

Dinosaur teeth from the Barremian of Uña, Province of Cuenca, Spain



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The dinosaur fauna from the Barremian locality of Uña, east-central Spain, is described on the basis of isolated teeth. Apart from an unidentified sauropod and a probably new basal euornithopod, the fauna is noteworthy for its high diversity of theropods. The latter clade is represented by teeth of velociraptorine and dromaeosaurine dromaeosaurids, as well as *Richardoestesia*-like and *Paronychodon*-like teeth, making the theropod tooth fauna from Europe strikingly similar to the Late Cretaceous faunas from North America. However, the reported presence of more basal theropods from other Early Cretaceous localities in Europe indicate that this was a transitional fauna between the typical Late Jurassic and the typical Late Cretaceous theropod faunas of the Northern Hemisphere.

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1. Introduction

Dinosaurs are usually regarded as large animals. While hundreds of tons of large dinosaur bones have been collected from localities all over the world, small dinosaur remains, especially isolated elements, have long been neglected, with few exceptions (e.g., Estes, 1964). Only in the last 20 years has more attention been paid to small isolated dinosaur teeth and bones, and several of these recent studies have demonstrated the high potential of isolated teeth for our understanding of dinosaur faunas (e.g., Currie *et al.*, 1990; Antunes & Sigogneau, 1992; Fiorillo & Currie, 1994; Ruiz-Omeñaca *et al.*, 1996; Baszio, 1997a, b; Zinke, 1998; Sankey, 2001). However, most of the remains described come from Upper Cretaceous rocks and small dinosaurs from the Lower Cretaceous are still very poorly known.

The locality Uña is situated in east-central Spain, in the province of Cuenca, north-east of the city of Cuenca (Figure 1). The vertebrate-bearing layer is part of the Uña Formation, which consists of carbonates and clastic rocks with interbedded coals, laid down in an alluvial plain environment (Gierlowski-Kordesch *et al.*, 1991). It has been dated as Barremian on the basis of palynomorphs (Mohr, 1987) and charophytes (Schudack, 1989). A rich microvertebrate fauna, including fishes, anurans, squamates,

crocodiles, mammals (see Kriwet, 1999, and references therein), and dinosaurs, was extracted from a lignite intercalated in limestones. The dinosaur fauna was briefly characterized by Rauhut & Zinke (1995),

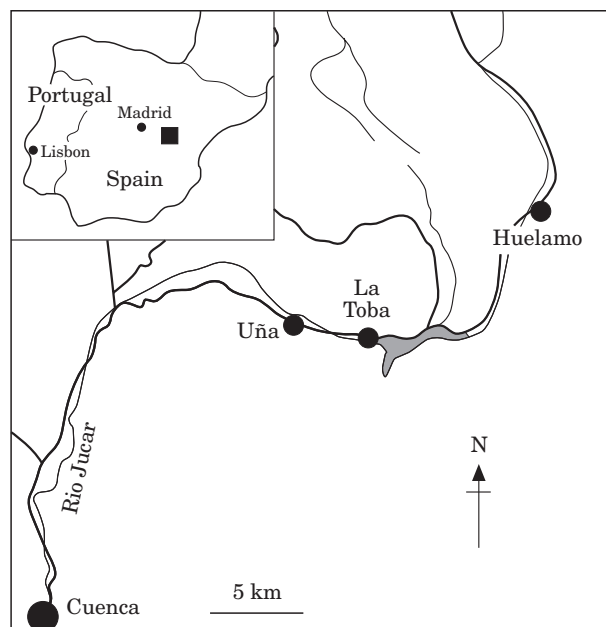


Figure 1. Map showing the locality of Uña in the province of Cuenca, east-central Spain.

based on isolated teeth. These remains are described and discussed in detail in the present paper.

2. Material and methods

Only isolated teeth have been studied. Although bone fragments are quite common in the locality, most of them are too fragmentary for identification. The high quantity of isolated teeth, however, allows for an identification of several morphotaxa, due to the constancy of certain characters. All specimens described here are housed in the vertebrate collections of the Institut für Paläontologie der Freien Universität Berlin (IPFUB).

For the description of the teeth, the values of FABL (Fore-Aft Basal Length; measured at the level of the basal end of the posterior carina, perpendicular to the longitudinal axis of the tooth), BW (Basal Width; measured at the same level as the FABL, and perpendicular to the latter in the horizontal plane) and TCH (Tooth Crown Height; vertical distance from the outer rim of the tooth socket to the tip, perpendicular to both FABL and BW), are given (see Farlow *et al.*, 1991). In addition, the DSDI (Denticle Size Difference Index; ratio between number of denticles over a given length on the mesial carina, divided by the number of denticles over the same length on the distal carina) is given in the description of theropod teeth (see Rauhut & Werner, 1995). For calculating the DSDI, only complete tooth crowns have been considered to reduce the risk of misidentification. The given mean DSDI values should be considered with caution, since the sample sizes are rather small.

3. Systematic palaeontology

Dinosauria: Owen, 1842

Saurischia: Seeley, 1887

Theropoda: Marsh, 1881

Theropoda *incertae sedis*

cf. *Richardoestesia* Currie, Rigby & Sloan, 1990

cf. *Richardoestesia* sp.

Figure 2A

Referred material. Forty-seven teeth: IPFUB Uña Th 1–20, 64, 68, 81.

Description. These teeth are characterised by their strongly elongate and only slightly recurved shape. As is usual for theropod lateral teeth, they are laterally compressed and most show serrated carinae. In some specimens, the distal carina is convex antapically rather than concave. The denticles are chisel-shaped

and relatively small in relation to tooth size. In several teeth, serrations are only found on the distal carina and a few specimens even show two unserrated carinae. The DSDI varies between 1.08 and 1.5, and the mean value is 1.24 (data taken from 13 teeth). The TCH of most specimens is 3–5 mm, and the FABL of the largest crowns is slightly more than 2 mm. The teeth show shallow longitudinal grooves on the antapical parts of their labial and lingual sides.

Discussion. The teeth described above are similar to the teeth of the Upper Cretaceous theropod *Richardoestesia* from several Upper Cretaceous formations, especially the Dinosaur Park and Aguja formations, of North America. They share with the North American teeth the elongated shape, relatively small denticles, convex antapical parts of the distal carina in some specimens, and the presence of grooves on the sides (Currie *et al.*, 1990; Sankey, 2001). Furthermore, the DSDI corresponds well to that of the Upper Cretaceous genus (Rauhut & Werner, 1995). With respect to their elongate crown and low degree of curvature, they more closely resemble the teeth of *R. isosceles* than those of *R. gilmorei*. However, the temporal distance between the Uña and Aguja formations is a strong argument against an assignment of the teeth from Spain to the species *R. isosceles*, although they might represent a closely related taxon. Very similar teeth are, furthermore, also found in the Upper Jurassic of Guimarota (Zinke, 1998) and the Lower Cretaceous of North America (Kirkland & Parrish, 1995). Thus, since the characteristics used to establish *R. isosceles* have a much broader distribution than previously recognized, and the species is solely based on teeth, it should be regarded as a *nomen dubium*. Although the same might be said about the teeth of *Richardoestesia gilmorei*, the type mandibles of this taxon are clearly distinct from all other theropods known so far (Currie *et al.*, 1990). However, more material is needed to establish firmly the validity of this taxon, in particular its distinctiveness from other theropods with the same kind of teeth, for which no skeletal material is known so far.

cf. *Paronychodon* Cope, 1876

cf. *Paronychodon* sp.

Figure 2B–D

Referred material. Fourteen teeth: IPFUB Uña Th 53, Th 55–61, Th 69.

Description. The teeth are moderately recurved, but only slightly compressed laterally. The lingual side is flattened with a central longitudinal ridge present

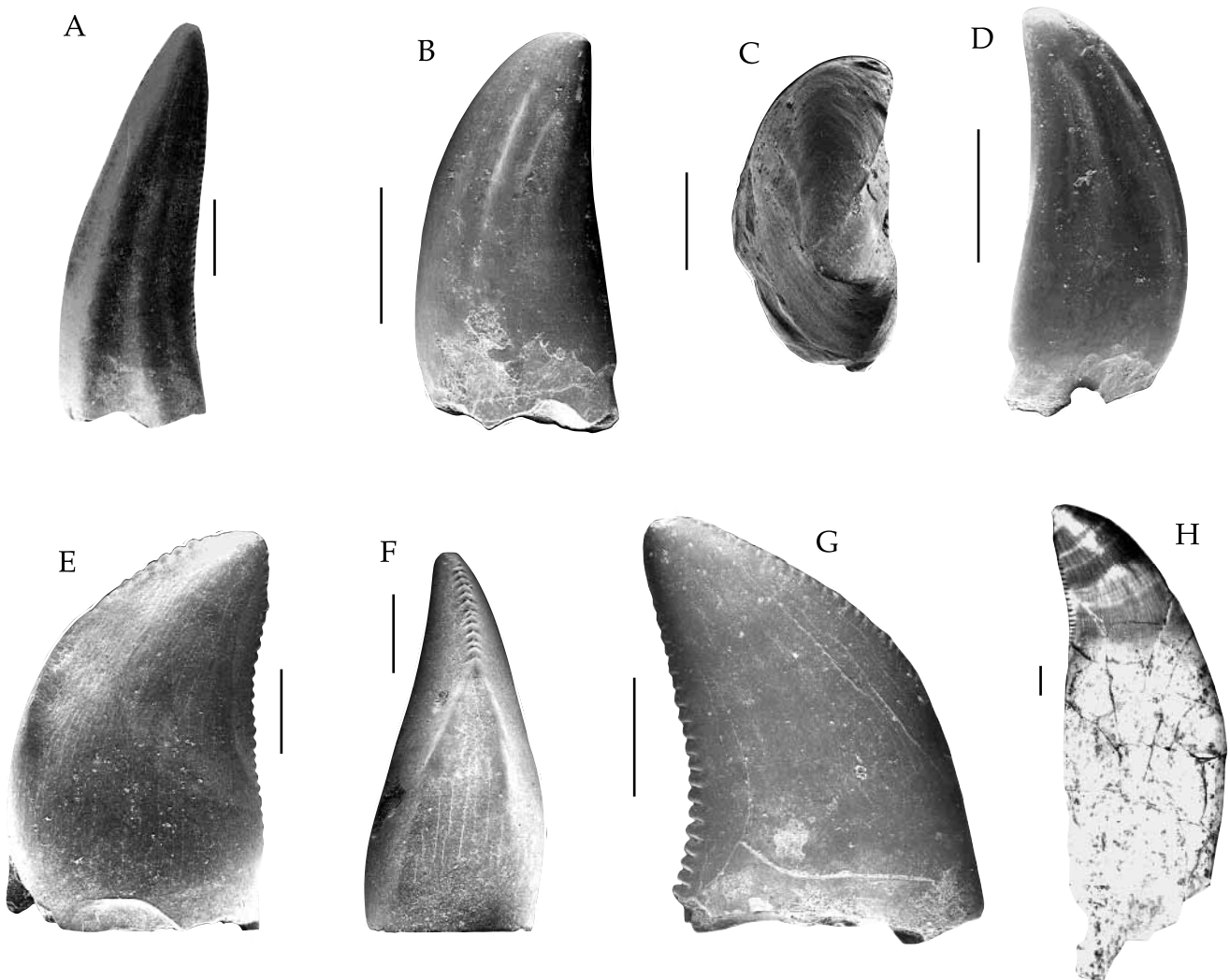


Figure 2. Theropod teeth from the Barremian of Uña. A, tooth of cf. *Richardoestesia* in lingual or labial view. B–D, tooth of cf. *Paronychodon* in labial (B), apical (C) and lingual (D) views. E, F, tooth of a dromaeosaurine dromaeosaurid in lingual (E) and mesial (F) views. G, tooth of a velociraptorine dromaeosaurid in lingual view. H, tooth of a velociraptorine dromaeosaurid with preserved root. Scale bars represent 1 mm (A–D, G, H) and 0.5 mm (E, F).

(Figure 2D). Both unserrated carinae are bent towards the lingual side, giving the appearance of two longitudinal grooves between the carinae and the medial ridge. In some specimens, faint longitudinal grooves are also present along the midline of the mesio-distally convex labial side (Figure 2B). In occlusal view, the tips of the teeth are slightly twisted towards the labio-distal side (Figure 2C). None of the teeth exceeds 6 mm in height, and the greatest FABL is approximately 2.5 mm. In some of the teeth, there is a suggestion of a slight constriction between the crown and root.

Discussion. These teeth are very similar to teeth from the Upper Cretaceous of North America described

as *Paronychodon lacustris* by Cope (1876) and to a tooth from the Maastrichtian of Portugal described as *Euronychodon portucalensis* by Antunes & Sigogneau-Russell (1991), to which taxon they were originally assigned by Rauhut & Zinke (1995). However, since the tooth of *Euronychodon* is virtually indistinguishable from teeth of *Paronychodon*, the former genus is a probable junior synonym of the latter. Zinke & Rauhut (1994) discussed the significance of longitudinal ridges and grooves on theropod teeth and came to the conclusion that at least some of the teeth showing this character, such as those found in the jaw described by these authors, might represent a sister group of troodontids. However, the teeth of *Paronychodon* (*sensu* Currie *et al.*, 1990) show

significant differences from the teeth found in the jaw described by Zinke & Rauhut (one side flattened, ridges mainly on one side, no serrations), and might not, therefore, belong to this group (*contra* Zinke & Rauhut, 1994). The systematic position of *Paronychodon* is, therefore, still uncertain. There is no obvious reason to refer these teeth to the Dromaeosauridae, as tentatively suggested by Antunes & Sigogneau-Russell (1991) for the tooth from Portugal. On the other hand, the assignment of *Paronychodon* to the Troodontidae (as a *nomen dubium*) by Osmólska & Barsbold (1990), probably based on the slight constriction between crown and root, is also doubtful, since this character may be found in other theropods (Zinke & Rauhut, 1994), and it is also present in toothed birds (Currie, 1987) and some other vertebrates (e.g., crocodiles). Finally, the suggestion that these teeth may be referable to *Pelecanimimus* by Rauhut & Zinke (1995) is most probably wrong (Pérez-Moreno, pers. comm. 1995).

A new interpretation proposed here is that the cf. *Paronychodon* teeth from Uña might represent bird teeth. Characters in favour of this interpretation are the constriction between crown and root (Currie, 1987) and the inwardly bent carinae as well as the labio-distal twist of the tooth tip; the latter two characters are also found in *Archaeopteryx* (Weigert, 1995; compare Figure 2C with Weigert, 1995, fig. 7.1.). The fact that the teeth of the Upper Cretaceous toothed birds *Hesperornis* and *Ichthyornis* differ in not showing inturned carinae and a labio-distal twist of the tip of the crown (Marsh, 1880) might indicate that these characters are archaeopterygiform synapomorphies, thus making cf. *Paronychodon* a possible late survivor of the Archaeopterygiformes. That the archaeopterygiform lineage survived into the Late Cretaceous is demonstrated by *Rahonavis* from the Maastrichtian of Madagascar (Forster *et al.*, 1998). However, teeth of *Archaeopteryx* differ from *Paronychodon* teeth in their sigmoidal shape (Weigert, 1995). The solution to this problem has to come from new finds of more complete material.

Dromaeosauridae Matthew & Brown, 1922

Dromaeosaurinae (Matthew & Brown, 1922) (*sensu* Currie *et al.*, 1990)

Gen. et sp. indet.

Figure 2E, F

Referred material. Thirty-seven teeth: IPFUB Uña Th 37, 39, 48, 49, 67, 71–80.

Description. The tooth crowns are broadly oval in cross section at their base, but become more flattened

towards the apex. The teeth are moderately to strongly recurved. In most specimens, both carinae are serrated, with the mesial carina showing denticles only on its apical part. Some specimens show only weakly developed denticles on the mesial carina and only few denticles on the distal one, and one tooth lacks serrations completely. The denticles are chisel-shaped. The DSDI varies between 0.86 and 1.17, with a mean value of 1.03 (data taken from nine teeth). The most remarkable feature of these teeth is a strong twist of the mesial carina to the lingual side in its lower half. The enamel is smooth and no down-pointing grooves are present at the bases of the denticles. All teeth are very small, with a FABL of less than 3 mm and a TCH of less than 5 mm. In some specimens, a very weak constriction between crown and root seems to be present. One specimen (Th 39) shows a split anterior carina (Figure 2F).

Discussion. The most striking character of these teeth is the lingual twist of the anterior carina. A twist like that has only been described for the Upper Cretaceous genus *Dromaeosaurus* (Currie *et al.*, 1990; Currie, 1995); therefore, the teeth from Uña are referred to the Dromaeosaurinae. A difference between the teeth of *Dromaeosaurus* and the specimens from Spain is found in the position of this twist: while it occurs just beneath the apex in the Upper Cretaceous genus (Currie *et al.*, 1990), it is found in the middle of the carina in the elements described above. This indicates that the latter specimens represent a different, perhaps more primitive, taxon of dromaeosaurine.

Velociraptorinae Barsbold, 1983 (*sensu* Currie *et al.*, 1990)

Gen. et sp. indet.

Figure 2G, H

Referred material. Sixty-seven teeth: IPFUB Uña Th21–36, 38, 40–47, 50–52, 63, 65, 66, 70.

Description. The teeth are strongly compressed laterally and significantly recurved. Both carinae or only the distal carina are denticulate. The specimens with two serrated carinae show a significant difference in the size of the denticles of the mesial and distal serrations; the DSDI varies between 1.11 and 2, with a mean value of 1.52 (data taken from 15 teeth). The denticles are chisel-shaped and rounded, or very slightly inclined apically. Most of the teeth are small, with a FABL of less than 5 mm, but the largest specimen (Th 66) shows a FABL of approximately 8 mm and a TCH of 15 mm. The tooth enamel is

smooth in most specimens; only a few show faint longitudinal ridges on both sides. No downpointing grooves are present at the base of the denticles.

Discussion. Within theropods, a mean DSDI of over 1.2, as in the specimens from Uña, is typical for the teeth of velociraptorine dromaeosaurids, and is only found in few other theropods of uncertain systematic position (*Richardoestesia* and *Dryptosaurus*; see Currie *et al.*, 1990; Rauhut & Werner, 1995) and the basal tyrannosauroid *Eotyrannus* (Naish, pers. comm. 2001). While *Dryptosaurus* is poorly known and its systematic position is far from clear, the teeth of *Richardoestesia* differ from the specimens from Spain in their overall shape and the relative size of the denticles (Currie *et al.*, 1990) and those of *Eotyrannus* in being less markedly recurved (Naish, pers. comm. 2001). Since the teeth from Uña show great similarities to teeth of velociraptorine dromaeosaurids in respect to their shape and the high DSDI (Ostrom, 1969; Currie *et al.*, 1990), they are referred to the Velociraptorinae. Within velociraptorines, they are more similar to the Mongolian genus *Velociraptor* (pers. obs.) than to the North American genera *Deinonychus* (Ostrom, 1969) and *Saurornitholestes* (Currie *et al.*, 1990) in that the denticles are chisel-shaped rather than strongly inclined apically. However, this similarity does not necessarily imply close relationships between the Uña velociraptorine and *Velociraptor*, since chisel-shaped denticles are the plesiomorphic condition within theropods.

Ruiz-Omeñaca *et al.* (1996) and Canudo *et al.* (1997) also described some velociraptorine dromaeosaurid-like teeth from the Barremian locality Vallipón (Province of Teruel), indicating that this group was quite common in the Iberian Peninsula during the Early Cretaceous.

Sauropodomorpha Huene, 1932

Sauropoda Marsh, 1878

Sauropoda indet.

Figure 3

Referred material. One tooth: IPFUB Uña Sd 1.

Description. Sd 1 is a badly preserved crown of a small sauropod tooth (Figure 3). The enamel is mainly preserved in the apical parts of the crown, and the basal part is broken. The base of the tooth is broadly oval in cross section, but the crown becomes more flattened apically. It is straight in lingual view, but slightly bent to the lingual side in mesial view. Both carinae are slightly turned towards the lingual side,

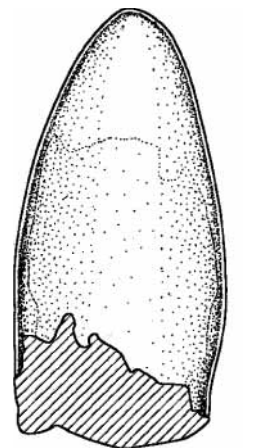


Figure 3. Tooth of an undetermined sauropod from the Barremian of Uña in lingual view.

giving the tooth a spoon-like appearance. The enamel is smooth at the tip, but there seems to have been enamel ornamentation near the base. The TCH of the tooth as preserved is 16 mm.

Discussion. The tooth is readily identified as a sauropod tooth on the basis of its spatulate shape. Its systematic position within sauropods, however, is difficult to establish, owing to the poor preservation of the specimen and the fact that spatulate teeth are found in a wide variety of sauropods. The tooth differs from those of the most basal sauropods in the lack of marginal denticles and from diplodocoids in the overall shape (Upchurch, 1998; Wilson & Sereno, 1998). Since the vast majority of Cretaceous sauropods identified from Europe so far are members of the Macronaria (Wilson & Sereno, 1998), and members of this group with spatulate teeth are known from the Barremian of Spain (Sanz *et al.*, 1987), it seems rather probable that the tooth from Uña belongs to a representative of this clade.

Ornithischia Seeley, 1887

Ornithopoda Marsh, 1881

Euornithopoda Sereno, 1986

Gen. et sp. indet.

Figure 4A–E

Referred material. Fourteen teeth: IPFUB Uña Or 1–10.

Description. Four of the 14 specimens are premaxillary teeth (Figure 4A). These specimens are asymmetrically subconical and significantly compressed laterally. A well-developed constriction is present between

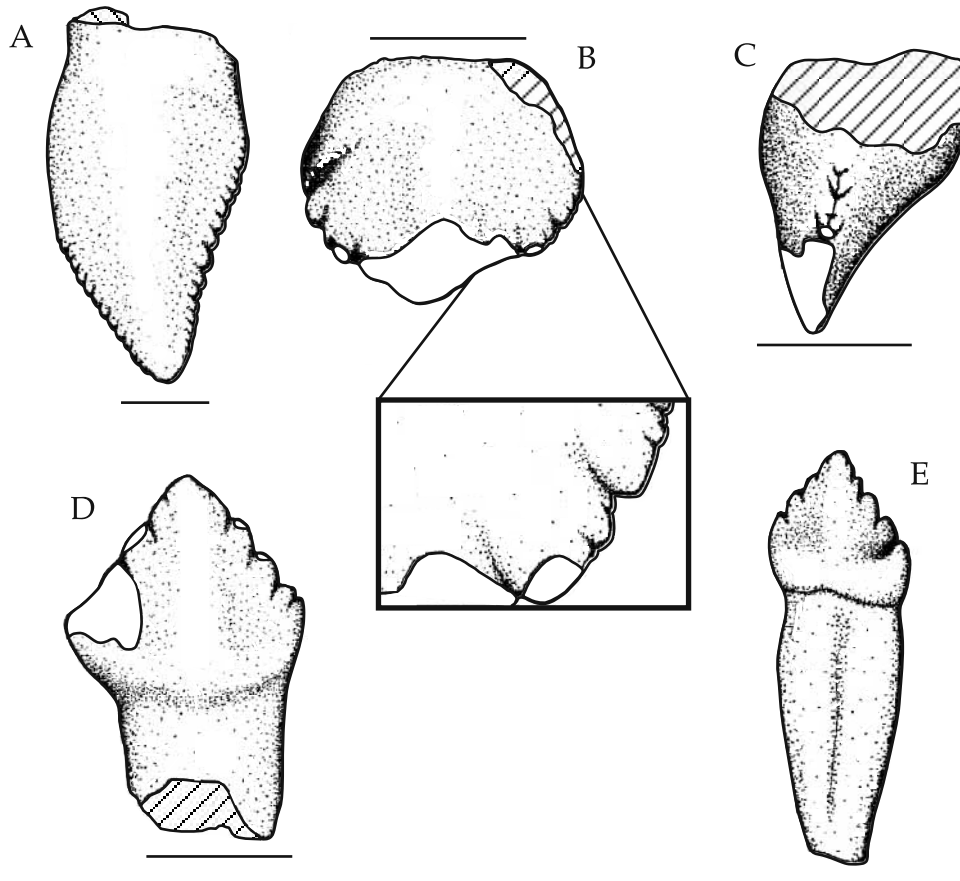


Figure 4. Hypsilophodontid teeth from the Barremian of Uña. A, premaxillary tooth in lingual view. B, C, maxillary tooth in lingual (B with enlargement of denticles) and mesial (C) views. D, dentary tooth in labial view. E, dentary tooth with preserved root in labial view. Scale bars represent 1 mm.

crown and root and the crown is slightly recurved. Both well-developed carinae bear denticles which end well above the base, more apical on the mesial carina than on the distal one. A weak cingulum is present at the base. At the sides, the cingulum extends apically to where the denticles begin. The FABL of the well preserved specimen Or 3 is 2 mm, the TCH 4.4 mm. There are 4.5 denticles per 1 mm on the distal and 5 denticles per 1 mm on the mesial carina. The smallest specimen shows a FABL of approximately 0.5 mm.

Four of the remaining teeth are maxillary teeth (Figure 4B, C). They are low triangular, laterally compressed, and show a higher labial than lingual side. As in *Phyllodon* from the Upper Jurassic of Portugal (Thulborn, 1973; Rauhut, 2000a, 2001), the crowns are rather symmetrical. They bear 4–5 denticles on each carina. The ends of the denticles are only preserved in one specimen, and there they are subdivided into two to three smaller denticles with the apical one of these subdivided being the largest (Figure 4B). In all specimens, a short denticulate

cingulum is present on the distal part of the lingual side. A broad primary ridge connects the apex with the swollen base, and in the largest specimen, all denticles are supported by secondary ridges. Whether such secondary ridges are also present in other specimens of similar size cannot be determined, since these teeth are heavily worn. The FABL of the teeth varies between 0.7 and 1.8 mm.

The remaining six teeth are dentary teeth (Figure 4D, E). Or 1 shows a complete crown with preserved root (Figure 4E). The tooth is very small, with a FABL of only 1.1 mm and a complete tooth length (including root) of 4.3 mm. The TCH is 1.5 mm. The crown is slightly asymmetrically triangular and laterally compressed. Both labial and lingual sides are subequal in height. The tooth bears three well-developed and one small denticle on both mesial and distal carinae. The denticles are not subdivided. The lowermost denticle on the distal carina is bent lingually onto a short but well-developed cingulum, which bears one more denticle. The base of the crown

is significantly swollen. A broad primary ridge extends from the base to the apical denticle; no secondary ridges are present. The root is almost twice as long as the crown. There is a striking constriction between root and crown and the root tapers towards its lower end. A significant longitudinal groove on both the lingual and labial side divide the root into two subequal parts.

Two other dentary teeth are very similar to Or 1, but the crowns are more symmetrical (Figure 4D). They are broadly triangular and bear four denticles on each carina. In Or 3, the denticles show a low antapical 'shoulder' reminiscent of the subdivision of the denticles in the maxillary teeth. As in Or 1, a short cingulum is present. The base is significantly swollen and the primary ridge is well developed. No secondary ridges are present. One of the teeth shows a broken part of the root, which is pseudobilobate as in Or 1. The FABL of the larger of these two specimens is 1 mm.

The other teeth preserved are even smaller, with a FABL of not more than 0.5 mm. One of these specimens (Or 7) is significantly broader than high and resembles the smallest teeth assigned to the Late Jurassic basal euornithopod *Phyllodon* (Rauhut, 2001, fig. 3L).

Discussion. Owing to the similar morphology, the teeth are thought to represent a single taxon, although it cannot completely be ruled out that more than one taxon is represented. The morphology of the teeth is in general accordance with that of typical 'hypsilophodontids' (e.g. Galton, 1983, 1995; Bakker *et al.*, 1990; Rauhut, 2001). However, it should be mentioned that newer research indicates that the Hypsilophodontidae *sensu* Sues & Norman (1990) are probably paraphyletic (Naish, pers. comm. 2001), so the term might only be used to refer to non-iguanodontian euornithopodans.

Several differences indicate that the teeth from Uña represent a so-far-unknown taxon of basal euornithopods. The premaxillary tooth is more strongly labiolingually compressed than in other members of this clade. Moreover, a subdivision of the marginal denticles in maxillary teeth has so far only been described in the Late Jurassic genera *Phyllodon* (Thulborn, 1973; Rauhut, 2001) and *Drinker* (Bakker *et al.*, 1990). However, in these taxa, the denticles are symmetrically divided, with a large medial cusp flanked by two subequal lateral cusps. In contrast, the basal euornithopod from Uña shows asymmetrically subdivided denticles, with the most apical cusp of every denticle being the largest. Although the shared derived character of possessing subdivided denticles

might indicate close relationships between especially *Drinker* and the Uña 'hypsilophodontid', the latter clearly represents a distinct taxon. However, no new name is proposed here because of the problems often created by naming dinosaur taxa on the basis of isolated teeth alone (see e.g., Currie, 1987; Dodson, 1990).

Ruiz-Omeñaca & Cuenca-Bescós (1995) described a distinctive 'hypsilophodontid' femur from the Barremian of Galve (Province of Teruel, Spain); the teeth described above may be referable to the same species (see also Ruiz-Omeñaca, 2001).

4. Discussion

The lignite coals of Uña have yielded a diverse fauna of small-bodied dinosaurs. The lack of larger animals and the apparent dominance of predatory dinosaurs might be for taphonomic reasons, as has been argued for the lithologically similar locality of Guimarota (Rauhut, 2001).

The high diversity and taxonomic composition of the theropod assemblage is especially noteworthy. With respect to represented theropod tooth morphologies, the fauna from Uña is strikingly similar to latest Cretaceous theropod faunas from North America (Currie *et al.*, 1990; Fiorillo & Currie, 1994; Baszio, 1997a). Velociraptorine and dromaeosaurine teeth, as well as teeth assignable to *Richardoestesia* and *Paronychodon*, are usually found in Campanian–Maastrichtian localities on that continent. Although other groups commonly present in North American Upper Cretaceous localities, namely tyrannosauroids, ornithomimosaurids and troodontids, are absent in Uña, they have been reported from other Lower Cretaceous sites in Europe (Estes & Sanchiz, 1982; Pérez-Moreno *et al.*, 1994; Hutt *et al.*, 2001). In this respect, the theropod fauna from the Barremian of Europe seems, on a broad taxonomic level, to be similar to the Late Cretaceous theropod faunas of North America. However, several more primitive lineages, such as allosauroids (Hutt *et al.*, 1996) and compsognathids (*Aristosuchus pusillus* from the Hauterivian–Barremian Wessex Formation of southern England) are also still present. Thus, the European Early Cretaceous theropod fauna represents a transitional fauna between the Late Jurassic basal tetanuran (allosauroids and 'megalosaurs')/basal coelurosaur faunas and the Late Cretaceous tyrannosaur/maniraptoran faunas of the Northern Hemisphere. That this transition had already begun in the Late Jurassic is shown by the presence of possible dromaeosaurid, troodontid, *Richardoestesia*-like, and

tyrannosauroid teeth and some possible tyrannosauroid bones in the Morrison Formation of North America (Madsen, 1974; Britt, 1991; Chure, 1995; Chure & Madsen, 1998) and the Alcobaça Formation of Portugal (Zinke, 1998; Rauhut, 2000a).

The presence of most of these groups (tyrannosauroids, dromaeosaurids, troodontids) had to be expected on the basis of recent cladistic analyses of theropod interrelationships (e.g. Sereno, 1999; Holtz, 2000; Rauhut, 2000b). However, the *Richardoestesia*-like teeth remain enigmatic. If theropod teeth are indeed of taxonomic value, at least at higher levels, their presence in the Upper Jurassic indicates a separate lineage of theropods that had a stratigraphic range from at least the Upper Jurassic to the uppermost Cretaceous. Apart from teeth, this lineage is only represented by the type mandibles of *Richardoestesia gilmorei* from the Dinosaur Park Formation (Campanian) of Alberta (Currie *et al.*, 1990), although, based on the tooth evidence, it had a wide distribution within western Laurasia by the Early Cretaceous (Kirkland & Parrish, 1995; this work). The reason more is not known about this lineage might be the relatively small size of its members, as indicated by the small size of all teeth known. Alternatively, the *Richardoestesia*-like teeth might represent juveniles of one of the better known groups of theropods. Again, the solution to this problem has to come from new discoveries of more complete material.

5. Conclusions

As has been shown in other cases, small dinosaur teeth from the Barremian of Uña provide important new information on the Early Cretaceous dinosaur fauna from the Iberian Peninsula. Taxa that have hitherto not been reported from Spain include a new basal euornithopod, dromaeosaurine dromaeosaurids, cf. *Paronychodon*, and cf. *Richardoestesia*. Many of these taxa represent lineages that thrived in the Northern Hemisphere since at least the Late Jurassic, but little is still known about their early evolutionary history. The Early Cretaceous in Europe seems to have been an age of transition between the typical Late Jurassic and Late Cretaceous theropod faunas of the Northern Hemisphere.

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