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Romain Vullo

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Une nouvelle espèce de Lapparentophis *du Crétacé moyen des Kem Kem, Maroc, et remarques sur la distribution des serpents lapparentophiidés*

Romain Vullo

Université de Rennes, CNRS, Géosciences Rennes, UMR 6118, 35000 Rennes, France

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ABSTRACT

Two isolated trunk vertebrae from the ?uppermost Albian–lower Cenomanian Kem Kem beds of Morocco are described and assigned to *Lapparentophis*, an early snake genus known from coeval deposits in Algeria. The Moroccan specimens represent a new species, *Lapparentophis ragei*, which can be distinguished from the type and only known species, *Lapparentophis defrennei*, by its smaller size, its more elongate vertebrae, the presence of parazygosphenal foramina, and paradiapophyses extending anteroventrally closer to the cotyle. The discovery of *Lapparentophis* in the Kem Kem beds adds to the relatively diverse snake assemblage previously reported from this formation and extends the geographical range of the genus. The distribution of *Lapparentophis* and lapparentophiid-grade (?lapparentophiid) snakes is discussed. This poorly known family of terrestrial snakes seems to be restricted to the latest Albian–early Cenomanian of North Africa, with the exception of *Pouitella* from the early–middle Cenomanian of France. As for many other vertebrate taxa of this period, this distribution is consistent with a dispersal event from Africa to the western part of the European archipelago.

Mots clés :
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RÉSUMÉ

Deux vertèbres dorsales provenant de l'Albien terminal–Cénomanien inférieur des Kem Kem (Maroc) sont décrites et attribuées à *Lapparentophis*, un serpent basal connu dans des dépôts équivalents en Algérie. Les spécimens marocains représentent une nouvelle espèce, *Lapparentophis ragei*, qui diffère de la seule autre espèce connue, *Lapparentophis defrennei*, par sa plus petite taille, ses vertèbres plus allongées, la présence de foramens parazygosphéniens et des paradiapophyses plus rapprochées antéroventralement du cotyle. La découverte de *Lapparentophis* dans les Kem Kem accroît la diversité de l'assemblage de serpents déjà décrit dans ces niveaux et étend la distribution géographique du genre. La distribution de *Lapparentophis* et des serpents de grade lapparentophiidés (? Lapparentophiidae) est discutée. Cette famille de serpents terrestres, qui demeure mal connue, semble être restreinte à l'Albien terminal–Cénomanien inférieur d'Afrique du Nord,

E-mail address: romain.vullo@univ-rennes1.fr

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à l'exception de *Pouitella* du Cénomanien inférieur–moyen de France. Comme pour de nombreux autres groupes de vertébrés, cette distribution est en accord avec l'existence d'une migration depuis l'Afrique vers la partie occidentale de l'archipel européen.

1. Introduction

Although primitive snakes have been reported as early as the Middle Jurassic based on a few jaw fragments from the Bathonian of England (Caldwell et al., 2015), the middle part of the Cretaceous coincides with an explosive increase in the snake fossil record worldwide (e.g., Albino et al., 2016; Apesteguía and Zaher, 2006; Caldwell and Lee, 1997; Caldwell et al., 2015; Cuny et al., 1990; Gardner and Cifelli, 1999; Hsiou et al., 2014; Klein et al., 2017; Lee et al., 1999; Rage, 1988; Rage and Escuillié, 2000; Rage and Werner, 1999; Rage et al., 2016; Tchernov et al., 2000; Xing et al., 2018). Snakes are particularly well represented in the vertebrate assemblages from the mid-Cretaceous (Albian–Cenomanian) of North Africa, with various, mostly terrestrial forms described from Morocco (Klein et al., 2017; Rage and Dutheil, 2008), Algeria (Cuny et al., 1990; Hoffstetter, 1959), Libya (Nessov et al., 1998; Rage and Cappetta, 2002), Sudan (Rage and Werner, 1999; Werner and Rage, 1994), and Egypt (Nopcsa, 1925). The genus *Lapparentophis* (and the family Lapparentophiidae) was recognised based on three isolated vertebrae found in deposits of late Albian–Cenomanian age at In Akhamil in eastern Algeria (Hoffstetter, 1959). So far, *Lapparentophis* is only known from the type locality and includes a single species, *L. defrennei*. In addition, a few vertebrae of possible lapparentophiid snakes have been described from coeval deposits in northern Algeria (Cuny et al., 1990) and Sudan (Rage and Werner, 1999; Werner and Rage, 1994). Outside Africa, the poorly known genus *Pouitella* is the only other taxon tentatively referred to Lapparentophiidae (Rage, 1988). Here I report the first occurrence of *Lapparentophis* from the rich and diverse vertebrate assemblage of the Moroccan Kem Kem beds. The material, consisting of two well-preserved and isolated vertebrae, represents a new species.

2. Geological and palaeontological settings

The two specimens come from the lower part of the Kem Kem beds cropping out at El Begâa, a productive fossil site located a few km east of Taouz (southeastern Morocco) (see Cavin et al., 2010). The lower part of the Kem Kem beds lie within the Ifezouane Formation, which is composed mainly of sandstone characterized by cross-stratified structures and channel structures filled with microconglomerates (Cavin et al., 2010). These beds are ?latest Albian to early Cenomanian in age and were deposited in fluvial and deltaic environments (Cavin et al., 2010). The Ifezouane Formation is renowned for its rich and diverse vertebrate assemblage including selachians, bony fishes, lissamphibians, turtles, squamates, pterosaurs, crocodyliforms and dinosaurs (see Cavin et al., 2010). The squamate assemblage consists mostly of snakes, including various forms such as *Simoliophis* cf. *libycus*, *Norisophis begaa*, an indeterminate madtsoiid, a possible nigerophiid and an incertae sedis snake (Klein et al., 2017; Rage and Dutheil, 2008). In addition, three lizard specimens have been reported so far from the Kem Kem Beds, corresponding to an isolated vertebra of an indeterminate form (Rage and Dutheil, 2008), a jaw fragment assigned to an acrodontan (*Jeddaherdan aleadonta*; Apesteguía et al., 2016), and a dentary of a borioteiioid (*Bicuspidon hogreli*; Vullo and Rage, 2018).

3. Systematic palaeontology

Lepidosauria Haeckel, 1856
Squamata Oppel, 1811
Ophidia Brongniart, 1800
Lapparentophiidae Hoffstetter, 1959
Lapparentophis Hoffstetter, 1959

Type species. *Lapparentophis defrennei* Hoffstetter, 1959.

Lapparentophis ragei sp. nov.

Etymology. The specific epithet is in honour of my late friend and colleague Jean-Claude Rage, who first suggested that the material studied here may belong to *Lapparentophis*, and in recognition of his innumerable and invaluable contributions to palaeoherpetology and palaeobiogeography.

Type material. MHNM.KK387 (holotype) and MHNM.KK388 (paratype), two nearly complete trunk vertebrae (Fig. 1) housed in the "Muséum d'Histoire Naturelle de Marrakech" (MHNM), Morocco.

Type locality and horizon. El Begâa locality near Taouz, southeastern Morocco; Kem Kem beds, Ifezouane Formation, ?latest Albian–early Cenomanian in age (see Cavin et al., 2010).

Diagnosis. A species of *Lapparentophis* differing from the type and only other species, *L. defrennei*, in the following features: smaller size, more elongate (as long as wide) vertebrae, presence of parazygosphenal foramina, paradiapophyses (synapophyses) extending anteroventrally closer to the cotyle.

Description. Both specimens are equally-sized, non-pachyostotic mid-trunk vertebrae that come from a similar position. The tip of the neural spine is broken on both specimens. Several features (i.e., robust general morphology, centrum moderately elongate, neural canal smaller than cotyle and condyle, prezygapophyses well developed) suggest that both vertebrae are from adults (e.g., Gardner and

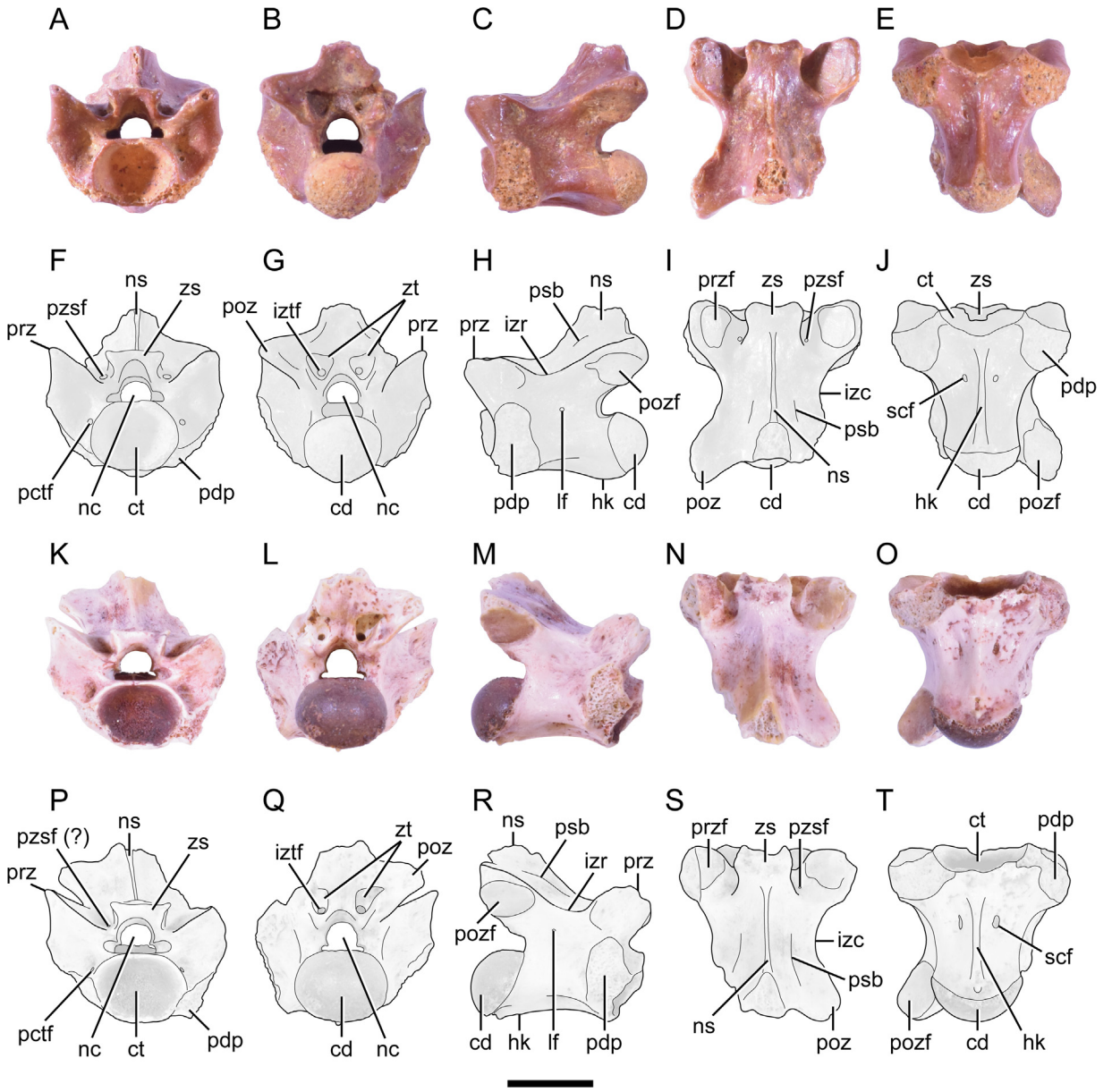

Fig. 1. Photographs and interpretative line drawings of trunk vertebrae of *Lapparentophis ragei* sp. nov., holotype MHNM.KK387 (A–J) and paratype MHNM.KK388 (K–T) in anterior (A, F, K, P), posterior (B, G, L, Q), left lateral (C, H), right lateral (M, R), dorsal (D, I, N, S), and ventral (E, J, O, T) views. Abbreviations: cd: condyle; ct: cotyle; hk: haemal keel; izc: interzygapophyseal constriction; izr: interzygapophyseal ridge; iztf: intrazygantral foramen; lf: lateral foramen; nc: neural canal; ns: neural spine; pctf: paracotylar foramen; pdp: paradiapophysis; poz: postzygapophysis; pozf: postzygapophyseal articular facet; prz: prezygapophysis; przf: prezygapophyseal articular facet; psb: parasagittal bulge; pzsf: parazygosphenal foramen; scf: subcentral foramen; zs: zygosphene; zt: zygantrum. Scale bar: 5 mm.

Fig. 1. Photographies et dessins interprétatifs des vertèbres dorsales de *Lapparentophis ragei* sp. nov., holotype MHNM.KK387 (A–J) et paratype MHNM.KK388 (K–T) en vues antérieure (A, F, K, P), postérieure (B, G, L, Q), latérale gauche (C, H), latérale droite (M, R), dorsale (D, I, N, S) et ventrale (E, J, O, T). Abréviations : cd : condyle ; ct : cotyle ; hk : carène hémale ; izc : constriction interzygapophysaire ; izr : ride interzygapophysaire ; iztf : foramen intrazygantral ; lf : foramen latéral ; nc : canal neural ; ns : épine neurale ; pctf : foramen paracotylien ; pdp : paradiapophyse ; poz : postzygapophyse ; pozf : facette articulaire postzygapophysaire ; prz : prézygapophyse ; przf : facette articulaire prézygapophysaire ; psb : renflement parasagittal ; pzsf : foramen parazygosphénien ; scf : foramen subcentral ; zs : zygosphène ; zt : zygantrum. Barre d'échelle : 5 mm.

Cifelli, 1999). The description provided here is mainly based on the holotype (Fig. 1A–J); the paratype (Fig. 1K–T) generally displays the same features, unless indicated otherwise. Measurements of both vertebral specimens are provided in Table 1.

In anterior view (Fig. 1A, F, K, P), the type vertebra shows no dorsoventral depression. The cotyle is slightly wider than high. The zygosphene is relatively small, clearly narrower than the cotyle; it shows a slightly convex dorsal margin and two lateral bulges. The roof of the zygosphene

Table 1
Measurements (in mm) for vertebrae of *Lapparentophis ragei* sp. nov.
Tableau 1
Mesures (en mm) des vertèbres de *Lapparentophis ragei* sp. nov.

	Holotype MHNM.KK387	Paratype MHNM.KK388
Maximum length of vertebra	10.7	10.2
Centrum length(from cotylar rim to posteriormost end of condyle)	8.3	8.4
Cotyle height	4.1	4.2
Cotyle width	5.5	5.6
Condyle height	3.7	3.9
Condyle width	4.3	5.1
Width across prezygapophyses	10.1	10.6
Width of interzygapophyseal constriction	5.8	6.2
Zygosphene width	3.5	3.5

is thicker than the cotylar rim. The zygosphenal facets are oblique. The neural canal is trifoliate and wider than high; it is markedly smaller than the cotyle. The lateral margins of the high prezygapophyseal buttresses are subvertical and slightly concave. The prezygapophyseal articular facets are markedly oblique, extending laterodorsally at 40° from horizontal; their medial ends are positioned at the level of the dorsoventral midpoint of the opening for the neural canal and their distal ends lie just above the level of the zygosphenal roof. Paracotylar and small parazygosphenal foramina are present in the holotype; however, parazygosphenal foramina seem to be absent (or minute?) in the paratype. The paradiapophyses extend dorsally just above the level of the dorsal rim of the cotyle and anteroventrally lie close to the cotylar rim (i.e., no paracotylar notches are present). The neural arch is relatively narrow and moderately elevated. Posteriorly, the neural spine is well separated from the roof of the neural arch.

In posterior view (Fig. 1B, G, L, Q), the condyle is slightly wider than high. The neural canal, markedly less trifoliate that in anterior view, is higher than wide; it is noticeably smaller than the condyle. A shallow median ridge is present on the floor of the neural canal. The zygantrum is slightly narrower than the condyle; it shows oblique, well-developed articular facets and a pair of large intrazygantral foramina. There are no parazygantral foramina. The neural spine is well differentiated from the postzygapophyses, i.e., the posterior margin of the neural arch between the neural spine and each postzygapophysis is markedly concave.

In lateral view (Fig. 1C, H, M, R), the vertebra appears rather elongate, with a moderately elevated neural arch. The neural spine is restricted to the posterior half of the neural arch; its oblique anterior border rises steeply. The paradiapophyses are large; they are anteroposteriorly broad and dorsoventrally tall. The junction between the diapophyseal and parapophyseal articular facets is marked by a slight constriction; the parapophyseal facet is larger than the diapophyseal facet. The interzygapophyseal ridge is salient and dorsally concave; small lateral foramina are present ventral to this ridge. The axis of the cotyle–condyle system is slightly oblique (i.e., the cotyle and the condyle are oriented slightly downward and slightly upward, respectively). The ventral margin of the centrum is concave and bears a shallow haemal keel.

In dorsal view (Fig. 1D, I, N, S), the interzygapophyseal constriction is well marked. The width across the prezygapophyses is slightly greater than across the postzygapophyses. The neural arch shows a weak parasagittal bulge on each side of the base of the neural spine. The posterior margin of the neural arch forms a broad concavity, without a distinct median notch. The zygosphene shows a gently concave anterior margin and a slight anterolateral truncation. The obovate prezygapophyseal articular facets are acute anterolaterally. There are no prezygapophyseal processes.

In ventral view (Fig. 1E, J, O, T), the centrum is subtriangular; its lateral margins are markedly concave lateroposteriorly. The shallow, ridge-like haemal keel is well marked; it originates anteriorly from near the cotylar rim and extends posteriorly to the condyle, where it forms a small tubercle. A pair of subcentral foramina is present. The paradiapophyses are large, with anteroposteriorly well-developed parapophyseal articular facets reaching the cotylar rim (i.e., no paracotylar notches are present). The postzygapophyseal articular facets are obovate, i.e., longer than wide.

4. Discussion

Lapparentophiids are rare mid-Cretaceous terrestrial snakes that are known only from a few isolated vertebrae. *Lapparentophis defrennei* (and the family Lapparentophiidae) was erected on the basis of three trunk vertebrae from the ?uppermost Albian–Cenomanian of In Akhamil, Algeria (Hoffstetter, 1959). This species is significantly larger than *Lapparentophis ragei* and is characterized by more massively built trunk vertebrae (Fig. 2). A re-examination of the type material of *Lapparentophis defrennei* has confirmed that no parazygosphenal foramina are present, unlike in *L. ragei*; in addition, prezygapophyses are more extended laterally, with more developed prezygapophyseal articular facets; the neural arch bears a well-developed bulge posterior to the prezygapophyseal articular facets; paracotylar notches are present; the zygosphene is more truncated anterolaterally; the interzygapophyseal ridge is less marked; the centrum is more robust; the axis of the cotyle–condyle system is less oblique; and the haemal keel is less marked (Fig. 2).

Three other isolated vertebrae from the mid-Cretaceous of North Africa were tentatively assigned to Lapparentophiidae (or identified as belonging to lapparentophiid-grade snakes). A single, poorly preserved vertebra was briefly described from the uppermost Albian of El Kohol, Algeria (Cuny et al., 1990). This incomplete specimen, consisting

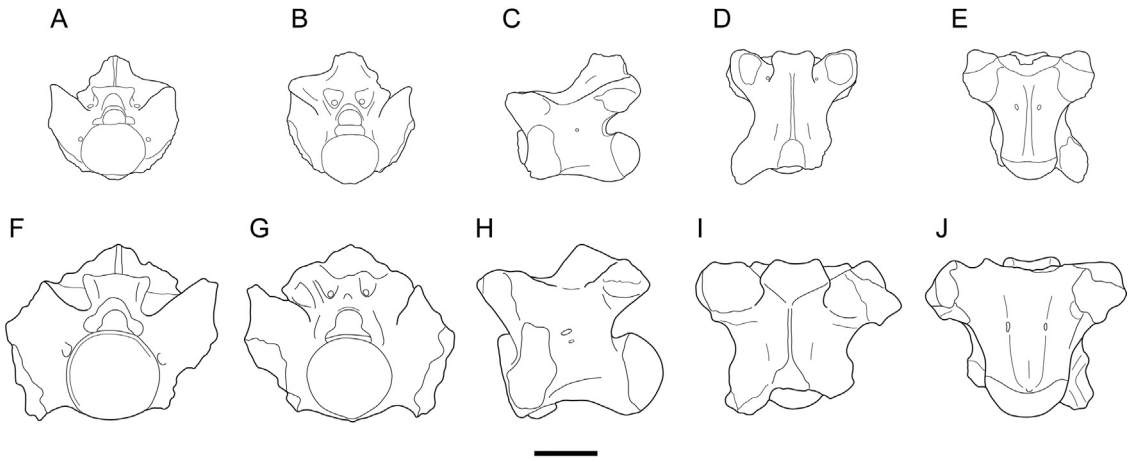

Fig. 2. Comparison of the holotype trunk vertebrae of *Lapparentophis ragei* sp. nov. (A–E) and *L. defrennei* (F–J) in anterior (A, F), posterior (B, G), left lateral (C, H), dorsal (D, I), and ventral (E, J) views. Line drawings of the vertebra of *Lapparentophis defrennei* after Hoffstetter (1959: fig. 2a). Scale bar: 5 mm.
Fig. 2. Comparaison des vertèbres dorsales (holotypes) de *Lapparentophis ragei* sp. nov. (A–E) et *L. defrennei* (F–J) en vues antérieures (A, F), postérieures (B, G), latérales gauches (C, H), dorsales (D, I), et ventrales (E, J). Dessins de la vertèbre de *Lapparentophis defrennei* d'après Hoffstetter (1959 : fig. 2a). Barre d'échelle : 5 mm.

only of the centrum, is about half the size of the Kem Kem specimens described here. In ventral view, it is similar in shape to the centrum of *Lapparentophis ragei*; however, in the El Kohol vertebra, the lateral margins of the centrum are more inflated and the haemal keel is wider and less sharp (Cuny et al., 1990: fig. 1). In addition, two isolated vertebrae representing two distinct ?Lapparentophiidae ("lapparentophiid-grade snakes A and B") were described from the Cenomanian of Wadi Abu Hashim, Sudan (Rage and Werner, 1999; Werner and Rage, 1994). The lapparentophiid-grade snake A from Wadi Abu Hashim, which may represent a new genus and species according to Rage and Werner (1999), is known from a single small trunk vertebra, wider than long. This form is similar in size to *Lapparentophis ragei*; however, it can be distinguished from the latter by its less elongate vertebrae, its higher neural arch, its wider and blunter haemal keel, and the absence of both paracotylar and parazygosphenal foramina (Rage and Werner, 1999: fig. 2). The lapparentophiid-grade snake B from Wadi Abu Hashim is only represented by a small (2.7 mm long), elongate caudal vertebra and, therefore, cannot be compared with either of the Kem Kem trunk vertebral specimens. The generally accepted Cenomanian age of the Wadi Milk Formation, which yielded a rich assemblage of snakes (including the two lapparentophiid-grade forms A and B discussed above) and other vertebrates at Wadi Abu Hashim (Rauhut, 1999; Werner, 1994), has recently been challenged based on palynological data (Eisawi, 2015) and detrital zircon geochronology (Owusu Agyemang et al., 2019). These two studies suggested a Campanian–Maastrichtian age for this formation. However, the palynological data presented by Eisawi (2015) are from the Shendi Formation, a supposed lateral equivalent of the Wadi Milk Formation, and thus do not provide a direct age estimate for the Wadi Abu Hashim vertebrate assemblage. Similarly, the six Late Cretaceous zircon grains reported by Owusu Agyemang et al. (2019) come from the Jebel el Gamman region, while no Cretaceous zircons were found in the Wadi Abu Hashim region. In addition, the five potentially age-constraining grains suggesting a maximum depositional age of 79.2 ± 2.4 Ma (middle Campanian) come from four sandstone samples that correspond to four distinct horizons distributed through the upper and lower members of the Wadi Milk Formation (Owusu Agyemang et al., 2019: figs. 3 and 7). According to Dickinson and Gehrels (2009) and Rossignol et al. (2019), such results should be considered not statistically robust. Furthermore, the occurrence of some vertebrate taxa (e.g., distobatid sharks; Vullo and Néraudeau, 2008) in the Wadi Abu Hashim assemblage is not consistent with a post-Cenomanian age. For these reasons, the Sudanese lapparentophiid-grade snakes described by Rage and Werner (1999) are still regarded here as Cenomanian in age.

Pouitella (type and only known species: *P. pervetus* Rage, 1988), from the early–middle Cenomanian of western France (holotype and only known specimen from Brézé and still undescribed material from Lussant; see Cuny et al., 1990), is a poorly known basal snake showing a general morphology and a level of evolution similar to *Lapparentophis* (Rage, 1988). This led Rage (1988) to provisionally place *Pouitella* within Lapparentophiidae. This placement is here reinforced by the presence of parazygosphenal foramina in *Lapparentophis ragei*, an unusual apomorphic feature also observed in *Pouitella pervetus* (Rage, 1988) and otherwise known among snakes only in two or three latest Cretaceous madtsoiids (Laduke et al., 2010) and in a few post-Cretaceous taxa (Head, 2005; McCartney et al., 2018; Rage, 1983, 2001, 2008; Rage et al., 2003, 2008). *Pouitella* is therefore confirmed as a member of Lapparentophiidae, thus representing the only known occurrence of this family in Laurasia. This suggests that a dispersal event from Africa to Europe may have occurred in lapparentophiid snakes, which is consistent with the presence of several other vertebrate taxa with Gondwanan affinities in the Cenomanian

of western Europe (see Csiki-Sava et al., 2015; Vullo and Rage, 2018).

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