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THE TAXONOMIC STATUS OF *MEGALOSAURUS BUCKLANDII* (DINOSAURIA, THEROPODA) FROM THE MIDDLE JURASSIC OF OXFORDSHIRE, UK

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Abstract: The lectotype of the Middle Jurassic theropod dinosaur *Megalosaurus bucklandii*, a right dentary, can be diagnosed on the basis of two unique characters: a longitudinal groove on the ventral part of the lateral surface of the dentary and a slit-like anterior Meckelian foramen. This taxon, the first dinosaur to be scientifically described, is therefore valid. Currently, however, no further material can be referred to this species with any certainty. *Megalosaurus bucklandii* occupies an uncertain systematic position but is not an abelisaurid or coelophysoid. Additionally, it does not possess the diagnostic dentary characters that are present in all known spinosauroids. Owing to this uncertainty, use of the family Megalosauridae should be discontinued until such time as its systematic position becomes clearer.

Key words: Dinosauria, Theropoda, *Megalosaurus,* Bathonian.

MEGALOSAURUS is a theropod dinosaur from the Middle Jurassic of England. It is historically important as the first dinosaurian taxon to be recognised as reptilian and formally described in the scientific literature (Buckland 1824) as well as being one of the taxa upon which Richard Owen (1842) originally based the Dinosauria. The type species, *Megalosaurus bucklandii*, was erected by Mantell (1827) based on the collection of material from Stonesfield, Oxfordshire, UK that formed the basis for Buckland's original description. Until recently *Megalosaurus* occupied a central position in studies of non-coelurosaurian theropods and was often proposed as a typical early 'carnosaur' in the older literature (e.g. von Huene 1926). The taxon is also important as it is a representative of the poorly known Middle Jurassic dinosaur fauna (Rauhut 2003; Holtz *et al.* 2004).

In the years following the description of the syntype series, material from a range of Middle Jurassic–Lower Cretaceous localities in England and northern France was unjustifiably referred to *M. bucklandii*, reaching an acme in Phillips (1871). Subsequently, the species was restricted to material from the type horizon, the Stonesfield Slate, by von Huene (1923). This material consists of numerous unassociated elements belonging to large theropods and representing much of the skeleton (Buckland 1824; Phillips 1871). Cladistic analyses (Holtz 1994, 2000) have found the taxon to be a basal tetanuran and one of a succession of outgroups to a more derived clade comprising allosauroids and coelurosaurs. The analysis of Holtz *et al.* (2004) found *Megalosaurus* to be a spinosauroid related to *Poekilopleuron* and *Torvosaurus*. Allain and Chure (2002), however, proposed that multiple taxa were represented in the large theropod material from the Stonesfield Slate, an observation confirmed by Day and Barrett (2004). It was suggested that the taxon should be restricted to the lectotype dentary (OUMNH J.13505) and it was recommended that *Megalosaurus*, as formerly considered, should not be included in cladistic analyses as such analyses would be utilising a chimera (Allain and Chure, 2002). The latter authors also failed to find diagnostic features of the dentary and thus considered *Megalosaurus* to be a *nomen dubium*.

In order for the fairly abundant and well-preserved Middle Jurassic theropod record of Britain to be of use to palaeontologists, a degree of taxonomic stability must be achieved. Re-evaluation of the lectotype of *M. bucklandii* suggests that the taxon can be diagnosed, but its phylogenetic position within Theropoda remains uncertain.

Institutional abbreviations. BMNH, Natural History Museum, London; BYU, Brigham Young University Museum of Geology,

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Provo; FMNH, Field Museum of Natural History, Chicago; MNHN, Muséum National d'Histoire Naturelle, Paris; OUMNH, Oxford University Museum of Natural History, Oxford; UCMP, University of California Museum of Paleontology, Berkeley; UMNH VP, University of Utah Museum of Natural History, Salt Lake City.

GEOLOGICAL SETTING

The lectotype and paralectotype series, and much of the referred material, was recovered from the Stonesfield Slate. This is a recurrent lithological facies that occurs at three levels within the Taynton Limestone Formation. It consists of beds of laminated calcareous sandstone that are restricted to the vicinity of the village of Stonesfield, Oxfordshire (Boneham and Wyatt 1993). The Taynton Limestone Formation pertains to the *Procerites progracilis* (ammonite) Zone, which is thought to have been deposited in the lower part of the middle Bathonian (Torrens 1980). The Stonesfield Slate has produced one of the most diverse Middle Jurassic vertebrate faunas known, including the remains of turtles, crocodilians, pterosaurs, dinosaurs, pliosaurs, ichthyosaurs and cynodonts (Benton and Spencer 1995).

SYSTEMATIC PALAEONTOLOGY

DINOSAURIA Owen, 1842
THEROPODA Marsh, 1881
Incertae sedis

Genus MEGALOSAURUS Buckland and Conybeare, *in* Buckland 1824

Type species. Megalosaurus bucklandii Mantell, 1827.

Diagnosis. As for the type species, *M. bucklandii*.

Remarks. The generic name *Megalosaurus* was first used in Parkinson (1822, p. 298) but this publication did not include a description, definition or any indication of types as required for the name to be available under Article 12 of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature 1999). Buckland (1824, p. 391) proposed the name accompanied by the explanation, 'In consideration therefore of the enormous magnitude which this saurian attains, I have ventured, in concurrence with my friend and fellow-labourer, the Rev. W. Conybeare, to assign to it the name of *Megalosaurus*'. This was accompanied by a detailed description including figures and is thus taken as the original source for the name.

Megalosaurus bucklandii Mantell, 1827
Text-figures 1–2

1826 *Megalosaurus conybeari* Ritgen, p. 354 (*nomen nudum*).
1827 *Megalosaurus bucklandii* Mantell, p. 67, pl. 18, fig. 2; pl. 19, figs 1, 8, 12, 14–16.
1832 *Megalosaurus bucklandi* von Meyer, p. 110.

Lectotype. OUMNH J.13505, a partial right dentary. OUMNH J. 13505b and 13505c, blocks of matrix containing the impressions of the lateral and medial sides of the dentary respectively and fragments of the superficial layers of the bone.

Locality and horizon. Unknown horizon within the Taynton Limestone Formation, middle Bathonian *Procerites progracilis* (ammonite) Zone, Stonesfield, Oxfordshire, UK.

Previous diagnosis. Twelve to thirteen teeth in maxilla and dentary, tooth carinae positioned anteriorly and posteriorly, not obliquely. Dentary straight, with symphysial facet. Vertebrae short; scapula large, with anterior expansion of middle part of blade; humerus stout; pubis with small distal thickening, extensive symphysis, no foot; ischium down-curved posteriorly; femur massive, lesser trochanter placed well down shaft; tibia stout, 83 per cent of femur length (after Waldman 1974, p. 326).

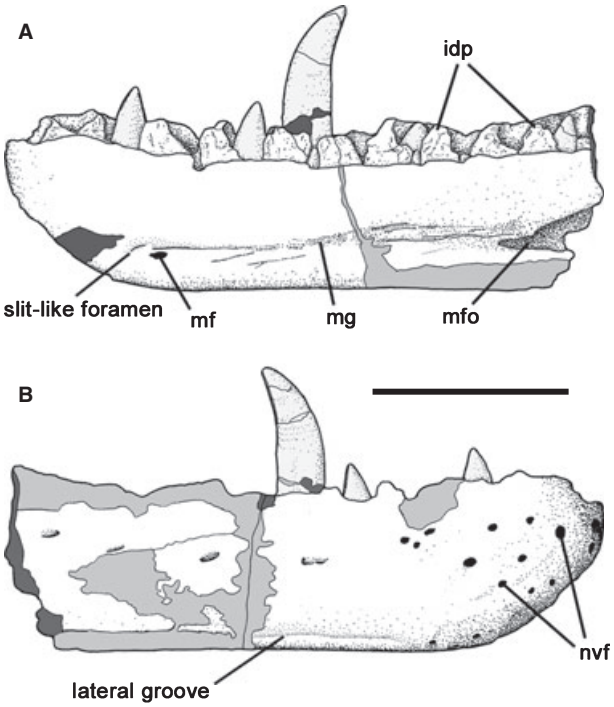
Revised diagnosis. Theropod dinosaur with the following autapomorphic features of the dentary: 13–14 teeth, a longitudinal groove in the ventral part of the lateral surface and a slit-like foramen anterior to the termination of the Meckelian groove.

Remarks. The binomen *Megalosaurus conybearei* was used by Ritgen (1826) but not accompanied by any description, diagnosis or indication as required under Article 12 of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature 1999) and is thus a *nomen nudum*. *Megalosaurus bucklandii* was used by Mantell (1827) in a publication including descriptions and figures of the syntype material. This spelling of the species epithet was used subsequently by only a few early authors (e.g. Mantell 1833; Eudes-Deslongchamps 1838) prior to Molnar *et al.* (1990) who incorrectly attributed the name to Ritgen (1826). Since that time it has been used as the presumed valid name in a handful of publications. *Megalosaurus bucklandi* was proposed by von Meyer (1832) and this spelling has been used by the vast majority of subsequent authors. Nevertheless it is an objective junior synonym of *M. bucklandii* Mantell, 1827.

The lectotype appeared in the collections of the Oxford Anatomy School at Christchurch College in 1797. The School's minute book for 24 October 1797 records this entry: 'Large jaw bone with two serrated teeth, in calc

schistus from Stonesfield, purchased for 10s 6d' (Günther 1925, p. 191). At this time the collection was being built by Dr (later Sir) Christopher Pegge, the Reader in Anatomy. Buckland was friendly with Dr Pegge but even if he had not been he would surely have known the collection as he was also a fellow of Christchurch.

The original syntype series of *Megalosaurus bucklandii* includes the various isolated, unassociated elements mentioned and figured by Mantell (1827) following the material originally attributed to this taxon by Buckland (1824), including: dorsal (OUMNH J. 13577) and caudal (OUMNH J. 13579) vertebrae, a sacrum (OUMNH J.13576), a right ilium (OUMNH J.29881: misidentified as a coracoid), a pubis (OUMNH J. 13563: misidentified as a fibula), an ischium (OUMNH J.13565: misidentified as a clavicle), a right femur (OUMNH J.13561), a metatarsal (OUMNH J. 13572), and two ribs (OUMNH J.13580, J.29792). Unfortunately, other material included in the original description (including a tooth and some fragments of bone) cannot be reliably identified among the OUMNH collections. Molnar *et al*. (1990) formally proposed designation of the dentary (OUMNH J.13505) as the lectotype, rendering the rest of the syntype series paralectotypes. However, as none of the paralectotypes can be convincingly referred to the same taxon as the lectotype dentary we follow Allain and Chure (2002) in restricting the hypodigm of *Megalosaurus bucklandii* to the lectotype pending the discovery of additional comparable material.

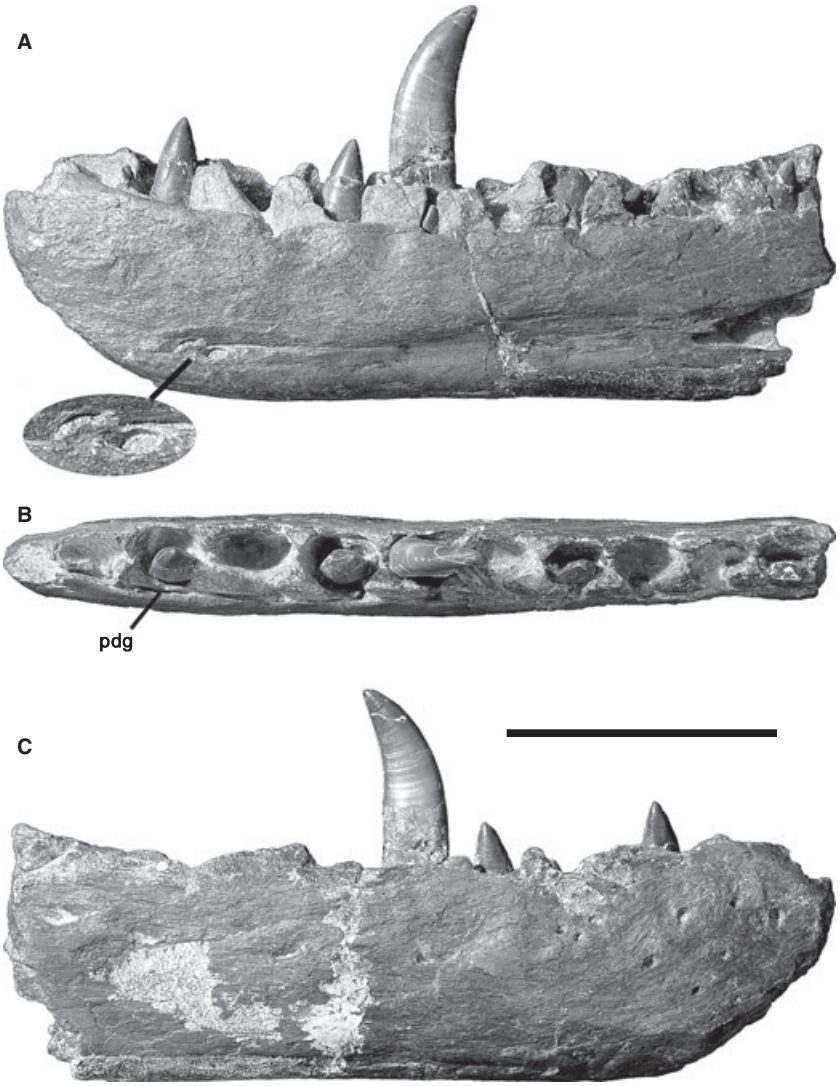


TEXT-FIG. 1. Interpretive drawing of lectotype right dentary (OUMNH J.13505) of *Megalosaurus bucklandii* from the Taynton Limestone Formation of Stonesfield, Oxfordshire, UK. A, medial and B, lateral views; idp, interdental plates; mg, Meckelian groove; mf, Meckelian foramen; mfo, Mecklian fossa; nvf, neurovascular foramina. Light grey represents tooth; medium grey, areas restored in plaster; dark grey, broken surface. Scale bar represents 100 mm.

Description. The type right dentary, OUMNH J.13505 is almost complete though missing much of the delicate portion posterior to the opening of the Meckelian fossa. The lateral and medial surfaces have been restored in part as indicated in Text-figure 1: however, there is no indication of damage in the figures of Buckland (1824, pl. 40, fig. 2) or Owen (1857, pl. 11, fig. 2). It is straight in dorsal view, unlike the medially curving dentary of *Allosaurus* (UMNH VP 9366). In lateral view it has a slightly sinuous ventral margin, being weakly convex anteriorly and weakly concave posteriorly, and a weakly convex dorsal margin, both of which are usual for carnivorous theropods.

Eleven alveoli are preserved, although more were certainly present. Waldman (1974) estimated that 12–13 teeth would have been present in the complete dentary based on comparison with *Allosaurus*. However, 13 teeth are present in the type of *Dubreuillosaurus valesdunensis* (MNHN 1998–13) with only ten positioned anterior to the position of the break in OUMNH J.13505. As such it is likely that more teeth, perhaps 14, were originally present in the latter specimen. The alveoli have transversely compressed oval outlines in dorsal view except for the anteriormost alveolus, which is small and subcircular. The fourth alveolus is the largest, having the greatest anteroposterior length. The third and fifth alveoli appear to have greater transverse widths (Text-fig. 2B): however, this is the result of resorption of the medial walls of the alveoli to accommodate replacement teeth and does not reflect their original dimensions. Although it is largest, the fourth alveolus is not transversely expanded. In coelophysoids (*Dilophosaurus*, UCMP 37303) and spinosauroids (*Baryonyx*, BMNH R9951; *Dubreuillosaurus*, MNHN 1998–13; *Eustreptospondylus*, OUMNH J.13558; *Magnosaurus*, OUMNH J.12143/1a–b; and *Torvosaurus*, BYU 2003) the third alveolus is the largest, and in these taxa the lateral wall of the dentary swells laterally to accommodate the enlarged alveolus. In OUMNH J.13505 the dentary is transversely expanded between the third and sixth alveoli but this is a much more gentle expansion and is subequal on both sides of the tooth row.

The interdental plates are poorly preserved but were probably subpentagonal in outline, with vertical, subparallel sides basally, but becoming pointed towards the apex. This shape is common among theropods, although some of the interdental plates of abelisaurids (*Majungatholus*, FMNH PR 2100) have a rectangular outline. In OUMNH J.13505 the interdental plates posterior to the fifth and sixth tooth positions respectively have the appearance of having rectangular outlines. However, at this level both the lateral wall of the dentary and the interdental plates are broken dorsally and the shape of the interdental plates cannot be assessed with certainty. On the basis of the shapes of more anteriorly and posteriorly positioned interdental plates these plates were probably subpentagonal and not square in outline. The interdental plates of *Megalosaurus* are unfused and do not have



TEXT-FIG. 2. Photographs of OUMNH J.13505 in A, medial (with magnification of Meckelian foramina × 2), B, dorsal and C, lateral views; pdg, paradental groove. Scale bar represents 100 mm.

the rugose medial surfaces that are present in abelisaurids (Carrano *et al.* 2002).

The paradental groove for the dental artery separates the medial faces of the interdental plates from the medial wall of the dentary. It is open dorsally, defining a distinct gap between those two structures anteriorly until the fifth interdental plate where it becomes closed, allowing the two structures to contact one another. In most other Jurassic theropod taxa the groove is either open for the entire length (*Allosaurus*, UMNH VP 9366; *Dilophosaurus*, UCMP 37303; *Magnosaurus*, OUMNH J.12143/1a–b) or closed for the entire length (*Torvosaurus*, BYU 2003) of the dentary. However, in '*Megalosaurus*' *hesperis* (BMNH R332) and *Dubreuillosaurus valesdunensis* (MNHN 1998–13) the situation is similar to that in OUMNH J.13505. This character should be treated cautiously as it may be the result of post-burial plastic deformation of the element: however, it appears to be present in both left and right elements of '*Megalosaurus*' *hesperis* (BMNH R332).

The medial wall of the dentary beneath the interdental places is relatively flat. Anteriorly, there is no evidence of a definite symphysial area, though this region has been slightly abraded. Only the anterior part of the Meckelian fossa is preserved. The Meckelian groove continues along the ventral part of the medial surface from the anterior and anterodorsal bounds of the fossa, paralleling the ventral margin of the element. Posteriorly it is broad and indistinct, housing two finer, more distinct and slightly sinuous grooves. Anterior to the level of the sixth alveolus it becomes narrow and more distinct, terminating at the level of the posterior margin of the third alveolus. Ventral to this termination an oval foramen is present. Anterior to the termination a distinct, slit-like, opening is present that may be a second foramen (Text-fig. 2A). Two such foramina are present in most Jurassic theropods in which this region is preserved [*Allosaurus*, UMNH VP 9366; *Ceratosaurus*, UMNH VP 5278; *Dubreuillosaurus*, MNHN 1998–13; *Eustreptospondylus*, OUMNH J.13558; *Magnosaurus*, OUMNH J.12143/1a–b); *Monolophosaurus* (Zhao and Currie 1993); and *Sinraptor* (Currie and Zhao 1993)], although it is possible that only one is present in *Dilophosaurus* (UCMP 37303). The presence of only a single foramen is a feature

shared with some abelisaurids (e.g. *Majungatholus*, FMNH PR 2100) and the Rhaetian taxon '*Zanclodon*' *cambrensis* (BMNH R2912). None of the listed taxa possesses an anterior foramen that is dorsoventrally compressed.

A number of subcircular foramina are present with a random distribution in the anterior parts of the lateral and ventral surfaces of the dentary. A further four are widely spaced in a longitudinal row posterior to these and just dorsal to mid-height on the lateral surface (Text-fig. 2). They open dorsolaterally and are anteroposteriorly long ovals in shape. In common with *Allosaurus* (UMNH VP 9366) these are not set in a lateral groove, as are at least some in *Ceratosaurus* (UMNH VP 5278), *Dilophosaurus* (UCMP 37303), *Dubreuillosaurus* (MNHN 1998–13), *Eustreptospondylus* (OUMNH J13558), *Magnosaurus* (OUMNH J.12143/1a–b), *Majungatholus* (FMNH PR 2100), *Monolophosaurus* (N. Smith, pers. comm. 2006), *Sinraptor* (Currie and Zhao 1993; Gao 1999), *Torvosaurus* (BYU 2003). The dorsal part of the lateral wall is damaged and restored but only in places, giving it an unnatural jagged appearance. Parts have also been restored centrally and in the ventral part posteriorly. A longitudinal groove is present near the ventral margin and parallel to it (Text-fig. 1A). This has not been observed in any other non-avian theropod dinosaur.

Only one fully-erupted tooth is present, in the sixth alveolus. Partially erupted teeth are present in alveoli 3, 5 and 8, and replacement teeth are visible between the interdental plates adjacent to the fourth, fifth, sixth, eighth and ninth alveoli. The teeth are recurved, transversely compressed and serrated as is generally typical of theropods. They are almost symmetrical: the posterior carina, which continues to the base of the tooth, is positioned on the midline and the anterior carina, continuing about one-third of the way down the tooth, is only slightly laterally deflected basally. 'Blood grooves', fine grooves continuing onto the crown from between the serrations, are not present. Gentle transverse wrinkles continuing around the side of the crown and slightly upturned towards the carinae anteriorly and posteriorly are distinct laterally but only weak medially.

DISCUSSION

The lectotype of *Megalosaurus* bears two potential apomorphies (contra Allain and Chure 2002) and is distinct from all other Jurassic theropods for which the dentary is known.

A second dentary from the type locality and horizon of *Megalosaurus bucklandii* was reported and figured in medial view by Owen (1857, pl. 12, figs 1–3) and mentioned again by Owen (1883). This specimen formed a part of the Duke of Marlborough's collection at Blenheim Palace. Attempts to relocate this specimen have proved unsuccessful thus far. Although at least some of the other large theropod elements from the Stonesfield Slate almost certainly belonged to the same taxon as OUMNH J.13505, no records of association between the material exist. As there is evidence for more than one large theropod taxon in the Stonesfield fauna (Allain and Chure 2002; Day and Barrett 2004) none of these elements can be referred to *M. bucklandii* with any certainty.

Megalosaurus bucklandii shares features with a range of theropods from different taxonomic groupings. The distributions of these characters have not yet been assessed in numerical phylogenetic analyses. It does not possess an enlarged third dentary tooth, a character found by Rauhut (2003) to be a synapomorphy of Neotheropoda (under ACCTRAN optimisation) with subsequent loss in the clade comprising Ceratosauria and Tetanurae and redevelopment in Spinosauroidea. It also lacks rugose medial surfaces of the interdental plates, which have been found to be a synapomorphy of the Abelisauridae (Carrano *et al.* 2002). Consequently, *Megalosaurus bucklandii* is probably a member of the clade comprising Ceratosauria and Tetanurae, but lies outside Abelisauridae. There is currently no positive evidence on which to refer *M. bucklandii* to Spinosauroidea and the characteristic morphology of the dentary that is present in all known spinosauroids is absent in *Megalosaurus*. This conclusion differs from that of Holtz *et al.* (2004), whose phylogenetic analysis found *Megalosaurus* to be a spinosauroid. However, the latter placement probably relates to the inclusion of data from Stonesfield theropod elements that cannot confidently be referred to this taxon (see Allain and Chure 2002).

Various taxa have been referred to the Megalosauridae Huxley, 1869, including *Chilantaisaurus tashuikouensis* (Hu 1964), *Gasosaurus* (Dong and Tang 1985), '*Szechuanosaurus*' *zigongensis* (Gao 1993) and *Poekilopleuron* (Allain 2002). However, dentaries are not known in any of these taxa. Some recent authors have used the family Megalosauridae to refer to basal members of the Spinosauroidea. These include Holtz *et al.* (2004), who referred *Megalosaurus bucklandii*, *Afrovenator*, *Eustreptospondylus, Piatnitzkysaurus, Poekilopleuron*, *Dubreuillosaurus* (as 'unnamed eustreptospondyline') and *Torvosaurus* to this clade, and Allain (2002) who included *Dubreuillosaurus*, *Torvosaurus*, *Afrovenator* and *Eustreptospondylus* in Megalosauridae. Since *Megalosaurus* has not been shown to share any characters of systematic significance with spinosauroids it is recommended that this practice, as well as the practice of referring to any other taxa as 'megalosaurid' be discontinued until further information on the systematic position of *Megalosaurus* is revealed.

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