### A new species of the plagiaulacoid multituberculate mammal *Eobaatar* from the Early Cretaceous of southern Britain

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Until recently, the only mammal remains to be obtained from the Early Cretaceous (Barremian, Wealden Group) Wessex Formation of the Isle of Wight, southern England were a poorly preserved left m2 and a well preserved left I2 crown representing one or possibly two plagiaulacoid multituberculate species. These were recovered in the early 1970s but despite subsequent efforts by a number of workers to recover additional Mesozoic mammal remains none were forthcoming until comprehensive bulk screening of the Wessex Formation was undertaken in a study commenced in 2002. This study resulted in the recovery of a number of new specimens representing an assemblage of at least six taxa. Among these are a well-preserved plagiaulacoid multituberculate left m1 and a similarly preserved left I3. The former permits diagnosis of a new species of eobaatarid, *Eobaatar clemensi* sp. nov. The previously recovered left m2 is also tentatively assigned to the same taxon. In addition, another left m1, somewhat worn as a result of dietary attrition, was recently obtained by a private collector. This is of very similar morphology to the holotype of *E. clemensi* but slightly larger. It is undoubtedly referable to the same taxon and provides some insight into intraspecific size, and other minor morphological variations in the teeth of the new species. The I3 may also be referable to the new species, in which case it is the first well preserved I3 of a member of Eobaataridae to be fully described.

Key words: Mammalia, Multituberculata, Plagiaulacoidea, Wealden, Barremian, Cretaceous, England.

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### Introduction

Only five purportedly mammalian specimens, all isolated teeth or fragments thereof, were reported from the Wealden Supergroup of mainland Britain during a period extending from the early 1890s to the 1960s (Woodward 1891, 1911; Lydekker 1893; Simpson 1928). In the 1960s Early Cretaceous mammals had only been recovered from two other localities and horizons; the Berriasian Purbeck Limestone Formation near Swannage in Dorset, southern England (at that time thought to be of Late Jurassic age), and the Aptian-Albian Trinity Group near Forestburg, Texas. Inspired by the tantalizing 19th and early 20th century reports of mammals from the Wealden Supergroup, a team led by the late Professor Kenneth A. Kermack re-examined previously reported specimens and commenced a detailed search for sites which might yield new mammal material (Clemens 1963; Kermack et al. 1965; Clemens and Lees 1971). Clemens (1963) demonstrated that of the early discoveries only two specimens could be unequivocally shown to be both mammalian, and derived from Wealden strata. These are a tooth and tooth fragment pertaining to the plagiaulacoid multituberculate Loxaulax valdensis Simpson, 1928 originally described by Woodward (1911) as a species of *Dipriodon*. Despite this somewhat disappointing start, Kermack and co-workers were successful in their search, recovering new specimens representing a number of taxa. However, the techniques employed (Lees 1964), which included acid dissolution of cemented bone beds and separation of residues using brominated hydrocarbons, were time consuming, hazardous, and expensive.

New specimens were recovered from three localities (Fig. 1): from a bone bed at Cliff End near Hastings which had also previously yielded the tooth and tooth fragment of *Loxaulax valdensis*; and from two inland localities, a pebble bed at Tyghe Farm and a bone bed at Paddockhurst Park. The Cliff End and Tyghe Farm sites are considered to be of early Valanginian age whereas Paddockhurst Park is probably of middle Valanginian age (Allen and Wimbledon 1991). For a description of the localities, see Clemens (1963), and for a general review and summary of the temporal and geographical distribution of the Plagiaulacoidea see Kielan-Jaworowska et al. (2004).

For a short time in the late 1960s and early 1970s, knowledge of the discovery of new mammal fossils from Wealden strata of mainland Britain prompted a small number of enthusiasts to search for mammal remains in the Wealden Group of the Isle of Wight (e.g., Butler and Ford 1975; Freeman 1975). Relatively crude bulk screening techniques were employed by

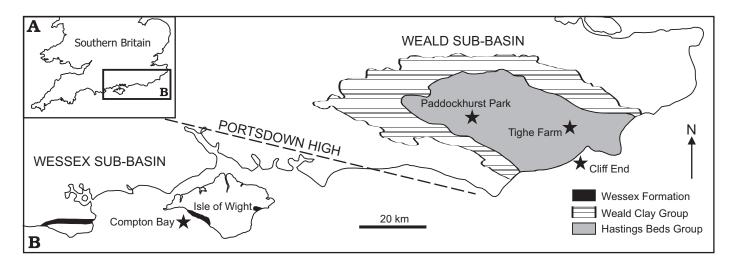


Fig. 1. British Wealden Supergroup outcrop areas (excluding the relatively small areas on the Isle of Wight and Isle of Purbeck occupied by the Vectis Formation) and mammal localities reported during the 19th and 20th centuries. A. Outline location map. B. Location of the Weald and Wessex sub-basins.

all and of these Freeman (1975) was alone in processing residues using high-density liquid separation techniques (the late Richard L.E. Ford personal communication 1976). Only Ford successfully obtained mammal remains comprising two multituberculate teeth, a left m2 and a left I2 (Figs. 2A, B, 8B, 10C) both from a sample taken from bed CL3 (Stewart 1978) in Compton Bay (Figs. 3, 4; Butler and Ford 1975). These were tentatively referred to Loxaulax sp., but in light of more recent discoveries, this assignment was incorrect. The amount of work required to recover these specimens was considerable (the late Richard L.E. Ford personal communication 1976) and mammal remains were not recovered from any other sampled horizons in both the Barremian Wessex Formation and the overlying upper Barremian to lower Aptian Vectis Formation. Discouraged by this, Ford and others at that time ceased work on the Wealden Group mammals of the Isle of Wight. At about the same time work to recover mammal remains from the Wealden Supergroup of mainland Britain also stopped and no further mammal remains were recovered from the Wealden Supergroup of Britain until comprehensive bulk screening of Wessex Formation strata was undertaken in an ongoing study commenced in 2002 (Sweetman 2006a, b, 2007, 2008).

Institutional abbreviations.—BMNH, the Natural History Museum, London, UK; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany.

Other abbreviation.—NGR, National Grid Reference.

# The Wessex Formation mammal assemblage

Mammal remains representing at least six taxa have now been recovered from a number of horizons and localities on both the south-west and south-east coasts of the Isle of Wight (Figs. 3, 4). However, of these, bed 38 (Radley 1994) at the top of the

Wessex Formation at Yaverland (Fig. 4) is the most productive. The assemblage includes: a gobiconodontid (Sweetman 2006b); one or possibly two multituberculates reported here; a spalacolestine spalacotheriid (Sweetman 2008); a dryolestid (SCS unpublished data); a stem boreosphenidan, possibly a member of the Aegialodontia; and more than one other taxon of as yet uncertain affinities (Sweetman 2006 a, 2007). The latter are currently represented by ante-molariform teeth and possible milk teeth.

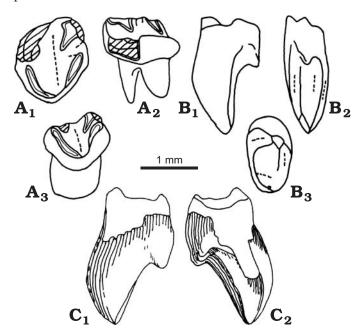


Fig. 2. **A**, **B**. Multituberculate teeth from the Wessex Formation of the Isle of Wight tentatively referred by Butler and Ford (1975) to *Loxaulax* sp. **A**. Left m2 (part of SMNS 51981) in occlusal  $(A_1)$ , mesiolabial  $(A_2)$ , and distolabial  $(A_3)$  views (hatched areas represent broken surfaces) (see also Fig. 8B). **B**. Left I2 (part of SMNS 51981) in labial  $(B_1)$ , mesial  $(B_2)$ , and occlusal  $(B_3)$  views (see also Fig. 10C). **C**. For comparison, right I2 from Cliff End provisionally referred by Clemens (1963) to *Loxaulax valdensis* Simpson, 1928 in labial  $(C_1)$  and lingual  $(C_2)$  views.

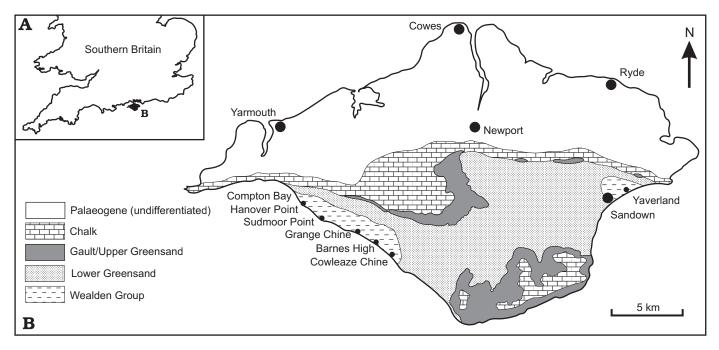


Fig. 3. A. Outline location map of Southern Britain. B. Outline geological map of the Isle of Wight.

The Wealden mammal assemblages of mainland Britain and of the Isle of Wight show some similarities in general composition. However, they appear to be entirely different in detail with no shared genera. Furthermore, the Valanginian assemblage of mainland Britain, which includes the spalacotheriid Spalacotherium tricuspidens Owen, 1854, appears to have more in common with the mammal assemblage of the Berriasian Purbeck Limestone Formation, which also includes S. tricuspidens (Kielan-Jaworowska et al. 2004), than it does with the Barremian assemblage of the Isle of Wight which includes a derived spalacolestine spalacotheriid (Sweetman 2008). However, the sample size is as yet small for both Wealden assemblages. In contrast, the microvertebrate assemblage of the Wessex Formation as a whole shows considerable similarity to that reported from the Barremian of Spain (e.g., Sweetman 2006a, b), including some shared genera, e.g., Eobaatar Kielan-Jaworowska, Dashzeveg, and Trofimov, 1987 (Hahn and Hahn 1992, 2001; Badiola et al. 2008; this study) and the scincomorph lizard Meyasaurus Vidal, 1915 (Sweetman 2007).

### Geological setting

On the Isle of Wight the exposed Wessex Formation is about 180 m thick (Stewart 1978, 1981) and comprises a sequence of fluvial, lacustrine and terrestrial deposits laid down on a low gradient, coastal floodplain. The high sinuosity river system responsible for these deposits provided considerable habitat diversity (Martill and Naish 2001 and references cited therein; Underhill 2002). However, the climate, which supplied year-round precipitation, also engendered considerable environmental stress on the biota during times of extreme heat. At

these times evaporation exceeded precipitation causing drought conditions (Haywood et al. 2004). During times of drought, thunderstorm activity ignited wildfires following which the denuded landscape was rendered vulnerable to erosion. Occasionally, heavy rainfall after such an event was sufficient to cause extensive runoff and erosion, and generate debris flows incorporating eroded floodplain sediments, copious amounts of plant material, both burnt and un-burnt, and animal remains including the bones, teeth and complete or partial carcasses of vertebrates. The debris flows were deposited in topographical lows of variable extent and where exposed comprise the so called plant debris beds (sensu Oldham 1976) of the Wessex Formation (Insole and Hutt 1994). These beds, formerly termed lignites (White 1921) make up only about 4% of the succession (Stewart 1978; Fig. 4) but they have yielded the majority of large and small vertebrate remains recovered from the Wessex Formation.

The majority of overbank mudstones and other fluvial and terrestrial deposits were subject to prolonged periods of sub-aerial weathering, soil-forming processes and oxidization prior to final burial. In most cases these processes have led to the destruction of organic matter and where large bones are encountered they are invariably demineralized to a greater or lesser extent. In contrast, while many of the plant debris beds show evidence of similar process towards their upper surfaces, the large amount of decaying plant material contained within them produced anoxic conditions which were conducive to the preservation of bone. For this reason the majority of samples taken for the purpose of recovering microvertebrate remains were taken from these beds (Fig. 4). Mammal remains have been recovered from six horizons (Fig. 4). The remainder of the microvertebrate assemblage comprises a diverse assemblage of chondrichthyan and oste-

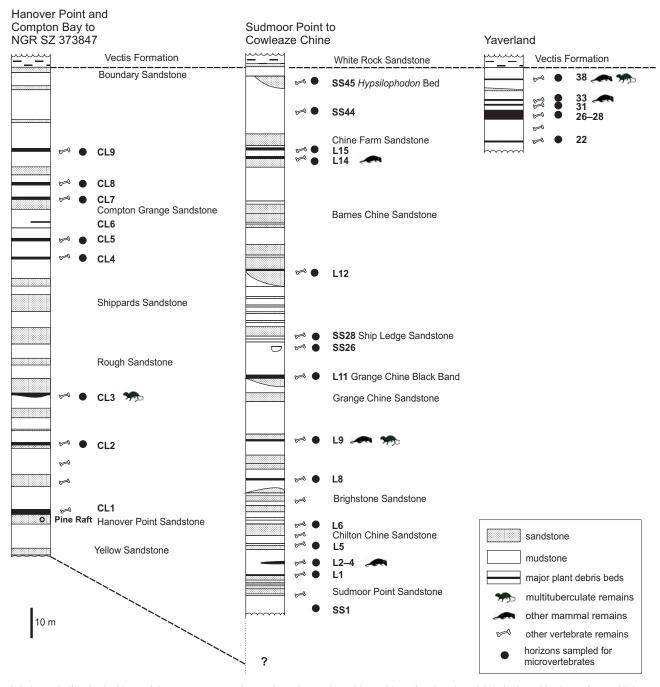


Fig. 4. Schematic lithological logs of the Wessex Formation to show the stratigraphic position of major plant debris beds and horizons from which mammal remains have been recovered (south-west coast sections based on Stewart 1978; south-east section after Radley 1994).

ichthyan fishes, lissamphibians, including several salamanders, an albanerpetontid and several frogs, probably the most diverse lizard assemblage yet recovered from any Early Cretaceous sequence, and numerous archosaurs (Butler and Ford 1975; Freeman 1975; Buffetaut and Ford 1979; Evans et al. 2004; Sweetman 2004, 2006a, b, 2007, 2008; Sweetman and Underwood 2006).

Multituberculate remains have been recovered from three horizons (Fig. 4), beds CL3 (now largely eroded away in current cliff exposures) and L9 (Stewart 1978) on the south-west coast and bed 38 (Radley 1994) at Yaverland on the south-

east coast (Figs. 3, 4). All are typical plant debris beds in terms of their sedimentology and their stratigraphic distribution indicates that the taxon described here was present throughout deposition of the exposed Wessex Formation. The absolute ages of individual beds are poorly constrained and correlation between beds is rendered problematic by the laterally discontinuous nature of the majority of Wessex Formation strata. However, palynological data (Harding 1986; Hughes and McDougall 1990) and fossil wood carbon isotope data (Robinson and Hesselbo 2004) indicate that the Hauterivian–Barremian boundary lies close to the base of the

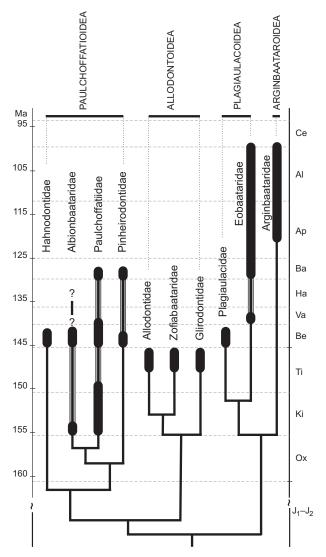


Fig. 5. A phylogenetic tree for the Plagiaulacida. After Hahn and Hahn (2004) with amendments and additions. Geological time scale from Gradstein et al. 2004. Temporal distribution of taxa from Kielan-Jaworowska et al. 2004. Abbreviations for Jurassic and Cretaceous stages: Al, Albian; Ap, Aptian; Ba, Barremian; Be, Berriasian; Ce, Cenomanian; Ha, Hauterivian;  $J_1 – J_2$ , Middle and Lower Jurassic; Ki, Kimmeridgian; Ox, Oxfordian; Ti, Tithonian; Va, Valanginian.

Wessex Formation exposed at Hanover Point (NGR SZ 3798370; Fig. 3) and that deposition of the overlying, lagoonal Vectis Formation commenced in the late Barremian (Kerth and Hailwood 1988; Stewart et al. 1991; Feist et al. 1995; Robinson and Hesselbo 2004).

### Phylogeny of Plagiaulacida

While the phylogeny of Plagiaulacida Ameghino, 1889 remains the subject of some debate, that proposed by Hahn and Hahn (2004) has received wide acceptance. However, their phylogenetic tree (Hahn and Hahn 2004: 154, fig. 16) was not drawn to temporal scale and the temporal distribution of

some taxa, including Eobaataridae, was not accurately depicted. In view of this a revised tree adopting the topology of Hahn and Hahn (2004), the geological time scale of Gradstein et al. (2004) and the temporal distribution of taxa recorded by Kielan-Jaworowska et al. (2004 and references cited therein) is provided here (Fig. 5). However, it should be noted that within Plagiaulacida the systematic positions of two taxa have changed since the review provided by Kielan-Jaworowska et al. (2004). Parendotherium Crusafont-Pairó and Adrover, 1966 has been transferred from the Plagiaulacoidea (Eobaataridae) to the Paulchoffatioidea and Janumys Eaton and Cifelli, 2001, recorded as family incertae sedis by Kielan-Jaworowska et al. (2004), has now been placed in Eobaataridae (Hahn and Hahn 2006). Furthermore, with regard to Eobaataridae, two new species have recently been recorded from the Early Cretaceous (probably Barremian) of Japan: Hakusanobaatar matsuoi Kusuhashi, 2008 and Tedoribaatar reini Kusuhashi, 2008.

### Systematic palaeontology

Mammalia Linnaeus, 1758 Allotheria Marsh, 1880 Multituberculata Cope, 1884 Plagiaulacida Ameghino, 1889

[nomen correctum McKenna, 1971, ex Plagiaulacoidea Ameghino, 1889]

Plagiaulacoidea Hahn and Hahn, 2004 Family Eobaataridae Kielan-Jaworowska, Dashzeveg, and Trofimov, 1987

Genus *Eobaatar* Kielan-Jaworowska, Dashzeveg, and Trofimov, 1987

*Type species: Eobaatar magnus* Kielan-Jaworowska, Dashzeveg, and Trofimov, 1987, Höövör ("Höövör Beds"), Early Cretaceous (Aptian or Albian): Gobi Desert, Mongolia.

Eobaatar clemensi sp. nov.

Figs. 6-8.

*Etymology*: In honour of Professor William A. Clemens, in recognition of his pioneering work on mammals of the Wealden Supergroup of south-east England, and his outstanding contribution to the field of Mesozoic mammalian palaeontology.

*Type material*: Holotype: BMNH M 45482, a well preserved left m1 tooth crown (Figs. 6, 7A). Paratype: BMNH M 45557, a well preserved but somewhat worn left m1 from which only part of the mesial root is missing (Fig. 7B).

*Tentatively referred material*: Part of SMNS 51981, a poorly preserved left m2 (Figs. 2A, 8B); BMNH M 45483, a well preserved left I3 crown and partial root (Figs. 9, 10B).

Horizons and localities: Holotype, BMNH M 45482, bed L9 (Stewart 1978) exposed about 300 m north-west of Grange Chine on the south-west coast of the Isle of Wight, NGR SZ 41781 81880; paratype, BMNH M 45557, and tentatively referred specimen, BMNH M 45483, bed 38 (Radley 1994) exposed about 600 m north-east of Yaverland car park on

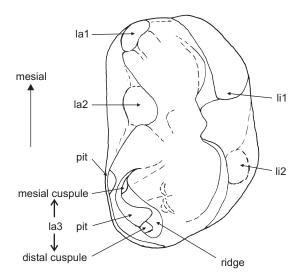


Fig. 6. Outline drawing of the holotype specimen, BMNH M 45482, to show disposition of cusps and pits, and cusp abbreviations used in the text.

the south-east coast of the Isle of Wight, NGR SZ 61693 85223; tentatively referred specimen, part of SMNS 51981, bed CL3 (Butler and Ford 1975; Stewart 1978) exposed in Compton Bay on the south-west coast of the Isle of Wight, exact locality unknown but close to NGR SZ 3785 8391 (Figs. 3, 4).

Diagnosis.—Autapomorphy: m1 with two crescentic lingual cusps and three labial cusps of which the mesial-most two comprise blunt cones (m1 unknown for Eobaatar minor, E. hispanicus, Hakusanobaatar, and Tedoribaatar). Resembles Bolodon osborni and E. magnus in possession of a distal-most labial cusp comprising a complex structure incorporating pits, grooves and ridges. The lingual margin is convex, shorter than the straight labial margin and the distal margin lies at an acute angle distally to the mesiodistal axis of the crown. Differs from Loxaulax and Janumys but resembles E. magnus and Bolodon in possession of two lingual cusps. Differs from E. magnus in lack of subdivision of mesial lingual cusp. Differs from Bolodon but resembles Eobaatar and Loxaulax in the degree of asymmetry of the crown (less asymmetric in Bolodon). Differs from Eobaatar but resembles Loxaulax and Bolodon in possession of three labial cusps. Differs from Loxaulax in complex morphology of the distal-most labial cusp. Where known, differs from Paracimexomys group cimolodontans in confinement of coalescence of cusps and cusp ornamentation to the distal-most labial cusp. Differs from Arginbaatar in cusp morphology and possession of ornamented enamel (m1 incompletely known for Ameribaatar).

Description.—BMNH M 45482 (Figs. 6, 7) is the well preserved and almost unworn crown of a lower left m1 of a plagiaulacoid multituberculate. Crown length is 1.4 mm labially, 1.1 mm lingually and crown width is 0.9 mm. There are two rows of cusps aligned mesiodistally separated by a valley. Two cusps are present lingually and three labially. As in other plagiaulacoid multituberculates, cusps on the lingual margin are higher than those on the labial margin. The lin-

gual margin is convex and significantly shorter than the straight labial margin.

The mesial margin of the crown lies at right angles to the central valley whereas the distal margin lies at about  $45^{\circ}$  to it. The crown strongly overhangs the roots but of the latter almost no trace remains (but see below a description of BMNH M 45557).

Lingual cusps are crescentic, convex lingually and concave labially. The li1 is mesiodistally longer than li2. Distolabially the margins of both cusps bear narrow, vertical wear facets covered by very fine horizontal scratches. The facet on the distolabial margin of li1 extends to and across the valley separating it from la2. It also extends up the mesiolingual margin of that cusp. The facet on the distolabial margin of li2 extends across the distal extremity of the valley separating the cusp rows and onto the distal margin of the distal-most cuspule of la3 (see below). The mesiolabial margin of li1 is unworn. The mesiolabial margin of li2 bears numerous horizontal scratches but is not faceted. Apically, both lingual cusps are recurved distally, this being more pronounced in li1 than li2. The apex of li1 is more pointed than that of li2, which has been blunted by wear or post mortem abrasion. The cusps are separated by a deep transverse groove the base of which is U-shaped. This is formed by the almost vertical distal surface of li1 and the less steeply inclined mesial surface of li2. The base of the trough lies above the base of the

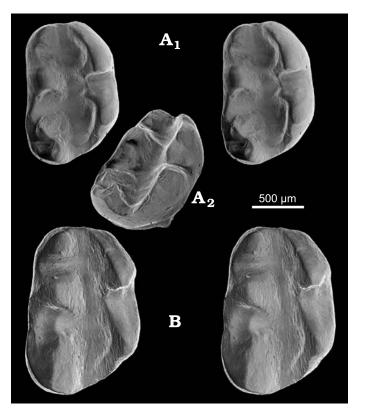


Fig. 7. Scanning electron micrographs of plagiaulacoid multituberculate *Eobaatar clemensi* sp. nov. from the Early Cretaceous Wessex Formation, Isle of Wight. **A**. BMNH M 45482, holotype left m1 in occlusal (A<sub>1</sub>, stereo pair) and oblique distolingual (A<sub>2</sub>) views. **B**. BMNH M 45557, paratype left m1 in occlusal view (stereo pair).

valley separating the lingual and labial cusp rows. In labial view it lies at the level of the apex of la2, which is the tallest cusp in the labial row. The valley separating the cusp rows is little affected by wear and the enamel exhibits a number of shallow pits and grooves. The distal margin of the valley is raised above the level of the valley floor along most of its length. Wear at the distal margin does not extend deeply enough to allow wear of the valley floor except at its mesial end and in the area between the distolabial margin of li1 and the mesiolingual margin of la2.

On the labial side of the crown, two distinct cusps, la1 and la2, are present mesially. The distal half of the labial cusp row is occupied by a more complex structure as further described below. The smallest cusp in the row, la1, is convex mesially and labially. The lingual surface comprises a small, steeply inclined wear facet covered with very fine, mesiodistally aligned, horizontal scratches extending to the base of the valley separating the cusp rows. The distal surface is slightly concave and the shallow transverse trough separating it from la2 is U-shaped. The largest and tallest cusp in the labial row is la2. It is somewhat convex labially, more so lingually. It is concave mesially and distally, the concavity being more pronounced on the distal surface. The lower half of the mesiolingual margin of la2 bears a wear facet as described above. The apices of this cusp and la1 are blunt, sloping downward mesially at a shallow angle. Fine mesiodistally aligned scratches can be seen on the apex of la2 indicating that it and la1 have been blunted by wear rather than post-mortem abrasion. The distal half of the labial margin of the crown bears a structure unlike all other cusps. It comprises two cuspules partially separated distolabially by a comma-shaped pit. A very small pit is also present on the extreme labial margin of the crown mesial to the commashaped pit. The mesial surface of this cuspidate area also differs from all others in that it does not rise smoothly from the transverse trough separating it from the adjoining cusp. Also, its steeply inclined lingual surface is somewhat rugose and ridged. The apex of the distal-most of the two cuspules is lower than that of the cuspule mesial to it and is very slightly worn or abraded. The base of the distolingual margin of the distal cuspule bears a steeply inclined facet as described above. This area probably represents the division of a single large cusp (la3) by the inclusion of pits and grooves but it may represent the coalescence of two small cusps.

BMNH M 45557 (Fig. 7B) is slightly larger than BMNH M 45482 but proportionately and in general morphology both are very similar. Crown length is 1.6 mm labially and 1.4 mm lingually and crown width is 1.1 mm. Intraspecific variation in molar size is commonly observed in multituberculates (e.g., Kielan-Jaworowska et al. 1987) and in view of the close similarity of this specimen to BMNH M 45482 it is confidently placed in the same taxon. The most noticeable difference between BMNH M 45557 and 45482 is the extent of wear affecting the former. All cusps remain well defined but wear extends to affect the whole of the valley separating the lingual and labial cusps. It has also largely, but not entirely, obliterated the

concavities seen on the labial surfaces of li1-2 as seen in BMNH M 45482, and has entirely obliterated the distal cuspule forming part of la3. Wear here has removed the enamel to reveal the underlying dentine. It is likely that before wear the morphology of la3 in BMNH M 45557 would have been similar to that of la3 in BMNH M 45482. However, a groove defining the mesiolingual margin of the mesial cuspule of BMNH M 45557 is considerably broader than a similar groove, seen in BMNH M 45482. This suggests that the morphology of la3 is somewhat variable. A further difference between BMNH M 45482 and 45557 is the proportionately larger la1 seen in the latter. The lingual surfaces of li1-2 are unaffected by wear whereas the labial surfaces of labial cusps have been worn. Wear here takes the form of a facet which forms an oblique angle (apicolabially) to the apicobasal axis of the crown. The facet is more strongly developed distally where it is particularly noticeable on the distolabial margin of la2 and along the entire margin of la3.

As in BMNH M 45482, the crown overhangs the roots but in BMNH M 45557 the distal root is preserved in its entirety. It is mesiodistally compressed, tapers apically both mesiodistally and labiolingually and is somewhat recurved mesially. The mesial and distal surfaces of the root are slightly concave whereas the much narrower lingual and labial surfaces are uniformly convex. The pulp cavity is open but the opening is small at the apex of the root. Apically, about three quarters of the mesial root is missing. The preserved basal part, while of similar general morphology to the distal root, is considerably more gracile being narrower both mesiodistally and labiolingually. A labiolingually narrow ridge separates the roots. This continues as a faint ridge on the mesial surface of the distal root where it extends for approximately half the distance to the apex.

Discussion.—While these specimens share a number of characters of the m1 of members of Plagiaulacidae and some members of the Paracimexomys group cimolodonts the unique combination of characters seen in BMNH M 45483 and 4557 set them apart from any of these. As set out above, significant differences exist between the morphology of the specimens from the Wessex Formation and, where known, the m1 of members of Eobaataridae, but these differences are not considered to be diagnostic at a generic level (Zofia Kielan-Jaworowska, personal communication 2006). That being the case, similarities to the m1 of Eobaatar indicate that the specimens from the Wessex Formation represent a new species of this taxon. However, m1 is unknown for *Eobaatar* minor Kielan-Jaworowska, Dashzeveg, and Trofimov, 1987 from the Aptian-Albian of Mongolia and also for E. hispanicus Hahn and Hahn, 1992 from the Barremian of Spain. In view of the temporal and geographical separations between E. minor and congeneric material from the Isle of Wight it appears unlikely that the latter is also conspecific. Also, although direct comparisons are not possible, it would appear from published data that m1 of the Isle of Wight species is intermediate in size between that of E. magnus Kielan-Jaworowska, Dashzeveg, and Trofimov, 1987 and that expected

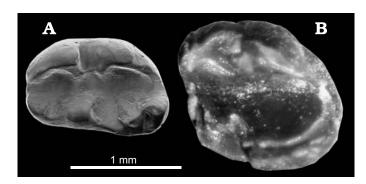


Fig. 8. Plagiaulacoid multituberculate *Eobaatar clemensi* sp. nov. from the Early Cretaceous Wessex Formation, Isle of Wight. A. Scanning electron micrograph of BMHH M 45482 in occlusal view. B. Normal light photograph of the m2 part of SMNS 51981 in occlusal view, to show its possible relationship to m1(s) BMNH M 45482 and 45557 (it was not possible to obtain scanning electron micrographs of the specimen which was glued to card by the original collector).

for E. minor. The Barremian occurrence of E. hispanicus, relatively close geographically to a coeval occurrence of that genus in southern Britain, raises the possibility that the lower molars from the Isle of Wight are those of this species. However, the upper premolars upon which E. hispanicus is based appear to be too large to be referable to the taxon described here (Hahn and Hahn 1992). Furthermore, palaeogeographical models (e.g., Smith et al. 1994; Scotese 2002) suggest that Britain and Iberia may have been separated by marine barriers since the Early Jurassic. That being the case, disbursal of small terrestrial tetrapods between the two areas would have been substantially restricted if not prevented for considerable periods of time. Thus, while synonymy of the Isle of Wight species of Eobaatar with E. hispanicus can not be entirely ruled out, it appears unlikely, and is supported by other data. Based on current observations, all small tetrapods described from the Barremian of Spain are either generically or specifically distinct from those occurring in the Barremian assemblage of southern Britain with only two congeneric taxa (Sweetman 2007). In light of the above, erection of a new species to accommodate material referable to Eobaatar from the Barremian of southern Britain seems justified.

## The m2 part of SMNS 51981 and its relationship to BMNH M 45482

The heavily worn and abraded left m2 forming part of SMNS 51981 (Figs. 2B, 8B) was recovered from bed CL3 exposed in Compton Bay on the south-west coast of the Isle of Wight (Figs. 4, 5) (Butler and Ford 1975), exact locality unknown but close to NGR SZ 3785 8391. It shares with BMNH M 45482 and 45557 an asymmetrical outline in which the lingual margin is shorter than the labial margin. It is also similar in that the lingual margin is convex whereas the labial margin (before post-mortem damage) is straight. Unfortunately, the mesiolabial corner of the tooth is broken away and elsewhere heavy wear from occlusion with the upper dentition has obliterated the labial cusps. Little can therefore be deter-

mined with regard to labial cusp morphology. Lingually, two relatively robust cusps are present but these have also been affected by wear, abrasion and breakage. The worn, chipped and abraded condition of the specimen renders an accurate determination of its pre-ware morphology problematic. However, the gross morphology of the specimen is consistent with a referral to Eobaataridae. Furthermore, its size also suggests that it should be referred to *Eobaatar clemensi* sp. nov., rather than to a new species of *Loxaulax*. However, in view of the heavy wear and abrasion affecting the specimen this referral must remain tentative.

#### A multituberculate I3 from Yaverland

BMNH M 45483 is the well preserved and unworn crown and partial root of a multituberculate left I3 (Figs. 9, 10B), recovered from bed 38 (Radley 1994) at Yaverland on the south east coast of the Isle of Wight, NGR SZ 61693 85223 (Figs. 3, 4).

Description.—The crown of left I3 BMNH M 45483 substantially overhangs the single root, which is thin-walled with a wide pulp cavity. This, together with the entirely unworn condition of the crown, suggests that, while fully formed, the tooth may have been unerupted. The tooth is essentially tricuspid but a cuspule is also present close to the base of the crown at its mesiolingual extremity (Fig. 9B, C). In lingual view, the crown is 1.1 mm high measured from the apex of the mesial apical cusp to the base of the enamel above the root. In occlusal view it measures 0.8 mm from the

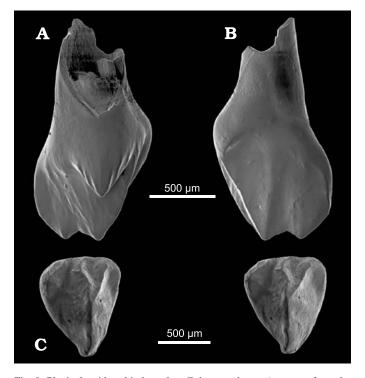


Fig. 9. Plagiaulacoid multituberculate *Eobaatar clemensi* sp. nov. from the Early Cretaceous Wessex Formation, Isle of Wight. Scanning electron micrographs of BMNH M 45483, a multituberculate left I3, in mesiolabial (**A**), lingual (**B**), and occlusal (**C**, stereo pair) views.

apex of the mesiolabial cusp to the distal margin of the crown and 0.85 mm from the apex of the mesiolingual cuspule to the distal margin of the crown. Mesially the crown is 0.7 mm wide measured from the apex of the mesiolabial cusp to the apex of the mesiolingual cuspule. The central cusps are strongly labiolingually compressed and separated apically by a V-shaped notch (Fig. 9A, B). The lingual surfaces of these cusps are relatively smooth whereas the labial surfaces are rugose. The distal surface of the distal apical cusp is convex distally with a faint central ridge. The lingual surface is convex lingually and bounded distally by a narrow ridge. Labially a broad ridge occupies the mesial margin of the cusp but distally it is concave. The apex is pointed and bounded mesially by a crest which descends to the distobasal extremity of the mesial apical cusp, the distal surface of which also comprises a ridge. The mesial apical cusp is convex labially and bears a pronounced central ridge on the lingual side. This descends at a steep angle distally to meet the central convexity of the distal apical cusp about two thirds of the distance below its apex. The ridge then curves smoothly mesially where it expands to comprise the mesiolingual cuspule. The mesiolingual surface of the mesial apical cusp is concave above the mesiolingual cuspule. Mesially a sigmoidal groove extends from the apex of the mesial apical cusp to the point where the crown retreats to meet the root. The base of the crown is here, as elsewhere, convex and smooth. Labially the sigmoidal groove is bounded by a similarly sigmoidal ridge, which is more pronounced than a similar ridge bounding it lingually. The mesiolabial cusp comprises a mesiolabiallydistolingually compressed cone from the apex of which, extending basally, there are a number of ridges. The mesiolabial and distolingual surfaces of the mesiolabial cusp are convex whereas the mesiolingual and distolabial surfaces comprise rounded crests. The valley separating the mesiolabial cusp from the remainder of the crown is V-shaped.

Affinities.—In a review of the dentition of Plagiaulacida, Hahn and Hahn (2004) state in their description of the dentition and diagnosis of Plagiaulacoidea that the I3 of plagiaulacoid multituberculates is small being only about half the size of I2 and with only one anterolabial cuspule. Also in their description of the dentition of Eobaataridae they note that I3 are unknown for Eobaatar, Loxaulax, and Monobaatar and that I3 of Sinobaatar is inadequately described. I3 for Janumis, recently placed in Eobaataridae (Hahn and Hahn 2006), is also unknown. Subsequent to this review two new eobaatarid genera from the Early Cretaceous of Japan have been described but the anterior upper dentition is known for only one of these, Hakusanobaatar Kusuhashi, 2008. From the illustrations and brief description provided by Kusuhashi (2008) it appears that the morphology of I3 in Hakusanobaatar differs from that observed in other plagiaulacoids in that it is monocuspid. An indeterminate eobaatarid upper right, deciduous I3 from the upper Barremian of Spain has been described and figured by Cuenca-Bescós et al. (1995: fig. 4). This shows some similarity in gross morphology to BMNH M 45483 but being a deciduous tooth no direct comparisons can be made.

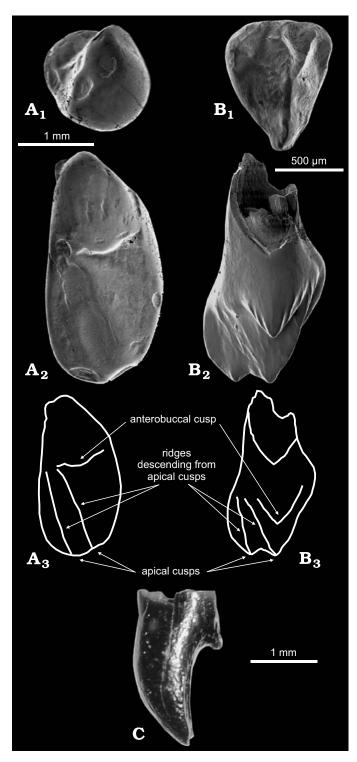


Fig.10. A. BMNH M 45658, an I2 tentatively referred to *Loxaulax valdensis* from the Early Cretaceous Hastings Beds Group, mainland Britain, in occlusal (A<sub>1</sub>) and distal (A<sub>2</sub>) views, line drawing (A<sub>3</sub>) to show features giving the erroneous impression that BMNH M 45658 may be a left I3. See text for a discussion. **B.** BMNH M 45483 a left I3 assigned to *Eobaatar clemensi* from the Early Cretaceous Wessex Formation, Isle of Wight, in occlusal (B<sub>1</sub>) and anterolabial (B<sub>2</sub>) views, line drawing (B<sub>3</sub>) as seen in B<sub>2</sub>. **C.** Normal light photograph of an indeterminate plagiaulacoid left I2 (part of SMNS 51981) from the Early Cretaceous Wessex Formation, Isle of Wight, in labial view (it was not possible to obtain scanning electron micrographs of the specimen which was glued to card by the original collector).

An upper incisor (Fig. 10A), now with accession number BMNH M 45658, figured by Clemens and Lees (1971: pl. 2: B) is assigned by them with question to *Loxaulax valdensis*. They state that the specimen is figured in lingual view with a magnification of 12.5× but it is actually shown at a magnification of 25× and if, as suggested by these authors it is an I2, it is figured in distal view. As figured and captioned, this abraded specimen appears to have a cusp disposition similar to BMNH M 45483 when seen in anterolabial view (Fig. 10A, B) suggesting that it may be an I3. However, recent re-examination serves to confirm that the apical depressions observed on BMNH M 45658 (Fig. 10A) are not the eroded apices of two apical cusps. This, together with the tooth's outline in occlusal view (Fig. 10A<sub>1</sub>) and its similarity in size to a well-preserved I2 tooth crown from the same locality, BMNH M 21100, indicate that it is indeed an I2 and not an 13. Therefore, with data currently available there is nothing to preclude assignment of the Isle of Wight I3, BMNH M 45483, to Eobaatar clemensi sp. nov. represented by the lower molars BMNH M 45482 and BMNH M 45557.

### Plagiaulacoidea indeterminate

The left I2 part of SMNS 51981 (Figs. 2B, 10C) is a well preserved bicuspid crown recovered from bed CL3 (Stewart 1978) on the south-west coast of the Isle of Wight (Figs. 3, 4) (Butler and Ford 1975), exact locality unknown but close to NGR SZ 3785 8391. Isolated I2s apparently representing plagiaulacoid multituberculates have been recovered from many sites yielding more diagnostic material. In most cases they are considered to be indeterminate and Parendotherium Crusafont-Pairó and Adrover, 1966, the holotype of which is an I2 with morphology similar to that of the plagiaulacid Bolodon, has recently been transferred to the Paulchoffatioidea (Hahn and Hahn 2006). However, I2 for Loxaulax (Figs. 2C, 10A) has been tentatively identified and is similar to I2s recovered from the Cherty Freshwater Member of the Purbeck Limestone Formation of Dorset, southern England. Among the latter is one specimen assigned to the plagiaulacid Bolodon osborni (Kielan-Jaworowska and Ensom 1992: pl. 4: 1-3). As noted above, the I2 described by Butler and Ford (1975) is too small to be placed with Loxaulax valdensis and it also differs from the I2 of this taxon but resembles that of Bolodon. Hakusanobaatar and a number of other taxa in the morphology of the basal cusp (Figs. 2C, 10C); a single cusp is present in Bolodon, Hakusanobaatar and the Isle of Wight specimen whereas the I2 tentatively assigned to L. valdensis has a basal cusp comprised of three cuspules (Clemens 1963). Enamel completely covers the crown of SMNS 51981 and of the I2 tentatively assigned to L. valdensis. In Eobaatar ?i1 is gliriform leading Hahn and Hahn (1992, 2004) to postulate that I2 would be similarly gliriform. I2 is unknown in currently described species of *Eobaatar* but indeterminate I2s referable to an eobaatarid have been reported from the Upper Barremian of Spain (Cuenca-Bescós et al. 1995) and that of Hakusanobaatar has been figured and briefly described (Kusuhashi 2008: 382–383, figs. 2A, 3C). Those from Spain appear to have normal enamel and while that of *Hakusanobaatar* has not been described, in the diagnosis of this taxon Kusuhashi (2008) states that "enamel is possibly not limited to the outer surface of the lower incisor". This suggests that enamel may also completely cover the crown of I2. However, if Hahn and Hahn (2004) are correct with respect to enamel covering the I2 of *Eobaatar*, the I2 from the Wessex Formation does not belong with the m1s described above.

I2 of the holotype of *Bolodon crassidens* is broken off but the base of the root is preserved, Simpson (1928) recording its maximum length as 2.2 mm. The broken I2 assigned to B. osborni by Kielan-Jaworowska and Ensom (1992: pl. 4: 3) measures just 0.9 mm at an apparently similar position. In comparison, at the same point, the Isle of Wight specimen measures 1.2 mm. BMNH M 21100, the I2 tentatively assigned to Loxaulax valdensis, measures 1.6 mm and the indeterminate I2s figured by Kielan-Jaworowska and Ensom (1992) measure 1.4 mm (pl. 4: 1) and 1.3 mm (pl. 4: 2). In the case of plagiaulacoid I2s exhibiting normal enamel cover, gross morphology is broadly similar in all taxa but some intraspecific variation in tooth size can be anticipated. The morphology of the principal cusp of the Isle of Wight specimen does not resemble that of the I2 of Hakusanobaatar and precludes assignment to this taxon. In view of this, and probable intraspecific variation in tooth size, it is not possible with currently available data to provide a higher taxonomic identification of the Isle of Wight specimen and it is here considered to be Plagiaulacoidea indet. However, it may represent a second Wessex Formation plagiaulacoid.

The third, undescribed, mammal tooth reported by Buffetaut and Ford (1978) also forms part of SMNS 51981 and comprises a small fragment superficially resembling the apex of the I2 accessioned under the same number. It is also here considered to be indeterminate and only questionably referable to Mammalia.

### Conclusions

A comprehensive programme of bulk screening has resulted in the recovery of the first well-preserved and determinate multituberculate teeth to be obtained from of the Barremian Wessex Formation of the Isle of Wight. Not surprisingly, in light of the occurrence of eobaatarids in the Valanginian of Britain and the Hauterivian–Barremian transition, and the Barremian of Spain, these also represent an eobaatarid. Despite the apparently close ties between the Barremian tetrapod assemblages of Britain and Spain (e.g., Sweetman 2006a, b, 2007) none of the taxa recorded from the Wessex Formation appear to be conspecific with those occurring in Spain. However, the assemblages do have at least two genera in common including the multituberculate *Eobaatar* reported here. Until this study, the only description of the plagiaulacoid m2 recovered from the Wessex

Formation in the 1970s by the late Richard L.E. Ford was that of Butler and Ford (1975) and the specimen, which was obtained after Ford's death by the SMN, remained largely ignored (Rainer Schoch personal communication 2004). Butler and Ford's (1975) brief account, and the line drawings that accompanied it (reproduced here as Fig. 2A), did not permit further analysis of the specimen's taxonomic position in light of discoveries made after its recovery. Furthermore, even if the specimen had been re-examined its poor state of perseveration would have rendered any higher taxonomic identification problematic due to the absence of directly comparable and better preserved material from the Wessex Formation. The recent recovery of well-preserved lower molars permitting such comparison indicates that the specimen can be tentatively assigned to the same species, Eobaatar clemensi sp. nov. With currently available data, the I3 recovered from the Wessex Formation can also be tentatively referred to E. clemensi and if this assignment is correct, BMNH M 45483 represents the first well preserved I3 of a member of Eobaataridae to be fully described. The I2 reported by Butler and Ford (1975), while undoubtedly the I2 of a plagiaulacoid multituberculate, is otherwise indeterminate.

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### References

- Allen, P. and Wimbledon, W.A. 1991. Correlation of NW European Purbeck-Wealden (non marine Lower Cretaceous) as seen from the English type-areas. *Cretaceous Research* 12: 511–526.
- Badiola, A., Canudo, J.I., and Cuenca-Bescós, G. 2008. New multituberculate mammals from the Hauterivian/Barremian transition of Europe (Iberian Peninsula). *Palaeontology* 51: 1455–1469.
- Buffetaut, E. and Ford, R.L.E. 1979. The crocodilian *Bernissartia* in the Wealden of the Isle of Wight. *Palaeontology* 22: 905–912.

- Butler, P.M. and Ford, R. 1975. Discovery of Cretaceous Mammals on the Isle of Wight. *Proceedings of the Isle of Wight Natural History and Archaeological Society* 6: 662–663.
- Clemens, W.A. 1963. Wealden mammalian fossils. *Palaeontology* 6: 55–69.
  Clemens, W.A. and Lees, P.M. 1971. A review of English Early Cretaceous mammals. *In*: D.M. Kermack and K.A. Kermack (eds.), Early Mammals, 117–130. *Zoological Journal of the Linnean Society of London* (Supplement 1) 50: 1–203.
- Crusafont-Piaró, M. and Adrover, R. 1966. El Primer mamífero del Mesozoico Español. *Publicacaiones de la Paleontolgía Universidad de Barcelona* 13: 28–33.
- Cuenca-Bescós, G., Canudo, J.I., and Ruiz Omeñaca, J.I. 1995. Los mamíferos del Barremiense superio (Cretácico inferior) de Vallipón (Castellote, Teruel). *Beca del Museo de Mas de las Matas* 1995: 105–137.
- Eaton, J.G. and Cifelli, R.L. 2001. Multituberculate mammals from the Early–Late Cretaceous boundary, Cedar Mountain Formation, Utah. *Acta Palaeontologica Polonica* 46: 453–518.
- Evans S.E., Barrett, P.M., and Ward, D.J. 2004. The first record of lizards and amphibians from the Wessex Formation (Lower Cretaceous: Barremian) of the Isle of Wight, England. *Proceedings of the Geologists' Association* 115: 239–247.
- Feist, M., Lake, R.D., and Wood, C.J. 1995. Charophyte biostratigraphy of the Purbeck and Wealden of southern England. *Palaeontology* 38: 407–442.
- Freeman, E.F. 1975. The isolation and ecological implications of the microvertebrate fauna of a lower Cretaceous lignite bed. *Proceedings of the Geologists' Association* 86: 307–312.
- Gradstein, F.M., Cooper, R.A., Sadler, P.M., Hinnov, L.A., Smith, A.G.,
  Ogg, J.G., Villeneuve, M., McArthur, J.M., Howarth, R.J., Agterberg,
  F.P., Robb, L.J., Knoll, A.H., Plumb, K.A., Shields, G.A., Strauss, H.,
  Veizer, J., Bleeker, W., Shergold, J.H., Melchin, M.J., House, M.R.,
  Davydov, V., Wardlaw, B.R., Luterbacher, H.P., Ali, J.R., Brinkhuis,
  H., Hooker, J.J., Monechi, S., Powell, J., Röhl, U., Sanfilippo, A.,
  Schmitz, B., Lourens, L., Hilgen, F., Shackleton, N.J., Laskar, J., Wilson, D., Gibbard, P., and Kolfschoten T. van 2004. A Geologic Time
  Scale 2004. 500 pp. Cambridge University Press, Cambridge.
- Hahn, G. and Hahn, R. 1992. Neue Multituberculaten-Zähne aus der Unter-Kreide (Barremium) von Spanien (Galve und Uña). *Geologica et Palaeontologica* 26: 143–162.
- Hahn, G. and Hahn, R. 2001. Multituberculaten-Zähne aus der Unter-Kreide (Barremium) von Pié Pajarón (Prov. Cuenca, Spanien). *Paläontologische Zeitschrift* 74: 587–589.
- Hahn, G. and Hahn, R. 2004. The dentition of Plagiaulacida (Multituberculata, Late Jurassic to Early Cretaceous). Geologica et Palaeontologica 38: 119–159.
- Hahn, G. and Hahn, R. 2006. Catalogus Plagiaulacidorum cum figuris (Multituberculata suprajarassica et subcretacea). *Fossilium Catalogus, 1: Animalia Pars 140*, 1–348. Backhuys Publishers, Leiden.
- Harding, I.C. 1986. An Early Cretaceous dinocyst assemblage from the Wealden of southern England. *In*: D.J. Batten and D.E. Briggs (eds.), Studies in Palaeobotany and Palynology in Honour of N.F. Hughes. *Special Papers in Palaeontology* 35: 95–109.
- Haywood, A.M., Valdes, P.J., and Markwick, P.J. 2004. Cretaceous (Wealden) climates: a modelling perspective. Cretaceous Research 25: 303–311.
- Hughes, N.F. and McDougall, A.D. 1990. New Wealden correlation for the Wessex Basin. *Proceedings of the Geologists' Association* 101: 85–90.
- Insole, A.N. and Hutt, S. 1994. The palaeoecology of the dinosaurs of the Weald. *Proceedings of the Geologists' Association* 87: 443–446.
- Kermack, K.A., Lees, P.M., and Mussett, F. 1965. *Aegialoden dawsoni*, a new trituberculasectorial tooth from the Lower Wealden. *Proceedings of the Royal Society of London*, B 162: 535–554.
- Kerth, M. and Hailwood, E.A. 1988. Magnetostratigraphy of the Lower Cretaceous Vectis Formation (Wealden Group) on the Isle of Wight, southern England. *Journal of the Geological Society, London* 145: 351–360.
- Kielan-Jaworowska, Z. and Ensom, P.C. 1992. Multituberculate mammals from the Upper Jurassic Purbeck Limestone Formation of southern England. *Palaeontology* 35: 95–126.

- Kielan-Jaworowska, Z., Cifelli, R.C., and Luo, Z.-X. 2004. Mammals From the Age of Dinosaurs: Origins, Evolution and Structure. 630 pp. Columbia University Press, New York.
- Kielan-Jaworowska, Z., Dashzeveg, D., and Trofimov, B.A. 1987. Early Cretaceous multituberculates from Mongolia and a comparison with Late Jurassic forms. Acta Palaeontologica Polonica 32: 3–47.
- Kusuhashi, N. 2008. Early Cretaceous multituberculate mammals from the Kuwajima Formation (Tetori Group), central Japan. Acta Palaeontologica Polonica 53: 379–390.
- Lees, P.M. 1964. The flotation method of obtaining mammal teeth from Mesozoic bone-beds. *Curator* 7: 300–306.
- Lydekker, R. 1893. On the mammalian incisor from the Wealden of Hastings. Quarterly Journal of the Geological Society of London 49: 281–283.
- Martill, D.M. and Naish, D. (eds.) 2001. Dinosaurs of the Isle of Wight. Palaeontological Association, London, Field Guides to Fossils 10: 1–433
- McKenna, M.C. 1971. Multituberculata. McGraw-Hill Encyclopedia of Science and Technology, 736–737. McGraw-Hill Book Company, New York
- Oldham, T.C.B. 1976. The plant debris beds of the English Wealden. *Palae-ontology* 19: 437–502.
- Radley, J.D. 1994. Stratigraphy, palaeontology and palaeoenvironment of the Wessex Formation (Wealden Group, Lower Cretaceous) at Yaverland, Isle of Wight, southern England. *Proceedings of the Geologists' Associa*tion 105: 199–208.
- Robinson, S.A. and Hesselbo, S.P. 2004. Fossil-wood carbon-isotope stratigraphy of the non-marine Wealden Group (Lower Cretaceous, southern England). *Journal of the Geological Society, London* 161: 133–145.
- Scotese, C.R. 2002. Palaeomap Project. World Wide Web resource, www. scotese.com.
- Simpson, G.G. 1928. A Catalogue of the Mesozoic Mammalia in the Geological Department of the British Museum. 215 pp. Oxford University Press, London.
- Smith, A.G., Smith, D.G., and Funnell, B.M. 1994. Atlas of Mesozoic and Cenozoic Coastlines. ix + 99 pp. Cambridge University Press, Cambridge.
- Stewart, D.J. 1978. The Sedimentology and Palaeoenvironment of the Wealden Group of the Isle of Wight, Southern England. 347 pp. Unpublished PhD. thesis, Portsmouth University.
- Stewart, J.D. 1981. A field guide to the Wealden Group of the Hastings area

- and the Isle of Wight. *In*: T. Elliot (ed.), *Field Guides to Modern and Ancient Fluvial Systems in Britain and Spain*, 3.1–3.32. International Fluvial Conference, University of Keele, Keele.
- Stewart, J.D., Ruffell, A., Wach, G., and Goldring, R. 1991. Lagoonal sedimentation and fluctuating salinities in the Vectis Formation (Wealden Group, Lower Cretaceous) of the Isle of Wight, southern England. Sedimentary Geology 72: 117–134.
- Sweetman, S.C. 2004. The first record of velociraptorine dinosaurs (Saurischia, Theropoda) from the Wealden (Early Cretaceous, Barremian) of southern England. *Cretaceous Research* 25: 353–364.
- Sweetman, S.C. 2006a. The tetrapod microbiota of the Wessex Formation (Lower Cretaceous, Barremian) of the Isle of Wight, UK. In: P.M. Barrett and S.E. Evans (eds.), Ninth International Symposium on Mesozoic Terrestrial Ecosystems and Biota, Abstracts and Proceedings, 127–129. Natural History Museum, London.
- Sweetman, S.C. 2006b. A gobiconodontid (Mammalia, Eutriconodonta) from the Early Cretaceous (Barremian) Wessex Formation of the Isle of Wight, Southern Britain. *Palaeontology* 49: 889–897.
- Sweetman, S.C. 2007. Aspects of the Microvertebrate Fauna of the Early Cretaceous (Barremian) Wessex Formation of the Isle of Wight. 315 pp. Unpublished PhD thesis, University of Portsmouth.
- Sweetman, S.C. 2008. A spalacolestine spalacotheriid (Mammalia, Trechnotheria) from the Early Cretaceous (Barremian) of southern England and its bearing on spalacotheriid evolution. *Palaeontology* 51: 1367–1385.
- Sweetman, S.C. and Underwood, C.J. 2006. A neoselachian shark from the non-marine Wessex Formation (Wealden Group: Early Cretaceous, Barremian) of the Isle of Wight, Southern England. *Palaeontology* 49: 457–465.
- Underhill, J.R. 2002. Evidence for structural controls on the deposition of the Late Jurassic–Early Cretaceous Purbeck Limestone Group, Dorset, southern England. *In*: A.R. Milner, and D.J. Batten (eds.), Life and Environments in Purbeck Times. *Special Papers in Palaeontology* 68: 12–40.
- White, H.J.O. 1921. A short account of the geology of the Isle of Wight. *Memoirs of the Geological Survey of the United Kingdom.* 219 pp. HMSO, London.
- Woodward, A.S. 1891. On a mammalian tooth from the Wealden Formation of Hastings. *Proceedings of the Zoological Society of London* 5: 85–86.
- Woodward, A.S. 1911. On some mammalian teeth of the Wealden of Hastings. *Quarterly Journal of the Geological Society of London* 158: 525–528.