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The geographic and phylogenetic position of sauropod dinosaurs from the Kota formation (Early Jurassic) of India

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Abstract

The earliest sauropods are the Late Triassic *Isanosaurus* from Thailand, the Early Jurassic *Barapasaurus* and *Kotasaurus* from the Kota Formation of the Pranhita-Godavari Basin of India and *Vulcanodon* from Zimbabwe, and a variety of Middle Jurassic genera from many localities in Gondwana and Laurasia except North America. These early sauropod genera are related, but their phylogenetic positions remain unresolved. Sauropods originated in Laurasia (Thailand and vicinity) or Pangea (broadly, Thailand, China, India), with at least three additional steps involving expansion and diversification through the Middle Jurassic.

Keywords: Sauropod; Kota; Pranhita-Godavari Basin

1. Introduction

The Early Jurassic sauropods *Barapasaurus* and *Kotasaurus* from the Kota Formation in the Pranhita-Godavari Basin are among the earliest known sauropod dinosaurs. Accordingly, their geographic position on the Indian subcontinent in the Early Jurassic indicates an early Gondwana distribution of sauropods, with subsequent dispersal that eventually became cosmopolitan. Their phylogenetic position places them at or near the ancestry of sauropods. However, the origin and history of the Indian sauropods remain enigmatic.

Recent studies have established an expanded and considerably more detailed record of early sauropod evolution (Table 1), including the first record of Triassic sauropods. The recently described sauropod *Isanosaurus attavipachi* from Thailand (Buffetaut et al., 2000) places sauropods in Laurasia prior to their expansion through Asia and some of the southern continents in the Early Jurassic. Other, more recently described dinosaurs from China, Morocco, and Germany confirm sauropod geographic distribution in Asia and Europe. This contribution reviews the geographic position of India in the Early Jurassic and the phylogenetic positions of its two sauropod dinosaurs, both from the Pranhita-Godavari Basin.

2. Late Triassic sauropod dinosaur of Thailand

Buffetaut et al. (2000) recently described the sauropod *Isanosaurus attavipachi* from the Late Triassic of Thailand, prompting this review of sauropod origins and early geographic distribution. *Isanosaurus attavipachi* is the earliest geologic record (Norian-Rhaetian) of a sauropod dinosaur, placing the origin of sauropods no later than Late Triassic, perhaps even Middle Triassic. According to the published diagnosis, this is "a primitive sauropod with a robust femur bearing a very prominent, acuminate, S-shaped fourth trochanter located in the proximal half of the bone" (Buffetaut et al., 2000, p. 72). The proximal position of the fourth trochanter resembles that of *Barapasaurus* and *Kotasaurus*, but the greater trochanter is weakly developed and the shaft is much more robust than in the Indian sauropods.

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Table 1
Traditional classification of the basal sauropod genera discussed in this paper, after McIntosh (1990) and Upchurch (1998). Derived sauropods in the families Brachiosauridae and Diplodocidae are not listed. The taxonomic positions of *Isanosaurus* and other genera not described in McIntosh (1990) are provisional. Additional Early and Middle Jurassic genera not listed herein are problematical

Sauropodomorpha von Huene, 1932
Sauropoda Marsh, 1878
Vulcanodontidae Cooper, 1984
Barapasaurus Jain et al., 1975
Kotasaurus Yadagiri, 1988
Vulcanodon Raath, 1972
Ohmdenosaurus Wild, 1978
Zizhongosaurus Dong et al., 1983
Isanosaurus Buffetaut et al., 2000
Cetiosauridae Lydekker, 1888
Cetiosaurus Owen, 1841
Yunnanosaurus Young, 1942
Rhoetosaurus Longman, 1927
Omeisaurus Young, 1939
Amygdalodon Cabrera, 1947
Patagosaurus Bonaparte, 1979
Shunosaurus Dong et al., 1983
Datousaurus Dong and Tang, 1984
Gongxianosaurus shibeinsis He et al., 1998
Tehuelchesaurus Rich et al., 1999

3. Early Jurassic sauropod dinosaurs

3.1. India

Barapasaurus tagorei Jain et al., 1975, is known from several partial skeletons in the vertebrate palaeontology collections of the Indian Statistical Institute, Kolkata. These individuals range in ontogenetic development from juvenile to adult. The geologic setting (Jain et al., 1962; Kutty et al., 1987; Robinson, 1970; Bandyopadhyay and RoyChowdhury, 1996; Bandyopadhyay et al., 2002 in press) and reasonable assignment of these individuals to *Barapasaurus tagorei* indicate an early, coeval population, which together constitute the hypodigm for the species. Jain et al. (1975) and Jain et al. (1979) presented osteological descriptions of some of the diagnostic elements in the hypodigm, thereby confirming certain aspects of the anatomy as a primitive sauropod, but with certain features that resemble those of prosauropods. According to the original description by Jain et al. (1975), *Barapasaurus tagorei* is a large sauropod with slender limbs, spoon-shaped teeth with coarse denticles on posterior and anterior keels, opisthocoelous anterior dorsal vertebrae, sacrum consisting of four co-ossified vertebrae and narrow width between the sacricostal yokes, deep medial wall of the ilium, and shallow curvature of the proximal part of the anterior border of the scapula. In some respects, this genus resembles prosauropod dinosaurs, especially the slender limbs, distinctive fourth trochanter of the femur, and the small pelvic basin (Jain et al., 1979). The age of the Kota Formation is generally considered Early Jurassic (Jain, 1973; Kutty, 1969; Yadagiri and Prasad, 1977; Rudra and Maulik, 1994; Bandyopadhyay and RoyChowdhury, 1996; Bandyopadhyay et al., 2002 in press), but an age assignment of Middle Jurassic has been proposed (Prasad and Manhas, 2002 and references therein).

Yadagiri et al. (1980) and Yadagiri (1988, 2001) described a second sauropod from the Kota Formation, *Kotasaurus yamanpalliensis*, from a locality in the Pranhita-Godavari basin approximately 40 km north of the type locality of *Barapasaurus tagorei*. The species is known from at least 12 individuals and more than 800 skeletal elements (Yadagiri, 2001) housed in the Geological Survey of India. Yadagiri (2001) distinguished *Kotasaurus* from *Barapasaurus* on the basis of osteological details including simple dorsal vertebrae and low iliac blade. Like Jain et al. (1975) and Jain et al. (1979) for *Barapasaurus*, Yadagiri (2001) recognized certain characteristics of *Kotasaurus*, such as less expanded humerus with slight twist at both end and lacking anteroposterior expansion in the dorsal end, retention of lesser trochanter of the femur, and the osteology of the astragalus that resemble those of prosauropods as well as *Vulcanodon*.

3.2. Africa

Vulcanodon karibaensis Raath, 1972, from the Early Jurassic (?Hettangian) of Zimbabwe (Raath, 1972; Cooper, 1984 and references therein), is generally considered older than the Indian sauropods of the Kota Formation. Many details of the osteology of this genus, including four fused sacral vertebrae, broadly articulated pubes and ischia, pubes with a prominent distal 'apron', ilium with long pubic peduncle and short ischiadic peduncle, indicate close relationship with the Indian sauropod *Barapasaurus*. Cooper (1984) recognized this close relationship and established the family Vulcanodontidae for *Barapasaurus* and *Vulcanodon*.

3.3. Asia

Zizhongosaurus chuanchengensis(Dong et al., 1983) was described on the basis of a dorsal arch, fragmentary pubis, and humerus from the Early Jurassic of Sichuan, People's Republic of China. According to McIntosh (1990), the material is insufficient for taxonomic assignment, but is important for its geographic and temporal position. *Gongxianosaurus shibeinsis* He et al., 1998 is a sauropod from the Early Jurassic Ziliujing Formation of Sichuan, China, based on several teeth and a premaxilla (He et al., 1998; Barrett, 1999). Barrett (1999) recently described the partial maxilla with dentition of the sauropod *Yunnanosaurus robustus* Young, 1951 from the Lower Lufeng Formation (Sinemurian-Pliensbachian) of Yunnan Province, People's Republic of China. Others, including Dong (1992), have considered *Yunnanosaurus* (*Y. robustus* Young, 1951 and *Y. huangi* Young, 1942) to be prosauropods. Because the available material for these three species

is insufficient for phylogenetic analysis, their taxonomic status and position are (Table 1) questionable. However, their stratigraphic position and geographic setting are important for biogeography of the early sauropods.

3.4. Europe

Ohmdenosaurus liasicus Wild, 1978 from the Toarcian (Late Early Jurassic) of Germany was described on the basis of a tibia and astragalus. It is approximately the same age (Early Jurassic) as *Barapasaurus* and *Kotasaurus*, and has been described in some respects as less derived than the Zimbabwean and Indian sauropods (McIntosh, 1990).

4. Middle Jurassic sauropod dinosaurs

Sauropod geographic distribution and diversity continued to expand in the Middle and Late Jurassic (McIntosh, 1990; Upchurch, 1995, 1998; Wilson and Sereno, 1998; Zhang, 1998). New records of basal sauropods (Table 1) have added considerably to the confirmed distribution of sauropods.

4.1. Gondwana

Records of unidentified sauropods in Gujarat confirm the continued existence of sauropods in India (Satyanarayana et al., 1999; Jana and Das, 2002). *Atlasaurus imelakei* Monbaron et al., 1999, a Middle Jurassic sauropod from Morocco, indicates the continued existence of sauropods in Africa. According to Monbaron et al. (1999), *Atlasaurus imelakei* is closely related to Late Jurassic brachiosaurid sauropods. Other Middle Jurassic sauropods in the derived families Diplodocidae and Brachiosauridae were widespread, with records in Argentina, England, France, and Madagascar.

The oldest sauropod in Australia is *Rhoetosaurus brownei* Longman, 1927, a Middle Jurassic cetiosaur (McIntosh, 1990). The earliest sauropods in South America are from Patagonia, southern Argentina: *Patagasaurus fariasi* Bonaparte, 1979, based on several partial skeletons; *Amygdalodon patagonicus* Cabrera, 1947, from a partial skeleton; and the recently described *Tehuelchesaurus benitezii* *Rich et al., 1999*, based on a partial skeleton from Chubut Province. *Tehuelchesaurus*, a late Middle Jurassic cetiosaur, closely resembles the broadly contemporary Chinese cetiosaur *Omeisaurus tianfuensis*, according to Rich et al. (1999), although that genus is generally regarded as Late Jurassic (McIntosh, 1990). Rich et al. (1999) interpreted the resemblance between *Tehuelchesaurus* and *Omeisaurus* as an indication that South American sauropods (and other terrestrial faunas) and Chinese sauropods were not isolated in the Middle Jurassic, contrary to Russell (1993), who postulated that Central Asian faunas were isolated during this time.

4.2. Laurasia

Among the well known Middle Jurassic sauropods of Asia are *Shunosaurus lii* Dong et al., 1983 from southern China and Tibet (Dong, 1992); and two others, generally regarded as cetiosaurs (McIntosh, 1990) from southern China, *Omeisaurus tianfuensis* He et al., 1984, and *Datousaurus bashanensis* Dong and Tang, 1984 (Dong, 1992; He et al., 1988). Both of the cetiosaur species are derived with respect to Early Jurassic sauropods. They confirm the continued presence of sauropods in Asia into the Middle Jurassic. In addition, *Cetiosaurus* and related forms are known from England (Jones, 1970; McIntosh, 1990).

Sauropods were absent in North America prior to the Late Jurassic (Gillette, 1996a,b), a paradox that may be explained by geographic barriers that prevented dispersal until their expansion in the Upper Jurassic Morrison beds of western United States. By Late Jurassic, sauropods were nearly cosmopolitan (McIntosh, 1990; Hunt et al., 1994), and reached great abundance and diversity. Late Jurassic and Cretaceous sauropods, however, are beyond the scope of this review.

5. Phylogeny of basal sauropods

The phylogenetic relationships of the Late Triassic and Early Jurassic sauropods are subjects of considerable interest. Recent studies on early sauropod relationships have focused on traditional osteological comparisons (e.g. Bonaparte, 1986; McIntosh, 1990) and cladistic analyses (e.g. McIntosh, 1990; Calvo and Salgado, 1995; Wilson and Sereno, 1998; Upchurch, 1995, 1998). *Isanosaurus*, *Barapasaurus*, *Kotasaurus*, and *Vulcanodon* all retain certain osteological features that indicate relationship with prosauropods, with which they were contemporaneous. The other Early Jurassic sauropods are not known well enough to afford confident comparisons.

Recent taxonomic assignments and cladistic analyses have consistently recognized *Vulcanodon* and *Barapasaurus* as basal sauropods (McIntosh, 1990; Calvo and Salgado, 1995; Wilson and Sereno, 1998; Upchurch, 1995, 1998). The recently published description of *Kotasaurus* by Yadagiri (2001) and the eventual publication of the comprehensive osteology of *Barapasaurus* should substantially improve the knowledge of these two genera and allow for more extensive analysis. To date, no published cladistic analysis has included *Isanosaurus*; therefore, the cladistic relationships between the Indian, Zimbabwean, and Thai sauropods remain unresolved.

6. Paleogeography of basal sauropods

The occurrence of *Isanosaurus* in the Late Triassic of Thailand indicates an earlier origin of sauropods, perhaps

from the Middle Triassic, as predicted by Wilson and Sereno (1998). Considering the extensive and abundant global record of dinosaurian faunas of the Late Triassic, the sole occurrence of *Isanosaurus* is problematical; the simplest explanation of this obvious rarity is that Late Triassic sauropod populations were restricted to a small geographic area (Fig. 1) and had not yet diversified.

The Early Jurassic sauropods, *Barapasaurus* and *Kotasaurus* of India, and *Vulcanodon* of Zimbabwe, have primitive features that have been variously described as prosauropod, or an indication of prosauropod ancestry (e.g. Raath, 1972; Jain et al., 1975, 1979; Cooper, 1984). These Gondwanan genera therefore seem to be closely related to the Late Triassic sauropod, *Isanosaurus*, a Laurasian genus. An osteological description of *Barapasaurus* should more fully establish phylogenetic relationships of these four genera. However, published information indicates that all four are basal sauropods. The other Early Jurassic sauropods, *Zizhongosaurus*, *Gongxianosaurus*, *Yunnanosaurus*, and *Ohmdenosaurus*, are based on fragmentary and incomplete skeletons, precluding confident taxonomic assignment and phylogenetic analysis. Nevertheless, in the Late Triassic and Early Jurassic, sauropods are restricted to southern and western Laurasia (Thailand, China, Germany) and eastern Gondwana (Zimbabwe, India). Although details of the paleogeography are not clear, these early sauropods occur in middle latitudes, with a Tethyan distribution, rather than at higher latitudes (Smith et al., 1994).

This distribution (Fig. 2) implies certain limitations, perhaps physiological constraints, which precluded global expansion into the American continents and other southern landmasses until the Middle and Late Jurassic. Expansion of sauropod populations into Australia and South America in the Middle Jurassic (Fig. 3) preceded the introduction of sauropods in the Late Jurassic of North America. Limitations that had prevented sauropods from widespread distribution in the Early Jurassic were lost or overcome by the Late Jurassic, perhaps as a consequence of the post-Toarcian global recession of sea level (earliest Middle Jurassic). Except for Antarctica (Hammer and Hickerson, 1999), all continents have records of Late Jurassic and Cretaceous dinosaurs.

Monbaron et al. (1999) recognized a major, early radiation from relatively small sauropods of the basal Jurassic to gigantic forms in the middle Jurassic such as *Atlasaurus* from Morocco. According to their interpretation, this radiation coincided with high levels of CO_2 in middle Mesozoic time and possibly higher levels of plant productivity. They also described the land masses presently represented by southeastern United States and western Africa as contiguous in the middle Jurassic (Bathonian-Callovian), 'so that Moroccan sauropods, at a latitude of 25–27°N of the Middle Jurassic equator, probably resembled those inhabiting the western side of the rift in the southeastern USA.' However, to date, there are no published records of Middle Jurassic sauropods anywhere in North America (McIntosh, 1990; Gillette, 1996a,b), including the southeastern states. Monbaron et al. (1999) also suggested that middle Jurassic dinosaurs of China are endemic.

Wilson and Sereno (1998) recognized the likelihood of a Late Triassic origin, or earlier, for sauropods, and discussed the biogeographic implications of neosauropod evolution, but did not present biogeographic interpretations for basal sauropods (Sauropoda and Eusauropoda) in the Early Jurassic. Russell (1993) argued for two terrestrial biogeographic provinces in the Middle Jurassic, one in Central Asia and the other Neopangea. Rich et al. (1999) contested that interpretation in their description of the sauropod *Tehuelchesaurus benitezii* from the Callovian (late Middle Jurassic) of Argentina, which closely resembles *Omeisaurus tianfuensis* from China, thereby indicating a broad and

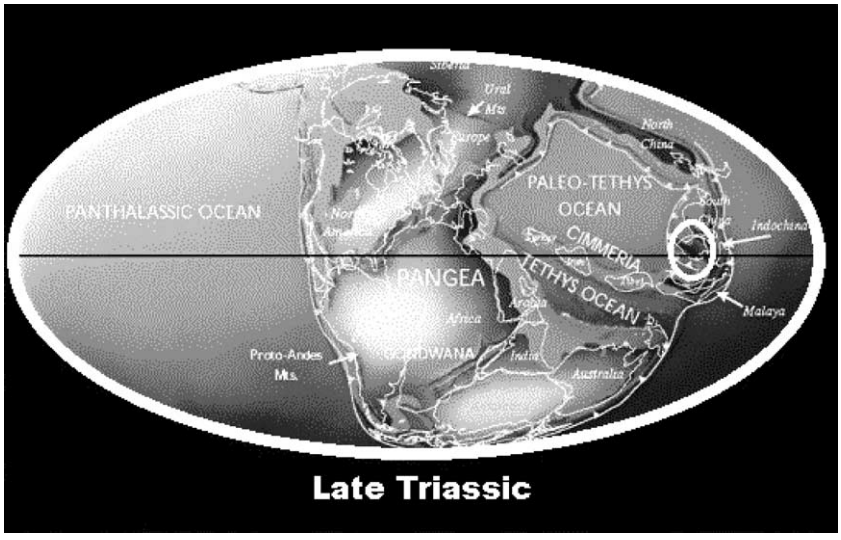

Fig. 1. Biogeography of early sauropods. Late Triassic: *Isanosaurus*, from Thailand. Map after Early Triassic globe of Scotese (2001, 2002).

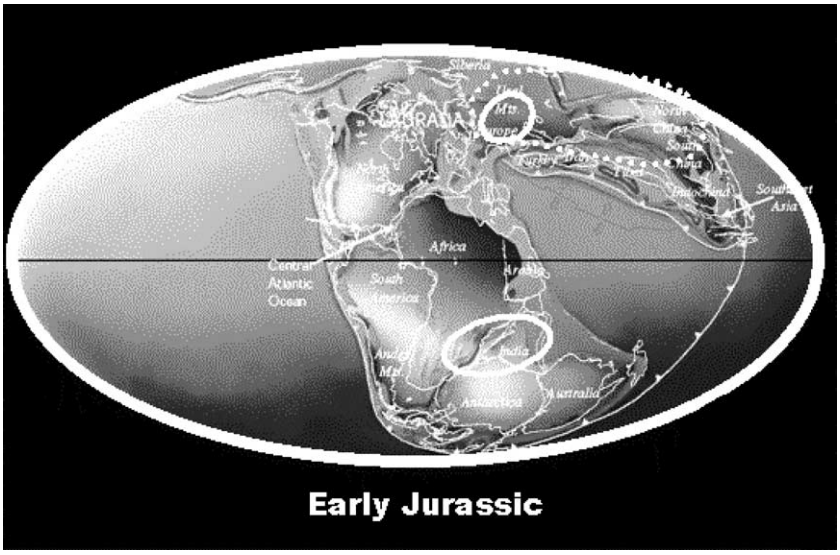

Fig. 2. Biogeography of early sauropods. Early Jurassic: *Barapasaurus* and *Kotasaurus*, from India; *Vulcanodon*, from Zimbabwe; *Zizhongosaurus*, *Gongxianosaurus*, *Yunnanosaurus*, and *Ohmdenosaurus*, from China; *Ohmdenosaurus*, from Germany. Dotted line indicates area of probable contiguous distribution. Map after Early Jurassic globe of Scotese (2001, 2002).

continuous Pangean distribution of sauropods. Hunt et al. (1994) recognized three major peaks in sauropod diversity, in the Late Jurassic, Early Cretaceous, and Late Cretaceous and one minor peak in the Middle Jurassic. They correlated these peaks with highstands of sea level.

According to the interpretations in this paper, early sauropod evolution and paleogeography are more complicated, involving at least four stages through the end of the Jurassic: 1. Origin in Middle or Late Triassic, with initial geographic distribution limited to southeastern Asia. 2. Expansion of distribution and increase of diversity in Early Jurassic through southern Laurasia and eastern Gondwana. In addition, the three well known Early Jurassic sauropods, *Barapasaurus*, *Kotasaurus*, and *Vulcanodon*, were already gigantic. The femur in the mounted skeleton of *Barapasaurus* at the Indian Statistical Institute exceeds 1 m in length, and others in the ISI collection are considerably larger. Accordingly, these genera demonstrate an earlier achievement of gigantism (Early Jurassic) than Monbaron et al. (1999) recognized. 3. Continued geographic expansion in the Middle Jurassic to include Australia and South America, but not North America, including derived sauropods that achieved still greater size. 4. Expansion into North America in the Late Jurassic, with some

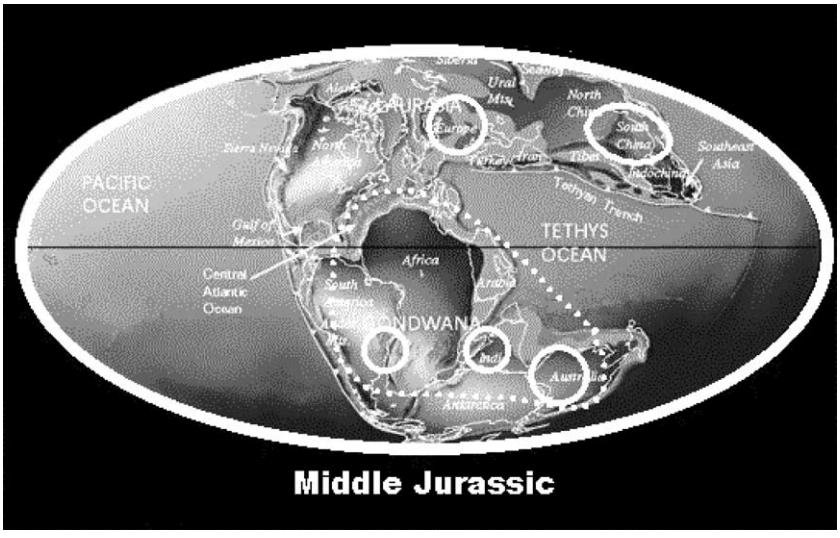

Fig. 3. Biogeography of early sauropods. Middle Jurassic: *Atlasaurus*, from Morocco; *Cetiosaurus*, from England; *Rhoetosaurus*, from eastern Australia; *Patagosaurus*, *Amygdalodon*, and *Tehuelchesaurus*, from southern Argentina; *Shunosaurus*, *Datousaurus*, *Omeisauru,* and *Gongxianosaurus* from China. Dotted line indicates area of probable contiguous distribution. Map after Late Jurassic map of Scotese (2001, 2002).

sauropods (e.g. *Brachiosaurus*, *Supersaurus*, *Seismosaurus*) achieving prodigious size. By the end of the Jurassic, sauropod populations had extended to all continents except Antarctica, although paleogeographic patterns suggest they should be discovered there eventually. Cretaceous sauropod evolution is beyond the scope of this paper. Without doubt, a comprehensive review of sauropod evolution would recognize several additional stages.

7. Conclusions

Recent discoveries of sauropodomorphs have added increased complexity to the early evolution of the sauropods. The occurrence of a primitive sauropod in the Late Triassic of Thailand might indicate a Laurasian origin of sauropods. However, according to published information, the Thai species resembles the two Early Jurassic genera *Barapasaurus* and *Kotasaurus*, perhaps indicating a restricted Pangaean origin instead. Subsequent evolution of the early sauropods in the Middle Jurassic involved expansion into eastern Laurasian and Gondwanan continents, and culminated in the Late Jurassic with a nearly global distribution and considerable variation. Because *Barapasaurus* and *Kotasaurus* are known from nearly complete skeletons, their osteology and stratigraphic position are critical to understanding the origin and evolution of sauropods.

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