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NOTE

A NEW SYMMETRODONT FROM THE EARLY CRETACEOUS OF ENGLAND

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Mesozoic symmetrodont mammals have long been of interest because of their 'reversed triangle' cusp pattern, considered a significant advance in molar evolution. Unfortunately, they are poorly represented in the fossil record. The genus *Spalacotherium* Owen 1854 was created from material collected from the earliest Cretaceous of Dorset, England. Other acute-angle symmetrodonts have been found from the lower Cretaceous of Spain (Krebs, 1985) and Texas (Patterson, 1956), the middle and late Cretaceous of Utah (Cifelli and Madsen, 1986, 1999; Cifelli, 1990; Cifelli and Gordon, 1999), and the late Cretaceous of Alberta (Fox, 1972, 1976, 1985). A complete skeleton of a symmetrodont, *Zhangheotherium*, was recently found in China (Hu et al, 1997), but generally knowledge of symmetrodont diversity is poor.

MATERIALS AND METHODS

Until the exciting recent discoveries of new sites (Ensom, 1988; Sigogneau-Russell and Ensom, 1998; Ensom and Sigogneau-Russell, 2000), almost all Mesozoic mammals from the Isle of Purbeck, Dorset, England, were obtained in the 1850s, from Beckles' Pit in the Mammal Bed of Durlston Bay. A specimen is now described, representing a new species, which I found in 1969, approximately 4 m above the Mammal Bed horizon, and just to the south of the original pit. No further portion of the jaw was found at the time and subsequent searching at this locality of both this horizon and the Mammal Bed were unrewarding. The jaw has suffered breakage, but virtually no abrasion, prior to deposition and some crushing subsequently. The specimen was manually cleaned and Alvar 1570 was used to repair the cusps.

The teeth are described using standard dental nomenclature. Dimensions were measured using a binocular microscope. Tooth measurements are to the nearest 0.05 mm to allow for slight abrasion in some specimens. Enamel thickness is measured to the nearest 15 microns.

Institutional Abbreviations—**BMNH**, Natural History Museum, London; **CAMSM**, Sedgwick Museum, Cambridge; **DORCM**, Dorset County Museum; **OMNH**, Oklahoma Museum of Natural History; **MNA**, Museum of Northern Arizona; **UA**, University of Alberta.

SYSTEMATIC PALEONTOLOGY

Order SYMMETRODONTA Simpson 1925
Family SPALACOTHERIIDAE Marsh, 1887
Type genus *SPALACOTHERIUM* Owen, 1854
SPALACOTHERIUM HOOKERI, sp. nov.

Holotype—BMNH 44970, partial left dentary with distal five molars (m3-m7) in situ.

Type Locality and Horizon—Durlston Bay, Swanage, Dorset, England, immediately to the south of the site of Beckles' Mammal Pit, on the downthrown side of the Tilly Whim Fault (National Grid Reference SY036783). Cherty Freshwater Member (Lulworth Formation) of the Purbeck Limestone Group, in a calcareous shale below the New Vein, a bioclastic limestone correlated with DB 101, dated as earliest Cretaceous (Berriasian) (Clements, 1993; Ensom and Sigogneau-Russell, 2000). The bed in which BMNH 44970 was found is correlated with DB 96. This is close to the horizons in which *Spalacotherium evansae* was found (Ensom and Sigogneau-Russell, 2000), particularly the lower horizon DB 98-100.

Diagnosis—Differs from *Spalacotherium tricuspidens* by its smaller size. Differs from *S. henkeli* by its smaller size, paraconid and metaconid sub-equal in size and absence of extensions under the anterior and posterior tips of the cingulum. Differs from *S. evansae* by its complete molar cingulum. Differs from *S. taylori* by its more complete, smoother, narrower cingulum. *S. taylori* is also more symmetrical in occlusal outline without the distinct asymmetry of the roots, but this may be related to a more mesial position in the jaw.

Etymology—hookeri for Dr. Jerry Hooker, of Natural History Museum, London, in recognition of his wide ranging contribution to the study of fossil mammals.

Description

BMNH 44970 comprises the distal portion of the horizontal ramus of a left dentary and the final five molars (Figs. 1, 2; Table 1). The ultimate molar is considerably smaller and distinctive in shape and is identified with confidence. The molars are identified as m3–7 on the basis of *Spalacotherium* having seven lower molars (Clemens, 1963a). A distal alveolus and part of the mesial alveolus for m2 are also present. The alveoli for m2 suggest that the tooth was similar in size to m3 but with slightly more diverging roots. The jaw has suffered some post-deposition lateral crushing and some of the cusps of the molars are broken, particularly on m4 and m5. The horizontal ramus is rather deeper below m3 than further distally, although this is slightly distorted by crushing. The dorsal border is gently concave in medial view. The ramus thickens distally in lateral view as it forms what was presumably the mesial margin of the masseteric fossa. The rise up to the ascending ramus appears to be more gradual than in *S. tricuspidens* and begins mesial to m7, making the final molar less prominent in BMNH 44970 than in *S. tricuspidens* with its straighter alveolar border. There is a distinct meckelian groove present (Fig. 1A), extending parallel to the ventral border to at least the level of m2. As the posterior section is damaged, evidence of any mandibular foramen is lost.

With the exception of the ultimate molar (m7), the molars are as for Simpson's (1928) description of *Spalacotherium tricuspidens*. The trigonid cusps form an angle of approximately 60°. There is a complete, smooth cingulum, which, although narrow, is sharply defined. The cingulum is narrowest labially, just above the root separation, and widens to either side, especially above the distal root. The distolingual stylar cusp overlaps the mesiolingual stylar cusp of the succeeding tooth in an imbricating relationship. Simpson (1928) noted that the molars of *S. tricuspidens* increase in height to m4. This cannot be definitely confirmed in BMNH 44970 as the protoconid is incomplete in m4 and m5, but it appears to be the case and m4 is the largest tooth in occlusal measurement.

The ultimate molar in BMNH 44970 is complete and similar to the ultimate molar of *Spalacotherium tricuspidens*, being reduced in size, more symmetrical than the preceding molars, and with the metaconid smaller than the paraconid (Figs. 1, 2). The cingulum is narrow and close to the alveolar border, with no distolingual or mesiolingual stylar cusps, and complete except for a very short section labial to the protoconid.

Wear of the protocristid is clearly seen on m3 running from the tip of the protoconid. It is most marked near the tip. Similar wear can also be seen on m6, although to a lesser extent as would be expected. Oblique scratches can be seen on the mesial and distal surfaces of the protoconids in m3 and m6 of BMNH 44970, but distinct facets cannot be determined. Wear is very marked on the cingulum, particularly mesially. Distally the cingulum is protected by the mesiolingual cuspule of the succeeding tooth but distal cingulum wear can be seen on the ultimate molar.

A rectangular groove extends down lingually from the smoothed tip of

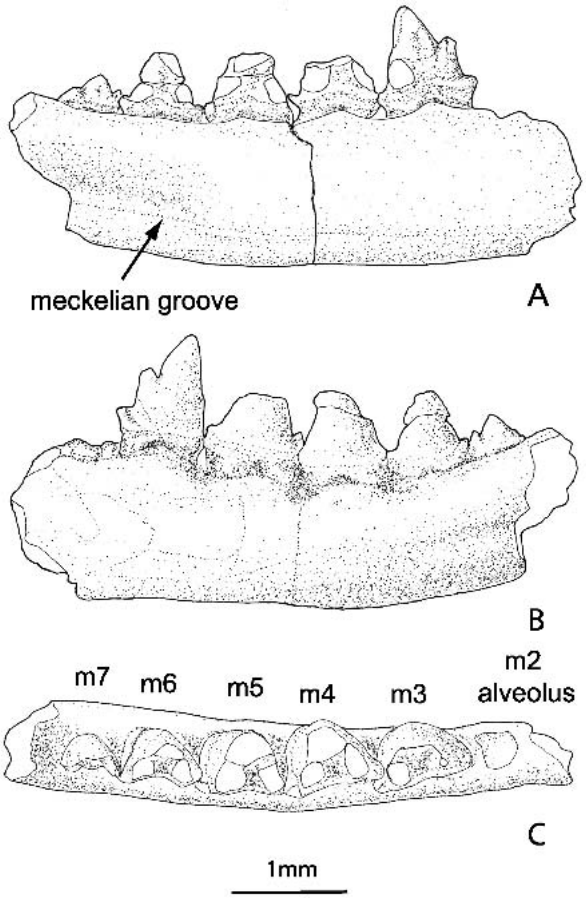

FIGURE 1. *Spalacotherium hookeri*, sp. nov., holotype (BMNH 44970), partial left dentary in lingual (**A**), labial (**B**), and occlusal (**C**) views.

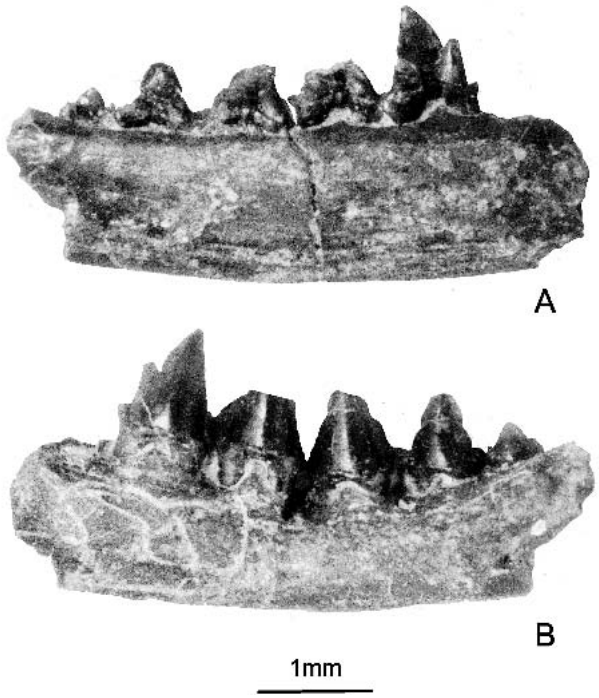

FIGURE 2. *Spalacotherium hookeri*, sp. nov., holotype (BMNH 44970), partial left dentary in lingual (**A**) and labial (**B**) views.

the paraconid of m3, continuous with the wear of the lingual paracristid. The wear extends into the dentine but the edges of the enamel are smooth. Although in an unusual position, this wear appears to have occurred during the life of the animal, as there is no evidence for post-mortem abrasion. Damage to the specimen seems to have been due to cracking and subsequent breakage and the blade and cingulum edges are sharp. This paraconid groove may have been formed by malocclusion, or possibly the paraconid tip was broken during life, enamel flaked off the cusp lingually and the area was smoothed by wear from food.

Isolated Wealden Symmetrodont Teeth

Three isolated symmetrodont molars are included in this paper, as they have not previously been described and further demonstrate the diversity of symmetrodont teeth occurring in the early Cretaceous. They are from the Wealden of southern England and were found by the University College London team led by Professor K. A. Kermack. BMNH 44971 is from Cliff End, BMNH 44972 from Tighe B, and BMNH 44973 from Tighe A (Table 2). A description of these localities is given in Clemens (1963b) and Clemens and Lees (1971).

BMNH 44972 (Figs. 3C, D, 4C) is an isolated left lower molar, slightly larger than *Spalacotherium taylori*. The trigonid is acute-angled (54°) and slightly asymmetrical. The protoconid is broken off at the level of separation of the paraconid and just above that of the metaconid, but it can be seen that the paraconid and metaconid separate from the protoconid at a similar height above the cingulum. The cingulum is well developed and smooth lingually but appears to have been very narrow labially as it passes round the base of the protoconid. The tooth is slightly rolled and the cusp tips and edges of the cingulum are rounded, so it is not possible to be completely certain. There are distinct mesial and distal stylar cusps. The roots are broken just below the crown labially, but a portion is preserved lingually due to the slope of the base of the crown. The roots are fairly symmetrical in outline. Wear can be clearly seen on the distal face of the protoconid with scratches running obliquely from the protocristid and distal wear of the cingulum can also still be seen. Mesially, the wear is less clear, particularly as the protoconid is broken. There appears to be wear on the cingulum at the mesial stylar cuspule and mesiolabially.

BMNH 44973 (Figs. 3E, F, 4D) is also an isolated left lower molar, larger than BMNH 44972, but not as large as BMNH 44971. The trigonid is acute-angled (54°), similar to BMNH 44972. The protoconid is complete, although worn, but the paraconid is broken and part of the lower portion of the mesial cingulum, including any stylar cuspule, is lost. The cingulum is generally similar to that of *Spalacotherium taylori* (Fig. 4), being broad and smooth, and almost dying out labially. Mesially, there is a clear facet on the cingulum and scratches on the mesial face of the

TABLE 1. Measurements include the cingulum and are to the nearest 0.05 mm, except *Spalacotherium evansae* (Ensom and Sigogneau-Russell, 2000), *S. henkeli* (Krebs, 1985) and *S. tricuspidens* BMNH 45471 (Clemens and Lees, 1971). Length is mesiodistal and width is labiolingual.

Specimen	Molar position	Length	Width
Spalacotherium hookeri	m3	1.10	0.80
BMNH 44970	m4	1.10	0.80
	m5	1.00	0.80
	m6	0.85	0.70
	m7	0.60	0.45
S. tricuspidens BMNH 46019	m4	1.60	1.50
	m5	1.60	1.50
	m6	1.40	1.35
	m7	1.05	0.95
S. henkeli Galve Th 11	—	2.18	1.30
S. taylori BMNH 21103	—	0.80	0.55
S. evansae DORCM GS 355	'1st molar'	0.75	0.65
	'2nd molar'	0.54	0.42
	'3rd molar'	0.37	0.30
BMNH 44971	—	1.65	0.95
BMNH 44972	—	0.85	0.90
BMNH 44973	—	1.10	1.10
S. tricuspidens BMNH 45471	—	1.5	0.8

TABLE 2. Horizons and localities of specimens of *Spalacotherium* from southern England (sequence based on Ruffell et al 1996).

Group	Formation	Specimen	Locality
Hastings	Upper Tunbridge Wells sands		
	Grinstead Clay	*Spalacotherium taylori*	Paddockhurst Park
	Lower Tunbridge Wells sands		
	Wadhurst Clay	BMNH 44972, 44973	Tighe Farm (Telham Pebble Bed)
		BMNH 44971	Cliff End Bone Bed
		BMNH 45471	Cliff End Bone Bed
	Ashdown		
Purbeck	Durlston		
	Lulworth	*S. tricuspidens*	Durlston Bay
		S. hookeri	Durlston Bay
		S. evansae	Durlston Bay / Langton Matravers

protoconid. Distally, the protocristid has heavy wear, but no discrete facet on the distal face of the protoconid. Wear on the distolabial cingulum is less than on the mesial cingulum.

BMNH 44971 (Figs. 3A, B, 4A, B) is an isolated, left lower molariform tooth with an obtuse-angled (120°) trigonid. It is larger in size than the previous two teeth and comparable in size with *Spalacotherium tricuspidens*. The tooth is rolled, with the tips of the cusps and the cingulum abraded, and the roots are broken just below the crown. The tooth is low-crowned and the cingulum is broad, smooth, and complete. The labial cingulum appears to be narrower, but the abrasion of the tooth makes this hard to determine. The paraconid separates from the protoconid near to the base of the crown, and is rather conical in appearance. The heavy wear on the tips of the trigonid cusps is still apparent and there is considerable wear on the protocristid. Fox (1976:1113) noted similar wear in *Symmetrodontoides canadensis* (UA 12086): "A broad strap-like wear facet extends from the apex of the protoconid down its posterior edge and continues onto the apex of the metaconid." This wear pattern is also seen in obtuse-angled *Kuehneotherium* molars (pers.obs.).

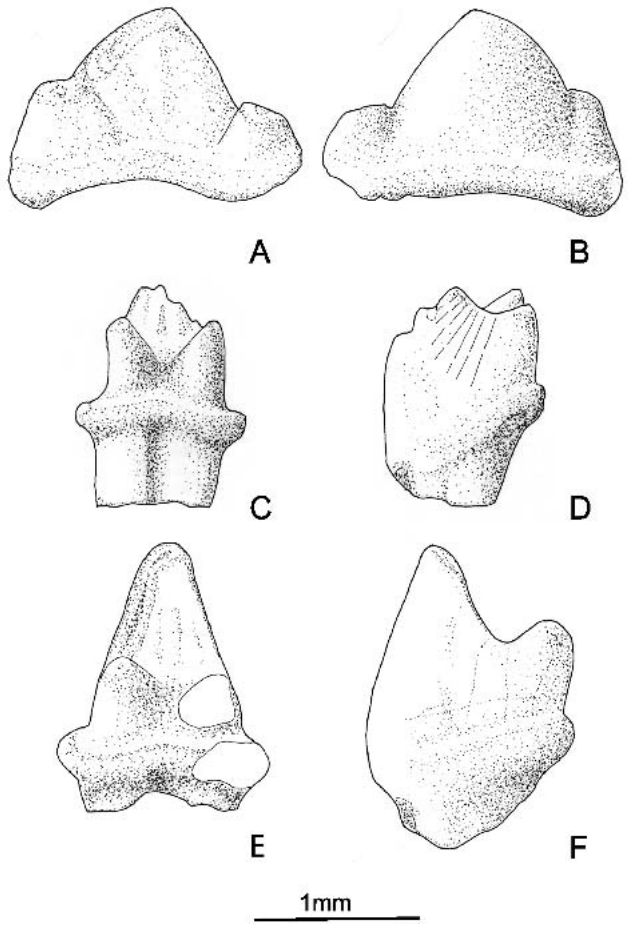

FIGURE 3. Isolated Wealden teeth, all left lower molars. **A**–**B**, BMNH 44971, in lingual (**A**) and labial (**B**) views. **C**–**D**, BMNH 44972, in lingual (**C**) and distal (**D**) views. **E**–**F**, BMNH 44973, in lingual (**E**) and distal (**F**) views.

DISCUSSION

Spalacotherium hookeri

Spalacotherium hookeri differs from *S. henkeli* and *S. tricuspidens* on the basis of its smaller size (Table 1) and, in the former case, lack of the extensions under the anterior and posterior tips of the cingulum (Krebs 1985). Although *S hookeri* is otherwise very similar to *S. tricuspidens*, the size difference is considered significant enough to create a new species (Fig. 5). Both holotypes are mature specimens and so can be readily compared. The holotype for *S. tricuspidens* (BMNH 46019) is also a partial left dentary with m4–7. Simpson (1928:102) noted that the specimens of *S. tricuspidens* in the Natural History Museum, London "show no measurable differences in size and appear to have been little variable". The other comparable specimen of *S. tricuspidens* is CAMSM J11378. This specimen is just slightly larger than the BMNH specimens (Clemens, 1963a).

Otherwise, apart from a slight difference in the ultimate molar, the molars are very similar. This difference is the extent of the labial cingulum in the final molar. Simpson (1928:101) notes that the cingulum in *Spalacotherium tricuspidens* is "obsolete externally" whereas it is complete, except for a very short section labial to the protoconid, in *S. hookeri*. However, there is some suggestion of variation in *S. tricuspidens*. In the holotype BMNH 46019 there is no cingulum labial to the

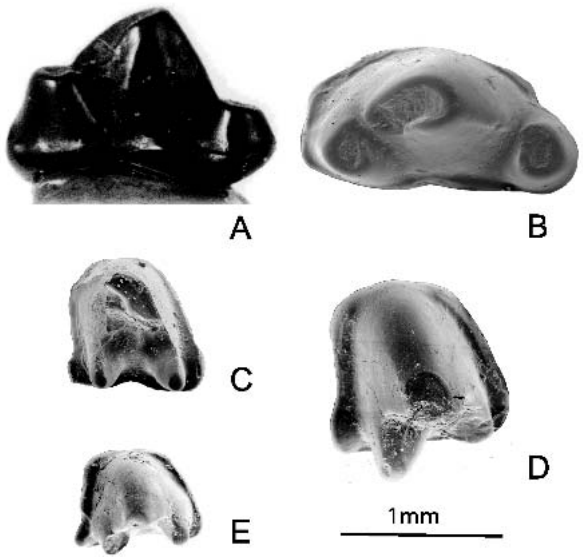

FIGURE 4. Isolated Wealden teeth, all left lower molars. **A**, BMNH 44971, lingual view. **B**–**E**, Scanning electron micrographs of casts, all occlusal view. **B**, BMNH 44971. **C**, BMNH 44972. **D**, BMNH 44973. **E**, *Spalacotherium taylori*, holotype (BMNH 21103).

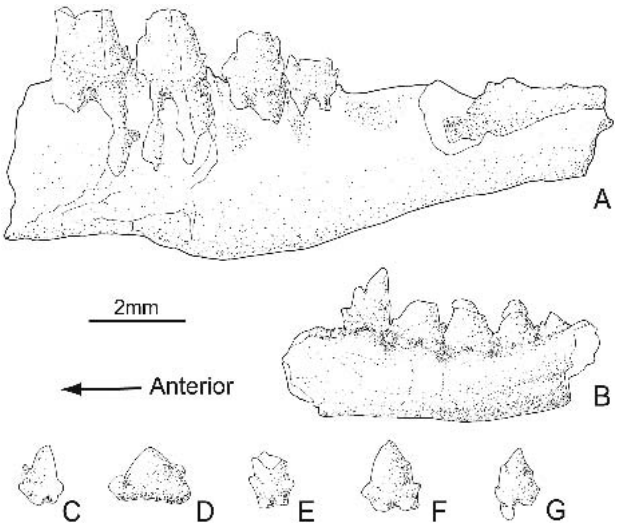

FIGURE 5. Drawings to same scale to show comparative size of *Spalacotherium hookeri* with other specimens. **A**, *S. tricuspidens*, holotype (BMNH 46019). **B**, *S. hookeri*, sp. nov., holotype (BMNH 44970). **C**, *S. evansae*, molar from holotype (reversed) (DORCM GS 355). **D**, BMNH 44971. **E**, BMNH 44972. **F**, BMNH 44973. **G**, *S. taylori*, holotype (BMNH 21103).

protoconid but there are mesial and distal salients extending labially from the lingual cingulum cusps. In BMNH 47749A, the cingulum extends rather further labially and is only absent from the most labial section. I would suggest that final molars might be variable and that this detail of the cingulum is not a definitive feature for identification unless a larger sample subsequently shows consistency.

There are two differences in the mandible but they may also represent individual variation. One is the anterior extent of the meckelian groove (Figs. 1A, 2A). In *Spalacotherium tricuspidens*, Simpson (1928:101) stated that "just below the dental foramen a well-marked internal groove starts, curving downward and forward to become obsolete beneath the middle molars". In *S. hookeri*, instead of curving down and dying out, the groove continues forward, parallel to the ventral border, to at least the level of m2. Another difference is the shape of the ascending ramus distal to the ultimate molar (Fig. 5A, 5B). Simpson (1928:102) noted for *S. tricuspidens*, "the coronoid process does not curve upward from the last molar, as in most mammals, but rises abruptly from the alveolar border . . . about 2.5 mm behind m7." The slope appears to be more gradual and begins at the final molar in *S. hookeri*, although, due to breakage distal to the final molar and some crushing, it is difficult to be absolutely sure. These possible differences are noted but there is insufficient evidence to include them in a diagnosis unless further specimens confirm their validity.

The wear seen in both *Spalacotherium tricuspidens* and *S. hookeri* appears to be very similar as far as can be determined, although the degree of wear is slightly less in *S. hookeri*. In the holotype of *S. tricuspidens*, the protoconids are broken, but a distal facet with oblique scratches can be seen on m6 and possibly m7. Wear of the paracrista from the paraconid tip can be seen on m4, similar to that seen on m3 in *S. hookeri*. Wear is most noticeable on the labial cingulum in both specimens, particularly mesially, but distal cingulum wear can be seen on m7 in both specimens.

The manner of interlock of the lower molars is diagnostic in symmetrodonts. In both *Spalacotherium hookeri* and *S. tricuspidens* the distolingual stylar cusp overlaps the mesiolingual stylar cusp of the succeeding tooth, in a rather imbricating relationship. This overlap is also demonstrated in *S. taylori* by a clear inter-tooth wear facet labial to the distal stylar cuspule (Fig. 4E). This unique pattern of overlapping was included in a revised diagnosis of the Spalacotheriidae, ". . . whereby the distal cingulum cusp of one molar is placed [lingual] to the mesial cingulum cusp of the succeeding tooth" (Cifelli and Madsen, 1999:174). This overlap pattern differs from *Kuehneotherium* where the distal stylar cusp fits between two mesial stylar cusps, of which the lingual is the larger (Mills, 1984). Inter-tooth wear between the mesial cusps can be clearly seen on *Kuehneotherium* molars (pers. obs.).

The manner of interlock was noted when comparing BMNH 44970 with other *Spalacotherium* specimens. Although showing the same basic unique interlock, modification is seen in *S. evansae* which is not seen in *S. tricuspidens* or BMNH 44970. Some lower molars of *S. evansae* have two mesiolingual stylar cusps, identified as e and f (Ensom and Sigogneau-Russell, 2000). A clear example is DORCM GS 360 (pers. obs.). The larger and most labial cuspule, f, is denoted as a tinodontid-type cuspule but I suggest they may not be equivalent. An alternative interpretation is that cuspule f is the equivalent of the mesiolingual cuspule seen in *S. tricuspidens*, and the smaller cuspule e has developed medial to it on the lingual cingulum. If so, the interlock in *S. evansae* is essentially a distal imbrication as described in *S. hookeri*, perhaps with extra stability lingually. I suggest that this is not comparable with *Tinodon* and *Kuehneotherium*, where the most lingual cuspule is prominent in the interlock and fits lingual to the distal cuspule, or hypoconulid, of the preceding tooth.

In comparing BMNH 44970 with *Spalacotherium taylori* (Fig. 4E), the differences are mainly in the development of the cingulum, as noted in the diagnosis. It is rather difficult to otherwise compare the two specimens as *S. taylori* is an obtuse-angled tooth and may be from a more mesial position than the teeth in BMNH 44970 (Clemens, 1963b; Clemens and Lees, 1971). The cingulum of *S. taylori* is broader and rather crenulate lingually but almost dies out labially. *S. taylori* is rather smaller than BMNH 44970, comparable in size to m6, one of the smaller molars (Table 1). *S. taylori* is also more symmetrical in occlusal outline and does not have the distinct asymmetry of the roots of BMNH 44970, which has a larger, more labially extending, distal root.

Spalacotherium evansae differs from BMNH 44970 in the lack of a labial cingulum and smaller size (Ensom and Sigogneau-Russell, 2000) (Table 1). Many of the teeth from the sample of *S. evansae* are also more acutely angled (pers. obs.). In the holotype of *S. evansae*, DORCM GS 355, the final molar is more reduced than that of BMNH 44970 and lacks a metaconid, similar to that of *Spalacolestes* (Cifelli and Madsen, 1999; Ensom and Sigogneau-Russell, 2000).

Isolated Wealden Symmetrodont Teeth

BMNH 44972 and BMNH 44973, both left lower molars from Tighe Farm, appear to be from the central, or centrodistal, region of the tooth row. Both are smaller than *Spalacotherium tricuspidens* or *S. henkeli* (Table 1). BMNH 44972 differs from BMNH 44973 in its smaller size and greater symmetry, including the roots (Figs. 4C, D). BMNH 44973 shows similarities in cingulum development to *S. taylori* (Fig. 4E), but is larger and more acute-angled, although this latter probably reflects tooth row position. BMNH 44972 is similar in size and cingulum development to *S. hookeri* but is more acute-angled. Both the above specimens are a little older than *S. taylori* although from a similar area (Table 2). BMNH 44972 and BMNH 44973 are considered to belong to the genus *Spalacotherium* but, without incontrovertible specific characters, they are currently designated as *Spalacotherium* sp.

BMNH 44971, the obtuse-angled molar from Cliff End, is similar in size to *Spalacotherium tricuspidens* and was compared to its first lower molar. Although similar in general form, BMNH 44971 is more obtuse-angled and has a stronger, more complete cingulum. *Tinodon bellus* from the Morrison Formation of Wyoming, also has an obtuse-angled first lower molar and is of a similar size, but does not have a labial cingulum. In tinodontids the anterior molars normally have equal or sub-equal paraconid and metaconid, whereas BMNH 44971 is more asymmetrical in lateral outline. It should be noted that a small symmetrodont from the Purbeck has been assigned to the genus *Tinodon* and named *T. micron* (Ensom and Sigogneau-Russell, 2000). However, *T. micron* has only short posterior and anterior labial cingula and has a well developed mesial stylar cusp e. BMNH 44971 is not considered to be a tinodontid due to its complete labial cingulum, asymmetrical lateral outline, and lack of cusp e.

Kielan-Jaworowska et al. (1998) and Luo et al. (2002) have demonstrated that penultimate and ultimate permanent premolars in stem symmetrodonts, tinodontids, and eupantotheres all have straight alignment of the cusps. This rules out the possibility that BMNH 44971 is a permanent premolar.

A preferred alternative identification is that BMNH 44971 is a deciduous lower premolariform from a posterior locus of a large spalacotheriid (Luo, pers. comm.). Cifelli (1999) described a series of deciduous teeth from the medial Cretaceous Cedar Mountain fauna of Utah and casts of these teeth were made available to the author. OMNH 33026 (dp4, re-

ferred to *Spalacolestes cretublatta*) and the larger OMNH 33027 and MNA V6247 (dp3 and dp4 respectively, referred to *Spalacotheridium noblei*) are very comparable to BMNH 44971, particularly the obtuse-angled trigonid, low crown, and rather separate paraconid (Cifelli 1999:figs. 4, 6). The lack of roots in BMNH 44971 is consistent with a relatively worn deciduous tooth as they may have been resorbed, pending replacement.

Another very similar tooth, in a dentary fragment, is UA 12086, one of three specimens referred to *Symmetrodontoides canadensis* (Fox, 1976) from the upper Milk River Formation of Alberta. This is also a low-crowned, obtuse-angled mesial lower molar, with a well developed complete cingulum and a strap-like wear facet. Although initially designated as m1 (Fox, 1976) the subsequent finds from the Cedar Mountain fauna suggest that the tooth is dp4 (Cifelli, 1999).

Noting that enamel tends to be noticeably thinner on deciduous premolars than on molars, Cifelli (1999:262, fig.11) measured this on *Spalacolestes cretublatta* from the Cedar Mountain fauna, with a caveat that enamel thickness changes according to position on the crown, and measurements at homologous positions may be difficult to obtain. He found that the enamel thickness was considerably less on the teeth identified as deciduous premolars than on the molars (32 microns and 73 microns respectively). If BMNH 44971 is a deciduous premolar it could be expected to have thinner enamel than a comparable molar, such as *Spalacotherium tricuspidens* from the Purbeck. The enamel can be measured on BMNH 44971 where a cross section is exposed by wear along the distal blade of the protoconid, and there is a distinct boundary between the black enamel and the light brown dentine. Several molars of *S. tricuspidens* have broken protoconids and the enamel thickness was measured on four of them (m5 of the holotype BMNH 46019; m2 of BMNH 44750; m4 and m5 of BMNH 44749). Care was taken to measure the thickness of the enamel perpendicular to the orientation of the prismatic, or preprismatic, structure and also at a position approximately half way down the distal protoconid blade. The enamel thickness of BMNH 44971 is 60 microns, whereas that of the *S. tricuspidens* molars is 150 microns (all four teeth are very similar in enamel thickness). This is a similar ratio to that measured by Cifelli (1999) in the teeth of *Spalacolestes cretublatta* (see above), and is contributory evidence that the Wealden BMNH 44971 is a deciduous premolar.

BMNH 44971 is consistent in size with BMNH 45471 (previously W-3) another isolated molar from Cliff End, this time an upper molar, possibly M1, which has been referred to *Spalacotherium tricuspidens* (Clemens and Lees, 1971). However, BMNH 45471 differs from M1 of *S. tricuspidens* from the Purbeck in being lower crowned, more oblique-angled, and mesiodistally elongate. Clemens and Lees (1971) also note that the paracone and cusp in the position of a metacone appear to be lower and less massive. These differences suggest that BMNH 45471 may be a deciduous upper premolar. If so, the most posterior locus is indicated, as BMNH 45471 is less mesiodistally elongate than the deciduous upper premolars from the Cedar Mountain fauna (Cifelli, 1999) or *Mictodon simpsoni* (Fox, 1984), probably representing the milk dentition of the spalacolestine symmetrodont *Symmetrodontoides canadensis* (Averianov, 2002). BMNH 45471 is not sufficiently worn to measure the enamel thickness. I suggest that, as both the Cliff End teeth, BMNH 45471 and BMNH 44971, appear to most closely resemble *S. tricuspidens,* but differ as noted above, they be designated as *S.* cf. *tricuspidens*.

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LITERATURE CITED

Averianov, A. O. 2002. Early Cretaceous "symmetrodont" mammal *Gobiotheriodon* from Mongolia and the classification of "Symmetrodonta." Acta Palaeontologica Polonica 47:705–716.

Cifelli, R. L. 1990. Cretaceous mammals of southern Utah. III. Therian mammals from the Turonian (early Late Cretaceous). Journal of Vertebrate Paleontology 10:332–345.

Cifelli, R. L. 1999. Therian teeth of unusual design from the medial Cretaceous (Albanian-Cenomanian) Cedar Mountain Formation, Utah. Journal of Mammalian Evolution 6:247–270.

Cifelli, R. L., and C. L. Gordon. 1999. Symmetrodonts from the Late Cretaceous of Southern Utah and distribution of archaic mammals in the Cretaceous of North America. Brigham Young University Geology Studies 44:1–15.

Cifelli, R. L., and S. K. Madsen. 1986. An Upper Cretaceous symmetrodont (Mammalia) from southern Utah. Journal of Vertebrate Paleontology 6:258–263.

Cifelli, R. L., and S. K. Madsen. 1999. Spalacotheriid symmetrodonts (Mammalia) from the medial Cretaceous (upper Albian or lower Cenomanian) Mussentuchit local fauna, Cedar Mountain Formation, Utah, USA. Geodiversitas 21:167–214.

Clemens, W. A. 1963a. Late Jurassic mammalian fossils in the Sedgwick Museum, Cambridge. Palaeontology 6:373–377.

Clemens, W. A. 1963b. Wealden Mammalian Fossils. Palaeontology 6: 55–69.

Clemens, W. A., and P. M. Lees. 1971. A review of English Early Cretaceous mammals; pp. 117–130 in D. M. Kermack and K. A. Kermack (eds.), Early Mammals. Zoological Journal of the Linnean Society 50 (Supplement 1).

Clements, R. G. 1993. Type section of the Purbeck Limestone Group, Durlston Bay, Swanage, Dorset. Proceedings of the Dorset Natural History and Archaeological Society 114:181–206.

Ensom, P. 1988. Excavations at Sunnydown Farm, Langton Matravers, Dorset. Amphibians discovered in the Purbeck Limestone Formation. Proceedings of the Dorset Natural History and Archaeological Society 109:148–150.

Ensom, P., and D. Sigogneau-Russell. 2000. New symmetrodonts (Mammalia, Theria) from the Purbeck Limestone Group, Lower Cretaceous, southern England. Cretaceous Research 21:767–779.

Fox, R. 1972. An Upper Cretaceous symmetrodont from Alberta, Canada. Nature 239:170–171.

Fox, R. 1976. Additions to the mammalian local fauna from the Upper Milk River Formation (Upper Cretaceous), Alberta. Canadian Journal of Earth Sciences 13:1105–1118.

Fox, R. 1984. A primitive, "obtuse-angled" symmetrodont (Mammalia) from the Upper Cretaceous of Alberta, Canada. Canadian Journal of Earth Sciences 21:1204–1207.

Fox, R. 1985. Upper molar structure in the Late Cretaceous symmetrodont *Symmetrodontoide*s Fox, and a classification of the Symmetrodonta. Journal of Paleontology 59:21–26.

Hu, Y.-M., Y.-Q. Wang, Z.-X. Luo, and C.-K. Li. 1997. A new symmetrodont mammal from China and its implications for mammalian evolution. Nature 390:137–142.

Kielan-Jaworowska, Z., R. L. Cifelli, and Z.-X. Luo. 1998. Alleged Cretaceous placental from down under. Lethaia 31:267–268

Krebs, B. 1985. Theria (Mammalia) aus der Unterkreide von Galv (Provinz Teruel, Spanien). Berliner Geowissenschaftliche Abhandlungen A 60:29–48

Luo, Z.-X., Z. Kielan-Jaworowska, and R. L. Cifelli. 2002. In quest for a phylogeny of Mesozoic mammals. Acta Palaeontologica Polonica 47:1–78.

Marsh, O. C. 1870. American Jurassic mammals. American Journal of Science 33:326–348.

Mills, J. R. E. 1984. The molar dentition of a Welsh pantothere. Zoological Journal of the Linnean Society 82:189–205.

Owen, R. 1854. On some fossil reptilian and mammalian remains from the Purbecks. Quarterly Journal of the Geological Society of London 10:420–433.

Patterson, B. 1956. Early Cretaceous mammals and the evolution of mammalian molar teeth. Fieldiana (Geology) 13:1–105.

Ruffell, A., A. Ross, and K. Taylor. 1996. Early Cretaceous Environments of the Weald. Geologists' Association Guide, number 55, 81 pp.

Sigogneau-Russell D., and P. C. Ensom. 1998. *Thereuodon* (Theria, Symmetrodonta) from the Lower Cretaceous of North Africa and Europe, and a brief review of symmetrodonts. Cretaceous Research 19:1–26.

Simpson, G. G. 1928. A Catalogue of the Mesozoic Mammalia in the Geological Department of the British Museum. Trustees of the British Museum, London, 215 pp.

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