New dinosaur sites correlated with Upper Maastrichtian pelagic deposits in the Spanish Pyrenees: implications for the dinosaur extinction pattern in Europe

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Six new dinosaurs sites have been found close to the Cretaceous/Tertiary boundary in Arén (south-central Pyrenees, Huesca, Spain) in coastal and non-marine deposits of the Arén and Tremp Formations. The sites contain articulated remains (skull elements, vertebrae, hind-limb bones) and isolated teeth and bones of hadrosaurids, three types of theropod teeth, one sauropod, at least seven types of eggshells (six ornithoid types and one Megaloolithidae probably from a sauropod), remains of other vertebrates, and four charophyte species. The fossil-bearing rocks have been correlated with marine sediments containing planktonic foraminifera from the uppermost Maastrichtian *Abathomphalus mayaroensis* Biozone. These rich and diversified dinosaur assemblages enable more accurate dating of the faunal changes that took place during the Maastrichtian in Europe and support the hypothesis of a sudden dinosaur extinction at the Cretaceous/Tertiary boundary.

KEY WORDS: Cretaceous/Tertiary boundary; Maastrichtian; marine-continental correlations; dinosaurs; charophytes; Pyrenees.

1. Introduction

Dinosaur remains are mostly found in non-marine rocks; therefore, their accurate age determination is often problematic. This paper presents one of the rare cases where dinosaur sites can be accurately dated, and the first to be directly correlated with the uppermost Cretaceous planktonic foraminiferal biozone. Six new dinosaur-rich sites were discovered by L. Ardèvol (GeoPlay) and F. López Olmedo (INYPSA) in uppermost Cretaceous rocks on the northern limb of the Tremp syncline near Arén (Huesca, south-central Pyrenees, Spain; Figure 1; López-Olmedo & Ardèvol, in press). The sites, named Blasi 1, 1b and 2–5, contain articulated and scattered dinosaur bones, teeth and eggshell fragments, together with remains of

other vertebrates (bony fishes, amphibians, lepidosaurs, turtles and crocodiles); charophytes occur only at Blasi 2. The fossil-bearing rocks are located on top of the Arén Formation and in the lower part of the Tremp Formation. Downdip these dinosaur localities can be correlated with deep marine sediments containing planktonic foraminifera from the topmost Maastrichtian *Abathomphalus mayaroensis* Biozone, near the Cretaceous/Tertiary boundary (Figure 2).

Other European dinosaur localities in non-marine rocks previously considered to be Maastrichtian by authors (e.g. Grigorescu, 1983; Buffetaut & Le Loeuff, 1991; Buffetaut *et al.*, 1997; Gheerbrant *et al.*, 1997; Laurent *et al.*, 1999; Garcia *et al.*, 1999), need to be recalibrated in the light of the new chronostratigraphic scale of Gradstein *et al.* (1995) and

refinements in marine-continental biostratigraphic correlation (Riveline *et al.*, 1996). The changes introduced to the duration of the stages has led to rocks previously assigned to the Early Maastrichtian (Figure 3) to be dated as Late Campanian, particularly those containing *Septorella* charophyte assemblages.

The dinosaur-rich Arén sites, among the youngest in the world, are crucial for establishing the pattern of the Late Cretaceous dinosaur succession and extinction in Europe. In particular, they contradict the hypothesis that dinosaur diversity decreased before their extinction, and that the extinction was earlier in Europe than in North America (Colombo, 1996; Galbrun, 1997), already challenged by López-Martínez *et al.* (1998) and Casanovas *et al.* (1999a).

2. Geological setting and depositional framework

The dinosaur-bearing strata are exposed along the northern limb of an east–west-trending syncline (Tremp) in the south-central Pyrenean thrust unit (Figure 1). This belt exposes rocks that reflect sediment deposition along the axis of an elongate foredeep basin, which deepens westward to the Atlantic Ocean. The foredeep was filled with basinal turbidites and prodelta shales, followed by deltaic sandstones and fluvial red beds (Arén Sandstone and Tremp Formation, respectively; Figure 2). These deposits are 3400 m thick and range in age from Santonian to Maastrichtian.

The sands of the Arén Sandstone are composed of quartz with scarce feldspar, chert, quartzite, mica, and fossil debris, and show medium- and large-scale cross bedding (Nagtegaal *et al.*, 1983). These rocks are transitionally overlain by lagoonal/marsh marls and red beds of the lower part of the Tremp Formation (Liebau, 1973; Díaz-Molina, 1987; Krauss, 1990). The Blasi 1 site is located on top of the Arén Sandstone whereas Blasi 2–5 are located within the lower part of the Tremp Formation (Figures 1, 2).

The depositional assemblages of the Upper Cretaceous foredeep have been divided into four depositional sequences (Arén 1–4) bounded by sequence boundaries H1–5 (Figure 2; Ardèvol *et al.*, 2000). The Arén dinosaur sites occur in delta-front, lagoonal, and fluvial deposits of the Arén 4 sequence, dated as latest Maastrichtian (Figure 2). The chronostratigraphy of the sequences and dinosaur sites is discussed below (Section 6). The sites are described in ascending stratigraphic order.

3. Dinosaur sites

The stratigraphic location of the fossil sites is indicated in the cross-section (Figure 2), and their fossil content in Table 1. Blasi 1 is situated on top of a 60-m-thick sandstone unit of the marine Arén Formation, which dips 30° to the south. The sandstone is a mixed arenite with white, coarse, well-rounded quartz grains. Iron nodules and remnants of iron crusts are locally present. Large dinosaur bones and crocodilian teeth are scattered over an area of several hundred square metres. Most of the bones are fragmentary limb remains lacking proximal or distal ends, but there are several associated bones belonging to a hadrosaurid skull (Figures 5–7).

Blasi 2 occurs in a 6.5-m-thick interval of grey marls that overlie the sandstones of Blasi 1 (Figure 2). Nearly 5000 kg of sediment have been washed, resulting in the extraction of vertebrate microfossils (fish, amphibians, squamates and turtles), some dinosaur teeth (theropods, hadrosaurids, a sauropod) and eggshells (Tables 1, 2). Plant debris, charophytes and gastropods are common, but mammal remains have not been found. Blasi 1b is situated 150 m to the east in an equivalent stratigraphic position. It has only yielded large, weathered and fragmentary dinosaur bones: three dorsal vertebrae and a few rib remains of a hadrosaurid, and limb bone fragments of an indeterminate dinosaur (Table 1).

Blasi 3 is situated in a 1-m-thick channelized sandstone body that overlies the marls of Blasi 2 (Figure 2). The fine-grained, matrix-supported feldspathic sandstone contains *Ophiomorpha* burrows. The site has yielded about 70 dinosaurian bones, most of which probably belong to a single hadrosaurid individual. They were scattered over an area of about 70 m^2 (Tables 1, 2). All together, 19 caudal vertebrae were present in an area 4 m^2: eight caudal vertebrae are preserved in anatomical connection, while additional caudal vertebrae and chevron bones are slightly disarticulated (Figure 4). Other hadrosaurid material consists of a maxilla fragment, poorly preserved isolated teeth, two cervical vertebrae, several distal caudal centra and chevrons, several rib remains, one ilium and two femora. Moreover, isolated teeth from a large theropod dinosaur, crocodilian bones and turtle plates have also been found (Tables 1, 2).

Blasi 4 and Blasi 5 occur 3 km to the west, 70 m and 100 m respectively above Blasi 3 (Figure 2). Blasi 4 is on top of a 0.5-m-thick, channelized, microconglomerate bed. It contains a few fragments of hadrosaurid bones, mainly vertebrae, as well as crocodilian and turtle remains and internal casts of bivalves. Blasi 5 is in a grey mudstone intercalation within shaly red beds; it has yielded turtle plates, crocodilian osteoderms and several fragments of vertebrae and long bones apparently belonging to hadrosaurs (Table 1).
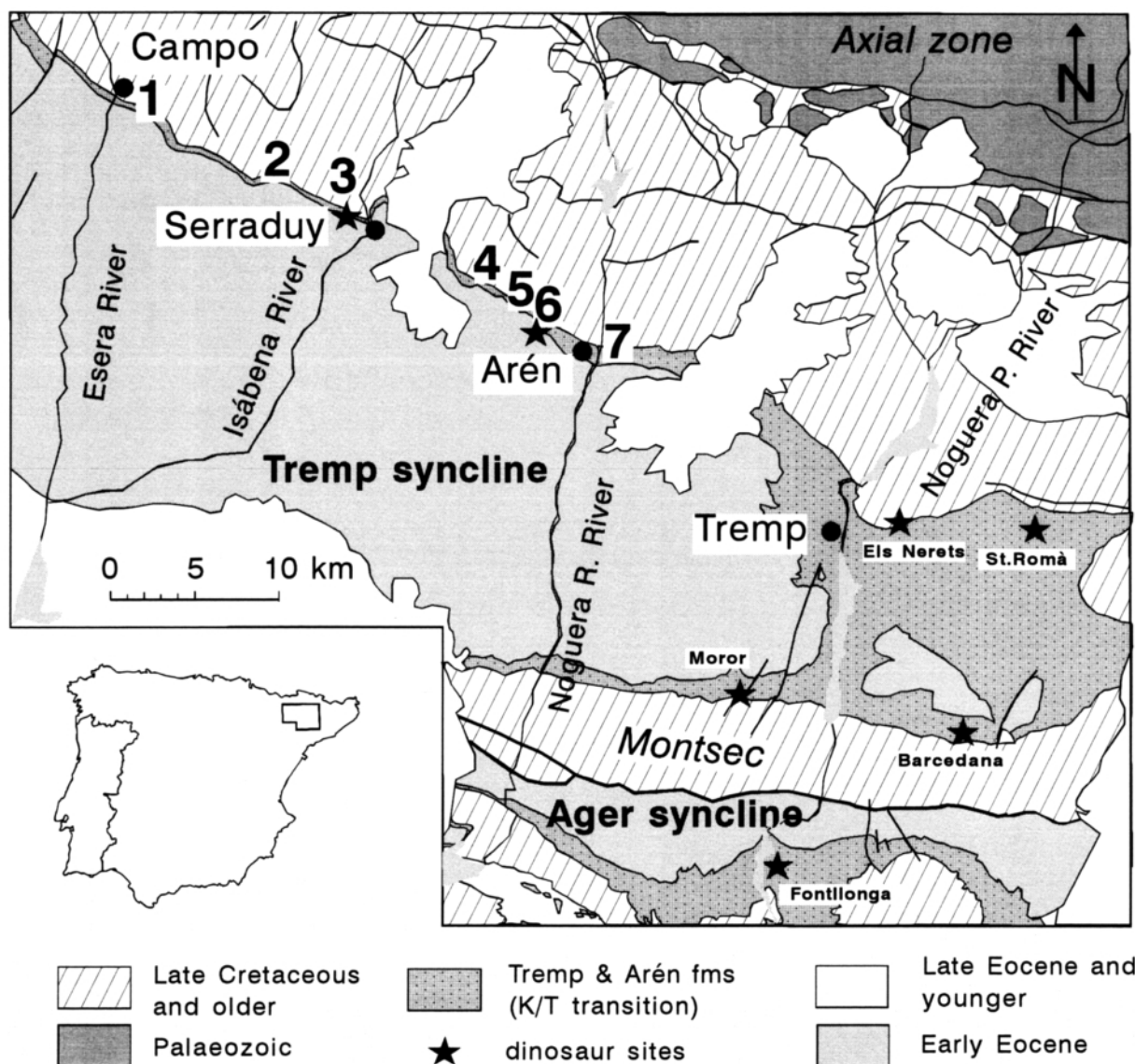
Figure 1. Simplified geologic map of the Tremp and Ager synclines (south-central Pyrenees, Spain). Numbers refer to the stratigraphic sections in Figure 2.

The vertebrate fossils from Arén are mostly fragmentary with a high proportion of splinters, with the notable exceptions of the associated remains from Blasi 1 and 3 and the articulated remains from Blasi 3, which indicate an absence of reworking processes and rapid burial probably after necrokinesis. Conversely, the microconglomeratic matrix of the Blasi 4 site covers the fracture surfaces of the bones, suggesting resedimentation and transport prior to final burial.

4. The dinosaurs

We have recognized at least eight dinosaur taxa: one type of hadrosaur on the basis of bones and teeth, a sauropod (one tooth and one Megaloolithidae eggshell-type), three types of theropod teeth and six 'ornithoid' eggshell-types from theropod dinosaurs and birds. The fossil material from the Arén sites is housed in the Museo Paleontológico of the Universidad de Zaragoza, Spain (MPZ).

4.1. Hadrosaurid ornithopods

Blasi 1 hadrosaurid. Hadrosaurid skull bones and a lower jaw with teeth have been recovered from Blasi 1. The material, which probably belongs to a single individual, consists of a left jugal, a fragmentary left maxilla with teeth, a left dentary preserving
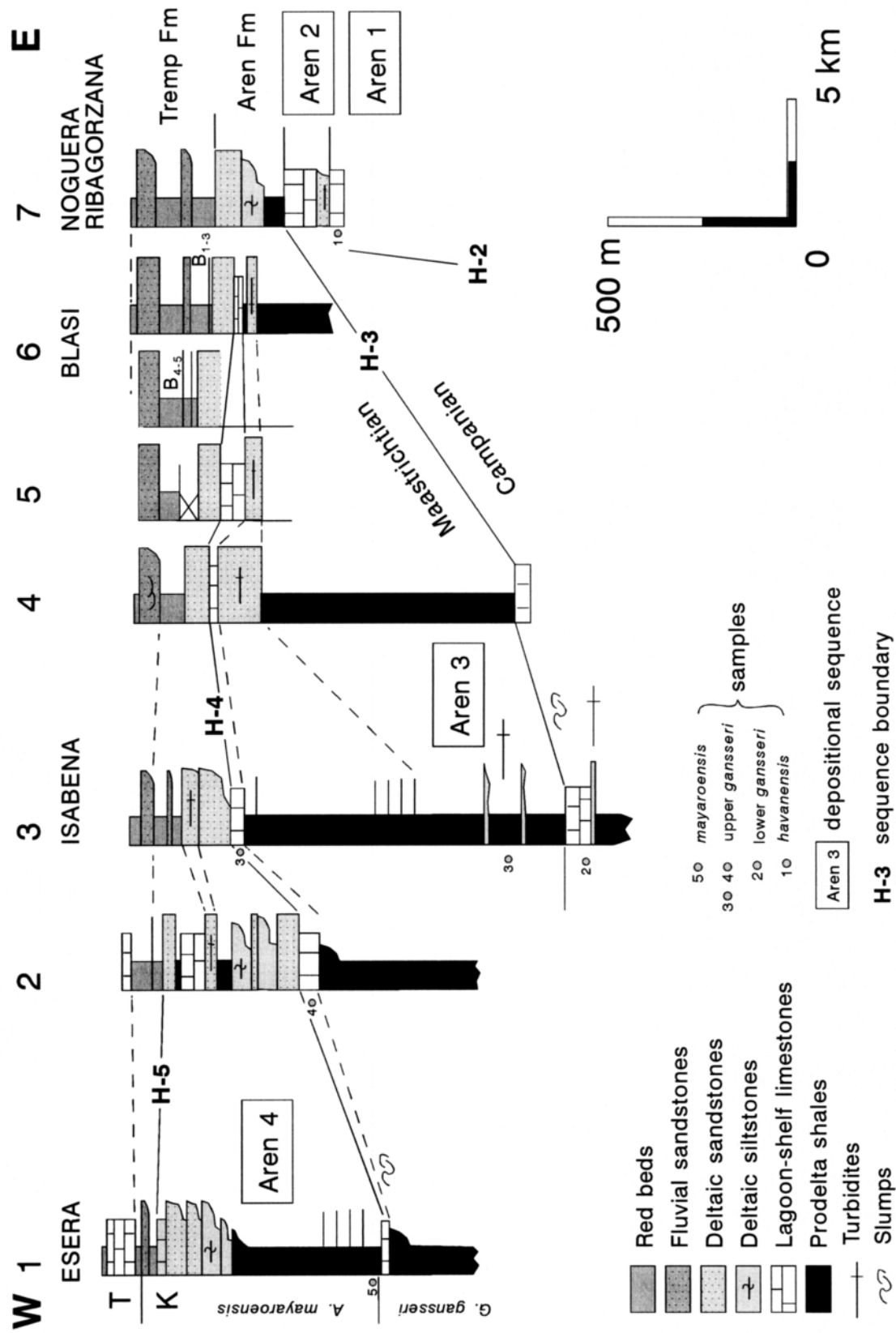
Figure 2. West-east cross-section showing the correlation of the stratigraphic sections located in Figure 1. Arén 1–4 sequences and H-2–5 sequence boundaries are shown, as well as the lithostratigraphic boundary between the Arén and Tremp formations and the location of the K/T boundary. Samples refer to the planktonic foraminiferal study. The Blasi dinosaur sites B1–3 and B4–5 are indicated.
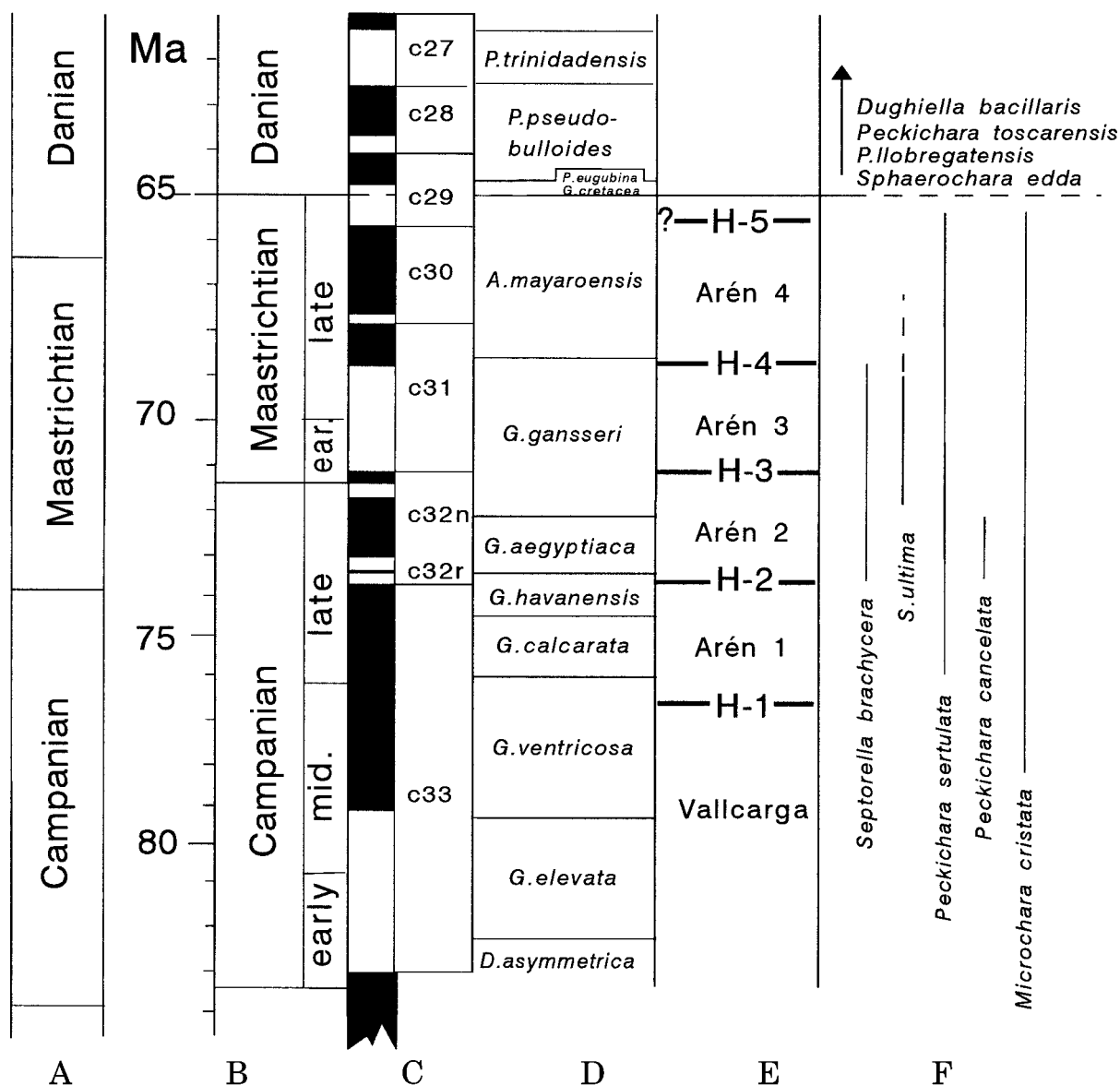
Figure 3. Chronology of the Cretaceous–Tertiary transition in the south-central Pyrenees. The Arén dinosaur sites are located in the Arén 4 sequence. A, chronostratigraphy according to Haq *et al.* (1987); B, chronostratigraphy according to Gradstein *et al.* (1995); C, magnetostratigraphy from Cande & Kent (1995); D, planktonic foraminiferal biostratigraphy according to Robaszynski and Caron (1995); E, sequence stratigraphy from Ardèvol *et al.* (2000); F, charophyte data modified from Galbrun *et al.* (1993) and Riveline *et al.* (1996).

most of the dental battery, and a right surangular. Other skull remains are too fragmentary for proper identification.

Jugal (BLA-99/667, Figures 6, 7). The jugal is a W-shaped gracile bone, very short rostrocaudally (preserved length, 14.5 cm). The rostral end is partially broken and it is not possible to determine whether it was broadly convex as in lambeosaurines, or distinctly angular as in hadrosaurines and *Telmatosaurus* (Weishampel & Horner, 1990). The rostral

process looks short and very expanded ventrally, forming a large articulation surface with the maxilla. The ventral margin is incised and caudally forms a distinctly concave flange ventral to the infratemporal fenestra. The facet for the quadratojugal is not well defined, but seems relatively small. The postorbital and caudal processes are nearly parallel, the former more elongate (albeit incomplete). The joint with the postorbital is a flat surface. The tip of the caudal process is curved rostrally. The mesiodistal length of
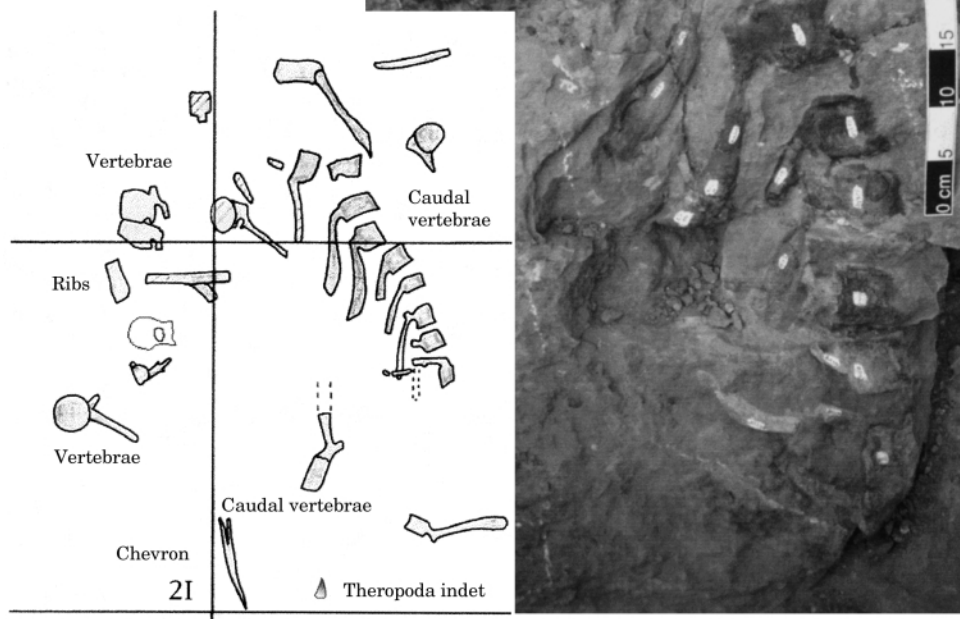
Figure 4. Map and photograph of part of the Blasi 3 dinosaur site, showing articulated caudal vertebrae, ribs and chevrons of a hadrosaurid, and an isolated theropod tooth.

the orbit appears to be comparatively much greater than that of the infratemporal fenestra.

Maxilla (BLA-99/666, Figures 5, 7). Only a fragmentary left maxilla is known (preserved length 13 cm). The proximal, dorsal and distal ends are broken. The lateral side is poorly preserved and the articular surface for the jugal is missing. In medial view, the maxillary surface is flat and exhibits a series of special foramina. The maxillary dental battery preserves the last 16 dental positions, five more tooth positions appearing in a proximal displaced fragment. Each tooth position has one or two functional teeth and at least two replacement teeth. The maxillary teeth are narrow mesiodistally and bear a prominent median carina. At least one tooth shows small papillae. The mean mesiodistal length of the teeth is 5.6 mm.

Dentary (BLA-99/665, Figures 6, 7). The left dentary is 33 cm long and relatively slender. It is roughly rectangular, with parallel dorsal and ventral margins. The rostral portion is ventrally deflected, with a moderate diastema between the predentary surface and the first dentary tooth. The coronoid process is projected rostrally and forms an angle of 75° with the jaw axis. The lateral side shows a series of small nutritional foramina. A large foramen is present anteroventrally on the symphyseal region. The dental battery is made up of 33 tooth positions, each with 4–5 successional teeth including two well-preserved functional teeth and up to three replacement teeth. The alveolar wall is broken and the enamelled surface of most of the teeth is missing. The mean mesiodistal length of the teeth is 6 mm, only slightly greater than

that of the maxillary teeth. The crowns are diamond-shaped and bear a single median carina. Their height/length ratio is about 3.5 in the anterior positions. Most of the teeth are straight, apart from those of the ends which are slightly curved distally. The angle between the crown and the root cannot be measured.

Surangular (BLA-99/664, Figures 6, 7). A right surangular is almost complete and relatively large (11 cm long as preserved). There is no surangular foramen.

The presence in the Blasi 1 hadrosaurid of a dental battery composed of closely packed tooth families, narrow maxillary teeth, and more than 29 dentary tooth positions are hadrosaurid synapomorphies (Weishampel & Horner, 1990; Weishampel et al., 1993). The absence of a surangular foramen is common to all hadrosaurids except *Protohadros* (Head, 1998).

The Blasi 1 hadrosaurid clearly differs from *Telmatosaurus transsylvanicus* in having a shorter jugal that is more expanded rostrally, narrower dentary teeth not recurved distally, and a single prominent carina in the dentary teeth (Weishampel et al., 1993). It is also more derived than *Telmatosaurus* and two indeterminate euhadrosaurians from Fontllonga and Valencia (Company et al., 1998; Casanovas et al., 1999a) in having a coronoid process inclined rostrally, a median single carina on the dentary teeth, and a complete absence of secondary ridges on the crowns. Based on these characters, the Blasi 1 hadrosaurid could be assigned to the Euhadrosauria as a member of the clade Hadrosaurinae plus Lambeosaurinae (Weishampel et al., 1993; Casanovas et al., 1999a).

By comparison with the derived hadrosaurids, the Blasi 1 hadrosaur shows a mosaic of both hadrosaurine and lambeosaurine features. The shallow caudal jugal process and its scalloped ventral margin are regarded as synapomorphies for 'brachylophosaur' hadrosaurines (Horner, 1988; Weishampel et al., 1993). On the other hand, the flat and dorsoventrally expanded rostral process, and the height of the postorbital process are reminiscent of lambeosaurines, mainly *Hypacrosaurus altispinus* (Gilmore, 1924). The presence of very high dentary crowns seems to be more frequent in lambeosaurines than in hadrosaurines (see Horner, 1990; Casanovas et al., 1999a). The Blasi 1 hadrosaurid differs from the lambeosaurine *Pararhabdodon* of Sant Romà (Figure 1; Casanovas et al., 1999b) in having a less prominent mandibular diastema.

Based on both jugal and dentary characters, the Blasi 1 hadrosaurid may be a new taxon provisionally assigned to Euhadrosauria indet.

Other hadrosaurid material from Blasi 2 and 3. There is no evidence of the occurrence of more than one hadrosaurid species in the Arén sites, but the material is probably too scanty and fragmentary for an accurate account. Isolated hadrosaurid teeth have been recovered from Blasi 2 and 3 (Figure 8). Dentary teeth are similar to those of Blasi 1. Shed maxillary crowns from Blasi 2 may have a strong carina, more prominent than that of the maxillary teeth from Blasi 1.

Hadrosaurid postcranial remains from Blasi sites consist of portions of the vertebral column (including articulated parts) and bones from the appendicular skeleton; the vertebrae show typical hadrosaur features, such as the strongly opisthocoelous cervical centra and amphiplatyan dorsal and caudal vertebrae; the caudal centra bear double separate facets for the chevrons, which form an angle equivalent to that of neural spines (Figure 4; Weishampel & Horner, 1990). The neural spines of the proximal caudals are relatively tall and caudally angled as in *Pararhabdodon*, in contrast to *Telmatosaurus* (Figure 4; compare with Weishampel et al., 1993 and Casanovas et al., 1999b). A hadrosaurine-like, slender, incomplete humerus bears a modestly developed, angular, deltopectoral crest. A rather complete femur, 73 cm long, lacking the distal condyles, is straight as is usual in hadrosaurids. This suggests a body length of about 6 m. Other preserved elements are: a proximal fragment of ulna, a distal end of tibia, a III metatarsal and a phalanx.

4.2. Sauropods

An isolated tooth in Blasi 2 documents the presence of a sauropod, already attested by eggshells. The material is too scanty for accurate identification.

4.3. Theropods

Theropods are represented by three types of isolated teeth from Blasi 2 and 3 (Figure 9, Table 2). Dromaeosauridae indet. A is a large form from Blasi 3, the distal denticles being bigger than the mesial (3 vs. 5 denticles per mm: Currie et al., 1990); since the distal denticles are inclined it may belong to the Velociraptorinae (sensu Rauhut & Werner, 1995). Small teeth fragments from Blasi 2 could belong to this taxon.

Dromaeosauridae indet. B is another small dromaeosaurid from Blasi 2. It differs from type A in having only distal denticles, which are not inclined, and 6–16 denticles per mm. The small size and straight form of the denticles suggest affinities with the
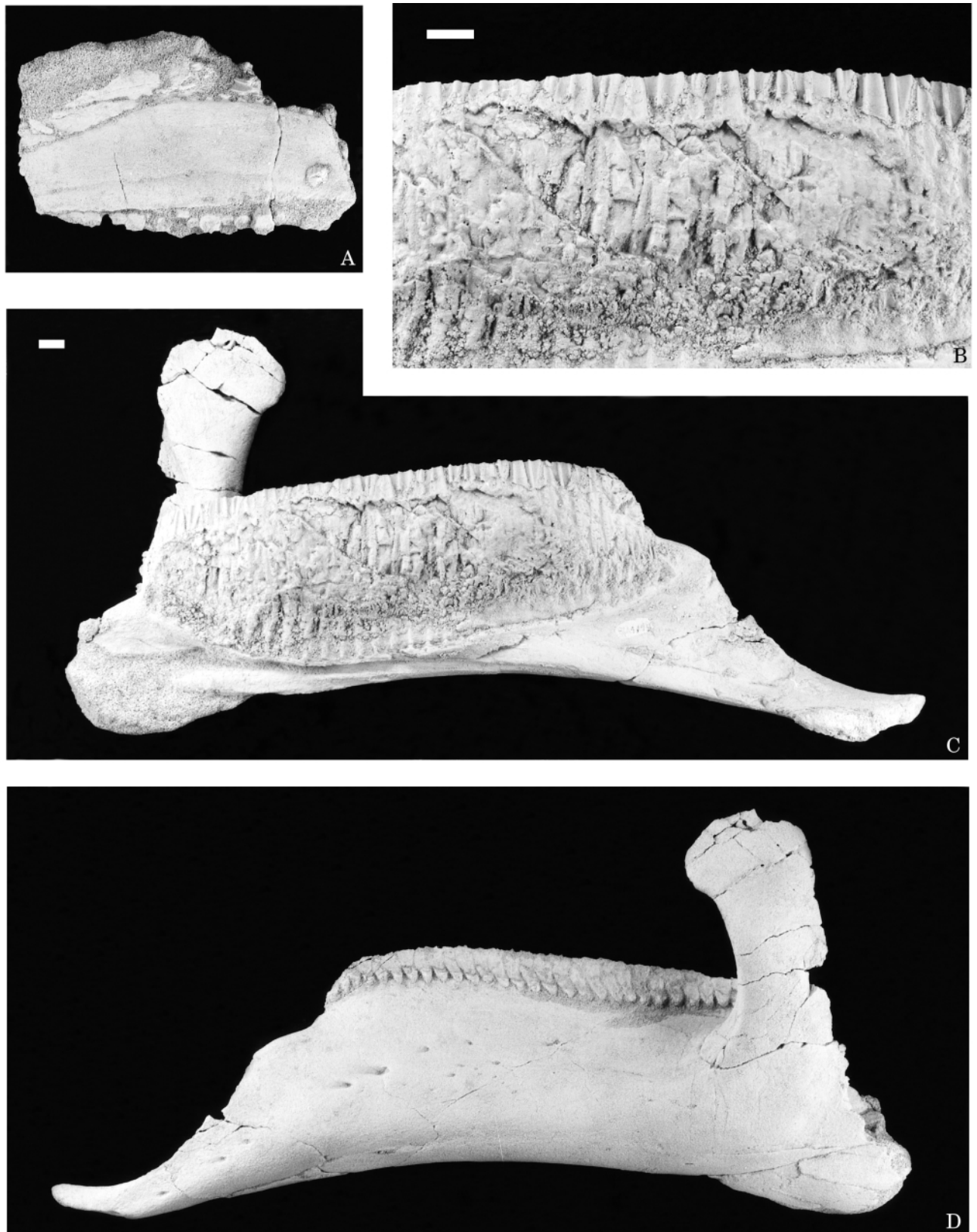
Figure 5. Euhadrosauria indet.: skull bones and lower jaw from Blasi 1 (Arén, Huesca; Late Maastrichtian). A, left maxilla (MPZ 99/666); B–D, left dentary (MPZ 99/665): A, D, lateral views; B, C, medial views. Scale bars represent 10 mm.
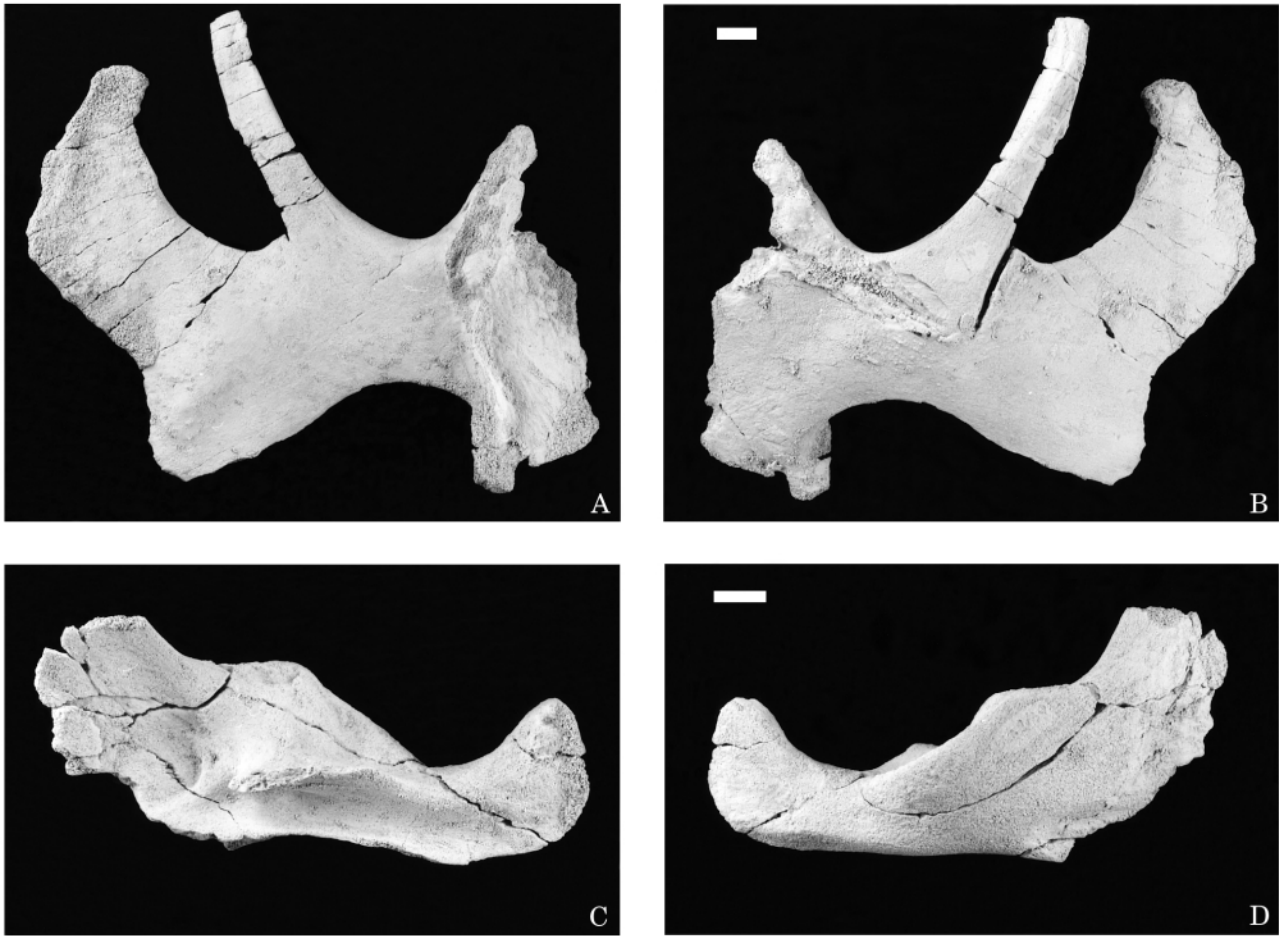
Figure 6. Euhadrosauria indet.: skull bones and lower jaw from Blasi 1 (Arén, Huesca; Late Maastrichtian). A, B, left jugal (MPZ 99/667); C, D, right surangular (MPZ 99/664): A, C, medial views; B, D, lateral views. Scale bars represent 10 mm.

Dromaeosaurinae (Currie *et al.*, 1990). Dromaeo-saurids are a common group of theropods in Upper Cretaceous deposits of southern and central Europe (see Csiki & Grigorescu, 1998).

Small unserrated teeth from Blasi 2 with vertical crests are attributed to cf. *Euronychodon* sp. (Antunes & Sigogneau Russell, 1991). The status of *Euronychodon* is uncertain. It represents a peculiar, small coelurosaurian theropod having close affinities with either maniraptorans or ornithomimosaurs (see Csiki & Grigorescu, 1998).

Other similar teeth from Blasi 2 but without crests, here assigned to Coelurosauria indet., may correspond to one of these small forms or to a different type.

4.4. Eggshells

Blasi 2 has provided about 200 eggshell fragments of at least seven types (López-Martinez *et al.*, 1999a).

One type is 0.75 mm thick and has an undulating external surface with scattered depressions, a tubo-spherulitic structure, mamillary cores well-separated from each other, and shell units that coalesce upwards. It is similar in construction but thinner than *Megaloolithus pseudomamillare*, a Megaloolithidae with coalescent shell units found in Peru, France and Spain (Vianey-Liaud & López-Martínez, 1997; Vianey-Liaud *et al.*, 1997). The oofamily Mega-loolithidae is attributed to sauropod titanosaur dinosaurs (Chiappe *et al.*, 1998).

The other six eggshell-types have 'ornithoid' prismatic structure. This ootype has been found associated with embryos of theropod dinosaurs and birds (Varrichio *et al.*, 1997). They measure 0.6–0.18 mm in thickness and differ in their mamillary core, prism and micropore patterns, type of external surface sculpture, and presence or absence of an external zone.
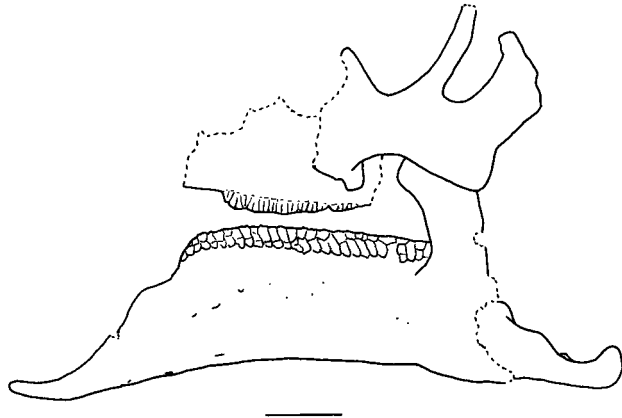
Figure 7. Euhadrosauria indet. from Blasi 1 (Arén, Huesca). Reconstruction of the skull and lower jaw in left lateral view (right surangular reversed). Scale bar represents 50 mm.

5. Other vertebrate remains

The Arén vertebrate fossils also include remains of actinopterygians, amphibians, squamates, turtles and crocodilians, mostly found at Blasi 2 (Table 1). Actinopterygians are represented by lepisosteiforms (ganoid scales and teeth), pycnodontiforms (teeth) and indeterminate teleosteans. The herpetofauna is represented by indeterminate amphibians, squamates (teeth from lizards and possible iguanids) and abundant turtle and crocodilian remains.

The remains of turtle shell plates and plate fragments are referable to a single pleurodiran taxon. The ornamentation of the plates is smooth with very fine, dichotomized *sulci*, typical of bothremydids such as *Polysternon* and *Elochelys* (Lapparent & Murelaga, 1996). The size of the plates indicates a rather thick carapace about 30 cm long and 25 cm wide. It suggests that they belong to cf. *Polysternon* sp., already found in Lower Maastrichtian deposits at Fontllonga 6 (Ager syncline: Murelaga *et al.*, 1998). This genus is common in Campanian and Maastrichtian freshwater deposits of the Ibero-Armorican realm, but it is also found in coastal deposits, because these turtles would have made use of marine littoral streams to migrate (Broin, 1977; Lapparent & Murelaga, 1996).

Crocodilian remains consist mostly of isolated teeth and osteoderms. The tooth shapes indicate at least three different forms in the assemblage: (1) a tribodont (button-like) form from Blasi 2 is similar to those of the small alligatorid *Acynodon*, hitherto known from Spain and France (Buscalioni *et al.*, 1997); (2) a striated, 'trematochampsid'-like form from Blasi 2; and (3) smooth, conical teeth from Blasi 1 and 2 that probably represent an alligatoroid.

6. The charophytes

6.1. Assemblage composition

The Blasi 2 charophyte assemblage includes four species: *Feistiella* sp. nov. (Porocharaceae), *Amblyochara concava* ssp. Grambast-Fessard, *Amblyochara* sp. A Feist and *Peckichara sertulata* Grambast (Characeae).

The new species of *Feistiella* is referable to the genus on the basis of its small apical pore, which is always open, and its undivided basal plate. The subglobular middle-sized gyrogonites differ from all the described species of *Feistiella* and of *Porochara*, whose basal plates have not been described. *Feistiella* has been reported from Berriasian–Upper Maastrichtian strata (Schudack, 1986); moreover, new material from the Dano-Montian locality of Péloua in the Northern Pyrenees (Massieux *et al.*, 1989) has revealed the persistence of the genus during the Early Tertiary.

Amblyochara concava ssp. Grambast-Fessard is assigned to *Amblyochara* on the basis of its undifferentiated apical part, the concave spiral cells and the very thin basal plate, and to *A. concava* because of its subglobular general shape and the protruding junction line of the spirals at the apex. The gyrogonite shape resembles that of the type species from the Montian Mons locality, which is however, larger (Table 3). The size of the Blasi species recalls *A. concava mucronata* Feist from Barranco de La Posa, in the Tremp Basin (Feist & Colombo, 1983), now attributed to the latest Campanian, but it differs in being more globular.

Amblyochara sp. A Feist is characterized by large (1050–1080 × 1150–1100 μm), ovoid gyrogonites having barely visible spiral sutures and a slightly tapering base. It has been reported under the name *A. begudiana* from the Upper Maastrichtian 'Marnes d'Auzas' in southern France (Massieux *et al.*, 1979), as well as from the Fontllonga section where it occurs in three uppermost Maastrichtian levels of the Tremp Formation (chrons C31n to C29r; Galbrun *et al.*, 1993, fig. 6).

The Blasi *Peckichara* specimens are referable to *P. sertulata* on account of their general shape and dimensions. They differ in that the intercellular crest is thick or double instead of lamellar as in the type material from the upper Rognacian of southern France (Grambast, 1971; Westphal & Durand, 1990). Hence they recall *Peckichara* sp. 1 Feist, which occurs in chron C30n in the Fontllonga section (Late Maastrichtian; Galbrun *et al.*, 1993). The latter species is, however, larger and the morphology of the basal part differs. *Peckichara sertulata* ranges from Late Campanian to Late Maastrichtian (Figure 3; Galbrun *et al.*, 1993; Riveline *et al.*, 1996).
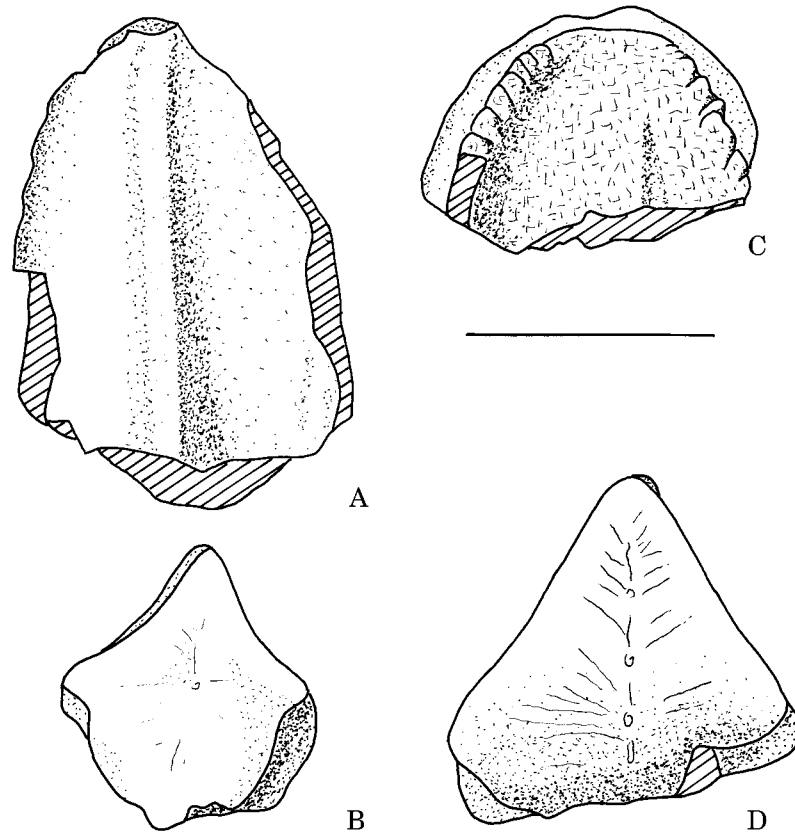
Figure 8. Isolated hadrosaurid teeth from Blasi 2. A, left dentary tooth (MPZ 99/668) in lingual view. B, shed maxillary tooth (MPZ 99/669) in occlusal view. C, right maxillary tooth (MPZ 99/670) in labial view. D, shed maxillary tooth (MPZ 99/671) in occlusal view. Scale bar represents 5 mm. Note the papillae and rough enamel in MPZ 99/670, and the absence of papillae and smooth enamel in MPZ 99/668.
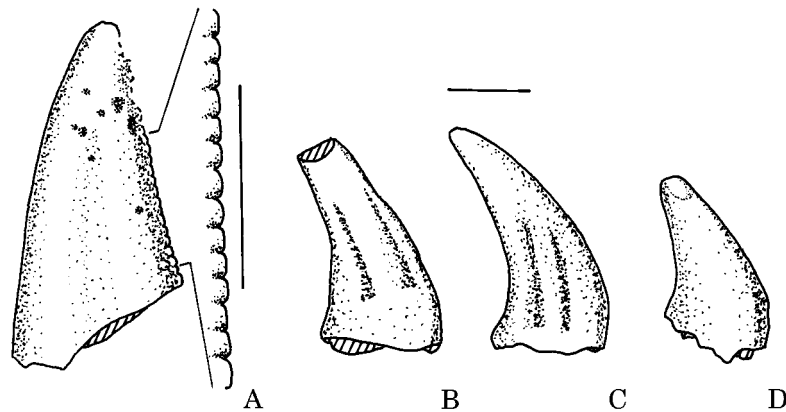
Figure 9. Theropod teeth from Blasi 2. A, Dromeosauridae indet., type B (MPZ 98/72), with detail of distal denticles. B, cf. *Euronychodon* sp. (MPZ 98/76). C, cf. *Euronychodon* sp. (MPZ 98/77). D, Coelurosauria indet. (MPZ 98/82). Views A and D are labial/lingual; B and C are lingual. Note the pits on the enamel of MPZ 98/72, possibly related to corrosion by digestion, and the wear facet in MPZ 98/82. Scale bars represent 1 mm.

6.2. Biostratigraphic and palaeoecological indications

According to the ranges of the four species (Table 4), the age of the Blasi assemblage appears to be Late Maastrichtian. The peculiar morphology of the Blasi representative of *P. sertulata*, recalling *P.* sp. 1, is compatible with the young dating suggested by the marine fossils (see below).
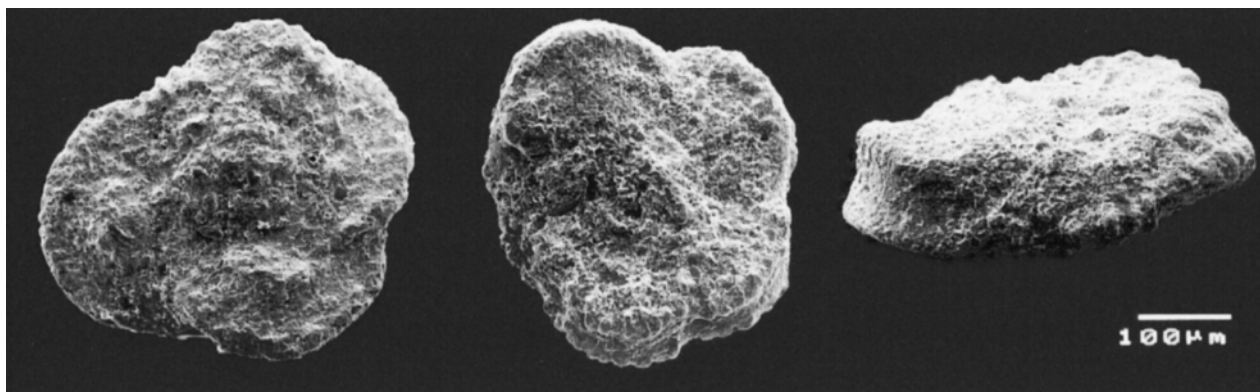
Figure 10. The planktonic foraminifer *Abathomphalus mayaroensis* from the Esera valley (Arén 4 sequence, sample 5, section 1; Figure 2). A, spiral side; B, umbilical side; C, lateral view.

In contrast to most charophyte species, which occupy freshwater biotopes, representatives of the Porocharaceae can tolerate a wide range of salinities, from freshwater–oligohaline to brachyhaline (Schudack *et al.*, 1998). In the Pyrenees, *Feistiella* has been found previously only at the base of the Tremp Formation, in contact with the marine Arén Sandstone [F. ('*Porochara*') *oblonga* Grambast in Llimiana, and F. ('*Porochara*') *malladae* (Bataller) in Barranco de la Posa (Feist & Colombo, 1983)]. Thus, the Blasi 2 assemblage confirms its transitional position between marine and freshwater deposits, indicating saline influences in the Blasi 2 area.

7. Dating the Arén dinosaur sites

Marine–continental correlations can be physically traced from east to west along the northern flank of the Tremp syncline, owing to the excellent exposure. The dinosaur-bearing strata have been dated by means of planktonic foraminifera, present in laterally equivalent basinal deposits. We follow here the depositional-sequence framework introduced by Ardèvol *et al.* (2000), which distinguish four westward-prograding depositional sequences, Arén 1–4 (Figure 2). Each sequence builds a clinoform made up of basinal turbidites, deltaic deposits and continental red beds. The locations of micropalaeontological samples and the foraminiferal assemblages that enable these four depositional sequences to be dated, are shown here. In addition, magnetostratigraphy, charophyte and palynomorph data have been taken into account.

The upper interval of the Arén 1 depositional sequence contains foraminifera from the *Globotruncanella havanensis* Biozone (sample 1, section 7; Figure 2). The new biostratigraphic scale divides the former *Globotruncana falsostuarti* Biozone into *Globotruncanella havanensis* and *Globotruncana aegyptiaca* biozones, and places them in the Late Campanian instead of the Early Maastrichtian (Robaszynski & Caron, 1995; Gradstein *et al.*, 1995).

The Arén 2 sequence can be assigned to the *Globotruncana aegyptiaca* Biozone and the lower part of the *Gansserina gansseri* Biozone, because the upper interval of this sequence has provided the foraminifera *Contusotruncana fornicata*, *C. walfischensis*, *Globotruncana arca*, *G. ventricosa*, *Globotruncanita stuarti*, *G. stuartiformis*, *Pseudotextularia nuttalli*, *Rugoglobigerina milamensis*, and others (sample 2, section 3; Figure 2).

The lower interval of the Arén 3 sequence contains planktonic foraminifera from the upper *Gansserina gansseri* Biozone (lower sample 3, section 3; Figure 2). Consequently, the H-3 sequence boundary between the Arén 2 and Arén 3 sequences is situated in the middle part of the *Gansserina gansseri* Biozone, which approximately coincides with the Campanian/Maastrichtian boundary (Figure 3).

Towards the upper part of Arén 3 sequence, the planktonic foraminifera decrease from about 20 to 12 species, among those present being *Globotruncana arca*, *Globotruncanita stuarti*, *Pseudotextularia nuttalli*, *Pseudoguembelina palpebra*, *Planoglobulina brazoensis* and *P. acervulinoides*. The uppermost interval of the Arén-3 sequence has been attributed to *Abathomphalus mayaroensis* Biozone by García Senz *et al.* (in press). However, additional sampling has led to the rejection of this age. Instead, it is taken to correspond to the highest part of the *Gansserina gansseri* Biozone, based on rich samples with more than 30 planktonic species, among which are *Contusotruncana walfischensis*, *P. acervulinoides*, *P. multicamerata*, *Pseudotextularia intermedia*, *Racemiguembelina fructicosa*, *R. powelli*, *Rugoglobigerina hexacamerata* and

Table 1. Faunal list of the vertebrates from Arén sites, Late Maastrichtian, Huesca Province, southern Pyrenees.

	Blasi					
	1	1b	2	3	4	5
Lepisosteiformes						
Lepisosteidae indet.			x			
Pycnodontiformes indet.			x			
Teleostei indet.			x			
Amphibia indet.			x			
Squamata						
Lacertilia indet.			x			
Iguanidae indet.			x			
Chelonii						
Pleurodira						
Bothremydidae						
cf. *Polysternon* sp.			x	x	x	x
Crocodyliformes						
Crocodylia indet. (osteoderms)			x			x
'Trematochampsidae' indet.			x	x		
Eusuchia						
Eusuchia indet. (vertebra)				x		
Alligatoroidea indet.	x		x	x		
Alligatoridae						
Acynodon sp.			x			
Dinosauria						
Sauropoda indet.			x			
Theropoda						
Theropoda indet.				x		
Tetanurae						
Coelurosauria indet.			x			
Dromaeosauridae indet. A (Velociraptorinae?)			?	x		
Dromaeosauridae indet. B (Dromaeosaurinae?)			x			
cf. *Euronychodon* sp.			x			
Ornithopoda						
Hadrosauridae						
Hadrosauridae indet.		x		x	x	x
Euhadrosauria indet.	x		x			

R. milamensis (upper sample 3, section 3, and sample 4, section 2; Figure 2). Consequently, the age of the Arén 3 sequence ranges from Early to early Late Maastrichtian (Figure 3).

The lowermost interval of the Arén 4 sequence approximately coincides with the appearence of *Abathomphalus mayaroensis* (latest Maastrichtian Biozone), since it has provided at least 32 species of planktic foraminifera, among them being *Abathomphalus mayaroensis*, *Contusotruncana contusa*, *C. walfischensis*, *Planoglobulina acervulinoides*, *Pseudotextularia intermedia*, *Racemiguembelina fructicosa* and *Rugoglobigerina hexacamerata* (sample 5, section 1; Figure 2). This interval is above the Horizon-4 sequence boundary, which can be traced landward about 60 m below the Blasi 1 site (Figure 2).

The upper boundary of the Arén 4 sequence in the Esera valley (Horizon 5) coincides with the top of the Arén Formation (section 1; Figure 2), dated as Late Cretaceous on the basis of fossil content (Garrido Mejías & Ríos Aragües, 1972). Consequently, the Arén 4 sequence and its dinosaur sites described in this paper are situated in the *Abathomphalus mayaroensis* Biozone, dated as latest Maastrichtian. The Blasi 1–3 sites correlate with the lower part of this biozone, thus around 68 Ma, and the Blasi 4–5 sites with the middle part, about 67 Ma (Figures 2, 3). The *A. mayaroensis* Biozone in the Tremp Basin reaches its

Table 2. Measurements in mm and characters of Theropoda from Arén; FABL, fore-aft basal length.

Site	Code	Name	FABL	height	basal width	dent/mm mesial	dent/mm distal
Blasi 3	MPZ98-67	Theropoda indet.	27	>27.5	13	broken	broken
	MPZ98-68	Dromeosauridae indet. (Velociraptorinae?)	16	>18	—	4.83–5.23	2.81–3.01
Blasi 2	MPZ98-69	Theropoda indet.	—	1.7	—	—	2.81
	MPZ98-70	Theropoda indet.	—	2.3	—	—	3.74
	MPZ98-71	Theropoda indet.	—	1.5	—	—	4.18
	MPZ98-72	Dromeosauridae indet. (Dromeosaurinae?)	2.23	4.32	1.07	—	7.57
	MPZ98-73	Dromeosauridae indet. (Dromeosaurinae?)	2.19	3.35	0.93	—	6.54 mid 13.15 base 10.87 all
	MPZ98-74	Dromeosauridae indet. (Dromeosaurinae?)	1.39	3.02	0.6	—	irregular 8.77
	MPZ98-75	Dromeosauridae indet. (Dromeosaurinae?)	1.39	2.65	0.74	—	8.2–10.87
	MPZ98-76	cf. *Euronychodon* sp.	1.49	2.74	0.6	—	15.87
	MPZ98-77	cf. *Euronychodon* sp.	1.39	2.79	0.6	—	—
	MPZ98-78	cf. *Euronychodon* sp.	1.21	2.23	0.84	—	—
	MPZ98-79	Coelurosauria indet.	1.86	1.86	1.02	—	—
	MPZ98-80	Coelurosauria indet.	1.81	2.56	0.88	—	—
	MPZ98-81	Coelurosauria indet.	1.39	1.91	0.74	—	—
	MPZ98-82	Coelurosauria indet.	1.21	2.42	0.74	—	—

Table 3. Comparison of the *Amblyochara concava* ssp. from Blasi 2 with the two subspecies of *A. concava*.

Amblyochara	length μm	width μm	ISI (l/w × 100)	N (number of spirals visible in profile)
A. concava concava	950–1150	950–1300	90–102	7–8
A. concava ssp.	575–750	575–760	82–135	7–9
A. concava mucronata	500–775	725–950	70–90	5–7

maximum thickness, being about 200–250 m in the Blasi section and more than 650 m in the Esera valley (sections 1 and 6; Figure 2).

According to the fossil content of the Esera and Isábena sections, the position of the Cretaceous/Tertiary boundary is situated in the middle part of the Tremp Formation, about 50 m above the top of Arén Formation. This is based on the occurrence of auto-chtonous rudists and the ammonite *Pachydiscus gollevillensis* 48 m above the Arén Formation in the Esera section (Eichenseer, 1988), and dinosaur sites in stratigraphically equivalent rocks in the Isábena section. The H-5 sequence boundary and the lower part of the overlying depositional sequence is therefore situated in the uppermost Cretaceous. The position of the Cretaceous/Tertiary boundary in the Tremp Basin agrees with that of the Ager valley, situated near the lower/middle boundary of the Tremp Formation (López-Martínez *et al.*, 1998). There is no basis, therefore for a Tertiary age determination for the top of the Arén 4 sequence as suggested by Fondecave-Wallez *et al.* (1990) and Galbrun *et al.* (in press). The method used by the former ('grade-dating' analysis) is based on the assumption that the selected foraminiferal lineage evolved gradually, but the results of this method have already been rejected in Northern Pyrenees by Bilotte *et al.* (1999). Galburn *et al.* interpreted as chron C28r a long reverse magnetozone across the transition between the Aren and Tremp Formations, which in fact ties in better with chron C29r.

8. Other Maastrichtian dinosaur localities in the south-central Pyrenees

Previous dinosaur discoveries in the south-central Pyrenees dated as Late Maastrichtian have been reported to the east of Arén (Lleida, Figure 1). On the northern limb of the Tremp syncline, the Els Nerets site (=Vilamitjana; Casanovas *et al.*, 1987), with

Table 4. Chronological ranges of the charophyte species from Blasi 2.

Stages \ Species	*Feistiella* sp.	*Amblyochara concava* ssp.	*Amblyochara* sp. A	*Peckichara sertulata*
Dano-Montian	■	■	■ (lower part)	
Latest Maastrichtian	■	■		■
Early Late Maastrichtian	■	■		■
Early Maastrichtian	■	■		■

titanosaurid and hadrosaurid remains, occurs in the uppermost interval of the Arén 2 sequence, dated as latest Campanian (Ardévol *et al.*, 2000; see above and Figures 1, 2). The Sant Romà site, with only hadrosaurids (type locality for *Pararhabdodon isonensis*; see Casanovas *et al.*, 1999b and references therein) is 70 m below lacustrine limestones dated Late Maastrichtian on the basis of charophytes (*Peckichara sertulata*, *Maedleriella* sp. A and *Peckichara* with tubercles; Feist & Colombo, 1983).

On the southern limb of the Tremp syncline, sites at Moror and Barcedana have provided sauropod and hadrosaurid bones (Figure 1). These are below grey marl beds with two charophyte species of the genus *Septorella* (Brinkmann, 1984; Masriera & Ullastre, 1988). *Septorella brachycera* disappears within the early Chron C31n (Galbrun *et al.*, 1993; Riveline *et al.*, 1996; about 68.5 Ma according to Cande & Kent, 1995), just below the *Abathomphalus mayaroensis* datum (Pujalte *et al.*, 1995; Figure 3); thus these sites cannot be younger than early Late Maastrichtian.

Westward from Arén, large titanosaurids have been reported from Serraduy (Huesca, Canudo *et al.*, 1999). They correspond to the upper part of the Arén 4 sequence of latest Maastrichtian age (upper *Abathomphalus mayaroensis* Biozone; Figure 2).

South of the Montsec thrust, the Fontllonga site in the Ager syncline (Figure 1) has yielded a hadrosaurid dentary, dated in the highest part of Chron C30n (latest Maastrichtian, about 66 Ma; Casanovas *et al.*, 1999b). In this area, dinosaur footprints have been recorded on uppermost Maastrichtian rocks close to the Cretaceous/Tertiary boundary, dated in Chron C29r, 15 m above the hadrosaur site and 3 m below both a δ^{13}C isotopic anomaly and Paleocene

fossil sites (López-Martínez *et al.*, 1998, 1999b; Peláez-Campomanes *et al.*, 2000).

Summarizing, other dinosaur sites in the south-central Pyrenees have yielded: (1) titanosaurs and hadrosaurs (*Pararhabdodon*) ranging in age from latest Campanian (Els Nerets) to Early Maastrichtian (Moror and Barcedana); (2) two different hadrosaurs (*Pararhabdodon* and a primitive Euhadrosaur dated as Late Maastrichtian; Sant Romà and Fontllonga); (3) a large sauropod from the latest Maastrichtian (Serraduy); and (4) diverse dinosaur footprints high in chron C29r, reaching the top of the Cretaceous. These records show the continuity and sustained diversity of dinosaur fauna in the Spanish Pyrenees during the Late Maastrichtian, now reinforced with four more taxa from the new Blasi sites (a third hadrosaur and three theropods). Moreover, there is a coincidence between the highest stratigraphic record of the Spanish dinosaurs and the Cretaceous/Tertiary boundary, marked by the younger part of chron C29r and a δ^{13}C isotopic anomaly.

9. Other Maastrichtian dinosaur localities in Europe

Latest Cretaceous dinosaur sites have been extensively reported from many parts of Europe: Petites-Pyrénées; Plantaurel, Hautes-Corbières, Bas-Languedoc (French Pyrenees); Aix en Provence (France); Transylvania (Romania); Limburg (Netherlands, Belgium); Bavaria (Germany) and Crimea (Ukraine). Some uncertainty exists concerning the accurate dating of the sites because many of them occur in non-marine rocks which cannot be correlated with marine deposits; moreover, where associated marine fossils exist, their stratigraphic

ranges are often ill-defined. The chronological evidence is discussed here in relation to the timescale of Gradstein et al. (1995).

In southern Europe, some dinosaur sites from the northern Pyrenees and Provence have been dated as Late Maastrichtian on the basis of the occurence of the charophyte *Septorella* (Buffetaut & Le Loeuff, 1991; Buffetaut et al., 1997; Gheerbrant et al., 1997; Laurent et al., 1999), but this genus in fact appeared in Late Campanian and disappeared early in the Late Maastrichtian, before the arrival of *Abathomphalus mayaroensis* (see above, Figure 3).

This observation applies to the Le Jadet and Lestaillats sites in the Petites Pyrénées, which has yielded dinosaurs (hadrosaurids, nodosaurids and theropods), crocodilians, turtles and actinopterygians (Paris & Taquet, 1973; Buffetaut & Cavin, 1995; Laurent et al., 1999). These sites occur in calcarenites below the 'Marnes d'Auzas', which are more than 200 m thick in the type section and contain *Septorella* near the top (Bilotte et al., 1983; Bilotte, 1985; Lepicard, 1985; Lepicard et al., 1985; Breton et al., 1995). Hence, the age of these dinosaur sites is probably greater than Early Maastrichtian (Figure 3). Other dinosaur sites with indeterminate hadrosaurids and theropods have been found in the basal part of the 'Marnes d'Auzas' (Peyrecave A and B, Tricouté 1 and 2, Auzas; Gheerbrant et al., 1997); they contain both species of *Septorella* and, therefore, range in age from Late Campanian to early Late Maastrichtian. Finally, the upper part of the Marnes d'Auzas contains only one *Septorella* species or none; as a result it may be dated as mid–late Late Maastrichtian; this is the case of the Mérigon site (Ariège) with remains of turtles, crocodilians, pterosaurs and hadrosaurid dinosaurs and the charophytes *Microchara cristata* and *Maedleriella* sp. A (Bilotte, 1985; Lepicard et al., 1985; Tambareau et al., 1997; Buffetaut et al., 1997; Figure 3).

The last occurrence of the charophyte *Septorella ultima* is considered to be coeval with that of *Septorella brachycera* (early Late Maastrichtian, about 69 Ma, Riveline et al., 1996; Figure 3). However, the record of *S. ultima* in several localities where *S. brachycera* is absent suggests that it survived longer (Figure 3). The Le Bexen site (eastern Corbières; Laurent et al., 1997), which has provided chelonians, crocodilians, pterosaurs, and hadrosaurid (*Pararhabdodon* sp.) and dromaeosaurid dinosaurs, has yielded only *Septorella ultima* and may thus be mid Late Maastrichtian age.

The Languedoc-Provence dinosaur sites have not yet provided reliable evidence of age despite some tentative magnetostratigraphic correlations (Westphal & Durand, 1990; Galbrun, 1997). In the Aix Basin (Provence), the Vitrolles-Couperigne dinosaur site has yielded an ornithopod skeleton (*Rhabdodon priscus*), dromeosaurid teeth and three types of eggshells (Garcia et al., 1999). It has been dated as Early Maastrichtian on the basis of the presence of the charophyte *Peckichara cancellata* (early 'Rognacian'); in fact, recent recalibration of the range of this species places it entirely within the Late Campanian (Riveline et al., 1996).

In Eastern Europe, dinosaurs are known mainly from the Romanian Haţeg Basin and from Sebes, Transylvania (Grigorescu, 1992). Several scattered localities in red beds that are >1000 m thick have yielded sauropods (the titanosaurid *Magyarosaurus*), four theropods (dromaeosaurids, troodontid-like small theropods, cf. *Euronychodon*, and neoceratosaurs), ornithopods (the euornithopod *Rhabdodon* and the hadrosaurid *Telmatosaurus*) and ankylosaurs (the nodosaurid *Struthiosaurus*) together with fishes, amphibians, turtles, crocodilians, pterosaurs and mammals (Weishampel et al., 1991, 1993; Grigorescu et al., 1994; Csiki & Grigorescu, 1998). These sites have been considered to be Late Maastrichtian on the grounds that the youngest underlying marine deposits are Late Campanian–Early Maastrichtian; in fact the age-range of the foraminifer *Lepidorbitoides minor*, for long considered to be a Maastrichtian marker species, is Late Campanian according to recent calibrations (lower *Gansserina gansseri* Biozone; Caus et al., 1988). The middle part of the dinosaur-bearing red beds is supposed to be Maastrichtian because it contains the palynomorph *Pseudopapillopollis praesubhercynicus* (Weishampel et al., 1991; Grigorescu et al., 1994); however this criterion is unreliable, because there is a continuous succession of palynomorph taxa across the Cretaceous/Tertiary transition in the Tethys area, the stratigraphic ranges of which are imprecisely known (Méon, 1991; Médus et al., 1992; López-Martínez et al., 1999b).

In Northern Europe, the Dutch-Belgian Limburg region has provided mainly hadrosaurids and theropods from the Maastricht Formation (Emael, Nekum and lower Meerssen members; see Mulder et al., 1997, 1998 for a review). The stratigraphically higher findings have been placed in the *Belemnitella junior* Biozone, assigned to the early Late Maastrichtian (Mulder et al., 1997; Smit et al., 1998); the top of this biozone, i.e., the base of the overlying *B. casimirovensis* Biozone, has been correlated with the base of the *A. mayaroensis* Biozone by Swinburne (1990; c. 69 Ma) by means of $^{87}Sr/^{86}Sr$ isotopic ratios. Using this same method Vonhof & Smit (1996) have, however, arrived at a different estimation for the base of this biozone, dated at approximately 150 000 years

before the end of the Cretaceous Period. Thus, either wrong dating or a highly diachronous boundary between *Belemnitella junior* and *B. casimirovensis* biozones (4 Ma; Christensen, 1996) has affected the calibration of the youngest dinosaur sites in Northern Europe.

In Central Europe, postcranial hadrosaurid remains have been found in marine deposits of the prealpine Helvetikum Zone in Bavaria (Wellnhofer, 1994). These deposits have been assigned to the *Gansserina gansseri* Biozone, suggesting a Late Campanian–early Late Maastrichtian age. Also near Sebastopol (Crimea, Ukraine), hadrosaurid limb bones have been found in deposits with the bivalve *Aequipecten meridionalis*, which have been attributed either to the uppermost Maastrichtian *B. casimirovensis* Biozone (Jeletzky, 1962) or to the Danian (see Brinkmann, 1988). Even if this last age determination cannot be trusted, the Crimean locality would be one of the youngest dinosaur sites in Europe, along with those in the south-central Pyrenees.

10. The dinosaur extinction pattern in Europe

A better understanding of the ages of dinosaur assemblages using new chronostratigraphic correlations, mainly those of the Pyrenees, allows the pattern of latest Cretaceous dinosaur succession and extinction in Europe to be approached more precisely. Previous studies, mainly supported by sites in southern France, have concluded that a faunal replacement of dinosaurs occurred in Europe during the Maastrichtian (Le Loeuff *et al.*, 1994; Buffetaut & Le Loeuff, 1997). Late Campanian–Early Maastrichtian dinosaurs would have consisted of dromeosaurid and abelisaurid theropods, titanosaurids, nodosaurids and the ornithopod *Rhabdodon*, while the Late Maastrichtian fauna would have consisted only of hadrosaurids and dromeosaurids (Buffetaut *et al.*, 1997; Le Loeuff, 1998). Titanosaurids were supposed to have declined until they completely disappeared prior to the Late Maastrichtian, whereas hadrosaurids appeared in the Late Maastrichtian as a result of environmental changes linked to a major marine regression.

However, the recent discoveries in Spain together with updated age determinations suggest a different faunal succession. Theropod, titanosaur and hadrosaur dinosaurs show a continuous record from Late Campanian to latest Maastrichtian in Europe. During this long period, the coexistence of titanosaurid sauropods and hadrosaurs is well documented (Casanovas *et al.*, 1987; Pereda Suberbiola & Sanz, 1999; Canudo *et al.*, 1999). The theropod *Euronychodon* is another element continuously present from Late Campanian to

latest Maastrichtian (Antunes & Sigogneau-Russell, 1991; Sigé *et al.*, 1997; Csiki & Grigorescu, 1998; this paper).

The main change during the latest Cretaceous dinosaur succession in Europe was the disappearance during the mid Late Maastrichtian of the euornithopod *Rhabdodon* and the nodosaurid ankylosaurs (*Struthiosaurus*), both of which are common in Upper Campanian and ?Lower Maastrichtian sites in Europe (Brinkmann, 1988; Pereda Suberbiola, 1992; Garcia *et al.*, 1999). Their absence from Upper Maastrichtian deposits indicates that these dinosaurs were probably extinct before the mid Late Maastrichtian (*contra* Weishampel *et al.*, 1991 and Pereda Suberbiola, 1992).

Dinosaur diversity in Europe during the Late Campanian and Maastrichtian was sustained by an increase in numbers of hadrosaurid and theropod taxa, compensating for the loss of the two groups that had become extinct. Therefore, the youngest European dinosaur faunas do not indicate a decreasing diversity.

With respect to the final extinction of all (non-avian) dinosaurs, some authors have suggested that European dinosaurs disappeared well before the Cretaceous/Tertiary boundary. Based on the last occurrence of *in situ* eggshells, Colombo (1996) and Galbrun (1997) have postulated that the extinction of European dinosaurs occurred at least 2 myr before the end of the Maastrichtian (Chron C30n or C31n). The discoveries in the Ager valley (López-Martínez *et al.*, 1998, 1999b; Casanovas *et al.*, 1999b) and at Arén indicate, however, that diverse and abundant dinosaurs were alive close to the end of the Cretaceous Period.

11. Conclusions

This paper documents the occurrence of rich and diverse dinosaur remains of Late Maastrichtian age in the south-central Pyrenees. The Arén sites have provided at least eight dinosaur species, among bones and eggshells: a hadrosaurid provisionally referred to as Euhadrosauria indet., a sauropod, and six distinct theropods (six prismatic eggshell types and teeth from a dromaeosaurine, a velociraptorine and a cf. *Euronychodon*). In addition, the Arén vertebrate assemblages include three crocodilians (the alligatorid *Acynodon*, an indeterminate alligatoroid and a 'trematochampsid'-like mesoeucrocodylian), a turtle (the bothremydid cf. *Polysternon*), squamates, amphibians and fish (lepisosteiformes, pycnodontiformes, teleosteans). Blasi 2 also contains a charophyte assemblage of four species: *Amblyochara*

concava, *Amblyochara* sp. A, *Peckichara sertulata*, and a possible euryhaline marker, *Feistiella* sp. nov.

The dinosaur-bearing deposits at Arén have been correlated in a basinward direction with rocks belonging to the lower and middle part of the uppermost Maastrichtian *Abathomphalus mayaroensis* (planktonic foraminiferal) Biozone, thus not far below the Cretaceous/Tertiary boundary. This is the first report of dinosaur localities correlated with the *Abathomphalus mayaroensis* Biozone, and one of the rare cases of confident, high-resolution stratigraphic correlation between dinosaur sites and marine deposits. Other tentative Late Maastrichtian dinosaur localities in Europe are not well-constrained stratigraphically, or are older.

The composition of Arén assemblages does not support the idea of dinosaurian faunal replacement during the Late Maastrichtian. The main changes concern the extinction of the nodosaurid *Struthiosaurus* and the euornithopod *Rhabdodon*, well represented during the Late Campanian–?Early Maastrichtian. Minor changes are characterized by an increment of hadrosaurids and theropods and a probable decrease in sauropod numbers. Overall, diversity was sustained during the latest Cretaceous in Europe.

The rich dinosaur assemblages from Arén serve to refute previous assumptions of a gradual and diachronous extinction of the dinosaurs, suggesting instead a sudden demise close to the end of the Cretaceous in Europe. However, the decline of some dinosaur groups during the Maastrichtian is also supported by the data. Owing to the still-scattered nature of the fossil record of dinosaurs, more research will be necessary if the end-Cretaceous impact event is to be linked to the final extinction of the dinosaurs in the southern Pyrenees.

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