First rebbachisaurid dinosaur (Sauropoda, Diplodocoidea) from the early Cretaceous of Spain: palaeobiogeographical implications

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Key words. – Dinosauria, Sauropoda, Rebbachisauridae, Cretaceous, Burgos, Iberian Peninsula.

Abstract. – Sauropod remains from the early Cretaceous (late Barremian–early Aptian) of Salas de los Infantes (Burgos, Spain) are described. The material consists of several caudal vertebrae, chevrons, a pair of ischia and a femur that is presumed to belong to a single medium-sized individual. Based on the tall neural arches and broad neural spines of the anterior caudal vertebrae, the specimen is referred to the Diplodocoidea. Moreover, it shows affinities with the Rebbachisauridae, a basal clade of diplodocoids. Both the caudal vertebrae and ischium of the Burgos sauropod are similar in form to those of 'Rebbachisaurus' tessonei from the Albian-Cenomanian of South America. However, there are some differences with regard to this taxon, so the Burgos sauropod is provisionally referred to as Rebbachisauridae indet. Rebbachisaurids are known in the Aptian-Cenomanian of the western Gondwanan landmasses (Africa and South America), although further remains have been reported from the Coniacian-Santonian of Argentina and the Hauterivian–Barremian of Croatia. The Burgos diplodocoid appears to be one of the earliest representative of the Rebbachisauridae. This discovery supports previous evidence of a land connection between Europe and Africa across the Tethys seaway sometime in the early Cretaceous.

INTRODUCTION

The fossil record of dinosaurs from the early Cretaceous of the Cameros Basin, in northern Spain (provinces of Burgos, La Rioja and Soria) is mainly represented by footprints [see Sanz et al., 1997 ; Lockley and Meyer, 2000 and references therein]. Additional dinosaur remains include theropods such as the spinosaurid *Baryonyx* [Viera and Torres, 1995 ; Fuentes et al., 2001], ornithopods like *Iguanodon* [Maisch, 1991], hypsilophodontids and dryosaurusids [Ruiz-Omeñaca, 2001 ; Fuentes and Mejide, 2001], and thyreophorans such as the ankylosaur *Polacanthus* [Sanz, 1983 ; Pereda Suberbiola et al., 1999] and an indeterminate stegosaur [Pereda Suberbiola et al., 2003]. Sauropods are represented by scarce remains, mostly of them still undescribed. Sanz et al. [1992] mentioned limb bones and vertebrae of an indeterminate sauropod from the late Jurassic-early Cretaceous near Lara (Burgos) and an isolated femur from Tera (Soria). Platt and Meyer [1991] listed sauropod remains (e.g., rib, vertebra, limb fragments) from the Berriasian Rupel Formation of Mamolar (Burgos), Mambrillas de Lara (Burgos) and Espejón (Soria). Torcida [1996] noted the discovery of large brachiosaurid-like bones from Aldea del Pinar (Burgos) and of teeth, vertebral and limb bones from sev-
eral localities of the Lower Wealden (Berriasian-Valanginian) of southeast Burgos, currently kept in the Museo de Dinosauros de Salas de los Infantes, Burgos (MPS collection\(^1\), unpublished). Some of these remains could belong to Titanosauriformes.

Recent field work in the early Cretaceous (Barremian-Aptian) rocks of the western Cameros Basin near Salas de los Infantes (Burgos) has yielded vertebrae, girdle and limb bones of a medium-sized diplodocoid. These remains are described below and referred to the Rebbachisauridae.

GEOLOGICAL SETTING

The dinosaur locality is Tenadas de los Vallejos II, situated near the villages of La Revilla and Ahedo at about 10 km southwest of Salas de los Infantes, province of Burgos, Spain (fig. 1). The site is located in the southern part of the Contreras anticline, western Cameros Basin. The fossiliferous beds are red clays intercalated with alluvial sandstones of the Castrillo de la Reina Formation, which correspond to the fifth sedimentary sequence of Mas et al. [1993] and Martín-Closas and Alonso [1998]. These are regarded as late Barremian to early Aptian in age (Salas Group; Aptian [sensu Platt, 1989]).

The sauropod bones consist of caudal vertebrae, haemal arches, rib fragments, two ischia and one femur. These remains were found disarticulated in the same level and in close proximity to each other, so they presumably belong to the same individual. Other dinosaur remains found in the Tenadas de los Vallejos II locality include two cervical vertebra of a spinosaurid theropod (A.C. Milner, J. Le Lœuff, pers. comm.).

SYSTEMATIC PALAEONTOLOGY

Sauropodomorpha Huene, 1932
Sauropoda Marsh, 1878
Diplodocoidea Upchurch, 1995
Rebbachisauridae Bonaparte, 1997
Gen. et sp. indet.
(figs. 2-3)

Referred material. MPS-RV II-2, 3, 4, 9, 10, 11, 12, 13, 15, 17, anterior and middle caudal vertebrae; MPS-RV II-23, haemal arch; MPS-RV II-14, rib fragment; MPS-RV II-6, 7, 8, other vertebral remains; MPS-RV II-18, 19, left and right ischium; MPS-RV II-16, left femur; MPS-RV II-22, indeterminate bone.

Locality and horizon. Tenadas de los Vallejos II (La Revilla-Ahedo), near Salas de los Infantes, province of Burgos, Spain; Castrillo de la Reina Formation, western Cameros Basin, Lower Cretaceous, Barremian-Aptian [Platt, 1989; Mas et al., 1993; Martín-Closas and Alonso, 1998].

Description

For measurements see table I.

Caudal vertebrae and haemal arches (fig. 2). Ten caudal vertebrae are known, including vertebrae from the anterior and middle regions of the tail. All the centra are amphiplatyan to slightly amphicoelous. In the anteriormost caudals, the anterior articulation surface is flat and the posterior articulation is slightly concave. Pleurocoels are absent. The centrum of the best preserved anterior caudal (MPS-RV II-15; figs. 2A-E) is anteroposteriorly shorter than high, and transversely higher than wide (anterior articulation) or as high as wide (posterior articulation). The lateral faces are concave. The ventral side has separate articulation surfaces for the haemal arches which are more marked distally than proximally. Between the anterior and

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1. Abbreviation : MPS, Museo de Dinosaurios – Paleontología, Salas de los Infantes, Burgos, Spain.

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FIG. 1. – Synoptic map of the main geological units of western Cameros Basin, Burgos, Spain. The dinosaur locality is marked by an asterisk.

FIG. 1. – Carte avec les principales unités géologiques de l’Ouest du bassin de Cameros, Burgos, Espagne. Le gisement à dinosaure est indiqué par un astérisque.

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posterior chevron surfaces, there are prominent ridges that delimit a shallow and wide longitudinal groove. The transverse processes are broken, but they are well-developed, forming a deep projection that extends from the centrum to the neural arch. As preserved, they are not wing-like but appear to be formed by fusion of a dorsal and a ventral bar [see Calvo and Salgado, 1996]. The neural arch is dorsoventrally tall, about 1.9 higher than the centrum. The neural spine is cruciform-shaped, with four laminae at right angles, including a prespinal lamina, a postspinal lamina and two lateral laminae (suprapostzygapophyseal laminae [see Upchurch, 1998, fig. 10] ; spinopostzygapophyseal laminae [sensu Wilson 1999b : fig. 4]). The prespinal lamina is more marked at the basal part of the neural spine than towards the top. In dorsal view, the postspinal lamina is much more developed than the prespinal one. The lateral laminae have small wing-like projections near the top of the neural spine. Anterior caudal vertebrae located more posteriorly in the tail series (e.g., MPS-RV II-3 ; figs. 2G-H) show a longitudinal ridge (rudimentary transverse process ?) on the upper third of the lateral surface of the centrum. The centrum of MPS-RV II-3 is comparatively longer than that of anteriormost caudals. The neural canal is much higher than wide ; the ventral longitudinal groove is very shallow. The chevrons of the anterior caudals (MPS-RV II-23 ; fig. 2F) are V-shaped and open at their proximal ends.

The middle caudal vertebrae (MPS-RV II-2, 4 ; figs. 2I-J) have slightly amphicoelous centra that are longer than high or wide. They are characterised by two longitudinal ridges on the lateral side of the centra, the upper ridge being more prominent than the lower one. The neural arches are placed over the middle of the centra. The prezygapophyses slightly overhang the anterior margin of the centra. The neural spines are broken. Ventrally, the articulation surfaces for the haemal arches are visible on both anterior and posterior ends.

Additional remains from the axial skeleton consist of a rib fragment and indeterminate vertebral bones.

Ischium (figs. 3A-C). Both ischia are preserved, the left ischium is more complete than the right one (MPS-RV II-18, 19). The bones are approximately 80 cm long from the

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**TABLE I. – Measurements (in mm) of the rebbachisaurid dinosaur from the early Cretaceous of Burgos, Spain.**

<table>
<thead>
<tr>
<th>Caudal vertebra</th>
<th>MPS-RV II-15</th>
<th>II-3</th>
<th>II-2</th>
<th>II-4</th>
<th>II-11</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total height</td>
<td>390</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Height of neural arch (from dorsal surface of centrum to top of neural spine)</td>
<td>250</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Height from postzygapophyses to top of neural spine</td>
<td>190</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maximum width of neural spine (near the top)</td>
<td>85</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Anteroposterior length of neural spine</td>
<td>55</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Centrum length (anterior)</td>
<td>98</td>
<td>150</td>
<td>155</td>
<td>150</td>
<td>130</td>
</tr>
<tr>
<td>(posterior)</td>
<td>135</td>
<td>135</td>
<td>125</td>
<td>95</td>
<td>115</td>
</tr>
<tr>
<td>Centrum width (anterior)</td>
<td>115</td>
<td></td>
<td>135</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(posterior)</td>
<td>135</td>
<td>135</td>
<td>135</td>
<td>130</td>
<td>135</td>
</tr>
<tr>
<td>Neural canal height</td>
<td>29</td>
<td>40</td>
<td>25</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Haemal arch</th>
<th>MPS-RV II-23</th>
</tr>
</thead>
<tbody>
<tr>
<td>Height</td>
<td>135</td>
</tr>
<tr>
<td>Length</td>
<td>30</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Ischium</th>
<th>MPS-RV II-18 (left)</th>
<th>MPS-RV II-19 (right)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length (distance from proximal corner of pubic peduncle to distal end)</td>
<td>790</td>
<td>805</td>
</tr>
<tr>
<td>Maximal dimensions of pubic peduncle</td>
<td>117 x 82</td>
<td>115 x 63</td>
</tr>
<tr>
<td>Minimal length of the neck of pubic peduncle</td>
<td>55</td>
<td></td>
</tr>
<tr>
<td>Distance from the pubic peduncle to distal margin of the bone</td>
<td>160</td>
<td></td>
</tr>
<tr>
<td>Dorsoventral length of the pubic peduncle</td>
<td>120</td>
<td></td>
</tr>
<tr>
<td>Distal width</td>
<td>90</td>
<td></td>
</tr>
<tr>
<td>Distal thickness</td>
<td>25</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Femur</th>
<th>MPS-RV II-16 (left)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length</td>
<td>1080</td>
</tr>
<tr>
<td>Proximal length</td>
<td>230</td>
</tr>
<tr>
<td>Distal width</td>
<td>235</td>
</tr>
</tbody>
</table>

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*Bull. Soc. géol. Fr., 2003, n° 5*
proximal corner of the acetabular region to the distal end (see table I). The ischial shaft is very slender and almost straight. The iliac peduncle is more prominent than the pubic one, but the articular margin of the latter is comparatively longer. Medially, there is a concavity that forms part of the acetabulum. The distal end of the ischial shaft is bladelike and narrow, only slightly expanded relative to the rest of the shaft. The ischia are not coossified at their distal ends, but they show a very rugose symphyseal surface. The distal ends are almost horizontal and form a nearly coplanar structure in cross-section. Distally, the shaft is flattened dorsoventrally and has subequal medial and lateral depths;
the maximum width is almost four times its minimal thickness.

Femur (figs. 3D-E). As reconstructed, the femur (MPS-RV II-16) is 108 cm long. The shaft is straight and relatively slender, with expanded proximal and distal ends. The femoral head is almost perpendicular to the shaft. It rises very slightly above the greater trochanter. The lesser trochanter is not developed. The lateral margin of the shaft is straight. There is no a prominent bulge on the proximal third of the lateral surface. The cross-sectional shape of the shaft is suboval, with the long axis oriented lateromedially. The fourth trochanter is reduced to a low ridge located above the midlength of the shaft, between the midline and the caudomedial margin. The distal condyles are prominent, the medial condyle larger than the lateral one, and separated from each other by a deep intercondylar groove.

Ontogenetic growth. The neural arches of the caudal vertebrae are firmly co-ossified to the centra, so the skeletal remains probably belong to a mature individual. The relative size of the bones suggests a medium-sized individual whose total length is approximately 10-12 m.

DISCUSSION

Affinities of the Burgos sauropod

The dinosaur remains from Tenadas de los Vallesjos II (Burgos) are referred to Sauropoda on the basis of the bladelike distal shaft of the ischium; elliptical (long axis oriented mediolaterally) cross-sectional shape of the femur; and femoral fourth trochanter reduced to crest or ridge [see Wilson and Sereno, 1998; Wilson, 2002]. The material of Burgos also shows synapomorphies of Neosauropoda: anterior caudal neural arches with prespinal and postspinal laminae (also present in Jobaria); chevrons without a proximal “crus” bridging dorsal margin of haemal canal; and ischial shaft flat, nearly coplanar (also in Jobaria) [Wilson, 1999a, 2002]. Moreover, the Burgos sauropod shares at least a synapomorphy with the Diplodocoidea sensu Upchurch, 1995 [senior synonym of Diplodocimorpha Calvo and Salgado, 1996]: tall neural arch in anterior caudal vertebrae. In diplodocoids, the neural arch is at least 1.5 higher than the centrum [Calvo and Salgado, 1996; 2.5 higher according to Wilson and Sereno, 1998]. In fact, the neural arch is at least two times higher than the centrum in the anterior caudals of ‘Rebbachisauridae’ and the dicraeosaurid Dicraeosaurus, while it is between 1.5 and 2 in the diplodocoids Diplodocus and Barosaurus [see Calvo and Salgado, 1996]. In the Burgos sauropod, the neural arch of the single complete anterior caudal vertebra is about 1.9 higher than the centrum.

Diplodocoids consist of diplodocids, dicraeosaurids and rebbachisaurids [Sereno et al., 1999; Wilson, 1999a, 2002]. Upchurch [1999] regarded nemegtosaurids as members of Diplodocoidea but they appear to be more closely related to titanosaurs within Titanosauriformes [Salgado and Calvo, 1997; Curry Rogers and Forster, 2001; Wilson, 2002]. The Burgos diplodocoid exhibits the following synapomorphy of the clade Rebbachisauridae + (Diplodocidae + Dicraeosauridae): anterior caudal neural spines broad, i.e. transverse breadth approximately 50 % greater than the anteroposterior length [Wilson, 2002]. Moreover, it does not show synapomorphies of the clade formed by the Dicraeosauridae (Dicraeosaurs, Amargasaurus) and Diplodocidae (Diplodocus, Apatosaurus, Barosaurus, Seismosaurus, Supersaurus). For example, the anterior cau-
Rebbachisaurids are basal diplodocoids outside the Diplodocidae-Dicraeosauridae clade. Bonaparte [1997] erected the Rebbachisauridae mainly on the basis of characters of the scapula and dorsal vertebrae. The Burgos specimen does not preserve synapomorphies of Rebbachisauridae listed by Wilson [2002] but it closely resembles rebbachisaurids in the form of both the anterior caudal vertebrae and ischium. The Spanish taxon exhibits a combination of primitive and derived characters that is only known in rebbachisaurids [see Calvo and Salgado, 1996; Upchurch, 1998; Wilson, 2002]: (1) ‘petal’-shaped anterior caudal neural spines [Wilson, 2002 regarded the ‘petal’-shaped posterior dorsal neural spines as synapomorphic for Rebbachisauridae (paralleled in dicraeosaurids), but this character is also present in the anteriormost caudals; see Calvo and Salgado, 1996: figs. 9-10]; (2) transversely expanded, cruciform-like in dorsal view, anterior caudal neural spines (known in all diplodocoids but Haplocanthosaurus); 3) amphiplatyian or platycoelous anterior caudal centra, without pleurocoels (known in ‘R.’ tessonei, Haplocanthosaurus, Dicraeosaurus and Apatosaurus within Diplodocoidea); 4) triangular-shaped, tapering distally anterior caudal transverse processes (only known in ‘R.’ tessonei and Haplocanthosaurus among diplodocoids); 5) anterior caudal chevrons with open proximal articulation (only present in rebbachisaurids and Haplocanthosaurus among diplodocoids); 6) very slender ischium, with a narrow and flat distal end, nearly coplanar in cross-section (only Rebbachisaurus tessonei and Haplocanthosaurus priscus [Hatcher, 1903] show a similar morphology among diplodocoids).

It is difficult to compare the Burgos remains with those of Rebbachisaurus garasabae from the middle Cretaceous of Morocco as the latter has no homologue elements except caudal vertebrae [Lavocat, 1954]. Unfortunately, most of the remains of R. garasabae kept at the Museum National d’Histoire Naturelle de Paris is still unprepared (P. Taquet, pers. comm.). The Burgos diplodocoid is most similar to ‘Rebbachisaurus’ tessonei, a rebbachisaurid from the middle Cretaceous of Argentina [Calvo and Salgado, 1996]. However, the incomplete nature of the Burgos remains does not allow us to recognize either the diagnostic characters of ‘Rebbachisaurus’ tessonei as described by Calvo and Salgado [1996] or Wilson [2002] as Rayososaurus, with perhaps, the exception of anterior caudal transverse processes composed of two lateral bars (while wing-like in most diplodocoids). A comparison of the Burgos sauropod with ‘R.’ tessonei shows several minor differences: the neural arch of the anterior caudal is just 1.9 higher than the height of the centrum (versus 2.5 in ‘R.’ tessonei [see Calvo and Salgado, 1996: fig. 10]); the postspinal lamina is greater than the prespinal lamina in anterior caudals (in contrast to ‘R.’ tessonei); the lateral laminae have small wing-like projections towards the top of the neural spine (absent in ‘R.’ tessonei), and the ischium is straighter and the dorsalventral length of the pubic articular surface is comparatively longer than in the South American specimen.
dantary was originally attributed to the Titanosauridae [Huene, 1929]. Powell [1986] and Chiappe et al. [2001] have supported the titanosaur affinities of this taxon [see also Salgado and Calvo, 1997]. In contrast, McIntosh [1990] regarded the dentary of A. wichmannianus as diplodocoid, and Jacobs et al. [1993] removed it from the Titanosauridae to the Diplodocidae. Wilson and Sereno [1998] and Upchurch [1999] interpreted the dentary of ‘A. wichmannianus’ as that of a late diplodocoid, while Sereno et al. [1999] and Wilson [2002] referred it to the Rebbachisauridae. With regard to other possible late Cretaceous diplodocoids, there is poor evidence to support the occurrence of the diplodocid Dyslocosaurus polyonchius in the Maastrichtian Lance Formation of Wyoming, North America. Derivation of this specimen from the late Jurassic of the Morrison Formation is more likely [McIntosh et al., 1992].

Rebbachisaurids have not been described in Europe, with the exception of Histriasaurus boscariollii from the early Cretaceous of Croatia [Dalla Vecchia, 1998]. This taxon is based on an isolated dorsal vertebra from the late Hauterivian-early Barremian of Istria [Dalla Vecchia, 1998, figs. 13-D-E]. The specimen is similar to mid-posterior dorsal vertebrae of Rebbachisaurus garasbae from Morocco and Rebbachisaurus tessonei from Patagonia in having a ‘petal’-shaped posterior dorsal neural spine, but differs in having a hypophene-hypantrum complex. Histriasaurus is a member of the Diplodocoidea on the basis of the tall neural arch, which is three times higher than that of the centrum [sensu Calvo and Salgado, 1996], and the presence of a postspinal lamina on the neural spine [Upchurch, 1998]. It differs from dicraeosaurids in retaining pleurocoels, and is probably different from diplodocids in having the neural spine 75 per cent higher than the neural arch. The affinities of Histriasaurus with the Rebbachisauridae need to be confirmed but this taxon testifies of the presence of a basal diplodocid in the early Cretaceous of Croatia [Dalla Vecchia, 1998].

Besides Histriasaurus and the Burgos rebbachisaurid, diplodocoids are rare in the Wealden succession of Europe as they are only represented by scarce remains. Charig [1980] described a sled-shaped diplodocid chevron from the Barremian Wessex Formation of the Isle of Wight (England), but the referral of this bone to the Diplodocidae must be provisional [Naish and Martill, 2001]. Other possible diplodocid material from the same area and horizon consists of isolated remains [see Upchurch, 1995; Naish and Martill, 2001]. Cetiosaurus iswarthii from the Middle Jurassic (Callovian) of England was referred to the Diplodocidae by McIntosh [1990], but it could be a basal neosauropod [Wilson et al., 1999]. In the Iberian Peninsula, the only known diplodocoids are Dinheirosaurus lourinhanensis from the late Jurassic (Kimmeridgian) Camadas de Alcobaça Formation of Lourinhã, Portugal [Bonaparte and Mateus, 1999] and Losillasaurus giganteus from the late Jurassic-early Cretaceous transition of Valencia, Spain [Casanovas et al., 2001]. Losillasaurus lacks several diplodocid and dicraeosaurid synapomorphies, and differs from rebbachisaurids in having hypophene-hypantrum complex on dorsal vertebrae, slightly opisthocoelous dorsal centra, and slightly prococoelous anterior caudal centra. It has been regarded as sister-group to the clade Barosaurus + Diplodocus + Dicraeosaurus by Casanovas et al. [2001]. In other words, Losillasaurus is a diplodocid, but it is probably not a rebbachisaurid. In Portugal, Bonaparte and Mateus [1999] considered Dinheirosaurus as a member of the Diplodocidae on the basis of features of the presacral vertebrae. Both Losillasaurus and Dinheirosaurus are regarded as members of the clade formed by dicraeosaurids and diplodocids by Wilson [2002]. Finally, Cuenca Bescós et al. [1997] referred tentatively an isolated tooth from the late Jurassic of the Villar del Arzobispo Formation of Teruel (Spain) to as Diplodocidae indet., and Martínez et al. [2000] described as diplodocid a tooth from the late Jurassic of the Lastres Formation of Asturias (Spain). This material seems too incomplete for an accurate identification.

PALAEOBIOGEOGRAPHICAL IMPLICATIONS

The discovery of a rebbachisaurid sauropod in the early Cretaceous (Barremian-Aptian) of Burgos demonstrates the presence of this basal clade of diplodocoids in the Iberian Peninsula. It confirms the presence of rebbachisaurids in Europe, and adds to previous reports of the Rebbachisauridae in Africa and South America.

From a biogeographical point of view, the occurrence of a rebbachisaurid in the Barremian-Aptian of Spain suggests a land connection between Europe and Africa during the early Cretaceous (although an alternative scenario involving an earlier dispersal episode cannot be excluded as basal diplodocoids are known as early as the late Jurassic). This hypothesis supports previous evidence based on the intercontinental distribution of dinosaurs across the Tethys sea-way, such as the dryosaurid ornithopods [Galton and Taquet, 1982] and spinosaurid theropods [Sereno et al., 1999].

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