DIVERSITY OF TRICONODONT MAMMALS FROM THE EARLY CRETACEOUS OF NORTH AFRICA – AFFINITIES OF THE AMPHILESTIDS

by

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SUMMARY

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ABSTRACT

The mammalian fauna (represented only by isolated teeth) from the early Cretaceous of Morocco includes a number of non-'therian' specimens, characterized by the antero-posterior alignement of the main molar cusps. This assemblage is very heterogenous, including forms (among them *Gobiconodon palaios* sp. nov.) that can be related to Laurasian triconodonts, and several forms so far known only in this part of Gondwana (among them *Kryptotherium polysphenos* gen. et sp. nov.). The latter, in particular, exemplifies the diversity of the mammalian dental morphology in the Mesozoic, often largely underestimated. In the last part of this paper, the 'therian' affinity of the 'amphilestids' is discussed, on the basis of the arrangement of molar cusps, the interlocking mechanism and the occlusal pattern.

RESUME

La faune mammalienne (limitée à des dents isolées) du Crétacé inférieur du Maroc comprend un certain nombre de non-'thériens', caractérisés par l'alignement antéro-postérieur des principaux tubercules des molaires. Cet assemblage est cependant hétérogène, comportant des formes (par ex. *Gobiconodon palaios* sp. nov.) qui peuvent être rapprochées de triconodontes laurasiatiques, et plusieurs autres jusqu'ici limitées à cette partie du Gondwana (par ex. *Kryptotherium polysphenos* gen. et sp. nov.). Cette dernière en particulier témoigne de la diversité de la morphologie dentaire des mammifères durant le Mésozoïque, diversité souvent largement sous-estimée. Dans la dernière partie de cet article est discutée l'affinité supposée des 'amphilestides' avec les 'thériens', sur la base de la disposition des tubercules des molaires, du mécanisme de l'engrènement des dents successives et du mode occlusal.

INTRODUCTION

Mammalian molars of a triconodont-type (cusps antero-posteriorly aligned) are found throughout the Mesozoic era and are known from the southern as well as the northern hemisphere by four families (not taking into account *Sinoconodon* PATTERSON & OLSON, 1961): Triconodontidae MARSH, 1887, Amphilestidae OSBORN, 1888 (considered as composed of Amphilestinae and Gobiconodontinae by Chow & Rich (1984) and Kielan-Jaworowska & Dashzeveg (1998)), Morganucodontidae KÜHNE, 1958 and Austrotriconodontidae BONAPARTE, 1992. These families were once grouped in the order Triconodonta OSBORN, 1888, but the monophyly of this taxon has recently been repeatedly challenged (e.g. Rowe 1988; Rougier *et al.* 1996; Kielan-Jaworowska 1997; Rougier 1999; Luo *et al.* 2002). In particular, the upper Jurassic-Cretaceous Triconodontidae appear to be phylogenetically separated from the Triassico-Jurassic Morganucodontidae (a family excluding *Megazostrodon* CROMPTON & JENKINS, 1968), although sharing a similar occlusal pattern (Cifelli *et al.* 1998).

Morganucodontidae, Gobiconodontinae and Triconodontidae are known by skeletal as well as dental elements. Triconodontidae are the most systematically diverse and have been significantly enriched by recent discoveries in the Cretaceous of North America (Cifelli & Madsen 1998; Cifelli *et al.* 1998; Engelmann & Callison 1998; Cifelli *et al.* 1999), of Africa (Heinrich 1998) and China (Ji *et al.* 1999). Amphilestinae and Austrotriconodontidae rest only on jaws or even on isolated teeth, as do the peculiar triconodont genera (family indet.) previously described from the Early Cretaceous of Morocco (*Ichthyoconodon* and *Diskrytodon* SIGOGNEAU-RUSSELL, 1995).

Again represented by isolated teeth and coexisting with evolved tribosphenic 'therians' in this Gondwanan locality, are a number of additional triconodonts *sensu lato*, the subject of the present study.

Terminology: As a "linguistic convenience" (Luo *et al.* 2002: 4), I use the "widely understood" (id.) terms: 'mammals', 'therians', 'amphilestids', 'triconodonts', being aware that these terms either do not cover monophyletic units or are now used formally for more restricted groupings.

Institutional abbreviations. - AMNH - American Museum of Natural History, New York; BMNH, Natural History Museum, London; SA - synclinal d'Anoual, Maroc; specimens in the Museum national d'Histoire naturelle, Paris; OMNH – Oklahoma Museum of Natural History, Norman, Oklahoma; POQ MNHN- Pontalun Quarry, Wales, Great Britain; specimens in the Museum national d'Histoire naturelle, Paris; SNP MNHN – Saint-Nicolas-de-Port; specimens in the Museum national d'Histoire naturelle, Paris; SMP-SMU – Shuler Museum of Paleontology, Southern Methodist University, Texas; USNM, United States National Museum, Washington D.C.; YPM, Yale Peabody Museum, New Haven, Connecticut.

L, length; W, width.

SYSTEMATIC PALAEONTOLOGY

Family **AMPHILESTIDAE** OSBORN, 1888
Subfamily **GOBICONODONTINAE** CHOW and RICH, 1984

Genre *GOBICONODON* TROFIMOV, 1978

***Gobiconodon palaios* sp. nov.**

Holotype: SA 107, a right upper molar (M1?). L = 1.55 mm; W = 0.80 mm.

Attributed material: SA 111, a right ?upper molar (M2?): L = 1.25. SA 119, a right upper molar (M1?): L = 1.45; W = 0.63. SA 130, a left upper molar (M2?): L = 1.50; W = 0.95. SA 138, a right upper molar: L = 1.33; W = 0.83. SA 141, a left upper molar: L = 1.45; W = 0.75. SA 146, anterior third of a left upper molar: W = 0.45. SA 153, anterior two-thirds of a left upper molar: L (as preserved) = 1.20. W = 0.90. SA 80, a worn right upper molariform: L = 1.26; W = 0.52. SA 93, a partial left ?upper premolar (posterior part): L = 1.04+; W = 0.71. SA 129, a partial right ?upper premolar (posterior part): W = 0.59.

Type horizon and locality: Anoual Syncline, Talsinnt Province, Morocco. sequence B of the Red Beds; ?Berriasian.

Etymology: *palaios*, Gr., old (with respect to the other species of the genus).

Diagnosis: Triconodont-type upper molars which share with those of other species of *Gobiconodon* the "incipient triangular pattern, with cusp A slightly more lingual than cusps B and C" (Kielan-Jaworowska & Dashzeveg 1998: 417). Differ from those of *G. borissiaki* TROFIMOV, 1978 and *G. ostromi* JENKINS & SCHAFF, 1988, by being respectively 1/2 and 1/3 smaller. Differ from those of *G. hoburensis* (TROFIMOV, 1978) by being relatively narrower labio-lingually. Differ from all species (except perhaps the Spanish one (Cuenca-Bescos & Canudo, 1999), incompletely known) by a slight asymmetry of cusps B and C and a lesser occlusal angulation of cusps.

Description:

The holotype (Fig. 1 and Pl. 1, 1) is a well preserved right upper molariform tooth, showing the antero-posterior near-symmetry, the slight anterior indentation and the complete labial cingulum seen in triconodont upper molars. However, the crown is not absolutely straight antero-posteriorly, cusps C and slightly more B, being labially displaced. The tooth is relatively large, compared to those of the other Moroccan mammals, with the anterior and posterior cusps being half the size (in length and height) of cusp A, but not very well detached from the latter. This cusp A is relatively low and pinched labially with mesial and distal wings; the labial face of all three cusps is more angular than the lingual face.

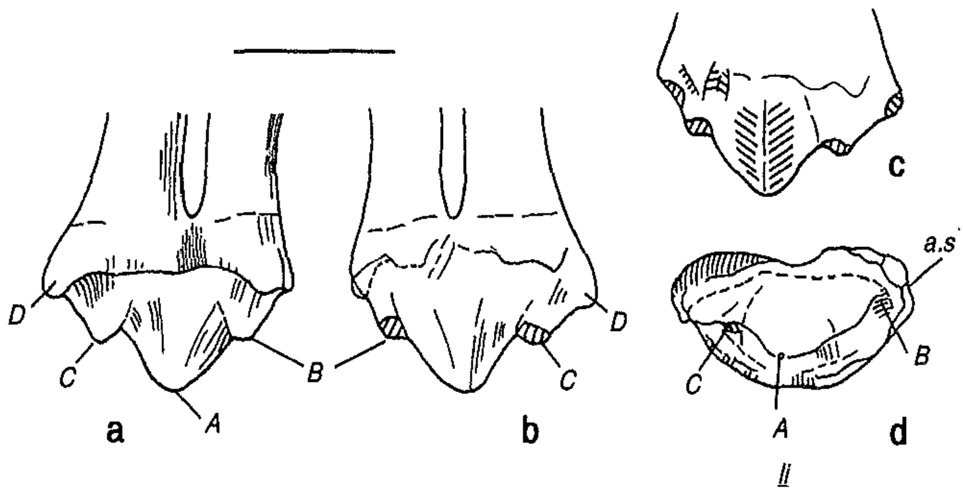

Figure 1 .— *Gobiconodon palaios* sp.nov. holotype SA 107, right upper molar. **a**, labial view ; **b**, lingual view; **c**, lingual view showing wear facets; **d**, occlusal view. a.s, anterior sulcus; li, lingual. In this figure and the followings: hatching = wear facet; cross hatching = broken surface. Scale = 1mm.

A strong cingulum encircles the crown; it emerges antero-labially in a high point, is very faintly denticulated labially and becomes fainter in the middle of A. Lingually, the cingulum is very briefly interrupted at the same level; it is also faintly undulated. A very narrow and faint vertical sulcus is detectable in the anterior cingulum, but cusp F is hardly individualized. The crown is sustained by two stubby roots disposed obliquely in labial view, the posterior one being slightly wider and angular anteriorly and posteriorly. The tooth is well preserved, except for the anterior crests of B and C, which are slightly abraded. A wear facet is detectable on the posterior face of A; that on the anterior face of A is less clear; there is also a possible wear facet on the anterior face of B. Finally, a circular notch is worn in the cingulum between A and B.

SA 111 (Fig. 2a-c) is unworn but incomplete dorsally and was found in two pieces: it has only the three main cusps preserved and part of the cingulum (that surmounting B lingually). This tooth could represent the same taxon as the holotype, though B is almost as large as A, and C only slightly lower (but such variability in the proportions of cusps can also be observed along the jaw of the triconodontid *Trioracodon bisulcus* (MARSH, 1880) (YPM 10344 for example) or *Gobiconodon* sp. (MNHN, undescribed specimen). The anterior sulcus is better indicated than on the holotype and cuspules E and especially F can be recognized. Cusp D seems to have been reduced. Again cusp B is more labially displaced than C. SA 111 seems to have been an erupting tooth.

SA 119 (Fig. 2d-e) has an occlusal contour close to that of the holotype, though being slightly narrower labio-lingually. Cusps B and C have been worn off, while cusp A remains relatively high. Both cingula are complete. A strong wear facet has also affected the anterior crest of A and B, and the cingulum above B.

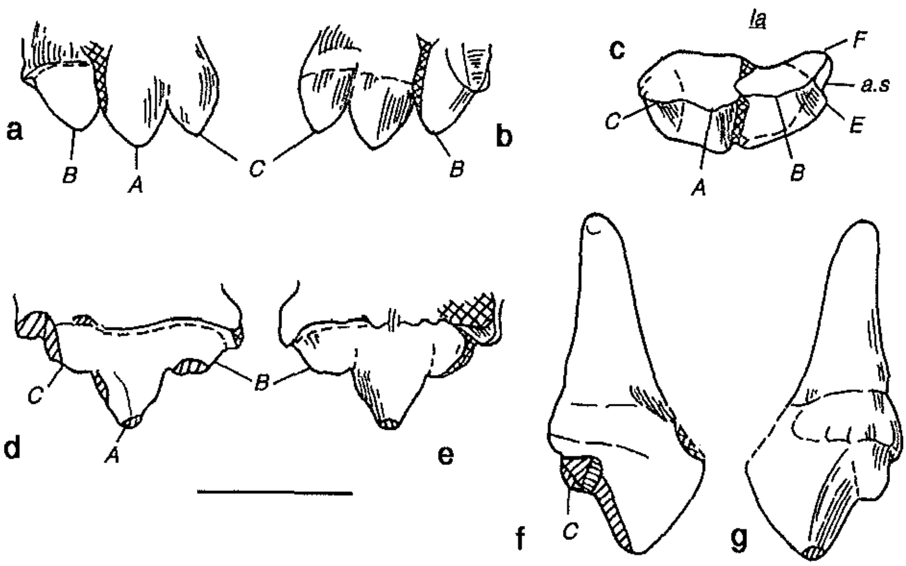

Figure 2 .— *Gobiconodon palaios* sp. nov. **a-c**, SA 111, right upper molariform, in lingual, labial and occlusal views; **d-e**, SA 119, right upper molariform, in lingual and labial views; **f-g**, SA 93, ?left upper premolar, in lingual and labial views. a.s, anterior sulcus; la, labial. Scale =1mm.

SA 130 (Fig. 3) is also complete but for cusps C and D which have been truncated. It differs from the holotype tooth by being more curved antero-posteriorly, hence a more pronounced ectoflexus. Moreover, cusp B is slightly more detached, the anterior sulcus is clearer and higher, the lingual cingulum is thicker and seems to have been complete as in SA 119. Finally, both roots bear a vertical crest in their latero-labial angle. A small wear facet is present on the lingual cingulum on each side of A and above B; another facet is present on the anterior and possibly the posterior face of A, as well as a narrow diamond-shaped one at the mid base of A.

SA 138 is a molar of which the anterior part has been damaged and the three main cusps abraded; cusp D is very small. The contour of the crown is more asymmetrical with a square anterior face (accentuated by erosion), and is thicker labio-lingually even than on SA 130. The ectoflexus is well marked and both cingula are complete. No wear is distinguishable on the lingual cingulum, itself thicker than on the preceding teeth.

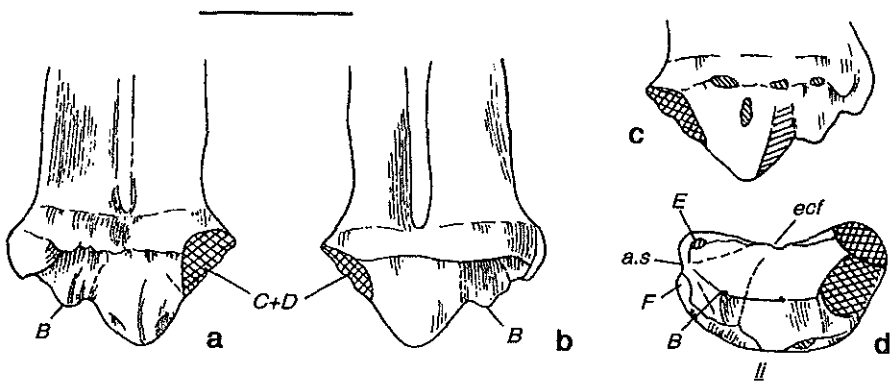

Figure 3 .— *Gobiconodon palaios* sp. nov., SA 130, left upper molar. **a**, labial view ; **b**, lingual view; **c**, lingual view with wear facets; **d**, occlusal view. a.s, anterior sulcus; ecf, ectoflexus; li, lingual. Scale = 1mm.

SA 141 is a very worn upper left molar, with a damaged anterior border, hence again a square anterior contour. It shows a similar thickness to the previous tooth, with B bulging out lingually, but the ectoflexus is less accentuated. Both cingula were complete, the lingual one having been severely worn, especially between A-C and A-B. The medio-lingual face of A shows a clear wear facet.

If SA 153 is the anterior part of a left tooth, then it is remarkable by B being hardly displaced labially. Moreover the labial cingulum is so developed that if forms a ledge under B and A, as well as anteriorly; the lingual cingulum is particularly thick. This seems also to have been the case in the fragment SA 146.

SA 80 is again slightly curved in occlusal view and might have belonged to the same taxon, but the crown is practically completely worn off up to the cingulum level. It may be the remnant of a deciduous tooth.

SA 93 (Fig. 2f-g) has one central relatively high cusp A, a low C cusp, both being practically aligned. A cingulum disappears lingually and labially under A. This specimen could be the posterior part of a premolar of the same taxon; no upper premolar has been figured for the other species of the genus. Wear has affected the posterior side of A and both sides of C. SA 129 is even more poorly preserved.

Discussion

Such a morphology as found in the above-described upper teeth, in particular the incipient triangular pattern with A placed slightly more lingually than B and C, is strongly reminiscent of that encountered on the anterior upper molars of the various species of *Gobiconodon*: these characters are indeed the only derived upper molar features of the genus cited by Kielan-Jaworowska & Dashzeveg in the generic diagnosis (1998: 417). Also, the mode of wear seems to be similar (*id.*, fig. 9), with even the same vertical notch in the lingual cingulum being observed in an undescribed specimen of *Gobiconodon* from Khovboor, suggesting a similar occlusal pattern as in this taxon. However, if the displacement of B and C is weak on M1 in the Mongolian species of the genus, it is stronger in the following molars, giving the teeth a rectangular outline that we do not see in any of the specimens from Morocco. Thus, the Moroccan form appears to be less specialized than the other species of *Gobiconodon* in its curvature, since it is doubtful that only anterior molars would be present in the available sample. Another difference concerns the faint asymmetry of B and C, the former cusp being usually slightly more labial than the latter in the Moroccan form. In fact, the morphology of these teeth, especially those with the lesser curvature, could be very easily derived from a megazostrodont-type upper molar (Crompton 1974, fig. 6B), whose occlusal mode is closer to that of 'amphilestids' than to morganucodontids. However, it cannot be excluded that these upper molariform teeth represent those of amphilestines, for which no ascertained specimen is known so far.

Family ?AMPHILESTIDAE

Genus *KRYPTOTHERIUM* gen. nov.

Type species: *Kryptotherium polysphenos* sp. nov.

Etymology: *kruptos*, Gr., mysterious; *therios*, Gr., mammal; allusion to the uncertain nature of this small mammal.

Diagnosis: Non-therian mammals whose lower molars display an asymmetrical and curved crown composed of a major central cusp, a variable number of tiny anterior cuspules and two posterior accessory cusps. Cusp d is as long antero-posteriorly as c. This morphology is unknown in other Mesozoic mammals. No cingulum nor anterior indentation, as in *Ichthyoconodon* SIGOGNEAU-RUSSELL, 1995; but differs from this genus by the number and proportions of cusps. Differs from *Diskrytodon* SIGOGNEAU-RUSSELL, 1995, by the absence of an anterior indentation and a cingulum, by a relatively larger cusp d and the multiplicity of anterior cusps.

Kryptotherium polysphenos sp. nov.

Holotype: SA 22, a right lower molar: L = 1.38mm; W = 0.70mm.

Attributed material: Sa 69, a right lower molar: L = 1.42; W = 0.56. SA 70, a right lower molar: L = 1.41; W = 0.55. SA 101, a left lower molar: L = 1.40; W = 0.58. SA 34, anterior part of a left lower ?premolar: L = 0.59+.

Type horizon and locality: Anoual Syncline, Talsinnt Province, Morocco. Sequence B of the Red Beds; ?Berriasian.

Etymology: *polus*,, Gr. many; *sphenos*, Gr., wedge, relative to the peculiar molar morphology.

Diagnosis: As for genus.

Description:

The hypodigm of the new taxon consists of five lower molars. On the holotype SA 22 (Fig. 4 a-d and Pl. 1, 2), the crown is very narrow transversely, but not straight; instead, it is curved slightly antero-posteriorly and dorso-ventrally. It is composed of six cusps, three minute ones preceding the main one and increasing in size towards the rear. Following Crompton's (1974) nomenclature, one might interpret them as b, e and f, the latter two being antero-posteriorly aligned instead of transversely disposed, or as b, and a subdivided cuspule e. The main cusp (a) is itself followed by two cusps of decreasing size, but larger than the anterior ones, interpreted as c and d. On the lingual face, the cusps are strongly pinched, cusp a even having "wings" on each side; while on the opposite face, cusps are more regularly convex, except cusp a which is almost angular. Sharp crests separate the labial and lingual faces of each cusp, but on the most posterior cusp (d), the posterior crest is displaced labially so that, lingually, d presents a long oblique face. On the lingual face, cusp a is nearly median, but on the labial face and due to the convexity of this cusp, the three anterior cuspules make up less of the crown. At the base of these is an oblique depression. There were two roots, the anterior one being the only one preserved on SA 22; it is roughly circular in cross section, and strongly curved posteriorly; it is about as high as the crown. There is no indication of a cingulum, nor of an anterior indentation, such as are usually known in other 'triconodonts'; on the contrary, a faint wear facet is detectable labially at the base of the anterior cuspules, that might suggest overlapping of adjacent teeth. Moreover, there is a short, distinct facet in the middle of a and another longer one on the anterior face of the same cusp. Finally, there is a fainter facet on the anterior (and posterior?) faces of c, and b is labially abraded.

SA 101 (Fig. 4e-h) is very similar to SA 22, though being less convex antero-posteriorly and dorso-ventrally, and with cusp a shorter relative to c. The most posterior cusp, d, is strongly divergent. The two roots are broken off. Between the base of cusp a and the anterior cuspules, there is a sort of antero-labial indentation which may be slightly worn and would again confirm the interpretation of these cuspules as e and f; the postero-labial face of c and d may also show slight wear.

SA 69 (Fig. 5a-c), now damaged, followed the same pattern, except that there were only two anterior cusps, hence practically no antero-labial depression; the crown was also less curved. It was nearly unworn, with only the anterior side of c and less clearly d having been slightly touched by wear. No roots were preserved.

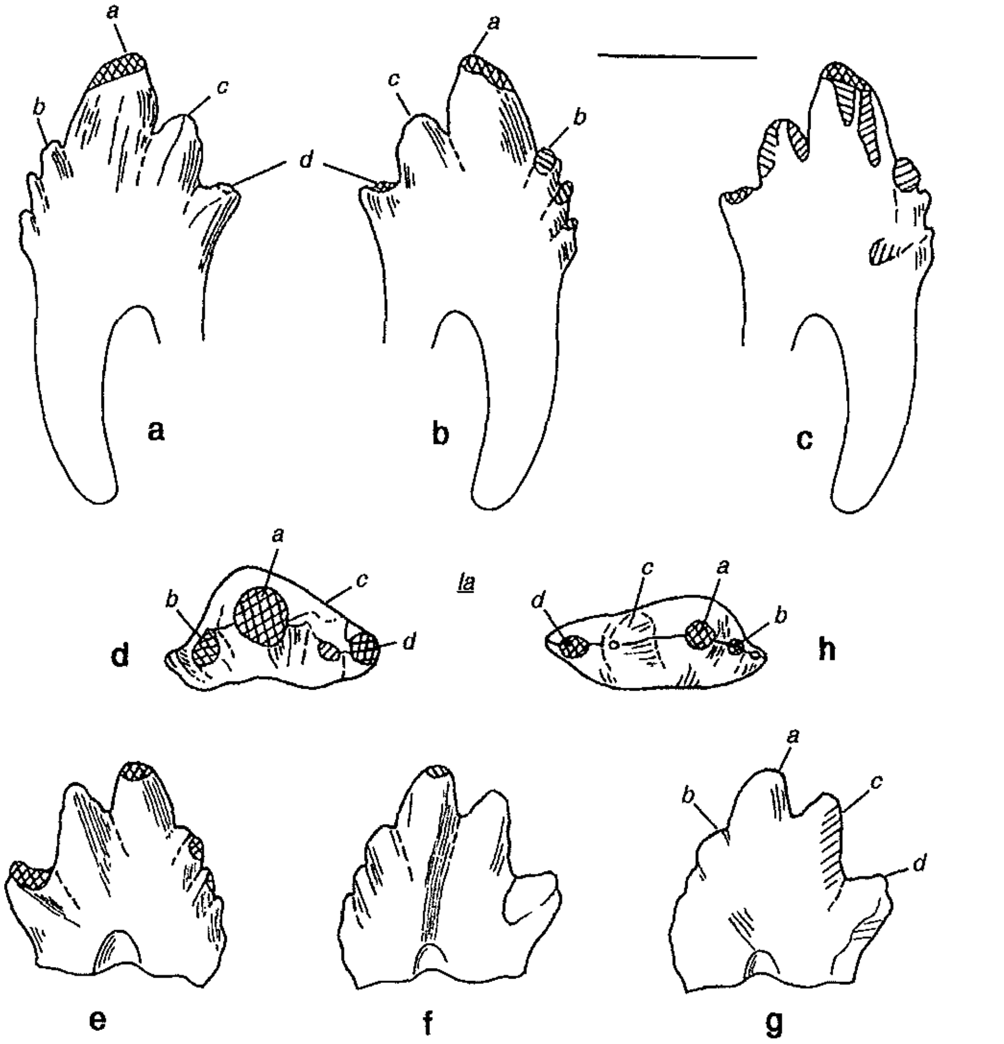

Figure 4.— *Kryptotherium polysphenos* gen. et sp. nov. **a-d**, holotype SA 22, right lower molar in lingual, labial, labial with wear facets and occlusal views: **e-h**, SA 101, left lower molar in lingual, labial, labial with wear facets and occlusal views. la, labial. Scale = 1mm.

SA 70 (Fig. 5d-g) is incomplete, but it shares the number and disposition of cusps with SA 69, except that a tiny cuspule follows the most posterior one. Wear facets are present on cusp a (whose tip is broken): one on the anterior border, a longer one on its anterior face. The various morphologies observed among these teeth could easily correspond to different positions in the jaw.

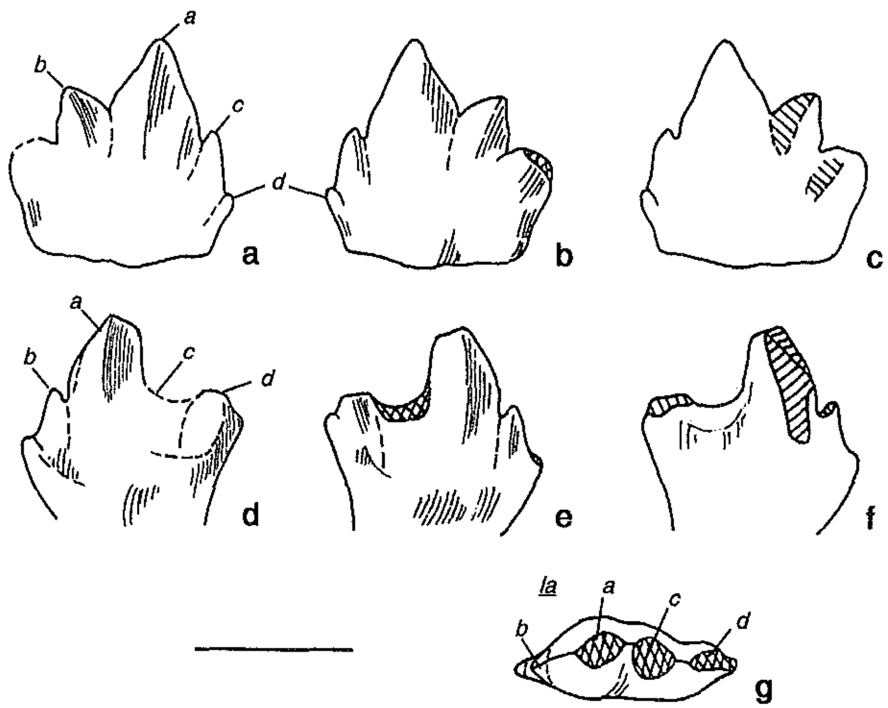

Figure 5.— *Kryptotherium polysphenos* gen. et sp. nov. **a-c**, SA 69, right lower molar in lingual, labial and labial with wear facet views; **d-g**, SA 70, right lower molar in lingual, labial, labial with wear facets and occlusal view. la, labial. Scale 1mm.

Finally, SA 34 (Fig. 6a-c) could be interpreted as the anterior part of a similar tooth with the two anterior cuspules and part of the main one. However, a is higher relative to the anterior cuspules: could the tooth represent a last lower premolar? A deep wear surface hollows the antero-labial base of a; but an occlusal wear is clearly detectable on the main cusp of p3 of *Priacodon ferox* YPM 606. The anterior root, the only one preserved, is different from that of SA 22, being straight and crested anteriorly.

Discussion

Besides their having two roots, triconodont-type lower mammalian molars are characterized not only by the longitudinal alignment of their cusps, but also by a symmetrical disposition of the latter, accessory cusps being usually equally distributed anteriorly and posteriorly relative to the main one. An exception to this rule is provided by the earliest members, the morganucodonts (Late Triassic-Early Jurassic), in which, at least in the lower jaw, the main cusp a is anteriorly situated (in relation with the poor development and cingular nature of the anterior cusp b). This was probably also the case in the Chinese genus *Klamelia* CHOW & RICH, 1984 (all molars are incomplete), and definitely so in the Late Cretaceous Argentinian *Austrotriconodon sepulvedai*

BONAPARTE, 1992. But in none of these genera does one observe the multiplication of cusps anteriorly, nor the incurvation of the crown in an horizontal and vertical plane.

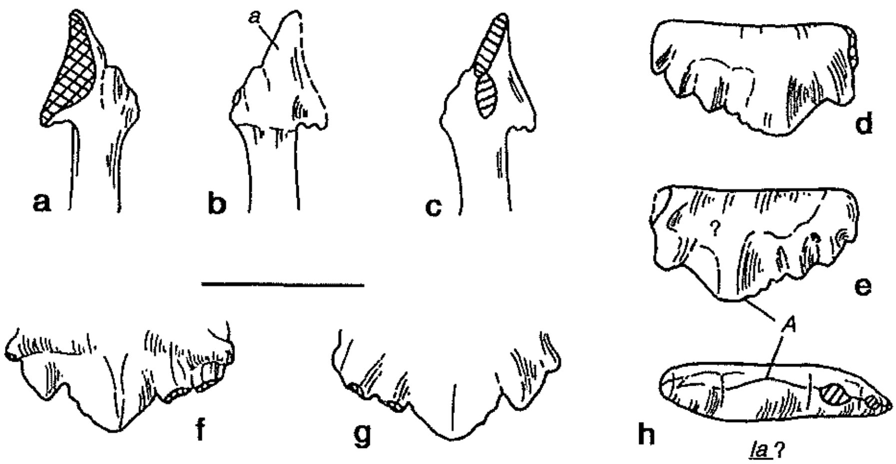

Figure 6.— **a-c**, *?Kryptotherium polysphenos* gen. et sp. nov. SA 34, ?left lower premolar in lingual, labial and labial with wear facets views ; **d-e**, gen. indet. SA 77, ?left upper molar in ?labial and ?lingual views; **f-h**, gen. indet. SA 133, ?right upper molar in ?labial, ?lingual and occlusal views. la, labial. Scale = 1mm.

This antero-posterior curvature of the crown in the teeth studied, a character slightly expressed on the molars of the Mongolian species of *Gobiconodon* (see for ex. Kielan-Jaworowska & Dashzeveg 1998, fig. 7D), and the fact that no lower tooth could be found referable to *Gobiconodon palaios*, lead inevitably to the suggestion that these lower teeth may belong to the latter taxon. The shape of cusp a as well as the fan-like disposition of the cusps are indeed reminiscent of the lower molars of other species of *Gobiconodon*. However, the total absence of molar interlocking, of a cingulum and of symmetry in the distribution of the cusps constitute major differences (though Kielan-Jaworowska & Dashzeveg (1998: 422) mention "a small lingual cingulum" and a "weak lingual cingulum" for m1 and m2 respectively of *Gobiconodon borissiaki*). Moreover, even if the approximate longitudinal alignment of cusps put these five teeth in the 'triconodont' realm, such a strongly asymmetrical morphology is unlike not only that of the gobiconodontines, but that of most 'triconodonts', with the exceptions already mentioned. Whether cusp e (or b) is here subdivided into two units, or whether these cuspules represent e and f antero-posteriorly aligned, the situation is also unique for this order; the same is true for the antero-posterior length of d relative to c. The absence of a lingual cingulum, coupled with that of a typical anterior indentation between e and f, is seen also in the large *inc. sed. Ichthyoconodon* from the same locality, and in the southern African genus *Tendagurodon* HEINRICH, 1998; but the distribution and shape of the cusps on the teeth of these mammals are completely different. Since the cingulum is developed even at the cynodont level (though not in *Sinoconodon*), its absence on the Moroccan teeth must be considered as a derived character (the same absence in late Triconodontidae upper molars has been interpreted similarly by Cifelli & Madsen

(1998); so must be the subdivision of the anterior cusps into several units, as well as the modified molar interlocking possibly into an antero-posterior overlapping; such an overlapping is known in *Klamelia*. These considerations led me to put the Moroccan lower molars in a new genus. It may be of interest to remark that, for one of the readers of an earlier version of this paper, the suggestion made above, of these teeth being the lower molars of *Gobiconodon palaios*, appeared as "impossible", while another reader saw no obstacle to this attribution. My choice of the word "suggestion" stands in the middle, though it favors the second position.

The mode of wear has been used to distinguish, among 'triconodonts', the morganucodontids and triconodontids from *Megazostrodon* and amphilestids (Crompton & Jenkins 1968, Jenkins & Crompton 1979, Crompton & Luo 1993, Cifelli *et al.*, 1998a, Kielan-Jaworowska & Dashzeveg 1998); this point will be discussed below. The distribution of wear facets in *Kryptotherium* does not seem to correspond to any of the two types, though being perhaps closer to the gobiconodontine-amphilestine type. This would constitute one more argument to group the two above-described Moroccan sets of teeth in one taxon; the obstacles enumerated above lead me to provisionnally keep the two taxa separately, pending further discoveries. In any case, the existence, in one single locality, of several unorthodox 'triconodonts' illustrates our persistently very limited understanding of mammalian life in the Mesozoic.

? *Kryptotherium polysphenos*

Indeed, two teeth, SA 77, ?left (L = 1.30+; W = 0.48) (Fig. 6d-e) and SA 133, ?right (L = 1.42; W = 0.46) (Fig. 6f-h) may be akin to *Kryptotherium* as possible upper molars. Only the crown is preserved; it is very narrow transversally and low. It consists of one main long and low cusp, situated between, on one side, two short, equal cusps disposed step-like plus one antero-basal cuspule, and, on the other side, one columnar cusp slightly larger than the opposite ones. This last cusp is itself bordered on SA 133 by a "cingular" cusp: a convex thickening rather than a cingulum encircles anterior and posterior cusps on this last tooth. By the number and shape of their cusps, these upper teeth evoke the lower teeth of *Kryptotherium*, but the three ?anterior cuspules are more spread out than on the latter and there is no antero-posterior or dorso-ventral convexity of the crown. As on the lower molars of *Kryptotherium*, no sign of interlocking is present here either, nor of an anterior overlapping. On SA 77, the medio-?lingual face of every cusp has been eroded *?post mortem;* SA 133 is practically unworn. These peculiar crowns may also be deciduous? or could even have belonged to a dinosaur! (the underside of the teeth is rounded, with no indication of roots).

Family *incertae sedis*

Genus indet.

The two following sets of asymmetrical teeth were first thought to represent 'triconodont' premolars, but the persistent presence of occlusal wear makes this assumption doubtful (R. Cifelli, pers. comm.).

Because of its asymmetrical labial convexity, the absence of an anterior indentation and the proportions of the various cusps, SA 41, left (L = 1.19; W = 0.58) (Fig. 7a-d) was first considered as affine to *Kryptotherium* and perhaps assignable to this taxon. Like SA 69 and 70, it has two anterior cusps and two posterior ones; but the most anterior one is a part of the short cingulum which underlines b at its base: no cingulum has been observed on the teeth described above. Moreover, cusps a, c and d are here more closely appressed to each other, while they diverge like in a fan on the molars described above; on the contrary, b is here more detached. Finally and mostly,

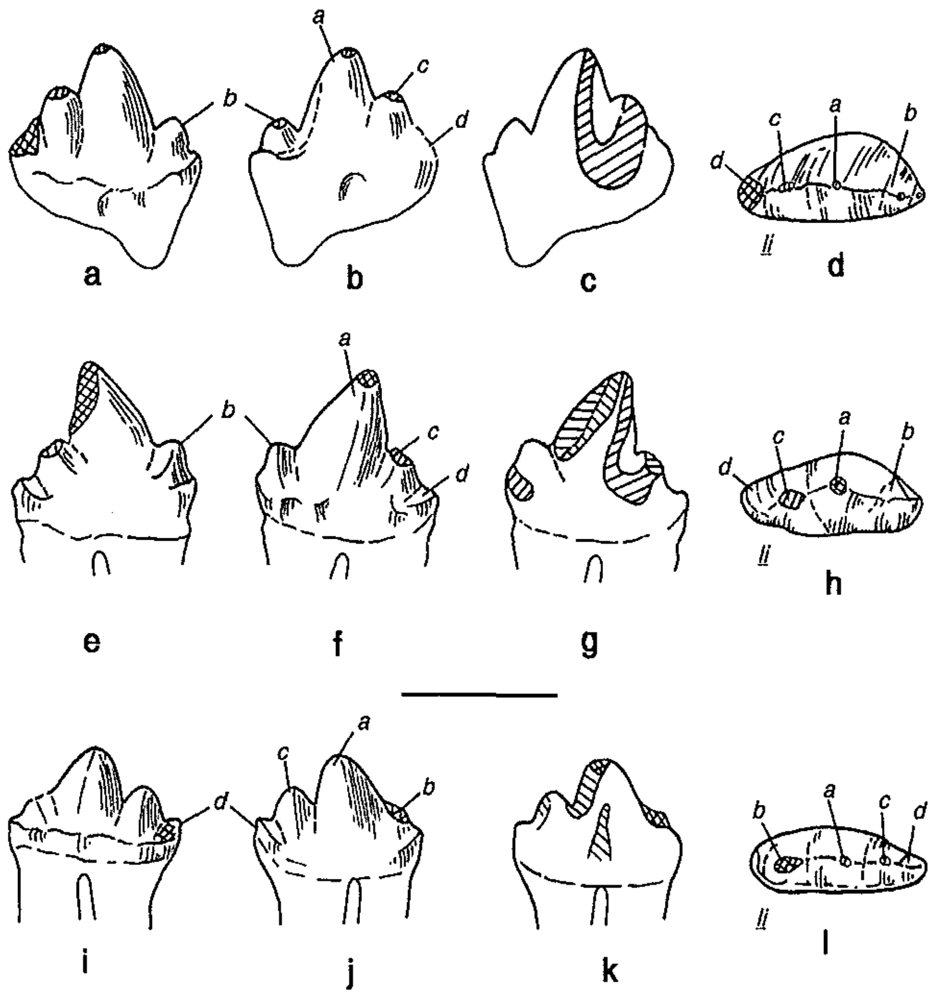

Figure 7.— Gen. indet. **a-d**, SA 41, left lower molariform, in lingual, labial, labial with wear facets and occlusal views; **e-h**, SA 3, left lower molariform in lingual, labial, labial with wear facets and occusal views ; **i-l**, SA 52, right lower molariform in lingual, labial, labial with wear facets and occlusal views. li, lingual. Scale = 1mm.

wear is typically of the triconodontid-morganucodontid type, with clear facets abrading the labial faces of a and c.

SA 3, left (L = 1.06; W = 0.49) (Fig. 7e-h and Pl. 1, 4) has been previously described in detail (Sigogneau-Russell *et al.* 1990); it closely approaches SA 41 but for a slighter posterior inclination of cusp a, a better alignment of the cusps and a slightly transversally thinner crown. The latter is also straighter than that of the molars of *Kryptotherium*. A sulcus separates the crown from the two subequal roots, the posterior one being convex anteriorly. Again, the type of wear is closer to that of morganucodontids-triconodontids: very clear U-shaped wear surfaces unite the postero-labial face of the main cusp and the labial face of the first posterior one; moreover the anterior face of a is possibly worn, as well as its medio-labial face.

SA 14, left (L = 1.13+; W = 0.39) is an incomplete tooth, with a long and relatively low cusp a; b was smaller than c and encircled by a faint and short cingulum; d was present but is broken. The antero-labial face of a and the labial face of b have been flattened by wear; the posterior face of a also has a narrow wear facet that joins another one on the anterior face of c. Finally, this latter cusp is also worn on its medio-labial face.

SA 5, left (L = 0.62+; W = 0.42) (Sigogneau-Russell *et al.* 1990) is the anterior part of a tooth with a tiny cuspule b encircled by a cingulum and half of a high cusp a. This part of the tooth is supported by a very long slender root. No wear is discernible.

These four teeth strongly evoke the lower molars of *Morganucodon* itself, with only a more convex labial face; but they are also reminiscent of larger lower premolars of several triconodontid taxa: *Astroconodon denisoni* PATTERSON, 1951 (SMP-SMU 61989; Slaughter 1969), *Priacodon ferox* (MARSH, 1880) (YPM 606), *Triconodon mordax* OWEN, 1859 (BMNH 47763b). But again, occlusal wear is considered as an obstacle to a premolar identification. In any case, that these four teeth represent a morganucodontid rather than an amphilestid as previously suggested for SA 5 (Sigogneau-Russell *et al.* 1990), appears more likely.

SA 52, right (L = 1.10; W = 0.50) (Fig. 7i-l) is undoubtedly a lower molar. The crown is lower than on the preceding four teeth. The cusps are nearly aligned antero-posteriorly: but cusp b is slightly more lingual and seems to have been subequal to c (b is damaged); moreover, its anterior base is encircled by a thickening, forming even in fact a cuspule. This thickening continues as an irregular cingulum on the whole lingual face. This morphology is again surprisingly close to that of a molar of *Morganucodon* from Wales, except that the cingulum becomes faint under a instead of forming a kuehneocone. Roots are elongate. The only clear wear facet lies on the posterior face of a and c and thus does not preclude a morganucodontid affinity.

Family *incertae sedis*

Genus indet.

Another taxon is possibly represented by three teeth displaying a much stronger asymmetry than the previous four specimens, due to the poor development of the anterior cusp b.

They are very similar lower teeth, whether premolars or molars: SA 17, right (L = 1.13; W = 0.42) (Fig. 8a-d), SA 66, left (L = 1.52; W = 0.48) (Fig. 8e-h), SA 113, left (L = 1.14; W = 0.43) (Fig. 8i-k). Their morphology is at first slightly reminiscent of that of SA 3 or SA 41, but the crown is very narrow transversely, b is reduced to a tiny cuspule at the base of a, c and d are low but well defined. There is no cingulum, only a lingual thickening at the base of c on SA 113 and SA 17. The relatively low crown is supported by two subequal and long roots. Wear is quite strong, and is again of the morganucodontid -triconodontid pattern : a wear facet is clearly visible on the middle of cusps a and c on SA 113 and SA 17, while on SA 66 the base of c is deeply hollowed.

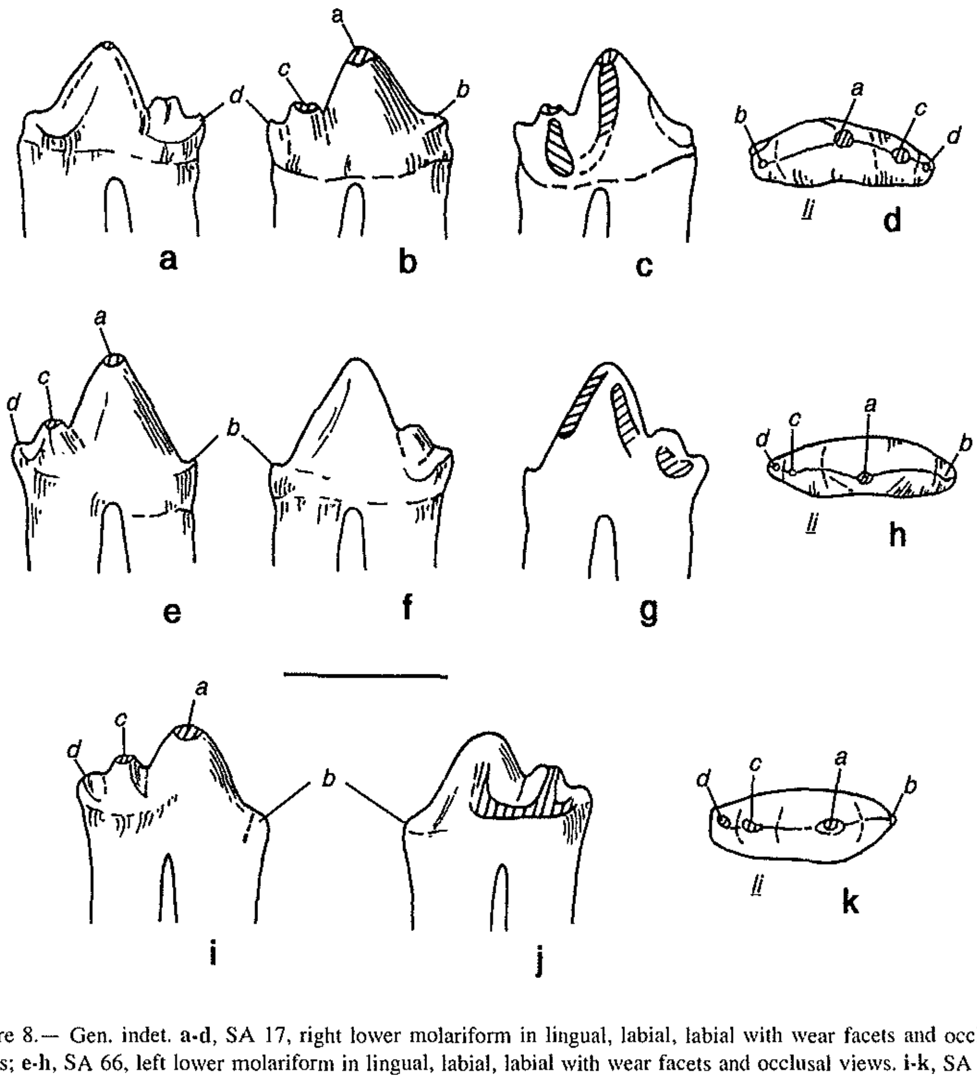

Figure 8.— Gen. indet. a-d, SA 17, right lower molariform in lingual, labial, labial with wear facets and occlusal views; e-h, SA 66, left lower molariform in lingual, labial, labial with wear facets and occlusal views. i-k, SA 113, left lower molariform in lingual, labial and occlusal views. li, lingual. Scale = 1mm.

On the latter tooth, there is also a faint facet on the antero-labial and postero-labial sides of a.

Again, these teeth differ from the lower molars of *Kryptotherium*: the crests separating the labial and lingual faces of the cusps are less sharp, cusp c is not so well detached, cusp b is not subdivided and in fact hardly indicated; and mostly, wear creates a different pattern. They were suspected to represent upper premolars: *Priacodon grandaevus* USNM 269 shows a very similar last upper premolar; but again, the heavy wear speaks again such an interpretation.

Family AMPHILESTIDAE OSBORN, 1888
Subfamily AMPHILESTINAE OSBORN, 1888

Genus indet.

SA 2, right (L = 0.93+) (Fig. 9a-c) has already been described (Sigogneau-Russell *et al.* 1988, Sigogneau-Russell *et al.* 1990). It is the only 'triconodont' tooth from the collection to have a typical anterior indentation between e and f. Moreover, this

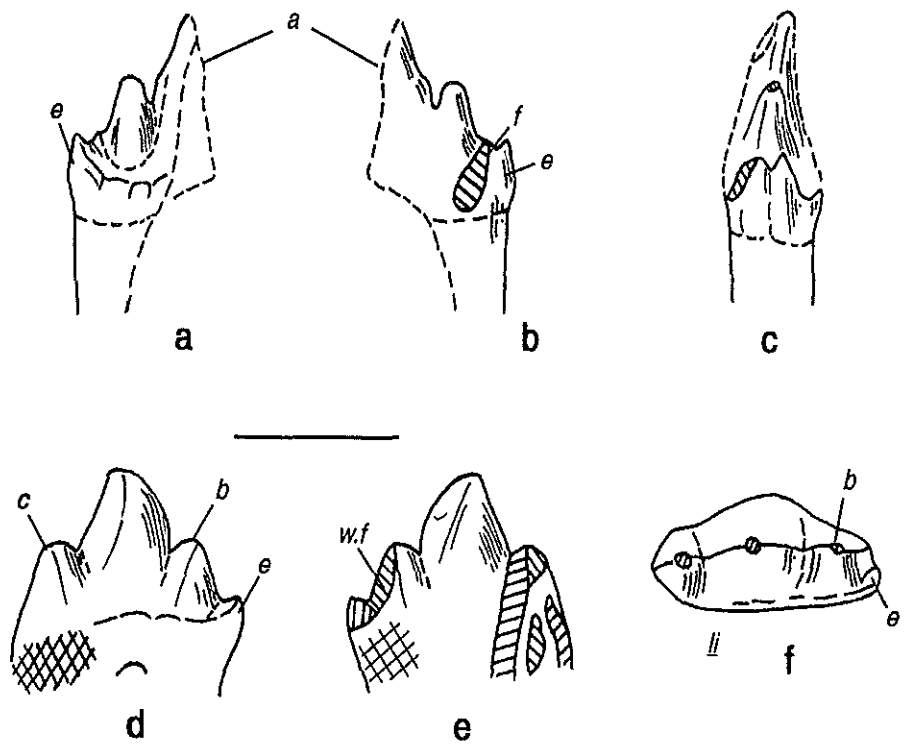

Figure 9.— **a-c**, Amphilestidae indet., SA 2, right lower molariform in lingual, labial and anterior views ; **d-f**, ?Amphilestidae indet. SA 86, left lower molariform, in lingual, labial with wear facets and occlusal views. li, lingual. Scale = 1mm.

indentation is of the amphilestid type (see below), with these two cuspules of nearly equal height and pressed against each other, only separated by a linear sulcus. Wear has flattened the labial face of f : such a feature is observable on the molars of *Amphilestes* OWEN, 1845, where it also extends the whole height of cusp b.

?Family AMPHILESTIDAE

Gen. indet.

One incomplete left lower tooth, SA 86 (L = 1.40; W = 0.65) (Fig. 9d-f) could also be considered as amphilestid. It is a transversally narrow tooth with a relatively high and slightly asymmetrical cusp a, bordered anteriorly and posteriorly by a small cusp, both being subequal lingually; but labially, b and c have a very different shape, with c being more cylindrical; all cusps are aligned longitudinally. A cingulum borders the crown lingually, hardly rises in the middle and culminates in a small cusp e anteriorly. A clear vertical wear facet gouges the anterior face of c: such a feature has been observed on an unpublished amphilestid tooth from Kirtlington (BMNH J .744); however, in this latter case, the crown is more symmetrical. Another wear facet has eroded the antero-labial face of b, and the posterior side of c bears two wear facets forming an angle. In spite of its amphilestid characters, the very slight asymmetry and the absence of anterior indentation leave this tooth *incertae sedis*.

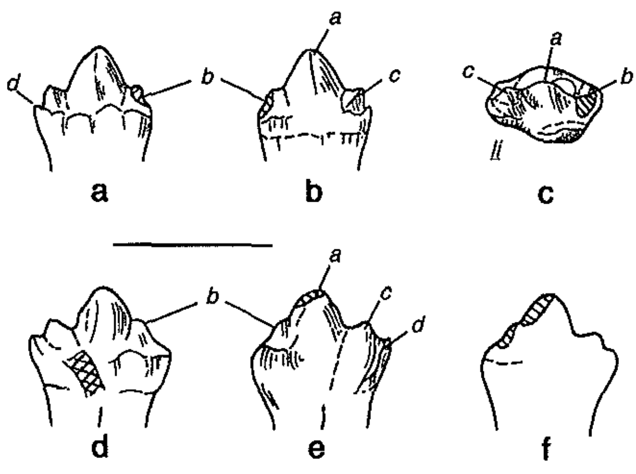

Figure 10.— ?Amphilestidae indet. a-c, SA 9, left lower molariform, in lingual, labial and occlusal views; d-f, SA 20, left lower molariform, in lingual, labial and labial with wear facets views. li, lingual. Scale = 1mm.

A tiny left molar SA 20 (L = 0.90; W = 0.59) (Fig. 10d-f and Pl. 1, 3) could represent a last molar of the same taxon as above. It is robust, with a short cusp b poorly differentiated from cusp a and encircled by a thick and festooned cingulum; but here b is slightly labial relative to c; d is very small. There is no anterior indentation, only a notch antero-lingually displaced. The lingual cingulum was probably complete (the tooth has been secondarily damaged). The two roots are fused, but separated all along their height and on both sides by a sulcus. Wear may have slightly affected the anterior part of a and b. Very small last molars are known in the amphilestid *Comodon gidleyi* (SIMPSON, 1925). SA 20 looks very close to the latter, differing in the relative development of cusps: subequal b and c are cingular in *Comodon*. A reduced last molar is also known in the triconodontid *Corviconodon* CIFELLI *et al.*, 1998, but it is very different from SA 20.

It is not clear whether SA 9 (L = 0.72; W = 0.54) (Fig. 10a-c), itself probably a last lower left molar (not right as indicated in Sigogneau-Russell *et al.*, 1990, fig. 6) could be classified in the same taxon as SA 20. The crown is smaller than on SA 20, cusps b and c are nearly equal and symmetrically disposed relative to a; the lingual cingulum is complete and circles labially around b and c; d is barely developed. There is only one root, with one slight lingual sulcus. Wear has abraded b anteriorly; cusps a and c may have suffered some wear. This tooth is even closer to the last molar of *Comodon* than is SA 20, though b and c are again not cingular in our specimen. If these teeth are indeed amphilestid, they enlarge the range of dental variation in this family.

Family *incertae sedis*

Gen. indet.

Completely different are two lower (pre)molars: Sa 53 (Fig. 11a-c) is a relatively large right tooth (L = 1.72; W = 0.62) with only two main cusps, a and c, widely separated from each other and with an angular lingual face. Cusp a is anteriorly situated, b remaining basal and minuscule; d follows c as a mere step on the posterior crest of the latter. The posterior crest of a is sharper than the anterior crest. There is a shallow basin labially between a and c, bordered basally by a faint step; a and c are aligned, but d is slightly displaced lingually. The two roots are widely separated, with the anterior one being curved posteriorly. A circular wear facet is visible at the base of c and another faint one on the anterior face of a and possibly c. Sa 128, left (L = 1.39+: W = 0.51) (Fig. 11 d-f), incomplete anteriorly, is close to SA 53, but the posterior crest of a is more concave.

The morphology of these teeth somewhat recalls the second set of molariforms described above (SA 17 for example: small b, shallow basin under c, same wear at the base of c), but the posterior part of the crown appears very different, the size is much larger and the occlusal view shows a slight antero-posterior curvature. In fact, if these teeth are not milk teeth as the divergence of the roots might suggest, the morphologically closest triconodont form appears to be the holotype tooth of the South American *Austrotriconodon sepulvedai*, because of the preeminence of a, the asymmetry of its crests and the presence of a lingual basin. However, the latter is four times larger, c is smaller than d and a cingulum turns around the base of d, lingually and labially, while this latter cusp is here reduced to a bump. Such a bump is seen on *A. mckennai* BONAPARTE, 1986, a tooth twice as large as that of our specimen, less asymmetrical and with a posterior crest of c not being concave. Again, the eventuality of SA 53 and SA 128 being upper premolars should not be excluded (see the North American triconodontid *Astroconodon denisoni* SLAUGHTER, 1969: fig. 1C)

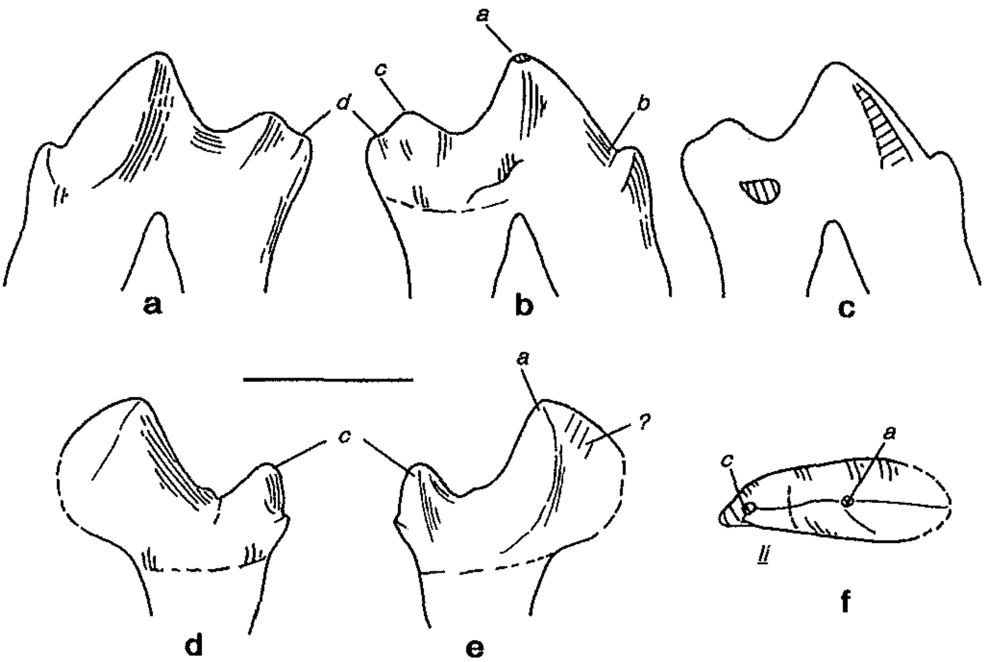

Figure 11.— Gen. indet. **a-c**, SA 53, right lower molariform, in lingual, labial, labial with wear facets views; **d-f**, SA 128, left lower molariform in labial, lingual and occlusal views. li, lingual. Scale = 1mm.

Conclusion

The assemblage presented here is remarkably heterogenous. If none of the molars can be attributed to the monophyletic Cretaceous Triconodontidae (Cifelli *et al.*, 1998), united by the strict interlocking of teeth and heightening of cusp d, some of the molariforms indicate the presence of triconodontids or late morganucodontids. On the other hand, the presence of gobiconodontines is, if not attested, at least strongly suggested (though homoplasy should never be excluded). This last group of mammals is already known to have had a large geographical extension, having been mentioned in Mongolia (Trofimov 1978; Kielan-Jaworowska & Dashzeveg 1998), North America (Jenkins & Schaff 1988), Siberia (Maschenko & Lopatin 1998), Spain (Cuenca Bescos & Canudo 1999), China (Godefroit & Guo 1999; Wang *et al.* 2001). The Moroccan species would be the oldest representative of this subfamily so far known, and would enforce Cifelli's suggestion (2000: 61) of "faunal ties" between the different continents concerned. Finally, *Kryptotherium*, if really a separate taxon from the new gobiconodontine, would still come close to amphilestines. Some isolated molars are even reminiscent of the amphilestine *Comodon*. In summary, this diverse Moroccan assemblage of 'triconodont' teeth contains taxa so far unknown in other more or less contemporaneous localities, while others seem to point to Laurasian (and Gondwanan?) families.

RELATIONSHIPS OF 'AMPHILESTIDS'

It is currently assumed (Luo 1994; Cifelli *et al.* 1998) that there are two modes of occlusion among 'triconodonts', one shared by Morganucodontidae and Triconodontidae (one-to-one relationships, Crompton 1974; Jenkins & Crompton 1979), the other by Amphilestinae and Gobiconodontinae (two-to-one). The last two subfamilies (included in the same family by Kielan-Jaworowska & Dashzeveg 1998) would then be closer to 'therians' (Jenkins & Crompton 1979), with which amphilestids would also share the mode of interlocking and the arrangement of cusps. Kielan-Jaworowska & Dashzeveg (1998) have discussed these three points. I shall here add a few comments.

Arrangement of cusps

Typically linear and presumably primitive, in morganucodontids as well as in triconodontids, the arrangement of lower molar cusps is said to be slightly triangular in amphilestines (Osborn 1888, Mills 1971, Crompton 1974, Kielan-Jaworowska & Dashzeveg 1998). The subfamily Amphilestinae (= Amphilestidae *in* Rougier 1999, who considers this family as paraphyletic) includes five genera, two from the Middle Jurassic of England, *Phascolotherium* OWEN, 1838 and *Amphilestes*, three from the Morrison Formation of North America, *Comodon*, *Aploconodon* SIMPSON, 1925 and *Triconolestes* ENGELMANN & CALLISON, 1998, all represented by lower molars only. Of the three lower jaws of *Amphilestes broderipii* (two in Oxford, holotype in York), none was prepared on both sides prior to 1999, so that no occlusal view was in fact directly available. Crompton (1974) drew his opinion on the triangular disposition of cusps in *Amphilestes* from stereophotographs, and said that in labial view, cusp a is more salient than b and c. It can easily be objected that the same is true for the lower molars of *Morganucodon* (see for example Kermack *et al.* 1973), *Brachyzostrodon* SIGOGNEAU-RUSSELL, 1983, or, for that matter *Phascolotherium*, for which one jaw (BMNH M7595) is available in occlusal view. Examination of this view (Pl. 1, 7) shows that, if a is more salient labially, all three cusps are nevertheless disposed in a linear pattern. This was already the conclusion of Goodrich (1894) and Simpson (1928). Finally, direct observation made on the newly cleaned specimen of *Amphilestes* (Oxford J. 20079, Pl. 1, 5) shows that the cusps are indeed aligned. The same is true for the preserved cusps of the unique molar of *Triconolestes*. However, in *Comodon* (Pl. 1, 6) and *Aploconodon*, one observes a very slight curvature in occlusal view. In our fauna, on the five teeth (SA 2, SA9, SA 20, SA52, SA86) suspected to be amphilestines, cusps b, a and c are disposed linearly. Moreover, if one compares a molar of *Comodon* to the most obtuse molar of *Tinodon* MARSH, 1879, for example (Pl. 1, 8-9), the morphology is quite different, with, in the former, cusp a narrower, b and c more deeply incised labially, and more angular also labially. The difference is even stronger between *Tinodon* and *Phascolotherium* (Pl. 1, 7 and 8).These observations do not favor a 'therian' relationships for amphilestines based on the arrangement of cusps, nor even the interpretation that 'therian' teeth would represent a further development of the

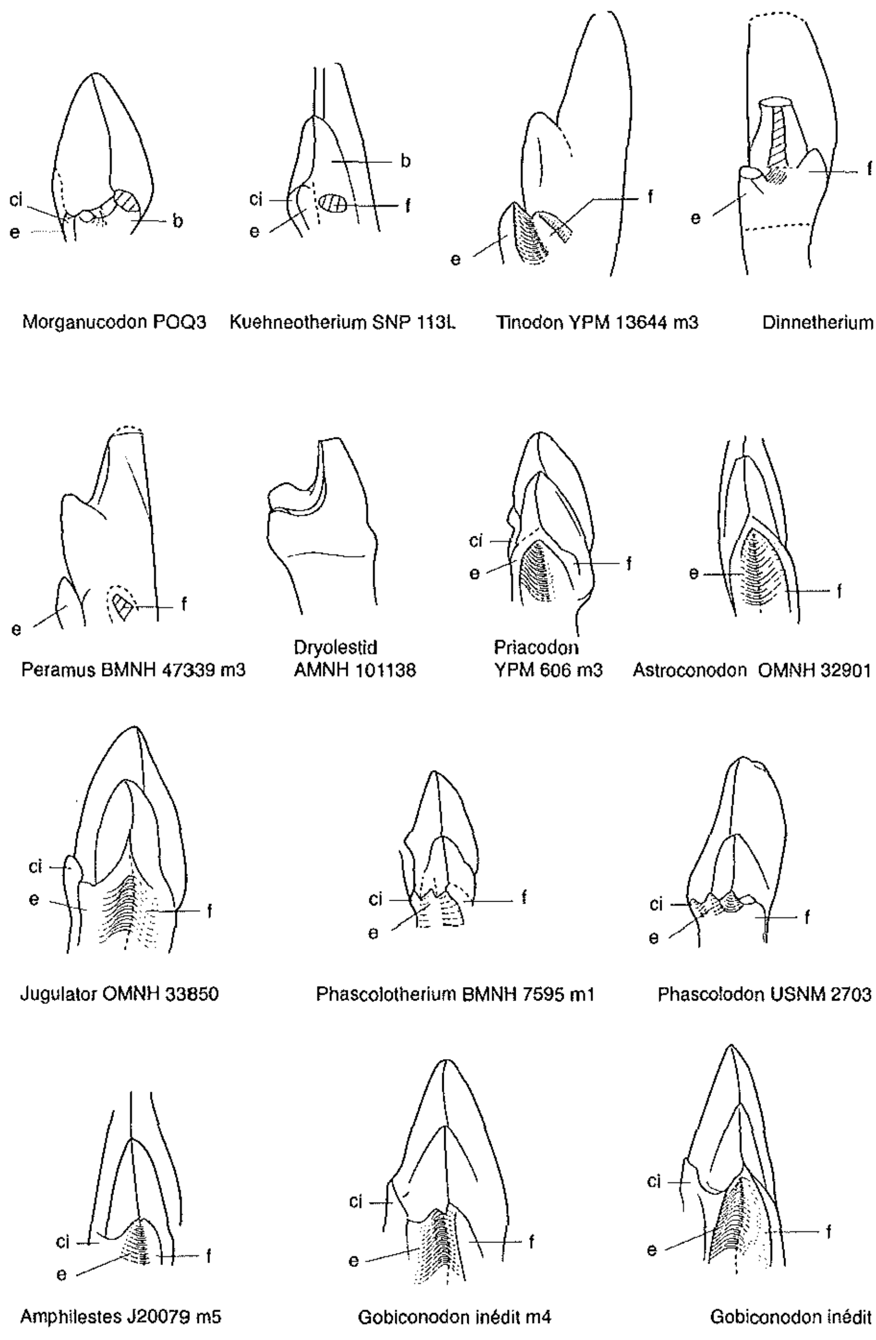

Figure 12.— Analysis of cusps e and f in the various genera considered in this study.

'amphilestid' condition. As for gobiconodontines, "in all three species of *Gobiconodon*, the cusps of lower molariforms are arranged mesio-distally" (Kielan-Jaworowska & Dashzeveg 1998: 432).

Upper molars are unknown in amphilestines. In gobiconodontines, (Jenkins & Schaff 1988, Kielan-Jaworowska & Dashzeveg 1998) M3 to M5 at least present a marked curvature of the crown; but again this configuration, with B and C of approximately the same size and disposition, is unmatched in early 'therian' upper molars, whether those of symmetrodonts or cladotheres: the stylocone (cusp B) is directly labial, even in the earliest forms (the particular case of "*Eurylambda*" is discussed in Ensom & Sigogneau-Russell 2000 and in Rougier 2002); so that this more or less symmetrical curvature of gobiconodontine upper molars is not necessarily indicative of a relationship with 'therians'.

Interlocking

Adjacent morganucodont lower molars interlock between b and e, while interlocking intervenes between e and f in amphilestines, gobiconodontines and some 'therians'. On the other hand, Kielan-Jaworowska & Dashzeveg (1998: 431-432) state that "Triconodontidae... display the interlocking mechanism of *Morganucodon* pattern, different from that of *Kuehneotherium, Tinodon* and Gobiconodontinae". Similarly, Cifelli & Madsen (1998: 409) observe, in Triconodontidae, "an extensively developed molar interlocking system, in which a groove extending the entire anterior face of a molar houses a ridge" (in fact cusp d) "developed on the posterior face of its predecessor".

First, morganucodonts (and *Megazostrodon)* molars interlock between b and e, because b is still cingular: in some molars of *Morganucodon* (MNHN POQ 26 and POQ 32) b is in the process of being detached from the cingulum and a tiny cuspule f is discernible at its base. Secondly, a survey of some 30 lower molars of kuehneotheriids from Saint-Nicolas-de-Port, France (Godefroit & Sigogneau-Russell 1999) shows that only half of them have an individualized cuspule f (the latter is more frequent in the *Kuehneotherium* hypodigm from Wales). Moreover, f as a cuspule is rare in other 'therians': it is limited to primitive symmetrodonts (tinodontids *sensu* Fox 1985), is even inconstant there (being often absent in the anterior molars), to peramurans and early tribosphenids (antero-labial cuspule), although the antero-labial cingulum of modern 'therians' is probably homologous (Butler 1978). Most of all, these cusps e and f appear quite different between 'therians' and 'non-therians' (Fig. 12): in the former, e is a high point of the cingulum, whereas f is a short protuberance at the labial base of the paraconid, postero-ventrally inclined. In triconodontids **and** gobiconodontines, e and f are two vertical, high and parallel columns. In fact, the similarity between the latter two in this respect is very striking.This "columnar" character is usually less accentuated in early triconodontids and varies along the jaw, while in the middle-late Cretaceous forms, e and f become stylised, being mostly defined by the deep sulcus which separates them and encroach upon the expanding d; but the pattern stays the same. In gobiconodontines, e and f remain better defined, but the pattern is again very similar to that of triconodontids. Consequently, the space separating e and f is wide in 'therians', while it is a narrow, V-shaped groove in triconodontids and gobiconodontines. As for the amphilestine condition, it appears definitely closer to that of the latter two in the shape of e and f and in that of the groove (see for instance BMNH M35000), although these cusps are usually lower with respect to the height of the crown and visible mostly on the last molars (as in early triconodontids). As mentioned above, the total absence of interlocking apparently occurs only in *Klamelia*, *Tendagurodon* and *Triconolestes*, all genera of possible 'amphilestid' affinities; and of course in *Kryptotherium* gen. nov. and *Ichthyoconodon*. The situation is unknown in *Liaotherium* ZHOU *et al.*, 1991, included in ?Amphilestidae by the authors. Fig. 12 shows the survey of this condition in all the forms mentioned. It should finally be stressed that the amount of interlocking is very variable along the jaw in all cases where material is available, being more accentuated posteriorly; that the condition in *Phascolotherium* and *Amphilestes* is difficult to observe because teeth are strongly appressed, and that in one unpublished tooth of *Gobiconodon*, the sulcus between e and f goes down the roots as in Triconodontidae (Cifelli *et al.* 1998).

This brief survey shows that this character of interlocking can no longer be invoked as an argument to unite amphilestines or gobiconodontines with 'therians'. In fact, it is doubtfully useful in determining affinities, since one finds a similar pattern in gobiconodontines and triconodontids.

Occlusion

Mills (1971), Crompton (1974), Jenkins & Crompton (1979) Cifelli *et al.* (1998) pointed out that the amphilestine occlusal pattern was different from that of morganucodontids and triconodontids and was close to that of symmetrodonts. Jenkins & Schaff (1988) and Kielan-Jaworowska & Dashzeveg (1998) arrive at the same conclusion with gobiconodontines. Such a conclusion was deduced, for Mills (1971: 53-54) "from the pattern of wear in *Amphilestes* (which) is essentially of the *Kuehneotherium* type".... "the principal upper cusp occludes against the mesial cuspule of the more posterior lower molar". Crompton (1974: 430) used stereophotographs of the Oxford specimen of *Amphilestes* to consider that "the principal cusp of the upper molar occluded between cusps f and b and in this respect they resemble the Late Jurassic symmetrodont *Tinodon*".

However, while wear facets of morganucodontids, triconodontids and gobiconodontines have been extensively figured, those of amphilestines have never been. I have examined (Fig. 13) all available specimens of Middle-Late Jurassic amphilestines (except *Triconolestes*): *Comodon* and *Aploconodon* from the Morrison Formation, *Phascolotherium* and *Amphilestes* from the Stonesfield Slates as well as an unpublished amphilestid tooth from Kirtlington (BMNH M35000). On the other hand, Godefroit & Sigogneau-Russell (1999) have, after Mills (1971), established a wear series in the French kuehneotheriids.

It can reasonably be assumed that the first wear facet to appear on a lower molar is caused by the main cusp of the corresponding upper, that is A; which gives us the position of A relative to the lower molar. In morganucodonts, from Mills' analysis, wear begins on the posterior face of a and the anterior face of c; then comes the anterior face of a. It follows that, in this family, A occludes posteriorly to a, or a occludes between B and A as shown in Mills (1971, fig. 1) and as stated by Luo (1994).

In the triconodontid *Corviconodon* (Cifelli *et al.* 1998), and other triconodontids, as well as in *Jeholodens* as reconstructed in Ji *et al.* (1999), cusp A similarly occludes between a and c. In *Phascolotherium* BMNH M7595, as far as wear facets are discernible, the first wear occurs on c and d; in *Amphilestes* (Oxford J 20079), a vertical facet wears the anterior face of b. From these two cases, it can be deduced that A occludes between two lower molars. In *Gobiconodon hoburensis* (Kielan-Jaworowska & Dashzeveg 1998, fig. 8), b and d of adjacent teeth are the first to be worn; hence A occludes again between two lower teeth (though the cingular facet on top of B is difficult to account for in this scenario). In *Kuehneotherium,* on the other hand, according to Mills (1984, fig. 5), the first facet, due to cusp A of the upper molar, appears on cusp c, which leads to an occlusion little different from that of *Morganucodon* (A between a and c), but Godefroit & Sigogneau-Russell (1999) conclude from their observations that A of the upper molars of *Kuehneotherium* would better occlude between two lower molars. Finally, in *Tinodon* (USNM 1648), the anterior part of A would occlude against the posterior flank of c; thus A would occlude between c and a of the adjacent teeth (as previously recognized by Crompton & Jenkins 1967, fig. 1).

Before any conclusion can be drawn, it should be stressed that wear facets are not always unequivocal, so that, if the number of specimens is limited, they should be regarded with caution. Moreover, in some forms at least and as already acknowledged by Mills (1984), results depend on the tooth observed. Nevertheless, it does seem that the type of occlusion of gobiconodontines at least and perhaps amphilestines, too, is closer to that of tinodontids than to that of triconodontids or morganucodontids. The same is true for *Megazostrodon*, no longer considered as a morganucodontid: in this genus, the occlusion has been reconstructed as similar to that of tinodontids (Crompton 1974). However, morganucodontids and triconodontids, though sharing a similar occlusal mode (Cifelli *et al.* 1998) are said to not constitute a monophyletic unit in all recent cladistic analyses. It thus should be considered that the occlusal mode is an adaptive process, which does not necessarily link phylogenetically the forms exhibiting a similar mode, whereas it certainly separates those functioning according to a different one.

In summary, if the proportions and structure of the cusps, as well as the mode of occlusion, possibly unite gobiconodontines and amphilestines, there is no solid argument, in our state of knowledge, that can be invoked to link these forms with 'therians'. The points invoked by Mills (1971) in favor of this theory, in addition to those cited above, are: 1) the posterior face of lower molars is more transverse than the anterior face: but this is not noticeable in *Amphilestes* and hardly so in other amphilestines or gobiconodontines; 2) the anterior cusp (b) is not cingular; nor is it in triconodontids; 3) the lower lingual cingulum is non cuspidate; it is certainly so in *Phascolotherium* and *Gobiconodon ostromi.*

In fact it is probably wise to admit that teeth alone do not yield enough data to assert affinities of amphilestines-gobiconodontines versus triconodontids or 'therians'. At a time when cranial and postcranial material of Mesozoic mammals is becoming more and more abundant, data provided by the dental morphology alone appear less and

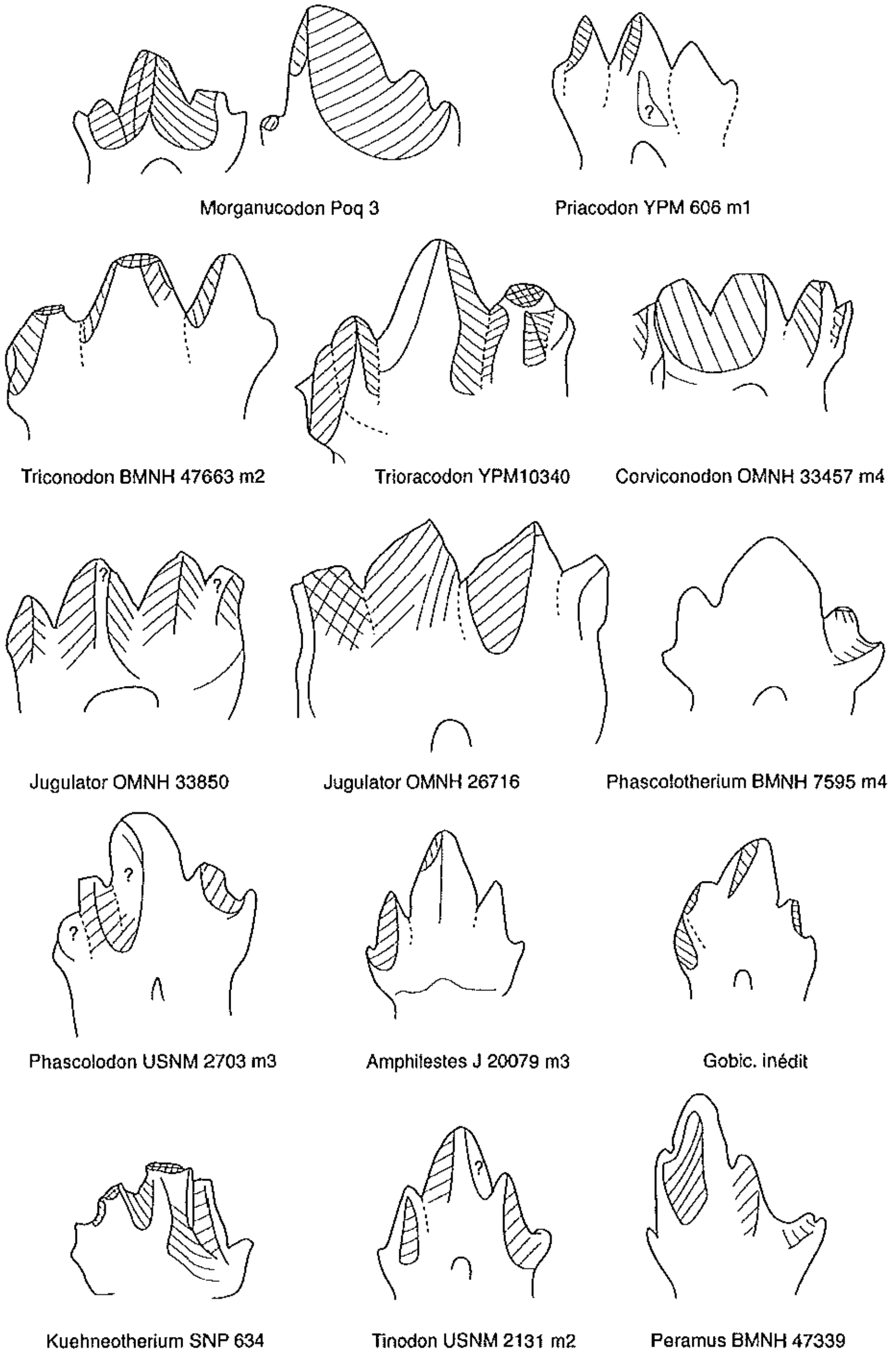

Figure 13.— Disposition of wear facets on some lower molars of the various genera considered in this study. Front is to the left.

less reliable. However, when these teeth come from a geological period and an area practically devoid of such fossils, they have the merit to testify to the yet underestimated diversity of mammals, if not to elucidate their phylogenetic relationships.

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REFERENCES

BONAPARTE, J.F., 1986. — Sobre *Mesungulatum houssayi* y nuevos mamíferos Cretácicos de Patagonia, Argentina. *Actas IV Congreso Argentino de Paleontología y Biostratigrafía*, 2: 48-61.

BONAPARTE, J.F., 1992. — Una nueva especie de Triconodonta (Mammalia), de la Formación Los Alamitos, Provincia de Río Negro y comentarios sobre su fauna de mamíferos. *Ameghiniana*, 29 : 99-110.

BUTLER, P.M., 1978. — Molar cusp nomenclature and homology. In BUTLER, P.M. & JOYSEY, K.A. (eds), *Development, Function and Evolution of teeth*. Academic Press, London: 439-454.

CHOW, M. & RICH, T.H.V., 1984. — A new triconodontan (Mammalia) from the Jurassic of China. *Jour. Vert. Paleont.*, 3 (4): 226-231.

CIFELLI, R.C., 2000. — Cretaceous mammals of Asia and North America. *Paleont. Soc. Korea Special Publ.*, 4: 49-84.

CIFELLI, R.L., 2002. — *Comodon* Kretzoi and Kretzoi, 2000 replaces *Phascolodon* Simpson, 1925 (Mammalia), not *Phascolodon* Stein, 1859. *Acta Pal. Pol.*, 47: 184.

CIFELLI, R.L. & MADSEN, S.K., 1998. — Triconodont mammals from the medial Cretaceous of Utah. *Jour. Vert. Paleont.* 18 (1): 237-241.

CIFELLI, R.L., WIBLE, J.R. & JENKINS, F.A., Jr., 1998. — Triconodont mammals from the Cloverly Formation (Lower Cretaceous), Montana and Wyoming. *Jour. Vert. Paleont*, 18 (2): 403-411.

CIFELLI, R.L., LIPKA, T.R., SCHAFF, C. R.& ROWE, T.B., 1999. — First Early Cretaceous mammal from the eastern seaboard of the United States. *Jour. Vert. Paleont.*, 19: 199-203.

CROMPTON, A.W., 1974. — The dentitions and relationships of the southern African Triassic mammals, *Erythrotherium parringtoni* and *Megazostrodon rudnerae. Bull. Brit. Mus. (Nat. Hist.)*, 24: 399-437.

CROMPTON, A.W. & JENKINS, F.A. Jr, 1967. — American Jurassic symmetrodonts and Rhaetic 'pantotheres'. *Science*, 155: 1006-1008.

CROMPTON, A.W. & JENKINS, F.A., Jr, 1968. — Molar occlusion in Late Triassic mammals. *Biol. Rev.*, 43: 427-458.

CROMPTON, A.W. & LUO, Z.-H., 1993. — Relationships of the Liassic mammals *Sinoconodon, Morganucodon oehleri* and *Dinnetherium*. In SZALAY, F.S., NOVACEK, M.J. & MCKENNA, M.C. (eds), *Mammal Phylogeny: Mesozoic Differentiation, Multituberculates, Monotremes, Early Therians and Marsupials*. Springer Verlag, New York: 30-44.

CUENCA BESCOS, G. & CANUDO, J.L., 1999. — A Lower Cretaceous traveler: *Gobiconodon* ('Triconodont', Mammalia) from Vallipón (Upper Barremian), Teruel, Spain. *IV European Workshop on Vertebrate Paleontology, Albarracin, Spain:* 41.

DATTA, P.M. & DAS, D.P., 1996. — Discovery of the oldest fossil mammal from India. *Ind. Min.*, 50: 217-222.

ENGELMANN, G.F. & CALLISON, G., 1998. — Mammalian faunas of the Morrison Formation. In CARPENTER, K., CHURE, D.J. & KIRKLAND, J.I. (eds), *The Jurassic Morrison Formation: An Interdisciplinary Study. Modern Geology*, 23 (2): 343-379.

ENSOM, P.C. & SIGOGNEAU-RUSSELL, D., 2000. — New symmetrodonts (Mammalia, Theria) from the Purbeck Limestone Group, Early Cretaceous of southern England. *Cret. Res.*,.21 : 767-779.

FOX, R., 1985. — Upper molar structure in the Late Cretaceous symmetrodont *Symmetrodontoides* Fox, and a classification of the Symmetrodonta. *Jour. Pal.*, 59: 21-26.

GODEFROIT, P. & GUO, D.-Y., 1999. — A new amphilestid mammal from the Early Cretaceous of Inner Mongolia (P.R. China). *Bull. Inst. Roy. Sc. Nat. Belgique, Sc. Terre*, 69- supp.B : 7-16.

GODEFROIT, P. & SIGOGNEAU-RUSSELL, D, 1999. — Kuehneotheriids from Saint-Nicolas-de-Port (Late Triassic of France). *Geol. Belgica*, 2/3-4: 181-196.

GOODRICH, E.S., 1894. — On the Fossil Mammalia of the Stonefield Slate. *Quat. Jour. Microsc. Soc.*, 35: 407-431.

HEINRICH, W.-D., 1998. — Late Jurassic mammals from Tendaguru, Tanzania, East Africa. - *Jour. Mamm. Evol.*, 5: 269-290.

JENKINS, F.A., Jr & CROMPTON, A.W., 1979. — Triconodonta. In LILLEGRAVEN, J.A. , KIELAN-JAWOROWSKA, Z. & CLEMENS, W.A. (eds), *Mesozoic Mammals, The first two-thirds of mammalian history*. University of California Press, Berkeley: 74-90.

JENKINS, F.A., Jr & SCHAFF, C.R, 1988. — The Early Cretaceous mammal *Gobiconodon* (Mammalia, Triconodonta) from the Cloverly Formation in Montana. *Jour. Vert. Paleont.*, 8: 1-24.

JI, Q., LUO, Z & JI, S., 1999. — A Chinese triconodont mammal and mosaic evolution of the mammalian skeleton. *Nature*, 398: 326-330.

KERMACK, K.A., MUSSETT, F. & RIGNEY, H.W., 1973. — The lower jaw of *Morganucodon. Zool. Jour. Linn. Soc. London*, 53: 87-175.

KIELAN-JAWOROWSKA, Z., 1997. — Characters of multituberculates neglected in phylogenetic analyses of early mammals. *Lethaia*, 29: 249-266.

KIELAN-JAWOROWSKA, Z. & DASHZEVEG, D., 1998. — Early Cretaceous amphilestid ('triconodont') mammals from Mongolia. *Acta Pal. Pol.*, 43 (3): 413-438.

LUO, Z.-H., 1994. — Sister taxon relationships of mammals and the transformations of the diagnostic mammalian characters. In FRASER, N.C. & SUES, H.-D. (eds), *In the shadow of the dinosaurs - Early Mesozoic tetrapods*. Cambridge University Press, Cambridge, Cambridge and New York: 98-128.

MCKENNA, M.C. & BELL, S.K., 1997. — *Classification of Mammals Above the Species Level*. Columbia University Press, New York, 631 p.

MASCHENKO, E.N. & LOPATIN, A.V., 1998. — First record of an Early Cretaceous triconodont mammal in Siberia. *Bull. Inst. Roy. Sc. Nat. Belgique, Sc. Terre*, 68 :233-236.

MILLS, J.R.E., 1971. — The dentition of *Morganucodon*. In KERMACK, D.M. & KERMACK, K.A. (eds), *Early Mammals*. *Zool. Jour. Linn. Soc. London*, 50, Supplement 12: 29-63.

MILLS, J.R.E., 1984. — The molar dentition of a Welsh pantothere. *Zool. Jour. Linn. Soc. London*, 82: 189-205.

OSBORN, H.F., 1888. — On the structure and the classification of the Mesozoic Mammalia. *Jour. Acad. Nat. Sci. Philadelphia*, 9: 186-264.

PROTHERO, D.R., 1981. — New Jurassic mammals from Como Bluff, Wyoming, and the inter-relationships of non-tribosphenic therians. *Bull. Amer. Mus. Nat. Hist.*, 167: 278-325.

ROUGIER, G.W., 1999. — An Early Cretaceous Japanese triconodont and a revision of triconodont phylogeny. *Jour. Vert. Paleont.*, 19, *Abstracts*: 72A.

ROUGIER, G.W., 2002. — A new specimen of *Eurylambda* and its bearing on cusp homologies and relationships among basal mammaliaformes. *Jour. Vert. Paleont.*, *22, Abstracts* : 101A.

ROUGIER, G.W., WIBLE, J.R. & HOPSON, J.A., 1996. — Basicranial anatomy of *Priacodon fruitaensis* (Triconodontidae, Mammalia) from the Late Jurassic of Colorado, and a reappraisal of mammaliaform interrelationships. *Amer. Mus. Novit.*, 3183: 1-38.

ROWE, T., 1988. — Definition, diagnosis and origin of Mammalia. *Jour. Vert. Paleont.*, 8: 241-264.

SIGOGNEAU-RUSSELL, D., 1983. — Nouveaux taxons de mammifères rhétiens. *Acta Pal. Pol.*, 28 : 233-249.

SIGOGNEAU-RUSSELL, D., 1995. — Two possibly aquatic triconodont mammals from the Early Cretaceous of Morocco. *Acta Pal. Pol.*, 40: 149-162.

SIGOGNEAU-RUSSELL, D., MONBARON, M. & RUSSELL, D.E., 1988. — Découverte de Mammifères dans le Mésozoïque moyen d'Afrique. *C. R. Acad. Sci.*, Paris, .II, 307: 1045-1050.

SIGOGNEAU-RUSSELL, D., MONBARON, M. & de KAENEL, E., 1990. — Nouvelles données sur le gisement à mammifères mésozoïques du Haut-Atlas marocain. *Geobios* 23 : 461-483.

SIMPSON, G.G., 1928. — *A Catalogue of the Mesozoic Mammalia in the Geological Department of the British Museum*. Oxford University Press, London, 215 p.

SIMPSON, G.G., 1929. — American Mesozoic Mammalia. *Mem. Peabody Mus. Yale Univ.*, 3: Part 1, I-XII+1-350.

SLAUGHTER, B.H., 1969. — *Astroconodon*, the Cretaceous triconodont. *Jour. Mammal.*, 50: 102-107.

TROFIMOV, B.A., 1978. — The first triconodonts (Mammalia, Triconodonta) from Mongolia (in Russian). *Dokl. Akad. Nauk SSSR*, 243: 213-216.

WANG, Y., HU, Y., MENG, J & LI, C, 2001. — An Ossified Meckel's Cartilage in Two Cretaceous Mammals and Origin of the Mammalian Middle Ear. *Science*, 294 (5541): 357-361.

ZHOU, M., CHENG, Z. & WANG, Y., 1991. — A mammalian lower jaw from the Jurassic of Lingyuan, Liaoning. - *Vert. PalAs.* 29: 165-175.

PLATE 1

Figure **1**, *Gobiconodon palaios* gen. et sp. nov., holotype SA 107, right upper molar in occlusal view.

Figure **2**, *Kryptotherium polysphenos* gen.et sp. nov., holotype SA 22, right lower molar in occlusal view.

Figure **3**, ?Amphilestidae indet. SA 20 in occlusal view.

Figure **4**, Gen. indet. SA 3 in lingual view.

Stereophotos X 20.

Figure **5**, third left molar of *Amphilestes* (Oxford J. 20079), X 45.

Figure **6**, a left molar of *Comodon* (holotype, USNM 2703), X 45.

Figure **7**, the first four right molars of *Phascolotherium* (BMNH 7595), X 15.

Figure **8**, the first left molar of *Tinodon*. (USNM 2131), X 45.

Figure **9**, the first three left molars of the same, X 15.

SEM photos in occlusal view.

PLATE 1