

A megatheropod tooth from the late Tithonian – middle Berriasian (Jurassic-Cretaceous transition) of Galve (Aragón, NE Spain)

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With 4 figures and 1 table

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Abstract: We herein describe the biggest theropod tooth hitherto found in Spain. The tooth (IPS-G1) comes from the Villar del Arzobispo Formation (Upper Tithonian-Middle Berriasian) in the Galve Sub-basin. The specimen is a nearly complete maxillary tooth with a FABL of 34 mm and DSDI = 1. Considering its geological age and the crown morphology (including the size), it is most likely that the tooth belongs to an allosauroid. This clade of theropods was present in the Late Jurassic of Portugal and the Early Cretaceous (Berriasian and Barremian) of England. The tooth represents the first allosaurid from Spain, and the biggest theropod from the European Berriasian.

Zusammenfassung: Wir beschreiben hier den größten bisher in Spanien gefundenen Theropoden Zahn. Dieser Zahn (IPS-G1) stammt aus der Villar-del-Arzobispo-Formation (spätes Tithonium – mittleres Berriasium) im Teilbecken von Galve. Das Exemplar ist ein beinahe vollständiger Oberkieferzahn mit einer Basislänge (FABL) von 34 mm und DSDI = 1. In Anbetracht seines geologischen Alters und der Morphologie der Zahnkrone (auch deren Größe) stammt der Zahn mit großer Wahrscheinlichkeit von einem Allosauroiden. Diese Theropoden-Gruppe kam im Oberjura von Portugal und in der Unterkreide (Berriasium und Barremium) von England vor. Der Zahn stellt den ersten Allosauriden aus Spanien und den größten Theropoden des europäischen Berriasium dar.

1. Introduction

A common feature in different lineages of theropods has been the increase of the size. Big theropods have traditionally been included in Camosauria, though modern cladistic studies indicate that gigantism has been developed in different clades: Megalosauridae in the Middle Jurassic (HOLTZ 2000; ALLAIN 2002), Allosauroidae (including Allosauridae and Carcharodontosauridae) in the Late Jurassic–Early Cretaceous, Spinosauridae in the Early Cretaceous, Therizinosauridae and Tyrannosauridae in the Late Cretaceous. Not only the skeleton as a whole but also the study of isolated teeth make the characterisation of these theropod clades possible (CURRIE et al. 1990; SERENO et al. 1996; CHARIG & MILNER 1997; BAKKER & BIR 2004).

The fossil remains of big theropods are scarce and fragmentary in Europe, whereas there is a significant record of herbivores (WEISHAMPEL et al. 2004). There are temporal intervals, like the Berriasian, without any data of skeletal remains. Only small or medium-sized theropods from this age are poorly known, and few species have been named. From other parts of Europe are the dromaeosaurids *Nuthetes destructor* (OWEN, 1854) from the Purbeck Limestone of the United Kingdom, and *Dromaeosauroides bornholmensis* CHRISTIANSEN & BONDE, 2003 from the Jydegaard Formation of Denmark (MILNER 2002; CHRISTIANSEN & BONDE 2003), as well as the maniraptoran "*Prodeinodon dunkeri*" (DAMES, 1884) from the Wealden of Germany (RUIZ-OMENACA & CANUDO 2003). In Portugal, RAUHUT & KRIWET (1994) cited a tetanuran tooth with a crown height of approximately 80 mm from beds that have sometimes been considered to be Berriasian in age, although the recent evidence seen to indicate a Tithonian age (WEISHAMPEL et al. 2004). Some fragmentary remains come from Spain (BARCO & RUIZ-OMENACA 2001a, 2001b). The palaeoichnological record indicates the presence of big theropods in the European Berriasian terrestrial ecosystems (LOCKLEY et al. 2000; BARCO et al. 2005b), but up to the present there has been no evidence of their skeletal remains. The aim of this work is two-fold: on the one hand we describe the largest theropod remains from the Berriasian of Europe, and on the other we prove the importance of the study of isolated theropod teeth in the general context of the dinosaur biogeographical reconstruction of Mesozoic ecosystems.

2. Geological and geographical location

Galve is a village located in north-eastern Spain some 40 km north of Teruel (Fig. 1). The outcrops of Galve are included in a wide and well-exposed synclinal structure and comprise a nearly 1-km-thick succession of shallow marine and continental sedimentary units, ranging from the Tithonian to the

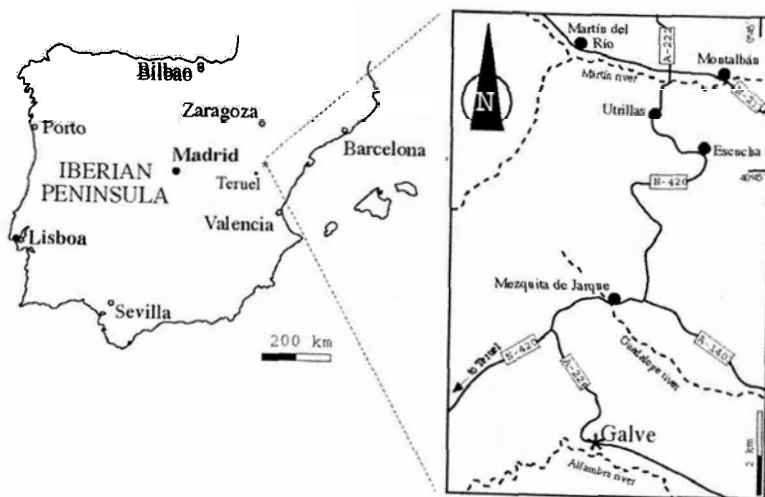


Fig. 1. Geographical situation of Galve (Aragón, Spain)

late Barremian–Aptian (SORIA et al. 1995). These Upper Jurassic–Lower Cretaceous outcrops are located in the north-western part of the Maestrazgo Basin, and have been included in the so-called Galve sub-basin (SALAS et al. 2001). The Galve region is justifiably famous for its archosaur remains (SANZ et al. 1987; BUSCALIONI & SANZ 1990), for its mammal assemblages (HAHN & HAHN 1992; CANUDO & CUENCA-BESCÓS 1996) and other vertebrate faunas (see BARCO et al. 2004).

The Galve stratigraphic sequence can be divided into five lithostratigraphic units (Figs. 2 and 3) characterised by different facies and fossil associations (DÍAZ et al. 1984). The lower two units are the Higuieruelas and Villar del Arzobispo formations and represent the last stages of development of the marine Jurassic platform. In the middle and upper parts of the Villar del Arzobispo Formation, levels with biogenic sedimentary structures dominated by dinosaur tracks record the episodic setting of shallow-marine to coastline environments that mark the transition between marine and con-

lithological units in the Galve area (SORIA et al. 1995). The Villar del Arzobispo Formation, known in the local literature as Purbeck facies, is overlain by a low-angle angular unconformity. The unconformity is also marked by an important lithological and environmental change, represented by the setting of the continental red clays of the bottom of the El Castellar Formation (PÉREZ-LORENTE et al. 1997). This unit and the overlying Camarillas Formation, known in the local literature as Wealden facies, represent the continental facies of the early Cretaceous age (upper Hauterivian-lower Barremian). The vertebrate localities are found throughout the whole sequence (Fig. 2).

The age of the upper part of the Higuieruelas Formation and most of the Villar del Arzobispo Formation is constrained by the presence of the benthic foraminifera *Anchispirocyclus lusitanica*, which spans from the middle Tithonian to the early Berriasian (e.g., HARDENBOL et al. 1998). In addition, basin-wide correlation based on sequence stratigraphic analysis (BÁDENAS et al. 2004; IPAS et al. 2004) indicates that the younger strata recorded in the Villar del Arzobispo Formation most probably correspond to the early and middle Berriasian, which has been dated by the associations of charophytes found in the contemporary lacustrine and palustrine sediments recorded in other localities of the Maestrazgo Basin (MARTÍN-CLOSAS 1989).

Dinosaur remains found in the Villar del Arzobispo Formation in Galve include sauropods, theropods and ornithomorphs (CUENCA-BESCÓS et al. 1997; PÉREZ-LORENTE et al. 1997; RUIZ-OMEÑACA et al. 2004) (Fig. 2). Most of them are not identifiable beyond family level because of their fragmentary nature. The most significant one is the new sauropod *Galvesaurus heneroi* BARCO, CANUDO, CUENCA-BESCÓS & RUIZ-OMEÑACA 2005, which represents a new primitive neosauropod from the Jurassic-Cretaceous transition of the Iberian Peninsula (BARCO et al. 2005). Theropods are represented by three parallel trackways from Las Cerradicas tracksite (Theropoda indet., PÉREZ-LORENTE et al. 1997), two small isolated teeth from the Cuesta Lonsal 1 and Las Cerradicas 2 sites (Theropoda indet. and Coelurosauria indet.), and one caudal centrum from the Carretera site (Theropoda indet., BARCO & RUIZ-OMEÑACA 2001a, b), and the tooth studied in this paper.

Fig. 2. Stratigraphical log of the Galve area, with situation of dinosaur record. Modified from RUIZ-OMEÑACA et al. (2004).

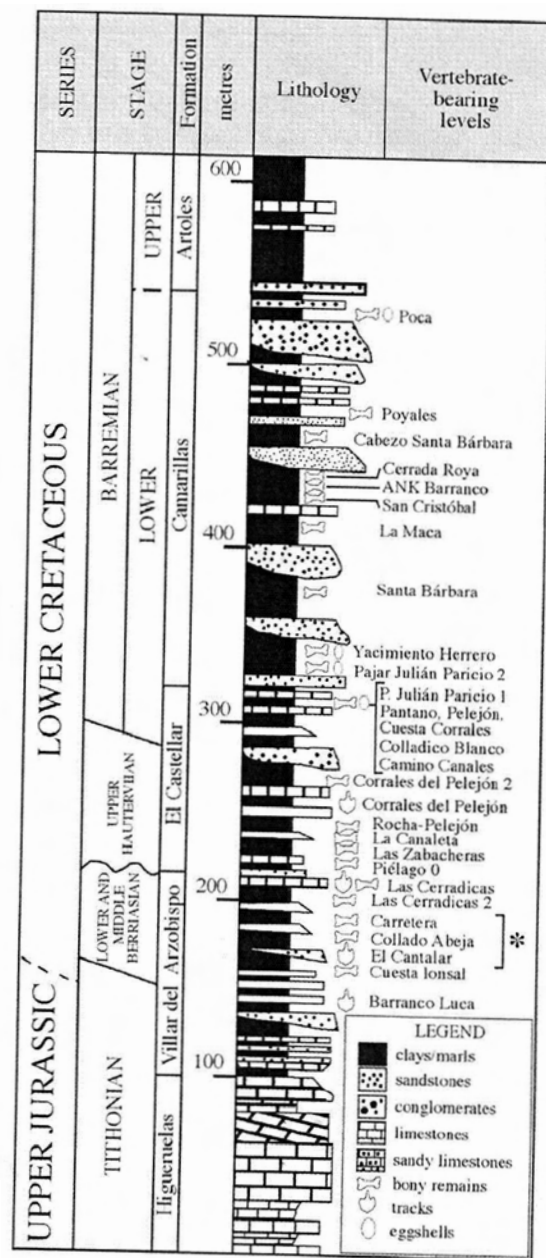


Fig. 2 (Legend see p. 80)

3. Material and methods

3.1. Tooth study

The importance of this fossil calls for a short history of the circumstances in which the tooth was found and the preliminary studies of it. The tooth described in this paper was found at the beginning of the 1960s. It was a shepherd who informed the local amateur Mr. JOSÉ MARÍA HERRERO, who himself had already discovered a number of significant dinosaur remains from Galve, that he had found a first fragment of the specimen. Later Mr. HERRERO went back to the site where the shepherd had found the fragment and recovered the other part of the tooth. A survey of the history of Galve and this local amateur is given in BARCO et al. (2004).

In the 1960s palaeontologists from the "Instituto de Paleontología Miquel Crusafont" in Sabadell began their exhaustive work with the aim of finding mammals (see the history in CANUDO & CUENCA-BESCÓS 1996). It was at this time that Mr. HERRERO lent the tooth to the Institute for the purpose of scientific study, and since then it has been housed in Sabadell. The first published reference to this tooth is by CRUSAFONT-PAIRÓ & ADROVER (1966). In their preliminary report, these authors assigned the tooth to "*Charcharodontosaurus*". This genus belongs to a group of advanced allosauroids only known in the Early Cretaceous and lowermost Late Cretaceous (CORIA & SALGADO 1995; SERENO et al. 1996; ALLAIN 2002) from Gondwana and may be Laurasia (see discussion below). Two years later, KÜHNE & CRUSAFONT-PAIRÓ (1968) assigned the tooth to *Megalosaurus*. Both identifications were based on the great size of the tooth, and lacked systematic study with descriptions or comparisons. The first and only previous illustration of the tooth is in a book for the general public by SANTAFÉ-LLOPIS & CASANOVAS-CLADELLAS (1993: fig. 40), where it is identified as a carnosaur ("Carnosaurio"). In this book, the locality where the tooth was found is not indicated, and the authors do not describe the specimen. The same photograph has been reproduced in BARCO et al. (2004: fig. 4.17). Elsewhere, the tooth has been briefly described, and the authors discuss previous identifications and consider its assignation to Theropoda indet (RUIZ-OMENACA et al. 1997, 1998; "Theropoda indet. A" in RUIZ-OMENACA et al. 1998).

In previously published papers the precise stratigraphical situation of this fossil was not taken into account, because prior to our paper Mr HERRERO had not revealed the exact site of the tooth discovery. As explained elsewhere, the majority of the vertebrate remains collected at Galve have been discovered in sediments from the Uppermost Hauterivian and Lower Barremian (SANZ et al. 1987; RUIZ-OMENACA et al. 2004). During the preparation of this study, Mr. JOSÉ MARÍA HERRERO has told us that the tooth

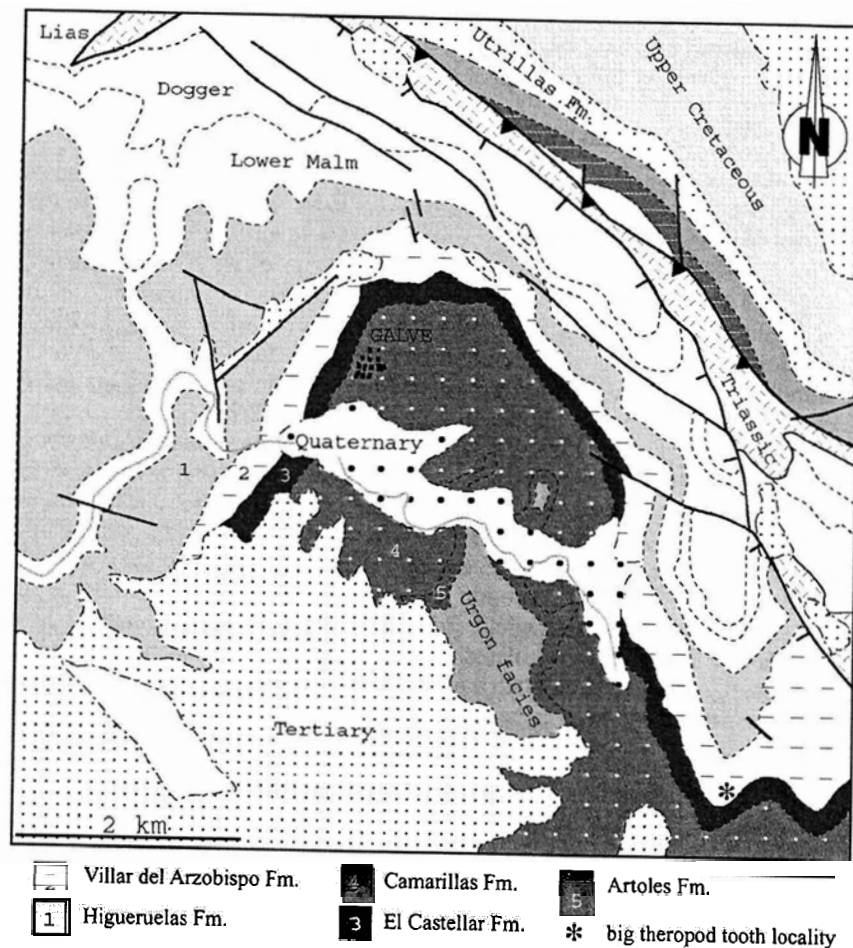


Fig. 3. Geological map of the Galve area, with the situation of the IPS-G1 locality. Based on DIAZ-MOLINA et al. (1984) and SORIA et al. (1995)

site is located in a level that we identify as Villar del Arzobispo Formation, with an age that ranges from late Tithonian to middle Berriasian (Fig. 2). Also, a taphonomic survey reveals that the preservation status of the tooth as

well as the matrix that is still attached to the specimen is similar to that of other remains from this formation.

3.2. Theropod dental morphology and taxonomy

Theropod crowns are characterised by a simple laterally compressed conical form with few homologous points or landmarks. However, recent studies agree that theropods might be taxonomically identified on the basis of isolated teeth (RAUHUT & WERNER 1995; SANKEY et al. 2002; SWEETMAN 2004). The main difficulty is to know the intraspecific variation, for the position of the tooth-crown along the dental series is hard to establish. Theropods are generally not considered to be heterodont taxa, but this is an oversimplification based on the terms homodont and heterodont as applied to vertebrates in general. Without claiming that theropods have the heterodonty of mammals, with only one dental replacement we can observe a morphologic heterodonty in theropods. In single individuals the premaxillary series forms an array of teeth that are morphologically distinct from the lateral series. When there is an accurate record in the same geological formation it is possible to use isolated theropod teeth for diagnosing taxa to family and, in some cases, to a lower taxonomic level (CURRIE et al. 1990; SANKEY et al. 2002, this work). In geological formations without cranial material it is possible at least to assign isolated theropod teeth to the main clades. Nevertheless, this must be done with caution for the sake of the non-proliferation of new specific and generic names.

Institutional abbreviation: ISP: "Instituto de Paleontologia Miquel Crusafont", Sabadell (Spain).

3.3. Nomenclature and tooth measurements

We use anatomical nomenclature used in the description of vertebrate studies (see for an overview SMITH & DODSON 2003). The theropod teeth have few landmarks; in fact they are simple structures with single cusp differing in the complex cuspidate mammal teeth. Tooth measurements were taken using the criteria established by CURRIE et al. (1990), FARLOW et al. (1991), RAUHUT & KRIWET (1994), BUSCALIONI et al. (1997) and SMITH & DODSON (2003). Tooth curvature was measured according to the method of SANKEY et al. (2002) and the denticle size difference index has been calculated following RAUHUT & WERNER (1995). The variables used in this paper are shown in Table 1.

Table 1. Measurements of the IPS-G1 from the Villar del Arzobispo Formation (late Tithonian-middle Berriasian) in Galve (Aragón, Spain). *: Approximately.

Variable Name	Abbreviation	Description	IPSG-1
Fore-an Basal Length	FABL	Length of the crown long axis	33.41 mm
Crown Basal Width	CBW	Width orthogonal to FABL	16.88 mm
Crown Base Ratio	CBR	FABL/CBW	1.98
Crown Height	CH	Height orthogonal to base (distal)	78.50 mm
Apical Distance	AD	Distance from apex to base (mesial)	82.74 mm
Crown Angle	CA	Angle between FABL and AD lines	69°
Crown Height Ratio	CHR	CH/FABL	2.35
Mesial Apical Denticle Density	MA	No. of mesial apical denticles per 5 mm	12
Mesial Center Denticle Density	MC	No. of mesial center denticles per 5 mm	11
Mesial Basal Denticle Density	MB	No. of mesial basal denticles per 5 mm	0
Distal Apical Denticle Density	DA	No. of distal apical denticles per 5 mm	11
Distal Center Denticle Density	DC	No. of distal center denticles per 5 mm	11
Distal Basal Denticle Density	DB	No. of distal basal denticles per 5 mm	13
Average Mesial Denticle Density	MAVG	Average no. of mesial denticles per 5 mm	11.5
Average Distal Denticle Density	DAVG	Average no. of distal denticles per 5 mm	11.5
Denticle Density Size index	DSDI	MAVG/DAVG	1

4. Systematic palaeontology

Class	Dinosauria OWEN, 1842
Order	Saurischia SEELEY, 1888
Suborder	Theropoda MARSH, 1881
	Tetanurae GAUTHIER, 1896
	Avetheropoda PAUL, 1988
Superfamily	Allosauroidae CURRIE & ZHAO, 1993

Allosauroida indet.

Fig. 4

Material: One left maxillary isolated tooth (IPS-G1), currently housed at the "Museo Fundación Conjunto Paleontológico de Teruel-Dinópolis" (Aragón).

Description: The tooth crown of IPS-G1 is almost complete, only flawed by the glued break. In this specimen, part of the root and some of the denticles are broken away. The presence of the root implies that IPS-G1 is not a shed tooth. Small root traces of recent vegetation are present superficially on the enamel surface. The tooth has a small wear facet at the distal side of the tip. The tooth is labiolingually compressed in such a way that the FABL is twice the labiolingual width (Crown Base Ratio: 1.98). The tooth is distally curved, and the tip is medially inclined. The specimen measures 98.86 mm from base to tip, although the preserved base is a portion of the root; when measured up to the enamel limit, the tooth is 75.58 mm. A wear facet also erodes the tip; if we reconstruct the tip the tooth measures approximately 78.5 mm (Table 1). The medial wear facet, the tip medially inclined and the medial displacement of the mesial carina imply that IPS-G1 is a left maxillary tooth.

The crown section is tear-shaped, with the distal part sharper. The root is only separated by a slight constriction. This character is not clearly developed as in advanced coelurosaurs and in toothed birds. The crown is oval with concave labial and lingual sides (eight-shape in cross section). The enamel is smooth and covers the surface of the tooth crown. There is no wrinkling of the enamel.

Both mesial and distal carinae bear denticles in IPS-G1. The mesial carina is situated at the mesio-labial corner. In mesial view, it begins at the apex and runs down to nearly 3/5 of the tooth height. It forms a slight curvature. The distal carina is situated at the rearmost part of the tooth at its symmetry plane and runs down to the base of the enamel.

The denticles are relatively small in relation to the tooth size: both carinae possess just under 11 denticles per 5 mm in their middle part (DSDI = 1). The distal denticles measure about 1.3 mm in height and 1 mm in length (Table 1). They are set virtually perpendicular to the axis of the carina and are rectangle-shaped in lateral view. Denticle size and morphology are similar in both carinae, with the exception of the basal ends, where the denticles decrease in size quickly. Each denticle is relatively broad (labiolingually) and chisel-like in form. The interdenticle slits are relatively deep. Shallow and poorly defined blood grooves extend onto the surface of the tooth from between the bases of adjacent denticles. The mesial carina only has denticles in the apical half.

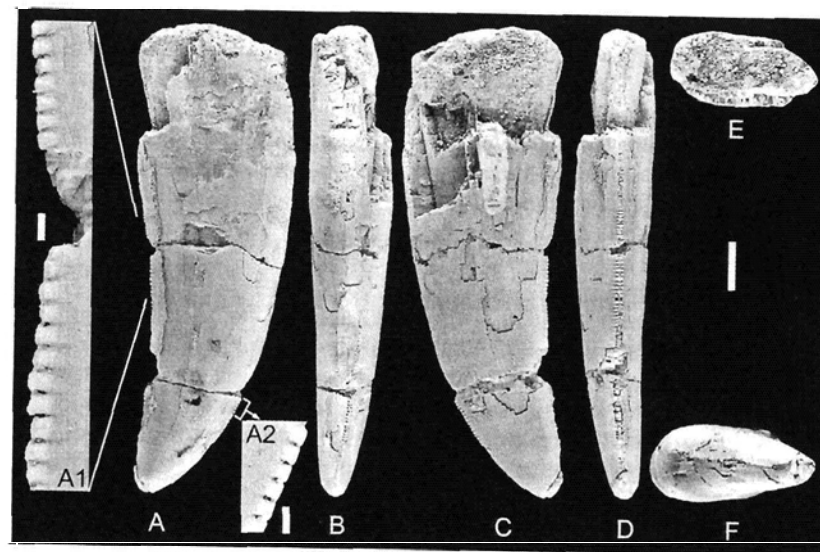


Fig. 4. Allosauroida? indet., left maxillary tooth (IPS-G1) from the late Tithonian – middle Berriasian of Galve (Spain, Villar del Arzobispo Formation), in lingual (A), mesial (B), labial (C), distal (D), basal (E) and apical (F) views, with details of the mesial and distal denticles (A1, A2). Scale bar: 10 mm (A–F) or 1 mm (A1, A2).

5. Discussion

Large theropods are characterised by big skulls with relatively few but large and stout teeth. Their function was probably to serve as primary killing tools, supported by strong jaw and neck muscles (SANDER 1997). Relative theropod tooth size can vary significantly, but we can make an estimation of the relative size of IPS-G1 dinosaur from other Theropoda taxa known. A comparison with teeth from the big allosauroid *Acrocanthosaurus* (NCSM 14345, in HARRIS 1998) shows that the owner of IPS-G1 may have had a skull length of 1 m and a total length of 9.5 m: IPS-G1 was thus from a big theropod.

Traditionally, the name Carnosauria has been used to include a variety of large theropods, yet large forms comprise several natural lineages (HOLTZ

2000; ALLAIN 2002). Gigantism in theropod dinosaurs is present in different clades. Differences in the size and shape of the teeth and the size, shape and number of denticles are used to help identify the different theropod groups. For systematic purposes, there now follows a comparison of IPS-G1 with the teeth of several lineages of theropods that attain a big size: Ceratosauridae, Abelisauridae, "Megalosauridae", Spinosauridae, Allosauridae, Sinraptoridae, Carcharodontosauridae, Dromaeosauridae and Tyrannosauridae.

5.1. Comparison with ceratosaurians (Ceratosauridae and Abelisauridae)

Ceratosaurian dinosaurs form a major clade of theropods, and one of its primary branches (Neoceratosauria) included some big theropods such as Ceratosauridae and Abelisauridae (MADSEN 1976; CORIA & SALGADO 1998; RAUHUT 2004). The presence of a flat or even slightly concave area adjacent to the marginal carinae in the lateral teeth is a character shared by *Ceratosaurus* and some abelisaurids. This character seems to represent a neoceratosaurian synapomorphy (RAUHUT 2004). However this area is mesiodistally convex in IPS-G1.

The family Ceratosauridae includes species from the Late Jurassic of North America, Europe and Africa (MADSEN & WELLES 2000). Some *Ceratosaurus* teeth from the Morrison Formation in Como Bluff (Wyoming, USA) show a crown height of 80 mm (see fig. 14.2 of BAKKER & BIR 2004). There are two different morphologies of *Ceratosaurus* teeth. MADSEN (1976) and MADSEN & WELLES (2000) figured teeth with longitudinal ridges, structures not present in IPS-G1. However, *Ceratosaurus* teeth described by BAKKER & BIR (2004) have smooth enamel. These authors describe the *Ceratosaurus* crowns with a teardrop cross-section and its carinae running up the midline fore and aft. The cross-section of the base of the tooth crown is subject to change along the tooth row, with anterior crowns having more asymmetric sections than posterior ones. Follow RAUHUT (2004) is possible to separate *Ceratosaurus* teeth from basal tetanuran teeth, on the basis of the more strongly flattened teeth, rather than the cross-section of the crown. The IPS-G1 tooth differs from *Ceratosaurus* teeth because it is more flattened and its mesial carina does not run to the basal part.

Abelisauridae is a family reported from the Late Cretaceous of several regions of Gondwana (NOVAS 1997; SAMPSON et al. 1998; CORIA & SALGADO 1998). Despite the fact that several examples of cranial material are known for abelisaurids, there is no information on the dentition of this group. Recently, BITTENCOURT & KELLNER (2002) and CANUDO et al. (2004) have described some teeth attributed to Abelisauridae, but they did not find

dental synapomorphic characters for diagnosing this family. It is a tentative identification based on the elimination of other clades such as Spinosauridae or Carcharodontosauridae. The teeth attributed to Abelisauridae present denticles in both carinae from apex to base. The denticles of IPS-G1 are absent at the basal part of the mesial carina, this being the main difference with respect to ceratosaurians.

5.2. Comparison with spinosauroids (Torvosauridae and Spinosauridae)

Spinosauroida is a Tetanurae clade that includes at least two families: Torvosauridae (or "Megalosauridae") and Spinosauridae (SERENO et al., 1998; ALLAIN 2002; HOLTZ & OSMOLSKA 2004). "Megalosauridae" is a family of large basal tetanurans very common in the Middle Jurassic of Europe. They were also present in the Late Jurassic of North America and Early Cretaceous of North Africa (SERENO et al. 1998; ALLAIN 2002; BAKKER & BIR 2004). There are significant differences between "Megalosauridae" teeth and IPS-G1. First of all, the teeth of European Middle Jurassic megalosaurids have mesial denticles larger than the distal ones (DSDI is less than 1.0, MILNER 2002), while in IPS-G1 their size is the same (DSDI is 1). In Late Jurassic megalosaurids from North America (BAKKER & BIR 2004), the apical serrations are much larger than the middle ones in the posterior row, whereas they show the same size in IPS-G1. Moreover, their enamel is wrinkled, whereas it is smooth in IPS-G1.

The Spinosauridae are medium to large-sized tetanurans with representatives from the uppermost Hauterivian to the Cenomanian (Cretaceous) of Europe, North Africa and South America (CHARIG & MILNER 1997; SERENO et al. 1998). However, modern cladistic analysis points to a Jurassic origin of the clade (ALLAIN 2002). Spinosauridae include two subfamilies grouped according to the characters of jaws and teeth: Baryonychinae and Spinosaurinae. Teeth from baryonychines have serrated mesial and distal carinae with extremely fine denticles, approximately seven per millimetre, much smaller than those in IPS-G1, and characteristic longitudinal ridges extending along the height of the crown (CHARIG & MILNER 1997; CANUDO & RUIZ-OMENACA 2003). They differ from IPS-G1, which has no ornamentation. Spinosaurines have teeth with reduced labiolingual compression, and slightly recurved or straight crowns without denticles (MILNER 1997). The tooth ISP-G1 is well flattened and presents denticles in both carinae.

5.3. Comparison with Allosauroidae or Carnosauria (Carcharodontosauridae, Sinraptoridae and Allosauridae)

Allosauroidae *sensu* ALLAIN (2002) or Carnosauria *sensu* HOLTZ & OSMOLSKA (2004) is an avetheropodan clade that includes at least three families: Carcharodontosauridae, Allosauridae and Sinraptoridae (ALLAIN 2002; HOLTZ & OSMOLSKA 2004). Carcharodontosaurids come from the uppermost Early Cretaceous and Late Cretaceous of Africa and South America (CORIA & SALGADO 1995; SERENO et al. 1996) and are not known from Laurasia. In fact their current occurrence suggests a gondwanian distribution.

Some Allosauroidae, like *Acrocanthosaurus* from the Lower Cretaceous of North America and *Neovenator* from the Lower Cretaceous of United Kingdom, have been sometimes regarded as carcharodontosaurids (RAUHUT 2003; HOLTZ et al. 2004). This discussion is out of our paper, but *Acrocanthosaurus* and *Neovenator* have tooth without curved enamel wrinkles (see below). Maybe represent a sister group of gondwanian carcharodontosaurids with a laurasian representation.

The carcharodontosaurids *Giganotosaurus carolinii* CORIA & SALGADO, 1995 and *Carcharodontosaurus saharicus* (DÉPERET & SAVORNIN, 1927) were similar to *Tyrannosaurus* in size, and probably longer and heavier. A distinctive character of carcharodontosaurid teeth is the presence of curved enamel wrinkles anterior to the serrations on the lingual and/or medial sides (SERENO et al. 1996; VERALLI & CALVO 2004; CANUDO et al. 2004). The tooth IPS-G1 has smooth enamel without wrinkles, unlike carcharodontosaurids.

Allosaurids have a wide distribution. They are known from the Late Jurassic and Early Cretaceous of North America, Portugal, the United Kingdom and France (MADSEN 1976; PÉREZ-MORENO et al. 1993, 1999; HUTT et al. 1996; HARRIS 1998; MILNER 2002; BAKKER & BIR 2004; HOLTZ et al. 2004), but up to the present they have not been found in Spain. The tooth IPS-G1 has a general morphology similar to that of allosaurids. The DSDI for the Late Jurassic *Allosaurus* and Early Cretaceous *Acrocanthosaurus* as well as for IPS-G1 is 1 (RAUHUT & WERNER 1995; HARRIS 1998). The size and morphology of denticles are plesiomorphic and similar in IPS-G1 and allosaurids. The denticles of these allosaurids are sharp (chisel-like) with an acute apex directed toward the crown tip (BAKKER & BIR 2004). In *Allosaurus fragilis* the mesial row of serrations on each tooth is shorter than the distal one (MADSEN 1976), as in IPS-G1. The systematic interest of this character can be object of discussion. The length of carina mesial could vary within the tooth row and especially, with the state of eruption of teeth (O. RAUHUT, personal communication). Similar serration pattern is

present in *Neovenator salerii* (HUTT et al. 1996) from the Barremian of England. Its teeth present 12 serrations per 5 mm (11 in IPS-G1). The enamel of the allosaurids is smooth without wrinkles (BAKKER & BIR 2004), unlike in carcharodontosaurids. Allosaurids are well known in the Kimmeridgian-Tithonian of Portugal (PÉREZ-MORENO et al. 1999; ANTUNES & MATEUS 2003) and in the Lower Cretaceous of the United Kingdom (HUTT et al. 1996). Possibly, although smaller, allosaurid teeth from the Berriasian of the United Kingdom have also been described (MILNER 2002).

Sinraptorids are a group of highly pneumatized Late Jurassic Chinese allosauroids represented by at least two genera, *Sinraptor* and *Yangchuanosaurus* (DONG et al. 1978; CURRIE & ZHAO 1994). There are possible presences outside China: *Metriacanthosaurus* from the Jurassic of England (PAUL 1988) and *Lourinhanosaurus antunesi* MATEUS, 1998 from the Kimmeridgian-Tithonian of Portugal (MATEUS 1998), but it is necessary to have more material in order to confirm the existence of this group in Europe. Teeth from *Sinraptor dongi* CURRIE & ZHAO, 1994 have not been described in detail. Those of *Sinraptor hepingensis* GAO, 1992 are serrated on anterior and posterior edges, with 24 denticles per 10 mm. The fourth maxillary tooth has a FABL of 28 mm (GAO 1992). The upper and lower teeth of *Yangchuanosaurus shangyuensis* DONG et al., 1978 are laterally flattened and curved posteriorly, with serrated anterior and posterior ridges (12 denticles per 5 mm), a number similar to *Sinraptor*, allosaurids and IPS-G1. From the above, it seems that given current knowledge the teeth of sinraptorids are indistinguishable from those of allosaurids.

5.4. Comparison with Dromaeosauridae

Dromaeosaurids are small to medium-sized maniraptoriform theropods, but there are also some big ones (KIRKLAND et al. 1993; NORELL & MAKOVICKY 2004). Dromaeosaurids are abundant and widely distributed in the Cretaceous of Laurasia (CURRIE et al. 1990; MILNER 2002; SANKEY et al. 2002; SWEETMAN 2004), and apparently scarcer, but they were also present in Gondwana (RAUHUT & WERNER 1995; NOVAS & POL, 1995). Isolated teeth of dromaeosaurids are very abundant in the Hauterivian and Barremian of the Iberian Peninsula (RAUHUT 2002; CANUDO & RUIZ-OMEÑACA 2003) as well as in Portugal and Great Britain (RAUHUT 2002; SWEETMAN 2004).

Traditionally, Dromaeosauridae have been divided into two subfamilies: Velociraptorinae and Dromaeosaurinae. The teeth of Velociraptorinae are characterised by the absence of denticles in the mesial carina or by mesial denticles smaller than the distal ones (CURRIE et al. 1990). Thus, the velo-

ciraptorinae denticle size difference index is approximately 1.5 (RAUHUT & WERNER 1995), very different from IPS-G1. A different pattern is present in Dromaeosaurinae; the type species *Dromaeosaurus* has teeth with a DSDI of 0.937 (3 denticles in mesial and 3.2 in distal, CURRIE 1995). A similar pattern has been observed in other dromaeosaurids, such as *Utahraptor* from the Barremian of the USA. The teeth of the holotype of *Utahraptor* show a DSDI variation from 0.846 to 0.916 (KIRKLAND et al. 1993). This pattern is different from IPS-G1, where the DSDI is equal to one.

5.5. Comparison with Tyrannosauroidae

Tyrannosauroids were the largest Late Cretaceous carnivorous dinosaurs, with especially large heads, heterodont dentition and robust bodies (CURRIE et al. 2003). Furthermore, current evidence suggests that Late Jurassic and Early Cretaceous tyrannosauroids (except Tyrannosauridae sensu stricto) were rather small dinosaurs (HUTT et al. 2001; RAUHUT 2003). Late Cretaceous tyrannosaurids show denticles similar in size and shape to IPS-G1: chisel-shaped and oriented parallel to the base of the tooth, with 2 denticles per millimetre (approximately 10 per 5 mm) and DSDI = 1. However, the serrations of tyrannosaurid teeth show well developed blood grooves between the bases of the denticles, oriented towards the base of the crown (CURRIE et al. 1990; FARLOW et al. 1991; ABLER 1992). These significant blood grooves are not present in IPS-G1. Moreover, the crowns of tyrannosaurid teeth are nearly conical in shape and slightly laterally compressed (SAMMAN et al. 2002), whereas IPS-G1 is well-compressed labiolingually. Early Cretaceous tyrannosauroids such as *Eotyrannus* from the Wessex Formation (Barremian) have a DSDI = 1.5 (HUTT et al. 2001). This value is high compared to Late Cretaceous tyrannosaurids and the Galve IPS-G1 tooth, and it is more similar to dromaeosaurids (HUTT et al. 2001).

6. Conclusions

The Berriasian theropod record from Laurasia is poorly known, but could be very useful for a better understanding of the faunal change between the old Jurassic and the modern Cretaceous dinosaur assemblages, which is poorly documented in Europe. The Iberian Peninsula record is of special interest from the palaeobiogeographic point of view because of its location between Laurasia and Gondwana. In the Galve area (NE Spain) there is a significant dinosaur record of the upper Tithonian-middle Berriasian interval. The dinosaurs are represented, at least, by two small and one large Theropoda (IPS-G1), one Sauropoda and one Ornithopoda (ichnological remains).

The tooth studied in this paper is the first representative of a very big theropod from the Berriasian of Iberia. IPS-G1 had been previously assigned to "*Charcharodontosaurus*" and *Megalosaurus*, but it has never been formally described before. It is a plesiomorphic tooth, with smooth enamel, chisel-shaped denticles of the same average size in both carinae and without blood grooves. After comparisons with several groups of large theropods, we conclude that IPS-G1 differs from the teeth of ceratosaurids, abelisaurids, spinosaurids, carcharodontosaurids, dromaeosaurids and tyrannosauroids. The basal tetanurans, torvosaurids ("megalosaurids") and allosauroids present similar tooth crowns and it is difficult to identify isolated tooth crowns. In general they show a DSDI around 1 and have chisel-like denticles, both are symplesiomorphies of theropods. If we consider the temporal and geographic context of tooth studied (there are no "megalosaurids" in European Cretaceous), IPS-G1 could represent an allosauroid different from Carcharodontosauridae.

Up to the present, the presence of very big theropods in the Berriasian of Europe has only been supported by ichnological evidence from the Wealden of Germany (LOCKLEY 2000) and the Huertiles Alloformation in Spain (Camereros Basin), provinces of Soria (BARCO et al. 2005) and La Rioja (CASANOVAS et al. 1995). The presence of big allosauroids in the Berriasian of Europe was previously suggested by the gigantic theropod footprints from the provinces of Soria and La Rioja (BARCO et al. 2005), and by an isolated tooth from the United Kingdom (MILNER 2002). The tooth IPS-G1 represents the first skeletal fossil remain of Allosauroidae from Spain and the biggest theropod tooth of the European Berriasian.

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References

- ABLER, W. L. (1992): The serrated teeth of tyrannosaurid dinosaurs, and biting structures in other animals. – *Paleobiology*, **18** (2): 161–183.
- ALLAIN, R. (2002): Discovery of megalosaur (Dinosauria, Theropoda) in the middle Bathonian of Normandy (France) and its implications for the phylogeny of basal Tetanurae. – *J. Vertebr. Paleont.*, **22** (3): 548–563.
- ANTUNES, M. T. & MATEUS, O. (2003): Dinosaurs of Portugal. – *C. R. Palevol*, **2** (1): 77–95.
- BÁDENAS, B., SALAS, R. & AURELL, M. (2004): Three orders of regional sea-level changes control facies and stacking patterns of shallow carbonates in the Maestrat Basin (Tithonian-Berriasian, NE Spain). – *Int. J. Earth Sci.*, **93**: 144–162.
- BAKKER, T. T. & BIR, G. (2004): Dinosaur crime scene investigations: Theropod behavior at Como Bluff, Wyoming, and the evolution of birdness. – In: CURRIE, P. J., KOPPELHUS, E. B., SHUGAR, M. A. & WRIGHT, J. L. (Eds.): Feathered dragons: Studies on the transition from dinosaurs to birds, p. 301–342; Bloomington (Indiana Univ. Press).
- BARCO, J. L., CANUDO, J. I., CUENCA-BESCÓS, G. & RUÍZ-OMEÑACA, J. I. (2005a): Un nuevo dinosaurio saurópodo, *Galvesaurus herreroi* gen. nov., sp. nov., del tránsito Jurásico-Cretácico en Galve (teruel, NE de España). – *Naturaleza Aragonesa*, **15**: 4–17.
- BARCO, J. L., CANUDO, J. I., RUÍZ-OMEÑACA, J. I. & RUBIO DE LUCAS, J. L. (2005b): Evidencia icnológica de un dinosaurio terópodo gigante en el Berriasiense (Cretácico Inferior) de Laurasia (Las Villasecas, Soria, España). – *Rev. Soc. Españ. Paleont. número extr.* **10**, 59–71.
- BARCO, J. L. & RUÍZ-OMEÑACA, J. I. (2001a): Primeros dientes de terópodo (Dinosauria, Saurischia) en la Formación Villar del Arzobispo (Titónico-Berriasiense): yacimientos Cuesta Lonsal y Las Cerradicas 2 (Galve, Teruel). In: MELÉNDEZ, G., HERRERA, Z., DELVENE, G. & AZANZA, B. (Eds.): XVII Jornadas de la Sociedad Española de Paleontología, **1**: 239–246; Zaragoza (Universidad de Zaragoza).
- BARCO, J. L. & RUÍZ-OMEÑACA, J. I. (2001b): Primeros restos postcraneales de terópodo (Dinosauria, Saurischia) en la Formación Villar del Arzobispo (Tithónico-Berriasiense): un centro vertebral caudal del yacimiento Carretera (Galve, Teruel). In: MELÉNDEZ, G., HERRERA, Z., DELVENE, G. & AZANZA, B. (Eds.): XVII Jornadas de la Sociedad Española de Paleontología, **1**: 247–254; Zaragoza (Universidad de Zaragoza).
- BARCO, J. I., RUÍZ-OMEÑACA, J. I., CANUDO, J. I., CUENCA-BESCÓS, G., AMO SANJUÁN, O., PÉREZ-LORENTE, F., RUBIO, C. y HERRERO, M. A. (2004): Guía del Parque Paleontológico de Galve. – 109 pp.; Zaragoza (Ayuntamiento de Galve y Paleoymás).
- BITTENCOURT, J. S. & KELLNER, A. W. A. (2002): Abelisauria (Theropoda, Dinosauria) teeth from Brazil. – *Boletim do Museu Nacional, Geologia*, **63**: 1–8.
- BROCHU, C. A. (2003): Osteology of *Tyrannosaurus rex*: insights from a nearly complete skeleton and high-resolution computed tomographic analysis of the skull. – *J. Vertebr. Paleont.*, **22** (Suppl. to no. 4): 1–138.
- BUSCALIONI, A. D., GASPARINI, Z., PÉREZ-MORENO, B. P. & SANZ, J. L. (1997): Argentinean theropods: first morphological analysis on isolated teeth. – In: First European Workshop on Vertebrate Palaeontology. Geological Museum, Copenhagen University. Geological Society of Denmark, On Line Series, **1** (www.purl.dk/net/9710-0100).
- BUSCALIONI, A. D. & SANZ, J. L. (1990): The small crocodile *Bernissartia fagesii* from the Lower Cretaceous of Galve (Teruel, Spain). – *Bull. Inst. Roy. Sci. Natur. Belgique, Sci. Terre*, **60**: 129–150.
- CANUDO, J. I. & CUENCA-BESCÓS, G. (1996): Two new mammalian teeth (Multituberculata and Peramurina) from the Lower Cretaceous (Barremian) of Spain. – *Cret. Res.*, **17** (2): 215–228.
- CANUDO, J. I. & RUÍZ-OMEÑACA, J. I. (2003): Los restos directos de dinosaurios terópodos (Excluyendo Aves) en España. – In: PÉREZ-LORENTE, F. (Ed.): Dinosaurios y otros reptiles mesozoicos en España (IER, Ciencias de la Tierra, **26**), p. 347–374; Logroño (Instituto de Estudios Riojanos).
- CANUDO, J. I., SALGADO, L., BARCO, J. L., BOLATTI, R. & RUÍZ-OMEÑACA, J. I. (2004): Dientes de dinosaurios terópodos y saurópodos de la Formación Cerro Lisandro (Cenomaniense superior-Turonense inferior, Cretácico superior) en Río Negro (Argentina). – *Geo-Temas*, **6** (5): 31–34.
- CASANOVAS, J. L., FERNÁNDEZ, A., PÉREZ-ORENTE, F. & SANTAFÉ, J. V. (1995): Un terópodo camosaurio en el camino a Treguajantes (La Rioja, España). – *Ciencias de la Tierra*, **18**: 13–14.
- CHARIG, A. J. & MILNER, A. C. (1997): *Baryonyx walkeri*, a fish-eating dinosaur from the Wealden of Surrey. – *Bull. Nat. Hist. Mus. London (Geol. Ser.)*, **53** (1): 11–70.
- CORIA, R. & SALGADO, L. (1995): A new giant carnivorous dinosaur from the Cretaceous of Patagonia. – *Nature*, **377**: 224–226.
- (1998): A basal Abelisauria Novas, 1992 (Theropoda-Ceratosauria) from the Cretaceous of Patagonia, Argentina. – *Gaia*, **15**: 89–102.
- CHRISTIANSEN, P. & BONDE, N. (2003): The first dinosaur from Denmark. – *N. Jb. Geol. Paläont., Abh.*, **227**: 287–299.
- CRUSAFONT-PAIRÓ, M. & ADROVER, R. (1966): El primer representante de la clase mamíferos hallado en el Mesozoico de España. – *Teruel*, **35**: 139–143.
- CUENCA-BESCÓS, G., CANUDO, J. I. & RUÍZ-OMEÑACA, J. I. (1997): Dinosaurios del tránsito Jurásico-Cretácico en Aragón. – In: GAMEZ VINTANED, J. A. & LIÑÁN, E. (Eds.): V Jornadas Aragonesas de Paleontología “Vida y ambientes del Jurásico”. Homenaje científico a la Prof. Asunción Linares, p. 193–221; Zaragoza (Institución “Fernando el Católico”).
- CURRIE, P. J. (1995): New information on the anatomy and relationships of *Dromaeosaurus albertensis* (Dinosauria: Theropoda). – *J. Vertebr. Paleont.*, **15**: 576–591.
- CURRIE, P. J., HURUM, J. H. & SABATH, K. (2003): Skull structure and evolution in tyrannosaurid dinosaurs. – *Acta Palaeont. Polon.*, **48** (2): 227–234.
- CURRIE, P. J., RIGBY, J. K. Jr. & SLOAN, R. E. (1990): Theropod teeth from the Judith River Formation of southern Alberta, Canada. – In: CARPENTER, K. & CURRIE, P. J. (Eds.): Dinosaur systematics. Approaches and Perspectives, p. 107–125; Cambridge (Cambridge Univ. Press).

- CURRIE, P. J. & ZHANG, X. J. (1994): A new large theropod (Dinosauria, Theropoda) from the Jurassic of Xinjiang, People's Republic of China. – *Can. J. Earth Sci.*, **30** (10/11): 2037–2081.
- DEPÉRET, M. C. & SAVORNIN, J. (1927): La faune de Reptiles et de Poissons Albiens de Timoun (Sahara, Algérie). – *Bull. Soc. Géol. France*, **4** (27): 257–265.
- DÍAZ, M., YÉBENES, A., GOY, A. & SANZ, J. L. (1984): Landscapes inhabited by Upper Jurassic/Lower Cretaceous archosaurs (Galve, Teruel, Spain). – In: REIF, W. E. & WESTPHAL, F. (Eds.): *Third symposium on Mesozoic Terrestrial Ecosystems, Short Papers*, p. 67–72; Tübingen (Attempto).
- DONG, Z. M., ZHANG, Y. H., LI, X. & ZHOU, S. W. (1978): Note on a new carnosaur *Yangchuanosaurus shangyuensis* gen. et sp. nov. from the Jurassic of Yangchuan District, Sichuan Province. – *Kexue Tongbao*, **23**: 298–302. (in Chinese, English translation available at The Polyglot Paleontologist: <http://ravenel.si.edu/paleo/paleoglot/>).
- FARLOW, J. O., BRINKMAN, D. L., ABLER, D. L. & CURRIE, P. J. (1991): Size, shape, and serration density of theropod dinosaur lateral teeth. – *Mod. Geol.*, **16** (1–2): 161–198.
- GAO, Y. (1992): *Yangchuanosaurus hepingensis*, a new species of carnosaur from Zigong, Sichuan. – *Vert. Palasiatica*, **30** (4): 313–324. (in Chinese, English translation available at The Polyglot Paleontologist: <http://ravenel.si.edu/paleo/paleoglot/>).
- HAHN, G. & HAHN, R. (1992): Neue Multituberculaten-Zähne aus der Unter-Kreide (Barremium) von Spanien (Galve und Uña). – *Geologica et Palaeontologica*, **26**: 143–162.
- HARDENBOL, J., THIERRY, J., FARLEY, M. B., JACQUIN, T., DE GRACIANSKI, P. C. & VAIL, P. R. (1998): Mesozoic and Cenozoic sequence chronostratigraphic framework of European basins. – In: DE GRACIANSKI, P. C., HARDENBOL, J., JACQUIN, T. & VAIL, P. R. (Eds.): *Mesozoic and Cenozoic Sequence Stratigraphy of European basins*. – SEPM, spec. vol., **60**, charts 1–8.
- HARRIS, J. D. (1998): A reanalysis of *Acrocanthosaurus atokensis*, its phylogenetic status, and paleobiogeographic implications, based on a new specimen from Texas. – *New Mexico Mus. Nat. Hist. Sci. Bull.*, **13**: 1–75.
- HOLTZ, T. R., Jr. (2000): A new phylogeny of the carnivorous dinosaurs. – *Gaia*, **15**: 5–61.
- HOLTZ, T. R., MOLNAR, R. E. & CURRIE, P. H. (2004): Basal Tetanurae. – In: WEISHAMPEL, D. B., DODSON, P. & OSMOLSKA, H. (Eds.): *The Dinosauria*, p. 71–110; Berkeley (Univ. California Press).
- HOLTZ, T. R. & OSMOLSKA, H. (2004): Saurischia. – In: WEISHAMPEL, D. B., DODSON, P. & OSMOLSKA, H. (Eds.): *The Dinosauria*, p. 21–24; Berkeley (Univ. California Press).
- HUTT, S., MARTILL, D. M. & BARKER, M. J. (1996): The first European allosaurid dinosaur (Lower Cretaceous, Wealden Group). – *N. Jb. Geol. Paläont., Mh.*, **1996**: 635–644.
- HUTT, S., NAISH, D., MARTILL, D. M., BARKER, M. J. & NEWBERY, P. (2001): A preliminary account of a new tyrannosauroid theropod from the Wessex Formation (Early Cretaceous) of southern England. – *Cret. Res.*, **22** (2): 227–242.
- IPAS, J., AURELL, M. & BADENAS, B. (2004): Propuesta de correlación de las Secuencias del Titónico (Jurásico Superior) entre los sectores septentrional y oriental de la Cuenca Ibérica. – *Geotemas*, **6** (2): 79–82.
- KIRKLAND, J. I., BURGE, D. & GASTON, R. (1993): A large dromaeosaur (Theropoda) from the Lower Cretaceous of eastern Utah. – *Hunteria*, **2** (10): 1–16.
- KÜHNE, W. G. & CRUSAFONT-PAIRO, M. (1968): Mamíferos del Wealdense de Uña, cerca de Cuenca. Nota preliminar. – *Acta Geol. Hisp.*, **3** (5): 133–134.
- LOCKLEY, M. G. (2000): An amended description of the theropod footprint *Bueckburgichnus maximus* KUHN 1958, and its bearing on the megalosaur tracks debate. – *Ichnos*, **7**: 217–225.
- LOCKLEY, M. G., MEYER, C. A. & DOS SANTOS, V. F. (2000): *Megalosauropus* and the problematic concept of Megalosaur footprints. – *Gaia*, **15**: 312–337.
- MADSEN, J. H. Jr. (1976): *Allosaurus fragilis*: A revised osteology. – *Utah Geol. Min. Surv., Bull.*, **109**: 1–163.
- MADSEN, J. H. Jr. & WELLES, S. P. (2000): *Ceratosaurus* (Dinosauria, Theropoda); a revised osteology. – *Utah Geol. Surv., Miscell. Publ.*, **2000** (2): 1–80.
- MARTÍN-CLOSAS, C. (1989): Els caròfits del Cretaci inferior de les conques perifèriques del Bloc de l'Ebre. – Tesis doctoral, Universidad de Barcelona, 581 pp.
- MATEUS, O. (1998): *Lourinhanosaurus antunesi*, a new Upper Jurassic allosaurid (Dinosauria: Theropoda) from Lourinha (Portugal). – *Mem. Acad. Ciênc. Lisboa, Clas. Ciênc.*, **37**: 111–124.
- MILNER, A. (2002): Theropod dinosaurs of the Purbeck limestone group, Southern England. – *Palaeontology, spec. Pap.*, **68**: 191–201.
- NORELL, M. A. & MAKOVICKY, P. J. (2004): Dromaeosauridae. – In: WEISHAMPEL, D. B., DODSON, P. & OSMOLSKA, H. (Eds.): *The Dinosauria*, p. 196–209; Berkeley (Univ. California Press).
- NOVAS, F. E. (1997): Abelisauridae. – In: CURRIE, P. J. & PADIAN, K. (Eds.): *Encyclopedia of Dinosaurs*, p. 1–2; San Diego (Academic Press).
- NOVAS, F. E. & POL, D. (2005): New evidence on deinonychosaurian dinosaurs from the Late Cretaceous of Patagonia. – *Nature*, **433**: 858–861.
- PAUL, G. S. (1988): *Predatory dinosaurs of the world*. – 464 pp.; New York (Simon & Schuster).
- PÉREZ-LORENTE, F., CUENCA-BESCÓS, G., AURELL, M., CANUDO, J. I., SORIA, A. R. & RUÍZ-OMENACA, J. I. (1997): Las Cerradillas tracksite (Berriasian, Galve, Spain): Growing evidence for quadrupedal ornithomimids. – *Ichnos*, **5** (2): 109–120.
- PÉREZ-MORENO, B., CHURE, D. J., PIRES, C., MARQUES DA SILVA, C., DOS SANTOS, V., DANTAS, P., POVOAS, L., CACHAO, M., SANZ, J. L. & GALOPIN DE CARVALHO, A. M. (1999): On the presence of *Allosaurus fragilis* (Theropoda: Carnosauria) in the Upper Jurassic of Portugal: first evidence of an intercontinental dinosaur species. – *J. Geol. Soc., London*, **156** (3): 449–452.

- PÉREZ-MORENO, B., SANZ, J. L., SUDRE, J. & SIGÉ, B. (1993): A theropod dinosaur from the Lower Cretaceous of southern France. – *Rev. Paléobiol.*, vol. spéc., 7: 173-188.
- RAUHUT, O. W. M. (2002): Dinosaur teeth from the Barremian of Uña, Province of Cuenca, Spain. – *Cret. Res.*, 23 (2): 255-263.
- (2003): A tyrannosaurid dinosaur from the Upper Jurassic of Portugal. – *Palaeontology*, 46: 903-910.
- (2004): Provenance and anatomy of *Genyodectes serus*, a large-toothed ceratopsian (Dinosauria: Theropoda) from Patagonia. – *J. Vertebr. Paleont.*, 24 (4): 894-902.
- RAUHUT, O. W. M. & KRIWET, J. (1994): Teeth of a big Theropod Dinosaur from Porto das Barcas (Portugal). – *Berliner geowiss. Abh.*, E13: 179-185.
- RAUHUT, O. W. M. & WERNER, C. (1995): First record of the family Dromaeosauridae (Dinosauria: Theropoda) in the Cretaceous of Gondwana (Wadi Milk Formation, northern Sudan). – *Paläont. Z.*, 69: 475-489.
- RUÍZ-OMEÑACA, J. I. & CANUDO, J. I. (2003): Un nuevo dinosaurio terópodo ("*Prodeinodon*" sp.) en el Cretácico Inferior de La Cantalera (Teruel). – *Geogaceta*, 34: 111-114.
- RUÍZ-OMEÑACA, J. I., CANUDO, J. I., AURELL, M., BÁDENAS, B., BARCO, J. L., CUENCA-BESCÓS, G. & IPAS, J. (2004): Estado de las investigaciones sobre los vertebrados de Jurásico Superior y Cretácico Inferior de Galve (Teruel). – *Estud. Geol.*, 60: 179-202.
- RUÍZ-OMEÑACA, J. I., CANUDO, J. I. & CUENCA-BESCÓS, G. (1997): Primera evidencia de un área de alimentación de dinosaurios herbívoros en el Cretácico Inferior de España (Teruel). – *Monogr. Acad. Cienc. Exa., Fis., Quím. Nat. de Zaragoza*, 10: 1-48.
- RUÍZ-OMEÑACA, J. I., CANUDO, J. I., CUENCA-BESCÓS, G. & AMO, O. (1998): Theropod teeth from the Lower Cretaceous of Galve (Teruel, Spain). – In: JAGT, J. W. M., LAMBERS, P. H., MULDER, E. W. A. & SCHULP, A. S. (Eds.): Third European Workshop on Vertebrate Paleontology, Maastricht, 6-9 May 1998. Programme and Abstracts. Field Guide, p. 62-63; Maastricht (Natuurhistorisch Museum Maastricht).
- SALAS, R., GUIMERÁ, J., MAS, R., MARTÍN-CLOSAS, C., MELÉNDEZ, A. & ALONSO, A. (2001): Evolution of the Mesozoic Central Iberian Rift System and its Cenozoic inversion (Iberian chain). – In: CAVAZZA, W., ROBERTSON, A. & ZIEGLER, P. A. (Eds.): Peritethyan rift/wrench basins and passive margins. – *Peri-Tethyan Memoir*, 6: Peritethyan Rift/Wrench Basins and Passive Margins. – *Mém. Mus. Nat. Hist. Natur. Paris*, 186: 145-185.
- SAMMAN, T., POWELL, G. L., CURRIE, P. J. & HILLS, L. V. (2002): Determining tooth positions in the jaw of tyrannosaurid dinosaurs-biting off more than you can chew? – *J. Vertebr. Paleont.*, 22 (Suppl. to no. 3): 101A-102A.
- SAMPSON, S. D., WITMER, L. M., FORSTER, C. A., KRAUSE, D. W., O. CONNOR, P. M., DODSON, P. & RAVOAVY, F. (1998): Predatory Dinosaur Remains from Madagascar: Implications for the Cretaceous Biogeography of Gondwana. – *Science*, 280: 1048-1051.
- SANDER, P. M. (1997): Teeth and Jaws. – In: CURRIE, P. J. & PADIAN, K. (Eds.): *Encyclopedia of Dinosaurs*, p. 717-725; San Diego (Academic Press).
- SANKEY, J. T., BRINKMAN, D. B., GUENTHER, M. & CURRIE, P. J. (2002): Small theropod and bird teeth from the Late Cretaceous (Late Campanian) Judith River Group, Alberta. – *J. Paleont.*, 76: 751-763.
- SANTAFÉ-LLOPIS, J. V. & CASANOVAS-CLADELLAS, M. L. (1993): Dinosaurios en la Comunidad Valenciana. – 205 pp.; Valencia (Generalitat Valenciana).
- SANZ, J. L., BUSCALIONI, A. D., CASANOVAS, M. L. & SANTAFÉ, J. V. (1987): Dinosaurios del Cretácico Inferior de Galve (Teruel, España). – *Estud. Geol.*, volumen extraordinario Galve-Tremp, p. 45-64.
- SERENO, P. C., BECK, A. L., DUTHEIL, D. B., GADO, B., LARSSON, C. E., LYON, G. H., MARCOT, J. D., RAUHUT, O. W., SADLEIR, R. W., SIDOR, C. A., VARRICCHIO, D. D., WILSON, G. P. & WILSON, J. A. (1998): A long-snouted predatory dinosaur from Africa and the evolution of spinosaurids. – *Science*, 282: 1298-1302.
- SERENO, P. C., DUTHEIL, D. B., IAROCHE, M., LARSSON, H. C. E., LYON, G. H., MAGWENE, P. M., SIDOR, C. A., VARRICCHIO, D. J. & WILSON, J. A. (1996): Predatory dinosaurs from the Sahara and late Cretaceous faunal differentiation. – *Science*, 271: 986-991.
- SMITH, J. B. & DODSON, P. (2003): A proposal for a standard terminology of anatomical notation and orientation in fossil vertebrate dentitions. – *J. Vertebr. Paleont.*, 23 (1): 1-12.
- SORIA, A. R., MELÉNDEZ, A., CUENCA-BESCÓS, G., CANUDO, J. I. & LIESA, C. L. (1995): Los sistemas lacustres del Cretácico Inferior de la Cordillera Ibérica Central: la Cubeta de Aliaga. – In: MELÉNDEZ, A. & AURELL, M. (Eds.): Grupo Español de Sedimentología. XIII Congreso Español de Sedimentología. Teruel, 1995. Guía de Excursiones, p. 91-141; Zaragoza (Universidad de Zaragoza).
- SWEETMAN, S. C. (2004): The first record of velociraptorine dinosaurs (Saurischia, Theropoda) from the Wealden (Early Cretaceous, Barremian) of southern England. – *Cret. Res.*, 25 (3): 353-364.
- VERALLI, C. & CALVO, J. (2004): Dientes de terópodos carcharodontosáuridos del Turoniano superior-Coniaciano inferior del Neuquén, Patagonia, Argentina. – *Ameghiniana*, 41: 587-590.
- WEISHAMPEL, D. B., BARRETT, P. M., CORIA, R., LE LOEUFF, J., XU, X., ZHAO, X., SHANI, A., GOMANI, E. M. P. & NOTO, C. R. (2004): Dinosaur Distribution. – In: WEISHAMPEL, D. B., DODSON, P. & OSMOLSKA, H. (Eds.): *The Dinosauria*, p. 517-606; Berkeley (Univ. California Press).

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