A diplodocid sauropod dinosaur from the Late Jurassic Cañadón Calcáreo Formation of Chubut, Argentina

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A DIPLODOCID SAUROPOD DINOSAUR FROM THE LATE JURASSIC CAÑADÓN CALCÁREO FORMATION OF CHUBUT, ARGENTINA

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ABSTRACT—Late Jurassic dinosaur faunas from the Southern Hemisphere are still poorly known, and it thus remains unclear whether or not the famous Tendaguru fauna (Kimmeridgian–Tithonian, Tanzania) represents a typical Gondwanan dinosaur assemblage of that time. In South America, only the Oxfordian–Kimmeridgian Cañadón Calcáreo Formation of Chubut Province, Argentina, has yielded more than isolated Late Jurassic dinosaur remains so far. Here we report fragmentary remains of a diplodocid sauropod from this unit, representing the first record of this family from the Late Jurassic of South America. Incorporating the basal macronarian Tehuelchesaurus, an unidentified brachiosaurid, the dicraeosaurid Brachytrachelopan, and the diplodocid described here, the taxonomic composition of the sauropod fauna from the Cañadón Calcáreo Formation is remarkably similar to that of the Tendaguru Formation, but also to roughly contemporaneous faunas in North America and Europe. The diverse non-neosauropodan sauropod fauna known from the early Middle Jurassic (Aalenian–Bajocian) of the same depositional basin within Chubut Province is congruent with the dominance of non-neosauropodan sauropods in continental faunas globally to at least the Bathonian. These assemblages suggest a rapid faunal turnover within sauropod faunas in the late Middle Jurassic-earliest Late Jurassic at least in western Pangea, through which basal eusauropods were replaced by diplodocid and macronarian neosauropods. Taking paleogeographical reconstructions into account, this faunal replacement might have taken place in a surprisingly short time interval of maximally five million years close to the end of the Middle Jurassic.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

INTRODUCTION

Jurassic dinosaur faunas of Gondwana are still poorly known, and our understanding of Late Jurassic Gondwanan dinosaurs is largely based on the fauna of the Tendaguru Formation of Tanzania (Rauhut and López-Arbarello, 2008). However, in the absence of comparative material from other Late Jurassic Gondwanan localities, it is difficult to evaluate to what extent the Tendaguru fauna is representative of Late Jurassic dinosaur faunas from other regions of Gondwana. Therefore, any report of Late Jurassic dinosaur remains from the Southern Hemisphere is significant.

Comparative material from the Late Jurassic of Africa is otherwise restricted to fragmentary remains from the Kadzi Formation of Zimbabwe, which seem to indicate a rather similar fauna, at least in respect of the sauropod dinosaurs (Raath and McIntosh, 1987). In South America, Late Jurassic dinosaurs are so far mainly known from the Cañadón Calcáreo Formation of Chubut Province, Argentina (Rauhut and López-Arbarello, 2008). Dinosaurs reported from this formation include the basal macronarian Tehuelchesaurus (Rich et al., 1999; Carballido et al., 2011), the dicraeosaurid Brachytrachelopan (Rauhut et al., 2005), and an indeterminate probable brachiosaurid (Rauhut, 2006a). Here we report fragmentary sauropod remains from this formation that represent a distinct lineage of sauropod dinosaurs for this unit.

GEOLOGIC AND PALEONTOLOGIC CONTEXT

The specimens described here come from the Cañadón Calcáreo Formation, a unit of terrestrial sediments that are exposed along the central Chubut River in Chubut Province, Argentina (Fig. 1). The Cañadón Calcáreo Formation represents the Jurassic post-rift infill of the Cañadón Asfalto Basin and consists of a basal lacustrine part, followed by fluvial and overbank deposits (Prosp rio, 1987; Figari and Courtade, 1993; Figari, 2005; Rauhut, 2006a, 2006b). The basal part of the Cañadón Calcáreo Formation was recently dated as latest Oxfordian (157 Ma; Cúneo et al., 2013). According to Figari (2005), the total thickness of the Cañadón Calcáreo Formation reaches 1400 m at its type locality, and the equivalent dates obtained from the type locality of the formation and the Puesto Almada locality represent the top of the basal lacustrine section (Cúneo et al., 2013). Thus, the upper fluvial and overbank deposits are probably somewhat younger and might reach into the Kimmeridgian. However, a Tithonian date mentioned by Rauhut et al. (2005), Rauhut (2006a), and more precisely at 147 ± 3 Ma by Cabalieri et al. (2010) might be in error, because this K-Ar date, derived from olivine crystals, comes from a tuff in a very similar stratigraphic position (possibly even the same tuff layer) as the samples dated at 157.387 ± 0.045 Ma with the more reliable U-Pb ID-TIMS method by Cúneo et al. (2013). The specimens described here were found eroded on the surface, but they come...
from the fluvial part of the formation, with part of a large scapula
having been present in situ at the time of initial discovery. Thus,
these remains are probably slightly younger than the latest
Oxfordian age of the base of the formation and might tentatively
be regarded as Kimmeridgian in age. Apart from sauropods, vertes-
brates from the Cañadón Calcáreo Formation include a rich
fish fauna in the basal lacustrine part of the unit (the ‘Almada
fauna’; López-Arbarello et al., 2008, 2013), the basal crocodylo-
morph Almadasuchus (Pol et al., 2013), and fragmentary ther-
pod remains (Rauhut, 2002).

SYSTEMATIC PALEONTOLOGY
SAURISCHIA Seeley, 1887
SAUROPODA Marsh, 1878
NEOSAUROPODA Bonaparte, 1986a
DIPLODOCOIDEA Marsh, 1884
DIPLODOCIDAE Marsh 1884
Gen. et sp. indet.

Material—Three dorsal vertebral centra, fragmentary scapula
(not collected). The material is kept in the collections of the
Museo Paleontológico Egidio Feruglio (MPEF) in Trelew,
Argentina, under accession number MPEF-PV 1324.
Locality and Horizon—The material comes from a coarse-
grain sandstone within the upper part of the Cañadón Calcáreo Formation, probably Kimmeridgian. The locality lies
c. 20 km north of the village of Cerro Cóndor on the eastern
side of the Chubut River. Exact locality data is available from
the authors upon request.

DESCRIPTION
The material comprises three partial vertebrae, which mainly
have their centra preserved (MPEF-PV 1324). Two of these ver-
tebrae are mid- to mid-posterior dorsals, as demonstrated by
the lack of parapophyses on the preserved parts; the third also
belongs to the dorsal series, but is too poorly preserved to deter-
mine its position within the column. In the first report on these
remains, Rauhut (2006a, 2006b) also mentioned a fragmentary
scapula, but this bone had been largely destroyed by erosion
when the materials were collected in 2008. However, even upon
initial discovery, this element was already too poorly preserved
to yield any useful information.

The dorsal vertebrae represent a large sauropod (see measure-
ments in Table 1). The probably more anterior vertebral cen-
trum (MPEF-PV 1324-2) is poorly preserved and partially
deformed (Fig. 2A). The right half of the centrum and the entire
neural arch (with the exception of a small part of the anterior
left wall of the neural canal) are missing. The centrum is higher
than long. Its anterior articular surface is flat, whereas the poste-
rior surface is mildly concave. The lateral side of the centrum
is marked by a large pneumatic opening that occupies most of its
dorsal half. The foramen is a rounded trapezoid in outline, being
higher anteriorly, where its dorsal margin is approximately level
with the ventral margin of the neural canal. Its maximal length is
100 mm (about 45% of centrum length), and its maximal height
90 mm. Anteriorly, a sharply defined, triangular depression is
present anterior to the pneumatic opening (Fig. 2A). This
depression extends some 25 mm further anterior than the open-
ing and almost reaches the anterior margin of the centrum. It is
offset from the centrum by a notable, rounded step and a marked
change in surface texture, the surface of the depression being
smooth, as is the case with the internal surfaces of the pneumatic
opening. Posteriorly, there is no marked step between the lateral
side of the centrum and the rim of the pneumatic opening, but
the latter rises steeply from opening to lateral surface. The ven-
tral margin of the opening curves gradually into the lateral sur-
face of the centrum; a clear line extending across this curve from
the ventral margin of the anterior depression to the posterover-
tral edge of the pneumatic opening separates the smooth internal
surface of the pleurocoel from the lateral surface of the centrum.
The opening extends deep into the centrum and ramifies exten-
sively into the ventral part of the centrum and the neural arch. In
the anterior part of the internal cavity, a stout lamina extends
from the dorsal part of the anterior margin of the pneumatic

<table>
<thead>
<tr>
<th>Dimension</th>
<th>MPEF 1324-1</th>
<th>MPEF 1324-2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length</td>
<td>240</td>
<td>215(+)</td>
</tr>
<tr>
<td>Anterior height</td>
<td>250</td>
<td>260</td>
</tr>
<tr>
<td>Anterior width</td>
<td>275</td>
<td></td>
</tr>
<tr>
<td>Mid-width</td>
<td>170</td>
<td></td>
</tr>
<tr>
<td>Mid-height</td>
<td>190</td>
<td></td>
</tr>
</tbody>
</table>

Measurements in mm. (+) indicates that the centrum is incomplete.
opening horizontally and medially, and separates the main cavity from the cavity leading into the neural arch anteriorly.

The second, probably more posterior vertebral centrum (MPEF-PV 1324-1) is undistorted and almost complete, missing only minor parts of the posterior rim and ventral surface, as well as the neural arch (Fig. 2B–E). The centrum is slightly wider than high, with oval articular surfaces (Fig. 2C, D). The anterior articular surface is very slightly convex, whereas the posterior surface is slightly concave, with a markedly deeper concavity in its central part. The centrum is notably constricted both transversely and dorsoventrally in its central part. The ventral side is broad and gently convex transversely, before it flexes abruptly into the lateral sides lateroventrally. The lateral side of the centrum is dominated by an extremely large pneumatic opening that occupies the entire dorsal half of this side (Fig. 2B). Its maximal length is 180 mm (75% of centrum length), and the maximal height is 100 mm. The opening has a gently concave ventral margin, an angular posterior margin, and two straight to very slightly convex dorsal margins that meet slightly anterior to the mid-length of the opening at a wide angle. The dorsal margin of the pneumatic opening is approximately level with the dorsal margin of the vertebral centrum. As in the more anterior vertebra, a notably offset, small triangular depression is present anterior to the opening; due to the great anterior extension of the latter, this depression is placed within the anterior margin of the main pneumatic opening and faces more posteriorly than laterally (Fig. 2E). Again, the bone surface within this depression is markedly smooth. The pneumatic opening expands extensively into the centrum, leaving only a thin bony wall of less than 10 mm thickness in the midline. As in the more anterior vertebra, a stout, horizontal lamina is present in the anterodorsal part of the cavity (Fig. 2E), and a shorter and lower, slightly inclined lamina is present in its anteroventral part. A marked ridge extends from the ventral side of the dorsal lamina anteroventrally towards the anterior base of the ventral lamina. In the posterior part of the cavity, a notable, rectangular depression is present dorsally towards the posterior end of the centrum, being defined by stout ridges dorsally and ventrally. The internal cavity furthermore expands notably ventrally into the centrum and dorsally into the neural arch, probably leading to a connection with supraneural camerae. However, the presence of the latter cannot be established, because the neural arch is largely missing. The small portion of the anterolateral walls of the neural canal preserved shows that the latter was large and considerably higher than wide. On the right side, the base of a stout, laterally directed centroprezeugaphyseal lamina is present on the preserved part of the wall of the neural canal; its ventral end is flush with the dorsal margin of the centrum.
SYSTEMATIC AFFINITIES

In order to test the phylogenetic affinities of the specimens described here, a phylogenetic analysis was carried out. For this, we incorporated the Cañadón Calcáreo material into the data matrix used by Carballido and Sander (2014), to which some new characters as well as characters used in previous studies were added (see Supplementary Data 1). The resulting matrix has 72 operational taxonomic units scored for 370 characters. Ordering of characters is as in Carballido and Sander (2014). The tree search was conducted in TNT 1.1 (Goloboff et al., 2008), starting from 1000 replicates of Wagner trees followed by TBR branch swapping, saving 10 trees per replicate. We obtained six maximum parsimony trees (MPTs) of 1074 steps that were recovered in 40% of the replicates. The strict consensus recovered the specimen as a diplodocid, in a basal polytomy within the group. Within the MPTs, the Cañadón Calcáreo specimen takes three different equally parsimonious positions within this group (Fig. 3).

The position here recovered for the Cañadón Calcáreo specimen is supported by a combination of characters. The presence of pneumatic openings (character 139) in middle to posterior dorsal vertebrae is a synapomorphy of the clade including mamenchisaurids and more derived sauropods. Among neosauropods, the plesiomorphic condition (absence of posterior dorsal pneumatic openings) is only present in dicraeosaurid sauropods (Janensch, 1929a; Salgado and Bonaparte, 1991). In the Cañadón Calcáreo specimen, the openings lead into large intercostal spaces and the articular surface is higher than wide. Thus, close relationships with Haplocanthosaurus (Cope, 1877; Osborn and Mook, 1921) and its non-opistocoelous condition (character 174) exclude this group (Fig. 3).

The presence of a diplodocid in the Late Jurassic Cañadón Calcáreo Formation is relevant for understanding the biogeographic history of the clade in South America as well as for understanding the dynamics of Jurassic faunal assemblages of Gondwana through time.

In order to test the robustness of the phylogenetic hypothesis recovered in the analysis, the specimen described here was forced into different phylogenetic positions. Four extra steps are needed to place MPEF-PV 1324 as sister taxon to Flagellicaudata, or as a basal rebbachisaurid, whereas five extra steps are needed if the specimen described here is placed as sister taxon to Neosauropoda or as a basalmost macronarian. Therefore, although fragmentary, the phylogenetic position of the Cañadón Calcáreo specimen among diplodocids is fairly well supported.

DISCUSSION

The presence of a diplodocid in the Late Jurassic Cañadón Calcáreo Formation is relevant for understanding the biogeographic history of the clade in South America as well as for understanding the dynamics of Jurassic faunal assemblages of Gondwana through time.

Diplodocids were completely unknown from South America prior to the recent work of Gallina et al. (2014), who described an Early Cretaceous diplodocid sauropod from Patagonia. The presence of a diplodocid in the early Late Jurassic of Patagonia favors one of the two biogeographic histories for the group discussed by Gallina et al. (2014), an early spread of diplodocids to South America, during their main time of dispersal, prior to the effective separation of northern and southern land masses. The alternative hypothesis discussed by these authors, a late colonization of South America by this clade (at around the Jurassic–Cretaceous boundary), would not predict the presence of this group in South America by the Oxfordian/Kimmeridgian.

From the viewpoint of the study of Jurassic sauropod faunal assemblages, the identification of a diplodocid from the Late Jurassic of the Cañadón Calcáreo Formation increases the sauropod diversity of this unit to at least four taxa. Sauropods present in the formation thus include two basal macronarians, Tehuelchesaurus (Rich et al., 1999; Carballido et al., 2011) and a probable brachiosaurid (Rauhut, 2006a), as well as two diplodocids, the dicraeosaurid Brachytrachelopan (Rauhut et al., 2005) and the material described here. Thus, as in other Late Jurassic terrestrial ecosystems, such as the Morrison Formation (Foster, 2003) and the Tendaguru Formation (Aberhan et al., 2002; Rauhut et al., 2005) and the Tendaguru Formation (Aberhan et al., 2005), a wide variety of sauropod taxa are present.
Bussert et al., 2009), sauropods obviously constituted an important component of the herbivorous vertebrate fauna of the Cañadón Calcáreo Formation.

All taxa reported in the Cañadón Calcáreo Formation represent neosauropod lineages. Underlying the Cañadón Calcáreo Formation there is another terrestrial unit in the same depositional basin, the Cañadón Asfalto Formation. The base of the Cañadón Asfalto Formation has recently been dated as Toarcian (178 Ma; Cúneo et al., 2013), but other parts of the formation have yielded early Middle Jurassic ages (171 Ma, Aalenian [Salani, 2007]; 167 Ma, earliest Bathonian [Cabaleri et al., 2010]); thus, this unit is 10–20 Ma older than the Cañadón Calcáreo Formation. The Cañadón Asfalto Formation also contains a rich dinosaur fauna, in which at least four different taxa of sauropods have been identified so far (Patagosaurus and Volkkheimetta [Bonaparte, 1979, 1986b] and two unnamed taxa [Rauhut, 2003; Pol et al., 2009]). All of these taxa represent basal, non-neosauropod eusauropods, belonging to at least three different lineages (Rauhut, 2002; Pol et al., 2011). Thus, there was an important faunal turnover in the sauropod faunas in the second half of the Middle Jurassic in this region, in which all basal eusauropod lineages were replaced by neosauropods.

Furthermore, the taxonomic composition of the fauna of the Cañadón Calcáreo Formation is, at a higher taxonomic level, remarkably similar to that of the Tendaguru Formation and, to a slightly lesser extent, to that of the Morrison Formation and various units in Europe. All of these units contain brachiosaurids, basal macronarians, and diplodocids (Janensch, 1929b; Foster, 2003; Rauhut, 2006a; Remes, 2006, 2009; Carballido et al., 2011; Mannion et al., 2012, 2013; Carballido and Sander, 2014). The fauna of Tendaguru furthermore shares the presence of closely related dicraeosaurids with that of the Cañadón Calcáreo Formation (Janensch, 1929b; Rauhut et al., 2005), and there is an emerging consensus that this clade is also represented in the Morrison Formation by Suuwassea, which represents its most basal member (Salgado et al., 2006; Whitlock, 2011; Mannion et al., 2012; Carballido and Sander, 2014). Thus, this neosauropod fauna, including representatives of all major basal clades (with the conspicuous absence of rebbachisaurids; see Mannion et al., 2012), seems to have been established in both Gondwana and at least western Laurasia by the Kimmeridgian at the latest. However, Middle Jurassic faunas of Gondwana and western Laurasia seem to be dominated by basal, non-neosauropodan sauropods, at least until the Bathonian. Basal sauropods from that age are known from England (Upchurch and Martin, 2003), Morocco (Lapparent, 1955; Lüang, 2008), and Madagascar (Buffetaut, 2005; Mannion, 2010); furthermore, the basal sauropod Rheosaurus from Australia is also of Bathonian or Callovian age (Nair and Salisbury, 2012). Lapparentosaurus from the Bathonian of Madagascar has variously been considered to be a macronarian neosauropod (e.g., Upchurch; 1998; Upchurch et al., 2004), but a recent reconsideration of this taxon placed it outside Neosauropoda (Mannion et al., 2013). Likewise, Aetosaurus from the Bathonian of Morocco (Monbaron et al., 1999) has been regarded as a neosauropod by several authors (Upchurch et al., 2004; Lüang and Mahammed, 2010), but found to be outside this clade in more recent analyses (Royo-Torres et al., 2006; Wilson and Upchurch, 2009; D’Emic, 2012; Mannion et al., 2013). Other possible occurrences of neosauropods from the Bathonian include wide-gauge trackways from the White Limestone Formation of England (Day et al., 2002), although caution is needed when interpreting trackways, because biomechanically similar animals might have made similar tracks (Henderson, 2006). Thus, basal sauropods were obviously still widespread in the Bathonian, and the scarce evidence for neosauropods at that time suggests that they were not abundant or dominant. This is also supported by a number of other, probably Middle Jurassic sauropods of uncertain exact age, including Jobaria (Sereno et al., 1999) and Spinophorosaurus from Niger (Remes et al., 2009) and Chebsaurus from Algeria (Mahammed et al., 2005; Lüang and Mahammed, 2010), all of which represent non-neosauropods.

In this respect, it is also interesting to note that neosauropods are conspicuously absent from eastern Asia until the Early Cretaceous, with the possible exception of the putative basal taxa Abrosaurus, Bellusaurus, and Daurosaurus (Upchurch et al., 2004; D’Emic, 2012; Carballido and Sander, 2014; but see Wilson and Upchurch, 2009; Royo-Torres and Upchurch, 2012; Mannion et al., 2013). There is, furthermore, currently no evidence for the diplodocid-basal macronarian-brachiosaurid assemblage present in Gondwana and western Laurasia in eastern Asia at any time in the Jurassic. It should be pointed out that many of the allegedly Late Jurassic dinosaur faunas of China are poorly dated, and some of these assemblages, such as that from the Shangshaximiao Formation of Sichuan, might be Middle Jurassic in age rather than Late Jurassic (see, e.g., Averianov et al., 2007). However, the fact that non-neosauropodan sauropods, mainly mamenchisaurids, are present in the better constrained Shishugou Formation (dated as Oxfordian; Russell and Zhong, 1993; see Clark et al., 2006; Choiniere et al., 2010a) and the probably Tithonian Kalazha Formation (Dong, 1997; Eberth et al., 2001), whereas no neosauropod remains have been described from any Late Jurassic unit in China, indicates that this might be a genuine feature of Chinese Late Jurassic sauropod faunas. This absence of the diverse neosauropod fauna of western Laurasia and Gondwana in eastern Asia might thus indicate that the proliferation of this fauna happened after the separation of the latter area from the rest of Pangea by epicontinental seas in the Bathonian/Callovian (Upchurch et al., 2002). Thus, both the fossil record of sauropods in the Middle Jurassic as well as the absence of this fauna from eastern Asia are consistent with the hypothesis that the faunal change from basal eusauropod-dominated faunas to the diplodocid-basal macronarian-brachiosaurid faunas occurred in western Pangea between the Bathonian and the Kimmeridgian, and thus in a geologically relatively short period of time of maximally 10 Ma.

Another tectonic event of the Jurassic might help to further constrain the time of this faunal replacement. Gallina et al. (2014) noted that sea floor spreading around the Americas had started by the Bajocian and on this basis suggested that the radiation of diplodocoids should have taken place at or prior to this time. However, according to most reconstructions, the final separation of the northern continents from Gondwana took place between the northern and southern continents in the Late Jurassic, which would indicate a faunal replacement within some five million years. This hypothesis is consistent with the sparse evidence of Oxfordian sauropod faunas of western Laurasia and Pangea, because brachiosaurids were probably present in the Oxfordian of Tanzania (Janensch, 1961; Bussert et al., 2009) and France (Mannion et al., 2013) and the oldest known diplodocid comes from Oxfordian sediments of
western Georgia in eastern Europe (Gabunia et al., 1998; Mannion et al., 2012). However, the Callovian and Oxfordian sauropod fossil record is still extremely poor, and more material from sediments of this age from western Laurasia and Gondwana is needed to test this hypothesis.

Rapid evolution during the Middle Jurassic is also found in other groups of terrestrial vertebrates, although the very poor fossil record of Middle Jurassic terrestrial vertebrates makes an evaluation difficult in most cases. In theropod dinosaurs, recent research indicates that most higher clades of coelurosauruses originated and diversified during that time (Choiniere et al., 2010b; Rauhut et al., 2010; Xu et al., 2010; Sullivan et al., 2014). However, there does not seem to be a marked faunal turnover from the Middle to the Late Jurassic, as is the case in sauropods. Although the (still very poorly known) Middle Jurassic theropod faunas seem to be dominated by megalosaurid megalosauroids (see Carrano et al., 2012), whereas neotetanurans are more common in the Late Jurassic, the transition seems to be more gradual, because there are a number of neotetanurans known from the Middle Jurassic, and megalosaurids survive to at least the Kimmeridgian–Tithonian. The same seems to be true for ornithischian dinosaurs, the very limited number of lineages of which in the Early Jurassic conflicts with the high diversity of this group in the Late Jurassic (e.g., Butler et al., 2008), indicating rapid diversification during the Middle Jurassic. However, again, there does not seem to be marked and rapid faunal turnover from the Middle to the Late Jurassic.

Thus, a common pattern of rapid faunal turnover from the Middle to the Late Jurassic is, given the current state of knowledge, not recognizable. This might therefore be an evolutionary event that is unique to sauropods, but more evidence, especially from the Middle Jurassic, is needed to fully understand the evolutionary dynamics of terrestrial vertebrates during the Jurassic.

CONCLUSIONS

Three dorsal vertebrae from the Oxfordian–Kimmeridgian Cañadón Calcáreo Formation of Chubut Province, Argentina, represent the first diplodocid sauropod reported from the Jurassic of South America. This diplodocid is part of a diverse sauropod fauna that furthermore includes dicraeosaurids, brachiosaurids, and basal macronarians, being similar in this respect to contemporaneous sauropod faunas from other continents, most notably the Morrison Formation of North America, various units from Portugal, and the Tendaguru Formation of Tanzania. Taking into consideration this wide distribution of various clades of neosauropods in the Late Jurassic, the scarcity of this group in Middle Jurassic rocks, and the apparent dominance of various lineages of basal eusauropods at that time, rapid evolution and dispersal of neosauropods in the late Middle Jurassic is indicated. Coupled with extinction of most non-neosauropod clades towards the end of this epoch, this led to drastic turnover in sauropod faunas in at least the western hemisphere in the second half of the Jurassic.

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