

SAUROPOD DINOSAURS FROM THE LOWER CRETACEOUS OF EASTERN ASIA: TAXONOMIC AND BIOGEOGRAPHICAL IMPLICATIONS

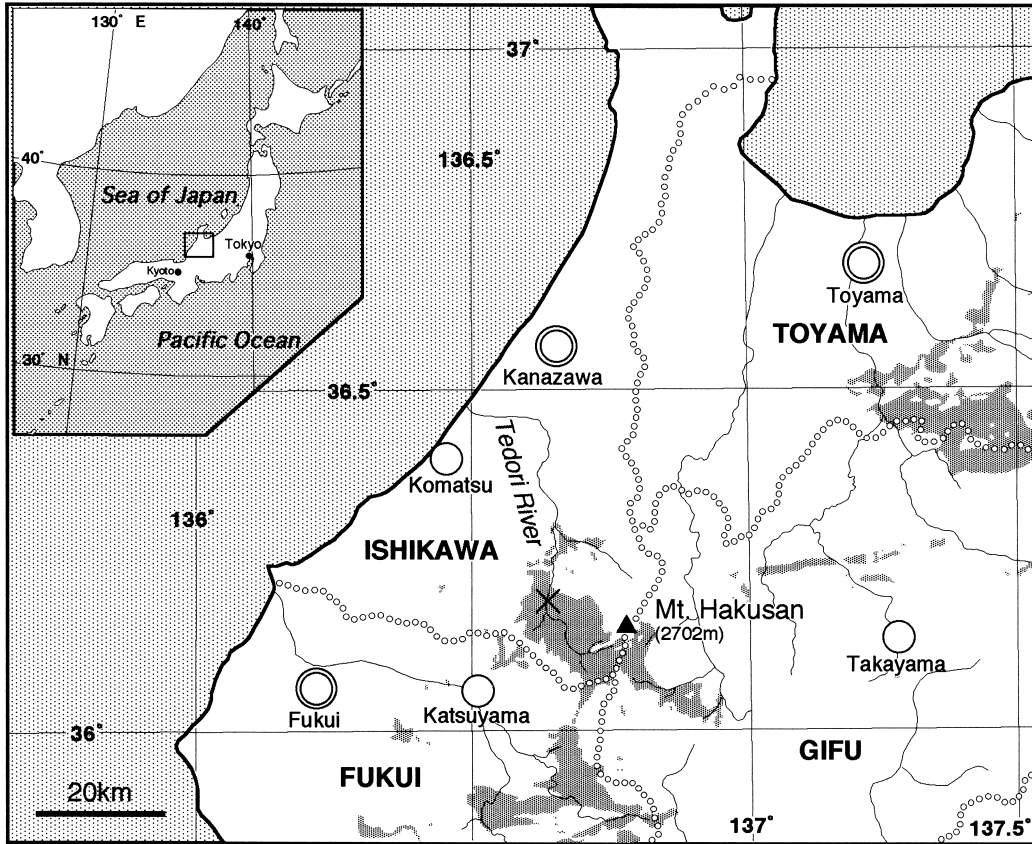
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ABSTRACT. Sauropod dinosaurs are poorly represented in the Lower Cretaceous of eastern Asia. Here, we describe a number of isolated sauropod teeth from the Kuwajima Formation (?Berriasian–?Hauterivian) of Shiramine, Japan. The mosaic of shared derived characters and symplesiomorphies displayed by the teeth indicate that they are referable to a basal member of the titanosauriform radiation. A taxonomic review of previously described sauropod specimens from eastern and south-eastern Asia reveals that a diversity of sauropods (including a titanosaurian, a basal titanosauriform and a ?euhelopodid, as well as several forms of indeterminate systematic position) was present in this region in the Early Cretaceous. This diversity conflicts with previous suggestions that eastern Asia was biogeographically isolated from the rest of Laurasia until the late Early Cretaceous and that the sauropod fauna was limited to the endemic East Asian clade Euhelopodidae. The presence of titanosauriform sauropods in the basal Cretaceous of Japan and Thailand indicate that the proposed faunal isolation of eastern Asia ended approximately 20 myr earlier than usually suggested.

KEY WORDS: Titanosauriform sauropods, Kuwajima Formation, Early Cretaceous, eastern Asia, Japan.

DINOSAUR remains were first recovered from the Lower Cretaceous Kuwajima Formation (Tetori Group) of Shiramine, Ishikawa Prefecture, in 1985. The locality, known locally as Kaseki-Kabe or 'Fossil Bluff' (Text-fig. 1), initially yielded fragmentary teeth of theropod (Manabe *et al.* 1989) and iguanodontid dinosaurs (Hasegawa *et al.* 1995). Until recently, only a handful of specimens were known from Kaseki-Kabe, due to the difficulties associated with collecting at this locality; the fossiliferous horizons crop out several metres above ground level in an almost vertical cliff section. However, the construction of a road tunnel through the cliff section (during 1997–2000) has greatly increased access to the fossiliferous horizons (Matsuoka 2000). Previous finds of well-preserved fossil wood at Kaseki-Kabe have led to its recognition as a site of national scientific importance; consequently, an agreement was drawn up between the Japanese Ministry of Construction, the local village authorities and various research institutes in order to secure the rock debris removed during the tunnelling operation for scientific study. Around 270 m³ of rock debris were set aside and the material is housed in several warehouses in the Shiramine area. The debris is being systematically prospected for new fossil material; around 60 m³ of rock have been processed so far (Matsuoka 2000).

The Kuwajima vertebrate fauna from Shiramine is now known to include theropod, hypsilophodontid and iguanodontid dinosaurs, tritylodontid synapsids, anurans, turtles, lizards, pterosaurs, fish, birds and choristoderes (Manabe *et al.* 1989, 2000; Azuma and Tomida 1995; Hasegawa *et al.* 1995; Setoguchi *et al.* 1999; Barrett and Manabe 2000; Matsuoka 2000; Matsuoka and Setoguchi 2000). Dinosaur footprints have been reported (Manabe *et al.* 1989; Matsuoka *et al.* 2001), and abundant plant and invertebrate material is also present (Maeda 1961). This material is currently under study by a Japanese multi-institutional research team sponsored by the Shiramine Village Board of Education and by an Anglo-Japanese team under the leadership of Dr Susan E. Evans (University College, London) and MM.



TEXT-FIG. 1. Map of north-central Honshu, Japan, showing the position of the Shiramine locality (X). The dark grey stippling indicates the distribution of the Tetori Group sediments (after Maeda 1961).

In this paper we describe a number of sauropod teeth from Shiramine. Sauropods are poorly represented in the Japanese fossil record (Azuma and Tomida 1998). A large, partial humerus recovered from the Lower Cretaceous (upper Aptian–lower Albian) Miyako Group of Iwate Prefecture, northern Honshu, was one of the first dinosaur specimens to be described from Japan and was referred to the Diplodocidae, on the basis of supposed similarities to *Mamenchisaurus*, which was considered to be a diplodocid at this time (Hasegawa *et al.* 1991). Further consideration of the specimen, however, could not identify any synapomorphic features that would permit the referral of this humerus to any particular sauropod clade; consequently, this material is now regarded as Sauropoda indeterminate (Azuma and Tomida 1998). Isolated teeth have been recovered from the Akaiwa Subgroup (Barremian–Aptian) of Fukui Prefecture (Azuma and Tomida 1998); the Futaba Group (Coniacian–Santonian) of Fukushima Prefecture (Azuma and Tomida 1998); and the Wakino Subgroup (Berriasian–Hauterivian) of Fukuoka Prefecture (Okazaki 1992, cited in Azuma and Tomida 1998). Most of these teeth are currently undescribed, though they are generally referred to as spatulate (Azuma and Tomida 1998). A tooth (Tanimoto and Mizutani 1999a, b) and partial postcranial skeleton have been collected from the Lower Cretaceous (Berriasian–Hauterivian) Matsuo Group of Mie Prefecture (Mie Prefecture Excavation and Research Group for Dinosaur Fossils 1997; Tomida *et al.* 2001). A sauropod footprint has been reported from the Itoshiro Subgroup (Valanginian) of Toyama Prefecture (Goto 1992, cited in Azuma and Tomida 1998). The teeth from

Shiramine thus provide additional data on the occurrence of Japanese sauropods and on the palaeobiogeography of eastern Asia in the Late Mesozoic.

Institutional abbreviations. AMNH, American Museum of Natural History, New York, USA; CMNH, Carnegie Museum of Natural History, Pittsburgh, USA; DNM, Dinosaur National Monument, Vernal, Utah, USA; FMNH, Field Museum of Natural History, Chicago, USA; HMN, Humboldt Museum für Naturkunde, Berlin, Germany; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, People's Republic of China; MACN, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; MCNA, Museo de Ciencias Naturales de Alava, Vitoria-Gasteiz, Spain; PMU, Palaeontological Museum, University of Uppsala, Sweden; SBEI, Museum of the Shiramine Board of Education, Shiramine, Japan; USNM, United States National Museum, Smithsonian Institution, Washington DC, USA; WDIS, Dinamation International Society, Wyoming, USA; ZDM, Zigong Dinosaur Museum, Zigong, People's Republic of China.

GEOLOGICAL SETTING

The Tetori Group crops out in central Honshu (Fukui, Gifu, Ishikawa and Toyama prefectures; Text-fig. 1) and is composed of alternating beds of sandstones, mudstones and conglomerates of Middle Jurassic–Early Cretaceous age (Maeda 1961; Matsukawa and Obata 1994). These sediments represent a variety of depositional environments; marine conditions prevailed during the Middle and Late Jurassic and were succeeded by Early Cretaceous freshwater depositional environments characterised by wide meandering river systems (Evans *et al.* 1998). The Tetori Group is traditionally divided into three subgroups: the Middle–Upper Jurassic Kuzuryu Subgroup (Bajocian–Oxfordian), the Upper Jurassic–Lower Cretaceous Itoshiro Subgroup (Kimmeridgian–Hauterivian) and the Lower Cretaceous Akaiwa Subgroup (Barremian–Aptian) (Maeda 1961; Matsukawa and Obata 1994; Azuma and Tomida 1998; Matsukawa and Nakada 1999).

The Kuwajima Formation crops out around the village of Shiramine, Ishikawa Prefecture. It comprises the uppermost part of the Itoshiro Subgroup in this region and is the lateral equivalent of the Okurodani Formation in neighbouring Gifu Prefecture (Maeda 1961). The Okurodani Formation has also yielded a diverse fossil fauna (Evans *et al.* 1998). Fission-track and K–Ar dates obtained from several tuff layers in the Okurodani Formation (Itoshiro Subgroup) and the overlying Bessandani Formation (Akaiwa Subgroup) indicate that the section spanning the upper part of the Itoshiro Subgroup and the lower part of the Akaiwa Subgroup can be dated to between 140 and 120 Ma (Gifu-Ken Dinosaur Research Committee 1993). Consequently, the fossil assemblages from both the Okurodani and Kuwajima formations must have been deposited at some time during the interval defined by the Berriasian–Barremian stages (cf. Gradstein *et al.* 1995). As the upper boundary of the Itoshiro Subgroup appears to be no younger than Hauterivian (on the basis of biostratigraphical correlations: Maeda 1961; Matsukawa and Obata 1994) this limits the age of both the Okurodani and Kuwajima formations to Berriasian–Hauterivian.

The Kuwajima Formation consists of alternating beds of fine- and coarse-grained sandstones and mudstones (Hasegawa *et al.* 1995; Isaji 2000). Several facies (Facies I, carbonaceous swamp; Facies II, shallow lake; Facies III, vegetated swamp) have been identified in the sequence, each of which has yielded a variety of vertebrate remains (Isaji 2000). The fossils are well preserved and lack signs of extensive transport or crushing. Articulated specimens are extremely rare, but small isolated elements are abundant and often complete. The sauropod teeth were recovered from Facies II, in a bed of dark grey fine-grained silty sandstone (Isaji 2000).

SYSTEMATIC PALAEONTOLOGY

SAUROPODA Marsh, 1878

EUSAUROPODA Upchurch, 1995

NEOSAUROPODA Bonaparte, 1986
TITANOSAURIFORMES Salgado *et al.*, 1997

gen. et sp. indeterminate

Plate 1, figures 1–16

Material. Nine isolated teeth (SBEI 13, 155, 160, 183, 318, 583, 815, 1284, 1473).

Locality and horizon. Kaseki-Kabe, near Shiramine Village, Ishikawa Prefecture, western Honshu, Japan. Kuwajima Formation (Itoshiro Subgroup, Tetori Group), Berriasian–Hauterivian, Lower Cretaceous.

Description. The crown is mesiodistally narrow and is not significantly wider than the root (Plate 1). The mesial and distal margins of the crown extend parallel to each other for much of the length of the crown but converge apically. In some teeth (e.g. SBEI 160; Pl. 1, figs 13–16), the crown displays a slight mesiodistal constriction at a point approximately half-way along its length; similar constrictions are also present on some teeth of *Brachiosaurus* (Janensch 1935–36). The crown apex is inclined slightly lingually and distally with respect to the long axis of the tooth. The markedly convex central portion of the labial crown surface is bounded mesially and distally by shallow troughs or grooves (referred to hereafter as ‘labial grooves’), which extend parallel to the mesial and distal crown margins. The lingual surface is either weakly concave, with a low, mesiodistally broad ridge (referred to hereafter as the ‘lingual ridge’) extending along the length of the crown surface, or planar. In those teeth where the lingual ridge is present, it almost obliterates the lingual concavity. The slenderness index (SI) of the tooth crowns (the ratio of crown height to maximum crown width; *sensu* Upchurch 1998) ranges between 2.0 and 3.0. Denticles are absent. The enamel has a wrinkled texture.

The apical regions of the crowns are D-shaped in cross-section (taken perpendicular to the long axis of the crown). The cross-section is asymmetrical in apical or basal view, with the apex of the D situated closer to the mesial margin of the crown than to the distal margin. Consequently, the mesial part of the labial surface is angled more steeply with respect to the mesiodistal axis of the tooth crown than the distal part of the labial surface. A tangent drawn from the mesial labial crown surface and extended to the mesiodistal axis of the tooth crosses the axis at an angle of approximately 85 degrees, whereas a tangent drawn from the distal labial crown surface crosses the mesiodistal tooth axis at an angle of approximately 45 degrees. The basal portion of the crown has a subelliptical cross-section.

Large, steeply inclined wear facets are present on the mesial and distal margins of most teeth and the two facets are often contiguous, forming a V-shaped wear surface. Each wear facet displays well-defined step-flush enamel-dentine contacts (Pl. 1, figs 1–4, 13–16). The most extensive wear tends to be situated on the distal margin of the crown. One tooth (SBEI 583; Pl. 1, figs 9–12) lacks high-angled mesial and distal wear facets, but possesses a mesiodistally wide, apicobasally short wear facet that extends over the lingual surface of the crown apex. A small apical wear facet is also present on the lingual surface of SBEI 1473, but this facet occurs in combination with a large, high-angled distal wear facet. The morphology of the wear facets is consistent with a precise occlusion. V-shaped facets indicate that upper and lower tooth rows interdigitated along at least a part of their length during jaw closure, suggesting a powerful cropping action. The apical wear facets provide evidence of a precise shearing bite (Calvo 1994; Barrett and Upchurch 1995; Christiansen 2000; Upchurch and Barrett 2000).

The large size and cross-sectional morphology of three isolated basal tooth crowns/roots (SBEI 159, SBEI 168 and SBEI 1287) suggest that these specimens may also be referable to the Sauropoda, but this assignment should remain tentative as the material is extremely fragmentary.

SYSTEMATIC POSITION OF THE SHIRAMINE SAUROPOD TEETH

Recent cladistic analyses of the Sauropoda have utilised several detailed and explicit dental characters (Upchurch 1998; Wilson and Sereno 1998). The phylogenetic distribution of the various character states

EXPLANATION OF PLATE 1

Figs 1–16. Indeterminate titanosauriform teeth from the Kuwajima Formation (Lower Cretaceous) of Shiramine, Ishikawa Prefecture, Japan. 1–4, SBEI 183 in lingual, labial, mesial and distal views. 5–8, SBEI 13 in lingual, labial, mesial and distal views. 9–12, SBEI 583 in lingual, labial, distal and mesial views. 13–16, SBEI 160 in lingual, labial, mesial and distal views. All $\times 1.5$.

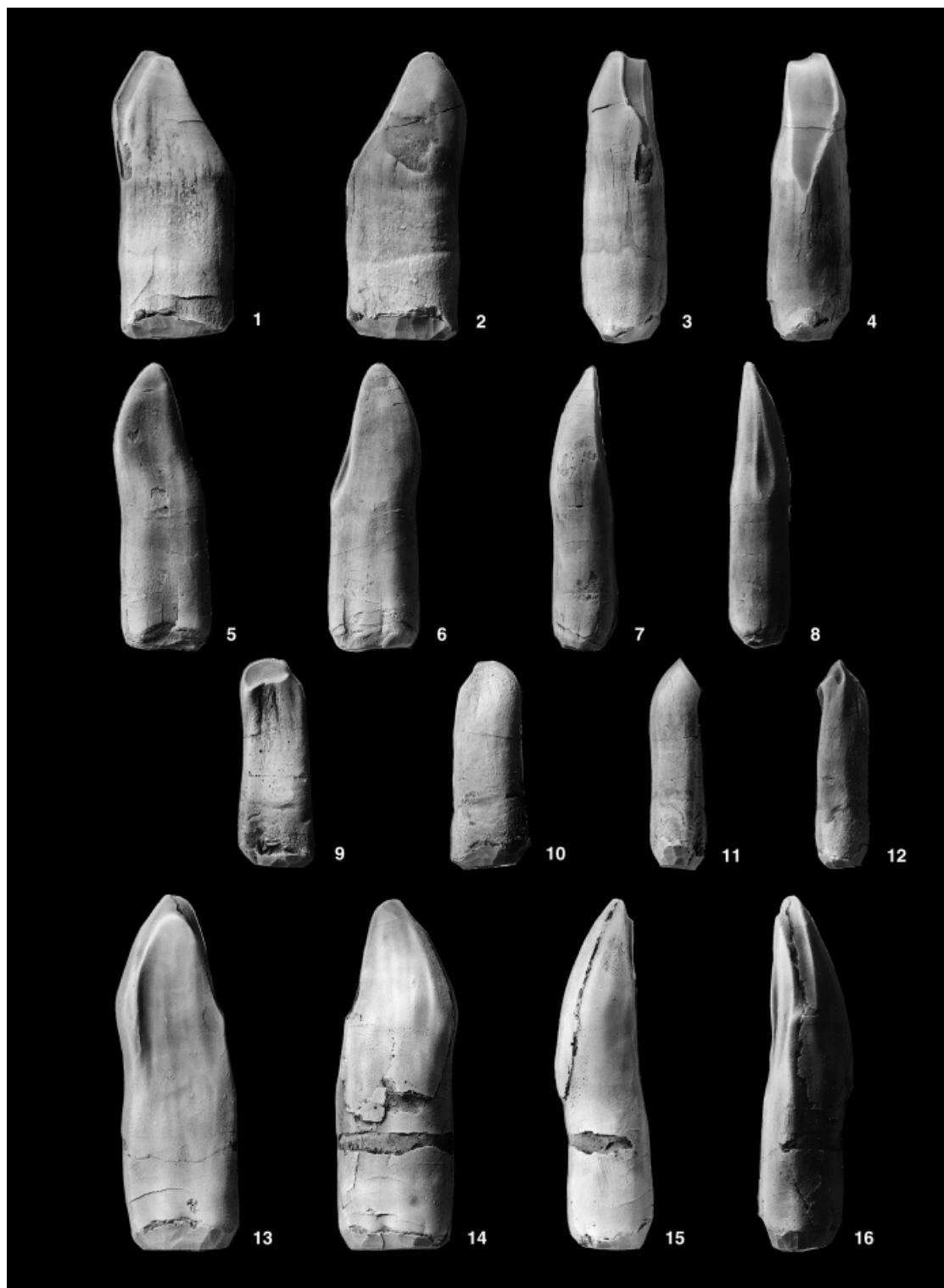


TABLE 1. Sauropod specimens examined for comparison with the Shiramine sauropod teeth.

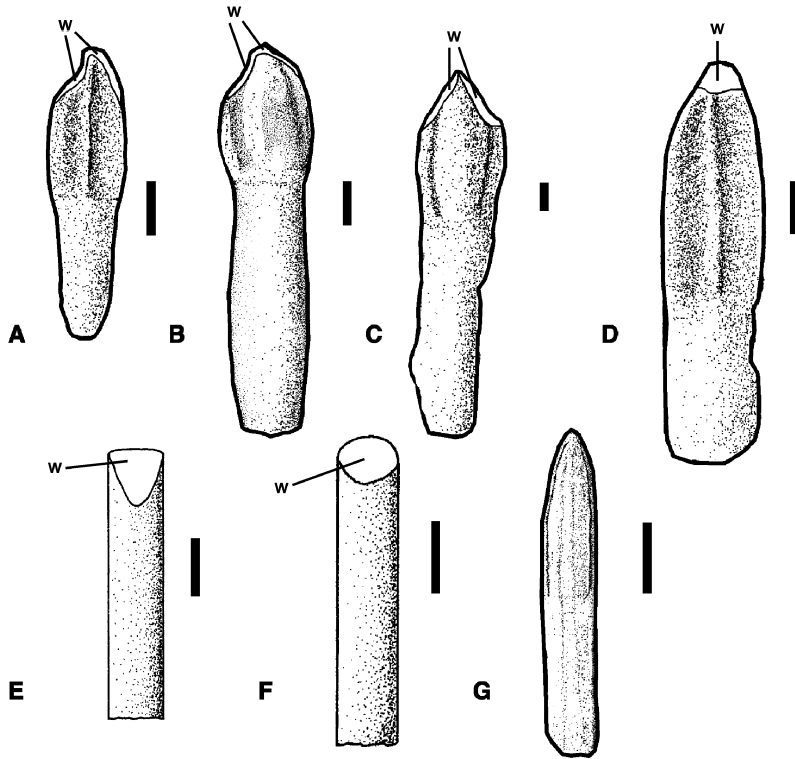
Taxon	Specimen number(s)
<i>Apatosaurus</i>	WDIS 0099
<i>Brachiosaurus</i>	HMN S11, HMN S66, HMN S116, HMN WJ470
<i>Camarasaurus</i>	AMNH 467, CMNH 11338, CMNH 21751, DNM 28
<i>Dicraeosaurus</i>	HMN d429
<i>Diplodocus</i>	AMNH 969, CMNH 11161, USNM 2672
<i>Euhelopus</i>	PMU M2983
<i>Lirainosaurus</i>	MCNA 7440-1
<i>Omeisaurus</i>	ZDM T5703
<i>Patagosaurus</i>	MACN 124, MACN CH933-4
<i>Shunosaurus</i>	IVPP 7261-5, ZDM T5402-3
' <i>Titanosaurus</i> '	MACN unnumbered
cf. <i>Rapetosaurus</i>	(FMNH field nos. 93-73/95029, 93074, 93-06/95034)

offers some insights into the systematic position of the sauropod teeth from Shiramine (Text-figs 2-3). The D-shaped apical cross-section of the tooth crowns, the possession of wrinkled enamel and the presence of a precise interlocking (interdigitating) occlusion (evidenced by the presence of large, V-shaped wear facets), indicate that these teeth are referable to the Eusauropoda (Wilson and Sereno 1998). Moreover, the absence of denticles supports assignment either to the Eusauropoda (Upchurch 1998) or the Neosauropoda (Wilson and Sereno 1998), depending upon the phylogeny adopted.

The Shiramine teeth possess a mosaic of dental character states that makes their referral to any particular sauropod clade problematic. (Sauropod taxa examined for comparative purposes are listed in Table 1.) Titanosauriforms ('brachiosaurids' and titanosaurs *sensu lato*; see Salgado *et al.* 1997), diplodocoids (diplodocids, dicraeosaurids, nemegtosaurids and others; *sensu* Upchurch 1995, 1998) and some euhelopodids (e.g. *Shunosaurus* and *Euhelopus*) have narrow tooth crowns with mesial and distal margins that extend parallel to each other along most of the length of the crown (Wiman 1929; Zhang 1988; McIntosh 1992; Calvo 1994; Upchurch 1994, 1995, 1998; Salgado and Coria 1997; Wilson and Sereno 1998; Upchurch and Barrett 2000; PMB pers. obs.; Text-fig. 2). This contrasts with the robust, mesiodistally expanded ('spatulate') tooth crowns seen in many non-titanosauriform, non-diplodocoid taxa, such as *Camarasaurus* (Carey and Madsen 1972; McIntosh *et al.* 1996), the euhelopodid *Omeisaurus* (He *et al.* 1988) and *Patagosaurus* (Bonaparte 1986). The possession of parallel-sided tooth crowns therefore represents a synapomorphy uniting the Shiramine teeth with diplodocoids, titanosauriforms or euhelopodids (excluding *Omeisaurus*).

The cylindrical and subcylindrical ('peg-like') teeth of diplodocoids and titanosaurids (see, for example, figures in Holland 1924; von Huene 1929; Text-fig. 2) each represent the end point of trends toward tooth crown narrowing and lengthening that occurred independently in Titanosauriformes and Diplodocoidea (Upchurch 1994, 1998; Wilson and Sereno 1998; Text-fig. 3). Although the teeth from Shiramine are parallel-sided, they are not subcylindrical or cylindrical in cross-section (see above), but retain the D-shaped cross-section seen in other non-diplodocoid, non-titanosaurid eusauropods. Consequently, referral of the Shiramine teeth to either Diplodocoidea or Titanosauridae seems unlikely. Moreover, the long, slender tooth crowns of diplodocoids and derived titanosaurids have SIs >4.0 (Upchurch 1998), while the Shiramine teeth have a maximum SI of 3.0. The latter is, however, close to the lower end of the SI range for titanosauriforms: the teeth of *Brachiosaurus* and *Pleurocoelus* have SIs ranging between 2.0 and 4.0 (see figures in Leidy 1865; Janensch 1935-36; Ostrom 1970). There is a small overlap between the SIs of the Shiramine teeth and the range of SIs present in non-titanosauriform, non-diplodocoid sauropods, such as *Camarasaurus*, *Euhelopus* and *Patagosaurus* (e.g. McIntosh *et al.* 1996), which all have SIs ranging from 1.5 to 2.5 (PMB, pers. obs.).

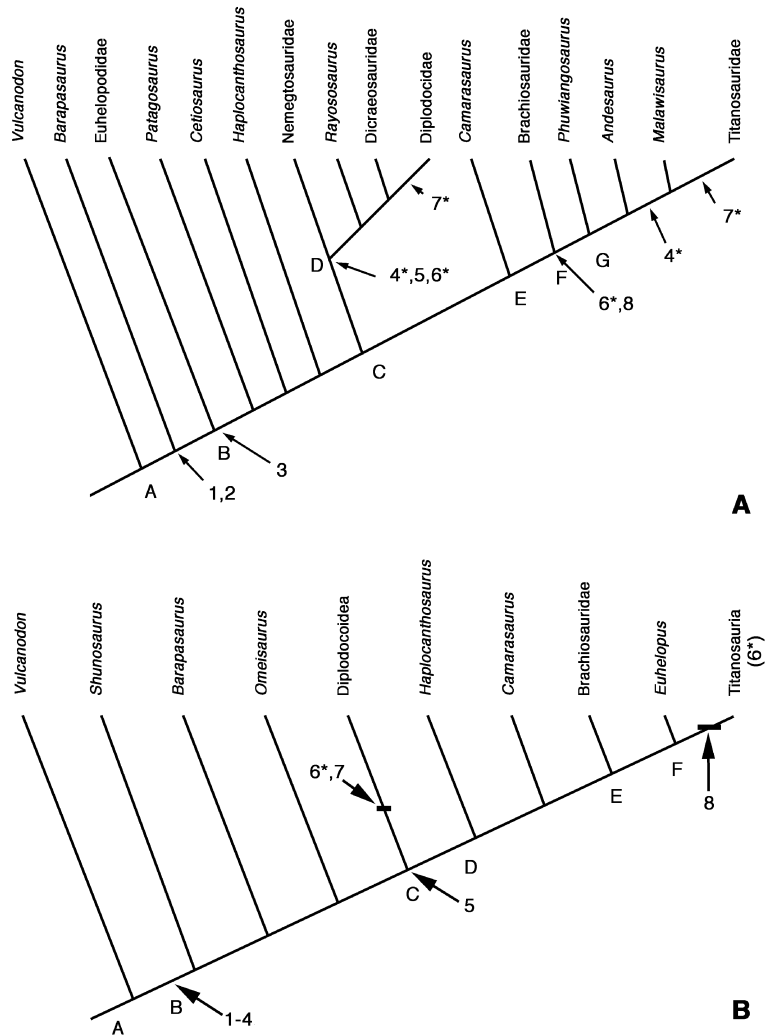
Differences in many other character states prevent referral of the Shiramine teeth to either Titanosauridae or Diplodocoidea. The teeth of diplodocoids and of titanosauriforms more derived than



TEXT-FIG. 2. Representative sauropod teeth for comparison with the material from Shiramine. A, *Euhelopus*. B, *Patagosaurus*. C, *Camarasaurus*. D, *Brachiosaurus*. E, indeterminate titanosaurid (MACN uncatalogued). F, *Diplodocus* (CM 11161). G, *Dicraeosaurus*. A and D are in lingual view; B–C and E–G are in labial view. (A–D and G are modified from Upchurch and Barrett 2000, with permission.) Scale bars represent 10 mm.

Malawisaurus have lost the lingual concavity and ridge, a loss that occurred independently in each of these clades (Upchurch 1998; Text-fig. 3). In contrast, the teeth of basal titanosauriforms (*Brachiosaurus*, *Pleurocoelus*), euhelopodids and the Shiramine sauropod retain the lingual concavity and ridge (a primitive character state for sauropods; Upchurch 1998) (Wiman 1929; Janensch 1935–36; Ostrom 1970; Zhang 1988; Text-fig. 2). The presence of labial grooves is a primitive character state for sauropods and these features are found in euhelopodids, basal titanosauriforms, the Shiramine teeth and in some diplodocoids (e.g. dicraeosaurids) (Wiman 1929; Janensch 1935–36; Zhang 1988; Upchurch 1998). However, derived titanosaurids and diplodocids have independently lost the labial grooves (Upchurch 1998). Moreover, the retention of V-shaped wear facets and a precise interlocking (interdigitating) occlusion excludes the Shiramine teeth from Titanosauoidea and from non-nemegtosaurid diplodocoid clades: these animals either lacked a precise occlusion (diplodocids) or had teeth that met in direct opposition, rather than interlocking (dicraeosaurids, titanosaurids) (Barrett and Upchurch 1995; Upchurch and Barrett 2000). Mesial and distal wear facets have been reported on some tooth crowns of the nemegtosaurid diplodocoid *Nemegtosaurus* (Nowinski 1971), but other features of nemegtosaurid teeth (see above) clearly distinguish them from those of the Shiramine sauropod. Diplodocoid and titanosaurid teeth possess large apical wear facets, but the slenderness of the tooth crown often gives these facets a 'chisel-like' appearance in comparison with the mesiodistally broad, apicobasally short wear facets seen in SBEI 583.

The Shiramine teeth bear a strong superficial resemblance to those of the euhelopodid *Euhelopus*



TEXT-FIG. 3. Phylogenetic distribution of sauropod dental character states. A, phylogeny simplified from Upchurch (1998). 1, lingual concavity present; 2, labial grooves present; 3, loss of marginal denticles; 4, loss of lingual concavity; 5, tooth crowns with $SI \geq 5.0$; 6, mesial and distal margins of tooth crown subparallel; 7, loss of labial grooves; 8, tooth crowns with $SI \geq 4.0$. * indicates convergent acquisition of a particular character state. A, Sauropoda; B, Eusauropoda; C, Neosauropoda; D, Diplodocoidea; E, 'Brachiosauria'; G, Titanosauroidae. F is equivalent to the Titanosauriformes of other authors; 'Brachiosauria' is equivalent to the Macronaria of Wilson and Sereno (1998). The name *Rayososaurus* is used for the material previously referred to '*Rebbachisaurus*' *tessonei* (see Wilson and Sereno 1998). B, phylogeny from Wilson and Sereno (1998). 1, spatulate tooth crowns; 2, wrinkled tooth enamel; 3, precise occlusion between tooth crowns; 4, V-shaped wear facets; 5, loss of marginal denticles; 6, cylindrical tooth crowns; 7, high-angled planar wear facets; 8, low-angled planar wear facets. In this scheme, cylindrical tooth crowns are only found in derived titanosaurs and are not diagnostic of the group as a whole. * indicates convergent acquisition of a particular character state. A, Sauropoda; B, Eusauropoda; C, Neosauropoda; D, Macronaria; E, Titanosauriformes; F, Somphospondyli. Note that the component taxa of Upchurch's (1995, 1998) Euhelopodidae are widely distributed on Wilson and Sereno's cladogram.

(Wiman 1929; Text-fig. 2A). However, this similarity is based solely on the shared retention of many primitive eusauropod character states, namely: the presence of large V-shaped wear facets; low SIs (seen in one of the Shiramine teeth); the presence of labial grooves; and the retention of the lingual ridge and concavity (Upchurch 1998; Wilson and Sereno 1998). The teeth of several basal titanosauriforms (*Brachiosaurus* and teeth referred to 'Astrodon' or *Pleurocoelus*) also retain many of these primitive eusauropod features (see Leidy 1865; Janensch 1935–36; Ostrom 1970). However, unlike euhelopodid teeth, the tooth crowns of basal titanosauriforms have higher SI values that range between 2.0 and 4.0. This range accommodates the relatively elongate crowns of some of the Shiramine teeth (SI of 3.0, see above), unlike the SI ranges of euhelopodids and other non-titanosauriform, non-diplodocoid sauropods (see above). Moreover, the lingual ridges present on *Brachiosaurus* teeth are mesiodistally broad (Janensch 1935–36; PMB, pers. obs.) and cover much of the lingual concavity, as is also seen in the teeth from Shiramine. In contrast, the lingual ridges of *Euhelopus* teeth are much narrower (Wiman, 1929). Finally, the range of tooth wear seen in the Shiramine sauropod matches closely the variation in tooth wear seen in *Brachiosaurus*. *Brachiosaurus* teeth often possess large, mesiodistally broad, apicobasally short wear facets (see Janensch 1935–36; Upchurch and Barrett 2000) that are almost identical to the apical wear facet seen on SBEI 583. Moreover, some *Brachiosaurus* teeth possess high-angled mesial and distal wear facets but no apical wear (as also seen in SBEI 183) while others display a combination of apical wear and mesial and distal wear (Janensch 1935–36; Upchurch and Barrett 2000; PMB, pers. obs.). The latter combination of wear features is seen in another of the sauropod teeth from Shiramine (SBEI 1473).

Taking all of the aforementioned dental characters into account, the mosaic of primitive and derived character states present in the Shiramine teeth appears to exclude them from Euhelopodidae, Titanosaurioidea and Diplodocoidea. On the basis of current evidence, assignment to the Titanosauriformes is the most plausible systematic hypothesis. The Shiramine sauropod appears to be a basal member of the titanosauriform radiation (as the teeth lack many titanosauroid synapomorphies), and may be closely related to the brachiosaurids. This assignment should be regarded as tentative, however, pending the discovery of additional material.

SUPPOSED NEMEGTOSAURID TEETH FROM JAPAN

Tanimoto and Mizutani (1999a) described a sauropod tooth from the Lower Cretaceous (Berriasian–Hauterivian) Matsuo Group of Toba City, Mie Prefecture, and tentatively referred it to the Titanosaurioidea. Subsequently, this tooth was transferred to the Nemegtosauridae (Tanimoto and Mizutani 1999b). The published figures indicate that the tooth crown is D-shaped in cross-section and possesses large, high-angled wear facets on the mesial and distal crown margins; the crown is mesiodistally narrow and not greatly expanded relative to the root (Tanimoto and Mizutani 1999a, b). The lingual surface is concave and appears to have a low and very broad lingual ridge. It is not possible to assess precisely the SI of the tooth from the available information, but measurements taken from the published photographs indicate an SI much lower than 4.0. This combination of character states suggests that the tooth is not referable to the Nemegtosauridae: nemegtosaurid teeth are peg-like, lack a lingual concavity, and have SIs >5.0 (Nowinski 1971; Upchurch 1998). In terms of overall morphology, the Toba sauropod tooth appears to be very similar to the teeth of *Pleurocoelus* (e.g. Ostrom 1970), suggesting that it might be referable to the Titanosauriformes; the combination of character states present in the tooth and in the associated postcrania (Y. Tomida, pers. comm. 1999) are consistent with this interpretation.

A putative nemegtosaurid tooth (SBEI 12) reported from the Kuwajima Formation of Shiramine (Barrett and Manabe 2000; Manabe and Barrett 2000) has subsequently been reidentified as the tooth of a large pterosaur. As a result, no nemegtosaurid material has been recovered from the Japanese Cretaceous to date.

A REVIEW OF SAUROPOD TAXA FROM THE LOWER CRETACEOUS OF EASTERN ASIA

Early Cretaceous sauropod material from eastern Asia is extremely fragmentary and provides only a very limited amount of systematic and taxonomic information. Furthermore, dating of the deposits from which

sauropod material has been recovered is not well established: the age of a horizon cannot usually be established to the level of standard European stages. Consequently, most of the relevant stratigraphical units are either described simply as 'Early Cretaceous' (e.g. Weishampel 1992) or assigned to the '*Psittacosaurus* fauna', a complex of stratigraphic horizons of supposed Berriasian–Aptian age united by the occurrence of the ceratopian dinosaur *Psittacosaurus* (e.g. Dong 1992, 1993, 1995). While these shortcomings to some extent frustrate attempts to test biogeographical scenarios that require a higher degree of systematic and temporal resolution, consideration of this material is necessary as it offers important information on sauropod diversity in eastern Asia at this time. This material is reviewed briefly below.

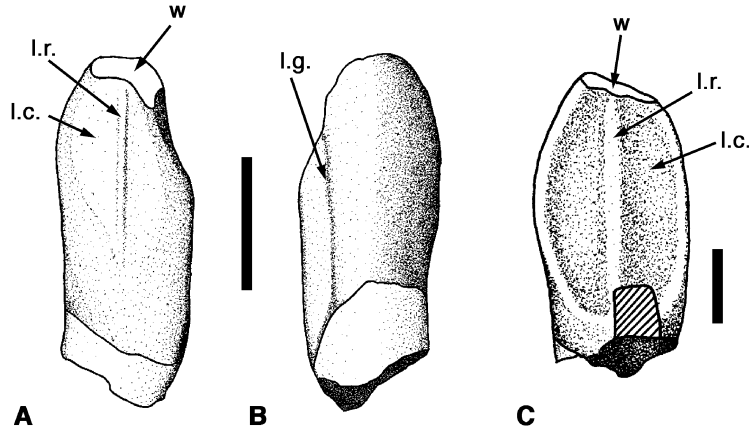
'*Asiatosaurus*' Osborn, 1924

Osborn (1924) based '*Asiatosaurus mongoliensis*' on two large (up to 70 mm in apicobasal length) partial tooth crowns from the Khukhtetskaya Svita (Aptian–Albian; Weishampel 1992) of Ovorkhangai, Mongolia. Each of these crowns possesses a suite of eusauropod character states: D-shaped cross-section; presence of labial grooves; presence of a lingual concavity and ridge; and large, high-angled mesial and distal wear facets (see Osborn 1924). The holotype tooth (AMNH 6264) has a very small lingual ridge, confined to the base of the lingual concavity, and a SI of 2.5 (the base of the crown is broken, so this represents a minimum value). In contrast, the paratype tooth (AMNH 6296) has a mesiodistally broad lingual ridge, which extends basally from the crown apex and covers much of the lingual concavity, and a SI of 2.1. Calvo (1996) suggested that the combination of a *Brachiosaurus*-like mesiodistally narrow tooth crown with *Camarasaurus*-like, high-angled, mesial and distal wear facets was sufficient grounds for recognising '*A. mongoliensis*' as a valid taxon. However, both of these character states also co-occur in some teeth of *Brachiosaurus* and *Dicraeosaurus* (Janensch 1935–36) and are distributed more generally within the Eusauropoda (Upchurch 1998; Wilson and Sereno 1998). Consequently, neither tooth possesses any unique diagnostic features that support the validity of the taxon. '*Asiatosaurus mongoliensis*' should, therefore, be regarded as a *nomen dubium* (McIntosh 1992; contra Calvo 1996). Moreover, no characters provide support for the referral of these teeth to any particular eusauropod clade and they should be regarded as Eusauropoda indeterminate.

A second species of '*Asiatosaurus*' was erected by Hou *et al.* (1975) on the basis of a tooth, three cervical vertebrae and some fragmentary ribs from the Napan Formation of Guangxi Province, PR China. The tooth of '*A. kwangshiensis*' appears to possess most of the eusauropod character states listed for '*A. mongoliensis*' above, although it differs in its lack of large mesial and distal wear facets (Hou *et al.* 1975; Text-fig. 4c). The tooth has a SI of 1.9. The presence of large pleurocoels in the cervical vertebrae indicates that '*A. kwangshiensis*' is not a member of the Euhelopodidae (*sensu* Upchurch 1995, 1998), but belongs to a clade consisting of either Neosauropoda + non-euhelopodid eusauropods (Upchurch 1998) or Neosauropoda + *Omeisaurus* (Wilson and Sereno, 1998), depending upon the preferred phylogeny. The features listed in the diagnosis of '*A. kwangshiensis*' (spatulate teeth; large, procoelous cervical vertebrae with pleurocoels; long dorsal ribs with broadly expanded proximal ends) are not autapomorphic, but have a wider distribution within Sauropoda, and this species should be regarded as a *nomen dubium* (McIntosh 1992).

'*Chiayusaurus*' Bohlin, 1953

'*Chiayusaurus lacustris*' was named on the basis of an isolated tooth from the Xinminbao Group (Barremian–Albian) of Gansu, PR China (Bohlin 1953; Tang *et al.* 2001; Text-fig. 4A–B). The tooth is spatulate, has a crown that is slightly expanded mesiodistally and is D-shaped in cross-section. A lingual concavity and narrow lingual ridge are present and the crown also possesses labial grooves. The crown apex bears a small apical wear facet and a high-angled wear facet is present along the distal crown margin. The crown has a SI of approximately 1.8 (see Bohlin 1953). This combination of character states places '*Chiayusaurus*' within Eusauropoda (Upchurch 1995, 1998; Wilson and Sereno 1998), but does not permit referral to any particular sauropod clade. Although the tooth is almost identical to the teeth of *Euhelopus*



TEXT-FIG. 4. A–B, holotype tooth of '*Chiayusaurus lacustris*' (redrawn from Bohlin 1953) in lingual (A) and labial (B) views. C, holotype tooth of '*Asiatosaurus kwangshiensis*' (redrawn from Hou *et al.* 1975) in lingual view. Abbreviations: l.c., lingual concavity; l.g., lingual groove; w, wear facet. Scale bars represent 10 mm (A–B) and 20 mm (C).

(Bohlin 1953), it possesses no autapomorphic features that support its referral to this genus. Calvo (1996) considered '*C. lacustris*' to be a junior synonym of '*Asiatosaurus mongoliensis*' on the basis of similarities in the pattern of tooth wear, but the proposed autapomorphies of '*A. mongoliensis*' have a wider distribution within Sauropoda and are not adequate for a diagnosis (see above). Moreover, the type teeth of '*C. lacustris*' and '*A. mongoliensis*' share no unique derived character states that would justify their synonymy (contra Calvo 1996). '*Chiayusaurus lacustris*' possesses no autapomorphies that justify its status as a valid taxon and it should, therefore, be regarded as a *nomen dubium* (McIntosh 1992), Eusauropoda indeterminate.

A second species, '*C. asianensis*' has been erected for an isolated tooth from the Hasandong Formation (Hauterivian) of South Korea (Lee *et al.* 1997, 2001). The tooth crown is narrow, parallel-sided and slender (SI = 3.3). There is a prominent lingual concavity that contains a small lingual ridge. At least one labial groove is present and large, high-angled wear facets extend along the mesial and distal margins of the crown (Lee *et al.* 1997). Consequently, this tooth shares no apomorphic features with the type tooth of '*C. lacustris*' (see description above) and, in fact, differs from the latter in several respects. Moreover, the type tooth of '*C. asianensis*' possesses no autapomorphic character states; one proposed autapomorphy, the distribution of the wear surfaces around the crown margin, has a broader distribution within Sauropoda (Upchurch 1998; Wilson and Sereno 1998; Upchurch and Barrett 2000). The combination of character states present in '*C. asianensis*' is suggestive of titanosauriform affinities and this taxon should be regarded as a *nomen dubium*, Titanosauriformes indeterminate.

Euhelopus Romer, 1956

Euhelopus zdanskyi was established on the basis of two partial skeletons, one with an associated partial skull, from the Meng-Yin Formation of Shandong Province, People's Republic of China (Wiman 1929). The age of the Meng-Yin Formation is currently uncertain (Wu *et al.* 1994). Consideration of the dinosaur fauna and of freshwater invertebrates has led some authors to suggest a Late Jurassic age (e.g. Young 1958; Chen 1982; Dong 1992); however, other biostratigraphical evidence has been advanced in favour of an Early Cretaceous age (Dong 1993, 1995).

The validity of *Euhelopus* is supported by numerous autapomorphies (McIntosh 1992; Wilson and Sereno 1998) and its anatomy is reasonably well known (Wiman 1929; Mateer and McIntosh 1985; McIntosh 1992). The phylogenetic position of *Euhelopus* is controversial, however, and has been the subject of some debate. Upchurch (1995, 1998) has suggested that *Euhelopus* is a member of the

Euhelopodidae, a monophyletic group of Chinese taxa that occupies a basal position within Eusauropoda. In contrast, several other authors have considered *Euhelopus* to be a neosauropod and either placed it within Camarasauridae (McIntosh 1992) or considered it to be the sister-taxon to the Titanosauria (Gauthier 1986; Wilson and Sereno 1998). Wilson and Sereno (1998) found little support for euhelopodid monophyly and suggested that Euhelopodidae was a paraphyletic assemblage composed of basal eusauropods (*Shunosaurus* and *Omeisaurus*) and a titanosauriform (*Euhelopus*).

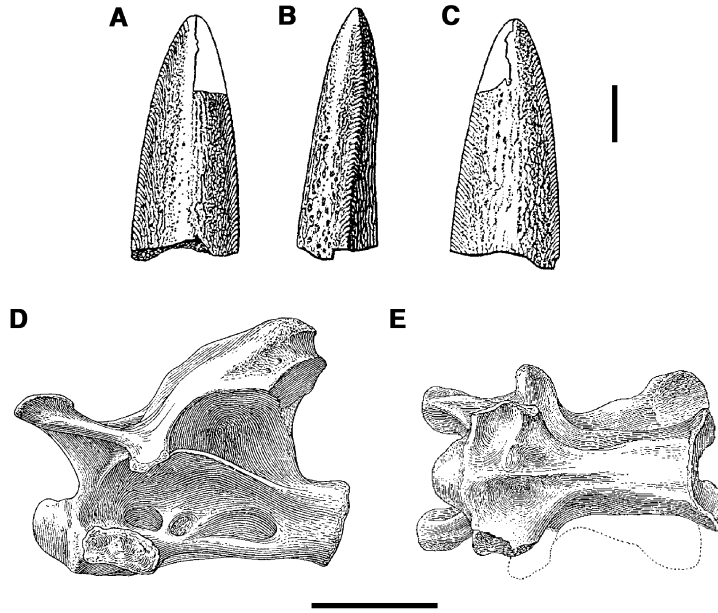
On the basis of the available data, we follow Upchurch (1995, 1998) in regarding the Euhelopodidae as a monophyletic clade, though we are also mindful of Wilson and Sereno's (1998) alternative hypothesis. The justification for our decision is based upon: the number of characters used in each analysis; the number of taxa included; and the strength of the various phylogenetic hypotheses in the face of several robustness tests. Upchurch's (1998) phylogeny is based on 205 characters scored for 26 individual sauropod taxa, whereas Wilson and Sereno (1998) presented only 109 characters scored for ten sauropod taxa, three of which are composite taxa (Diplodocoidea, Brachiosauridae and Titanosauria) whose monophyly and ingroup relationships were not tested explicitly in the analysis. Moreover, Upchurch (1998; Wilkinson *et al.* 2000) thoroughly explored the strengths and weaknesses of his data set using a large number of analytical approaches (such as matrix randomisation tests, decay analysis and double decay analysis). In contrast, the testing of the Wilson and Sereno (1998) data set did not approach this level of statistical rigour. The phylogenetic position of the various euhelopodid taxa has a direct bearing on several biogeographic scenarios and is discussed further below.

'*Mongolosaurus*' Gilmore, 1933

This taxon is based upon several teeth, a basioccipital, an atlas, an axis and a third cervical vertebra that were recovered from the On Gong Formation of Inner Mongolia (Gilmore 1933; Text-fig. 5). The teeth have very slender crowns and are subcylindrical in cross-section, indicating that they are referable to either Titanosauroidae or Diplodocoidea (Upchurch 1995, 1998; Wilson and Sereno 1998; Text-fig. 5A–C). Several features of the basioccipital and cervical vertebra suggest that '*M. haplodon*' cannot be referred to either Diplodocidae or Dicraeosauridae, however. The basioccipital is damaged and lacks the distal ends of the basiptyergoid processes; nevertheless, several characters can be coded for this element. The basioccipital condyle is posteroventrally oriented with respect to the long axis of the skull (the primitive condition for sauropods), in contrast to the ventrally oriented basioccipital condyle characteristic of dicraeosaurids and diplodocids (Upchurch 1998). Moreover, the proximal portions of the basiptyergoid processes indicate that they diverged from each other at an angle of approximately 45 degrees and that they extended ventrolaterally from the base of the braincase (Gilmore 1933). In contrast, the basiptyergoid processes of diplodocids and dicraeosaurids extend in an anteroventral direction; furthermore, in dicraeosaurids the basiptyergoid processes diverge at an angle of approximately 20 degrees (Upchurch 1998).

Several features of the cervical vertebrae also indicate that '*M. haplodon*' cannot be referred to the Dicraeosauridae. Dicraeosaurids are characterised by cervical vertebrae whose total height (height of neural arch + height of centrum) is approximately 1.5 times greater than the anteroposterior length of the centrum; in comparison, '*M. haplodon*' (Gilmore 1933) and all other sauropods have relatively short neural spines, resulting in a ratio of total vertebral height to centrum length of approximately 1.0 in these taxa (Upchurch 1998). The cervical vertebra of '*M. haplodon*' has a large pleurocoel that is subdivided by an accessory oblique lamina (Text-fig. 5D), a synapomorphy of either *Haplocanthosaurus* + Neosauropoda (Upchurch 1998) or *Omeisaurus* + Neosauropoda (Wilson and Sereno 1998). Dicraeosaurids, however, lack divided cervical pleurocoels (a secondary reversal; Upchurch 1998). Moreover, the cervical vertebrae of dicraeosaurids and diplodocids have deeply excavated, concave ventral surfaces; all other sauropods (including '*M. haplodon*'; Text-fig. 5E) have cervical vertebrae with either very shallow-convex or flat ventral surfaces transversely (Upchurch 1998).

Further consideration of the cervical vertebrae suggests that referral of '*M. haplodon*' to the Euhelopodidae is also unlikely. Euhelopodids have transversely compressed anterior cervical vertebrae, with centra that are approximately 1.25 times higher than wide; other sauropods (including '*M. haplodon*';



TEXT-FIG. 5. Type material of '*Mongolosaurus haplodon*'. A–C, tooth in labial (A), mesial (B) and lingual (C) views. D–E, third cervical vertebra in lateral (D) and ventral (E) views (from Gilmore 1933, courtesy of the American Museum of Natural History). Scale bars represent 5 mm (A–C) and 100 mm (D–E).

Gilmore 1933) have relatively wider anterior cervical centra that are only ≤ 1.0 times higher than wide (Upchurch 1998). Moreover, euhelopodids lack subdivided cervical pleurocoels (Upchurch 1998). Most euhelopodids (*Mamenchisaurus*, *Omeisaurus* and *Shunosaurus*) possess a midline keel on the posterior half of the ventral surface of the centrum (Upchurch 1998). '*M. haplodon*' lacks this keel and is, therefore, apparently excluded from the Euhelopodidae. However, this character state has a complex distribution; one euhelopodid (*Euhelopus*) lacks the midline ventral keel, as do several other sauropods (*Barapasaurus*, *Dicraeosaurus*, *Patagosaurus* and others). The cervical neural spine of '*M. haplodon*' is posterodorsally inclined (Gilmore 1933), a character state seen in all sauropods with the exception of titanosaurs and *Euhelopus* (Wilson and Sereno 1998).

In summary, the presence of peg-like teeth in '*M. haplodon*' supports referral to the Neosauropoda, as does the phylogenetic distribution of several derived character states of the cervical vertebrae. Several character states preclude referral of '*M. haplodon*' to the Euhelopodidae or to other basal eusauropods. Referral of this taxon to Diplodocidae and Dicraeosauridae are unlikely on the basis of the available evidence and at least one derived character state of titanosaurs argues against referral to the Titanosauria. More precise phylogenetic placement of '*M. haplodon*' is not possible on the basis of current material: a basal position within either Diplodocoidea or Titanosauroidea is equally plausible on the basis of the available data (see also Upchurch 1995). '*M. haplodon*' appears to lack any unambiguous autapomorphic features and should be regarded as a *nomen dubium*, Neosauropoda indeterminate.

Phuwiangosaurus Martin, Buffetaut and Suteethorn, 1994

Phuwiangosaurus sirindhornae is known from the Lower Cretaceous (?Valanginian–?Barremian) Sao Khua Formation of Thailand and is represented by hundreds of disarticulated postcranial elements, including those of juveniles, and rare cranial remains (Martin *et al.* 1994, 1999; Buffetaut and Suteethorn 1999). Various postcranial autapomorphies support the validity of this taxon, but the phylogenetic position

of *Phuwiangosaurus* is disputed. Martin and colleagues have suggested that *Phuwiangosaurus* is a nemegtosaurid on the basis of tooth morphology (Martin *et al.* 1999; Buffetaut and Suteethorn 1999). However, the 'nemegtosaurid dental characteristics' listed by these authors are diplodocoid and titanosaurid symplesiomorphies (Upchurch 1998; Wilson and Sereno 1998): therefore, they cannot be used to determine the systematic status of *Phuwiangosaurus*. Derived character states that unite *Phuwiangosaurus* with the nemegtosaurids to the exclusion of other sauropod clades have yet to be identified.

The phylogenetic analyses of Upchurch (1995, 1998, 1999) indicate that *Phuwiangosaurus* is not closely related to the nemegtosaurids (which Upchurch considers to be members of the diplodocoid lineage; but see Salgado and Calvo 1997, Wilson and Sereno 1998, and Curry Rogers and Forster 2001 for alternative viewpoints), but is a basal member of the Titanosauroidae. Wilson and Sereno (1998) did not include *Phuwiangosaurus* in their analysis, but did refer it to the Titanosauriformes (based on the identification of several titanosauriform synapomorphies in this material), a systematic position that is close to the one advocated by Upchurch (1998). For the time being, we follow Upchurch's (1998, 1999) conclusions regarding the systematic position of this genus as his study is the only one that has included *Phuwiangosaurus* in a full cladistic analysis.

'*Ultrasaurus*' Kim, 1983

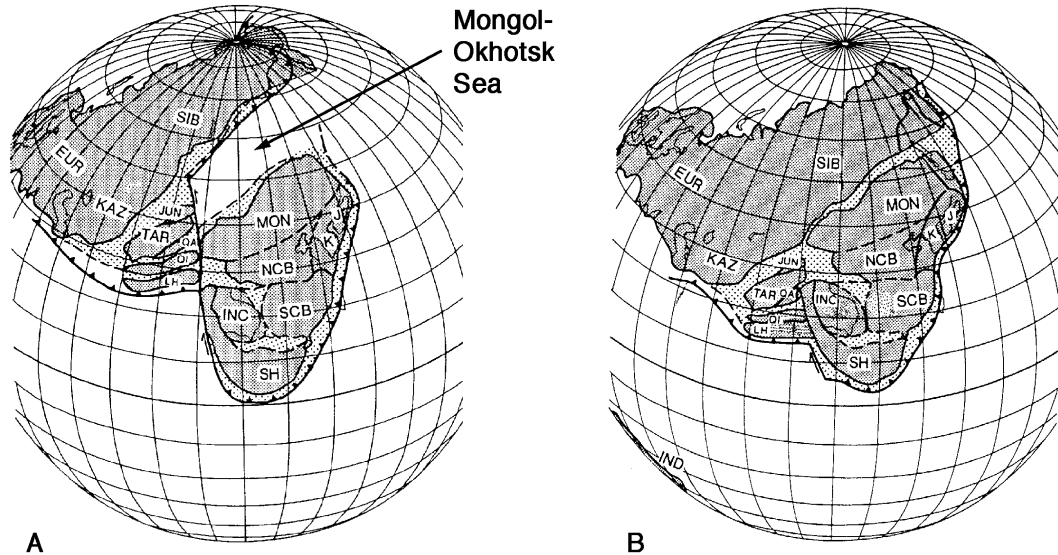
Kim (1983) based '*Ultrasaurus tabriensis*' on the proximal part of a left humerus (initially misidentified as the proximal end of a right ulna; Lee *et al.* 1997) from the Gugyedong Formation (Aptian; Lee *et al.* 1997) of South Korea. However, reassessment of this material has demonstrated that it displays no autapomorphic features and should be regarded as a *nomen dubium* (McIntosh 1992; Lee *et al.* 1997). The absence of a well-developed process on the lateral margin of the proximal end of the humerus excludes '*Ultrasaurus*' from a clade composed of derived titanosaurids (Upchurch 1998), but the humerus possesses no other character states that permit the referral of this taxon to any particular sauropod clade and should be regarded as Sauropoda indeterminate.

Indeterminate sauropod material

Several fragmentary specimens document the presence of neosauropods in the Early Cretaceous of China. A partial vertebra from the Xinminbao Group of Gansu Province (Bohlin 1953; Barremian–Albian, Tang *et al.* 2001) displays the cancellous bone texture characteristic of titanosauriform sauropods (Upchurch 1998; Wilson and Sereno 1998). Two partial tooth crowns from the Xinminbao Group, described as 'aff. *Chiayusaurus*' and 'aff. *Mongolosaurus*' respectively (Bohlin 1953), are slender (with SIs of >3.0), parallel-sided and have D-shaped cross-sections. One tooth (that of 'aff. *Mongolosaurus*') possesses extensive mesial and distal wear facets (Bohlin 1953). These tooth crowns are very similar to those from Shramine (see above) and it is likely that they are also referable to the Titanosauriformes. An isolated tooth from the Early Cretaceous (Barremian–Aptian) Jinju Formation of South Korea has recently been referred to the Brachiosauridae and has been hailed as the first evidence of this family to be found in Asia (Lim *et al.* 2001). However, although the tooth crown is parallel-sided and has a high SI (*c.* 3.0), it lacks the characteristic chisel-like wear facets seen on the anterior teeth of *Brachiosaurus* (contra Lim *et al.* 2001). Consequently, there is no evidence to support the identification of this tooth as that of a brachiosaurid, though the combination of character states displayed by the tooth does suggest that it pertains to an indeterminate basal titanosauriform.

DISCUSSION

During the Early Cretaceous, the various terranes that comprise south-western Japan were situated at the easternmost margin of continental Asia (Kojima 1989; Enkin *et al.* 1992; Otsuki 1992; Azuma and Tomida 1995; Isozaki 1996). The Tetori Basin encompassed a broad coastal plain located on the Hida terrane, which was positioned between the Sino-Korean continent, located to the north-west, and an accretionary



TEXT-FIG. 6. Palaeogeographic maps showing the position of Japan and the Sino-Korean continental blocks relative to the rest of eastern Asia in A, the Late Jurassic and B, the Early Cretaceous (both after Enkin *et al.* 1992, © 1992 American Geophysical Union; reproduced by permission of American Geophysical Union). Abbreviations refer to major tectonic divisions: EUR, Europe; INC, Indo-China; IND, India; J, Japan; JUN, Junggar; K, Korea; KAZ, Kazakhstan; LH, Lhasa; MON, Mongolian; NCB, North China; QI, Qiangtang; SCB, South China; SH, Shan Thai; SIB, Siberian; TAR, Tarim.

prism, composed of the Tamba-Mino-Ashio terrane, situated to the south-east (Kojima 1989; Otsuki 1992; Azuma and Tomida 1995; Isozaki 1996; Evans *et al.* 1998). This coastal plain was traversed by wide, meandering river systems that transported sediments derived from the Sino-Korean continent into the Tetori Basin (Taira and Matsuo 1983, 1984). The transport and deposition of these sediments in a non-marine setting demonstrates that a land connection existed between south-west Japan and eastern Asia during the Early Cretaceous (Azuma and Tomida 1995). The proximity of Japan to the Sino-Korean continent (Text-fig. 6), and the establishment of land connections between these areas, suggest that the faunas of the two regions should be very similar.

Consideration of palaeogeography and of the composition of various terrestrial vertebrate faunas led Russell (1993, 1995) to propose that central and eastern Asia had been isolated from Pangaea during Middle Jurassic–Early Cretaceous times. During this period, the vertebrate fauna of central and eastern Asia displayed a high degree of endemism, with little or no evidence for the presence of vertebrate taxa from other palaeobiogeographic provinces. According to Russell's (1993) thesis, the appearance of more cosmopolitan forms, such as iguanodontian dinosaurs and paramacellodid lizards, during the Aptian and Albian signalled a reduction in endemism and indicated an end to geographical isolation. Upchurch (1995) provided some support for Russell's hypothesis, arguing that eastern Asia was home to a monophyletic radiation of euhelopodid sauropods. Possible palaeogeographical mechanisms for the isolation of central and eastern Asia included the presence of the extensive Mongol-Okhotsk Sea (that separated eastern Asia from Siberia for much of the Mesozoic before finally closing during the Early Cretaceous; Enkin *et al.* 1992; Text-fig. 6) (Upchurch 1995), possible breaches of the Junggar-Tarim-Mongolian land bridge (that formed a tenuous link between eastern and central Asia during the Triassic and Jurassic; Enkin *et al.* 1992; Text-fig. 6) (Upchurch 1995) and the formation of epicontinental seas between Europe and central Asia (Russell 1993). Luo (1999) also concurred with Russell (1993) in suggesting that eastern Asia had acted as a refugium during Early Cretaceous times, permitting the survival of various 'relict' taxa (including compsognathid theropods and 'rhamphorhynchoid' pterosaurs) that had supposedly become extinct

elsewhere by the end of the Jurassic (but see Manabe *et al.* 2000 and Unwin *et al.* 2000 for an alternative viewpoint).

The presence of titanosauriform sauropods in Lower Cretaceous deposits in Japan provides some new data with which to test the hypothesis of eastern Asian isolation. If euhelopodid monophyly is accepted, then it is possible that all Chinese sauropods from the Middle and Upper Jurassic were members of a single radiation (Upchurch 1995, 1998). The phylogenetic position of several enigmatic sauropod taxa [e.g. *Bellusaurus* (Dong 1990) and *Klamelisaurus* (Zhao 1993)] from the Middle and Upper Jurassic of China cannot be ascertained on the basis of current evidence; however, these animals do possess some character states that might be indicative of euhelopodid affinities (Upchurch 1995). Upchurch's (1995, 1998) analyses and synapomorphy lists thus suggest that all non-euhelopodid sauropod lineages, including titanosauriforms, are currently unknown from the Middle–Upper Jurassic of eastern Asia. The appearance of titanosauriform sauropods in the basal Cretaceous of Japan would, therefore, suggest that the geographical isolation of eastern Asia ended during the latest Jurassic or earliest Cretaceous, rather than during the late Early Cretaceous as previously suggested (Russell 1993, 1995; Luo 1999). This scenario implies immigration of titanosauriforms into eastern Asia from Europe or central Asia just before their appearance in Japan during the Early Cretaceous.

However, this conclusion is weak if based only on the presence of indeterminate titanosauriform material in the Japanese Lower Cretaceous. Wilson and Sereno's (1998) phylogeny suggests that Upchurch's (1995) biogeographic conclusions might be in error, as they do not recognise euhelopodid monophyly; indeed, their alternative scheme of relationships suggests that a number of sauropod lineages were present in China during the Middle and Late Jurassic, including several basal eusauropods (*Omeisaurus* and *Shunosaurus*) and a titanosauriform (*Euhelopos*). If this alternative phylogeny proves to be correct, then the presence of titanosauriform sauropods in the Japanese Lower Cretaceous would be unsurprising, as a representative of that clade would have been present in the Late Jurassic (or Early Cretaceous; see above for problems relating to the dating of the Meng-Yin Formation) of China. Moreover, as admitted by Upchurch (1995), the relationships of taxa such as *Bellusaurus* (see above) are still not firmly established, suggesting that, even if Upchurch's (1998) phylogeny is essentially correct, there is still potential for non-euhelopodid sauropods to have been present in China during the Jurassic. Nevertheless, as Upchurch's (1998) phylogeny is currently the best supported (see above), we prefer the former hypothesis in which the Early Cretaceous occurrence of Japanese titanosauriforms places some constraint on the end of eastern Asian isolation, though we recognise that this situation may change when further evidence becomes available.

Other sauropods from the Lower Cretaceous of eastern Asia provide additional support for an earlier than expected end to isolation. The occurrence of the basal titanosaur *Phuwiangosaurus* in the ?Valanginian–?Barremian of Thailand convincingly demonstrates the presence of a non-euhelopodid taxon in eastern Asia before the Aptian/Albian. Moreover, fragmentary remains of '*Mongolosaurus*', '*Chiayusaurus asianensis*', '*Asiatosaurus kwangshiensis*' and several other unnamed forms (see above) testify to the presence of non-euhelopodid sauropods (indeterminate neosauropods, titanosauriforms) in the Lower Cretaceous of China and Mongolia. However, the biogeographic utility of the latter specimens, with the exception of '*C. asianensis*', is hampered by the lack of precise dates for their various localities. The Hauterivian age of '*C. asianensis*' (Lee *et al.* 2001) and the Barremian–Albian age of indeterminate titanosauriforms from Gansu and South Korea (see above) provide additional support for the early immigration of titanosauriform sauropods into eastern Asia.

This biogeographic scenario is the same as that suggested by consideration of the iguanodontian ornithopods from the Lower Cretaceous Okurodani and Kuwajima formations of Japan (Hasegawa *et al.* 1995). Iguanodontian ornithopods are currently unknown from the Jurassic and lowermost Cretaceous of central and eastern Asia, and until recently the earliest occurrence of iguanodontians in this region was marked by the appearance of *Probactrosaurus* in several units of Aptian/Albian age in Mongolia and northern China (e.g. Rozhdestvensky 1966; Jerzykiewicz and Russell 1991; Weishampel 1992). The identification of iguanodontian teeth in the basal Cretaceous of Japan therefore suggested an end to eastern Asian isolation prior to the Aptian/Albian date proposed by Russell (1993). Moreover, the recent discovery of a new iguanodontian (*Jinzhouosaurus*; Wang and Xu 2001) from the Yixian Formation of north-eastern China (now generally considered to be of Barremian age; Swisher *et al.* 1999; Barrett 2000) confirms

the pre-Aptian occurrence of this clade in East Asia, as does the occurrence of *Probactrosaurus mazongshanensis* (Lu 1997) in the Barremian–Albian Xinminbao Group (Tang *et al.* 2000).

CONCLUSION

The Kuwajima Formation is offering important new insights into the terrestrial and freshwater biotas of East Asia during the Early Cretaceous. In addition to increasing our knowledge of Early Cretaceous faunas, this material has also permitted the testing of existing palaeobiogeographic scenarios. Current data, though limited, suggest that eastern Asian isolation ended approximately 20 myr earlier than previously suggested. Moreover, the material from Shiramine, and reassessment of material from other parts of East Asia, indicate that titanosauriform sauropods were an integral part of faunas in this region during the Early Cretaceous. Recovery of more material from the Shiramine locality, and from others like it, should provide more much-needed information on the diversity and distribution of dinosaur faunas in Asia.

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