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HIGH EUROPEAN SAUROPOD DINOSAUR DIVERSITY DURING JURASSIC–CRETACEOUS TRANSITION IN RIODEVA (TERUEL, SPAIN)

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Abstract: Up to now, more than 40 dinosaur sites have been found in the latest Jurassic – earliest Cretaceous sedimentary outcrops (Villar del Arzobispo Formation) of Riodeva (Iberian Range, Spain). Those already excavated, as well as other findings, provide a large and diverse number of sauropod remains, suggesting a great diversity for this group in the Iberian Peninsula during this time. Vertebrae and ischial remains from Riodevan site RD-13 are assigned to *Turiasaurus riodevensis* (a species described in RD-10, Barrihonda site), which is part of the Turiasauria clade. This is the first time that a taxon is attributed to *Turiasaurus* genus out of its type site. A Neosauropod caudal vertebra from the RD-11 site has been classified as Diplodocinae indet., supporting the previous attribution on an ilion also found in Riodeva

(CPT-1074) referring to the Diplodocidae clade. New remains from the RD-28, RD-41 and RD-43 sites, of the same age, among which there are caudal vertebrae, are assigned to Macronaria. New sauropod footprints from the Villar del Arzobispo Formation complete the extraordinary sauropod record coming to light in the area. The inclusion of other sauropods from different contemporaneous exposures in Teruel within the Turiasauria clade adds new evidence of a great diversity of sauropods in Iberia during the Jurassic–Cretaceous transition. Turiasauria distribution contributes to the understanding of European and global palaeobiogeography.

Key words: Sauropoda, Turiasauria, Diplodocoidea, Macronaria, Tithonian–Berriasian, Iberian Peninsula, Riodeva.

SAUROPODA have been widely recorded in the Mesozoic, from their origin in the Triassic until their extinction in the Upper Cretaceous (Upchurch *et al.* 2004). The diversity of groups oscillated, hence Upchurch and Barrett (2005) noted a decrease in sauropod diversity in the Oxfordian, although this increased considerably during the Jurassic to reach its peak at the end of this period (Kimmeridgian–Tithonian) with more than 30 taxa recorded in each stage. Later, in the Lower Cretaceous, data point to low diversity (Berriasian–Aptian) with less than 10 taxa in each stage; the Berriasian has the lowest number of taxa (Hunt *et al.* 1994; Upchurch and Barrett 2005). This reduction in the diversity of sauropod taxa could either be or not be attributed to the substitution of dinosaur faunas proposed between the Jurassic and the Cretaceous for the different groups (Serenó 1997, 1999). Within this context, the results achieved by the Fundación Conjunto Paleontológico de Teruel-Dinópolis during several excavations in Riodeva (southern Teruel province, Spain) since 2002 show a large diversity of sauropods living

on the Iberian plate during the Jurassic–Cretaceous transition. Until now, more than 40 dinosaur sites have been discovered, 15 of them containing sauropod remains (Table 1), and three of them have already been intensively excavated. The RD-10 (Barrihonda-El Humero) site includes a new large sauropod genus and species, *Turiasaurus riodevensis* Royo-Torres, Cobos and Alcalá, 2006. Other fossil bones found in Riodeva are attributed to different groups of sauropods such as diplodocids, stegosaurids, theropods (large and small sized) and basal ornithomorphs (Royo-Torres *et al.* 2006; Alcalá *et al.* 2007). Isolated crocodile teeth, partially articulated turtle shells, many fish teeth and scales, vegetable remains and invertebrates have also been recovered. Some contemporaneous sauropod ichnite tracksites have also been recorded in Riodeva.

In this study, we present the findings of the sites El Carrillejo (RD-11), Puntal de Santa Cruz (RD-13) and San Lorenzo (RD-28), plus other more fragmentary remains found in the localities RD-1, RD-5, RD-8, RD-9, RD-20, RD-27, RD-41 and RD-43 and a new dinosaur

TABLE 1. Sites with sauropod dinosaurs remains in Riodeva (Teruel, Spain).

Site	Material	CPT	Systematic
RD-1 (A)	Fragment of ulna and femur	CPT-973 and CPT-974	Sauropoda indet.
RD-5 (Pino de Jarque 2)	Right ilium	CPT-1074	Diplodocidae indet.
RD-8 (La Cueva)	Fragment of right ulna	CPT-1098	Sauropoda indet.
RD-9 (La Loma)	Right distal of pubis	CPT-1109	Sauropoda indet.
RD-10 (Barrihonda-El Humero)	An articulated left forelimb	CPT-1195 to CPT-1210	<i>Turiasaurus riodevensis</i> (holotype)
RD-10 (Barrihonda-El Humero)	Skull fragments, eight teeth, six cervical vertebrae with ribs, two proximal dorsal vertebrae, one middle dorsal vertebra, fragments of other dorsal vertebrae, eight dorsal ribs, partial sacrum, two distal caudal, one fragment of the scapula, one sternal plate, one distal fragment of femur, one proximal fragment of the tibia, one fibula, two astragalus and one pes.	CPT-1211 to CPT-1261	<i>Turiasaurus riodevensis</i> (paratype)
RD-10 (Barrihonda-El Humero)	Three dorsal spines vertebrae	CPT-2688, CPT-1181, CPT-1182	<i>Turiasaurus riodevensis</i> (referred material)
RD-11 (El Carrillejo)	Anterior caudal vertebra	CPT-1575	Diplodocinae indet.
RD-13 (Puntal de Santa Cruz)	Axis, one cervical vertebra?, five dorsal centra, two dorsal spines, one sacral spine, one anterior caudal vertebra, fragments of prezygapophyses, postzygapophyses and proximal ischium	CPT-1609 to CPT-1657 and CPT-1661 to 1674	<i>Turiasaurus riodevensis</i>
RD-20 (Pino de Jarque-Muro)	Fragment of ulna	CPT-1717	Sauropoda indet.
RD-27 (La Cautiva 2)	Anterior caudal vertebra	CPT-1966	Eusauropoda indet.
RD-28 (San Lorenzo)	Anterior caudal vertebra	CPT-1846	Macronaria indet.
RD-36 (Las Perplejas)	Sauropod tracks		Sauropoda indet.
RD-41 (La Quineta 1)	Posterior caudal vertebra	CPT-3295	Macronaria indet.
RD-43 (Las Viñas)	Anterior caudal vertebra	CPT-3296	Macronaria indet.

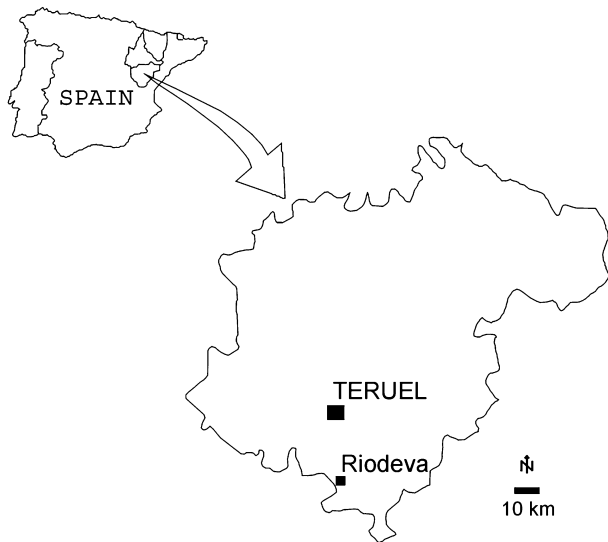
ichnite site named Las Perplejas (RD-36). The materials are property of the Aragón Government and are housed at the Museum Fundación Conjunto Paleontológico de Teruel-Dinópolis (Teruel, Spain). All of them are included in the Villar del Arzobispo Formation exposures (Tithonian–Berriasian) in Riodeva (Teruel).

GEOGRAPHIC AND GEOLOGICAL SETTING

The Riodeva dinosaur sites are located in the southern Iberian Range, in the province of Teruel (Spain) (Text-fig. 1). The outcrop bearing dinosaur deposits is in a triangular depression of 18 km² deeply incised by stream channels. Eastward and westward from these exposures, folded limestone Jurassic formations create a high

relief, while eastward and northward both unconformable Cretaceous and Tertiary deposits overlay Riodeva deposits.

The dinosaur-bearing deposits consist of more than 200-m thick sandstone and red silty clay layers corresponding to the Villar del Arzobispo Formation (Mas *et al.* 1982, 1984). The Villar del Arzobispo Formation has also been recognized in other exposures where dinosaur bones or footprints have been previously found, like Galve (Ruiz-Omeñaca *et al.* 2004), Formiche Alto (Cobos *et al.* 2005) or El Castellar (Alcalá *et al.* 2007), in Teruel, and Losilla de Aras-Alpuente (Santisteban 2004), in Valencia. Fieldwork surveys (Text-fig. 2) proved that underlying marine deposits of the Higuieruelas Formation gradually pass to the transitional deposits of the Villar del Arzobispo Formation in a regressive trend in parts of the Iberian basin (Bádenas and Aurell 2001).



TEXT-FIG. 1. Geographic setting of Riodeva (UTM 659049 and 4443553) in Teruel Province, Spain.

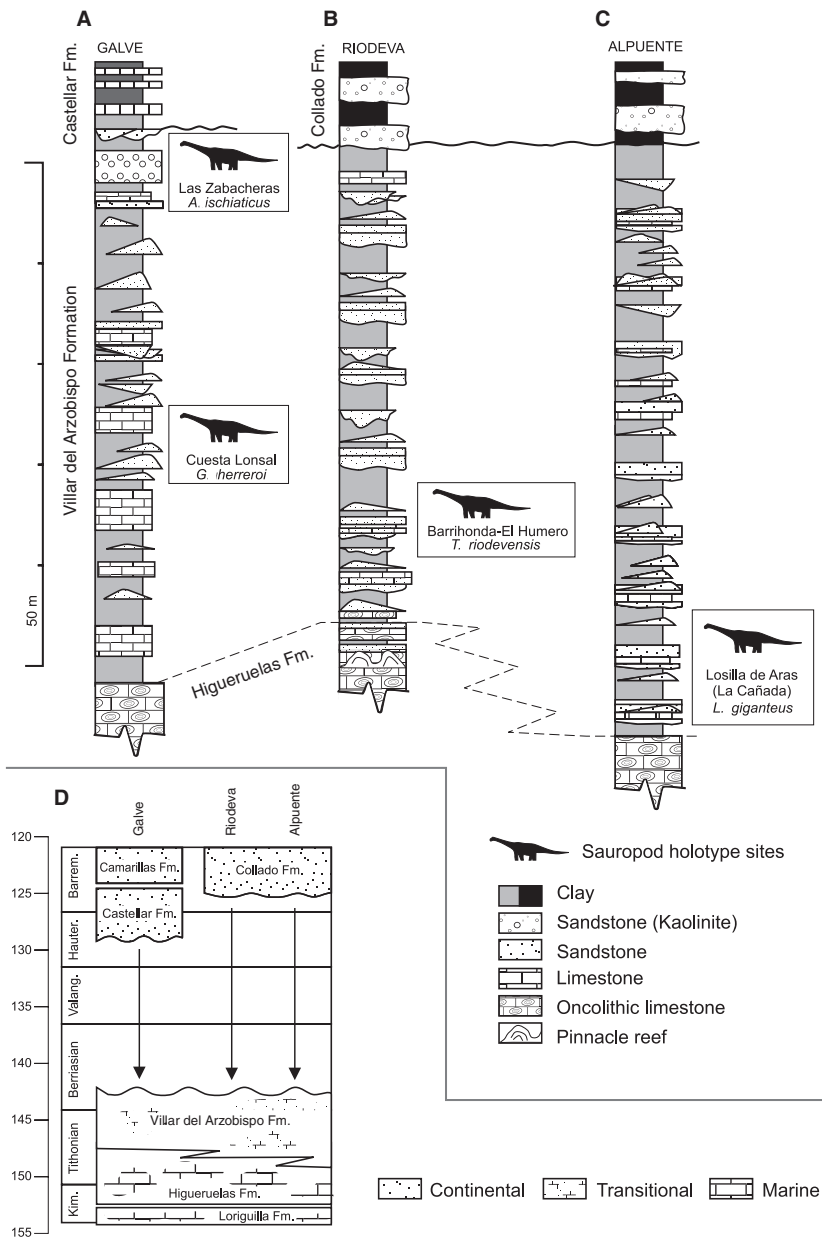
These sedimentary deposits in Riodeva are structured in a series of at least 13 sequences, each constituted by 2–10 m thick, white-yellowish sand beds at the base and overlaid by a similar thickness of red and gray silty clays (Luque *et al.* 2005). The contact between each sequence is sharp and erosive, with the basal sandy beds showing a lateral extension of several hundreds of meters. Paleocurrents show dominant NW–SE and NE–SW trends. A detailed analysis of the sequences allowed us to divide the series in three stratigraphic units (Luque *et al.* 2005):

1. Transitional contact with the underlying shallow marine carbonates showing clastic-carbonated deposits with a tidal influence.
2. Intermediate clastic section, more carbonated at the base, showing a shallowing trend tide influenced at the base and more fluvial at the upper part. It is the thickest section and contains the greater part of the dinosaur remains.
3. Uppermost section showing thin carbonated levels at the top suggesting more of a marine influence. The overlying Barremian Collado Formation lies unconformably above it.

The lateral changes in facies suggest a more continental environment in Riodeva than those of the other fossiliferous sites such as Galve, El Castellar or Losilla de Aras-Alpuente (Text-fig. 2). Sedimentary sequences show a general regressive trend (Bádenas and Aurell 2001), related to global regression recorded during the end of the Jurassic (Haq *et al.* 1987; Hallam 2001; Ford and Golonka 2003). The age of the Villar del Arzobispo Formation in Riodeva is obtained through geological correlation because of its current lack of precise biochronological markers (only poorly preserved ostracods have been

recorded). In the area where the Villar del Arzobispo Formation was defined, both *Anchispirocyclus lusitanica* and *Everticyclus virguliana*, foraminifers of Late Kimmeridgian to Portlandian (latterly specified as Tithonian–Berriasian) age, were first found (Mas *et al.* 1984). Subsequently, *Alveosepta jaccardi* of the mid-Kimmeridgian age and benthonic foraminifers that range from the mid-Tithonian to the mid part of the Early Berriasian, as well as *Feurtillia frequens* (probably Berriasian), were recovered (Aurell 1990). According to the foraminiferal assemblage with *Alveosepta powersi* and *Anchispirocyclus lusitanica*, the underlying Higuieruelas Formation spans the interval from the Kimmeridgian/Tithonian boundary and to the Early Tithonian (Aurell 1990). Recently, Bádenas *et al.* (in press) dated the base of the Villar del Arzobispo Formation as near the Kimmeridgian/Tithonian boundary in the westernmost outcrops and Middle Tithonian in the Riodeva area. All these data suggest that diachronism of the Villar del Arzobispo Formation is coherent with the regressive trend of the sedimentary succession. The Higuieruelas Formation at the Riodeva exposures includes the foraminifer *Anchispirocyclus lusitanica*, indicating that the dinosaur-bearing deposits are not older than Tithonian (Fezer 1988). The lack of biochronological markers, the erosional surface at the top and the consequent sedimentary hiatus overlying the Riodeva succession prohibit a precise age determination of the uppermost exposures of the Villar del Arzobispo Formation in Riodeva; in any case, this age would exceed the Berriasian.

The terrigenous deposits containing the dinosaur sites in Riodeva (Text-fig. 2) were mainly formed in tidal environments but changing over time from subtidal to supratidal in each sequence. Cyclic processes, probably climate-forced, gave rise to a series of shallowing upward parasequences showing marine influenced deposits at the base and more continental deposits at the top. Fine, well-laminated sandstones can be found at the base of the parasequences, sometimes including a thin layer of limestone rich in ostracods, gastropods and echinoids or fine coal remains. Dinosaur remains are found as clasts both within the sandstones overlying the marine-influenced fine carbonate-siliciclastic beds and on the top of these sandstones. In many cases, the thickest sand beds show a multi-channel structure, sand waves and point bars, increasing the depositional energy flow upward, being richer in conglomerates. Higher fossil bone concentrations are found at the top of these beds, included in the overlying sandy clays. Bones in the red clays are much more scarce and scattered, but not absent (RD-41). Red clays show a number of paleosols sometimes related to overbank deposits on the muddy supratidal to alluvial flat, indicating shorter scale cycles. Sauropod footprints have been found in some fine sandstone to siltstone beds at the lower part of the sequence. The main site, Las Perple-



TEXT-FIG. 2. Stratigraphic sections of the localities where the Villar del Arzobispo Formation sauropods have been found and their temporal relationship. A, Galve (Ruiz-Omeñaca *et al.* 2004; Barco *et al.* 2005). B, Riodeva (Luque *et al.* 2005). C, Alpuente (Casanovas-Cladella *et al.* 1999; Casanovas *et al.* 2001). D, Lithostratigraphic chart of the South Iberian Basin of the Iberian Range during the Late Jurassic–Early Cretaceous (Salas *et al.* 2001).

jas, corresponds to tidally influenced sand bar deposits included in the basal section of the Villar del Arzobispo Formation in Riodeva.

The extrapolation of the new stratigraphic and sedimentological data obtained in Riodeva to other outcrops with dinosaur sites, allows us to suggest an older age to those levels of Galve where the *Aragosaurus ischiaticus* Sanz, Buscalioni, Casanovas and Santafé, 1987 holotype was discovered, previously considered as belonging to the lower and middle detritic levels of the El Castellar Formation, Hauterivian–Barremian in age (Sanz *et al.* 1987; Soria de Miguel 1997; Ruiz-Omeñaca *et al.* 2004). The first works describe these levels as Unit 3 (Díaz Molina *et al.* 1984; Díaz Molina *et al.* 1985; Díaz Molina

and Yébenes 1987), but they could not be directly dated, and their age has been inferred in Galve from charophyte remains found in the overlying Unit 4 and by correlation with the type locality at El Castellar (Ruiz-Omeñaca *et al.* 2004). In this locality, the base of the El Castellar formation shows well-cemented coarse sandstones and purplish clays, slightly different from the red clays and sandstones of Galve that, on the other hand, are very similar to the detritic layers of the Villar del Arzobispo Formation. The study of these facies in the south of the Iberian Range has proved that the Villar del Arzobispo formation is more detritic upward (Luque *et al.* 2005; Santisteban 2004; Santisteban and Esperante 2004), and it could be easy to mistake these deposits

from others that are also detritic but suprajacent. This idea leads to a new interpretation for the age of the Las Zabacheras site in Galve (Teruel, Spain), where *Aragosaurus* was found. It could be contemporaneous to the Riodeva dinosaur sites (Tithonian–Berriasian age). This geological reinterpretation also gives coherence to other findings of dinosaurs in sites included at the base of the El Castellar Formation, whose remains are more typical of the Upper Jurassic or the Jurassic/Cretaceous boundary than that of the Lower Cretaceous, like the record of *Stegosauria* indet. in Galve (Pereda Suberbiola and Galton 2001; Pereda Suberbiola et al. 2005). It could be coherent with the remains of stegosaurids found in the levels of the Villar del Arzobispo Formation in El Castellar and Riodeva (Royo-Torres et al. 2006; Alcalá et al. 2007) and with those assigned to *Dacentrurus armatus* (Owen, 1875) in the area of Los Serranos in Valencia (Casanovas-Cladellas et al. 1995, Casanovas-Cladellas et al. 1999).

SYSTEMATIC PALAEOLOGY

Institutional abbreviations. FCPT-D, for the institution Fundación Conjunto Paleontológico de Teruel-Dinópolis, Spain and CPT, for the fossil material deposited at the Museum Fundación Conjunto Paleontológico de Teruel; MIGM, Museu Geológico do Instituto Geológico e Mineiro, Portugal; MPZ, Museo Paleontológico de la Universidad de Zaragoza, Spain; MUJA, Museo Jurásico de Asturias Spain; RD, Riodeva fossil site.

Anatomical abbreviations. sprl, spinoprezygapophysial lamina; prsl, prespinal lamina; posl, postspinal lamina; pcpl, posterior centroparapophyseal lamina (laminae abbreviations after Wilson, 1999).

Remarks. The large diversity of sauropods found in the Riodeva sites includes the following clades: basal Eusauropoda Turiasauria, Diplodocidae and Macronaria.

DINOSAURIA Owen, 1842

SAURISCHIA Seeley, 1888

SAUROPODOMORPHA Huene, 1932

SAUROPODA Marsh, 1878

EUSAUROPODA Upchurch, 1995

TURIASAURIA Royo-Torres, Cobos and Alcalá, 2006

Turiasaurus riodevensis Royo-Torres, Cobos and Alcalá, 2006

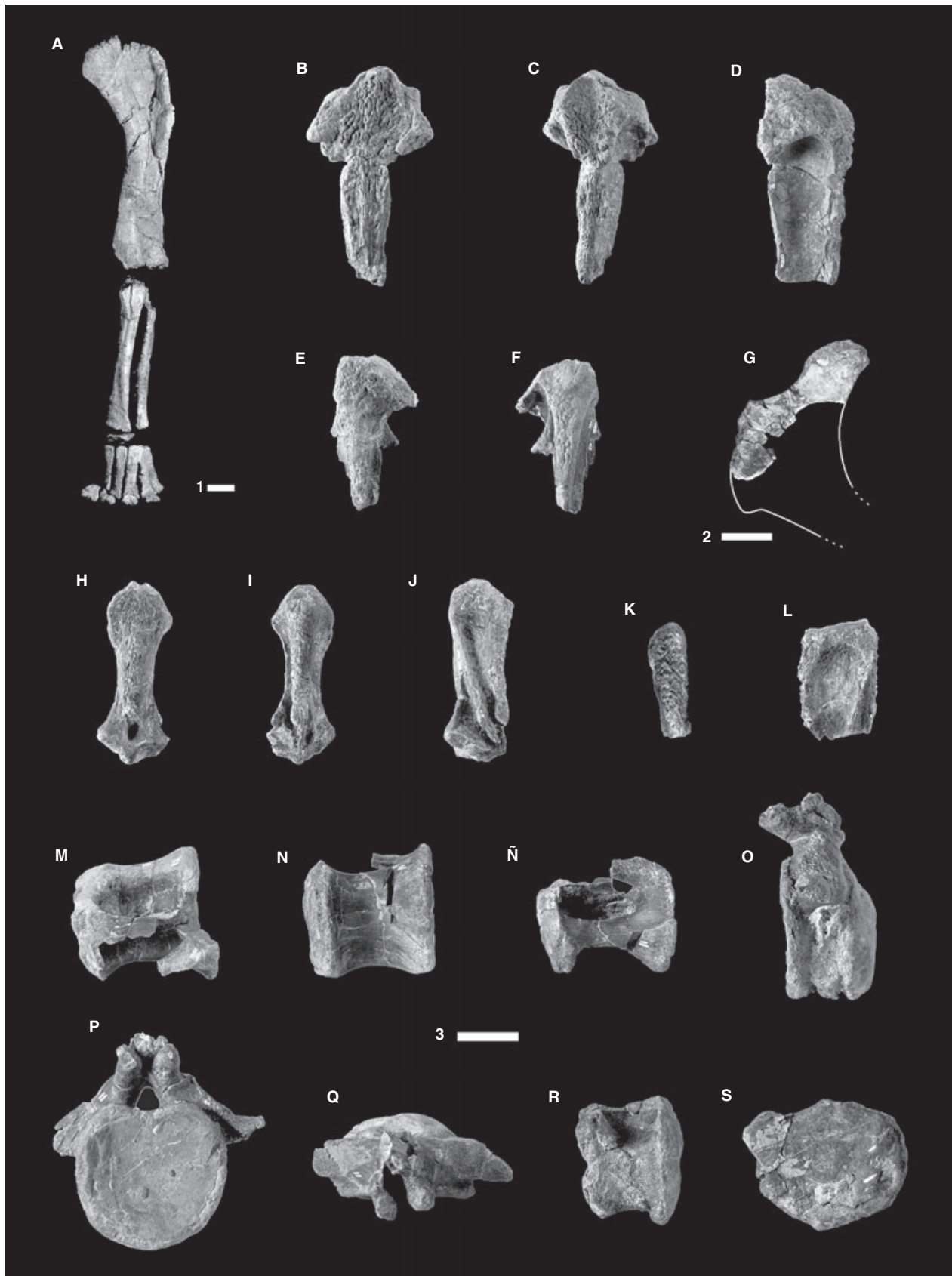
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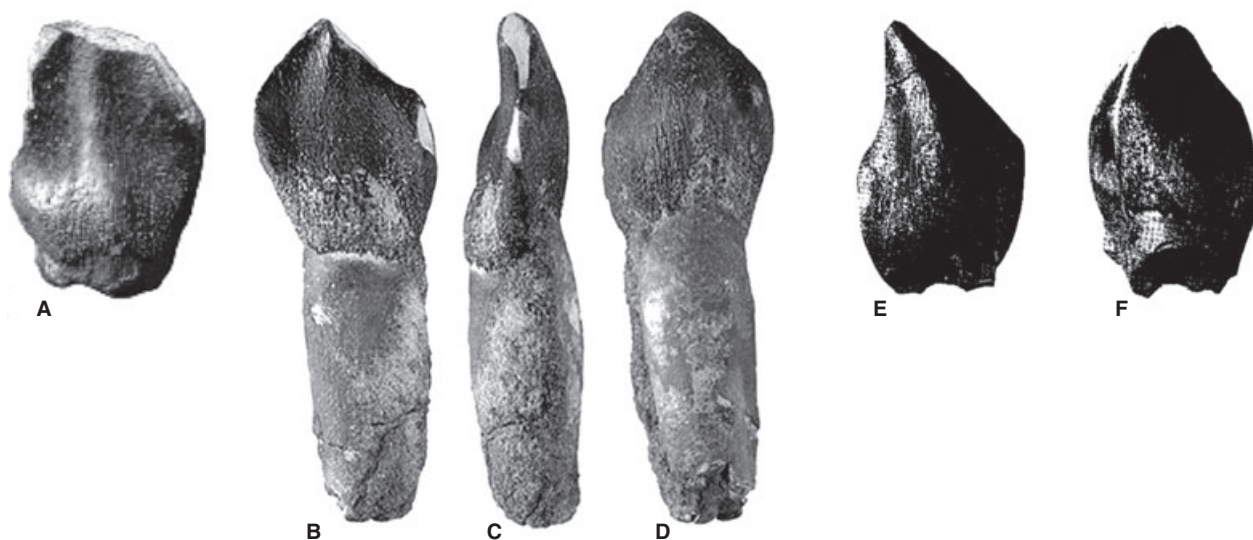
From the RD-10 site (Barrionda-El Humero), which is the most outstanding and is providing many remains, *Turiasaurus riodevensis* has been described, with partially articulated materials

(Text-fig. 3; Table 1) and its holotype being an articulated left forelimb (CPT-1195 to CPT-1210) (Royo-Torres et al. 2006). Besides the material referred for the paratype, new materials have been recovered. Three new dorsal spine vertebrae have been prepared, and they refer to this taxon (Text-fig. 3). They have an absence of prsl and posl laminae and a presence of lateral triangular processes in the neural spines of dorsal vertebrae as in *T. riodevensis* dorsal vertebrae.

Another outcrop with new material is the Puntal de Santa Cruz site (RD-13), which includes one axis, one cervical vertebra centrum, five dorsal vertebra centra, two dorsal vertebra spines, one sacral vertebra spine, one caudal anterior vertebra (out spine), fragments of prezygapophyses, postzygapophyses and a right proximal ischium fragment with the iliac pedicel. The acetabular region and part of the pubic pedicel are well preserved (Text-fig. 3) (CPT-1609 to 1657 and CPT-1661 to 1674). The anterior and mid-dorsal vertebrae are opisthocoelic, but the most posterior dorsal vertebra has a flat articulation anteriorly and is concave posteriorly, without marked opisthocoelia, a character that leaves it out of Macronaria (Wilson, 2002). The presence of triangular lateral processes (Text-fig. 3) in spines are similar to those of *Haplocanthosaurus priscus* Hatcher, 1903, *Losillasaurus giganteus* Casanovas-Cladellas, Santafé and Sanz, 2001 and have the same morphology as in *Turiasaurus* (Royo-Torres et al., 2006). The ischium is characterized by a large acetabular opening and a robust iliac pedicel of the elliptic section. The sauropod material from RD-13 has been compared to that of the Iberian sauropods: *Lourinhasaurus alenquerensis* Dantas, Sanz, Da Silva, Ortega, Santos, and Cachao, 1998, *Aragosaurus ischiaticus*, *Dinheirosaurus lourinhanensis* Bonaparte and Mateus, 1999, *Galveosaurus herreroi* Sánchez-Hernández, 2005, and *Lusotitan atalaiensis* (Lapparent and Zbyszewski, 1957) in Antunes and Mateus (2003), being distinguishable from all of them (Royo-Torres et al. 2007). So, the main differences are the presence of procoelus anterior caudal vertebrae in RD-13 and the absence of prsl and posl laminae on dorsal vertebrae. The presence of primitive characters in RD-13, such as posterior dorsal vertebra without opisthocoelia, simple pleurocoels in presacral vertebrae and a solid internal bone structure in vertebrae and ribs (Wilson 2002), leads us to include it in Eusauropoda and out of the Neosauropoda (Royo-Torres et al., 2007). We have compared it with *Losillasaurus*, and they share some characters. But RD-13 is different from *Losillasaurus* because the first has dorsal vertebrae with convex prezygapophyses and the sprl are less developed, while in *Losillasaurus* the dorsal surfaces of the prezygapophyses are flat. In addition, the anterior caudal vertebrae from the Riodeva sauropod have the transversal processes pointing forwards, while those of *Losillasaurus* point backwards. From the comparison between CPT-1609 caudal and other material from Riodeva such as the CPT-1966 caudal (Royo-Torres and Cobos 2005, see below), noticeable differences emerge, such as the presence of a keel in the ventral surface and great anteroposterior compression of the anterior caudal centrum in the latter, absent both in the CPT-1609 caudal vertebra of RD-13.

Comparing it with *Turiasaurus riodevensis*, RD-13 has some convex prezygapophyses, a diagnostic character of the medium dorsal vertebrae of this species; in addition, it has similarities with the individual found in the RD-10 type site as opisthoco-





TEXT-FIG. 4. Teeth attributed to Turiasauria. A, tooth (MUJA-0635) from Late Jurassic of Asturias after García-Ramos *et al.* (2002) in lingual view. B–D, tooth of *Turiasaurus riodevensis* (CPT-1215) in lingual, distal and labial views (Royo-Torres *et al.* 2006). E, tooth of *Neosodon* (BHN2R 113) in labial view. F, tooth of *Neosodon* (BHN2R 1101) in labial view (Buffetaut and Martín 1993). Scale bar represents 10 mm.

lous cervical and anterior dorsal vertebrae centra, simple well-developed pleurocoels, absence of prsl and posl laminae and presence of lateral triangular processes in neural spines of dorsal vertebrae. Thus, RD-13 belongs to the same taxon as the sauropod from RD-10: *Turiasaurus riodevensis*. The new remains of *Turiasaurus* show us how the spines vary in the axial series, and cervical vertebrae are bifid, while dorsal vertebrae are simple, with a transition in anterior dorsal vertebrae. Pleurocoels in dorsal series are simple, and the last dorsal vertebra lacks the opisthocoelous articulation. The anterior caudal vertebrae are procoelus, while the posterior are opisthocoelous, indicating that there is a change in the articulation of the caudal series.

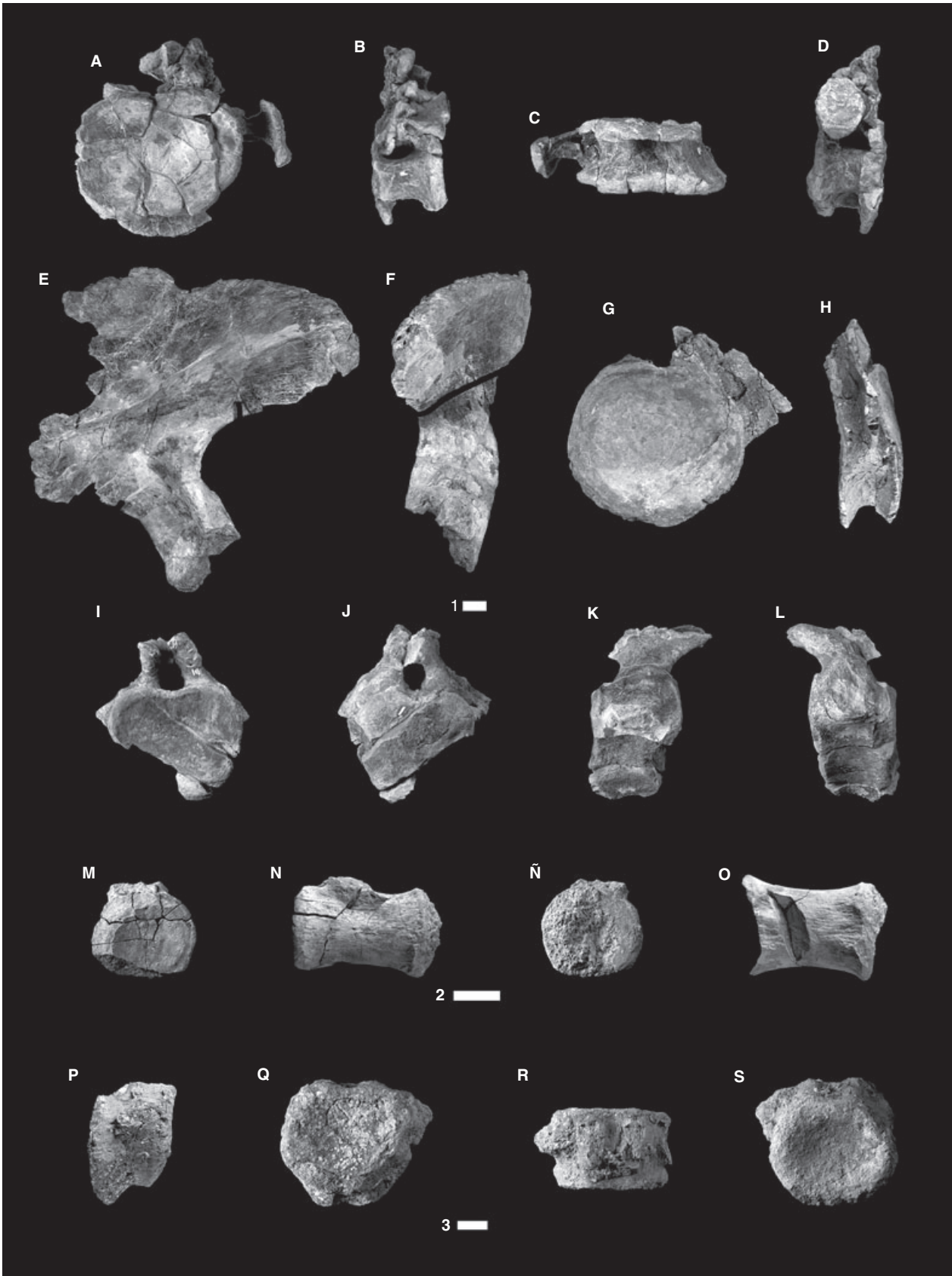
Bearing these materials from Riodeva and the tooth of *Turiasaurus* in mind, it is possible to include some teeth from the Iberian Peninsula and Europe in the Turiasauria clade. In the Iberian Peninsula, a tooth (MUJA-0635, Text-fig. 4), very similar to those of *Turiasaurus* (figured in Royo-Torres *et al.* 2006), has been found in the Upper Jurassic deposits in the province of Asturias (Spain) (Martínez *et al.* 2000) as well as in Portugal, where another similar tooth housed in the MIGM (Lisbon, Portugal), and assigned to *Pelorosaurus* Mantell, 1850 shows great similarities (pers. obs., MIGM sample 4832, S. Martinho do Porto, Deposit archive of Los Olmos). In the

rest of Europe, *Turiasaurus* teeth match the description given for a tooth of *Cardiodon* Owen, 1840–45 by Upchurch *et al.* (2004) in England. It is also similar to *Neosodon* Moussaye, 1885 teeth (Text-fig. 4) recorded in the Late Jurassic of France and Portugal (Buffetaut and Martín 1993), but it differs from *Turiasaurus* because its teeth are less concave in the lingual face and have greater dorsoventral development in the apex end. The characters shared by all these teeth that could lead us to interpret them as Turiasauria are tooth with heart-shaped crowns (when unworn), a pointed and asymmetrical crown apex that is strongly compressed labiolingually and tooth crowns with convex labial surfaces with a bulge that extends from the base towards the apex.

Eusauropoda indet.

An anterior caudal vertebra has been described from the RD-27 (La Cautiva 2) site (CPT-1966) (Text-fig. 5). This vertebra shares a marked anteroposterior compression of the centrum (with a ratio between the anteroposterior length and the dorsoventral length of 0.3 or smaller), a slight procoelia and the presence of a

TEXT-FIG. 3. Material from Barrionda-El Humero (RD-10). A, holotype from *Turiasaurus riodevensis*, a complete forelimb including humerus, radius, ulna, carpal, five metacarpals and seven phalanges (CPT-1195 to CPT-1210), material referred to *T. riodevensis* consists of dorsal spine vertebrae (CPT-2688). B, posterior view; C, anterior view and D, right lateral view. Material from Puntal de Santa Cruz site (RD-13) referred to *T. riodevensis*: dorsal spine (CPT-1633) in E, posterior view; F, anterior view, right proximal ischia (CPT-1640); G, medial view, posterior dorsal spine vertebrae (CPT-1611); H, posterior view; I, anterior view; J, right lateral view, sacral spine vertebrae (CPT-1637); K–L, anterior and left lateral views, dorsal centrum (CPT-1636); M–N, dorsal, ventral and left lateral views, anterior caudal vertebrae (CPT-1609); O, left lateral view; P, anterior view; Q, dorsal view and posterior dorsal vertebrae (CPT-1610) in R, right lateral and S, anterior views. Scale bar 1 is 20 cm represents A, scale bar 2 is 20 cm represents G and scale bar 3 is 10 cm represents B–F and H–S.



crest on the ventral surface with anteroposterior direction, with two anterior caudal vertebrae of European sauropods. The first belongs to *Cetiosauriscus greppini* Huene, 1922, from the Kimmeridgian in Switzerland (Meyer and Thüring 2003), and the second is a caudal found in the area of Gognac (France) from the Tithonian (Le Loeuff *et al.* 1996). These three sauropod fossil samples, present in Spain, France and Switzerland, have similar characteristics in the anterior caudal vertebrae and are included as indeterminate eusauropods because their shape, morphology and relative proportions are similar (Royo-Torres and Cobos 2005). We do not include them within Turiasauria, because the anterior caudals present in Turiasauria genera do not have a ventral crest, and the anteroposterior development of the vertebra centrum is greater, although this character could be exclusive of the first or second caudal vertebra of some of the species of this clade.

NEOSAUROPODA Bonaparte, 1986

DIPLODOCOIDEA Marsh, 1884

FLAGELLICAUDATA Harris and Dodson, 2004

DIPLODOCIDAE Marsh, 1884

Diplodocidae indet.

Description. An ilium (CPT-1074) found on the RD-5 site (Pino de Jarque 2) was studied and included in Diplodocidae. The main diagnostic character is a pubic peduncle with an acute angle with respect to the sacral axis (Salgado *et al.* 1997) and a lateral profile (Text-fig. 5) similar to those of *Diplodocus carnegii* Hatcher, 1901 and *Barosaurus lentus* Marsh, 1890 (Lull 1919; McIntosh 2005; Royo-Torres and Cobos 2004). The preacetabular process is low and triangular in shape, similar to diplodocids and different to the other neosauropod ilia such as *Camarasaurus* (Ostrom and McIntosh, 1966) or *Brachiosaurus* (Janensch, 1961).

DIPLODOCINAE Marsh, 1884

Diplodocinae indet.

Description. At the El Carrillejo site (RD-11), we have recovered several vertebrae and indeterminate bones (Text-fig. 5) (CPT-1575 to CPT-1586). One of the anterior caudal vertebrae (CPT-1575) retains the following plesiomorphic feature: the anterior face is concave, and the posterior convex without the presence

of a condyle. It shows synapomorphies of the clade Diplodocinae according to Wilson's (2002) analysis: it is procoelous, and the centrum is characterized by deep pleurocoels and a marked ventral wrinkle with anteroposterior direction (Royo-Torres *et al.* 2007).

MACRONARIA Wilson and Sereno, 1998

Macronaria indet.

Description. We have recorded three sites with different caudal vertebrae: RD-28 (San Lorenzo) with an anterior caudal vertebra, RD-41 (La Quineta 1) with a posterior caudal vertebra and RD-43 (Las Viñas) with a middle anterior caudal vertebra.

At the RD-28 (San Lorenzo) site a caudal vertebra has been recovered (CPT-1846), which is different from the rest of the anterior caudal vertebrae registered in the Riodeva area. Vertebra CPT-1846 (Text-fig. 5) rules out diagenetic deformation. It preserves the centrum and part of the neural arch (pedicels and prezygapophyses) and is characterized by a bigger lateromedial dimension in the vertebral centrum than the dorsoventral length. The anterior face is concave and the posterior plane convex, showing an incipient procoelia. The neural arch is situated in the anterior half without reaching the articular face. Prezygapophyses point towards the anterior and are robust. The difference between the caudal centra of basal sauropods and eusauropods non-neosauropods lies in the relationship between the dorsoventral length and the lateromedial length. Thus, the anterior caudal centra have greater dorsoventral development in *Kotasaurus yamanpalliensis* Yadagiri, 1988 (Yadagiri 2001), *Shunosaurus* Dong, Zhou and Zhang, 1983 (Zhang *et al.* 1984) and *Mamenchisaurus hochuanensis* Young and Zhao, 1972 (Ouyang and Ye 2002), while in CPT-1846 lateromedial development is greater. The difference with the caudal vertebrae of diplodocids such as *Diplodocus* and *Barosaurus* is that the ventral and lateral faces are flat without either pleurocoels or wrinkles. The presence of a slight procoelia and the interior of the bone without holes differentiates CPT-1846 from the caudal vertebrae of titanosaurs (Wilson 2002) such as *Saltasaurus loricatus* Bonaparte and Powell, 1980 and *Neuquensaurus australis* (Lydekker, 1893). At least two characters let us place caudal CPT-1846 among sauropods from Macronaria. The articulation is more derived than the amphicoelias articulation in the caudal vertebrae of *Camarasaurus*, and the presence of a neural arch in the anterior position is a proposed character for Titanosauriformes (Salgado *et al.* 1997). Moreover, the anterior caudals are similar to anterior caudal vertebrae from Macronaria *Lourinhasaurus*,

TEXT-FIG. 5. Material from El Carrillejo site (RD-11): anterior caudal vertebra (CPT-1575) of Diplodocinae indet. A, anterior view; B, left lateral view; C–D, ventral (C) and right lateral (D) views. Material from Pino de Jarque 2 site (RD-5): right ilium (CPT-1074) of Diplodocidae indet. E, lateral and F, anterior views. Material from La Cautiva 2 site (RD-27): anterior caudal vertebra (CPT-1966) of Eusauropoda indet. G, anterior and H, right lateral views. Material from San Lorenzo site (RD-28): anterior caudal vertebra (CPT-1846) of Macronaria indet. I, anterior view; J, posterior view; K–L, right lateral and left lateral views. Material from La Quineta 1 site (RD-41): posterior caudal vertebra (CPT-3295) of Macronaria indet. M, anterior; N, left lateral; Ñ, posterior and O, ventral views. Material from Las Viñas site (RD-43): anterior caudal vertebra (CPT-3296) of Macronaria indet. P, right lateral; Q, anterior; R, dorsal and S, posterior views. Scale bar 1 is 10 cm represents A–L, scale bar 2 is 10 cm represents M–O and scale bar 3 is 10 cm represents P–S.

Aragosaurus and *Tastavinsaurus sanzi* Canudo, Royo-Torres and Cuenca-Bescós, 2008 (Royo-Torres 2005; Royo-Torres *et al.* 2006; Canudo *et al.* 2008).

The RD-41 (La Quineta 1) site has a posterior caudal vertebra (CPT-3295) with the centrum and part of the neural arch (pedicels) (Text-fig. 5). The articulation is between flat and biconcave. The neural arch is situated in an anterior position but without reaching the articular face. At the RD-43 (Las Viñas) site, a middle-anterior caudal vertebra has been recovered (CPT-3296). It still has the centrum and the base of the pedicels (Text-fig. 5). The articular face shape is concave in the anterior and posterior, without pleurocoels or a ventral hole. The neural arch is situated in the anterior position, similar to RD-28 and 41. They are similar to the caudal of *Camarasaurus* Cope, 1877 (Ostrom and McIntosh 1966; McIntosh *et al.* 1996), *Brachiosaurus brancai* Janensch, 1914 (Janensch 1950) and *Areia Branca* sauropod (Yagüe *et al.* 2006). This fact and their characters allow us to include these caudal vertebrae within the Macronaria clade.

Sauropoda indet.

Description. The prospections in Riodeva led to the discovery of a large number of sites with sauropod remains on the surface. The study of many isolated remains (Text-fig. 6) let us identify

them as Sauropoda indet., but we are not able to be more precise in their determination.

The material we present is from the following sites: RD-1, RD-8, RD-9 and RD-20. Site RD-1 (Riodeva A) has a proximal half of an ulna (CPT-973) with a triangular section and a femur diaphysis (CPT-974) with a section between elliptic and circular. Site RD-8 (La Cueva) has a proximal half of a right ulna (CPT-1098) with a triangular section. Site RD-9 (La Loma) has a distal end of a right pubis (CPT-1109). It has an elliptic section, the ventral surface is wrinkled and has a trapezoidal contour, with the ventral surface rounded in lateral view. Finally, site RD-20 has a proximal ulna fragment (CPT-1717) with a triangular section.

Two sites with dinosaur ichnites have been discovered at the base of the Villar del Arzobispo Formation in Riodeva. At the RD-36 (Las Perplejas) site, about 60 imprints of manus and pes of sauropod dinosaurs have been found, without any definite pattern to identify the trackways. They are interpreted as a disruption of the substrate homogeneity caused by bioturbation of sauropods. The morphology of pes varies between elliptic and circular with 20 and 70 cm of maximum length and the manus with a half-moon shape between 10 and 40 cm of maximum width (Text-fig. 6). So, the proportion between manus and pes is 1:2, similar to that found in *Turiasaurus riodevensis* bones, but the poor conservation of the tracks and the absence of trackways



TEXT-FIG. 6. Isolated material of Sauropoda indet. draws in line. Proximal ulna fragment (CPT-1717) from Pino de Jarque Muro site (RD-20). A, dorsal view; B, anterior view and C, ventral view. Proximal ulna fragment (CPT-1098) from La Cueva site (RD-8). D, dorsal view and E, anterior view. Distal end pubis from La Loma site (RD-9). F, lateral view and G, anterior view. Femur diaphysis (CPT-974) from Riodeva A site (RD-1). H, ventral view; I, anterior view and J, lateral view. Proximal ulna fragment from Riodeva A site (RD-1). K, anterior view; L, dorsal view and M, ventral view. Ichnites of sauropods from Las Perplejas tracksite (RD-36). N. Scale bar 1 is 10 cm represents A–M and scale bar 2 is 1 m represents N.

lead us to classify it as Sauropoda indet. This data can be added to that previously recorded in this formation with a great abundance of sauropod footprints in other localities (Cobos *et al.* 2005) except at the Las Cerradicas site in Galve, where the ornithopod imprints are dominant (Pérez-Lorente *et al.* 1997) with at least four trackways with ornithopod manus and pes (Royo-Torres and Cobos 2007). So, the record of ichnites in the Villar del Arzobispo Formation also reflects the abundance of sauropods in these tidal environments of the Jurassic–Cretaceous transition.

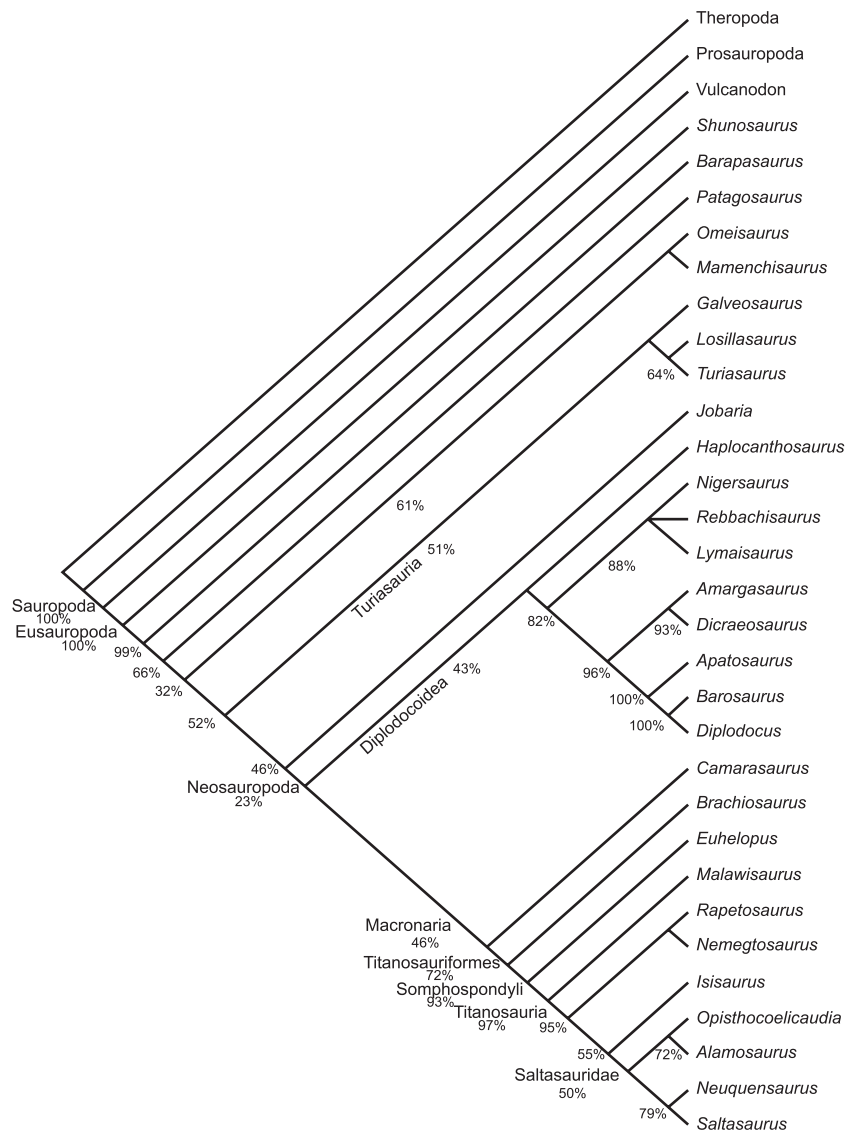
PHYLOGENETIC DISCUSSION

The great variety of sauropod dinosaurs from the Tithonian–Berriasian age recovered in the Villar del Arzobispo Formation in Riodeva indicates the high diversity of this group at the end of the Jurassic and the beginning of the Cretaceous in the Iberian Range, with the presence of groups of basal eusauropods and neosauropods. This diversity is also confirmed by the presence of other sauropods of the same age found in different places on the Iberian Peninsula and by the reinterpretation of others found in Teruel.

The data from the cladistic analysis allow us to recognize that three of these sauropods, *Turiasaurus riodevensis*, *Losillasaurus giganteus* and *Galveosaurus herreroi*, whose type locality is also in the aforementioned Villar del Arzobispo Formation of the Iberian Range, are included in the clade Turiasauria (Royo-Torres *et al.* 2006). *Losillasaurus* was firstly proposed as Diplodocoidea (Casanovas *et al.* 2001) although posterior cladistic analysis placed it out of Neosauropoda (Harris and Dodson 2004; Harris 2006a; Rauhut *et al.* 2005; Remes 2006) and being recently included in Turiasauria (Royo-Torres *et al.* 2006). *Galveosaurus* has been proposed as a possible Eusauropoda (Sánchez-Hernández 2005; Canudo *et al.* 2006) and a possible Neosauropoda (Barco *et al.* 2005), suggesting first its inclusion in Diplodocoidea (Barco, 2005) and later in Macronaria? using a modified Wilson's matrix (Wilson 2002; Barco *et al.* 2006). However, the cladistic analysis carried out by Royo-Torres *et al.* (2006) using Upchurch's matrix (Upchurch *et al.* 2004) includes *Galveosaurus* in the Turiasauria clade, so it is a non-Neosauropoda. Hence, in addition to the published Upchurch matrix (Royo-Torres *et al.* 2006), we include here our own analysis based on Wilson's matrix (Wilson 2002) with last modifications for *Omeisaurus* Young, 1939 and *Mamenchisaurus* from Harris and Dodson (2004). The first analysis carried out with a heuristic search option shows the following result: number of trees retained = 6, tree length (TL) = 462, consistency index (CI) = 0.6190, homoplasy index (HI) = 0.3810 and retention index (RI) = 0.7764, a topology with Turiasauria formed by *Galveosaurus*, *Losillasaurus* and *Turiasaurus*, under Neos-

auro-poda and *Jobaria* appears in polytomy with Neosauropoda. Afterwards, the character was reweighted according to rescaled consistency index and base weight 1. This operation was performed until it stabilized in three retained trees with the following result: TL = 228.51822, CI = 0.8303, HI = 0.1697 and RI = 0.9098, the polytomy between *Jobaria* and Neosauropoda disappears, and the topology is similar to that obtained by Wilson (2002, 2005) and Harris and Dodson (2004) including the group Turiasauria as a monophyletic clade within Eusauropoda not Neosauropoda (see Table 2 and Text-fig. 7). The robustness of this analysis has been explored using bootstrap. A 50% majority rule bootstrap analysis was carried out using 1000 replicates with heuristic search in PAUP* 4.0b10 (Swofford 2002) with all characters having equal weight and type order (TL = 450, CI = 0.6190, HI = 0.3810, RI = 0.7764) with the result being similar to previous analyses (see Table 2 and Text-fig. 7), which also confirms the same topology for Turiasauria. The difference between both analyses is because of the changes carried out on the characters by Barco *et al.* (2006). The matrix by Barco *et al.* (2006) has introduced two new characters from other analyses (C235 by Salgado *et al.* (1997) and C236 by Upchurch *et al.* (2004)), and seven original characters were changed (C102, C103, C110, C116, C118, C130 and C172). Furthermore, they misinterpreted some characters in the original material that in this study have the following codifications according to Wilson's matrix: (C86) mid-cervical centra with a ratio between 2 and 3 of its antero-posterior length and its height in the posterior face, (92) the dorsal neural spines broader transversely than antero-posteriorly, (C98) lamina pcp1 slightly developed in the anterior-middle dorsal vertebrae, (120) this character as a result of the absence of anterior caudal vertebrae is codified with a question mark, (C146) depth of chevron haemal canal is incomplete and cannot be observed, (C161) deltopectoral crest of humerus markedly expanded distally, (C163 and 164) humeral distal condyles divided and exposed on anterior portion of humeral shaft, and (C192) the ischial blade has the same length as the pubic blade in the ischia. We have also added in our cladistic analysis new data (C154, C155, C157, C207) about the scapula (CLH-14), coracoid (CLH-s/n) and fibula proximal end (CLH-21) (pers. obs. at the Palaeontological Collection of Galve) to reinforce it, codified with a question mark by Barco *et al.* (2006). As a final test, a topological constraint was created to force *Galveosaurus* to cluster within the Neosauropoda (like Barco *et al.* 2006 proposed). This analysis with a heuristic search found six MPTs of 464 steps in length. A Templeton's test was then used to compare the 'constrained MPTs' with the 'unconstrained MPTs' (Templeton 1983). The results (p-value = 0.72–0.79) indicate that placement of *Galveosaurus* within the

TEXT-FIG. 7. Phylogenetic relationships of *Turiasaurus riodevensis* following Wilson (2002) using PAUP* 4.0b10 (Swofford 2002). The figure represents a strict consensus cladogram after reweighting characters by maximum value of rescaled consistency index. Percentages are bootstrap values in a 50% majority-rule bootstrap analysis with 1000 replicates. The data matrix contains 234 characters considering 27 taxa of sauropods such as Wilson (2002) and Harris and Dodson (2004) adding three genera from the Villar del Arzobispo Formation: *Galveosaurus*, *Losillasaurus* and *Turiasaurus* (see Table 2 for data matrix).



Neosauropoda is not a significantly worse statistic explanation of the data than its position within the Turiasauria. At the moment, our cladistic analysis using the matrix and characters of Wilson (2002, 2005) and Upchurch *et al.* (2004) includes *Galveosaurus* within the Turiasauria.

Diplodocinae clade is represented by isolated remains in Riodeva. Its dispersion expands to other places with exposures of similar age, which confirms its presence throughout the Iberian Peninsula. Apart from the previously mentioned ilium (Royo-Torres and Cobos 2004) and the caudal vertebra here described, in Spain Diplodocidae teeth have been described in the Villar del Arzobispo Formation in Galve (Cuenca-Bescós *et al.* 1997) and in the Lastres Formation in Asturias (Martínez *et al.* 2000). In Portugal, the species *Dinheirosaurus lourinhanensis* from the Kimmeridgian is defined (Bonaparte and

Mateus 1999) and included in Diplodocinae (Rauhut *et al.* 2005).

The caudal vertebra attributed to Macronaria in Riodeva indicates the presence and dispersion of this group in Spain at the end of the Jurassic. This group is clearly established in the Iberian Peninsula: the sauropod *Lourinhasaurus alenquerensis*, from the Kimmeridgian in Portugal (Dantas *et al.* 1998), is placed within Macronaria according to the last analyses (Royo-Torres *et al.* 2006), besides that of Areia Branca sauropod material (Yagüe *et al.* 2006). On the other hand, applying the stratigraphic and sedimentological data obtained in Riodeva to other places with dinosaur sites allows us to propose the attribution of the holotype of *Aragosaurus ischiaticus* to the Villar del Arzobispo Formation (Tithonian–Berriasian). This new dating would set light on the morphological resemblance observed in the postcranial skeleton

(humerus, ischion, pubis and caudal vertebrae) of *Aragosaurus* (now Tithonian–Berriasian) and *Lourinhasaurus* (Kimmeridgian). These two taxa would be part of a clade of basal Macronaria, more derived than *Camarasaurus* and more primitive than *Brachiosaurus* (Royo-Torres 2009).

PALEOBIOGEOGRAPHIC DISCUSSION

As we have pointed out previously, in Riodeva, there is a high diversity of sauropods with the presence of samples of Turiasauria, Diplodocidae and Macronaria in the Tithonian–Berriasian. This diversity of sauropods was already documented in the Iberian Peninsula in the Kimmeridgian of Portugal and Asturias. This high diversity allows us to consider palaeobiogeographical questions about their global distribution and representation at the end of the Jurassic. The relationship, diversity and difference of dinosaur taxa between Laurasia and Gondwana have been explained because of the fragmentation of Pangea in the Mid Jurassic (Sereno 1997, 1999; Upchurch *et al.* 2002). In this sense, the palaeogeographical history of Europe during the later Jurassic and Early Cretaceous is complex, because it was composed of several major islands: e.g. Britain, Iberia and Eastern Europe (Upchurch *et al.* 2002). In this group of emerged lands and shallow marine platforms, the Iberian plate could have been very relevant as an intercontinental bridge connecting Gondwana with the rest of Europe and, during the first stages of this splitting, with North America (Sereno 1999). This geographical continuity would have been temporary and weaker throughout time and would have depended on variations in the sea level and tectonic movements.

The presence of the Diplodocinae and Titanosauriformes groups in the Iberian Peninsula at the end of the Late Jurassic would point to a relationship with the North-American and African sauropods. In this way, Diplodocidae was well represented in the Morrison Formation (North America), where there are up to six known genera of Diplodocidae (Upchurch *et al.* 2004; Harris 2006b) but fewer in Africa, with a scarce number in the Tendaguru Formation: just two genera, *Torniera africana* Fraas, 1908 (Upchurch *et al.* 2004; Remes 2006) and *Australodocus bohetii* Remes, 2007. The presence of *Dinheirosaurus lourinhanensis* in Portugal and the isolated remains from Riodeva and Asturias widen this dispersion to the European subcontinent. This connection can be reinforced by the presence of other groups of sauropods such as Titanosauriformes in those continents, pointing also to the biogeographic relationship between them, although there are remarkable differences within the represented genera and the ratio between the groups, being Diplodocidae more abundant in North America and Titanosauri-

formes in Africa (Rees *et al.* 2004). Other dinosaur findings strengthen the idea that there were bridges connecting the continents at the end of the Jurassic, such as the genus *Stegosaurus* Marsh, 1877a and *Allosaurus* Marsh, 1877b found in the Morrison Formation (USA) (Madsen 1976; Turner and Peterson 1999; Galton and Upchurch 2004) and in the Alcobaça Formation (Portugal) (Mateus 2006; Escaso *et al.* 2007; Malafaia *et al.* 2007). On the other hand, palaeogeographical data indicate that between North America and Africa there was already an oceanic crust since the Middle Jurassic, and it continued in the Upper Jurassic (Golonka *et al.* 1996; Ford and Golonka 2003). Then some dinosaurs such as Diplodocids and Titanosauriformes might have crossed this barrier from north Greenland into Europe and later into Africa in the Upper Jurassic. But other authors deny this possibility and say that in the Callovian, North America was physically separated from Gondwana and Europe by epeiric seas (Smith *et al.* 1994). The presence of different diplodocines in the Late Jurassic of both Laurasia and Gondwana supports an early diversification of the Diplodocoidea prior to the separation of the northern and southern landmasses in the late Middle Jurassic (Remes and Rauhut 2005; Harris 2006b; Remes 2007).

The European sauropod teeth record included within the Turiasauria clade taxa such as *Neosodon* in France and *Cardiodon* in England provides information about the dispersion of this clade around the Old World Continent. We can assert that this group of basal eusauropods (Turiasauria), with spoon-like teeth, lived at least during the Mid, Late Jurassic and Tithonian–Berriasian in Europe. Up to the present, it is unknown whether this clade is only restricted to Europe as the present data indicate. The distribution of the new basal eusauropods of the Turiasauria clade can bring more relevant data about the dispersion of sauropods. If Turiasauria was limited to Europe during the Late Jurassic – and their probable maintenance there until the Berriasian – this would indicate an evolutionary origin related to the isolation of the differently emerged European lands from the rest of the continents, that is to say an evolutionary vicariant process. However, the presence of shared groups (Diplodocinae, allosaurs and stegosaurs) in the two or three regions of Europe, Africa and North America suggests that the palaeogeographical connections existed and should have also conditioned the dispersion of Turiasauria. In this second case, we could expect new findings to enlarge the presence of this clade in other continents.

CONCLUSIONS

The sites from Riodeva (Teruel, Spain) have a high diversity of sauropods in the Tithonian–Berriasian. This diver-

sity is coherent with other findings in Portugal and Spain at the end of the Jurassic. The new remains include the first record of *Turiasaurus* away from the RD-10 site, where the holotype of the genus was found, as well as the remains of Diplodocinae, Macronaria, Eusauropoda indet. and Sauropoda indet. These data corroborate the hypothesis suggested in previous studies about the existence of basal eusauropods and also the high diversity of neosauropods at the end of the Jurassic in Europe. Moreover, a revision of the context of the *Aragosaurus ischiaticus* site places it within the Villar del Arzobispo Formation of Tithonian–Berriasian age, and it is related to *Lourinhasaurus* from Portugal and other remains from Riodeva RD-28, RD-41 and RD-43 sites. These taxa provide new data to document the early evolution of sauropods, keeping in mind the importance of their interpretation to support the presence or not of intercontinental bridges during the fragmentation of Pangea in the Late Jurassic. Within this context, the palaeogeographical position and the richness of dinosaurs in the Iberian Peninsula, particularly in the Villar del Arzobispo Formation, constitute an exceptional source of data.

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