



General palaeontology, systematics and evolution (Vertebrate palaeontology)

A tall-spined ornithopod dinosaur from the Early Cretaceous of Salas de los Infantes (Burgos, Spain)

Un dinosaure ornithopode à haute épine neurale du Crétacé inférieur de Salas de los Infantes (Burgos, Espagne)

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ABSTRACT

A tall-spined ornithopod dinosaur from the Pinilla de los Moros Formation (Upper Hauterivian-Lower Barremian) of Salas de los Infantes (Burgos, Spain) is described. The material consists of seven associated axial remains, including five middle dorsal vertebrae, a fragmentary neural spine and a dorsal rib, from a single medium-sized individual. This material was previously referred to *Iguanodon cf. fittoni*. It is characterised by having a high dorsal neurapophysis that is approximately 4.5 times the height of the centrum. The elongation and vertical orientation of the dorsal neural spines allow it to be distinguished from other ornithopods from the Wealden of Europe, including *Hypsosaurus* and *Barilium* from the Valanginian, and *Iguanodon* and *Mantellisaurus* from the Barremian-Aptian. The material is here referred to Iguanodontia indet. because it is so incomplete, but it is potentially a distinct taxon. Among the ornithopods, only *Oviraptor* and the hadrosaurid *Hypacrosaurus* possess higher dorsal neural spines.

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RÉSUMÉ

Un dinosaure ornithopode à haute épine neurale provenant de la Formation Pinilla de los Moros (Hauterivien supérieur-Barrémien inférieur) de Salas de los Infantes (Burgos, Espagne) est décrit ici. Le matériel consiste en sept restes associés du squelette axial, y compris cinq vertèbres dorsales moyennes, une épine neurale fragmentaire et une côte dorsale, appartenant probablement à un seul individu de taille moyenne. Ce matériel a été auparavant rapporté à *Iguanodon cf. fittoni*. Il est caractérisé par une neurapophyse

Mots clés :

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Vertèbres dorsales

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¹ <http://www.aragosaurus.com>.

allongée, environ quatre fois et demie plus haute que la hauteur du centrum. La longueur et l'orientation verticale de l'épine neurale des vertèbres dorsales permettent de le différencier d'autres ornithopodes des faciès wealdiens d'Europe, y compris *Hypselospinus* et *Barilium* du Valanginien, *Iguanodon* et *Mantellisaurus* du Barrémien-Aptien. Il est ici rapporté à *Iguanodontia* indet. de part sa nature fragmentaire, mais représente potentiellement un nouveau taxon. Parmi les ornithopodes, seuls *Ouranosaurus* et l'hadrosauridé *Hypacrosaurus* possèdent des épines neurales dorsales plus hautes.

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1. Abbreviations

AMNH	American Museum of Natural History, New York, USA
GPI	Geologisch-Paläontologisches Institut, Münster, Germany
GPIT	Geologisches und Paläontologisches Institut der Universität Tübingen, currently the Institut für Geowissenschaften, Tübingen, Germany
IRSNB	Institut Royal des Sciences Naturelles de Belgique/Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussels, Belgium
MDE	Musée des Dinosaures, Espéraza, Aude, France
MDS	Museo de Dinosaurios, Salas de los Infantes, Burgos, Spain
MNHN	Muséum National d'Histoire Naturelle, Paris, France
NHMUK	The Natural History Museum, London, UK
NMN	National Museum of Niger, Niamey, Niger

2. Introduction

Salas de los Infantes (province of Burgos, northern Spain) is one of the most productive areas of dinosaur fossils in southern Europe. More than 30 outcrops are known in the vicinity of Salas de los Infantes, most of them of Early Cretaceous age (Torcida Fernández-Baldor, 2006). In geological terms, this area lies within the western Cameros Basin, which is located in the northwestern part of the Iberian Range. The dinosaur-bearing units of this area are the Pinilla de los Moros (Upper Hauterivian-Lower Barremian) and Castrillo de la Reina (Upper Barremian-Aptian) formations (Martín-Closas and Alonso Millán, 1998), both of fluvial origin. The sites around Salas have yielded abundant dinosaur remains, including spinosaurid and dromaeosaurid theropods, diplodocoid and titanosauriform sauropods, stegosaurian and ankylosaurian thyreophorans, basal euornithopods, dryosauroids and basal iguanodontian ornithopods (Pereda Suberbiola et al., in press and references therein; Torcida Fernández-Baldor, 2006). The dinosaur assemblage from Salas de los Infantes shares several taxa with the fauna of the Wealden Group of Britain (Martill and Naish, 2001), namely the theropod *Baryonyx*, the ankylosaur *Polacanthus* and, with reservations, the ornithopod *Iguanodon*. Moreover, dinosaur remains from the Barremian-Aptian of Salas de los Infantes also represent new taxa, such as a new rebachisaurid sauropod (Torcida Fernández-Baldor et al., in press).

Most of the fossil remains found in this region are kept at the MDS. A small collection is housed in the Institut und Museum für Geologie und Paläontologie of the Universität Tübingen (GPIT), which is currently the Institut für Geowissenschaften (Germany). This collection was gathered in 1968 by the German geologist Gerd Dietl while doing fieldwork in Burgos for his MA thesis (Dietl, 1969). It consists of 25 bones, all but three belonging to iguanodontian ornithopods: seven vertebral remains were referred to *Iguanodon* cf. *fittoni* (Maisch, 1997), and a dentary fragment that preserves several teeth *in situ* has been assigned to *Iguanodontioidea* indet. (Ruiz-Omeñaca et al., 2008). The GPIT collection also contains a theropod tooth and two crocodilian teeth (still undescribed). The general aspect of the fossils and the conservation of the matrix suggest that they come from several different localities of the Wealden facies near Salas de los Infantes (Torcida Fernández-Baldor et al., 2008).

The aim of this article is to review the material previously referred to *Iguanodon* cf. *fittoni* and to discuss its affinities.

3. Geological setting

The fossils studied in this paper (GPIT 1802/1-7) were found in the “Tera-Beds” of Burgos, in the Cameros Basin (Dietl, 1969). The Tera Group is the oldest of the three lithostratigraphic units defined by Beuther (1966) in the western part of the Cameros Basin (the others are Oncala and Urbión Groups). Because the material was referred to *Iguanodon* cf. *fittoni*, Maisch (1997) tentatively correlated the “Tera-Beds” of Burgos with the Wadhurst Clay of the Wealden Basin, and regarded them as Berriasian-Valanginian in age.

The Tera Group in the north and south sectors of the western Cameros Basin (Burgos province; Fig. 1) comprises sedimentary rocks of Tithonian-Barremian age, now recognised as different geological formations (Clemente and Pérez Arlucea, 1993): Señora de los Brezales, Boleras, Jaramillo de la Fuente, Campolara, Río del Salcedal, Río de San Marcos, Peñacoba, Pinilla de los Moros, and Hortigüela (Martín-Closas and Alonso Millán, 1998: figs. 4, 7).

According to Dietl (1969) (pers. comm.), the ornithopod remains come from the “El Castro” area of Castrovido, in Salas de los Infantes (Burgos). The outcrops of this area correspond to the Pinilla de los Moros Formation (Fig. 1). This interpretation is consistent with the study of the matrix that is associated with the fossils in some areas. On the basis of charophyte biozonation, the Pinilla de los Moros Formation is dated as Late Hauterivian to Early Barremian in

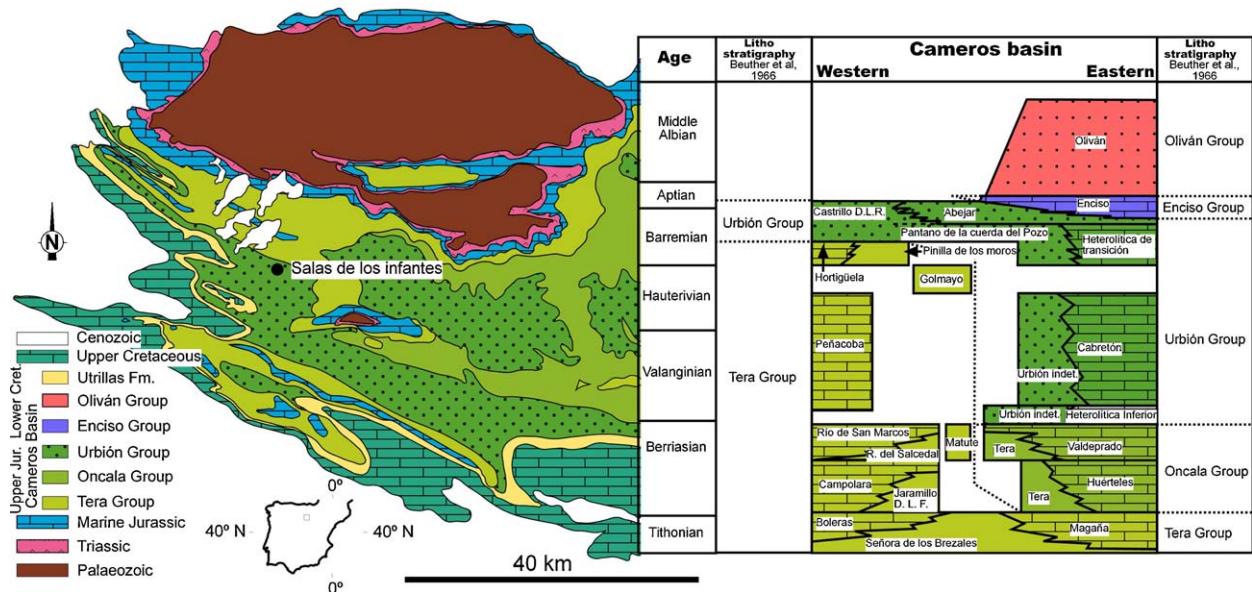


Fig. 1. Geological map of the western Cameros Basin, modified from Beuther et al. (1966) (pl. 36), and chronostratigraphic scheme of the Cameros Basin, as proposed by Martín-Closas and Alonso Millán (1998).

Fig. 1. Carte géologique de l'Ouest du Bassin de Cameros modifiée d'après Beuther et al. (1966) (pl. 36) et schéma chronostratigraphique du même bassin d'après Martín-Closas et Alonso Millán (1998).

the northern sector of the western Cameros Basin (Martín-Closas and Alonso Millán, 1998).

4. Systematic palaeontology

Dinosauria Owen, 1842

Ornithischia Seeley, 1887

Ornithopoda Marsh, 1881

Iguanodontia Dollo, 1888 (*sensu* Norman, 2004)

Iguanodontia indet.

Material: GPIT 1802/1–5, five dorsal vertebrae (one of them almost complete); GPIT 1802/6, a fragment of dorsal neural spine; and GPIT 1802/7, an incomplete dorsal rib. All the remains probably come from a single individual. Casts of the most relevant specimens are kept at Salas de los Infantes, Burgos (MDS collection).

Locality and horizon: "El Castro" in Castrovido, Salas de los Infantes (Burgos, Spain); Pinilla de los Moros Formation; Lower Cretaceous, Upper Hauterivian-Lower Barremian (Martín-Closas and Alonso Millán, 1998).

5. Description

The material was previously described in detail by Maisch (1997). It consists of five vertebrae, a fragment of neural spine and an incomplete rib, all from the dorsal region (Fig. 2). Maisch (1997) regarded the vertebrae as a series of five dorsals, most probably from the sixth to the ninth, and the eleventh. The vertebrae are so similar in both size and state of preservation that they probably pertain to the same individual. One of them, considered to be the first vertebra of the series (GPIT 1802/1), is almost complete, but the left prezygapophysis, left transverse process, and both postzygapophyses are missing (Fig. 2A). As in the other

vertebrae, the centrum is longer than high or wide (Table 1). The anterior articular surface is rather flat, and the posterior one is slightly concave. The lateral surfaces of the centrum are convex dorsoventrally and concave anteroposteriorly. The centrum has a longitudinal keel ventrally and ridges near the edges of the articular surfaces. The ventral surface of the centrum is flat to slightly concave in lateral view. A small nutrient foramen is located half way up on both lateral sides. The neurocentral suture is irregular. The right prezygapophysis does not protrude beyond the anterior articular surface of the centrum. The right transverse process associated to GPIT 1802/1 is oriented at about 50° to the horizontal. The dorsal edge of the parapophysis does

Table 1

Measurements (in mm) of the iguanodontian ornithopod from Salas de los Infantes (Burgos, Spain).

Tableau 1

Mesures (en mm) de l'ornithopode iguanodontien de Salas de los Infantes (Burgos, Spain).

Dorsal vertebrae	L	H	W	l	h	w
GPIT 1802/1	72	53	62	67	285	27
GPIT 1802/2	71	53	56	-	-	28
GPIT 1802/3	71	55	54	-	-	18
GPIT 1802/4	70	60	62	-	-	25
GPIT 1802/5	70	53	57	-	-	-
GPIT 1802/6	-	-	-	63	-	-

Dorsal rib

GPIT 1802/7 +250 (length)

Centrum: H: height; L: length; W: transverse width; neural spine: l: anteroposterior length; h: height; canal neural: w: transverse width.

Centrum: H: hauteur; L: longueur; W: largeur transversale; épine neurale: l: longueur antéropostérieure; h: hauteur; canal neural: w: largeur transversale.

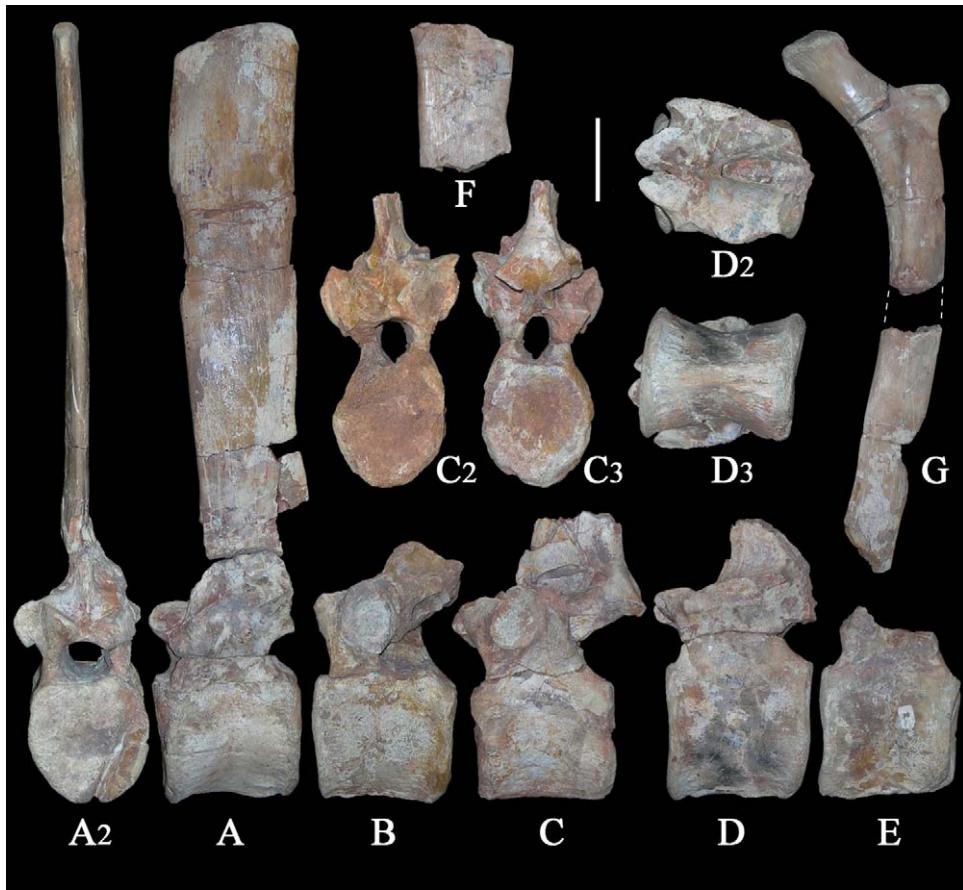


Fig. 2. Iguanodontia indet. from the Early Cretaceous of Salas de los Infantes, Burgos, Spain. A–E: GPIT 1802/1 to 5 (from left to right), dorsal vertebrae; F: GPIT 1802/6, fragment of neural spine; G: GPIT 1802/7, dorsal rib. Views: left lateral (A–E, F, G), anterior (A2, C2), posterior (C3), dorsal (D2) and ventral (D3). Scale bar: 5 cm.

Fig. 2. Iguanodontia indet. du Crétacé inférieur de Salas de los Infantes, Burgos, Espagne. A–E : GPIT 1802/1 à 5 (de gauche à droite), vertèbres dorsales ; F : GPIT 1802/6, fragment d'épine neurale ; G : GPIT 1802/7, côte dorsale. Vues : latérale gauche (A–E, F, G), antérieure (A2, C2), postérieure (C3), dorsale (D2) et ventrale (D3). Barre d'échelle : 5 cm.

not reach above the dorsal margin of the prezygapophysis. The neurapophysis is very elongated and is oriented vertically. It is approximately 4.5 times higher than the centrum. The anterior and posterior edges are almost parallel in lateral view; the distal part is slightly wider than the proximal part. The ratio of the height and the anteroposterior length of the neural spine (measured in the upper third) is equal to 4.25. The anterior edge of the neural spine is rather blunt whereas the posterior edge is sharp. In lateral view, the longitudinal axis of the posterior border of the neural spine is vertical and coincides with the posterior articular surface of the centrum (Fig. 2A).

The other vertebrae only preserve the centrum and the basal portion of the neural arch. In GPIT 1802/2, the parapophysis is larger and more elongated dorsoventrally; it protrudes just above the dorsal edge of the prezygapophysis (Fig. 2B). GPIT 1802/3 is the only vertebra of the series that preserves the postzygapophyses (Fig. 2C). The prezygapophyses, which have flat articular facets, are oriented at an angle of 90°. Unlike GPIT 1802/1, the neural canal is higher than wide. The anterior surface of the basal part of the neurapophysis has two lateral depressions. These depressions are present in GPIT 1802/2 and 3, but

are absent in GPIT 1802/4. The latter vertebra has small parapophyses as anterolateral extensions of the transverse processes, which are at the level of the dorsal edge of the prezygapophyses (Fig. 2D). The length of the centrum is comparable to the other vertebrae, but the centrum is as high as wide. GPIT 1802/5 is a very incomplete vertebra (Fig. 2E). The parapophysis is merely a small knob.

GPIT 1802/6 is an isolated proximal fragment of neural spine that does not fit with any of the vertebrae (Fig. 2F). Its anteroposterior length is similar to the neural spine of GPIT 1802/1. As suggested by Maisch (1997), it presumably comes from a middle dorsal vertebra.

Finally, GPIT 1802/7 is an incomplete double-headed rib (Fig. 2G). It consists of two fragments: the head and a portion of the shaft. Both the capitulum and tuberculum have oval articular facets; the facet of the capitulum is smaller and more convex than that of the tuberculum.

6. Discussion

The combination of characters present in the vertebrae GPIT 1802/1–5 – absence of pleurocoels, presence of amphiplatyan to platycoelous (posterior articular surface)

centra that exhibit a sinuous suture with the neural arches – supports ornithischian and ornithopod affinities (Knoll, 2009; Norman, 2004).

The presence of centra that are longer than wide, with articular surfaces flat to slightly concave, and of para-

pophyses that are located above the neurocentral suture throughout the series indicates that the vertebrae come from the dorsal region. The most anterior dorsals can be ruled out, because GPIT 1802/1–5 do not retain cervical features (e.g., short, opisthocoelous centra). Moreover, the

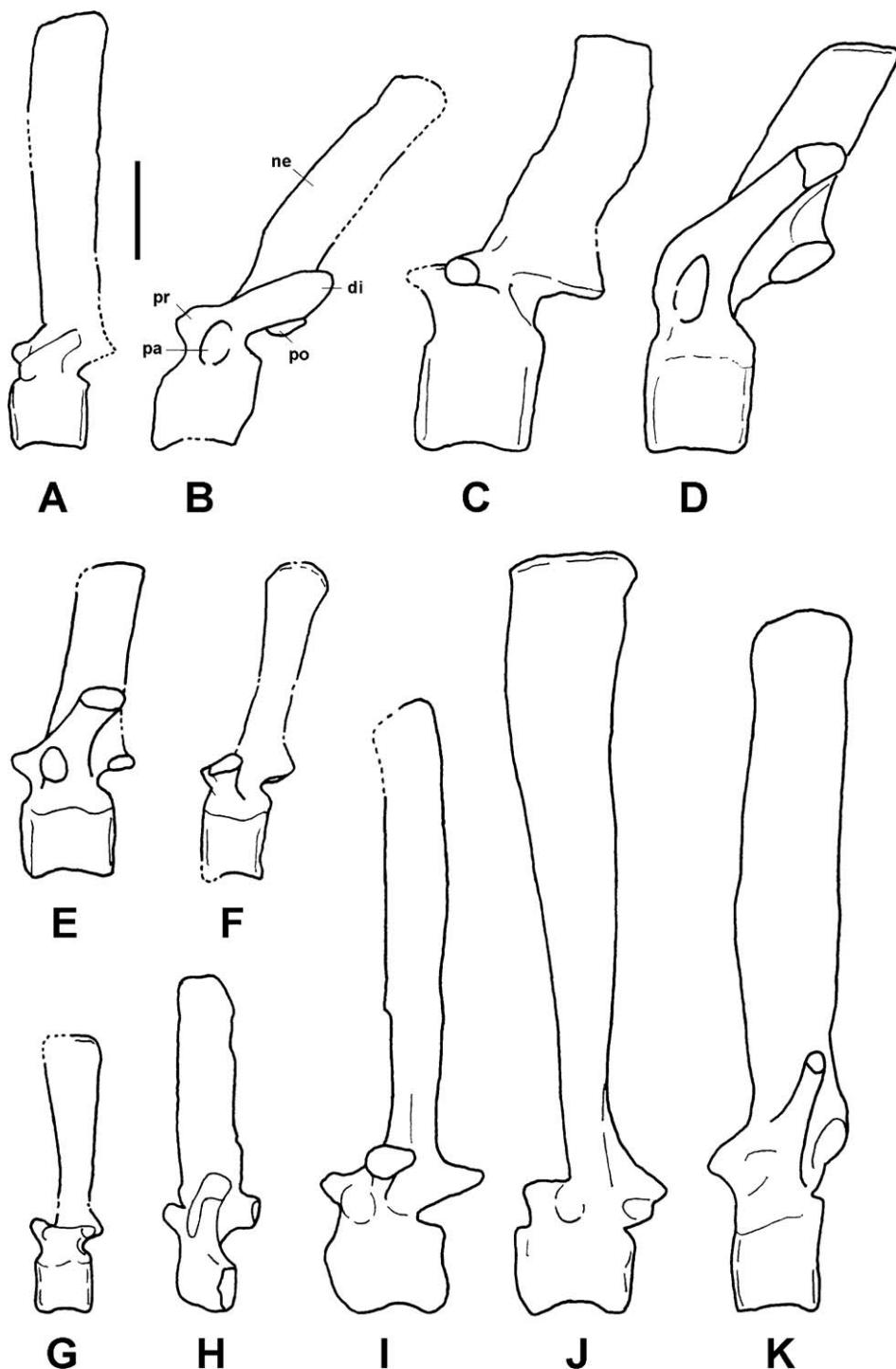


Fig. 3.

shape and position of the parapophyses and the comparison of the vertebrae with reconstructions of the dorsal vertebral column of ornithopods such as *Iguanodon* and *Mantellisaurus* (Norman, 1980, 1986) indicate that they are middle dorsals (i.e., between the fifth and the eleventh of the series).

The degree of fusion between the vertebral centra and the base of the neural arches indicates that GPIT 1802/1–7 represent a subadult or adult individual (Galton, 2009; Irmis, 2007). Based on the size of the vertebrae and after a comparison with ornithopod skeletal reconstructions (Norman, 2004; Paul, 2008), the Salas material can be regarded as that of a middle-sized iguanodontian (estimated body length about 5 m).

The most striking feature observed in the dorsal vertebrae of Salas is the elongation of the neurapophysis. In GPIT 1802/1, which is regarded as the fifth or sixth dorsal, the neural spine is approximately 4.5 times the height of the centrum (Fig. 3A). Maisch (1997) referred GPIT 1802/1–7 to *Iguanodon* cf. *fittoni* because the dorsal vertebrae bear a long neural spine that is totally vertical. *I. fittoni* was originally described from the Valanginian of England. Other material from the same formation was named *I. hollingtoniensis* by Lydekker (1889). Recently, Norman (2010) referred the species *fittoni* to the genus *Hypselospinus* (*Wadhurstia* Carpenter and Ishida, 2010 is a junior synonym). According to Norman (2004, 2010), *I. hollingtoniensis* is a junior subjective synonym of *I. fittoni* (see also Paul, 2008; Galton, 2009). The holotype of *I. hollingtoniensis* includes several dorsal vertebrae, but only a few are more or less complete (NHMUK R604 partim). The neural spine of an anterior-middle dorsal vertebra differs from that of GPIT 1802/1 in that it is shorter (no more than 3.5 times the height of the centrum) and steeply inclined posteriorly, forming an angle of about 50° to the horizontal (Fig. 3B; Norman, 2010: figs. 9A–B). In a posterior dorsal vertebra, the (broken) neurapophysis is more vertical and the angle to the horizontal is about 75° (Norman, 1987b: fig. B, left). In both vertebrae of *I. hollingtoniensis*, the neural spine is narrower than that of GPIT 1802/1 (height/anteroposterior length ratio more than 4.5 versus approximately 4.25 in the Salas ornithopod).

Barilium dawsoni was a sympatric contemporary of *H. fittoni* (Norman, 2010). *Torilion Carpenter and Ishida, 2010* is a junior synonym of *Barilium* Norman, 2010. The dorsal vertebrae (NHMUK R798, R805, R3788) have a short neural spine whose height does not exceed 2.5 times that of the centrum (Fig. 3C; Lydekker, 1888: fig. 38; Norman, 2010: figs. 4A–B). The neurapophysis is oblique, more inclined posteriorly in the middle dorsals (ca. 65° to the horizontal in NHMUK R798) than in the posterior dorsals (ca. 80° in NHMUK R805). The neural spine of *B. dawsoni* is broader than that of *H. fittoni* and of the Salas ornithopod (height/anteroposterior length ratio equal to or less than 3).

Iguanodontians from the upper part of the Wealden Group (Barremian-Aptian) of Britain and its equivalent units in mainland Europe are represented by at least two species: *Iguanodon bernissartensis* and *Mantellisaurus atherfieldensis* (Norman, 2010; Paul, 2007, 2008). The validity of *Vectisaurus valdensis* from the Isle of Wight (Galton, 1976) and *Dollodon bampingi* from Belgium (*Dollodon seelyi* in Carpenter and Ishida, 2010) is controversial (Norman, 1990, in press).

I. bernissartensis is currently the only valid species of *Iguanodon* (Paul, 2008; Norman, in press; contra Norman, 2004). It bears low dorsal neurapophyses that do not exceed 2.5 times the height of the centrum, and are inclined posteriorly at about 65–70° to the horizontal (Fig. 3D; Norman, 1980: figs. 36c, 39b, 40a).

In *Mantellisaurus atherfieldensis*, the dorsal neurapophyses are higher than in *I. bernissartensis* (Norman, 2004: fig. 19.16), but the height does not exceed three times that of the centrum (Figs. 3E–F; Norman, 1986: figs. 29, 31, 32, appendix 2). The neural spines are almost vertical, forming an angle of approximately 80–85° to the horizontal.

The dorsal neurapophyses of the holotype of *Vectisaurus valdensis* (NHMUK R2494–2500) are broken. Referred material includes an associated series of dorsal vertebrae with elongate neural spines that are vertically oriented (NHMUK R8649), which are now part of the holotype of the recently described taxon *Proplanicoxa galtoni* (Carpenter and Ishida, 2010). The neurapophyses are wider at the dorsal end than in the proximal region. According to Galton

Fig. 3. Comparative drawings of middle dorsal vertebrae from several ornithopod dinosaurs in left lateral view. A: GPIT 1802/1, Iguanodontia indet., Hauerivian-Barremian Salas de los Infantes (Burgos, Spain); B: NHMUK R604, *Hypselospinus fittoni*, Valanginian of Sussex (Norman, 2010: fig. 9A); C: NHMUK R798, *Barilium dawsoni*, Valanginian of Sussex (Norman, 2010: fig. 4A; reversed); D: IRSNB “individu S”, *Iguanodon bernissartensis*, Barremian to basal Aptian of Belgium (Norman, 1980: fig. 34, dorsal 6); E: IRSNB 1551, *Mantellisaurus atherfieldensis* [*Dollodon bampingi*] of Paul, 2008; *Dollodon seelyi* of Carpenter and Ishida, 2010, Barremian to basal Aptian of Belgium (Norman, 1986: fig. 29B, reconstructed dorsal 6); F: GPI-S.31, *Mantellisaurus atherfieldensis*, Barremian-Aptian of Westphalia (Norman, 1987a: fig. 9c); G: NHMUK R8649, *Proplanicoxa galtoni* [*Vectisaurus valdensis*], Barremian of the Isle of Wight (Galton, 1976: fig. 2A, D9; reversed); H: MDE uncatalogued (cast), cf. *Rhabdodon priscus*, Campanian of Languedoc (Buffetaut et al., 1996: fig. 6b; reversed); I–J: NMN GDF 300 (casts in MNHN), *Ouranosaurus nigeriensis*, Aptian of Niger (Taquet, 1976: fig. 38, No. 17 [dorsal 5] and No. 19 [dorsal 7]); K: AMNH 5206, *Hypacrosaurus altispinus*, Maastrichtian of Alberta (Brown, 1913: fig. 2a; reversed). Abbreviations: di: diapophysis; ne: neurapophysis; pa: parapophysis; po: postzygapophysis; pr: prezygapophysis. All figures on the same scale. Scale bar represents 10 cm.

Fig. 3. Dessins comparatifs des vertèbres dorsales moyennes de plusieurs ornithopodes en vue latérale gauche. A: GPIT 1802/1, Iguanodontia indet., Hauerivien-Barremien Salas de los Infantes (Burgos, Espagne); B: NHMUK R604, *Hypselospinus fittoni*, Valanginien de Sussex (Norman, 2010 : fig. 9A); C: NHMUK R798, *Barilium dawsoni*, Valanginien de Sussex (Norman, 2010 : fig. 4A; inversée); D: IRSNB « individu S », *Iguanodon bernissartensis*, Barremien inférieur de Belgique (Norman, 1980 : fig. 34, dorsale 6); E: IRSNB 1551, *Mantellisaurus atherfieldensis* [*Dollodon bampingi*] de Paul, 2008 ; *Dollodon seelyi* de Carpenter et Ishida, 2010, Barremien-Aptien inférieur de Belgique (Norman, 1986 : fig. 29B, dorsale 6); F: GPI-S.31, *Mantellisaurus atherfieldensis*, Barremien-Aptien de Westphalie (Norman, 1987a : fig. 9c); G: NHMUK R8649, *Proplanicoxa galtoni* [*Vectisaurus valdensis*], Barremien de l'Île de Wight (Galton, 1976 : fig. 2A, D9 ; inversée); H : MDE non catalogué (moulage), cf. *Rhabdodon priscus*, Campanien du Languedoc (Buffetaut et al., 1996 : fig. 6b ; inversée); I–J: NMN GDF 300 (moulages au MNHN), *Ouranosaurus nigeriensis*, Aptien de Niger (Taquet, 1976 : fig. 38, n° 17 [dorsal 5] et n° 19 [dorsale 7]); K: AMNH 5206, *Hypacrosaurus altispinus*, Maastrichtien d'Alberta (Brown, 1913 : fig. 2a ; inversée). Abréviations : di : diapophyse ; ne : neurapophyse ; pa : parapophyse ; po : postzygapophyse ; pr : prézygapophyse. Toutes les figures à la même échelle. Barre d'échelle : 10 cm.

(1976: fig. 2), the ratio between the height of the neural spine and the centrum is approximately 3.7 (Fig. 3G) in the middle dorsals and can reach 3.8 in the posteriormost dorsals. Reexamination of NHMUK R8649 indicates that the neural spines are incomplete. In the best preserved vertebra, the ratio is about 3.2.

Among European ornithopods, only the Late Cretaceous rhabdodontid *Rhabdodon* could have had such high neural spine (Fig. 3H; Buffetaut et al., 1996). As to other ornithopod species outside Europe, only a few have higher dorsal neural spines than the Salas taxon, i.e. *Ouranosaurus nigeriensis* from the Aptian of Niger (Taquet, 1976), *Hypacrosaurus altispinus* from the Maastrichtian of Canada (Brown, 1913) and an unnamed iguanodontian from the Albian of the United States (Scheetz et al., 2010). The mid-dorsal neuropophyses of *Ouranosaurus* are the highest of the series, approximately 7 to 7.5 times as high as the centra (NMN GDF 300; casts in MNHN; Taquet, 1976: figs. 37, 38, 73), whereas the anterior and posterior dorsal neuropophyses are slightly lower (ratio: 5 to 5.5) (Fig. 3I–J). The neural spines are petal-shaped and wider distally than proximally, except in the first middle dorsals where they are narrow and parallel-sided (Fig. 3I). The neural spines are vertical in the middle dorsals and become slightly inclined anteriorly in the posterior dorsals (Taquet, 1976). *Hypacrosaurus altispinus* possesses the tallest neural spines among hadrosaurids (Horner et al., 2004). Those of the middle dorsal vertebrae are approximately five times as high as the centrum, and are vertically oriented (AMNH 5204, 5206, 5217; Brown, 1913: fig. 2; Horner et al., 2004: fig. 20.9a; Fig. 3K). Finally, an unnamed iguanodontian from Utah is characterized by dorsal neural spines 5.5 times as high as the centrum (Scheetz et al., 2010).

The function of the high neural spines in *Ouranosaurus* and other long-spined dinosaurs is the source of some debate. It has been suggested that such high neural spines could be related to thermal biology (Bailey, 1997), but the precise function of these structures remains uncertain.

7. Conclusions

The dorsal vertebrae from the Lower Cretaceous (Upper Hauterivian-Lower Barremian Pinilla de los Moros Formation) near Salas de los Infantes (Burgos, Spain) represent a tall-spined ornithopod, the first found in the Iberian record. This material is here regarded as that of a medium-sized (roughly 5 m long) iguanodontian. It was previously assigned to *Iguanodon cf. fittoni* but differences in the elongation of the middle dorsal neuropophyses (4.5 times as high as the centrum) and their vertical orientation indicate that it is not referable to that (or any other known) iguanodontian species. We regard the Salas ornithopod as a potentially distinct taxon, but suggest that it would be inadvisable to erect a new genus and species given the incomplete material available. Among ornithopods, several lineages of Cretaceous iguanodontians have representatives that bear greatly elongated (e.g., more than four times as high as the centrum) neural spines in the dorsal vertebrae. The elongation of the dorsal neuropophyses reaches its greatest expression in *Ouranosaurus* (with a ratio of up to 7.5 times).

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References

- Bailey, J.B., 1997. Sailbacks or buffalo-backs? Neural spine elongation in dinosaurs. *J. Paleontol.* 71, 1124–1146.
- Beuther, A., 1966. Geologische Untersuchungen in Wealden und Utrillas-Schichten im Westteil der Sierra de los Cameros (Nordwestliche Iberische Ketten, Spanien). *Beih. Geol. Jb.* 44, 103–121.
- Beuther, A., Dahm, H., Kneuper-Haack, F., Mensink, H., Tischer, G., 1966. Der Jura und Wealden in Nordost-Spanien. *Beih. Geol. Jb.* 44, 1–225 (47 pls).
- Brown, B., 1913. A new trachodont dinosaur. *Hypacrosaurus*, from the Edmonton Cretaceous of Alberta. *Bull. Am. Mus. Nat. Hist.* 32, 395–406.
- Buffetaut, E., Costa, G., Le Loeuff, J., Martin, M., Rage, J.C., Valentín, X., Tong, H., 1996. An Early Campanian vertebrate fauna from the Villeveyrac Basin (Hérault, southern France). *N. Jb. Geol. Paläont. Mh.* 1, 1–16.
- Carpenter, K., Ishida, Y., 2010. Early and "Middle" Cretaceous Iguanodonts in time and space. *J. Iberian Geol.* 36, 145–164.
- Clemente, P., Pérez Arlucea, M., 1993. Depositional architecture of the Cuerda del Pozo Formation. Lower Cretaceous of the extensional Cameros Basin, north-central Spain. *J. Sedim. Petrol.* 63, 437–452.
- Dietl, G., 1969. Geologische Kartierung des Jura in der Umgebung von Honoria (westliche Keltiberische Ketten, Spanien). Master thesis, Universität Tübingen (unpublished).
- Dollo, L., 1888. Iguanodontidae et Camptonotidae. *C. R. Hebd. Acad. Sci. Paris* 106, 775–777.
- Galton, P.M., 1976. The dinosaur *Vectisaurus valdensis* (Ornithischia: Iguanodontidae) from the Lower Cretaceous of England. *J. Paleontol.* 50, 976–984.
- Galton, P.M., 2009. Notes on Neocomian (Lower Cretaceous) ornithopod dinosaurs from England – *Hypsilophodon*, *Valdosaurus*, "*Campsaurus*", "*Iguanodon*" – and referred specimens from Romania and elsewhere. *Rev. Paleobiol.* 28, 211–273.
- Horner, J.R., Weishampel, D.B., Forster, C.A., 2004. Hadrosauridae. In: Weishampel, D.B., Dodson, P., Osmólska, H. (Eds.), *The Dinosauria*, Second edition. University of California Press, Berkeley, pp. 438–463.
- Irmis, R.B., 2007. Axial skeleton ontogeny in the Parasuchia (Archosauria: Pseudosuchia) and its implications for ontogenetic determination in archosaurs. *J. Vert. Paleontol.* 27, 350–361.
- Knoll, F., 2009. A large iguanodont from the Upper Barremian of the Paris Basin. *Geobios* 42, 755–764.
- Lydekker, R., 1888. Catalogue of the Fossil Reptilia and Amphibia in the British Museum. Part I. Containing the Orders Ornithosauria, Crocodilia, Dinosauria, Squamata, Rhynchocephalia, and Proterosauria. British Museum of Natural History, London, 309 p.
- Lydekker, R., 1889. Notes on new and other Dinosaurian remains. *Geol. Mag.* 3 (6), 352–357.
- Maisch, M.W., 1997. The Lower Cretaceous dinosaur *Iguanodon cf. fittoni* Lydekker, 1889 (Ornithischia) from Salas de los Infantes (Province Burgos, Spain). *N. Jb. Geol. Paläont. Mh.* 4, 232–241.
- Marsh, O.C., 1881. Principal characters of the American Jurassic dinosaurs. Part V. *Am. J. Sci.* 21, 417–423.
- Martill, D.M., Naish, D., 2001. Dinosaurs of the Isle of Wight. Palaeontological Association, London. Field Guide to Fossils 10, 433 p.

- Martín-Closas, C., Alonso Millán, A., 1998. Estratigrafía y bioestratigrafía (Charophyta) del Cretácico inferior en el sector occidental de la Cuenca de Cameros (Cordillera Ibérica). *Rev. Soc. Geol. España* 11, 253–269.
- Norman, D.B., 1980. On the ornithischian dinosaur *Iguanodon bernissartensis* from the Lower Cretaceous of Bernissart (Belgium). *Mem. Inst. R. Sci. Nat. Belg. Sci. Terre* 178, 1–105.
- Norman, D.B., 1986. On the anatomy of *Iguanodon atherfieldensis* (Ornithischia: Ornithopoda). *Bull. Inst. R. Sci. Nat. Belg., Sci. Terre* 56, 281–372.
- Norman, D.B., 1987a. A mass-accumulation of vertebrates from the Lower Cretaceous of Nehden (Sauerland), West Germany. *Proc. R. Soc. Lond. B* 230, 215–255.
- Norman, D.B., 1987b. Wealden dinosaur biostratigraphy. In: Currie, P.T., Koster, E.H. (Eds.), Fourth Symposium on Mesozoic Terrestrial Ecosystems, Short Papers. Drumheller: Tyrrell Museum of Palaeontology, Drumheller, pp. 161–166.
- Norman, D.B., 1990. A review of *Vectisaurus valdensis*, with comments on the family Iguanodontidae. In: Carpenter, K., Currie, P.J. (Eds.), Dinosaur Systematics: Approaches and Perspectives. Cambridge University Press, Cambridge, pp. 147–161.
- Norman, D.B., 2004. Basal Iguanodontia. In: Weishampel, D.B., Dodson, P., Osmólska, H. (Eds.), The Dinosauria, Second Edition. University of California Press, Berkeley, pp. 413–437.
- Norman, D.B., 2010. A taxonomy of iguanodontians (Dinosauria: Ornithopoda) from the lower Wealden Group (Cretaceous: Valanginian) of southern England. *Zootaxa* 2489, 47–166.
- Norman, D.B., in press. Iguanodontian dinosaurs from the Lower Cretaceous of Britain and Belgium: a brief review. In: Godefroit, P. (Ed.), Bernissart Dinosaurs and Early Cretaceous Terrestrial Ecosystems, Series Life in the Past, 464 pp. Indiana University Press, Bloomington and Indianapolis. See http://www.iupress.indiana.edu/catalog/product_info.php?products_id=922060.
- Owen, R., 1842. Report on British Fossil Reptiles. Part 2. Report. Brit. Ass. Adv. Sci. (Plymouth) 11, 60–204.
- Paul, G.S., 2007. Turning the old into the new: a separate genus for the gracile iguanodont from the Wealden of England. In: Carpenter, K. (Ed.), Horns and beaks: ceratopsian and ornithopod dinosaurs. Indiana University Press, Bloomington & Indianapolis, pp. 69–77.
- Paul, G.S., 2008. A revised taxonomy of the iguanodont dinosaur genera and species. *Cret. Res.* 29, 192–216.
- Pereda Suberbiola, X., Ruiz-Omeñaca, J.I., Canudo, J.I., Torcida, F., Sanz, J.L., in press. Dinosaur faunas from the Early Cretaceous (Valanginian-Albian) of Spain. In: Godefroit, P. (Ed.) Bernissart Dinosaurs and Early Cretaceous Terrestrial Ecosystems, Series Life in the Past, 464 pp. Indiana University Press, Bloomington & Indianapolis. See http://www.iupress.indiana.edu/catalog/product_info.php?products_id=922060.
- Ruiz-Omeñaca, J.I., Pereda Suberbiola, X., Torcida Fernández-Baldor, F., Maisch, M., Izquierdo, L.A., Huerta, P., Contreras, R., Montero Huerta, D., Pérez Martínez, G., Urién Montero, V., Welle, J., 2008. Resto mandibular de ornitópodo iguanodontideo (Dinosauria) del Cretácico Inferior de Salas de los Infantes (Burgos) en las colecciones del Institut für Geowissenschaften de Tübingen (Alemania). *Geogaceta* 45, 63–66.
- Scheetz, R., Britt, B., Higgerson, J., 2010. A large, tall-spined iguanodontid dinosaur from the Early Cretaceous (Early Albian) Basal Cedar Mountain Formation of Utah. *J. Vert. Paleontol.* 28 (Suppl. 3), 158A.
- Seeley, H.G., 1887. On the classification of the fossil animals commonly named Dinosauria. *Proc. Roy. Soc. Lond.* 43, 165–171.
- Taquet, P., 1976. Géologie et Paléontologie du gisement de Gadoufaoua (Aptien du Niger). Centre National de la Recherche Scientifique, Cahiers de Paléontologie, Paris, 191 p.
- Torcida Fernández-Baldor, F., 2006. Restos directos de dinosaurios en Burgos (Sistema Ibérico): un balance provisional. Colectivo Arqueológico-Paleontológico de Salas. III Jornadas Internacionales sobre Paleontología de los Dinosaurios y su Entorno, Actas, Salas de los Infantes, Burgos, Spain, pp. 105–128.
- Torcida Fernández-Baldor, F., Canudo, J.I., Huerta, P., Montero, D., Pereda Suberbiola, X., Salgado, L., in press. *Demandasaurus darwini*, a new rebbachisaurid sauropod from the Early Cretaceous of the Iberian Peninsula. *Acta Palaeontol. Pol.* 56, 3.
- Torcida Fernández-Baldor, F., Ruiz-Omeñaca, J.I., Pereda Suberbiola, X., Maisch, M.W., Izquierdo, L.A., Huerta, P., Contreras, R., Montero Huerta, D., Pérez Martínez, G., Urién Montero, V., Welle, J., 2008. La colección de restos de dinosaurios del Cretácico Inferior de Salas de los Infantes (Burgos, España) depositada en el Institut und Museum für Geologie und Paläontologie de Tübingen (Alemania). In: Ruiz-Omeñaca, J.I., Piñuela, L., García-Ramos, J.C. (Eds.), XXIV Jornadas de la Sociedad Española de Paleontología, Libro de resúmenes. MUJA, Colunga, Spain, pp. 205–206.