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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 diplococid 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 diplococid 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 diplococid 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 (Proserpio, 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 Cabaleri 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

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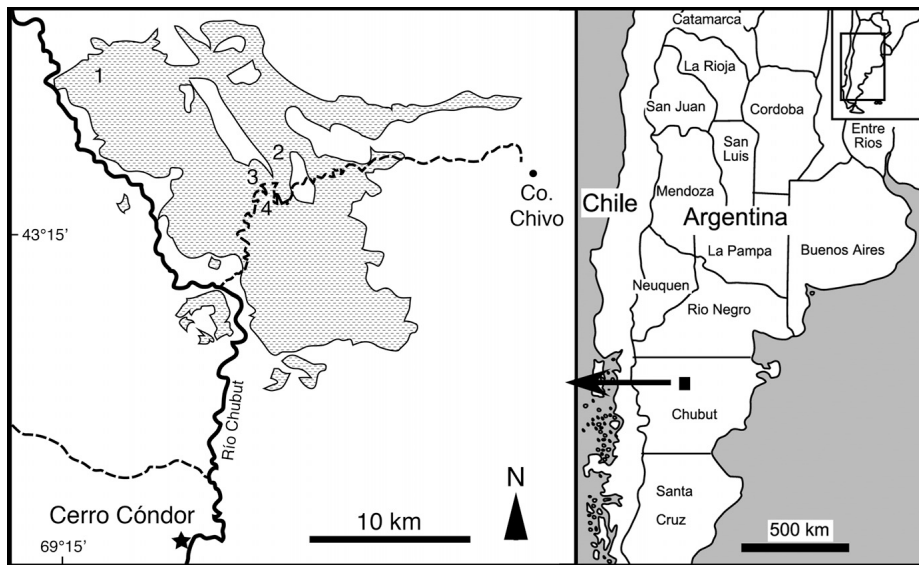


FIGURE 1. Sauropod localities in the Cañadón Calcáreo Formation of northern central Chubut. Stippled area indicates outcrops of the Cañadón Calcáreo Formation (based on geological map in Figari, 2005). **1**, type locality of *Tehuelchesaurus benitezii*; **2**, type locality of *Brachyrachelopan mesai*; **3**, locality that yielded brachiosaurid remains described by Rauhut (2006a); **4**, site of the remains described here.

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, vertebrates from the Cañadón Calcáreo Formation include a rich fish fauna in the basal lacustrine part of the unit (the ‘Almada fauna’; López-Arbarelo et al., 2008, 2013), the basal crocodylomorph *Almadasuchus* (Pol et al., 2013), and fragmentary theropod 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-grained sandstone within the upper part of the Cañadón Calcáreo Formation, probably Kimmeridgian. The locality lies ca. 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 vertebrae 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 determine 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 measurements in Table 1). The probably more anterior vertebral centrum (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 posterior 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 is 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 opening 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 ventral margin of the opening curves gradually into the lateral surface of the centrum; a clear line extending across this curve from the ventral margin of the anterior depression to the posteroventral 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 extensively 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 1. Measurements of the sauropod vertebral centra MPEF 1324.

Dimension	MPEF 1324-1	MPEF 1324-2
Length	240	215(+)
Anterior height	250	260
Anterior width	275	
Mid-width	170	
Mid-height	190	

Measurements in mm. (+) indicates that the centrum is incomplete.

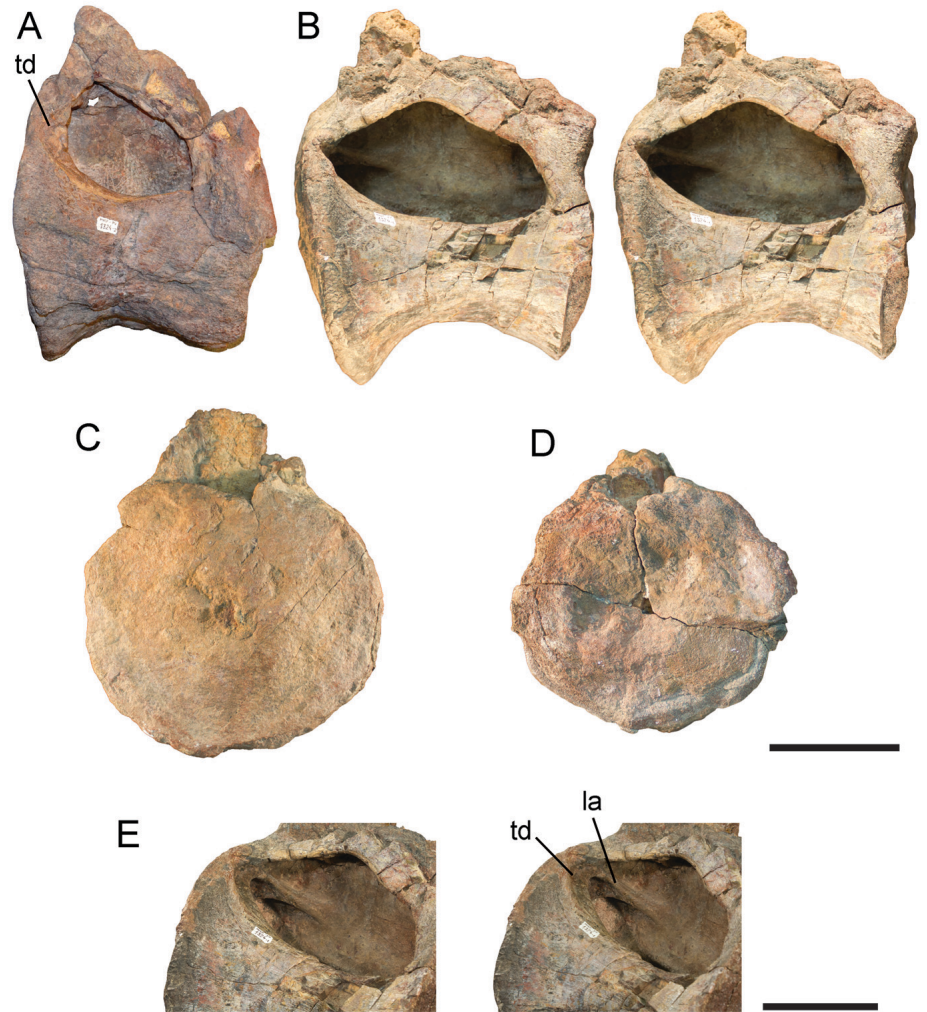


FIGURE 2. Diplodocid dorsal vertebral centra from the Cañadón Calcareo Formation. **A**, anterior to mid-dorsal (MPEF-PV 1324-2) in left lateral view; **B-E**, posterior dorsal (MPEF-PV 1324-1); **B**, left lateral view (stereophotographs); **C**, anterior view; **D**, posterior view; **E**, detail of the pneumatic opening and depression anteroventral to the opening in posterolateral view (stereophotographs). **Abbreviations:** *la*, lamina within the pneumatic cavity; *td*, triangular depression anterior to the pneumatic opening. Scale bars equal 10 cm.

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 centroprezygapophyseal 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 internal camerae (character 139), an ambiguous synapomorphy of Neosauropoda with a reversal in *Haplocanthosaurus* and dicraeosaurids. The subcircular shape of the centrum (character 162) and its non-opisthocoelous condition (character 174) exclude the materials described here from camarasauromorph sauropods, which are characterized by their opisthocoelous and dorsoventrally compressed posterior dorsal centra. As noted in the description, the dorsal margin of the pneumatic openings forms an angular shape (character 346), as in the diplodocids *Apatosaurus* and *Diplodocus* (Hatcher, 1901; Gilmore, 1936), differing from the more rounded shape of these openings in most sauropods, including brachiosaurids (Janensch, 1950). Other characters shared by the specimen described here and diplodocids include the dorsal extension of the pneumatic opening, with the dorsal margin being at the same level as the floor of the neural canal (character 347, present in *Apatosaurus* and *Diplodocus*; Hatcher, 1901; Gilmore, 1936), and the presence of a small fossa at the anterior margin of the opening (character 348, shared with

Diplodocus; Hatcher, 1901). One further character (not included in the formal analysis, because positional variation and continuous size variation make a formal definition difficult) shared with at least some diplodocids is the large size of the pneumatic opening, in which the posterior and anterior edges are close to the articular surfaces of the centrum. This is comparable to the situation in *Apatosaurus* and *Diplodocus*, but differs from the small openings of other diplodocids such as *Barosaurus* and *Dinheirosaurus* (McIntosh, 2005; Mannion et al., 2012). In the Cañadón Calcáreo specimen, as well as in *Diplodocus*, *Apatosaurus*, and rebbachisaurids, the pneumatic opening is placed at about the mid-length of the vertebrae or close to it, at an approximately equal distance from the anterior and posterior ends (character 240), and not anteriorly, as in most sauropods, including the diplodocids *Dinheirosaurus* and *Barosaurus*.

A taxon not included in the analysis, but for which comparable material is known, is the basal diplodocoid *Amphicoelias* (Cope, 1877; Osborn and Mook, 1921). However, the only known posterior dorsal vertebral centrum of *Amphicoelias* is very different from the material described here: the pneumatic opening is rather small, placed in the anterior half of the centrum, has its dorsal margin clearly below the level of the neural arch, and is rounded, rather than angular, dorsally (Osborn and Mook, 1921: fig. 120). Furthermore, there is no indication of a depression at the anterior rim of the opening, as found in the specimens from the Cañadón Calcáreo Formation, and the anterior articular surface is higher than wide. Thus, close relationships with *Amphicoelias* can be excluded.

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 a basal rebbachisaurid, whereas five extra steps are needed if the specimen described here is placed as sister taxon to Neosauropoda or as a basal 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 diplodocoids, the dicraeosaurid *Brachyracheloptan* (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;

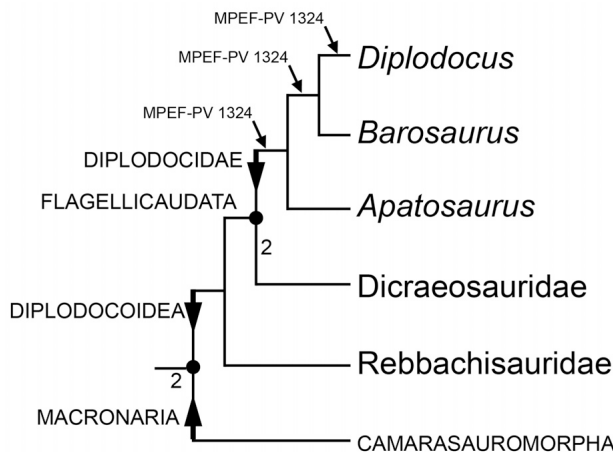


FIGURE 3. Phylogenetic position of the taxon represented by MPEF-PV 1324. For details of phylogenetic analysis see text and Supplementary Data.

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 *Volkheimeria* [Bonaparte, 1979, 1986b] and two unnamed taxa [Rauhut, 2003; Pol et al., 2009]). All of these taxa represent basal, non-neosauropodan 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 higher taxonomic levels, 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; Läng, 2008), and Madagascar (Buffetaut, 2005; Mannion, 2010); furthermore, the basal sauropod *Rhoetosaurus* 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, *Atlasaurus* from the Bathonian of Morocco (Monbaron et al., 1999) has been regarded as a neosauropod by several authors (Upchurch et al., 2004; Läng and Mahammed, 2010), but found to be outside this clade in most 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 (Serenio et al., 1999) and *Spinophorosaurus* from Niger (Remes et al., 2009) and *Chebsaurus* from Algeria (Mahammed et al., 2005; Läng 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 *Daanosaurus* (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 Shishou Formation (dated as Oxfordian; Russell and Zheng, 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 towards the end of the Middle Jurassic (Ford and Golonka, 2003; Iturralde-Vinent, 2006), and sea floor spreading had proceeded to the eastern Caribbean by the Oxfordian at the latest (Pindell and Kennan, 2009), but faunal exchange might have been possible before that time. Furthermore, the widespread basal sauropods in the Bathonian, the lack of any positive evidence for neosauropods in earlier sediments, and the absence of diplodocoids from the Late Jurassic of Asia (see discussion above) make a radiation and dispersal of diplodocoids over most continents in pre-Bathonian times unlikely (though not impossible). Nevertheless, it seems unlikely that there was substantial faunal exchange between the northern and southern continents in the Late Jurassic, as already argued by Remes and Rauhut (2005), Remes (2006), and Gallina et al. (2014). Thus, the great diversification and dispersal of the different neosauropod lineages at least across central Pangea might have taken place in the latest Middle to earliest 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

LITERATURE CITED

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 coelurosaurs 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-neosauropodan 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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