

Gabriel Lio^{*, **}, Federico Agnolin^{*, **}, Andrea Cau^{***} &
Simone Maganuco^{****}

Crocodyliform affinities for *Kemkemia auditorei* Cau & Maganuco, 2009 from the Late Cretaceous of Morocco

Abstract - *Kemkemia auditorei* Cau & Maganuco, 2009 was recently described as a new genus and species of theropod dinosaur on the basis on an isolated distal caudal vertebra. The holotype and only known specimen comes from Kem Kem beds (Upper Cretaceous) of Morocco. In the present paper we review the phylogenetic position of *Kemkemia* and we conclude that this taxon belongs to Crocodyliformes. It shares with crocodyliforms the presence of a concavity at the posterolateral margin of neural spines, an inflated neural canal, and reduced prezygapophyses, among other traits. This combination of characters clearly distinguishes *Kemkemia* from theropod dinosaurs. In this way, *Kemkemia* is here considered as a Crocodyliformes *incertae sedis*, and based on the absence of unique characters, the genus and species *Kemkemia auditorei* is proposed as a *nomen dubium*.

Key words: *Kemkemia*, Crocodyliformes, Cretaceous, Morocco.

Riassunto - Affinità di *Kemkemia auditorei* Cau & Maganuco, 2009, dal Cretacico superiore del Marocco, con i Crocodyliformes.

Kemkemia auditorei Cau & Maganuco, 2009 è stato descritto come nuovo genere e nuova specie di dinosauro teropode sulla base di una vertebra caudale distale isolata. L'olotipo e unico esemplare proviene dai livelli del Kem Kem (Cretacico superiore) del Marocco. Nel presente articolo si revisiona la posizione filogenetica di *Kemkemia* e si attribuisce questo taxon ai Crocodyliformes. Esso condivide con i Crocodyliformes, tra i vari caratteri, la presenza di una concavità nel margine posterolaterale della spina neurale, un canale neurale espanso e ridotte prezigapofisi. Questa combinazione di caratteri distingue chiaramente *Kemkemia* dai dinosauri teropodi.

* Laboratorio de Anatomía Comparada y Evolución de Vertebrados, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Angel Gallardo 470 (1405BDB), Buenos Aires, Argentina; e-mail: alioramus@hotmail.com

** Área de Paleontología, Fundación de Historia Natural "Félix de Azara". Departamento de Ciencias naturales y Antropología, CEBBAD - Universidad Maimónides, Hidalgo 775, 7° piso (1405BDB), Buenos Aires, Argentina; e-mail: fedeagnolin@yahoo.com.ar

*** Museo Geologico "Giovanni Capellini", Via Zamboni 63, 40126 Bologna, Italy; e-mail: cauand@gmail.com

**** Museo di Storia Naturale di Milano, Corso Venezia 55, 20121 Milano, Italy; e-mail: simonemaganuco@iol.it

Alla luce di ciò, l'esemplare viene assegnato ai Crocodyliformes *incertae sedis* e, sulla base dell'assenza di caratteri unici, sia il genere *Kemkemia* sia la specie *K. auditorei* devono essere considerati *nomen dubium*.

Parole chiave: *Kemkemia*, Crocodyliformes, Cretacico, Marocco.

Introduction

Kemkemia auditorei was described by Cau & Maganuco (2009) as an enigmatic theropod dinosaur of uncertain affinities. They based their description on a single and isolated distal caudal vertebra coming from the Upper Cretaceous (Cenomanian; Sereno *et al.*, 1996) Kem Kem beds of Morocco, Africa. Cau & Maganuco (2009), sustained the taxonomic validity of *Kemkemia* on the presence of some putative autapomorphies and a unique combination of characters. The data analyzed by Cau & Maganuco (2009) suggest the existence of a previously unknown lineage of theropods differing from other taxa in the presence of elongate distal caudals bearing transversely robust neural spines, and reduced prezygapophyses. Cau & Maganuco (2009) do not attempt to refer *Kemkemia* to a precise particular theropod subclade although they suggested probable ceratosaurian affinities for the Moroccan genus. The presence of a large amount of unusual characters in *Kemkemia* lead us to re-examine the phylogenetic position of this taxon.

A detailed comparison of *Kemkemia* with different archosaurian clades was carried out. This overview suggests that this genus may not belong to Theropoda nor Dinosauria. Instead *Kemkemia* appears to be well nested within crocodyliform archosaurs. The aim of the present paper is to exclude *Kemkemia* from Dinosauria, and sustain its crocodyliform affinities.

Abbreviations. MSNM, Museo di Storia Naturale di Milano; V, Vertebrate.

Systematic Palaeontology

Crocodyliformes Hay, 1930 (*sensu* Clark, 1986)

Kemkemia auditorei Cau & Maganuco, 2009 *nomen dubium*

Holotype. MSNM V6408, isolated distal caudal vertebra (Fig. 1).

Locality and Horizon. The specimen comes from the surroundings of Erfoud, east of the village of Taouz, Errachidia Province, Morocco, Africa (Cau & Maganuco, 2009). The holotype was collected at the Kem Kem Beds (Cenomanian, Upper Cretaceous; Sereno *et al.*, 1996).

Discussion

Referral of *Kemkemia* to Crocodyliformes

In this section we discuss the characters employed by Cau & Maganuco (2009) allowing the former referral of *Kemkemia* to Theropoda, as well as the combination of features that lead us to assign this taxon to Crocodyliformes. Cau & Maganuco (2009) based the referral of *Kemkemia* to Theropoda on the basis of the following characters:

1) Presence of spinal laminae in caudal neural arches. This trait lead Cau & Maganuco (2009) to restrict the comparisons of *Kemkemia* with saurischian dinosaurs, because the presence of spinal laminae (in the case of *Kemkemia* both pre- and post-spinal laminae were present; Cau & Maganuco, 2009) was considered a derived feature shared only by selected saurischians, such as Neotheropoda and Neosauropoda (Wilson, 1999).

However, the presence of such laminae is also observed in several crocodyliforms (e.g. *Baurusuchus*, *Akanthosuchus*, *Caiman*; O'Neill *et al.*, 1981; Nascimento & Zaher, 2010; pers. obs.; Fig. 2A) indicating that this trait is more widespread than previously thought. Its presence in crocodyliforms weakens putative saurischian affinities for *Kemkemia*.

2) Cau & Maganuco (2009) included *Kemkemia* within Neotheropoda, distinguishing it from Sauropoda on the base of a combination of features. Neotheropoda and *Kemkemia* share a relatively elongate and amphicoelous vertebral centrum, anteroposteriorly elongate neural arches, dorsoventrally narrow zygapophyses, and anteroposteriorly short neural spine that does not extends posteriorly

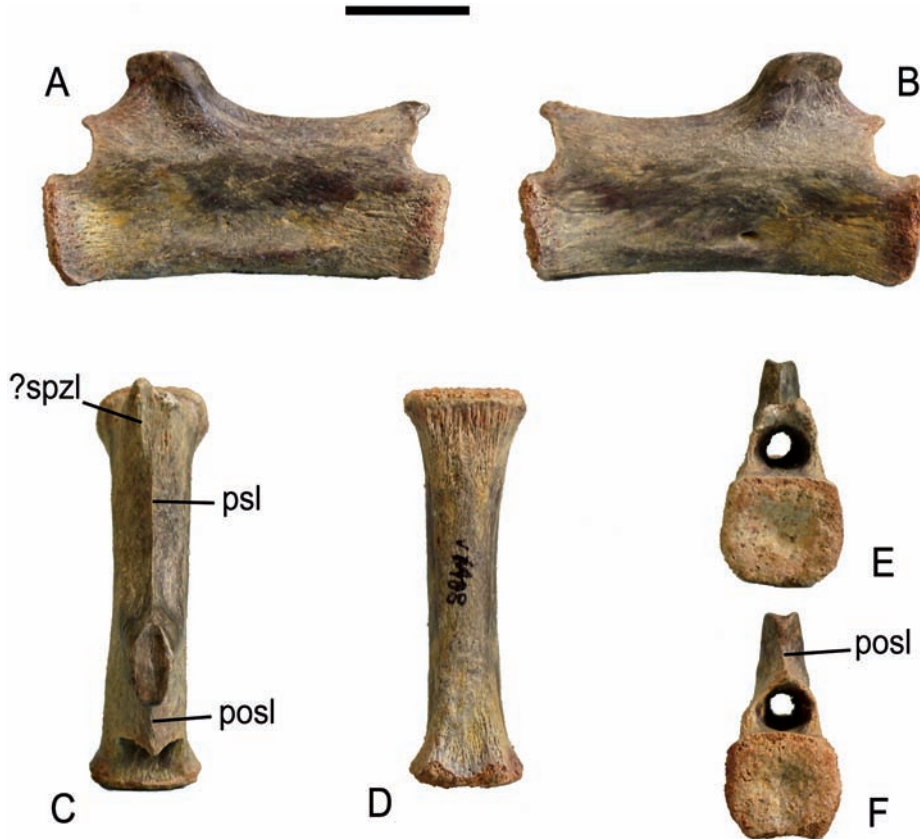


Fig. 1 - Specimen MSNM V6408. A) in right lateral view, B) left lateral view, C) dorsal view, D) ventral view, E) proximal view, F) distal view. Abbreviations: ?spzl) ?spinoprezygapophyseal lamina; psl) pre-spinal lamina; posl) postspinal lamina. Scale bar equals 2 cm. (Photos by SM).

beyond the postzygapophyses. However, we must point here that this combination of traits is widely present among other archosaurus, including ornithischian dinosaurs (e.g. *Fabrosaurus*, *Camptosaurus*; Thulborn, 1972; Galton & Powell, 1980) and crocodyliforms (e.g. *Baurusuchus*, *Pachycheilosuchus*, *Akanthosuchus*, *Caiman*, *Araripesuchus* (O'Neill *et al.*, 1981; Rogers, 2003; Turner, 2006; Nascimento & Zaher, 2010; pers. obs.; Fig. 2B-C). In this way, although the combination of characters enumerated above allow us to differentiate *Kemkemia* from sauropods, it may not be useful to distinguish the vertebra from ornithischians or crocodyliforms.

3) Cau & Maganuco (2009) indicated other characters that may prove to be useful to differentiate *Kemkemia* from Sauropod dinosaurs. These include the presence of a very large neural canal, and the persistence of chevron facets and pre- and post-spinal laminae in distalmost caudals. However, as will be discussed below, all these features are clearly seen in crocodyliforms, including most crocodylians, as exemplified by *Caiman*.

4) Cau & Maganuco (2009) also pointed out a peculiarity of *Kemkemia* that distinguishes it from all known theropods. Caudal vertebrae in Theropoda, distal to the transition point, show very prominent and elongate prezygapophyses. These zygapophyses are reduced only in the distal-most vertebrae, where the neural spine is completely absent. On the contrary, in *Kemkemia* the neural spine is short and low but robust, whereas the zygapophyses are highly reduced. The combination of both characters was considered by Cau & Maganuco (2009) as unique to *Kemkemia*.

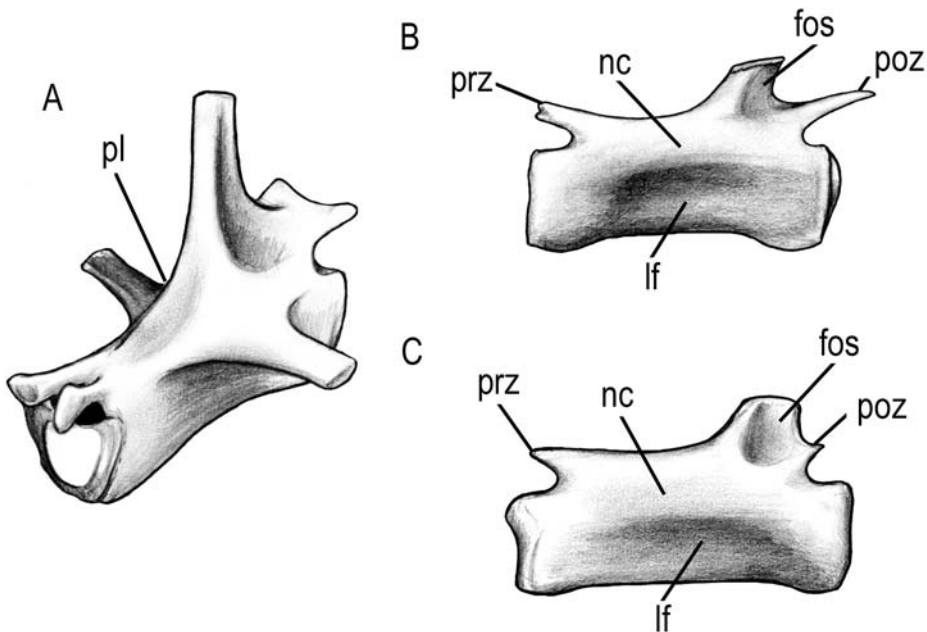


Fig. 2 - A) Anterodorsal view of the 13th caudal vertebra of the living crocodylian *Caiman latirostris*. B) Left lateral view of the 25th caudal vertebra of *Caiman latirostris*. C) Left lateral view of distal caudal vertebra of *Kemkemia auditoi* (MSNM V6408, Holotype). Abbreviations: fos) posterior fossa of the neural arch; lf) Lateral fossa; nc) neural canal; pl) prepsinal lamina; poz) postzygapophysis; prz) prezygapophysis. Scale bar: 1 cm.

However, the condition mentioned above is widely present in crocodyliform caudals, such as those of *Baurusuchus*, *Pachycheilosuchus*, *Protosuchus* and *Caiman* (Nascimento & Zaher, 2010; Rogers, 2003; Colbert & Mook, 1951; pers. obs.).

Cau & Maganuco (2009) proposed a set of autapomorphies that distinguishes *Kemkemia* from remaining theropods. However, the features cited by these authors are present in crocodyliform archosaurs and may serve to nest *Kemkemia* within this archosaur clade. Such characters are discussed below:

1) Inflated neural canal, broader than the width of the centrum at mid-length (Fig. 2B-C). In *Kemkemia* the neural arch is anteroposteriorly elongate, occupying approximately 90% of total centrum length. The neural canal was considered by Cau & Maganuco (2009) as inflated in *Kemkemia*, and described it as very large and rounded, showing a transverse diameter almost 50% of the diameter of the anterior articular surface of the centrum (Cau & Maganuco, 2009). Moreover, due to this transverse inflation, the neural canal is visible for almost all its length when the vertebra is viewed ventrally. This set of characters was considered as autapomorphic by Cau & Maganuco (2009). Nevertheless, the peculiar condition of the neural canal is not unique to *Kemkemia*, being widely present in distal caudal vertebrae of living and fossil crocodyliforms (e.g. *Caiman*; *Uruguaysuchus* Rusconi, 1933). In *Caiman*, as also occurs in *Kemkemia*, the lateral walls of the neural canal are very convex and ventrally delimited by a longitudinal concavity that is apparent in the lateral view of the vertebral centrum. This morphology can also be observed in *Baurusuchus* (Nascimento & Zaher, 2010), *Araripesuchus* (Turner, 2006), and *Simosuchus* (Georgi & Krause, 2010), suggesting that it may be a feature diagnostic of crocodyliforms.

2) Strongly reduced finger-like prezygapophyses lacking articular facets and failing to reach the level of the articular end of the centrum (Fig. 2B-C). In most Theropoda the prezygapophyses of distal caudals are very elongate representing at least 1/4 of total vertebral length, a condition synapomorphic of that clade (Rauhut, 2003). On the contrary, in *Kemkemia* the prezygapophyses are strongly reduced and finger-like, a trait that clearly departs from this general pattern (Cau & Maganuco, 2009). This putative *Kemkemia* autapomorphy is already present in several crocodyliforms (e.g. *Protosuchus*, *Baurusuchus*, *Simosuchus*, *Caiman*; Colbert & Mook, 1951; Georgi & Krause, 2010; Nascimento & Zaher, 2010). Moreover, Cau & Maganuco (2009), indicate that contrasting with all theropods, the prezygapophyses of *Kemkemia* do not reach the anterior articular facet of the centrum. This feature is clearly seen in several crocodyliforms, including *Simosuchus* and *Caiman* (Georgi & Krause, 2010; pers. obs.). In this way, extremely reduced prezygapophyses lacking distinct articular facets may be considered a feature shared by both *Kemkemia* and crocodyliforms.

3) Shallow fossa on the distal half of the lateral surface of the neural spine bounded distally by the postspinal lamina (Fig. 2B-C). As pointed out by Cau & Maganuco (2009), the posterior lateral surfaces of the neural spine are concave. These concavities are distally limited by the postspinal lamina, and as a consequence, the anterior portion of the neural spine is transversely broader than the posterior one. Because this morphology is absent in all known theropods, Cau & Maganuco (2009) interpreted it as an autapomorphy of *Kemkemia*. However, the presence of such concavities appears to be present also in several crocodyliforms. In *Caiman*, this condition is observed in all caudal vertebrae posterior to the 7th caudal, and in *Baurusuchus* this morphology is also present in most caudal

vertebrae, including the anterior ones (Nascimento & Zaher, 2010). In the single available caudal vertebra of *Araripesuchus* (Turner, 2006) a similar fossa is also exhibited.

As indicated above, most of the characters representing putative autapomorphic and synapomorphic traits of *Kemkemia* proposed by Cau & Maganuco (2009) are, in fact, crocodyliform characters. However, there are two putative autapomorphies that may be unique to *Kemkemia* and may validate this taxon: 1- mediolaterally concave dorsal surface to the neural spine, and 2- robust neural spine (in which the mediolateral width at the apex is at least 30% of the width of the cranial articular surface of the centrum). Curiously, both conditions are present in dorsal and sacral vertebrae of living crocodylians (e.g. *Caiman*), but are absent in anterior and posterior caudal vertebrae.

Based on the discussion above, *Kemkemia* is here considered as belonging to Crocodyliformes rather than to Theropoda.

Phylogenetic position of *Kemkemia* among Crocodyliformes

The referral of *Kemkemia* to Crocodyliformes is here sustained by a large amount of features, including prezygapophyses reduced without well defined articular facets, an inflated neural canal, and the presence of a fossa on the posterior lateral surface of the neural spine (see above).

Due to the poorly informative nature of the elements at hand, the systematic position of *Kemkemia* within crocodyliforms is rather difficult to assess. For example, *Kemkemia* is clearly distinct from *Baurusuchus* in lacking the dorsal tilting of prezygapophyses seen in the latter genus (Nascimento & Zaher, 2010), also differs from *Notosuchus* in bearing postspinal laminae in the distal caudals (Pol, 2005), and from *Simosuchus* in showing distal caudals more slender and elongate (Georgi & Krause, 2010). In addition, *Kemkemia* differs from Eusuchia and several basal neosuchians in lacking procoelous caudal vertebrae (e.g. Atoposauridae, *Susisuchus*, *Isisfordia*; Martin *et al.*, 2010; Salisbury *et al.*, 2003; 2006). In this way, *Kemkemia* is here considered as a non-eusuchian crocodyliform of uncertain affinities.

Distal caudal vertebrae in many archosaur lineages are usually regarded as lacking robust phylogenetically informative characters. In general, in most archosaur phylogenetic analyses the character statements describing caudal vertebral morphology form no more than 2-5% of the characters involved (pers. obs.). The most notable exception are sauropod phylogenetic analyses, where caudal vertebral morphology forms about 10-14% of the character statements included (pers. obs.). In crocodylomorph phylogenetic studies, most authors have focused their analyses on cranial characters, underestimating the amount of phylogenetically informative characters of the postcranial skeleton, and rarely have included caudal vertebral characters (pers. obs.). In this way, the lack of accurate descriptions on the postcranial anatomy, even in taxa that are well preserved and almost complete, prevent to make well-grounded comparisons with available *Kemkemia* specimen. Thus, we are not able to draw clear conclusions about the validity of this taxon, pending more comparisons and more complete data sets. In this way due to the isolated nature and phylogenetically uninformative condition of the holotype and only known specimen of *Kemkemia auditorei* Cau & Maganuco, 2009, this taxon is here considered as a *nomen dubium* (*sensu* Mones, 1986).

Conclusions

In the present paper we made an assessment of the phylogenetic position of *Kemkemia auditorei*. We conclude that this taxon does not belong to Theropoda but may be included within Crocodyliformes. The isolated nature of the material available and the difficulty of finding informative characters of the distal caudals, preclude the assignation of *Kemkemia* to any crocodyliform clade. This lead us to propose this taxon as a *nomen dubium* and asks for more attention in postcranial characters in crocodyliform taxonomy and systematics.

Finally, the implications of *Kemkemia* regarding theropod diversification as advocated by Cau & Maganuco (2009) are no longer valid due to the new taxonomic arrangement here proposed.

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