Theropod dinosaurs from the Upper Cretaceous of the South Pyrenees Basin of Spain

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The dinosaur record in the South Pyrenees Basin is diverse and rich. A total of 142 theropod teeth were studied for this paper, which constitutes one of the richest samples for these remains in Europe. Eight upper Campanian to upper Maastrichtian outcrops from the Pyrenees produced six non-avian theropod taxa (Theropoda indet., Coelurosauria indet., ?*Richardoestesia*, ?Dromaeosauridae indet., ?*Pyroraptor olympius*, ?*Paronychodon*). These six taxa are added to two previously described theropods (a *Richardoestesia*-like form and a possible ornithomimosaurid), indicating that there was considerable theropod diversity on the Iberian Peninsula during the Late Cretaceous.

Key words: Dinosauria, Theropoda, teeth, Cretaceous, Spain, South Pyrenees.

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Introduction

On the Iberian Peninsula, few theropod teeth have been recovered in association with their cranial and postcranial skeletal remains. In southern Europe, isolated theropod teeth tend to be scattered amongst the remains of other dinosaurs, and have no relation to skeletal remains attributable to any defined theropod taxon (Buffetaut and Le Loeuff 1991). *Pyroraptor olympius* is an exception in that two isolated teeth were associated with postcranial skeletal remains (Allain and Taquet 2000). The vast majority of Upper Cretaceous (Campanian–Maastrichtian) theropod fossils in Europe consist of isolated teeth, and they provide the greatest potential for identifying which theropod taxa were present in the region.

The dinosaur record in the South Pyrenees Basin is rich, comprising 147 dinosaur sites that can be assigned to four time intervals from late Campanian to late Maastrichtian (López-Martínez 2003b). In this paper, teeth are used to identify the Upper Cretaceous theropod dinosaurs from this region. Laño is the richest site for theropod teeth in this area, and for the Upper Cretaceous of Europe. Outside of the South Pyrenees Basin, fewer than a dozen teeth have been found in the rest of Spain (Pol et al. 1992; Pereda-Suberbiola 1999b, Prieto-Márquez et al. 2000; Company 2004).

Institutional abbreviations.—AMNH, American Natural History Museum, New York, USA; DPM, Departamento de Paleontología de Madrid, Complutense University of Madrid, Spain; MCNA, Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Spain; MPZ, Museo Paleontológico, Universidad de Zaragoza, Zaragoza, Spain.

Other abbreviations.—FABL, fore-aft-basal length; PCA, principal components analysis.

Material and methods

Eight localities (from east to west: Laño in Treviño; Blasi 1, 2B and 3 in Huesca; Vicari 4, Montrebei, Figuerola 2, and Fontllonga 6 in Lleida) produced the 142 theropod teeth used in this study. Laño, the richest site, produced 120 of these teeth. The sample is relatively small, when compared with Upper Cretaceous North American sites, each of which can produce up to thousands of specimens (Currie et al. 1990;

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Farlow et al. 1991; Sankey 2001; Sankey et al. 2002; Samman et al. 2005; Smith 2005). However, for Europe, this is one of the largest Cretaceous theropod tooth samples that has been examined. Several publications (Csziki and Grigorescu 1998; Codrea et al. 2002; Laurent et al. 2002; Allain and Pereda-Suberbiola 2003; Smith et al. 2005) mention European theropod teeth without providing figures on their abundances. Where numbers are given, the sample varies from one to 58 (Buffetaut et al. 1986, 1988; Antunes and Sigogneau-Russell 1991, 1992; Sigé et al. 1997; Le Loeuff and Buffetaut 1998; Allain and Taquet 2000; Garcia et al. 2000; Laurent 2002; Lindgren et al. 2009; Ösi et al. 2010).

Theropod teeth were measured for this study using a Leica Wild M-10 stereo microscope. Measurements included: crown height, fore-aft-basal length (FABL), basal width of the crown, anterior denticle density, and posterior denticle density. The last two measurements were recorded as the number of denticles per millimeter, and were taken at the mid-heights of the carinae. Qualitative characteristics (such as the shape of a denticle) were noted, as these are often important in the identification of theropod teeth (Currie et al. 1990). For example, *Troodon* teeth have strongly hooked denticles, velociraptorine teeth have distally-hooked and sharply-pointed denticles, and dromaeosaurines and other theropods have denticles that are squared-off and chisel-like distally. The presence of longitudinal ridges was noted, as this is common in teeth attributed to *Paronychodon lacustris*.

Statistical analyses were carried out using SPSS 21.0 (IBM Corp. Released 2012. IBM SPSS Statistics for Windows, Version 21.0. Armonk, NY: IBM Corp.). A total of 650 teeth—representing 21 species and eleven families—were included in these analyses. Bivariate analyses of the Pyrenean sample and taxa were compared with a sample of a further 17 theropod species, largely from North America, but with some South American (*Aucasaurus*, *Mapusaurus*) and Asian (*Fukuiraptor*, *Tarbosaurus*) species. These analyses were performed to compare the relationship between tooth size and denticles per millimeter. Principal components analysis (PCA) was performed to separate the specimens according to the variance of the height, FABL, basal width, and denticle size. The data were log-transformed for the analyses.

Three discriminant analyses were performed on the log-transformed values of the Pyrenean sample to verify the preliminary assignments of the specimens. Analyses were carried out at both species and family level.

Geological setting

The Late Cretaceous theropod localities considered here are all located in the South Pyrenees Basin (Garrido Mejías and Ríos Aragües 1972), extending over some 1500 km from east (Provence, France) to west (Cantabrian Platform), with an average width of 200 km from north (Aquitaine Basin) to south (Ebro Basin). The eight sites have been dated by means of biostratigraphy using planktonic foraminifera, charophytes, pollen (Galbrun et al. 1993; López-Martínez et al. 1998; López-Martínez 2003a) and magnetostratigraphy (Galbrun et al. 1993; López-Martínez et al. 2006; Pereda-Suberbiola et al. 2009; Riera et al. 2009).

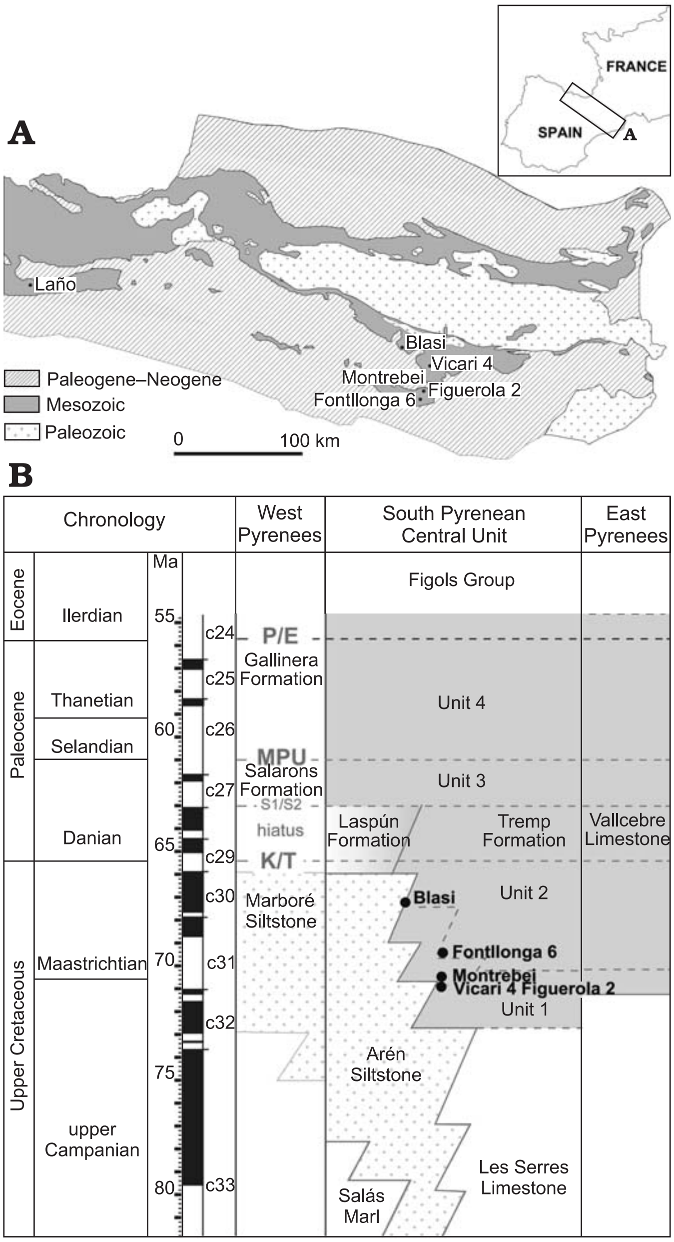

Fig. 1. **A**. Locations of the palaeontological sites of Laño, Vicari 4, Montrebei, Fontllonga 6, Figuerola 2, and Blasi. **B**. Correlation of the uppermost Cretaceous and lowermost Tertiary deposits in the southern Pyrenees, showing the stratigraphic levels of the studied localities. MPU, Mid-Paleocene unconformity; S1, S2, depositional sequences (Robador 2005).

The first site, where practically all the material has been found, is Laño in the Basque-Cantabrian Region. The Laño site (Fig. 1) is situated in an abandoned sand quarry within the Condado de Treviño, 25 km south of the city of Vitoria-Gasteiz (Alava province). This quarry is on the south flank of the Sub-Cantabrian Synclinorium, a great structure composed mostly of Upper Cretaceous and Palaeogene deposits that extend more than 100 km from east to west (Astibia et al. 1987, 1990; Baceta et al. 1999). Most of the vertebrate fossils have been recovered from upper Campanian–lower Maastrichtian siliciclastic rocks in three beds, known as L1A, L1B, and L2. These beds are part of a Late Cretaceous alluvial system composed mainly of fluvial sand and silt, interpreted as channel deposits of an extensive braided river system (Astibia et al. 1990). Unusually, the fossiliferous beds are associated with iron crusts, and the fossil bones are often covered by iron oxides (Elorza et al. 1999; Pereda-Suberbiola et al. 2000). Laño has yielded a diverse continental vertebrate assemblage, which consists of nearly 40 species of actinopterygians, lissamphibians, lepidosaurs, turtles, crocodyliforms, dinosaurs, pterosaurs, and mammals. In addition to theropods, other dinosaurs include the titanosaurian sauropod *Lirainosaurus astibiae* (Sanz et al. 1999; Díez Díaz et al. 2011, 2012), the ornithopod *Rhabdodon* (Pereda-Suberbiola and Sanz 1999) and the ankylosaur *Struthiosaurus* (Pereda-Suberbiola 1999a).

The seven other sites are in the Montsec Thrust sheet (Tremp Syncline in the north, Tremp-Graus Basin) and the Sierras Marginales Thrust sheet (Ager Syncline in the south). The Montsec Thrust separates these two structures. In both synclines, the Cretaceous–Tertiary transition is represented by red-bed deposits of the Tremp Formation (Mey et al. 1968; López-Martínez et al. 1998, 1999; Riera et al. 2009). Two of the sites are in the Ager Syncline at the base of Unit 2; Figuerola 2 is late Campanian in age, and Fontllonga 6 is early Maastrichtian (López-Martínez et al. 1998). The rest of the sites are in the Tremp Syncline. Vicari 4 and Montrebei are found at the base of the Tremp Formation near the contact with the Arén Sandstone; the age of Vicari 4 is late Campanian, and Montrebei is latest Campanian to basal Maastrichtian (Vicens et al. 2001). Blasi 1 is in the Arén Formation, and Blasi 2B and 3 in the Tremp Formation; all three are late Maastrichtian (López-Martínez et al. 2001; López-Martínez 2003b; Pereda-Suberbiola et al. 2009; Fig. 1).

The Figuerola 2 fossiliferous level consists of 2.5 m of grey marl, upon which is superimposed a layer of 0.5 m made up exclusively of oncolites. Above this layer there is 4.5 m of grey marl. In the marl, bone fragments, scales of bony fish, ray teeth, dinosaur eggshells, and theropod teeth have been found. At the Fontllonga 6 site, theropod teeth appear in a level composed of 1.8 m of grey marl with yellowish and brownish alterations. Fossil remains are found covered with carbonate crusts and oncolitic layers.

Montrebei and Vicari 4 theropod teeth are found in thin levels (0.5 m) of dark marl that is rich in organic matter associated with fish teeth and scales, crocodile teeth, and eggshells.

Blasi 2B occurs in a 6.5 m thick interval of grey marl that overlie the sandstone of Blasi 1. Nearly 5000 kg of sediment have been washed, resulting in the extraction of vertebrate microfossils (fish, amphibians, squamates, and turtles), including some dinosaur teeth (theropods, hadrosaurids) and eggshell fragments. Plant debris, charophytes and gastropods are common (López-Martínez et al. 2001; Blain et al. 2010). Two hadrosaurids have been described in the Blasi section—*Blasisaurus* in Blasi 1 (Cruzado-Caballero et al. 2010) and *Arenysaurus* in Blasi 2 (Pereda-Suberbiola et al. 2009).

The sedimentological interpretations of these formations and their relationships are complex. Several authors have supported a model of barrier islands and coastal lagoons for the formation of these deposits (Nagtegaal et al. 1983; Diaz-Molina 1987; Diaz-Molina et al. 2007). According to this model, longitudinal platform currents would have built a barrier island that became the Arén Sandstone deposits. After that, Tremp Formation deposits were formed in lagoons protected from the waves. At the top of the Arén Sandstone, palaeosols, ferruginous encrustations and nodules are commonly found, which implies that the Tremp Formation marly sediments did not form until after a period of emersion and subaerial exposure of the barrier island (Díaz-Molina 1987) (Fig. 1).

Systematic palaeontology

Dinosauria Owen, 1842

Saurischia Seeley, 1888

Theropoda Marsh, 1881

Theropoda indet.

Fig. 2A, D–H.

Material.—There are thirteen large, isolated theropod teeth from Blasi 1, 2B, and 3, Laño, and Montrebei (upper Campanian–upper Maastrichtian) that can be separated into two morphotypes. Morphotype 1: two teeth (MPZ2004/3 and 4/4) from Blasi 1, one tooth (MPZ2004/5) from Blasi 2B, and two teeth (MPZ2004/8 and 98/67) from Blasi 3); four teeth (MCNA 22051, 4520, 14521, and 1852) from Laño (lateral equivalent of Sedano Formation, upper Campanian–lower Maastrichtian); one tooth (DPM-MON-T10) from Montrebei (Tremp Formation, upper Campanian–lower Maastrichtian) (Fig. 2E–H; SOM: Table 1 [Suplementary Online Material available at http://app.pan.pl/SOM/app60-Torices_etal_SOM.pdf]). Morphotype 2: one tooth (MPZ98/68) from Blasi 1 and two teeth (MCNA 1853, 14522) from Laño (Fig. 2A, D; SOM: Table 1).

Description

Morphotype 1.—Teeth have crowns whose height varies between 18 and 62 mm, FABL between 11 and 27 mm, and basal widths between 4.4 and 13 mm. Their carinae have large rectangular denticles. Their anterior denticle densities vary between 2 and 5 denticles/mm, and posterior denticle densities range between 2 and 3 denticles/mm. The largest anterior and posterior denticles are more or less the same size, although the anterior ones tend to be a bit smaller than the posterior ones. The teeth are vertically elongate with straight or slightly curved borders in lateral view.

Variation in tooth morphology along the jaw has been observed in theropods and there is a tendancy towards increased labiolateral compression towards the posterior regions of the

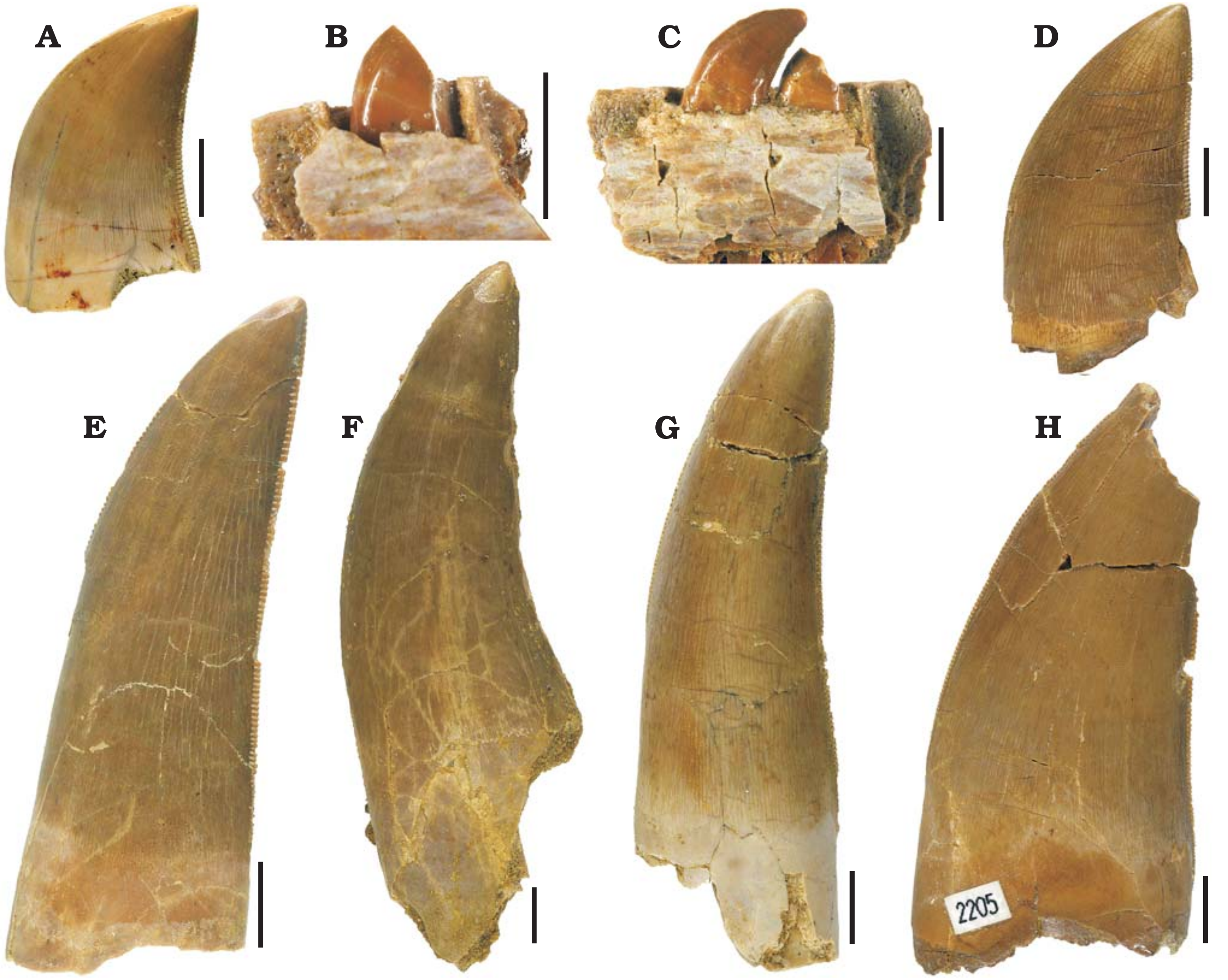

Fig. 2. Theropod dinosaurs teeth from upper Campanian–lower Maastrichtian, Laño. **A**, **D**. Theropoda indet. Morphotype 2. **A**. MCNA 14522. **D**. MCNA 1853. **B**, **C**. ?*Pyroraptor olympius* Allain and Taquet, 2000. **B**. MCNA 14623. **C**. MCNA 14624. **E**–**H**. Theropoda indet. Morphotype 1. **E**. MCNA 1852. **F**. MCNA 14520. **G**. MCNA 14521. **H**. MCNA 2205. All lateral views. Scale bars 5 mm.

jaws (Currie et al. 1990; Smith 2005; Reichel 2010). Some Morphotype 1 teeth have rounded cross-sections that may indicate that they are from anterior positions in the jaws.

Morphotype 2.—Teeth are smaller (between 20 and 24 mm) than those of Morphotype 1 (although there is slight overlap between the ranges) and are strongly curved. Their FABLs are 12 and 13 mm, and their basal widths are 6.2 and 7.3 mm. Their denticles have the same morphologies as Morphotype 1. Anterior denticle density is 4 denticles/mm and posterior denticle density is 3 denticles/mm.

Discussion

Morphotype 1.—In Europe, several large theropods (including abelisaurids and megalosaurids) have been described from Upper Cretaceous sites (Le Loeuff and Buffetaut 1991; Le Loeuff 1992; Pereda-Suberbiola 1999b; Pereda-Suberbiola et al. 2000). Remains attributed to Megalosauridae (teeth and a radius) have been described in Portugal and Spain, but this fragmentary material is probably not diagnostic enough to classify at family level (Pereda-Suberbiola 1999b).

The only species of large theropod defined for the Late Cretaceous of Europe is, at the moment, *Tarascosaurus salluvicus* from Var (southern France), which is represented by two dorsal vertebrae and a femur (Le Loeuff and Buffetaut 1991). This taxon is probably an abelisauroid (Carrano and Sampson 2008) but it was considered a nomen dubium by Allain and Pereda-Suberbiola (2003). In Laño, this taxon was identified on the basis of two femora by Le Loeuff and Buffetaut (1991) and Le Loeuff (1992), and afterwards it has subsequently been referred to Neoceratosauria indet. (Pereda-Suberbiola 1999b; Pereda-Suberbiola et al. 2000).

Abelisauroidea, the clade to which *Tarascosaurus* belongs (Le Loeuff and Buffetaut 1991; Le Loeuff 1992), is characteristic of the late Mesozoic of Gondwana (Sereno et al. 2004); they could have reached Europe during the Early Cretaceous (Pereda-Suberbiola 2009) or even during the Jurassic as recently suggested (Ezcurra and Agnolin 2012; see Pol and Rauhut 2012; Rauhut 2012 for a different interpretation). *Camarillasaurus cirugedae* (Barremian; Sánchez-Hernandez and Benton 2014), *Genusaurus sisterornis* (Albian;

Accarie et al. 1995), *Tarascosaurus salluvicus* (Campanian), *Betasuchus bredai* (Maastrichtian) and other taxa not formally named from the Campanian–Maastrichtian (Buffetaut and Le Loeuff 1991; Allain and Pereda-Suberbiola 2003) indicate the presence of multiple ceratosaur lineages (including abelisauroids) in Europe through the end of the Cretaceous (Carrano and Sampson 2008). According to Allain (1998), European species could represent an independent line of ceratosaurs that evolved in isolation.

Neoceratosaurs are known from the Late Jurassic to the latest Cretaceous (Carrano et al. 2002; Sereno et al. 2004; Carrano and Sampson 2008) in other parts of the world, and include both small sized theropods (such as *Masiakasaurus*, which is 1.8–2 m in total length; Carrano et al. 2002) and large ones (such as *Carnotaurus* at 7.5 m, Bonaparte et al. 1990; and *Majungatholus* at 6–7 m, Krause et al. 2007). Allain et al. (2007) described the neoceratosaur *Berbesaurus liassicus* from the Jurassic of Morocco, but not everyone agrees with its classification (Carrano and Sampson 2008; Xu et al. 2009).

Morphotype 1 teeth, unlike those of neoceratosaurs, lack ornamentation in the tooth enamel. Ornamentation in the form of wrinkles in the enamel is also commonly found in theropods like basal tetanurans, carcharodontosaurids and some tyrannosaurids (Brusatte et al. 2007). With the exception of two teeth that are assigned to *Daspletosaurus* and *Dilophosaurus*, Morphotype 1 teeth group in their own category in the discriminant analysis at generic/species level (SOM: Table 2). At family level, only one of the teeth grouped with the Neoceratosauridae, whereas most of the other Morphotype 1 teeth showed stronger affinities to Tyrannosauridae. The statistically uncertain affinities of Morphotype 1 teeth suggests that they should be identified only as indeterminate theropods until diagnostic postcranial material is found associated with the teeth.

Morphotype 2.—Teeth are shorter than those classified as Morphotype 1 and have more strongly curved crowns. However, measurements of the denticles are similar to those of Morphotype 1, and these teeth could belong to the same taxon. Heterodonty in large theropods is widespread enough to encompass these two morphotypes in the same taxon (Smith 2005; Reichel 2010). It is also possible that Morphotype 2 could represent the juveniles of Morphotype 1. The curvatures of Morphotype 2 crowns are similar to those of the juveniles of *Tyrannosaurus rex* described by Baszio (1997: pl. 7: 94, 96, 101), whereas adult *Tyrannosaurus rex* teeth are more similar to Morphotype 1.

Statistically, Morphotype 2 groups on its own in the discriminant analyses at species level (SOM: Table 2). At family level, the analysis reassigned the three teeth to Neovenatoridae (Benson et al. 2010). This clade is formed by some problematic allosauroids that survived into the Cretaceous. The appearance of this clade in the Late Cretaceous of Europe would have interesting palaeobiogeographic implications because the only known Late Cretaceous neovenatorid is from South America. However, until more diagnostic material is found, these teeth should more conservatively be referred to as indeterminate Theropoda.

Coelurosauria Huene, 1914

Coelurosauria indet.

Material.—Fifty isolated teeth: MPZ98/79–82 from Blasi 2B (Tremp Formation, late Maastrichtian); MCNA 14523–14565 from Laño (lateral equivalent of Sedano Formation, upper Campanian–lower Maastrichtian); DPM-MON-T3, T6 from Montrebei (Tremp Formation, upper Campanian–lower Maastrichtian); DPM-VIR4-T5 from Vicari 4 (Tremp Formation, upper Campanian) (Fig. 3M–P; SOM: Table 1).

Description.—The indeterminate coelurosaurian teeth are small and lack denticles. Height varies between 1.5 and 8.1 mm. The anterior carina of each is convex, whereas the posterior one is concave in lateral view.

The most prominent features of the indeterminate coelurosaurian teeth are their small sizes and the absence of denticles. Similar teeth are known from several European and North American sites. Teeth with similar characteristics from the Hateg Basin were classified as indeterminate theropods (Antunes and Sigogneau-Russell 1991; Pol et al. 1992; Csiki and Grigorescu 1998; Garcia et al. 2000; López-Martínez et al. 2001; Grigorescu 2003).

Discussion.—Coelurosauria is a large clade that includes many non-avian and avian theropod families. Most Cretaceous forms are small (under 2 m long), although some (some ornithomimids, most tyrannosauroids, and several dromaeosaurids) reached large sizes (Turner et al. 2007; Zanno and Makovicky 2013). Amongst small theropods, there are genera with distally curved teeth that do not have denticles and are similar to those from Blasi 2B. These genera include the ornithomimosaur *Pelecanimimus* (Pérez-Moreno et al. 1994), troodontids like *Byronosaurus* and *Mei* (Norell et al. 2000; Xu and Norell 2004), alvarezsaurids like *Mononykus* and *Shuvuuia* (Chiappe et al. 1998; Suzuki et al. 2002), and Mesozoic birds with teeth (Chiappe et al. 2002). Differentiation can be difficult, although in birds there is a constriction at the base of the crown (Sankey et al. 2002) that it has not been observed in any of the teeth in this study.

Statistically, these teeth grouped together in all three discriminant analyses (SOM: Table 2), although some specimens grouped with *Paronychodon* because of similarities in size. However, they lack the characteristic longitudinal ridges of *Paronychodon*.

Family indet.

Genus *Paronychodon* Cope, 1876

Type species: *Paronychodon lacustris* Cope, 1876; Montana, USA; Campanian.

?*Paronychodon* sp.

Fig. 3Q.

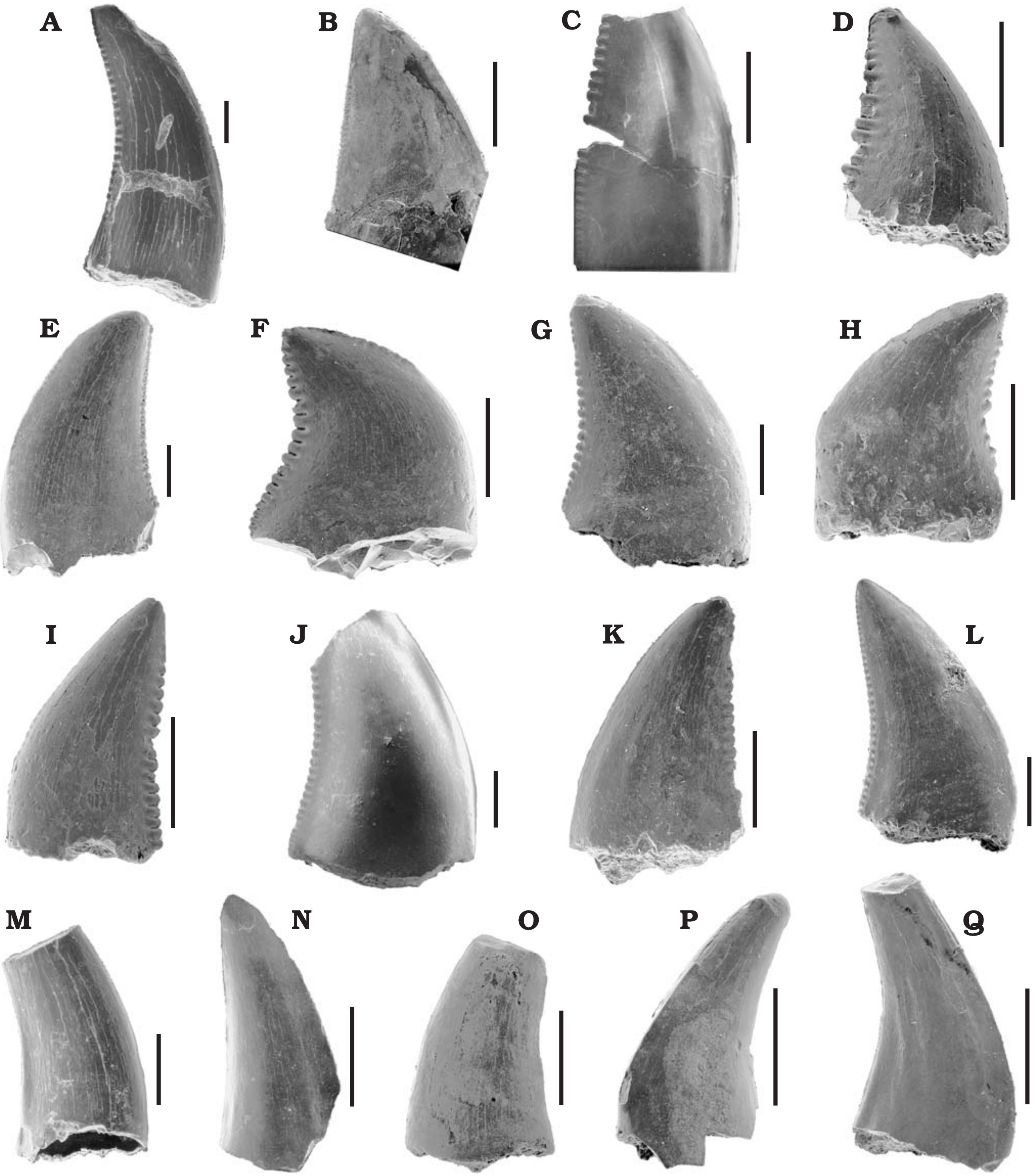

Fig. 3. Theropod dinosaurs teeth from upper Campanian–Upper Maastrichtian, Spain. **A**. ?*Pyroraptor olympius* Allain and Taquet, 2000, DPM-MON-T1, Montrebei. **B**, **C**. ?Dromaeosauridae indet. **B**. MPZ2004/6, Blasi 2B. **C**. DPM-FON6-T2, Fontllonga 6. **D**–**L**. ?*Richardoestesia* sp., Laño. **D**. MCNA 14610. **E**. MCNA 14607. **F**. MCNA 14606. **G**. MCNA 14608. **H**. MCNA 14609. **I**. MCNA 14611. **J**. MCNA 14568. **K**. MCNA 14607. **L**. MCNA 14619. **M**–**P**. Coelurosauria indet. **M**. DPM-MON-T6, Montrebei. **N**. DPM-MON-T3, Montrebei. **O**. MPZ98/80, Montrebei. **P**. MPZ98/82, Blasi 2B. **Q**. ?*Paronychodon* sp., MPZ98/76, Blasi 2B. All lateral views. Scale bars 1 mm.

1991 *Euronychodon portucalensis* Antunes and Sigogneau-Russell, 1991: 118–119, fig. 15A.

2001 cf. *Euronychodon* sp.; López-Martínez et al. 2001: 49, 51, fig. 9B, C, D.

2004 cf. *Euronychodon* sp.; Torices et al. 2004: 72–73.

Material.—Three teeth (MPZ98/76–78) from Blasi 2B (Tremp Formation, late Maastrichtian) (Fig. 3Q; SOM: Table 1).

Description.—*Paronychodon* teeth are relatively tall, elongate and curve gently (Currie et al. 1990). Usually, the pos-

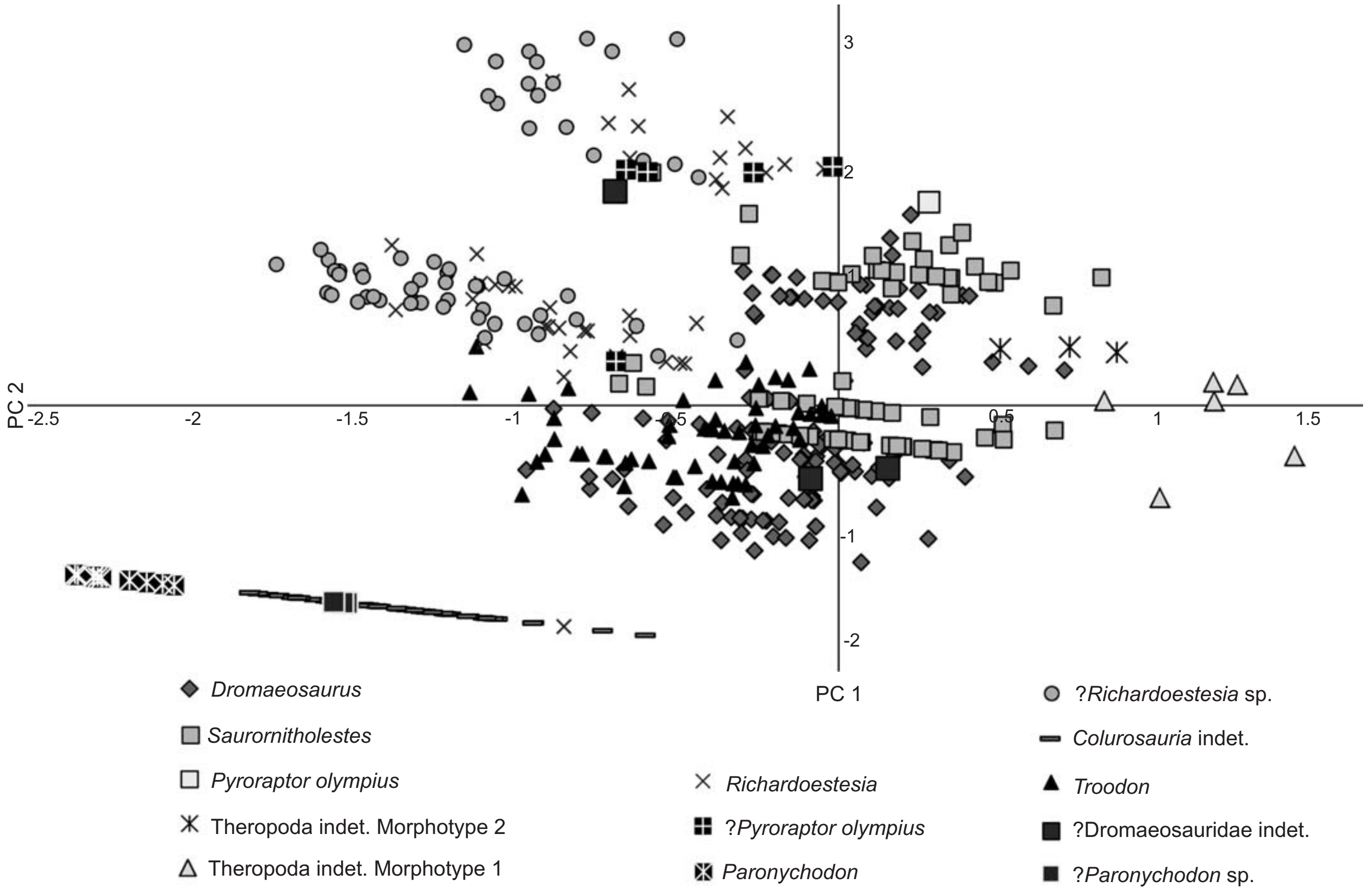

Fig. 4. Principal component analysis of the South Pyrenees Basin sample and the Royal Tyrrell Museum of Palaeontology sample; a chart displaying two first principal components, PC1 and PC2.

terior carina is more or less straight and the anterior one is convex in lateral view, but both carinae can be convex. The enamel is sometimes folded, and three or more longitudinal ridges appear on one or both flanks of the teeth. Denticles are never present (Currie et al. 1990).

Three teeth from Blasi 2B are referred to ?*Paronychodon* sp. They have similar measurements and morphological characteristics to the ones described as Coelurosauria indet. They are small, and their heights are less than 3 mm, their FABL varies between 1.21 and 1.49, and their basal widths range between 0.60 and 0.84. They lack denticles on their anterior and posterior carinae, but longitudinal ridges can be observed on the labial and lingual sides of their crowns.

Discussion.—*Paronychodon* is an enigmatic theropod taxon that has teeth ornamented with longitudinal ridges (Canudo and Ruiz-Omeñaca 2003). The position of this genus within Theropoda is uncertain. There is no clear reason to assign it to Dromaeosauridae, as Antunes and Sigogneau-Russell (1991) tentatively suggested. On the other hand, the assignment of *Paronychodon* (as a nomen dubium) to Troodontidae by Osmólska and Barsbold (1990) and Makovicky and Norell (2004), is probably based on the slight constriction between crown and root; this is insufficient because this character can be found in other theropods (Zinke and Rauhut 1994), in toothed birds (Currie 1987), and in some other vertebrates, such as crocodyliforms. Rauhut and Zinke (1995) suggested that *Paronychodon* teeth can be attributed to *Pelecanimimus*, but this seems unlikely (Rauhut 2002). Rauhut (2002) proposed that they could belong to birds. The longitudinal ridges in *Paronychodon* teeth have been attributed to growth abnormalities (Currie et al. 1990). Other authors consider them normal and refer "paronychodontids" to primitive maniraptoriform theropods, as close relatives of troodontids, ornithomimosaurs, or even birds (Zinke and Rauhut 1994; Csiki and Grigorescu 1998; Rauhut 2002).

Teeth from our sample are similar to *Paronychodon lacustris* from the Upper Cretaceous of North America that have been classified as *Paronychodon lacustris* (Currie et al. 1990) and group together perfectly (Fig. 4). They are also similar to a Portuguese tooth classified as *Euronychodon portucalensis* (Antunes and Sigogneau-Russell 1991). Other similar teeth have been identified as cf. *Paronychodon* or cf. *Euronychodon* in French, Romanian, and Spanish sites.

North American teeth of *Paronychodon* are indistinguishable from *Euronychodon*, so it is probable that *Euronychodon* is a synonym (Rauhut 2002). Pyrenean teeth previously classified as cf. *Euronychodon* (Torices et al. 2004) are therefore renamed here as ?*Paronychodon*.

Statistically, these teeth grouped consistently in all three discriminant analyses. Although one specimen grouped with indeterminate coelurosaurians because of similar size, its assignment is certain because of the presence of longitudinal ridges in its enamel (SOM: Table 2).

Family indet.

Genus *Richardoestesia* Currie, Rigby, and Sloan, 1990

Type species: *Richardoestesia gilmorei* Currie, Rigby, and Sloan, 1990; Dinosaur Provincial Park; Campanian.

?*Richardoestesia* sp.

Fig. 3D–L.

2003 Dromaeosauridae indet. 4; Torices 2002: 141.
2004 cf. Dromaeosauridae morphotype 8; Torices et al. 2004: 73.
2004 cf. Dromaeosauridae indet. 4; Torices et al. 2004: 73.
2005 Maniraptoriformes indet.; Canudo et al. 2005: 34.

Material.—Four teeth (MPZ98/72–74, 2004/7) from Blasi 2B (Tremp Formation, late Maastrichtian); sixty-four isolated teeth (MCNA 14566–14621) from Laño (lateral equivalent of Sedano Formation, upper Campanian–lower Maastrichtian); two teeth (DPM-MON-T5, T9) from Montrebei (Tremp Formation, upper Campanian–lower Maastrichtian); two teeth (DPM-VIR4-T6, T7) from Vicari 4 (Tremp Formation, upper Campanian) (Fig. 3D–L; SOM: Table 1).

Description.—*Richardoestesia* specimens are small theropod teeth (crown height between 1.4 and 5.1 mm, FABL between 1 and 5.1 mm, and basal width between 0.4 and 2.2 mm) with posterior denticle densities between 6 and 11.4 denticles/mm. Sixteen of the sixty four specimens have anterior denticles that are smaller than the posterior ones, and with densities between 8.1 and 16.3 anterior denticles/mm. Denticles are small and rectangular. In some of the teeth, it is possible to see that the posterior denticles are tilted slightly towards the apices of the teeth, which is characteristic of the genus *Richardoestesia.*

The morphologies of the teeth have great variability, from teeth with convex anterior borders and concave posterior borders to teeth with convex anterior borders and straight posterior borders. In some teeth, both edges are slightly convex, and the teeth resemble isosceles triangles.

The four specimens of *Richardoestesia* from the Blasi 2B site have almost straight (slightly biconvex) carinae, and compressed basal sections (basal widths are about half their FABLs). The tips of three of the teeth are broken and one of them is slightly worn, and their roots are not preserved. Their denticles are rectangular.

The two specimens from Montrebei have convex anterior borders and straight posterior ones. They are compressed lateromedially and their basal widths are nearly half of the corresponding FABLs. The tips show wear that in DPM-MON-T5 affects the anterior carina, and there is some breakage affecting the posterior carina in both teeth. The density of posterior denticles ranges from 7.8 to 9 denticles/mm. The morphology of each denticle is rectangular. Only DPM-MON-T9 has denticles on the anterior carina that are smaller than the posterior ones; the density is 11.5 anterior denticles/mm. The morphology of each anterior denticle is also rectangular in lateral view, but the denticles are only found on the apical half of the carina.

The material from Vicari 4 consists of one entire tooth, and the apex of another. The complete tooth has a convex anterior carina and a concave posterior one in lateral view. Both teeth are laterally compressed with basal widths that are about half of the FABLs. Posterior denticle density is 9.5 denticles/mm. The morphology of each denticle is rectangular, and some of them (including DPM-VIR4-T7) do not show any wear.

The 56 teeth of Laño constitute most of the *Richardoestesia* sample. They consist of complete teeth and fragments that retain only the middle parts of the teeth, the apices, or the posterior carinae. They all have denticles on the posterior carinae, with densities between 6.5 and 11.4 denticles/mm. In sixteen of the specimens, anterior denticles are also present, with densities between 8.1 to 16.3 denticles/mm. The shape of each posterior denticle is rectangular, and in some cases a slight tilt toward the apex of the tooth can be observed. The morphology of each anterior denticle is also rectangular, but its overall size is much smaller than an equivalent posterior denticle. The morphologies of the tooth crowns cover the three types: (i) biconvex teeth; (ii) teeth with convex anterior carinae and straight posterior ones; and (iii) teeth with convex anterior carinae and concave posterior ones. Those with strongly concave posterior borders are usually lower in height than those with straight edges, which are more elongate vertically. The lower heights suggest that this morphology may represent posterior maxillary or posterior dentary teeth.

Teeth identified as *Richardoestesia* in the Royal Tyrrell Museum of Palaeontology (Drumheller, Canada) collections were measured. The height varies from 2.5 to 10.8 mm, the FABL varies between 1.37 and 4.67 and basal width ranges from 0.66 to 2.83 mm. Denticle densities vary from 5 to 12.5 posterior denticles/mm, and 5 to 10 anterior denticles/mm when anterior denticles are present. Each of these measurements overlap perfectly with those of the Pyrenean sample (Figs. 4 and 5).

Discussion.—The morphologies and measurements of many Spanish specimens fall within the ranges of variability of teeth from North America that are identified as *Richardoestesia* (Currie et al. 1990) (Figs. 4 and 5). *Richardoestesia gilmorei* was described by Currie et al. (1990) on the basis of a pair of lower jaws containing a replacement tooth. Isolated teeth were assigned to this species based on the characteristics of the denticles, particularly their small size. *Richardoestesia* denticles are the smallest seen in any of the small theropods from the Upper Cretaceous. Usually they do not have anterior denticles, but when present, they are even tinier than the posterior denticles.

In *Richardoestesia* collections from the Late Cretaceous of Canada and the USA, various researchers (Currie et al. 1990; Baszio 1997; Sankey et al. 2002) have observed two different morphologies: (i) tall and straight teeth, and (ii)

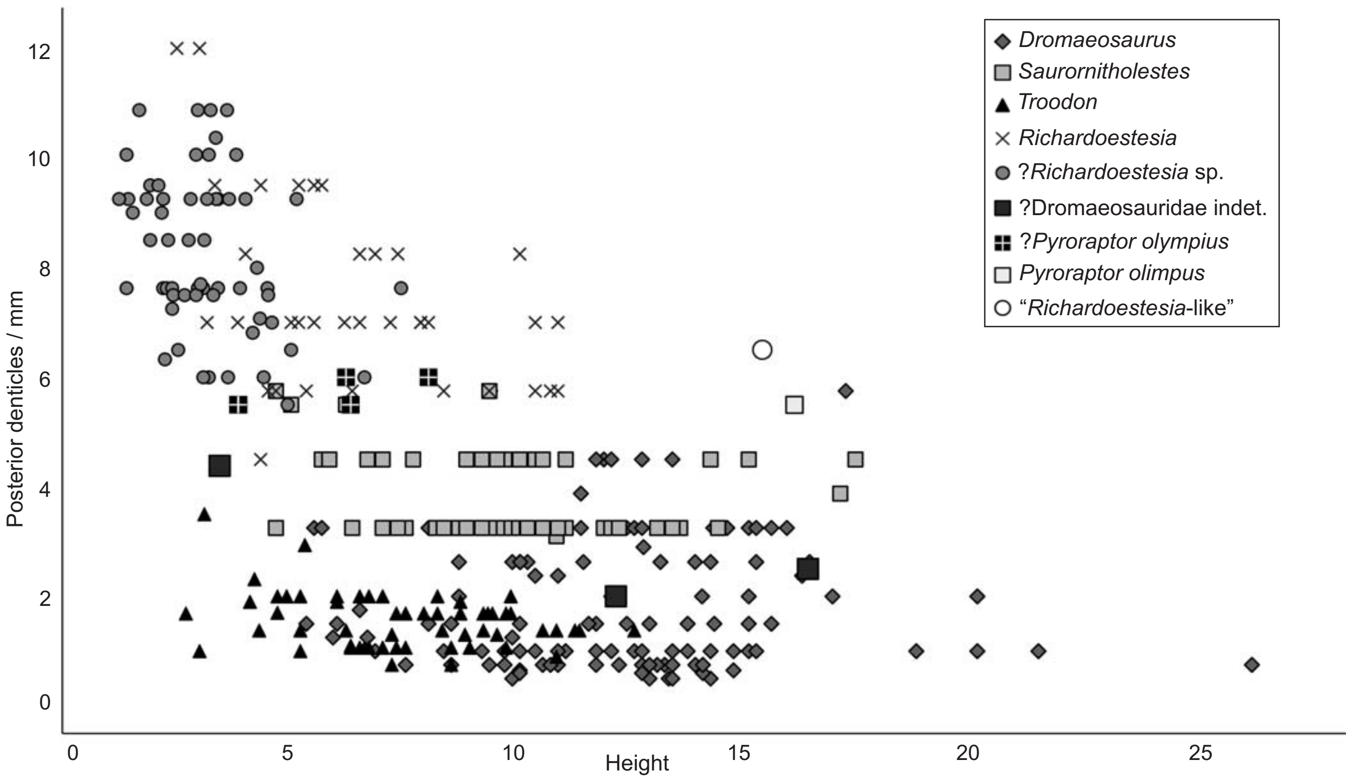

Fig. 5. Bivariate analysis comparing height (in mm) against posterior denticles per millimeter, ?Dromaeosauridae, ?*Pyroraptor olympius*, and ?*Richardoestesia* from the South Pyrenees area are compared against a sample of *Dromaeosaurus*, *Saurornitholestes*, *Richardoestesia*, and *Troodon* from the collections of the Royal Tyrrell Museum of Palaeontology, the *Richardoestesia*-like tooth from the site of Suterranya, Catalonia, Spain (Prieto-Márquez et al. 2000) and *Pyroraptor olympius* Allain and Taquet, 2000 from Provence (Ronan Allain, personal communication 2013).

shorter and curved teeth. Currie et al. (1990) considered the possibility that these two morphologies represent positional variation along the dental series, with the straighter ones coming from the anterior parts of the jaws. However, they also alluded to the possibility that the two morphotypes represented two different taxa. Baszio (1997) preferred the latter option, and he distinguished the straight teeth as a distinct species (*Richardoestesia* sp.) that Sankey (2001) named *Richardoestesia isosceles*. The latter paper also recognizes differences in the morphologies of the denticles between *Richardoestesia gilmorei* and *Richardoestesia isosceles*. The denticles of *Richardoestesia isosceles* are more square and lack interdenticular spaces (Sankey et al. 2002). Although *Richardoestesia gilmorei* and *Richardoestesia isosceles* form two distinct morphological groups, they are not distinguishable from each other when considering variables such as crown height and FABL. In principle, the differences in the general morphology of the tooth that Baszio (1997) used to distinguish *Richardoestesia* sp. teeth from those of *Richardoestesia gilmorei* are not sufficient proof because morphological variability within even a single theropod jaw can be remarkable (Smith 2005, Reichel 2010). Company et al. (2005) proposed that *Richardoestesia isosceles* might be a ziphodont crocodyliform.

Teeth identified as cf. *Richardoestesia* have been recovered from the Upper Jurassic of Portugal, the Lower Cretaceous of Spain (Zinke 1998; Rauhut 2002) and the Upper Cretaceous of Romania (Codrea et al. 2002; Weishampel et al. 2010). The measurements and morphological characteristics of the teeth and their denticles are also perfectly compatible with those in the Spanish sample from the Upper Cretaceous.

A tooth from L'Abella in the Upper Cretaceous of the Pyrenees was referred to as *Richardoestesia*-like (Prieto-Márquez et al. 2000). This tooth has a FABL of 3.1 mm and a posterior denticle density of 7 denticles/mm. The anterior edge is broken, so it is impossible to know whether or not it possessed anterior denticles. The denticles are rectangular. It is a taller tooth (15.3 mm) than the rest of the specimens assigned to the genus (the average height is 4.9 mm) (Fig. 5). In the discriminant analysis performed, this tooth is clearly isolated by its height from both the North American and Pyrenean samples (SOM: Table 2), which suggests it might be a new taxon.

Dromaeosauridae Matthew and Brown, 1922

Genus *Dromaeosaurus* Matthew and Brown, 1922

Type species: *Dromaeosaurus albertensis* Matthew and Brown, 1922; Red Deer River, Campanian.

?Dromaeosauridae indet.

2002 Dromaeosauridae indeterminate 2; Torices 2002: 141.
2004 cf. Dromaeosauridae morphotypes 2, 5 and 6; Torices et al. 2004: 73.
2005 Maniraptoriforme indet.; Canudo et al. 2005: 34.

Material.—Four specimens: MPZ2004/6 from Blasi (Arén Formation, upper Maastrichtian); MCNA 14622 from Laño (lateral equivalent of Sedano Formation, upper Campanian–lower Maastrichtian); DPM-FON6-T2 from Fontllonga 6 (Tremp Formation, lower Maastrichtian); DPM-FIG2-T1+T2 from Figuerola 2 (Tremp Formation, upper Campanian) (Figs. 3B, C, SOM: Table 1).

Description.—The measurements of the teeth of indeterminate dromaeosaurids vary from a minimum crown height of 3.4 mm (as estimate from a broken specimen) to 17.5 mm, FABLs of 2.6 to 16 mm, and basal widths between 1.3 and 5.8 mm. Crown shapes in lateral or medial views correspond to two types: (i) biconvex borders or (ii) a convex anterior border and a straight posterior one. These laterally compressed teeth have denticulate carinae. Denticle densities vary between 3.5 to 8.1 anterior denticles/mm and 2.5 to 4.9 mm posterior denticles/mm. The denticles are rectangular, slightly rounded and chisel-like (Currie et al. 1990).

The indeterminate dromaeosaurid from Laño consists of only the tip of a tooth that has a convex anterior border and straight posterior one. Denticle densities are 8.1 anterior denticles/mm and 4.9 posterior denticles/mm.

The specimen from Fontllonga 6 is biconvex in morphology and has large denticles with a density of 3 posterior denticles/mm. The tooth from Figuerola 2 lacks enamel, although it is possible to see traces of the denticles and measure their density (2.5 posterior denticles/mm).

The teeth from Blasi have convex anterior borders and straight posterior ones. Their anterior denticle densities vary between 3.5 and 5 denticles per millimeter, whereas their posterior denticle densities vary between 2.9 and 3 denticles/mm.

Discussion.—All *Dromaeosaurus* teeth in the collections of the Royal Tyrrell Museum of Palaeontology and those from the holotype (AMNH 5356) of *Dromaeosaurus albertensis* Matthew and Brown, 1922 were measured. The height of the teeth of this sample varies between 5.33 and 26 mm, FABL varies between 2.17 and 8.83, and basal width ranges from 1.67 to 9.17. Anterior denticle density is 1 to 8.75 denticles/mm, whereas posterior denticle density is 1 to 6.25 denticles/mm. The measurements of the teeth from the Pyrenean sample fall within the ranges of these measurements and those described in the literature (Currie et al. 1990; Baszio 1997; Sankey et al. 2002). The rectangular, chisel-like morphologies of the denticles match those described for dromaeosaurids (Figs. 4, 5).

The discriminant analyses suggest that all teeth fall in the Dromaeosauridae; two of them are grouped with *Dromaeosaurus* teeth and one is placed with ?*Pyroraptor* teeth (SOM: Table 2). The last tooth was not identified as *Pyroraptor* because its denticles resemble the taller, narrower ones of dromaeosaurids than the lower, broader ones of *Pyroraptor*.

It should be noted, however, that there is a diagnostic characteristic of *Dromaeosaurus* that is not found in any of the Spanish teeth. The anterior carina of each tooth of *Dromaeosaurus* extends along the midline from the apex to mid-height of the tooth, and then twists onto the lingual surface (Currie et al. 1990). The absense of this feature in the Spanish teeth suggests that they cannot be assigned to the genus *Dromaeosaurus.* They are designated here as indeterminate dromeosaurid teeth.

Genus *Pyroraptor* Allain and Taquet, 2000

Type species: *Pyroraptor olympius* Allain and Taquet, 2000, Provence.

?*Pyroraptor olympius* Allain and Taquet, 2000

2002 Dromaeosauridae indeterminate 3; Torices 2002: 141–143.
2004 cf. Dromaeosauridae indeterminate Morphotype 3; Torices et al. 2004: 73.

Material.—Four teeth (MCNA 14623–14626) from the Laño (lateral equivalent of Sedano Formation, upper Campanian–lower Maastrichtian); one (DPM-MON-T1) from Montrebei (Tremp Formation, upper Campanian–lower Maastrichtian) (Figs. 2B, C, 3A)

Description.—The teeth assigned to ?*Pyroraptor olympius* are laterally compressed with convex anterior borders and concave posterior ones. Their heights vary between 3.8 and 8 mm, FABLs between 2.5 and 5.4 mm, and basal widths range between 1.4 and 2.4 mm. Anterior denticle densities vary between 8 and 9.8 denticles/mm and posterior denticle densities are 6 to 6.5 denticles/mm. The denticles are square.

Three of the teeth were found in situ within a dentary bone fragment and the other one was found isolated but in association with the dentary fragment (MCNA 14623–14626). In this fragment, it can be seen that the interdental plates are fused together, which is characteristic of dromeosaurids and has been observed in *Deinonychus*, *Dromaeosaurus*, and *Saurornitholestes* (Currie et al. 1990; Currie 1995). This character has also been observed in some larger theropods like carcharodontosaurids, megalosaurids and neovenatorids (Brusatte et al. 2008, 2012; Benson 2010). Characteristics of these teeth are similar to those of the dromaeosaur *Pyroraptor olympius* (Allain and Taquet 2002) in the density of denticles (6 posterior denticles/mm) and the square denticle morphology, so the probability is high that our sample could belong to the same taxon.

Discussion.—Statistically, the teeth from the Pyrenean sample grouped together with *Pyroraptor* teeth in the three discriminant analyses performed (SOM: Table 2).

Therefore, considering the characters that identify our sample as a dromaeosaurid, the similarity of morphological and numerical data to those of *Pyroraptor* teeth and the correct assignation by the discriminant analyses of our sample to *Pyroraptor*, these teeth are best identified as ?*Pyroraptor olympius*.

Results

Principal components analysis of the log-transformed data of the Pyrenean and North American samples indicates that two components explain the variance of the data (Fig. 4). PC1 shows a heavy loading in the tooth size variables (height, FABL, basal width) and PC2 shows a heavier loading in the denticle variables. Graphically the representation of the two components groups the different taxa with some overlap especially between *Dromaeosaurus*, *Saurornitholestes*, and *Troodon*. The rest of the taxa are grouped better allowing comparison of the two samples and helping the identification of the Pyrenean sample.

Bivariate analyses show that there is a strong correlation (significant at 0.01) between the five variables—crown height, fore-aft-basal length (FABL), basal width, posterior denticle density, and anterior denticle density. In Fig. 5, the relationship between tooth size, represented by crown height, and denticle size, represented by number of posterior denticles per millimeter, is shown for small theropods from the two samples. The different taxa are grouped with some overlap, especially between *Dromaeosaurus*, *Saurornitholestes*, and *Troodon*. In this case, the different morphology of their denticles is the key for their identification in spite of the overlapping of the numerical data.

The discriminant analyses gave poor results, correctly identifying only 58.5% of specimens at species level and 67.4% at family level. The reason for these poor results is the enormous amount of overlap between the teeth of large theropods (especially between tyrannosaurids). There is some overlap in the small theropods but to a lesser degree. The third discriminant analysis was performed for the Pyrenean sample, and this gave better results, with the percentage of correctly identified species as 79.2% (SOM: Table 2).

Discussion

Many newly discovered teeth from the Campanian–Maastrichtian of the South Pyrenees Basin significantly increase our knowledge about theropod diversity in the Iberian Peninsula at the end of the Cretaceous.

In this work, seven morphotypes of theropod teeth are identified from the South Pyrenees Basin. Two morphotypes of Theropoda indet. are separated in the discriminant analyses even though their denticle densities and denticle morphologies are nearly identical. The main difference between them is crown shape. Heterodonty has been observed in the jaws of large theropods (Smith 2005; Reichel 2010). Elongate, more rounded teeth characterize the anterior parts of the jaws, and shorter, more recurved teeth belong to the posterior parts (Smith 2005). For this reason, the most conservative approach would be to assign these two morphotypes to a single taxon. Two morphotypes of dromeosaurid teeth have been identified as ?Dromaeosauridae indet. and ?*Pyroraptor olympius*. The two morphotypes group separately in the discriminant analysis and ?*Pyroraptor* teeth group together with the teeth from the holotype of *Pyroraptor* giving strength to this assignment. The variabilities of their denticle densities both fall within the range of variability (2.5–6.5 denticles/mm) of *Dromaeosaurus*, but the morphologies of their respective denticles are different (?Dromaeosauridae indet. are taller and narrower than those of ?*Pyroraptor olympius*). For this reason it is reasonable to assign these morphotypes to two different taxa. Teeth identified as ?*Richardoestesia* are distinctive in size and denticle density. They group well statistically in the discriminant analysis with the North American sample of *Richardoestesia*. Teeth described as ?*Paronychodon* teeth have diagnostic longitudinal ridges that separate them from smaller, non-denticulate teeth. Apart from the teeth studied in this work, another tooth needs to be considered. It was found at the Suterranya site, near the Vicari 4 site, described by Prieto-Márquez et al. (2000) and determined to be a *Richardoestesia*-like theropod. This tooth was included in the discriminant analysis and did not group with any of the taxa described in this paper because of its size (Fig. 5; SOM: Table 2), suggesting it may belong to another theropod taxon. The remains of a possible ornithomimosaur were identified from Laño (Astibia et al. 1990), and this may be evidence of another theropod taxon in the area that may not be represented by teeth.

A total of eight taxa of theropods are present in the South Pyrenees Basin. There are six taxa present at Laño, and eight in the central Pyrenees sites (four taxa in Blasi, one in Figuerola 2, one in Fontllonga 6, three in Montrebei and three inVicari 4) (SOM: Table 3).

The change in diversity of theropod dinosaurs through the Late Cretaceous (late Campanian–late Maastrichtian) can be analysed from the sites of South Pyrenees Basin (SOM: Table 3). Figuerola 2, Suterranya, and Vicari 4 represent upper Campanian deposits, where four theropod taxa are present. Laño and Montrebei represent upper Campanian–lower Maastrichtian deposits, where there are six taxa represented. In the lower Maastrichtian, there is only one site, Fontllonga 6, where only one kind of theropod is present. And finally, in the upper Maastrichtian (represented by deposits from Blasi 1, 2B, and 3), there are five taxa of theropods.

Comparing the diversity of Campanian–Maastrichtian theropods in the Iberian Peninsula with the rest of Europe at the same time, the faunal associations follow similar patterns. Based on teeth, a large theropod and a series of small theropods (typically dromaeosaurids and other theropods with teeth that lack denticles) can be recognized. Compared to the rich associations of France, Portugal and Romania (teeth and other fossils), the Spanish fauna of theropods is as good or better in terms of number of taxa represented. France has six taxa of theropods, Portugal has five, Hungary has one taxon in the Early Santonian, and Romania has nine (Buffetaut et al. 1986; Antunes and Sigogneau-Russell 1991; Buffetaut and Le Loeuff 1991, 1997; Le Loeuff and Buffetaut 1991, 1998; Csiki and Grigorescu 1998; Pereda-Suberbiola 1999b; Allain and Taquet 2000; Garcia et al. 2000; Allain and Pereda-Suberbiola 2003; Bonde and Christiansen 2003; Grigorescu 2003; Jagt et al. 2003; Csiki et al. 2010; Weishampel et al. 2010; Brusatte et al. 2013) (SOM: Table 4).

Most of the studies on theropod tooth assemblages in Europe have been done using qualitative (but not quantitative) comparisons, mostly with North American faunas. Only Ösi et al. (2010) used statistical analyses to help identify Hungarian theropods (Santonian). In terms of composition, there are many similarities between different European sites, based on the presence of dromaeosaurids, ?*Paronychodon,* other coelurosaurians, and a large theropod. However, they differ from the South Pyrenees Basin in that most of these other deposits seem to lack identifiable *Richardoestesia* teeth. In the Hateg basin of Romania, Codrea et al. (2002) mention three teeth similar in morphotype to *Richardoestesia*, but ultimately classified them as Theropoda incertae sedis. In the Spanish deposits, specimens of *Troodon* or troodontids have not been recognized, but they have been described from the Portuguese and Romanian deposits (SOM: Table 4).

In the South Pyrenees Basin and most other European outcrops, the remains (mostly teeth, but some postcranial material) of large theropods, have been found (Buffetaut et al. 1986; Antunes and Sigogneau-Russell 1991; Buffetaut and Le Loeuff 1991, 1997; Le Loeuff and Buffetaut 1991, 1998; Pereda-Suberbiola 1999b; Allain and Taquet 2000; Garcia et al. 2000; Allain and Pereda-Suberbiola 2003; Bonde and Christiansen 2003; Jagt et al. 2003). It is worth mentioning that no large theropod teeth have been recovered in the Hateg Basin of Romania. Nopcsa (1902) described some theropod teeth as *Megalosaurus hungaricus* but these teeth came from Borod Basin (possibly Santonian) and not from the Hateg Basin. Unfortunately, the specimens have been lost (Csiki and Grigorescu 1998; Csiki et al. 2010; Brusatte et al. 2013). The absence of large theropods from the Hateg fauna has been attributed to the palaeoenvironments during the Cretaceous (Csiki and Grigorescu 1998; Csiki et al. 2010; Brusatte et al. 2013).

The establishment of a chronostratigraphical framework (from Upper Campanian to Upper Maastrichtian) for theropod teeth from the Pyrenees Basin provides another tool for evaluating the ages of palaeontological sites. Palaeoenvironmentally, the Arén and Tremp Formations were formed by a barrier island and coastal lagoon system. The taphonomic characteristics are roughly equivalent although each of the sites in these formations has its own peculiarities. The sites were prospected and sampled with approximately the same intensity, although the Fontllonga 6 sample is inadequate because of its small size. The Laño deposits were formed in an alluvial system and the palaeoenvironmental taphonomic characteristics are different from other Pyrenean sites. The intensity of sampling in the Laño deposits was higher and produced a larger sample. Even so, most of the taxa that appear in Laño are present in the rest of Pyrenean sites and fit within the framework of changes over time.

In the South Pyrenees Basin, it appears that overall diversity increases from four theropods (an indeterminate coelurosaurian, ?*Richardoestesia* sp., a *Richardoestesia*-like form described by Prieto-Márquez et al. 2000, and an indeterminate dromeosaurid) in the late Campanian to six Maastrichtian taxa (Theropoda indet., Coelurosauria indet., ?*Richardoestesia* sp., ?Dromaeosauridae indet., ?*Pyroraptor olympius*, and ?Ornithomimosauria indet. described by Astibia et al. 1990). Although only one taxon (?Dromaeosauridae indet.) appears in the early Maastrichtian, this is a sampling problem that cannot be resolved at this time. The presence of five theropod taxa (indeterminate theropod, indeterminate coelurosaurian, ?*Paronychodon* sp., ?*Richardoestesia* sp., ?Dromaeosauridae indet.) in the late Maastrichtian suggests there was no significant decrease in the theropod diversity at the end of the Cretaceous in this region (SOM: Table 3). These results agree with Lillegraven and Eberle (1999), who observed that diversity remained high in North America until the uppermost levels, although they do not rule out a gradual (non-catastrophic) extinction of the dinosaurs. Sheehan et al. (2000) and Lyson et al. (2011) found similar results in the uppermost three meters of the Hell Creek formation. However, the diversity of dinosaurs in North America is considerably less in the Hell Creek Formation than it is in the Judith River Formation (Weishampel et al. 2004).

Conclusions

The study of 142 isolated teeth from the Campanian–Maastrichtian of the South-Pyrenean Basin suggests six species of toothed theropods (five small, one large) were present in the region. The taxa identified include two morphotypes of an indeterminate theropod (which could correspond to juveniles and adults of the same species, or tooth row variation), Coelurosauria indet., ?*Paronychodon* sp., ?*Richardoestesia* sp., ?Dromaeosauridae indet., ?*Pyroraptor olympius*. Other two taxa, a *Richardoestesia*-like form (Prieto-Márquez et al. 2000) and a possible ornithomimosaur are added to the final diversity. In total, there are eight theropod taxa present in the South Pyrenees Basin at the end of the Cretaceous.

At least five families appear to be present. The indeterminate theropod teeth identified as Morphotype 1 and Morphotype 2 represent a large theropod of uncertain affinities. Statistically these teeth show more affinities at the family level in the analyses with tyrannosaurids, and only one tooth grouped with Neoceratosauridae. A possible ornithomimosaurid is represented by some phalanges. The family Dromaeosauridae is represented by teeth identified as ?Dromaeosauridae indet. and ?*Pyroraptor olympius*. Specimens identified as ?*Richardoestesia* sp. represent Maniraptoriformes, but the family of this genus is still uncertain. Similarly, the families represented by the indeterminate coelurosaurian and ?*Paronychodon* sp. are unknown.

With this study the number of theropod taxa known from the South Pyrenees Basin is exponentially increased. This shows the value of isolated teeth to reconstruct the composition of dinosaur palaeofaunas when other more complete material is not present allowing us to make interpretations about the evolution of their diversity through time. In this case, apparently theropod diversity in the north of Spain does not experience a significant decline at the end of the Cretaceous (Campanian and Maastrichtian).

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