

# DIVERSITY OF TRICONODONTS IN THE MIDDLE JURASSIC OF GREAT BRITAIN

PERCY M. BUTLER and DENISE SIGOGNEAU-RUSSELL

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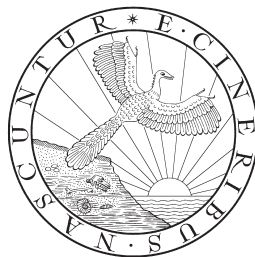
We describe a range of triconodont mammalian teeth from the Forest Marble (Middle Jurassic) of Kirtlington Quarry (Oxfordshire), Watton Cliff, and Swyre (both Dorset), and demonstrate the presence of a variety of morganucodontans, including *Morganucodon tardus* sp. n., *Cherwellia leei* gen. et sp. n., and *Stylidens hookeri* gen. et sp. n. “Amphilestidae” are represented by three species, *Phascolotherium simpsoni* sp. n., *P. cf. bucklandi*, and *Amphilestes* cf. *A. broderipii*, as well as by upper molars referable to *Phascolotherium*. Gobiconodontidae and Triconodontidae are represented by, respectively, *Gobiconodon bathoniensis* sp. n., and *Eotricodon sophron* gen. et sp. n.

Key words: “Amphilestids”, Bathonian, gobiconodontids, morganucodontids, triconodontids.

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## INTRODUCTION

Early mammals with triconodont teeth, characterized by three main, longitudinally aligned cusps, were formerly grouped in the order Triconodonta Osborn, 1888 (*e.g.*, Lillegraven *et al.* 1979). As conceived by Simpson (1928), the order Triconodonta contained only Triconodontidae Marsh, 1887, with subfamilies Triconodontinae Marsh, 1887 and Amphilestinae Osborn, 1888. Subsequent revisions led to a notable expansion of the concept of Triconodonta. Thus, Jenkins and Crompton (1979) reestablished the family level for Triconodontidae and Amphilestidae, and included Morganucodontidae Kühne, 1958. The family Megazostrodonidae Gow, 1986 was added to separate *Megazostrodon* Crompton *et* Jenkins, 1968, from Morganucodontidae, where the genus had been initially included. Chow and Rich (1984) recognized Gobiconodontinae as a subfamily of “Amphilestinae”; Jenkins and Schaff (1988) subsequently raised the former to family status.

Subsequent work recognised the triconodont molar pattern as plesiomorphic for Mammalia, and rejected Triconodonta as a paraphyletic grouping comprising markedly different mandibular, cranial and postcranial morphologies. As a result, Morganucodontidae and Megazostrodonidae, which do not fall into crown Mammalia, were excluded from the class as a whole (Rowe 1988; Rougier *et al.* 1996); but they were later reincorporated as the stem mammalian order Morganucodonta Kermack *et al.*, 1973 by Kielan-Jaworowska *et al.* (2004). “Amphilestidae” and Gobiconodontidae, together with Triconodontidae, are treated by these authors as Eutriconodonta Kermack *et al.*, 1973. Additional finds in South America (Rougier *et al.* 2007), Morocco (Sigogneau-Russell 1995, 2003a), Tanzania (Heinrich 1998), North America (Cifelli and Madsen 1998; Rose *et al.* 2001), China (Ji *et al.* 1999; Li *et al.* 2000, 2003; Rougier *et al.* 2001; Kusuhashi *et al.* 2009; Gao *et al.* 2010), Central Asia (Martin and Averianov 2007, 2010), Mexico (Montellano *et al.* 2008), and the UK (Clemens 2011) have extended our knowledge of the diversity of “triconodont” mammals. In several cases, however, only isolated molars have been found and their relationships remain unclear.

This paper presents new triconodont teeth from the late Bathonian (Middle Jurassic) of Britain. The Jurassic Period, which lasted 56 Ma (Gradstein *et al.* 2012), remains very sparing of mammalian fossils, with the “middle Jurassic [being] the most poorly represented epoch in mammalian history”, and “most of the known record comes from Britain” (Kielan-Jaworowska *et al.* 2004, p. 33). For many years, however, the only Middle Jurassic mammals with triconodont teeth from Britain were the two species of “amphilestids” from the middle Bathonian “Stonesfield Slate”, Taynton Limestone Formation: *Amphilestes broderipii* (Owen, 1845) and *Phascolotherium bucklandi* (Broderip, 1828), collected in the late 18<sup>th</sup> and early 19<sup>th</sup> centuries and restudied by Simpson (1928). More recently Freeman (1976, 1979) described a collection of mammals from the Kirtlington Mammal Bed, Forest Marble Formation (late Bathonian) of the Old Cement Works Quarry, Kirtlington, Oxfordshire, including a morganucodontan, *Wareolestes rex* Freeman, 1979. In the 1980s, intensive work in this quarry and at two other Forest Marble sites, Watton Cliff and Swyre, Dorset, by the late Prof. K.A. Kermack and colleagues from University College, London, resulted in the discovery, among other material, of some 700 isolated mammalian teeth (Kermack 1988). These have formed the basis for a number of papers describing constituents of the fauna: docodonts (Kermack *et al.* 1987; Sigogneau-Russell 2001, 2003b), allotherians (Kermack *et al.* 1998; Butler and Hooker 2005), shuotheriids (Sigogneau-Russell 1998), and trechnotherians (Sigogneau-Russell 2003c).

The triconodont teeth from the Forest Marble Formation of Kirtlington, Watton Cliff, and Swyre (Freeman’s and University College collections) described in this paper are now housed in the Earth Sciences Department, Natural History Museum, London, UK.

**Institutional abbreviations.** — M (Mammalia) and OR (Old Register), specimens deposited at the Natural History Museum, London, UK (full current acronym includes the prefix .PV; former acronyms include BMNH and NHM); MNHN SA, specimens from synclinal d’Anoual, Morocco, and deposited at Museum national d’Histoire naturelle, Paris, France; OUM, Oxford University Museum, Oxford, UK; PM TGU, Paleontological Museum, Tomsk State University, Russia.

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tion of the drawings), from the Paleontology Department, Museum national d'Histoire naturelle, Paris, have given some life to the dry descriptions of the authors. Finally, Françoise Pilard, from the same Institution, kindly agreed to make endless modifications and additions to the figures, long after her retirement.

## TRICONODONT MOLAR PATTERN

The basic triconodont molar cusp pattern, with cusps in line, inherited from that of cynodonts, is relatively simple: two-rooted lower molars, relatively narrow transversely with a dominant middle cusp (a, according to the nomenclature used for *Morganucodon* Kühne, 1949 by Crompton and Jenkins 1968), flanked by lower mesial (b) and distal (c) cusps, the latter being followed by a small "talonid" cusp (d). More mesial cuspules (e and f) may delimit a sulcus, into which fits the d cusp of the preceding tooth. A lingual cingulum is usually present, with, at least in the early forms, a dominant cuspule under the distal part of a: the Kuehnecone of Parrington 1967 (= g of Crompton and Jenkins 1968, already present in the cynodont *Thrinaxodon*). Two-rooted upper molars are structurally similar to the lowers, but are relatively wider transversely and lower crowned, with less elevated cusps. Cusp A, in the centre again, dominates the mesial (B) and distal (C) cusps; more distal cusp D is more or less well defined. A complete cingulum encircles the crown lingually and labially. Accessory mesial cingular cuspules (E lingually and F labially) may be present.

Within this rather uniform morphological scheme, however, wear facets show that two types of occlusal relationships occurred (Mills 1971; Crompton 1974). In the morganucodontan Morganucodontidae, lower cusp a occludes immediately anterior to upper cusp A, between A and B; in the eutriconodontan Triconodontidae, though considered as not being directly related to the former, similar occlusion occurs (Crompton 1974; Cifelli *et al.* 1998). In the other eutriconodontan families, the "Amphilestidae" and Gobiconodontidae, by contrast, lower and upper teeth alternate, with the result that lower cusp a occludes farther forward, anterior to B and near the junction between two upper molars. To complicate matters, in the morganucodontan Megazostrodonidae genus *Megazostrodon* Crompton *et Jenkins*, 1968, occlusion has been shown (Crompton 1974) to be of the "amphilestid" type; but *Dinnetherium* Jenkins *et al.*, 1983, also a megazostrodonid according to the characters of its lower jaw (Gow 1986), has a morganucodontid type of occlusion.

Generally in mammals, upper and lower molars evolve together so that cusps can be homologised by their occlusal relations. Applying this criterion, Mills (1971) concluded that the cusps of *Morganucodon* and *Megazostrodon* were not homologous. We consider the resemblance too detailed to support this hypothesis. Either the two types of occlusion evolved independently in pre-occlusal triconodont teeth (*e.g.*, *Sinoconodon* Patterson *et Olson*, 1961); or, more probably, one type (the *Morganucodon* type?) evolved first and was converted into the other by changing the relative position of opposing teeth. In support of the latter alternative, Parrington (1978) noted some variation in the occlusal pattern in *Morganucodon*, and a distinct arrangement occurs in *Bridetherium* (Clemens, 2011).

In morganucodontids the functional pattern is produced as the result of wear. In *Morganucodon* this results in the removal of much of the B and C (b and c) cusps (see Crompton and Jenkins 1968). The *Megazostrodon* type of occlusion, in which A and a occlude into the pre-formed valleys between two opposing teeth, might be advantageous in requiring less loss of tooth material. Perhaps for this reason the alternating type of occlusion characterises the amphilestids and later mammals in general. Only the Triconodontidae retain the *Morganucodon* arrangement; they appear to have reduced tooth loss by developing more accurately fitting cusps. However, intermediates between the two modes of occlusion have not been identified.

## SYSTEMATIC PALEONTOLOGY

Class **Mammalia** Linnaeus, 1758

Order **Morganucodonta** Kermack *et al.*, 1973

The morganucodontan molar structure remains the basic triconodont one, though cusp b may not be separated from the cingulum on the lower molars. It has been most studied in *Morganucodon*, of which there is

plentiful material from the Rhaetic and Early Jurassic of Britain and China (*e.g.*, Mills 1971; Parrington 1971, 1978; Kermack *et al.* 1973; Crompton 1974; Crompton and Luo 1993). Associated teeth and jaws are known for three other Early Jurassic genera: *Erythrotherium* Crompton, 1964, *Megazostrodon* Crompton, 1974, and *Dinnetherium* Jenkins *et al.*, 1983 (see also Crompton and Luo 1993). The last two genera were placed by Gow (1986) in a separate family Megazostrodonidae on the basis of mandibular characters, despite their different modes of occlusion, as noted above. The order Morganucodonta as compiled by Kielan-Jaworowska *et al.* (2004) includes, besides the above-mentioned genera, *Wareolestes* Freeman, 1979, *Helvetiodon* Clemens, 1980, *Brachyzostrodon* Sigogneau-Russell, 1983, *Indotherium* Yadagiri, 1984, *Gondwanadon* Datta *et al.*, 1996 (in fact possibly a sinoconodontid), and *Indozostrodon* Datta *et al.*, 2001. Of these, *Wareolestes*, *Brachyzostrodon*, and *Indozostrodon* were placed in the family Megazostrodonidae by Kielan-Jaworowska *et al.* (2004), the others remaining in the Morganucodontidae. It is well worth keeping in mind that the familial position of several of these taxa, independent (as noted above) of the type of occlusion, remains highly speculative. This remark applies to the placing of taxa known only by isolated teeth and, in particular, to four of the five types of morganucodontan described in this paper, which are all classified as Morganucodonta incertae sedis.

Morganucodontans (with the exception of *Dinnetherium*) also differ from eutriconodontans in the mode of interlocking of adjacent teeth: d makes contact between b and e, instead of e and f (Sigogneau-Russell 2003a). Owing to a lingual ridge connecting it to e, b has an anterior face, more or less transverse to the longitudinal axis of the crown. On upper molars, B is similarly linked to the labial cusp E. In “amphilestids”, b and B are more distally placed, on the longitudinal main crest of the tooth, and the interlocking groove is between E (e) and F (f). B is also transversely developed on upper molars of gobiconodontids, but this is due to a curvature of the crown. It should be noted that the articulation of the d cusp in the e–f embrasure of “amphilestid” lower molars is shared not only “with obtuse-angled symmetrodonts” (Kielan-Jaworowska *et al.* 2004, p. 237), but also with triconodontids (Cifelli *et al.* 1998) and gobiconodontids (Kielan-Jaworowska and Dashzeveg 1998, p. 422; e–f groove of Sigogneau-Russell 2003a, p. 47, fig. 12).

### Family **Morganucodontidae** Kühne, 1958

#### Genus **Morganucodon** Kühne, 1949

Type species: *Morganucodon watsoni* Kühne, 1949.

#### *Morganucodon tardus* sp. n.

(Fig. 1A)

LSID urn:lsid:zoobank.org:act:EC47A860-3226-4FF5-A1B1-80CE730A3770

Holotype: M34984, a right upper molar, lightly worn.

Etymology: From Latin *tardus*, late; this is the geologically youngest species of the genus.

Horizon and locality: Watton Cliff, Dorset, UK; late Bathonian.

**Diagnosis.** — Differs from *Morganucodon watsoni* Kühne, 1949 by the relative proportions of the three main cusps as seen in side view (A being larger and less pointed), and by the wider and non-crenulated labial cingulum. Differs from *M. peyeri* Clemens, 1980 and *M. oehleri* Rigney, 1963 by the non-crenulated labial cingulum. Differs from *M. heikuopengensis* (Young, 1978) in its larger size and relative proportions of the three main cusps.

**Description.** — M34984 (L = 1.42 mm, W = 0.88 mm) is a small right upper molar (size range of *Morganucodon watsoni*). It shows the transverse disposition of the anterior cusp (B) and a horizontal labial cingulum ledge. The lingual cingulum is faintly crenulated and narrow. A and C are aligned, B is more labial and linked to both cingula, as is the very small D cusp. A is much higher than B and C; its mesial profile is moderately convex, so that its tip is not as sharp as in specimens of *M. watsoni*. E is weakly developed and F absent, hence there is no anterior sulcus, just a flattening. Wear has affected the lingual face of B and the anterior part of the cingulum. Cusps are flatter labially than in *Morganucodon watsoni*, the labial cingulum is wider and the cingular denticulations negligible. No complete upper molar of *Morganucodon peyeri* is known, but from the synthesis given by Clemens (1980, p. 78), the main discrepancy lies again in the weak labial cingulum. From the brief description given by Luo and Wu (1994), *M. oehleri* may resemble *M. tardus* in the great height of the A cusp, but it differs in the strongly crenulated labial cingulum. As for *M. heikuopengensis*, it is more like *M. watsoni* in these characters. Among the molariforms from the Early Jurassic of Wales described by Clemens (2011), those labelled as Group 2 have the greatest resemblance to *M. tardus*, but they are much smaller.

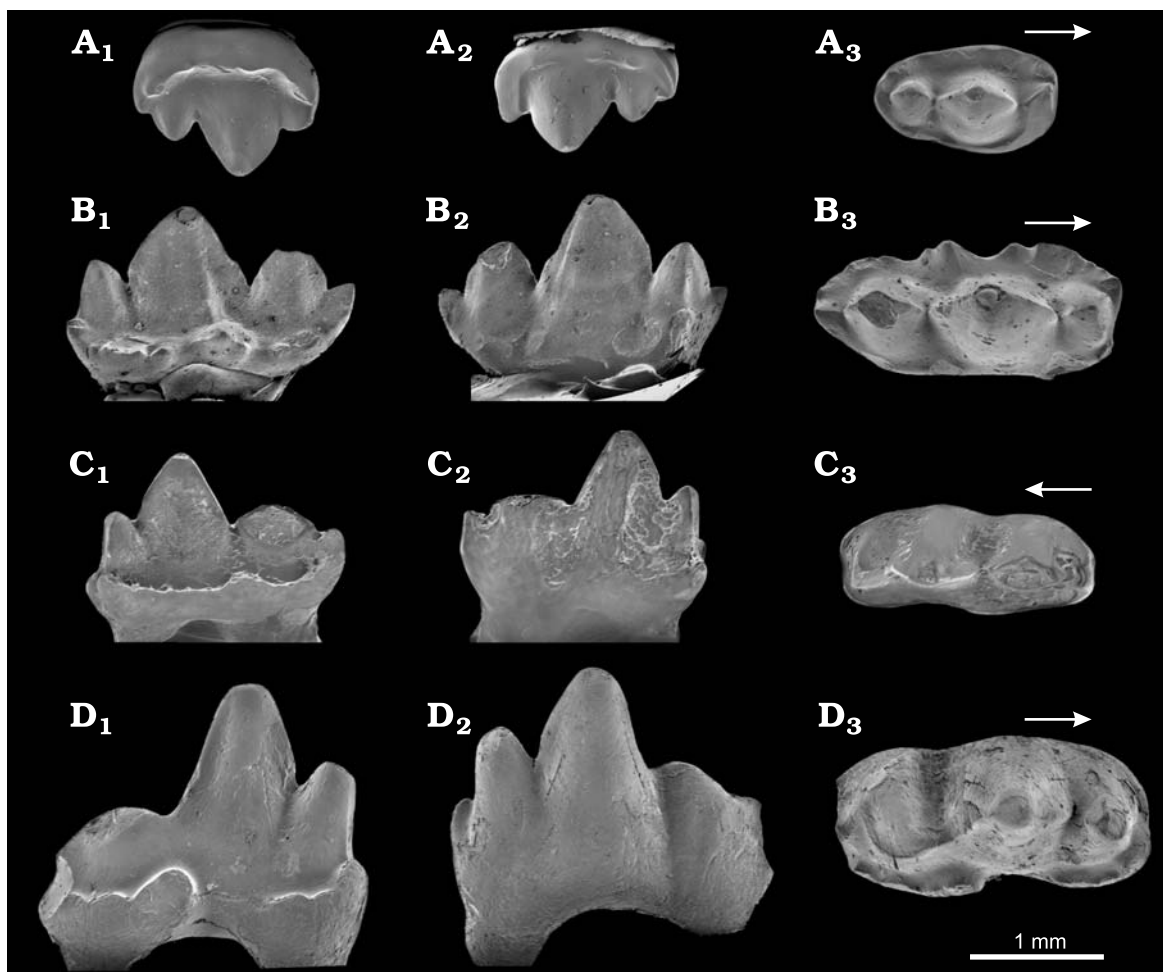


Fig. 1. Morganuodonton from the Middle Jurassic of Great Britain. **A.** *Morganuocodon tardus* sp. n., holotype M34984, Watton Cliff, Dorset, UK; late Bathonian, right upper molar in labial (A<sub>1</sub>), lingual (A<sub>2</sub>), and occlusal (A<sub>3</sub>) views. **B.** *Cherwellia leei* gen. et sp. n., holotype M46811, Old Cement Works Quarry, Kirtlington, Oxfordshire, UK; late Bathonian, right lower molar in lingual (B<sub>1</sub>), labial (B<sub>2</sub>), and occlusal (B<sub>3</sub>) views. **C.** *Stylidens hookeri* gen. et sp. n., holotype M84127, Watton Cliff, Dorset, UK; late Bathonian, right lower molar in lingual (C<sub>1</sub>), labial (C<sub>2</sub>), and occlusal (C<sub>3</sub>) views. **D.** *Stylidens* gen. n., sp. indet, M46554, Swyre, Dorset, UK; late Bathonian, left lower molar in lingual (D<sub>1</sub>), labial (D<sub>2</sub>), and occlusal (D<sub>3</sub>) views. SEM photos; roots cropped as needed. Arrows point anteriorly.

#### Family indet.

#### Genus *Wareolestes* Freeman, 1979

Type species: *Wareolestes rex* Freeman, 1979.

**Emended diagnosis.** — Morganuodonton with upper molar having a relatively high and robust cusp A, pyramidal with lingual and labial ridges on its slopes. B and C subequal, B slightly smaller, but not incorporated into the cingulum, which is continuous from E around the mesial border. D is a relatively small cusp on the cingulum. Lingual cingulum non-crenulated and narrow, rising to a point below A, where it is almost interrupted. Labial cingulum broader and cuspidate, with the highest cusp opposite to A, to which it is linked by a ridge. Cusp F hardly individualized. Owing to damage of the type specimen, it is not clear whether the labial cingulum was divided into two parts, as cited in the diagnosis of family Megazostrodonidae by Kielan-Jaworowska *et al.* 2004.

Differs from the M2 of *Megazostrodon* by larger size, more dominant cusp A, presence of enamel ridges, and of a cingulum cusp labial to A. Differs from the upper molars referred to *Brachyostrodon* (Hahn *et al.* 1991) by slightly larger general size, cusp A less globular and relatively higher, better individualisation of cusp D, coarser enamel ridges, lingual cingulum rising sharply in the middle of A, presence of a median labial cingulum cusp. Differs from *Indozostrodon* mostly by the relative proportions of cusps A, B, and C.

*Wareolestes rex* Freeman, 1979

(Fig. 2A)

Holotype: M36525, a right upper molar (originally described as a right lower molar); L = 2.31 mm, W = 1.24 mm.

Type horizon and locality: From the Old Cement Works Quarry, Kirtlington, Oxfordshire, UK; late Bathonian.

**Discussion.** — Morganucodonta, and more precisely Megazostrodonidae, were judged to be represented at Kirtlington by the genus *Wareolestes* Freeman, 1979, based on one molar identified by its author as a lower, and diagnosed as possessing “a kuehnecone directly lingual to the main cusp ... and a poorly defined buccal cingulum” (Freeman 1979, p. 158). According to Freeman’s determination, cusp “b” (broken) was nearly as high as “c” but shorter mesio-distally. Enamel ridges striate the disto-lingual side of the middle cusp “a”. The “lingual cingulum” forms a high wall anteriorly, but “e” and “f” are hardly distinct; the small cingular cusp “g” is connected to the main cusp by a ridge, and is followed posteriorly by two cusps. The “labial cingulum” is faint (“subdued”; Freeman 1979, p. 159), non-cuspidate, and interrupted under the high central cusp, but it widens posteriorly. Wear is detectable on the side opposite to “g”, below the tip of the main cusp and less clearly down it and on the distal cusp.

Freeman’s identification of the holotype of *Wareolestes rex* as a lower molar thus rested largely on the presence of what was considered as a Kuehnecone, g. However, on lower molars of other morganucodontans (*Morganucodon*, *Megazostrodon*, *Brachyostrodon*), cusp g stands below the a–c notch, while the supposed “g” in *Wareolestes* is more mesial, directly opposite the main cusp, to which it is connected by a ridge. Moreover, the presence of two cingula (labial and lingual) suggests an upper molar, as Hahn *et al.* (1991) noted. Also, the presence of “well-developed labial cingular cusps” is cited as a diagnostic character for megazostrodonid upper molars by Kielan-Jaworowska *et al.* (2004, p. 179). Finally the “b” cusp is independent from the anterior cingulum, like the B cusp on upper molars of morganucodontans. The main difficulty with the interpretation of M36225 as an upper molar lies in the fact that the main cusp is higher relative to tooth length than on the uppers of *Brachyostrodon*; however it is nearly as high on M1 of *Megazostrodon* (Crompton 1974, pl. 2B; it is lower on other molars of the genus) and equally high on the holotype of *Helvetiodon* that Clemens (1980) provisionally interpreted as an upper molar.

We therefore reinterpret the holotype of *Wareolestes rex* as an upper molar; in that case, the strong cingulum with the “g” cusp has to be labial (as in *Brachyostrodon*; Hahn *et al.* 1991): a large lingual cusp would interfere with occlusion against the lower molar, which bites lingual to the upper. Wear is very slight, but it supports the new interpretation: a polished facet on the tip of A extends onto the side with the weak cingulum, which must therefore be lingual.

*Helvetiodon* was classified as a morganucodontid by Kielan-Jaworowska *et al.* (2004); however, the strong cingular cusps and the division of the labial cingulum in two parts suggests that it might be closer to the megazostrodonids, and possibly related to *Wareolestes*. Indeed, the upper molar, while being much smaller, resembles M36525 in the high, robust cusp A; but B is a small cusp on the cingulum. The lateral cingula of the two genera correspond best if the holotype of *Helvetiodon schutzi* Clemens, 1980 is a left tooth, not a right tooth as interpreted by Clemens (1980). Then the enlarged cingulum cusp of *Helvetiodon* is labial, and the interrupted cingulum, absent under A, is lingual. With this orientation, *Helvetiodon* differs from *Wareolestes* in the more distal position of the labial cingulum cusp, in the small cingular cusp B, and in the presence of denticulations on the lingual cingulum.

Known only by a single molar, the familial affinity of *Wareolestes rex* is uncertain. The labial cingulum, though its mesial part is broken, was evidently more complex than in *Morganucodon*, and the presence of a G cusp contrasts with the ectoflexus of *Megazostrodon*. Evidence of function is inconclusive. The relationships of A to b and c of the lower molar are unclear. Hahn *et al.* (1991) noted that, in the megazostrodonid *Brachyostrodon*, wear is largely confined to the tips of the cusps. Similarly, in *Wareolestes*, the form and size of cusp A seems better adapted for a puncturing than for a shearing function.

*Wareolestes* sp. indet.

(Fig. 2B)

**Referred specimen.** — M46775 (Old Cement Works Quarry, Kirtlington, Oxfordshire, UK; late Bathonian).

**Description.** — M46775, the distal half of a molar with the middle cusp broken in the middle, is about 25% smaller (L = 1.00 mm, W = 0.70 mm) than, but apparently close to, the holotype of *Wareolestes rex*. We

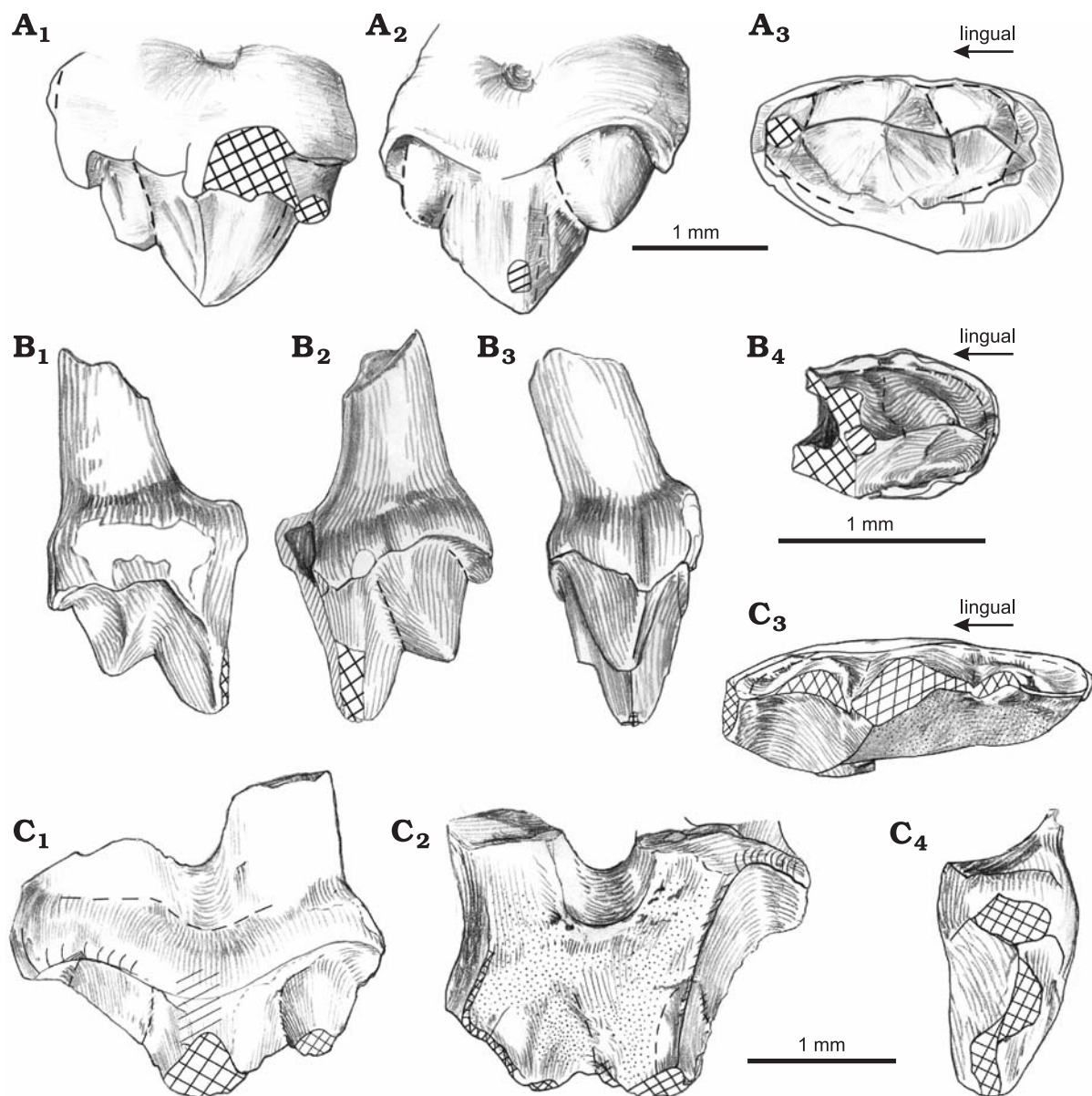


Fig. 2. Morganucodonta from the Middle Jurassic of Great Britain. All specimens from the Old Cement Works Quarry, Kirtlington, Oxfordshire, UK; late Bathonian. **A.** *Wareolestes rex*, holotype M36525, right upper molar in labial (A<sub>1</sub>), lingual (A<sub>2</sub>), and occlusal (A<sub>3</sub>) views. **B.** *Wareolestes* sp. indet., M46775, right upper molar in labial (B<sub>1</sub>), lingual (B<sub>2</sub>), distal (B<sub>3</sub>), and occlusal (B<sub>4</sub>) views. **C.** Gen. et sp. indet., M46194, right upper molar in labial (C<sub>1</sub>), lingual (C<sub>2</sub>), occlusal (C<sub>3</sub>), and mesial (C<sub>4</sub>) views. Arrows point anteriorly. Cross hatching refers to a broken surface and parallel hatching indicates wear.

interpret it as a right upper molar. Cusps C and D, which are well preserved, stand in line on the posterior crest of A. Vertical wrinkling of the posterior surface of A is not discernible, but C has a vertical ridge on its labial side, which is much fainter on the holotype of *W. rex*. On both sides, the cingulum is well indicated and grossly denticulate. Labially, it rises in the middle where it links to the middle ridge of A, but, owing to breakage, the presence of a “G-like” cusp cannot be confirmed. Lingually, it bears low undulations, one close to D and two further forward. Finally, a slight indentation is present on the distal face of D; this feature is absent on the holotype, and could well question the mesio-distal orientation adopted here. The proximal half of the distal root is preserved. It is inclined lingually at about 20° to the vertical axis of the crown. If the root was vertical, the lingual surface of the crown, which occludes with the lower teeth, would be inclined lingually. This resembles *Morganucodon* where, according to Mills (1971, p. 37), “the long axis of the upper molars leans notably lingually”, so that the functioning surface is vertical (Mills 1971, p. 41, fig. 2B). The enamel is partly missing; hence, no wear facet is discernable.

M46775 differs from the holotype of *Wareolestes rex* not only by its smaller size, but also by the slightly taller cusps, the more accentuated lingual cingulum, the presence of a labial ridge on C, and absence of wrinkling of the enamel of cusp A. It is possible that the tooth represents an “amphilestid”; however, the state of preservation does not allow definitive identification.

Gen. et sp. indet.

(Fig. 2C)

M46194 (L as preserved = 2.80 mm, W = 1.10 mm), from Kirtlington, is the largest morganucodontan tooth in the collection. It is poorly preserved, having suffered much post mortem damage as well as wear, making interpretation somewhat uncertain. It is described as a left upper molar. As seen in crown view, the blunt, wider end is taken as mesial, the narrower end as distal. The crown is proportionately narrower than that of the holotype of *Wareolestes rex*, but the enamel is missing on a large part of the lingual face. Cusps were aligned; the mesial one, B, has been completely removed by wear, but it was larger than in *Wareolestes*. Cusp A was large, robust, and centrally placed. C and D are similar in proportions to those of *Wareolestes*. The labial cingulum forms a regular bulge, without any denticulations unlike in megazostroodontids. There may have been a lingual cingulum, the two cingula meeting anteriorly into cusps E and F, but the area is damaged. The mesial root was slightly larger than the distal one. A possible rectangular “wear” surface is observed in the middle of the main cusp, labially. Two interpretations can be offered: if the rectangular surface on the main cusp represents wear, then it could indicate the labial face of a lower molar, as also suggested by the relative narrowness of the tooth. If this surface is an artefact, then it represents an upper molar (the interpretation adopted here) with a cusp B completely worn lingually by cusp a of the lower molar. It would then differ from the holotype of *Wareolestes rex* not only by its size and proportions, but also by its pointed distal end, by B larger than C, by its stronger labial cingulum and the relative size of the roots (mesial one larger). In any case, the tooth is evidence of another type of morganucodontan in the fauna, but its state of preservation does not allow confident identification.

### ?Order **Morganucodonta** Kermack *et al.*, 1973

As mentioned above, in morganucodontans, cusps b–B may have an anterior face, more or less oblique relative to the longitudinal axis of the crown; this is because lingual and labial crests of these cusps link them independently to the anterior cusps e and f (E and F). It is mostly on this criterion that the following molars are considered as possibly belonging to this order, though uncertainties remain.

Family indet.

Genus *Cherwellia* gen. n.

LSID urn:lsid:zoobank.org:act:E1F7A297-9D98-4DB2-A334-D1280CFD6D4B

Type species: *Cherwellia leei* sp. n.

Etymology: From the River Cherwell, which flows near Kirtlington.

**Distribution.** — As for the type and only species.

**Diagnosis.** — As for the type and only species.

*Cherwellia leei* sp. n.

(Fig. 1B)

LSID urn:lsid:zoobank.org:act:57BA710D-0094-46D5-90F0-307E012C4787

Holotype: M46811, a right lower molar.

Etymology: For the British artist Mr. A.J. Lee, whose drawings were of so much help in the preparation of this paper.

Horizon and locality: Old Cement Works Quarry, Kirtlington, Oxfordshire, UK; late Bathonian.

**Diagnosis.** — Relatively large lower molar showing the morganucodontan disposition of b and the presence of a g cusp. Differs from *Morganucodon* by cusp a relatively lower and less acute with a more convex mesial crest, the deeper incisures between the three main cusps, b as high as c but shorter mesio-distally, and presence of cusp f. In the morganucodontid *Gondwanadon*, which also has e and f cusps, b is larger than c, and the three cusps are less deeply separated. Differs from megazostroodontids in the proportions of the main cusps, the presence of f (except *Dinnetherium*), and the occlusal relations, which appear to be of *Morganucodon* type.



**Description.** — M46811 (L = 2.60 mm, W = 1.09 mm) is a right lower molar, as indicated by the absence of a labial cingulum and the presence of a lingual g cusp. Cusp a is relatively low, broadly triangular in lateral view, and separated from b and c by deep notches. Cusp b is comparatively large, equal in height to c, but shorter mesiodistally; it is obliquely disposed, linked by a lingual ridge to a distinct e. Cusp f is weaker, labial to the base of b, and there is a very shallow anterior indentation (rather a flattening) between e and f. Cusp d is small relatively to c and reached by the complete lingual cingulum, which forms a ledge and shows a moderate g cusp opposite to the groove between a and c.

Wear has created three flat oval surfaces at the labial base of the tooth: between a and b, between a and c, and below c; the median crest of a and c is also narrowly flattened by a vertical wear facet, as is also the labial face of b. Such wear is the first to show up in morganucodontan lower molars (“In *Megazostrodon*...as in *Eozostrodon*, wear commences on the cingular area”; Crompton 1974, p. 419; or at the base of the cusps, see Mills 1971, p. 40, fig. 1). If the occlusal pattern of M 46811 is of the *Morganucodon* type, and if it is a lower molar, the upper cusp A would occlude between a and c, wear on b would be due to B, and the more distal wear on c would be due to C.

**Comparison.** — As mentioned above, the absence of a labial cingulum and the presence of a g cusp identify the tooth as a lower molar. However, the weakness of the anterior indentation, the lowness of a, the relative size of d, the large size of b, the small size of cuspule f, and the deep incisures between cusps a–b and a–c all differ from morganucodontid lower molars of the Early Jurassic. On the contrary, b is also large in the megazostrodonid *Megazostrodon*, but M46811 differs in the lower and broader a, smaller d, the presence of cuspule f, and the more crenulated lingual cingulum with a smaller g. Also, wear on the anterior surface of b, due to A, is absent. M46811 differs from *Brachyzostrodon* by its less sturdy main and cingular cusps, presence of f, and smooth enamel. Moreover, wear on the anterior surface of b is absent. *Dinnetherium* shares with M46811 the *Morganucodon* type of occlusal cusp relationships (Crompton and Luo 1993) and the presence of f, but in *Dinnetherium* the cusps are high and acute, b is equal to c, and g is rudimentary. Finally, the size of M46811 is close to that of *Wareolestes rex*: could this tooth be a lower molar of this taxon? The relative height of the more blade-like cusp a, compared to the stout, crushing, cusp A of the holotype of *Wareolestes rex* precludes their mutual occlusion. The same relationship applies to the problematic M46194 (listed as gen. et sp. indet. above): its massive A cusp could not have functioned with the smaller a cusp of M46811. Thus this tooth indicates the presence of another morganucodontan taxon in the fauna.

#### Genus *Stylidens* gen. n.

LSID urn:lsid:zoobank.org:act:C9874C21-6E13-49E9-8946-4B74F9BE01A0

Type species: *Stylidens hookeri* sp. n.

Etymology: From Latin *stylus*, pointed instrument and *dens*, tooth, in reference to the shape of the cusps.

**Distribution.** — As for the type and only species.

**Diagnosis.** — As for the type and only species.

#### *Stylidens hookeri* sp. n.

(Fig. 1C)

LSID urn:lsid:zoobank.org:act:6F2A6053-AF28-4FED-8186-603D59AA9F06

Holotype: M84127, a right lower molar with tip of cusp c broken off (Fig. 1C).

Etymology: For Dr. J. Hooker, in recognition of his contributions to knowledge of British fossil mammals.

Type horizon and locality: Watton Cliff, Dorset, UK; late Bathonian.

**Diagnosis.** — Lower molar with cusps a and b acutely conical. Sulcus between a and c wider than between a and b, and continuous with a vertical groove on the labial side. Differs from other morganucodontans, including *Cherwellia*, by the height and disposition of the cusps, recalling the situation in *Amphilestes* Owen, 1859, but differing from the latter in the asymmetrical crown, the transverse disposition of b, the indication of a g cusp, and the type of occlusal relations.

**Description.** — M84127 (L = 1.85 mm, W = 0.80 mm) is a relatively large and unworn but damaged right lower molar. Cusp b has a transverse anterior face due to crests linking it to e and f. The main cusp a is anterior to the middle, as in *Morganucodon*; it is a high, narrow cone, with an apical angle of 50° laterally. Cusp b is also a narrow cone, about half the height of a; the base of c (tip broken off) shows that it was notably larger than b. The sulcus between a and c is wider and lower than that between a and b; it is continued labially by a

groove that extends to the base of the crown. The distal crest of a is diverted slightly more lingually than the mesial crest. The lingual face of cusp b is clearly distally orientated. The lingual cingulum is faintly crenulated, and g is represented by a long bump rather than a cusp. There is no labial cingulum, but the posterior part of the labial margin is swollen. The distal root, the only one partially preserved, is slightly flattened transversely and inclined distally. Wear is detectable at the base of the groove between a and c; it indicates that the occlusion of A against a and c was more accurately related to the a–c notch than in *Morganucodon*, and hence more like that of the Triconodontidae.

**Comparisons.** — M84127 shows some resemblance to *Cherwellia*, especially in the relationship between b, e, and f at the mesial end of the crown. However, in *Stylidens*, the a cusp is taller, narrower, more acute, and meets b and c at a higher level; such differences exceed those observed along the jaw in *Morganucodon* for instance (Kermack *et al.* 1973), Cusp f also occurs in *Dinnetherium*, but b and c are of equal size, hence the tooth is more symmetrical. The general outline and shape of the cusps evoke the eutriconodontan *Amphilestes* (see below), in which b is upright, taller than c, and slightly diverted lingually. However, the mesial and distal cusps are here not symmetrically disposed, and the tooth is straight longitudinally, whereas there is a slight curvature on *A. cf. broderipii* (M46744; see below); the crown is less compressed, and e and f are bumps rather than columns. Finally, each of these cuspules is linked by a crest to b, which thus has an anterior face, as in morganucodontans.

*Stylidens* sp. indet.

(Fig. 1D)

M46554 (L = 2.64 mm, W = 1.20 mm) is a left lower molar with cusp c broken off. It is from the late Bathonian of Swyre, Dorset, UK. This tooth is morphologically close to M84127, with the same mesiodistal compression, the same conical shape of a (apical angle of 40° laterally) and b, and with similar labial grooves between a and c. However, not only is the size notably larger, but b is barely transverse, having only one weak crest going to e, so that its lingual face is barely oblique; and the f cuspule is replaced by a low cingulum. The lingual cingulum is more grossly denticulate with a more salient g cusp, and it is interrupted in the middle of a. There were two subequal, circular roots, in vertical line with the cusps, the distal one being slightly inclined distally. The enamel is not well preserved, but d is apparently worn and so is the sulcus between a and c basally, where A may have occluded, as in M84127 and morganucodontids. Though a wide range of size has been reported to exist in *Morganucodon* (Parrington 1971, p. 257), the differences concerning b and f cast doubt on the attribution of M 46554 to the species *Stylidens hookeri*, but a close relationship is undeniable.

Finally, the two teeth representing the genus *Stylidens* agree in several points with *Cherwellia* (M 46811; Fig. 1B); especially the anterior end of M84127 (but not M46554) and M46811 (b, e, and f) are quite similar. However, the main cusps are relatively taller and unite at a higher level in *Stylidens*. Finally, *Cherwellia* and *Stylidens* differ from *Bridetherium* Clemens, 2011, by being more asymmetrical, e and g better developed, the a cusp lower in proportion to crown length, the more distal g cusp, and the proportionally larger b and c.

Altogether, these isolated specimens do not help to trace the evolutionary history of Morganucodonta during the Middle Jurassic, nor do they help to clarify the confused problem of the evolution of dental occlusion in this order. Nonetheless, the specimens document previously unappreciated diversity of morganucodontans (including the family Morganucodontidae) during the Middle Jurassic.

### Order Eutriconodonta Kermack *et al.*, 1973

#### Family “Amphilestidae” Osborn, 1888

Lower molars belonging to members of this family share with those of eutriconodontan Gobiconodontidae “their basic structure” (Kielan-Jaworowska and Dashzeveg 1998, p. 417), while they differ from those of the Triconodontidae by the dominance of cusp a over b and c (Simpson 1925a, 1928). They are characterized by a high, centrally placed cusp a, subequal b and c, and an e–f interlocking mechanism with cusp d of the preceding lower molar. Occlusion differs from that of the Morganucodontidae and Triconodontidae and is of the megazostroodontid, gobiconodontid and “therian” type, with alternating upper and lower molars (Mills 1971).

Chow and Rich (1984) recognized two subfamilies of “Amphilestidae”, “Amphilestinae”, and Gobiconodontinae; the latter was elevated to familial rank by Jenkins and Schaff (1988), a position adopted by Kielan-Jaworowska *et al.* (2004). These two families differ from each other by the proportions of the dentary, the dental formula, and the modalities of dental replacement. Moreover, the Gobiconodontidae are

derived in the enlargement of the anterior dentition and the arched disposition of cusps of upper molars (except in *Gobiconodon zofiae* Li *et al.*, 2003).

Simpson (1928) included four genera in the “Amphilestinae”, all known by lower dentitions only: *Amphilestes* Owen, 1871, *Phascolotherium* Owen, 1838, both from the middle Bathonian of the “Stonesfield Slate”, UK; and *Comodon* Kretzoi *et Kretzoi*, 2000 (replacement name for *Phascolodon* Simpson, 1925b) and *Aploconodon* Simpson, 1925b, from the Morrison Formation of North America. Kielan-Jaworowska *et al.* (2004) added the questionably referred genera *Klamelia* Chow *et Rich*, 1984 (characterized by unequal b and c cusps on lower molars), *Liaotherium* Zhou *et al.*, 1991 (known only by a dentary bearing an incomplete last molar), *Tendagurodon* Heinrich, 1998 (distinctive in lacking a lingual cingulum), *Triconolestes* Engelmann and Callison, 1998 (distinctive cusp pattern), and *Paikasigudodon* Prasad *et Manhas*, 2002 (the first “amphilestid” genus diagnosed on an upper molar; see below). The inclusion of these diverse and poorly known genera understandably compelled Kielan-Jaworowska *et al.* (2004) to recognize Amphilestidae as a probably paraphyletic “Amphilestidae”, definable only on primitive characters.

More recently, a genus has been described from the Early Cretaceous of western Siberia, *Kemchugia* Averianov *et al.*, 2005, based on an upper molar and a partial lower molariform (see below). Subsequently, Rougier *et al.* (2007) described *Hakusanodon*, based on a lower jaw from the Lower Cretaceous of Japan, which they considered “as closely related to Eurasian and North American Jurassic amphilestids” (Rougier *et al.* 2007, p. 73). Hooker and Lawson (2011) described an unnamed partial lower molar as representing the youngest member of the family (Cenomanian, UK). Finally, the discovery of *Juchilestes* Gao *et al.*, 2010, based on a partial skull with complete upper and lower dentitions, sheds new light on “amphilestid” relationships.

#### Genus *Amphilestes* Owen, 1859

Type species: *Amphilestes broderipii* (Owen, 1845).

##### *Amphilestes* cf. *A. broderipii* (Fig. 3A, B)

The genus *Amphilestes* was rediagnosed (Simpson 1928, p. 71) on its dental formula and on “molar cusps high and slender, molar cingulum rising below the main cusp, molar enamel not pitted”. Two teeth from the late Bathonian correspond to the above generic diagnosis: M35000, from Watton Cliff; and M46744, from Kirtlington.

M35000 (lower right molar; L = 1.45 mm, W = 0.70 mm; Fig. 3A), was previously figured by Freeman (1979, p. 149, pl. 16, figs 1, 2) but not described. It is in the size range of *A. broderipii*. As in this species, the three main cusps are closely apposed, though the tip of cusp c diverges slightly. Cusp a is broken off; its base shows that it was narrower mesiodistally than in the Oxford specimen of *A. broderipii* (OUM J 20079). Cusp b is slightly higher than c, and more closely joined to a. Mesially, e and f form two high vertical columns separated by a narrow sulcus; distally, cusp d is in line with c. These cusps, as well as cusps e and f, are relatively higher than in the three original specimens of *A. broderipii*. In occlusal view, a slight convexity of the crown can be seen, with c slightly more lingual than a and b. The lingual cingulum forms a ledge mesially and distally but is much narrower in the middle where it rises under a, as in *A. broderipii*. One of the illustrations published in Freeman (1979, p. 149, pl. 16, fig. 2) gives the impression of the tooth having two cingula; based on this view, Averianov *et al.* (2005) identified it as an “amphilestid” upper molar. However, reexamination of the specimen itself shows that the “labial cingulum” is the swollen margin of the crown under b and c (similar to *Megazostrodon* m1 and m2, Crompton 1974, p. 408, fig. 6); it is rounded in profile and not sharp like the lingual cingulum. We thus maintain that M 35000 is a lower molar.

M46744 (lower right molar; L = 1.27 mm, W = 0.52 mm; Fig. 3B), from Kirtlington, appears very similar; its cusps are more closely aligned but the labial face is again convex. Cusp a is narrower mesio-distally than in the Oxford specimens (OUM J.20078, 20079); b and c have been truncated. Lingual to d is a minute cuspule, absent in M 35000. Cusp e is slightly lingual to b, as on M 35000; cuspule f has been hollowed vertically by wear. A deep groove has been worn labially between a and b (due to occlusion with cusp C of the corresponding upper molar), as well as near the base between a and c (due to occlusion with cusp B of the following upper tooth) and also on d. The removal of cusp f and wear of d would be attributable to the tip of A at the end of the masticatory stroke, as it bit between two lower teeth. Thus alternation would apply, not only to the teeth, but also to the individual cusps (see below). The two Oxford specimens of *A. broderipii*

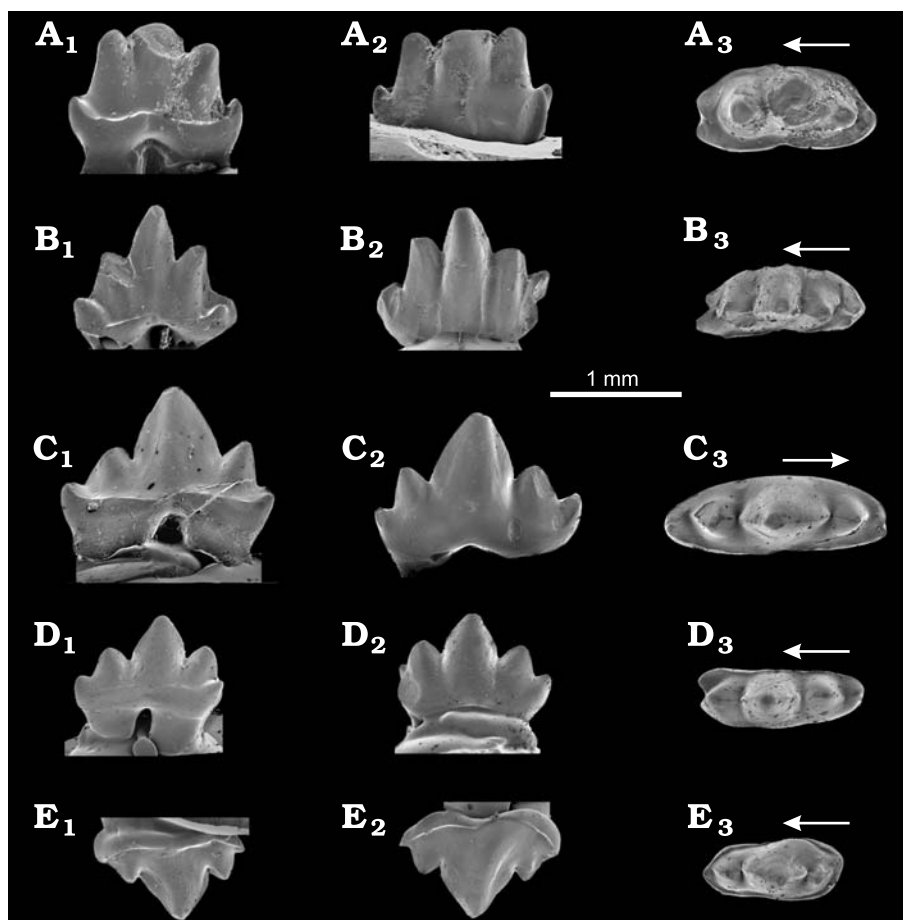


Fig. 3. “Amphilestidae” from the Middle Jurassic of Great Britain. **A, B.** *Amphilestes* cf. *A. broderipii*. **A.** M35000, Watton Cliff, Dorset, UK; late Bathonian, right lower molar in lingual (A<sub>1</sub>), labial (A<sub>2</sub>), and occlusal (A<sub>3</sub>) views. **B.** M46744, Old Cement Works Quarry, Kirtlington, Oxfordshire, UK; late Bathonian, right lower molar in lingual (B<sub>1</sub>), labial (B<sub>2</sub>), and occlusal (B<sub>3</sub>) views. **C.** *Phascolotherium* cf. *P. bucklandi*, M46694, Old Cement Works Quarry, Kirtlington, Oxfordshire, UK; late Bathonian, left lower molar in lingual (C<sub>1</sub>), labial (C<sub>2</sub>), and occlusal (C<sub>3</sub>) views. **D, E.** *Phascolotherium simpsoni* sp. n. **D.** Holotype M46115, Watton Cliff, Dorset, UK; late Bathonian, left lower molar in lingual (D<sub>1</sub>), labial (D<sub>2</sub>), and occlusal (D<sub>3</sub>) views. **E.** M46440, Old Cement Works Quarry, Kirtlington, Oxfordshire, UK; late Bathonian, right upper molar in labial (E<sub>1</sub>), lingual (E<sub>2</sub>), and occlusal (E<sub>3</sub>) views. SEM photos; roots cropped as needed. Arrows points anteriorly.

(OUM J.20078 and J.20079) are mostly unworn; only the base of the sulcus between a and c is worn on m3 of J.20078, while on J.20079 it is b of m3 which is vertically worn.

The attribution of M35000 and M46744 to the type species remains uncertain, mostly because of the height of the mesial and distal cusps, hence the tentative referral.

#### Genus *Phascolotherium* Owen, 1838

Type species: *Phascolotherium bucklandi* (Broderip, 1828).

**Referred species.** — The type, and *Phascolotherium simpsoni* sp. n.

**Comments.** — The emended generic diagnosis of Simpson (1928, p. 73) states: “molar cusps larger, less slender, more compressed [than *Amphilestes*]; internal cingulum rising slightly at two places, just anterior and posterior to the main cusp; molar enamel pitted or finely rugose”. The following additional information is derived from M7595, *Phascolotherium bucklandi*, which has been freed from matrix and can now be viewed from both sides. In *Phascolotherium*, cusps are relatively lower than in *Amphilestes* and they are triangular rather than columnar in side view (although the distinction is not as sharp in the first molar of *Amphilestes*). Cusp a is longer mesiodistally and its mesial and distal crests are curved in lateral view, but the whole cusp is less convex labially than in *Amphilestes*. Cusps b and c are smaller relative to a, and slightly divergent instead of vertical. On m1 to m3, a small circular facet on the labial side represents f, which would

have been worn off by the tip of A. Contact between the teeth obscures the relationship between e and f, but it would seem that these cusps are less deeply separated from each other than in *Amphilestes*. Finally, the cingulum is variable in configuration on the molars of the jaw of M7595, and even appears to be crenulated on some. Not much difference in size is observed from m1 to m4.

Three specimens are known from Stonesfield, all belonging to the single species *P. bucklandi*. The rugosity of enamel referred to in the diagnosis is present in all three specimens (Simpson 1928, p. 75) and is therefore unlikely to be due to immaturity or postmortem damage; enamel structure is probably involved. Yet all the late Bathonian specimens which in other respects resemble *Phascolotherium bucklandi* have smooth enamel. This might justify generic separation, but in view of the lack of other significant differences, we refrain from this step pending a closer examination of the enamel of *P. bucklandi*.

*Phascolotherium* cf. *P. bucklandi*

(Fig. 3C)

M46694, (left lower molar; L = 1.55 mm, W = 0.55 mm; Fig. 3C), from Kirtlington, shows the same size, shape and general proportions of the cusps as those of M7595. The cusps are aligned; b and c are relatively low and divergent as on the holotype (OR112) of *P. bucklandi*, but cusp a is not as broad in lateral view; cusps e and f are hardly separated and not higher than d. The lingual cingulum, which is nearly level, rises slightly toward the middle (a character seen in *Amphilestes*), where it diminishes for a short distance under a; the two elevations characteristic of *P. bucklandi* are absent. A vertical furrow hollows the base of the tooth between a and c (owing to occlusal wear by corresponding cusp B); moreover the distal side of c and the mesial side of d are worn (due to A) and there is a small facet on f (due to A on the preceding upper molar). Except for the smooth enamel and the course of the cingulum, this tooth could be classified as *P. bucklandi*.

*Phascolotherium simpsoni* sp. n.

(Figs 3D–E, 4, 5A–C)

LSID urn:lsid:zoobank.org:act:53A32C2E-85C5-467B-8750-22CCCAF634B6

Holotype: M46115, a left lower molar.

Etymology: To honour the contribution of G.G. Simpson to the knowledge of the “British Mesozoic Mammalia”.

Type locality and horizon: Watton Cliff, Dorset, UK; late Bathonian.

**Referred material.** — M46513, right lower molar; M46036, anterior half of a right lower molar; M46503, right lower molar; M46440, right upper molar; M46762, right upper molar; M46538, left upper molar; M46536, ?left upper molar. All referred specimens are from Old Cement Works Quarry, Kirtlington, Oxfordshire, UK; late Bathonian.

**Diagnosis.** — Lower molars differ from those of *Amphilestes* in having cusps b and c more separate and slightly divergent. Differs from *Phascolotherium bucklandi* in smaller size, cusp a less enlarged in comparison with b and c; e and f better developed and separated by a deep indentation; lingual cingulum without elevations; smooth enamel.

#### DESCRIPTION

**Lower molars.** — The holotype, M46115 (L = 1.20 mm, W = 0.50; Fig. 3D) is 30% smaller than the teeth of *Phascolotherium bucklandi* and is more similar in size to those of *Amphilestes broderipii*. It shows a deep mesial indentation between cusps e and f (which is lower), somewhat as in *Amphilestes*. In crown view the labial border is slightly convex, the lingual border straight, a contour recalling that of *Comodon* (Sigogneau-Russell 2003a). In lateral view, the cusps are broadly triangular, with b and c divergent from a, as in *Phascolotherium bucklandi*; but these cusps are larger relative to a, somewhat as in *Amphilestes*. However, b and c are less upright and their crests slightly convex in lateral view, especially when compared with M35000 and M46744 (although the difference is less with respect to the anterior molars of *Amphilestes* as seen in OUM J.20078). Finally, the faintly crenulated cingulum is horizontal and does not rise in the middle as in *Amphilestes*, nor does it show the elevations characteristic of *Phascolotherium bucklandi*. The enamel is smooth. Cusp f and the base of cusp b have been worn labially into a round wear facet (probably due to A of the preceding upper molar) as on the first three molars of *P. bucklandi* M7595; there is also possible wear on the mesial and distal faces of a.

Three other lower molars are referred to *Phascolotherium simpsoni* but differ from the holotype in some details.

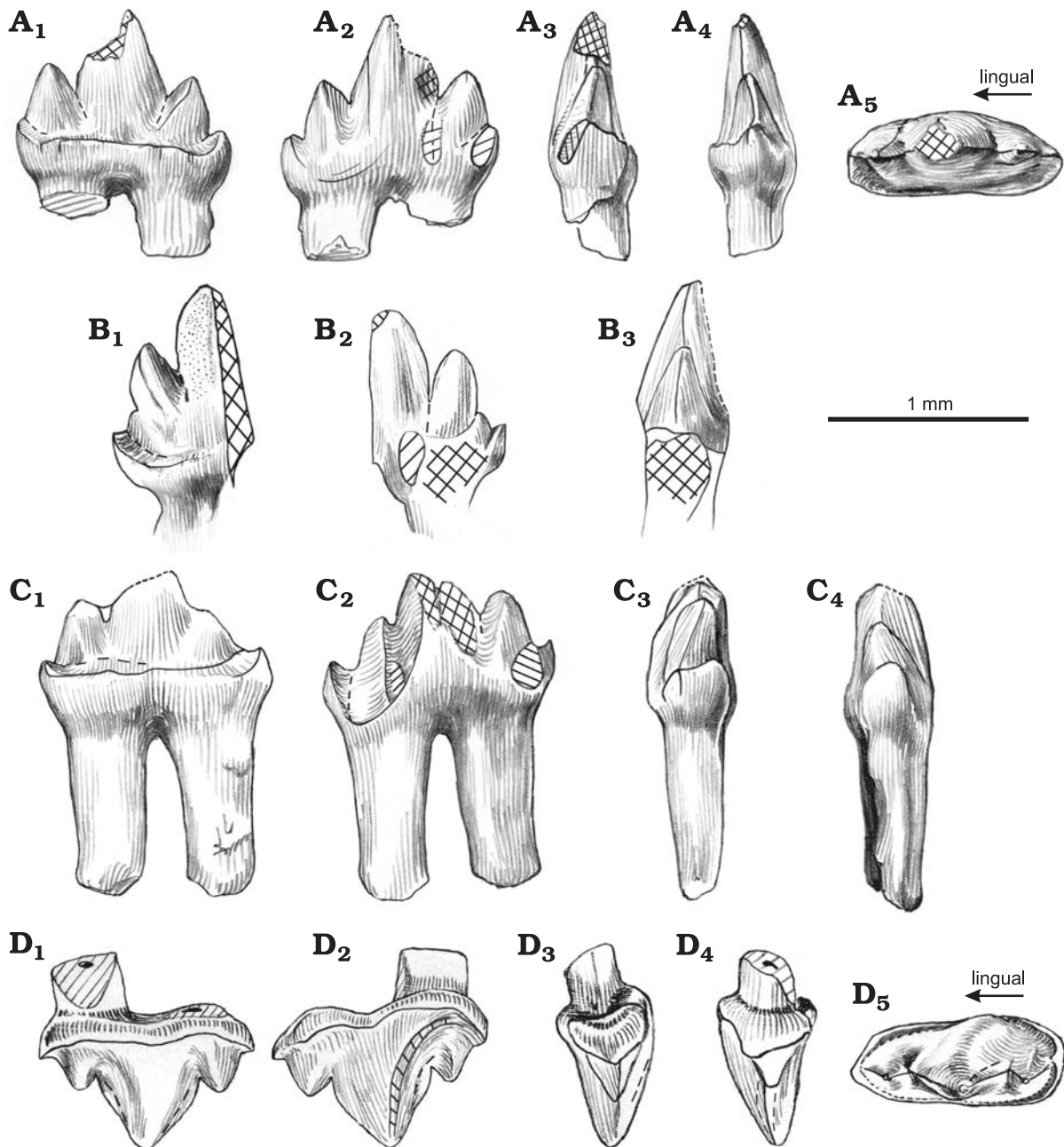


Fig. 4. *Phascolotherium simpsoni* sp. n. ("Amphilestidae") from the Middle Jurassic of Great Britain. All specimens from the Old Cement Works Quarry, Kirtlington, Oxfordshire, UK; late Bathonian. **A.** M46513, right lower molar in lingual (A<sub>1</sub>), labial (A<sub>2</sub>), mesial (A<sub>3</sub>), distal (A<sub>4</sub>), and occlusal (A<sub>5</sub>) views. **B.** M46036, right lower molar in lingual (B<sub>1</sub>), labial (B<sub>2</sub>), and mesial (B<sub>3</sub>) views. **C.** M46503, right lower molar in lingual (C<sub>1</sub>), labial (C<sub>2</sub>), mesial (C<sub>3</sub>), and distal (C<sub>4</sub>) views. **D.** M46440, right upper molar in labial (D<sub>1</sub>), lingual (D<sub>2</sub>), mesial (D<sub>3</sub>), distal (D<sub>4</sub>), and occlusal (D<sub>5</sub>) views. Arrows point anteriorly. Cross hatching refers to a broken surface, parallel hatching indicates wear, and dots indicate broken edges.

M46513 (right lower molar; L = 1.12 mm, W = 0.45 mm; Fig. 4A) has the size of the holotype, M46115. Cusp a is strongly convex labially; cusps b and c are intermediate between those of *Amphilestes broderipii* and *Phascolotherium bucklandi* in shape and direction; e and f are of unequal height, f being higher than e; they are nearly fused, with no sulcus between them. The cingulum is horizontal and finely crenulated. Wear has created a narrow groove between a and b (due to C) and an oval facet on f (due to A); this again recalls *Amphilestes*. Another wear surface may be present on the base of the distal face of c.

M46036 (right lower molar; L = 0.58 mm, W = 0.40 mm, as preserved; Fig. 4B) seems to be the mesial half of a large tooth similar to M 46513. The b cusp is high and upright. Wear has eroded the base of the tooth between a and b.

M46503 (right lower molar; L = 1.15 mm, W = 0.45 mm; Fig. 4C) is poorly preserved, but enough remains to show a near symmetrical configuration of the three main cusps in lingual view, b and c being closer to a than in M46513. A complete lingual cingulum, not rising in the middle, terminates in the e cusp mesially and the d cusp distally. Mesially, a narrow sulcus isolates a badly preserved f cusp; this mesial indentation is intermediate in depth between that of M46115 and that of M46513. Wear, heavier than in other specimens, has affected at least the distolabial part of the tooth. This tooth seems to be closer to *Amphilestes broderipii* according to the shape of the cusps and the closer approximation of b and c to a, but it may differ in the lesser height of the cusps, although this is uncertain owing to the wear.

**Upper molars.** — Upper molars, also from Kirtlington, may be identified by the presence of both labial and lingual cingula and other characteristics. These are of appropriate size and morphology to occlude with the lower molars of *Phascolotherium simpsoni*, and are referred to the species by analogy with the associated upper and lower dentition known for *Juchilestes* (Gao *et al.* 2010). They are described individually in the paragraphs that follow.

M46440 (right upper molar; L = 1.08 mm, W = 0.46 mm; Figs 3E and 4D) could well fit with the smaller lower molars M46115 and M46513. From the inclination of the partially preserved distal root and the shape of cusp A, M46440 is interpreted as a right molar. The crown is relatively lower than that of the lower teeth, and there is a labial cingulum as well as a lingual one; these cingula are narrow, smooth, and vaguely sinuous. An elevation of the cingula forms a cuspule (?E), directly mesial to B, but F is not individualized and no mesial indentation is detectable. D is slightly displaced lingually from the A–C line; it would probably lie lingual to E of the next tooth. All cusps are triangular in lateral view, even more so than on the lower molars described above. Cusp A is longer mesiodistally at the base, and B and C are relatively smaller than the corresponding cusps of lower molars belonging to *Phascolotherium simpsoni*. Surprisingly, assuming the specimen is a right tooth, the crown is wider distally than mesially, unlike amphilestid lower molars, and B is slightly larger than C. Cusp A bears a ridge on its lingual side, turning distally toward the base. This divides the lingual surface into a convex mesial part and a concave distal part. There were two roots, the distal one only basally preserved. Wear has flattened the lingual ridge of A, especially at its recurved base, creating a narrow elongated facet facing distally. The short lingual ridge of C is not worn.

M46762 (right upper molar; L = 0.85 mm, W = 0.37 mm; Fig. 5A) is smaller than M46440, and its enamel is not as well preserved, but it is very similar and offers the same challenge as to its orientation. The differences with M46440 concern B and C, which are small and less detached from A, only the latter having a triangular shape in lateral view. Its lingual ridge and concavity are also less accentuated. There is no E cusp; D is again lingually placed, and the complete distal root is inclined backward. No wear facet is discernible, except perhaps on the cingulum above C. M46762 could be interpreted as a distal molar of the same taxon as M46440 (though the wear [?] above C would imply the presence of a more distal lower molar).

M46538 (?left upper molar; L = 0.95 mm, W = 0.40 mm; Fig. 5B) is of the same size as M46762, but with sharper cusps. The lingual cingulum is weaker and may even be incomplete mesially. Cusp E is absent, but there is a small labial cusp F, separated by a groove from the mesial ridge of B. D is less lingually placed than on M46440. The rounded ridge on A is present lingually. The distal root is vertical, long, and slender, and decreases in diameter apically. Perhaps this tooth is a deciduous premolar.

M46536 (?right upper molar; L = 1.12 mm, W = 0.50 mm; Fig. 5C), an upper molar broken by a vertical crack across A, is close to M46440 in size and in the lingual convexity of A, but it has straighter labial crests and C seems to have been more vertically oriented and closely apposed to A. Cusp E is not individualized. The narrow cingulum on both sides of the tooth remains equal along its entire course. No wear is detectable. The attribution of this tooth remains debatable, given the characters noted above and also the contour of the crown view. An alternative possibility is that it is an upper molar of *Amphilestes* cf. *A. broderipii*.

## DISCUSSION

**Comparisons, lower molars.** — Outside of the “amphilestids” from the Middle Jurassic of the UK, the closest form to *P. simpsoni* may be the Morrison (Late Jurassic) genus *Comodon* (= *Phascolodon* Simpson, 1925b), based on lower molars. The latter agrees with *P. simpsoni* in size, proportions and shape of cusps, situation of e and f, wear (groove between a and c), and smooth enamel. *Comodon* was said to “closely [resem-

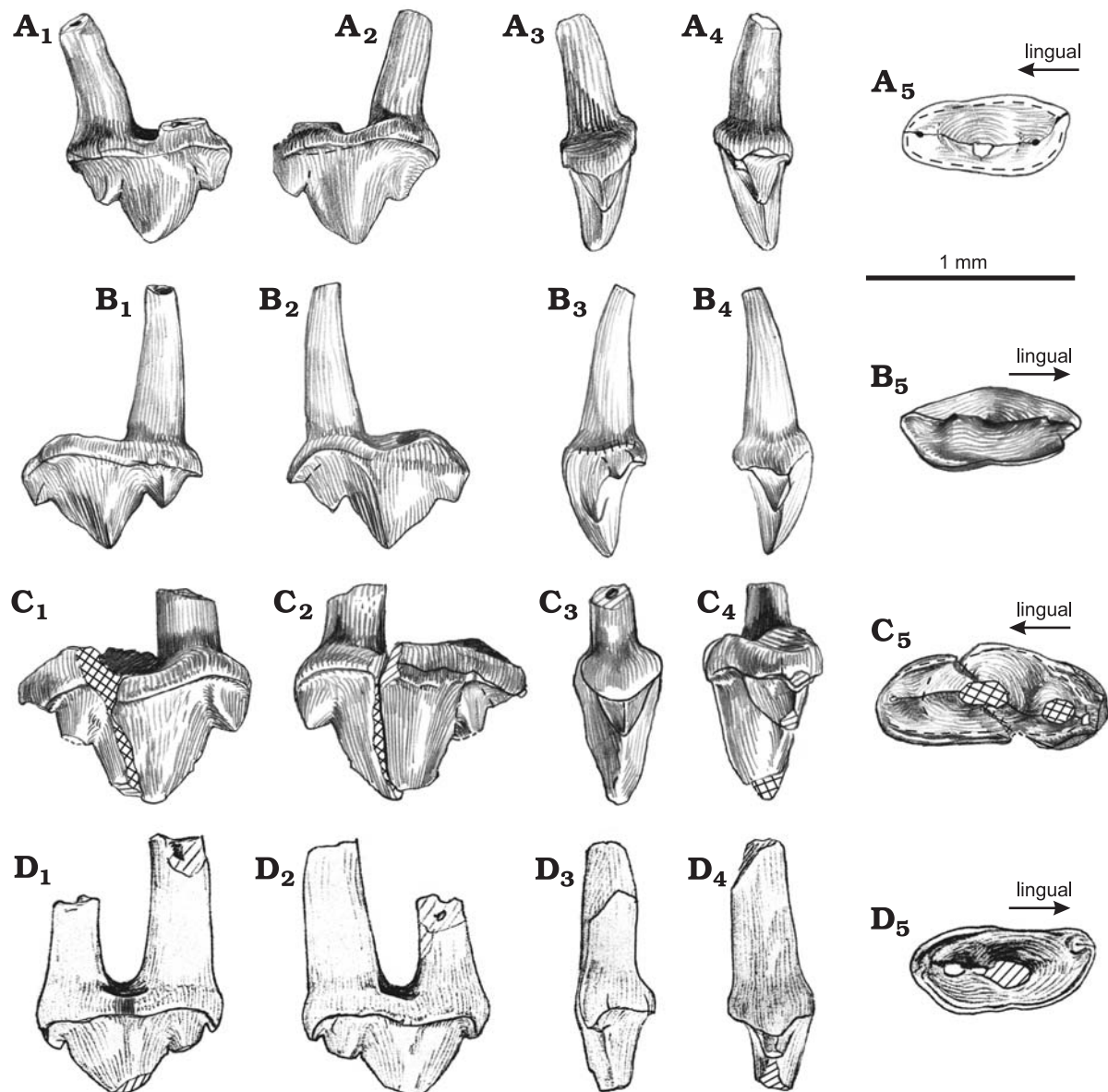


Fig. 5. “Amphilestidae” and ?“Amphilestidae” from the Middle Jurassic of Great Britain, upper molars. All specimens from the Old Cement Works Quarry, Kirtlington, Oxfordshire, UK; late Bathonian. **A–C.** *Phascolotherium simpsoni* sp. n. **A.** M46762, right upper molar in labial (A<sub>1</sub>), lingual (A<sub>2</sub>), mesial (A<sub>3</sub>), distal (A<sub>4</sub>), and occlusal (A<sub>5</sub>) views. **B.** M46538, left upper molar in labial (B<sub>1</sub>), lingual (B<sub>2</sub>), mesial (B<sub>3</sub>), distal (B<sub>4</sub>), and occlusal (B<sub>5</sub>) views. **C.** M46536, right upper molar in labial (C<sub>1</sub>), lingual (C<sub>2</sub>), mesial (C<sub>3</sub>), distal (C<sub>4</sub>), and occlusal (C<sub>5</sub>) views. **D.** Gen. et sp. indet., M46441, left upper molar in labial (D<sub>1</sub>), lingual (D<sub>2</sub>), mesial (D<sub>3</sub>), distal (D<sub>4</sub>), and occlusal (D<sub>5</sub>) views. Arrows point anteriorly. Cross hatching refers to a broken surface and parallel hatching indicates wear.

ble] *Phascolotherium*” (Simpson 1925b, p. 335), but it “can be readily distinguished by the smooth enamel, by the character of the cingulum” [weaker in *Comodon*?], “and the reduction of the last molar” (Simpson 1929, p. 31); a slight curvature of the crown should be added (Sigogneau-Russell 2003a, p. 55, pl. 1, figs 6–8). However, the smooth enamel of the Kirtlington specimens reduces the gap between the two genera.

A lower molar from the Early Cretaceous of West Siberia (PM TGU 16/6 404 — not 401) was attributed by Averianov *et al.* (2005, p. 5, fig. 2G–I) to “Amphilestidae indet.” It more closely resembles *Amphilestes* in the shape of the lateral cusps and the narrowness of the primary cusps; but it has only a slight anterior indentation and *f* is very weak. The roots are more widely separated than on the Bathonian teeth, suggesting the possibility that a replacement tooth may have developed in the space between them.

The partial lower tooth attributed by the same authors to *Kemchugia* (Averianov *et al.* 2005, p. 5, fig. 3; PM TGU 16/6-410) seems to have a low, divergent *d* cusp and a mesiodistal alignment of *a* and *c* as in



*Phascolotherium*, but the apparently intact anterior border seems to preclude the presence of a b cusp, or at least indicates that it was much smaller than c. This tooth could be a first molar, on which the b cusp is reduced as in *Gobiconodon borissiaki* Trofimov, 1978 (see Kielan-Jaworowska and Dashzeveg 1998) but not as on m1 of the Stonesfield specimens of *Amphilestes* or *Phascolotherium*.

Though described as family indet., the Early Cretaceous genus *Hakusanodon* Rougier *et al.*, 2007, based on a lower jaw, is shown within the “amphilestids” in the cladogram of these authors. It differs from *Amphilestes* and resembles *Phascolotherium* in the loss of anterior premolars. However, it differs from both Bathonian genera in that cusp a is slightly recumbent, b is taller than c, f and the mesial indentation are absent, and the lingual cingulum is represented only by mesial and distal segments. In addition, on OUM J.20079 of *Amphilestes*, b appears slightly wider — if not slightly higher — than c, and it is higher on M35000, attributed above to *Amphilestes* cf. *A. broderipii*. Furthermore, the variability of this character along the toothrow should be considered. None of the “family indet.” specimens from the late Early Jurassic of Mexico (Montellano *et al.* 2008) resembles the Kirtlington specimens. Finally, *Juchilestes* lower molars differ from the teeth described above by the straighter disposition of the cusps, the absence of a lingual concavity, of a labial “bulging base of cusp a” (Rougier *et al.* 2007, p. 80), and the absence of cusp f.

The cladistic analysis of Gao *et al.* (2010) confirms that “Amphilestidae” are not monophyletic: the authors distinguish two groups, the first containing *Amphilestes* and *Phascolotherium*, representing stem taxa to *Tinodon* and the Trechnotheria; the second, a clade containing *Hakusanodon*, *Juchilestes*, *Comodon*, *Amphidon*, and *Aploconodon*, which is closer to gobi-conodontids.

This study, which reveals confusing combinations of similarities and differences in molar structure, underscores the fragility of current phylogenetic relations among taxa based on isolated teeth (for instance, a phylogenetically important area like the angular region of the lower jaw of *Amphilestes* is not preserved).

**Occlusion** (Fig. 6). — The traditional view of alternate occlusion among “amphilestids” rested originally on the observation by Mills (1971, p. 53) that “the dental occlusion of *Phascolotherium* is essentially of the *Kuehneotherium* type”. In fact, a slight triangulation of a with b and c had been claimed for *Amphilestes* (Osborn 1888; Mills 1971; Crompton 1974); however, careful examination of OUM J.20079 following recent preparation (Sigogneau-Russell 2003a) showed that the tips of the cusps are in a straight line, though the base of cusp a projects labially because of its larger size; this results in the convexity of the labial margin of the lower tooth. Also, because a is much higher than b or c, it appears out of line if the tooth is not seen exactly from above. Nevertheless, two of our specimens belonging to *Amphilestes* cf. *A. broderipii* (M35000, M46744) are very shallowly concave on the lingual outline, thus suggesting a slight triangulation.

The identification of M46440 and others as upper molars of *Phascolotherium simpsoni* supports this alternate type of occlusion, in which the A cusp of the upper tooth would naturally bite into the embayment between two lower convexities. The ridge on the lingual side of A corresponds to the embrasure between two lower teeth, separating the occlusal domains of c

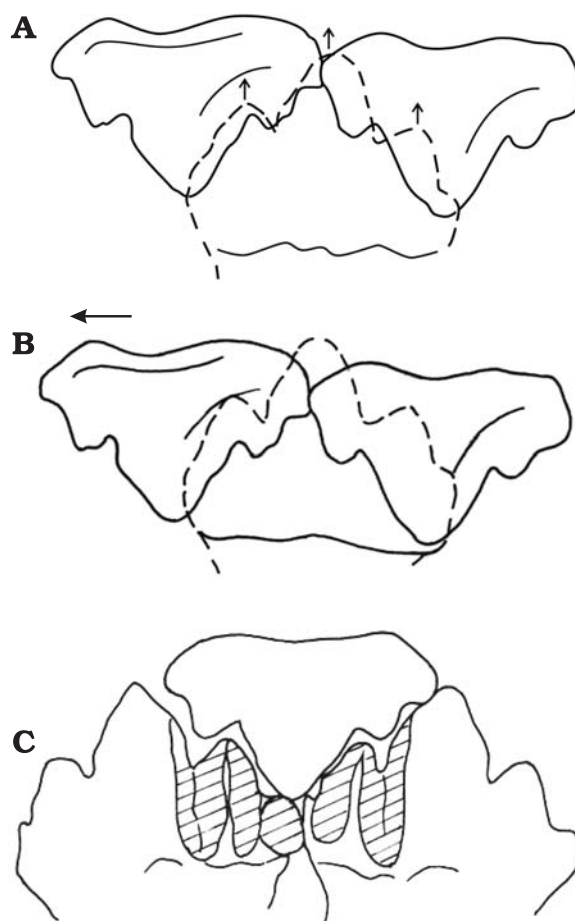


Fig. 6. *Phascolotherium simpsoni* sp. n. from late Bathonian. Proposed occlusal relationships between upper (M46440 Old Cement Works Quarry, Kirtlington, Oxfordshire, UK) and lower (M46115, Watton Cliff, Dorset, UK) molars. A, B. Successive stages in upward movement of the lower tooth (dotted line). C. The facets (parallel hatching) produced by an upper tooth. Arrow points anteriorly.

mesially and b distally. Superposition of drawings shows that the cusps of M46440 are in correct position to cause wear such as that seen on M46503. Wear on lower molars takes the form of steeply inclined strips on the edges of the cusps and in the grooves between their bases. Fig. 6A<sub>3</sub> shows the maximum potential position of the facets; individual differences may be ascribed to degree of wear and small variations in tooth position. The facets were presumably produced by the tips of upper cusps, when the lower teeth travelled upward and lingually as the jaws closed.

**Upper molars.** — Until recently, no “amphilestid” upper molar had been recognized with certainty: the Indian genus *Paikasigudodon* Prasad *et* Manhas, 2002, defined on an upper molar, has recently been referred to the family (Kielan-Jaworowska *et al.* 2004, p. 240) but these authors recognize this placement as “highly uncertain”: the asymmetrical outline of the tooth, its minute cingular denticulations, the proportions of the cusps and the absence of D, the presence of accessory anterior and posterior cuspsules, the quasi absence of a lingual cingulum (assuming that the specimen is an upper molar, an interpretation that is itself questionable) justify such doubts.

Averianov *et al.* (2005, p. 3) reidentified as a new “amphilestid” *Kemchugia magna* an upper molar (PM-TGU 16/6-401; Averianov *et al.* 2005, p. 5, fig. 2A–C) from the Early Cretaceous of Siberia, previously published in 2003 by Leshchinskiy *et al.* (2003, p. 351, fig. 1a–c) as Morganucodontidae indet. (PM-TGU 16/6-301). The authors distinguished this tooth from those of Morganucodontidae by “a more vertical and higher central cusp A and less height differential between cusps B and C” (Averianov *et al.* 2005, p. 4) with cingular cusp E less lingually situated; and from the Gobiconodontidae by the absence of an ectoflexus. Cusp E has possibly been misidentified (the real cusp E is visible lingually (Leshchinskiy *et al.* 2003, p. 351, fig. 1c). Moreover, the same relative size of A can be observed on M1–M2 of *Megazostrodon* or the eutriconodontan *Jeholodens* Ji *et al.*, 1999. In fact, identification of *Kemchugia* as an “amphilestid” rested partly on a referred, incomplete lower molar, PM-TGU 16/6-410, which shows (Averianov *et al.* 2005, p. 6, fig. 3) facets “1” (formed by occlusion of cusps C–a) and “2” (formed by occlusion of cusps c–A) as defined by Crompton (1971) on triangular-cusped teeth (and as such not applicable here), “consistent with the embrasure dental occlusion characteristic for amphilestids” (Averianov *et al.* 2005, pp. 4, 5, fig. 3). These facets could as well be identified as those figured by Mills (1971, p. 40, fig. 1) for the early stages of wear in *Morganucodon*. Moreover, the seemingly intact mesial border indicates that the b cusp was very small or absent, so that the tooth would not occlude with the upper molar. Finally, the anterior cuspsules e and f, characteristic of “amphilestids”, are unknown for this incomplete tooth, which could be a first molar in which the b cusp is reduced, as in *Gobiconodon borissiakii* (see Kielan-Jaworowska and Dashzeveg 1998). In any case, compared to the upper molars referred above to *Phascolotherium*, that of *Kemchugia* is wider distally, with higher cusps, a mesiodistally narrower A, upright B and C which are joined to A at a higher level, and strongly crenulated cingula. Finally, the lingual ridge of A is absent.

The upper molars of *Juchilestes* differ from those of *Phascolotherium simpsoni* in the same ways as do the lowers: by the straighter disposition of the cusps, the lack of a labial concavity in occlusal view, and the lesser lingual bulging of the cingulum. This supports the phylogenetic hypothesis of Gao *et al.* (2010), who recognized the clade including *Amphilestes* and *Phascolotherium* as distinct from another comprising *Juchilestes* and its relatives.

### ?Family “Amphilestidae” Osborn, 1888

Gen. et sp. indet.

(Fig. 5D)

One additional upper molar from the Old Cement Works Quarry, Kirtlington (Oxfordshire, UK; late Bathonian), M46441 (left upper molar; L = 0.92 mm, W = 0.45 mm; Fig. 5D), is of uncertain affinities; we describe it under this heading for lack of a definitive identification. Like the upper molars of *Phascolotherium simpsoni*, this tooth also bears a cingulum labially and lingually. It is similar in size to M46538, referred to *P. simpsoni*, but it is more asymmetrical, the small B cusp arising from the cingulum; A is then placed more anteriorly, as on premolars of morganucodontans. The cingulum is complete and lacks denticulations. E and F are absent; D is in line with A and C; the lingual ridge of A is not developed. The tips of the cusps are abraded and A may have been slightly reduced by wear. The roots are vertical and stouter than on M46538, the distal one being the largest. This tooth could be interpreted as an upper premolar (though lower premolars of *Amphilestes* and *Phascolotherium* are strictly symmetrical).

### Family **Gobiconodontidae** Chow *et* Rich, 1984

Gobiconodontidae are distinguished from “Amphilestidae” by their more robust teeth and cranial elements, specialized anterior dentition, curving upper tooth row, and replacement of at least some molariforms (e.g., Jenkins and Schaff 1988; Kielan-Jaworowska and Dashzeveg 1998; Meng *et al.* 2005; Yuan *et al.* 2009). Most gobiconodontid occurrences are of Early Cretaceous age, possible exceptions being *Klamelia* Chow *et* Rich, 1984, from the Late Jurassic of China (excluded from the family by Kielan-Jaworowska *et al.* 2004); and *Huasteconodon* Montellano *et al.*, 2008, represented by a remarkably small (upper molar length, 0.55 mm) fossil from the late Early Jurassic of Mexico. Kielan-Jaworowska *et al.* (2004) included in the Gobiconodontidae the type genus *Gobiconodon* and the Chinese genera *Hangjinia* Godefroit *et* Guo, 1999, and *Repenomamus* Li *et al.*, 2000. *Hangjinia* is defined on a lower jaw with partial teeth; *Repenomamus* has been more recently returned to its own family, Repenomamidae Li *et al.*, 2000, by Hu *et al.* (2005). Finally, *Meemannodon* Meng *et al.*, 2005 has been described from the Early Cretaceous of China, also based on a lower jaw.

Specimens from Kirtlington and Swyre form the basis for recognition of *Gobiconodon bathoniensis* sp. n., described below. Additional specimens not surely referable to the species, genus, or family are described under separate headings following treatment of *G. bathoniensis* sp. n.; a brief summary is presented at the end of the section on Gobiconodontidae.

#### Genus **Gobiconodon** Trofimov, 1978

Type species: *Gobiconodon borissiaki* Trofimov, 1978

##### *Gobiconodon bathoniensis* sp. n.

(Figs 7A–C, 8A, B)

LSID urn:lsid:zoobank.org:act:222BC89E-E0B0-4690-968D-7E3287C5740D

Holotype: M46527, upper right molar (Figs 7A, 8A).

Etymology: From Latin *Bathonium*, in reference to the geological age (based on outcrop at Bath, UK).

Type horizon and locality: Old Cement Works Quarry, Kirtlington, Oxfordshire, UK; late Bathonian.

**Referred material.** — M46083 and M46189, both upper left molars from Kirtlington; M46031, ?last upper right molar, from Swyre, Dorset, UK; late Bathonian.

**Diagnosis.** — Small-sized upper molars, whose main cusps show an “incipient triangular pattern, cusp A being placed more lingually than cusps B and C” (Kielan-Jaworowska and Dashzeveg 1998, p. 417), generally diagnostic of the genus *Gobiconodon*, and differing from the pattern seen in *G. luoiianus* Yuan *et al.*, 2009. Differs from *G. hoburensis* (Trofimov, 1978), *G. borissiaki* Trofimov, 1978, *G. ostromi* Jenkins *et* Schaff, 1988, *G. hopsoni* Rougier *et al.*, 2001, and *G. zofiae* Li *et al.*, 2003, in that teeth in corresponding serial positions are narrower, with the occlusal contour triangular rather than rectangular, and the ectoflexus shallower (though this feature varies from M1 to M5 in the above species). Differs from *G. zofiae*, where cusps of molars are aligned antero-posteriorly, cusp D is said to be “degenerated” (Li *et al.* 2003, p. 1129), and E larger than B. Closest in size to *G. hoburensis* and *G. palaios* Sigogneau-Russell, 2003a. Differs from *G. hoburensis* with cusp A relatively higher and shorter, and lateral cusps better detached from A; last molar more reduced. Differs from *G. palaios* in shallower ectoflexus and D cusp more pointed in crown view. Differs from the other Jurassic form, *Huasteconodon* Montellano *et al.*, 2008, in its larger size, larger cusp C, occlusal shape, lesser ectoflexus, and roots narrower transversely, not visible in occlusal view.

**Description.** — The holotype, M46527 (right upper molar; L = 1.30 mm, W = 0.57 mm; occlusal angle = 160°; Figs 7A, 8A) shows a curvature of the crown in occlusal view, with the lingual edge evenly convex, the labial edge barely concave, the mesial end truncated, and the distal end pointed. Cusp A is narrow, sharp, centrally placed, and high relative to B and C; in side view, it has the shape of an equilateral triangle, as in the Mongolian species of *Gobiconodon*, *G. borissiaki*, and *G. hoburensis*. B is smaller and slightly more labially placed than C. The F cuspule, mesiolabial to B, is as large as the D cusp; the latter is fully labial, so that the C–D crest is oblique; the B–F region is even more bent labially. There is an encircling cingulum, wider on the labial side, and faintly crenulated in places. The mesial root is flat mesially, its greater diameter pointing obliquely toward the mesiolabial end of the crown. The distal root, which is broken, was flattened labiolingually and also obliquely disposed under the crown, so that the bases of the roots are closer lingually than

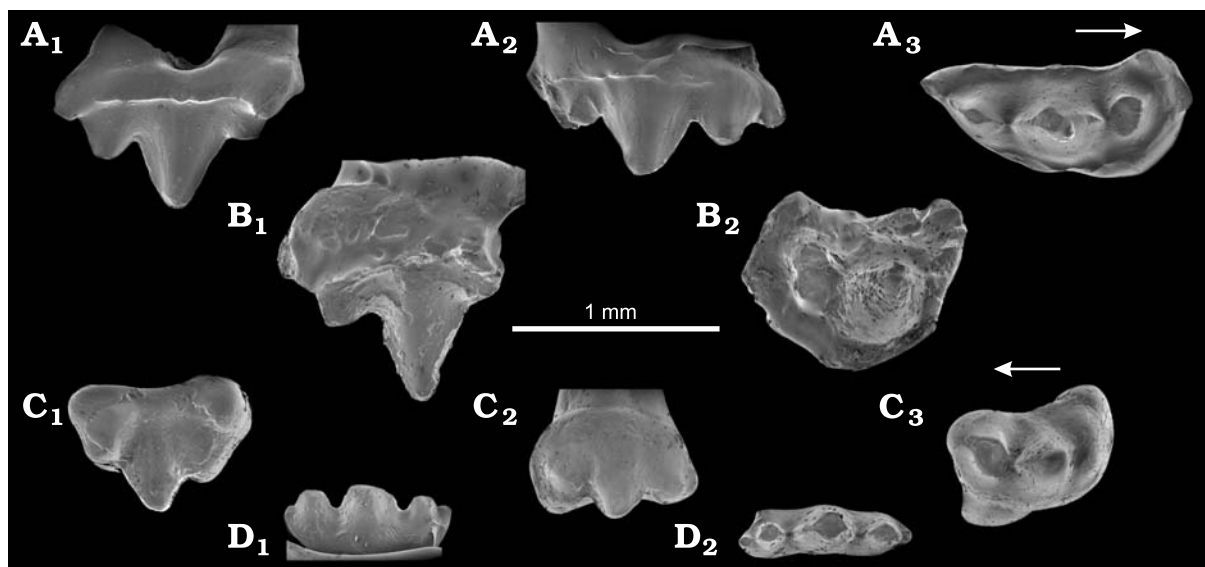


Fig. 7. Gobiconodontidae and Triconodontidae from the Middle Jurassic of Great Britain. A–C. *Gobiconodon bathoniensis* sp. n. A. Holotype M46527, Old Cement Works Quarry, Kirtlington, Oxfordshire, UK; late Bathonian, right upper molar in labial (A<sub>1</sub>), lingual (A<sub>2</sub>), and occlusal (A<sub>3</sub>) views. B. M46083, Old Cement Works Quarry, Kirtlington, Oxfordshire, UK; late Bathonian, left upper molar in labial (B<sub>1</sub>) and occlusal (B<sub>2</sub>) views. C. M46031, Swyre, Dorset, UK; late Bathonian, right upper molar in labial (C<sub>1</sub>), lingual (C<sub>2</sub>), and occlusal (C<sub>3</sub>) views. D. *Eotriconodon sophron* gen. et sp. n., holotype M46736, Old Cement Works Quarry, Kirtlington, Oxfordshire, UK; late Bathonian, right lower molar in lingual (D<sub>1</sub>) and occlusal (D<sub>2</sub>) views. SEM photos; roots cropped as needed. Arrows points anteriorly.

labially. Wear facets are visible on the mesial faces of F and B (by contact with D of the succeeding tooth). Possible wear on the lingual cingulum would presumably be due to occlusion with lower molar cusp a or c, and wear on the cingulum distal to C would be due to occlusion with lower molar cusp a.

M46083 (left upper molar; L = 1.40 mm, W = 0.85 mm; angle = 165°; Fig. 7B) has cusps B and C abraded, and the distal part of the lingual edge broken off. It is similar to M46527 but the crown is proportionately broader and more curved in occlusal view than the holotype, with C displaced as labially as B, and F even more prominent labially. The labial cingular ledge is even wider; it is also more grossly denticulate with a higher cusplule distally. The lingual cingulum is again faintly undulating. The ectoflexus is deeper than on the holotype. The mesial root is stouter; the distal one has been broken off, but their bases are again closer lingually than labially. The enamel is only partially preserved, but it does seem that wear had heavily affected the mesial faces of F, B and A, and possibly the lingual cingulum; the tip of A remains intact. The greater curvature and more pronounced ectoflexus indicate that this tooth occupied a more distal position than the holotype.

M46189 (left upper molar; L = 1.05 mm, W = 0.52 mm; angle = 155°; Fig. 8B) is notably smaller than the two teeth described above; it is also proportionately narrower. The crown is badly eroded, and worn the same way as the holotype and M46083 (and M46563; see below, under Gobiconodontidae gen. et sp. indet.), with A remaining unworn, while B and C are heavily worn. The crown is again curved in occlusal view, with a truncated mesial end and a pointed D, the latter being more labial than C. There may have been two cingula but erosion has minimized the evidence. The mesial root has broken off; the distal root is flattened labio-lingually and the two root bases are again divergent. This tooth is interpreted as possibly a worn molar of a first generation, or a more anterior member of the series containing M46527 and M46083.

M46031 (right upper molar; L = 0.92 mm, W = 0.52 mm; angle = 137°; Fig. 7C) is puzzling: it is even shorter mesiodistally than the preceding tooth but relatively wider labiolingually. B and C are displaced labially, B more than C. F protrudes labially. B and C are equal in height and much lower than A, which is conical. D is rudimentary on the distal crest of C. All three main cusps are set close to each other. There is a trace of E mesial to B, in the shape of a wear facet. The lingual cingulum is not discernible but the enamel is missing at that level; labially, the cingulum was present at least distally and possibly also mesially. The crown was supported by a single root, wider mesially and furrowed with a faint sulcus lingually, as if formed by the union of two roots; its labial face has been broken away, exposing the pulp cavity. Again, B and C have been abraded, the tip of A remaining intact. Lingually, wear has affected the mesial crest of A, the

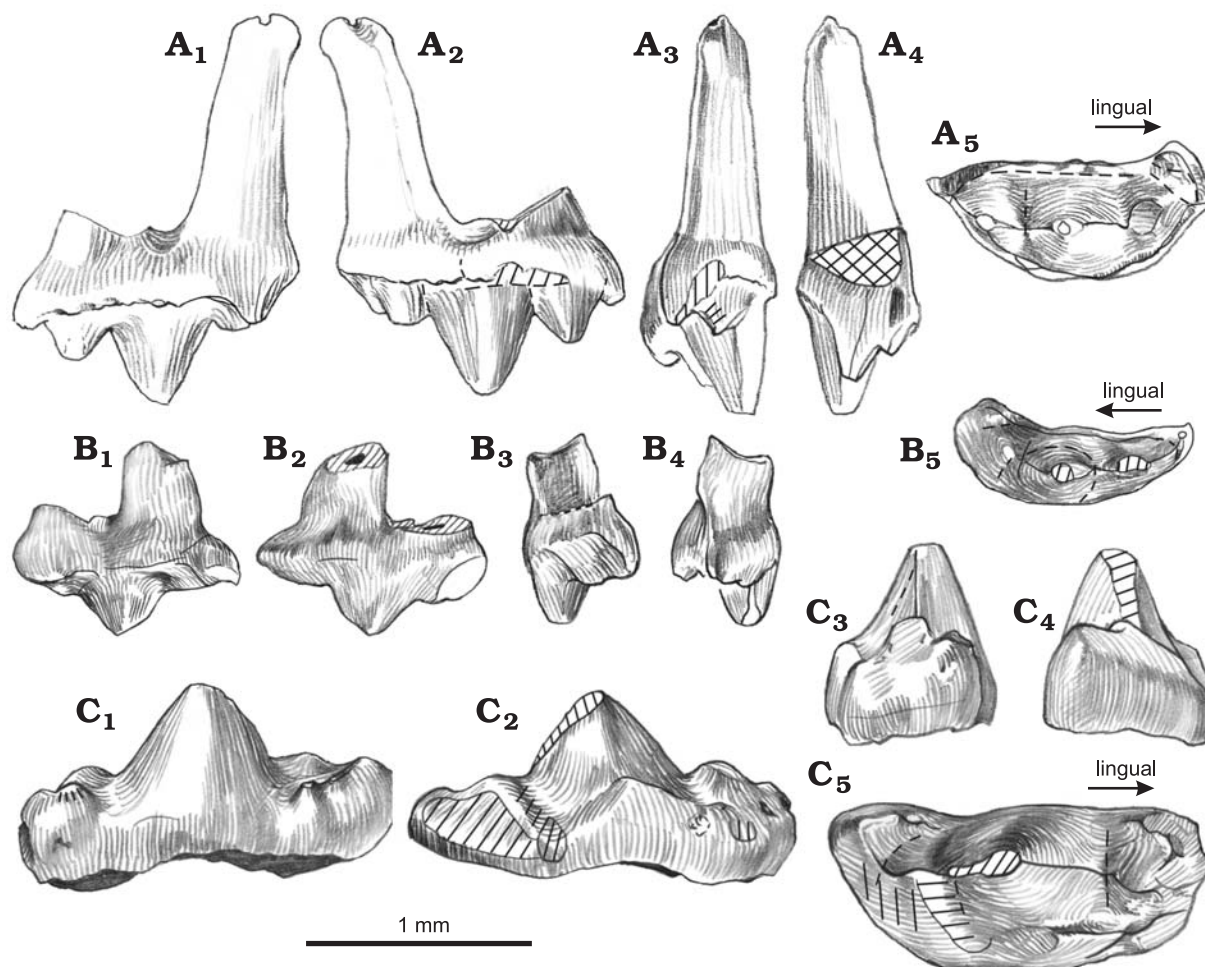


Fig. 8. Gobiconodontidae from the Middle Jurassic of Great Britain. All specimens from the Old Cement Works Quarry, Kirtlington, Oxfordshire, UK; late Bathonian. **A, B.** *Gobiconodon bathoniensis* sp. n. **A.** Holotype M46527, right upper molar in labial (A<sub>1</sub>), lingual (A<sub>2</sub>), mesial (A<sub>3</sub>), distal (A<sub>4</sub>), and occlusal (A<sub>5</sub>) views. **B.** M46189, left upper molar in labial (B<sub>1</sub>), lingual (B<sub>2</sub>), mesial (B<sub>3</sub>), distal (B<sub>4</sub>), and occlusal (B<sub>5</sub>) views. **C.** *Gobiconodon* sp. indet., M46563, right lower molar in labial (C<sub>1</sub>), lingual (C<sub>2</sub>), mesial (C<sub>3</sub>), distal (C<sub>4</sub>), and occlusal (C<sub>5</sub>) views. Arrows point anteriorly. Cross hatching refers to a broken surface and parallel hatching indicates wear.

mesial face of B as far as F, and the distal crest of C leading to a small D cusp. By the relative development of the two lobes and the general proportions recalling the M5 of *Gobiconodon hoburensis*, this tooth can be interpreted as a last upper molar, even though the latter is two-rooted in *Gobiconodon borissiaki* (Kielan-Jaworowska and Dashzeveg, 1998, fig. 1) and *G. zofiae* (Li *et al.* 2003).

**Discussion.** — These gobiconodontid upper molars are small, comparable in size to those of *G. palaios*, from the ?Berriasian of Morocco. In *G. zofiae* there are five lower molars but only four upper molars; in *G. luoiianus* both upper and lower dentitions include five molars. M46031, if a last upper molar, could therefore be M4 or 5 (see summary and discussion in Yuan *et al.* 2009).

In *Gobiconodon zofiae*, M1 is narrower than M2–M3, and M3 is the broadest; the same is true in *G. borissiaki* and *G. hoburensis*. We have attempted to reconstruct the dentition in order of differences in width/length (Fig. 9A): M46189, M46527, and M46083 progressively increase in size and relative width, and might be M1–M3. Comparing this hypothetical series with *G. hoburensis* and *G. borissiaki*, we note that the teeth of *G. bathoniensis* are narrower, and M2 and M4 are smaller relative to M3, M2 having a shallower ectoflexus. The F cuspule is well defined, mesiolabial to B and projecting labially beyond the border, and the E cuspule is a widening of the cingulum mesial to B, at the mesial extremity of the tooth; the effect is that this mesial end is obliquely truncate. In *G. borissiaki* and *G. hoburensis*, E is represented by a ridge on B, running toward the mesial apex of the tooth, while F is weakly developed (Kielan-Jaworowska and Dashzeveg 1998, figs 1–4). Moreover, in *G. bathoniensis*, the lingual margin is convex, giving the teeth a triangular

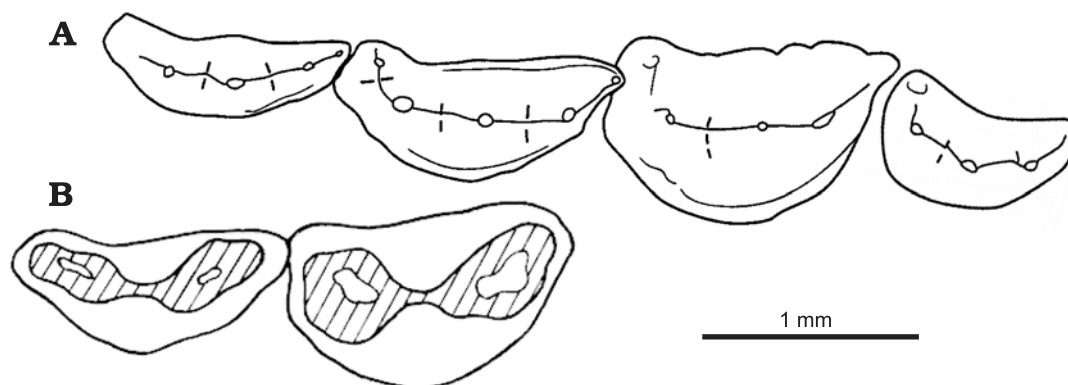


Fig. 9. *Gobiconodon bathoniensis* sp. nov. from late Bathonian. **A.** Reconstructed left upper molar series; from left to right: M46189, M46527, and M46083 (Old Cement Works Quarry, Kirtlington, Oxfordshire, UK), M46031 (Swyre, Dorset, UK). **B.** Root pattern of M46527 and M46083.

shape, as in *G. palaios*; whereas in other species, the lingual margin is nearly straight, with a slight median concavity, and the mesial and distal margins are more transverse, so that the teeth are more quadrangular. The last molar of *G. borissiakii* and *G. hoburensis* shows various degrees of reduction of its distal part (least in *G. ostromi*). *G. palaios* is known by isolated molars that vary in relative width and probably represent more than one serial position (?M2, 3). It resembles *G. bathoniensis* not only in size, but also in having upper molars with narrow crowns that are triangular rather than quadrate, with the labiodistal end pointed. We also note that abrasion in *G. palaios* MNHN SA 119 (Sigogneau-Russell 2003a, p. 31, fig. 2d–e) is of the same type as on M46189 and M46083, with B and C cut off but A nearly intact; such a state of wear has not been illustrated in the other Cretaceous species. Finally, asymmetry of roots (Fig. 9B) has not been mentioned in the Cretaceous species except *G. palaios*.

In fact, the differences between *G. bathoniensis* and the Cretaceous species (except *G. palaios*) might provide grounds for generic separation. In any case, *G. bathoniensis*, with teeth narrow and triangular, ectoflexus faint, and labiodistal corner pointed, probably represents a primitive condition in *Gobiconodon*, only slightly modified in *G. palaios*; it is to be anticipated that other anatomical differences, in particular in the anterior dentition, would help to assess the specific distinction.

The upper gobiconodont tooth from the late Barremian of Spain, which is slightly larger than M46083, is described as possessing “cusps nearly subequal in height and reduced lingual cingulum [...] occlusal outline more rounded than in *G. borissiakii*, *G. hoburensis* and *G. ostromi*” (Cuenca Bescos and Canudo 1999, p. 41). The lingual side of the B cusp is broken, but the mesial end is pointed, and there is a small ?F, followed by a shallow ectoflexus. The most obvious difference from *G. bathoniensis* is that the tooth is broader distally and rounded, rather than pointed, and the lingual profile is less convex; B and C are said to be larger relative to A than in the previously known species. However, given the poor state of preservation of this tooth and the variation along the dental series already mentioned for other species of the genus, it is not possible to make a more detailed comparison.

*Huasteconodon wiblei* is known by a fragment of maxilla containing two molars and the alveoli of a third, from the late Early Jurassic of Mexico (Montellano *et al.* 2008). The teeth are about half the size of those of *Gobiconodon bathoniensis*, but they show some resemblances. They are narrow, in contrast to most Cretaceous species; the A cusp is more lingual than B and C; and D projects at the distolabial corner of the tooth, at the end of an oblique A–C–D ridge. There is a difference in the ectoflexus, which has the form of a deep indentation of the margin labial to cusp A.

Gen. et sp. indet.

(Figs 8C, 10)

The following three teeth (all from the Old Cement Works Quarry, Kirtlington, Oxfordshire, UK; late Bathonian) differ from the upper molars of *Gobiconodon bathoniensis* in that the three main cusps are in line, the mesial area being oriented directly forward instead of being oblique. The outline is therefore oval rather than triangular. It is possible that they are gobiconodontid lower molars, and they are provisionally described as such. Alternatively, if uppers, they could represent a new genus of Gobiconodontidae.

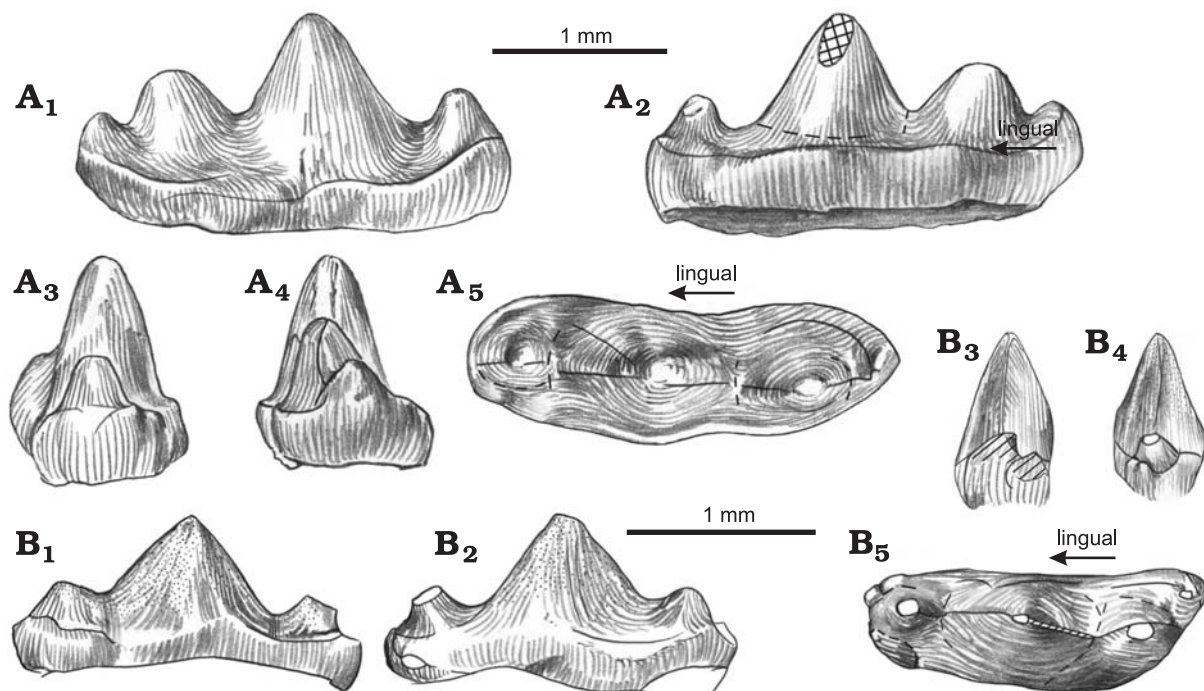


Fig. 10. Gobiconodontidae gen. et sp. indet., specimens provisionally identified as lower molars, from the Old Cement Works Quarry, Kirtlington, Oxfordshire, UK; late Bathonian. **A.** M46815, left lower molar in labial (A<sub>1</sub>), lingual (A<sub>2</sub>), mesial (A<sub>3</sub>), distal (A<sub>4</sub>), and occlusal (A<sub>5</sub>) views. **B.** M46300, left lower molar in labial (B<sub>1</sub>), lingual (B<sub>2</sub>), mesial (B<sub>3</sub>), distal (B<sub>4</sub>), and occlusal (B<sub>5</sub>) views. Arrows point anteriorly. Cross hatching refers to a broken surface and parallel hatching indicates wear.

**Description.** — M46563 (?right lower molar; L = 1.72 mm, W = 0.75 mm; Fig. 8C) is similarly constructed to M46527, but reversed labio-lingually. It is less arched and relatively longer, the labial border is broadly convex, the distal end is pointed with d more lingual than c, the mesial end transverse; the lingual face is straighter than is the labial face of M 46527 and b is in line with a and c, so that the b–e–f-complex is directly anterior to a. Cusp a remains high but is relatively wider than in the upper teeth and less acute. A high labial cingular cusp protrudes at the mesial base of a, which was not individualized on the holotype upper tooth of *Gobiconodon bathoniensis* (M 46527). Most notable is the absence of a lingual cingulum; but the e and f cusps are well developed, and a tiny lingual cuspsule is mesial to d. The pulp cavity is open. Strong wear affected the distal crest of cusp a, cusp b and even more cusp c, a groove having been cut between the latter and a, and extending to the labial cingulum, which is worn.

These features could have been interpreted as M46563 being a milk upper molariform, or rather a first generation upper molar, since gobiconodontid molars are known to be replaced (Jenkins and Schaff 1988; Kielan-Jaworowska and Dashzeveg 1998), but its size speaks against this interpretation. On the other hand, considered as a right lower tooth, M46563 resembles the lower molars of *Gobiconodon borissiakii* (Kielan-Jaworowska and Dashzeveg 1998, p. 419, fig. 1D) in the rectilinear arrangement of b, a and c, and the general outline (labially convex, lingually straight, distal end pointed); however, it differs in the small size of b and c relative to a, in the absence of an interlocking mesial groove, and in the presence of a labial marginal cusp. In any case, this specimen is too large to occlude with the upper molars of *G. bathoniensis*.

M46815 (left lower molar; L = 2.00 mm, W = 0.80 mm; Fig. 10A) is longer and relatively narrower than M46563, with low cusps. It appears to be an unerupted crown on which the enamel is incompletely developed and pitted. Cusps b and especially c are larger in comparison with M46563; b and d are slightly displaced lingually. The mesial border is rounded. There is a complete encircling cingulum but no cingular cusps, except mesially where one can detect incipient e and f cusps. No root is present, and the pulp cavity is fully exposed. No wear is discernible. If this tooth belongs to the same taxon as M46563, it may be from a more distal position in the dentition; or, given the absence of wear, a newly erupted tooth; in any case it is again too large to belong to *G. bathoniensis*.

M46300 (left lower molar; L = 1.48 mm, W = 0.64 mm; Fig. 10B) closely resembles M46563, except that it is smaller and relatively narrower. Cusps b and c remain small; d is displaced lingually. A labial cingulum

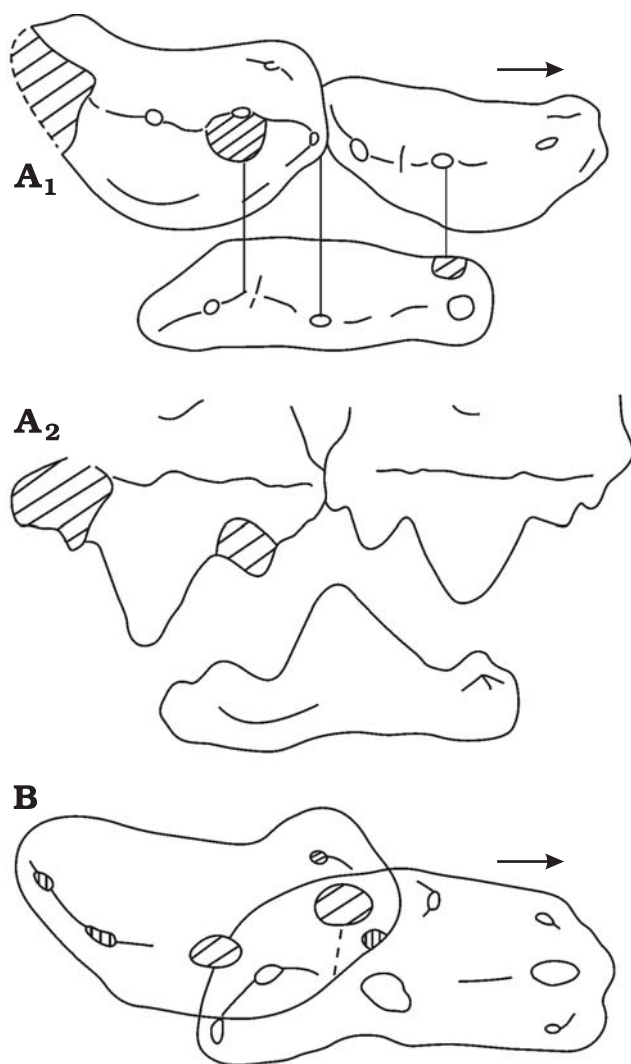


Fig. 11. *Gobiconodon bathoniensis* sp. n. from the Old Cement Works Quarry, Kirtlington, Oxfordshire, UK; late Bathonian. **A.** Postulated lower molar M46300 in relation to upper molar M46083 (reversed) and M46527, in occlusal ( $A_1$ ) and side ( $A_2$ ) views. **B.** Postulated occlusion (occlusal view) between lower molar M46563 and a hypothetical upper tooth based on M46083.

(1998), taking into account the greater height of the cusps in the latter. We therefore speculate that M49300 may be a lower molar of *G. bathoniensis*. M46563, because of its resemblance to M49300, would therefore also be a lower molar, but presumably of a larger species. Its wear facets indicate the same occlusal relationships, with the exception that the facet on the labial side of c is much more extensive, reaching the peculiar marginal cusp. It would seem that the corresponding upper tooth (not represented in the available sample) had a much larger B cusp (Fig. 11B).

### ?Family **Gobiconodontidae** Chow *et* Rich, 1984

Gen. et sp. indet.

(Fig. 12A, B)

**Description.** — Three teeth (all from the Old Cement Works Quarry, Kirtlington, Oxfordshire, UK; late Bathonian) are possibly gobiconodontid premolars. M46077 (left; L = 1.20 mm, W = 0.70 mm; Fig. 12A) is a relatively large tooth with an asymmetrical crown. In outline it is triangular, with lingual apex. The crown is dominated by a high, acute A cusp, recurved distally at the tip. This cusp bears, lingually, a strong vertical crest creating a concave distal half, while it is strongly convex labially. C is low relative

is faintly indicated distally but lacks the cingulum cusp; the lingual cingulum is clearly developed with an elevation at the level of the mesial half of a. The top of b has been abraded and there appears to be a small facet on f; otherwise no wear is distinguishable, and the enamel is definitely pitted. The roots had not developed, therefore it was probably incompletely erupted (hence the pitted enamel?); its size makes it more likely to occlude with the uppers of *G. bathoniensis*.

Enamel pitting is known only in the Stonesfield material of the “amphilestid” *Phascolotherium* and was included by Simpson (1928) in its generic diagnosis. However, M46815 and M46300, both with pitted enamel, show little resemblance to the *Phascolotherium* teeth described in this paper: they differ from them in their asymmetry, the wider separation of the mesial cusp from the main cusp, as well as in the lowness of the crown. On the other hand, there is greater resemblance to the upper teeth of *Gobiconodon*, as noted above, but with differences suggesting that they could be lower teeth of this genus in spite of the lowness of the main cusp and presence of the labial cingulum.

**Occlusion.** — As a gobiconodont lower molar, M46300 would fit between the upper molars of *G. bathoniensis* M46527 and M46183. Superposition of drawings indicates occlusal relations (Fig. 11A<sub>1</sub>): the tip of cusp a would fit into the interdental embrasure between C and D anteriorly and E posteriorly. Cusp c occludes with B, accounting for a facet on the lingual surface of that cusp on M 46563. The tip of the upper cusp A would pass between b and the more mesial d, meeting f at the end of the stroke. These relationships agree with those of *Gobiconodon borissiaki* and *G. hoburensis* described by Kielan-Jaworowska and Dashzeveg



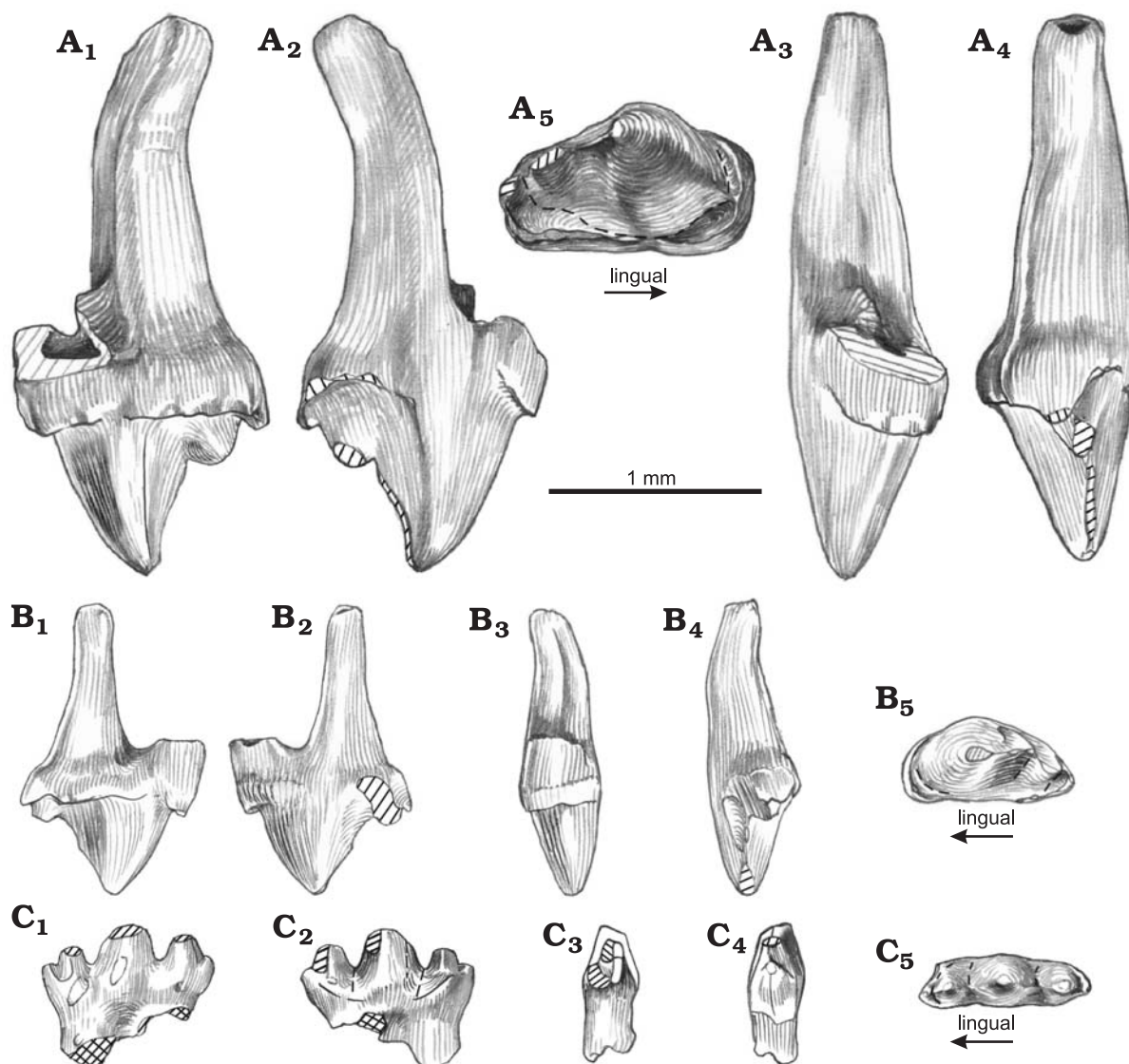


Fig. 12. Eutriconodonta and Triconodontidae from the Middle Jurassic of Great Britain. All specimens from the Old Cement Works Quarry, Kirtlington, Oxfordshire, UK; late Bathonian. **A, B.** ?Gobiconodontidae, gen. et sp. indet. **A.** M46077, left upper premolar in labial (A<sub>1</sub>), lingual (A<sub>2</sub>), mesial (A<sub>3</sub>), distal (A<sub>4</sub>), and occlusal (A<sub>5</sub>) views. **B.** M46597, right upper premolar in labial (B<sub>1</sub>), lingual (B<sub>2</sub>), mesial (B<sub>3</sub>), distal (B<sub>4</sub>), and occlusal (B<sub>5</sub>) views. **C.** *Eotriconodon sophron* gen. et sp. n., holotype M46736, right lower molar in lingual (C<sub>1</sub>), labial (C<sub>2</sub>), mesial (C<sub>3</sub>), distal (C<sub>4</sub>), and occlusal (C<sub>5</sub>) views. Arrows point anteriorly. Cross hatching refers to a broken surface and parallel hatching indicates wear.

to A; there is no B cusp. A complete labial crenulated cingulum is prolonged mesially and expands in two slight bumps (E and F?) but with hardly an indentation between them. Distally the cingulum culminates in a D cusp and wraps around to encircle C lingually. There were two roots, which had a similar arrangement as on the gobiconodontid molars: the distal root, the only one preserved, is long, massive, flattened mesio-distally but obliquely orientated, lingually and distally; it diverged from the mesial root toward the labial side of the tooth. The mesial root was clearly smaller. A flange joins the bases of the roots, which were close together. The posterior crest of A and the tip of C are abraded; incipient wear is observable on the cingulum linguo-distally.

Because of its triangular shape and asymmetrical pattern, this tooth can only be an upper premolar. The absence of B and its low length/width ratio distinguish it from gobiconodontid molars. It somewhat resembles a last premolar of *Megazostrodon* (in particular, it has the same labial ledge above C as figured by Crompton (1974, p. 406, fig. 4C; p. 407, fig. 5A; pl. 2A); it could qualify as an upper premolar of *Gobiconodon bathoniensis*, although the marked labial convexity of A and the asymmetry of the roots may also suggest a trechnotherian premolar.

M46823 (L = 0.82 mm, W = 0.45 mm) is quite similar to, but much smaller than M46077, and cusp A is not posteriorly recurved. E and F are separated by a slight indentation; the labial cingulum points under the middle of A. The distal root is relatively shorter, and apparently no stronger than the mesial root (missing). Wear has touched the same areas as on M 46077, but more extensively and it extends to D.

M46597 (right; L = 0.90 mm, W = 0.45 mm; Fig. 12B) is morphologically very close to M46823, with A less convex labially and C more distant from A; the labial cingulum is also weaker. The two roots were subequal, but the distal one is disposed obliquely as in M46077. The distal side of C is worn vertically.

If these teeth have been correctly identified, they would indicate that the premolar dentition in the Bathonian gobiconodontids was less specialised than in the Cretaceous species (no premolar is preserved for *Huasteconodon*). Not only are the roots unfused, but the crown retains the structure characteristic of morganucodontans.

#### DISCUSSION: GOBICONODONTIDAE

The family Gobiconodontidae has been shown to have had an extensive geographical distribution, being recorded from Mongolia (Trofimov 1978; Kielan-Jaworowska and Dashzeveg 1998; Godefroit and Guo 1999; Rougier *et al.* 2001), North America (Jenkins and Schaff 1988; Montellano *et al.* 2008), Siberia (Maschenko and Lopatin 1998), Spain (Cuenca Bescos and Canudo 1999), China (Wang *et al.* 2001; Yuan *et al.* 2009), North Africa (Sigogneau-Russell 2003a), and southern Britain (Sweetman 2006). Its presence in the Bathonian of Kirtlington confirms an early origin of the family, as already suggested by the Mexican species (*Huasteconodon wiblei*; late Early Jurassic), since all other occurrences date from the Cretaceous. This revives the suggestion already proposed (Sigogneau-Russell 2003a) that a megazostrodonid-gobiconodontid relationship may not be as far-fetched as it would seem: anterior molariform replacement, supposedly present in *Megazostrodon* (Gow 1986), exists in *Gobiconodon* (Jenkins and Schaff 1988; Wang *et al.* 2001; Luo *et al.* 2004). True, the specialisations of the anterior part of the lower jaw of the latter genus are not indicated in *Megazostrodon*, but we are ignorant of this anatomical region in the pre-Cretaceous Gobiconodontidae.

The presence of megazostrodonids as well as gobiconodontids on each side of the Tethys implies exchanges between Laurasia and Gondwana; such exchanges during the Jurassic have long been documented (Galton 1977; Rage 1988) and supported by palaeogeographic reconstructions (Barron *et al.* 1981; Smith *et al.* 1994). However, we are left to explain the absence of gobiconodontids in the Late Jurassic Morrison Formation of North America or the Early Cretaceous Purbeck Limestone Group, as well as in most Gondwanan Mesozoic localities.

#### Family **Triconodontidae** Marsh, 1887

##### Genus *Eotriconodon* gen. n.

LSID urn:lsid:zoobank.org:act:283D5F57-6AF4-49A3-B551-8EB4DBAF1795

Type species: *Eotriconodon sophron* sp. n.

Etymology: From Greek *eos*, dawn; in reference to the age of the new form with respect to most other triconodontids.

**Distribution.** — As for the type and only species.

**Diagnosis.** — As for the type and only species.

##### *Eotriconodon sophron* sp. n.

(Figs 7D, 12C)

LSID urn:lsid:zoobank.org:act:1FA19E1C-7C1C-40C9-84A4-BC0C03DF0F8C

Holotype: M46736, a right lower molar.

Etymology: From *sophron*, discrete.

Type horizon and locality: Old Cement Works Quarry, Kirtlington, Oxfordshire, UK; late Bathonian.

**Diagnosis.** — Similar to most triconodontids in having lower molars with three main cusps (a–c) mesiodistally aligned and subequal; distinct from all comparable taxa in its miniscule size, the absence of a lingual cingulum (derived), and the presence of cusps e and f, detached from b (primitive).

**Description.** — The only tooth in the Kirtlington collection attributable to the Triconodontidae is a tiny right lower molar, M46736 (L = 0.80 mm, W = 0.27 mm). It includes three main, subequal cusps, of

which the central (a) is just the largest; the mesial (b) is only slightly lower and shorter than c. These three cusps are mesiodistally aligned and widely separated. In crown view the labial margin is slightly convex owing to the larger size of a; the lingual margin is straight. The a cusp is constricted distally, especially on the labial side. Cusp b is preceded by two cusps, e and f; e is columnar and is directly mesial to b, while f is more distally situated, forming a ledge labially under b; e and f are separated by a vertical groove. Cusp d is very small and in line with a, b, and c. There is no distinct labial cingulum, unless it is represented by cuspule f under b, and a ledge between a and c; more noteworthy is the fact that the lingual cingulum is also absent. Two roots were present, connected proximally by a flange. Intercuspal valleys are rounded, as if opposing cusps passed between them. The tips of the cusps have been abraded. An extended contact facet is clearly detectable mesially between e and f. Wear facets are also clearly indicated on the distal face of a and c, and less clearly on the mesial side of a and b: these facets determine which is the labial side, in spite of the latter having a basal ledge, while the lingual side lacks a cingulum (a lingual cingulum is almost universally present among other Triconodontidae and is found among other basal mammaliaforms and mammals). Some wrinkling of the enamel is visible at the labial crown base between a and f.

**Discussion.** — Crown morphology, especially the low cusp a and the relative proportions and disposition of the three main cusps, identifies M46736 as belonging to a triconodontid. A distal constriction of cusp a is observed in several triconodontids, especially *Priacodon* Marsh, 1887, which retains a degree of cusp inequality (Simpson 1929). Also, the valleys separating these cusps are rounded at the bottom to allow for the passage of upper cusps through them, as in other triconodontids. The fact that e and f are distinct cusps anterior to b could be considered as a primitive condition relative to that of Early Cretaceous triconodontids, where these cusps are stylised and more or less fused distally to the body of the crown (Sigogneau-Russell 2003a); but the columnar shape of e also favours triconodontid affinity. However, M46736 is unlike most triconodontid lower molars in the absence of a lingual cingulum, a character shared with the highly derived *Alticonodon* Fox, 1969, with m1 of *Jeholodens*, and the Volaticotheriini (Gaetano and Rougier 2011). “Amphilestids” differ from *Eotricodon* in the elevated, dominant cusp a, indicating a different mode of occlusion, but there is some resemblance in the interlocking cusps e and f of *Phascolotherium* cf. *P. bucklandi* M46115. The first — and only preserved — molar of the triconodontid *Victoriaconodon* Montellano *et al.*, 2008, from the late Early Jurassic of Mexico, is of practically the same small size as M46736; but it differs in several respects that raise the question whether it belongs to the same family: b and c cusps are lower and smaller relative to a and less widely separated from it, with narrow and not V-shaped valleys; an e cusp is present but not an f; and there is a nearly complete lingual cingulum.

Martin and Averianov (2010) have recently described a triconodontid tooth from the Callovian of Kyrgyzstan, which they claimed to be the geologically oldest record for the family (*Victoriaconodon* was not mentioned). It consists of a very fragmentary lower right molar that is larger than the holotype of *Eotricodon sophron*. Its main triconodontid character is the mesial embayment delimited by two vertical crests, of which the lingual one is said to be the more pronounced. The specimen is unique in apparently possessing a supernumerary cusp apposed to the distal crest of cusp a. Its taxonomic position requires confirmation from additional material.

The most recent addition to knowledge of early Triconodontidae is *Argentoconodon fariatorum* Rougier *et al.*, 2007, from the late Early or early Middle Jurassic Cañadón Asfalto Formation, Argentina. Originally compared with “Amphilestidae” on the basis of the holotype, an isolated molariform, *Argentoconodon* is now known by associated upper and lower dentitions. Phylogenetic analysis (Gaetano and Rougier 2011) places it in the Triconodontidae, within a clade containing *Volaticotherium* (from the late Middle or early Late Jurassic of China; Meng *et al.* 2006) and *Ichthyoconodon*, from the ?Berriasian of Morocco (Sigogneau-Russell 1995). Analysis by Gaetano and Rougier (2011) places volaticotheriines in the triconodontid subfamily Alticonodontinae, mainly known from North America (Cifelli and Madsen 1998; Cifelli *et al.* 1998) but also now represented in the Early Cretaceous of China (Kusuhashi *et al.* 2009).

Summing up, pre-Late Jurassic records of Triconodontidae are rare (four, including *Eotricodon*) and poorly represented by fossils. Scarcity of triconodontids in Kirtlington suggests the possibility that we may be, in the Bathonian, close to the origin of the family, or at least to its eastern extension if the identification of *Victoriaconodon* is confirmed. Nonetheless, the absence of a lingual cingulum in *Eotricodon*, a derived character, implies an earlier diversification of this family, as suggested by Gaetano and Rougier (2011).

## CONCLUSIONS

Progress in understanding “triconodontan” evolution depends on the occurrence of morphologically informative, associated dental and non dental material; peculiar isolated teeth cannot be safely referred to recognized taxa. Kielan-Jaworowska *et al.* (2004) list 14 “triconodont” genera (seven morganucodontans, seven eutriconodontans) based on isolated teeth, and our study increases this number. Some of the latter may belong to groups yet unknown. Only in the case of “amphilestids” can our material be closely compared with mandibular specimens from the Stonesfield Slate. Other comparisons are more distant, namely: gobiconodontids from the Early Cretaceous, triconodontids from the Late Jurassic–Early Cretaceous, and morganucodontids from the Early Jurassic. All we can hope for is that future discoveries will include osteological material and associated dentitions which will clarify the taxonomic position of the isolated teeth described above, hence help in understanding the evolutionary pathways followed by “triconodont” mammals.

Despite these difficulties, the some thirty teeth described in this paper are sufficient to provide a rough picture of the faunal composition. Although all are variants of the plesiomorphic triconodont molar pattern, they show great diversity. This is particularly so in the order Morganucodonta, of which six specimens are referable to four or perhaps five genera. Of these, *Wareolestes* Freeman, 1979 has been reinterpreted with a change of orientation of the type specimen. *Morganucodon tardus*, named herein, is morphologically conservative and in this sense may be regarded more as a survivor from the Early Jurassic, whereas *Cherwellia* and *Stylidens* (both also proposed on the basis of species named herein) are more divergent and appear to be more recently evolved; the poorly preserved M46194 may represent another taxon. The “Amphilestidae” are represented by seven lower molars which vary in details of cusp form, interlocking cuspules, and lingual cingulum. A new species, *Phascalotherium simpsoni*, is proposed. Four upper molars are referred to this species. A fifth upper tooth, M 46441, is of questionable affinities because of its asymmetry. Ten teeth are identified as representatives of the Gobiconodontidae, of which four upper molars form the basis for *Gobiconodon bathoniensis*, a new species closely resembling *G. palaios*, from the Early Cretaceous of Morocco. Three lower molars and three possible upper premolars are referred to the family. By contrast, the Triconodontidae are represented by only a single specimen of the new genus and species *Eotriconodon sophron*.

As previously mentioned (Sigogneau-Russell 2003c), the Kirtlington mammalian fauna does not show close faunal links with the sympatric younger (earliest Cretaceous) Purbeck mammalian fauna. Thus Triconodontidae are rare in Kirtlington and gobiconodontids are absent in Purbeck. The difference could be ecological, though the two assemblages are considered to have accumulated in lacustrine environments. On the other hand, both areas are likely to have had terrestrial links during the Late Jurassic. It is true that the presence, in Kirtlington, of a shuotheriid genus known also in China (Sigogneau-Russell 1998), and the occurrence of strikingly similar volaticotheriine “triconodonts” in Argentina, Morocco, and China (Meng *et al.* 2006; Gaetano and Rougier 2011) suggest that we very poorly master the faunal peregrinations in these ancient times. Indeed, much remains to be discovered or explained concerning early mammalian evolution, and ever-hopeful cladists should consider exploring both the field and long-unopened drawers.

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