

The plated dinosaurs (Ornithischia, Stegosauria) of eastern Iberia (Spain): Taxonomy, diversity, and ecology

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ABSTRACT

Although stegosaurs have a long history in Europe, they were first discovered in Spain only in the late twentieth century. Since then, discoveries have increased markedly, particularly in the provinces of Teruel and Valencia (eastern Spain). In this work, several new specimens from the Villar del Arzobispo Formation are systematically studied. Recovered from nine fossil sites, they are referred to as *Stegosauria* indet., *Neostegosauria* indet., and *Dacentrurinae* indet., thereby expanding the known stegosaurian record. The Spanish ‘historical material’ is also revisited and systematically reassessed, revealing that this collection is currently dispersed across several institutions and collections. Furthermore, the review of all known specimens from the region results in the taxonomic reassignment of additional material. The stegosaurian record is exclusively composed by dacentrurines, which exhibit high morphological homogeneity. Four specimens can be attributed to *Dacentrurus armatus*, with no current evidence for additional dacentrurine species or the presence of stegosaurines. The abundance of *D. armatus* and indeterminate dacentrurine remains suggests these stegosaurs were very common and firmly established in the Late Jurassic coastal ecosystems of eastern Iberia. In contrast, the absence of stegosaurines likely reflects ecological preferences for inland biotopes, together with fossilization bias. The richness and good preservation of both osteological and ichnological record make the eastern Iberian Peninsula one of the most important regions worldwide for the study of these dinosaurs.

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Final citation: Sánchez-Fenollosa, Sergio, Cobos, Alberto, and Suñer, Maite. 2026. The plated dinosaurs (Ornithischia, Stegosauria) of eastern Iberia (Spain): Taxonomy, diversity, and ecology. *Palaeontologia Electronica*, 29(1):a13.

<https://doi.org/10.26879/1637>

palaeo-electronica.org/content/2026/5818-stegosaurs-of-eastern-iberia

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Keywords: Dacentrurinae; *Dacentrurus armatus*; systematics; Villar del Arzobispo Formation; Teruel; Valencia

Submission: 6 October 2025. Acceptance: 10 March 2026.

INTRODUCTION

Stegosaurs are thyreophoran dinosaurs mainly characterised by two parasagittal rows of osteoderms that extend from the neck to the tip of the tail (Sereno, 1986; Galton and Upchurch, 2004; Maidment et al., 2008; Raven and Maidment, 2017; Sánchez-Fenollosa and Cobos, 2025). In Europe, the first stegosaur described was *Dacentrurus armatus* (Owen, 1875), based on the posterior half of a skeleton from the Upper Jurassic of the UK (Owen, 1875; Galton, 1985). Over the following decades, additional stegosaurian material was recovered from several Upper Jurassic localities across Europe (Owen, 1877; Seeley, 1893; Nopcsa, 1911a; Lapparent and Zbyszewski, 1957; Galton, 1981a, 1983, 1991; Casanovas-Cladellas et al., 1999). In 2009, a new European dacentrurine, *Miragaia longicollum* Mateus et al., 2009, was described from a nearly complete anterior half of a skeleton in the Upper Jurassic of Portugal. This species was diagnosed from anatomical elements not preserved in the holotype of *D. armatus* (Galton, 1985). Since its description, the validity of *M. longicollum* has been repeatedly debated and reassessed (Ortega et al., 2009; Cobos et al., 2010; Cobos and Gascó, 2013; Escaso, 2014; Maidment et al., 2015).

A relatively complete dacentrurine specimen (MG 4863) from the Upper Jurassic of Portugal was later described as sharing several features with the holotype of *M. longicollum* (ML 433) and differing from that of *D. armatus* (NHMUK PV OR46013) (Costa and Mateus, 2019; Costa et al., 2025). However, these proposed characters cannot be reliably assessed in one or both holotypes and/or appear to have limited taxonomic and phylogenetic value (Sánchez-Fenollosa et al., 2025a). Some were also briefly challenged by Allain et al. (2022). In this context, broad comparative approaches that integrate the European Upper Jurassic stegosaurian record and account for intraspecific and intraindividual variability, as documented in other stegosaurs and ornithischians (e.g., Hennig, 1925; Galton, 1974, 1981a, 1981b, 1982a, 1982b; Boyd et al., 2009; Maidment et al., 2015; Baron et al., 2017; Verdú et al., 2017; Hüb-

ner, 2018; Ösi et al., 2019), are essential for establishing robust and consistent species delimitation.

Recently, Sánchez-Fenollosa et al. (2025a) reassessed all relatively complete European Upper Jurassic dacentrurine material, including a newly described specimen. They concluded that: 1) diagnosing two contemporaneous dacentrurines from non-overlapping anatomical elements introduces significant taxonomic uncertainty, 2) the comparable material of the *M. longicollum* type cannot be distinguished from that of the *D. armatus* type, 3) the European Upper Jurassic dacentrurine record exhibits high morphological homogeneity, 4) *M. longicollum* is currently best regarded as a junior synonym of *D. armatus*, 5) there is at present no solid evidence for more than one dacentrurine species, and 6) the synonymisation of *Dacentrurus* Lucas, 1902 and *Alcovasaurus* Galton and Carpenter, 2016 is not supported morphologically.

New phylogenetic analyses have further expanded Dacentrurinae by recovering *Alcovasaurus longispinus* (Gilmore, 1914) and *Kentrosaurus aethiopicus* Hennig, 1915a as members of this clade (Sánchez-Fenollosa and Cobos, 2025). These results suggest a more complex evolutionary history for Dacentrurinae, indicating greater taxonomic diversity and broader geographic distribution than previously recognised.

The presence of stegosaurs in the Iberian Peninsula has been acknowledged since the mid-twentieth century (Lapparent and Zbyszewski, 1957). In Spain, however, the first stegosaurian evidence was not reported until 1995, with the discovery of an isolated dermal spine (Casanovas-Cladellas et al., 1995a). Soon after, further discoveries followed, including the first Spanish record of *D. armatus* (Casanovas-Cladellas et al., 1995b, 1995c).

The Iberian Peninsula is now a key region for systematic and palaeobiological research on stegosaurs, containing by far the largest number of stegosaurian fossils in Europe (e.g., Casanovas-Cladellas et al., 1999; Mateus et al., 2009; Cobos et al., 2010; Company et al., 2010; Escaso, 2014; Costa and Mateus, 2019; Sánchez-Fenollosa et al., 2022a, 2025a; Sánchez-Fenollosa and Cobos, 2025). In particular, the Villar del Arzobispo Formation (eastern Spain) is one of the European litho-

stratigraphic unit richest in stegosaurian material. Its record includes both ichnological and osteological remains from numerous sites (e.g., Casanovas-Cladellas et al., 1999; Cobos et al., 2010; Company et al., 2010; Sánchez-Fenollosa et al., 2022a, 2025a; Castanera et al., 2024; Sánchez-Fenollosa and Cobos, 2025).

Considering recently proposed taxonomic frameworks and evolutionary hypotheses, this study focuses on stegosaurian dinosaurs from eastern Iberia. The main objectives are to: 1) provide osteological descriptions of both unpublished and 2) 'historical' fossils, 3) assess their taxonomic affinities, 4) document the current location and status of the 'historical' specimens, 5) conduct a comprehensive taxonomic review of all known stegosaurian material from eastern Iberia, and 6) discuss the implications for understanding stegosaurian diversity and ecology in the Late Jurassic coastal ecosystems of the region.

Institutional Abbreviations

IPS (or ICP), Institut Català de Paleontologia Miquel Crusafont, Sabadell, Spain; **MAP**, Museo Aragonés de Paleontología (**CPT**, Museo Fundación Conjunto Paleontológico de Teruel-Dinópolis, was used for accessions prior to 2011), Teruel, Spain; **MCNV**, Museo de Ciencias Naturales de Valencia, Valencia, Spain; **MG**, Museu Geológico, Lisboa, Portugal; **MHNN**, Muséum d'Histoire Naturelle du Havre, Le Havre, France; **ML**, Museu da Lourinhã, Lourinhã, Portugal; **MPA**, Museo Paleontológico de Alpuente, Alpuente, Spain; **NHMUK**, Natural History Museum, London, UK; **SHN**, Sociedade de História Natural, Torres Vedras, Portugal.

GEOGRAPHICAL AND GEOLOGICAL CONTEXT

All the specimens studied here (Appendices 1, 2, 3) came from the eastern Iberian Peninsula (provinces of Teruel and Valencia, Spain) (Figure 1).

Geologically, all the fossil sites (Appendices 1, 2, 3) are located within the South-Iberian and the Maestrazgo basins (Figure 1). These basins form part of the Mesozoic Iberian Extensional System (also known as the Iberian Basin), which developed in eastern Iberia from the late Oxfordian to the middle Albian and subsequently inverted during the Cenozoic Alpine Orogeny (Salas et al., 2001; Mas et al., 2004; Campos-Soto et al., 2021). The South-Iberian and Maestrazgo basins were surrounded to the west and north-east by the Iberian

and Ebro massifs, respectively, and were separated by the Valencian Massif (Mas et al., 2004; Campos-Soto et al., 2019). The Maestrazgo Basin, in particular, comprises several sub-basins separated by tectonic structures (Salas and Guimerà, 1996; Salas et al., 2001).

All the fossils studied here (Appendices 1, 2, 3) came from beds of the Villar del Arzobispo Formation (sensu Campos-Soto et al., 2019, 2021). This detrital-carbonate lithostratigraphic unit is formed by sandstone and clay levels with intercalations of limestone and marls (Mas et al., 1984). According to Campos-Soto et al. (2019), it is divided into two informal parts: 1) an essentially carbonate lower part (CLP) and 2) an essentially siliciclastic upper part (SUP) (Figure 1C).

The Villar del Arzobispo Formation (Kimmeridgian–Tithonian or, locally, Kimmeridgian–early Berriasian in the Las Zabacheras-Galve area sensu Campos-Soto et al., 2017, 2019) conformably overlies the oncolitic limestones of the Higuieruelas Formation (Kimmeridgian sensu Campos-Soto et al., 2016; Pacios et al., 2018). It is, in turn, unconformably overlain by Lower Cretaceous siliciclastic and/or carbonate units, depending on the region (Figure 1C).

MATERIALS AND METHODS

The new stegosaurian fossils studied here were recovered from several sites (Figure 1). They comprise: 1) an anterior caudal vertebra (CPT-1075; RD-5), 2) a dermal spine fragment (MAP-8435; MR-9), 3) a partial sacrum (CPT-1986; Jab.1), 4) an anterior dorsal vertebra, a posterior dorsal vertebra, a mid caudal vertebra with its chevron, and a partial left terminal dermal spine (MPA D-0287, MPA D-0279, MPA D-0276, and MPA D-0267; By Pass), 5) a cervical centrum (CPT-1705; RD-17), 6) a mid caudal centrum (CPT-1977), 7) a posterior caudal centrum (CPT-763; CT-10), 8) a posterior caudal centrum and several caudal dermal spine fragments (MPA-1218, MPA-1221, MPA-1222, and MPA-1223; Los Arenales), 9) a posterior caudal centrum (MAP-8436; MC-2), and 10) three posterior caudal vertebrae (MAP-8426, MAP-8425, and CPT-1950; RD-29).

The first-recorded stegosaurian specimens from Spain ('historical material') were revisited and studied. This research reveals that currently these fossils are dispersed in several institutions and collections (Appendix 2). They were recovered from several sites (Los Serranos region; Figure 1) and comprise: 1) a partial right caudal dermal spine

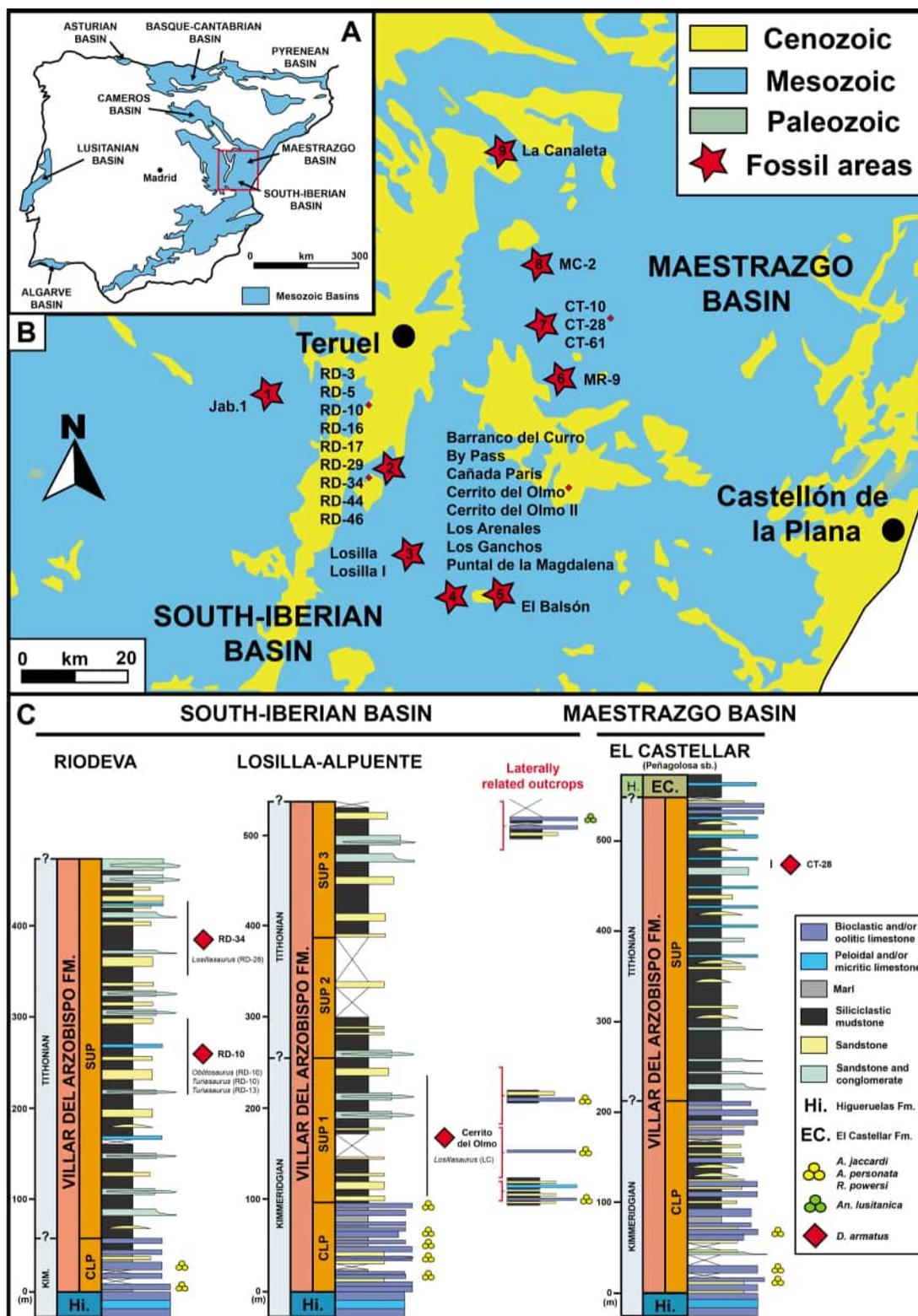


FIGURE 1. A, B, location and geological setting of all fossil areas (1, Jabaloyas; 2, Riodeva; 3, Aras de los Olmos; 4, Alpuente; 5, La Yesa; 6, Mora de Rubielos; 7, El Castellar; 8, Monteagudo del Castillo; 9, Galve) with osteological stegosaurian remains (eastern Spain, South-Iberian and Maestrazgo basins). C, stratigraphic sections of the Villar del Arzobispo Formation in the Riodeva, Losilla-Alpuente, and El Castellar areas. Cartography and stratigraphic sections modified from Campos-Soto et al. (2019).

(MCNV Lo-1; Losilla [Lo]), 2) a right femur (CO II-1; Cerrito del Olmo II [CO-II]), 3) a cervical centrum, two posterior cervical vertebrae, an anterior dorsal vertebra, and a dorsal centrum (MCNV Lo I-6, IPS-37432, IPS-37431, IPS-37433, and IPS-37435; Losilla I [Lo I]), and 4) three mid cervical vertebrae, three posterior cervical vertebrae, two dorsal centra, two dorsal neural arch fragments, several partial dorsal ribs, and an anterior caudal vertebra (MCNV CO-9, MCNV CO-5, MCNV CO-1, MCNV CO-17, MCNV CO-24, MCNV CO-2, MCNV CO-4, MCNV CO-7, MCNV CO-18, MCNV CO-19, MCNV CO-21, MCNV CO-13, MCNV CO-14, MCNV CO-15, MCNV CO-25, and MCNV CO-10; Cerrito del Olmo [CO]). Additional indeterminate and non-stegosaurian fossils from this last site were also revisited (MCNV CO-6, MCNV CO-8, MCNV CO-20, MCNV CO-22, MCNV CO-23, MCNV CO-26, and MCNV CO-27) (Appendix 2).

Revisiting the collections of the Museo de Ciencias Naturales de Valencia in 2023, we identified an unpublished stegosaurian posterior caudal vertebra (MCNV-VCP). This element was not mentioned by Casanovas-Cladellas et al. (1999), and no associated documentation is preserved in the museum's records. However, it was stored together with fossils from the Losilla I and Cerrito del Olmo sites, suggesting that it was likely recovered from one of these sites.

New fossils from the municipalities of Riodeva, Mora de Rubielos, Jabaloyas, El Castellar, and Monteagudo del Castillo are housed in the Museo Aragonés de Paleontología (Teruel, Aragón, Spain). Specimens from the municipality of Alpuente are housed in the Museo Paleontológico de Alpuente (Alpuente, Valencian Community, Spain). By contrast, the 'historical material' revisited here is housed in the Museo de Ciencias Naturales de Valencia (Valencia, Valencian Community, Spain) and the Institut Català de Paleontologia Miquel Crusafont (Sabadell, Catalonia, Spain), with the exception of CO II-1 (an isolated femur), which remains in the collection of J.P. Albir. This fossil was collected before the enactment of the Ley del Patrimonio Cultural Valenciano (Ley 4/1998, Valencian Cultural Heritage Law). Under present legislation, therefore, its housing in a private collection is permitted. Since this specimen is legally held and had already been described and figured (see Casanovas-Cladellas et al., 1999), its inclusion in this study is regarded as ethically acceptable.

All fossils were measured using either a calliper or a measuring tape (Appendix 1).

A systematic study was conducted through comparative anatomy, considering both morphometric data and qualitative anatomical features of each element. The material was compared primarily with Jurassic and Cretaceous stegosaurs, and in some cases with other ornithischians (cited on the text).

Only the specimens described in detail (Appendix 4) are included in this section and in the 'Systematic Palaeontology' section. However, many additional specimens were examined and taxonomically reviewed to better decipher and understand the Late Jurassic stegosaurian diversity of eastern Iberia (see 'Discussion' section and Appendix 3).

SYSTEMATIC PALAEOLOGY

DINOSAURIA Owen, 1842
sensu Langer et al., 2020
ORNITHISCHIA Seeley, 1887
sensu Madzia et al., 2021
THYREOPHORA Nopcsa, 1915
sensu Madzia et al., 2021
STEGOSAURIA Marsh, 1877
sensu Madzia et al., 2021
Gen. and sp. indet.

Referred material. An anterior caudal vertebra (CPT-1075) from the RD-5 fossil site (Figure 2A–E).

A distal fragment of dermal spine (MAP-8435) from the MR-9 fossil site (Figure 2F–H).

A partial right caudal dermal spine (MCNV Lo-1) from the Lo fossil site (Figure 2I–K).

Locality, horizon, and age. Pino de Jarque 2 (RD-5) site in the municipality of Riodeva, province of Teruel, Aragon, Spain. South-Iberian Basin, Villar del Arzobispo Formation, Upper Jurassic, upper Kimmeridgian–Tithonian (Figure 1).

El Batán (MR-9) site in the municipality of Mora de Rubielos, province of Teruel, Aragon, Spain. Maestrazgo Basin, Peñagolosa sub-basin, Villar del Arzobispo Formation, Upper Jurassic, upper Kimmeridgian–Tithonian (Figure 1).

Losilla (Lo) site in the municipality of Aras de los Olmos, province of Valencia, Valencian Community, Spain. South-Iberian Basin, Villar del Arzobispo Formation, Upper Jurassic, upper Kimmeridgian–Tithonian (Figure 1).

Description. (Appendix 4).

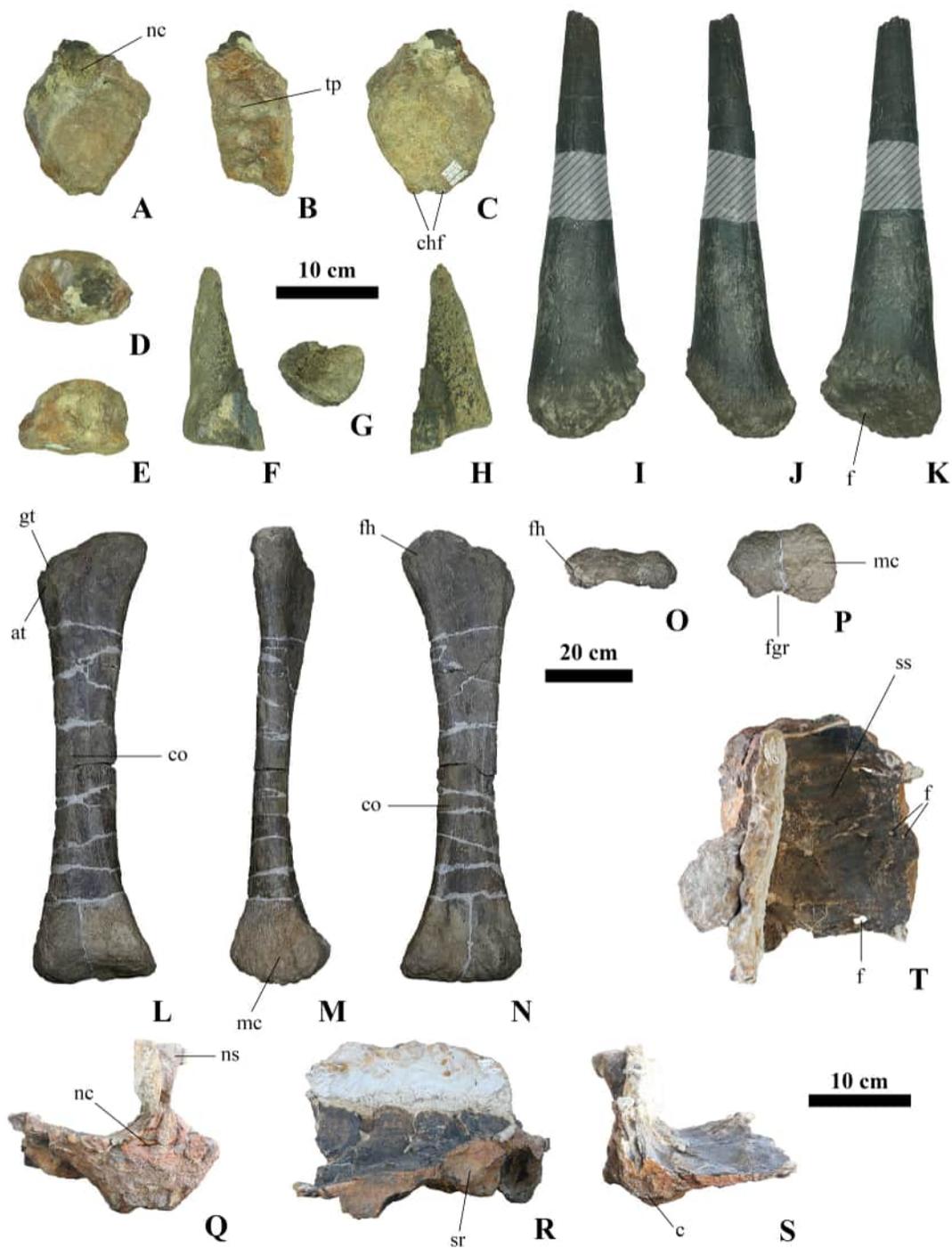


FIGURE 2. **A–E**, anterior caudal vertebra (CPT-1075) (RD-5, Riodeva, Teruel) referred to as *Stegosauria* indet. in anterior (A), left lateral (B), posterior (C), dorsal (D), and ventral (E) views. **F–H**, dermal spine fragment (MAP-8435) (MR-9, Mora de Rubielos, Teruel) referred to as *Stegosauria* indet. in ?dorsal (F), cross-section (G), and ?ventral (H) views. **I–K**, right caudal dermal spine (MCNV Lo-1) (Lo, Aras de los Olmos, Valencia) in dorsal (I), lateral (J), and ventral (K) views. **L–P**, right femur (CO II-1) (CO II, Alpuente, Valencia) referred to as *Stegosauridae* indet. in anterior (L), medial (M), posterior (N), proximal (O), and distal (P) views. **Q–T**, sacrum (CPT-1986) (Jab.1, Jabaloyas, Teruel) referred to as *Neostegosauria* indet. in anterior (Q), right lateral (R), posterior (S), and dorsal (T) views. **Abbreviations:** at, anterior trochanter; c, centrum; chf, chevron facet; co, cord-like ridge; f, foramen; fgr, flexor intercondylar groove; fh, femoral head; gt, greater trochanter; mc, medial condyle; nc, neural canal; ns, neural spine; sr, sacral rib; ss, sacral shield; tp, transverse process.

Comparisons and taxonomic assignment

RD-5 specimen (Figure 2A–E). The anterior caudal vertebra CPT-1075 exhibits a combination of characters indicating stegosaurian affinities (Galton, 1982a, 1985; Dong et al., 1983; Zhou, 1984; Carpenter et al., 2001; Maidment et al., 2015; Hao et al., 2018; Tumanova and Alifanov, 2018; Dai et al., 2022; Sánchez-Fenollosa et al., 2022a, 2025a; Li et al., 2024a; Jia et al., 2025): 1) absence of pleurocoels, 2) transverse processes located on the centrum, and 3) a centrum strongly compressed anteroposteriorly.

Given these features, and considering its isolated and fragmentary condition, CPT-1075 is tentatively referred to as *Stegosauria* indet.

MR-9 specimen (Figure 2F–H). The fragmentary shaft MAP-8435 is broad and straight in lateral and medial views, resembling other stegosaurian dermal spines (Figure 2I–K; Galton, 1982a, 1985; Dong et al., 1983; Zhou, 1984; Carpenter et al., 2001; Maidment et al., 2015; Galton and Carpenter, 2016; Dai et al., 2022; Sánchez-Fenollosa et al., 2022a). This contrasts with the recurved and compressed dermal spines of contemporary ankylosaurs such as *Mymoorapelta maysi* Kirkland and Carpenter, 1994 (Kirkland and Carpenter, 1994; Kirkland et al., 2025) and *Gargoyleosaurus parkpinorum* Kilbourne and Carpenter, 2005 (Kilbourne and Carpenter, 2005; Kirkland et al., 2025), as well as with Early Cretaceous ankylosaurs such as *Hylaeosaurus armatus* Mantell, 1833 (Raven et al., 2020), *Vectipelta barretti* Pond et al., 2023 (Pond et al., 2023), and *Europelta carbonensis* Kirkland et al., 2013 (Kirkland et al., 2013). Although the Early Cretaceous ankylosaur *Polacanthus foxii* Owen in Anonymous, 1865 exhibits a straight dermal spine, it is more compressed than that of stegosaurs (Raven et al., 2020).

MAP-8435, like other stegosaurian dermal spines (Figure 2I–K; Galton, 1982a, 1985; Dong et al., 1983; Zhou, 1984; Carpenter et al., 2001; Maidment et al., 2015; Galton and Carpenter, 2016; Dai et al., 2022; Sánchez-Fenollosa et al., 2022a), lacks a posterior groove. This differs from the condition observed in the Late Jurassic ankylosaurs *My. maysi* (Kirkland and Carpenter, 1994; Kirkland et al., 2025) and *G. parkpinorum* (Kilbourne and Carpenter, 2005; Kirkland et al., 2025).

Considering these features, and the specimen's fragmentary and isolated nature, MAP-8435 is also tentatively referred to as *Stegosauria* indet.

Losilla specimen (Figure 2I–K). The right caudal dermal spine MCNV Lo-1 exhibits all the stegosaurian features noted above. Furthermore, it also lacks both a hollow base and any longitudinal groove on its lateral or medial surfaces. These characters further distinguish it from ankylosaurian dermal spines (e.g., Kirkland and Carpenter, 1994; Kilbourne and Carpenter, 2005; Galton, 2016; Kirkland et al., 2025).

The small size and slight concavity of the base, together with the subcircular cross-section of the shaft, are similar to that observed in the slender caudal dermal spine of the *D. armatus* holotype (Galton, 1985). Comparable morphologies are also present in several specimens from the Villar del Arzobispo Formation, including the La Canaleta specimen (Pereda-Suberbiola et al., 2005), the Barranco del Curro specimen (MPA D-316, Company et al., 2010), and the Puntal de la Magdalena specimen (Sánchez-Fenollosa et al., 2022a). This condition contrasts with the large-based stocky caudal dermal spines seen in several dacentrurine specimens from the European Upper Jurassic (e.g., Galton, 1985, 1991; Company et al., 2010; Escaso, 2014; Costa and Mateus, 2019; this paper). Finally, this specimen also differs from the subcircular cross-section with a narrow anterior edge that is observed in the contemporary *Stegosaurus stenops* Marsh, 1887 (Maidment et al., 2015; Galton and Carpenter, 2016).

Given these features and its isolated nature, MCNV Lo-1 is referred to as *Stegosauria* indet. This dermal spine was previously referred to as *Stegosauridae* indet. (Casanovas-Cladellas et al., 1995a), *D. armatus* (Casanovas-Cladellas et al., 1999), *Thyreophora* indet. (Maidment et al., 2008), and *Stegosauria* indet. (Galton, 2016).

Given these features and its isolated nature, MCNV Lo-1 is referred to as *Stegosauria* indet. This dermal spine was previously referred to as *Stegosauridae* indet. (Casanovas-Cladellas et al., 1995a), *D. armatus* (Casanovas-Cladellas et al., 1999), *Thyreophora* indet. (Maidment et al., 2008), and *Stegosauria* indet. (Galton, 2016).

STEGOSAURIA Marsh, 1877 sensu Madzia et al., 2021

STEGOSAURIDAE Marsh, 1880 sensu Madzia et al., 2021

Gen. and sp. indet.

Referred material. A right femur (CO II-1) (Figure 2L–P).

Locality, horizon, and age. Cerrito del Olmo II (CO II) site in the municipality of Alpuente, province of Valencia, Valencian Community, Spain. South-Iberian Basin, Villar del Arzobispo Formation, Upper Jurassic, upper Kimmeridgian–Tithonian (Figure 1).

Description. (Appendix 4).

Comparisons and taxonomic assignment. The right femur CO II-1 is slender, columnar, and straight, resembling other stegosaurian femora (e.g., Galton, 1982a, 1985, 1991; Dong et al.,

1983; Zhou, 1984; Maidment et al., 2015; Galton and Carpenter, 2016; Hao et al., 2018; Dai et al., 2022). The anterior trochanter is fused to the greater trochanter, as in many subadult and adult stegosaurs (e.g., Galton, 1982a, 1985, 1991; Dong et al., 1983; Zhou, 1984; Maidment et al., 2015; Hao et al., 2018; Dai et al., 2022). This contrasts with the condition observed in *A. longispinus*, in which the anterior trochanter is separated from the greater by a deep cleft (Galton and Carpenter, 2016).

CO II-1 lacks a fourth trochanter as in most stegosaurids (Galton, 1982a, 1985; Dong et al., 1983; Maidment et al., 2015; Galton and Carpenter, 2016). This condition clearly differs from the prominent ridge-like fourth trochanter observed in huayangosaurids (Maidment et al., 2006; Hao et al., 2018; Dai et al., 2022). Sánchez-Fenollosa and Cobos (2025) have been identified an extremely reduced or absent fourth trochanter as a synapomorphy of Stegosauridae.

Cord-like ridges are present in CO II-1. Costa and Mateus (2019) interpreted the presence of longitudinal cord-like ridges, two posterior and one anterolateral, with distal bifurcation, as an autapomorphy of *M. longicollum* (based on specimen MG 4863). However, such features are strongly influenced by intraspecific variation and ontogeny (Galton, 1982a, 1982b, 1991); we conclude that they should therefore be treated with caution and regarded as non-diagnostic.

Given these observations and the isolated nature of the specimen, CO II-1 is referred to as Stegosauridae indet. This femur was previously assigned to *D. armatus* (Casanovas-Cladellas et al., 1999).

STEGOSAURIDAE Marsh, 1880 sensu Madzia et al., 2021

NEOSTEGOSAURIA Sánchez-Fenollosa and Cobos, 2025

Gen. and sp. indet.

Referred material. A partial sacrum (CPT-1986) (Figure 2Q–T).

Locality, horizon, and age. Fuente del Canal (Jab.1) site in the municipality of Jabaloyas, province of Teruel, Aragon, Spain. South-Iberian Basin, Villar del Arzobispo Formation, Upper Jurassic, upper Kimmeridgian–Tithonian (Figure 1).

Description. (Appendix 4).

Comparisons and taxonomic assignment. The presence of a solid sacral shield in CPT-1986 resembles the condition observed in neostegosaurs such as *A. longispinus* (Galton and Carpen-

ter, 2016), *K. aethiopicus* (Hennig, 1925; Galton, 1982a), *D. armatus* (Galton, 1985, 1991; Sánchez-Fenollosa et al., 2025a), *Hesperosaurus mjosi* Carpenter et al., 2001 (Carpenter et al., 2001), *S. stenops* (Maidment et al., 2015), *Wuerhosaurus homheni* Dong, 1973 (Dong, 1990), and *Yanbeilong ultimus* Jia et al., 2025 (Jia et al., 2025). By contrast, it lacks the large foramina between sacral ribs observed in huayangosaurids such as *Huayangosaurus taibaii* Dong et al., 1982 (Zhou, 1984; Maidment et al., 2006) and *Gigantospinosaurus sichuanensis* Ouyang, 1992 (Hao et al., 2018), early-diverging stegosaurids such as *Chungkingosaurus jiangbeiensis* Dong et al., 1983 (Dong et al., 1983) and *Tuojiangosaurus multispinus* Dong et al., 1977 (Maidment and Wei, 2006), and ankylosaurs (Carpenter et al., 2013). The presence of a solid sacral shield has been identified as a synapomorphy of Neostegosauria by Sánchez-Fenollosa and Cobos (2025).

Given this feature and considering the isolated and fragmentary condition of the specimen, CPT-1986 is referred to as Neostegosauria indet.

NEOSTEGOSAURIA Sánchez-Fenollosa and Cobos, 2025

DACENTRURINAE Mateus, Maidment, and Christiansen, 2009 sensu Sánchez-Fenollosa and Cobos, 2025

Gen. and sp. indet.

Referred material. A cervical centrum (MCNV Lo I-6), two posterior cervical vertebrae (IPS-37432 and IPS-37431), an anterior dorsal vertebra (IPS-37433), and a dorsal centrum (IPS-37435) from the Lo I fossil site (Figure 3; Appendix 2).

An anterior dorsal vertebra (MPA D-0287), a posterior dorsal vertebra (MPA D-0279), a mid caudal vertebra with its chevron (MPA D-0276), and a partial left terminal dermal spine (MPA D-0267) from the By Pass fossil site (Figure 4). Note that additional stegosaurian fossils were recovered from this site, but some of them are still unprepared and their study is beyond the scope of this work.

A cervical centrum (CPT-1705) from the RD-17 fossil site (Figure 5A–E).

A mid caudal centrum (CPT-1977) from Riodeva (unknown fossil site) (Figure 5F–J).

A posterior caudal vertebra (MCNV-VCP) from the Lo I or CO fossil site (Figure 5K–O).

A posterior caudal centrum (CPT-763) from the CT-10 fossil site (Figure 5P–T).

A posterior caudal centrum (MPA-1218) (Figure 5U–Y) and several caudal dermal spine

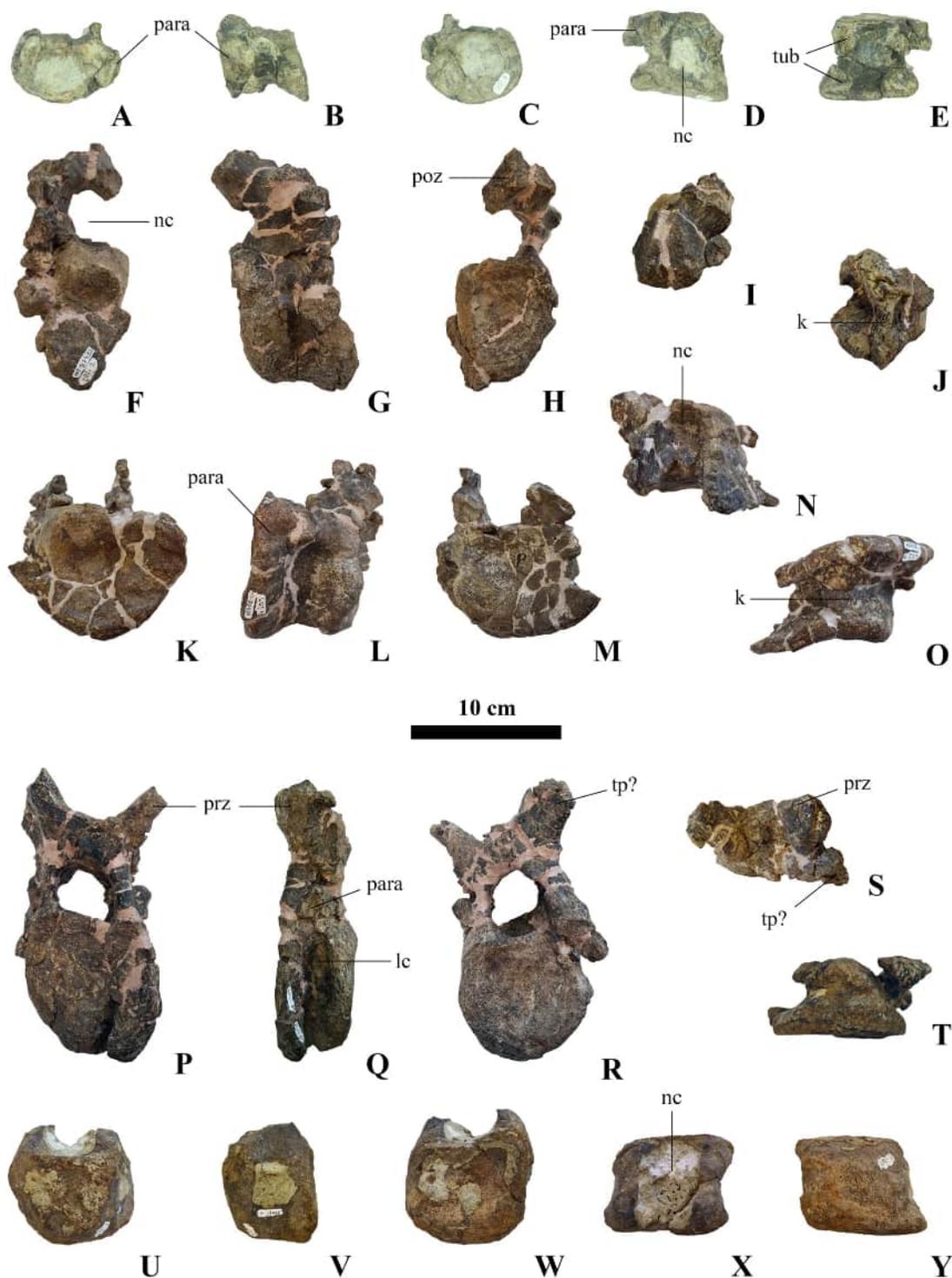


FIGURE 3. Dacentrinine fossils from the Losilla I (Lo I) site (Aras de los Olmos, Valencia). **A–E**, cervical centrum (MCNV Lo I-6) in anterior (A), left lateral (B), posterior (C), dorsal (D), and ventral (E) views. **F–J**, posterior cervical vertebra (IPS-37432) in anterior (F), right lateral (G), posterior (H), dorsal (I), and ventral (J) views. **K–O**, posterior cervical vertebra (IPS-37431) in anterior (K), left lateral (L), posterior (M), dorsal (N), and ventral (O) views. **P–T**, anterior dorsal vertebra (IPS-37433) in anterior (P), left lateral (Q), posterior (R), dorsal (S), and ventral (T) views. **U–Y**, dorsal centrum (IPS-37435) in anterior (U), left lateral (V), posterior (W), dorsal (X), and ventral (Y) views. **Abbreviations:** k, keel; lc, lateral concavity; nc, neural canal; para, parapophysis; poz, postzygapophysis; prz, prezygapophysis; tp?, transverse process; tub, tuberosity.

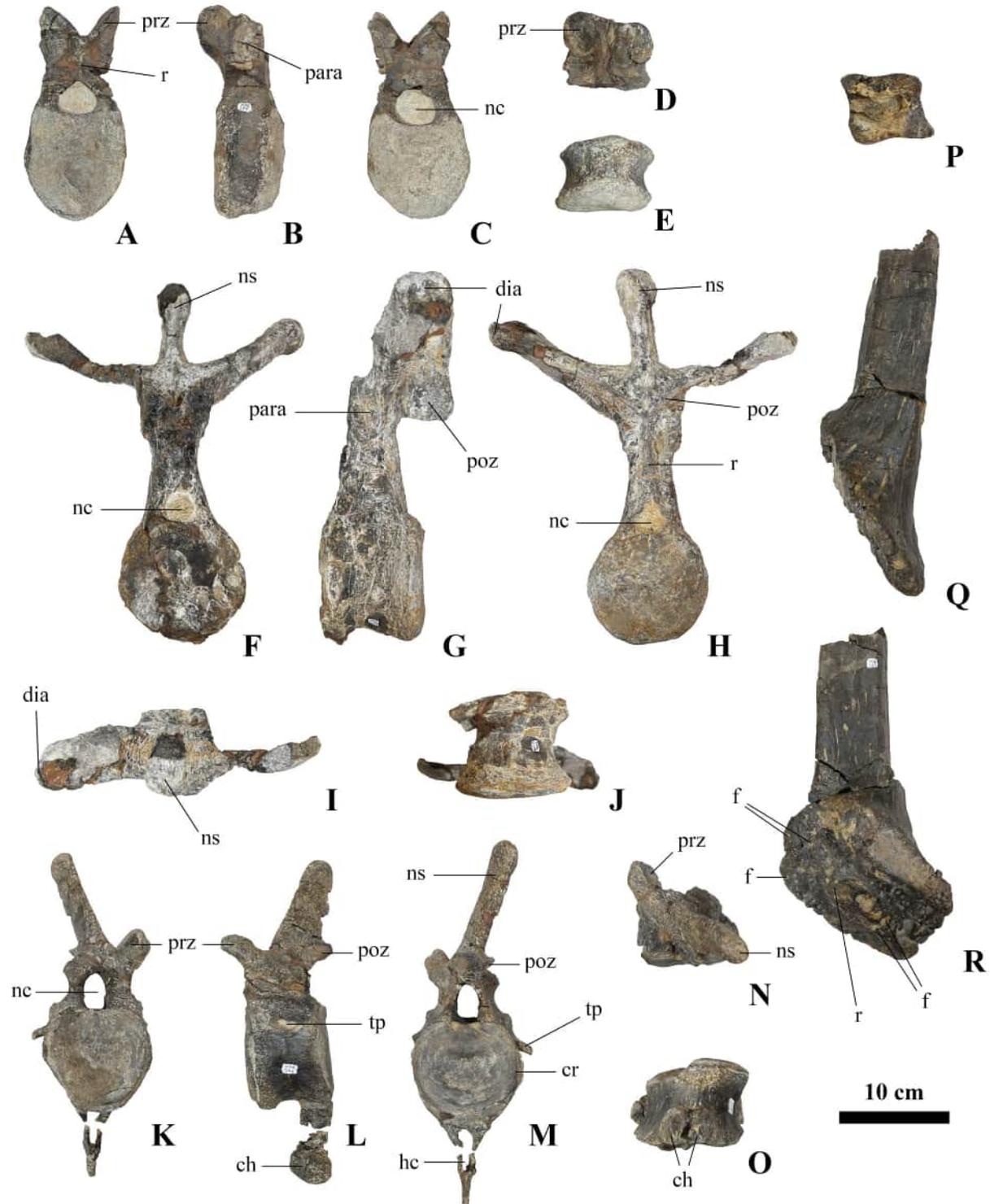


FIGURE 4. Dacentrurine fossils from the By Pass site (Alpuente, Valencia). **A–E**, anterior dorsal vertebra (MPA D-0287) in anterior (A), left lateral (B), posterior (C), dorsal (D), and ventral (E) views. **F–J**, posterior dorsal vertebra (MPA D-0279) in anterior (F), left lateral (G), posterior (H), dorsal (I), and ventral (J) views. **K–O**, mid caudal vertebra (MPA D-0276) in anterior (K), left lateral (L), posterior (M), dorsal (N), and ventral (O) views. **P–R**, left terminal dermal spine (MPA D-0267) in cross-section (P), dorsal (Q), and medial (R) views. **Abbreviations:** cr, concentric ridge; ch, chevron; dia, diapophysis; f, foramen; hc, haemal canal; nc, neural canal; ns, neural spine; para, parapophysis; poz, postzygapophysis; prz, prezygapophysis; r, ridge; tp, transverse process.

fragments (MPA-1221, MPA-1222, and MPA-1223) from the Los Arenales fossil site.

A posterior caudal centrum (MAP-8436) from the MC-2 fossil site (Figure 5Z–DD).

Three posterior caudal centra (MAP-8426, MAP-8425, and CPT-1950) from the RD-29 fossil site (Figure 6).

Locality, horizon, and age. Losilla I (Lo I) site in the municipality of Aras de los Olmos, province of Valencia, Valencian Community, Spain. South-Iberian Basin, Villar del Arzobispo Formation, Upper Jurassic, upper Kimmeridgian–Tithonian (Figure 1).

By Pass and Los Arenales sites in the municipality of Alpuente, province of Valencia, Valencian Community, Spain. South-Iberian Basin, Villar del Arzobispo Formation, Upper Jurassic, upper Kimmeridgian–Tithonian (Figure 1).

El Vago de Blasco (RD-17) and San Lorenzo 2 (RD-29) sites in the municipality of Riodeva, province of Teruel, Aragon, Spain. South-Iberian Basin, Villar del Arzobispo Formation, Upper Jurassic, upper Kimmeridgian–Tithonian (Figure 1).

Berzal Norte 2 (CT-10) site in the municipality of El Castellar, province of Teruel, Aragon, Spain. Maestrazgo Basin, Peñagolosa sub-basin, Villar del Arzobispo Formation, Upper Jurassic, upper Kimmeridgian–Tithonian (Figure 1).

MC-2 site in the municipality of Monteagudo del Castillo, province of Teruel, Aragon, Spain. Maestrazgo Basin, Galve sub-basin, Villar del Arzobispo Formation, Upper Jurassic, upper Kimmeridgian–lower Berriasian (Figure 1).

Description. (Appendix 4).

Comparisons and taxonomic assignment

Losilla I specimen (Figure 3). The cervical vertebrae are wider than long similar to those of *D. armatus* (Casanovas-Cladellas et al., 1995b; Galton, 1985, 1991; Mateus et al., 2009; Costa and Mateus, 2019). This condition differs from the longer than wide posterior cervical centra of other stegosaurs, such as the huayangosaurid *Gi. sichuanensis* (Hao et al., 2018), the early-diverging stegosaurid *T. multispinus* (Dong et al., 1983), the stegosaurines *Jiangjunosaurus junggarensis* Jia et al., 2007 (Jia et al., 2007), *Loricatosaurus priscus* Nopcsa, 1911b (Galton, 1990), *H. mjosi* (Carpenter et al., 2001), and *S. stenops* (Escaso et al., 2007a; Maidment et al., 2015), and the dacentrurine *K. aethiopicus* (Hennig, 1925).

The dorsal centra are likewise wider than long, differing from the elongate centra of huayangosaurids (Maidment et al., 2006; Hao et al., 2018; Dai et al., 2022; Li et al., 2024a), early-diverging stegosaurids such as *C. jiangbeiensis* and *T. multispinus* (Dong et al., 1983), stegosaurines (Galton, 1985; Carpenter et al., 2001; Escaso et al., 2007a; Maidment et al., 2008, 2015; Jia et al., 2025), and the dacentrurines *A. longispinus* (Gilmore, 1914; Galton and Carpenter, 2016) and *K. aethiopicus* (Hennig, 1925; Galton, 1982a). However, this condition is similar to that of the dacentrurines *Adratiklit boulahfa* Maidment et al., 2020 (Maidment et al., 2020), *Thyreosaurus atlasicus* Zafaty et al., 2024 (Zafaty et al., 2024), and *D. armatus* (Galton, 1985, 1991; Escaso et al., 2007b; Mateus et al., 2009; Costa and Mateus, 2019; Sánchez-Fenollosa et al., 2025a). This character is exclusively present in these taxa (Sánchez-Fenollosa and Cobos, 2025), but it is also in several stegosaurian specimens from the Upper Jurassic and Berriasian (Lower Cretaceous) of Europe (Figure 4A–C, F–H; Pereda-Suberbiola et al., 2003; Cobos et al., 2010; Company et al., 2010; Cobos and Gascó, 2013; Allain et al., 2022).

Due to the presence of a synapomorphic character limited to certain dacentrurines, the absence of any identifiable autapomorphies, and the fragmentary nature, the Losilla I specimen is referred to as Dacentrurinae indet. Historically, this specimen was attributed to *D. armatus* (Casanovas-Cladellas et al., 1995c).

By Pass specimen (Figure 4). The dorsal vertebrae exhibit centra that are wider than long, resembling those of the dacentrurines *Ad. boulahfa* (Maidment et al., 2020), *Th. atlasicus* (Zafaty et al., 2024), and *D. armatus* (Galton, 1985, 1991; Escaso et al., 2007b; Mateus et al., 2009; Costa and Mateus, 2019; Sánchez-Fenollosa et al., 2025a), as well as several European stegosaurian specimens from the Upper Jurassic and Berriasian (Figure 3P–R; Pereda-Suberbiola et al., 2003; Cobos et al., 2010; Company et al., 2010; Cobos and Gascó, 2013; Allain et al., 2022). However, this contrast with the plesiomorphic condition (Sánchez-Fenollosa and Cobos, 2025), dorsal centra longer than wide, observed in other stegosaurs (Hennig, 1925; Dong et al., 1983; Galton, 1985; Carpenter et al., 2001; Maidment et al., 2006, 2008, 2015; Galton and Carpenter, 2016; Hao et al., 2018; Dai et al., 2022; Li et al., 2024a; Jia et al., 2025).

The neural arch of the posterior dorsal vertebra MPA D-0279 is greatly elongated similar to

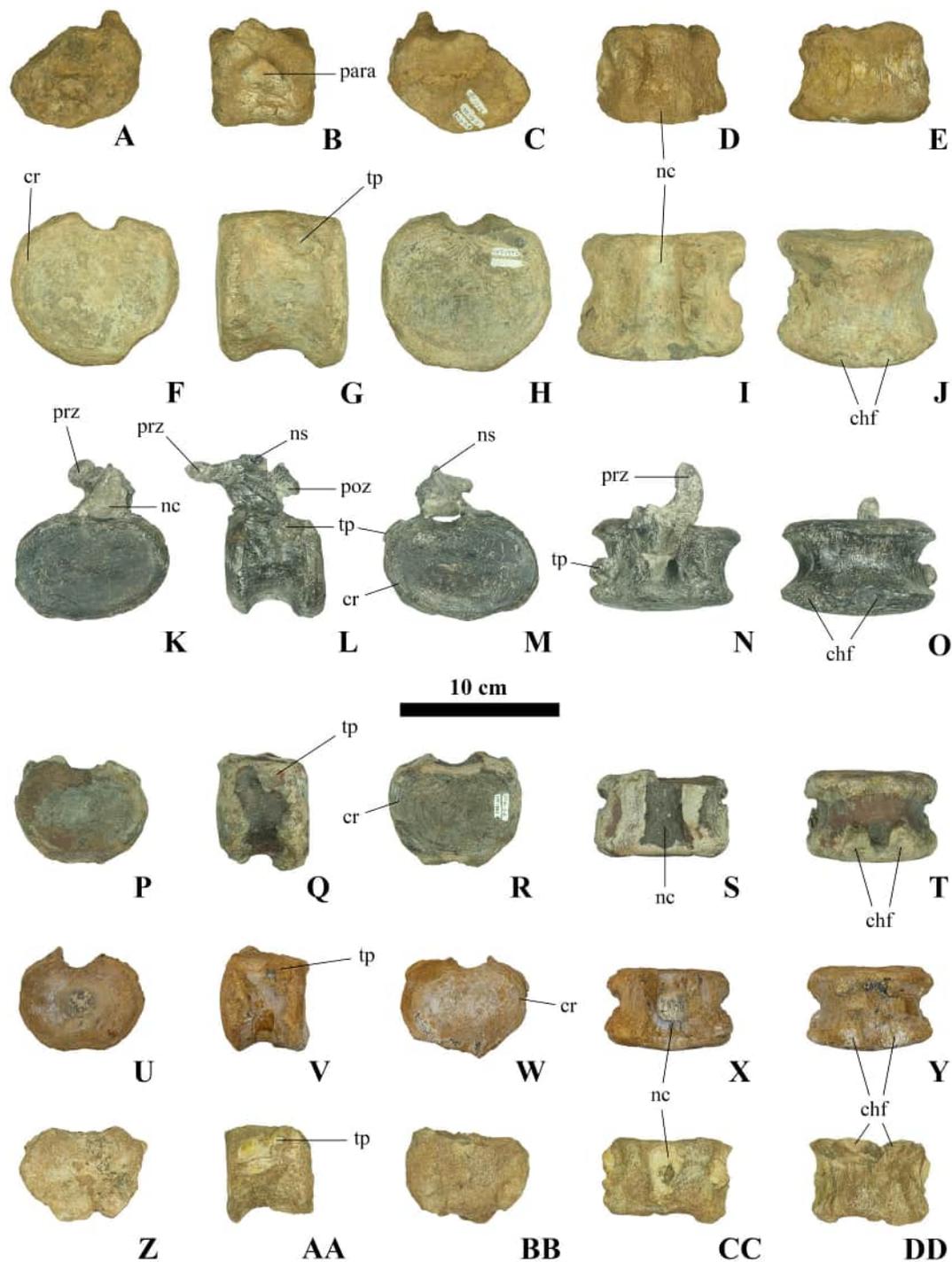


FIGURE 5. Some dacentrurine fossils from several sites. **A–E**, cervical centrum (CPT-1705) (RD-17, Riodeva, Teruel) in anterior (A), left lateral (B), posterior (C), dorsal (D), and ventral (E) views. **F–J**, mid caudal centrum (CPT-1977) (Riodeva, Teruel) in anterior (F), left lateral (G), posterior (H), dorsal (I), and ventral (J) views. **K–O**, posterior caudal vertebra (MCNV-VCP) (Losilla I or Cerrito del Olmo) in anterior (K), left lateral (L), posterior (M), dorsal (N), and ventral (O) views. **P–T**, posterior caudal centrum (CPT-763) (CT-10, El Castellar, Teruel) in anterior (P), left lateral (Q), posterior (R), dorsal (S), and ventral (T) views. **U–Y**, posterior caudal centrum (MPA-1218) (Los Arenales, Alpuente, Valencia) in anterior (U), left lateral (V), posterior (W), dorsal (X), and ventral (Y) views. **Z–DD**, posterior caudal centrum (MAP-8436) (MC-2, Monteagudo del Castillo, Teruel) in anterior (Z), left lateral (AA), posterior (BB), dorsal (CC), and ventral (DD) views. **Abbreviations:** cr, concentric ridge; chf, chevron facet; nc, neural canal; ns, neural spine; para, parapophysis; poz, postzygapophysis; prz, prezygapophysis; tp, transverse process.

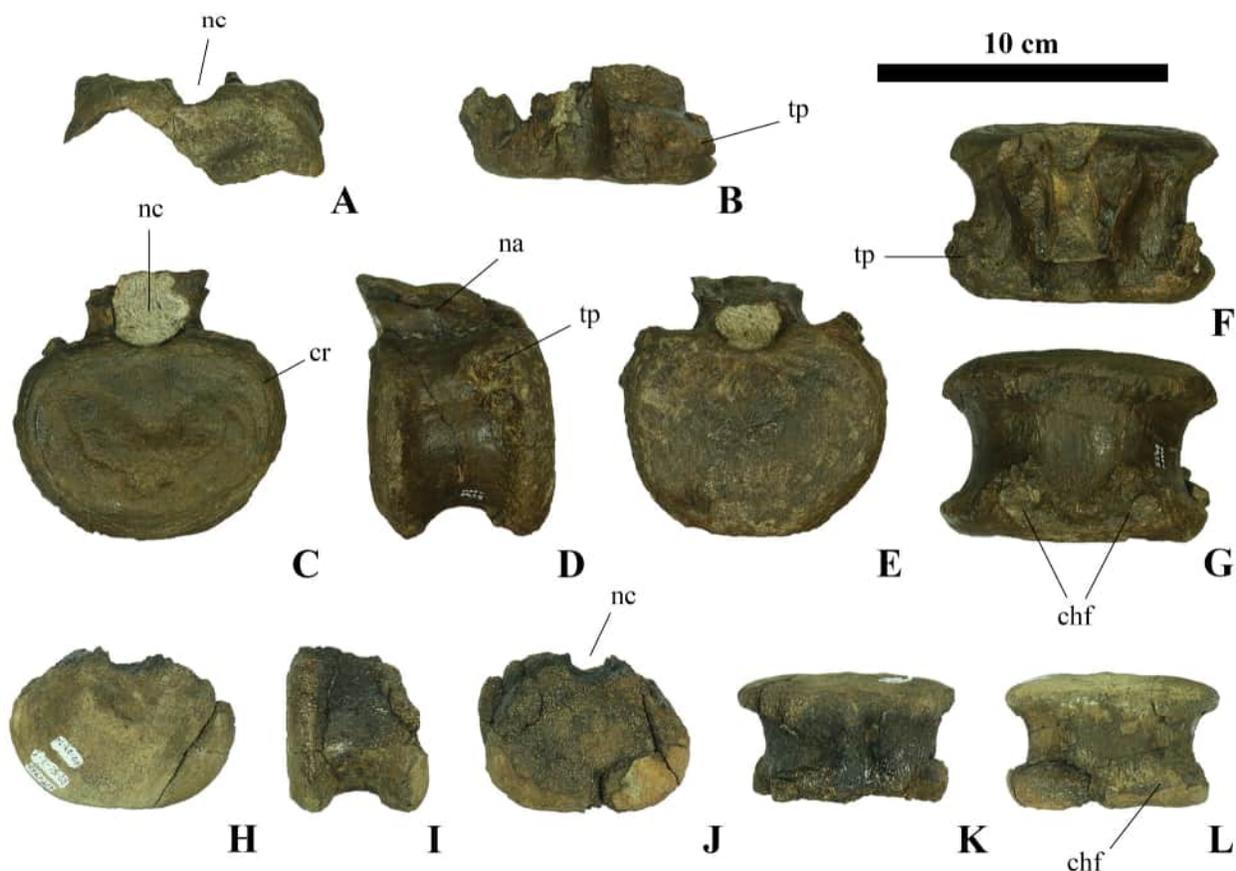


FIGURE 6. Dacentrurine fossils from the RD-29 site (Riodeva, Teruel). **A–B**, proximal posterior caudal centrum (MAP-8426) in anterior (A), and dorsal (B) views. **C–G**, proximal posterior caudal vertebra (MAP-8425) in anterior (C), left lateral (D), posterior (E), dorsal (F), and ventral (G) views. **H–L**, distal posterior caudal centrum (CPT-1950) in anterior (A), left lateral (B), posterior (C), dorsal (D), and ventral (E) views. **Abbreviations:** cr, concentric ridge; chf, chevron facet; na, neural arch; nc, neural canal; tp, transverse process.

those of stegosaurids (Galton, 1982a, 1985; Dong et al., 1983; Carpenter et al., 2001; Maidment et al., 2008, 2015, 2020; Galton and Carpenter, 2016; Zafaty et al., 2024; Jia et al., 2025; Sánchez-Fenolosa et al., 2025a), but contrasting with the shorter arches of huayangosaurids (Maidment et al., 2006; Hao et al., 2018; Dai et al., 2022; Li et al., 2024a). Additionally, it also differs from the greatly enlarged neural canal of the dacentrurine *K. aethiopicus* (Galton, 1982a; pers. obs. [NHMUK PV R37170]), as well as from the deeply excavated neural arch above the canal observed in the Early Cretaceous stegosaurines *W. homheni* (Maidment et al., 2008) and *Y. ultimus* (Jia et al., 2025).

The mid caudal vertebra MPA D-0276 has a centrum that is wider than long and heart-shaped, resembling those of the dacentrurines *K. aethiopicus* (Hennig, 1925) and *D. armatus* (Galton, 1985; Costa and Mateus, 2019; Sánchez-Fenolosa et al., 2022a, 2025a). Its neural spine is characterised by an expanded and rounded apex. This condition

contrasts with the unexpanded (or slightly) apex observed in huayangosaurids and early-diverging stegosaurids (Dong et al., 1983; Zhou, 1984; Hao et al., 2018; Tumanova and Alifanov, 2018), as well as with the bifurcated apex of the dacentrurine *A. longispinus* and the stegosaurine *S. stenops* (Ostrom and McIntosh, 1966; Escaso et al., 2007a). MPA D-0276 possesses a chevron fused to the vertebra, as seen in some caudal vertebrae of the *D. armatus* holotype (Galton, 1985) and the CT-28 specimen (Sánchez-Fenolosa et al. 2025a).

The terminal dermal spine MPA D-0267 is stocky and presumably elongate. In dacentrurines, a long terminal pair is documented in *K. aethiopicus* (Galton, 1982a; Mallison, 2011) and proposed for *A. longispinus* (Galton and Carpenter, 2016). This features, as well as the presence of a large base and/or a shaft with a rhomboidal (or lenticular) cross-section, is also observed in several dacentrurine specimens from the European Upper Jurassic (Galton, 1985, 1991, 2016; Company et

al., 2010; Escaso, 2014; Costa and Mateus, 2019), and in the Los Arenales specimen described here (MPA-1221, MPA-1222, and MPA-1223).

In particular, MPA D-0267 closely resembles the terminal caudal spine pair of the Barranco del Curro specimen (Company et al., 2010) and the Portuguese specimen SHN.LPP 123 (Escaso, 2014), especially in the presence of a large convex base and a shaft with a rhomboidal cross-section. In the latter two specimens, the bases are dorso-posteriorly fused to each other with the distal vertebrae within their bases. This condition, superficially reminiscent of the ankylosaurid tail club, is unique in the stegosaurian record worldwide and potentially diagnostic; however, the fragmentary nature of both specimens precludes a taxonomic assignment beyond Dacentrurinae indet. By contrast, MPA D-0267 is preserved as an isolated element, possibly due to taphonomic processes (the dorsal margin of the base is broken), although intraspecific variability (e.g., ontogeny or sexual dimorphism) cannot be ruled out.

Given the presence of synapomorphic characters exclusive to dacentrurine stegosaurs, together with the absence of any identifiable autapomorphies, these fossils are referred to as Dacentrurinae indet. As not all stegosaurian material from this site has been studied, future research may allow for a more precise taxonomic assignment.

RD-17 specimen (Figure 5A–E). The cervical centrum CPT-1705 is wider than long, closely matching the condition in *D. armatus* (Casanovas-Cladellas et al., 1995b; Galton, 1985, 1991; Mateus et al., 2009; Costa and Mateus, 2019). This contrasts with the elongate posterior cervical centra of other stegosaurs, such as the huayangosaurid *Gi. sichuanensis* (Hao et al., 2018), the early-diverging stegosaurid *T. multispinus* (Dong et al., 1983), the stegosaurines *J. junggarensis* (Jia et al., 2007), *L. priscus* (Galton, 1990), *H. mjosi* (Carpenter et al., 2001), and *S. stenops* (Escaso et al., 2007a; Maidment et al., 2015), and the dacentrurine *K. aethiopicus* (Hennig, 1925).

On this basis, and given the lack of clear apomorphies and its fragmentary nature, CPT-1705 is tentatively referred to as Dacentrurinae indet.

CPT-1977, MCVN-VCP, CT-10, Los Arenales (MPA-1218), MC-2, and RD-29 specimens (Figures 5F–DD, 6). These specimens represent mid or posterior caudal vertebrae. All are wider than long and have heart-shaped articular facets, resembling those of the dacentrurines *K. aethiopicus* (Hennig, 1925; pers. obs. [NHMUK PV R37155 and R37154]) and *D. armatus* (Galton, 1985; Costa

and Mateus, 2019; Sánchez-Fenollosa et al., 2022a, 2025a). Posterior caudals of *A. longispinus* share these features (Gilmore, 1914; Galton and Carpenter, 2016), although Gilmore (1914) noted that its mid caudals are elongated with hexagonal facets, more similar to the condition present in the stegosaurines *L. priscus* (Galton, 1985, 1990), *H. mjosi* (Carpenter et al., 2001), and *S. stenops* (Escaso et al., 2007a; Maidment et al., 2015). Huayangosaurids and early-diverging stegosaurids also show elongate mid and/or posterior caudal vertebrae (Dong et al., 1983; Maidment et al., 2006; Hao et al., 2018; Dai et al., 2022).

Importantly, stegosaurines lack transverse processes in the distal half of the tail (Galton, 1985, 1990; Carpenter et al., 2001; Maidment et al., 2015), whereas such processes are present in the mid and/or posterior caudal vertebrae studied here, as well as in those of the dacentrurines *A. longispinus* (Gilmore, 1914; Galton and Carpenter, 2016), *K. aethiopicus* (Hennig, 1925), and *D. armatus* (Galton, 1985; Costa and Mateus, 2019; Sánchez-Fenollosa et al., 2025a).

These features restricted to dacentrurine stegosaurs, combined with the absence of clear apomorphies and the fragmentary nature of the material, support referral of these specimens to Dacentrurinae indet.

DACENTRURINAE Mateus, Maidment, and Christiansen, 2009 sensu Sánchez-Fenollosa and Cobos, 2025

DACENTRURUS Lucas, 1902

DACENTRURUS ARMATUS (Owen, 1875)

Synonymy. *Omosaurus armatus* Owen, 1875; *Stegosaurus armatus* Lydekker, 1888; *Omosaurus lennieri* Nopcsa, 1911a; *Dacentrurus lennieri* Hennig, 1915b; *Dacentrurosaurus armatus* Hennig, 1925; *Miragaia longicollum* Mateus, Maidment, and Christiansen, 2009; and *Dacentrurus longicollum* Raven and Maidment, 2017.

Diagnosis. *D. armatus* possesses the following autapomorphies (Sánchez-Fenollosa and Cobos, 2025; Sánchez-Fenollosa et al., 2025a): A premaxilla with 1) an anterior tip that drawn into a point; and 2) an anterolateral margin ventrally projected; a supraoccipital with 3) a posteroventrally orientation with an angle greater than 90° with the dorsal plane of the skull roof; a cervical series with 4) at least 17 cervical vertebrae; and 5) at least anterior and mid cervical ribs fused to the vertebrae; cervical vertebrae with 6) two spinopostzygapophyseal laminae that extend anterolaterally from the top of the postzygapophyses to both sides of the base of

the neural spine and culminate on its anterior margin; mid and posterior cervical vertebrae with 7) neural spines positioned in the anterior half of the centrum; anterior caudal vertebrae with 8) short neural spines and expanded and rounded apices; an ilium with 9) a wide and short preacetabular process; and 10) a broad base of the preacetabular process and a smooth curvature between the anterior margin of the sacral shield and the dorsal margin of the preacetabular process; and a pubis with 11) a dorsoventrally expanded anterior end of the prepubis

Holotype. NHMUK PV OR46013, a partial skeleton including axial and appendicular elements, and osteoderms (Owen, 1875; Galton, 1985).

Type locality, horizon, and age. Unknown horizon. The fossils were discovered in a clay pit at the Old Swindon Hill, Swindon, Wiltshire, England, United Kingdom. Lower part of the Kimmeridge Clay Formation, Upper Jurassic, Kimmeridgian (Galton, 1985; Martill et al., 2006).

Referred material. Three mid cervical vertebrae (MCNV CO-9, MCNV CO-5, and MCNV CO-1), three posterior cervical vertebrae (MCNV CO-17, MCNV CO-24, MCNV CO-2, and MCNV CO-4), two dorsal centra (MCNV CO-7 and MCNV CO-18), two dorsal neural arch fragments (MCNV CO-19 and MCNV CO-21), several partial dorsal ribs (MCNV CO-13, MCNV CO-14, MCNV CO-15, and MCNV CO-25), and an anterior caudal vertebra (MCNV CO-10) (Figures 7–9; Appendix 2).

Other referred material. MHNH A (Nopcsa, 1911a; Galton, 1991), ML 433 (Mateus et al., 2009; Sánchez-Fenollosa and Cobos, 2025), ML 433-A (Mateus et al., 2009), MG 4863 (Costa and Mateus, 2019), the Pedras Muitas specimen (Galton, 1991; Escaso, 2014), the Murteiras specimen (Galton, 1991; Escaso, 2014), the Atalaia specimen (Galton, 1991; Escaso, 2014), SHN.LPP 016 (Escaso et al., 2007b), the RD-10 specimens (Cobos et al., 2010; Sánchez-Fenollosa et al., 2022a), the CT-28 specimen (Sánchez-Fenollosa et al., 2025a), and the RD-34 specimen (Sánchez-Fenollosa and Cobos, 2025).

Locality, horizon, and age. Cerrito del Olmo (CO) site in the municipality of Alpuente, province of Valencia, Valencian Community, Spain. South-Iberian Basin, Villar del Arzobispo Formation, Upper Jurassic, upper Kimmeridgian–Tithonian (Figure 1).

Locality, horizon, and age of other referred material. All specimens are known from the Upper Jurassic (Kimmeridgian–Tithonian) of western Europe (France, Portugal, and Spain) (Sánchez-

Fenollosa and Cobos, 2025; Sánchez-Fenollosa et al., 2025a).

Systematic remarks. The CO specimen is classified as *D. armatus* because it possesses characters 5, 6, and 7 from the diagnosis.

Description. (Appendix 4).

Comparisons and taxonomic assignment. The posterior cervical centra are wider than long similar to those of *D. armatus* (Galton, 1985, 1991; Mateus et al., 2009; Costa and Mateus, 2019). This condition differs from the elongate, longer than wide posterior cervicals of other stegosaurs (Hennig, 1925; Dong et al., 1983; Galton, 1990; Carpenter et al., 2001; Escaso et al., 2007a; Jia et al., 2007; Maidment et al., 2015; Hao et al., 2018).

Cervical ribs are fused to vertebrae, a condition also present in *D. armatus* (Galton, 1991; Mateus et al., 2009; Cobos et al., 2010; Costa and Mateus, 2019; Sánchez-Fenollosa and Cobos, 2025). This contrast with the unfused ribs of the huayangosaurids *Hu. taibaii* (Maidment et al., 2006), *Gi. sichuanensis* (Hao et al., 2018), the stegosaurines *J. junggarensis* (Jia et al., 2007), *L. priscus* (Galton, 1990), *H. mjosi* (Carpenter et al., 2001; Maidment et al., 2018), and *S. stenops* (Escaso et al., 2007a; Maidment et al., 2015), and the dacentrurines *A. longispinus* (Galton and Carpenter, 2016), *K. aethiopicus* (Hennig, 1925; Pereda-Suberbiola et al., 2013), and *Ad. boulahfa* (Maidment et al., 2020). This character has been regarded as an autapomorphy of *D. armatus* (Sánchez-Fenollosa et al., 2025a).

The postzygapophyses are elongated and overhang the posterior centrum facet, resembling those of the huayangosaurid *Gi. sichuanensis* (Hao et al., 2018; Li et al., 2024b), the stegosaurines *J. junggarensis* (Jia et al., 2007) and *L. priscus* (Galton, 1990), and the dacentrurines *K. aethiopicus* (Hennig, 1925; Pereda-Suberbiola et al., 2013), *Ad. boulahfa* (Maidment et al., 2020), and *D. armatus* (Galton, 1991; Mateus et al., 2009; Costa and Mateus, 2019; Sánchez-Fenollosa and Cobos, 2025). They do not, however, overhang in the huayangosaurid *Hu. taibaii* (Maidment et al., 2006), and they also contrast with the greatly elongate postzygapophyses present in the stegosaurines *H. mjosi* (Carpenter et al., 2001; Maidment et al., 2018) and *S. stenops* (Escaso et al., 2007a; Maidment et al., 2015).

MCNV CO-1 and MCNV CO-2 both exhibit two spinopostzygapophyseal laminae extending anterolaterally from the postzygapophyses to the base of the neural spine, terminating at its anterior margin. This mirrors the condition in *D. armatus*

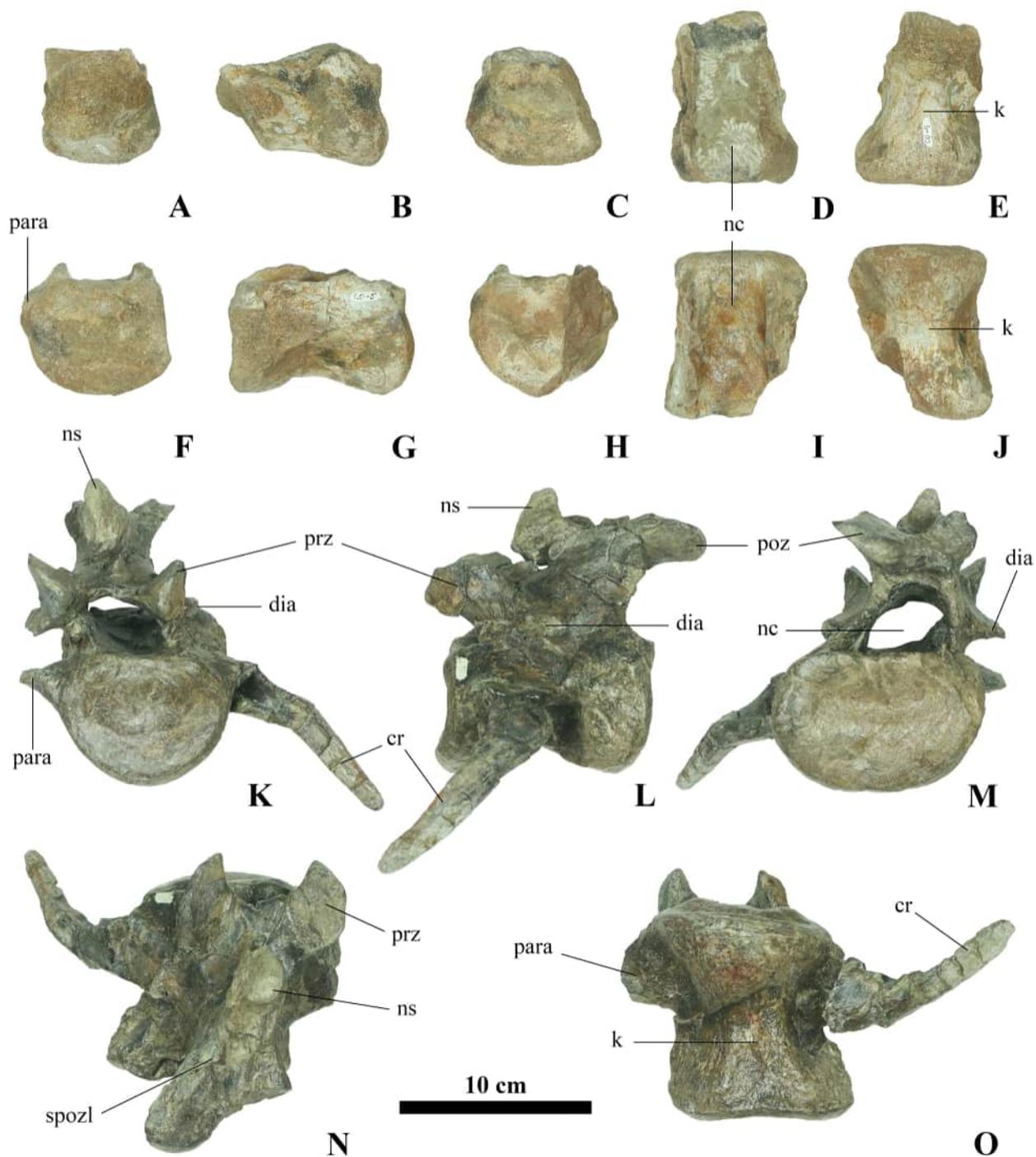


FIGURE 7. Mid cervical vertebrae of *Dacentrurus armatus* (Owen, 1875) from the Cerrito del Olmo site (Alpuente, Valencia). **A–E**, mid cervical centrum (MCNV CO-9) in anterior (A), left lateral (B), posterior (C), dorsal (D), and ventral (E) views. **F–J**, mid cervical centrum (MCNV CO-5) in anterior (F), left lateral (G), posterior (H), dorsal (I), and ventral (J) views. **K–O**, mid cervical vertebra (MCNV CO-1) in anterior (K), left lateral (L), posterior (M), dorsal (N), and ventral (O) views. Note that the cervical rib is not correctly reattached in the current mount (see Casanovas-Cladellas et al., 1995b, plate I). **Abbreviations:** cr, cervical rib; dia, diapophysis; k, keel; nc, neural canal; ns, neural spine; para, parapophysis; poz, postzygapophysis; prz, prezygapophysis; spozl, spinopostzygapophyseal lamina.

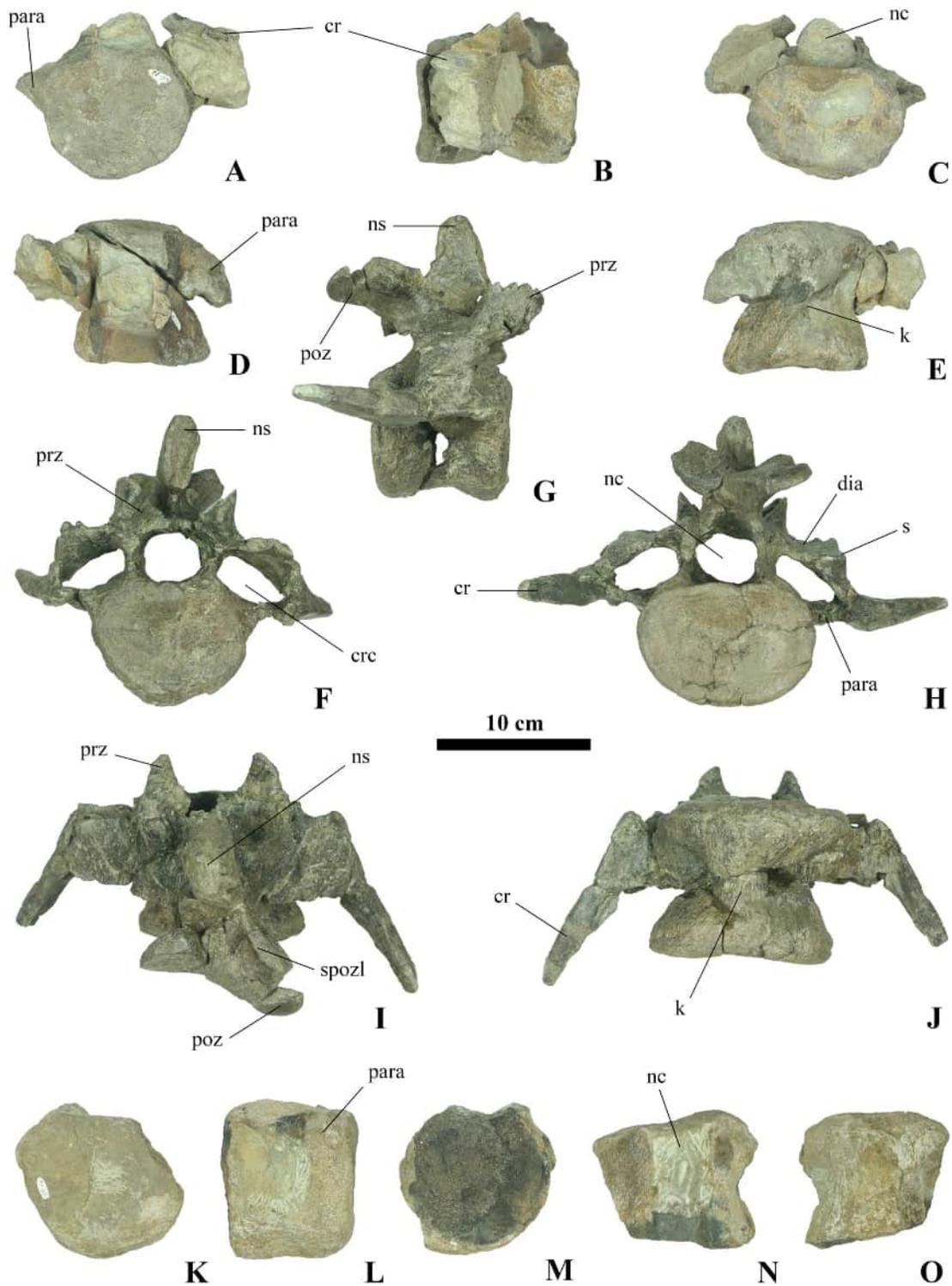


FIGURE 8. Posterior cervical vertebrae of *Dacentrurus armatus* (Owen, 1875) from the Cerrito del Olmo site (Alpuente, Valencia). **A–E**, posterior cervical vertebra (MCNV CO-17 and CO-24) in anterior (A), left lateral (B), posterior (C), dorsal (D), and ventral (E) views. **F–J**, posterior cervical vertebra (MCNV CO-2) in anterior (F), right lateral (G), posterior (H), dorsal (I), and ventral (J) views. **K–O**, posterior cervical centrum (MCNV CO-4) in anterior (K), right lateral (L), posterior (M), dorsal (N), and ventral (O) views. **Abbreviations:** cr, cervical rib; crc, cervical rib canal; dia, diapophysis; k, keel; nc, neural canal; ns, neural spine; para, parapophysis; poz, postzygapophysis; prz, prezygapophysis; s, suture; spozl, spinopostzygapophyseal lamina.

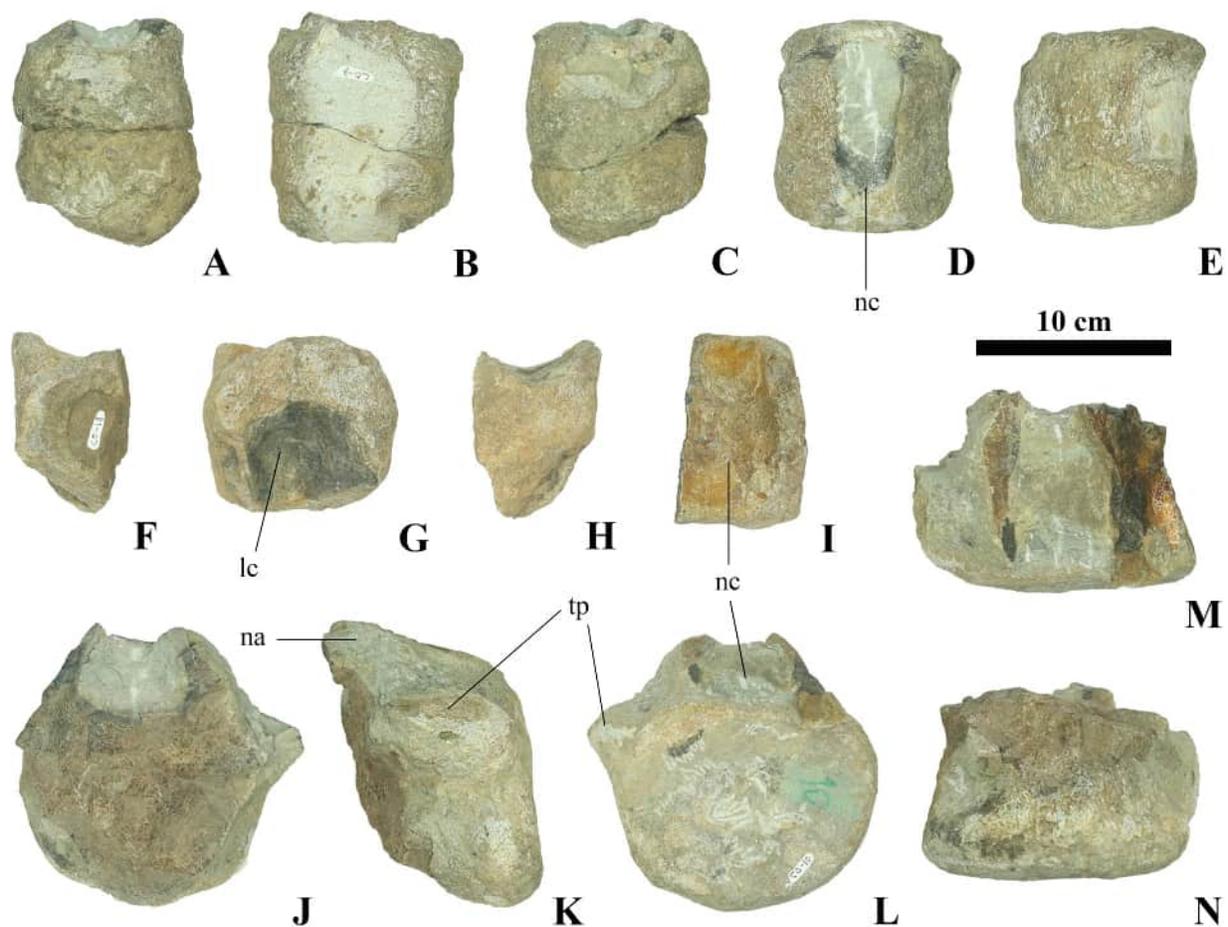


FIGURE 9. Dorsal and caudal centra of *Dacentrurus armatus* (Owen, 1875) from the Cerrito del Olmo site (Alpuente, Valencia). **A–E**, dorsal centrum (MCNV CO-7) in anterior (A), left lateral (B), posterior (C), dorsal (D), and ventral (E) views. **F–I**, dorsal centrum (MCNV CO-18) in anterior (F), right lateral (G), posterior (H), and dorsal (I) views. **J–N**, posterior cervical centrum (MCNV CO-10) in anterior (J), left lateral (K), posterior (L), dorsal (M), and ventral (N) views. **Abbreviations:** na, neural arch; nc, neural canal; lc, lateral concavity; tp, transverse process.

(Mateus et al., 2009; Costa and Mateus, 2019; Sánchez-Fenollosa and Cobos, 2025). In other stegosaurs, these laminae are absent or terminate at the posterior spine margin (Galton, 1990; Maidment et al., 2015, 2018, 2020; Li et al., 2024c). This feature has likewise been considered as an autapomorphy of *D. armatus* (Sánchez-Fenollosa et al., 2025a).

In the mid and posterior cervical vertebrae, the neural spine is positioned in the anterior half of the centrum, again matching with *D. armatus* (Mateus et al., 2009; Costa and Mateus, 2019; Sánchez-Fenollosa and Cobos, 2025). In contrast, in other stegosaurs the neural spine is positioned in the posterior half (Hennig, 1925; Galton, 1990; Carpenter et al., 2001; Maidment et al., 2006, 2015, 2018; Escaso et al., 2007a; Pereda-Suberbiola et al., 2013) or spanning both halves (Maid-

ment et al., 2020; pers. obs. [NHMUK PV R37367 and R37368]). This character has also been regarded as an autapomorphy of *D. armatus* (Sánchez-Fenollosa et al., 2025a).

The mid cervical vertebra MCNV CO-1 bears a slightly expanded neural spine, while the posterior cervical MCNV CO-2 shows a stronger transverse expansion. A similar anteroposterior pattern and degree of expansion occur in the *D. armatus* specimen ML 433 (pers. obs.). Specimen MHNH A also appears to possess strongly expanded neural spines (Galton, 1991). By contrast, the expansion is clearly less pronounced in other specimens of the same species, such as MG 4863 (Costa and Mateus, 2019) and probably RD-34 (Sánchez-Fenollosa and Cobos, 2025 [only one mid cervical vertebra described]). Since the degree of expansion varies along series and across specimens,

this character is best treated, at least for now, as non-diagnostic (contra Costa and Mateus, 2019).

The dorsal centrum MCNV CO-7 exhibits a subtle lateral concavity, while in MCNV CO-18 it is deeply concave. Similar intraindividual variation has been reported for the dorsal series of *D. armatus* (Sánchez-Fenollosa et al., 2025a).

Given the presence of three autapomorphies of *D. armatus*, this specimen is referred to this species. It was previously assigned to *D. armatus* (Casanovas-Cladellas et al., 1995b; Sánchez-Fenollosa et al., 2025a) and *Dacentrurus* sp. (Maidment et al., 2008).

DISCUSSION

Stegosauria from the Eastern Iberian Peninsula: A Taxonomic Reassessment and Updated Overview

The taxonomy of stegosaurs from the eastern Iberian Peninsula, as elsewhere in western Europe, has been complex and subject to repeated revisions (Galton, 1991; Maidment et al., 2008; Mateus et al., 2009; Cobos et al., 2010; Cobos and Gascó, 2013; Costa and Mateus, 2019). A recent systematic study re-evaluated the European stegosaurian record, incorporating all relatively complete specimens then available and providing a consistent, coherent, and parsimonious taxonomic framework (Sánchez-Fenollosa et al., 2025a). That work proposed a set of autapomorphies for *D. armatus* based on its hypodigm (holotype and referred material) and used them to assign several eastern Iberian specimens to this species (CO, RD-10, and CT-28; Figures 7–10G–I). Later, Sánchez-Fenollosa and Cobos (2025) assigned an additional specimen to *D. armatus* (RD-34; Figure 10A). This individual includes the most complete stegosaurian skull yet reported from Europe and permitted the recognition of a new cranial autapomorphy for the species (Sánchez-Fenollosa and Cobos, 2025). As a result of these developments, several fragmentary specimens from the eastern Iberian Peninsula (CO II [Figure 2L–P], Lo I [Figure 3], RD-3 [Figure 10B, C], RD-16, RD-44, and RD-46 [Figure 10D–F]) that had previously been referred to *D. armatus* (sensu Casanovas-Cladellas et al., 1999; Cobos and Gascó, 2013) were excluded from the revised hypodigm and left without a clear taxonomic assignment.

RD-3 and RD-46 specimens exhibit dorsal centra that are wider than long. This synapomorphic condition is exclusive to certain dacentrurines, such as *Ad. boulahfa* (Maidment et al., 2020), *Th.*

atlasicus (Zafaty et al., 2024), and *D. armatus* (Galton, 1985; Escaso et al., 2007b; Mateus et al., 2009; Costa and Mateus, 2019; Sánchez Fenollosa et al., 2025a). Accordingly, both specimens are here reclassified as Dacentrurinae indet. (Appendix 3). By contrast, RD-16 and RD-44 specimens are represented by highly incomplete and fragmentary material, precluding any assignment more specific than Stegosauria indet. (Appendix 3).

In 2022, three specimens (Cañada París, MPA-653, and MPA-1086) were tentatively referred to as cf. *Dacentrurus* sp. on the basis of features suggesting greater affinity with *D. armatus* than with another European Late Jurassic stegosaur (Sánchez-Fenollosa et al., 2022a). However, those same features also occur in *K. aethiopicus* from the Upper Jurassic of Africa (Hennig, 1925; pers. obs. [NHMUK PV R37155 and R37154]). At the time, *K. aethiopicus* was not considered a member of Dacentrurinae, but a recent phylogenetic study placed it within this clade (Sánchez-Fenollosa and Cobos, 2025). Consequently, this material can now be justifiably referred to as Dacentrurinae indet. (Appendix 3). Following the same rationale, several new specimens examined here (Figures 5, 6) have also been referred to as Dacentrurinae indet. (see ‘Systematic Palaeontology’ section).

Two specimens (El Balsón and Barranco del Curro) previously attributed to Dacentrurinae indet. (Company et al., 2010) retain here that taxonomic rank (Appendix 3). The El Balsón specimen includes a dorsal vertebra with a centrum wider than long, a synapomorphy of certain dacentrurines (Maidment et al., 2020; Zafaty et al., 2024; Sánchez-Fenollosa and Cobos, 2025; Sánchez Fenollosa et al., 2025a). Additional material from the same specimen, not listed by Company et al. (2010), has since been recovered and may allow a more precise assignment in future studies.

The Barranco del Curro specimen (Figure 10J) exhibits stocky and elongated terminal caudal spines with a large convex base and a rhomboidal cross-section along the shaft, closely resembling the left terminal caudal spine MPA D-0267 from the By Pass specimen (Figure 4P–R). Moreover, the Barranco del Curro specimen strongly resembles the Portuguese specimen SHN.LPP 123 (Escaso, 2014) morphologically, as both preserve the last two caudal spine pairs (see for more details the ‘Comparisons and taxonomic assignment’ section of the By Pass specimen). In both cases, the penultimate pair is also stocky and has a large base that, unlike the terminal pair, is concave. This morphology closely matches that of MG 4863-39, sug-

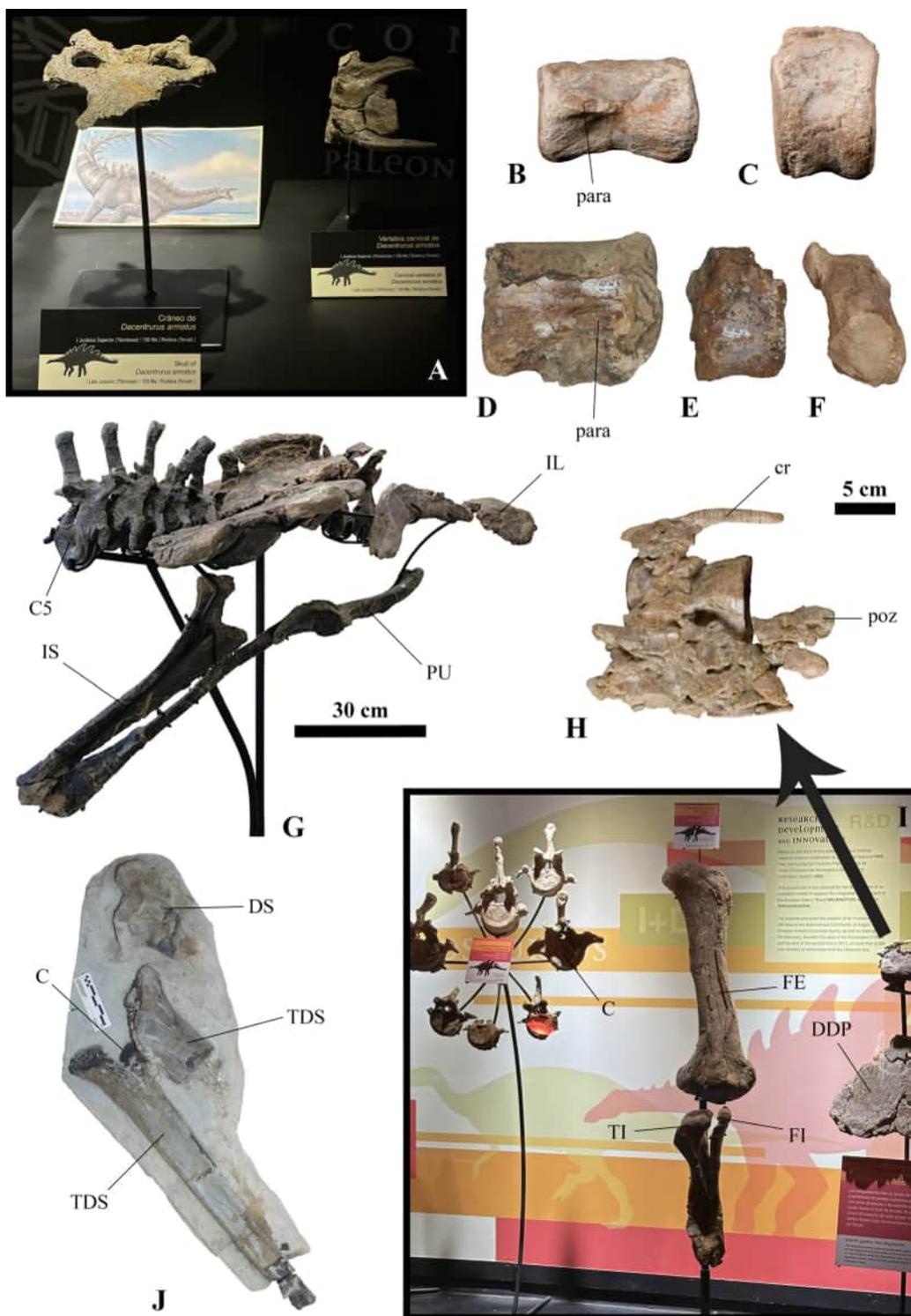


FIGURE 10. Some dacentrurine specimens from eastern Iberia (Spain). **A**, skull and cervical vertebra of *Dacentrurus armatus* (Owen, 1875) (RD-34). **B**, **C**, cervical (B) and dorsal centra (C) in lateral view (RD-3). **D–F**, cervical (D), dorsal (E), and caudal centra (F) in lateral view (RD-46). **G**, mounted sacropelvic region of *D. armatus* (CT-28). **H**, **I**, some axial, appendicular and dermal elements of *D. armatus* (RD-10). **J**, right penultimate dermal spine and pair of terminal dermal spines articulated with the last two caudal vertebrae (Barranco del Curro). **Abbreviations:** C, caudal vertebra; cr, cervical rib; DDP, dorsal dermal plate; DS, dermal spine; FE, femur; FI, fibula; IL, ilium; IS, ischium; para, parapophysis; poz, postzygapophysis; PU, pubis; TDS, terminal dermal spine; TI, tibia.

gesting that this spine most likely corresponds to a distal caudal position, probably from the antepenultimate pair, rather than from the anterior region of the tail as interpreted by Costa and Mateus (2019). Dacentrurines such as *K. aethiopicus* (Galton, 1982a; Mallison, 2011) also have an elongated terminal dermal spine pair, a feature considered as a synapomorphy of the clade (Sánchez-Fenollosa and Cobos, 2025). In *A. longispinus*, the presence of an elongated terminal pair has been proposed (Galton and Carpenter, 2016), although no articulated specimens confirm this condition.

Considering the current Upper Jurassic European dacentrurine record, the hypothesized osteoderm distribution in *D. armatus* depicted in Figure 11 represents the most plausible reconstruction. This arrangement includes paired plates in the cervical and dorsal region that progressively increase in size (based on ML 433, NHMUK PV OR46013, and CPT-1288), with the possible presence of transitional spine-like plates. No evidence of gular ossicles and parascapular spines has been found in any dacentrurine from the European Upper Jurassic. The caudal region is inferred to bear spines that progressively increase in size posteriorly and shift laterally from an initially more dorsal position. Two clearly differentiated morphotypes can be recognized: 1) a slender morphotype with a small base and a circular cross-section shaft (e.g., NHMUK PV OR46013 and MPA D-0316), interpreted as occupying a more anterior position; and 2) a stocky morphotype with a large base and a rhomboidal (or lenticular) cross-section shaft (e.g., NHMUK PV OR46320, MG 4863-39, SHN.LPP 123, MPA D-0267, and MPA D-0313/315). The terminal pair is fused to each other at the tip of the tail (based on SHN.LPP 123 and MPA D-0313/315) and likely reached 1–1.5 m in length. More complete and articulated specimens are necessary to assess and corroborate this hypothesis.

The specimens from CT-61 (a left humerus, Sánchez-Fenollosa et al., 2022a), La Canaleta (a dermal spine, Pereda-Suberbiola et al., 2005), and Puntal de la Magdalena (a dermal spine, Sánchez-Fenollosa et al., 2022a) remain as *Stegosauria* indet. due to their isolated and fragmentary condition (Appendix 3). No systematically informative characters are preserved to justify a more precise assignment.

In summary, the osteological stegosaurian record from eastern Iberia comprises indeterminate stegosaurs, stegosaurids, neostegosaurs, dacentrurines, and the species *D. armatus* (see Appendix 3 for details).

The ichnological stegosaurian record includes numerous tracks and natural casts from several sites (Cobos et al., 2010, 2012; Mampel et al., 2011; Alcalá et al., 2012; Herrero and Pérez-Lorente, 2013, 2017; Campos-Soto et al., 2017; Castanera et al., 2024). Most of these have been assigned to the ichnospecies *Deltapodus ibericus* Cobos et al., 2010 (Castanera et al., 2024). Notably, this record contains the holotype of *De. ibericus* and includes two tracksites representing the only known evidence of gregarious behaviour in stegosaurs worldwide (Castanera et al., 2024).

The abundance of stegosaur-bearing sites, both osteological (Appendix 3) and ichnological (Castanera et al., 2024), together with the good preservation and relative completeness of several specimens, makes the eastern Iberian Peninsula one of the most important regions globally for stegosaurian research and the richest from the European Upper Jurassic. Its relevance is expected to grow as further systematic and palaeobiological studies are undertaken on both new and previously described material.

Notes on the Diversity and Ecology of Late Jurassic Stegosaurs in the Coastal Ecosystems of Eastern Iberia

The Villar del Arzobispo Formation is a transitional lithostratigraphic unit that outcrops in the South-Iberian and Maestrazgo Basins (eastern Iberia) (e.g., Campos-Soto et al., 2019, 2021). Deposited within a coastal fluvial system discharging into a shallow marine platform, it preserves a spectrum of palaeoenvironments. These include very shallow marine platforms, tidal flats, beaches, distributary channels, estuaries, wetlands, floodplains, and fluvial channels (e.g., Santisteban and Santos-Cubedo, 2010; Campos-Soto et al., 2017, 2019, 2021).

The stegosaurian record from eastern Iberia is restricted to dacentrurines, with no evidence supporting the presence of stegosaurines (Appendix 3). At present, all relatively complete dacentrurine specimens described from this region show a high degree of morphological homogeneity, with no robust evidence for more than one species. Four of these specimens can be referred to as *D. armatus* (Sánchez-Fenollosa and Cobos, 2025; Sánchez-Fenollosa et al., 2025a; this paper), which currently represents the only stegosaur reliably identified in the Villar del Arzobispo Formation (Appendix 3).

Interestingly, the osteological stegosaurian record of the Villar del Arzobispo Formation closely resembles that of other Upper Jurassic European



FIGURE 11. Life reconstruction of *Dacentrurus armatus*. Note proposed osteoderm distribution. Illustration by A. Blázquez. Courtesy of FCPT-D.

lithostratigraphic units, including the Kimmeridge Clay Formation (Kimmeridgian sensu Martill et al., 2006), the Argiles d' Octeville Formation (Kimmeridgian sensu Gallois, 2005), and the Lourinhã Formation (Kimmeridgian–Tithonian sensu Mateus et al., 2017). Each of these is similarly dominated by indeterminate dacentrurine remains and/or *D. armatus* (Galton, 1985, 1991; Mateus et al., 2009; Escaso, 2014; Costa and Mateus, 2019).

During this epoch, western Europe comprised several major islands separated by shallow continental seas, which at intervals allowed faunal exchange and dispersal events. Overall, the low morphological disparity observed among Kimmeridgian–Tithonian dacentrurine material from western Europe (see Sánchez-Fenollosa et al., 2025a and references therein) suggests that allopatric speciation was limited in at least some taxa. In fact, the occurrence of palaeosols and recurrent mega-tracksites during the Oxfordian–Berriasian on the Jura carbonate platform supports the existence of a faunal corridor that was intermittently open during sea-level lowstands, connecting several of

these major landmasses (Meyer et al., 2006; Waite et al., 2013; Marty et al., 2018).

A partial skeleton from the Upper Jurassic of Portugal (western Iberia), described by Escaso et al. (2007a) and referred to as *S. cf. unguulatus* Marsh, 1879 (*S. stenops* sensu Maidment et al., 2015), provides the only unequivocal evidence of stegosaurines in the European Upper Jurassic. This discovery is one of the strongest indications of faunal similarity between North America and Europe during the late Kimmeridgian–early Tithonian, supporting episodic dispersal events and faunal exchange across the proto-North Atlantic Ocean (e.g., Pérez-Moreno et al., 1999; Escaso et al., 2007a; Brikiatis, 2016), along with limited vicariant isolation and slightly morphological divergence in some taxa. The presence of stegosaurines in the European Middle Jurassic (Galton, 1985, 1990) shows that members of this clade were already established in the region prior to these Late Jurassic connections.

The abundant record of dacentrurines in the Villar del Arzobispo Formation (Appendix 3) indicates that this lineage was firmly established in the

Late Jurassic coastal ecosystems of eastern Iberia. In contrast, stegosaurines may have preferred more continental biotopes. This inference is consistent with their greater abundance (e.g., Siber and Möckli, 2009; Maidment et al., 2015) in the continental interior palaeoenvironments (Turner and Peterson, 2004; Myers et al., 2014) of the Morrison Formation. Consequently, their apparent absence in eastern Iberia likely reflects both ecological preferences and fossilisation bias.

Several stegosaurian trackways and tracks have been documented in the Villar del Arzobispo Formation (Castanera et al., 2024 and references therein). Given the abundance of *D. armatus* osteological remains in the region, this species is the most plausible trackmaker, particularly since no evidence of stegosaurines is present. At some tracksites (CT-1 and AG-3), parallel trackways and accumulations with preferred orientation have been interpreted as evidence of gregarious behaviour (Castanera et al., 2024). This suggests that dacentrurines in eastern Iberia may have moved in groups, at least in certain seasons, life stages, or in sex-based cohorts.

The Late Jurassic sedimentary and palynological record of eastern Iberia presents features typical of both arid or semiarid and humid settings (Santisteban and Holgado, 2011; Campos-Soto et al., 2021; Santos et al., 2023). The palaeoclimate has been reconstructed as warm and strongly seasonal, with monsoonal-type precipitation (Campos-Soto et al., 2021). During dry seasons, reduced resources likely forced some dinosaurian species to move to more favourable areas. Considering ichnological evidence, it is plausible that stegosaurs migrated in aggregations. A comparable palaeoclimate has also been proposed for western Iberia, concretely in the Portuguese Lourinhã Formation (Myers et al., 2012). Seasonal aggregated migratory patterns are widely reported in extant large terrestrial mammals (e.g., Harris et al., 2009).

Based on current evidence, together with the stegosaur *D. armatus*, a wide range of vertebrate groups inhabited the coastal ecosystems of eastern Iberia during the Late Jurassic. Sauropods included turiasaurs (Casanovas-Cladellas et al., 2001; Royo-Torres et al., 2006, 2021), macronarians (Pérez-Pueyo et al., 2019), diplodocids (Royo-Torres et al., 2009), and brachiosaurids (Suñer et al., 2022). Systematic study of several theropod teeth has confirmed the presence of three groups: allosaurids, megalosaurids, and dromaeosaurids (Gascó et al., 2012; Cobos et al., 2014). More recently, evidence has been presented for dryo-

saurids and both small- and large-sized ankylopollexians (Sánchez-Fenollosa et al., 2022b, 2023, 2025b). Crocodylomorphs were at least represented by machimosaurine thalattosuchians (Royo-Gómez, 1926; Gamonal et al., 2018) and bernissartiid neosuchians (Sánchez-Fenollosa et al., 2021). In addition, pterodactyloids (Holgado et al., 2025), pleurosternid testudinatanans (Pérez-García et al., 2015), and albanerpetontid lissamphibians (Marquina-Blasco et al., 2020) were also present. Finally, spores, pollen, and macrofloral remains demonstrate that plant communities were dominated by mosses, ferns, bennettitaleans, cycads, and conifers (López-Fernández et al., 2021; Santos et al., 2023).

CONCLUSIONS

Several new stegosaurian specimens from the Villar del Arzobispo Formation have been systematically studied here. They came from nine fossil sites in provinces of Teruel and Valencia (Spain) and are referred to as *Stegosauria* indet. (CPT-1075 [RD-5]; MAP-8435 [MR-9]), *Neostegosauria* indet. (CPT-1986 [Jab.1]), or *Dacentrurinae* indet. (MPA D-0287, MPA D-0279, MPA D-0276, and MPA D-0267 [By Pass]; CPT-1705 [RD-17]; CPT-1977; CPT-763 [CT-10]; MPA-1218, MPA-1221, MPA-1222, and MPA-1223 [Los Arenales]; MAP-8436 [MC-2]; MAP-8426, MAP-8425, and CPT-1950 [RD-29]).

The first-recorded stegosaurian material from Spain (Los Serranos region, Valencia) has been revisited and systematically studied. This research shows that the material is now distributed across two public museums and a private collection. It is here classified as *Stegosauria* indet. (MCNV Lo-1 [Losilla]), *Stegosauridae* indet. (CO II-1 [Cerrito del Olmo II]), *Dacentrurinae* indet. (MCNV Lo I-6, IPS-37432, IPS-37431, IPS-37433, and IPS-37435 [Losilla I]), and *D. armatus* (MCNV CO-9, MCNV CO-5, MCNV CO-1, MCNV CO-17, MCNV CO-24, MCNV CO-2, MCNV CO-4, MCNV CO-7, MCNV CO-18, MCNV CO-19, MCNV CO-21, MCNV CO-13, MCNV CO-14, MCNV CO-15, MCNV CO-25, and MCNV CO-10 [Cerrito del Olmo]). Several elements have been reidentified anatomically, and a previously unreported posterior caudal vertebra (MCNV-VCP) has been documented in the Museo de Ciencias Naturales de Valencia, most likely recovered from either Losilla I or Cerrito del Olmo.

In addition, a review of all known stegosaurian fossils from the eastern Iberian Peninsula has led to the taxonomic reassignment of several specimens: Cañada París, RD-3, RD-16, RD-44, RD-46,

MPA-653, and MPA-1086. A comprehensive approach that integrates the full Upper Jurassic stegosaurian record is essential for establishing robust and consistent species delimitations.

The Upper Jurassic stegosaurian record of the eastern Iberian Peninsula is currently represented exclusively by dacentrurines, which exhibit high morphological homogeneity. Among these, four specimens (Cerrito del Olmo, CT-28, RD-10, and RD-34), can be attributed to *D. armatus*, with no solid evidence for additional dacentrurine species or the presence of stegosaurines.

The abundance of *D. armatus* alongside numerous indeterminate dacentrurine specimens suggests that this lineage was firmly established in the Late Jurassic coastal ecosystems of eastern Iberia. In contrast, stegosaurines may have inhabited more inland or continental biotopes, and their absence in this regional record likely reflects ecological preferences combined with fossilisation bias.

Overall, the exceptional richness and preservation of both osteological and ichnological material make the eastern Iberian Peninsula one of the most important regions worldwide for the study of stegosaurs. Ongoing work and future research will provide new and valuable data on their morphological disparity, systematics, and palaeobiology.

ACKNOWLEDGMENTS

This research was funded by the Gobierno de Aragón through the research group E04_23R FOCONTUR, the Ministerio de Ciencia, Innovación y Universidades (MICIU, Gobierno de España) through the Unidad de Paleontología de Teruel, and the Instituto Aragonés de Fomento. It was also supported by the project PID2024-162804NB-I00

funded by the MICIU /AEI /10.13039/501100011033 / FEDER, UE

We thank to the colleagues from the Fundación Conjunto Paleontológico de Teruel-Dinópolis (Teruel, Spain) for its support. We acknowledge T. Palacios for the discovery of the sacrum from Jabaloyas, D. Vidal for the dermal spine fragment from Mora de Rubielos, and E. Guillén for the caudal centrum from Monteagudo del Castillo. We are grateful to C. Santisteban for the background information provided about the historical material. We acknowledge A. Galobart and J.M. Robles for providing access to the collection of the Institut Català de Paleontologia Miquel Crusafont (Sabadell, Spain) and B. Poza for providing access to the collection of the Museo de Ciencias Naturales de Valencia (Valencia, Spain). We thank to J.P. Albir for allowing us access to his collection. We are grateful to A. Blázquez for the illustration of *D. armatus* used in this work. We appreciate the constructive comments and suggestions provided by the handling editor A. Demers-Potvin, two anonymous reviewers, and J.I. Kirkland, which contributed to improving this manuscript.

AUTHOR CONTRIBUTIONS

Conceptualization: S.S.-F., A.C., and M.S.; Resources: S.S.-F., A.C., and M.S.; Investigation: S.S.-F., A.C., and M.S.; Data Curation: S.S.-F.; Methodology: S.S.-F., A.C., and M.S.; Formal Analysis: S.S.-F.; Validation: S.S.-F., A.C., and M.S.; Writing – Original Draft: S.S.-F.; Writing – Review & Editing: S.S.-F., A.C., and M.S.; Visualization: S.S.-F.; Supervision: S.S.-F., A.C., and M.S.; Project Administration: A.C. and M.S.; Funding Acquisition: A.C. and M.S.

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APPENDICES

APPENDIX 1.

Measurements of the stegosaurian fossils described in this study.

TABLE A1. Measurements (in mm) of the stegosaurian fossils described in this study. **Abbreviations:** AAFH, anterior articular facet height; AAFW, anterior articular facet width; CL, centrum length; DW, distal width; L, length; MW, mid width; NAH, neural arch height; PAFH, posterior articular facet height; PAFW, posterior articular facet width; PW, proximal width; W, width.

RD-5 (RIODEVA, TERUEL) – STEGOSAURIA INDET.						
	CL	AAFH	AAFW	PAFH	PAFW	NAH
Anterior caudal vertebra (CPT-1075)	47.4	71.5	69.2	80.6	92.2	-
MR-9 (MORA DE RUBIELOS, TERUEL) – STEGOSAURIA INDET.						
	L					
Dermal spine fragment (MAP-8435)	186					
LOSILLA (ARAS DE LOS OLMOS, VALENCIA) – STEGOSAURIA INDET.						
Right caudal dermal spine (MCNV Lo-1)	403					
CERRITO DEL OLMO II (ALPUENTE, VALENCIA) – STEGOSAURIDAE INDET.						
	L	PW	DW	MW		
Right femur (CO II-1)	910	250	225	125		
JAB.1 (JABALOYAS, TERUEL) – NEOSTEGOSAURIA INDET.						
	L	W	AAFH	AAFW		
Sacrum (CPT-1986)	250	215	51.1	80.2		
LOSILLA I (ARAS DE LOS OLMOS, VALENCIA) – DACENTRURINAE INDET.						
	CL	AAFH	AAFW	PAFH	PAFW	NAH
Cervical centrum (MCNV Lo I-6)	47.9	42.9	56.6	47.2	64.1	-
Posterior cervical vertebra (IPS-37432 or Lo I-2)	55.1	81.8	64.6	73.7	59.8	-
Posterior cervical vertebra (IPS-37431 or Lo I-1)	60.7	78.7	102.7	64.8	89	-
Anterior dorsal vertebra (IPS-37433 or Lo I-3)	44.1	88.6	88.4	75.1	83	-
Dorsal centrum (IPS-37435 or Lo I-7)	61.7	60.9	68.4	69.5	80.4	-
BY PASS (ALPUENTE, VALENCIA) – DACENTRURINAE INDET.						
Anterior dorsal vertebra (MPA D-0287)	57.7	96.4	88.5	87	92.5	-
Posterior dorsal vertebra (MPA D-0279)	86.1	109.3	111.5	101.4	109.9	262
Mid caudal vertebra (MPA D-0276)	73.3	92.4	97.7	91	102.5	157
	L					
Left terminal dermal spine (MPA D-0267)	339					
RD-17 (RIODEVA, TERUEL) – DACENTRURINAE INDET.						
	CL	AAFH	AAFW	PAFH	PAFW	NAH
Cervical centrum (CPT-1705)	56.1	55	73	56.8	80.5	-

UNKNOWN SITE (RIODEVA, TERUEL) – DACENTRURINAE INDET.						
Mid caudal centrum (CPT-1977)	69.3	79.3	97.4	77.8	98.2	-
UNKNOWN SITE (LOSILLA I or CERRITO DEL OLMO) – DACENTRURINAE INDET.						
Posterior caudal vertebra (MCNV-VCP)	54.5	60.9	95.8	58.1	94.6	99.8
CT-10 (EL CASTELLAR, TERUEL) – DACENTRURINAE INDET.						
Posterior caudal centrum (CPT-763)	52.5	58.5	84.6	58.8	84	-
LOS ARENALES (ALPUENTE, VALENCIA) – DACENTRURINAE INDET.						
Posterior caudal centrum (MPA-1218)	51	53.3	82.8	54.6	82.8	-
MC-2 (MONTEAGUDO DEL CASTILLO, TERUEL) – DACENTRURINAE INDET.						
Posterior caudal centrum (MAP-8436)	48.3	51.9	71.5	45.9	73.9	-
RD-29 (RIODEVA, TERUEL) – DACENTRURINAE INDET.						
Posterior caudal centrum (MAP-8426)	-	-	-	-	-	-
Posterior caudal vertebra (MAP-8425)	56.5	65.3	95.1	63.3	89.8	-
Posterior caudal centrum (CPT-1950)	41.3	44.9	72.6	40.8	67.3	-
CERRITO DEL OLMO (ALPUENTE, VALENCIA) – DACENTRURUS ARMATUS						
Mid cervical centrum (MCNV CO-9)	85.1	-	-	51	52.8	-
Mid cervical centrum (MCNV CO-5)	91.6	56.6	68.4	58.3	-	-
Mid cervical vertebra (MCNV CO-1)	101.6	63.2	82.1	65.1	92.2	151.2
Posterior cervical vertebra (MCNV CO-17 and CO-24)	91.5	79.1	91.4	71.2	99.2	-
Posterior cervical vertebra (MCNV CO-2)	91.1	83.8	98.6	78.6	111.1	210.0
Posterior cervical centrum (MCNV CO-4)	82.1	88.5	96.6	83.8	85.2	-
Dorsal centrum (MCNV CO-7)	69.8	77.8	67.4	79.1	68.3	-
Dorsal centrum (MCNV CO-18)	75.2	-	-	59	43	-
Anterior caudal vertebra (MCNV CO-10)	71.5	65.4	92.9	83.4	105.9	-

APPENDIX 2.

Remarks on the first stegosaurian material from Spain and a revised fossil list.

The first-recorded stegosaurian specimens from the Los Serranos region (Valencia, Spain) are of considerable importance to Spanish dinosaurian palaeontology. This is because they represent the earliest fossils attributed to this group found in Spain. These remains were discovered during prospecting and excavation campaigns in the early 1990s. After recovery, all material was transported to the ICP, where it was housed, prepared, and studied. Later, at the request of the Generalitat Valenciana (Government of the Valencian Community), part of the collection was returned to Valencia and deposited at the MCNV, together with other dinosaurian remains, including the holotype of *Losillasaurus giganteus* Casanovas-Cladellas et al., 2001 (Casanovas-Cladellas et al., 2001).

Although these fossils constitute the first Spanish stegosaurs, the label 'historical material' is applied informally, since additional stegosaurian remains from the region were reported only a few years later in a conference communication (see Royo-Torres et al., 2003).

Casanovas-Cladellas et al. (1999) published the last comprehensive list of stegosaurian fossils recovered from the region in the 1990s. Based on that list, we began our search and examination of the 'historical' specimens. The material has been identified between two public institutions (ICP and MCNV) and a private collection. Several fossils listed in the original publication, however, could not be located (Lo I-4, Lo I-5, Lo I-8, CO-3, CO-11, CO-12, and CO-16). Except for Lo I-4, these elements were at least partially described and figured by Casanovas-Cladellas et al. (1995b, 1995c).

Three centra from the Cerrito del Olmo site (MCNV CO-6, MCNV CO-8, and MCNV CO-26) were reassigned to an ornithopod dinosaur by Pereda-Suberbiola et al. (2009). During our study, numerous fossils have been reidentified anatomically. The fragmentary state of certain elements (MCNV CO-20, MCNV CO-22, MCNV CO-23, and MCNV CO-27) has hindered their anatomical identification and prevented any reliable taxonomic assignment. We also report an almost complete posterior caudal vertebra (Figure 5K–O) with no provenance data (see also 'Materials and Methods' section).

In this study, we have referred fossils to a specimen only when their location, anatomical identification, and taxonomic assignment are unambiguous. Accordingly, the stegosaurian material from the Losilla I and Cerrito del Olmo sites differs from that reported by Casanovas-Cladellas et al. (1999).

Casanovas-Cladellas et al. (1999) were unclear about whether the dermal spine from Losilla (Lo) and the vertebrae from Losilla I (Lo I) came from the same site, and also whether the femur from Cerrito del Olmo II (CO II) and the fossils from Cerrito del Olmo (CO) belonged to the same site. This uncertainty prompted Galton (2016) to state: 'However, Casanovas-Cladellas et al. 1995b: 270 list Lo 1-1 to Lo 1-8 as additional bones (mostly vertebrae) that were subsequently excavated from the same Losilla site, and presumably from the same level (X. Pereda-Suberbiola pers. comm. 2016), so this dermal spine is probably not an isolated find'. Nevertheless, two of us (SS-F. and MS), together with the original discoverers, have verified that these are in fact distinct fossil sites. Therefore, the Spanish stegosaurian 'historical material' came from four different sites.

TABLE A2. Updated and revised list of the ‘historical material’ recovered from the Losilla (Lo), Losilla I (Lo I), Cerrito del Olmo (CO), and Cerrito del Olmo II (CO II) sites (Los Serranos region, Valencia, Spain). Blue: non-stegosaurian or indeterminate fossils. Red: currently unlocated fossils.

CASANOVAS-CLADELLAS ET AL. (1999)		THIS PAPER	
Lo-1	Right caudal spine	MCNV Lo-1	Right caudal dermal spine
Lo I-1	Posterior cervical vertebra fragment	IPS-37431	Posterior cervical vertebra
Lo I-2	Dorsal vertebra fragment	IPS-37432	Posterior cervical vertebra
Lo I-3	Almost completed dorsal vertebra	IPS-37433	Anterior dorsal vertebra
Lo I-4	Caudal centrum fragment	-	-
Lo I-5	Caudal centrum fragment	-	-
Lo I-6	Caudal centrum fragment	MCNV Lo I-6	Cervical centrum
Lo I-7	Dorsal centrum	IPS-37435	Dorsal centrum
Lo I-8	Dorsal centrum	-	-
CO-1	Cervical vertebra	MCNV CO-1	Mid cervical vertebra
CO-2	Cervical vertebra	MCNV CO-2	Posterior cervical vertebra
CO-3	Cervical centrum	-	-
CO-4	Dorsal centrum	MCNV CO-4	Posterior cervical centrum
CO-5	Cervical centrum	MCNV CO-5	Mid cervical centrum
CO-6	Caudal centrum	MCNV CO-6	Ornithopoda indet.
CO-7	Dorsal centrum	MCNV CO-7	Dorsal centrum
CO-8	Caudal centrum	MCNV CO-8	Ornithopoda indet.
CO-9	Cervical centrum fragment	MCNV CO-9	Mid cervical centrum
CO-10	Caudal centrum fragment	MCNV CO-10	Anterior caudal vertebra
CO-11	Anterior dorsal rib	-	-
CO-12	More posterior dorsal rib	-	-
CO-13	Dorsal rib proximal fragment	MCNV CO-13	Dorsal rib proximal fragment
CO-14	Dorsal rib distal fragment	MCNV CO-14	Dorsal rib proximal fragment
CO-15	Dorsal rib distal fragment	MCNV CO-15	Dorsal rib distal fragment
CO-16	Right ischium fragment	-	-
CO-17	Centrum fragment	MCNV CO-17	Posterior cervical vertebra (and CO-24)
CO-18	Centrum fragment	MCNV CO-18	Dorsal centrum
CO-19	Indet.	MCNV CO-19	Dorsal neural arch fragment
CO-20	Indet.	MCNV CO-20	Indet.
CO-21	Indet.	MCNV CO-21	Dorsal neural arch fragment
CO-22	Indet.	MCNV CO-22	Indet.
CO-23	Caudal centrum fragment	MCNV CO-23	Vertebral centrum
CO-24	Cervical caudal fragment	MCNV CO-24	Posterior cervical vertebra (and CO-17)
CO-25	Three rib fragments	MCNV CO-25	Dorsal rib
CO-26	-	MCNV CO-26	Ornithopoda indet.
CO-27	-	MCNV CO-27	Indet.
-	-	MCNV-VCP	Posterior caudal vertebra
CO II-1	Right femur	CO II-1	Right femur

APPENDIX 3.

Osteological stegosaurian record from eastern Iberia.

TABLE A3. Osteological stegosaurian record from eastern Iberia (South-Iberian and Maestrazgo basins, Villar del Arzobispo Formation [sensu Campos-Soto et al., 2019], Spain).

SITE	PREVIOUS SYSTEMATICS	CURRENT SYSTEMATICS	MATERIAL	MUNICIPALITY	REFERENCES
Barranco del Curro	Dacentrurinae indet.	Dacentrurinae indet.	Two caudal centra, a partial left scapula, a left femur, and four caudal dermal spines	Alpuente (Valencia)	Company et al., (2010); this paper
By Pass	Stegosauridae indet.	Dacentrurinae indet.	Two dorsal vertebrae, a mid caudal vertebra with its chevron, a terminal dermal spine, and undescribed fossils	Alpuente (Valencia)	Suñer and Martín, (2009); this paper
Cañada París	cf. <i>Dacentrurus</i> sp.	Dacentrurinae indet.	Two caudal neural arches, and five caudal centra	Alpuente (Valencia)	Sánchez-Fenollosa et al., (2022a); this paper
Cerrito del Olmo (CO)	<i>Dacentrurus armatus</i>	<i>Dacentrurus armatus</i>	Six cervical vertebrae, two dorsal centra, two dorsal neural arch fragments, several dorsal ribs, and an anterior caudal vertebra (and a posterior caudal vertebra?)	Alpuente (Valencia)	Casanovas-Cladellas et al., (1995b); Sánchez-Fenollosa et al., (2025a); this paper
Cerrito del Olmo II (CO II)	<i>Dacentrurus armatus</i>	Stegosauridae indet.	A right femur	Alpuente (Valencia)	Casanovas-Cladellas et al., (1999); this paper
CT-10 (Berzal Norte 2)	-	Dacentrurinae indet.	A posterior caudal centrum	El Castellar (Teruel)	This paper
CT-28 (San Cristóbal)	<i>Dacentrurus armatus</i>	<i>Dacentrurus armatus</i>	Twelve dorsal vertebrae, several dorsal ribs, five sacral vertebrae, five anterior caudal vertebrae, a posterior caudal vertebra, two partial ilia, a right ischium, a right pubis, and a partial hindlimb (femur and tibia)	El Castellar (Teruel)	Sánchez-Fenollosa et al., (2025a)
CT-61	Stegosauria indet.	Stegosauria indet.	A left humerus	El Castellar (Teruel)	Sánchez-Fenollosa et al., (2022a)
El Balsón	Dacentrurinae indet.	Dacentrurinae indet.	Four dorsal vertebrae, several dorsal ribs, a partial femur, and undescribed fossils	La Yesa (Valencia)	Company et al., (2010)
Jab.1 (Fuente del Canal)	-	Neostegosauria indet.	A partial sacrum	Jabaloyas (Teruel)	This paper
La Canaleta	Stegosauria indet.	Stegosauria indet.	A dermal spine	Galve (Teruel)	Pereda-Suberbiola et al., (2005)
Los Arenales	-	Dacentrurinae indet.	A posterior caudal centrum and several dermal spine fragments	Alpuente (Valencia)	This paper
Los Ganchos	Stegosauria indet.	Stegosauria indet.	Undescribed	Alpuente (Valencia)	Suñer et al., (2022)
Losilla (Lo)	Stegosauria indet.	Stegosauria indet.	A dermal spine	Aras de los Olmos (Valencia)	Casanovas-Cladellas et al. (1995a); Galton, (2016); this paper
Losilla I (Lo I)	<i>Dacentrurus armatus</i>	Dacentrurinae indet.	Three cervical vertebrae and two dorsal vertebrae (and a posterior caudal vertebra?)	Aras de los Olmos (Valencia)	Casanovas-Cladellas et al., (1995c); this paper
MC-2	-	Dacentrurinae indet.	A posterior caudal centrum	Monteagudo del Castillo (Teruel)	This paper

SITE	PREVIOUS SYSTEMATICS	CURRENT SYSTEMATICS	MATERIAL	MUNICIPALITY	REFERENCES
MR-9 (El Batán)	-	Stegosauria indet.	A dermal spine fragment	Mora de Rubielos (Teruel)	This paper
Puntal de la Magdalena	Stegosauria indet.	Stegosauria indet.	A dermal spine	Alpuente (Valencia)	Sánchez-Fenollosa et al., (2022a)
RD-3 (El Romeral)	<i>Dacentrurus armatus</i>	Dacentrurinae indet.	A cervical centrum and a dorsal centrum	Riodeva (Teruel)	Cobos et al., (2010); Cobos and Gascó, (2013); this paper
RD-5 (Pino de Jarque 2)	-	Stegosauria indet.	An anterior caudal centrum	Riodeva (Teruel)	This paper
RD-10 (Barrihonda-El Humero)	<i>Dacentrurus armatus</i>	<i>Dacentrurus armatus</i>	A cervical vertebra, nine caudal vertebrae, an ilio-sacral block, two ischia, two pubes, a left partial hindlimb (femur, tibia, fibula, calcaneum, astragalus and metatarsal II), and a dorsal dermal plate	Riodeva (Teruel)	Cobos et al., (2010); Sánchez-Fenollosa et al., (2022a, 2025a)
RD-16 (Prado de las Arenas)	<i>Dacentrurus armatus</i>	Stegosauria indet.	A partial right femur	Riodeva (Teruel)	Cobos et al., (2010); Cobos and Gascó, (2013); this paper
RD-17 (El Vago de Blasco)	-	Dacentrurinae indet.	A cervical centrum	Riodeva (Teruel)	This paper
RD-29 (San Lorenzo 2)	-	Dacentrurinae indet.	Three posterior caudal vertebrae	Riodeva (Teruel)	This paper
RD-34 (Están de Colón)	<i>Dacentrurus armatus</i>	<i>Dacentrurus armatus</i>	A partial cranium, a mid cervical vertebra, and undescribed fossils	Riodeva (Teruel)	Sánchez-Fenollosa and Cobos, (2025)
RD-44 (La Quineta 2)	<i>Dacentrurus armatus</i>	Stegosauria indet.	A partial left hindlimb	Riodeva (Teruel)	Cobos et al., (2010); Cobos and Gascó, (2013); this paper
RD-46 (Barranco Conejero)	<i>Dacentrurus armatus</i>	Dacentrurinae indet.	Two cervical centra, a dorsal centrum, and a caudal centrum	Riodeva (Teruel)	Cobos and Gascó, (2013); this paper
Unknown (CPT-1977)	-	Dacentrurinae indet.	A mid caudal centrum	Riodeva (Teruel)	This paper
Unknown (MPA-653)	cf. <i>Dacentrurus</i> sp.	Dacentrurinae indet.	A mid caudal centrum	Alpuente (Valencia)	Sánchez-Fenollosa et al., (2022a); this paper
Unknown (MPA-1086)	cf. <i>Dacentrurus</i> sp.	Dacentrurinae indet.	A mid caudal centrum	Alpuente (Valencia)	Sánchez-Fenollosa et al., (2022a); this paper

APPENDIX 4.

Osteological descriptions of the new specimens and the 'historical material'. Both included in the 'Material and Methods' and 'Systematic Palaeontology' sections.

RD-5 specimen (Figure 2A–E; Stegosauria indet.). CPT-1075 is a distal anterior caudal vertebra. The centrum is amphicoelous and strongly compressed anteroposteriorly, being wider lateromedially than tall dorsoventrally and long anteroposteriorly, and also taller dorsoventrally than long anteroposteriorly (Appendix 1). The anterior articular facet is eroded (Figure 2A), whereas the posterior facet is well-preserved, wider lateromedially than tall dorsoventrally (Appendix 1), and heart-shaped (Figure 2C). In lateral view, broken transverses processes are present in the upper half of the centrum and located next to the neural arch (Figure 2B). Ventrally, the surface is slightly eroded but chevron facets are preserved in the posterior region (Figure 2C, E).

MR-9 specimen (Figure 2F–H; Stegosauria indet.). MAP-8435 consists of a distal fragment of a dermal spine. It is heavily eroded, exposing cancellous bone along most of the shaft. Cortical bone is preserved only on the medial surface of the proximal part (Figure 2F–H). The shaft is straight and exhibits a D-shaped cross-section (Figure 2G).

Losilla specimen (Figure 2I–K; Stegosauria indet.). MCNV Lo-1 is a right caudal dermal spine. It is partially preserved and composed by two fragments now reconstructed together (Figure 2I–K). Overall, it is slender and has a small base (Figure 2I–K). The base is subcircular in outline and bears marginal rugosities (Figure 2I–K). Its surface is slightly concave and contains several nutrient foramina (Figure 2K). The shaft is straight (Figure 2I–K) and has a subcircular cross-section. The maximum width of the shaft lies just above its base.

CO II specimen (Figure 2L–P; Stegosauridae indet.). CO II-1 is a complete right femur. In anterior and posterior views, it is columnar and straight (Figure 2L, N). The proximal region is lateromedially expanded (Figure 2L, N, O). The femoral head projects dorsomedially and is convex and rounded (Figure 2L, N). The dorsal margin slopes ventrolaterally towards the greater trochanter, with a smooth femoral neck (Figure 2L, N). The anterior trochanter lies on the anterolateral surface and is completely fused to the greater trochanter (Figure 2L). Its dorsal margin is positioned below that of the crista trochanteris (Figure 2L). The fourth trochanter is inappreciable. The shaft cross-section is elliptical. A pronounced cord-like ridge extends proximodistally along the lateral anterior surface from the anterior trochanter but does not reach the condyle (Figure 2L). On the posterior surface, a smooth cord-like ridge extends proximodistally along the medial region from the upper half of the diaphysis to the medial condyle (Figure 2N). In the distal region, the femur is expanded both anteroposteriorly and lateromedially (Figure 2L–N, P). The medial condyle is larger in both dimensions than the lateral one (Figure 2P). The two condyles are separated by distinct intercondylar grooves. The extensor intercondylar groove is wide lateromedially and shallow, whereas the flexor intercondylar groove is notably deeper anteroposteriorly (Figure 2P). The distal articular surface is heavily rugose (Figure 2P).

Jab.1 specimen (Figure 2Q–T; Neostegosauria indet.). CPT-1986 consists of a partial sacrum, preserving at least five vertebrae. The most anterior vertebra is the best preserved, although its anterior region is eroded (Figure 2Q). Its centrum is wider lateromedially than tall dorsoventrally (Appendix 1), subcircular in outline, and laterally fused to the sacral ribs. Only the right side of the sacrum is preserved, but it is also laterally broken (Figure 2R). Dorsally, the neural arches of the sacral vertebrae and the dorsal surfaces of the sacral ribs are co-ossified, forming a flat sacral shield (Figure 2T). Two small open foramina, along with several closed ones, are present on the dorsal surface of the sacral shield (Figure 2T). The neural spines are also fused together. They are short, posteriorly curved, and lateromedially compressed but expanded at their apices. Each sacral rib and neural spine can still be distinguished by sutures (Figure 2R, T). Ventrally, the surface of the sacrum is heavily eroded, and the vertebral centra are no longer discernible. The relatively small size of the specimen and the incomplete fusion (visible sutures and foramina) suggest that CPT-1986 likely belongs to a skeletally immature individual.

Losilla I specimen (Figure 3; Dacentrurinae indet.). MCNV Lo I-6 (Figure 3A–E) is a small cervical centrum. It is wider lateromedially than long anteroposteriorly (Appendix 1), longer anteropos-

teriorly than tall dorsoventrally (Appendix 1), and amphicoelous. Its articular facets are wider lateromedially than tall dorsoventrally (Appendix 1) and subelliptical to heart-shaped (Figure 3A, C). The lateral surfaces are concave. The left parapophysis is preserved on the anterior margin of the centrum (Figure 3B). Ventrally, no keel or groove is present, but four well-developed tuberosities are visible on both anterior and posterior margins (Figure 3E).

IPS-37432 (Lo I-2) (Figure 3F–J) and IPS-37431 (Lo I-1) (Figure 3K–O) are two posterior cervical vertebrae. IPS-37432 (Figure 3F–J) preserves the most part of the right half, whereas IPS-37431 (Figure 3K–O) preserves the centrum and pedicels. Both centra are amphicoelous, wider lateromedially and taller dorsoventrally than long anteroposteriorly (Appendix 1), and exhibit a longitudinal ventral keel (Figure 3J, O). In IPS-37431, the articular facets are wider lateromedially than tall dorsoventrally (Appendix 1) and heart-shaped (Figure 3K, M). Parapophyses are preserved in IPS-37431, located on the anterior margin in the upper half of the centrum (Figure 3L). Both vertebrae exhibit notably concavities on the lateral surfaces (Figure 3G, L) and a large neural canal (Figure 3F, H, N). In IPS-37432, the neural arch is not well-developed dorsally and almost entirely occupied by the neural canal (Figure 3F, H). Its postzygapophyses are partially preserved, projecting posteriorly beyond the articular facet of the centrum (Figure 3G, H).

IPS-37433 (Lo I-3) (Figure 3P–T) is an almost complete anterior dorsal vertebra. The centrum is amphicoelous, wider lateromedially than tall dorsoventrally and long anteroposteriorly (Appendix 1), taller dorsoventrally than long anteroposteriorly (Appendix 1), and heart-shaped. The lateral surfaces are deeply concave (Figure 3Q), and the ventral surface bears a longitudinal keel (Figure 3T). The neural canal is large and subcircular, occupying the entire surface of the short neural arch (Figure 3P, R). The left parapophysis is preserved at the base of the neural arch (Figure 3Q). The prezygapophyses are well preserved and do not extend beyond the articular facet of the centrum (Figure 3P, Q, S). They are notably separated each other and their articular facets face dorsomedially, are flat, and elliptical. The postzygapophyses are not preserved. The fragmented right transverse process is displaced dorsomedially, as visible in posterior and dorsal views (Figure 3R, S).

IPS-37435 (Lo I-7) (Figure 3U–Y) is a dorsal centrum. Like IPS-37433, it is amphicoelous, wider lateromedially than tall dorsoventrally and long anteroposteriorly (Appendix 1), taller dorsoventrally than long anteroposteriorly (Appendix 1), and heart-shaped, although less compressed anteroposteriorly. Both lateral surfaces exhibit a concavity just below the base of the neural arch (Figure 3V). The ventral surface is eroded (Figure 3Y).

By Pass specimen (Figure 4; Dacentrurinae indet.). MPA D-0287 (Figure 4A–E) is an anterior dorsal vertebra, while MPA D-0279 (Figure 4F–J) is a posterior dorsal vertebra. Both centra are slightly amphicoelous and wider lateromedially than long anteroposteriorly (Appendix 1). However, MPA D-0279 is proportionally longer anteroposteriorly (Appendix 1) and exhibits articular facets with a more circular shape than MPA D-0287 (Figure 4A, C, F, H). The centra have concave lateral surfaces (Figure 4B, G) and a gentle longitudinal ventral keel (Figure 4E, J). The neural arch of MPA D-0287 is dorsoventrally short (Figure 4A–C), while that of MPA D-0279 is proportionally more elongated (Figure 4F–H). A medial ridge runs dorsoventrally on both anterior and posterior surfaces of the neural arch (Figure 4A, C, H). Neural canals are subcircular to teardrop-shaped (Figure 4A, C, F, H). The parapophyses are concave and elliptical (Figure 4B, G). The prezygapophyses slightly extend beyond the anterior articular facet of the centrum in MPA D-0287 (Figure 4B), but are eroded in MPA D-0279 (Figure 4F, G, I). Their flat and elliptical articular facets face dorsomedially (Figure 4A, D). Since MPA D-0287 (Figure 4A–E) do not preserve postzygapophyses, transverse processes, and the neural spine, the description that follows pertains only to MPA D-0279 (Figure 4F–J). In this vertebra, the postzygapophyses are presumably located at the same level as the prezygapophyses and extend beyond the posterior articular facet of the centrum (Figure 4G). Their articular facets are flat, elliptical, face lateroventrally, and posteriorly separated by a wide longitudinal groove (Figure 4G, H). The transverse processes project outward with a great angle to the horizontal, and the right one is partially preserved (Figure 4F–H). The neural spine is compressed lateromedially but expands at its apex (Figure 4F, H).

MPA D-0276 (Figure 4K–O) is a mid caudal vertebra with its chevron. The centrum is amphicoelous, wider lateromedially than tall dorsoventrally and long anteroposteriorly (Appendix 1), taller dorsoventrally than long anteroposteriorly (Appendix 1), and heart-shaped (Figure 4K, M). Smooth

concentric ridges are visible on both articular facets (Figure 4K, M). The lateral surfaces are slightly concave and bear small transverse processes in the upper half (Figure 4K–M). The neural arch is short dorsoventrally and narrow lateromedially (Figure 4K, M). The neural canal is large, taller dorsoventrally than wide lateromedially, and elliptical (Figure 4K, M). Only the left prezygapophysis is preserved, and it is finger-like and extends anteriorly beyond the centrum facet (Figure 4K, L, N). Its articular facet is flat, elliptical, and dorsomedially oriented. However, the postzygapophyses do not extend beyond the posterior centrum facet and their flat and elliptical articular facets face ventrolaterally (Figure 4L, M). The neural spine projects dorsoposteriorly, is compressed lateromedially, and expands slightly at the apex (Figure 4L–N).

A nearly complete chevron is fused to the ventral posterior margin of the centrum (Figure 4K–M, O). It is Y-shaped in anterior and posterior views and short dorsoventrally (Figure 4K, M). The haemal canal is large, notably taller dorsoventrally than wide lateromedially, and elliptical in outline (Figure 4K, M). The chevron narrows strongly lateromedially towards the distal end (Figure 4K, M), but expands anteroposteriorly, forming a subcircular outline in lateral view (Figure 4L).

MPA D-0267 (Figure 4P–R) is a left caudal dermal spine belonging to the terminal pair. It is stocky and bears a large base (Figure 4Q, R). The base is longer anteroposteriorly than dorsoventrally and elliptical in outline (Figure 4R), although the dorsal margin is broken (Figure 4Q, R). Its surface is convex and exhibits a wide (especially at the mid) ridge directed anteroposteriorly, as well as numerous nutrient foramina (Figure 4R). Regarding the shaft, only the proximal region is preserved. It is straight with concave surfaces (Figure 4Q, R). The cross-section is rhomboidal in outline (Figure 4P).

RD-17 specimen (Figure 5A–E; Dacentrurinae indet.). CPT-1705 is a partially preserved cervical centrum. It is amphicoelous, wider lateromedially than tall dorsoventrally and long anteroposteriorly (Appendix 1), and taller dorsoventrally than long anteroposteriorly (Appendix 1). The articular facets are subcircular, each with a C-shaped concavity medially (Figure 5A, C). The left parapophysis is preserved and located on the lateral surface of the centrum (Figure 5B). Viewed laterally, the ventral margin is gently concave. Ventrally, CPT-1705 bears a wide but shallow longitudinal keel (Figure 5E).

CPT-1977 (Figure 5F–J; Dacentrurinae indet.). CPT-1977 is a mid caudal centrum. It is amphicoelous, wider lateromedially than tall dorsoventrally and long anteroposteriorly (Appendix 1), and taller dorsoventrally than long anteroposteriorly (Appendix 1). Both articular facets are heart-shaped and exhibit smooth concentric ridges in their surface (Figure 5F, H). The lateral surfaces are concave (more markedly in the right lateral) with transverse processes located in the upper posterior half of the centrum (Figure 5G). The neural canal is wider posteriorly (Figure 5I). The ventral surface lacks a keel or groove but bears chevron facets (Figure 5J). Posterior facets are more developed than the anterior.

MCNV-VCP (Figure 5K–O; Dacentrurinae indet.). MCNV-VCP is an almost complete posterior caudal vertebra. The centrum is amphicoelous, wider lateromedially than tall dorsoventrally and long anteroposteriorly (Appendix 1), and taller dorsoventrally than long anteroposteriorly (Appendix 1). Both articular facets are heart-shaped and show smooth concentric ridges (Figure 5K, M). The lateral surfaces are concave, and on the left, a transverse process is located in the upper posterior half of the centrum (Figure 5L). Ventrally, chevron facets are present, with posterior ones more developed (Figure 5O). The neural canal is taller dorsoventrally than wide lateromedially and elliptical in outline (Figure 5M). Only the right prezygapophysis is preserved. It is finger-like, projecting beyond the anterior centrum facet (Figure 5K, L, N). Its facet is dorsomedially oriented and elliptical. The postzygapophyses are small and do not project past the posterior centrum facet (Figure 5L–N). Their articular facets face lateroventrally and are subelliptical in outline (Figure 5L). The neural spine is strongly reduced in size, although it is likely incomplete (Figure 5L–N).

CT-10 specimen (Figure 5P–T; Dacentrurinae indet.). CPT-763 is a posterior caudal centrum. It shares the features of CPT-1977 (Figure 5F–J) but is more compressed dorsoventrally and anteroposteriorly.

Los Arenales specimen (Figure 5U–Y; Dacentrurinae indet.). MPA-1218 is a posterior caudal centrum, morphologically similar to CPT-763 (Figure 5P–T).

MPA-1221, MPA-1222, and MPA-1223 consist of several fragments of caudal dermal spine from the shaft, each exhibiting lenticular or rhomboidal cross-section.

MC-2 specimen (Figure 5Z–DD; Dacentrurinae indet.). MAP-8436 is a slightly eroded posterior caudal centrum that exhibits the same morphological features seen in CPT-763 (Figure 5P–T) and MPA-1218 (Figure 5U–Y).

RD-29 specimen (Figure 6; Dacentrurinae indet.). MAP-8426 (Figure 6A, B) and MAP-8425 (Figure 6C–G) are contiguous proximal posterior caudal vertebrae, whereas CPT-1950 (Figure 6H–L) is a distal posterior caudal centrum.

MAP-8426 (Figure 6A, B) is a fragmentary centrum, broken anteroposteriorly and dorsoventrally, with only part of the posterior upper half preserved (Figure 6A, B). Its posterior facet is concave and presumably heart-shaped (Figure 6A). The transverse processes arise from the upper rear of the centrum (Figure 6A, B).

MAP-8425 (Figure 6C–G) is amphicoelous and wider lateromedially and taller dorsoventrally than long anteroposteriorly (Appendix 1). The articular facets are wider lateromedially than tall dorsoventrally (Appendix 1), heart-shaped, and exhibit smooth concentric ridges (Figure 6C, E). Small transverse processes are set high and posteriorly on the lateral surfaces (Figure 6D, F). The neural arch is destroyed except for its base (Figure 6C–F). Ventrally, no keel or groove is present, but chevron facets occur, with the posterior pair being larger (Figure 6G).

CPT-1950 (Figure 6H–L) is slightly amphicoelous and wider lateromedially and taller dorsoventrally than long anteroposteriorly (Appendix 1). Its facets are remarkably wider lateromedially than tall dorsoventrally (Appendix 1). Compared to MAP-8425 (Figure 6C–G), this centrum is more compressed and has subelliptical facets (Figure 6H, J). The surface of the anterior articular facet exhibits smooth concentric ridges (Figure 6H). The lateral surfaces are concave (Figure 6I). The transverse processes are not visible, probably due to erosion of the centrum's upper half (Figure 6H–K). Ventrally, faint chevron facets are present (Figure 6L).

CO specimen (Figures 7–9; *Dacentrurus armatus*). MCNV CO-9 (Figure 7A–E), MCNV CO-5 (Figure 7F–J), and MCNV CO-1 (Figure 7K–O) are mid cervical vertebrae. Their centra are amphicoelous and longer anteroposteriorly than wide lateromedially and tall dorsoventrally (Appendix 1). The articular facets are wider lateromedially than tall dorsoventrally (Appendix 1) and subelliptical to heart-shaped in outline (Figure 7A, C, F, H, K, M). In MCNV CO-9, parapophyses are absent due to erosion, but in MCNV CO-5 (Figure 7F) and MCNV CO-1 (Figure 7K–O) they are preserved, situated in the anterior upper half of the centrum (Figure 7F, L, O). Ventrally, all three vertebrae exhibit a wide longitudinal keel (Figure 7E, J, O). The following description is based in MCNV CO-1, the only mid cervical vertebra that preserves the neural arch. Overall, it is anteroposteriorly elongated and dorsally short (Figure 7K–N). The neural canal is large and subcircular in outline (Figure 7K, M). The prezygapophyses lie ventral to the postzygapophyses and slightly overhang the anterior facet of the centrum (Figure 7L). They are separated by a large intra-prezygapophyseal lamina (Figure 7N), and their articular facets are flat, elliptical, and dorsomedially faced (Figure 7K, N). The diapophyses arise from the neural arch below the prezygapophyses (Figure 7K–M). The left cervical rib is fused to both the parapophysis and diapophysis, although it is not correctly reattached in the current mount (see Casanovas-Cladellas et al., 1995b, plate I). This rib is posteriorly directed, curves medially, overhangs the centrum, and terminates bluntly (Figure 7K–O; Casanovas-Cladellas et al., 1995b, plate I). The left postzygapophysis is complete, whereas the right one preserves only its anterior region (Figure 7M, N). The left postzygapophysis is finger-like, extending beyond the posterior facet of the centrum (Figure 7L, M). Its articular facet is flat, elliptical, and lateroventrally directed. Dorsally, two well-developed spinopostzygapophyseal laminae extend anterolaterally from the top of the postzygapophyses towards both sides of the neural spine base, culminating on its anterior margin (Figure 7N). The neural spine is positioned in the anterior half of the centrum (Figure 7K, L, N), is short, and appears to be modestly expanded lateromedially (Figure 7K, L, N).

MCNV CO-17 and MCNV CO-24 (Figure 8A–E), MCNV CO-2 (Figure 8F–J), and MCNV CO-4 (Figure 8K–O) are posterior cervical vertebrae. Their morphology closely resembles that of the mid cervical vertebrae described above, though their centra are wider lateromedially than long anteroposteriorly and tall dorsoventrally (Appendix 1). MCNV CO-2 (Figure 8F–I) has a neural arch that is less anteroposteriorly elongated yet dorsally more developed than that of MCNV CO-1 (Figure 7K–N). Additionally, its neural spine is longer dorsally and wider lateromedially than that of MCNV CO-1 (Figures 7K, L, 8F, G).

MCNV CO-7 (Figure 9A–E) and MCNV CO-18 (Figure 9F–I) are dorsal centra. MCNV CO-7 is notably eroded, so its proportions and morphology should be interpreted with caution. Its centrum is amphiplatyan, taller dorsoventrally than wide lateromedially and long anteroposteriorly (Appendix 1), and exhibits subtle lateral concavities beneath the base of the neural arch (Figure 9B). In contrast, MCNV CO-18 is heavily eroded and broken dorsoventrally and lateromedially, but a pronounced lateral concavity remains visible (Figure 9G).

MCNV CO-10 (Figure 9J–N) is an anterior caudal vertebra. Its centrum is wider lateromedially and taller dorsoventrally than long anteroposteriorly (Appendix 1). The anterior facet is heavily eroded (Figure 9J), while the posterior facet is well preserved, concave, wider lateromedially than tall dorsoventrally (Appendix 1), and weakly heart-shaped (Figure 9L). On the lateral surfaces, broken transverse processes are present in the upper half of the centrum (Figure 9K). The ventral surface is moderately eroded and lacks chevron facets (Figure 9N).