

New material and phylogenetic position of the basal iguanodont dinosaur *Delapparentia turolensis* from the Barremian (Early Cretaceous) of Spain

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Received: 27 December 2013 / Accepted: 18 December 2014 / Available online: 25 March 2015

Abstract

Delapparentia turolensis Ruiz-Omeñaca, 2011 is the only iguanodont taxon erected in the Barremian of Spain. It is described on the basis of a partial postcranial skeleton discovered in the 1950s near the village of Galve (Teruel Province), within the Camarillas Formation. Recently, new remains from the same individual have been recovered, and these are described here. Furthermore, after first-hand examinations of the holotype, the phylogenetic position of this taxon has been analysed for the first time, and its diagnosis is emended. *Delapparentia turolensis* is a large-sized, basal iguanodont which presents an autapomorphic, unusually high axial neural spine and a unique combination of postcranial characters. The ilium morphology differs from that of other basal iguanodonts and relates *Delapparentia* to the Valanginian *Barilium dawsoni* from England, with whom it shares two synapomorphies. In our phylogenetic analysis *Delapparentia* is recovered in a polytomy with *Kukufeldia*, *Lanzhousaurus*, *Barilium* and the clade equivalent to Iguanodontoidea.

Keywords: axial neural spine, Styrcosterna, *Iguanodon*, *Barilium*, Galve, Teruel

Resumen

Delapparentia turolensis Ruiz-Omeñaca, 2011 es el único taxón iguanodonte definido en el Barremiense de España. Está descrito a partir de un esqueleto postcraneal parcial descubierto en la década de 1950 próximo al pueblo de Galve (provincia de Teruel), dentro de la Formación Camarillas. Recientemente, se han recuperado nuevos restos del mismo individuo que se describen aquí. Además, tras examinar de primera mano el holotipo, se ha analizado la posición filogenética de este taxón por primera vez además de enmendar su diagnóstico. *Delapparentia turolensis* es un iguanodonte basal de gran tamaño, que presenta una espina neural axial autapomórfica, al ser inusualmente alta, y una combinación única de caracteres postcraneales. La forma del ilion es diferente de la de otros iguanodontes basales y relaciona a *Delapparentia* con *Barilium dawsoni* del Valanginiense de Inglaterra, al compartir de forma exclusiva dos sinapomorfías. En nuestro análisis filogenético *Delapparentia* se sitúa en una politomía con *Kukufeldia*, *Lanzhousaurus*, *Barilium* y el clado equivalente a Iguanodontoidea.

Palabras clave: espina neural del axis, Styrcosterna, *Iguanodon*, *Barilium*, Galve, Teruel

1. Introduction

Many Lower Cretaceous localities from the Iberian Peninsula have yielded iguanodont remains, some of which belong to one of several European taxa such as *Mantellisaurus* (Sanz *et al.*, 1984; Llandres Serrano *et al.*, 2013) or *Iguanodon* (Gasulla *et al.*, 2014), others of which are only described in Iberia, such as *Delapparentia* and *Proa* (Ruiz-Omeñaca, 2011; McDonald *et al.*, 2012b), while others belong to as yet

undescribed taxa (Fuentes Vidarte *et al.*, 2005; Gasca *et al.*, 2009; Pereda-Suberbiola *et al.*, 2011). Taking into account only the confirmed taxa, the Iberian fauna of basal iguanodonts is distributed over the course of the Early Cretaceous as follows: *Delapparentia turolensis* in the Barremian (Ruiz-Omeñaca, 2011), *Iguanodon bernissartensis* in the Aptian (Gasulla *et al.*, 2014), and *Proa valdearinnensis* in the Albian (McDonald *et al.*, 2012b). This limited faunal list contrasts with the diversity of iguanodonts in the faunas of the Lower

Cretaceous of Europe (Table 1), where the coexistence of at least two taxa has been registered for each time interval (Norman, 2010; 2011a).

However, it is possible that the Early Cretaceous Iberian iguanodontian faunas are in fact more diverse than can be known for certain at present. This is suggested by the presence of forms related to *Mantellisaurus* and *Owenodon* in the Barremian and Aptian of Spain (Ruiz-Omeñaca, 2006; Galton, 2012; Llandres Serrano et al., 2013; Gasulla et al., 2014), as well as the coexistence of potentially distinct taxa, such as a tall-spined iguanodontian from Burgos (Pereda-Suberbiola et al., 2011). An additional line of evidence is the differentiation of dental morphotypes recorded in some Iberian fossil localities (Gasca et al., 2008; Canudo et al., 2010; Gasca et al., 2014).

The Barremian iguanodont record from the Iberian Range is abundant but fragmentary and undiagnostic in most cases. *Delapparentia turolensis* is the only taxon described in this interval of time. It is described on the basis of a partial postcranial skeleton recovered from the La Maca-3 locality, which is located on a small hill two kilometres east of the village of Galve (Fig. 1). Early Cretaceous outcrops of Galve are located within the Galve Sub-basin, in the Maestrazgo Basin (Fig. 1). The fossiliferous levels comprise lutites that represent floodplain deposits located in the middle part of the Camarillas Formation (Fig. 1). This formation is a predominantly fluvial unit from the Wealden facies (Díaz Molina and Yébenes, 1987) and is Barremian (Early Cretaceous) in age (Canudo et al., 2012).

In addition to *Delapparentia*, the dinosaur record from the Camarillas Formation in Galve is composed of the basal ornithopod *Gideonmantellia amosanjuanae* (Ruiz-Omeñaca et al., 2012), represented by an isolated skeleton, as well as other taxa represented by isolated remains identified as Stegosauria indet., Ornithopoda indet., Iguanodontoidea indet., Sauropoda indet., Euhelopodidae indet., Allosauroida? indet., and several Maniraptoriformes (Sanz et al., 1987; Ruiz-Omeñaca et al., 2004; Ruiz-Omeñaca, 2011).

Fossil remains of *Delapparentia* were discovered and collected in the 1950s by the local amateur José María Herrero

in Galve (Teruel, Spain) and were initially described by Laparent (1960), who assigned them to *Iguanodon bernissartensis*. The holotype (Museo de Teruel, MPT/I.G.) was the only record of this taxon until recently (Gasca et al., 2014). Since its discovery, several fragmentary remains have been recovered during subsequent fieldwork at the outcrop and on the dump of the original excavation. One of these remains, together with previously unidentifiable fragments, has allowed us to reconstruct most of the neural arch of the axis. The proximal part of the left scapula has also recently been recovered, representing the first known remnant from the scapular girdle of *Delapparentia*. Ruiz-Omeñaca (2011) erected *Delapparentia* and identified it as a non-hadrosaurid iguanodontoid, but no phylogenetic analysis was presented. *Delapparentia* was included in a data matrix in subsequent studies of basal iguanodont phylogeny, but its phylogenetic position was not analysed (McDonald, 2012a; McDonald et al., 2012b).

The aim of this paper is to describe new, unpublished material belonging to the holotype specimen of *Delapparentia turolensis*, as well as reviewing the diagnosis after first-hand examinations of the previously published material and analysing the phylogenetic position of this taxon for the first time.

Institutional abbreviation: MPT: Museo de Teruel, Teruel, Spain.

2. Systematic Palaeontology

- Dinosauria Owen, 1842
- Ornithischia Seeley, 1887
- Ornithopoda Marsh, 1881
- Iguanodontia Dollo, 1888
- Styracosterna Sereno, 1986
- Delapparentia* Ruiz-Omeñaca, 2011
- Delapparentia turolensis* Ruiz-Omeñaca, 2011

Holotype: MPT/I.G., a partial postcranial skeleton that comprises the neural arch of the axis and another four cer-

Stage	Spain	England	References
Albian	<i>Proa valdearriñoensis</i>		McDonald et al. (2012b)
Aptian / Barremian	<i>Iguanodon bernissartensis</i> <i>cf. Mantellisaurus atherfieldensis</i>	<i>Iguanodon bernissartensis</i> <i>Mantellisaurus atherfieldensis</i>	Norman (2011b); Llandres Serrano et al. (2013); Gasulla et al. (2014)
Barremian	<i>Delapparentia turolensis</i>	" <i>Iguanodon seelyi</i> "*	Norman (2011b); Ruiz-Omeñaca (2011)
Hauterivian			
Valanginian		<i>Hypselospinus fittoni</i> <i>Barilium dawsoni</i> <i>Kukufeldia tilgatensis</i> * <i>Sellacoxa pauli</i> *	Carpenter and Ishida (2010); McDonald et al. (2010a); Norman (2011b)
Berriasian		<i>Owenodon hoggii</i>	Galton (2012)

*: Iguanodont taxa with questionable taxonomic validity

Table 1.- Simplified overview of European iguanodont distribution, based on Spanish and English Early Cretaceous records.

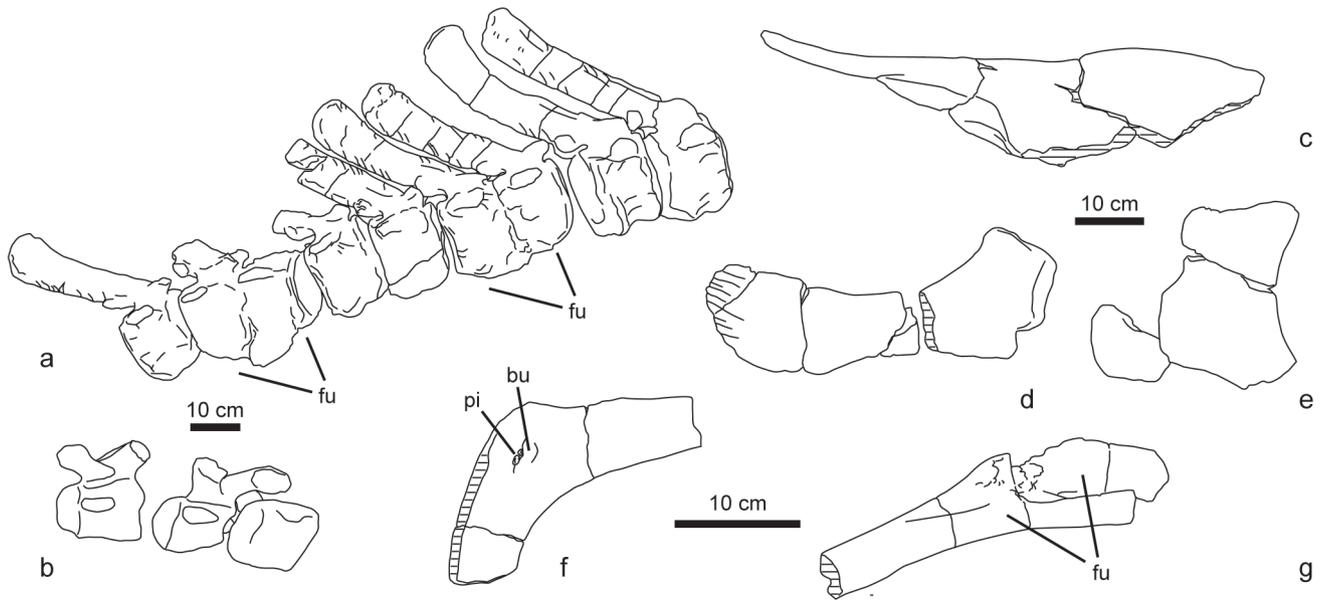


Fig. 2.- Selected remains of *Delapparentia turolensis* holotype (MPT/I.G.): anterior caudal vertebrae –discontinuous series– (a), cervical vertebrae (b), left ilium (c), pubis (d) and ischium (e), dorsal rib fragment with a striking structure (f) i.e. pneumatic foramina sensu Ruiz-Omeñaca (2011) and dorsal rib fragment with the tuberculum fused with the diapophysis of the corresponding dorsal vertebra. Vertebrae (a, b) figured as they are mounted in Dinópolis exhibition of Galve, Teruel. Abbreviations: fu – fused elements, pi – pit, bu – bulge.

sal and ventral edges that diverge towards its anterior end, the ventral edge being more concave than the dorsal in profile.

Comments: In the original diagnosis, Ruiz-Omeñaca (2011) provided the following autapomorphies for *Delapparentia turolensis*: 1) posterior dorsal ribs with long, parallel and unfused capitulum and tuberculum, 2) ossified sternal ribs, and 3) horizontal, twisted and lateromedially expanded preacetabular process of ilium (convergent in *Zalmoxes*), as well as the presence of anterior dorsal ribs with a pneumatic foramen and an ischium that is large in relation to the ilium. None of these has been retained in our proposal, at least in its original sense. The posterior dorsal ribs with long, parallel and unfused capitulum and tuberculum (1) were misinterpreted. These rib fragments (see Fig. 4H, I in Ruiz-Omeñaca, 2011) are actually posterior dorsal ribs with the tuberculum fused with the diapophysis of the corresponding dorsal vertebra (Fig. 2g). This could indicate a mature age – even an old state – in this individual and is coherent with the ossification observed between some caudal centra of the individual (Fig. 2a), which was previously reported and discussed by Lapparent (1960) and Ruiz-Omeñaca (2011). Partial ossification of sternal rib segments (2) has been reported in other iguanodont taxa such as *Mantellisaurus* and *Iguanodon* and other basal ornithopods such as *Dryosaurus*, *Camptosaurus* or *Zalmoxes* (Weishampel et al., 2003: character 11). As for the ilium, the horizontal, twisted and lateromedially expanded preacetabular process of the ilium (convergent in *Zalmoxes*, 3) has been modified because, despite being lateromedially expanded, the preacetabular process of *Delapparentia* differs with respect to the twisted dorsal margin of *Zalmoxes* (Weishampel et al.,

2003: fig. 22; Godefroit et al., 2009: fig. 18). The preacetabular process of *Zalmoxes* twists along its length such that the dorsal surface of the ilium becomes the lateral surface of the anterior end of the process, whereas in *Delapparentia* the lateral edge of the process comes from the lateroventral edge ending dorsal to the pubic peduncle, this morphology being closer to the typical horizontal boot of other iguanodonts (McDonald et al., 2012a) and similar to the morphology that Norman (2011a) describes as an autapomorphic character in *Barilium*. As regards the additional characters provided in the original diagnosis, the pneumatic foramen previously identified in the anterior dorsal ribs (Ruiz-Omeñaca, 2011: fig. 4G) is a slight pit with a bulge that seems rather to be a structure like a muscle attachment (Fig. 2f). Finally, an ischium that is large in size in relation to the ilium is ambiguous in nature as a character and in any case invalid because the ilium is actually less complete than Ruiz-Omeñaca (2011) considered (see description below).

Description and comparison

In this chapter only the new material (axis and scapula) is described in detail, as well as the older material that is relevant for the diagnosis. For a complete description of all postcranial remains of *Delapparentia turolensis* see Ruiz-Omeñaca (2011).

The fossil remains show good preservation, with no evidence of significant biostratinomic alteration. The post-burial distortion is not significant for the systematics. Most of the information loss in the holotype bones is a result of the inadequate collection of this material in the 1950s.

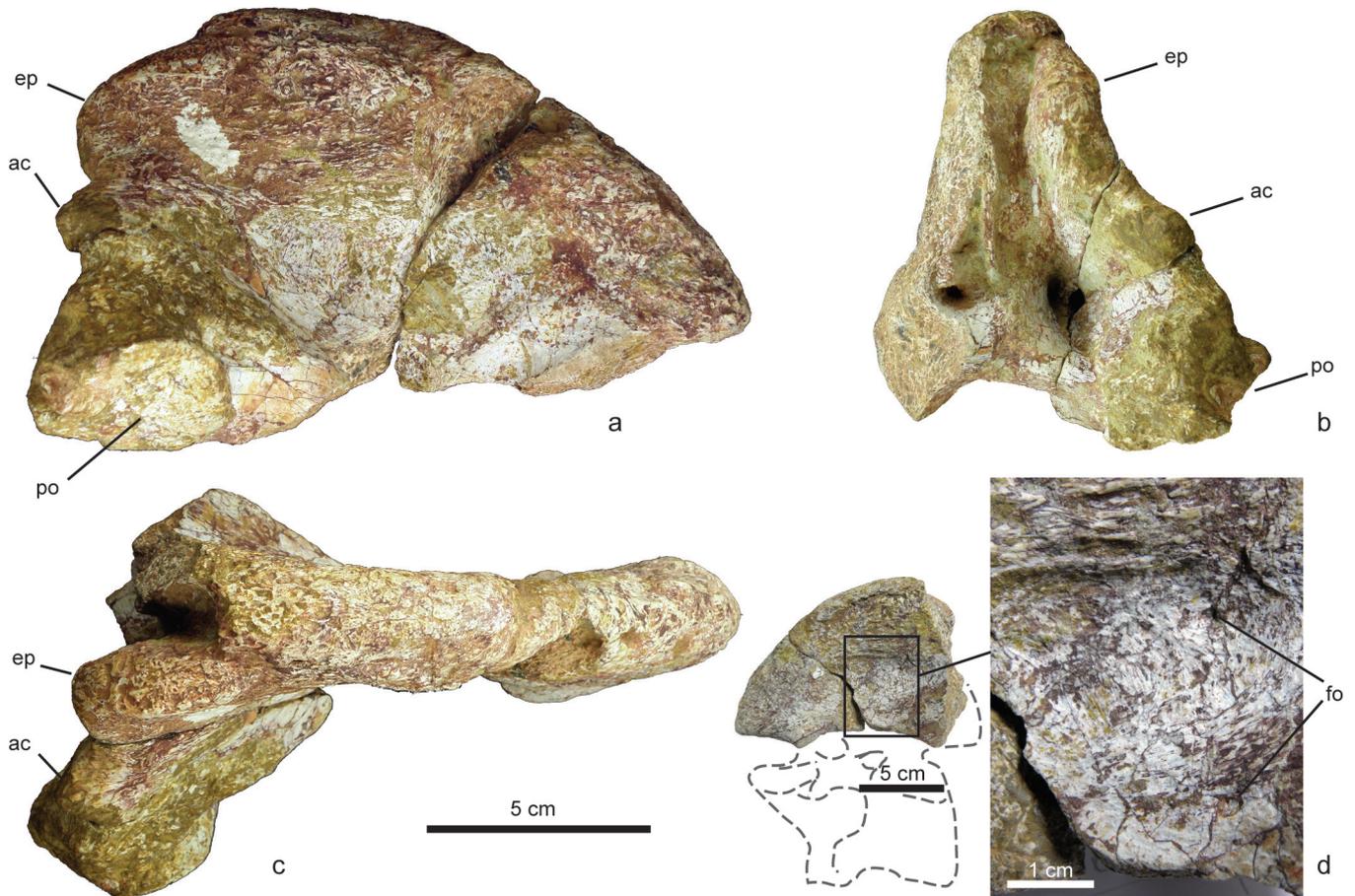


Fig. 3.- Axial neural spine of *Delapparentia turolensis* MPT/I.G., in right lateral (a), posterior (b) and dorsal (c) views; and magnification of the left lateral surface bearing two tiny foramina (d). Abbreviations: ep – epiphysis, ac – accessory bulge, po – postzygapophysis, fo – foramen.

Axis

Only the neural arch is known, with the regions of the neural spine and right postzygapophyseal complete, while no remains have been recovered below the roof of the neural channel, the prezygapophyses and the transverse processes being absent (Fig. 3).

The axial neural spine is lateromedially compressed and dorsally convex in lateral view (Fig. 3), forming a large blade-like structure similar to those of basal iguanodonts such as *Iguanodon* (Norman, 1980: Fig. 24), and quite dissimilar from the sloping, dorsally concave axial neural spines of more basal iguanodontians such as *Tenontosaurus tilletti* (Winkler et al., 1997) or *Camptosaurus dispar* (Gilmore, 1909). The neural spine is exceptionally tall. *Delapparentia* is the only taxon among the iguanodonts and basal ornithopods so that the height of the axial neural spine from the base of the postzygapophysis is clearly greater than half the length of the neural arch (Fig. 4). This relationship between height and length expressed as a percentage is 59% in *Delapparentia*, which contrasts with the lower values in other ankylopollexians (Fig. 4), such as 48% in *Camptosaurus dispar* (Gilmore, 1909), 46% in *Iguanodon* (Norman, 1980), 45% in

Ouranosaurus (Taquet, 1976), and 43% in *Taninus* (Wiman, 1929), and with much lower values such as 37% in *Mantellisaurus* (Norman, 1986), 28% in *Mantellisaurus* sp. (Norman, 1987), and 35% in *Bactrosaurus* (Godefroit et al., 1998).

The anterior end is hook-shaped, as in other basal iguanodonts such as *Iguanodon* (Norman, 1980). The lateral surfaces are slightly concave, with the presence of at least two tiny foramina visible in the left side (Fig. 3d). The apex of the neural spine is strongly convex and posteriorly placed as in *Iguanodon* (Norman, 1980), but unlike other basal iguanodonts such as *Iguanacolossus*, *Mantellisaurus* and *Ouranosaurus* and hadrosauroids such as *Bactrosaurus* and *Taninus*, where the apex of the neural spine is gently convex and there is a slight embayment between the apex and the posterior edge.

Posteriorly, the neural spine bifurcates in dorsal view to form two divergent, posterolaterally directed buttresses. Each buttress bears a posteriorly directed, blunt bulge (i.e. epiphysis) in the dorsal part, a small, posterolaterally directed, blunt bulge in the middle part, and ends in a large, lateroventrally oriented and elliptical postzygapophyseal facet. The epiphyses are positioned ventral to the dorsal margin of the neural spine, as in *Iguanodon* (Norman, 1980)

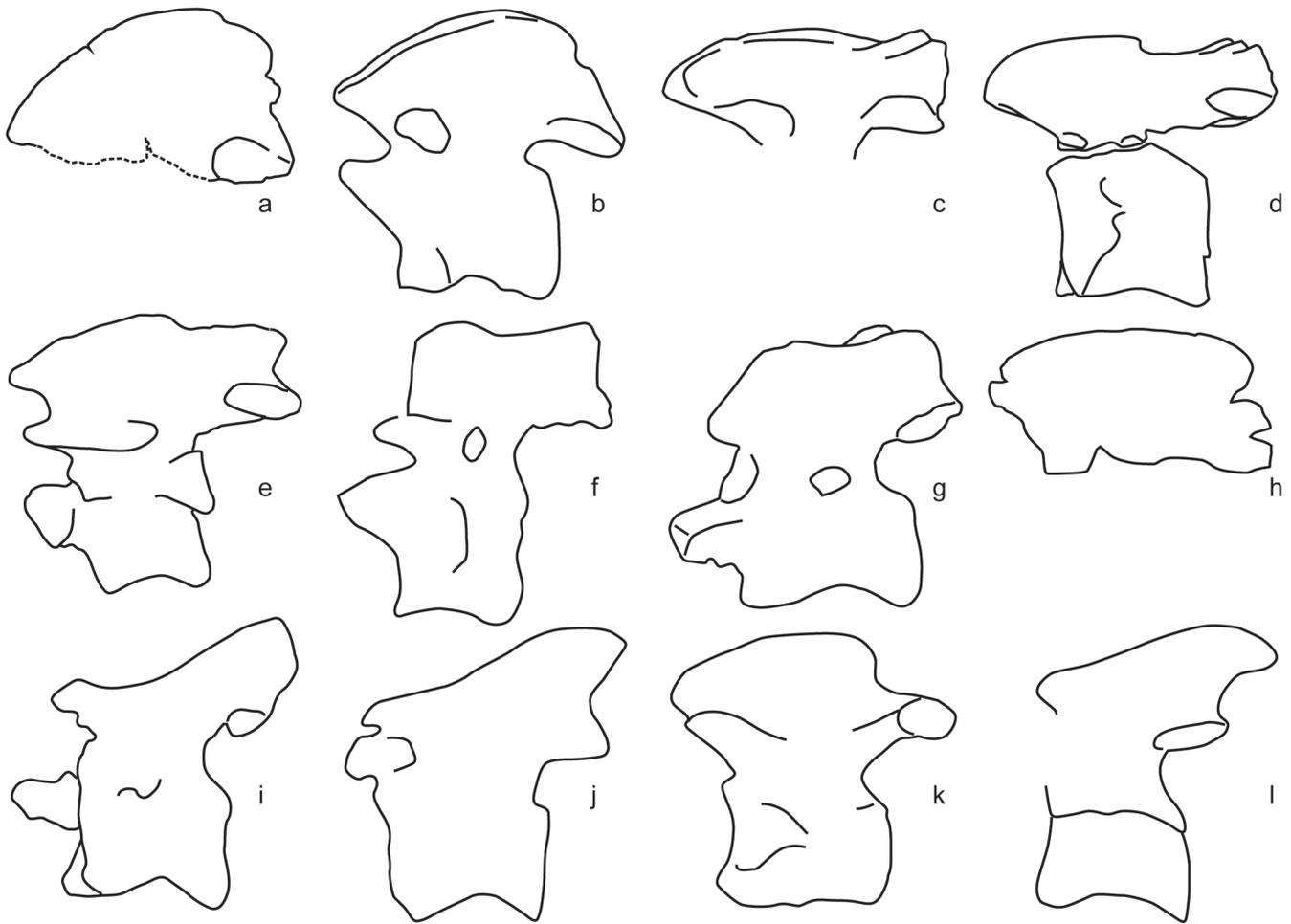


Fig. 4.- Comparisons of the axis in lateral view of (a) *Delapparentia* (right reversed), (b) *Iguanodon* (after Norman, 1980), (c) *Mantellisaurus* (after Norman, 1986), (d) *Mantellisaurus* sp. (after Norman, 1987), (e) *Bactrosaurus* (after Godefroit et al., 1998), (f) *Tanuis* (after Wiman, 1929), (g) *Ouranosaurus* (after Taquet, 1976), (h) *Iguanacolossus* (after McDonald et al., 2010b), (i) *Camptosaurus dispar* (after Gilmore, 1909), (j) *Tenontosaurus tilletti* (after Winkler et al., 1997), (k) *Zalmoxes robustus* (right reversed, Weishampel et al., 2003), (l) *Lesothosaurus* (right reversed, after Sereno, 1991).

and *Jinzhouosaurus* (Wang et al., 2011), and unlike *Mantellisaurus* (Norman, 1986) and *Ouranosaurus* (Taquet, 1976), where they are positioned approximately at the same level. A similar blunt accessory process between the epiphysis and postzygapophysis is also present in *Iguanodon* (Norman, 1980) and *Mantellisaurus* (Norman, 1986, 1987), and poorly defined in *Ouranosaurus* (Taquet, 1976), whereas it is absent in *Camptosaurus* (Gilmore, 1909), *Jinzhouosaurus* (Wang et al., 2011), *Bactrosaurus* (Godefroit et al., 1998) and *Tanuis* (Wiman, 1929).

Scapula

Only a proximal portion of the right scapula is preserved (Fig. 5). The anterior margin is lateromedially thickened along the articular surface for the coracoid. In profile, the edge between the glenoid – in the anteroventral margin – and the articular surface for the coracoid is pronounced, as in cf. *Barilium* (Norman, 2011a: Fig. 21), and unlike in other iguanodonts (e.g. *Mantellisaurus*, McDonald, 2012b: fig. 4;

Eolambia, McDonald 2012a: fig. 27). The acromion process is dorsally directed, as in other basal iguanodonts (e.g. *Eolambia*, McDonald et al., 2012a: fig. 27), and unlike in hadrosaurids (McDonald, 2012a: character 102). In lateral view, the shape of the acromion process is convex in general terms (Fig. 5a), although it is difficult to discern whether it is more similar to the subtriangular shape of *Barilium* or to the convexity usual in other iguanodonts (McDonald, 2012a: character 101). This difficulty is a consequence of the incompleteness of the process in its anterodorsal margin and the presence of a slight distortion.

Ilium

The completeness of the left ilium was originally overestimated by Ruiz-Omeñaca (2011). In fact, it is preserved more fragmentarily, with the ventral half and most of the preacetabular process lost due to their breakage during excavation. This reinterpretation is based on the presence of facets for the attachment of the sacral yoke in the ventralmost pre-

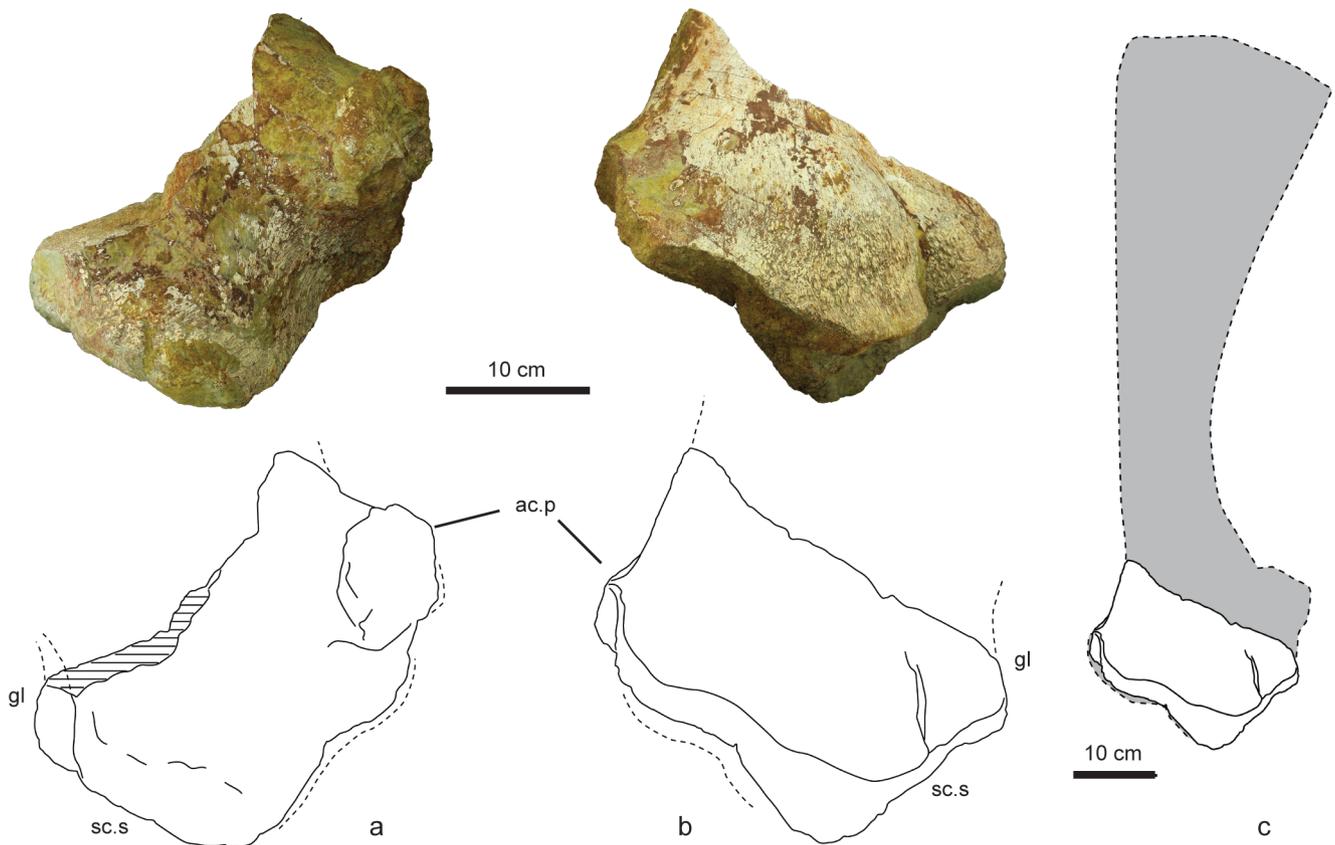


Fig. 5.- Right scapula of *Delapparentia turolensis* MPT/I.G., in lateral (a) and medial (b, c) views. In c the reserved remains of *D. turolensis* are drawn on the complete outline of scapula, reconstructed from the comparison with cf. *Barilium* sp. (NHMUK R2848, Norman, 2011a: fig. 21). Abbreviations: ac.p – acromion process, gl – glenoid, sc.s – scapulocoracoid sutural surface.

served part (Fig. 6). This implies that the entire ilium would be larger than expected. The ilium, as preserved, is 780 mm long and 170 mm deep. Using the ilium of *Barilium* (Norman, 2010: fig. 3) as a point of comparison to reconstruct the entire ilium of *Delapparentia*, it would have an approximate length of 1120 mm and a depth of 370 mm. The ilium of *Delapparentia* is bigger than the *Barilium* holotype and comes close in size to the biggest known individual of *Iguanodon* (NHMUK R2502, Norman, 2011b: fig. 27.50). The large size of the *Delapparentia* holotype may be due to the senile state of the individual, which is also suggested by the fusion of certain axial elements (dorsal ribs and neural arches, pairs of caudal centra) and the ossification of the sternal ribs.

The preacetabular process (Fig. 6) of the ilium projects anteriorly and terminates in a flattened, horizontal boot. The lateral surface of the preacetabular process twists around its long axis towards its anterior end so that it comes to face almost dorsally as in *Barilium* (Norman, 2011a) and unlike all other iguanodonts. The maximum lateromedial expansion occurs halfway along and decreases progressively in width towards the anterior end, which is complete and superficially eroded only at the edges of the tip.

In the preacetabular notch, the rim of the sacrodorsal rib facet is visible in lateral view (Fig. 6), which is a synapomor-

phy only shared with *Barilium* and the specimen NHMUK R2502 (holotype of *Iguanodon seelyi* and currently assigned to *Iguanodon bernissartensis*, Norman, 2011b: fig. 27.50).

In profile, the dorsal edge is nearly straight in the central portion of the body, as well as in the proximal part of the preacetabular process (i.e. dorsal to the preacetabular notch), as in *Camptosaurus* (McDonald, 2011), *Cedrorestes* (McDonald et al., 2010b: Fig. 18), *Hypselospinus* (Norman, 2010) and *Eolambia* (McDonald et al., 2012a), and unlike in other iguanodonts. The profile of *Delapparentia* differs slightly from *Barilium* (Norman, 2011a), with its gently convex dorsal margin, and from *Mantellisaurus* (Norman, 1986), with its dorsal margin straight in the central portion of the body but convex dorsal to the preacetabular notch, and differs clearly from basal iguanodonts such as *Iguanacolossus* (McDonald et al., 2010b), *Iguanodon* (Norman, 1980) and *Ouranosaurus* (Taquet, 1976), with a clearly convex dorsal edge, and from hadrosauroids such as *Gilmoresaurus* or *Corythosaurus* (McDonald et al., 2010b: fig. 17), with a marked convexity dorsal to the preacetabular notch. In dorsal view, the dorsal edge of the ilium is rounded dorsal to the pubic peduncle and progressively increases its width caudally to become a rugose, thick, flattened dorsal edge that faces dorsolaterally. This morphology differs clearly from the transversely com-

pressed dorsal edge of *Hypselospinus* (Norman, 2010) and is difficult to distinguish from *Barilium*, whose flat, transversely thick dorsal edge is considered autapomorphic by Norman (2011a). However, the posteriormost part of the dorsal edge preserved in *Delapparentia* represents a morphology differ-

ent from the laterally everted rim of iguanodontoids such as *Iguanodon* (Norman, 1980), *Proa* (McDonald et al., 2012b) and *Mantellisaurus* (Norman, 1986).

The lateral surface of the ilium is nearly flat, displaying a slight concavity dorsoventrally. The medial surface is flat-

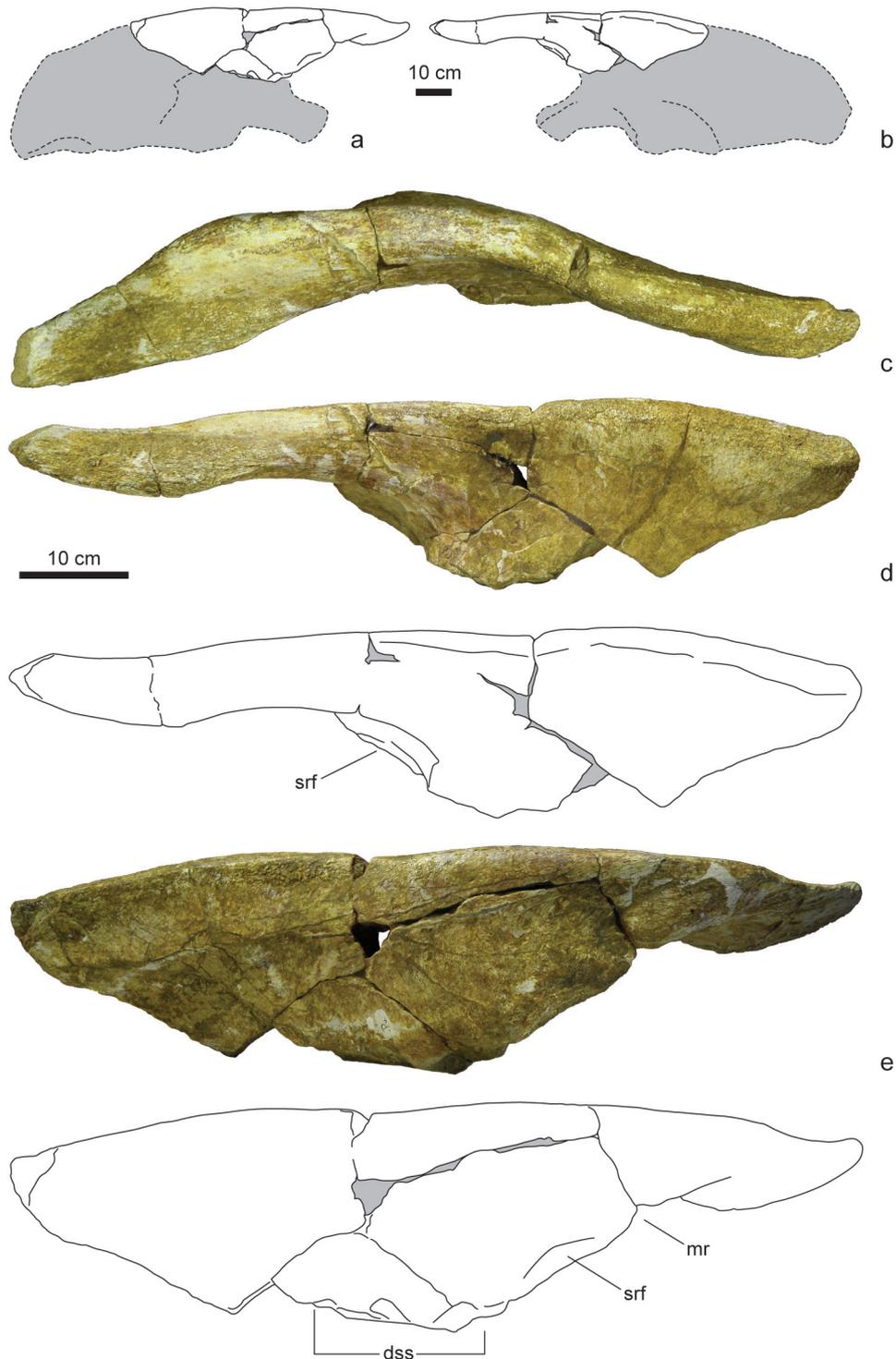


Fig. 6.- Left ilium of *Delapparentia turolensis* MPT/I.G., in medial (a, e), lateral (b, d) and dorsal (c) views. In a, b the preserved remains of *D. turolensis* are drawn on the complete outline of ilium, reconstructed from the comparison with *Barilium dawsoni* holotype (Norman, 2010: fig. 3). Abbreviations: srf – dorsosacral rib facet, mr – medial ridge on the preacetabular process, dss – dorsal sutural surface for the sacral ribs.

tened in its dorsal half and limits ventrally with some excavated facets for the attachment of the sacral yoke (Fig. 6). Only the dorsal border of this faceted area is preserved, which corresponds to dorsolateral extensions of the fused upper parts of the sacral ribs and transverse processes of the sacral vertebrae (Norman, 2011a).

Pubis

Only two fragments of the left pubis are preserved, comprising almost all the prepubic process, the iliac peduncle and acetabulum, whereas the postpubis and ischial peduncle are lost by breakage (Fig. 2d, Ruiz-Omeñaca, 2011: fig. 7). The prepubic process is well preserved in its dorsal and ventral edges and only slightly eroded in the anteroventral edge. The two fragments of the pubis do not fit exactly but the bone lost between the anterior end and the proximal part seems to be minimal. The prepubic process is expanded, with a thick, rounded dorsal edge and a thin, sharp ventral margin, which diverge towards its anterior end, as is usual in iguanodontoids (e.g. McDonald *et al.*, 2012a). In profile, the ventral margin is more concave than the dorsal margin, as in *Iguanodon* (Norman, 1980: fig. 65) and *Altirhinus* (Norman, 1998: fig. 33), though the opposite is usually the case in basal iguanodonts (e.g. *Mantellisaurus* holotype, NHMUK R5764; Norman, 2011a: fig. 27.45). In other iguanodonts the dorsal margin is more concave whereas the ventral margin is gently concave or straight (see Paul, 2008: fig. 3C) and even slightly convex as in *Eolambia* (McDonald *et al.*, 2012a). In spite of the similar outline of the prepubic blade, the anterior end of the prepubis in *Delapparentia*, with the most anterior point dorsally offset, differs from that of *Iguanodon* (Norman, 1980) and *Altirhinus* (Norman, 1998), which is ventrally offset; nonetheless, this difference should be taken with caution due to the above-mentioned slight incompleteness of the anteroventral edge of *Delapparentia*. The iliac peduncle projects posterodorsally, with a subrectangular articular facet, as is usual in other iguanodonts and different from *Proa*, which faces dorsally (McDonald *et al.*, 2012b: fig. 31). The pubis of the holotype of *Barilium* (Norman, 2011a: fig. 9) also differs in the acetabular region because it presents a ridge between the iliac peduncle and the acetabulum, forming a wider angle, whereas the angle is markedly more acute in *Delapparentia* (Ruiz-Omeñaca, 2011: fig. 7). This means that in *Delapparentia* the ischial peduncle is more prominent and angulated in relation to the acetabular border, whereas in *Barilium* the ischial peduncle is low and the acetabular border shallow.

3. Phylogenetic analysis

To explore the phylogenetic position of *Delapparentia turolensis* we incorporated the newly reported skeletal remains in the dataset of McDonald (2012a) and McDonald *et al.* (2012b). This allowed us to score two new characters (93, 102), one related to the axis and one to the scapula. Further-

more, we revised character 110, adding a new character state (2) to better describe the morphology of the preacetabular process of the ilium shared by *Delapparentia* and *Barilium dawsoni* (see discussion for details). We also rescored two characters in accordance with our reinterpretation of the ilium of *Delapparentia* (see description): character 112, concerning the morphology of the dorsal margin of the postacetabular process, was changed from state 3 (thickened and laterally-bulging everted rim along dorsal margin) to state 2 (mediolaterally thickened dorsal margin compared to dorsal margin above pubic peduncle). Also, character 114, concerning the orientation of the postacetabular process, was scored as ambiguous (?) due to the lack of most of the postacetabular process. These modifications resulted in *Delapparentia* being scored for a total of 10 characters (see Appendix 1). Although it is widely known that this dataset usually produces unsatisfactory results, especially concerning the low resolution of the obtained consensus, we have chosen it as it is currently the largest compilation of iguanodonts' osteological information available in the literature. We consider that the dataset can be greatly improved by the progressive addition and recodification of both taxa and characters, and subsequently the resolution of the consensus will be progressively improved in future iterations of the dataset. McDonald (2012a) proposal represents the first modern attempt to put together an inclusive dataset of iguanodonts, and should be considered as a valuable work-in-progress. In that sense, we are aware that some included problematic taxa, such as *Kukufeldia* and *Xuwulong*, may need further revision, but without first hand examination of the specimens we choose not to rescore or delete these taxa.

We conducted the analysis under TNT v1.1 (Goloboff *et al.*, 2008) using the settings of the "second run" in McDonald (2012a): all characters were equally weighted; twelve characters (10, 14, 20, 25, 46, 67, 81, 82, 83, 100, 127, and 130) were treated as additive. The resulting dataset was explored with Wagner starting trees (starting seed=1) and 10,000 replicates were used saving 10 trees per replication. This procedure resulted in 17,060 most parsimonious trees (MPTs) of 398 steps, a tree set similar in size to that obtained by McDonald (2012a). The resulting strict consensus is identical to the one obtained by McDonald (2012a), with the inclusion of *Delapparentia* within the huge polytomy of all taxa more derived than *Hypsilophodon*.

In order to improve the resolution, we tested different methods. McDonald *et al.* (2012b) used an Adams consensus tree to obtain a higher resolution. However, Adams consensus trees are widely known to report nodes that are not observed in any of the original MPTs (see for example Bryant, 2003). Due to the huge size of the tree set analysed, the necessary revision of all trees to ensure that no spurious nodes were obtained is difficult, so we consider that this kind of consensus is not ideal for this dataset. Following McDonald *et al.* (2012b), we calculated all Maximum Agreement Subtrees (MASTs) of the 17,060 MPTs obtained in the analysis us-

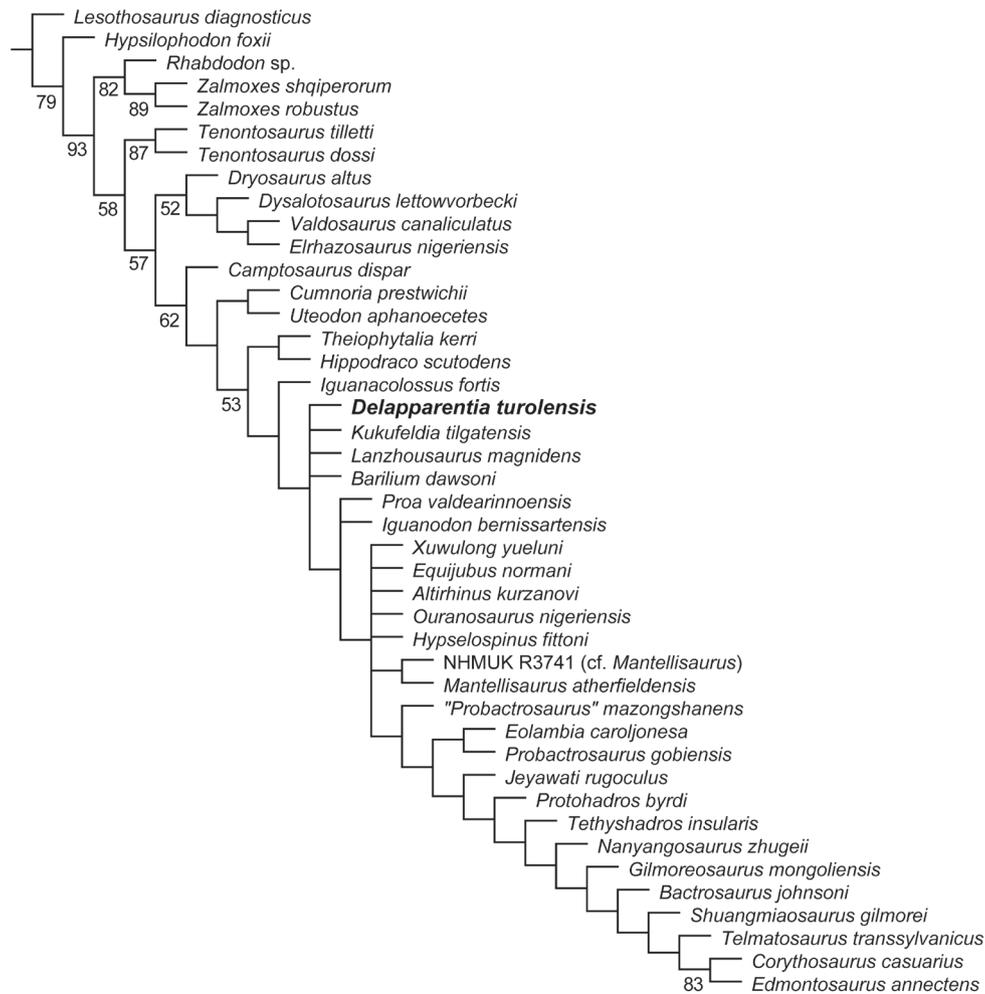


Fig. 7.- Consensus subtree of 17,060 most parsimonious trees of 398 steps. This topology is obtained after *a posteriori* pruning from the strict consensus all the taxa except for those included in a maximum agreement subtree, plus the European taxa *Delapparentia*, *Hypselospinus* and *Proa*. *Delapparentia* is recovered in a polytomy with *Kukufeldia*, *Lanzhousaurus*, *Barilium* and the clade equivalent to Iguanodontoidea. Numbers under nodes represent Bootstrap values over 50 after 1000 replications. See text for detailed description and discussion of the Bootstrap analysis.

ing PAUP* 4.0b (Swofford, 2003), as this generally resolves MASTs more quickly than TNT. We recovered a total of 288 equivalent MASTs, each including 40 taxa. Most of these MASTs differed in the alternative inclusion of a few taxa, the most relevant to our study being the permutation with *Proa* and *Iguanodon* as the basal members of Iguanodontoidea. We chose to figure the MAST which includes the greatest number of taxa that are close to *Delapparentia* in age or palaeobiogeographical distribution. Again, all these MASTs resulted in the pruning of *Delapparentia*. To study the approximate phylogenetic affinities of the Iberian taxon we *a posteriori* pruned in the strict consensus all the taxa not included in the MAST but *Delapparentia*, with TNT. We also retained in the consensus two taxa that have been previously reported from the Lower Cretaceous of Europe, *Hypselospinus* and *Proa*. The resulting consensus subtree is shown in Fig. 7.

Nevertheless, it is noteworthy that more exhaustive searches produced increasingly bigger tree sets –for example, an additional round of TBR (Tree Bisection and Reconnection)

using the 17,060 trees obtained above may lead to a tree set one order of magnitude bigger–. This problem directly correlates with the huge amount of missing data in the dataset (58% of the character states scored, most of them concentrated in a few poorly represented taxa, as noted by McDonald, 2012a). Exploratory searches of the dataset revealed that this increase in the number of trees obtained does not affect either the topology of the consensus or the size of the MASTs. We have chosen to restrict our comments to the smallest original tree set for comparative purposes and because a deep revision of the dataset and exploratory methodology is out of the scope of this paper, though it could prove an interesting path to follow in future work. To evaluate the support of our results, 1000 bootstrap replications were conducted in TNT, considering only the taxa included in the depicted subtree. Bootstrap values over 50 are shown in Fig. 7.

Delapparentia is recovered in a polytomy with *Kukufeldia*, *Lanzhousaurus*, *Barilium* and the clade equivalent to Iguanodontoidea. Other European iguanodonts from the Early Cre-

taceous are more derived than *Delapparentia*. *Proa* is recovered in a polytomy with *Iguanodon bernissartensis* and the clade that contains all more derived iguanodonts, including *Hypselospinus* and *Mantellisaurus*. Low bootstrap support is recovered for most nodes, with the exception of the clade that includes all iguanodonts more derived than *Hypsilophodon*, the *Zalmoxes* + *Rhabdodon* clade, the clades equivalent to the genus *Zalmoxes* and *Tenontosaurus*, and the *Corythosaurus* + *Edmontosaurus* clade.

4. Discussion

The axis of *Delapparentia* differs from that of other iguanodonts in presenting a high neural spine measured from the base of the postzygapophysis. This measurement is clearly greater than half the length of the neural arch. The axial neural arch is similar to that of *Iguanodon bernissartensis* (Norman, 1980) in presenting a dorsally expanded spine, a dorsal edge that is strongly convex, a distally placed apex with an absent posterior concavity, an epiphysis ventral to the apex, and the presence of an accessory bulge on the buttresses between the epiphysis and postzygapophysis. Furthermore, basal iguanodontoids such as *Mantellisaurus* (Norman, 1986) and *Ouranosaurus* (Taquet, 1976) differ from *Delapparentia* and *Iguanodon* in presenting an axial neural spine that has a gently convex apex placed near the mid-length of the neural arch, a slight concavity posterior to the apex, and an epiphysis placed at the same height as the apex.

The axis of *Barilium* is unknown; however, *Delapparentia* can be clearly differentiated from *Barilium* (Norman, 2011a) in the rest of the axial skeleton. The mid-anterior dorsal vertebrae with a gentle ventral midline keel in *Delapparentia* are absent in *Barilium*, the vertebrae having smoothly convex ventral surfaces (Norman, 2011a: fig. 4). The first anterior caudal centrum is higher than wide in *Delapparentia*, as is common in other basal iguanodonts, whereas in *Barilium* it is characteristically low and broad (Norman, 2011a: fig. 6). The two taxa also differ in the pubis, in the region of the iliac peduncle (see description and comparison above). Additionally, as well as the *Barilium* holotype, other material referred to the genus *Barilium* by Norman (2011a: NHMUK R3788, holotype of *Sellacoxa pauli* sensu Carpenter and Ishida, 2010) differs from *Delapparentia* in many pelvic features relating to the ilium, ischium and pubis (see related discussion of NHMUK R3788 below). Even so, the ilia of *Delapparentia* and *Barilium* are very similar – except in their slightly different dorsal edge in profile view – and exhibit two characters only shared between them, namely the lateral surface of the preacetabular process facing dorsally towards its anterior end, and the rim of the sacrodorsal rib facet that is visible, in lateral view, in the preacetabular notch. These synapomorphies were previously reported by Norman (2011a) as autapomorphies of *Barilium*. The similarities in the ilia suggest a close affinity between the English Valanginian *Barilium dawsoni* and the Spanish Barremian *Delapparentia turoloensis*. The af-

finity between these European Early Cretaceous taxa, which is also observed in the phylogenetic analysis we performed (Fig. 7), had previously gone unnoticed.

The modification of the matrix of McDonald (2012a) with additional character states and coding changes has contributed to *Delapparentia* being placed close to *Barilium*; concretely, in a polytomy with *Barilium*, *Kukufeldia* and *Lanzhousaurus* and outside the clade Iguanodontoidea. The English Valanginian *Kukufeldia* is known from a dentary (McDonald et al., 2010a) and has been proposed as a junior synonym of *Barilium* (Norman, 2011a). It lacks overlapping material with *Delapparentia*, so comparison is impossible. The Asian Early Cretaceous *Lanzhousaurus* (You et al., 2005) is known from a partial skeleton. As regards the overlapping material, among the most diagnostic bones are the pubes, which differ from *Delapparentia* in the prepubic profile. The ilium morphology of *Delapparentia* differs clearly from other iguanodontoids, as is reflected in the data matrix. More precisely, *Barilium* and *Delapparentia* share a synapomorphic preacetabular process (McDonald, 2012a: character 110) and lack the laterally everted rim shared by all other basal iguanodontoids, which becomes pendant in derived forms (McDonald, 2012a: character 112).

The ilium of *Delapparentia* is different from that of *Iguanodon*. Moreover, the two taxa differ in the last sacral vertebra, which is ventrally grooved in *Iguanodon* (i.e. *haemal sulcus*, Norman, 1980: fig. 45) and ventrally keeled in *Delapparentia* (Ruiz-Omeñaca, 2011). *Delapparentia* also differs from *Iguanodon* in the anterior end of the prepubic process (see description). The prepubic process of the pubis of *Proa* is not dorsoventrally expanded in its anterior end, and the ischial peduncle seems to be dorsally projected (McDonald et al., 2012b: fig. 8) unlike in *Delapparentia*, where it is posterodorsally projected. The axis and the ilium of *Mantellisaurus* show differences with respect to those of *Delapparentia* (see the description and comparison above) and also in the pubis (see holotype NHMUK R5764 in Norman, 2011a: fig. 27.45). Moreover, Ruiz-Omeñaca (2011) noted that the first chevron in *Delapparentia* is located between the third and fourth caudal vertebrae, as in *Iguanodon* and *Ouranosaurus* (Taquet, 1976: 119) and unlike *Mantellisaurus* (Norman, 1986: 310), where it is placed between the second and third caudals. The ilium and ischium of *Hypselospinus* (Norman, 2010, 2011b) are different from those of *Delapparentia*. The ischium of *Delapparentia* (Fig. 2e; Ruiz-Omeñaca, 2011: fig. 8) is more angled between the articular surface of the iliac peduncle and the acetabulum border, and this also results in the main axis of the ischial and pubic peduncles forming almost a right angle in *Delapparentia*, whereas this angle is markedly obtuse in *Hypselospinus* (Norman, 2011b: fig. 27.37B).

After examining the range of variation within the fossil record, Carpenter and Ishida (2010) noted that the ilium of basal iguanodonts is indeed diagnostic, so it can be used to separate taxa. In fact, the ilium of *Delapparentia* is useful for distinguishing this taxon from iguanodontoids, but not from

Barilium, though there are plenty of differences in the rest of the postcranial elements of these taxa. This advises against the use of ilium morphology as the only criterion in separating taxa.

The possibility of *Delapparentia* being a junior synonym of *Barilium*, leaving *Delapparentia turolensis* as a second species of *Barilium*, has to be discussed in depth, as *Delapparentia* presents two characters previously thought to be autapomorphies of *Barilium*.

First, despite the fragmentary nature of both holotypes there are a considerable number of differential characters within the overlapping material (mainly in the axial skeleton and pubis). As a result of this, the two taxa are not recovered as sister taxa in our analysis, but as close relatives, even if the synapomorphies are coded. Furthermore, a more exhaustive codification of the morphology of the axial skeleton, and other bones such as the pubis, would emphasize the differences between the two taxa.

Secondly, the criteria used to refer material to *Barilium* in previous papers need to be revised. Norman (2011a) describes NHMUK R3788 (holotype of *Sellacoxa pauli*; Carpenter and Ishida, 2010) as a compressed and distorted partial postcranial skeleton, and refers it to *Barilium* cf. *dawsoni*. However, NHMUK R3788 does not bear the diagnostic rim of the sacrodorsal rib facet visible, in lateral view, in the preacetabular notch, a character present in the ilia of the holotypes of both *Barilium dawsoni* (Norman, 2011a) and *Delapparentia turolensis* (this paper). It is a priori difficult to assume that this absence is caused by the possible masking effect of distortion or preservation. On the contrary, this character is actually present in the English Barremian ilium NHMUK R2502 (Norman, 2011b: fig. 27.50), which is the holotype of *Iguanodon seelyi* and referred to *Iguanodon bernissartensis* by this author. Furthermore, some of the remains which Norman (2011a) refers to *Barilium* do not present overlapping material with the holotype, and are referred on the basis of the occurrence of the fossil remains within the same geological unit in geographically close localities, on the assumption that iguanodontian palaeobiodiversity during the Late Jurassic and Early Cretaceous is often represented by robust/large and gracile/small osteological (and taxonomic) pairs. And this would disagree with other proposals (e.g. Paul, 2012). To contextualize the issue, a simplified taxonomic scenario for European iguanodonts is shown in Table 1.

All of the above problems, together with the important difference in age of the two taxa, advise against the synonymization of *Barilium* and *Delapparentia*, especially without first-hand examination of the different specimens assigned to *Barilium*. Nevertheless, this possibility must be considered if future remains of *Delapparentia* or *Barilium* are found.

5. Conclusion

Delapparentia turolensis is a large-sized Barremian basal iguanodont from Spain, which presents an autapomorphic,

unusually high axial neural spine and a unique combination of postcranial characters. The ilium morphology differs from that of other basal iguanodonts and relates *Delapparentia* to the Valanginian *Barilium dawsoni* from England, with whom it shares two synapomorphies. In our phylogenetic analysis, *Delapparentia* is recovered in a polytomy with *Kukufeldia*, *Lanzhousaurus*, *Barilium* and the clade equivalent to Iguanodontoidea.

Acknowledgements

This paper is part of the project CGL2010-16447, subsidized by the Spanish Ministerio de Economía y Competitividad, the European Regional Development Fund, and the Government of Aragón (*Grupos Consolidados* and *Dirección General de Patrimonio Cultural*). We thank the Museo de Teruel and FCPT-Dinópolis (especially Dr. R. Royo-Torres) for allowing us access to study the *Delapparentia* holotype. Rupert Glasgow revised the translation of the text into English. Finally, we thank Pascal Godefroit and David B. Weishampel for their helpful reviews.

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Appendix 1

Character scorings for *Delapparentia turolensis*, to be added to the matrix of McDonald (2012a), McDonald et al. (2012b). Character 110 has been modified to include a new character state (2, scored for *Delapparentia* and *Barilium*). With the modification used in this paper, the character reads as follows:

110. Ilium, preacetabular process twisting along its length: twisting absent (0); twisting such that the dorsal surface of the ilium becomes the lateral surface of the cranial end of the process (1); the lateral surface of the preacetabular process twists around its long axis towards its anterior end so that it comes to face almost dorsally (2)

Scoring of *Delapparentia*: 93 – 1, 94 – 1, 102 – 0, 109 – 1, 110 – 2, 111 – 0, 112 – 2, 115 – 1, 116 – 1, 132 – 0, the rest between 0 and 134 are ?.