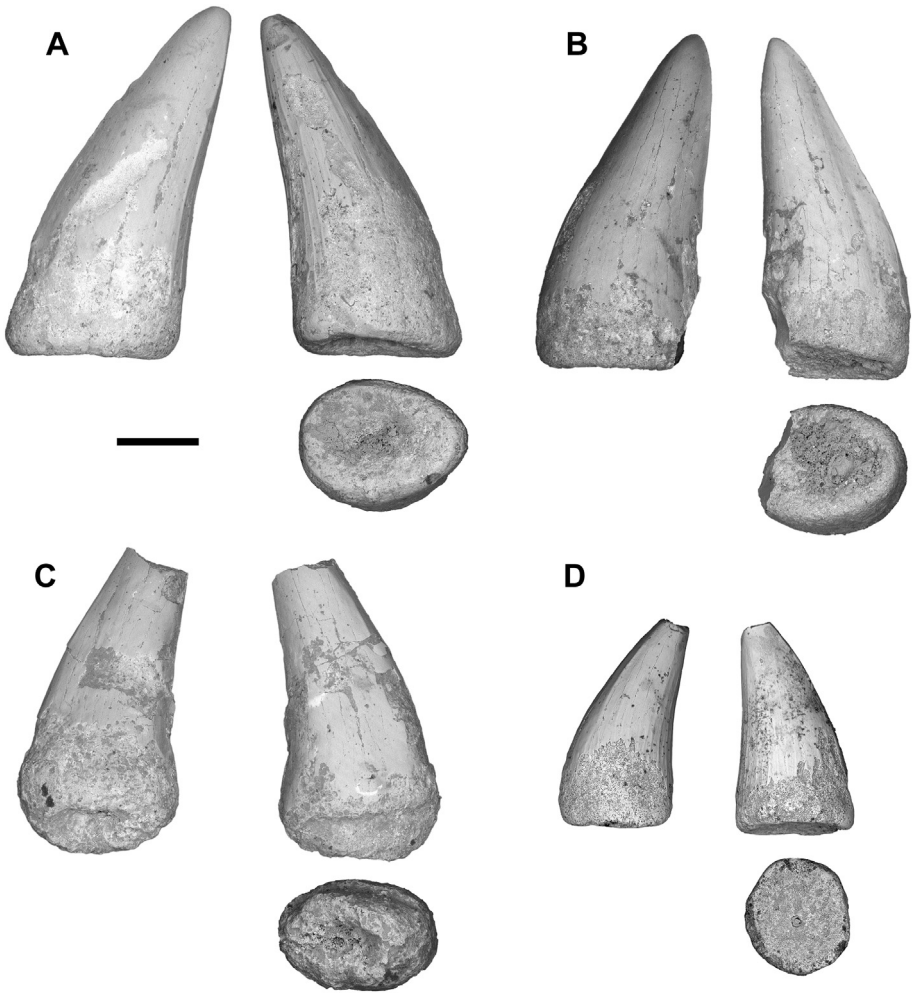


Fig. 7. Isolated teeth. **A**, MAR 2004/20/10; **B**, MAR 2004/20/7; **C**, MAR 2006/37/1; **D**, MAR 2006/37/5 (made with BSED detector). In **A**, **B** (left = labial view; right = lingual view; below right = basal view [top side = lingual, bottom side = labial]); in **C**, **D** (left and right = lateral views; below right = basal view). Scale bar equals 1 mm. SEM photographies: Microscopy Department/MNCN.

carina placed at 180°. Tooth surface lacks ornamentation. These corners are reminiscent of the carinae mentioned for Morphotype C, the flattened area might be evidence of the close contact with a neighbouring tooth.

4.1.2. Slope of the crown apex

The teeth show an inclination of the crown apices towards areas with ridges or at least where ridges are better defined (the lingual side of the tooth) (Fig. 12). The labial sides of the teeth have either fewer or no ridges. For the teeth with no ornamentation, the lingual side was deemed to be that towards which the crown apices were inclined. In lateral view, the curvature of the mesial face is always greater than that of the distal one.

Two possible crown-curve morphotypes were distinguished depending on the inclination of the posterior face of the crown (Fig. 13A–B): (A) continuous curvature (the most common); (B) double inclined, starting practically straight from the base to a point close to the middle of the crown, and then distally inclined from this point towards the apex (this morphotype was only observed in specimens MAR 2004/20/7 and MAR 2004/20/10).

4.2. Vertebrae

The differences seen in the length of the vertebrae (Table 2D) can be explained in two ways: (1) that the vertebrae belong to different animals at different points in their ontogenetic development; or (2) that there are vertebrae of different size in a single individual.

The components of lizard vertebral regions show different characteristics (Romer, 1956; Hoffstetter and Gasc, 1969; Houssaye et al., 2011): (1) cervical vertebrae: these show a hypapophysis, and paradiapophyses that extend ventrally beyond the ventral edge of the cotyle; (2) dorsal vertebrae: these have no hypapophysis but do have paradiapophyses, the ventral border of which occupies a more dorsal position the more posterior the vertebra lies; (3) sacral vertebrae: these have robust transverse processes and a centrum with no hemal arches; and (4) caudal vertebrae: with transverse processes and hemal arches (chevrons), except the first caudal vertebrae (or pygal vertebrae). The lack of hypapophyses, transverse processes and hemal arches indicates that the new vertebrae belong to the dorsal region; their paradiapophyses show that they occupy medial to posterior positions.

5. Discussion

5.1. Taxonomic determination

The morphological features of the isolated vertebrae and teeth are insufficient for a phylogenetic analysis to be performed. However, they are sufficient for the generic and specific assignment of

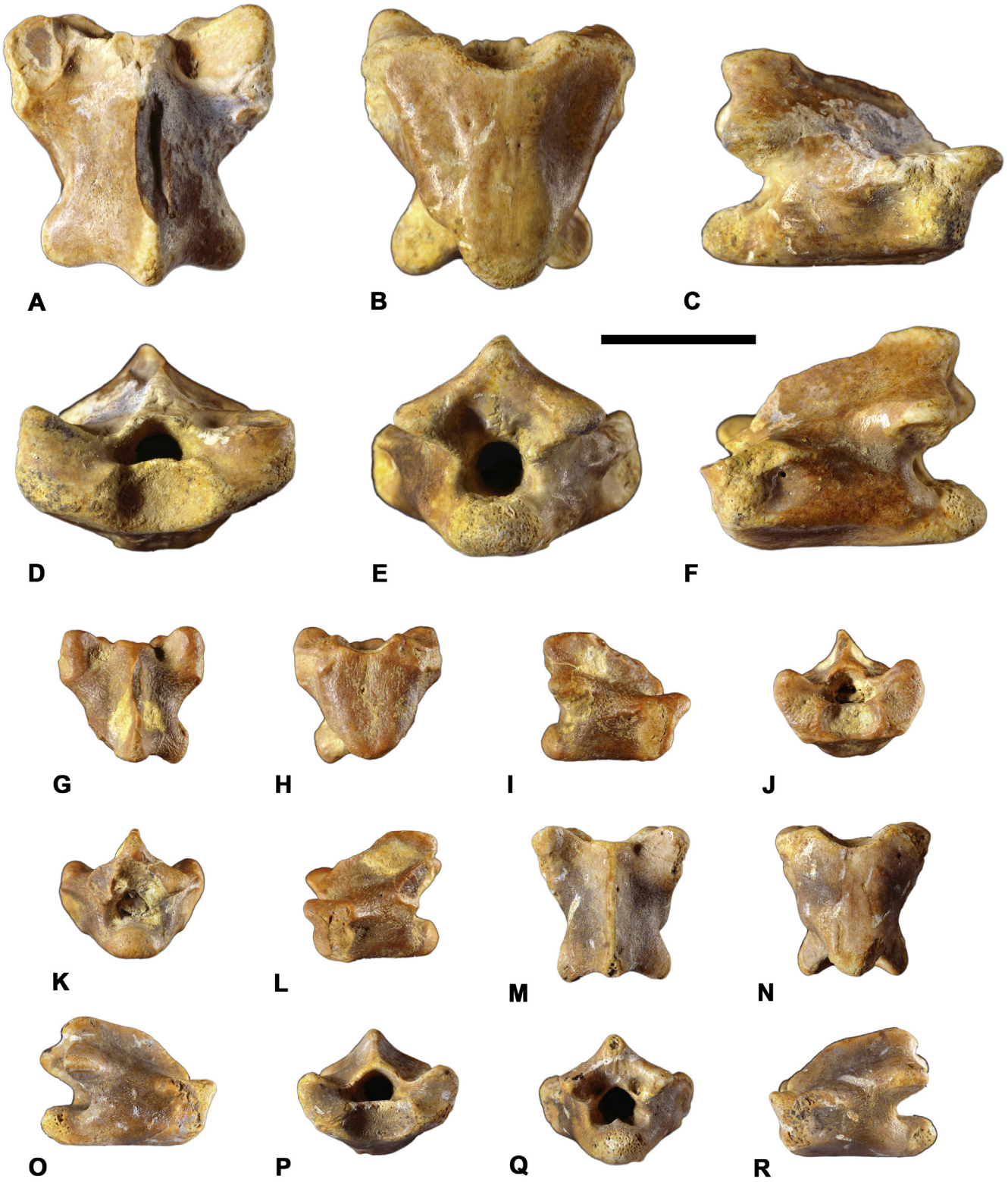


Fig. 8. Isolated mid-posterior dorsal vertebrae: **A**–**F**, MAR 2005/34/9; **G**–**L** (possible anterior dorsal), MAR 2011/13/1; **M**–**R**, MAR 2005/34/12. In **A**, **G**, **M**, dorsal views; **B**, **H**, **N**, ventral views; **D**, **J**, **P**, cranial views; **E**, **K**, **Q**, caudal views; **C**, **I**, **O**, right lateral views; **F**, **L**, **R**, left lateral views. Scale bar equals 1 cm. Photographs: Mario Torquemada (MAR).

the material. The systematics used here are those of Palci and Caldwell (2007, 2010).

The studied vertebrae are procoelic, as in other members of Squamata. Within this order, the following features suggest the studied material to be more likely that of a lizard (Romer, 1956; Hoffstetter and Gasc, 1969; Estes et al., 1988; Rage and Néraudeau, 2004; Houssaye, 2010): (1) the absence of zygantral facets; (2) the absence of prezygapophyseal processes; (3) the narrow dorsoventrally elongated paradiapophyses and non-subdivision of the joint facet; (4) the moderately concave posterior border of the neural arch (in dorsal view); (5) the absence of hypapophyses or hemal keels on the dorsal vertebrae; and (6) the

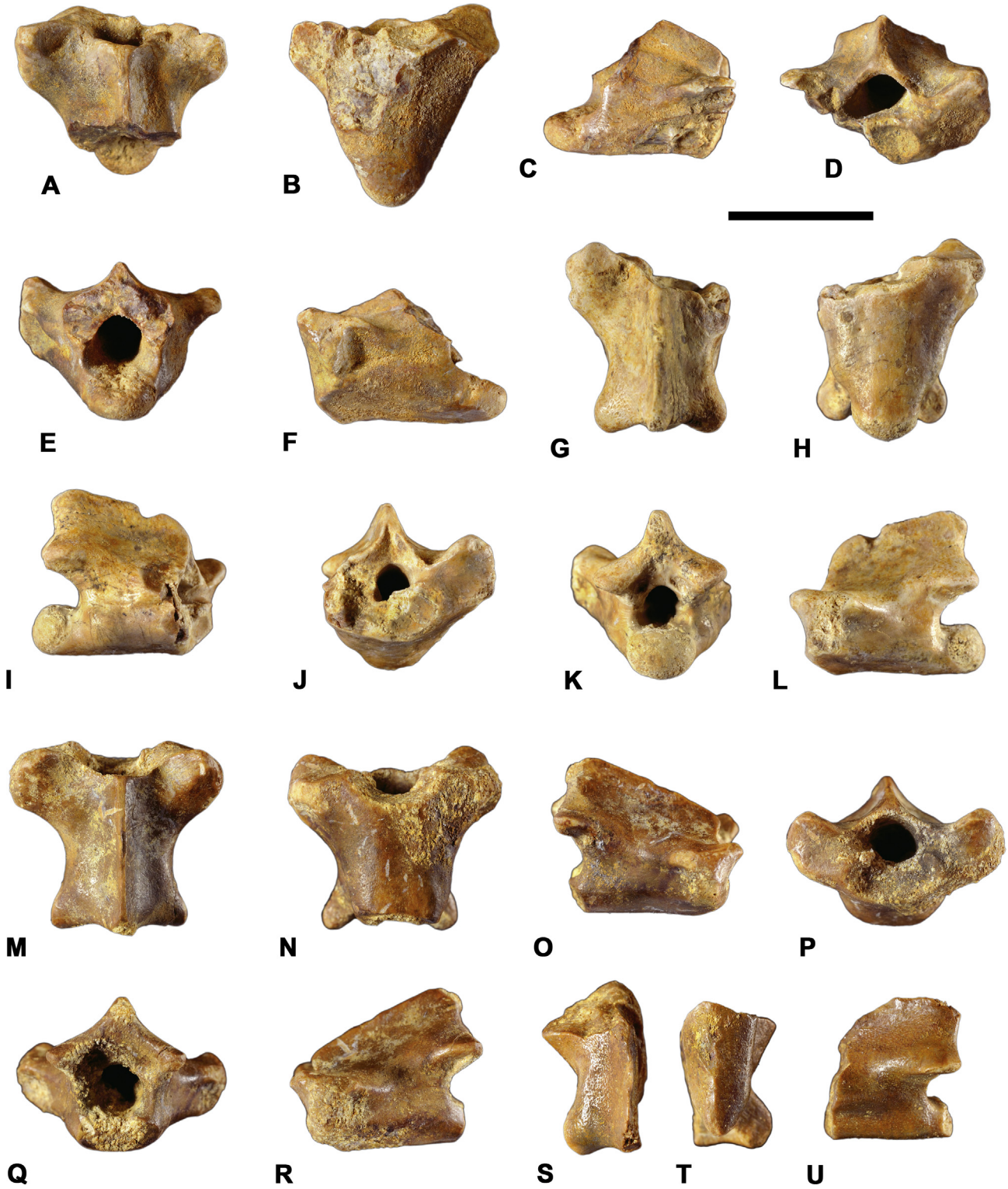


Fig. 9. **A**–**L**, isolated mid-posterior dorsal vertebrae: **A**–**F**, MAR 2007/29/3; **G**–**L**, MAR 2003/35/2. **M**–**R**, isolated posterior dorsal vertebra MAR 2007/29/4. **S**–**U**, isolated indeterminate vertebral fragment MAR 2005/34/10. In **A**, **G**, **M**, **S**, dorsal views; **B**, **H**, **N**, **T**, ventral views; **D**, **J**, **P**, cranial views; **E**, **K**, **Q**, caudal views; **C**, **I**, **O**, right lateral views; **F**, **L**, **R**, left lateral views. Scale bar equals 1 cm. Photographs: Mario Torquemada (MAR).

greater width of the prezygapophyses compared to the postzygapophyses. Note, however, that features (2), (4) and (5) are also seen in primitive snakes (Romer, 1956; Rage and Néraudeau, 2004). They differ from the pachyosteosclerotic vertebrae of *Pachyvaranus crassispondylus* Arambourg, 1952, in that they are larger (Houssaye et al., 2011: Table 1), and above all in having a zygosphene-zygantrum. This feature implies a possible affinity with Pythonomorpha (Lee, 1997; Houssaye et al., 2011), Iguanidae or Teioidea (see Gauthier et al., 2012 for the distribution of state 3 of character 468 in Squamata). However, the presence of pachyostosis and of

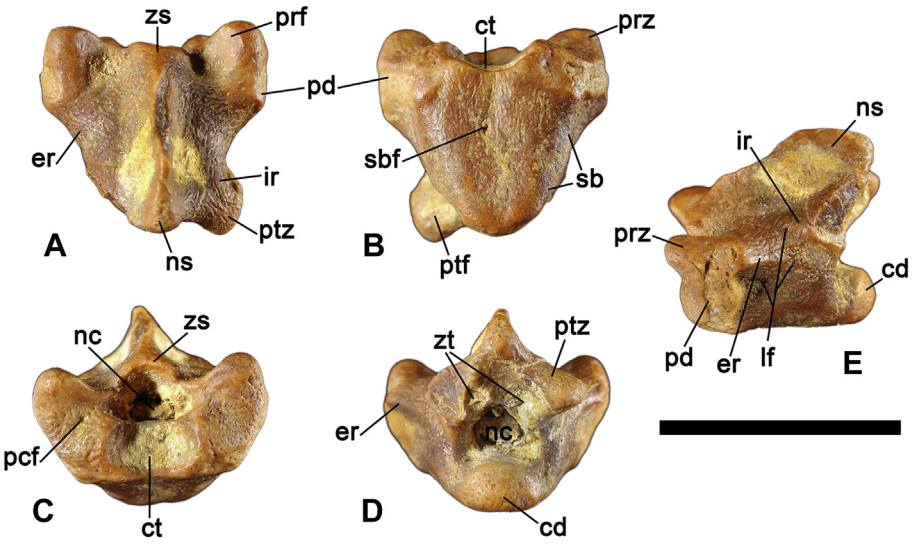


Fig. 10. Elements recognised in the vertebrae (MAR 2011/13/1). **A**, dorsal view; **B**, ventral view; **C**, cranial view; **D**, caudal view; **E**, lateral view. Scale bar equals 1 cm. Photographs: Mario Torquemada (MAR).

paracotylar foramina excludes an affinity with either teioids or iguanids (Rage and Néraudeau, 2004; Gauthier et al., 2012), leaving pythonomorphs as the only possible group.

Within Pythonomorpha (Mosasauroidea and Ophidiomorpha), the examined vertebrae differ from those of several hydropedal mosasauroids in terms of: (1) their smaller size; (2) the presence of pachyostosis; (3) the obliqueness of the cotyle-condyle axis; (4) the retention of the zygosphene-zygantrum system; and (5) the fact that the zygapophyses are not reduced nor orientated vertically in the trunk region (Russell, 1967; DeBraga and Carroll, 1993; Caldwell et al., 1995; Lee, 1997; Houssaye et al., 2008; Houssaye, 2009). They share some morphological patterns with plesiopedal mosasauroids, but the pachyostosis in the dorsal vertebrae (except for the most posterior one; see [Houssaye, 2013]) is much more intense.

The lengths of the studied vertebral centra (Table 2) are consistent with those of ophidiomorphs. However, the studied vertebrae differ from those of the stem ophidians *Aphanizocnemus libanensis* Dal Sasso and Pinna, 1997, *Coniasaurus* Owen, 1850 and *Dolichosaurus longicollis* Owen, 1850 by the presence of pachyostosis (Houssaye, 2013). *Acteosaurus tommasinii* von Meyer, 1860, *Adriosaurus* Seeley, 1881, *Eidolosaurus trauthi* Nopcsa, 1923 and *Pontosaurus* (Kornhuber, 1873) Kramberger, 1892 show a strong degree of pachyostosis (Nopcsa, 1923; Lee and Caldwell, 2000; Caldwell and Lee, 2004; Pierce and Caldwell, 2004; Caldwell, 2006; Houssaye, 2013), but the dorsal vertebrae of *Acteosaurus*, *Adriosaurus* and *Eidolosaurus* are much smaller than those of the new specimens, while those of *Pontosaurus* are slightly larger (Table 2). The new vertebrae are also different from those of *Acteosaurus*, which show a much more posterior constriction of the neural arch and smaller and subtriangular postzygapophyses (Palci and Caldwell, 2010). Finally, they also differ from those of *Eidolosaurus,* the centra of which are subrectangular in ventral view and have shallow, longitudinal furrows along the ventral surface (Nopcsa, 1923; Calligaris, 1988).

The new material was also compared to the vertebrae of four pythonomorphs incertae sedis. The studied vertebrae differ from

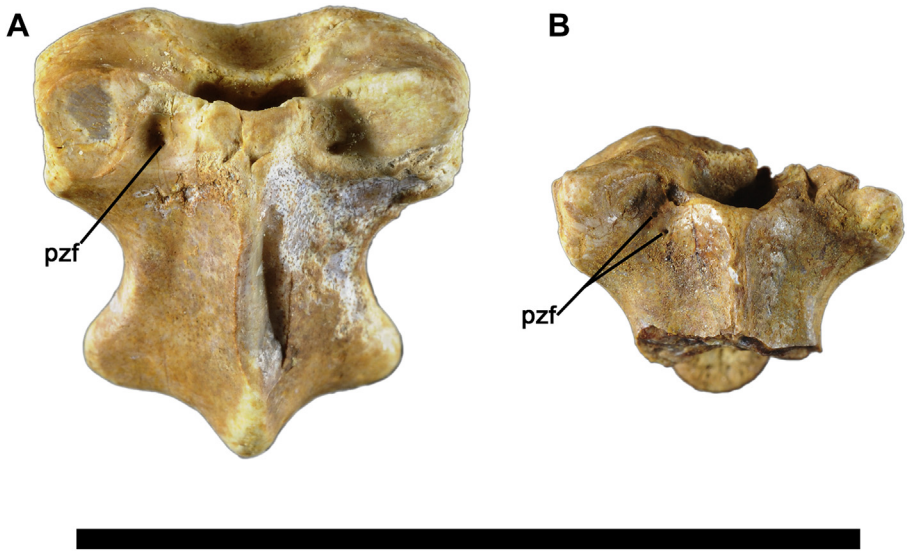


Fig. 11. Photographs in detail in order to show the presence of parazygosphenal foramina in the vertebrae. **A**, MAR 2005/34/9; **B**, MAR 2007/29/3. Scale bar equals 3 cm. Photographs: Mario Torquemada (MAR).

Table 3
Variables used to establish the different tooth morphotypes.

Specimens	Position of the primary carina	Position of the secondary carina	Beginning of the area with ridges	Amplitude of the area with ridges	Morphotypes
MAR 2004/20/7	10°	190°	smooth		A
MAR 2004/20/5	30°	270°	30°	240°	A
MAR 2004/20/6	0°–5°	225°	0°–5°	220°	A
MAR 2005/34/8	0° (Ni)		poorly preserved		?
MAR 2003/35/4	5°–10°	225°	5°–10°	220°	A
MAR 2004/20/10	0°	225°	30°	195°	A
MAR 2006/37/4	5°–10°	200°	90°	115°	A
MAR 2006/37/3	10°	240°	40°	200°	A
MAR 2006/37/2	10°–15°	270°	120°	150°	A
MAR 2008/29/1	0°	225°	135°	90°	A
MAR 2008/29/2	0°	225°	80°	145°	A
MAR 2007/29/5	0°	170°	5°	355°	B
MAR 2005/34/11	0°	135°	whole perimeter	360°	B
MAR 2006/37/5	45°	315°	45°	270°	C
MAR 2006/37/1		180°	smooth		D

All angles were measured clockwise. Ni = not included in the morphotypes in Fig. 11.

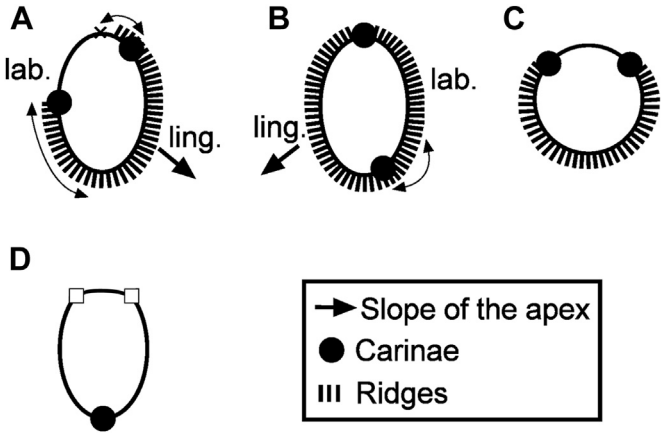


Fig. 12. Tooth morphotypes according to crown ornamentation, the slope of the apex and the position of the carinae (in apical view). The X mark the origin of the angular meaurements, which was made clockwise. Abbreviations—lab., labialmost point; ling., lingualmost point. **A**, MAR 2004/20/7, MAR 2004/20/5, MAR 2004/20/6, MAR 2003/35/4, MAR 2004/20/10, MAR 2006/37/4, MAR 2006/37/3, MAR 2006/37/2, MAR 2008/29/1, MAR 2008/29/2; **B**, MAR 2007/29/5, MAR 2005/34/11; **C**, MAR 2006/37/5; **D**, MAR 2006/37/1.

those of *Mesoleptos zendrinii* Cornalia and Chiozza, 1852, which has more localized and feebly intense pachyostosis (if present at all) (Houssaye, 2013). They also differ from those of the pythonomorph found at Lo Hueco, which show no pachyostosis at all (Houssaye et al., 2013a), and from those of the pythonomorph of Touraine, which has zygantral facets and sagittal furrows in the middle of the centrum (Houssaye, 2010). While the mean length of the vertebrae of the pythonomorph of Touraine is quite similar to that of the examined vertebrae, the mean length of *Mesoleptos* vertebrae is greater (Table 2).

The similarity of the studied vertebrae to those of the holotype of *Carentonosaurus mineaui* Rage and Néraudeau, 2004 is significant, especially in terms of the autapomorphies based on the presence of parazygosphenal foramina and the absence of zygantral facets. The degree of development of pachyostosis in the centrum is also similar (it is difficult to determine in the neural arches) (Houssaye et al., 2008), as are the measurements of these vertebrae (Table 2). Since no differences in size or morphology have been observed between our material and *Carentonosaurus mineaui*, we have decided that *Carentonosaurus* cf. *mineaui* is the best assignment to refer to the fossils here described, despite the differences in stratigraphic occurrence (Cenomanian vs Santonian).

5.2. The problem posed by the teeth

Since the vertebrae and teeth were found in the same sediment, the teeth can also be tentatively assigned to *Carentonosaurus* cf. *mineaui*. The only tooth described to date that might belong to this genus (Vullo et al., 2009: Fig. 3N–P) is similar in height (close to 5 mm) but its lack of carinae and poor state of preservation prevented its use in the identification of the present specimens.

The differing height, the three crown-curvature morphotypes and the arrangement of the carinae and ornamentation might indicate the existence of a certain heterodonty, both for the upper and lower dentition. This has been described in the mosasauroids *Russellosaurus coheni* Polcyn and Bell, 2005, and *Yaguarasaurus columbianus* Páramo, 1994, in which some teeth in the mid-maxilla and dentary bone are longer than their more anterior or posterior counterparts (Páramo-Fonseca, 2000; Polcyn and Bell, 2005). The maxillary teeth of *Yaguarasaurus* are also bigger than the premaxillary and mandibular teeth (Páramo, 1994; Páramo-Fonseca, 2000).

In *Adriosaurus suessi*, Lee and Caldwell (2000) identified an increase in the size of the teeth from the premaxilla and extreme anterior of the maxilla to the middle of the maxilla. In the mandibular and maxillary teeth of *Coniasaurus crassidens* Owen, 1850 and the maxillary teeth of *Coniasaurus gracilodens* Caldwell, 1999, heterodonty is based on an increase in the width of the crowns towards the posterior end of the jaw (Caldwell, 1999; Caldwell and Cooper, 1999; Liggett et al., 2005). However, in *C. gracilodens*, the posterior teeth are never so bulbous, expanded lingually or divided asymmetrically into two parts by labial furrows as they are in *C. crassidens* (Caldwell, 1999; Caldwell and Cooper, 1999). In both species, the apices are more rounded than in the present specimens (Caldwell, 1999; Caldwell and Cooper, 1999). In the examined reptile teeth, the rounding of the apices may be the result of processes that took place during fossilization (via exposure at the surface, short transport) and, unlike in *C. crassidens* (Caldwell and Cooper, 1999), there is no evidence of facets. The most anterior maxillary teeth of the latter would look very similar to the examined material except for a deep posterolateral furrow and crenulated carinae (Caldwell and Cooper, 1999). Thus, the dental

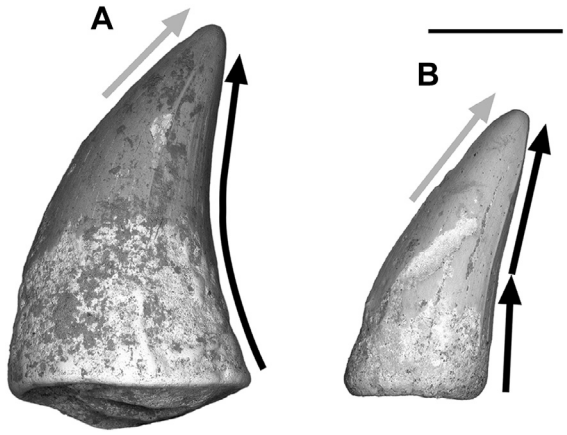


Fig. 13. Tooth morphotypes according to the crown curvature. **A**, morphotype A (MAR 2006/37/2); **B**, morphotype B (MAR 2004/20/10). Grey arrow marks inclination of the convex side; black arrow marks inclination of the concave side. Scale bar equals 2 mm. SEM photographies: Microscopy Department/ MNCN.

morphologies of these two *Coniasaurus* differ from those of the examined reptile.

The teeth of *Adriosaurus suessi*, *Aphanizocnemus*, *Pontosaurus kornhuberi* and *P. lesinensis* are pointy, laterally compressed and curved (Dal Sasso and Pinna, 1997; Lee and Caldwell, 2000; Pierce and Caldwell, 2004; Caldwell, 2006), as they are in other pythonomorphs and in the studied material. However, they have crowns ornamented with furrows and striations instead of ridges (e.g., *Pontosaurus kornhuberi*, *P. lesinensis*; Pierce and Caldwell, 2004; Caldwell, 2006). In *Coniasaurus* and *Pontosaurus*, the teeth remain inserted in pedestals or masses of ossified tissue (Caldwell, 1999; Caldwell and Cooper, 1999; Pierce and Caldwell, 2004; Caldwell, 2006), as in mosasauroids (Russell, 1967; Páramo, 1994; Polcyn et al., 1999; Bell and Polcyn, 2005; Polcyn and Bell, 2005; Caldwell, 2007; Dutchak and Caldwell, 2009). The basal cavities visible in the present material are probably due to the breakage of the cemented roots during reworking. These cavities correspond to the pulp cavity seen in mosasaurs (Kearney and Rieppel, 2006; Caldwell, 2007). The possibility exists that one of the present teeth was in an early stage of growth (Caldwell, 2007) and had not yet developed a root.

Comparing their arrangement with the teeth in the dental arch of fossil pythonomorphs (Russell, 1967; Páramo, 1994; Caldwell, 1999; Polcyn et al., 1999; Bardet et al., 2003; Polcyn and Bell, 2005; Dutchak and Caldwell, 2009) and extant Squamata (Gauthier et al., 2012), most of the present specimens can be said to be marginal teeth. Marginal teeth in *Mosasaurus hoffmanni* (Mantell, 1829) also show variations in the position of the secondary carina (Lingham-Soliar, 1995; Konishi et al., 2014), so that this carina changes its position from lateral in the anteriormost teeth to distal in the teeth occupying the most caudal positions in the tooth row. According to this pattern, the great majority of the specimens displaying morphotype A would come from intermediate positions (see Table 3), except for specimens MAR 2004/20/5 and MAR 2006/37/2, which might have occupied more anterior positions on the tooth row. Specimen MAR 2004/20/7, and possibly MAR 2006/37/4, might correspond to the most posterior teeth from this morphotype, since their secondary carinae are found on the distal side of the crown, at 190° and 200°, respectively.

Concerning morphotype B, specimen MAR 2007/29/5 probably occupied a much more posterior position than the other tooth belonging to this same morphotype, since the carina in the former is found at approximately 170° on the distal side of the crown (see Table 3). The tooth MAR 2006/37/1 (morphotype D) might be interpreted as coming from an anterior position on the tooth row because of the flattened surface observed between the two "corners" (squares in Fig. 12D), which makes it incisorlike. On the other hand, the position of its carina at 180° suggests that a distal position on the tooth row is more likely according to the criteria established by Lingham-Soliar (1995) or Konishi et al. (2014). This flattened surface could be a contact surface between contiguous teeth in an area more compressed on the tooth row. Since there is no way to infer in this fossil the direction in which the crown apex was inclined because it is broken, the position this tooth occupied remains uncertain. It might as well be a pterygoid tooth, the most probable position inferred for the small sized tooth MAR 2006/37/5, in which the basal outline shows practically no difference between its length and width (e.g., as seen in *Aigialosaurus bucchichi*, *Coniasaurus gracilodens*, *Russellosaurus*, *Tethysaurus*; Caldwell, 1999; Bardet et al., 2003; Polcyn and Bell, 2005; Dutchak and Caldwell, 2009).

The possibility of ontogenetic variability, as Konishi et al. (2014) observed in *Mosasaurus missouriensis* (Harlan, 1834), in place of individual variability also needs comment. These authors remark the presence of strong ornamentation on the marginal teeth of a small specimen of *M. missouriensis* and an ornamentation practically absent in the larger specimens of the same species. Most of the teeth here described are similar in size (see Table 1) and have ornamented crowns, including the smaller tooth. Since the largest teeth in our material (MAR 1981/3/5 and MAR 2005/34/8) are poorly preserved, the presence or absence of ornamentation on their surface cannot be observed. Thus, no conclusions can be drawn concerning whether the differences observed in the material are a consequence of variability within a single individual or if several individuals and different age stages are involved.

6. Conclusions

The morphological features of the examined dorsal vertebrae allow them to be assigned to the pythonomorph incertae sedis *Carentonosaurus* cf. *mineaui*, and are thus the first remains of this marine reptile to be found in the Cretaceous deposits of the Madrid region. The absence of any other fossil reptile material suggests that the teeth found may also belong to this taxon. If this is confirmed, they will be the first described teeth of *Carentonosaurus*.

Although all the *Carentonosaurus* remains were found reworked in Quaternary deposits inside galleries and rock shelters of karstic origin, they most likely come from the rocks forming the walls of these cavities. Accordingly, these specimens can be dated as Santonian, thus extending the biostratigraphic range of this genus, which until now was only known from the Cenomanian (Rage and Néraudeau, 2004; Bardet et al., 2008a; Vullo et al., 2011). Studies currently underway of the shark and ray teeth associated with the examined reptile remains should help to verify our conclusions concerning the age of the reworked fossils.

Among the features found in the reported vertebrae is the presence of pachyosteosclerosis. This increase in skeletal mass is observed in many Late Cretaceous marine squamates. It is considered a structural specialization developed in tetrapods that became secondarily adapted to life in water environments. It apparently plays an important role in hydrostatic buoyancy and body trim control, which is considered to help in shallow waters to remain stationary, swim slowly or walk on the bottom (Taylor, 2000; Houssaye, 2009, 2013; Housaye et al., 2011). The information provided by the Cretaceous lithofacies of the present site and previous works suggest that, during the Late Cretaceous, the region of the Sistema Central constituted a coastal margin of the Iberian Basin where the area of Pinilla del Valle was included (Gil et al., 2010). From the Albian to the Santonian-early Campanian, the Iberian microplate suffered several tectonic tilting, which influenced paleogeographical connections of the Iberian Basin with the Atlantic and the Tethys (Gil et al., 2010). Such connections could also explain the presence of this marine pythonomorph in other nearby geographical areas such as Asturias and southwestern France. The faunal richness of these waters, favored by the subtropical position of Iberia and warm currents from the Tethys (Gil et al., 2010), could have attracted other predators such as sharks, rays and malacophage fishes, whose remains are also found in the Calvero de la Higuera sites.

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