Two possibly aquatic triconodont mammals from the Early Cretaceous of Morocco

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Three mammalian molars from the Early Cretaceous of Morocco reveal the existence, at that time, of two new and peculiar species, one of them assigned to the Eotheria Triconodonta (uncertain family), *Dyskritodon amazighi* gen. et sp. n., the second only tentatively assigned to the Triconodonta, *Ichthyoconodon jaworowskorum* gen. et sp. n. The former is represented by a last lower molar which three main cusps (*a*, *c*, *d*) decrease regularly in size posteriorly while cusp *b* is very small and lingually situated, a unique condition for post-Liassic triconodonts. The second taxon (two specimens) is characterized by very narrow and trenchant teeth not intermeshing with adjacent ones, and carrying three subequal main cusps (*b*, *a*, *c*). Such dental morphology suggests that these mammals might have been semi-aquatic and piscivorous.

Key words: molars, Mammalia, Triconodonta, Early Cretaceous, Morocco.

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Introduction

The Anoual Syncline littoral sediments from the Early Cretaceous of Morocco have already yielded, among other vertebrates (Sigogneau-Russell *et al.* 1990; Duffin & Sigogneau-Russell 1993; Richter 1994), a rich and diversified mammalian fauna, a small part of which has been published: Triconodonta indet. (Sigogneau-Russell *et al.* 1990), three symmetrodonts (Sigogneau-Russell 1988, 1991), one pantothere (Sigogneau-Russell 1991), one multituberculate (Sigogneau-Russell 1991), and two tribotheres (Sigogneau-Russell 1991, 1992, 1995). This paper presents three new, relatively large and quite peculiar teeth; in fact, the first two teeth found looked so strange that, in spite of their two roots, I was long hesitant to include them in the Mammalia. But the third specimen belongs without

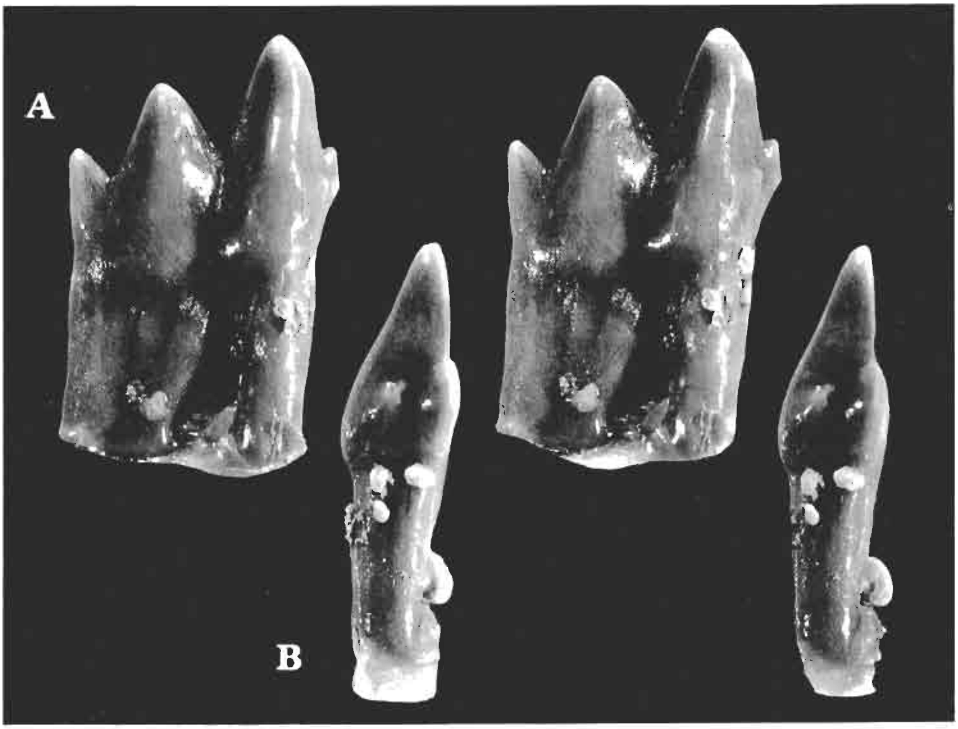


Fig. 1. *Dyskritodon amazighi* gen. et sp. n., right lower molar, holotype SA 92; top, labial view; bottom, anterior view. Stereophotos; × 20.

doubt to that class and, within the latter, clearly to the Eotheria Triconodonta. The two others are tentatively included in this order. The Triconodonta are known from the Rhaetic to the Campanian.

The specimens are housed in the palaeontological collections of the Museum National d'Histoire naturelle, Paris, France. SA, stands for synclinal d'Anoual.

Tooth MNHN SA 92

Measurements: length — 1.85mm; width — 0.75mm

Description (Figs 1, 2, 3M). — The crown is intact and still supported by two nearly complete roots. It is high and narrow, with three main cusps (2, 3, 4) aligned antero-posteriorly and decreasing strongly in height posteriorly. The main anterior cusp 2 is linked at its base with a much smaller cusp 1 slightly displaced towards the face interpreted as lingual; on the same face, cusp 1 is followed posteriorly by a faint cingulum, more prominent at the level of cusps 2 and 3, and ending as a vertical crest on cusp 4. Still lingually, cusps 2 and 3 are more angular than convex in

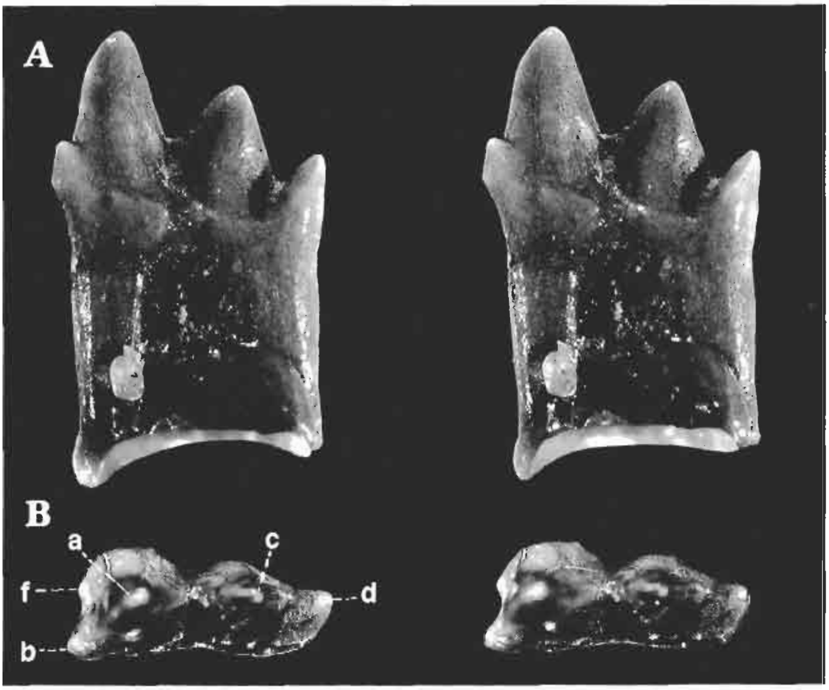


Fig. 2. *Dyskritodon amazighi* gen. et sp. n., right lower molar, holotype SA 92; top, lingual view; bottom, occlusal view. Stereophotos; × 20.

transverse section. The fourth cusp is disposed perpendicularly to 2 and 3, with a flat anterior face and a convex linguo-posterior face separated by the crest mentioned above. On the labial face, cusp 2 is extremely convex and moreover bulging at its base, which seems to give it a lingual inclination; due to this basal widening, an anterior face is individualized, at the base of which is a tiny cuspule followed by a cingulum; between this cuspule and cusp 1 is thus a shallow anterior notch. Cusp 3 is slightly less convex labially than cusp 2, but both 2 and 3 are pinched posteriorly and cusp 4 shows a short labial face separated from the posterior face by a ridge. Finally, these four cusps are linked by sharp crests. In occlusal view the contour of the crown is bilobate.

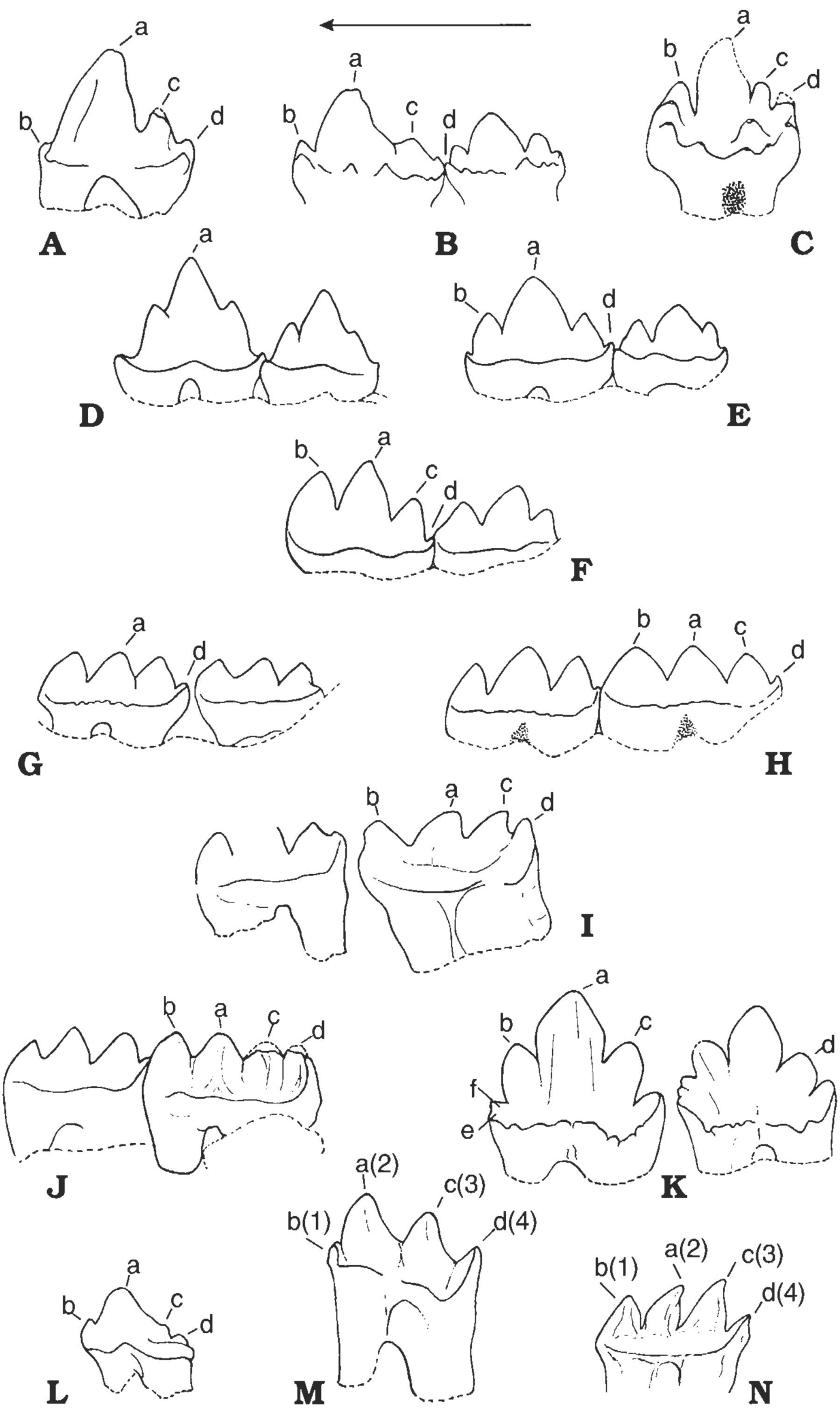
The anterior root is short antero-posteriorly and subcircular. The posterior root, which starts in fact beneath cusp 2, is elongated antero-posteriorly and flattened, except at the rear where it is rounded; its labial face, which is vertically striated, is incipiently divided by a sulcus. The morphology of the roots thus leads one to interpret this tooth as a last molar. Anteriorly and posteriorly the roots are very slightly overhung by the crown.

The tooth is quite unworn; the only wear facet suspected is a triangle on the anterior face of 3, and the anterior crest of 4 is labially truncated.

Interpretation. – The general morphology of the tooth SA 92 (major cusps antero-posteriorly aligned, lingual cingulum, anterior notch) is clearly that of a triconodont tooth. In consequence, and in conformity with the nomenclature proposed by Crompton & Jenkins (1968), cusps 1, 2, 3, and 4 are interpreted respectively as *b*, *a*, *c*, and *d* (Fig. 3M). But it is to be emphasized that cusp *b* is displaced lingually, and moreover is still included in the cingulum. Finally, the tiny cuspule mentioned at the labial base of *a* can only be interpreted as *f*; the anterior notch is thus in this case produced between *b* and *f*.

On triconodont molars, either cusp *a* dominates the crown (Morganucodontidae, Amphilestidae, Gobiconodontidae, Austroconodontidae) or *a*, *b*, and *c* are subequal (Triconodontidae) (Fig. 3A–L). But only in the Morganucodontidae does cusp *b* belong to the cingulum: 'most previous authors have regarded the lower molars (of *Morganucodon*) as triconodont, but this would seem to be an over-simplification. Both the principal and distal cusps might be classified as true cusps, but the mesial cusp (*b*) is a cingulum cusp' (Mills 1971). In all other Triconodonta (and in Theria) cusp *b* is a true cusp, more or less symmetrical with *c*, and the difference in size between the two remains slight. Besides, Mills, in the same paragraph, continues: 'It is quite common for major cusps to develop from cingula. It may be that this is actually occurring here (in *Morganucodon*) and we probably see a later stage of the process in the Triconodontinae'. The only other tooth of Triconodonta with an anterior dominant cusp and a cuspule *b* included in the cingulum is the last lower premolar: for example, USNM 2705 identified as ?*Priacodon*, USNM 2720 belonging to *Triconodon mordax* (Simpson 1928: fig. 24) or the P/5 of *Megazostrodon* (Fig. 3A; Crompton 1974). On all these teeth, the lingual cingulum is linked to the posterior cusp *d* in the way described for SA 92. However the differences between these premolars and SA 92 appear to be major ones; on the former, cusp *a* constitutes almost the whole crown, and cusp *c* is not clearly separated from it; as for *d*, it never is, on the premolars, more than an irregularity of the cingulum. On the contrary, in SA 92 the three cusps *a*, *c*, and *d* are equally distinct. Also, if the anterior notch is present on some last premolars, cuspule *b* in such cases is very low on the crown;

Fig. 3. Lingual views of molar teeth of Mesozoic mammals. ❑A. Right P/5 of *Megazostrodon rudnerae*. ❑B. Right lower molar of *Eozostrodon parvus*. ❑C. Penultimate left lower molar of *Megazostrodon rudnerae*, reversed (A–C, redrawn from Crompton 1974). ❑D. Two last right lower molars of *Amphilestes broderipii*. ❑E. Two last right lower molars of *Phascolotherium bucklandi*. ❑F. Two last lower right molars of *Priacodon ferox*. ❑G. Two last left lower molars of *Trioracodon ferox*, reversed. ❑H. Two last lower molars of *Triconodon mordax*, reversed (D, E–H, redrawn from Simpson 1928). ❑I. Two right lower molars of *Astroconodon denisoni* (redrawn from Slaughter 1969). ❑J. Two last lower right lower molars of *Alticonodon lindoei* (redrawn from Fox 1969 and 1976). ❑K. Two last right lower molars of *Gobiconodon ostromi*. ❑L. Left lower molar of *Austrotriconodon sepulvedai*, reversed (redrawn from Bonaparte 1992). ❑M. Last right lower molar of *Dyskritodon amazighi* gen. et sp. n. ❑N. Right lower molar of *Ichthyoconodon jaworowskorum* gen. et sp. n. The arrow points towards the front.


a
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here it is higher than the base of *c*. Finally, the P/3 of *Astroconodon* (Slaughter 1969) shows a crown morphology strongly recalling that of SA 92. But the inequality of the roots in the latter excludes the premolar interpretation: as I have suggested above, this is clearly a last lower molar. In all genera of Triconodonta where the last molar is known (Fig. 3), its morphology is not different from the more anterior molars, except in *Alticonodon* (Fox 1969, 1976) (Triconodontidae), where it even carries a supplementary cusp (4 instead of 3 because of the development of *d*).

Finally, in no Triconodonta is there a cuspule *f* (except perhaps in *Gobiconodon* (Jenkins & Schaff 1988), but *e* and *f* are poorly individualized); the anterior notch is usually hollowed between *b* and a more lingual cuspule, *e*; cuspule *f* is known only in Theria (Crompton & Jenkins 1968). It thus appears that SA 92 not only represents a new genus, but probably also a new family. It should be remembered that the five families so far known of Triconodonta differ in particular by the relative size of the main cusps (Lillegraven *et al.* 1979; Jenkins & Schaff 1988): $a > c > b > d$ in Morganucodontidae, $a > b \sim c > d$ in Amphilestidae, $a > c \sim b > d$ in Gobiconodontidae, $a \sim b \sim c > d$ in Triconodontidae, $a > b > c > d$ in Austroconodontidae.

Taxonomy of MNHN SA 92

Order Triconodonta Osborn 1888

Family *incertae sedis* (with relative size of cusps: $a > c > d > b$).

Dyskritodon gen. n.

Type species *D. amazighi* sp. n.

Etymology: *Dyskritos*, Greek, of uncertain position; *odous*, Greek, tooth.

Diagnosis. — Last molar wih high and narrow crown, with cusps *a, c, d,* decreasing regularly in height posteriorly; differs from all Triconodonta except Morganucodontidae by cusp *b* displaced lingually and included in the cingulum; differs from all Triconodonta by anterior notch displaced labially with presence of a cuspule *f*, a cuspule not present in any other Triconodonta.

D. amazighi sp. n.

Figs 1, 2, 3M.

Holotype: SA 92, lower right molar.

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

Etymology: *Amazighi*, Berber, in the Berberian language: in honour of the Berberian people who helped us during the 1988 expedition.

Diagnosis. — As for the genus.

Discussion. — The small size of cusp *b* could be considered primitive, but its unusual lingual position rather pleads in favor of a secondary reduction. The weakness of the cingulum, the trenchantness of the cusps and

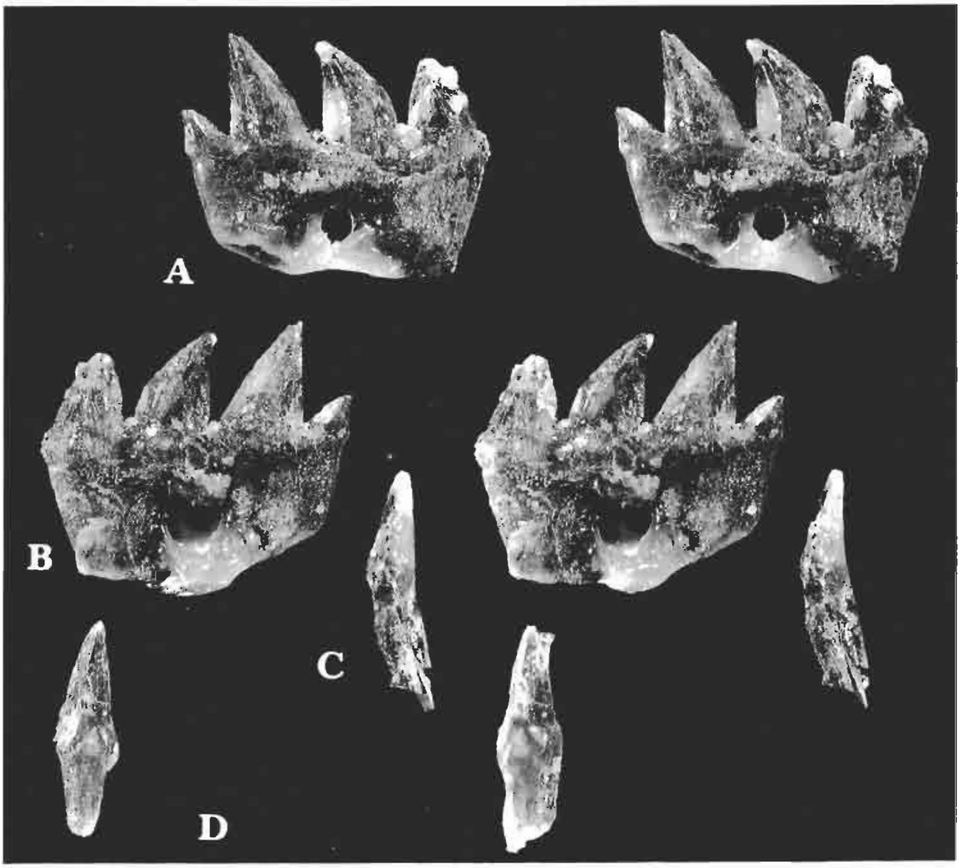

Fig. 4. *Ichthyoconodon jaworowskorum* gen. et sp. n., right lower molar, holotype SA 46 in lingual (A), labial (B), anterior (C), and posterior (D) views. Stereophotos; × 10.

the presence of a cuspule *f*, equally appear as derived characters. Overall, the peculiar morphology of this last molar, unlike that in all Triconodonta in which this tooth is known, suggests that the phyletic line to which *Dyskritodon* belonged was long developed in isolation. In any case, nothing links the new African genus with the late Cretaceous Argentinian *Austrotriconodon* (Bonaparte 1986, 1992, 1994), which is obviously a component of an endemic fauna.

Teeth MNHN SA 46 and SA 78

Measurements: MNHN SA 46 length — 4.00 mm; width — 0.96 mm
MNHN SA 78 length — 2.95 mm; width — 0.68 mm

Description (Figs 3N, 4, 5). — These two teeth are very different from SA 92, but quite similar to each other. SA 46 is complete except for the tip of the anterior cusp, but the tooth is poorly preserved in the sense that the enamel is eroded and that the roots have been crushed. It is a relatively large tooth, very compressed transversely. It bears four 'cusps' (a term which does not quit fit these trenchant blades), longitudinally aligned and deeply separated from each other. The three anterior cusps are subequal (1 slightly lower than 2 which is slightly lower than 3), but the last one is markedly lower. All of these cusps are quite strongly inclined posteriorly, and cusps 2 and 3 are even somewhat recurved, their posterior border being thus shorter than their anterior border. They are about equally convex on both faces, but the anterior and posterior pinching of each is more accentuated on the face interpretated as lingual. They are limited by anterior and posterior sharp crests. Finally, a faint bulge or cingulum underlines the bases of the crown on the two faces, but this is slightly thicker on the face identified as lingual. On both faces too, but mostly on the lingual face again, the cingulum ends on cusp 4 on which it makes a median ridge. The base of the posterior crest of the small cusp 4 describes a curve that thus slightly overhangs the root, and at the base of cusp 1 is a faint expansion from the cingulum that also overhangs the root. There is no anterior notch, only the trenchant edge of cusp 1.

The crown is supported by two roots, transversely flattened and deeply separated from each other. They are of subequal antero-posterior dimensions. These roots possess a very thin wall, hence a large pulp cavity; but the anterior one externally shows a fibrous texture which looks more like bone than dentine. The passage from the crown to the roots is marked by a slight narrowing, but the histological difference between the two parts seems at present weakly indicated, presumably due to the poor preservation of the crown enamel.

Given this state of preservation, it is impossible to state the degree and localisation of wear; it seems however that the cingulum has undergone an erosion on the face where the cusps are the most pinched, interpreted consequently as labial (assuming this a lower molar). This is particularly marked under cusps 2 and 3.

SA 78 is a smaller tooth. Its posterior cusp has been broken at the base, and cusp 2 is somewhat battered at the apex. The three anterior cusps are again subequal (1 slightly lower than 2 slightly lower than 3); cusp 1 also presents a step at its anterior base (presently slightly crushed) and there is no anterior notch either. The posterior slope of the cusps is weaker than on SA 46 and, above all, 2 and 3 are not curved; their anterior and posterior borders thus being equal. These borders are as trenchant as on SA 46. The transverse section of the cusps shows the same contour as on SA 46, with an angulation somewhat more marked on the side interpreted as lingual. The basal cingulum is faint labially and almost nonexistent lingually. Finally, two roots support the crown, the posterior one being complete and about equal to the height of the crown. The anterior root has a thick wall and thus a narrower pulp cavity than on SA 46.

The enamel is not intact, but not as deeply eroded as in the preceding tooth; and the wear on the external cingulum is more clearly expressed, a

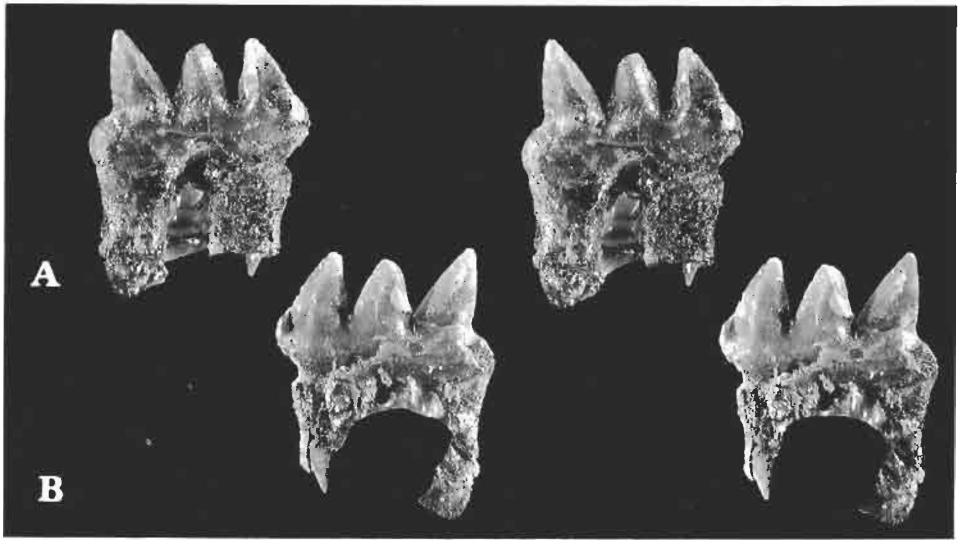

Fig. 5. *Ichthyoconodon jaworowskorum* gen. et sp. n., right lower molar SA 78 in lingual (A) and labial (B) views. Stereophotos; × 10.

wear which ascends somewhat on the axis of the cusps. There is no doubt that SA 46 and SA 78 represent the same taxon, a taxon that is apparently very rare in the fauna.

Interpretation. — The so-peculiar aspect of the teeth SA 46 and SA 78, and especially of the roots, has long cast doubt on their mammalian nature (in fact I even checked in the realm of scolecodonts). Outside the mammals, the first possible identification was that of a selachian, especially a dalatiine (Fig. 6A); this was definitely refuted because of the two roots (Cappetta personal communications 1992 and 1993). On the other hand, the structure of the crown appears different from that of fishes, and there is no acrodyne (Characidae are also devoid of acrodyne, but their structure is notably different; Schultze personal communication 1992). Attribution to the Squamata is considered as very improbable because of the roots (Rage personal communication 1993). Currie (written communication 1993) reckoned that no dinosaur is known with such teeth. Finally, pterosaurs (Fig. 6B) were definitely rejected by Wellnhofer and Wild (written communication 1993).

There remains the mammals: the possibility of their being last lower premolars of very specialised multlituberculates was proposed (Gingerich personal communication 1992); indeed in this order P/4 shows a transverse section approaching that of our teeth, and roots may have the same flattening and the same bony aspect. But the anterior part of the crown and that of the corresponding root show a thickening which is usually excavated to lodge the third premolar. Moreover, the deep separation of the cusps on the Moroccan teeth is the opposite of what one observes in multituberculates, where these cusps are quasi-totally fused.

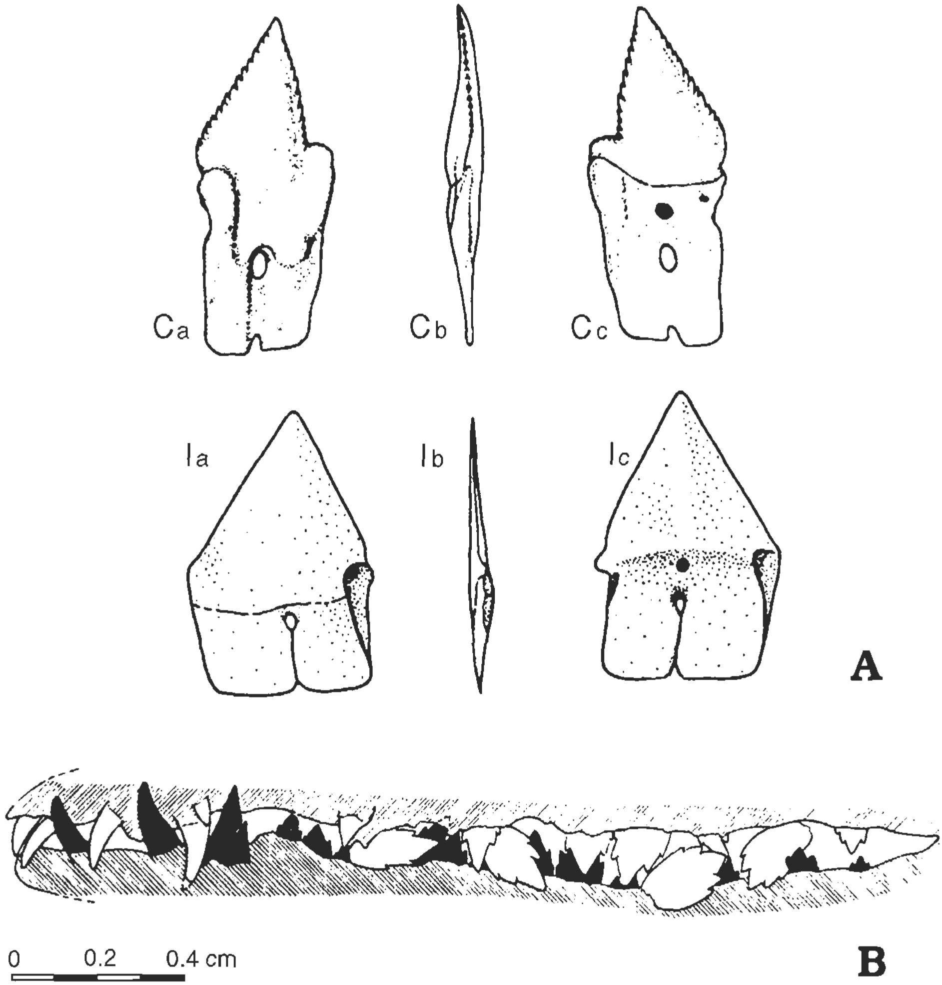

Fig. 6. □A. Dalatiine selachian teeth (*Scymnorhinus licha* top, *Isistius triangulus* bottom) in labial, mesial and lingual views; from Cappetta (1987). □B. Pterosaurian dentition (*Eudimorphodon ranzii*); white — upper teeth, black — lower teeth; from Wild (1978).

Assuredly, the alignement of the cusps of SA 46 and SA 78 evokes the Triconodonta, and more precisely, because of the subequality of the cusps, the Triconodontidae. However, in this order, molars always have an anterior notch for the talonid of the preceding tooth, while, in the Anoual species, it is more probable that such molars laterally overlapped each other. Also the cingulum is usually better developed in Triconodonta, although it is very reduced in Austroconodontidae and, in the triconodontine *Astroconodon*, it is said to be 'rounded rather than sharp' (Slaughter 1969). Finally, in no genus of Triconodonta does one observe such separation of the cusps nor their posterior recurvature (except on the last lower molar of *Astroconodon*), and the transverse compression of these teeth surpasses that of any triconodont.

In spite of such incongruencies, it is in the Triconodonta that I propose to place the strange Anoual animal. In this hypothesis, cusps 1, 2, 3, and 4 would be interpreted as *b, a, c, d*. The latter cusp has a typical triconodont morphology, and SA 46 and SA 78 would be right lower molars.

Only in the the family Triconodontidae are the cusps of subequal height, but it seems to me that the absence of an interlocking mechanism between teeth and the extreme sharpness of the cusps do not fit in this family. And, although some of the characteristics of these teeth are already found in the Jurassic Triconodontidae (two subequally convex sides, overhang of the posterior root by cusp *d*, size of *d* relative to *c*; Slaughter 1969), it is clear that we have here one of the most specialized genera of Triconodonta.

Taxonomy of MNHN SA 46 and SA 78

Order ?Triconodonta Osborn 1888

Family *incertae sedis* (relative size of cusps: $c \sim a \sim b > d$)

Ichthyoconodon gen. n.

Type species: *I. jaworowskorum* sp. n.

Etymology: *Ichthys*, Greek, fish; allusion to the aspect of these teeth and their supposed diet.

Diagnosis. — Molars with very high, narrow and trenchant crowns, with cusps *b, a,* and *c* subequal. Differs from all Triconodonta, and especially the Triconodontidae which have also subequal cusps, by their extreme trenchantness and deep separation, as well as by the absence of intermeshing between adjacent molars, suspectedly replaced by an overlap; differs also by cusp *c* slightly dominant. Cingulum faintly developed.

I. jaworowskorum sp. nov.

Figs 3, 4, 3N.

Holotype: SA 46, right lower molar.

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

Etymology: In honour of Zofia Kielan-Jaworowska and Zbigniew Jaworowski for their generous hospitality on many occasions.

Attributed material: SA 78, right lower molar.

Diagnosis. — As for genus.

Discussion. — If these teeth do belong to the order Triconodonta, they certainly represent the most derived form known of this order. However, some doubt will persist as to their attribution until more complete dentitions become available.

Conclusion

The cusp sharpness of these molars, combined with the preservation of such fragile elements in littoral sediments, led us to believe that they could not have undergone long transportation and, in consequence, that they could have belonged to a piscivorous and aquatic animal. After the idea was developed, I discovered similar reasoning had already been proposed by Slaughter for *Astroconodon* (1969), who based his suggestion on similar sedimentological and morphological arguments, underlining at the same time the convergence of his genus with some archaeocetes and pinnipeds.

As for a possible relationship between *Ichthyoconodon* and *Dyskritodon*, it seems to be eliminated by the characteristics of the anterior part of the teeth in the two cases (intermeshing in the former, overlapping in the latter), even if it may appear very surprising that two so specialized Triconodonta could have coexisted in apparently a single biotope. In any case, these finds, added to the numerous taxa already identified from the Anoual Syncline, attest to the variety of mammals which thrived in that part of Africa at the beginning of the Cretaceous.

Acknowledgments

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Resumé

Des sédiments littoraux du Crétacé inférieur du Haut-Atlas marocain, qui ont déjà livré de nombreux mammifères et autres vertébrés, ont été extraites trois dents très particulières, attribuées à deux nouveaux taxons de mammifères Eotheria: *Dyskritodon amazighi* gen. et sp. n., ordre Triconodonta, famille indet., et *Ichthyodonodon jaworowskorum* gen. et sp. n., ordre ?Triconodonta, famille indet. Le premier est représenté par une dernière molaire inférieure, elle-même caractérisée par la petitesse du tubercule *b*, sa position cingulaire et un peu linguale et la décroissance régulière des tubercules *a*, *c*, *d*. Le second taxon est représenté par deux molaires isolées; trois tubercules (*b*, *a*, *c*) y sont subégaux comme chez les Triconodontidae, mais la dominance de *c* est un caractère tout à fait unique. En outre ces tubercules sont plus étroits et tranchants que chez

tous les Triconodontes connus, et surtout il n'y a pas d'indentation antérieure témoignant de l'engrènement des dents adjacentes; il semblerait plutôt que ces dents se chevauchaient légèrement l'une l'autre. La morphologie dentaire de ces deux taxons, leur très bonne conservation en dépit de leur fragilité (tubercules élevés et minces), suggèrent que les animaux qui les portaient étaient semi-aquatiques et piscivores. Il s'agit en tous cas de deux formes très spécialisées, et ce tout à fait indépendamment l'une de l'autre.

Streszczenie

W osadach wczesnej kredy (beriasu) Maroka znalezione zostały trzy zęby o piłkowanych płaskich koronach typowych dla rybożernych, wodnych kręgowców. Choć powierzchownie przypominają pokrojem zęby rekinów bądź pterozaurów, ich plan budowy da się porównać jedynie z zębami prymitywnych ssaków trikonodontów. Jeden z tych zębów, o coraz niższych kolejnych czterech wierzchołkach, należy prawdopodobnie do nowej rodziny trikonodontów i nazwany został *Dyskritodon amazighi* gen. et sp. n. Dwa inne zęby, o trzech spośród czterech wierzchołków zbliżonej wysokości, reprezentują jeszcze bardziej tajemniczy gatunek *Ichthyoconodon jaworowskorum* gen. et sp. n.