First report on Cretaceous vertebrates from the Algerian Kem Kem beds. A new procoelous salamander from the Cenomanian, with remarks on African Caudata

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Abstract

In northwestern Africa, the Kem Kem plateau is a major source of continental Cenomanian fossils. The plateau extends across the Algerian-Moroccan border but, unlike the intensely worked Moroccan part, the Algerian side of the Kem Kem beds has received less attention. However, recent field work in Algeria resulted in the recovery of a locality that yielded a promising vertebrate assemblage. Among the fossils is a trunk vertebra belonging to a salamander, a group whose remains are extremely rare in Africa. The vertebra is procoelous and it presents combination of characters that suggest it belongs to a new taxon of unknown affinities. Although the putative new taxon is represented by a single specimen that is too poorly preserved to be formally named, the discovery is important for showing that salamanders were more diversified than expected in the Cretaceous of Africa.

Keywords

Kem Kem

Algeria

Cenomanian

Amphibia

Caudata

1. Introduction

Caudata (i.e. salamanders) are primarily Laurasian amphibians (Bailon et al., 2011; Gardner and Rage, 2016). Most extant and extinct species occur in North America, Europe and Asia, which are the territories that made up the former Laurasia. These past and present ranges suggest that salamanders originated in Laurasia (Gardner and Rage, 2016). Outside of Laurasia, living salamanders occur only in the northern parts of three former Gondwanan continents (Frost, 2017): South America, the African Plate (Africa plus the Arabian Peninsula and Middle East) and India. The colonization of India does not appear problematic, because the Indian Plate has been in contact with Eurasia for a longer time (latest Cretaceous to early Eocene? Kapur and Khosla, 2016; Verma et al., 2016) than South America and Africa, both of which have been linked to Laurasia only recently, during the Neogene. The colonization of these two southern continents by modern salamanders appears to be a Neogene phenomenon. In Africa, fossils of both living and extinct taxa are known; they are rare but range from the Middle Jurassic to the Pleistocene (Gardner and Rage, 2016, and references therein).

Here we describe the first salamander from the upper Cretaceous Kem Kem beds of Algeria. This specimen was collected from a locality known as Oued Bou Seroual.

2. African Caudata

A few fossils document the recent history of African Caudata. The earliest known of these fossils comes from the early Pleistocene of Morocco and was referred to as *Pleurodeles* cf. *waltl* (Bailon et al., 2011). *P. waltl* is a living species of European affinities, which is consistent with the Laurasian (Eurasian) origin for living salamanders inhabiting northernmost Africa. The date of dispersal of living salamanders into Africa is unknown, the only certainty is to assume that it is older than the early Pleistocene.

Aside from Pleistocene fossils, patchy older remains document a history clearly distinct from the recent colonization. They all come from the northern part of Africa and range from the middle Jurassic (Bathonian; Haddoumi et al., 2016) to the early-middle Eocene (Gardner and Rage, 2016). The relationships of these fossils are either unknown or disputed. Of particular importance are the remains from the Cenomanian-Santonian interval (Late Cretaceous) assigned to the endemic genus *Kababisha* (Evans et al., 1996) or to a closely related form, cf. *Kababisha* (Rage and Dutheil, 2008; Gardner and Rage, 2016). Their presence in the Late Cretaceous of Africa was regarded either as the result of vicariance (Rage et al., 1993) or of a dispersal from Laurasia (Evans et al., 1996). Here, we report on a new specimen from the Cenomanian of Africa, which likely represents a salamander distinct from *Kababisha*.

3. The Algerian Kem Kem and the fossiliferous locality

The Kem Kem plateau of Algeria is located in the western part of the Saharan platform at the junction between the mountain chain of Ougarta and the Moroccan Anti-Atlas (Zellouf, 1987) (Fig. 1A). The name Kem Kem has a Berber origin meaning torn or shredded (Lavocat, 1954); the name Hammada is also used, which means a vast and rocky plateau. This plateau is almost tabular with a slight inclination to the north, it is semi-desertic and excavated by a very

dense river network (Joly, 1962). It is 200 km long extending NE to SW from the village of Taouz in southeastern Morocco, to the village of Zegdou in southwestern Algeria (Joly, 1962) (Fig.1B). It is located approximately 1400 km southwest of Algiers and 350 km southwest of Bechar (Fig. 1A).

The wadis (i.e. rivers) that incise the surface of the Kem Kem as a dense network typically are not deep enough to expose the underlying marlstones and sandstones. In the Oued Bou Seroual area, however, the wadi Daoura does cut into the sandstone layer. A deposit rich in disarticulated micro-vertebrates was recovered recently in this region. It is situated in the central part of the Kem Kem plateau, 90 km northeast of Zegdou and 50 km east of the famous Gara Sbaa locality (Cenomanian, Morocco; Lavocat, 1948; Cavin et al., 2010) (Fig. 1B). The preliminary and unpublished list of vertebrates includes: Chondrichthyes (*Onchopristis dunklei*, *O. numidus*), Actinopterygii (Polypteriformes, Semionotiformes), Actinistia, Dipnoi, Amphibia (Anura), Squamata, Crocodylomorpha, Sauropoda, Theropoda, Pterosauria and, as reported here, a salamander.

4. Geological setting

The Cretaceous series of the Hammada, along the Algerian-Moroccan border was first and briefly described, on the Moroccan side, by Clariond (1933) during field work throughout the Hammada of Taouz. He described the following succession, from bottom to top: 120 m thick whitish and pinkish soft sandstone; 3 m thick calcareous sandstone with crystals of calcites and manganese spots, attributed to the Albian on the basis of the presence of the echinoderm *Dorocidaris taouzensis*; and a thick layer of limestones, which he divided into two parts, a lower part assigned to the Cenomanian, due to the presence of the ammonite *Neolobites vibrayanus*, and an upper part dated as Turonian on the basis of the presence of the gastropod *Nerinea requieni*.

Later Choubert (1948), Lavocat (1948, 1954), and Dubar (1949) divided the Kem Kem beds into three formations: a lower continental formation commonly called 'Grès infracénomanien' or 'Formation d'Ifezouane' assigned to the Albian (Choubert, 1948; Dubar, 1949; Ettachfini and Andreu, 2004); a second, lagoonal formation composed of colorful marlstones with gypsum, assigned to the lower Cenomanian and called 'Marne versicolore à gypse' (Choubert, 1948) or 'Formation d' Aoufous' (Dubar, 1949); and a third, marine formation of Cenomanian-Turonian age, comprised of white marly-limestones including flints, called 'Formation d'Akabou' (Dubar 1949).

Sereno et al. (1996) united the two lower formations of Dubar (1949), namely the Ifezouane and Aoufous formations into a single unit informally named the 'Kem Kem beds'. The Kem Kem beds were assigned to the lower Cenomanian (Sereno et al., 1996; Cavin et al., 2010) on the basis of close similarity between the vertebrate assemblage of these beds and that of Bahariya, in Egypt (Catuneanu et al., 2006).

The Kem Kem beds in Oued Bou Seroual, Algeria, are reported here for the first time and consist mainly of sandstone. The lower part includes thin reddish sandstones and yellowish coarse sandstones, overlaid by reddish coarse sandstones; all these sandstones show oblique and horizontal stratifications. The upper level comprises yellowish coarse sandstones interspersed with greenish coarse friable sandstone; this is the richest level in terms of the number of vertebrate fossils.

5. Material and methods

The poorly consolidated sandstones were screen washed using 1 mm, 800, 500 and 400 µm mesh-size sieves. Three kilograms of matrix from the Oued Bou Seroual area were processed. In spite of this small sample, the collected and treated sedimentary rocks delivered diverse vertebrate assemblage, which includes about a hundred remains identifiable at high

taxonomic level. The vertebrate micro-remains were subsequently sorted under stereomicroscope (model Leica A60). The described specimen is housed in the palaeontological collections of the Museum of the University of Sciences and Technology Houari Boumediene (MUHB), Algeria.

6. Systematic Palaeontology

Lissamphibia Haeckel, 1866

Caudata Scopoli, 1777

Family indeterminate

Material: one trunk or anteriormost caudal vertebra (MUHB 1010001).

6.1. Description

MUHB 1010001 (Fig. 2A-J) is a small, slightly distorted vertebra (maximum length from anterior rim of prezygapophysis to posterior rim of postzygapophysis = 2.1 mm). Its main characteristic is the procoelous nature of its centrum. In dorsal aspect, the vertebra is elongate and narrow. The prezygapophyses are well developed, but their shape cannot be determined precisely. The neural spine is very low. It appears as a ridge that runs along the entire length of the neural arch; posteriorly, the ridge forms a low, triangular tubercle, but anteriorly the ridge is so shallow that it is scarcely perceivable. The distal portions of the transverse processes are broken off. Only their bases are preserved; those are broad and positioned relatively posteriorly. In anterior view, the neural canal is large and the prezygapophyses are approximately level with the top of the canal. The anterior cotyle is filled by matrix. Short but strong anterior basapophyses are present on either side, lateroventral to the cotyle. The bases of the transverse processes are directed lateroventrally. They are not thick and they do not include a dorsal and a ventral elements; in other words,

they are not true rib-bearers. In lateral view, the base of the transverse process is attached obliquely (anterodorsally to posteroventrally) to the lateral wall of the neural arch. A low ridge extends between the transverse process and the ventral part of the posterior condyle, but there are no accessory ridges or flanges buttressing the process anteriorly. No vertebrarterial foramen pierces the basis of the transverse process and the vertebra lacks spinal foramina. The condyle clearly projects posteriorly; it appears as a bony continuation of the centrum and not as a calcified infilling of a posterior cotyle. On the ventral face, a shallow but sharp keel occupies the posterior two-thirds of the centrum length. There are no foramina on the ventral surface. In posterior view, the condyle shows a large notochordal pit.

6.2. Remarks

MUHB 1010001 shows a combination of characters that is encountered only in Caudata: presence of basapophyses; absence of buttresses on either side of the cotyle as a result of the high position of the prezygapophyses; marked anterior orientation of the prezygapophyses, which renders the interzygapophyseal constriction very shallow; presence of a ridge extending between the transverse process and the condyle; and condyle non-hemispheric, flat posteriorly, with a large notochordal pit. The vertebra lacks haemapophyses, therefore it comes either from the trunk or the anteriormost caudal regions. In addition, the absence of a double-processed rib-bearer (instead, seemingly replaced by a simple transverse process) suggests that the vertebra belongs to an elongate, snake-like salamander. The procoelous nature of the vertebra enables to narrow comparisons to procoelous salamanders, which are inferred to be snake-like forms.

The vertebrae of Caudata are either amphicoelous or opisthocoelous, with a very few exceptions that may be labelled procoelous. The nature of the posterior vertebral condyle, which renders the vertebrae procoelous, has been disputed (Evans et al., 1996). Rage et al.

(1993) regarded vertebrae with posterior condyles as really procoelous. However, according to Evans et al. (1996), the posterior condyle is not a true condyle; instead, it is made up by the infilling of the cotyle by calcified material and the vertebrae would be 'pseudoprocoelous'. It is true that the posterior condyle is made by additional material in large vertebrae, but in small vertebrae it appears to be a true, osseous condyle that is continuous with the centrum. The nature of the posterior condyle of these salamanders remains to be really investigated, but this issue is beyond the scope of our study.

Among Caudata, except some extant species of *Ambystoma* that are pseudoprocoelous (Evans et al., 1996), a posterior condyle occurs only in some extinct Gondwanan taxa, which are restricted to the Late Cretaceous. These fossils are *Kababisha humarensis* and *K. sudanensis* fom the Cenomanian (or perhaps Campanian-Maastrichtian; Eisawi, 2015) of Wadi Abu Hashim, Sudan (Evans et al., 1996), cf. *Kababisha* from the Cenomanian of Morocco (Rage and Dutheil, 2008) and from the Coniacian-Santonian of Niger (Rage et al., 1993; Gardner and Rage, 2016; JCR, work in progress), and *Noterpeton bolivianum* from the Maastrichtian of Bolivia, South America (Rage et al., 1993).

The vertebra from the Algerian Kem Kem beds is readily distinguished from those of other procoelous and/or pseudoprocoelous Caudata in being relatively more depressed and less narrow (Fig. 2A-J vs 2K-M), in lacking vertebrarterial foramina and the anterior accessory crests that buttress the transverse process, and in having strong anterior basapophyses. It should be noted, incidentally, that the presence or absence of vertebrarterial foramina was not addressed in the description of *Noterpeton* (Rage et al., 1993). Based on well-preserved specimens, it may be stated here that such foramina are present in *Noterpeton* as they are in other procoelous caudatans, except in the taxon from Oued Bou Seroual. The Algerian vertebra further differs from those of *K. humarensis* and *K. sudanensis* in being relatively more elongate (Fig. 2L, M). However, its elongation is somewhat reminiscent of a

vertebra referred to a juvenile individual of *Kababisha* by Evans et al. (1996: text-fig. 9G-J). Nevertheless, elongation of the specimen from Algeria is not related to a juvenile, age as demonstrated by its well-developed prezygapophyses and the moderate size of its neural canal.

In addition, the Algerian vertebra does not represent an intracolumnar variant in *Kababisha* or *Noterpeton*. In these two genera, all post-atlantal vertebrae are clearly taller and have anterior accessory crests or flanges. Consequently, we regard the salamander from Oued Bou Seroual as representing a new taxon, but defer naming it because currently only a single and incomplete vertebra is available.

7. Discussion

Assuming that Wadi Abu Hashim in Sudan is really Cenomanian in age as originally reported (Werner, 1994), and not Campanian-Maastrichtian as recently suggested (Eisawi, 2015), then the specimen from Oued Bou Seroual, cf. *Kababisha* from the Moroccan Kem Kem, and *Kababisha humarensis* and *K. sudanensis* from Sudan are the only salamanders known from the Cenomanian of Africa, and the only salamanders known from the Callovian-Turonian of Gondwana, an interval of approximately 76 million years. These Cenomanian taxa represent the earliest known procoelous or pseudoprocoelous salamanders, an assemblage that extends up to the Maastrichtian. All known Cenomanian salamanders from Gondwana have procoelous (or pseudoprocoelous) vertebrae, whereas those from the Cenomanian of Laurasia have amphicoelous vertebrae (Gardner and DeMar, 2013; Skutschas, 2013).

Unfortunately, the new salamander does not help to resolve origin of the Gondwanan procoelous salamanders, i.e. either the result of vicariance or of a dispersal from Laurasia. This will remain unresolved until new palaeontologic discoveries.

8. Conclusions

The Cretaceous Kem Kem beds, which extend through easternmost Morocco and westernmost Algeria, have produced numerous continental vertebrates of Cenomanian age in Morocco, but were not studied in Algeria. Recent field work on the Algerian side led to the recovery of a promising fossiliferous locality (Oued Bou Seroual). A small amount of fossiliferous matrix produced a fairly diverse assemblage of vertebrates. Among them is a caudate amphibian, i.e. a salamander, represented by a procoelous vertebra. In Africa, salamanders are exceptionally rare, with only rare fossils known from the Middle Jurassic-Holocene and four living species. The salamander from Oued Bou Seroual cannot be identified within Caudata because it is represented by a single vertebra that is both incomplete and enigmatic. However, it may be stated that this salamander is distinct from the rare representatives of the group known from Africa.

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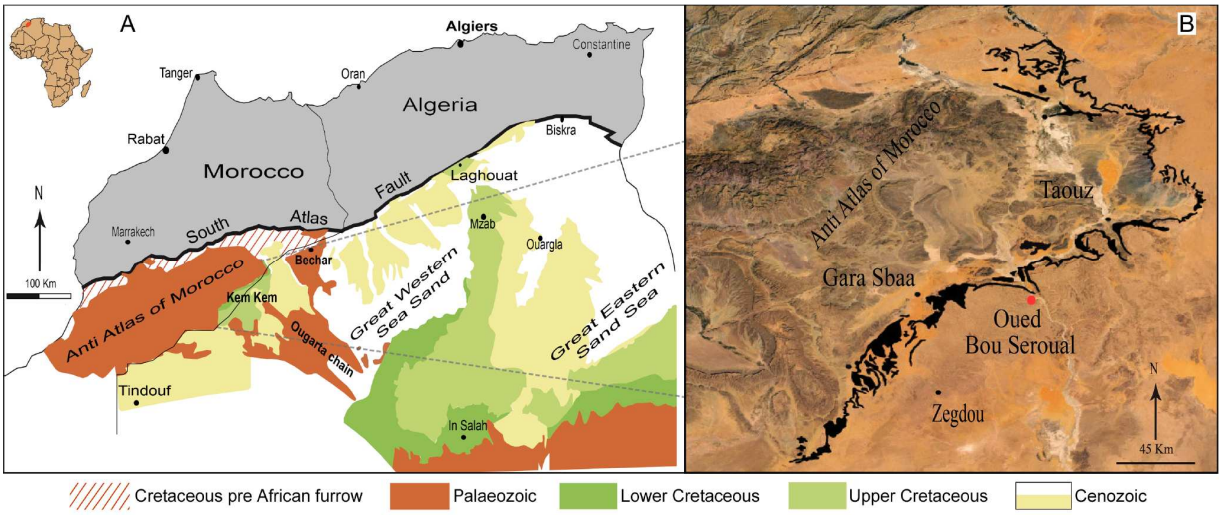
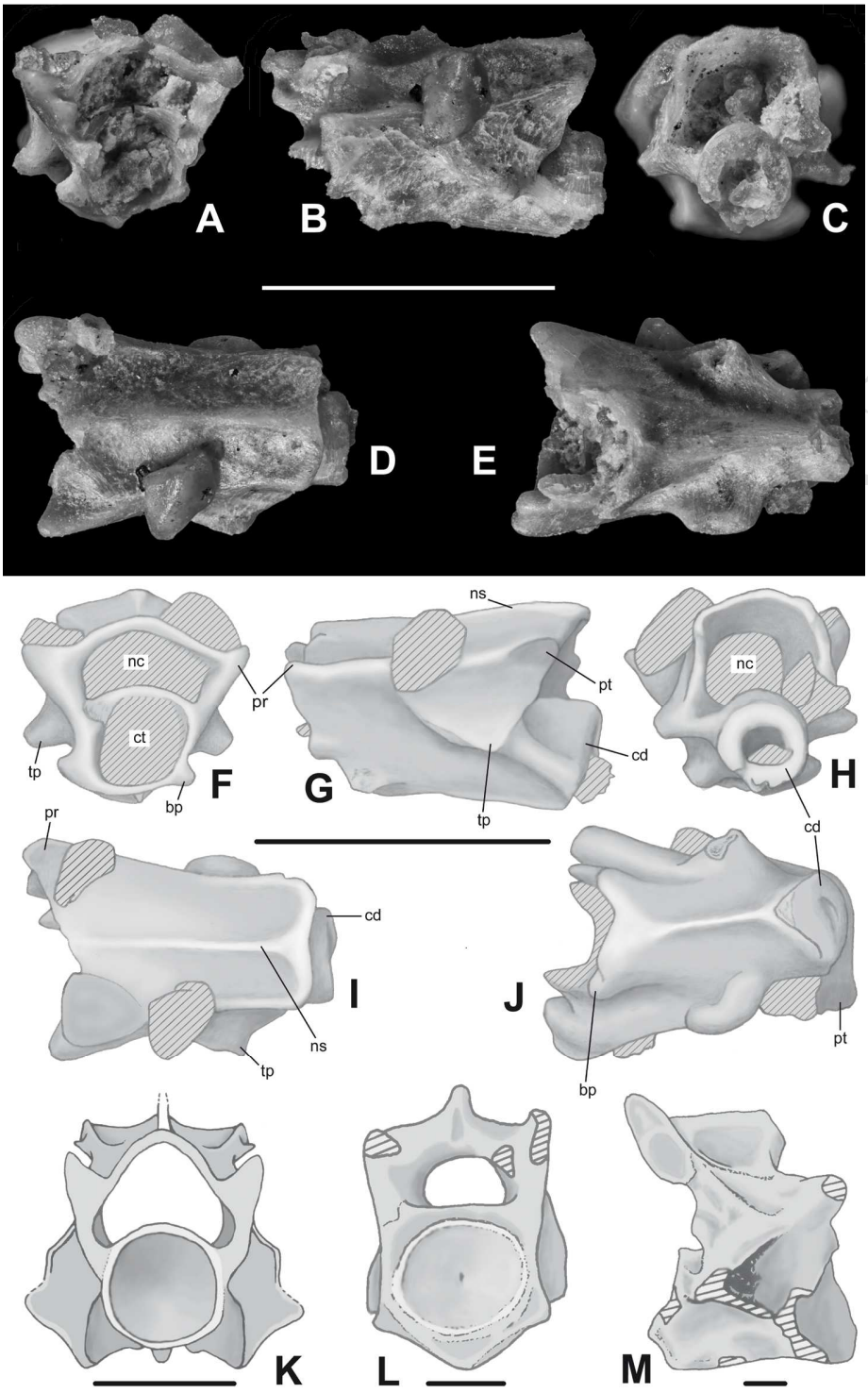
Legend of figures

Fig 1: A, geographical location of the Kem Kem plateau (grey area not mapped); modified from Benyoucef (2012). B, Satellite image of the area, with location of Oued Bou Seroual area, marked by a red dot. Image from Google Earth. [Print at 2-columns width]

Fig. 2. Upper Cretaceous salamander post-atlantal vertebrae from Gondwana. A-J: Caudata indet. from the Cenomanian of Oued Bou Seroual, Algeria, MUHB 1010001, trunk or anteriormost caudal vertebra, photographs (A-E) in anterior (A), left lateral (B), posterior (C), dorsal (D) and ventral (E) views and annotated drawings (F-J) in anterior (F), left lateral (G), posterior (H), dorsal (I) and ventral (J) views; (B, D, E, G, I, J with anterior to left). K: *Noterpeton bolivianum* (Maastrichtian, Bolivia), trunk vertebra in anterior view (from Rage et

al., 1993: fig. 2a; modified). L, M: *Kababisha humarensis* (Cenomanian or Campanian-Maastrichtian?, Sudan), anterior trunk vertebra in anterior view (L) and posterior trunk vertebra in right lateral view (M) (from Evans et al., 1996: figs 8a and 9c; modified). Abbreviations: bp, basapophysis; cd, condyle; ct, cotyle; nc, neural canal; ns, neural spine; pr, prezygapophysis; pt, postzygapophysis; tp, transverse process. Scale bars = 2 mm. [print at 1.5 column width]

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Highlight:

- The Cretaceous Kem-Kem area in northwestern Africa is a major palaeontological site.
- The Moroccan Kem Kem where intensively worked but the Algerian side was neglected.
- Recent finds in Algerian Kem Kem resulted in an exceptional Cenomanian fauna.
- The fauna includes a salamander, which is an exceptionally rare occurrence in Africa.