New stegosaurian (Ornithischia, Thyreophora) remains from Jurassic-Cretaceous transition beds of Valencia province (Southwestern Iberian Range, Spain).

Nuevos restos de estegosaurios (Ornithischia, Thyreophora) del tránsito Jurásico-Cretácico de la provincia de Valencia (Cordillera Ibérica Suroccidental, España)

J. Company¹, X. Pereda Suberbiola², J.I. Ruiz-Omeñaca³,⁴

¹Departamento de Ingeniería del Terreno, Universidad Politécnica de Valencia, 46022 Valencia, Spain. company@uv.es
²Universidad del País Vasco/Euskal Herriko Unibertsitatea, Facultad de Ciencia y Tecnología, Departamento de Estratigrafía y Paleontología, Apartado 644, 48080 Bilbao, Spain. xabier.pereda@ehu.es
³Museo del Jurásico de Asturias (MUJA), 33328 Colunga, Spain
⁴Grupo Aragosaurus-IUCA (www.aragosaurus.com), Área de Paleontología, Facultad de Ciencias, Universidad de Zaragoza, 50009 Zaragoza, Spain. jigruiz@unizar.es

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Abstract

New stegosaurian remains have been recently recovered from the Jurassic-Cretaceous transition sandstones of the Villar del Arzobispo Formation (Tithonian-Berriasian) in the Valencia province, eastern Spain. Specimens consist of two partially articulated (or closely associated) postcranial skeletons. The Baldovar specimen is composed of appendicular bones (scapula, femur) and two pairs of dermal tail spines, two of them articulated with two distal caudal vertebrae. The second specimen, unearthed in the vicinity of La Yesa village, consists of dorsal vertebrae and ribs, fragments of caudal centra and an incomplete femur. The new specimens are tentatively referred to the clade Dacentrurinae and may belong to *Dacentrurus* on the basis of features observed on the dorsal vertebrae and caudal dermal spines. Stegosaurs are represented so far in the Jurassic-Cretaceous transition of Spain by *Dacentrurus*. The presence of other taxa (*Stegosaurus*, *Miragaia*) in Spain, recently documented in the Late Jurassic of Portugal, cannot be attested on the basis of the currently recorded material.

Keywords: Dinosauria, Stegosauria, *Dacentrurus*, Iberian Range, Tithonian-Berriasian, Iberian Peninsula
Resumen

Nuevos restos fósiles de estegosaurios han sido recientemente hallados en niveles de areniscas del tránsito Jurásico-Cretácico de la formación Villar del Arzobispo (Titónico-Berriasiano) en la provincia de Valencia. Los especímenes consisten en dos esqueletos postcraneales parcialmente articulados (o en relación anatómica). El ejemplar de Baldovar consta de huesos apendiculares (escápula, fémur) y dos pares de espinas dérmicas de la cola, dos de ellas articuladas con dos vértebras caudales distales. Por su parte, el ejemplar de La Yesa se compone de vértebras dorsales y costillas, fragmentos de centros caudales y un fémur incompleto. Los fósiles se atribuyen al clado Dacentrurinae y podrían pertenecer a Dacentrurus en función de caracteres observados en las vértebras dorsales y las espinas dérmicas caudales. Los estegosaurios están representados hasta la fecha en el tránsito Jurásico-Cretácico de España por Dacentrurus. No puede confirmarse por el momento la presencia de otros taxones que están documentados en los yacimientos del Jurásico superior de Portugal (Miragaia, Stegosaurus).

Palabras clave: Dinosauria, Stegosauria, Dacentrurus, Cordillera Ibérica, Titónico-Berriasiano, Península Ibérica

1. Introduction

Omosaurus armatus, from the Early Kimmeridgian of Wiltshire (England), was the first articulated stegosaur described in the world and is the type species of Dacentrurus. Dacentrurus has been subsequently cited in other Late Jurassic localities of England, France and Portugal (see references in Galton and Upchurch, 2004; Weishampel et al., 2004; Maidment et al., 2008), and in several Late Jurassic-Early Cretaceous localities of Spain (see below).

Until recently, Dacentrurus was the only stegosaur documented in the Late Jurassic of Europe. However, remains of Stegosaurus and Miragaia have been described in the Late Kimmeridgian-Early Tithonian of Portugal (Escaso et al., 2007, 2008; Mateus, et al., 2009).

In Spain, remains of Dacentrurus have been recovered from several localities of the Jurassic-Cretaceous transition at the Iberian Range (Teruel and Valencia provinces, see Table 1). In addition, a dorsal vertebra and a dermal plate from the Early Cretaceous of Burgos, originally referred to an indeterminate stegosaur (Pereda-Suberbiola et al., 2003), were recently assigned to this genus (Maidment et al., 2008). The Spanish fossils have been referred to Dacentrurus based mainly on the presence of cervical ribs fused to respective vertebrae and/or dorsal vertebrae provided with wider than longer centra, features considered at present as synapomorphies of the clade Dacentrurinae (Mateus et al., 2009). These materials should be restudied in order to clarify its referral to Dacentrurus, Miragaia or to another undefined dacentrurine (Ruiz-Omeñaca et al., 2009).

In this paper we describe preliminarily new stegosaurian material from the Tithonian-Berriasian Villar del Arzobispo Formation cropping out near the villages of La Yesa and Baldovar (Valencia province, eastern Spain). The affinities of this material are discussed. Comparisons are made with the clade Dacentrurinae, and more specifically with Dacentrurus, the only stegosaur genus documented so far in the Spanish record.

Institutional abbreviations.- NHMUK, The Natural History Museum, London, UK; MCNV, Museo de Ciencias Naturales de Valencia, Spain; MPA, Museo Paleontológico de Alpuente, Valencia province, Spain; YPM: Yale Peabody Museum, New Haven, USA.

2. Location and Geological setting

The fossils consist of two partly articulated skeletons of stegosaurian dinosaurs unearthed from exposures of the lower part of the Villar del Arzobispo Formation in the South Iberian sub-basin of the Iberian basin (Southwestern Iberian Range). The new localities are placed near the villages of Baldovar (Barranco del Curro site) and La Yesa (El Balsón site), Valencia province, eastern Spain (Fig. 1).

The area exhibits extensive exposures of Upper Jurassic-Lower Cretaceous sediments represented by the transitional Villar del Arzobispo Formation (Tithonian-Berriasian), unconformably overlain by the more regressive El Collado Formation (Barremian). These units constitute an approximately 500-m-thick succession of interbedded bioclastic limestones, calcarenites and marly claystones, changing with the beginning of the second formation to a more siliciclastic sequence composed of sandstones, red and grey mudstones and locally conglomerates, in which subtidal to intertidal and supratidal facies have been recognized (Mas et al., 1984; Luque et al., 2005). The succession represents the installation of a regressive episode that took place during the Jurassic-Cretaceous transition. Both coastal non-marine units, known informally as “Purbeckian” and “Wealden” facies, have produced abundant remains of dinosaurs, including large sauropods, indeterminate theropods and stegosaurs. In this regard, the Villar del Arzobispo Formation is by far the most productive unit of the Iberian Range, and has yielded a number of fossiliferous localities, mainly concentrated in the South Iberian sub-basin (Ruiz-Omeñaca...
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<th>Taxon</th>
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<th>Age (Formation)</th>
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<tr>
<td>?Stegosauria indet.</td>
<td>&quot;Castellote NE&quot;, in Castellote (Teruel)</td>
<td>Lower Barremian-basal Aptian (Artoles Fm.)</td>
<td>Dorsal vertebrae</td>
<td>Ruiz-Omeñaca (2000); Maidment et al. (2008)*</td>
</tr>
<tr>
<td>Stegosauria indet.</td>
<td>&quot;Barranco Espina&quot;, in Galve (Teruel)</td>
<td>Lower Barremian (Camarillas Fm.)</td>
<td>Dermal spine</td>
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<tr>
<td>Stegosauria indet.</td>
<td>&quot;Aldea del Pinar&quot;, in Hontoria del Pinar (Burgos)</td>
<td>Hauterivian-Barremian (Piedrahita de Muñó Fm.) – provisional age</td>
<td>Dorsal vertebra and dermal plate</td>
<td>Pereda Suberiola et al. (2003); Maidment et al. (2008)*</td>
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<tr>
<td>Stegosauria indet.</td>
<td>&quot;La Canaleta&quot;, in Galve (Teruel)</td>
<td>Uppermost Hauterivian (El Castellar Fm.)</td>
<td>Dermal spine</td>
<td>Pereda-Suberiola et al. (2005); Maidment et al. (2008)*</td>
</tr>
<tr>
<td><em>Dacentrurus</em></td>
<td>&quot;San Cristóbal&quot;, in El Castellar (Teruel)</td>
<td></td>
<td>Dorsal and caudal vertebrae, synsacrum, ischium, pubis (mainly undescribed)</td>
<td>Cobos et al. (2009)</td>
</tr>
<tr>
<td>Aff. Dacentrurus sp.</td>
<td>&quot;Barrihonda-El Humero&quot;, in Riodeva (Teruel)</td>
<td>Tithonian-Berriasian (Villar del Arzobispo Fm.)</td>
<td>Cervical and caudal vertebrae, iliosacral block, ischia, pubes, femur, tibia, fibula, calcaneum, astragalus, dermal plate (mainly undescribed)</td>
<td>Cobos et al. (2008, 2009); Cobos (2009)</td>
</tr>
<tr>
<td>Dacentrurus armatus</td>
<td>&quot;Losilla I&quot;, in Aras de los Olmos (Valencia)</td>
<td></td>
<td>Cervical, dorsal and caudal vertebrae</td>
<td>Casanovas-Cladellas et al. (1997); Maidment et al. (2008)*</td>
</tr>
<tr>
<td>Dacentrurus armatus</td>
<td>&quot;Cerrito del Olmo I&quot;, in Alpuente (Valencia)</td>
<td></td>
<td>Cervical, dorsal and caudal vertebrae, ribs and ischium</td>
<td>Casanovas-Cladellas et al. (1995b); Maidment et al. (2008)*</td>
</tr>
<tr>
<td>Dacentrurus armatus</td>
<td>&quot;Cerrito del Olmo II&quot;, in Alpuente (Valencia)</td>
<td></td>
<td>Femur</td>
<td>Casanovas-Cladellas et al. (1999)</td>
</tr>
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</table>

Table 1. Previous record of stegosaurian dinosaurs in the Late Jurassic and Early Cretaceous of Spain. References of *Dacentrurus* in Valencia Teruel and Burgos provinces are emphasized in bold. New assignments of revised material are indicated.

Tabla 1. Registro previo de dinosaurios estegosaurios en el Jurásico Superior y Cretácico Inferior de España. En negrita se destaca la presencia de *Dacentrurus* en las provincias de Valencia, Teruel y Burgos. Se indican las nuevas asignaciones de los materiales revisados.
and Canudo, 2003 and references therein; Royo et al., 2006, 2009) which documents a rich and diverse Tithonian-Berriasian continental vertebrate fauna.

2.1. El Balsón site, La Yesa.

El Balsón site occurs in the lower part of the Villar del Arzobispo Formation, which consists of greenish-gray, massive mudstones and siltstones alternating with sandstone beds. The sequence overlies coarse calcarenite deposits with abundant bivalve moulds and oysters, indicating alternation of continental and marine conditions that point out to a siliclastic tidal flat origin of the terrigenous sediments.

Fossils are concentrated in the upper part of a fine-grained sand body. The stegosaurian remains consist of dorsal vertebrae and ribs, sparse fragments of caudal vertebrae, and a partial femur of a small-sized individual. These bones were found closely associated and at least some of them were preserved in close anatomical relation; thus they probably belong to the same individual (Fig. 2A). Bones surface are pristine, suggesting limited transport, and absence of reworking or prolonged subaerial exposure of the carcass before burial. The material is somewhat crushed and distorted by diagenetic compaction. The sandstone deposit has also produced actinopterygian teeth and abundant carbonized plant remains.

2.2. Barranco del Curro site, Baldovar.

Several postcranial elements of a second stegosaur specimen were found encrusted in a sandstone slab fallen down from a lateral bank of the Barranco del Curro creek. The fossil site is located about 6.5 km northwest to El Balsón (Fig. 1) site and placed at the same stratigraphic interval. The specimen has been only partially excavated, and a partial scapula, a complete femur and four dermal tail spines, two of them articulated with distal caudal centra, have been recovered to date. These remains are articulated or in close anatomical relation (Fig. 2B). Thus,
they may belong to a single individual. Again, the presence of relatively unweathered bones with little abrasion suggests rapid burial. Coal lenses and ferruginized vegetable remains are frequent in the sandstone bed.

3. Systematic Paleontology

3.1. El Balsón specimen

Dinosauria Owen, 1842
 Ornithischia Seeley, 1888
 Stegosauria Marsh, 1887
 Dacentrurinae Mateus, Maidment and Christiansen, 2009
 Dacentrurinae indet.
 (Figs. 2A, 3A-G)

Material: A partial skeleton composed at least by four dorsal vertebrae (MPA D-318/319/324/332), ten dorsal ribs (MPA D-320/322/323/330/333/335/337/338/344/348), fragments of caudal centra (uncatalogued), and a fragmentary femur (MPA D-317).

Locality and horizon: El Balsón site, near La Yesa village, Valencia province, Spain. Lower part of the Villar del Arzobispo Formation.

Age: Late Jurassic-Early Cretaceous (Tithonian-Berriasian).

Description

Dorsal vertebrae.- Four fairly complete posterior dorsal vertebrae have been recovered (Figs. 3A-C). The amphicoelous, massive centra of the dorsal vertebrae are wider transversely than long anteroposteriorly. The anterior and posterior articular faces are gently concave, with the anterior articular surface considerably expanded, especially ventrally. The lateral sides of the centra are depressed beneath the neural arch and end in a faint ventral keel, joining the anterior and posterior articular faces. The neural arch, which encloses a circular neural canal, is moderately high (the height of pedicels is more than 1.5 times the height of the centra), but not as tall as in other stegosaurs (Galton and Upchurch, 2004), acquiring a columnar aspect. The neural arch exhibits a sagittal, well marked ridge extending from the base of the postzygapophyses to the neural canal. A similar, but faint ridge runs the midline of the front of the neural arch.

The parapophyses, oval-shaped in outline, are placed lateral to the prezygapophyses in the recovered specimens, beneath the transverse processes, indicating a posterior position of the dorsals in the vertebral column. The transverse processes are long, stout, and exhibit a triangular cross section. They are upwardly directed and oriented approximately 25-30° above the horizontal. The prezygapophyses, whose articular surfaces are oriented upwards, inwards and slightly forwards, are ventromedially fused, but not the postzygapophyses, which are ventrally separated at the base of the neural spine by a rounded notch. The neural spine is short, moderately thickened distally and slightly directed backwards.

Dorsal ribs.- The ribs are slender elements provided of a long shaft, a reduced tuberculum and a well developed neck ending in a long capitulum (Figs. 3D-E). The cross section of the proximal half of the shaft is T-shaped, with the flat surface at its outside.

Femur.- Only a fragmentary femur 700 mm long has been preserved (Figs. 3F-G). It lacks the proximal third region and most of the distal end. The shaft is straight, elliptical in cross section, and the fourth trochanter is scarcely perceptible.
Discussion

The dorsal vertebrae from El Balsón site have massive centra that are wider than long. This character is regarded as a synapomorphy of the dacentrurines *Dacentrurus* (Galton and Upchurch, 2004; Maidment *et al*., 2008) and *Miragaia* (Mateus *et al*., 2009). Moreover, the vertebrae share two characters with those of *Dacentrurus armatus* (holotype, BMNH 46013). First, the ratio of the neural arch height (measured from the top of the centrum to the base of the prezygapophyses) to the neural canal height is approximately 2.63; this value is similar to that of *D. armatus* (2.60 in Maidment *et al*., 2008). Second, the ratio of the centrum height to the neural arch height is about 0.74 (this value is comparable to that (0.8) observed in *D. armatus* and *Stegosaurus armatus* (YPM 1850 and other specimens listed by Maidment *et al*., 2008).

These vertebral characters cannot be tested in *Miragaia longicollum* because only two anterior dorsal vertebrae are known in this taxon (Mateus *et al*., 2009). The dorsal vertebrae of La Yesa specimen have the ventral surfaces of the prezygapophyses fused where they meet on the midline, forming a concave, continuous U-shaped surface, as occurs commonly in stegosaurs and, convergently, in ankylosaurs (Maidment *et al*., 2008). In the clade *Lexovisaurus* (*Loricatosaurus* according to Maidment *et al*., 2009; see also Buffetaut and Morel, 2009) + *Stegosaurus + Dacentrurinae*, the prezygapophyses are fused in all dorsal vertebrae, but in other stegosaurs the fusion only occurs on the middle and posterior dorsals (Mateus *et al*., 2009). The dacentrurines *Dacentrurus* and *Miragaia* are coded as “?” for inapplicable by Mateus *et al*., 2009). Finally, the transverse processes of La Yesa stegosaur project about 25°-30° to the horizontal, as is in the dorsal vertebrae of *Dacentrurus armatus* (35° in the holotype BMNH 46013; Galton, 1985: Fig. 6B; see also Galton, 1991 for referred material at the Musée d’Histoire Naturelle du Havre destroyed in 1944). This angle is higher in other stegosaurs, such as *Huayangosaurus, Kentrosaurus, Lexovisaurus* and *Stegosaurus*.
Many thyreophorans have transverse processes that project dorsolaterally, rather than laterally. As noted by Maidment et al. (2008), the angle that the transverse processes make with the horizontal varies along the vertebral column, and is susceptible of deformation by taphonomical biases. Nevertheless, the low projection of the dorsal transverse processes relative to the horizontal distinguishes La Yesa taxon and Dacentrurus (Galton, 1985, 1991) from other stegosaurs. According to the features observed on its posterior dorsal vertebrae, and in absence of middle and posterior dorsal vertebrae in Miragaia, El Balsón stegosaur is provisionally referred to Dacentrurinae indet.

Fig. 4. H-M, Stegosaurian remains (Dacentrurinae indet.) from the Villar del Arzobispo Formation at Valencia province, Spain (Barranco del Curro site). A-C, left femur (MPA D-311) in anterior (A), medial (B) and posterior views (C). D-F, Left dermal tail spine (MPA D-316) in dorsal (D) and posterior (E) views, showing details of the cross sections of the spine (F). G-I, Distal tail spines and caudal vertebrae. G, sandstone slab with tail spines (MAP D-313/315) and associated caudal vertebrae (MAP D-327, 329). H, cross section of distal tail spine (MPA D-314). I, detail of caudal vertebrae co-ossified with the distal tail spines. Scale bar from A-E, G, I = 10 cm. Figures F, H not to scale.

3.2. Barranco del Curro specimen

Dacentrurinae indet.
(Figs. 2B, 4A-I)

Material: A partial skeleton composed of a complete femur (MPA D-311), a partial scapula (MPA D-312), four isolated dermal tail spines (MPA D-313/316), two of them articulated with two distal caudal centra (MPA D-327, 329).

Locality and horizon: Barranco del Curro site, placed in the vicinity of Baldovar village, Valencia province, Spain. Lower part of the Villar del Arzobispo Formation.

Age: Late Jurassic-Early Cretaceous transition (Tithonian-Berriasian).

Description

Caudal vertebrae.- Two distal caudal vertebrae coossified with the first pair of the terminal tail spines are partially exposed on the slab (Figs. 4G,I). The centra are short, platycoelous, narrow in their mid-section and expanded in the articular ends. The anterior end is slightly wider than the posterior end. The neural canal is broad but shallow, and the neural arch is placed posteriorly.

Scapula.- A fragmentary left scapula including most of the blade is preserved (Fig. 2B). The scapular blade is long, slenderly built, and parallel-sided. The dorsal margin is straight and the ventral margin gently curves at the contact with the proximal plate.

Femur.- A complete left femur 103 cm long is preserved (Figs. 4A-C). The femur is a straight bone, with a transversely wide columnar shaft, slightly compressed anteroposteriorly, showing at mid section a subrectangular shape. The head of the femur, not distinctly set off from the shaft, is markedly elevated above the greater trochanter, forming an angle of about of 110–115º with the long axis of the shaft. The lesser trochanter is fused to the greater trochanter. The distal condyles, badly eroded, are separated by a wide intercondylar groove. The fourth trochanter is scarcely noticeable.

Dermal tail spines.- Four tail spines are preserved in the slab (Figs. 4D-I). One pair is fused to distal caudal centra (Fig. 4G-I). These spines are elongate (at least 63 cm long as preserved), exhibiting a moderately expanded base and well defined lateral and medial edges. The cross section is subrhomboidal in outline, and the broken basal section shows a thick cortex surrounding a central cavity (Fig. 4H). The specimens are quite similar to an isolated spine from the close locality Aras de los Olmos (MCNV Lo-1) referred to Dacentrurus by Casanovas et al. (1999). These long spines are regarded as the terminal pair of the dermal armour, and were probably posterolaterally projected well beyond the distal end of the vertebral column, as in Stegosaurus (Gilmore, 1914; Carpenter and Galton, 2001) and Kentrosaurus (Galton, 1982).

Two incomplete, isolated spines are also preserved in the slab. They probably correspond to the second pair of distal caudal spines (see Carpenter and Galton, 2001). These spines are noticeably expanded at the base, oval on cross-section (see figures 4D-F), and appear to be shorter than the terminal spines (about 35 cm long as preserved). The material is provisionally referred to Dacentrurinae indet.

Discussion

The material of Baldovar is referred to Stegosauria by the presence of a parallel-sided blade of the scapula, an indistinct fourth trochanter on the femur, and paired dermal spines on the tail (Galton and Upchurch, 2004; Maidment et al., 2008). The spines, provided of well defined lateral and medial edges, look like those of Dacentrurus (BMNH 46013; MCNV Lo-1) in that the transverse width is greater than the anteroposterior length (Galton, 1985; Galton and Upchurch, 2004; this character is not taken into account by Maidment et al. 2008). Pending complete preparation of the dermal elements, the Baldovar material is provisionally referred to Dacentrurinae indet.

4. Conclusions

Stegosaurian remains are relatively common in the Upper Jurassic and in Jurassic-Cretaceous transitional formations of the Iberian Peninsula. Most of the Iberian material, which comes from Portuguese localities, has been referred to Dacentrurus. Recent discoveries in the Late Jurassic of Portugal indicate the presence of different taxa, such as Stegosaurus and Miragaia. In Spain, only Dacentrurus is known in the fossil record (Valencia, Teruel and, with reservations, Burgos provinces). In this paper, new stegosaurian fossils from two new localities (La Yesa and Baldovar) of the Jurassic-Cretaceous transition of Valencia are reported. The new specimens consist of partial postcranial skeletons with closely or fully articulated bones, including a noticeable terminal pair of dermal spines associated to distal caudal vertebrae in the Baldovar specimen – the first one found in the Spanish record. La Yesa specimen exhibits a combination of features on the dorsal vertebrae that is only known in the genus Dacentrurus. All the material is preliminarily re-
ferred to Dacentrurinae indet., as these features cannot be tested in Miragaia because the lack of homologous material in the Portuguese specimen.

Note Added in Proof:

Since this manuscript was submitted for publication, a new paper updating the stegosaur record of the Teruel province was published (Cobos et al., 2010). In this work, the postcranial remains from the “Barrihonda-El Humero”, “El Romeral”, “Prado de las Arenas” and “La Quineta 2” sites, in Riodeva (Table 1), are described and referred to aff. Dacentrurus sp. (Cobos, A., Royo-Torres, R., Luque, L., Alcalá, L., Mampel, L. (2010): An Iberian stegosaurs paradise: The Villar del Arzobispo Formation (Tithonian-Berriasian) in Teruel (Spain). Palaeogeography, Palaeoclimatology, Palaeoecology, 293: 223-236).

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