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A GOBICONODONTID (MAMMALIA, EUTRICONODONTA) FROM THE EARLY CRETACEOUS (BARREMIAN) WESSEX FORMATION OF THE ISLE OF WIGHT, SOUTHERN BRITAIN

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Abstract: Bulk screening of Early Cretaceous (Barremian) strata of the Wessex Formation, exposed in sections on the south-west and south-east coasts of the Isle of Wight, southern England, has resulted in the recovery of mammal remains, the first to be obtained from Wealden Group strata since the early 1970s. The fauna comprises at least six taxa represented by isolated teeth and in addition, in the case of an as yet undescribed spalacotheriid, a partial dentary. One of the teeth, a distal premolar, is of unique tricuspid, single-rooted morphology and represents the first British record of the Gobiconodontidae. Discovery of a gobiconodontid mammal in Early Cretaceous deposits of Britain sheds further light on the palaeogeographical distribution of an apparently successful clade of Early Cretaceous mammals and together with the occurrence of a gobiconodontid in the earliest Cretaceous of North Africa calls into question recent hypotheses concerning the area of origin of the Gobiconodontidae and mechanisms of dispersal therefrom.

Key words: Britain, Cretaceous, Gobiconodontidae, Mammalia, palaeogeography, premolar.

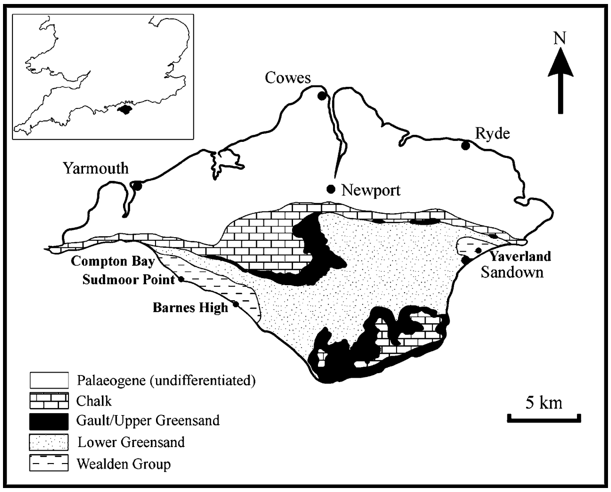
THE Early Cretaceous (Barremian, Wealden Group) Wessex Formation of the Isle of Wight, southern England (Text-fig. 1) has yielded a diverse macro-herpetofauna of international importance and without parallel elsewhere in Europe (e.g. Benton and Spencer 1995; Martill and Naish 2001 and references therein; Naish and Martill 2002; Naish *et al.* 2004; Sweetman 2004). In contrast, until recently the microvertebrate fauna was largely ignored although a number of workers have undertaken limited bulk screening operations in attempts to isolate it (Butler and Ford 1975; Freeman 1975; Buffetaut and Ford 1979; Evans *et al.* 2004). The only mammal remains described from the Wessex Formation are two isolated teeth recovered by the late R. L. E. Ford from Stewart's (1978) bed number CL3, which lies *c.* 50 m above the base of the exposed Wessex Formation at Compton Bay on the south-west coast of the Isle of Wight (Text-figs 1–2). These comprise a heavily worn left m2 and a well-preserved crown of a left I2 of a multituberculate provisionally referred to the genus *Loxaulax* Simpson, 1928 (Butler and Ford 1975). A third tooth referred to by Buffetaut and Ford (1979) is an indeterminate tooth fragment which may or may not be of mammalian origin (pers. obs. 2004).

The discovery of multituberculate teeth in the Wessex Formation and the earlier discovery of mammal teeth in the Wealden of the Weald (see Clemens 1963 for a review of early discoveries; Kermack *et al.* 1965; Clemens and Lees 1971) indicated that a sustained search for Wessex Formation mammals might prove worthwhile. However, it was the discovery in 1986 of unexpectedly rich microvertebrate-bearing horizons within the Early Cretaceous (Berriasian) Purbeck Limestone Formation at Sunnydown Farm in Dorset, southern England (Ensom 1987), that rekindled interest in British Early Cretaceous microvertebrates. Work undertaken since then (e.g. Ensom 1988; Ensom *et al.* 1991, 1994; Kielan-Jaworowska and Ensom 1992, 1994; Ensom and Sigogneau-Russell 1998; Evans and McGowan 2002; Evans and Searle 2002; Sigogneau-Russell and Kielan-Jaworowska 2002; Sigogneau-Russell 2003*a*) has reinforced the importance of the Purbeck Limestone Formation as a source of small Early Cretaceous vertebrates including mammals, archosaurs, lepidosaurs and lissamphibians. It also raised questions concerning the apparent paucity of the Wessex Formation fauna and prompted further sampling for microvertebrates (Evans *et al.* 2004; the comprehensive study by SCS currently in progress).

Mammal remains, the first to be recovered from Wealden Group strata since the early 1970s, have now been obtained from a number of horizons (Text-fig. 2). The fauna comprises at least six taxa including two multituberculates, a spalacotheriid, a zatherian or possibly eutherian, a ?dryolestid (B. Gasson, pers. comm. 2005) and the gobiconodontid described here. Examination of a partial, tooth-bearing dentary and attributed isolated upper and lower molars pertaining to a spalacotheriid indicates that this material represents a new taxon (SCS, work in progress). Furthermore, preliminary examination of isolated teeth belonging to other elements of the fauna indicates that the taxa concerned may also be new. The Wessex Formation mammal fauna is therefore of considerable potential importance both nationally and internationally. Further sampling of the most productive bed, Radley's (1994) bed 38 exposed at Yaverland on the south-east coast of the Isle of Wight (Text-figs 1–2), is being undertaken whenever exposures permit and it is hoped that this will result in the recovery of further mammal material, including molars/molariforms of taxa currently represented only by ante-molar/molariform teeth.

GEOLOGY

Inland exposures of the Wealden Group are poor but there are excellent exposures on the south-west and south-east coasts of the island (Text-fig. 1). Estimates for the total thickness of exposed Wessex Formation strata vary due to difficulty in estimating the throw on a significant fault in Compton Bay and minor faults elsewhere in the section, and to the laterally discontinuous nature of many of the beds. However, Stewart (1978, 1981) estimated the thickness to be *c.* 180 m. Exposed Wessex Formation strata comprise interbedded non-marine sandstones, calcrete conglomerates, massive, varicoloured mudstones, crevasse splay deposits and plant debris beds (*sensu* Oldham 1976) in which a number of facies associations have been recognized (Stewart 1978, 1981; Daley and Stewart 1979; Insole and Hutt 1994). These strata are entirely of Barremian age (Allen and Wimbledon 1991; Feist *et al.* 1995) but the Hauterivian/Barremian boundary may lie at the level of the Pine Raft, which is exposed at low water on the foreshore at Hanover Point [National Grid Reference (NGR) SZ 379837] (Harding 1986; Hughes and McDougall 1990). The Wessex Formation was deposited on a low-gradient, near-coast floodplain by a high-sinuosity river system flowing from west to east within a confined, fault-bounded valley (Stewart 1978, 1981; Daley and Stewart 1979; Stoneley 1982; Chadwick 1985; Ruffell 1992; Insole and Hutt 1994; Radley 1994; Wright *et al.* 1998; Underhill 2002). The freshwater/terrestrial Wessex Formation is overlain by *c.* 70 m of lagoonal strata which comprise the late Barremian to early Aptian Vectis Formation (Kerth and Hailwood 1988; Stewart *et al.* 1991; Feist *et al.* 1995; Robinson and Hesselbo 2004).



TEXT-FIG. 1. Outline geological and location maps of the Isle of Wight.

The Wessex Basin provided considerable habitat diversity. However, while precipitation remained high throughout the year, high summertime evaporation rates resulted in seasonal aridity (Haywood *et al.* 2004; but for an alternative interpretation of the cause of aridity, see Allen 1998). This may have rendered large areas of the floodplain inhospitable at times (Insole and Hutt 1994; Allen 1998) and also rendered vegetation susceptible to wildfires leaving the denuded landscape immediately thereafter prone to erosion by storm waters (Batten 1998). The plant debris beds, which have produced the bulk of vertebrate fossils recovered from the Wessex Formation but which make up only *c.* 1 per cent of the succession, represent deposits derived from such local fire and storm events (Insole and Hutt 1994). The fauna present in these beds is therefore representative of that present in the immediate vicinity rather than the hinterland. The microvertebrate fauna comprises mammals, dinosaurs, crocodiles, turtles, pterosaurs, lepidosaurs, lissamphibians, and chondrichthyan and osteichthyan fishes (Butler and Ford 1975; Freeman 1975; Buffetaut and Ford 1979; Evans *et al.* 2004; Sweetman 2004; Sweetman and Underwood 2006).

Bed 38 (Radley 1994), from which the specimen described here was obtained, is a typical Wessex Formation plant debris bed (Stewart 1978, 1981; Insole and Hutt 1994) occurring *c.* 4 m below the top of the Wessex Formation exposed at Yaverland on the south-east coast of the Isle of Wight (NGR SZ 617852, Text-figs 1–2). It contains a variably developed basal conglomeratic lag comprising reworked calcrete nodules, other intraformational clasts, and plant and vertebrate remains, above which there is a grey, silty clay containing locally abundant, poorly sorted plant material including fusain, unionoid bivalves and vertebrate remains. It is considered to be of latest Early Barremian age (Harding 1986; Kerth and Hailwood 1988; Hughes and McDougall 1990; Allen and Wimbledon 1991; Stewart *et al.* 1991; Feist *et al.* 1995; Robinson and Hesselbo 2004), but the precise age of bed 38 is poorly constrained. Charophytes recovered during the course of this study may provide better dating in due course (Feist *et al.* 1995; pers. obs.).

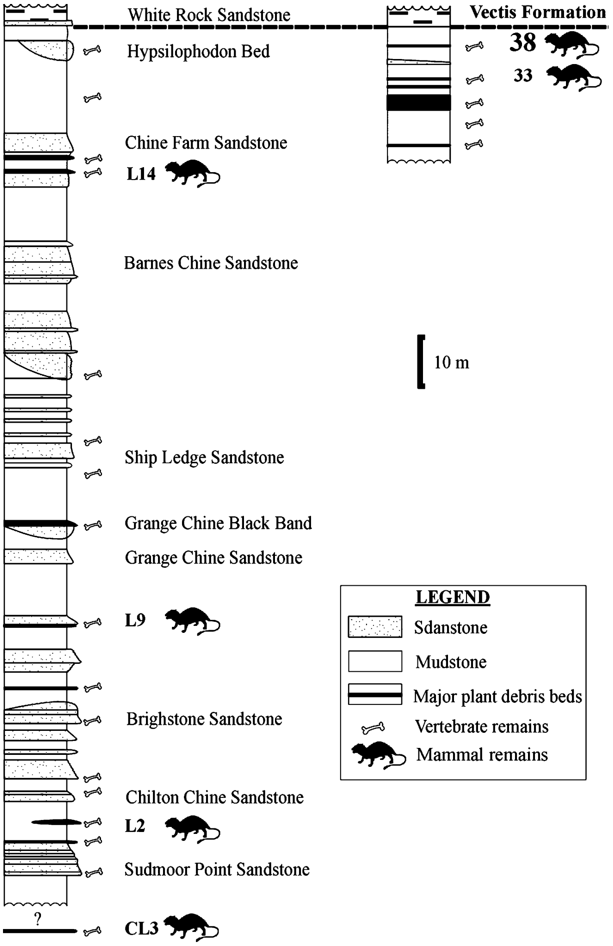
METHODS

Bed 38 (Radley 1994) is usually obscured by slumping of the cliff section and is only occasionally exposed on the foreshore. As a result it has not been possible to collect large bulk samples but small samples of between 10 and 30 kg are being taken whenever exposures are observed, the position of each being recorded using a GPS receiver. Samples were dried at 80°C for up to 12 h and processed using a bulk screening machine (Ward 1981) modified for use with re-circulated water. After processing, the residues were divided using a nest of sieves and plant material removed from each fraction hydromechanically. The sample which produced the specimen described here weighed *c.* 20 kg (dry weight before processing) and was collected from a cliff exposure at NGR SZ 61693 85223. It was obtained from the < 1·00 mm > 0·50 mm residue fraction, which also yielded a well-preserved, but probably indeterminate, double-rooted mammalian canine.

Digital images of the uncoated specimen were obtained using a scanning electron microscope. An environmental chamber was not available but acceptable images were obtained using low acceleration voltages to avoid excessive charging. Measurements of the specimen and specimens figured in the literature were taken digitally using digital image capture, analysis and processing software (SemAfore version 4.00, Insinööritoimisto J. Rimppi Oy).

Terminology. In the following description the terminology of Crompton and Jenkins (1968), Crompton (1974) and Jenkins and Schaff (1988) is employed.

Institutional abbreviations. BMNH, The Natural History Museum, London; MCZ, Museum of Comparative Zoology, Harvard, Cambridge, Massachusetts; PSS, Paleontological and Stratigraphic Section, Institute of Geology, Mongolian Academy of Sciences, Ulan Bator.



TEXT-FIG. 2. Schematic lithological logs of the Wessex Formation between (left) Sudmoor Point and Barnes High, SZ 392827–438807, on the south-west coast of the Isle of Wight (based in part on Stewart 1978) and (right) north-east of Yaverland Landslip, SZ 616851–618853, on the south-east coast (after Radley 1994).

SYSTEMATIC PALAEONTOLOGY

Class MAMMALIA Linnaeus, 1758
Order EUTRICONODONTA Kermack, Musset and Rigney, 1973
Family GOBICONODONTIDAE Chow and Rich, 1984
[*non* GOBICONODONTIDAE Jenkins and Schaff, 1988; REPENOMAMIDAE Li, Wang, Wang and Li, 2000]

Genus ?GOBICONODON Trofimov, 1978

Type species. Gobiconodon borissiaki Trofimov, 1978, from the Lower Cretaceous, Khoboor, Guchin Us Somon, Gobi Desert, Mongolia.

Taxonomy. In their review of 'triconodont' mammals, Kielan-Jaworowska *et al.* (2004) provisionally accepted the

Eutriconodonta as being monophyletic and included within it the monophyletic clade Triconodontidae and a paraphyletic group, the 'Amphilestidae'. Within the latter, Chow and Rich (1984) had previously erected the subfamily Gobiconodontinae to include *Gobiconodon* and *Klamelia*. Subsequently, Jenkins and Schaff (1988) raised the subfamily to family status but excluded *Klamelia* from their Gobiconodontidae, an exclusion accepted by Kielan-Jaworowska *et al.* (2004) who treated *Klamelia* as a eutriconodontan of 'amphilestid' grade. The family Repenomamidae was erected by Li *et al.* (2000) to accommodate *Repenomamus robustus* from the Yixian Formation of Liaoning Province, China, but Kielan-Jaworowska *et al.* (2004) concluded that *Repenomamus* is very similar to *Gobiconodon* and therefore placed it in the Gobiconodontidae. The taxonomy of Kielan-Jaworowska *et al.* (2004), which rendered Gobiconodontidae Jenkins and Schaff, 1988 and Repenomamidae Li, Wang, Wang and Li, 2000 junior subjective synonyms of Gobiconodontidae Chow and Rich, 1984, is accepted here although Hu *et al.* (2005) continued to use Repenomamidae in their description of *Repenomamus giganticus*, also from the Yixian Formation of Liaoning Province, China.

Material. One well-preserved, small, premolariform tooth, specimen number BMNH M 45513, Text-figure 3.

Horizon and locality. Bed 38 (Radley 1994) occurring *c.* 4 m below the top of the Wessex Formation exposed at Yaverland on the south-east coast of the Isle of Wight, southern England, NGR SZ 61693 85223 (Text-figs 1–2).

Description. A small, lower right, tricuspid tooth in which the crown and single root are well preserved. The crown is buccolingually compressed with a mesiodistal length of 0·74 mm and a buccolingual width of 0·37 mm. Crown height is *c.* 0·6 mm but the tip of cusp a is worn as further discussed below. The lingual surface of the crown appears almost planar in occlusal view (Text-fig. 3E) but there is a slight lingual convexity at the base of cusp a and stronger convexities at the bases of cusps b and c. The base of the buccal surface is universally convex (Text-fig. 3E). There is no trace of either a lingual or a buccal cingulid. Cusp a dominates the crown and is triangular in lateral profile with approximately straight mesial and distal edges (Text-fig. 3A–B, F). However, whereas the mesial surface is rounded the distal edge comprises a well-defined crest (Text-fig. 3C–E). No wear is present on the lingual surface but a single, prominent, oval wear facet is present on the buccodistal surface, which meets the apicobasal axis of the cusp at an acute angle (Text-fig. 3B–C, E–F). The enamel is smooth and highly reflective in normal light. It is thin (*c.* 15 μm) but, in view of a desire not to coat the specimen, its microstructure could not be examined and precise measurements of its thickness could not be determined. Cusp b is slightly smaller than cusp c and situated more apically than the latter (Text-fig. 3A–B, F). Both are small in comparison with cusp a and the apices of both cusps are slightly flexed buccally, the flexion being more pronounced in cusp c than in cusp b (Text-fig. 3C–E). The apicobasal axis of cusp a follows the apicobasal axis of the tooth whereas the apicobasal axes of cusps b and c intersect it at an acute angle root apically. In contrast to cusp a, cusps b and c are equally convex both buccally and lingually and have convex mesial and distal surfaces, respectively. The distal margin of cusp b and the mesial margin of cusp c comprise weakly developed crests (Text-fig. 3E). The apices of cusps b and c bear small, buccally orientated facets which meet the apicobasal axes of the cusps at an oblique angle. Unlike the wear facet on cusp a, which is smooth and attributable to occlusion with a tooth from the upper dentition, the facets on b and c have pitted surfaces (Text-fig. 3E). They may, therefore, represent abrasion caused by tooth/food contact or (perhaps less likely in view of the otherwise undamaged nature of the specimen) post-mortem damage rather than occlusion. The root is preserved in its entirety and while of approximately circular cross-section apically it is convex buccally and bears a concave depression crownward on the lingual side (Text-fig. 3A–B). In relation to the gum line, which indicates that the crown would have been very slightly procumbent, the root is markedly so, flexed buccally and recurved distally particularly towards the apex. The surface of the root is essentially smooth but very faint horizontal lines can be seen using optical microscopy in the region immediately below the crown on the lingual side. The mesial surface becomes somewhat rugose as the pulp cavity is approached (Text-fig. 3B, D). The latter opens buccodistally and is relatively small, being approximately one-third of the diameter of the root at its midpoint (Text-fig. 3B). Root length is *c.* twice crown height.

Remarks. In view of their limited taxonomic utility antemolar/molariform teeth of Mesozoic mammals other than those of multituberculates generally receive rather scant attention. Nevertheless, it is evident that all taxa possessed single-rooted incisors and some, single-rooted upper and/or lower canines (e.g. Simpson 1928, 1929; Lillegraven *et al.* 1979; Kielan-Jaworowska *et al.* 2004). Some Laurasian taxa also possessed single-rooted, anterior lower premolars, e.g. *Kuehneotherium* Kermack, Kermack and Mussett, 1968; *Manchurodon* Yabe and Shikama, 1938; some eutriconodontans (Jenkins and Schaff 1988; Kielan-Jaworowska and Dashzeveg 1998; Rougier *et al.* 2001); and Late Cretaceous deltatheroidians (Gregory and Simpson 1926; Kielan-Jaworowska *et al.* 2000). Some also possessed single-rooted, anterior upper premolars, e.g. *Docodon superus* Simpson, 1929, and possibly *Kurtodon* Osborn, 1887. However, in these taxa all such teeth bear simple crowns with at best a minimal development of accessory cusps. In contrast, distal premolars tend to have better-developed accessory cusps but where significant development of these cusps is observed, for example in members of the Triconodontidae (*sensu stricto*) and in closely related *Jeholodens* Ji *et al.*, 1999, with the exception only of certain members of one eutriconodontan family, it is invariably accompanied by the addition of a second root.

TEXT-FIG. 3. Scanning electron micrographs of BMNH M 45513 in A, lingual view; B, buccal view; C, distal view; D, mesial view; E, enlargement of crown in occlusal view; F, enlargement of crown in buccal view. Scale bars represent 500 μm.

AFFINITIES

The general crown morphology of BMNH M 45513, including the wear facet present on cusp a, confirms that it is the tooth of a mammal (Luo, pers. comm. 2004 and pers. obs.). The single root is indicative of a tooth from the anterior dentition but the well-developed accessory cusps show that it is a distal premolar and not a tooth from a more mesial position. Members of the eutriconodontan family Gobiconodontidae possess single-rooted distal premolars but this apomorphy is not shared by all members of the family and even at the specific level is variably present. Single-rooted, lower, distal premolars (p4) are present in the type species, *Gobiconodon borissiaki* Trofimov, 1978 (Kielan-Jaworowska and Dashzeveg 1998) and *G. hopsoni* (Rougier *et al.* 2001), whereas in *G. ostromi* Jenkins and Schaff, 1988, p4 is present in one specimen (MCZ 19860) but absent in another (MCZ 19965). Furthermore, in MCZ 19860 the right p4 is single-rooted whereas the left p4 is incipiently double rooted (Jenkins and Schaff 1988). In *G. hoburensis* the apparently small p4 (represented by alveoli only) is double-rooted (Kielan-Jaworowska and Dashzeveg 1998). However, among Laurasian Early Cretaceous mammals single-rooted distal premolars are only seen in members of the Gobiconodontidae. In view of this and the general crown morphology of BMNH M 45513 (tricuspid with cusp a dominant; small but well-developed accessory cusps b and c; mesiodistal alignment of cusps; buccal inflation of the crown; lack of cingulid; thin enamel lacking surface ornamentation), the specimen is identified as a right distal premolar, possibly a p4, of a gobiconodontid mammal and is tentatively referred to *Gobiconodon* Trofimov, 1978.

The p4 of the type species *Gobiconodon borissiaki* as seen in PSS 10-15a (Kielan-Jaworowska and Dashzeveg 1998, fig. 2) has suffered substantial wear, which has removed the apex of cusp a producing a horizontal wear facet and produced a substantial, steeply inclined facet buccally, below which there is a further oval, longitudinally elongate facet. Wear has also removed the apices of cusps b and c producing subhorizontal facets (Kielan-Jaworowska and Dashzeveg 1998, fig. 1D). Despite this, it is evident that the crown morphology of p4 seen in PSS 10-15a is very similar to that seen in BMNH M 45513. The latter differs from the former in being approximately half the size (digital measurements of maximum mesiodistal length of p4 taken from electronically scanned images of PSS 10-15a as seen in Kielan-Jaworowska and Dashzeveg 1998, fig. 2), greater buccal inflation of the crown basally in BMNH M 45513 and lack of lingual inflation below cusp a as seen in PSS 10-15a. BMNH M 45513 also exhibits apparently more pronounced development of cusps b and c, and a different wear pattern from that seen in the p4 of PSS 10-15a: lack of horizontal wear facet at the apex of cusp a; lack of oval, longitudinally elongate wear facet at the base of cusp a; and the apparently more distal disposition of the steeply inclined facet present on the buccal surface of cusp a. However, BMNH M 45513 is little worn in comparison with the p4 of PSS 10-15a and the differences in wear patterns may in part reflect this.

The root morphology of BMNH M45513 indicates that it is derived from a mature individual representing a taxon that was small in the context of the Gobiconodontidae. The type genus includes *Gobiconodon hopsoni* Rougier *et al.*, 2001, of similar body size to, but more robustly built than, the extant North American opossum *Didelphis virginiana* (Jenkins and Schaff 1988; Rougier *et al.* 2001). The family also includes the largest Mesozoic mammal yet discovered, *Repenomamus giganticus* Hu, Meng, Wang and Li, 2005, which had skull length of 160 mm and a body size comparable with that of a large Tasmanian devil, *Sarcophilus harrisii* (Hu *et al.* 2005). Based on the size of the tooth described here, the Isle of Wight gobiconodontid could have been similar in size to *Gobiconodon hoburensis* Trofimov, 1978, estimated by Kielan-Jaworowska and Dashzeveg (1998) to have had a skull length of *c.* 27 mm, thus being *c.* 1·8 times smaller than *G. borissiaki*. It also appears to represent a taxon that was somewhat smaller than that reported by Cuenca-Bescós and Canudo (2003) from the Upper Barremian of Spain. However, this estimate of size is speculative, being based on a single distal premolar, the size of which, relative to the remainder of the dentition, is variable within the Gobiconodontidae.

CONCLUSIONS

BMNH M 45513 represents the first British record of the Gobiconodontidae and only the second record of the clade from Europe, the other being an isolated M3 or M4 from the Upper Barremian of Spain (Cuenca-Bescós and Canudo 2003). Outside of Europe gobiconodontids are represented by isolated teeth and more complete cranial and postcranial remains from the Lower Cretaceous (?Berriasian) of North Africa (Sigogneau-Russell 2003b), the Lower Cretaceous (correlation still subject to debate but probably Hauterivian–Albian) of central and eastern Asia (Trofimov 1978; Chow and Rich 1984; Kielan-Jaworowska and Dashzeveg 1998; Maschenko and Lopatin 1998; Godefroit and Guo 1999; Averianov and Skutschas 2000; Li *et al.* 2001; Rougier *et al.* 2001; Tang *et al.* 2001; Hu *et al.* 2005), and the Aptian–Albian of North America (Jenkins and Schaff 1988; Carpenter *et al.* 2002).

Cuenca-Bescós and Canudo (2003) concluded that the Gobiconodontidae probably originated and diverged in central and eastern Asia, a view shared, with reservations due to lack of data, by Chow and Rich (1984). They also concluded that the currently known distribution of the Gobiconodontidae appears to represent at least two dispersal events, both of which originated in central Asia, the first involving a westward migration to western Europe during the late Barremian and a second involving a somewhat later eastward migration to western North America. The discovery of a gobiconodontid, *Gobiconodon palaios* Sigogneau-Russell, 2003*b*, in the lowermost Cretaceous (?Berriasian) of northern Gondwana and, perhaps less significantly, a gobiconodontid in the lower Barremian of Britain, now casts doubt on this hypothesis. The occurrence of gobiconodontid remains restricted to Aptian–Albian strata deposited to the west of the epicontinental sea that divided North American in the Early Cretaceous appears to support an eastward migration from Asia to North America (Jenkins and Schaff 1988; Carpenter *et al.* 2002). However, lack of gobiconodontid remains from strata deposited to the east of the epicontinental sea may well represent a collecting artefact reflecting the small number of Early Cretaceous mammal-bearing sites so far known from this region. Furthermore, Cifelli and Madsen (1999) cited the occurrence of a monophyletic subfamily of the Spalacotheriidae, the Spalacolestinae, in the upper Lower and Upper Cretaceous of North America as evidence of mammal migration from Europe to North America during the Early Cretaceous. While the Barremian occurrence of a gobiconodontid in Britain is significant in terms of the biogeographical distribution of the family, it is evident that lack of data, particularly in light of the earliest Cretaceous, Gondwanan occurrence of a gobiconodontid, currently renders any analysis of the area of origin of the Gobiconodontidae and mechanisms of dispersal therefrom problematic. It is, however, evident from study of the palaeogeographical distribution of the Gobiconodontidae and other elements of the Early Cretaceous faunas of Europe and Asia (e.g. Evans *et al.* 1998; Tsubamoto *et al.* 2004) that faunal interchange between Europe and Asia did occur before some palaeogeographical models (e.g. Smith *et al.* 1994; Smith and Rush 1997) indicated that this was possible. It is now apparent that these models are over-simplistic and that dispersal events were more complex than previously realised.

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