

New symmetrodonts (Mammalia, Theria) from the Purbeck Limestone Group, Lower Cretaceous, southern England



*P. Ensom and †D. Sigogneau-Russell

*Natural History Museum, Cromwell Rd, London SW7 5BD, UK

†Institut de Paléontologie, MNHN, 8 rue Buffon, 75005 Paris, France

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The genus *Spalacotherium* Owen was initially created from material collected in the Purbeck Group in 1854. A new species, *S. evansae*, is here described from a Purbeck site discovered in 1986; it is represented not only by lower and upper molars, but possibly also by milk molars. The genus *Tinodon* was, until now, known only from the slightly older Morrison Formation in Wyoming, USA; a few lower molars and an upper molar also from the site are attributed to a new and smaller species, *T. micron*, which adds one more genus that is common to the two formations. The attributed upper molar of *T. micron* is especially interesting in that it yields new data on a taxon widely discussed in symmetrodont phylogeny, while at the same time raising problems of cusp homology. © 2000 Academic Press

KEY WORDS: Symmetrodonta; Purbeck Limestone Group; Lower Cretaceous; Morrison Formation.

Le genre *Spalacotherium* Owen fût initialement créé à partir de spécimens provenant du Groupe de Purbeck en 1854. Cet article décrit une nouvelle espèce, *S. evansae*, provenant d'un site purbeckien découvert en 1986; celle-ci est représentée non seulement par des molaires inférieures et supérieures mais peut-être aussi par des molaires de lait. Le genre *Tinodon* n'était, jusqu'à maintenant, connu que dans la Formation Morrison du Wyoming, USA, un peu plus ancienne que celle de Purbeck; quelques molaires inférieures et surtout une molaire supérieure du même gisement sont attribuées à une nouvelle espèce, *T. micron*, ce qui ajoute un genre à la liste des taxons communs aux deux formations. La molaire supérieure de *T. micron* est particulièrement intéressante en ce qu'elle fournit des indications sur un taxon occupant une position clé dans la phylogénie des symmétrodontes, tout en soulevant le problème d'homologie des tubercules. © 2000 Academic Press

MOTS CLES: Symmétrodontes; Purbeck Limestone Group, Crétacé inférieur; Formation Morrison.

1. Introduction

In the collection assembled by one of us (PE) from Sunnydown Farm near Langton Matravers, Dorset, southern England (Nat. Grid. Ref. SY 9822 7880; Figure 1), therian symmetrodonts are not very abundant; however, they represent new taxa (one has already been published; Sigogneau-Russell & Ensom, 1998), and bring new data to the controversial question of cusp evolution in this order.

This new fauna was obtained by sieving clay from two horizons in the Cherty Freshwater Member (Lulworth Formation) of the Purbeck Limestone Group. The exact age of these strata (Late Jurassic–Early Cretaceous) remains uncertain (Allen & Wimbledon, 1991; Kielan-Jaworowska & Ensom, 1994) although the sampled horizons are thought to be Early Cretaceous. Samples from the lower horizon

(1.5 m below the upper horizon) at the same site have produced one specimen of *Spalacotherium evansae* sp. nov.; this came from a carbonaceous clay which underlies the New Vein, a bioclastic limestone correlated with DB 101 in Durlston Bay (Clements, 1993), 5 km east-southeast of Sunnydown Farm. All of the other specimens described in this paper came from an upper horizon, from a clay sample at and just below its interface with the 'Cap'; in Durlston Bay these beds were numbered DB 102/3 by Clements (1993). The clay was walked over by dinosaurs, the casts of their tracks being preserved on the base of the limestone (Ensom, 1988). Four specimens of *Spalacotherium evansae* sp. nov. were picked from a sample collected in Durlston Bay itself, SZ 0365 7839 (Figure 1); the rest came from the equivalent horizon at Sunnydown Farm. Similarly all the specimens of *Tinodon micron*

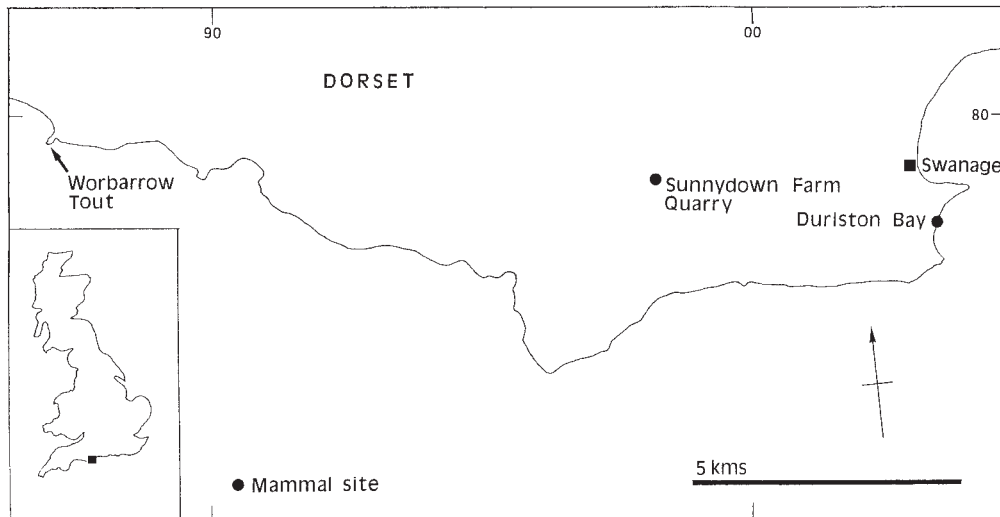


Figure 1. Map showing the location of mammal-producing localities mentioned in the text.

sp. nov. came from the upper horizon at Sunnydown Farm. The Purbeck Limestone Group, a succession of limestones and clays, was deposited in predominantly shallow, brackish to freshwater environments, though rare marine influences are recorded (Kelly, 1983).

2. Systematic palaeontology

Abbreviations. DORCM, Dorset County Museum, England; USNM, National Museum, Washington DC, USA; YPM, Yale Peabody Museum, Yale University, New Jersey, USA; BMNH, The Natural History Museum, London, England; MNHN SNP, Saint-Nicolas-de-Port locality, Museum national d'Histoire naturelle, Paris, France.

Spalacotheriidae Marsh, 1887

Spalacotherium Owen, 1854

Spalacotherium evansae sp. nov.

Figures 2–7, 10 (all except DORCM GS 694)

Derivation of name. After Dr Susan Evans (University College London), in recognition of her major contribution to the discovery and study of Mesozoic microvertebrate remains in Great Britain.

Holotype. DORCM GS 355, a fragmentary right lower jaw with one complete and two incomplete molars *in situ*.

Referred material. Right lower molars: DORCM GS 357, 360, 370, 371, 383, 389, 435, 488, 490, 534, 673, 674, 769, 853; right penultimate lower molar:

DORCM GS 380. Left lower molars: DORCM GS 323, 390, 669, 843, 914, 1043, 1075, 1076. Fragments: DORCM GS 721 and 842. Upper molars: DORCM GS 309, anterior corner of a right molar; DORCM GS 684, anterior right molar, nearly complete; DORCM GS 918, middle right molar, nearly complete; DORCM GS 961, partial right molar; DORCM GS 314, anterior half of a posterior left molar. DORCM GS 350, undetermined molar. Milk molars: DORCM GS 308, partial upper right; DORCM GS 312, upper left; DORCM GS 909, partial upper left; DORCM GS 373, lower left (see measurements, Table 1).

Horizon and locality. Cherty Freshwater Member, Purbeck Limestone Group, Durlston Bay (DB 102/103); upper horizon at Sunnydown Farm (equivalent to DB 102/103) and lower horizon at Sunnydown Farm (equivalent to DB98/100), Langton Matravers, Dorset, England (see Table 2 for details).

Diagnosis. Lower molars differ from those of *S. tricuspidentens* and *S. henkeli* by their smaller size, the incompleteness of the labial cingulum and the near equality of the roots with a similar labial extension; they further differ from those of *S. henkeli* by the absence of basal anterior and posterior swellings and by the paraconid being equal to or lower than the metaconid. They differ from the sole molar of *S. taylori* by the incomplete labial cingulum, and from all species by the individualisation, on some specimens, of a tinodontid-type cuspule f antero-labially (very narrow interlocking).

Table 1. Measurements in mm.

<i>Spalacotherium evansae</i>				
DORCM GS 355: length of mandibular fragment: 3.70; width in front of 'first' molar: 0.67				
		length	width	ling.height
	'1st' molar	0.75	0.65	0.92
	'2nd' molar	0.54	0.42	
	'3rd' molar	0.37	0.30	
DORCM GS	323	0.62+?	0.48	0.76
	357	0.44+	0.60	0.83
	360	0.60	0.51	0.63
	370	0.66	0.65	
	371	0.65+?	0.58	0.75
	383	0.74	0.77	
	437	0.71+	0.47	
	673	0.89	0.59+	
	674	0.70	0.63	
	1075	0.85	0.56	0.82
	1076	0.71	0.61	0.92
	350	0.40	0.24	
	380	0.54	0.32	
	309	0.91	0.69	
	314	1.03+	0.54	
	684	0.80	0.65	
	961	0.88+	0.70	
	918	0.68+	0.68	
	308	0.81+	0.36	
	312	1.10	0.41	
	373	0.87?	0.38?	
	909	0.95	0.45	
<i>Spalacotherium tricuspidens</i>				
BMNH 46019	'2nd' molar	1.62	1.48	
<i>S. henkei</i> Galve TH 11		2.18	1.30	
<i>S. taylora</i> BMNH M 21103		0.80	0.55	
' <i>Peralestes</i> '				
BMNH 47740	M1	1.26	1.02	
	M2	1.52	1.70	
	M3	1.87	1.46	
	M4	1.76	1.66	
	M5	1.37	1.65	
	M6	1.10+	1.40?	
<i>Tinodon micron</i>				
DORCM GS	1110	0.88	0.34	
	538	0.81+	0.42	
	1081	0.81+	0.44	
	694	1.21	0.62	
<i>Tinodon lepidus</i>				
USNM 2131	M3	1.90	0.73	1.40
	M4	1.74	1.00	1.62
	?M5	1.47	1.12	
YPM 13644	M2	1.82	0.75	1.31
	M3	1.60	1.00	1.28
	?M5	1.80	0.90	
' <i>Eurylambda</i> ' Morrison YPM 13639		1.91	0.92	
<i>Kuehneotherium</i> sp. MNHN SNP 50W		1.21	0.75	

Table 2. Purbeck specimens grouped by sample numbers; all prefixed DORCM GS.

Durlston Bay, upper horizon:	308, 309, 312, 314, sample 01.
Sunnydown Farm, upper horizon:	350, 355, sample 28; 488, 490, sample 30; 769, sample 35; 373, sample 40; 370, 371, 842, 843, sample 58; 380, sample 59; 360, 853, sample 61; 383, sample 62; 389, 390, sample 63; 909, sample 71; 914, sample 73; 437, sample 76; 918, sample 75; 721, sample 78; 928, sample 79; 534, 538, sample 88; 961, sample 95; 669, sample 103; 673, 674, sample 104; 684, sample 106; 694, sample 107; 357, sample 109; 435, sample 112; 1043, sample 114; 1075, 1076, 1078, 1081, sample 116; 1110, sample 119.
Sunnydown Farm, lower horizon:	323, sample 09.

Description of type (Figure 2). Two empty alveoli occupy the anterior portion of DORCM GS 355, in which the interradicular septum is much more developed than the intermolar one; the first alveolus is slightly shorter than the second. Then comes a complete molar followed by an incomplete small tooth and a very small last molar. The 'first' tooth is slightly tilted forward and labially as in *Spalacotherium tricuspidentens* (see Simpson, 1928) and the lingual alveolar border is higher than the labial one. The anterior protoconid crest is very slightly longer than the posterior one, again as in *S. tricuspidentens*, but the protoconid remains uncurved; it is high and strongly compressed labially. The posterior trigonid face is very slightly concave. The paraconid was probably lower than the metaconid (broken). The lingual cingulum is chevron-shaped and culminates anteriorly in a cusp e (secondarily truncated), itself closely followed labially by a second swelling (cuspsule f), the two being sepa-

rated by a minute depression. From this point a cingulum descends steeply; this weakens and disappears at the level of the anterior protoconid crest. Posteriorly, the hypoconulid is barely higher than cusp e but appears more protruding, and is similarly followed labially by a steep cingulum, which weakens and stops at the level of the posterior protoconid crest. Roots separate at mid-protoconid length and seem to have been equal in size.

The succeeding molar is much smaller; it is broken at the base of the cusps, almost at root level. Anteriorly is a long lobe for the paraconid and the anterolingual cusp, while the metaconid is followed posteriorly by a very short talonid; these proportions were inverse in the preceding molar.

The last tooth is extremely small and nearly complete, with a short protoconid (broken at the tip), a long anterior lobe with a distinct paraconid and an anterocingular extension; finally, the short posterior part is reduced to a cingulum without a distinct metaconid. These characteristics are also seen on the last molar of *Spalacolestes* (Cifelli & Madsen, 1999). The labial cingulum is distinct at least on the anterior half of the tooth.

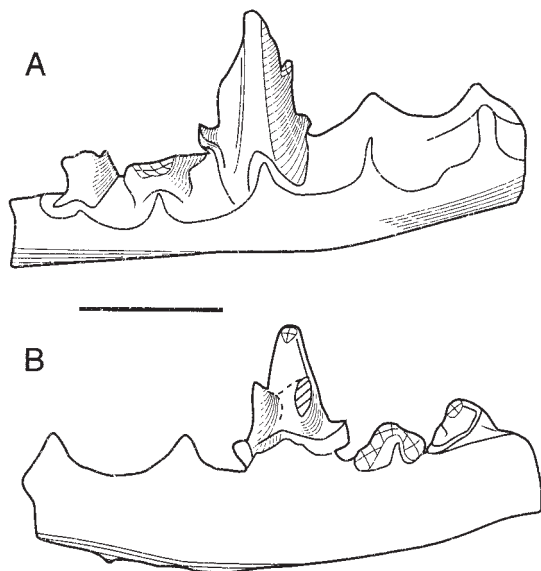


Figure 2. *Spalacotherium evansae* sp. nov., holotype, DORCM GS 355, right portion of lower jaw, in A, labial view; B, lingual view. Scale bar represents 1 mm.

Attributed lower molars. These are often merely fragments. The most complete specimens (Figure 3A) confirm the characters noted on the 'first' molar of the type, although some molars are even more compressed than the latter and cuspsule f is rarely distinct. Additionally, five teeth (DORCM GS 360, 371, 669, 1043, 1075, Figure 3B–D) have a similar morphology, but with a relatively lower protoconid, especially DORCM GS 1075; the latter is a complete tooth where, moreover, the paraconid is notably smaller than the metaconid. Such characters could be attributable to an anterior position in the series, but it should be stressed that these teeth also resemble the most compressed of the *Tinodon* lower molars (Figure 8) (as well as m_1 of *Spalacolestes*; Cifelli & Madsen, 1999, fig. 6). Teeth DORCM GS 323, 360, 383 and 1075

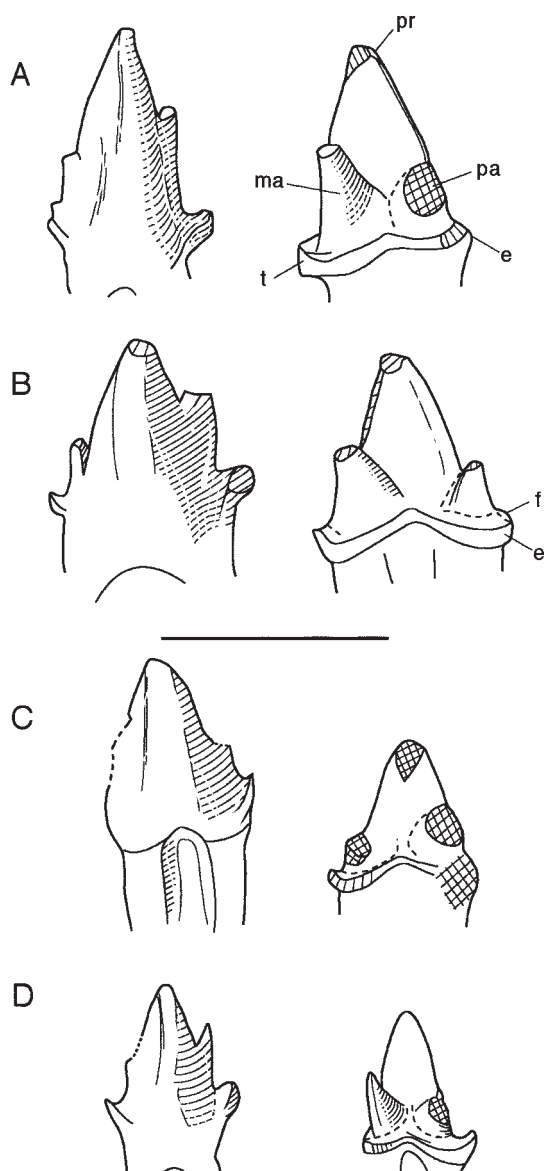


Figure 3. *Spalacotherium evansae* sp. nov., attributed lower molars: DORCM GS 1076 (A), 1075 (B), 371 (C), 360 (D), in labial and lingual views. Scale bar represents 1 mm; e, cuspule e; ma, metaconid; pa, paraconid; pr, protoconid; t, talonid.

clearly show a subdivision of the anterior cuspule into two elements (cusps e, f) separated by a very narrow slit, confirming the observation made on the type tooth.

Finally, two tiny teeth were certainly close to the posterior end of the series (Figure 4). DORCM GS 380 is undoubtedly a lower molar though the main three cusps are broken. These remain clearly distinguishable, the paraconid section being much more developed than that of the metaconid; the two cusps

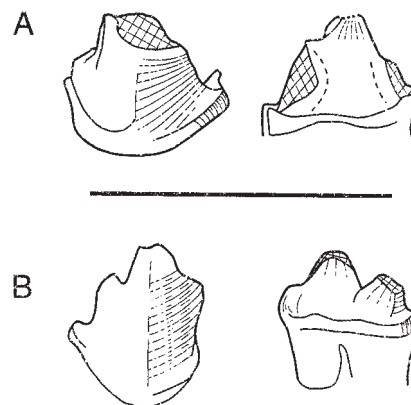


Figure 4. *Spalacotherium evansae* sp. nov., attributed lower molars: DORCM GS 380 (A), DORCM GS 350 (B), in labial and lingual views. Scale bar represents 1 mm.

are widely separated. The paraconid is preceded by a cingular shelf, festooned anteriorly so that cusps e and f can nearly be distinguished; the cingulum may have extended labially more than on the posterior teeth of the type jaw. Distally the talonid is practically non-existent, but again the cingulum extends further labially, only the anterior base of the protoconid remaining free of a cingulum. GS 380 is slightly smaller than the previous to last in the type jaw, but as it retains a metaconid we consider it as occupying this position.

The second tooth (DORCM GS 350) is even smaller but is better preserved than DORCM GS 380. It has a completely asymmetrical shape strongly reminiscent of the last molar of the type jaw, with one short side reduced to a cingulum and a longer side carrying a distinct cusp followed by a cingular lobe. If this tooth is compared to the last one of the type jaw, this cusp would then be the paraconid. However, contrary to the tooth in the jaw, no cingulum is discernible on the convex side. Moreover, this morphology of DORCM GS 350 is also reminiscent of the upper molar morphology (see below): it is interesting to note that on the '*Peralestes*' type maxilla, there is an inversion between the first molar where the posterior lobe is protruding, and the last molar where the anterior lobe is protruding. DORCM GS 350 could then represent the last upper molar with a long anterior lobe (the cusp would be B₁ as suggested for the attributed upper molars), or an anterior upper molar with a strong posterior lobe and a strong metacone (but the tooth seems too small for such a situation). Finally, there may be what could be considered a parastyle sulcus on the convex side of the short lobe: the designation of this tooth as upper or lower thus remains uncertain.

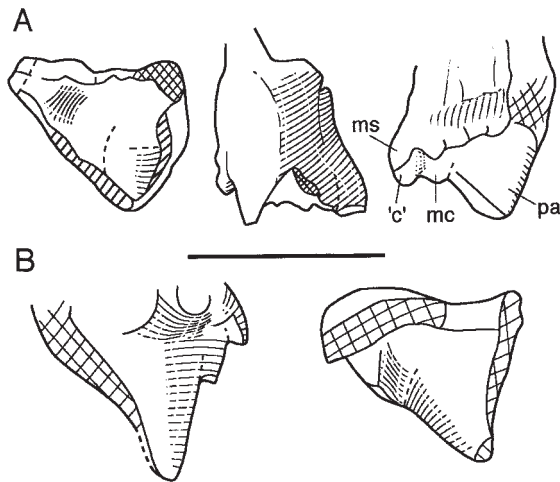


Figure 5. *Spalacotherium evansae* sp. nov., attributed upper molars. A, DORCM GS 309, in occlusal, lingual and labial views. B, DORCM GS 314, left, in lingual and labial views. Scale bar represents 1 mm; 'c', cuspule 'c'; mc, metacone; pa, paracone; ms, metastyle.

Wear facets (Figure 10). No uncontested wear facets are discernible on the type teeth, except perhaps on the anterior labial cingulum. On DORCM GS 1076, the summit of the anterior face of the protoconid is flattened by at least three distinct wear facets, while the posterior face consists of one large single wear facet with oblique scratches affecting even the hypoconulid. A similar, though less clear, situation is seen on DORCM GS 435 and 534; on DORCM GS 357 and 488 the posterior face is similarly unifaceted, in spite of the concavity of the protoconid. Among the five uncertain lower molars, DORCM GS 360 shows one large wear facet posteriorly, though very slightly angled between protoconid and metaconid, and at least two anteriorly, one below the other on the protoconid. The situation is the same on the anterior face of DORCM GS 1043. On DORCM GS 1075 the anterior face of the protoconid is again crossed by several facets, and that of the paraconid is clearly independent; the posterior face is transverse but again the wear facet is slightly angled; this would favour an attribution to *Timodon*. However, as this tooth probably belongs to the same dentition as DORCM GS 1076, though being lower and wider, this could also suggest that wear can vary slightly according to the position in the series, in relation to the differing configuration, especially in a primitive spalacotheriid; such a variation can be observed in *Timodon*. Finally on DORCM GS 383, the anterior face of e is clearly flattened, f not being touched.

Attributed upper molars (Figure 5). Five teeth are considered to represent the upper dentition of

S. evansae. DORCM GS 309, 684 and 918 are strongly asymmetrical and lack an ectoflexus. The paracone is moderately high and strongly compressed; the paracrista is lower than the metaconid. These three teeth are not sufficiently well preserved anteriorly to make possible a statement about the anterior cusps; it seems, however, that cusp B₁ (Hu *et al.*, 1997) was very weak or absent. Posteriorly, the metacone is well individualized and followed by what seems to be a fused 'c' and metastyle; but on DORCM GS 309, a small indentation separates these two cusps, the latter being extremely reduced. The labial cingulum is finely denticulated, at least in the preserved posterior half; the lingual cingulum is absent on the first two teeth, but present faintly on the posterior side of the paracone on DORCM GS 309. Roots are also asymmetrical: one is disposed antero-lingually, wide proximally but diminishing rapidly to become circular; the second is posterior, wider and flatter but presents a longitudinal sulcus or depression; the separation of the two roots is thus postero-lingual.

DORCM GS 961 is a shattered, incomplete upper right molar and DORCM GS 314 a left anterior fragment: the paracone is, in both cases, relatively higher than on the previous molars and slightly convex labially (concave on the latter); these teeth are also much less convex lingually, so that their attribution is not certain. But if these characteristics are simply owing to a different position in the jaw, they are very interesting because the preserved anterior crest shows a well-developed cusp, followed antero-labially by a strong elevation of the cingulum in a slightly recurved (incompletely preserved) cusp, which seems to mostly represent the parastyle. If the cusp on the paracrista is homologous to B₁ (as in '*Peralestes*', a taxon currently considered to be synonymous with *Spalacotherium*, in *Zhangheotherium* and *Spalacotheroides*), then no stylocone is discernible. The parastyle is not followed antero-lingually by a cingulum.

The whole postero-labial face is worn on DORCM GS 309 and mostly on 918, while in DORCM GS 684 (Figure 10) only the posterior base of the paracone and the edge of the metacone and 'c' are touched. It should be noted that this face is here slightly undulating while it is perfectly flat in *S. tricuspidentis* ('*Peralestes*').

Milk teeth (Figure 6). Cifelli (1999) has described what he considers to be symmetrodont deciduous teeth. Four teeth from our collection may be suggested to belong to that category: one left lower, DORCM GS 373; three uppers, DORCM GS 312, practically complete left; DORCM GS 308, right

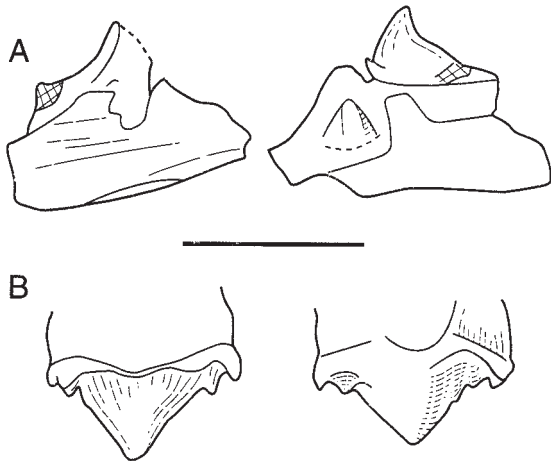


Figure 6. *Spalacotherium evansae* sp. nov., attributed milk molars. A, DORCM GS 373 (lower) in lingual and labial views. B, DORCM GS 312 (upper) in lingual and labial views. Scale bar represents 1 mm.

posterior part; and DORCM GS 909, left posterior part. They are very thin transversely, with particularly long and thin roots. On the lower molar (included in a jaw fragment from which another protoconid emerges in front of the tooth), a long, low, lingually recurved protoconid may be distinguished; a second tiny cusp emerges posteriorly. On the uppers, and especially on DORCM GS 312, the most complete of the three, the paracone is high and long, followed far distally by a clear cut metacone and a sharp metastyle; no lingual cingulum is present but we note a slight bulge under the metacone. Anteriorly, a small, sharp cusp situated against the cingulum could be the stylocone; it does not occupy the position of the supposed B_1 of DORCM GS 961 or 314 and is quite different in shape; the parastyle itself is reduced to a small disto-labial shelf. The teeth are slightly curved labio-lingually, and supported by roots that are slightly oblique relative to the long axis of the tooth. The upper milk teeth described for *Spalacolestes* by Cifelli (1999, figs 7, 8) have no cingula, but a tooth very similar to ours (Galve Th 17, undescribed) has been recovered from Barremian deposits of Galve (Spain). Whether these milk teeth belong to *Tinodon* or *Spalacotherium* is uncertain; however, the similarity with the tooth from Galve, where *S. henkeli* was identified (Krebs, 1985), has led us to prefer the latter attribution.

Once more the problem is raised concerning the identification of the preparacrista cusps: if our proposals are correct, B_1 would be present in the definitive molar while the stylocone remains distinct on the milk tooth. This would confirm the derived status of B_1 in

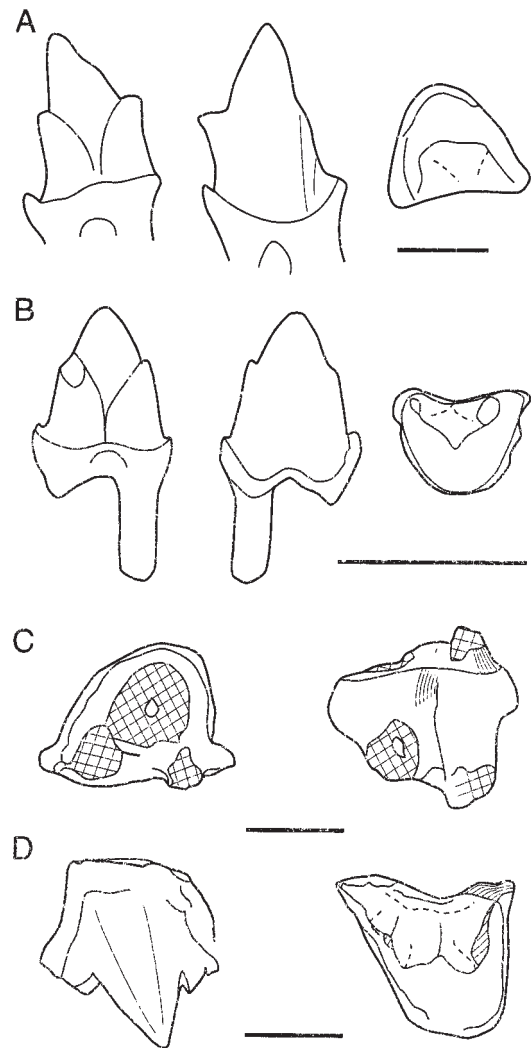


Figure 7. A, *Spalacotherium tricuspiciens*, left lower molar, in lingual, labial and occlusal views; redrawn from Simpson (1928). B, *S. taylori*, left lower molar BMNH M 21103, in lingual, labial and occlusal views; redrawn from Clemens & Lees (1971). C, *S. henkeli* 'Galve Th 11', right lower molar, in occlusal and lingual views; redrawn from Krebs (1985). D, '*Peralestes*' BMNH 47740, right M3, in lingual and occlusal views. Scale bars represent 1 mm.

symmetrodonts, which thus would have developed in parallel with the reduction of the stylocone.

Discussion. The attribution of the lower molars to symmetrodonts rests on the quasi-equality of the roots, the presence of a lingual cingulum, and the small size and sharpness of the hypoconulid. The attribution to the genus *Spalacotherium* (Figure 7) is based on the presence of a (partial) labial cingulum, the very compressed nature of the trigonid and the height of the protoconid. Unfortunately, of the six jaws of *S. tricuspiciens* originally figured by Owen

(1854, 1871), several of them with complete molars, none seems to have been preserved today in that condition, which renders comparison rather problematical: the absence of cuspule f in the type species should in particular be confirmed. In any case, no cuspule f is discernible on the type molar of the large species *S. henkeli* from Galve (Krebs, 1985).

A smaller species, *Spalacotherium minus*, was created by Owen (1854) for a jaw half the size of *S. tricuspidentis*, but Osborn (1888) and later Simpson (1928) included it in the hypodigm of *Peramus tenuirostris*. Finally, Clemens (1963) recognized one left lower molar from East Sussex, England, as belonging to the genus, though being notably smaller: it was later made the type of a new species, *S. taylori* (see Clemens & Lees, 1971); the size is close to that of the new Purbeck specimens, but the labial cingulum is complete, as in the two other species.

The incompleteness of the labial cingulum seen in *S. evansae* is also known in *Spalacotheroides* and *Zhangheotherium*, but its individual variation is not met within the other genera of spalacotheriids.

The attributed upper molars, as compared to those of 'Peralestes' (Figure 7D) are, apart from being smaller, more asymmetrical, possibly less compressed, and in any case without an ectoflexus. The lingual cingulum, if present, was very slight and limited; but the labial cingulum is finely denticulated as in 'Peralestes'.

In conclusion, the small size of the new species (close to that of *Kuehneotherium*), the presence of a tinodontid-type cuspule f on the lower molars, the incomplete labial cingulum of the lower molars and lingual cingulum of the uppers, and the slightly undulating posterior face of the latter, all seem to indicate a less derived state than that of the type species; similarly, the lesser development of B₁ on the upper molar, a cusp considered by Cifelli & Madsen (1999) to be derived for symmetrodonts but primitive for the Spalacotheriidae, could also be viewed as showing a plesiomorphic state in this particular species of the genus *Spalacotherium*. As an additional point of interest, this new material would tend to support the association of *Spalacotherium* and 'Peralestes'; note that the paracone of the attributed upper molars of *S. evansae* is not tilted backwards and correspondingly the protoconid of the lower molars is not tilted forward, contrary to what was underlined by Simpson (1928) for the type species of *Spalacotherium* and 'Peralestes'.

Tinodontidae Fox, 1985

Tinodon Marsh, 1879

Tinodon micron sp. nov.

Figures 8A–B, 9C–E, 10 (DORCM GS 694 only)

Derivation of name. Greek, *micron*, very small.

Holotype. DORCM GS 1110, a lower left molar whose paraconid is broken.

Referred material. DORCM GS 437, 538 and 1081, posterior two-thirds of left molars; DORCM GS 1078, incomplete right posterior half (uncertain attribution); DORCM GS 694, upper right molar.

Horizon and locality. Cherty Freshwater Member, Purbeck Limestone Group, upper horizon at Sunnydown Farm, Langton Matravers, Dorset, England.

Diagnosis. Lower molars differ from those of both *Tinodon bellus* and *T. lepidus* by their smaller size, the presence of posterior and anterior labial cingula, a less centrally acute lingual cingulum, and a lesser occlusal angulation of the cusps.

Description. DORCM GS 1110 (Figure 8A) has the tip of the protoconid and the paraconid missing. The main features concern what is interpreted as the paraconid, weakly detached at its base from the protoconid, while the metaconid is entirely posterior to the latter; these characters could well be attributed to an anterior position in the jaw. The cuspule interpreted as e is high and sharp, but flat anteriorly; no cuspule f is present (but it should be stressed that this cuspule is inconstant along the dental series in the other *Tinodon* species). Conversely, the hypoconulid is low and protrudes little distally. The two roots are very flat. Thus conformed, this tooth appears quite different from those of *Tinodon*, even from an anterior molar of that taxon on which, in particular, the metaconid is higher and more lingual. In fact, all other possibilities have been envisaged: premolar? milk tooth? of either *Tinodon* or *Spalacotherium*, with no means to solve the problem (in particular premolars of these genera have never been properly figured), and we probably would not have created a new species were it not for the upper molar (see below).

The referred cheek teeth (one shown in Figure 8B) do not help in the attribution. First, they are even less complete, the paraconid being totally missing: if developed, it was better detached than on the type tooth, since the preprotocristid is longer than the postprotocristid (contrary to what is observed on the latter), but still smaller than the metaconid. They

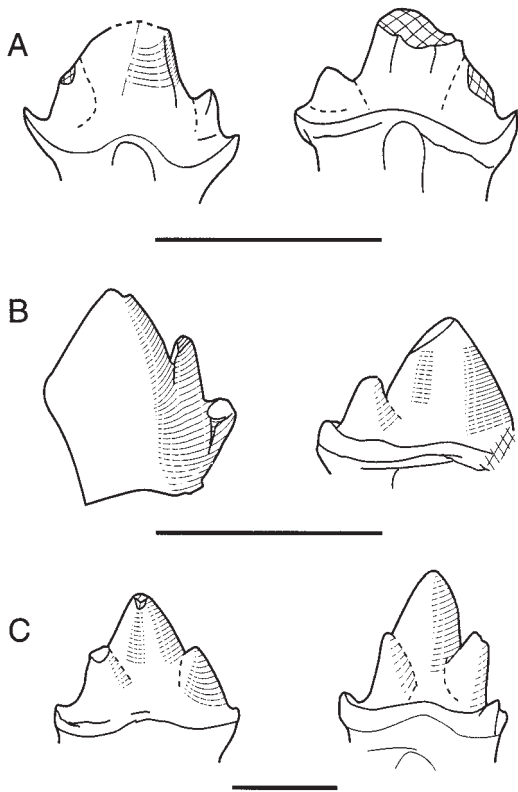


Figure 8. A, B, *Tinodon micron* sp. nov. A, holotype, DORCM GS 1110, left lower molar, in labial and lingual views. B, DORCM GS 1081, left lower molar, in labial and lingual views. C, *Tinodon bellus*, YPM 13644, M1 and M2, lingual views. Scale bars represent 1 mm.

differ further from DORCM GS 1110 by the metaconid being partly lingual to the protoconid, which might indicate a more posterior position in the jaw. The sharp hypoconulid is also quite different, especially labially where it is better detached and flattened by a wear facet in two cases; it is prolonged postero-labially by a slight, descending, short cingulum. The lingual cingulum is slightly undulating. The protoconid here is again thin labio-lingually, slightly convex lingually with a vertical ridge, and more or less angulated labially. Wear facet A (Crompton, 1971) persists on these teeth (Figure 10).

Discussion. Even though the characters distinguishing the lower molars of *Spalacotherium* and *Tinodon* are very clear on the preserved jaws described previously from the Purbeck (*Spalacotherium*) and Morrison (Wyoming, USA: *Tinodon*) Formations, these isolated teeth pose a problem. The main distinctive elements of the latter genus (weak transverse width and wide separation of para- and metaconid, shorter paraconid) are also found on the *Spalacolestes* m_1 as reconstructed

by Cifelli & Madsen (1999), so that the teeth identified here as belonging to *Tinodon* could as well be the anterior molars of *Spalacotherium evansae*; all the more so that on these teeth, and contrary to what is seen in the two other species of *Tinodon*, the cristids are unequal as they are in *Spalacotherium*. Conversely, the five teeth discussed above under *S. evansae* (DORCM GS 360, 371, 669, 1043, 1075), could be posterior molars of this small species of *Tinodon*: the trigonid compression varies greatly along the jaw in this genus (Figure 8C); in particular, DORCM GS 1075, with its small paraconid and well-individualized cusplule f could belong to *Tinodon*.

Finally, it was the presence or absence of a clear wear facet A that appeared determinant in the decisions: the five teeth just mentioned do not show it and are, therefore, attributed to *Spalacotherium*. On the contrary, and as noted earlier, the teeth attributed to *Tinodon micron* keep it: the metaconid shows two independent wear facets, one anteriorly, one posteriorly; the sole DORCM GS 1078, which also obviously had a small paraconid far from the metaconid, shows a completely transverse posterior face; hence its doubtful attribution to *Tinodon*.

Attributed upper molar. In fact, the justification for, and the main interest of, this new *Tinodon* species resides in the attributed upper molar, DORCM GS 694 (Figure 9). We could have designated this tooth as the type, and considered the incomplete lower molars as attributed, but of what genus? The synonymy *Tinodon*-'Eurylambda' is not proved, but on the other hand it seems ill-advised to create a new 'Eurylambda' species.

The genus 'Eurylambda' Simpson, 1929, with the single species *aequicrurius*, occupies a key position in phylogeny in that, together with *Tinodon*, it was made the type of the basal family of Theria. Moreover, studies by Crompton & Jenkins (1967, 1968) based on these genera have been the foundation for establishing the molar occlusion for these early Theria. Unfortunately 'Eurylambda *aequicrurius*' is known by a part of a right maxilla preserving a single upper molar (YPM 13639), from the Morrison Formation of Wyoming; moreover, this tooth is incomplete, lacking the antero-labial corner, an area important to assessing affinities within the Symmetrodonta. DORCM GS 694 is thus of special interest as it is apparently attributable to 'Eurylambda' and it preserves the anterior labial area.

This new tooth is complete in that all cusps are preserved, though the paracone has been severely truncated. It is notably smaller than the Morrison

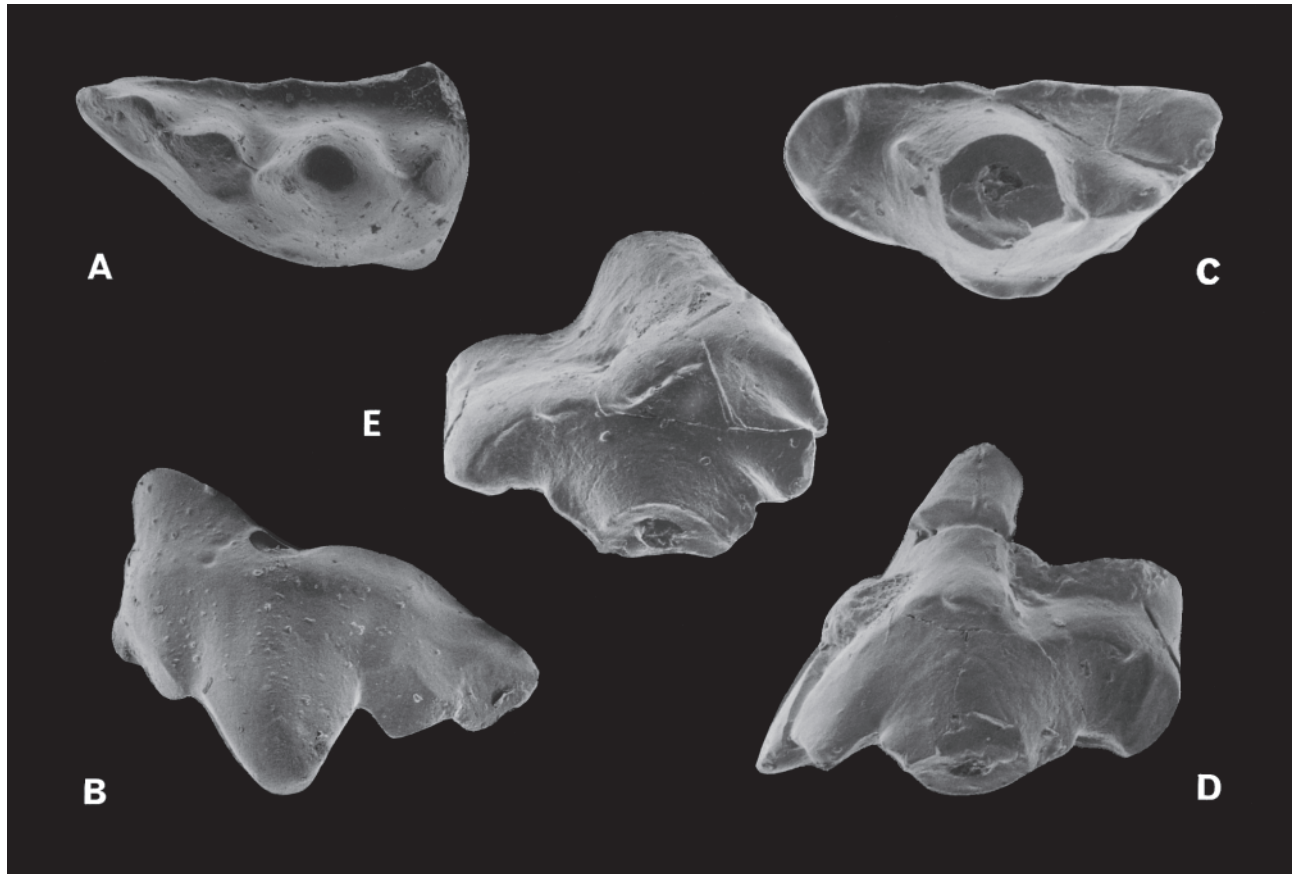


Figure 9. A, '*Eurylambda aequicururius*', holotype, YPM13639, right upper molar, occlusal view, $\times 30$. B, the same, lingual view, $\times 30$. C, *Tinodon micron*, attributed left upper molar, DORCM GS 694, occlusal view, $\times 45$. D, the same, lingual view, $\times 45$. E, the same, labial view, $\times 45$. All scanning electron micrographs.

tooth (length=1.21 versus 1.91 mm; width=0.62 versus 0.92 mm) and much more curved labio-lingually; it also differs in the quasi-absence of a cusp on the preparacrista, interpreted as a stylocone by [Crompton & Jenkins \(1967\)](#): a very faint bump on the preparacrista might represent it. More labially, the anterior part consists of a well-developed parastylar lobe, separated from the rest of the crown by a deep sulcus, and continued labially into a faintly cuspidate cingulum. The latter is less straight than on the type tooth. Lingually, the cingulum is more accentuated and complete than on the Morrison tooth, reaching at least the posterior third of the crown, but the tooth is damaged at its base at this level; on the type tooth the fainter cingulum is limited to the base of the paracone. Metacone and cusp 'c' are little different on the two teeth, except that 'c' is almost as high as the metacone in the new specimen, but flatter lingually; moreover it is only faintly separated from the metastyle, from which the cingulum descends vertically. On the Morrison specimen the metastyle forms a low cuspule separated from 'c' by a lingual sulcus. The two roots

are preserved: the anterior one is flattened labio-lingually, the posterior one antero-posteriorly, but set obliquely relative to the axis of the tooth.

Wear facets ([Figure 10](#)) are somewhat less accentuated than on the Morrison tooth, and the difference on the posterior side is assignable to the curvature of the tooth. One facet, oval-shaped and inclined lingually, wears the lingual side of the parastyle, which must have been caused by the protoconid of the lower molar; and clear facets cut the antero-lingual face of the metacone and postero-lingual face of the latter and cusp 'c'. In any case, transverse shear was not achieved. Finally, the posterior curvature of the tooth testifies that the anterior part of the corresponding lower molar was also compressed, as is exemplified by the most central teeth of the *Tinodon* dental series.

Can the very marked difference in importance of the preparacrista cusp in the two teeth that are known be compatible with intrageneric variation (or even accountable to a different position on the jaw: [Cifelli, pers. comm. 2000](#))? First, it is stressed again ([Sigogneau-Russell & Ensom, 1998](#)) that the cusp on

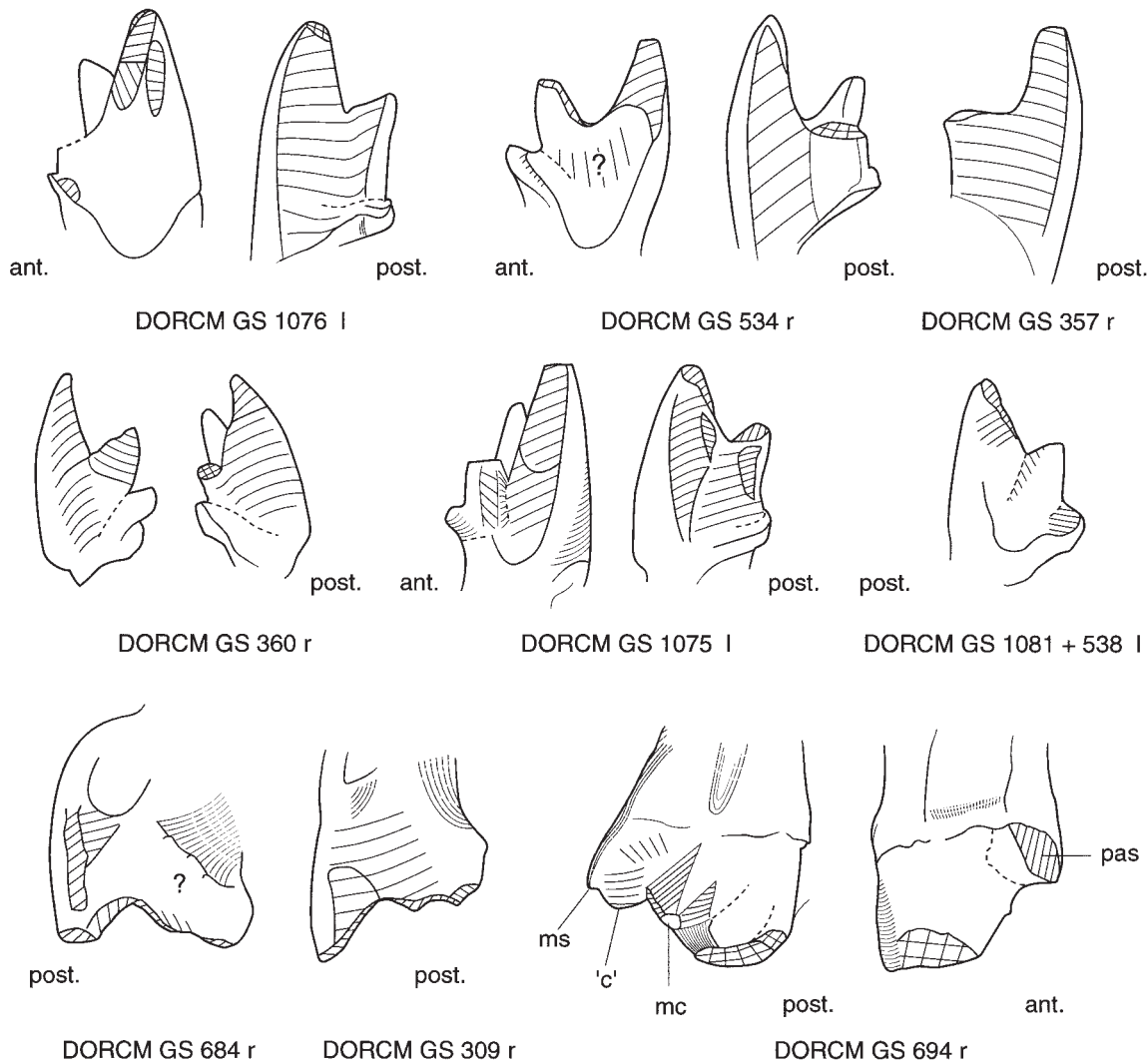


Figure 10. Wear facets observed on some of the teeth studied; all are attributed to *Spalacotherium evansae* sp. nov. except for DORCM GS 694, which is referable to *Tinodon micron* sp. nov.

the preparacrista on the type of '*Eurylambda*' is very lingually situated, more so than in all other therians, whether primitive or derived. Could this cusp then not be the stylocone, as identified by Crompton & Jenkins (1967), but rather equivalent to the accessory cuspule on the preparacrista of *Zhangotherium* (B_1 of Hu *et al.*, 1997) or '*Peralestes*' (Sigogneau-Russell & Ensom, 1998; Cifelli & Madsen, 1999)? In this context, it is interesting to note that Simpson (1929) had already observed the resemblance between '*Eurylambda*' (the Morrison tooth) and '*Peralestes*'; this resemblance is especially accentuated with the second molar of this taxon, but here the paracone is flatter labially. The stylocone would then have already been very reduced in '*Eurylambda*', and the difference between the two upper molars from Morrison and

Purbeck would affect the accessory cuspule, B_1 , absent in the latter: this cusp is also variable along the jaw in '*Peralestes*'. Moreover the resemblance between DORCM GS 694 and *Kuehneotherium* sp. SNP 50W (Figure 11) (no cusp B_1 and stylocone entirely labial) would confirm this interpretation. This would indicate that the reduction of the stylocone and development of a cusp B_1 were not limited to spalacotheriids. If, however, the anterior cusp of the Morrison tooth is indeed a stylocone, then one should envisage variation within a generic unit of earlier symmetrodonts.

Finally, the less distinct individualization of a meta-style on the Purbeck specimen could be attributable to it representing the last position in the molar series, although there is little variation in this area along the series in the jaw of '*Peralestes*'. Despite these

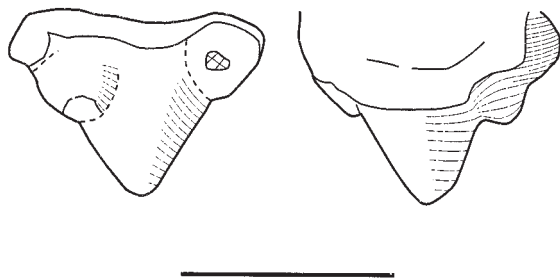


Figure 11. *Kuehneotherium* sp., upper molar SNP 50W, in labial and lingual views. Scale bar represents 1 mm.

differences, YPM 13639 and DORCM GS 694 exhibit striking resemblances, and we accordingly refer this tooth to the new *Tinodon* taxon.

Tinodon-Eurylambda was thought to be specialized by Patterson (1956) 'particularly as regards molar reduction' (p. 45), while Crompton & Jenkins (1967) saw it as 'conservative within symmetrodonts, having retained the primitive form of Rhaetic symmetrodonts' (p. 1008). The lower molars described above would support the latter statement. In the upper molars, the labio-lingual narrowness of the trigon, the persistence of the facet A and the more or less complete lingual cingulum are primitive relics; but the possible reduction of the stylocone and development of B₁, as well as the presence of a large cusp 'c' and of a detached parastyle (different, however, from the hook-like parastyle of late spalacotheriid symmetrodonts) are apomorphies relative to the condition seen in the primitive Theria (*Kuehneotherium*, *Woutersia*), some of which would parallel those of spalacotheriids.

3. Conclusion

The presentation of such isolated teeth as those described above may seem to be of slight interest in view of the more complete material coming to light in North America (Cifelli & Madsen, 1999) and China (Hu *et al.*, 1997). Our specimens nevertheless contribute in substantiating the variety of mammals during the middle Mesozoic and in throwing more light on relationships between the faunas of the Morrison Formation of North America and the Purbeck Limestone Group of England, while perhaps obscuring the concept of spalacotheriids!

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