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A new aquatic pythonomorph (Reptilia, Squamata) from the Turonian (Late Cretaceous) of France

Un nouveau pythonomorphe aquatique (Reptilia, Squamata) du Turonien (Crétacé supérieur) de France

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ABSTRACT

Disarticulated vertebrae from the Turonian of France display a distinctive suite of characters and probably represent a new pythonomorph. This taxon displays some degree of vertebral pachyostosis *s.s.*, often observed in varanoid squamates from the Cenomanian-Turonian interval of the 'Mediterranean' portion of the Tethys. The discovery of this new material highlights the importance of also describing possibly new taxa based on isolated remains.

RÉSUMÉ

Des vertèbres isolées, découvertes dans le Turonien de France, montrent un assemblage de caractères remarquables et représentent probablement un nouveau pythonomorphe. Ce taxon affiche un certain degré de pachyostose *s.s.* vertébrale, souvent observée chez les squamates varanoïdes de l'intervalle Cénomanien-Turonien de la portion méditerranéenne de la Téthys. La découverte de ce nouveau matériel souligne l'importance de décrire également des taxons potentiellement nouveaux, sur la base de restes isolés.

1. Introduction

Pythonomorpha *sensu* Lee (1997) underwent important radiations in the marine realm during the Late Cretaceous (Bardet et al., 2008). Within this clade, some Mosasauroidea, several non-Ophidia Ophidiomorpha, and all the "hind-limbed" snakes (except *Najash rionegrina* Apesteguia and Zaher, 2006), display signs of pachyostosis *sensu stricto* in their vertebrae and/or ribs (Table 1). This non-pathological specialization of the osseous structure is characterized by an increase of the cortical bone deposits that leads to a modification of the bone morphology by causing an increase in bone volume (de Buffrénil and Rage, 1993). Most of the Cenomanian-Turonian pythonomorphs are based on artic-

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Table 1
List of the fossil pythonomorphs displaying vertebral pachyostosis *s.s.*
Tableau 1
Liste des pythonomorphes fossiles présentant de la pachyostose *s.s.* vertébrale.

Systematic position	Taxon	References
Mosasauroidea	*Aigialosaurus dalmaticus*	(Kramberger, 1892; Dutchak and Caldwell, 2006)
	Haasiasaurus gittelmani	(Polcyn et al., 1999; Houssaye, 2008; Houssaye et al., 2008)
Pythonomorpha *Inc. sedis*	*Carentonosaurus mineaui*	(Rage and Néraudeau, 2004)
Non Ophidia Ophidiomorpha	*Adriosaurus suessi*	(Seeley, 1881; Lee and Caldwell, 2000)
	Adriosaurus microbrachis	(Palci and Caldwell, 2007)
	Eidolosaurus trauthi	(Nopcsa, 1923)
	Kaganaias hakusanensis	(Evans et al., 2006)
	Pontosaurus lesinensis	(Kornhuber, 1873; Kramberger, 1892; Pierce and Caldwell, 2004)
	Pontosaurus kornhuberi	(Caldwell, 2006)
'Hind-limbed snakes'	*Eupodophis descouensi*	(Rage and Escuillié, 2000)
	Haasiophis terrasanctus	(Rieppel et al., 2003; Tchernov et al., 2000)
	Mesophis nopcsai	(Bolkay, 1925)
	Pachyrhachis problematicus	(Haas, 1979; Lee and Caldwell, 1998; Lee et al., 1999)
	Pachyophis woodwardi	(Nopcsa, 1923; Lee et al., 1999)
	Simoliophis (all species)	(Sauvage, 1880)

ulated cranial and/or postcranial skeletons disposed on slabs. However, in France only disarticulated vertebrae have so far been discovered (Sauvage, 1880; Bardet et al., 1998; Rage and Néraudeau, 2004). Isolated vertebrae and articulated skeletons are hardly comparable, which is probably at the origin of synonymies. The description of specimens represented only by disarticulated vertebrae might therefore engender a parataxonomy within these taxa.

Disarticulated vertebrae discovered in the Turonian of western France seemingly represent a new genus and species of Pythonomorpha of which few vertebrae display signs of pachyostosis *s.s.* However, in view of the lack of clearly distinctive characters that would be unquestionably significant, this taxon will not be named pending on possible additional material or further analyses on previously described specimens. The aim of the present study is to present a description of this new material and to discuss the relevance of the use of a parataxonomy within Pythonomorpha.

2. Locality and sedimentological context

Twenty-five disarticulated vertebrae of a pythonomorph lizard were recently discovered in a quarry south of the locality Le Paluau (Fig. 1), 6 km north-east of the town of Bourgueil (Department of Indre-et-Loire, western France) by P.-A. Gillet. The specimens were recovered from the level C3c (Alcaydé, 1975) that is rich in bryozoa and bivalve fragments. This stratigraphical unit is composed of coarse glauconitic yellow sands containing heavy metals and displaying cross-bedding stratification. It is known as the 'Falun de Continvoir' and is dated from the late Turonian (Alcaydé, 1975). It should correspond to a shallow marine environment (H. Cappetta, pers. comm. 2007).

The vertebrae display the same general morphology and are therefore considered to belong to the same taxon. They were found together by screen-washing a small volume of sediment but display size differences that would indicate that they represent different ontogenetic stages, thus suggesting the presence of multiple individuals.

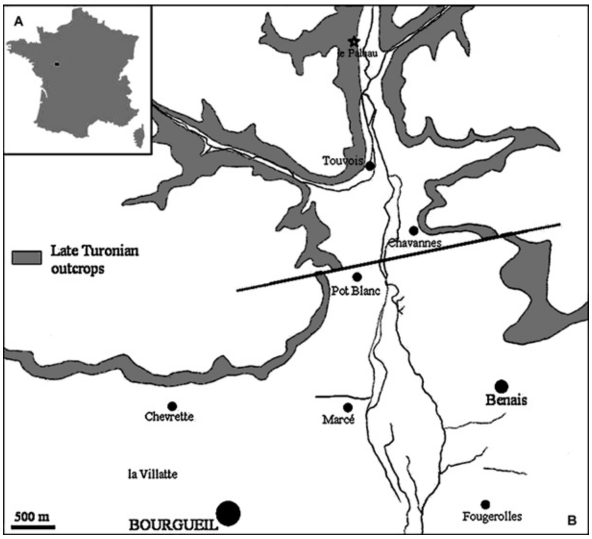

Fig. 1. Maps showing the location of the discovery site of this new material: Le Paluau in the northeast of the town of Bourgueil, Indre-et-Loire, western France. A. France; the discovery area is indicated by a black rectangle. B. Detail of the discovery area showing the distribution of the late Turonian outcrops (grey) and the discovery locality (⋆).

Fig. 1. Cartes montrant l'emplacement du site de découverte de ce nouveau matériel: Le Paluau au nord-est de la ville de Bourgueil, Indre-et-Loire, Ouest de la France. A. France ; le site de la découverte est indiqué par un rectangle noir. B. Détail du site de la découverte montrant la distribution des gisements du Turonien supérieur (gris) et la localité de la découverte (⋆).

3. Systematic paleontology

Reptilia Linnaeus, 1758.

Squamata Oppel, 1811.

Varanoidea Gray, 1827.

Pythonomorpha Cope, 1869.

Genus et species indet.

Material: MNHN MFR 5-16 isolated vertebrae. MNHN MFR 17-26 casts of isolated vertebrae (original material in the private collection of B. Guevel). MNHN MFR 6, anterior cervical; MNHN MFR 7,18,20,21,22* posterior cervicals; MNHN MFR 26,15* anterior dorsals; MNHN MFR 8,10,11,12,14,19,23*,24,25 mid-dorsals; and MNHN MFR 9,13*,16*,17 posterior dorsal vertebrae; all specimens from the same locality and horizon. *: juvenile and subadult specimens.

Description: Several common features are displayed by all vertebrae, whatever their original position along the vertebral column. All centra are procoelous.

In dorsal view, vertebrae are much wider anteriorly than posteriorly, resulting from the marked lateral projection of the paradiapophyses. Moreover, the width across the prezygapophyses is greater than that between the postzygapophyses. The narrowest part of the interzygapophyseal constriction is positioned posteriorly. The facets of the prezygapophyses are wider than those of the postzygapophyses. In dorsal vertebrae, the prezygapophyses are inclined at about 20 degrees to the horizontal and antero-laterally oriented. The paradiapophyses are enlarged by an epidiapophyseal process (*sensu* Rage and Néraudeau, 2004; see Text-Fig. 2 in Rage and Néraudeau, 2004 for illustration of morphological features described in the text) that appears as a blunt ridge. The posterior border of the neural arch forms a concavity. The anterior border of the zygosphene forms a notch and is thus concave. The neural spine is thin and extends from the anterior border of the zygosphene to the posterior edge of the neural arch.

In anterior view, vertebrae are dorso-ventrally depressed. This feature increases in intensity from cervicals to posterior dorsals. The neural canal is subtriangular in shape and narrower than the cotyle. The latter is slightly depressed and wider than the zygosphene and its dorsal border is very slender and gently convex. The roof of the zygosphene is thin.

In lateral view, the neural spine rises directly from the zygosphenal roof; as all neural spines are partially broken, it is not clear whether their anterior border is straight or curved. The articular facets of the zygosphene are ovoid, strongly inclined on the horizontal, and face ventro-laterally. The paradiapophyses are dorso-ventrally elongate. They seem to form a single articular facet.

In ventral view, the centrum, delimited by blunt subcentral ridges, is triangular. A sagittal shallow furrow begins in the middle of the centrum in dorsal vertebrae. There is no precondylar constriction.

In posterior view, the borders of the neural spine are thick. The zygantrum presents well-defined articular facets.

From one vertebra to another, the presence and the number of foramina (subcentral, paracotylar, lateral and/or zygantral) varies and do not appear to be associated with the position within the vertebral column.

Intracolumnar variation: Several characters vary significantly from one vertebra to another, indicating a great degree of intracolumnar variation. The original positions of the vertebrae along the vertebral column were estimated after comparisons with extant lizards and fossil pythonomorphs.

Cervical vertebrae

One vertebra (MNHN MFR 6; Fig. 2A–C) displays a hypapophyseal peduncle. It is relatively short and ends as an ovoid facet. The latter is antero-posteriorly elongate, concave, and faces postero-ventrally. The hypapophysis articulated on this facet and was thus posteriorly oriented. The presence of a hypapophysis allows identification of this vertebra as an anterior cervical one (Hoffstetter and Gasc, 1967; Rieppel, 1980; Caldwell, 2000). Another characteristic of this cervical vertebra consists in the important ventral projection of the paradiapophyses beyond the ventral border of the cotyle (Fig. 2A). The processes even protrude anterior to the cotyle, forming a weak notch at its base in ventral view (Fig. 2C). Some vertebrae display this projection but, instead of bearing a hypapophyseal peduncle, they present a ventral bulge at the position of the hypapophysis (Fig. 2D–G). They are interpreted as posteriormost cervicals (as in the mosasauroid *Platecarpus* Cope, 1869; Russell, 1967). Cervical vertebrae are poorly dorso-ventrally depressed and the prezygapophyses are strongly inclined on the horizontal (Fig. 2A,D) with elongated and oblique articular facets (except for MNHN MFR 7; Fig. 2E). The latter are more anteriorly oriented in anterior cervicals (Fig. 2B) and become more laterally oriented in more posterior ones. The dorsal part of the paradiapophyses is almost vertical. The cotyle and condyle are dorso-ventrally depressed and their axes are horizontal (Fig. 2A,D,G).

Anterior dorsal vertebrae

Two vertebrae possess paradiapophyses extending just above the ventral border of the cotyle and display no trace of hypapophyseal bulging in the posteroventral part of the centrum; they are therefore identified as anterior dorsal vertebrae. The dorsal part of the paradiapophyses slightly bends posteriorly. The cotyle-condyle axis is slightly oblique.

Mid-dorsal vertebrae

In mid-dorsal vertebrae (Fig. 2H–L), the ventral border of the paradiapophyses lies clearly above the level of the cotylar ventral rim, whereas their dorsal part bends posteriorly. Prezygapophyseal facets are ovoid, directed laterally and slightly anteriorly. The axis of the condyle is inclined so that it slightly faces posterodorsally whereas the cotyle faces anteroventrally.

Pachyostotic s.s. *vertebrae*

Several vertebrae display pachyostosis *s.s.* Pachyostosis *s.s.* corresponds to a hyperplasy of the periosteal tissues (de Buffrénil and Rage, 1993). As it increases the massiveness of the bone, it is morphologically observable. Two verte-

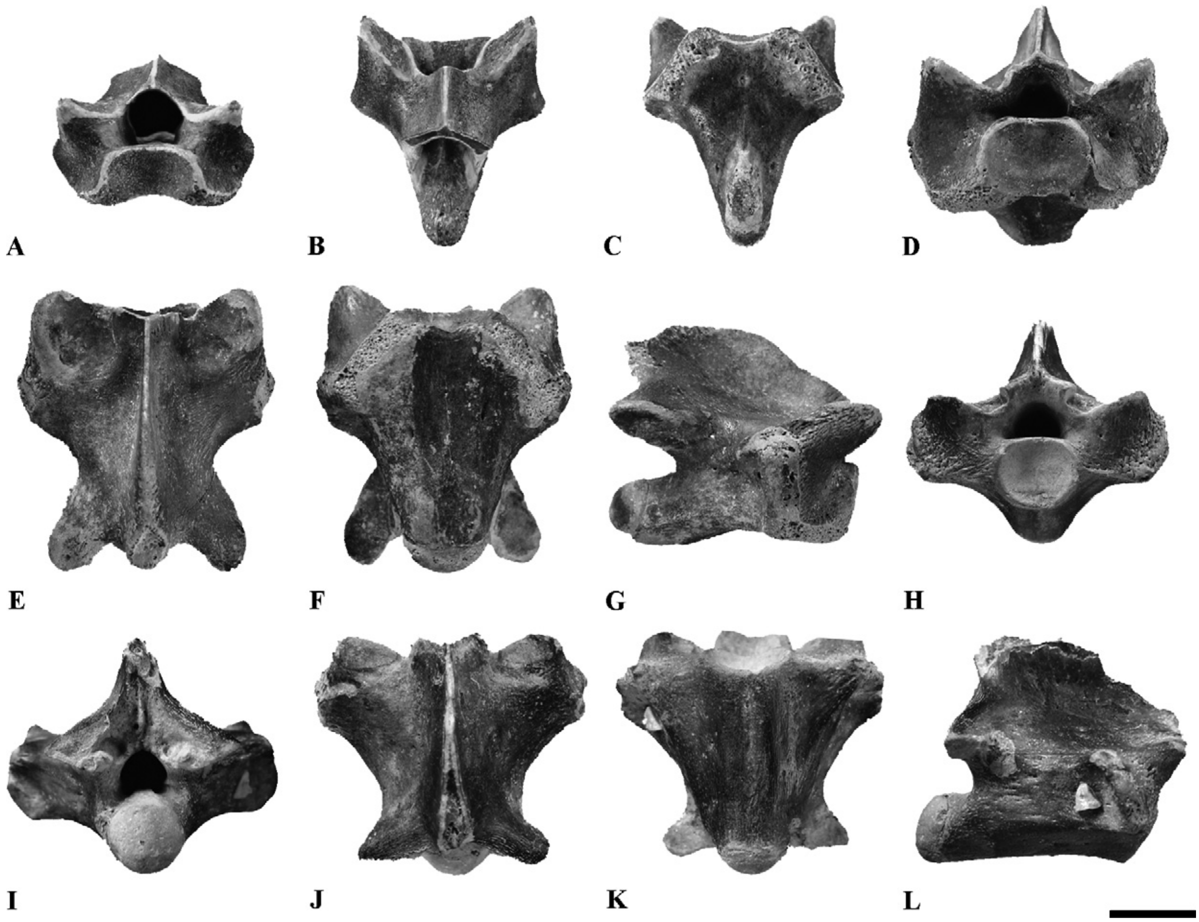

Fig. 2. Pythonomorpha *inc. sedis.* A -C. Anterior cervical vertebra MNHN MFR 6 in A, anterior, B, dorsal, and C, ventral views. D -G. Posterior cervical vertebra MNHN MFR 7 in D, anterior, E, dorsal, F, ventral, and G, right lateral views. H -L, Mid-dorsal vertebra MNHN MFR 5 in H, anterior, I, posterior, J, dorsal, K, ventral, and L, right lateral views. Scale bar represents 5 mm.

Fig. 2. Pythonomorpha *inc. sedis.* A -C. Vertèbre cervicale antérieure MNHN MFR 6 en vues A, antérieure, B, dorsale, et C, ventrale. D -G. Vertèbre cervicale postérieure MNHN MFR 7 en vues D, antérieure, E, dorsale, F, ventrale, et G, latérale droite. H -L, vertèbre dorsale moyenne MNHN MFR 5 en vues H, antérieure, I, postérieure, J, dorsale, K, ventrale, et L, latérale droite. L'échelle représente 5 mm.

brae are notably strongly pachyostotic *s.s.* and thus present a very bloated morphology (Fig. 3A–E). Six vertebrae display a thickening of the neural arch and are therefore also considered pachyostotic *s.s.* Pachyostosis *s.s.* obscures most of the morphological characters. Nevertheless, it can be determined that the prezygapophyses are weakly inclined to the horizontal, and the paradiapophyses are significantly higher than the ventral border of the centrum, and weakly inclined posteriorly. Moreover, the axis of the cotyle-condyle system is inclined.

Posterior dorsal vertebrae

Some vertebrae are extremely depressed dorso-ventrally and display strong lateral projections of the prezygapophysis-paradiapophysis complex (Fig. 3F–H). Moreover, the paradiapophyses are more posteriorly projected. The height between the base of the paradiapophysis and the prezygapophysis is, as a consequence, relatively short. The orientation of the cotyle-condyle system is only partly observable as most of the vertebrae in this grouping have a broken centrum. Nonetheless, the central articulations seem less inclined than in the more anteriorly located dorsal vertebrae.

Ontogenetic variations: Typical ontogenetic variations are observed. In addition to being smaller, vertebrae from juvenile individuals display weak ossifications of both the zygosphene-zygantrum complex and condyle, an important lateral depression of the cotyle, and a relatively wide neural canal (Scanlon et al., 2003; Rage and Néraudeau, 2004). Some vertebrae of juveniles display pachyostosis *s.s.*, which indicates that this specialization was already present at early ontogenetic stages.

4. Discussion

Remark about pachyostosis *s.s.*: Several vertebrae display pachyostosis *s.s.* Pachyostosis *s.s.* seems concentrated in the mid-dorsal portion of the vertebral column in pythonomorph lizards 'affected' by this specialization (Lee and Caldwell, 2000; Caldwell, 2006; pers. obs.). The vertebrae displaying this pattern (Fig. 3A–E) should therefore

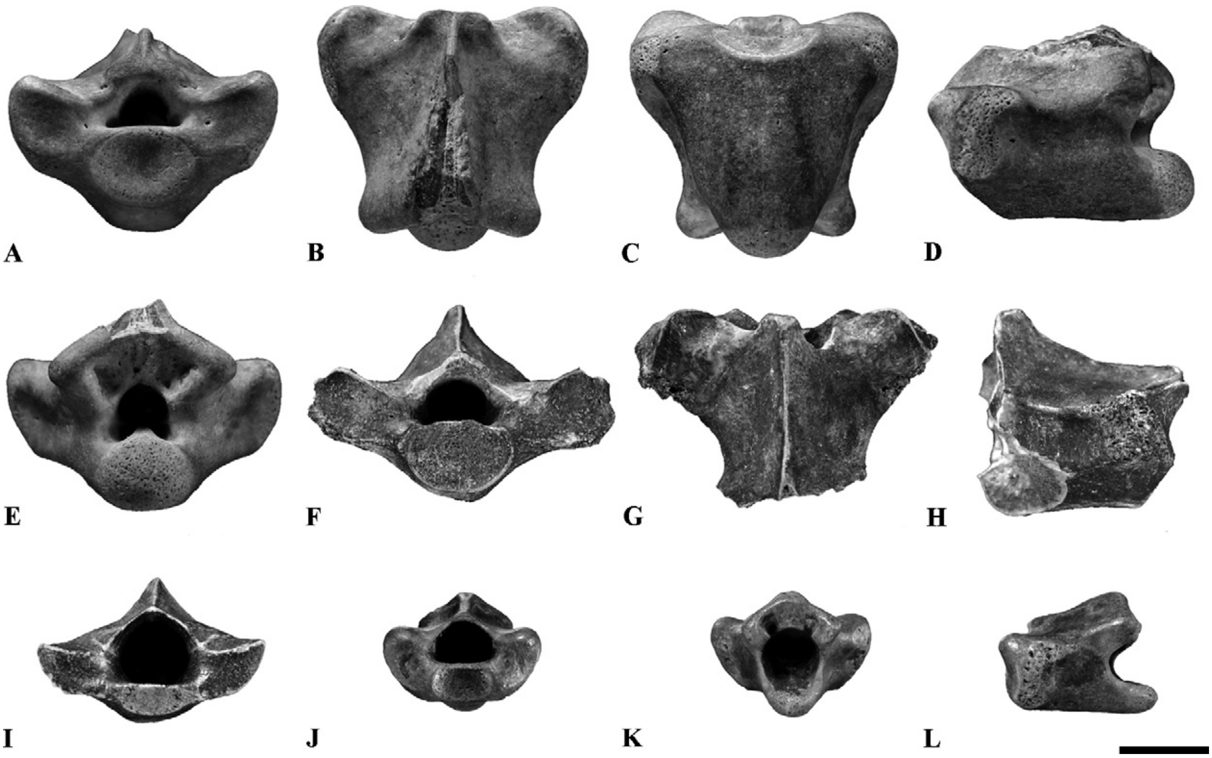

Fig. 3. Pythonomorpha *inc. sedis.* A–E. Pachyostotic *s.s.* mid-dorsal vertebra MNHN MFR 8 in A, anterior, B, dorsal, C, ventral, D, left lateral, and E, posterior views. F–H. Posterior dorsal vertebra MNHN MFR 9 in F, anterior, G, dorsal, and H, right lateral views. I. Juvenile posterior dorsal vertebra MNHN MFR 16 in anterior view. J–L. Juvenile slightly pachyostotic *s.s.* mid-dorsal vertebra MNHN MFR 15 in J, anterior, K, posterior, and L, left lateral views. Scale bar represents 5 mm.

Fig. 3. Pythonomorpha *inc. sedis.* A–E. Vertèbre dorsale moyenne pachyostotique *s.s.* MNHN MFR 8 en vues A, antérieure, B, dorsale, C, ventrale, D, latérale gauche, et E, postérieure. F–H. Vertèbre dorsale postérieure MNHN MFR 9 en vues F, antérieure, G, dorsale, et H, latérale droite. I. Vertèbre dorsale postérieure de juvénile MNHN MFR 16 en vue antérieure. J–L. Vertèbre dorsale moyenne légèrement pachyostotique *s.s.* de juvénile MNHN MFR 15 en vues J, antérieure, K, postérieure, et L, latérale gauche. L'échelle représente 5 mm.

correspond to mid-dorsals. Some other mid-dorsal vertebrae seem to present a slight thickening of the neural arch but it is not enough to consider them pachyostotic *s.s.* The determination of the relative position of non-pachyostotic *s.s.* mid-dorsals relative to the pachyostotic *s.s.* ones is difficult. Some may have been located anteriorly to the pachyostotic *s.s.* ones whereas others may have been located posteriorly to them.

Taxonomic determination: The vertebrae are procoelous, as in other squamates. The obliquity of the axis of the cotyle-condyle system is, within squamates, a derived characteristic of varanoid lizards and snakes (Varanoidea *sensu* Lee, 1997), which is consistent with the posterior position of the narrowest part of the interzygapophyseal constriction. The presence of a well developed, roofed and notched zygosphene, with articular facets directed latero-ventrally, is typical of pythonomorphs (Lee, 1997). The general morphology of the vertebrae is distinct from that observed in snakes. This is readily determinable but less obviously justifiable as some potential 'snake-like characters' are: difficult to describe unambiguously, shared by some lizards, absent in a few snakes.

Nevertheless, the combination of the following characters can be used to distinguish this taxon from snakes: the presence of a notched zygosphene, the greater width across the prezygapophyses than across the postzygapophyses, the absence of prezygapophyseal processes (Rage, pers. comm. 2007).

Moreover, the vertebrae differ from those of hydropedal mosasauroids *sensu* Bell and Polcyn (2005) by the combination of: the obliquity of the cotyle-condyle system, the absence of reduction or of vertical orientation of the zygapophyses in the dorsal region, the presence of well-developed zygosphene-zygantrum articulations all along the vertebral column (Debraga and Carroll, 1993).

This distinctive taxon differs from the plesiopedal mosasauroids *sensu* Bell and Polcyn (2005) *Aigialosaurus*, *Carsosaurus*, *Haasiasaurus*, *Komensaurus* and *Tethysaurus* in displaying some pachyostotic *s.s.* mid-dorsal vertebrae. For the same reason, it also differs from the non-Ophidia ophidiomorphs *sensu* Palci and Caldwell (2007) *Aphanizocnemus*, *Coniasaurus*, *Dolichosaurus*, *Kaganaias* and *Mesoleptos*. Within ophidiomorphs, it also differs from *Eidolosaurus* in the shape of the dorsal vertebral centra in ventral view; whereas it is rectangular in *Eidolosaurus*, it is triangular in this specimen. Moreover, it differs from *Adriosaurus* in the apparently much reduced extension of pachyostosis *s.s.* Indeed, specimens of *Adriosaurus*, which are much smaller than this one (mean dorsal vertebra length between 3.3 and 4.4 mm in the specimens of *Adriosaurus*; about 12.4 mm in this new specimen), display pachyostosis *s.s.* at least all along the dorsal region. The much more important extension of pachyostosis *s.s.* in *Adriosaurus* cannot be imputed to ontogeny as pachyostosis *s.s.* is considered increasing in intensity during ontogeny (Lee and Caldwell, 1998; Rieppel and Head, 2004).

It is very difficult to compare this material with the other pythonomorph taxa represented only by articulated specimens. Indeed, these specimens provide only incomplete information relative to the vertebral anatomy as they present only their dorsal, ventral or lateral views, while most of the diagnostic vertebral characters are on the anterior and posterior faces. Consequently, this new specimen cannot be differentiated from *Acteosaurus*, and *Pontosaurus*, which mainly differ by their size: mean dorsal vertebra length equals 5.3 mm in *Acteosaurus*, and 9.7 mm in *Pontosaurus lesinensis* (Palci, unpublished PhD thesis). The pythonomorph taxon *Carentonosaurus* is almost exclusively based on disarticulated vertebrae (plus one rib and a fragment of a pectoral girdle; Rage and Néraudeau, 2004). This new material differs from *Carentonosaurus* in having no parazygosphenal foramina (very frequent in the vertebrae of *Carentonosaurus*), and in having zygantral articular facets, which are surprisingly absent in *Carentonosaurus*.

For the same reasons as for this new taxon, *Carentonosaurus* vertebrae cannot be differentiated from those of *Adriosaurus*, *Acteosaurus* and *Pontosaurus*. Therefore, there may be synonymies between some of these taxa but it is currently impossible to identify them, so that parataxonomy is used. As the new fossil specimen differs from *Carentonosaurus*, it appears important to distinguish it. However, in order to avoid possible parataxonomy, this new specimen will remain unnamed pending on possible additional material or further analyses on previously described specimens.

As the material of this new specimen does not provide sufficient data to assign it either to Mosasauroidea or to (non-Ophidia) Ophidiomorpha, it is considered a pythonomorph *incertae sedis*.

The vertebra discovered in the Middle Turonian of Sainte-Maure, in Indre-et-Loire (western France), and described by Rage in 1989, looks very similar to the posterior cervical vertebrae of this taxon and therefore could be assigned to it. Indeed, it only differs from it in being slightly less depressed dorso-ventrally. Rage interpreted the specimen as a middle or posterior dorsal vertebra. This systematic assignment, based only on a single vertebra, is corrected thanks to the discovery of the new material described in this paper. The vertebra was assigned to the Dolichosauridae (group of pythonomorphs including some non-Ophidia Ophidiomorpha; Palci and Caldwell, 2007) and distinguished from Aigialosauridae but, at that time, the meaning of these groups and their contents were different from today (see Dutchak, 2005). The assignment of this vertebra to this possibly new pythonomorph extends the temporal range of the latter to the middle Turonian.

Interest of specimens based on isolated remains: Within pythonomorphs, diagnoses are mainly elaborated from more or less complete articulated skeletons (Lee et al., 1999; Lee and Caldwell, 2000; Rage and Escuillié, 2000). But these specimens are rare as their conservation requires particularly favourable environmental deposit conditions. On the other hand, many remains are constituted by isolated bones among which vertebrae are by far the most numerous (Caldwell, 1999; Caldwell and Cooper, 1999; Rage and Néraudeau, 2004). Unfortunately, as stated above, the latter can hardly be compared to specimens in connexion as many of the diagnostic vertebral characters are on the anterior and posterior faces and therefore not observable in articulated skeletons. However, isolated bones remain very informative. Within pythonomorphs, isolated vertebrae are sufficiently distinct from one taxon to another to be relevant for taxonomic determinations (Rage and Néraudeau, 2004). Unfortunately, this type of material is commonly not taken in consideration on the field or maintained undescribed in the collections as it is generally small and difficult to identify for scientists who are not used to pay much attention on isolated vertebrae. Because of this very feeble interest, many useful data are ignored. Isolated vertebrae are more numerous than articulated specimens and can provide data about the diversity of the taxa and be useful to understand the paleoecology, stratigraphic repartition and paleobiogeography of these organisms, even if they cannot be used in phylogeny (as characters of the axial skeleton used in phylogenetic analyses are generally very few; e.g. 32 out of 250 in Lee and Caldwell, 2000 among which only 24 can be observed on isolated vertebrae). Therefore, they cannot be ignored. That is why their taxonomic description is required. However, in order to avoid possible synonymies, they should preferably remain unnamed in some cases, like the present one. We can expect that, in the future, discoveries of associated skull remains and disarticulated vertebrae and/or the isolation of vertebrae (physical when possible or via microtomography) from articulated specimens will enable to assign some of these specimens to species based on articulated skeletons.

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