Dinosaurs and other fossil vertebrates from the Late Jurassic and Early Cretaceous of the Galve area, NE Spain

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Abstract

Since 1950, diverse assemblages of Mesozoic vertebrates have been described from the Galve area (Teruel Province, NE Spain). More than fifty taxa have been noted, including fishes, crocodyliforms, pterosaurs, dinosaurs and mammals. The Galve fossil sites occur in an Upper Jurassic to Lower Cretaceous succession spanning some 30 myr, divided into five formations, representing marginal marine and continental settings, with a Tithonian–early Barremian regression and a transgression from the Barremian onwards. New discoveries include teeth of the hybodont shark *Lonchidion microselachos*, spinosaurine theropods, Eusauropoda and the dryosaurid *Valdosaurus*. The 30-myr succession shows some possible evolutionary shifts, with a predominance of sauropods as herbivores in older strata, and ornithopods commoner in younger beds. There are some possible replacements among mammals in the latter part of the succession, with trechnotheres, such as spalacotheriids and dryolestoids, dominant in the El Castellar Formation, and multituberculates in the Camarillas Formation. Matching of the vertebrates from the Galve succession with those from age-equivalent units throughout Europe shows close similarity with the Purbeck–Wealden succession of southern England, among others. There are many similarities with dinosaur faunas from North America and Africa, but continent-scale faunal differentiation had clearly begun.
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1. Introduction

The Upper Jurassic to Lower Cretaceous vertebrate faunas from the Galve region in NE Spain have been described by many researchers over the past 50 years. The first vertebrate fossils, found by José María Herrero, were reported by Fernández-Galiano (1958, 1960) and Lapparent (1960). Herrero has continued collecting since the 1950s, while palaeontological teams from Spain, France and Germany have collaborated with him and collected materials at different times through the 1960s and up to the present day. Buscalioni and Sanz (1987), Canudo et al. (1996), Sánchez-Hernández (2002, 2004) and Ruíz-Omeñaca et al. (2004) have reviewed the vertebrate faunas, but there has never been a comprehensive overview of these rich deposits, nor a thorough comparison with other units of the same age. A recent review by Ruíz-Omeñaca et al. (2004) does not include more recent discoveries, and introduces changes to the names of several well-known outcrops and to the numbering scheme of fossils housed in the museum of Galve and in

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the Herrero collection. We do not adopt these changes to well-known usage, and comment on potential confusions where necessary.

The aims of this paper are to present the geological setting and the faunas from Galve, to describe new material, to reconstruct the palaeogeographical setting, and to compare the faunas with others of similar age elsewhere.

2. Geological setting

The Upper Jurassic to Lower Cretaceous sedimentary succession around Galve (Fig. 1) is part of the infill of the Maestrazgo Basin in the Central Iberian Range, in the centre of Teruel Province (Sanz et al., 1984; Díaz and Yébenes, 1987; Cuenca-Bescós et al., 1997; Ruíz-Omeñaca et al., 2004; Ipas et al., 2005; Liesa et al., 2006). The Galve sub-basin was formed by the activity of two main fault sets oriented NNW–SSE and ENE–WSW during the late Hauterivian creating the elongated basin that measures 40 km long and 20 km wide (Liesa et al., 2006). The fossiliferous part of the succession is some 600 m thick (Fig. 2), and has been divided into five formations, the Higueruelas, Villar del Arzobispo, El Castellar, Camarillas and Artoles formations. There are at least three unconformities: one between the Villar

del Arzobispo and El Castellar formations cutting out part of the Tithonian and lower Berriasian strata at the Jurassic/Cretaceous boundary; the second in the upper part of the El Castellar Formation, between the upper Hauterivian and lower Barremian; and the third between the Camarillas Formation and the Artoles Formation (lower/upper Barremian). The succession was first dated using from the overall fossil content of the different formations, but more precise correlations have been based on charophytes (Martín-Closas, 1989) and benthic foraminifera (Ruíz-Omeñaca et al., 2004).

Based on the simplified stratigraphic section shown in Fig. 2, the five formations in the Galve area are described, starting from the bottom of the succession.

2.1. Higueruelas formation

The Higueruelas Formation consists of 40–60 m of carbonates with marine fossils. The limestones are massive or bedded, with oncolitic, peloidal and bioclastic facies, with oolitic grainstones in the last few metres, according to Díaz and Yébenes (1987). The fossils include ostracods, echinoderms, bivalves and gastropods, among other marine invertebrates, which indicate an early to mid Tithonian age. This fossil association is typical of coastal marine deposition, but not too deep,
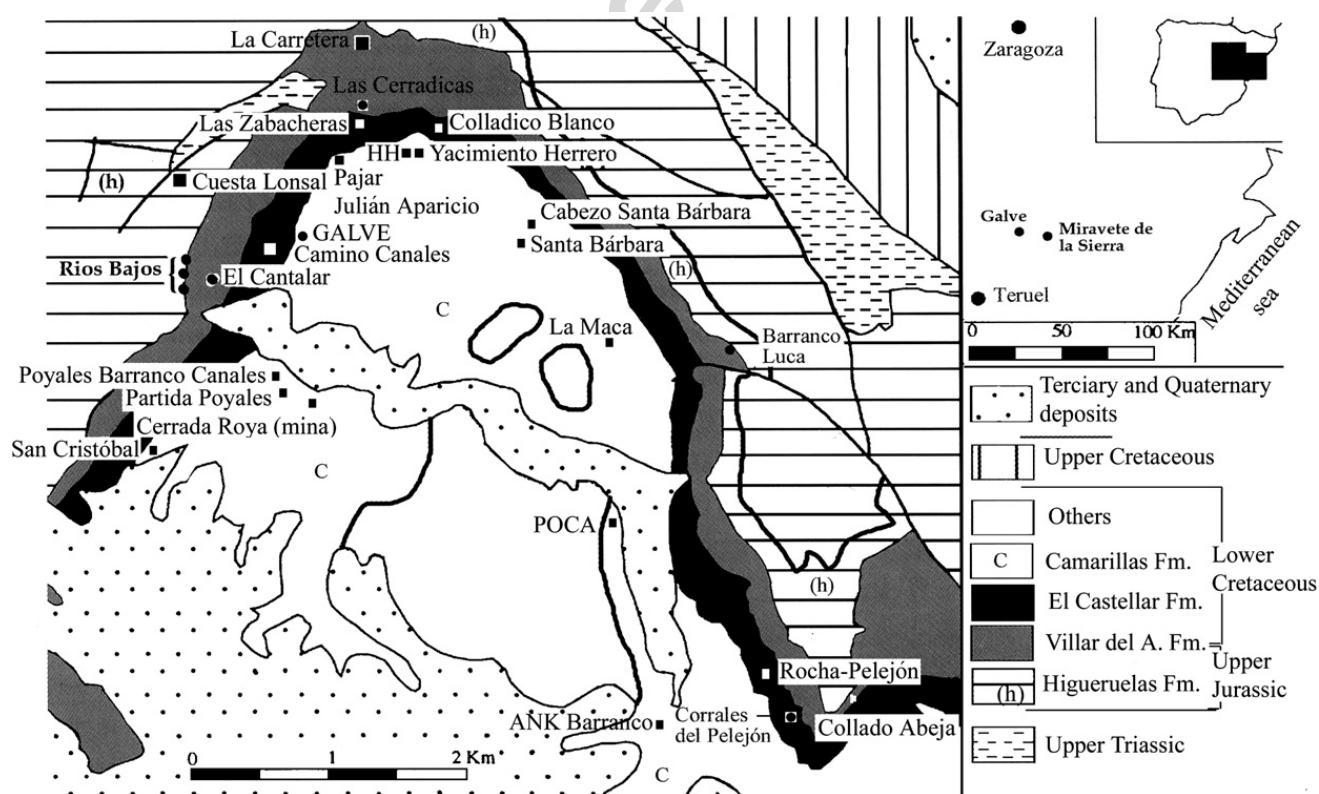
Fig. 1. Geographic setting of the Galve area within Spain and geological map, showing some of the fossil outcrops. The squares indicate fossil sites with vertebrate bones, while the circles show outcrops with footprints. Modified from Pérez-Lorente and Ortega (2003).
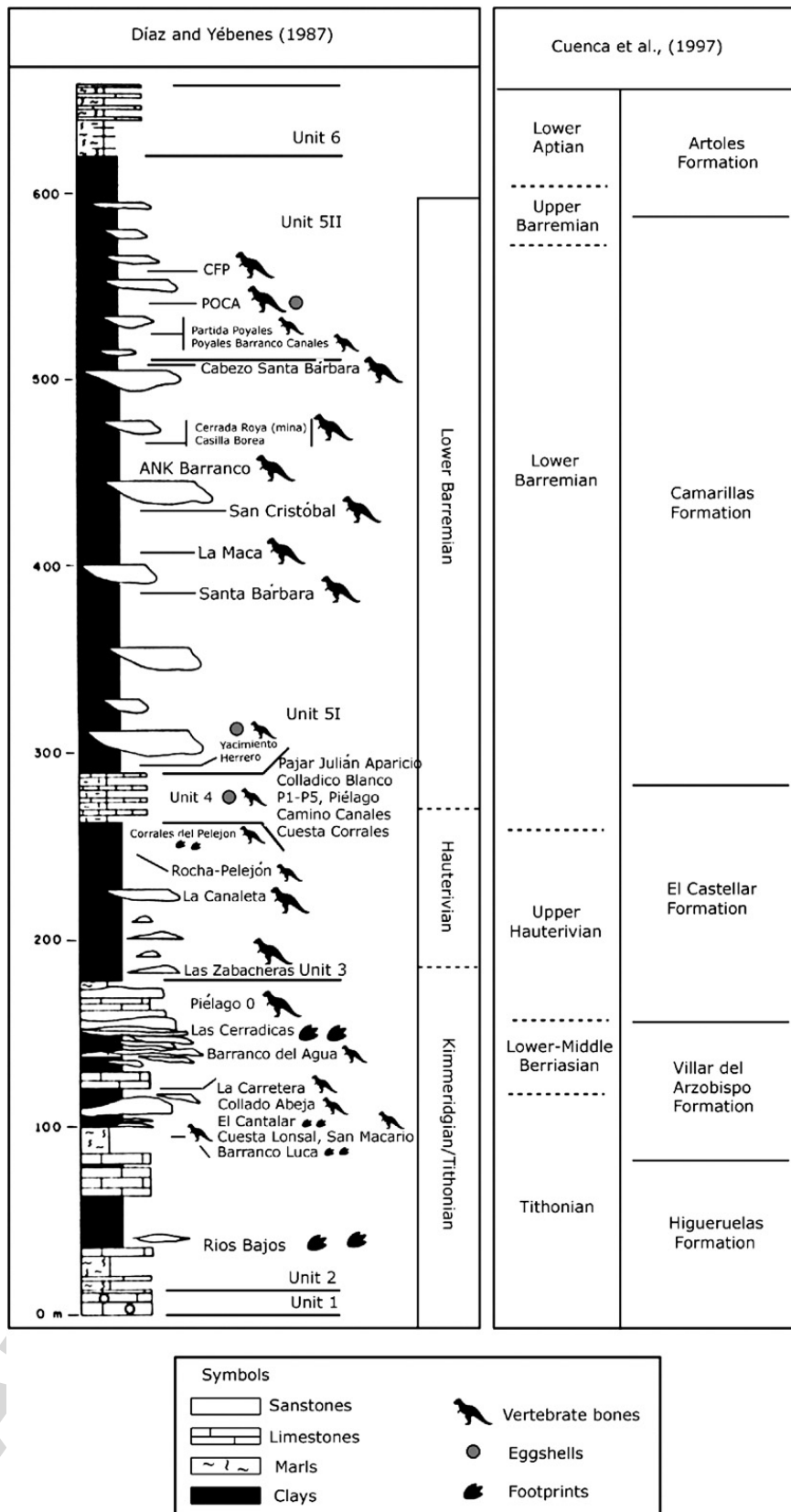
Fig. 2. Simplified stratigraphic column of the Upper Jurassic to uppermost Lower Cretaceous succession in the Galve syncline. The vertebrate fossil sites are indicated at their appropriate stratigraphic levels. After Díaz and Yébenes (1987) and Cuenca-Bescós et al., (1997).

and the sediments indicate deposition in the middle and internal parts of a carbonate ramp (Ipas et al., 2005).

In the upper part of this formation there is an outcrop with theropod footprints (Pérez-Lorente and Romero-Molina, 2001).

2.2. Villar del Arzobispo Formation

The Villar del Arzobispo Formation is a regressive 100 m-thick succession of marine limestones, sandstones and unconsolidated mudstones, with an association of foraminiferans including *Pseudocyclamina* gr. *lituus*, *Archispirocyclina lusitanica* and *Rectocyclamina arrabidensis* which give a Tithonian age at the top of this unit (Díaz and Yébenes, 1987). The formation spans the late Tithonian and the early and mid Berriasian (Fig. 2).

Two fossil sites are known towards the top of this unit: Cuesta Lonsal, source of the remains of a new cetiosaurid sauropod dinosaur (Sánchez-Hernández, 2005) and associated teeth and scales of fishes; and Las Cerradicas, which yielded the footprints of theropods and ornithopods, including the trail of an iguanodontian dinosaur that started with a quadrupedal gait and finished as a biped (Pérez-Lorente et al., 1997; this outcrop was initially dated as Berriasian, but Cuenca-Bescós et al. (1997) revised its age to Late Jurassic). There are also many ripples in these outcrops generated under fluvial influence. In similar beds, or slightly lower, is the El Cantalar outcrop, which produced footprints of an enormous crocodyliform with a total length of about 12 m, although its taxonomic attribution is unclear (Pérez-Lorente and Ortega, 2003).

2.3. El Castellar Formation

The El Castellar Formation consists of about 100 m of alternating varicoloured muds and fine to medium sandstones that pass upwards into grey marls interbedded with grey limestones. The muds are mainly red, brown and purple. The sandstones, with similar colours, exhibit parallel lamination and cross-bedding. They appear as tabular beds often channelized with bottom surfaces. Vertical bioturbation generated by roots is common. The bioclastic wackestones–packstones to mudstones–wackestones towards the top of this formation are tabular with occasionally ferruginous or brecciated tops. The remains of charophytes, ostracods, gastropods and fishes are common. The formation was deposited unconformably on the Villar del Arzobispo Formation, and in the upper part there is also a disconformity, but their duration cannot be assessed.

The El Castellar Formation is dated as late Hauterivian–early Barremian based on the charophyte assemblage, consisting of *Atopochara trivolvis* var. *triquetra*, *Globator maillardii* var. *trochiliscoides*, *Clavator harrisii* var. *reyi*, *Pseudoglobator adnatus* and *Pseudoglobator neimongolensis* var. *posticecapta*, all members of the *Triquetra* biozone (Martín-Closas, 1989). Specimens of *Hemiclavator adnatus* (late Valanginian–early Barremian) and *Globator maillardi* var. *trochiliscoides* (late Hauterivian–late Barremian) have also been found (Martín-Closas, 2000).

Díaz and Yébenes (1987) argued that deposition occurred on an alluvial plain near the coast, based on the bioclastic limestones, numerous sand beds, root marks and charophyte remains. Waning currents deposited abundant clays near the top of the unit, where the calcareous deposits are commoner. The root bioturbation and the ferruginized/brecciated surfaces indicate interruptions in the siliciclastic depositional environment corresponding to the tops of lagoonal systems. The depositional environment is considered as open lacustrine, with distributary channels and a lagoonal system. The palynological analysis by Díez et al. (1995) indicates a xenolithic flora with a predominance of *Classopollis* and *Trilobosporites* over ferns.

Towards the bottom of the El Castellar Formation is the Las Zabacheras outcrop, which yielded the eusauropod (Upchurch et al., 2004) *Aragosaurus ischiaticus* Sanz et al. (1987) and ornithopod remains. Towards the top of the El Castellar Formation is the Corrales del Pelejón outcrop, where dinosaur footprints (Pérez-Lorente and Ortega, 2003) are preserved among ripple marks. Further fossil sites have produced remains of theropod, ornithopod and sauropod dinosaurs (represented by teeth), lissamphibians, crocodyliforms, turtles, mammals (only teeth) and fish scales and teeth. A complete list is given below. The 'unit 4' of Díaz and Yébenes (1987) constitutes the upper part of the El Castellar Formation in the Galve area. Their 'unit 4' (Hauterivian–early Barremian) consists of carbonates (mudstones with charophytes, gastropods, bivalves and other invertebrate marine remains) alternating with grey marls and white sandstones, that were probably deposited in a lagoon, with ephemeral waters and high concentrations of salts.

2.4. Camarillas Formation

The Camarillas Formation is the thickest of all the units in the Galve region, comprising nearly 300 m of white and red channelized sandstones interbedded with massive varicoloured sandy silts and muds, divided into

two parts (unit 5I and unit 5II; Fig. 2), by Díaz and Yébenes (1987).

'Units 5I and 5II' of Díaz and Yébenes (1987) consist of near-shore fluvial-dominated sequences resting unconformably on 'Unit 4': clays, sands, marls and sandstones. Towards the top of this unit there are channel deposits. The terrigenous sediments are var-icoloured (red, green, violet) from oxidation and reduc-tion of iron minerals. The sandstones show planar cross-stratification and they fine upwards. In the lower and middle parts of this unit, plant remains have been found, including millimetre-thick coalified laminae. The grey limestone occurs as planar beds and varies between bioclastic packstone with numerous bivalve remains and mudstone. The Camarillas Formation passes up gradu-ally into the Artoles Formation.

The Camarillas Formation is the source of most of the vertebrate fauna described from the Galve area. Among the charophyte remains are *Atopochara trivolvis* var. *triquetra*, *Globator maillardii* var. *trochiliscoides*, *Clavator harrisii*, *Clavator harrisii* var. *reidii*, indicators of the *Triquetra–Neimongolensis* biozone and *Calcitrapus* subzone, dated as early Barremian (Martín-Closas, 1989). The top of unit 5I marks the maximum sea level in the section, and after that a new transgression occurs and the sediments above are more marine-influenced. The upper part of the Camarillas Formation (unit 5II of Díaz and Yébenes, 1987) consists of typical delta-front deposits, with mixohaline influences.

2.5. Artoles Formation

The Artoles Formation, some 8 m thick, comprises conglomerates, sandstones, clays, marls and shales. The clays show redox colours. The conglomerates and sandstones are typical of palaeochannel deposits. The limestones towards the top contain local floatstones or rudstones enriched with numerous ostreid bivalves. The green marls show occasional lenticular stratification, and these clays are the dominant lithology in the lower part of this formation. Biomicritic wackestone and packstone limestones at the top of this unit are rich in ostracods, bivalves, benthic foraminiferans, gastropods, aquatic plants, crocodyliforms and fishes, all character-istic of paralic lakes.

Some beds among the green marls have yielded charophytes, including *Atopochara trivolvis* var. *tri-quetra*, *Globator maillardii* var. *trochiliscoides*, *Clava-tor harrisii* var. *reyi*, *A. (Embergella) cruciata*, all indicators of the *Cruciata–Paucibracteatus* biozone. In the marine horizons the benthic foraminiferan *Paleor-bitolina lenticularis lenticularis* occurs. The *Cruciata–Pancibractratus* biozone in the lower levels (Martín-Closas, 1989; Martín-Closas and Alonso, 1998) is dated as late Barremian to early Aptian.

In some parts of the Galve sub-basin, limestones near the top of the Artoles Formation bear peloids, ostreid bivalve accumulations (ostreid tempestites) and lentic-ular bodies with planar cross-stratification interpreted as shoals or moving sand bodies on the platform. This upper part of the Artoles Formation, termed 'unit 6' by Díaz and Yébenes (1987), was interpreted as having been deposited in a bay. So, the sediments of the Artoles Formation were generated in a fluvial environment (delta front) that changes to a bay environment.

3. Systematic palaeontology

Many groups of vertebrates have been reported from the Galve deposits, as summarized by Buscalioni and Sanz (1987), Canudo et al. (1996), Sánchez-Hernández (2002, 2004) and Ruíz-Omeñaca et al. (2004). Here, we outline and revise these earlier reports, add information based on extensive studies of new collections and report a number of new records.

Museum abbreviations are: BMNH, Natural History Museum, London; MPG, Museo Paleontológico de Galve; MPT, Museo Paleontológico de Teruel; MPZ, Museo Paleontológico de la Universidad de Zaragoza; UCMP, Museum of Paleontology of the University of California.

3.1. Fishes

Fish remains from the Galve deposits consist of iso-lated vomers, scales, spines, teeth and coprolites. *Lonchidion microselachos* is a hybodontid shark species named by Estes and Sanchíz (1982) for teeth from the Camarillas Formation. Other sharks from Galve include *Acrodus* (Kühne, 1966) and *Polyacrodus parvidens* (Estes and Sanchíz, 1982), and bony fishes include Holostei (Kühne, 1966; Estes and Sanchíz, 1982; Buscalioni and Sanz, 1987), Amiidae and Pycnodonti-dae (Estes and Sanchíz, 1982; Krebs, 1985; Kriwet, 1998). Additionally, Kriwet and Kussius (1996) recorded *Lissodus* sp., *Egertonodus* sp., *Polyacrodus* sp., *Cretolamna* sp. and *Protolamna* sp. Furthermore, some isolated arrow-shaped teeth that recall those of amiids, are present in the Herrero collection. The fish fossils require fuller and more detailed analysis.

CHONDRICHTHYES Huxley, 1880
HYBODONTIFORMES Gluckman, 1964
HYBODONTIDAE Owen, 1846

Genus LONCHIDION Estes, 1964
Lonchidion microselachos Estes and Sanchíz, 1982.

3.1.1. Material

Teeth from the Cerrada Roya (mina) outcrop (Camarillas Formation, Barremian) can be referred to this form taxon. There are five specimens (Fig. 3), MPG P-CR(m)-1, MPG P-CR(m)-2, MPG P-CR(m)-3, MPG P-CR(m)-4 and MPG P-CR(m)-5.

3.1.2. Description

The five isolated teeth have smooth enamel on the labial and lingual sides. In the crown there is a central cusp, a marked labial process and an occlusal crest. The length of these four teeth is 1.7–3.1 mm (larger than the holotype, with a length of 1.2 mm according to Estes and Sanchíz, 1982). There is a constriction between the crown and the root. The crown height/root height ratio is 1.5 (MPG P-CR(m)-1), 1.1 (MPG PCR(m)-2), 1.2 (MPG P-CR(m)-3) and 1.4 (MPG P-CR(m)-4).

3.1.3. Discussion

Similar teeth have been attributed to a new species, *Lonchidion microselachos*, by Estes and Sanchíz (1982). Nevertheless the teeth studied by them, including the holotype MPT/I.G./5.240 (1982), lacked their roots. In the four teeth discussed here, the root is preserved and similar or smaller than the crown (Fig. 3). While we have followed Estes and Sanchíz (1982) in their classification of the Galve hybodontid material, some authors have questioned the validity of the genus *Lonchidion*, considering it synonymous with *Lissodus* (Duffin, 2001; Rees and Underwood, 2002; Duncan, 2004).

3.2. Lissamphibia

Lissamphibians from Galve include albanerpetontids, urodeles and anurans. Isolated urodele and anuran remains have been reported from the El Castellar Formation at Colladico Blanco, and have been identified as Prosirenidae indet. and Discoglossidae indet. (Kühne, 1966; Krebs, 1985; Canudo et al., 1996). From the Camarillas Formation outcrop at Yacimiento Herrero, Estes and Sanchíz (1982) reported Caudata *incertae sedis* as well as the urodele *Galverpeton ibericum* and the discoglossid *Eodiscoglossus santojae*. Albanerpetontid material from Galve was originally referred to *Albanerpeton* cf. *megacephalus* (Estes and Sanchíz, 1982) but would today be referred to *Celtedens*.

3.3. Sauria

Although lizard fossils are rare at Galve, non-diagnostic remains have been mentioned (Estes and Sanchíz, 1982), as have indeterminate scincids and paramacellodids (Richter, 1994b). Diagnostic remains have been referred to the paramacellodid *Paramacellodus* and the lacertiform *Meyasaurus* (Richter, 1994a), although Richter identified the latter as *Ilerdaesaurus*, a name shown by Evans and Barbadillo (1996) to be a junior synonym of *Meyasaurus*.

3.4. Testudines

Turtle remains are common in the Galve outcrops but remain poorly studied. Kohring (1990) mentioned eggshells of Bataguridae indet. (= Batagurinae, Geomydidae indet., according to Spinks et al., 2004). There is an almost complete carapace from Upper Jurassic sediments and
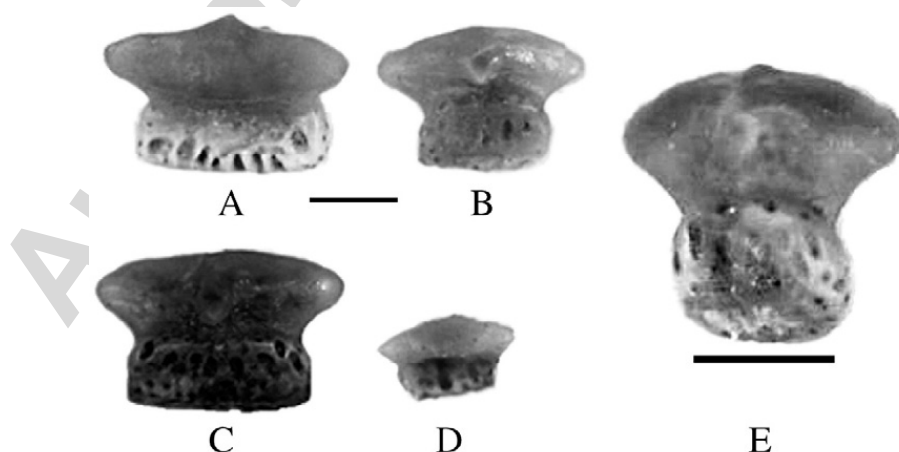

Fig. 3. *Lonchidion microselachos* teeth. (A) MPG P-CR(m)-1 in lingual view, (B) MPG P-CR(m)-2 in labial view; (C) MPG P-CR(m)-3 in labial view; (D) MPG P-CR(m)-4 in lingual view and (E) MPG P-CR(m)-6 in labial view. Scale bar: 1 mm.

many isolated pieces of others and different isolated bones, from different deposits of different age. Based on the ornamentation of the carapace fragments, at least three turtle taxa were present in the Galve area.

3.5. Crocodyliformes

Isolated crocodyliform teeth and osteoderms assigned to several taxa are common at Galve and crocodyliform eggshells are also known (Kohring, 1990). Estes and Sanchíz (1982) described teeth that they referred to Atoposauridae, ?Pholidosauridae and cf. *Bernissartia* sp. Berg and Crusafont (1970) mentioned isolated teeth of *Allognathosuchus*, but these were later referred to *Bernissartia* sp. (Buscalioni and Sanz, 1984). *Bernissartia* is also represented by a skull (Buscalioni et al., 1984) (Fig. 4). Four tooth morphotypes were reported by Sanz et al. (1984), identified as cf. *Theriosuchus* sp. (Fig. 4D), Bernissartidae, cf. *Machimosaurus* sp. (Fig. 4A) and Goniopholididae (Fig. 4E).

CROCODYLIFORMES Benton and Clark, 1988
NEOSUCHIA Benton and Clark, 1988
ATOPOSAURIDAE Gervais, 1871.

3.5.1. Material

Both teeth: MPG POCA.CA-9 and MPG PX-18 (Fig. 4B, C).

3.5.2. Description

The two teeth have lanceolate crowns and possess roots longer than the crowns are tall (4 mm versus 3 mm in MPG PX-18). Whereas the root of MPG PX-18 (Fig. 4B) is rectangular in cross-section, that of MPG POCA.CA-9 (Fig. 4C) is circular in cross-section. Both teeth have a constriction between the crown and root. The crowns lack ornamentation and possess slightly crenulated edges.

3.5.3. Discussion

The overall morphology and proportionally broad roots of these teeth allow them to be identified as those of crocodyliforms and in crown shape they are similar to teeth identified as atoposaurid (Kriwet et al., 1997; Schwarz and Salisbury, 2005). However, we note that teeth similar to MPG PX-18 have been figured for basal mesoeucrocodylians such as *Lusitanisuchus mitracostatus* (Schwarz and Fechner, 2004).

Fig. 4. Crocodilian remains: *Bernissartia* skull (above) and teeth of Bernissartidae indet. (A: MPG POCA.CA-23), ?Atoposauridae indet. (B: MPG POCA.CA-9, C: MPG PX-18), cf. *Theriosuchus* sp. (D: MPG POCA.CA-21) and Goniopholididae (E: MPG PX-12). Scale bars: 1 mm.

3.6. Pterosaurs

Though represented by only some isolated bones and numerous teeth, a relatively diverse pterosaur fauna has been reported from Galve, with ornithocheirids, istiodactylids, dsungaripterids and possible gnathosaurine ctenochasmatoids (Kühne, 1966; Krebs, 1985).

PTEROSAURIA Kaup, 1834
PTERODACTYLOIDEA Plieninger, 1901.

3.6.1. Material

More than thirty teeth (Fig. 5) from lower Barremian deposits (Cerrada-Roya mina outcrop, Camarillas Formation).

3.6.2. Description

Four distinct morphologies are present among the Galve pterosaur teeth:

Morphotype 1: 'Pencil-like' (viz, with straight crowns and subparallel margins); circular in cross-section; sometimes with longitudinal ridges; relatively large (Fig. 5A).

Morphotype 2: Smaller than morphotype 1; elongate, curved and pointed, with a narrow crown tip; crown without longitudinal ridges (Fig. 5B).

Morphotype 3: Subtriangular and broad-based; oval in cross-section; smaller than morphotypes 1 and 2 (Fig. 5C).

Morphotype 4: Subtriangular; labiolingually compressed; crown tip pointed and mesiodistally narrower than rest of crown; smaller than morphotypes 1 and 2 (Fig. 5D).

3.6.3. Discussion

The Galve pterosaur teeth could come from a number of clades. Pterosaurs were diverse in the Barremian, with both basal forms and representatives of all the major pterodactyloid clades known from this time. Until recently, it was thought that non-pterodactyloid pterosaurs were broadly absent from the Cretaceous, but examples of Anurognathidae and Rhamphorhynchidae such as *Dendrorhynchoides curvidentatus*, *Jeholopterus ningchengensis* and *Pterorhynchus wellnhoferi* are known from the Barremian Yixian Formation of China (Unwin et al., 2000; Czerkas and Ji, 2002; Wang et al., 2002). Basal pterosaurs have also been reported from the Lower Cretaceous (probably Berriasian) of Anoual, Morocco (Sigogneau-Russell et al., 1998), but so far there had been no evidence that such forms also persisted in Europe.

Ornithocheirids, though well known from the European Lower Cretaceous (Unwin, 2001), have only recently been confirmed from the Barremian, with the peculiar crested form *Caulkicephalus trimicrodon* from the Wessex Formation (Steel et al., 2005). However, older records from the Hastings Beds Group of the English mainland (Howse et al., 2001) demonstrate that

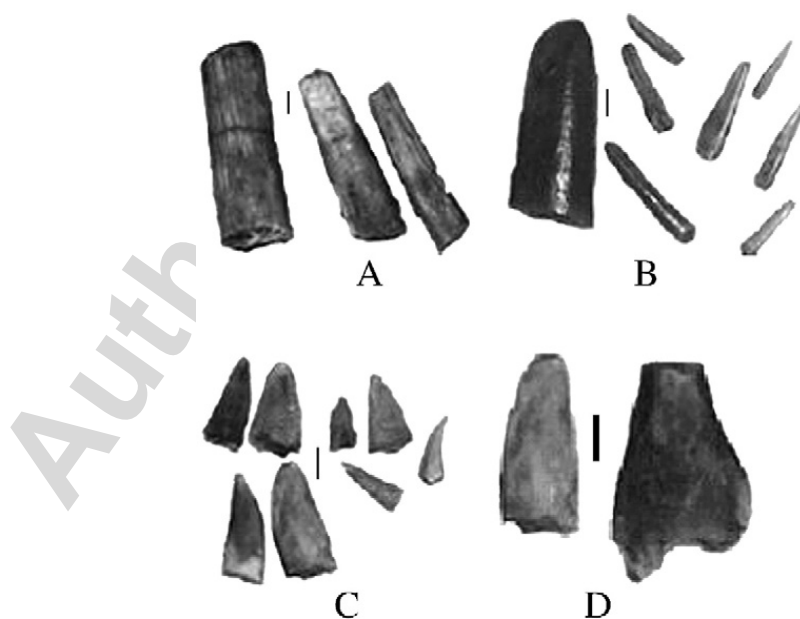Fig. 5. Pterosaur teeth from the Cerrada–Roya (mina) outcrop (Camarillas Formation, lower Barremian). 'Morphotype 1': Ornithocheiridae indet. (A), 'morphotype 2': Pterodactyloidea indet., with one Ornithocheirid tooth ('morphotype 1') on the left (B), 'morphotype 3': Ornithocheiridae indet. (C) and 'morphotype 4': Istiodactylidae indet., with an Ornithocheirid tooth ('morphotype 3') on the left (D). Scale bars: 1 mm.

ornithocheirids were present in Europe from the Valanginian at least, and Barremian pterodactyloid teeth from Teruel in Spain have been reported by Ruiz-Omeñaca et al. (1998). Yixian Formation forms include *Haopterus gracilis* and *Boreopterus cuiae* (Wang and Lü, 2001; Lü and Ji, 2005). Istiodactylids, named for *Istiodactylus latidens* from the Vectis Formation (Howse et al., 2001), but also known from the Wessex Formation (Steel et al., 2005) and Aptian Jiufotang Formation of western Liaoning (Wang et al., 2005; Andres and Ji, 2006), were also present at this time.

Ctenochasmatoids were present in the Early Cretaceous of Asia (Unwin et al., 2000; Lü, 2003; Wang et al., 2005) and South America (Chiappe et al., 2000). In Europe, gnathosaurine ctenochasmatids are known from the Purbeck Limestone Group (Howse and Milner, 1995) but it is unclear whether these specimens fall on the Jurassic or Cretaceous side of the boundary: Unwin et al. (2000) regarded the Purbeck pterosaurs as Berriasian, in common with most other Purbeck vertebrate fossils.

The distribution of dsungaripteroids in the Early Cretaceous appears to have been similar to that of ctenochasmatoids, with good records from the Berriasian–Aptian of Asia (Unwin et al., 2000; Maisch et al., 2004) and from an undated unit in Chile (Martill et al., 2000). Fragmentary records, including those reported here, and material from Romania (Benton et al., 1997), indicates the presence of the group in the European Lower Cretaceous.

Finally, there is little reason to expect the presence of azhdarchoids in the Lower Cretaceous of Spain. The controversial *Doratorhynchus validus*, named for a manual digit IV phalanx from the Purbeck Limestone Group that cannot be identified beyond Pterodactyloidea (Howse and Milner, 1995), has at times been identified as an azhdarchid azhdarchoid because of the similarity of a referred cervical vertebra to that of azhdarchids (e.g. Howse, 1986; Wellnhofer, 1991). However, this identification is widely doubted as the specimen differs in detail from azhdarchid vertebrae (Pereda Suberbiola et al., 2003). The poorly known, enigmatic lonchodectids were present from the Valanginian to the Cenomanian at least (Unwin, 2003), and thus may also be present in the Spanish Barremian.

The Galve pterosaur remains can be referred to several pterodactyloid clades, though identification is ambiguous in some cases. 'Morphotype 1' teeth (Fig. 5A) are referred to Ornithocheiridae, the only pterosaur clade that possesses teeth of this form (Kellner and Tomida, 2000). While the fang-like rostral teeth of

some ornithocheirids are curved, other taxa possess relatively straight teeth, though heterodonty in these animals renders it likely that specimens would possess both relatively straight fangs beside more curved ones. The Galve ornithocheirid teeth appear to be more circular in cross-section than those of *Ornithocheirus*, suggesting that they may not be referable to this taxon. The large ctenochasmatoid *Cearadactylus atrox* also possesses teeth of this form but the incompleteness of its teeth poor preservation prevents detailed comparison (Unwin, 2002).

'Morphotype 2' teeth (Fig. 5B) differ from those of most ornithocheirids in being more gracile and in lacking ornamentation. However, teeth of this form are present in the ornithocheirid *Boreopterus cuiae* (Lü and Ji, 2005). Gnathosaurine ctenochasmatids also possess teeth similar to 'morphotype 2' specimens (Wellnhofer, 1991), as does the probable ctenochasmatoid *Feilongus youngi* (Wang et al., 2005). Accordingly, we are unable to determine whether 'morphotype 2' teeth belong to ornithocheirids or ctenochasmatoids, and identify them simply as Pterodactyloidea indet. Although some fishes had similar teeth, some of the 'morphotype 2' teeth here have a deep apical groove toward the tip that divides the tooth interior it into two circular hollow canals. This is a feature of other pterosaur teeth, so we identify the 'morphotype 2' teeth as those of pterosaurs, rather than those of fishes.

'Morphotype 3' teeth (Fig. 5C) strongly resemble the smaller teeth that occur within the jaws of ornithocheirid taxa (Owen, 1874; Kellner and Tomida, 2000), including *Ornithocheirus*, *Anhanguera* and *Coloborhynchus*. It is not possible to identify them further and hence they are identified as Ornithocheiridae indet.

Finally, 'Morphotype 4' teeth (Fig. 5D) are similar to those of the istiodactylids *Istiodactylus latidens* and *Nurhachius ignaciobritoi* (Howse et al., 2001; Wang et al., 2005) and are therefore attributed to this group. Though Ruiz-Omeñaca et al. (1998) suggested that some pterosaur teeth from Vallipón, Teruel were possibly istiodactylid, the Galve teeth differ from those of *Istiodactylus* in lacking a vertical ridge on the lingual surface of the tooth, though *Nurhachius* also appears to lack these ridges.

3.7. Dinosaurs

3.7.1. Theropoda

Theropods are represented at Galve by isolated bones and teeth. Previous authors have attributed these to ?Coeluridae indet., Megalosauridae indet., Dromaeosauridae indet., Theropoda indet., Baryonychinae indet. and

Carcharodontosaurus indet. (Crusafont-Pairó and Adrover, 1966; Sánchez-Hernández, 2002) but, as discussed below, several of these identifications cannot be supported.

    THEROPODA Marsh, 1881a
    TETANURAE Gauthier, 1986
    SPINOSAUROIDEA Stromer, 1915
    SPINOSAURIDAE Stromer, 1915
    SPINOSAURINAE Stromer, 1915.

3.7.1.1. Material.   Six teeth identified as spinosaurine are known from the Cerrada–Roya (mina) outcrop of the Camarillas Formation: MPG CR(m)-1, MPG CR(m)-2, MPG CR(m)-4, MPG CR(m)-6, MPG SC-1 and MPG SC-2 (Fig. 6).

3.7.1.2. Description.   The teeth range in crown height from 12 to 21 mm, have an anteroposterior basal length ranging from 6 to 9 mm, and a bucco-lingual basal width of 4–6 mm (Table 1). The teeth from the Cerrada Roya

(mina) outcrop, CR(m), are bucco-lingually compressed, whereas those from the San Cristóbal outcrop, SC, are circular in cross-section (Fig. 6D and H). With the exception of MPG SC-2, all specimens possess unserrated distal and mesial carinae. While only one carina (the posterior) is present in MPG SC-2 (Fig. 6D), the absence of the other could be the result of abrasion. All specimens lack ornamentation on their crowns, with the exception of MPG SC-2, in which vertical ridges are present.

3.7.1.3. Discussion.   Teeth with a sub-circular cross-section, a straight (or relatively straight) crown, unserrated carinae, and an absence of crown ornamentation, are identified as those of spinosaurine spinosaurids when found in Cretaceous sediments of Africa and elsewhere. The presence of such teeth in the Lower Cretaceous of Spain is surprising as spinosaurines have not hitherto been reported in Europe.

    Spinosaurine teeth are notoriously hard to distinguish from those of some crocodyliforms and other theropod
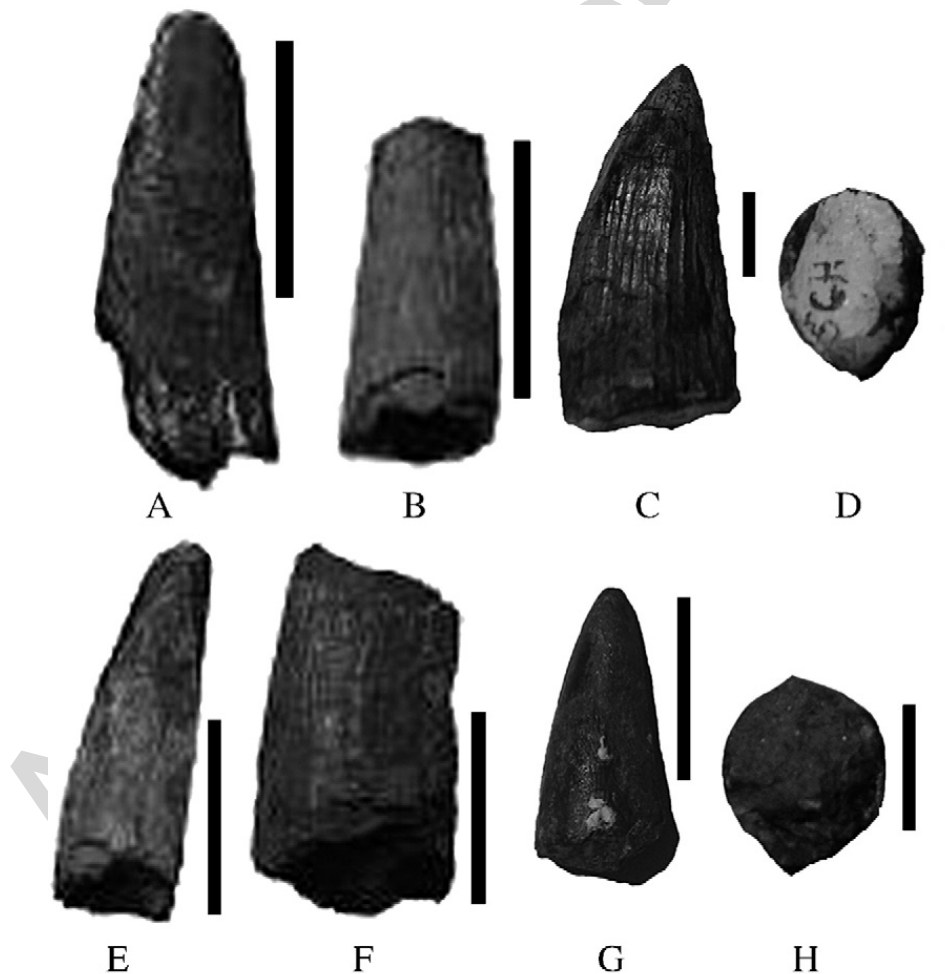

Fig. 6. Spinosaurine teeth from Galve outcrops. (A) MPG CR(m)-1; (B) MPG CR(m)-2; (C) MPG SC-2; (E), MPG CR(m)-4; (F) MPG CR(m)-6 and (G) MPG SC-1 are in lateral view; (D) MPG SC-2 and (H) MPG SC-1 are in occlusal view. Scale bars: 10 mm.

Table 1
Measurements of spinosaurid teeth from Galve

Fossil	Length (mm)	Depth at bottom (D_b, bucco-lingual) (mm)	Width at the bottom (W_b, anteroposterior) (mm)	W_b/D_b
MPG CR(m)-1	17	4	7	1.75
MPG CR(m)-2	12	4	6	1.5
MPG CR(m)-4	18	4	6	1.5
MPG CR(m)-6	17	6	9	1.5
MPG SC-1	16	7	9	1.3
MPG SC-2	21	8	12	1.5
Cf. *Baryonyx* [a] (PS-JTS, 20)	14	7	9	1.3
Cf. *Baryonyx* [a] (PS-C-1, 11)	27	14	10	0.7

[a] Measurements of two broken teeth from Lower Cretaceous of Burgos (Spain) according to Torcida Fernández-Baldor et al. (2003).

groups. The unequivocal crocodyliform teeth from Galve (e.g. Fig. 4) differ in being coarsely striated (Estes and Sanchíz, 1982), and in other features correspond to the teeth of *Theriosuchus*, *Machimosaurus*, *Goniopholis* or Bernissartidae (Estes and Sanchíz, 1982; Sanz et al., 1984). The Galve spinosaurine teeth further differ from those of crocodyliforms in lacking lingual curvature (Fig. 7). While serrations are absent on the teeth of several theropod clades (including spinosaurines, ornithomimosaurs, alvarezsaurids, oviraptorosaurs, troodontids and birds), the presence of unserrated carinae like those on the Galve teeth described here is rare, and restricted to Spinosaurinae, Alvarezsauridae and the troodontid *Byronosaurus jaffei*. However, as is the case with most other coelurosaurs that possess unserrated teeth, the teeth of alvarezsaurids and *Byro-nosaurus* possess a distinct constriction between the root and crown (Perle et al., 1994; Norell et al., 2000).

The six Galve teeth are therefore most similar to those of spinosaurines like *Spinosaurus aegyptiacus*. However, MPG SC-2 has coarse vertical ridges resembling those of the spinosaurine *Irritator challengeri* (Sues et al., 2002). The ratio of height to anterior–posterior length (= mesiodistal diameter) in *I. challengeri* varies from 2.5 to 3.1 (Sues et al., 2002). In the complete teeth from Galve, this ratio is 2.43 for MPG CR(m)-1, and 3 for MPG CR(m)-4, whereas it is 1.78 for MPG SC-1 and 1.75 for MPG SC-2.

While spinosaurines and their close relatives the baryonychines were until recently regarded as distinct 'family-level' taxa, most recent studies have united them as sister-taxa within Spinosauridae (Sereno et al., 1998;
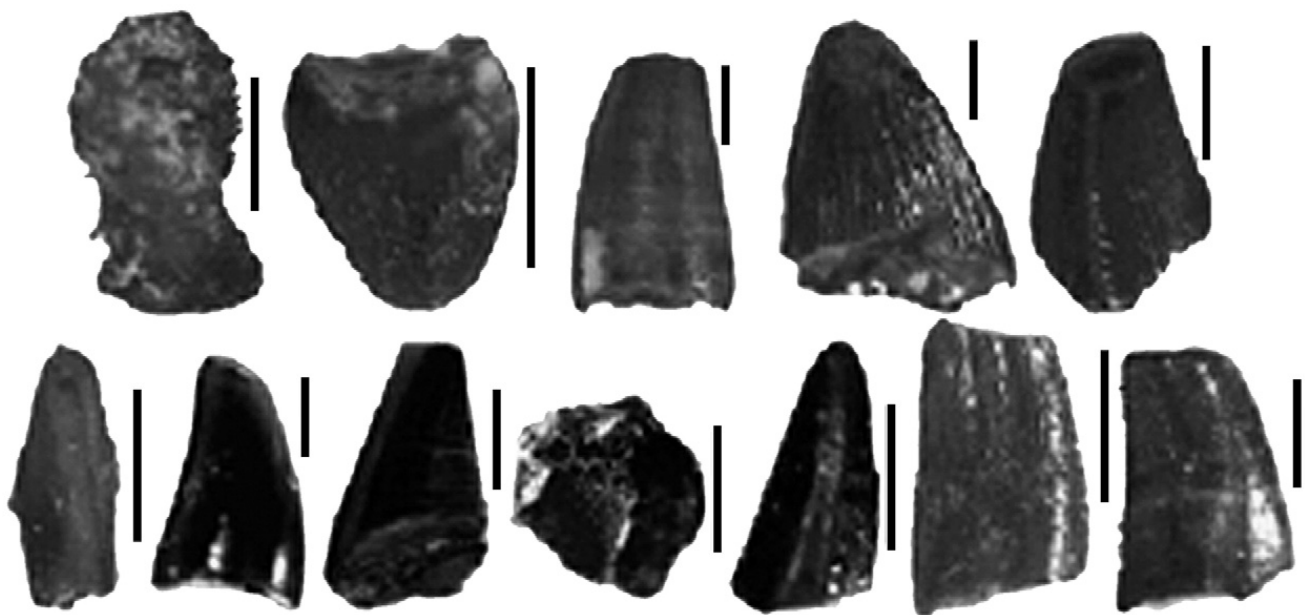

Fig. 7. Isolated crocodilian teeth (above) and baryonychine teeth (below). Although they have similar aspect, the position of their keels is different. From left to right (above): MPG PX-11, MPG PX-12, MPG PX-15, MPG PX-16, MPG PX-13; (below) MPG PX-23, MPG POCA-14, MPG POCA-15, cross-section of MPG POCA-18, MPG POCA-18, MPG POCA-6 and MPG POCA-7. Scale bars: 1 mm.

Sues et al., 2002; Holtz et al., 2004). The oldest baryonychines are from the Valanginian–Barremian of England and Spain (Viera and Torres, 1995; Charig and Milner, 1997; Fuentes Vidarte and Meijide Calvo, 2001; Torcida Fernández-Baldor et al., 2003), considerably older than spinosaurines from the Aptian and Albian of North Africa (Sereno et al., 1998; Benton et al., 2000) and the Albian of Brazil (Sues et al., 2002). In reporting Barremian spinosaurid teeth referred to Spinosaurinae (Fig. 6) we have extended the age range of this clade so that it almost matches that of its sister taxon Baryonychinae.

THEROPODA Marsh, 1881a
TETANURAE Gauthier, 1986
SPINOSAUROIDEA Stromer, 1915
SPINOSAURIDAE Stromer, 1915
BARYONYCHINAE Charig and Milner, 1986.

3.7.1.4. Material. Six possible baryonychine teeth are known from the PX (El Castellar Formation, lower Barremian) and POCA outcrops (Camarillas Formation, lower Barremian) of Galve: MPG PX-23, MPG POCA-6, MPG POCA-7, MPG POCA-14, MPG POCA-15 and MPG POCA-18 (Fig. 7, Table 2).

3.7.1.5. Description. Baryonychine teeth are superficially similar to those of some crocodyliforms, being sub-circular in cross-section and with reduced denticulation (Fig. 7). However, they can be distinguished from the teeth of crocodyliforms and other taxa by their particularly fine denticulation, their slight distal curvature, and by the presence of vertical striations. In the specimens described here, denticles are absent on the distal carina.

3.7.1.6. Discussion. The possession of characteristically fine denticulation allows these teeth to be identified as baryonychine. While some also possess the vertical striations typical of baryonychine teeth, such ornamentation is absent in MPG PX-23, MPG POCA-14, MPG POCA-15 and MPG POCA-18. Furthermore, the denticles on these specimens are restricted to the distal carina. A baryonychine tooth with denticulation on only one carina has been described by Infante et al. (2005) from an outcrop close to Galve, and Canudo and Ruíz-Omeñaca (2003) also reported Spanish baryonychine teeth in which denticles were absent from one carina. This is unlike the condition in *Baryonyx walkeri* where both carinae are serrated (Charig and Milner, 1997) and

Table 2
Theropod tooth measurements (in mm). H: height of the tooth measured in a straight line from the tip to the base of the crown along the posterior margin of the tooth (Currie et al., 1990). FABL: fore-aft basal length of the tooth (Currie et al., 1990); BW: basal labiolingual width (Farlow et al., 1994); d/mm: denticles per millimetre. All the teeth here are broken, so these values are rough measures. m: mesial crenulation, d: distal crenulation

Number	Attribution	H	FABL	BW	d/mm
MPG PX-2	Allosauroidea indet.	9	9	5	3.5d, m
MPG PX-5		16	9.5	6.2	6d, m
MPG PX-1	Dromaeosauridae indet.	11.5	5	4	5d
MPG PX-3		6.5	6	2.5	5d
MPG PX-4		9.5	5	3	?
MPG PX-17		8.5	4	2	5d
MPG PX-21		1.8	2	0.8	6d
MPG PX-22		2	1.8	0.8	6d
MPG POCA-1		1.6	1.1	0.6	14d
MPG POCA-2		1.6	1.2	0.8	14d
MPG POCA-3		1.2	1.6	0.6	9d
MPG POCA-4		1.8	1.5	0.6	10d
MPG POCA-5		2.54	1	0.8	10d
MPG POCA-12		3	2	1.5	8d
MPG POCA-13		4	3	2	10d, 12m
MPG POCA-14		3	1.8	1.5	13d
MPG POCA-18		2	1	0.5	11.5d
MPG PX-6	Coelurosauria indet.	2	0.9	0.4	–
MPG PX-8		3	1.3	0.5	–
MPG PX-9		2	1.3	0.8	–
MPG POCA-6	Baryonychinae indet.	3.9	1.9	0.9	>13
MPG POCA-7		3.1	1.5	?	10d
MPG POCA-14		3	1.8	1.5	13
MPG POCA-15		2.8	1.5	0.8	10
MPG POCA-18		2	1	0.5	11.5
MPG PX-23		1.3	0.7	0.4	?

could indicate that the Spanish specimens represent a different species.

THEROPODA Marsh, 1881a
TETANURAE Gauthier, 1986
ALLOSAUROIDEA Currie and Zhao, 1993
Allosauroidea indet.

3.7.1.7. Material. Two teeth, MPG PX-2 and MPG PX-5, are known from the PX outcrops of the El Castellar Formation (Fig. 8).

3.7.1.8. Description. Both teeth are lenticular in cross-section, recurved and with serrated mesial and distal carinae. In MPG PX-2 (Fig. 8A–D), both carinae are convex and show similar serration densities of approximately 3.5 denticles per millimetre. The mesial denticles are slightly inclined toward the crown tip. Several poorly developed parallel vertical striations are present on the sides of the crowns. In MPG PX-5 (Fig. 8E, F) the mesial carina is convex but the distal carina is concave. For measurements, see Table 2.

3.7.1.9. Discussion. Zinke (1998) noted that the teeth of *Allosaurus* are characterised by a FABL/BW ratio of 2:1 (though, using Zinke's data, it is actually 1.9:1). In the two teeth described here, this ratio is 1.8:1 and 1.5:1. Like *Allosaurus* teeth, and those referred to Allosauroidea by Zinke (1998), the two El Castellar Formation teeth are proportionally long mesiodistally for their labiolingual width, and this similarity supports their identification as allosauroid.

Infante et al. (2005) mentioned a tooth that is similar to MPG PX-2 and MPG PX-5 from the Mirabel Formation (lower Barremian) of Teruel. Based on the lenticular cross-section, similarly sized denticles on both

mesial and distal carinae, and the presence on the mesial carina of denticles restricted to the apical part, they classified the tooth as Allosauroidea indet. We follow the same argumentation, and regard MPG PX-2 as belonging to a similar taxon, although the restriction of mesial denticles to the apical zone of the crown cannot be checked in the specimen. MPG PX-5 preserves denticulation on the apical part of the mesial carina but the rest of the carina is broken. While this tooth is similar to those attributed to Dromeosaurinae (e.g. MPG PX-17), it differs in possessing mesial and distal denticulations and in having a similar number of denticles/mm on both carinae.

Finally, an isolated tooth of "median size" similar to MPG PX-2 and MPG PX-5 was reported from the Cuesta Lonsal outcrop of Galve by Canudo et al. (2005). They attributed this specimen to Theropoda indet., but it is probably also referable to Allosauroidea. An isolated left maxillary tooth, also probably from an allosauroid, has recently been reported from the Villar del Arzobispo Formation (Canudo et al., 2006).

THEROPODA Marsh, 1881a
TETANURAE Gauthier, 1986
COELUROSAURIA Huene, 1914
Coelurosauria indet.

3.7.1.10. Material. Three teeth (MPG PX-6, MPG PX-8 and MPG PX-9) from lower Barremian deposits of the El Castellar Formation (PX outcrops) (Fig. 9).

3.7.1.11. Description. These teeth are sharply pointed, labiolingually compressed, lenticular in cross-section, and lack denticles. They also lack any ornamentation on their surfaces. For measurements see Table 2.
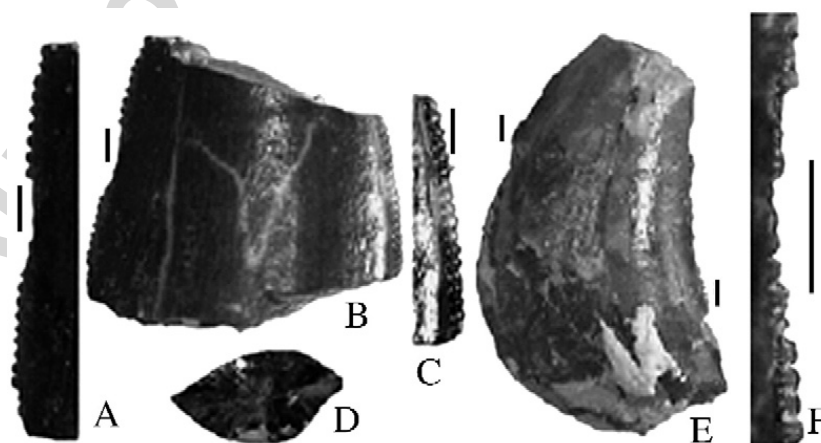

Fig. 8. Isolated Allosauroidea indet. teeth, MPG PX-2 (B) with a detail of its carinae (A, C) and cross-section (D); and MPG PX-5 (E) with a detail of its most complete carina (F). Scale bars: 1 mm.

3.7.1.12. Discussion. It is not possible to identify these teeth with confidence. They possess a superficial similarity to Upper Cretaceous teeth identified as avian (Sankey et al., 2002) but lack features that allow this to be tested. The three teeth are similar to MPZ96/65 from the Vallipón outcrop of Castellote (Teruel), determined as Coelurosauria indet. by Canudo and Ruíz-Omeñaca (2003). The age of this deposit is similar to that of the PX outcrops, and also geographically close to Galve.

> THEROPODA Marsh, 1881a
> TETANURAE Gauthier, 1986
> COELUROSAURIA Huene, 1914
> MANIRAPTORA Gauthier, 1986
> DROMAEOSAURIDAE Matthew and Brown, 1922
> Dromaeosauridae indet.

3.7.1.13. Material. There are sixteen teeth (MPG PX-1, MPG PX-3, MPG PX-4, MPG PX-6, MPG PX-7, MPG PX-17, MPG PX-21, MPG PX-22, MPG POCA-1, MPG POCA-2, MPG POCA-3, MPG POCA-4, MPG POCA-5, MPG POCA-12, MPG POCA-13 and MPG POCA-18), from lower Barremian deposits of the El Castellar Formation (PX outcrops) and Camarillas Formation (POCA outcrop) (Figs. 10, 11; Table 2).

3.7.1.14. Description. Mostly, these teeth are recurved, lenticular in cross-section and with the distal carina alone bearing serrations. However, those interpreted as being more rostral in their original position are more sub-circular in cross-sectional shape. In two of the teeth (MPG PX-17, Fig. 11A–C and MPG POCA-13, Fig. 11G–K), mesial denticles are present, and are smaller than the distal denticles. The denticles are sub-rectangular, separated by distinct interdenticle slits, but variable in terms of their height and spacing. For measurements see Table 2.
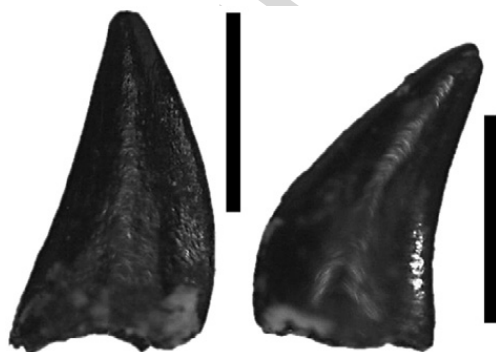

Fig. 9. Coelurosauria indet. teeth, MPG PX-8 (left) and MPG PX-9 (right). Scale bars: 1 mm.

3.7.1.15. Discussion. These small, denticle-bearing teeth are most similar, superficially at least, to those of dromaeosaurids. According to Currie et al. (1990) and Averianov et al. (2003), possession of distal denticles that are larger than those on the mesial carina is a characteristic feature of dromaeosaurid teeth. In the two teeth that bear denticles on both their mesial and distal carinae (MPG PX-17 and MPG POCA-13), the distal denticles are larger than the mesial denticles and the DSDI (denticle size difference index, *sensu* Rauhut and Werner, 1995) is 1.2. This is within the range of variation recorded for dromaeosaurids, but other theropods, notably *Ricardoestesia*, have similar values (Rauhut and Werner, 1995). While the denticles of some *Ricardoestesia* teeth are unlike those of the teeth reported here (in being taller and more closely packed, and continuous across the tooth apex), other specimens referred to this taxon are highly similar to some of the Galve teeth (Currie et al., 1990). They differ, however, in that the denticles of *Ricardoestesia* are so closely spaced that the interdenticle slits are almost obliterated, and in that *Ricardoestesia* teeth usually possess longitudinal grooves on the crown (Currie et al., 1990; Sankey et al., 2005). Accordingly, the Galve teeth are identified as Dromaeosauridae indet.

Although they lack denticles on their mesial carinae, the other teeth described here are otherwise similar to MPG PX-17 (Fig. 11A–C) and MPG POCA-13 (Fig. 11G–K) and are similarly identified as dromaeosaurid teeth. The absence of mesial denticles has been reported before in both dromaeosaurine and velociraptorine dromaeosaurids (Rauhut, 2002; Sweetman, 2004) and is not unique to the Galve specimens. Two different morphotypes, distinguishable by their denticle morphology, are present among the Galve teeth. In some specimens (MPG PX-1, MPG PX-3, MPG PX-6, MPG PX-7, MPG PX-21, MPG PX-22, MPG POCA-1, MPG POCA-2, MPG POCA-5 (Fig. 11) and MPG POCA-12), the denticles are chisel-shaped and placed perpendicularly relative to the long axis of the carina. They are most similar to dromaeosaurine teeth and are tentatively identified as Dromaeosaurinae indet. In other Galve teeth (MPG POCA-3, MPG POCA-4 and MPG POCA-18), the denticles are apically curved (but not to the extent seen in troodontids). Accordingly, these specimens are identified as Velociraptorinae indet. It should be noted however that some studies find 'velociraptorine' tooth morphology to occur in maniraptorans that are not members of the clade Velociraptorinae (Senter et al., 2004). If this is correct then 'velociraptorine' teeth represent a morphotype, not a taxon.
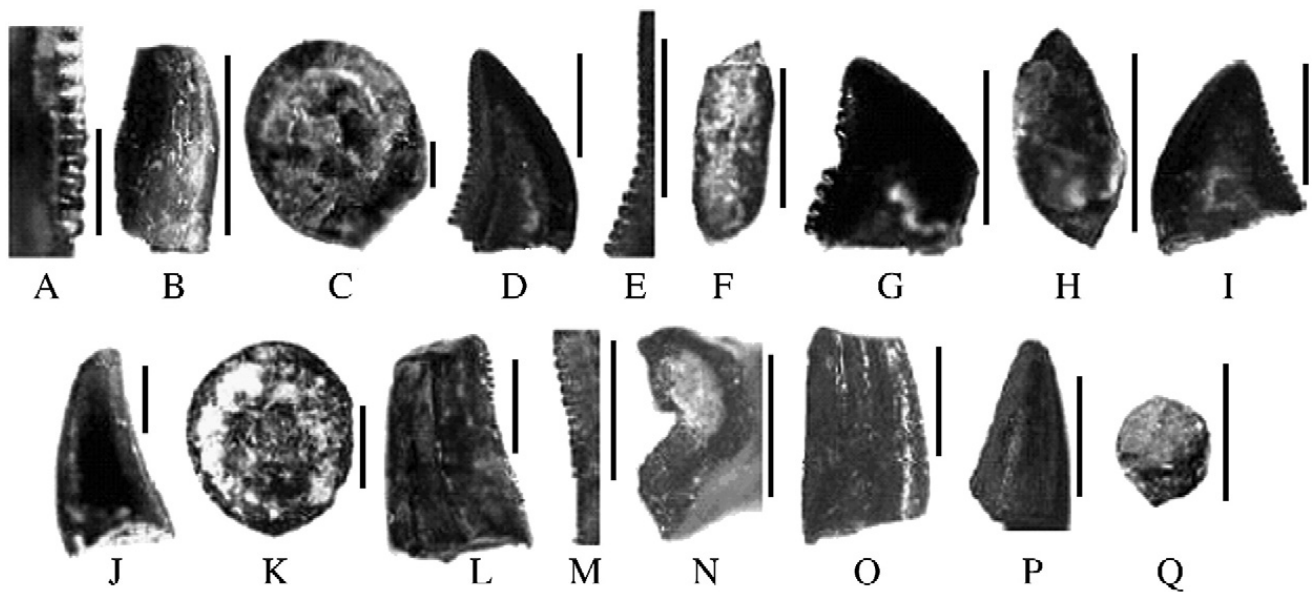
Fig. 10. Isolated theropod teeth from the Camarillas Formation deposits of Galve: Posterior crenulation of PX-1 (A), lateral (B) and basal (C) views of PX-1; lateral (D, E) and basal (F) views of POCA-1; lateral (G) and basal (H) views of POCA-3; lateral view (I) of POCA-2 which although is similar in form than POCA-3 the size of the denticles is smaller; lateral (J) and basal (K) views of POCA-14; lateral (L), posterior crenulation (M) and basal (N) view of POCA-7; lateral view (O) of POCA-6; lateral (P) and basal (Q) view of MPG SC-2. Scale bars (A–O): 1 mm and 10 mm (P–Q).

3.7.2. Sauropodomorpha

Two eusauropod taxa have been described from Galve: *Aragosaurus ischiaticus* from the Berriasian–upper Hauterivian (Sanz et al., 1987) and *Galveosaurus herreroi* from the upper Tithonian–Berriasian (Sánchez-Hernández, 2005). The former was originally described as a camarasaurid, was later identified as a titanosaur, and has most recently been considered Eusauropoda *incertae sedis* (Upchurch et al., 2004), while *Galveosaurus* appears to be a cetiosaurid (Sánchez-Hernández, 2005). Isolated sauropod bones and teeth are also known: Sanz et al. (1987) studied two teeth referred to cf. *Astrodon* (= *Pleurocoelus* according to McIntosh, 1990) sp. from the El Castellar Formation of Colladico Blanco, and from the Camarillas Formation of Partida Poyales, and suggested that they be identified as Camarasauridae indet. An isolated tooth from the Villar del Arzobispo Formation of La Carretera was described and considered as ?Diplodocidae by Cuenca-Bescós et al. (1997). Seven sauropod teeth and some isolated bones are described here.

SAUROPODA Marsh, 1878
Sauropoda indet.

3.7.2.1. Material. MPG S-YH-1 is an incomplete tooth crown from the Yacimiento Herrero outcrop (Camarillas Formation). Isolated bones include the proximal part of a femur (MPG S-LC-1) from the Las Cerradicas outcrop, Villar del Arzobispo Formation; a humerus (MPG S-FM-1) from the FM outcrop of the Villar del Arzobispo Formation; an incomplete fibula or ischium (MPG LZ-20) from the Las Zabacheras outcrop, El Castellar Formation; a tibia (MPG SM-1) from the San Macario outcrop (equivalent beds to the Cuesta Lonsal outcrop) of the Villar del Arzobispo Formation; a metatarsal (MPG BA-1) from the Barranco del Agua outcrop of the Villar del Arzobispo Formation; and an ungual phalanx (MPG CA-1) from the Collado de la Abeja outcrop, Villar del Arzobispo Formation.

3.7.2.2. Description and discussion. The incomplete tooth crown MPG S-YH-1 is semi-circular in cross-section, more convex labially than lingually, and lacking in surface ornamentation. When complete it would have been mesiodistally expanded. Although superficially similar to the teeth of *Camarasaurus*, it is attributed to Sauropoda indet. Cuenca-Bescós et al. (1997) and Barco et al. (1999) mentioned isolated postcranial sauropod remains from the Galve area, including a proximal part of an ulna from the Cuesta Lonsal outcrop, an ungual phalanx from the El Collado de la Abeja outcrop, a caudal vertebra from the Cerrada Roya outcrop, and a proximal part of a femur (CRH-1) from Las Cerradicas II. However, the specimen numbers given by these authors are different from those on the material analysed here (with the exception of the incomplete femur; although in the broken femur studied by us there is no number, as seen in Fig. 12 A–C) and they present
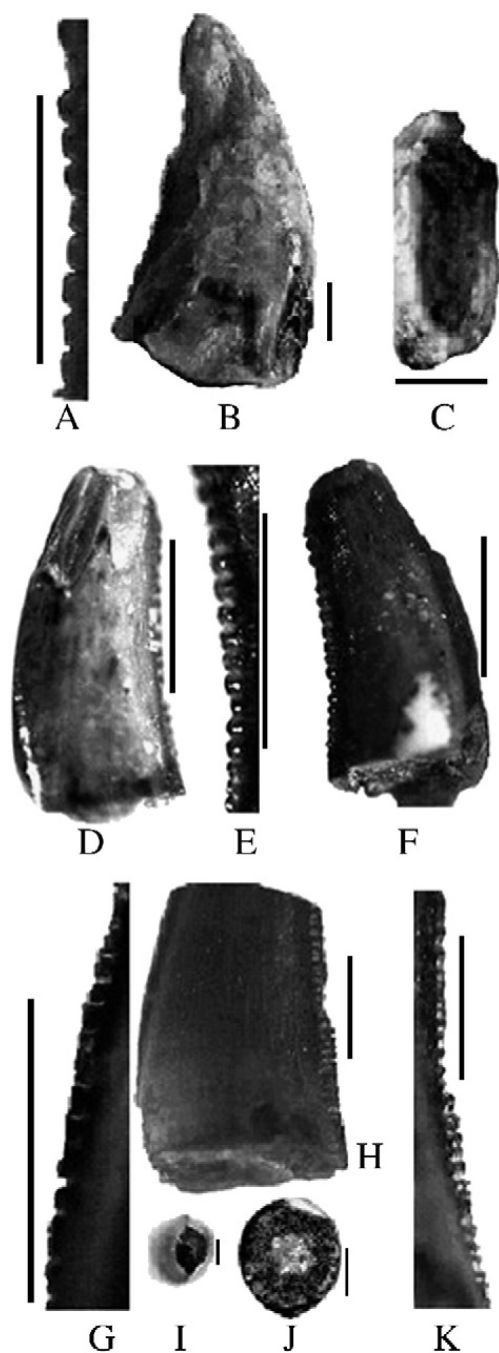
Fig. 11. Detail of three isolated dromaeosaurine teeth: a cheek tooth, MPG PX-17 (B), with a detail of its distal carina (A) and a basal view (C); a premaxillary tooth, MPG POCA-5, below, in both lateral views (D, F) and detail of the distal carina (E); MPG POCA 13 (G–K), with distal chisel shaped denticles (K) larger than on the mesial carina (G) and the apical (I) and basal (J) views. Scale bars: 1 mm.

no illustrations or measurements, so we cannot judge whether they were discussing the same specimens as here.

MPG S-LC-1 is the proximal end of a left femur (Fig. 12A–C) 190 mm long proximodistally. The femoral head is robust and not separated from the shaft by a constriction and the medial deflection of the head present in titanosauriforms is absent. In the absence of further information the specimen is identified as Eusauropoda indet. It is from the same formation that yielded *Galveosaurus herreroi* (Sánchez-Hernández, 2005), although from younger beds.

The isolated left humerus MPG S-FM-1 (Fig. 12D–F) is a slender bone 843 mm long, with proximal and distal ends that are expanded relative to the width of the shaft. The proximal end has a maximum width (310 mm) that exceeds that of the distal end (250 mm), while at mid-shaft the specimen is 130 mm wide. The deltopectoral crest extends distally to near the mid-length of the shaft and the distal articular condyles are barely separated. The distal articular surface is flat, as is typical for sauropods. Few derived characters are present that might allow the specimen to be identified. Its weakly developed deltopectoral crest and absence of an anterodistal concavity exclude it from Titanosauriformes, while the lack of distinct lateral and medial ridges anterodistally suggests exclusion from Neosauropoda. Accordingly, the humerus cannot be identified beyond Eusauropoda indet.

The incomplete bone MPG LZ-20 (Fig. 12G–I) is from the Las Zabacheras outcrop and was discovered a vertical distance of 200 m from the bed that yielded *Aragosaurus ischiaticus*. We have been unable to identify this element conclusively but it is most likely a fibula or ischium. The proximal end and shaft are complete but the distal end is absent.

The complete tibia MPG SM-1 (Fig. 12 J–L) is from a similar level of the Cuesta Lonsal outcrop to that which yielded *Galveosaurus herreroi*. Its total length is 1042 mm, and at mid-shaft it has a width of 264 mm. The proximal and distal ends are similar in width (305 mm and 315 mm respectively) and both with oval cross-sections. Distally, the shaft is deflected slightly posteriorly and two malleoli are present on the distal articular surface.

An isolated metatarsal (MPG BA-1; Fig. 12M–Q) also comes from the Villar del Arzobispo Formation. The bone is 230 mm long with markedly different proximal and distal ends, both of which are compressed anteroposteriorly. The proximal end is 220 mm wide while the distal end is 260 mm wide. The mediolaterally expanded proximal and distal ends of the specimen, combined with the relative gracility of the shaft, make it most like mt III of some neosauropods (Bonaparte et al., 2000).

Finally, MPG CA-1 is an isolated ungual phalanx (Fig. 12R–T) from an outcrop close to Cuesta Lonsal, where the remains of *Galveosaurus herreroi* were
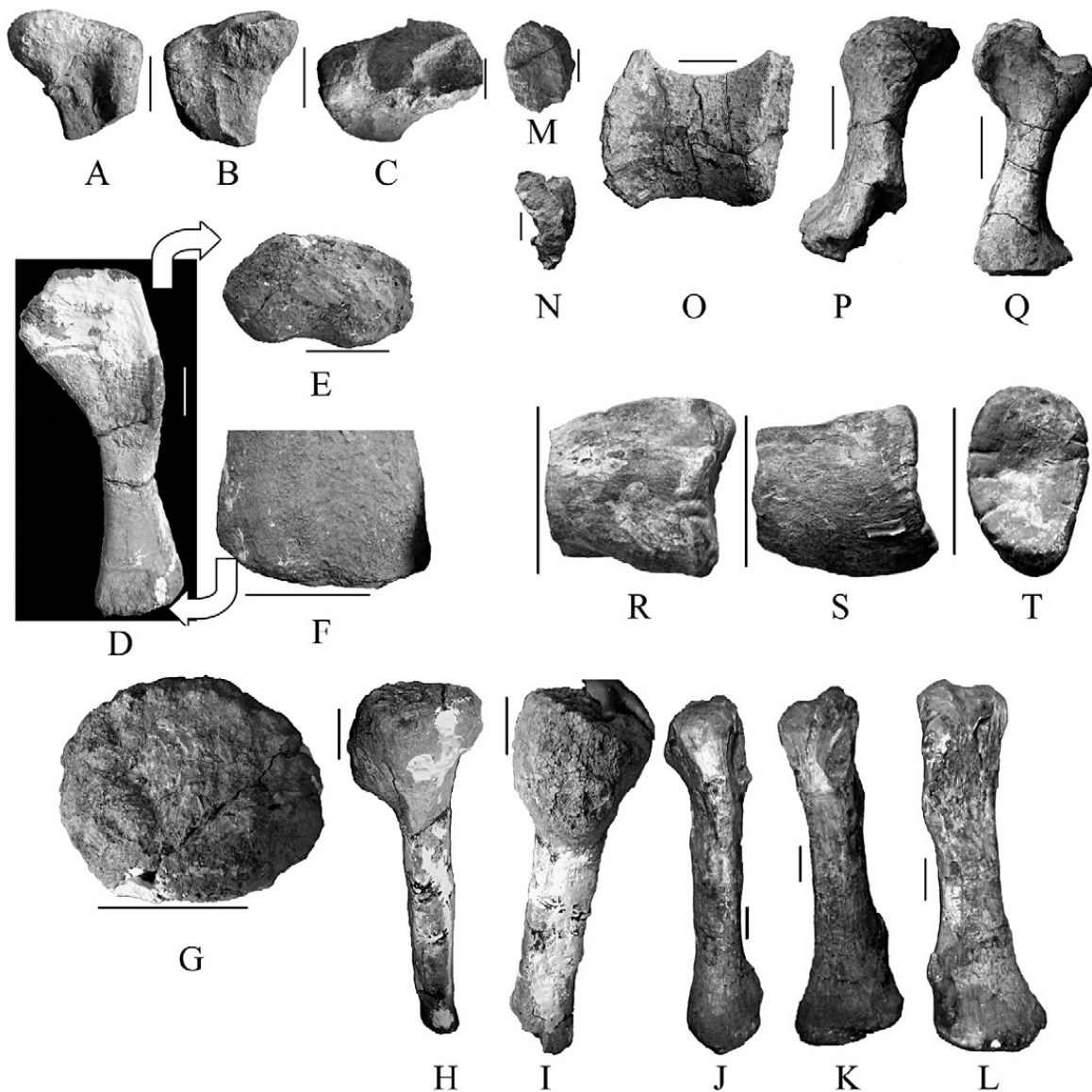
Fig. 12. Isolated sauropod postcranial elements: (A–C) broken femur MPG S-LC-1 in anterior (A), posterior (B) and proximal views (C); (D–F) left humerus MPG S-FM-1 in lateral view (D) and detail of the proximal (E) and posterior (F) ends; (G–I) possible ischium or fibula MPG LZ-20 in different views; (J–L) tibia MPG SM-1; (M–Q) metatarsus MPG BA-1 in dorsal (O) and lateral (P, Q) views, with a view of the two articular surfaces (M, N); (R–T) ungual phalanx MPG CA-1 in two lateral views (R, S) and view of the posterior articular surface (T). Scale bars: 100 mm.

found. It is laterally compressed with a concave proximal articular surface, but is incomplete distally. As is also the case in an ungual phalanx referred to *Aragosaurus ischiaticus* (MPG ZH-19), the specimen lacks the lateral grooves that are typical of unguals.

SAUROPODA Marsh, 1878
EUSAUROPODA Upchurch, 1995
Eusauropoda indet.

3.7.2.3. Material. Four isolated teeth: MPG S-V1 (Villaralbo outcrop, Camarillas Formation), MPG S-Mk1 (La Maca outcrop, Camarillas Formation), MPG S-POCA-1 (POCA outcrop, Camarillas Formation) and MPG S-SC1 (San Cristóbal outcrop, Camarillas Formation).

3.7.2.4. Description. All the teeth (Fig. 13) are slightly spatulate, concave lingually and convex labially, and with crowns that are D-shaped in cross-section and crown bases that are sub-circular in cross-section. They lack cingula, denticles, and a constriction between the root and crown, and are wider mesiodistally than labiolingually. Enamel is absent from the crown apex but, elsewhere on the crown, a wrinkled surface texture is present. MPG S-POCA-1 is unlike the other teeth in possessing longitudinal mesial and distal grooves on its lingual surface (Fig. 13R–S).

3.7.2.5. Discussion. The presence in the Galve teeth of a wrinkled enamel surface texture, of crowns that are

D-shaped in cross-section, and of V-shaped wear facets resulting from crown–crown occlusion demonstrate that these teeth are assignable to the Eusauropoda (Upchurch and Barrett, 2000; Wilson, 2002). The absence of denticles may indicate that these teeth belong to neosauropods, as denticles are generally present only in basal eusauropods. However, the cetiosaurid *Patagosaurus* lacks denticles (Upchurch and Barrett, 2000) and cetiosaurids appear to be basal eusauropods (Upchurch et al., 2004), so this does not apply to all non-neosauropod members of Eusauropoda. Spatulate teeth similar to the Galve specimens are widespread in eusauropods, being known in cetiosaurids, mamenchisaurids, *Camarasaurus*, brachiosaurids, and *Euhelopus*. With slenderness indices *sensu* Upchurch (1998) ranging from 2.2 to 2.7, the Galve teeth are less slender than the teeth of diplodocoids, brachiosaurids and titanosaurs (where SI values are 4.0 at least Upchurch, 1998), but comparable to SI values of cetiosaurids, mamenchisaurids, *Euhelopus* and *Camarasaurus*. Of these taxa, mamenchisaurids are unlike the Galve teeth in possessing denticles, *Euhelopus* differs in exhibiting asymmetrically distributed enamel and so-called crown buttresses on the labial sides of its teeth (Wilson and Sereno, 1998), and in *Camarasaurus* the crowns are somewhat more expanded mesiodistally than is the case in the Galve teeth. The strongest similarity therefore appears to be with cetiosaurid teeth.

A tooth with a similar crown width to the specimens described here was reported by Cuenca-Bescós et al. (1997) and Canudo et al. (1999) from the La Carretera outcrop of Galve (specimen MPZ 97/557, Villar del Arzobispo Formation, Tithonian–Berriasian) and attributed to Diplodocidae? indet. This identification is unlikely as the specimen possesses a lingually curved crown and mesial and distal carinae.

One of the teeth described here, MPG S-POCA-1 (Fig. 13R–T), is unusual compared to the others in possessing longitudinal mesial and distal grooves on its lingual surface. Wilson (2002) reported such structures as being uniquely present within Rebbachisauridae. However, MPG S-POCA-1 possesses mesial and distal V-shaped wear facets unlike those of rebbachisaurids (and other diplodocoids) and in crown shape more resembles brachiosaurid teeth. An isolated tooth studied by Sanz (1982) and initially considered close to *Brachiosaurus*, but later attributed to *Aragosaurus ischiaticus* (Sanz et al., 1987), is similar to MPG S-POCA-1 in SI (2.45 and 2.6 respectively), though smaller and more worn. Sanz et al. (1987), Ruíz-Omeñaca and Canudo (2003, 2005) described MPG S-POCA-1, but wrongly referred to it as MPG-PYHII-1 and described it as

coming from Partida Poyales. However, the tooth they figured is MPG S-POCA-1 from the POCA outcrop (J. M. Herrero, pers. comm., 2006). Ruíz-Omeñaca and Canudo (2003, 2005) attributed this specimen to '*Pleurocoelus*' *valdensis*, a taxon which they argue is valid and diagnosable. This genus has, however, been designated a *nomen dubium* by several authors (Upchurch, 1993; Martill and Naish, 2001; Weishampel et al., 2004a,b).

Based on the morphology of the wear facets, the interdigitation of the tooth crowns deduced from the V-shaped facets, the wrinkled enamel surface texture, and the low SI indices (ranging from 2.2 to 2.7), four of the teeth studied here are attributed to Eusauropoda indet. They may belong to Cetiosauridae but this cannot be verified. The unusual tooth MPG S-POCA-1 (Fig. 13R–T) probably belongs to a titanosauriform, and perhaps to a brachiosaurid.

SAUROPODA Marsh, 1878
EUSAUROPODA Upchurch, 1995
NEOSAUROPODA Bonaparte, 1986
MACRONARIA Wilson and Sereno, 1998
CAMARASAURIDAE Cope, 1877
Camarasauridae indet.

3.7.2.6. Material. MPG P4-1 and MPG P4-2 ('P4' outcrop, El Castellar Formation, Berriasian–Barremian; Fig. 13A–I).

3.7.2.7. Description. Both teeth possess spatulate crowns that are more convex on their presumed labial side than on their presumed lingual side, and are D-shaped in cross-section. Lingual convexity is most obvious in the better-preserved, smaller tooth (MPG P4-2; Fig. 13F–I). Prominent wear facets are present on both teeth and are either on the mesial or distal side of the crown (MPG P4-2), or occur across the mesial, apical and distal parts of the crown (MPG P4-1; Fig. 13A–E). In both teeth, clearly defined concave facets extend from the crown apex to near the crown's mesiodistally widest point and, in MPG P4-2 the facet appears to be formed of smaller concave facets. Whereas MPG P4-1 has smooth enamel lacking ornamentation, MPG P4-2 has a rough surface texture. The SI of the tooth crowns is 1.57 (MPG P4-1) and 1.4 (MPG P4-2).

3.7.2.8. Discussion. The D-shaped cross-section of the tooth crown and distinct evidence for tooth–tooth occlusion demonstrates that these teeth belong to members of Eusauropoda. The SI values of MPG P4-1 and MPG P4-2 (1.57 and 1.4 respectively) are
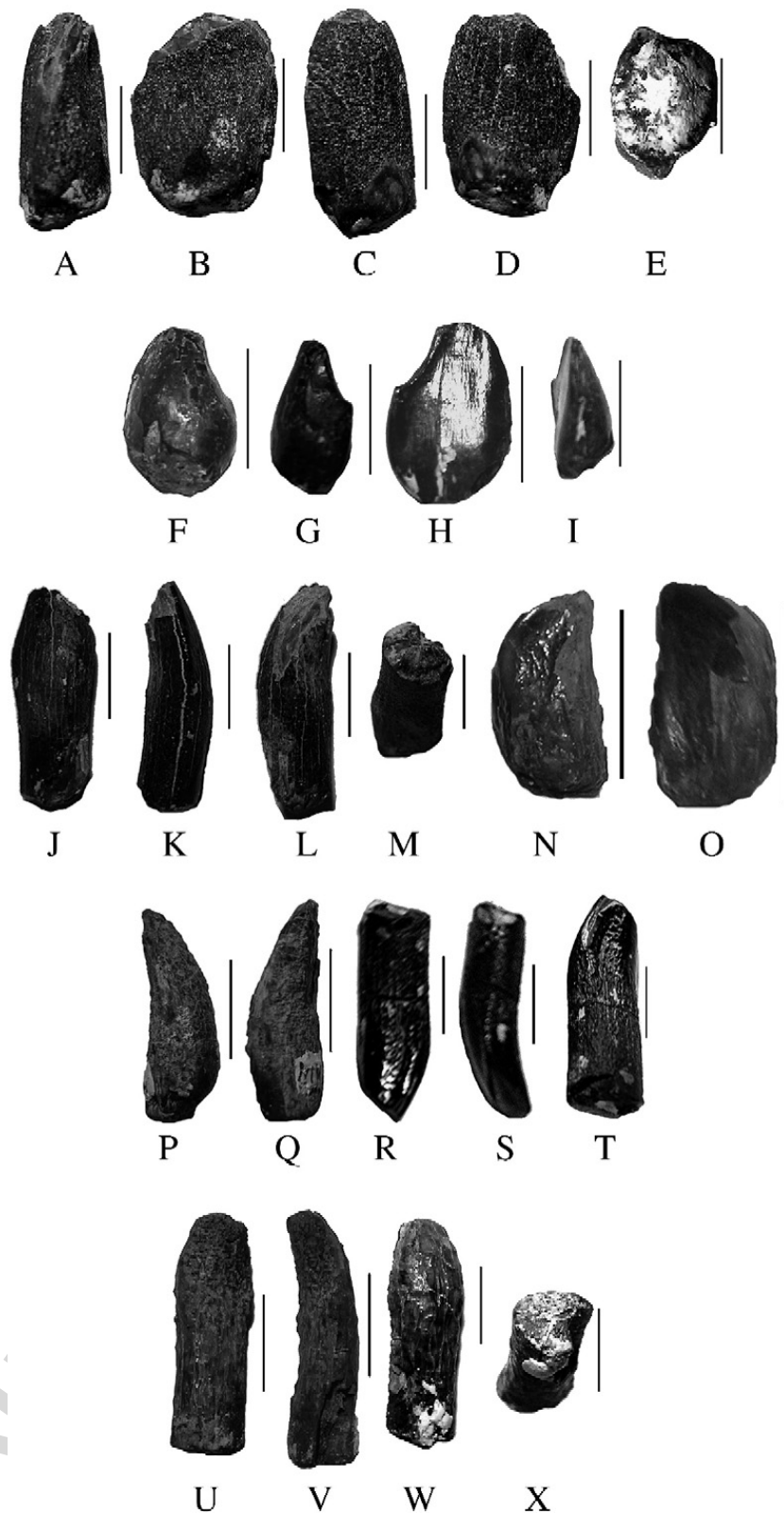
Fig. 13. Sauropod teeth from Galve deposits. First line: (from left to right) MPG P4-1 in mesial (A), lingual (B), lateral (C), labial (D) and occlusal views (E). Second line: MPG P4-2 in labial (F), mesial (G), lingual (H) and lateral (I) views. Third line: labial (J), lateral (K), mesial (L) and basal (M) views of MPG V1 and MPG YH-1 in labial (N) and lingual (O) views. Fourth line: two lateral views of MPG S-Mk1 (P, Q) and MPG POCA-1 in lingual (R, T) and mesial (S) views. Fifth line: MPG S-SC1 in lingual (U), lateral (V), labial (W) and basal (X) views. Scale bars: 1 mm.

close to the SI values of cetiosaurids, *Camarasaurus* and *Euhelopus*, where SI values range from 1.5 to 2.5 (Upchurch and Barrett, 2000). Among these taxa, the high-angle, mesially and distally placed concave wear facets on the Galve teeth, combined with their overall morphology, make them more like the teeth of *Camarasaurus* than those of any other sauropod (Upchurch and Barrett, 2000). Because *Camarasaurus* is restricted to the Kimmeridgian and Tithonian, we consider it most likely that the Galve teeth represent an as-yet-unnamed, closely related taxon, and they are therefore identified as Camarasauridae indet.

This is not the first record of possible camarasaurid teeth from the Lower Cretaceous of Europe. Sanz et al. (1987) described two teeth that they also classified as Camarasauridae indet. 'A form' (tooth PHIII-1) and Camarasauridae indet. 'B form' (tooth CBH-1). The second specimen is almost identical to MPG P4-2 but is different in size (see Table 3) and from a different outcrop (although Colladico Blanco is stratigraphically equivalent to the 'P4' outcrop).

The two Galve teeth are also reminiscent of the tooth that constitutes the holotype of *Oplosaurus armatus* from the Wessex Formation of the Isle of Wight (Naish and Martill, 2001). Although identified by Naish and Martill (2001) as possibly brachiosaurid, this tooth is closer to those of cetiosaurids, *Euhelopus*, or camarasaurids, and indeed Canudo et al. (2002) proposed that *Oplosaurus* might be a camarasaurid. It is possible that *Oplosaurus* and the Galve teeth MPG P4-1 and MPG P4-2 belong to the same camarasaurid taxon, though this remains untestable in the absence of better material.

SAUROPODA Marsh, 1878
EUSAUROPODA Upchurch, 1995

NEOSAUROPODA Bonaparte, 1986
TITANOSAURIFORMES Salgado et al., 1997
TITANOSAURIA Bonaparte and Coria, 1993
Titanosauria indet.

3.7.2.9. Material. In addition to the tooth attributed above to Titanosauriformes, a single caudal vertebra (MPG C.B.1-1; Fig. 14) from the lower Barremian Casilla Barea outcrop also appears to belong to this group of sauropods.

3.7.2.10. Description. The specimen is a caudal vertebra centrum with an incomplete neural arch. It is taller dorsoventrally (14 cm) than it is long proximodistally (11.5 cm). The centrum is strongly procoelous with the concave proximal articular surface being wider (19 cm) than it is tall (16 cm). An incomplete transverse process is present on the right side. Both prezygapophyses are preserved, but the neural spine has been lost.

3.7.2.11. Discussion. The strong procoely, dorsoventrally tall transverse processes, and large size of this specimen allow it to be identified as a proximal caudal vertebra of a sauropod. Based on its strong procoely, the specimen is identified as belonging to a titanosaur, and it is very like the proximal caudal vertebrae of titanosaurs such as *Isisaurus colberti*, *Gondwanatitan faustoi* and *Mendozasaurus neguyelap* (Jain and Bandyopadhyay, 1997; Kellner and de Azevedo, 1999; González Riga, 2003). Procoely is also present in the proximal caudal vertebrae of some diplodocoids, but is only weakly expressed compared to that present in MPG C.B.1-1. Outside Titanosauria, strong procoely as here also occurs in species referred to *Mamenchisaurus*. In these taxa, however, the articular surfaces of the proximal

Table 3
Measurements of the camarasaurid sauropod teeth from Galve

| Fossil	Length (mm)	Bucco-lingual diameter at the bottom (mm)	Mesiodistal diameter at the bottom (mm)
MPG POCA-1	33	8	9
MPG S-SC-1	27	7.5	8.3
MPG P4-1	13.5	5.2	6.5
MPG Mk-1	22	8	6
MPG V1	25	8	7
MPG P4-2	22	7	8
MPG YH-1	13	—	6
Cf. *Astrodon* [a] sp. (MPG PYII-1)	27.6	7.3	7.2
Cf. *Astrodon* [a] sp. (MPG CBH-3)	26	7.2	8
Camarasauridae A [a] (MPG PHIII-1)	22	10	14
Camarasauridae A [a] (MPG CBH-1)	20	8	13
Camarasauridae B [a] (MPG PHIII-5)		3.7	3.5

[a] Studied by Sanz et al. (1987).
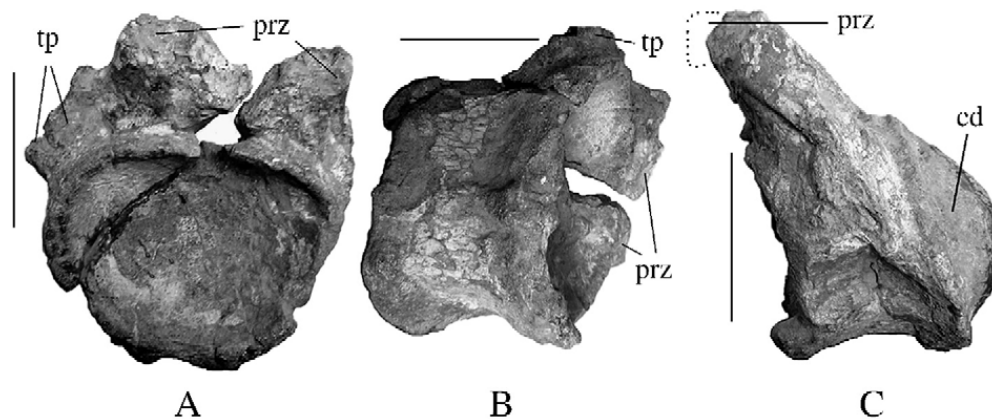
Fig. 14. Isolated titanosaurid caudal vertebra MPG C.B.1-1 in cranial (A), ventral (B) and left lateral (C) view. Abbreviations: cd, condyle; prz, prezygapophysis; tp, transverse process (based on Martínez et al., 2004). Scale bars: 100 mm.

caudal vertebrae are taller than they are wide and the transverse processes are not so extensive dorsoventrally as they are in MPG C.B.1-1 (Young and Zhao, 1972; Pi et al., 1996).

3.7.3. Ornithischia

The ornithischians reported from Galve belong to most of the major clades, with the exception of Marginocephalia. Following a recent proposal (Butler, 2005), we here regard Heterodontosauridae as a basal ornithischian clade and not as part of Ornithopoda. This hypothesis was considered by Santa Luca (1980) based on the absence of the obturator process of the ischium. Estes and Sanchíz (1982) referred a tooth from the Yacimiento Herrero outcrop (Camarillas Formation) to the heterodontosaurid *Echinodon* and we also report three teeth from the upper part of the Camarillas Formation (POCA and CFP outcrops) that can be attributed to Heterodontosauridae (though not to *Echinodon*). Thyreophorans are represented at Galve by a presacral dermal spine from the Ank-Barranco outcrop (lower Barremian) identified as Nodosauridae indet. by Pereda Suberbiola and Galton (2001), and by a caudal spine and a broken plate attributed to Stegosauria indet. (Pereda Suberbiola et al., 2005).

Remains of Ornithopoda are quite well represented in the Mesozoic deposits of Galve. These include isolated teeth from the Camarillas Formation that can be identified as Hypsilophodontidae indet. (described here) as well as a partial skeleton from Poyales Barranco Canales (Camarillas Formation) identified as *Hypsilophodon foxii* by Sanz et al. (1987) but considered to represent a new genus by Ruíz-Omeñaca et al. (2004). Other remains, including eggshells, teeth and postcrania have also been attributed to hypsilophodontids (Estes and Sanchíz, 1982; Carpenter and Alf, 1994; Ruíz-

Omeñaca, 2001; Ruíz-Omeñaca et al., 2004). Iguanodontians at Galve include remains referable to cf. *Valdosaurus* as well as elements referred to *Mantellisaurus* (*I.* cf. *atherfieldensis* in Sanz et al., 1984) and *Iguanodon bernissartensis* by Buscalioni and Sanz (1987). The latter record was regarded as erroneous by Ruíz-Omeñaca et al. (2004) who noted that the specimen actually represents a new (as yet unnamed) taxon, but without justification.

ORNITHISCHIA Seeley, 1888
HETERODONTOSAURIDAE Kuhn, 1966
Heterodontosauridae indet.

3.7.3.1. Material. Teeth MPG C7-15, MPG C7-16 (both from POCA outcrop) and MPG CFP-1 of the Herrero collection (Fig. 15). The strata exposed at the POCA and CFP outcrops form part of a suite of clays and marls that belong to the top of the Camarillas Formation (lower Barremian).

3.7.3.2. Description. All three teeth are small, lingually curved and labiolingually compressed and, when viewed mesially or distally, the crowns appear triangular. Because the crowns are worn apically, the presence of apical denticles cannot be determined. However, denticles are clearly absent from the basal, unworn parts of the crowns. The crown and root are structurally continuous, although the crown is markedly wider than the root. Both labial and lingual sides possess enamel although, while the lingual surface is unornamented, the labial surface bears three vertical ridges. A central ridge divides the labial surface into symmetrical halves, while two less prominent accessory ridges flank the mesial and distal edges of the crown. The crown surface in between these ridges is slightly concave. In MPG C7-15 (Fig. 15C–E) the

maximum width of the crown is 1.25 mm, while the crown height is 2 mm. The root is 0.6 mm in diameter. The second specimen (MPG C7-16; Fig. 15G–J) is similar, although larger, with a root 2 mm in diameter and a crown 5 mm in diameter and 6 mm in height. The third specimen (MPG CFP-1; Fig. 15F) is close to MPG C7–15 in dimensions, but poorly preserved. The specimen is 0.9 mm in crown height and 1.2 mm in maximum width.

3.7.3.3. Discussion. While heterodontosaurids are best known from the Lower Jurassic of South Africa, the reinterpretation of *Echinodon becklesii* from the Berriasian Lulworth Formation (Norman and Barrett, 2002) shows that the group survived into the Early Cretaceous in Europe. Nevertheless, the rarity of Lower Cretaceous heterodontosaurids suggests caution when identifying Cretaceous records of the group, and we

therefore first exclude other ornithischian groups present in the Lower Cretaceous. Basal ornithischians can be excluded because their teeth possess bulbous crown bases and numerous denticles (Sereno, 1991). Dryosaurids and other basal iguanodontians can be rejected based on the numerous ridges and denticles on their rather rectangular tooth crowns (Weishampel et al., 2004a,b), and camptosaurids and iguanodontid-grade taxa can be excluded on the basis of larger tooth size, the presence of more than three ridges on their tooth crowns, and their denticulate crown edges.

Like the teeth described here, *Hypsilophodon* and similar forms possess a prominent vertical crest but differ from MPG C7-15, MPG C7-16 and MPG CFP-1 in bearing denticles at the crown base. This is true even of small juvenile teeth of *Hypsilophodon* where denticles at the crown base are present on at least one of the carinae (Fuentes Vidarte and Meijide Calvo,
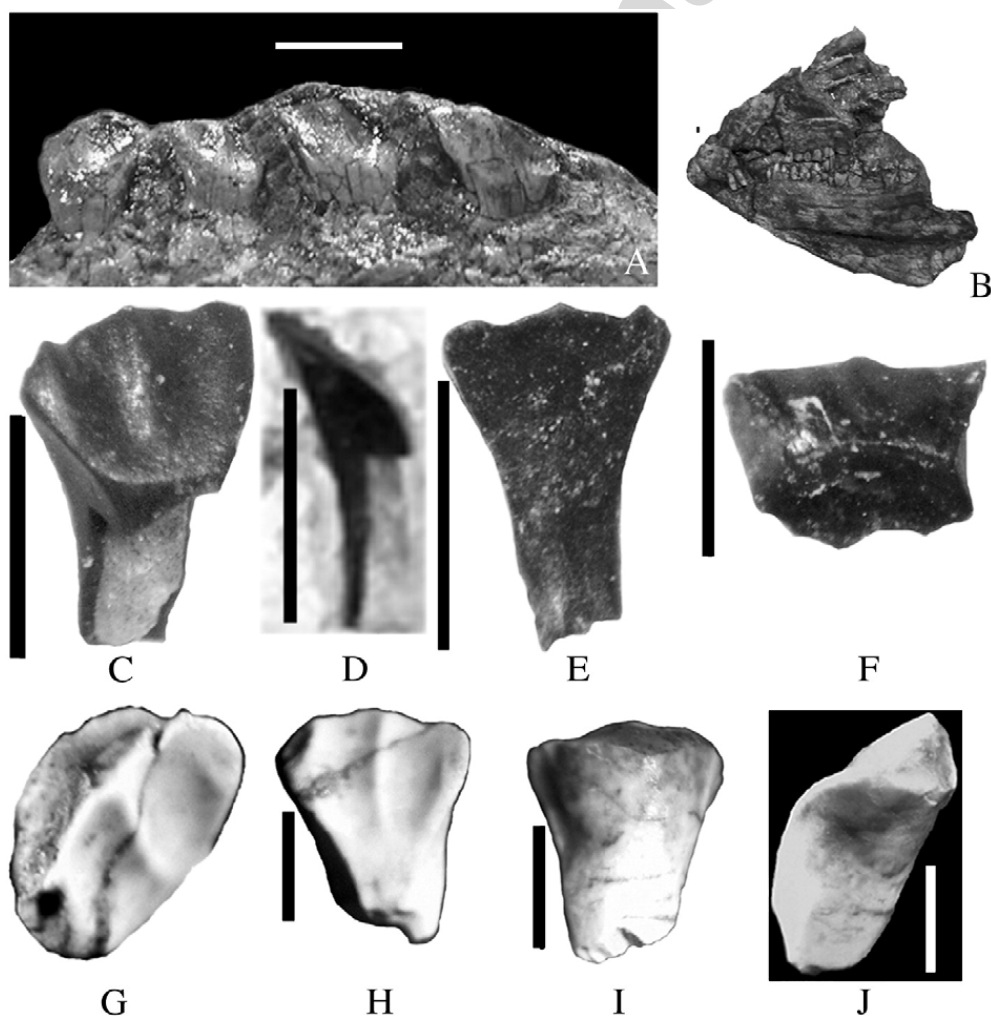

Fig. 15. Heterodontosaurid teeth. (A) *Abrictosaurus consors* teeth (BMNH RUB.54), (B) *Lycorhinus angustidens* dentition (carst from the original No. 3606, British Museum). (C–J) Teeth from Galve, MPG C7-15 in labial (C), mesial (D) and lingual (E) views, MPG CFP-1 in labial view (F), MPG C7-16 in apical–labial (G), labial (H), lingual (I), and lateral (J) views. Scale bars: 1 mm.

2001). Juvenile *Hypsilophodon* teeth are not only morphologically distinct from MPG C7-15, MPG C7-16 and MPG CFP-1, but are also larger. The three Galve teeth would have belonged to a tiny ornithischian a good deal smaller than *Hypsilophodon*.

Several features characterise these teeth: three vertical, parallel ridges are present on the labial side of the crown, and are spaced out equally across the labial surface; denticles are absent from the basal, unworn parts of the crown; the crown appears triangular in mesial or distal view; and the crown narrows towards the root and is not clearly demarcated from it. These are all characteristics of the teeth of Heterodontosauridae (Fig. 15A–B). This is not the first report of heterodontosaurids from the Lower Cretaceous of Galve: Estes and Sanchíz (1982) described a tooth that they attributed to aff. *Echinodon* sp. (although Pereda Suberbiola and Galton (2001) regarded this record as doubtful) and other authors (Galton, 2002; Ruíz-Omeñaca et al. 2004) referred to material identified as Heterodontosauridae indet. MPG C7-15, MPG C7-16 and MPG CFP-1 are unlike the teeth of *Echinodon* and are unlikely to belong to this taxon. We note also that a maxillary tooth from the Kimmeridgian of Guimarota, Portugal (Rauhut, 2001, Fig. 5) and some dentary teeth from the Barremian–Aptian of the El Pañascal site at Burgos, Spain (Torcida Fernández-Baldor et al., 2005) agree closely with the teeth identified here as heterodontosaurid.

ORNITHISCHIA Seeley, 1888
GENASAURIA Sereno, 1986
ORNITHOPODA Marsh, 1881b
Hypsilophodontidae indet.

3.7.3.4. Material. Seven teeth (MPG O-YH1 and 2; Fig. 16) from the "Yacimiento Herrero" outcrop, in the Camarillas Formation (lower Barremian) of Galve (Teruel, Spain).

3.7.3.5. Description. All the teeth are heavily worn and lack their apices. Five of the teeth are similar in morphology and identified as maxillary teeth (MPG O-YH3 to MPG O-YH7). In height, they range from 4 to 8 mm and in mesiodistal length from 3 to 12 mm (Table 4). The crowns are asymmetrical and lack both a constriction at the crown–root junction and a cingulum. They have a prominent central ridge on the lingual surface and a centrally placed concavity on the labial surface. In occlusal view, the crown apices are pentagonal (Fig. 16). MPG O-YH7 is broken longitudinally. MPG O-YH1 and MPG O-YH2 are larger and exhibit more secondary ridges than the other teeth. Because of their similar size, these two teeth are considered to belong to the same animal, and one that was larger than those represented by the other teeth.

3.7.3.6. Discussion. Comparison of these teeth with those of *Hypsilophodon foxii* suggests they represent a closely related taxon, and positions within the dental sequence may be allocated. Two of them (MPG O-YH1 and MPG O-YH2) can be identified as dentary teeth as the lingual surface bears a prominent, centrally placed vertical ridge, and several less prominent secondary ridges. The others (MPG O-YH3 to 7) can be identified as maxillary teeth as they bear denticles on both sides of their asymmetrical crowns. MPG O-YH3 and MPG O-YH6 are identified as left maxillary teeth and MPG
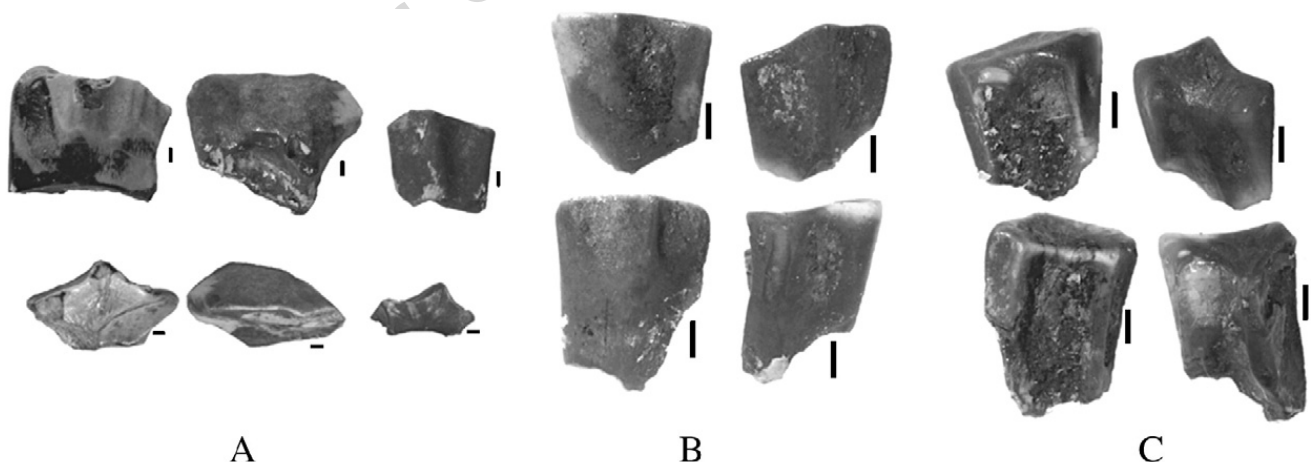
Fig. 16. Hypsilophodontidae indet. teeth. MPG O-YH1, MPG O-YH2 and MPG O-YH3 in lingual (A, upper line, from left to right) and occlusal views (A, lower line, from left to right); lingual view of the teeth MPG O-YH4, MPG O-YH5 (B, upper line, from left to right) and MPG O-YH6 and MPG O-YH7 (B, lower line, from left to right); and labial view of the teeth MPG O-YH4, MPG O-YH5 (C, upper line, from left to right) and MPG O-YH6 and MPG O-YH7 (C, lower line, from left to right). Scale bars: 1 mm.

Table 4
Measurements of the hypsilophodontid teeth from Galve

Fossil	Length	Bucco-lingual diameter at the bottom	Mesiodistal diameter at the bottom
	(mm)	(mm)	(mm)
MPG O-YH-1	8	7	12
MPG O-YH-2	8	7	12
MPG O-YH-3	8	3	7
MPG O-YH-4	5	2	4
MPG O-YH-5	6	1	3
MPG O-YH-6	4	0.5	4
MPG O-YH-7	6	3	3

O-YH4, MPG O-YH5 and possibly MPG O-YH7 are interpreted as right maxillary teeth.

While recent studies have not recovered a monophyletic Hypsilophodontidae (Weishampel et al., 2004a,b), the similarity of the Galve teeth to those of *H. foxii* indicates that they belong to a taxon more closely related to *H. foxii* than to any other ornithopod, and for this reason we provisionally recognise a clade for *H. foxii* and the unnamed Galve taxon.

ORNITHISCHIA Seeley, 1888
GENASAURIA Sereno, 1986
ORNITHOPODA Marsh, 1881b
IGUANODONTIA Sereno, 1986
PDRYOSAURIDAE Milner and Norman, 1984
VALDOSAURUS Galton, 1977
Valdosaurus sp.

3.7.3.7. Material. An isolated broken tooth (MPG C. A.S. 14) from the Villar del Arzobispo Formation (Tithonian–Berriasian) of Las Cerradicas, Galve (Fig. 17B–C).

3.7.3.8. Description. The specimen is an incomplete, labiolingually compressed crown bearing enamel both labially and lingually. It sports a central primary ridge on its labial surface and lacks wear facets. On either side of the central ridge, the labial surface of the crown is slightly concave. Accessory ridges occur in these regions, with more than eight being present mesial to the primary ridge, and three distal to it. Denticles occur along the crown edges, but they are not necessarily confluent with the vertical ridges. Ridges are absent on the crown's lingual surface (Fig. 17C). Mesiodistally, the specimen is c. 7 mm wide, and labiolingually it is c. 3 mm thick.

3.7.3.9. Discussion. This specimen is identified as a maxillary tooth because the apex is centrally positioned on the crown, and not located closer to the distal edge, as is the case in dentary teeth. Morphologically, MPG C.A.S. 14 corresponds most closely with maxillary teeth of the dryosaurid *Valdosaurus* (Fig. 17A). Though incomplete, the crown was clearly more rectangular than that of non-iguanodontian ornithopods and other ornithischians like thyreophorans. Furthermore, it differs from thyreophoran teeth in that their tooth crowns are bulbous above the cingulum, their vertical ridges are thicker, and their crowns are more triangular. The specimen matches dryosaurid teeth in possessing a single, prominent centrally placed vertical ridge, and in the morphology and spacing of its denticles and accessory ridges (Galton and Taquet, 1982; Galton, 1983). The tooth crowns of *Dryosaurus* (Galton, 1983, Fig. 4) are more symmetrical than those of *Valdosaurus* (Galton, 1983, Fig. 5). Galton's (1983) *Valdosaurus* tooth (YPM 1876) has a mesiodistal width of 12 mm and a total crown height of 20 mm, while the *Dryosaurus*
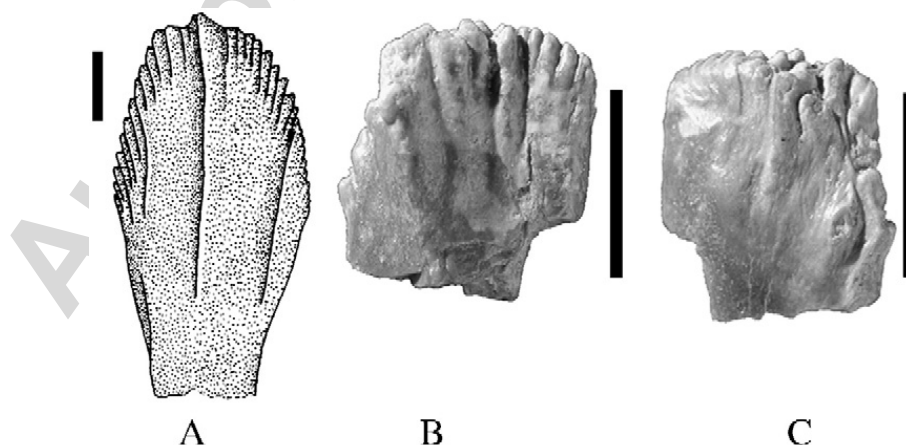

Fig. 17. Comparison between the tooth MPG CAS.14 (B) from the Barremian of Galve (Spain) and a maxillary *Valdosaurus canaliculatus* tooth (CM 3392; A) after Galton (1983) from the Lower Cretaceous of England. Detail of the tooth in buccal (B) and lingual (C) view. Scale bars: 5 mm.

tooth (YPM 9521) has a mesiodistal width of 6.5 mm and a total crown height length of 12.3 mm.

Valdosaurus is the only known Lower Cretaceous dryosaurid. Possible evidence for this taxon has been reported previously from the Lower Cretaceous of Spain: two femora from different outcrops of the Camarillas Formation of Galve were attributed to cf. *Valdosaurus* sp. by Sanz et al. (1984, 1987) and Buscalioni and Sanz (1987).

4. Vertebrate palaeontology

All vertebrates so far identified from the Galve deposits are listed below for each formation, based on previous work (Sánchez-Hernández, 2002, 2004) and new records. The classification used here for Dinosauria is from Weishampel et al. (2004a,b). Other remains have been classified following Buscalioni and Sanz (1987) and Sánchez-Hernández (2002). The multituberculate mammals have been classified according to Kielan-Jaworowska and Hurum (2001). The term 'Plagiaula-cida' is in quotation marks since it is considered paraphyletic in current cladistic analyses (Kielan-Jaworowska and Hurum, 2001). New taxa based on fossils from Galve are indicated by the author/s and year of publication.

4.1. Villar del Arzobispo Formation (Tithonian–Berriasian)

Fishes
  Osteichthyes
      Lepidotes sp.
      Pycnodontiformes indet.
  Testudines: Cryptodira
      Cryptodira indet.
Diapsida
  Squamata
      Squamata indet.
  Dinosauria
    Saurischia: Theropoda
      Theropoda indet.
      Coelurosauria indet.
    Saurischia: Sauropodomorpha: Sauropoda
      Sauropoda indet.
    Eusauropoda: Cetiosauridae
      Galveosaurus herreroi Sánchez-Hernán-dez, 2005
    Ornithischia: Ornithopoda
      Valdosaurus indet.
Trace fossils
      Theropoda indet. (trackways)
      Sauropoda indet. (trackways)
      Ornithopoda indet. (trackways)
      Archosauria indet. (trackways)

All the vertebrates described from the Villar del Arzobispo Formation consist of isolated bones and teeth, with the exception of the eusauropod *Galveo-saurus* where caudal vertebrae, a chevron, an ischium, a dorsal vertebra, a cervical vertebra, some rib fragments, a scapula, the two humeri, and a sternal plate are known (Sánchez-Hernández, 2005). Other isolated sauropod bones are described here. The dryosaurid ornithopod *Valdosaurus* is represented in these deposits by the incomplete tooth described in this paper. Fossil wood fragments are also quite common in this formation.

4.2. El Castellar Formation (Berriasian–early Barremian)

Fishes
  Osteichthyes
      Lepidotes sp.
      Pycnodontiformes indet.
      Amiiformes indet.
Lissamphibia
      Lissamphibia indet.
Reptilia
  Testudines: Cryptodira
      Cryptodira indet.
Diapsida
  Squamata
      Squamata indet.
  Crocodyliformes: Mesoeucrocodyliformes
    Atoposauridae
      Theriosuchus sp.
    Goniopholididae
      Goniopholis cf. *crassidens*
    Bernissartiidae
      cf. *Bernissartia* sp.
Pterosauria
      Pterosauria indet.
Dinosauria
  Saurischia: Theropoda
      Dromaeosauridae indet.
  Saurischia: Sauropodomorpha: Sauropoda
      Eusauropoda *incertae sedis*
      Aragosaurus ischiaticus Sanz et al., 1987
  Saurischia: Sauropodomorpha: Neosauropoda
      Camarasauridae indet.
  Ornithischia: Thyreophora: Stegosauria
      Stegosauria indet.
  Ornithischia: Heterodontosauridae

aff. *Echinodon* sp.
Ornithischia: Ornithopoda: Euornithopoda
 cf. *Hypsilophodon* sp.
 Valdosaurus indet.
Mammalia: Theriimorpha: Multituberculata
 'Plagiaulacida': Paulchoffatiidae
  Galveodon nannothus Hahn and Hahn, 1992
Mammalia: Trechnotheria
Symmetrodonta: Spalacotheriidae
 Spalacotherium henkeli Krebs, 1985
Dryolestoidea: Dryolestidae
 Crusafontia cuencana Henkel and Krebs, 1969
Zatheria: Peramuridae
 Peramuridae indet.
Trace fossils
 Theropoda indet. (trackways)
 Sauropoda indet. (trackways)
 Ornithopoda indet. (trackways)
 Dinosaur eggshells

The vertebrates from the El Castellar Formation are mostly isolated teeth and bones. Thus, mammals in the El Castellar Formation are only represented by teeth, whereas fish remains consist only of vertebrae, mandibles, scales, several teeth and coprolites. The urodele remains are more complete: Estes and Sanchíz (1982) described a dorsal vertebra of *Galverpeton ibericum* and a humerus and some cranial bones of another taxon larger than *Galverpeton* from the Colladico Blanco outcrop. These authors also described a tooth of aff. *Echinodon* sp. Some pterosaur (Pterosauria indet.) and sauropod (Camarasauridae and Sauropoda indet.) teeth have been described from the same outcrop. The Las Zabacheras site has yielded the remains of the sauropod *Aragosaurus*, consisting of a tooth, a radius, an ulna, metacarpals, phalanges, rib fragments, a scapula, coracoid, pubis, ischium, femur, caudal vertebrae and chevrons. A spine of an indeterminate Stegosauria were found in the La Canaleta outcrop. Turtle remains are present in all the localities, but have yet to be studied. Several isolated teeth and osteoderms of crocodyliforms are also present.

4.3. Camarillas Formation (early Barremian)

Fishes
Chondrichthyes: Elasmobranchii: Hybodontiformes
 Lonchidion microselachos Estes and Sanchíz, 1982

Hybodus parvidens (= *Polyacrodus parvidens*)
 Acrodus sp.
Chondrichthyes: Neoselachii: Squalomorpha
 Lamniformes indet.
Chondrichthyes: Batomorphii
 Batoidea
  Rhinobatos sp.
 Rajiformes
  Pristidae indet.
Osteichthyes
 Holostei indet.
 Lepidotes sp.
 Teleostei indet.
Halecomorphi
 Pycnodontiformes indet.
 Amiiformes indet.
Lissamphibia
 Lissamphibia indet.
Albanerpetontidae
 Celtedens cf. *megacephalus*
Anura: Discoglossidae
 Discoglossidae indet.
 Eodiscoglossus santonjae Sanchíz, 1998
Urodela
 Galverpeton ibericum Estes and Sanchíz, 1982
Reptilia
 Testudines
  Testudines indet.
  Cryptodira indet.
 Diapsida
 Squamata
  Squamata indet.
  Sauria: Scincomorpha
   Paramacellodidae indet.
   Scincidae indet.
   Meyasaurus sp.
 Crocodyliformes
  Crocodyliformes indet.
  Allognathosuchus sp.
  Mesoeucrocodyliformes
   Atoposauridae
    Theriosuchus sp.
   Goniopholididae
    Goniopholis cf. *crassidens*
   Bernissartiidae
    cf. *Bernissartia* sp.
    Bernissartia fagesii
 Pterosauria
  Pterosauria indet.
  Pterodactyloidea indet.

Ornithocheiridae indet.
Istiodactylidae indet.
Dinosauria
　Saurischia: Theropoda
　　Theropoda indet.
　Theropoda: Neotheropoda: Tetanurae
　　Spinosauridae
　　　Baryonychinae indet.
　　　Spinosaurinae indet.
　　Allosauroidea
　　　Allosauroidea indet.
　　Coelurosauria
　　　Coelurosauria indet.
　　　Dromaeosauridae indet.
　Saurischia: Sauropodomorpha
　　　Camarasauridae indet.
　　　Titanosauria indet.
　Ornithischia: Heterodontosauridae
　　　Heterodontosauridae indet.
　Ornithischia: Thyreophora: Ankylosauria
　　　Nodosauridae indet.
　Ornithischia: Ornithopoda
　　　Ornithopoda indet.
　　　Hypsilophodontidae indet.
　　　cf. *Hypsilophodon* sp.
　　　Hypsilophodon indet.
　Iguanodontia
　　Dryosauridae
　　　cf. *Valdosaurus* sp.
　　Iguanodontidae
　　　Iguanodontidae indet.
　　　Iguanodon sp.
　　　Iguanodon bernissartensis
　　　Mantellisaurus atherfieldensis
Mammalia
　　　　Mammalia sp.
Mammalia: Theriimorpha: Multituberculata
　'Plagiaulacida': Paulchoffatiidae
　　　Galveodon nannothus Hahn and Hahn,
　　　1992
　　　Paulchoffatiinae
　　　　Paulchoffatia sp.
　　　Kuehneodontinae
　　　　Kuehneodon sp.
　'Plagiaulacida': Pinheirodontidae
　　　Lavocatia alfambrensis Canudo and
　　　Cuenca, 1996
　'Plagiaulacida': Plagiaulacidae
　　　Plaugiaulax sp.
　　　Bolodon elongatus
　　　Bolodon sp.
　'Plagiaulacida': Eobaataridae

Eobaatar hispanicus Hahn and Hahn,
1992
Loxaulax sp.
Parendotherium herreroi Crusafont-Pairó
and Adrover, 1966
Mammalia: Dryolestoidea: Dryolestidae
　　Crusafontia cuencana
Trace fossils
　　Theropoda indet. tracks
　　Theropoda indet. eggshells:
　　　Elongatoolithidae indet.
　　　Macroolithus turolensis Amo et al., 2000
　　　Ageroolithus aff. *fontllongensis*
　　　Prismatoolithus sp.
　　Sauropoda indet. tracks
　　Bataguridae indet. (eggshells)
　　Crocodyliformes eggshells

As is the case in the other units, the fish, squamate, pterosaur and mammal remains of the Camarillas Formation are mostly represented by teeth and isolated bones. The turtle remains, although comparatively abundant, have yet to be studied. The crocodyliforms are represented by vertebrae, teeth, scutes and a skull found in the Cerrada Roya Mina outcrop and attributed to *Bernissartia fagesii*. Ornithischian dinosaurs are well represented, with teeth of *Hypsilophodon* and Hypsilophodontidae present (some of them described here) as well as an almost complete postcranial skeleton of *Hypsilophodon* from the Poyales Barranco Canales outcrop. Dryosaurids are represented by a broken femur of cf. *Valdosaurus* sp., and many isolated bones and teeth referred to *Iguanodon* and *Mantellisaurus* have also been reported. Three heterodontosaurid teeth have been described above from these deposits and thyreophorans are represented by an ankylosaurid presacral spine from the ANK-Barranco outcrop, and a tail spine attributed to Stegosauria indet. Theropods are also represented by isolated teeth and by ungual phalanges and other postcranial elements. Sauropod remains are scarce in the Camarillas Formation.

4.4. Faunal evolution

The composition of the vertebrate faunas seems to change through the succession, although the abundance of turtles and crocodyliforms remains about the same throughout. Vertebrates are most common in the Camarillas Formation. Among dinosaurs, sauropods are commoner in the basal two units while ornithopod fossils are more abundant in the Camarillas Formation. This could be interpreted as being in line with the

general replacement of sauropods by ornithopods across the Jurassic–Cretaceous boundary, although sauropods were clearly by no means eradicated.

Trechnotherian mammals like spalacotheriids and dryolestoids appear dominant in the El Castellar Formation, but they are not as well represented in the Camarillas Formation where multituberculates are more common.

5. Palaeobiogeography

The Galve vertebrate assemblages show similarities with those from the Purbeck and Wealden of England, Belgium, France and Germany, as well as with Early Cretaceous dinosaur-bearing beds in Portugal and Romania (Figs. 18, 19). More widely, many of the taxa are shared with faunas in North Africa and North America.

5.1. Comparisons with England

The Galve vertebrate-bearing Early Cretaceous may be matched with the Purbeck and Wealden succession of southern England (Fig. 18). This succession is exposed in two main basins, the Wessex and Weald basins, with the Purbeck Group, Wessex Formation (alluvial facies, Valanginian–Barremian) and Vectis Formation (mainly lacustrine–lagoonal deposits, Barremian–Aptian; Benton and Spencer, 1995; Robinson et al., 2002; Robinson

and Hesselbo, 2004). Correlations between Galve and England are based on charophytes (Martín-Closas, 1988; Allen and Wimbledon, 1991; Soulié-Märsche, 1994; Díez et al., 1995; Martín-Closas, 2000). Broadly speaking, the faunas from Galve match those in age-equivalent units of the Purbeck–Wealden succession of England. In some cases, the facies are similar, but in others they differ, and so the shared taxa probably represent a biological signal.

The Villar del Arzobispo Formation is dated as spanning the Jurassic–Cretaceous boundary (Fig. 18), and so is age-equivalent to the Purbeck/Durlston beds of southern England. Both units share cryptodire turtles, similar crocodilians (*Goniopholis* and *Bernissartia*, among others), pterosaurs, sauropods, iguanodontids, ankylosaurs and large theropods (Benton and Spencer, 1995). The facies represented by the two units are somewhat different – the upper part of the British Purbeck Limestone Group consists of freshwater limestones and clays, while the Villar del Arzobispo Formation comprises intertidal deposits – so the broad faunal similarities may indicate that both units were sampling a similar fauna in these two regions of Europe.

There is a long hiatus above the Villar del Arzobispo Formation (upper Tithonian/lower Berriasian) before the El Castellar Formation (upper Hauterivian/lower Barremian), which matches the upper part of the Wessex Formation in England. The Camarillas Formation sediments (fluvial origin, lower Barremian) are similar

System	Stage		Ma	ENGLAND		SPAIN
				Weald	Wessex +Isle of Wight	Galve
		Upper	125	Upper Weald Clay	Vectis Fm.	Artoles Fm.
	Barremian	Middle				Camarillas Formation
			132	Grinstead Clay		
						El Castellar Formation
(Neocomian) Lower Cretaceous	Hauterivian	Upper		Lower Weald Clay	Wessex Fm.	
		Middle				
		Lower	135			
	Valanginian	Upper		Upper Tunbridge Wells Sand		
		Middle				hiatus
		Lower		Lower Tunbridge Wells Sand		
				Wadhurst Clay		
				Ashdown Beds/ Fairlight Clay		
	Berriasian	Upper	141	Durlston Beds	Purbeck Beds	
		Middle				Villar del Arzobispo Formation
		Lower	146	Lulworth Beds		
Upper Jurassic	Tithonian	Upper			Portland Beds	

Fig. 18. Correlation between the Upper Jurassic/Lower Cretaceous formations of Galve (Spain) and England. The dashed lines indicate uncertain boundaries.

	GALVE, IBERIAN RANGE, NE SPAIN	PARIS BASIN, FRANCE	WESSEX SUB-BASIN, ENGLAND	WEALD SUB-BASIN, ENGLAND	(JURA) FRANCE & SWITZERLAND	BELGIUM RHINELAND ARDENNES	L.Saxon Basin NETHERLANDS & GERMANY	POLAND	DENMARK (Bornholm)
APTIAN (part)	Morella Formation		Vectis Fm.			Hautrage pocket			
BARREMIAN	Camarillas Formation	Sables et argiles p. / Sables de Perthes	Vectis Fm.	Upper Weald Clay		Nehden & Bernissart pockets			
HAUTERIVIAN	El Castellar Formation	Sables de C., C.Landon, Gres de P. & equivs.	Wessex Formation	Lower Weald Clay					Jydegard Formation
VALANGINIAN		Sables de Griselles & equivalents		Upper T.W. Fm. / Low.T.W. Fm. / Washurst Fm. / Ashdown Formation		Other pockets ?	Osterwald Member / Bückeburg Member	marine?	
BERRIASIAN	Villar del Arzobispo Formation	"Purbeck"	Cinder Bed... Purbeck(type)	Grays Lm. / Cinder Beds	De Vions Fm. / Pierre Châtel Fm. / "Purbeckian"		Katzberg Member	Purbeck	Robbedale Fm / Rabekke Fm.
TITHONIAN									

Fig. 19. Correlation between the subaerial 'synclinal of Galve' (Spain) deposits and subaerial NW of Europe sediments of similar age (after Allen and Wimbledon (1991). Dark grey areas indicate marine deposits. The hiatuses are marked in grey.

to the middle and upper parts of the Wessex Formation (alluvial floodplain and lacustrine origin), in England. The upper part of the Vectis Formation (lacustrine–lagoonal succession) is equivalent to the Artoles Formation (bay-marine deposits, late Barremian–Aptian). All the vertebrate taxa in the faunal list from the Upper Weald Clay (early Barremian) of Smokejacks Quarry (Surrey, England) given by Ross and Cook (1995), have also been found in the Camarillas Formation, which has produced other taxa not found at Smokejacks.

In the Wealden of England, *Iguanodon* iguanodontian ornithopods (conventionally referred to *Iguanodon*) are abundant in both the Isle of Wight and the Weald, while *Hypsilophodon foxii* is present only in the former, and *Hylaeosaurus* in the latter. In the Barremian deposits of Galve, abundant remains of *Iguanodon*, *Hypsilophodon* and one spine of *Polacanthus* have been found (Sánchez-Hernández, 2002, 2004). Genera shared between the Isle of Wight and Galve are the hybodontid shark *Lonchidion*, the crocodyliforms *Goniopholis*,

Bernissartia and *Theriosuchus*, and the dinosaurs *Hypsilophodon*, *Valdosaurus*, *Polacanthus*, *Iguanodon* and '*Pleurocoelus*'. Other less clearly identified taxa that are also shared include theropods (baryonychines and possibly dromaeosaurids), sauropods (brachiosaurids, diplodocids, or eusauropods; although the diplodocid and brachiosaurid remains are still unclear, as noted above), thyreophorans (stegosaurs) and cryptodires (Howse and Milner, 1993; Benton and Spencer, 1995; Martill and Naish, 2001; Weishampel et al., 2004a,b). These units also have albanerpetontids in common (Gardner, 2000; Gardner et al., 2003), similar families of pterosaurs and isolated bones of Lower Cretaceous stegosaurs (Barrett and Upchurch, 1995; Naish and Martill, 2001; Pereda Suberbiola et al., 2005).

5.2. Comparisons with other parts of Europe

Other parts of Europe have yielded similar dinosaurian remains from the Early Cretaceous, but finds are often incomplete, or require re-study (Weishampel et al.,

2004a,b). Broad correlations of these units are indicated in Fig. 19 (Allen and Wimbledon, 1991). There are similarities between the vertebrate faunas from the Galve succession and Upper Jurassic/Lower Cretaceous faunas from other parts of Europe, such as Belgium (the Barremian–Aptian Wealden deposits of Province de la Hainaut, with indeterminate large theropod *Megalosaurus* and *Iguanodon* remains), France (the Hauterivian–Albian unnamed deposits with remains of sauropods, theropods, *Iguanodon* and ankylosaurs), Portugal (in the Barremian and Aptian–Cenomanian sediments with theropod, sauropod, ankylosaur and *Iguanodon* remains similar to the Galve ones), Germany (the Berriasian–Aptian Nordrhein–Westphalen Wealden shares with the Galve Lower Cretaceous deposits the presence of large theropods, *Iguanodon*, *Megalosaurus*, *Hypsilophodon* and nodosaurid bones) or Romania (where the Berriasian bauxite deposits of Oradea share with Galve the presence of large theropods, *Megalosaurus*, *Valdosaurus*, *Iguanodon* and *Hypsilophodon*, among others). It should be noted that some of these apparent faunal similarities result from imprecise taxonomy however, and some apparently widespread taxa (e.g., *Iguanodon*) are almost certainly 'taxonomic wastebins'.

5.3. Wider palaeobiogeographic comparisons

Many of the Galve vertebrates are widely distributed: the fishes, turtles, crocodyliforms and pterosaurs belong to taxa that were present throughout Europe in the Early Cretaceous, some of them also in North America. The dinosaur *Iguanodon* is also known throughout Europe, and with isolated remains reported from North America (though see above). The same is true for *Allosaurus* (whose remains are present in Portugal and North America), dromaeosaurid teeth (reported from different European localities) and *Hypsilophodon*, whose remains have been reported from Spain, England and Romania. Some of the other dinosaurs are so incomplete, that any names given, such as *Megalosaurus*, *Hypsilophodon*, or *Astrodon* should be used with caution — and certainly

should not be used as a basis for inferring ancient distributions.

Valdosaurus is known from Galve, as well as from the Wessex Formation of the Isle of Wright and the Hastings Beds Group of West Sussex, in Berriasian–Barremian sediments of Romania, and from the late Aptian El Rhaz Formation of Niger (Galton and Taquet, 1982). Of course, whether this one genus truly spanned the whole of the Early Cretaceous must remain doubtful. The spinosaurine and baryonychine teeth from the Camarillas Formation suggest a faunal link with the Early Cretaceous of North Africa, but the baryonychine teeth also provide a geographic link with *Baryonyx* from southern England.

The Galve sauropods, on the other hand, appear to be isolated holdover taxa, relatives of Late Jurassic forms that survived into the Early Cretaceous, and it is tempting to speculate that the Iberian Peninsula was home to some relict sauropod taxa. There are two eusauropods from Galve, *Aragosaurus ischiaticus* (Berriasian–late Hauterivian) and *Galveosaurus herreroi* (Tithonian–Berriasian), and another from the Oxfordian–Kimmeridgian of Portugal, *Lourinhasaurus alenquerensis* (Weishampel et al., 2004a,b; Sánchez-Hernández, 2005). These basal sauropods lived at the same time as derived sauropods elsewhere in the world. This might indicate some kind of geographic isolation, perhaps in some way linked to the existence of internal seas. This faunal isolation might also explain the relict mammal taxa, according to Krebs (1985) and Kielan-Jaworowska et al. (2004). These authors have emphasized the presence in Portugal, Asia and Mongolia of some taxa found in Galve.

These results are not surprising, and they confirm previous palaeogeographic studies. For example, in a cluster analysis of dinosaur faunas, Holtz et al. (2004) found similar results, although their listings of dinosaurian taxa from Galve were incomplete. They paired the Camarillas Formation closely with the Oradea bauxites, those two with the Arcillas de

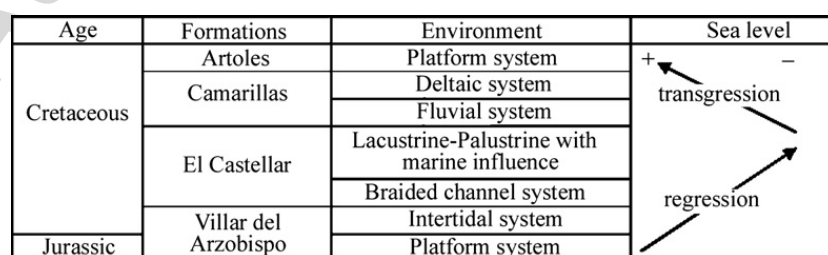| Age	Formations	Environment	Sea level
Cretaceous	Artoles	Platform system	+ −
	Camarillas	Deltaic system	transgression
		Fluvial system	
	El Castellar	Lacustrine-Palustrine with marine influence	
		Braided channel system	regression
Jurassic	Villar del Arzobispo	Intertidal system	
		Platform system	

Fig. 20. Cartoon showing the Upper Jurassic/Lower Cretaceous succession from Galve and relative sea level.

Morella fauna of Castellón, and those three in turn with a cluster of Wealden and other units from England and Spain. The Artoles Formation clustered closely with the Weald Clay of Surrey. The El Castellar Formation of La Rioja province though is found in two widely separated locations in their cluster analysis, pairing with a large cluster of mainly Late Jurassic localities from Portugal on the one hand, and with the Early Cretaceous Calizas de Lychnus, Burgos, Spain on the other. Such studies can give a spurious sense of exactitude, indeed especially when faunal lists are short, or determinations are uncertain. Nonetheless, Holtz et al. (2004) conclude that there was a single Europe-wide fauna of dinosaurs in the first half of the Early Cretaceous, extending from the Iberian Peninsula to Romania, and showing strong affinities with many North American faunas from the Midwest. The Iberian Peninsula shows some evidence of differentiation of dinosaurian faunas in the Late Jurassic and Late Cretaceous, according to their study.

6. Geological history

The geological history of the Galve area was controlled by a regression in the Late Jurassic, followed by an Early Cretaceous transgression (Fig. 20). The fully marine (platform) sediments of the lower Villar del Arzobispo Formation pass up into intertidal deposits in the upper part of the unit. The overlying El Castellar Formation was deposited in braided channel systems in the lower part, but with lakes near the coast in the upper part. The top of the El Castellar Formation and bottom of the Camarillas Formation are composed of sediments deposited in a siliciclastic marginal lacustrine environment with distributary channels, shoreface lake-fringing marsh facies associations (upper part of the El Castellar Formation), and a mouth-bar delta (upper part of the Camarillas Formation, according to Díaz and Yébenes, 1987) which developed into a new platform environment (Artoles Formation) in the Aptian. In this last formation, as in the Cameros basin (Doublet et al., 2003), there are storm-dominated limy facies consisting of limestone beds alternating with open lacustrine marls and deltaic sandstones.

The five formations in the Galve area (Figs. 1, 2) extend widely over the region to the Iberian Range (Alvarado et al., 1983), and they may be correlated with equivalent units with dinosaur remains in other regions, such as the Oncala Group of the Cameros basin (Cuenca-Bescós et al., 1997) in Soria, Burgos and La Rioja provinces, or the Morella Formation of Valencia, the first Aptian deposits (Canerot et al., 1982). Alvaro et al. (1979) have interpreted four principal steps in the Celtiberic (NE of Spain) aulacogen evolution; the

deposits of the Galve syncline are included within the "Flexor Phase". The palaeogeographic history of the Galve region shows a transgression towards the SE, with Galve itself lying entirely under the sea in the Late Jurassic, near the shore in the Early Cretaceous, and just on land in the Mid Cretaceous.

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