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New Fossils of Stegosaurs from the Upper Jurassic of the Eastern Iberian Peninsula (Spain)

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Abstract: The eastern Iberian Peninsula is one of the places with most stegosaur fossils in all of Europe. In the present study, we describe new remains from six different fossil sites from the Upper Jurassic of the Villar del Arzobispo Formation (Kimmeridgian–Tithonian). The remains comprise: a left humerus from CT-61 (El Castellar, Teruel), a dermal spine from Puntal de la Magdalena (Alpuente, Valencia), two caudal neural arches and five caudal vertebrae from Cañada París (Alpuente, Valencia), two caudal centra from Alpuente (Valencia) and four caudal vertebrae from Barrihonda-El Humero (Riodeva, Teruel). The left humerus (CT-61-1) and dermal spine (MPA D-110) are referred to Stegosauria indet. The caudal vertebrae from Alpuente (Cañada París specimen, MPA-653 and MPA D-1086) are referred to cf. *Dacentrurus* sp. Finally, the caudal vertebrae from Riodeva (Barrihonda-El Humero specimen) are referred to *Dacentrurus armatus* and assigned to a previously known caudal series from this site. The presence of abundant localities with stegosaurian remains reaffirms the important role of stegosaur dinosaurs in Late Jurassic coastal ecosystems.

Keywords: Dinosauria; Ornithischia; Stegosauria; *Dacentrurus*; systematics; Late Jurassic; Villar del Arzobispo Formation; Valencia; Teruel

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1. Introduction

Since the first European stegosaurian findings from the United Kingdom (UK) in the 19th century [1,2], the fossil record of this group of dinosaurs has expanded to the present day. Most of the findings comprise disarticulated, isolated and fragmentary material [3,4] and references therein. Furthermore, the majority of osteological remains, including the most relevant, come from the Jurassic period, the Cretaceous findings being scarcer and more fragmentary [3,5–7]. As of today, the European Jurassic stegosaurian record comprises four taxa: *Loricatosaurus priscus*, the holotype of which comes from the Callovian of the UK [8,9] and with referred material in other localities of the UK and France [3,10–12], *Dacentrurus armatus*, the holotype of which has been found in the Kimmeridgian–Tithonian of the UK [2,9], although other several fossils referred to this taxon have been discovered in localities from the UK, France, Spain and Portugal [9,13–16], *Stegosaurus* sp. from the Kimmeridgian–Tithonian of Portugal [17], and '*Miragaia*' from the Tithonian of Portugal [18,19]. There is a disagreement over whether this last taxon is valid or a junior synonym of *Dacentrurus* [7,15,16,19–23].

In the Iberian Peninsula, the presence of stegosaurs has been well known since the 1950s [24]. Among the osteological stegosaur remains from the Upper Jurassic of the Iberian Peninsula, the findings from the Lusitanian Basin stand out with several specimens referred to *Dacentrurus armatus* [13,16,24,25], three specimens referred to '*Miragaia*' [18,19] and three specimens assigned to *Stegosaurus* [16,17]. On the other hand, in the Gijón-Villaviciosa Basin, at least two specimens have been found and provisionally referred to Dacentrurinae indet. [26]. In the Maestrazgo Basin, the specimen from San Cristóbal

is classified as *Dacentrurus armatus* [15,20]. Finally, the fossils from several localities of the South-Iberian Basin (or Iberian-Levantine Basin) have been referred to Stegosauria indet. ([12]; Thyreophora indet. *sensu* [3]; Stegosauridae *sensu* [27]; and *Dacentrurus armatus sensu* [28]), Stegosauridae indet. [29], Dacentrurinae indet. [30] and *Dacentrurus armatus* [14,15,20].

The stegosaurian fossil record of the Villar del Arzobispo Formation, the lithostratigraphic unit from which the fossils studied in this work come, comprises osteological and ichnological remains. In particular, the osteological record of the Maestrazgo Basin is scarce and uniquely comprises the San Cristóbal specimen (CT-28, El Castellar, Teruel [15,21]) and an isolated slender spine from La Canaleta (Galve, Teruel, [6]; Villar del Arzobispo Formation (Upper Jurassic) *sensu* [31]). In contrast, the presence of ichnological sites is abundant, and all of the footprints are associated with the ichnogenus *Deltapodus* [32–34], including those of the CT-1 site, which contains the holotype of *Deltapodus ibericus* [15]. Regarding the South-Iberian Basin, several localities with osteological stegosaur remains have been found: El Romeral (RD-3, Riodeva, Teruel [15]), Barrihonda-El Humero (RD-10, Riodeva, Teruel [15]), Prado de las Arenas (RD-16, Riodeva, Teruel [15]), La Quineta 2 (RD-44, Riodeva, Teruel [15]), Barranco Conejero (Riodeva; Teruel [20]), Losilla (Alpuente, Valencia [14,27,28]), Cerrito del Olmo (Alpuente, Valencia [14,28,35]), By Pass (Alpuente, Valencia [29]), Barranco del Curro (Alpuente, Valencia [30]) and El Balsón (La Yesa, Valencia [30]).

In the current work, we describe new remains from six different fossil sites from the Upper Jurassic of the eastern Iberian Peninsula (South-Iberian Basin and Maestrazgo Basin) (Figure 1). One of these consists of new stegosaurian material from Barrihonda-El Humero [15], the type site of the largest sauropod from Europe *Turiasaurus riodevensis* [36]. The other localities are unpublished until now. The aim of this work is: (1) to provide a detailed description of these fossils; (2) to compare them with those of other Late Jurassic stegosaur taxa; and (3) to discuss the taxonomic affinity of the specimens.

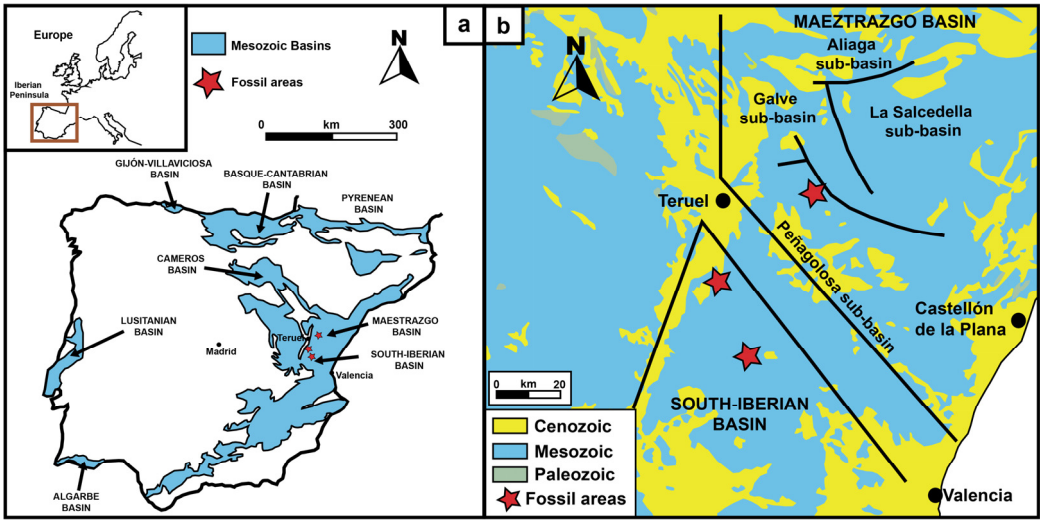

Figure 1. (**a**) Location of the fossil areas studied. (**b**) Geological map of the studied region that shows the limits of the basins and the more detailed location of the fossils areas. Cartography modified from [37].

Institutional Abbreviations

CPT: Fundación Conjunto Paleontológico de Teruel-Dinópolis, Teruel, Spain. MAP: Museo Aragonés de Paleontología, Teruel, Spain. MPA: Museo Paleontológico de Alpuente, Alpuente, Spain.

2. Geographical and Geological Context

The localities of Cañada París, Puntal de la Magdalena, MPA-653 and MPA-1086 are located in the municipality of Alpuente (Province of Valencia, Valencian Community, Spain). On the other hand, Barrihonda-El Humero (RD-10) is located in the municipality of Riodeva (Province of Teruel, Aragón, Spain). Finally, CT-61 is located in the municipality of El Castellar (Province of Teruel, Aragón, Spain) (Figure 1).

The fossils studied come from the Villar del Arzobispo Formation defined by [38]. The Villar del Arzobispo Formation is a detrital carbonate lithostratigraphic unit formed by sandstone and clay levels with intercalations of limestone and marls [38]. The materials of the Villar del Arzobispo Formation were deposited in the South-Iberian Basin (or Iberian-Levantine Basin) and in the Maestrazgo Basin (Figure 1), separated by an emergent massif with NW–NE orientation known as the Valencian Massif (or Sagunto-Teruel Massif), which was located where the Sierra de Javalambre is today [37,39,40].

The CT-61 site is located in the west of the Maestrazgo Basin, in the Peñagolosa sub-basin (Figure 1). In the South-Iberian Basin, the fossil sites of Cañada París, Puntal de la Magdalena, MPA-653 and MPA-1086 pertain to the Baldovar facies association. This facies association comprises parasequences of shallow marine or transition deposits dominated by tabular sandstones with a structure influenced by the presence of incised channels [41]. On the other hand, Barrihonda-El Humero (RD-10) pertains to the Riodeva facies association, which is mainly characterized by the scarcity of shallow marine deposits and the predominancy of transition and continental deposits (lutites and red clays). This facies association is structured in sections with vertical or progradational overlapping parasequences and amalgamated incised channel systems [41].

The Villar del Arzobispo Formation overlies the Higueruelas Formation (Tithonian or Tithonian-Berriasian *sensu* [42,43] or Kimmeridgian *sensu* [44,45]). Since the 1990s, the chronostratigraphic range of the Villar del Arzobispo Formation has been considered Tithonian–Berriasian [39,46], although recent studies assign it a Kimmeridgian–Tithonian range [37,47].

3. Materials and Methods

The studied fossils consist of: a left humerus (CT-61-1) from the CT-61 site (Figure 2; El Castellar, Teruel), a dermal spine (MPA D-110) from the Puntal de la Magdalena site (Figure 3; Alpuente, Valencia), two caudal neural arches (MPA D-108; MPA D-109) and five caudal centra (MPA D-114; MPA D-111; MPA D-112; MPA D-115; MPA D-113) from the Cañada París site (Figure 4; Alpuente, Valencia), two caudal centra (MPA-653; MPA-1086) from unknown sites (Figure 5; Alpuente, Valencia) and four caudal vertebrae (MAP-4682; MAP-4680; MAP-4683; MAP-4681) from the Barrihonda-El Humero site (Figure 6; Riodeva, Teruel).

Fossils from the municipality of Alpuente are deposited in the Museo Paleontológico de Alpuente, whereas the fossils from Riodeva and El Castellar are deposited in the Museo Aragonés de Paleontología.

All the pieces were measured with a caliper or a measuring tape (Table 1).

A systematic study was conducted through comparative anatomy, considering both the measurements and the anatomical features of each element. We compared the anatomy of the fossil bones to that of other Late Jurassic stegosaurs described in the literature. A taxonomic revision of the Upper Jurassic stegosaurs is beyond the scope of this paper. Hence, awaiting a detailed revision of the taxonomy, we preferred to synonymize '*Miragaia*' with *Dacentrurus* according to the most recent references [7,21].

We followed the open nomenclature terms definitions described by [48].

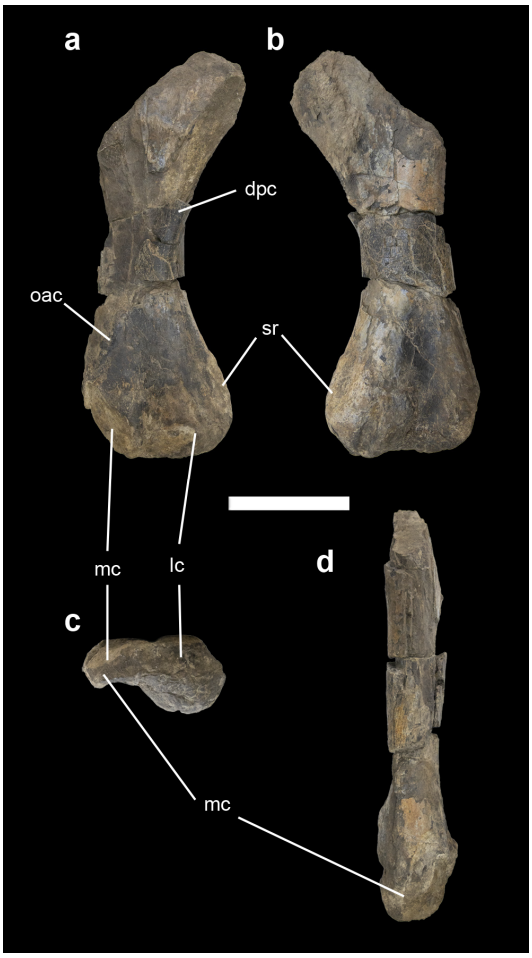

Figure 2. CT-61-1. Left humerus from CT-61 fossil site (El Castellar, Teruel, Spain) in anterior (**a**), posterior (**b**), distal (**c**) and medial (**d**) views. Abbreviations: dpc: deltopectoral crest; lc: lateral (radial) condyle; mc: medial (ulnar) condyle; oac: oblique anterior crest; sr: supinator ridge. Scale bar = 20 cm.

Figure 3. MPA D-110. Dermal spine from Puntal de la Magdalena fossil site (Alpuente, Valencia, Spain) in lateral (**a**), anterior (**b**) and medial (**c**) views. Scale bar = 5 cm.

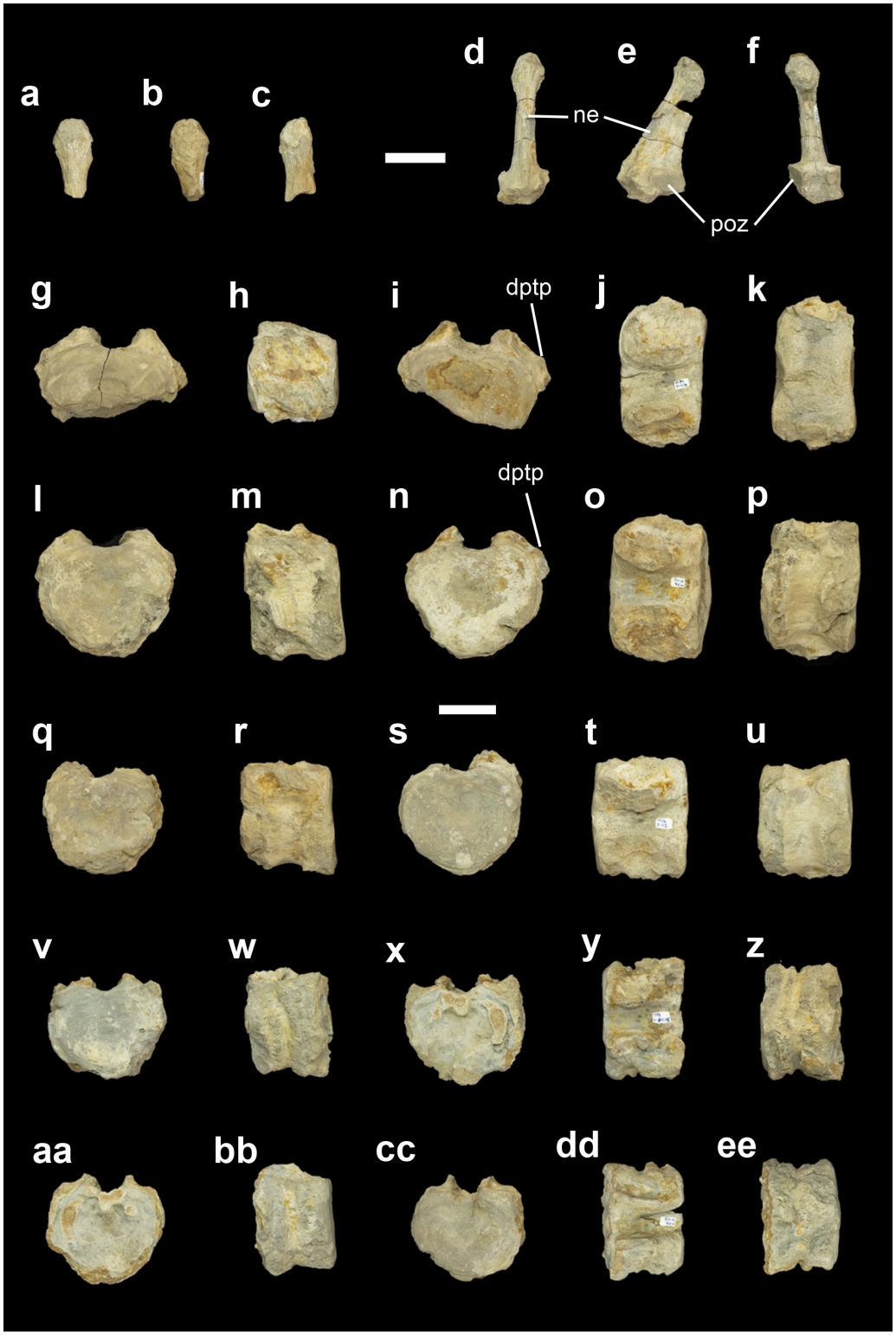

Figure 4. Fossils from Cañada París fossil site (Alpuente, Valencia, Spain). Apical fragment of a caudal neural arch (MPA D-108) (**a**–**c**), middle caudal neural arch (MPA D-109) (**d**–**f**), anterior caudal centra MPA D-114 (**g**–**k**) and MPA D-111 (**l**–**p**) and middle caudal centra MPA D-112 (**q**–**u**), MPA D-115 (**v**–**z**) and MPA D-113 (**aa**–**ee**) in anterior (**a**,**d**,**g**,**l**,**q**,**v**,**aa**), lateral (**b**,**e**,**h**,**m**,**r**,**w**,**bb**), posterior (**c**,**f**,**i**,**n**,**s**,**x**,**cc**), dorsal (**j**,**o**,**t**,**y**,**dd**) and ventral (**k**,**p**,**u**,**z**,**ee**) views. Abbreviations: dptp: dorsal process of the transverse process; ne: neural spine; poz: postzygapophyses. Scale bar = 5 cm.

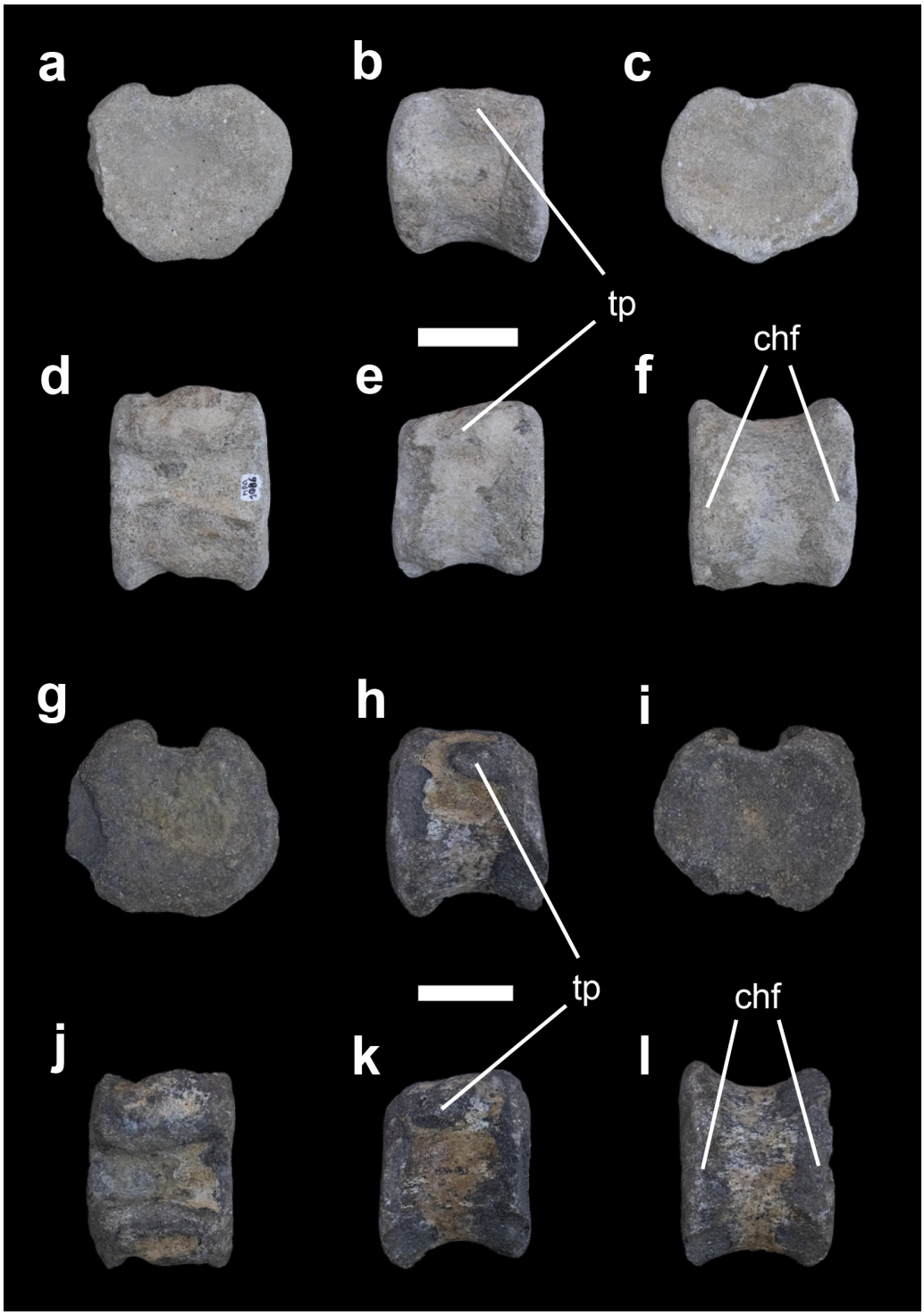

Figure 5. Vertebral centra from unknown fossil sites (Alpuente, Valencia, Spain). Middle caudal centrum (MPA-1086) in anterior (**a**), left lateral (**b**), posterior (**c**), dorsal (**d**), right lateral (**e**) and ventral (**f**) views. Middle caudal centrum (MPA-653) in anterior (**g**), left lateral (**h**,**k**), posterior (**i**), dorsal (**j**), right lateral (**k**) and ventral (**l**) views. Abbreviations: chf: chevron facet; tp: tranverse process. Scale bar = 5 cm.

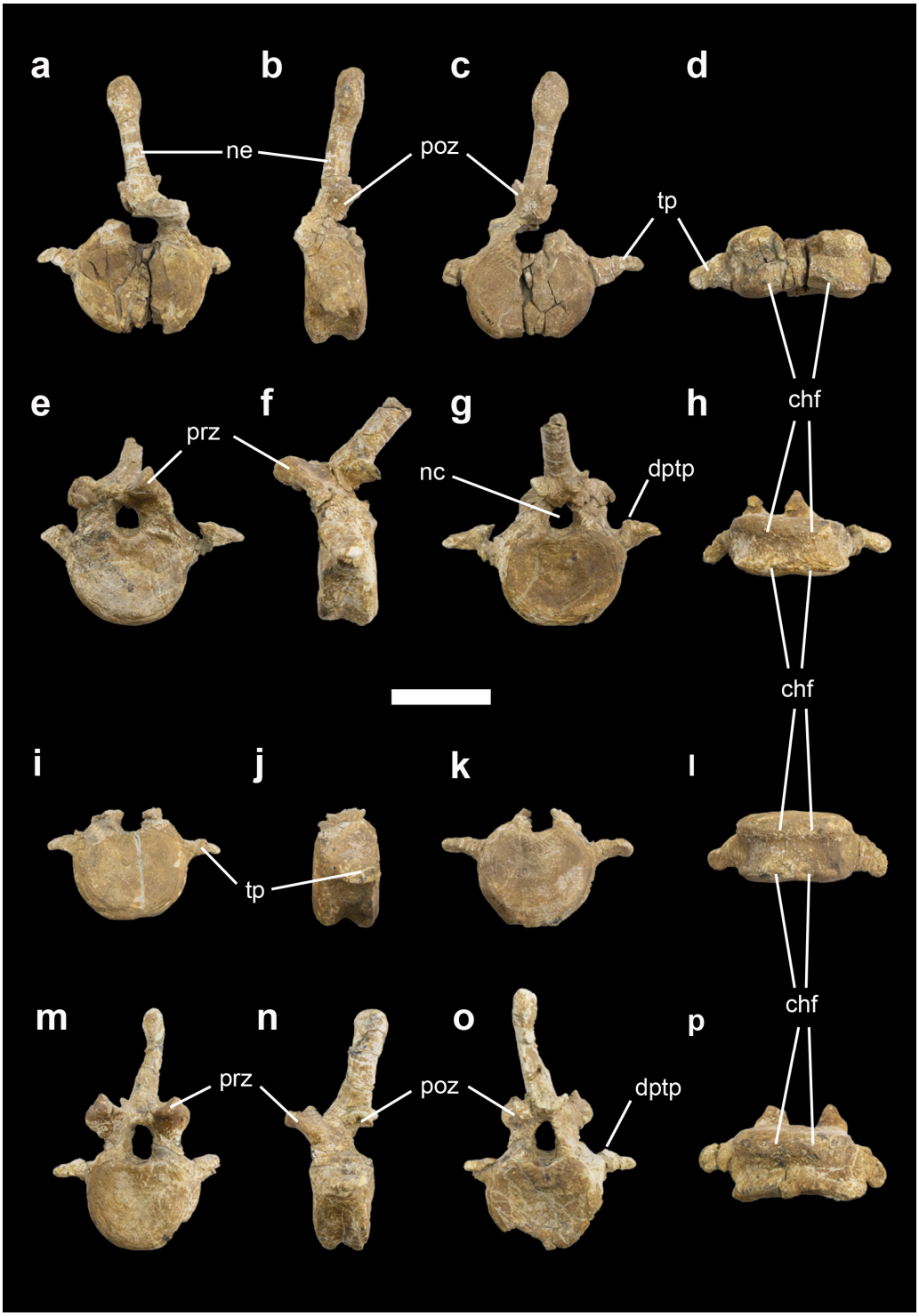

Figure 6. Caudal vertebrae from Barrihonda-El Humero fossil site (Riodeva, Teruel, Spain). Anterior caudal vertebrae MAP-4682 (**a**–**d**) and MAP-4680 (**e**–**h**), middle caudal vertebrae MAP-4683 (**i**–**l**) and MAP-4681 (**m**–**p**) in anterior (**a**,**e**,**i**,**m**), lateral (**b**,**f**,**j**,**n**), posterior (**c**,**g**,**k**,**o**) and ventral (**d**,**h**,**l**,**p**) views. Abbreviations: chf: chevron facet; dptp: dorsal process of the transverse process; nc: neural canal; ne: neural spine; poz: postzygapophyses; prz: prezygapophyses; tp: transverse process. Scale bar = 10 cm.

Table 1. Measurements (in mm) of the elements of the stegosaur specimens from the Villar del Arzobispo Formation studied in this work.

CT-61 Site	L	PW	DW			
Left humerus CT-61-1	628 *	237	267			
Puntal de la Magdalena	L	BH	BW			
Dermal spine MPA D-110	285 *	55	89			
Cañada París site	CL	AAFH	AAFW	PAFH	PAFW	NAH
Anterior caudal centrum MPA D-114	59	-	107	-	104	-
Anterior caudal centum MPA D-111	71	86	104	85	106	-
Middle caudal centrum MPA D-112	71	76	85	78	94	-
Middle caudal centrum MPA D-115	66	69	94	73	93	-
Middle caudal centrum MPA D-113	61	73	91	67	89	-
Caudal neural arch MPA D-108	-	-	-	-	-	68 *
Caudal neural arch MPA D-109	-	-	-	-	-	124
	CL	AAFH	AAFW	PAFH	PAFW	NAH
Middle caudal centrum MPA D-653	66	72	94	73	96	-
Middle caudal centrum MPA D-1086	65	70	82	68	84	-
Barrihonda-El Humero site	CL	AAFH	AAFW	PAFH	PAFW	NAH
Anterior caudal vertebra MAP-4682	49	82	121	79	115	170
Anterior caudal vertebra MAP-4680	47	65	108	84	112	98 *
Middle caudal vertebra MAP-4683	53	79	105	85	103	-
Middle caudal vertebra MAP-4681	53	79	91	88	105	147

Abbreviations: AAFH: anterior articular facet height; AAFW: anterior articular facet width; BH: base height; BW: base width; CL: centrum length; DW: distal width; L: length; NAH: neural arch height; PAFH: posterior articular facet height; PAFW: posterior articular facet width; PW: proximal width. *: measure influenced by the conservation state.

4. Results and Discussion

4.1. Systematic Paleontology (CT-61-1 and MPA D-110)

Dinosauria Owen, 1842 [49]
Ornithischia Seeley, 1887 [50]
Thyreophora Nopcsa, 1915 [51]
Stegosauria Marsh, 1877 [52]
Stegosauria indet

Referred material: A left humerus (CT-61-1) from the CT-61 fossil site. A dermal spine (MPA D-110) from the Puntal de la Magdalena fossil site.

Locality and horizon: CT-61 fossil site (CT-61-1) in the municipality of El Castellar (Province of Teruel, Spain), eastern Iberian Range, Maestrazgo Basin, Villar del Arzobispo Formation, Upper Jurassic (Kimmeridgian–Tithonian).

Puntal de la Magdalena fossil site (MPA D-110) in the municipality of Alpuente (Province of Valencia, Spain), eastern Iberian Range, South-Iberian Basin, Villar del Arzobispo Formation, Upper Jurassic (Kimmeridgian–Tithonian).

4.1.1. Descriptions

- CT-61-1 (Figure 2) is a left humerus. It is robust, short and has an expanded distal end. The lateral and medial margins are concave and almost straight, respectively, in anterior and posterior views. The humeral head is not preserved. Regarding the deltopectoral crest, it is mostly destroyed, with only its distal region preserved. On

the anterior surface, an oblique ridge extends from the distal base of the deltopectoral crest towards the medial (ulnar) condyle. A robust supinator ridge can be observed in the lateral surface of the distal end. The condylar region is rough and partially preserved. The anterior half of the medial condyle is not preserved. The medial condyle is slightly expanded posteriorly. The lateral (radial) condyle is robust and sub-circular in ventral view.

- MPA D-110 (Figure 3) is a proximal fragment of a slender dermal spine. The base of the spine is wider anteroposteriorly than dorsoventrally. In lateral and medial views, the basal region is moderately expanded with respect to the shaft. The surface of the base is slightly concave and C-shaped. Regarding the spine, the medial surface is slightly concave, especially in the proximal region. On the other hand, the lateral surface is slightly convex. The point of maximum width is located slightly above the beginning of the spine. Furthermore, approximately at this point, the spine begins to twist along its length. Anterior and posterior margins are convex and narrow. The cross-section is oval-shaped.

4.1.2. Comparisons and Discussions

- The left humerus CT-61-1 (Figure 2) shows a robust and strongly expanded transversally distal region that demonstrates thyreophoran affinities [53,54]. Furthermore, the presence of a pronounced anteroproximal expansion of the lateral condyle and an oblique ridge on the anterior surface that extends from the deltopectoral crest to the medial condyle support stegosaurian affinities [54]. In comparison to other stegosaurs, CT-61-1 shows an oblique crest less pronounced than *Stegosaurus* (Plate 33 [55]) or *Kentrosaurus* (Figure 4b [54]), being more similar to *Dacentrurus armatus* (Plate 17 [2]; Figure 9a–e [9]) and '*Miragaia*' (Figure S3 [18]).
- The presence of a base that is not hollow with rounded edges, the absence of a longitudinal groove on the lateral and medial surfaces, a straight spine in the lateral and medial views and the absence of a groove posteriorly for a following spine indicates that MPA D-110 (Figure 3) belongs to a stegosaur [12]. MPA D-110 presents a slightly concave base with a moderate expansion very similar to the slender spine of the holotype of *Dacentrurus armatus* (Figure 10d,e [9]) and three spines from different localities of the Villar del Arzobispo Formation (Figure 2a,b [6]; Figure 1 [27]; Figure 4d–f [30]). This condition is different from the massive spines with strongly expanded and concave bases of several specimens referred to *Dacentrurus* or '*Miragaia*' from Portugal and the UK (Figure 10f–m [9]; Figure 7a–c [13]; Figure 3.32 and 3.33 [16]; Figure 68 [19]). It is also different from the massive spines associated with the most caudal vertebrae related to *Dacentrurus* (Figure 3.34 [16]; Figure 4g–i [30]). The cross-section of MPA D-110 is oval, as is the spine of the specimen from Barranco del Curro (Figure 4f [30]). This is different from the sub-circular cross-section of the spine of the holotype of *Dacentrurus armatus* (Figure 1t [12]), the spine from Losilla (Figure 1 [27]) or the spine from La Canaleta [6] and from typical spines with a rhomboidal cross-section found in the Upper Jurassic of Europe, all of which are associated with *Dacentrurus* (Figure 10f–m [9]; Figures 5j and 7a–c [13]; Figure 3.33 [16]) or '*Miragaia*' (Figure 68a [19]). It is also different from the sub-circular cross-section with a narrow anterior edge observed in *Stegosaurus* [55].

4.2. Systematic Paleontology (Cañada París specimen, MPA-653 and MPA D-1086)

Stegosauria Marsh, 1877 [52]
Stegosauridae Marsh, 1880 [56]
Dacentrurus Lucas, 1902 [57]
cf. *Dacentrurus* sp.

Referred material: Two caudal neural arches (MPA D-108; MPA D-109) and five caudal centra (MPA D-114; MPA D-111; MPA D-112; MPA D-115; MPA D-113) from Cañada París fossil site (Figure 4). Two caudal centra (MPA-653; MPA-1086) from Alpuente (Figure 5).

Locality and horizon: Cañada París fossil site in the municipality of Alpuente (Province of Valencia, Spain), eastern Iberian Range, South-Iberian Basin, Villar del Arzobispo Formation, Upper Jurassic (Kimmeridgian–Tithonian).

Unknown fossil site 1 (MPA-653) and 2 (MPA-1086) in the municipality of Alpuente (Province of Valencia, Spain), eastern Iberian Range, South-Iberian Basin, Villar del Arzobispo Formation, Upper Jurassic (Kimmeridgian–Tithonian).

4.2.1. Descriptions

- MPA D-108 (Figure 4a–c) and MPA D-109 (Figure 4d–f) are two neural arch fragments. In particular, MPA D-108 consists of the apical region of a neural spine. The top of the neural spine has a circular morphology, and it is anteroposteriorly and mediolaterally expanded. Owing to these features, MPA D-108 belongs to the caudal series. On the other hand, MPA D-109 is an almost complete neural arch. The postzygapophyses are located above the prezygapophyses. The articulation surfaces of the postzygapophyses are anteroposteriorly directed and oval-shaped. With regard to the neural spine, it is short, and its lateral and medial surfaces are straight. The apex is anteroposteriorly and mediolaterally expanded and presents a circular morphology. Owing to the morphology of the postzygapophyses and the size of the postzygapophyses and the neural spine, we identified MPA D-109 as a middle caudal neural arch, more posterior than MPA D-108. MPA D-114 (Figure 4g–k), MPA D-111 (Figure 4l–p), MPA D-112 (Figure 4q–u), MPA D-115 (Figure 4v–z) and MPA D-113 (Figure 4aa–ee) are vertebral centra. MPA D-115 and MPA D-133 are contiguous vertebral centra. All centra are amphicoelous and wider than they are tall and long. As we move backward through the series, the centra tend to reduce their size, to become longer and to present a more marked heart-shaped morphology of the articulation facets. The lateral surfaces are concave with transverse processes located on the upper half. In the proximal region of the transverse processes of MPA D-114 and MPA D-111, a dorsal process is observed. In ventral view, all centra have chevron facets but lack a keel or groove. Owing to the presence of heart-shaped articulation facets, transverse processes (two of them with dorsal processes) and chevron facets, the vertebral centra from Cañada París were identified as caudal vertebrae from the anterior and middle region.
- MPA-1086 (Figure 5a–f) and MPA-653 (Figure 5g–l) are vertebral centra. Both are amphicoelous and wider than they are tall and long. The articulation facets are heart-shaped. The lateral surfaces are concave with transverse processes located in the upper half of the centrum. MPA-653 presents a deep concavity in the left lateral located immediately under the transverse process, whereas, in the right lateral, the concavity is more superficial. In ventral view, neither centra have a keel or a groove, but they do have chevron facets. The dimensions of the centra, the shape of the articular facets and the presence of transverse processes and chevron facets led us to identify them as middle caudal centra.

4.2.2. Comparisons and Discussions

Fossils from Cañada París (Figure 4) can be referred to Stegosauridae due to the presence of dorsal processes in the proximal region of the transverse processes in the anterior caudal vertebrae and neural spines, the apices of which are expanded relative to the rest of the spine [48].

All caudal centra (Figures 4 and 5) are characterized by being wider than they are tall and long, and heart-shaped, as in the type specimen of *Dacentrurus armatus* [9], a specimen from Portugal referred to '*Miragaia*' [19] and several specimens from the Villar del Arzobispo Formation assigned to *Dacentrurus* [15,20,35] (and pers. obs.) in contrast to the taller than wide and sub-hexagonal middle caudal centra of *Stegosaurus* [17,55,58], *Hesperosaurus* [59], *Loricatosaurus* [9,11] and *Alcovasaurus* (='*Miragaia*' *sensu* [19]) *longispinus* [60,61].

4.3. Systematic Paleontology (Barrihonda-El Humero specimen)

Stegosauridae Marsh, 1880 [56]
Dacentrurus Lucas, 1902 [57]
Dacentrurus armatus Owen 1875 [2]

Referred material: Four caudal vertebrae (MAP-4682; MAP-4680; MAP-4683; MAP-4681) (Figure 6).

Locality and horizon: Barrihonda-El Humero (RD-10) fossil site in the municipality of Riodeva (Province of Teruel, Spain), eastern Iberian Range, South-Iberian Basin, Villar del Arzobispo Formation, Upper Jurassic (Kimmeridgian–Tithonian).

4.3.1. Description

All centra are amphicoelous, wider than they are tall and long and heart-shaped (Figure 6). Similar to the centra from Cañada París, as we move backward through the series, the centra tend to increase their length, to reduce their height and width and to present a more marked heart-shaped morphology. In lateral view, all of them have transverse processes located at the upper half of the centrum. The transverse processes are posterolaterally projected and have a proximal dorsal process. No keel or groove is observed in the ventral surface, but chevron facets are present. MAP-4682 and MAP-4680 present a neural canal with a sub-circular morphology, whereas, in MAP-4681, it is oval-shaped. The prezygapophyses of MAP-4680 and MAP-4681 are finger-like, being convex laterally and straight medially. In both vertebrae, the prezygapophyses project anterodorsally, surpassing the articular facet of the centrum. The prezygapophyses and postzygapophyses are located at approximately the same level in lateral view. The postzygapophyses have an oval morphology. As we advance in the series, the postzygapophyses adopt a more anteroposterior orientation. The neural spine of MAP-4682 extends dorsally, and the sub-circular-shaped apex is anteroposteriorly and mediolaterally expanded. On the other hand, MAP-4680 and MAP-4681 have a neural spine with a more posterodorsal orientation (especially MAP-4680 due to diagenetic deformation) and a less expanded apex.

4.3.2. Comparisons and Discussions

The caudal vertebrae from Barrihonda-El Humero (Figure 6) present features such as heart-shaped articulation facets, wider than tall and long centra or the presence of transverse processes with a sub-triangular morphology, which makes them very similar to those of the holotype of *Dacentrurus armatus* [2,9] and a specimen from Portugal referred to '*Miragaia*' [19]. Previous to this work, several caudal vertebrae belonging to two different caudal series were described in Barrihonda-El Humero [15]; due to the dimensions and features of the vertebrae studied in this work (MAP-4682, MAP-4680, MAP-4683, MAP-4681), they form part of the caudal series made up of the vertebrae CPT-1453, CPT-4057 and CPT-4058. Other associated stegosaurian remains have been found at the Barrihonda-El Humero site [15]: a cervical vertebra (CPT-1330), an ilio-sacral block with two ischia and two fused pubes (CPT-1435), a left femur (CPT-1304), a fused tibia, fibula, astragalus and calcaneum block (CPT-1316; 1424), a metatarsal II (CPT-1454) and a dermal plate (CPT-1288). This material was previously assigned to *Dacentrurus armatus* [20] due to the presence of a distal ischial shaft with a straight dorsal margin [3,19,20,53]. For this reason, the vertebrae MAP-4682, MAP-4680, MAP-4683 and MAP-4681 are referred to *Dacentrurus armatus*.

5. Conclusions

The stegosaurian fossil record from the Villar del Arzobispo Formation constitutes one of the main sources of knowledge about this group of dinosaurs at the end of the Jurassic period in Europe. In the current study, new stegosaurian material from the South-Iberian Basin (or Iberian-Levantine Basin) and Maestrazgo Basin (Peñagolosa sub-basin) from six different fossil sites is identified and described.

The left humerus (CT-61-1) from CT-61 is referred to Stegosauria indet. due to the presence of: (1) a robust and expanded distal end, (2) a pronounced anteroproximal expan-

sion of the radial condyle and (3) an oblique ridge from the distal end of the deltopectoral crest to the medial condyle. The dermal spine (MPA D-110) from Puntal de la Magdalena is also referred to Stegosauria indet. due to: (1) the presence of a base that is not hollow with rounded edges, (2) the absence of a longitudinal groove on lateral or medial surfaces, (3) a straight spine in lateral and medial views and (4) the absence of a groove posteriorly for a following spine. On the other hand, the caudal vertebrae (MPA D-108; MPA D-109; MPA D-114; MPA D-111; MPA D-112; MPA D-115, MPA D-113; MPA-653; and MPA-1086) recovered from Alpuente show a combination of characters that demonstrate affinity with *Dacentrurus armatus* and other specimens recovered from the Upper Jurassic of Europe: (1) middle caudal centra that are wider than tall, (2) wider than long and (3) heart-shaped. For these reasons, and due to the lack of species-level or genus-level diagnostic characters, the caudal vertebrae from Alpuente are referred to cf. *Dacentrurus* sp. Finally, the new four caudal vertebrae from Barrihonda-El Humero are referred to a previously known caudal series formed by the vertebrae (from most anterior to posterior): CPT-1453, CPT-4057, CPT-4058, MAP-4682, MAP-4680, MAP-4683 and MAP-4681. All are assigned to *Dacentrurus armatus* because the dorsal surface of the distal ischial shaft previously described in the same locality is straight.

The discovery and study of these new stegosaurian remains, as well as several osteological and ichnological evidence previously described in the same lithostratigraphic unit (Villar del Arzobispo Formation), reaffirm the important role of stegosaur dinosaurs in Late Jurassic coastal ecosystems. Further and detailed studies of stegosaurian remains from the Villar del Arzobispo Formation will provide new and relevant systematic information about Late Jurassic European stegosaurs.

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