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References

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A Giant European Dinosaur and a New Sauropod Clade

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Fossils of a giant sauropod dinosaur, *Turiasaurus riodevensis*, have been recovered from terrestrial deposits of the Villar del Arzobispo Formation (Jurassic-Cretaceous boundary) of Riodeva (Teruel Province, Spain). Its humerus length (1790 millimeters) and estimated mass (40 to 48 metric tons) indicate that it may have been the most massive terrestrial animal in Europe and one of the largest in the world. Phylogenetic analysis indicates that the fossil represents a member of a hitherto unrecognized group of primitive European eusauropods that evolved in the Jurassic.

Most gigantic sauropods are neosauropods and have been found in the New World [such as *Seismosaurus* (1) and *Sauroposeidon* (2) in North America and *Argentinosaurus* (3) and *Puertasaurus* in South America (4)] or Africa [such as *Paralititan* (5) and *Brachiosaurus* (6)]. Here we describe a new giant European sauropod from Riodeva (Spain) as a new taxon, *Turiasaurus riodevensis* gen. et sp. nov., in Tithonian-Berriasian-aged deposits of the Villar del Arzobispo Formation (7) (figs. S1 and S2). The Barrihonda–El Humero site, where the new gigantic sauropod was found, has also yielded theropod teeth, postcranial remains of stegosaurs, and isolated elements of ornithomorphs, as well as fishes, turtles, and crocodylomorphs. The only other sauropod specimens reported from Riodeva were isolated elements from Pino de Jarque 2 and La Cautiva 2 (fig. S2): an ilium of a Diplodocidae indet (8) and a proximal caudal vertebra of a basal eusauropod (9).

Etymology. *Turiasaurus*, from Turia (word used since the 12th century from which Teruel derives) and *sauros* (Greek word, lizard); *riodevensis*, from Riodeva (village where the fossil site is located).

Holotype. An articulated left forelimb (Fig. 1, A to G) including humerus, radius, proximally incomplete ulna, carpal, five metacarpals, and seven phalanges (specimen numbers CPT-1195 to CPT-1210, housed in the Museo de la Fundación Conjunto Paleontológico de Teruel-Dinópolis, Teruel, Aragón, Spain).

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Paratype. Remains attributed to the same individual, found close to each other in an area of 280 m² (fig. S3), consisting of skull frag-

ments, eight teeth (Fig. 2), six cervical vertebrae (Fig. 1K) with ribs (Fig. 1, L and M) (probably cervicals 3 to 8), two proximal dorsal vertebrae, a middle dorsal vertebra (Fig. 1I), fragments of other dorsal vertebrae, eight dorsal ribs (five incomplete), a partial sacrum, two distal caudal vertebrae (Fig. 1T), a proximal fragment of the left scapula, a left sternal plate (Fig. 1J), a distal fragment of the left femur, a proximal fragment of the left tibia (Fig. 1, N and O), a distally incomplete left fibula (Fig. 1H), a complete left astragalus (Fig. 1, P and Q), two left pedal phalanges, and an incomplete right astragalus and pes (Fig. 1, R and S) (CPT-1211 to CPT-1261), housed in the Museo de la Fundación Conjunto Paleontológico de Teruel-Dinópolis, Teruel, Spain).

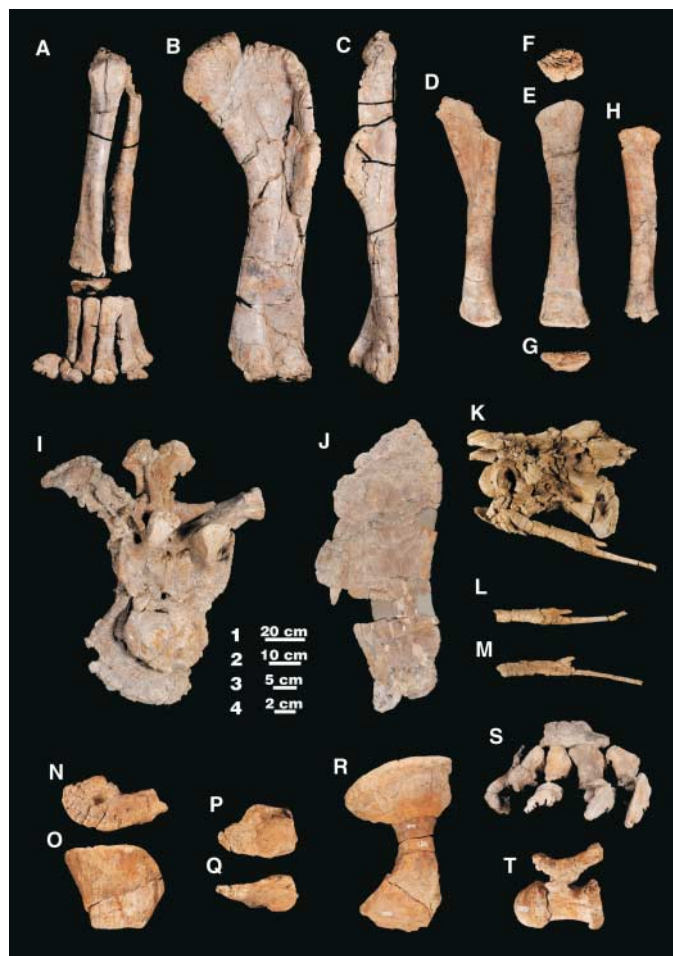


Fig. 1. Skeletal elements of *T. riodevensis* gen. et sp. nov.: left radius, ulna, carpal, and manus in cranial view (A); humerus in cranial (B) and lateral (C) views; left ulna in cranial view (D); left radius in medial (E), proximal (F), and distal (G) views; left fibula in medial view (H); middle dorsal vertebra in cranial view (I); left sternal plate in ventral view (J); cervical vertebra and rib in left lateral view (K); cervical rib in medial (L) and lateral (M) views; left tibia in proximal (N) and medial (O) views; left astragalus in proximal (P) and cranial (Q) views; metatarsal V in lateral view (R); right pes in cranial view (S); distal caudal vertebra in left lateral view (T). Scale bar 1 = 20 cm [(A) to (H), (N) to (Q), and (S)]; scale bar 2 = 10 cm [(I) to (M)]; scale bar 3 = 5 cm (R), and scale bar 4 = 2 cm (T).

Diagnosis. Autapomorphies of *Turiasaurus* include the following: prezygapophyseal and postzygapophyseal articular facets on middle dorsal vertebrae strongly convex and concave, respectively; strongly convex subcircular hyposphene on middle dorsal vertebrae; distal caudal vertebrae strongly opisthocelous; accessory process projecting caudodorsally from the dorsal margin of the shafts of proximal cervical ribs; distal humeral condyles strongly expanded cranially and caudally; radius and ulna distal condyles very compressed mediolaterally; carpal with two subcircular distal processes separated by a depression; cnemial crest of tibia reduced and directed cranially; fibula with roughened oval medial trochanter on middle-distal part; and metatarsal V with strongly expanded distal end.

Locality and horizon. Riodeva (fig. S1), Teruel Province, Aragón, Spain (grid coordinates Universal Transverse Mercator 659049 and 4443553), site RD-10 (known as Barrionda-El Humero), in the Villar del Arzobispo Formation (Tithonian-Berriasian), conformably overlying the Higuieruelas Formation (7). In Riodeva, the top of the Higuieruelas is dated as early Tithonian based on the occurrence of the foraminiferan *Anchispirocyclina lusitanica* (10).

The teeth of *Turiasaurus* (Fig. 2) have heart-shaped spatulate crowns that are arranged in the typical sauropodomorph overlapping imbricate arrangement. The tooth enamel is wrinkled, and crown-to-crown occlusion has produced V-shaped wear facets (11, 12). There are also some isolated and very reduced marginal tooth denticles on the mesial and distal edges of the teeth. The cervical and dorsal vertebral centra are opisthocelous and possess simple but well-developed pleurocoels. The neural spines appear to have been shallowly divided (bifurcate) on the midline, as in the distal cervicals and proximal dorsals of *Euhelopus* (13) and *Mamenchisaurus* (14). The dorsal neural spines are broader transversely than craniocaudally, a synapomorphy of Eusauropoda (11), and terminate dorsally in laterally directed triangular processes (Fig. 11). The internal bone structure is solid in the presacral vertebrae and ribs. A potentially diagnostic character, previously observed only in the Late Cretaceous Asian titanosaurs *Opisthocoeleicaudia* (15) and *Borealosaurus* (16), is the presence of strongly opisthocelous articulations in distal caudal vertebrae (Fig. 1T). Based on our phylogenetic results, this appears to represent a convergence between these taxa and *Turiasaurus*. In contrast to that of *Brachiosaurus*, which has a deltopectoral crest medially projected (11), the humerus of *Turiasaurus* has a robust deltopectoral crest oriented cranially, and the proximal third of the bone slants noticeably medially in cranial view (Fig. 1B). The ulna has a triradiate proximal end, and the radius possesses a subrectangular distal condyle, as in other sauropods (11). The

ratio of the length of the longest metacarpal (Mc II) to that of the radius is 0.369. The manual phalangeal formula is reduced to 2-2-2-2-?, with phalanges that are broader than they are

long. The proximal end of the tibia is compressed mediolaterally, representing a primitive state recorded in basal sauropods (11, 12). The astragalus is wedge-shaped in cranial view,



Fig. 2. Teeth of *T. riodevensis* (specimens CPT-1213, CPT-1215, and CPT-1217, from left to right). Lingual [(A), (D), and (G)], distal [(B), (E), and (H)], and labial [(C), (F), and (I)] views are shown.



Fig. 3. Phylogenetic relationships of *Turiasaurus* gen. nov. and the newly recognized clade Turiasauria. This analysis also groups European, Asian, and South American Middle-Upper Jurassic Euhelopodidae-related sauropods in a monophyletic clade. The figure represents a 50% majority-rule consensus cladogram based on 11 most parsimonious trees. The data matrix contains 309 characters and 33 taxa (12), adding three genera from the Villar del Arzobispo Formation: *Galveosaurus*, *Losillasaurus*, and *Turiasaurus* (table S3). The analysis was done with PAUP* 4.0b 10 (29); tree length = 611; consistency index = 0.5205; retention index = 0.7233.

and its distal surface is convex mediolaterally. The ascending process of the astragalus extends over the cranial two-thirds of the proximal surface, unlike the condition in neosauropods where this process reaches the caudal margin (11). The metatarsals are robust and display the typical sauropod “spreading” graviportal morphology (11). The pedal phalanges are broader than they are long, and the unguals of digits II and III have mediolaterally compressed and dorsoventrally tall proximal ends, as in other sauropods (11, 12).

Turiasaurus differs from other sauropods from the Iberian Range. *Aragosaurus* (17) is a taxon distinct from *Turiasaurus*, as demonstrated by differences in both morphology and age. *Losillasaurus* (18) and *Galveosaurus* (19–21), which also come from the Villar del Arzobispo Formation, are also different from the new Riodeva taxon. *Turiasaurus* possesses features that distinguish it from *Losillasaurus*, among them presacral vertebrae with bifurcate neural spines. Moreover, the prezygapophyses of *Turiasaurus* have a rugose ventral process that is better developed toward the proximal than toward the prezygapophyses themselves. A similar character is developed in the postzygapophyses but in a more dorsal position. Also, the dorsal vertebrae of *Turiasaurus* have convex and robust prezygapophyses and a convex hyposphene with a circular contour. Distal caudal vertebrae are opisthocoelous. With respect to the appendicular skeleton, the main differences are in the humeral condyles, which are well marked on the cranial face. Furthermore, in *Turiasaurus*, the radial and ulnar distal ends are strongly compressed mediolaterally, and the carpal has two distal processes. *Turiasaurus* also possesses features that distinguish it from *Galveosaurus*. In *Turiasaurus* the cervical vertebrae have a solid internal bone structure, the dorsal vertebrae are broader transversely, and the cervical and dorsal neural spines are bifid. Pleurocoels in dorsal vertebrae are smaller and shallower. The humeral distal condyles of *Turiasaurus* are more marked cranially. Furthermore, *Turiasaurus* also differs from Portuguese sauropods known from the Oxfordian-Kimmeridgian. The following features distinguish it from *Lourinhasaurus*: absence of a large postspinal lamina on the dorsal vertebrae, a differently shaped humerus with more marked distal condyles, and an elliptical morphology of the proximal end of the tibia (12, 22). *Dinheirosaurus* possesses the following features that are absent in *Turiasaurus*: an elongate pneumatic fossa on the lateral surfaces of the cervical neural spines, robust horizontal lamina linking the hyposphene with the posterior centrodiapophyseal lamina in dorsal vertebrae, and prespinal and postspinal laminae on dorsal vertebrae (23).

Phylogenetic analysis (Fig. 3 and table S1) indicates that *Turiasaurus* lies outside of

Neosauropoda and belongs to a new clade, named Turiasauria (24), together with *Losillasaurus* and *Galveosaurus*. Turiasauria is diagnosed by vertical cervical neural spines, posterior centroparapophyseal laminae on dorsal vertebrae, absence of prespinal and postspinal laminae on dorsal vertebrae, absence of the scapular acromial crest, proximal end of humerus deflected medially (Fig. 1B), prominent humeral deltopectoral crest, and finally by a vertical ridge developed on the caudal side of the distal half of the ulna. The geographic and stratigraphic ranges of this clade are uncertain, but Turiasauria probably represents a sauropod radiation that originated in Europe earlier than the Tithonian. Members of this clade may also have been present in France, Portugal, and England, where teeth similar to those of *Turiasaurus* have been recovered from the Jurassic [such as “*Neosodon*” (12, 25) and *Cardiodon* (12)]. All of these teeth share the following characters, and may be referable to Turiasauria: heart-shaped crowns (when unworn), a pointed and asymmetrical crown apex that is strongly compressed labiolingually, and crowns with convex labial surfaces with a bulge that extends from the base toward the apex.

Many of the elements of *Turiasaurus* are comparable in size with those of some of the largest known sauropods (tables S2 and S3). For example, the humerus of the type specimen is 1790 mm long, similar to the value estimated for *Argentinosaurus* (1810 mm) (5) and longer than that of *Paralititan* (1690 mm) (5). Only the humeri of brachiosaurids, which can exceed 2000 mm in length (6, 22) are longer. However, brachiosaurs, including *Brachiosaurus* itself, have apomorphically elongated forelimbs (11), which means that comparisons based solely on humerus length might underestimate the relative body size of a nonbrachiosaurid such as *Turiasaurus*. This explains why hindlimb elements of *Turiasaurus* are actually larger than those of the biggest *Brachiosaurus* specimens (table S3). For example, in *Turiasaurus*, the length of metatarsal II is 295 mm, whereas in *Brachiosaurus* (HMN SII) it is 276 mm (6). In *Turiasaurus*, the ungual phalanx on pedal digit I is 300 mm long, and 240 mm long in *Brachiosaurus* (HMN SII) (6). The largest sauropod specimens that had been reported from Europe are an isolated brachiosaurid cervical vertebra from the Lower Cretaceous Wessex Formation in southern England (26) and an isolated proximal caudal vertebra from another site in Riodeva (9). We estimate that *Turiasaurus* body mass was between 40 and 48 metric tons (27), weighing more than any other European sauropod. Particularly large sauropod genera, with body lengths exceeding 30 m and estimated masses of 40,000 kg or more, have previously been recognized only within the neosauropod radiations [diplodocoids (1) and titanosauriforms (2, 3, 28)], and it might have been supposed that truly gigantic forms

were restricted to Neosauropoda. *Turiasaurus* however, demonstrates that at least one of the more basal (non-neosauropod) lineages achieved gigantic size independently.

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