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Maxime Lasseron

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Des dents énigmatiques de la transition Jurassique–Crétacé du Maroc : les derniers cynodontes non mammaliaformes (Synapsida, Cynodontia) connus d'Afrique ?

Maxime Lasseron

CR2P – Centre de recherche en paléontologie – Paris, UMR 7207, MNHN–CNRS–Sorbonne Université, Muséum national d'histoire naturelle, 8, rue Buffon, CP38, 75005 Paris, France

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ABSTRACT

Two tooth morphotypes corresponding to one or two tetrapod species from the Late Jurassic or Earliest Cretaceous locality of Ksar Metlili (KM), Anoual Syncline (eastern Morocco), are reported and described. These teeth cannot be related to any of the identified vertebrate major groups of this site. They are tricusped and uniradiculate, with a high and large main central cusp mesio-distally surrounded by two smaller accessory cusps. Their morphology is reminiscent of several taxa such as pterosaurs, notosuchians and mammals, with which they are compared here. These morphotypes are tentatively referred to cf. Cynodontia indet. They would be the most recent non-mammaliaform cynodonts reported in Africa and among the latest described. The KM specimens display remarkable plesiomorphic dental features with respect to known contemporaneous non-mammaliaform cynodonts. They might indicate the survival of a relict lineage in a North African refugium.

RÉSUMÉ

Deux morphotypes de dents de la localité de Ksar Metlili (KM), dans le Jurassique supérieur ou le Crétacé basal du synclinal d'Anoual (Maroc oriental), et correspondant à une ou deux espèces de tétrapodes, sont signalés et décrits. Ces dents ne peuvent être rattachées à aucun des groupes majeurs de vertébrés identifiés dans ce site. Elles sont tricuspides et uniradiculées, avec une cuspide centrale principale haute et bien développée entourée par deux cuspides accessoires mésio-distales plus réduites. Leur morphologie rappelle plusieurs taxons tels que les ptérosaures, notosuchiens et mammifères, auxquels elles sont comparées ici. Ces morphotypes sont provisoirement attribués à cf. Cynodontia indet. Ils seraient les plus récents cynodontes non mammaliaformes signalés en Afrique et parmi les plus jeunes

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E-mail address: maxime.lasseron@edu.mnhn.fr

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décrits. Les spécimens de KM montrent des caractéristiques dentaires remarquablement plésiomorphes par rapport aux cynodontes non mammaliaformes contemporains connus. Ils pourraient appartenir à une lignée relique ayant survécu dans un refuge nord-africain.

1. Introduction

The Cynodontia is the youngest of the six therapsid lineages, which also include dinocephalians, biarmosuchians, gorgonopsians, anomodonts, and therocephalians (Abdala and Ribeiro, 2010; Botha et al., 2007), since the earliest known cynodont record and their first radiation date back from the Latest Permian, nearly 252 million years ago (Abdala and Ribeiro, 2010; Abdala et al., 2007; Botha et al., 2007; Ruta et al., 2013). It is the only surviving therapsid lineage, comprising the extant mammals (Botha et al., 2007; Hopson and Kitching, 2001; Rowe, 1988; Rubidge and Sidor, 2001). Moreover, these are the only therapsids which main diversification occurred in the Triassic (Abdala, 2007; Abdala and Ribeiro, 2010; Ruta et al., 2013).

Extinct representatives of the group are comprised in a paraphyletic assemblage known as non-mammaliaform cynodonts; they represent the stage at which many mammalian characteristics first appeared in therapsids (Botha et al., 2007; Hopson and Kitching, 2001; Martinelli et al., 2017a). Here, we report and describe a new dental material from the Late Jurassic or Earliest Cretaceous locality of Ksar Metlili, Anoual Syncline, eastern Morocco, identified as possible non-mammaliaform cynodonts species. We discuss the possible taxonomic affinities of this new material.

Abbreviations–CR2P = Research Centre on Palaeontology–Paris, France; KM = Ksar Metlili fossil locality, Ksar Metlili Formation, Late Jurassic–Earliest Cretaceous, Anoual Syncline, eastern Morocco; MNHN = National Museum of Natural History, Paris, France.

2. Location and geological setting

The fossils were discovered in the microvertebrate locality of Ksar Metlili, Morocco, which is located in the “Couches rouges” (“Red Beds”, or “Continental intercalaire”; Kilian, 1931), nearby the city of Anoual. This fossiliferous locality belongs to the Ksar Metlili Formation, which was considered to be Early Cretaceous (?Berriasian) in age for a long time (Haddoumi et al., 1998, 2008; Mojon et al., 2009; Sigogneau-Russell et al., 1990), but could be instead regarded as Late Jurassic at least (Lasseron et al., in prep.).

The mixing of continental (e.g., wood, mammals, dinosaurs, root traces; etc.), brackish (e.g., bivalves) and marine (e.g., echinoderms, corals, brachiopods, etc.) species in the KM Formation (Sigogneau-Russell et al., 1990), as well as the sedimentary facies (e.g., fine-to-medium-grained sandstones, overturned cross stratifications, ripple marks; Haddoumi et al., 2008) suggest a near-shore, river-dominated deltaic depositional environment, probably controlled by eustatic variations (Haddoumi et al., 2008; Sigogneau-Russell et al., 1990, 1998; Lasseron et al., in press).

The KM site delivered a rich and diverse microvertebrate fauna, with more than 24,500 identified specimens, representing at least 47 species. This vertebrate assemblage includes mammals, dinosaurs, pterosaurs, crocodylomorphs, turtles, lepidosaurs, lissampibians, lungfishes, coelacanths, actinopterygians, and chondrichthyans (Botha et al., 2007; Duffin and Sigogneau-Russell, 1993; Sigogneau-Russell et al., 1998; Watabe et al., 2007; Lasseron et al., in press).

3. Materials and methods

The teeth described here were recovered from blocks of calcareous sandstones collected in 2010, following acid attack of the matrix using 7% formic acid saturated with tricalcium phosphate. The recovered lithoclastic and bioclastic residue was then reconcentrated using hydrogen peroxide. Different size fractions were separated from each other using sieves of 5-, 2-, 1-, and 0.5-mm mesh, and finally sorted under a stereomicroscope.

The orientation of these isolated teeth was made following the criteria of Godefroit and Battail (1997). The most convex side of the crown is traditionally regarded as the labial face, so we applied this criterion to identify the lingual and labial faces of the KM specimens. The mammal lineage shows a general trend toward simpler and smaller dental structures in the anterior direction, and the accessory cusps are usually more numerous or better developed on the distal side, so the side bearing the most developed and differentiated accessory cusp has been considered as probably distal and the side bearing the most reduced one as mesial; the distal inclination of the cusps, when present, also helps to determine the mesial and distal faces of the teeth. All measurements were made on lingual face (Fig. 1).

These teeth are provisionally stored at the MNHN and will be housed, after study, at the Faculty of Sciences Aïn Chock, University Hassan II of Casablanca, Morocco. The collection numbers given here (prefix KM) are provisional; they will receive a permanent one (prefix FSAC) when the specimens will be relocated at Casablanca.

4. Systematic palaeontology

cf. **Synapsida** Osborn, 1903
cf. **Cynodontia** Owen, 1861
cf. Cynodontia gen. et sp. indet. (Figs. 2, 3, 4)

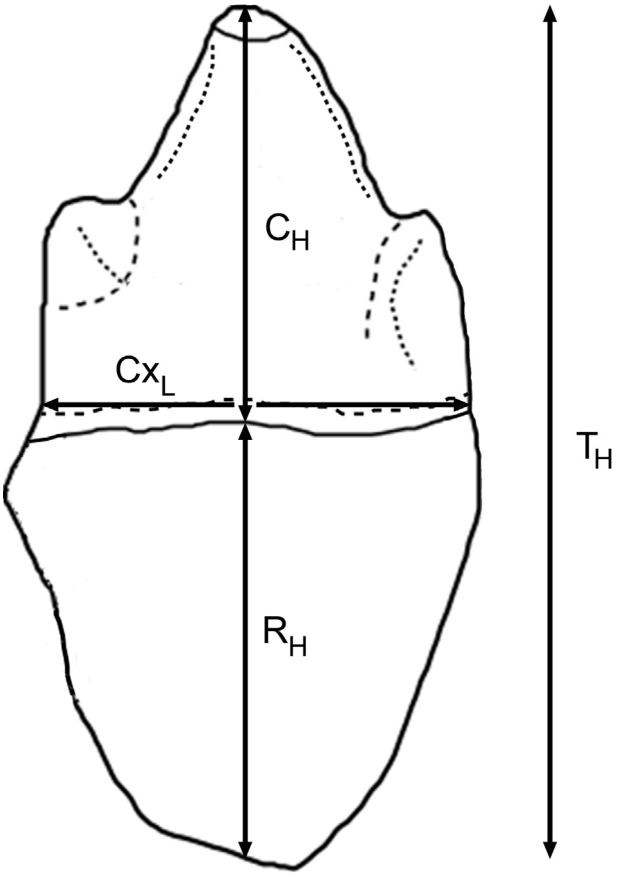

Fig. 1. Measurements made on the Ksar Metlili cf. non-mammaliaform cynodonts teeth. T_H = total height; C_H = crown height; R_H = root height; Cx_L = length at the cervix dentis.

Fig. 1. Mesures effectuées sur les dents de cf. cynodontes non mammaliaformes de Ksar Metlili. T_H = hauteur totale ; C_H = hauteur de la couronne ; R_H = hauteur de la racine ; Cx_L = longueur au niveau du cervix dentis.

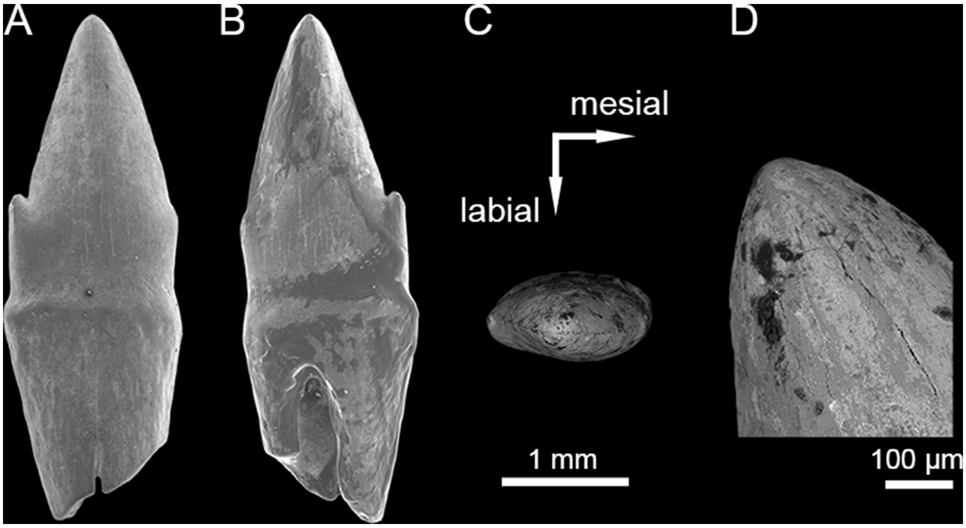

Fig. 2. Specimen KM-B'-44, tooth of cf. Cynodontia gen. et sp. indet., in (**A**) labial, (**B**) lingual and (**C**) occlusal views. (**D**) Close-up on the main central cusp apex, in lingual view. SEM views.

Fig. 2. Spécimen KM-B'-44, dent de cf. Cynodontia gen. et sp. indet., en vues (**A**) labiale, (**B**) linguale et (**C**) occlusale. (**D**) Détail de l'apex de la cuspide centrale principale, en vue linguale. Vues MEB.

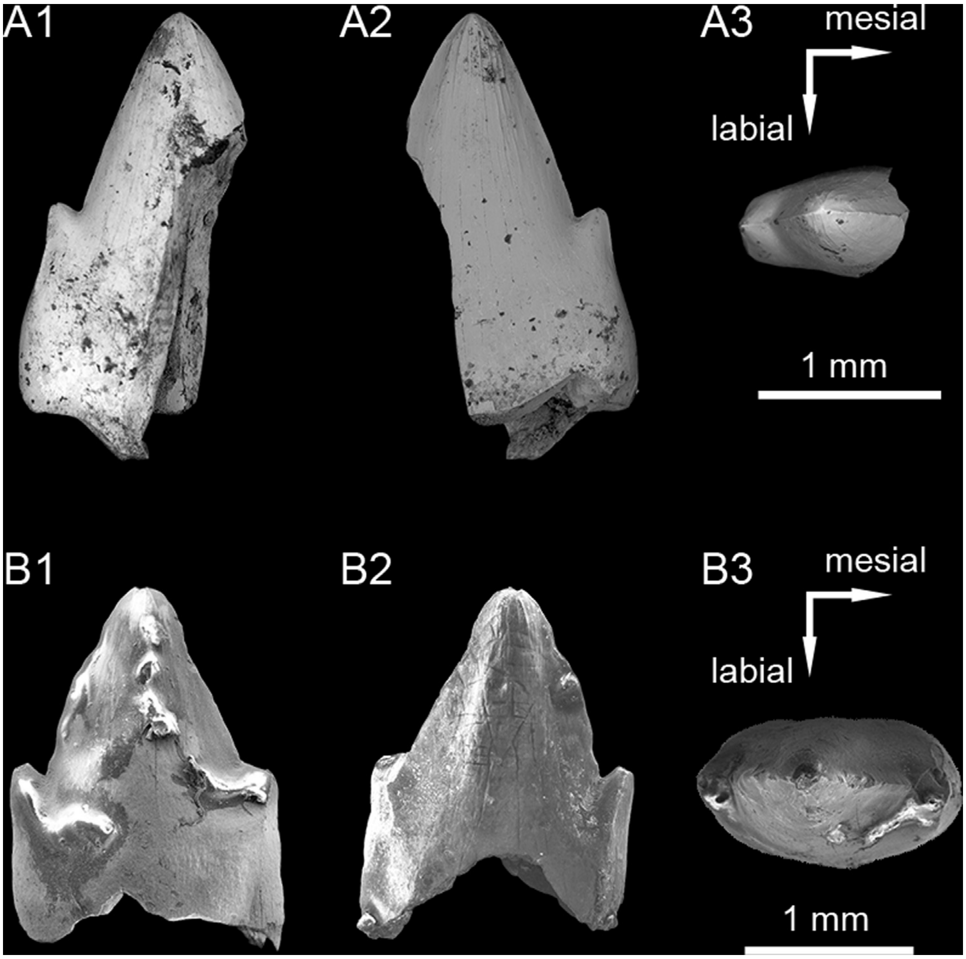

Fig. 3. Teeth of cf. Cynodontia gen. et sp. indet. **A.** Specimen KM-B'-43 in (A1) labial, (A2) lingual and (A3) occlusal views. **B.** Specimen KM-B'-98 in (B1) labial, (B2) lingual, and (B3) occlusal views. SEM views.

Fig. 3. Dents de cf. Cynodontia gen. et sp. indet. **A.** Spécimen KM-B'-43 en vues (A1) labiale, (A2) linguale et (A3) occlusale. **B.** Spécimen KM-B'-98 en vues (B1) labiale, (B2) linguale et (B3) occlusale. Vues MEB.

Referred material. KM-B'-44: complete?upper tooth crown with almost complete root (Fig. 2); KM-B'-43: distal part of an?upper tooth crown (accessory cusp and partial main cusp; Fig. 3A); KM-B'-98: complete?lower tooth crown (Fig. 3B); KM-?-1: almost complete?lower tooth (Fig. 4).

Description. The tooth KM-B'-44 (Fig. 2) is almost complete, with the whole crown and most of the root. It is uniradiculate, with a straight and hollow root almost as long as the crown, from which it is separated by a slight constriction (Figs. 2A, 2B); this constriction also marks the limit of the enamel and thus corresponds to the cervix dentis. The root shows an apical bulge. The tooth is strongly compressed transversely and broadly symmetrical in occlusal view (Fig. 2C). It bears a high main central cusp flanked by two small accessory cusps on both mesio-distal sides, one being strongly reduced relatively to the other one. The larger accessory cusp is probably distal and the reduced one is mesial, following the general trend toward simpler and smaller dental structures in the anterior direction in the mammal lineage. The distal cusp is clearly separated from the main central cusp and is about the third of the crown's size in height. The crown has a slight convexity that is probably labial, and so it is slightly curved lingually. The labial face is smooth (Fig. 2A), but the crown apex shows converging ridges on its lingual face (Fig. 2D). In KM-B'-44, the ridges extend approximatively to the middle of the crown height. Lingual and labial faces of the crown are separated by slight carinae.

The specimen KM-B'-43 (Fig. 3A) consists of a tooth fragment: only one accessory cusp and the main central cusp apex are preserved. As for KM-B'-44, the preserved accessory cusp (probably distal) is well developed, but, in comparison with KM-B'-44, it is higher relatively to the main central cusp, its height being about the half of that of the central one. The crown is slightly concave lingually. The lingual face of the main central cusp apex bears slight converging ridges, which extend to the middle of the crown height, just at the level of the accessory cusp edge (Fig. 3A2).

The specimen KM-B'-98 (Fig. 3B) is a complete tooth crown. As for the teeth KM-B'-44 and KM-B'43 (Figs. 2, 3A),

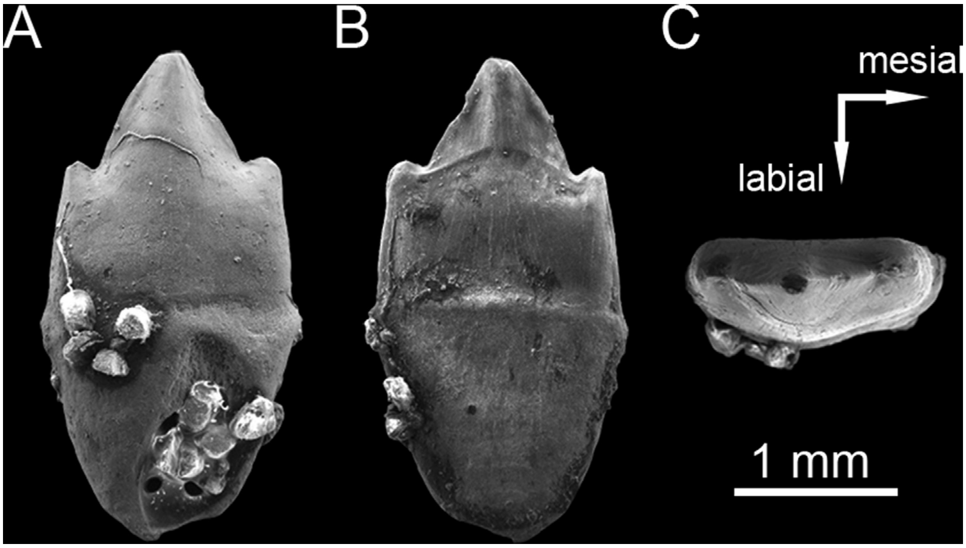

Fig. 4. Specimen KM-?-1, tooth of cf. Cynodontia gen. et sp. indet., in (**A**) labial, (**B**) lingual and (**C**) occlusal views. SEM views.
Fig. 4. Spécimen KM-?-1, dent de cf. Cynodontia gen. et sp. indet., en vues (**A**) labiale, (**B**) linguale et (**C**) occlusale. Vues MEB.

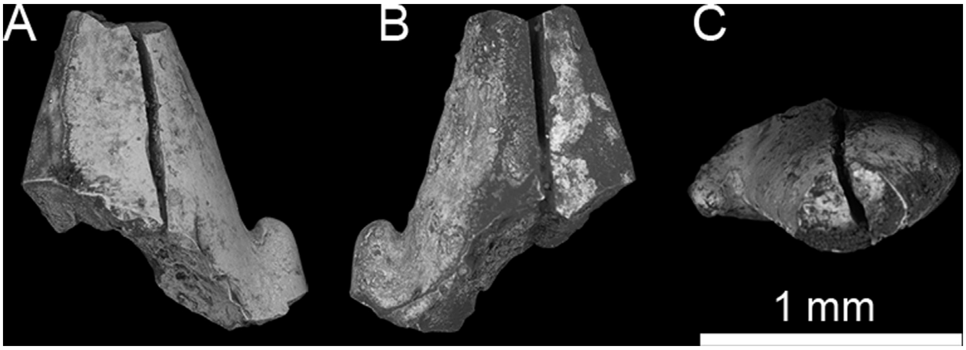

Fig. 5. Specimen KM-B'-99, tooth of cf. Cynodontia indet. (undetermined morphotype) in (**A**)?labial, (**B**)?lingual and (**C**) occlusal views. SEM views.
Fig. 5. Spécimen KM-B'-99, dent de cf. Cynodontia indet. (morphotype indéterminé) en vues (**A**) ?labiale, (**B**) ?linguale et (**C**) occlusale. Vues au MEB.

the distal accessory cusp is more differentiated than the other one and as for KM-B'-43, it is higher relatively to the main central cusp than in KM-B'-44 and measures about half of its height. The crown is slightly curved lingually. Because this tooth is stockier, wider and lower than the other two, we infer that it might belong to the lower tooth row.

The morphology of the specimen KM-?-1 (Fig. 4) is noticeably close to the morphotype of the three previous teeth described above, but without apical ridges (Fig. 4B). The transverse compression is not symmetrical and the labial face is inflated while the lingual face is flat (Fig. 4C). The two accessory cusps are about half of the tooth height; they are of similar size but poorly developed relatively to the main central cusp, in comparison with the three previous teeth. The crown is slightly curved lingually, as in the teeth described above, but the distal side of the crown is slightly convex, which is unseen in the three other. There are slightly marked anterior and posterior carinae. A ridge connecting the two accessory cusps with the base of the main central one on the lingual face can be seen on SEM views (Fig. 4B), even if it is difficult to detect with a stereomicroscope. As for KM-B'-98, its stocky morphology suggests that it belongs to the lower tooth row. The root is oval in cross section.

See Table 1 for the dimensions of KM-B'-44, KM-B'-43, KM-B'-98 and KM-?-1.

The three isolated teeth KM-B'-44, KM-B'-43 and KM-B'-98 described here share several features that could indicate and characterize a single and same species: (1) a broadly symmetrical transverse compression in occlusal view, and (2) an apical ornamentation consisting of ridges on the lingual face of the main central cusp. In addition, their dimensions are very similar (Table 1). The tooth KM-?-1, which differs by several features (e.g, no apical ridges, asymmetry of the lateral compression, similar size of the accessory cusps, slight convexity of the distal side of the crown), could represent a distinct species. The tentative referral of these morphotypes to Cynodontia is discussed in Section 5.

cf. Cynodontia indet. (Fig. 5)

Table 1
Dimensions (in mm) of the possible non-mammaliaform cynodont teeth from Ksar Metlili[a].
Tableau 1
Dimensions (en mm) des possibles dents de cynodontes non mammaliaformes de Ksar Metlili[b].

	cf. Cynodontia gen. et sp. indet.		cf. Cynodontia indet.		
	KM-B'-44	KM-B'-43	KM-B'-98	KM-?-1	KM-B'-99
T_H	4.02	?	?	3.01	?
C_H	2.17	2.43	2.15	1.54	1.29
R_H	1.85	?	?	1.47	?
Cx_L	1.40	0.93 (1.75)	1.43	1.52	1.16 (1.37)

[a] Estimated values for incomplete teeth are indicated in brackets. See Fig. 1 for abbreviation meaning.

[b] *Les valeurs estimées pour les spécimens incomplets sont indiquées entre parenthèses. Voir la* Fig. 1 *pour la signification des abréviations.*

Referred material. KM-B'-99: distal part of a tooth crown (Fig. 5).

Description. Only the tooth crown is preserved. The apex of the main central cusp and the mesial accessory cusp are missing (Fig. 5). The morphology of this tooth is closely related to other KM tricuspid teeth described here, but it is too incomplete to allow its formal specific assignation.

See Table 1 for the dimensions of KM-B'-99.

5. Comparisons and discussion

In the KM material described here, two dental morphotypes are characterized and are distinguished as representing one or two tetrapod species. However, we do not exclude that these morphotypes could also represent two ontogenetic stages and/or two dental positions of the same species.

The teeth attributed to the morphotype 1 (KM-B'-44, KM-B'-43, and KM-B'-98; Figs. 2, 3) are distinguished by their symmetrical transverse compression in occlusal view and their lingual apical ornamentation made of ridges converging on the apex of the main central cusp. In contrast, the material attributed to the morphotype 2 (KM-?-1; Fig. 4) has no apical ridges–and this absence does not seem to be due to wear, since the tooth does not bear any sign of it–, the transverse compression is not symmetrical and the distal side of the crown is slightly convex.

All these teeth are reminiscent of those of the pterosaurs *Eudimorphodon* (see Dalla Vechia, 2013; Jenkins et al., 2001; Kellner, 2015; Wellnhofer, 2003 for comparison) or *Peteinosaurus* (Dalla Vechia, 2013) with multi-cusped teeth. Nevertheless, these taxa are primarily Triassic in age, and all post-Triassic pterosaurs have single-cusped teeth or are toothless (Kellner, 2003). Considering that numerous pterosaurs are known in Late Jurassic to late Early Cretaceous Lagerstätten (Butler et al., 2009, 2013) and have yielded the best record of the pterosaur diversity, the occurrence of a fossil gap in this interval for similar pterosaur teeth seems unlikely. In addition, in *Eudimorphodon*, the crown is much shorter and higher than in cynodonts, and the enamel is strongly wrinkled, with numerous ridges (Hahn et al., 1984; Sigogneau-Russell and Hahn, 1994), while cynodont enamel is frequently smooth, as in KM-?-1 (Fig. 4), and may be wrinkled only at the tips of the main cusps (as in *Gaumia incisa*; Hahn et al., 1987; Sigogneau-Russell and Hahn, 1994), as in the KM morphotype 1. In the KM material, these ridges do not seem to result from acid attack because of their localised position. Hahn et al. (1984) also used other criteria to make the difference between *Eudimorphodon*-like pterosaur teeth and non-mammaliaform cynodont ones. Following the authors, the most important among them are (1) the constriction between the crown and the root, present in pterosaur teeth, but often absent or only slightly marked in cynodonts, and (2) the incipient division of the root in cynodonts, unseen in pterosaurs. The crown–root constriction is really slight in the KM specimens (Figs. 2, 4), close to what can be seen in *Gaumia*? *incisa* (Hahn et al., 1987), *Prozostrodon brasiliensis* (Martinelli et al., 2017b; Pacheco et al., 2018) or *Thrinaxodon liorhinus* (Abdala et al., 2013). The tooth KM-B'-44 (Fig. 2) shows an incipiently root division; the development of a double-rootedness has been reported for several non-mammaliaform cynodonts taxa, such as *Microconodon tenuirostris* (Sues, 2001) and *Rewaconodon tikiensis* (Datta et al., 2004), but as far as is known, all pterosaurs have a single and undivided root (Fröbisch and Fröbisch, 2006). Furthermore, cutting edges are often sharp in 'dromatheriid' cynodonts, but only weakly developed in *Eudimorphodon* (Fröbisch and Fröbisch, 2006); in the KM specimens, even if the carinae are slight, they are sharper than what can be seen in *Eudimorphodon* (see Hahn et al., 1984) in occlusal view. Thus, the pterosaur identity of the KM material can be confidently refuted, even though we cannot exclude the hypothesis of a basal and unknown lineage of pterosaurs maintained in the Late Jurassic or Earliest Cretaceous of Africa.

Another interesting systematic comparison of the KM material can be made with notosuchian crocodylomorphs. Representatives of this clade have developed an unexpected array of dental morphologies comparable to mammals and their extinct relatives, and several were initially identified as mammals because of their complex, multicuspid teeth and heterodont dentition (*Candidodon itapecuruense* and *Lavocatchampsa sigogneaurussellae*, for example; Martin and Lapparent de Broin, 2016). Some notosuchians, such as *Lavocatchampsa sigogneaurussellae* from the Kem-Kem Beds of the Cretaceous of Morocco (Martin and Lapparent de Broin, 2016), *Candidodon itapecuruense* from the late Early Cretaceous of Brazil (Carvalho, 1994; Carvalho and Campos, 1988; Santos et al., 2011) or *Malawisuchus mwakasyungutiensis* from the Early Cretaceous of Malawi (Gomani, 1997), have tricuspid teeth, with a large main central cusp flanked by two accessory cusps, one being smaller than the other one. Their crown–root junction is constricted. However, in these species, the crown–root constriction is strongly marked and the cingulum bears small and rather numerous cuspids arranged all around the tooth crown (Carvalho, 1994; Carvalho and Campos, 1988; Martin and Lapparent de Broin, 2016; Santos et al., 2011), which is not the case in the KM teeth described here. Moreover, the transverse compression is less distinct in notosuchian teeth than in the specimens reported here (see Carvalho, 1994; Martin and Lapparent de Broin, 2016; Santos et al., 2011 for comparison). Thus, a notosuchian identity of the KM teeth seems unlikely.

The difference in the development of the two accessory cusps reminds the mammal lineage, where the tooth complexification usually increases distally. The KM specimens are quite similar in morphology to single-rooted premolariform teeth of some eutriconodontan mammals such as the small gobiconodontid BMNH M 45513 described by Sweetman (2006) in the Barremian of southern England, or *Gobiconodon borrisiaki* from the Aptian-Albian of Mongolia (Kielan-Jaworowska and Dashzeveg, 1998). However, they differ from BMNH M 45513 in having a straight, not curved root and less clearly separated accessory cusps; in the KM specimens of morphotype 1 (KM-B'-44, KM-B'-43 and KM-B'-98; Figs. 2, 3), only the apex of the main central cusp is curved (lingually), whereas in BMNH M 45513 the base of the cusps is lingually convex (i.e. cusp base not inflated in the KM material); moreover, the roots of the KM specimens show an apical bulge, and the apex of the main cusp of the teeth attributed to morphotype 1 bears ridges, which is not the case in BMNHN M 45513 (Sweetman, 2006). They also differ from p2–p3 of *G. borrisiaki*, which are slightly bent mesiolingually in comparison with m1–m2 (Kielan-Jaworowska and Dashzeveg, 1998), a feature which seems absent in the KM specimens because of their straight root. The shape of the root is also different: in *G. borrisiaki*, the uniradiculate teeth as well as those with two roots, have a strong vertical constriction in the root (Kielan-Jaworowska and Dashzeveg, 1998; Sweetman, 2006), whereas in KM-?-1 the root is oval in cross section. Thus, we exclude the eutriconodontan hypothesis for the KM teeth attribution.

The KM teeth are somewhat similar to those figured by Lucas and Oakes (1988) and Godefroit and Battail (1997) and identified as non-mammaliaform cynodonts. The Tritylodontidae are the only Late Jurassic surviving family of this non-mammaliaform cynodonts (Ruta et al., 2013). However, Tritylodontidae have complex teeth, with several rows of curved cusps well adapted to their herbivorous diet (Velazco et al., 2017). In comparison, the KM teeth morphology is quite simple and is clearly different from the non-mammaliaform cynodonts from the Late Jurassic (see Hu et al., 2009; Maisch et al., 2004; Velazco et al., 2017; Watabe et al., 2007) for comparison material) or Early Cretaceous (see Lopatin and Agadjanian, 2008; Matsuoka and Setoguchi, 2000; Matsuoka et al., 2016; Setoguchi et al., 1999; Tatarinov and Mashchenko, 1999) for comparison material). Thus, the tritylodontid systematic hypothesis can be reasonably excluded.

Such quite simple tooth morphology is also found in the anterior dentition of probainognathian cynodonts, such as *Prozostrodon brasiliensis* (Barberena et al., 1987; Bonaparte and Barberena, 2001; Martinelli et al., 2017b; Pacheco et al., 2018) from the Late Triassic of Brazil. It also reminds even more basal cynodonts such as the Late Permian *Nanictosaurus* and *Cynosaurus suppostus* (Van den Brandt and Abdala, 2018; Van Heerden and Rubidge, 1990), or the Early Triassic *Thrinaxodon* (Abdala et al., 2013; Van Heerden and Rubidge, 1990), although the roots of the KM specimens seem to be shorter and the height of the main cusp in morphotype 1 is much higher.

The KM teeth are even more similar to those of Triassic non-mammaliaform cynodonts (Fig. 6). Their general morphology and their small size are reminiscent of the teeth of the Late Triassic non-mammaliaform cynodonts from Saint-Nicolas-de-Port (Rhaetian, France; Godefroit and Battail, 1997), such as *Gaumia* (Godefroit and Battail, 1997; Hahn et al., 1987; Figs. 6F, 6G) and *Pseudotriconodon* (Godefroit and Battail, 1997; Hahn et al., 1984; Lucas and Oakes, 1988; Fig. 6H). They share a high main central cusp surrounded by a smaller accessory cusp, one being less developed than the other one. A similar pattern can be seen also in the first postcanines of some Late Triassic Tritheledontidae, such as *Pachygenelus* (Gow, 1980). The KM specimens are also very similar to the tricuspid postcanine teeth of 'dromatheriids', such as *Microconodon tenuirostris* (Simpson, 1926; Sues, 2001; Sues et al., 1994; Fig. 6I), *Rewaconodon tikiensis* (Datta et al., 2004) and the recently described *Polonodon woznikiensis* (Sulej et al., 2018; Fig. 6J) from the early Late Triassic of United States, India and Poland respectively. However, in *Polonodon* the roots have a strong vertical constriction (Sulej et al., 2018), whereas in KM-?-1 the root is oval in cross section.

No wear facets are noticeable on these teeth, so it is difficult to define an occlusion pattern. However, because their morphology is close to that of Triassic non-mammaliaform cynodonts, we can suppose that the occlusion pattern was also similar. In *Thrinaxodon,* when the jaws are closed, the lower postcanines teeth lay lingual to the upper ones, but without any contact between the two sets (Crompton, 1972, 1995); they did not occlude with one another and so did not develop extensive intermolar contact and attrition wear facets (Crompton, 1972; Crompton and Jenkins, 1968). The main cusps of the upper and lower postcanines lay adjacent to the intervals between successive teeth (Crompton and Jenkins, 1968). A close pattern of the crown (but the roots are different) can be seen in the probainognathian *Probainognathus* (Crompton, 1995), *Brasilodon* and *Brasilitherium* (Bonaparte et al., 2003, 2005). In trithelodonts, such as *Pachygenelus* and *Diarthroganthus*, the postcanines developed wear facets on the lingual face of the upper ones and labial face of the lower ones, producing sharp edges along the apical border (Crompton, 1995); so, the tooth rows also lay medial relatively to each other, as in *Thrinaxodon* and *Probainognathus*, but with contact.

Thus, we tentatively propose a similar pattern of occlusion for the KM non-mammaliaform cynodonts, with lower tooth row occluding lingual relatively to the upper tooth row and, because there is no noticeable wear facets, maybe without direct contact between the lower and the upper teeth (Fig. 7) as in *Thrinaxodon*. Another explanation for this absence of wear facets is that the teeth presented here could be newly, recently erupted teeth, still unworn by food consumption; the KM possible cynodonts could be subadult individuals, with a tooth replacement frequency higher than in the adults. Tooth wear in this case would

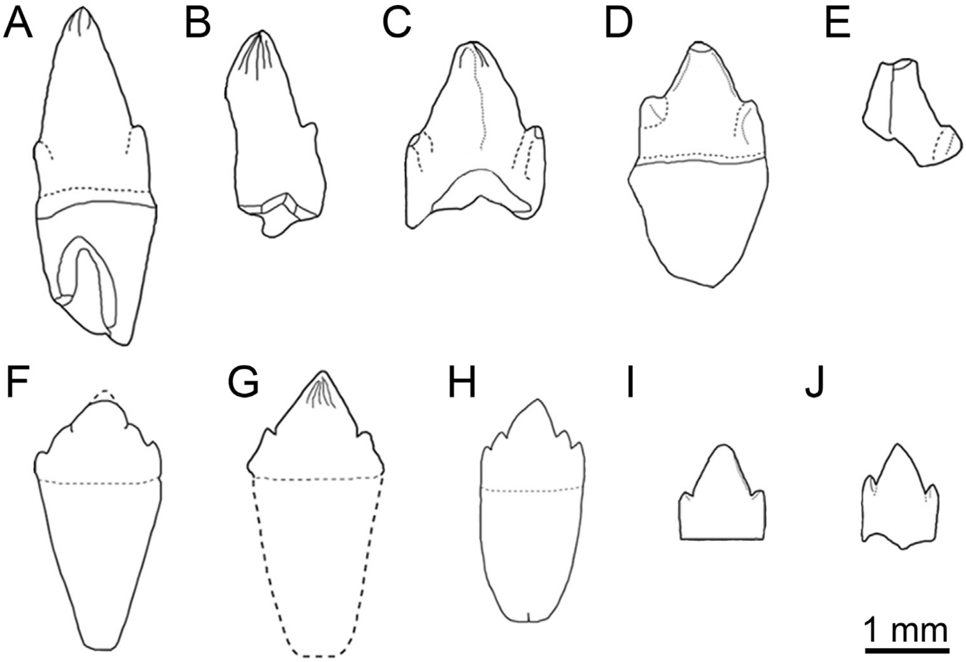

Fig. 6. Comparative sketches of the Ksar Metlili cynodont-like teeth and other non-mammaliaform cynodonts, in lingual view and at the same scale. cf. Cynodontia gen. et sp. indet., specimens (**A**) KM-B'-44, (**B**) KM-B'-43, (**C**) KM-B'-98, ?upper tooth and (**D**) KM-?-1, ?upper tooth. (**E**)?Cynodontia indet., specimen KM-B'-99. (**F**) *Gaumia longiradicata*. (**G**) *Gaumia? incisa*. (**H**) *Pseudotriconodon wildi*. (**I**) *Microconodon tenuirostris*, USNM 448600, upper tooth. (**J**) *Polonodon woznikiensis*, ZPAL V.34/51. (**F**, **G** from Hahn et al., 1987; H from Hahn et al., 1984; I from Sues et al., 1994; J from Sulej et al., 2018).

Fig. 6. Schémas comparatifs des dents de Ksar Metlili attribuées à des cynodontes, comparées à d'autres dents de cynodontes non mammaliaformes, en vue linguale et à la même échelle. cf. Cynodontia gen. et sp. indet., spécimens (**A**) KM-B'-44, (**B**) KM-B'-43, (**C**) KM-B'-98, dent ?supérieure, et (**D**) KM-?-1, dent ?supérieure. (**E**) ?Cynodontia indet., spécimen KM-B'-99. (F) *Gaumia longiradicata*. (**G**) *Gaumia ? incisa*. (H) *Pseudotriconodon wildi*. (**I**) *Microconodon tenuirostris*, USNM 448600, dent supérieure. (**J**) *Polonodon woznikiensis*, ZPAL V.34/51. (**F** d'après Sues et al., 1994 ; **G** d'après Sulej et al., 2018 ; **H**, I d'après Hahn et al., 1987 ; **J** d'après Hahn et al., 1984).

be expected in more advanced stages, as in *Bonacynodon schultzi* (Martinelli et al., 2016).

The KM teeth also show features that are rare for cynodonts, such as the apical bulge of the root or the ridges on the apex of the lingual face (see for example Martinelli et al., 2017a, b; Pacheco et al., 2018). Thus, if the hypothesis that these teeth belong to a bizarre and still unknown lineage of non-mammaliaform cynodonts is possible, we cannot exclude that they represent another taxon. This explains our attribution of the KM teeth in open nomenclature as cf. non-mammaliaform cynodonts.

After a first phase of diversification toward the end of the Permian and only a slight decrease after the Permian–Triassic extinction event (Abdala and Ribeiro, 2010; Botha et al., 2007), non-mammaliaform cynodonts had a remarkable diversification in the Middle Triassic (Abdala, 2004). However, their diversity dropped during the Jurassic: they are only represented by the family Tritylodontidae, with a few Asian genera (Averianov et al., 2017; Lopatin and Agadjanian, 2008; Hu et al., 2009; Maisch et al., 2004; Matsuoka and Setoguchi, 2000; Matsuoka et al., 2016; Setoguchi et al., 1999; Tatarinov and Mashchenko, 1999; Velazco et al., 2017; Watabe et al., 2017). Thus, the non-mammaliaform cynodont fossil record is really poor around the Jurassic–Cretaceous transition, and it is restricted to Asia. Hence, in the current state of the present fossil data, the KM cf. non-mammaliaform cynodonts are for sure the youngest known in Africa and in Gondwana, and among the youngest ever described in the world outside Asia.

The KM material would include the latest representatives of the non-mammaliaform cynodonts, but with strongly plesiomorphic dental features that remind the first members of the group and especially the Late Triassic ones. This could be explained in two ways: first, the KM species belong to a North African relict lineage, which had retained ancestral dental characteristics all along its evolution until the Late Jurassic-Early Cretaceous; second, the plesiomorphic dental features of the KM species are the result of a convergent evolution with Late Permian–Triassic cynodonts within a more recent lineage. The hypothesis of a relict lineage fits well with the occurrence of other relict lineages recently reported in the KM fauna, such as basal ornithischians and haramiyidan mammaliaforms (Lasseron et al., in press).

6. Conclusions

One or two putative new non-mammaliaform cynodonts are described from the Ksar Metlili Formation (Late Jurassic or Earliest Cretaceous), eastern Morocco. The KM new material documents a poorly known period and suggests that some non-mammaliaform cynodonts persisted until the Late Mesozoic not only in Asia, but also in Africa. The KM non-mammaliaform cynodonts would be the most recent known from Gondwana, and among the latest

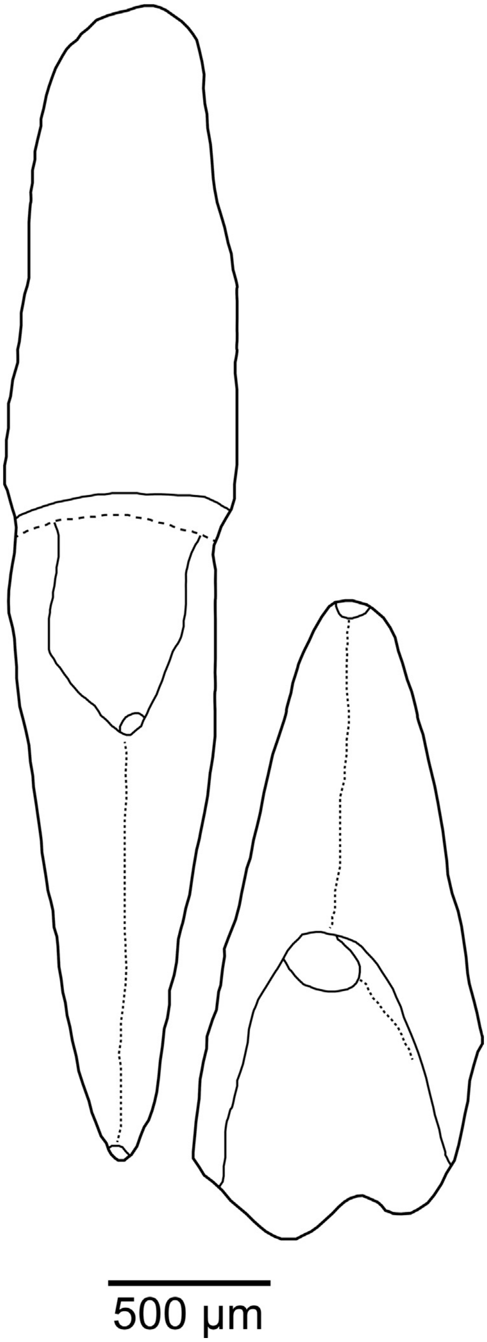

Fig. 7. Sketch of the pattern of occlusion proposed for the Ksar Metlili cf. non-mammaliaform cynodonts teeth, in distal view. Based on the specimens KM-B'-44 (left) and KM-B'-98 (right).

Fig. 7. Schéma du modèle d'occlusion proposé pour les dents de cf. cynodontes non mammaliaformes de Ksar Metlili, en vue distale. Il est basé sur les spécimens KM-B'-44 (à gauche) and KM-B'-98 (à droite).

known. However, an interesting point is that the morphology of KM non-mammaliaform cynodonts teeth does not seem to fit with their geological age. Their Late Mesozoic age would favour systematic relationships to Tritylodontidae, but their simple structure brings them closer to the Late Permian and Triassic non-mammaliaform cynodonts. The most likely explanation retained here is that the KM specimens belong to a relict lineage of non-mammalian cynodonts that retained basal dental features and survived until the Late Jurassic at least in a North African refugium, along with other relict lineages recently reported from the same site.

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