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Late Maastrichtian continental vertebrates from southwestern France: correlation with marine fauna

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Abstract

The Cassagnau locality (Marignac-Laspeyres, Haute-Garonne department) has yielded the richest vertebrate assemblage of Late Maastrichtian age in western Europe. Numerous bones can be referred to various fishes, amphibians, chelonians, squamates, crocodiles, dinosaurs and birds, some of which constitute the first Late Maastrichtian occurrences in Europe (a large varanoid lizard, a longirostrine crocodile, an enantiornithine bird) or in Southern France (a titanosaurid dinosaur). The latter discovery shows that at least five dinosaur families were represented in the Late Maastrichtian of western Europe. As for other localities of the French Petites Pyrénées, the age of the Cassagnau locality can be directly constrained by biostratigraphical and biochronological evidence based on associated marine and continental microfauna and microflora; therefore, the assemblages from these localities can be considered as reference assemblages for the continental Late Maastrichtian localities of Southern Europe, the age of which has been much disputed.

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1. Introduction

In Europe, the fossil record for the Late Maastrichtian continental vertebrates was almost non-existent in the early 1990s (Buffetaut and Le

Loeuff, 1991); even worse, the precise age of these continental localities is much disputed (Godefroit, 2000). The discovery of two rich localities in tidal marsh deposits of Southern France, where continental vertebrates are found associated with marine microfauna, allows us to define their Late Maastrichtian age more precisely. Remains of fossil vertebrates were mentioned in the Petites Pyrénées as early as 1834 when Dufrenoy reported a few fish remains. Later, Hébert (1862) and Leymerie (1868, 1881) noticed some fish or reptile bones in the Garumnian facies (see Plaziat, 1980

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for stratigraphic correlation of this facies). Only rare bone fragments were discovered during the 20th century (Paris and Taquet, 1973; Ségura, 1979; Bilotte, 1980; Le Loeuff et al., 1994; Buffet and Cavin, 1995), until we began systematic prospections and excavations in 1994 (Laurent et al., 1999). A rich locality was discovered in 1997 at Cassagnau (Marignac-Laspeyres, Haute-Garonne department) (Fig. 1A); its excavation in 1999 yielded a rich vertebrate assemblage partially described below.

2. Geological context

From outcrops in the subpyrenean anticlines of Plagne, Saint-Martory/Saint-Marcet and Aurignac, four major stacked stratigraphical units are defined for the Late Cretaceous and Paleocene strata of the Petites Pyrénées (Fig. 2): from the bottom to the top, the Plagne/Saint-Martory Marls Formation, the Ausseing group including the genuine Nankin Limestone, and the Auzas Marls Formation for the Late Cretaceous and

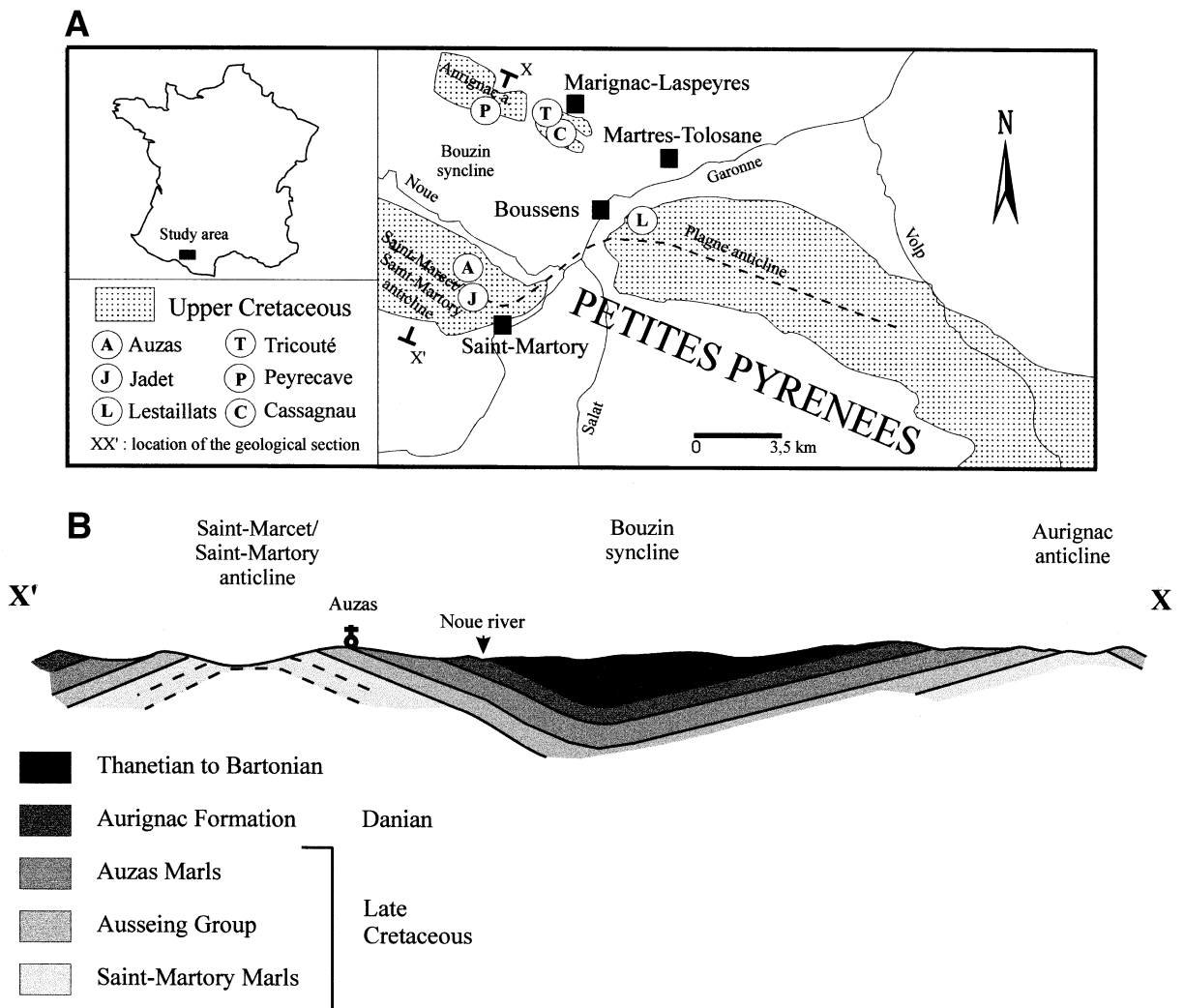


Fig. 1. (A) Map showing the location of Late Maastrichtian vertebrate localities of the Petites Pyrénées. (B) Geological section of the study area showing the relative position of the Late Cretaceous and Tertiary lithological units.

AGES	Aurignac anticline	Saint-Marcel / Saint-Martory Plagne anticlines		Deposital environments	Calcareous Nannofossils	Benthic Foraminifera	
DANIAN 65	Tucaou lithographical Limestones	Lacustrine Limestone	Aurignac Formation	Lacustrine			
	Cassagnau Evaporites	Hauric Dolomites		Sebkha			
MAASTRICHTIAN LATE 69.5	Auzas Marls (C) (F) (P)	Auzas Marls (A)	Ausseing Group	Alluvial plain to lagoon		* <i>Laffiteina mengaudi</i> <i>Hellenocyclus beotica</i>	
	Nankin limestones facies	Jadet Calcarenites (J)		Carbonated ramp		tidal marsh	<i>Orbitoides apiculata</i> <i>Omphalocyclus macroporus</i> <i>Siderolites calcitrapoides</i> <i>Lepidorbitoides socialis</i>
		Lestaillats Marls (L)		Carbonated ramp			
Nankin 2 Limestones							
EARLY 69.5 71.3	Saint-Martory Marls	Saint-Martory / Plagne Marls		Open marine facies	← <i>Arkhangelskiella cymbiformis</i> <i>Cribocorona gallica</i> <i>Lithraphidites quadratus</i>		

Fig. 2. Lithostratigraphical and environmental units of the Late Cretaceous and Early Paleocene in the Saint-Martory/Plagne and Aurignac anticlines.

the Aurignac Formation for the Paleocene consisting of the Cassagnau Evaporites and the Tucaou lithographical Limestones (Lepicard, 1985; Lepicard et al., 1985; Bilotte, 1991). The thickness of the Auzas Marls Formation is about 100 m; they result from terrigenous sedimentation starting in a paralic domain becoming gradually more and more confined and finishing (at the upper level) in the continental domain. This passage from the paralic to limnic domain expresses itself in a succession of environments defined on sedimentological and biological features (Bilotte, 1980; Lepicard, 1985; Lepicard et al., 1985): tidal marsh, tidal muddy channel, euryhaline lagoon, alluvial plain, fluvial channel, paleosol, including marine and continental fauna and flora with vertebrates which are studied in this paper.

The fossiliferous locality is situated to the east of the Aurignac anticline near the farm of Cassagnau, in the Auzas Marls, the last formation of the Late Cretaceous. Three main facies characterize the formation (Fig. 3):

Facies A: poorly stratified marls with ostreid coquina (*Ostrea cf. garumnica*, *Ostrea cf. verneuilii*) and benthic microfauna from a stenohaline but restrictive marine area (lagoon); the main organisms are Foraminifera (*Siderolites calcitrapoides*, *Orbitoides* sp., *Laffiteina mengaudi*, planche 1) and Ostracoda (*Cyanocytheridea* sp., *Oertiella* sp., *Limburgina* sp., *Uroleberis* sp., ...) (det. B. Andreu, work in progress).

Facies B: marls and sandstones with a euryhaline fauna: Bivalvia (*Cyrena garumnica*), Foraminifera (*Laffiteina mengaudi*) and Ostracoda (*Neocyprideis* sp., *Paracandona* sp.) characteristic for paralic brackish environments.

Facies C: gray marls, marly limestones, lacustrine limestones, fluvial sandstones and paleosols corresponding to distal paralic to limnic environments. The fauna and flora is principally: vertebrates (see below), molluscs (gastropoda and bivalves – *Cyrena garumnica*, *Islamia* sp.) (det. J. Villatte), ostracodes (*Paracandona* sp.) and charophytes (*Septorella brachycera*, *Amblyochara lae-*

vigata, *Microchara cristata*, *Maedleriella prisca*, *Peckichara* sp., *Feistiella* sp., ...) (det. M. Feist).

The two vertebrate sites called Cassagnau 1 (CAS1) and Cassagnau 2 (CAS2) are vertically separated by less than 15 m (Fig. 3); they are situated in the middle part of the Auzas Marls, in a transition zone between paralic and limnic deposits. The first Tertiary levels are about 50 m above the fossiliferous levels.

3. Biochronology

The Auzas Marls Formation is referred to the Late Maastrichtian on micropaleontological grounds (fauna and flora); the data were obtained in the formation itself or in the underlying units.

In the western termination of the Saint-Martory/Saint-Marcet anticline, the Saint-Martory

Marls occupy the medial axis of the structure and constitute the oldest lithological unit of the succession (Fig. 1B). In their upper part (Fig. 2), they have yielded a nanoflora with *Arkhangelskiella cymbiformis*, *Cribocorona gallica* and *Lithraphidites quadratus* (det. B. Lambert in Lepicard, 1985), a typical Tethyan Late Maastrichtian marine association (CC 25 in von Salis, 1998).

The overlying genuine Nankin Limestone (Nankin 2, Fig. 2, also known as the 'Calcaire à *Hemipneustes*') yields rich associations of large benthic foraminifera such as *Orbitoides apiculata*, *Lepidorbitoides socialis*, *Omphalocyclus macroporus*, *Siderolites calcitrapoides*, *Siderolites denticulatus*, ... (Bilotte, 1998), microfauna of which the Maastrichtian age is unanimously admitted.

The succeeding Auzas Marls themselves contain rare *Hellenocyclina beotica* in some marine facies at their type locality (Lepicard, 1985); this orbi-

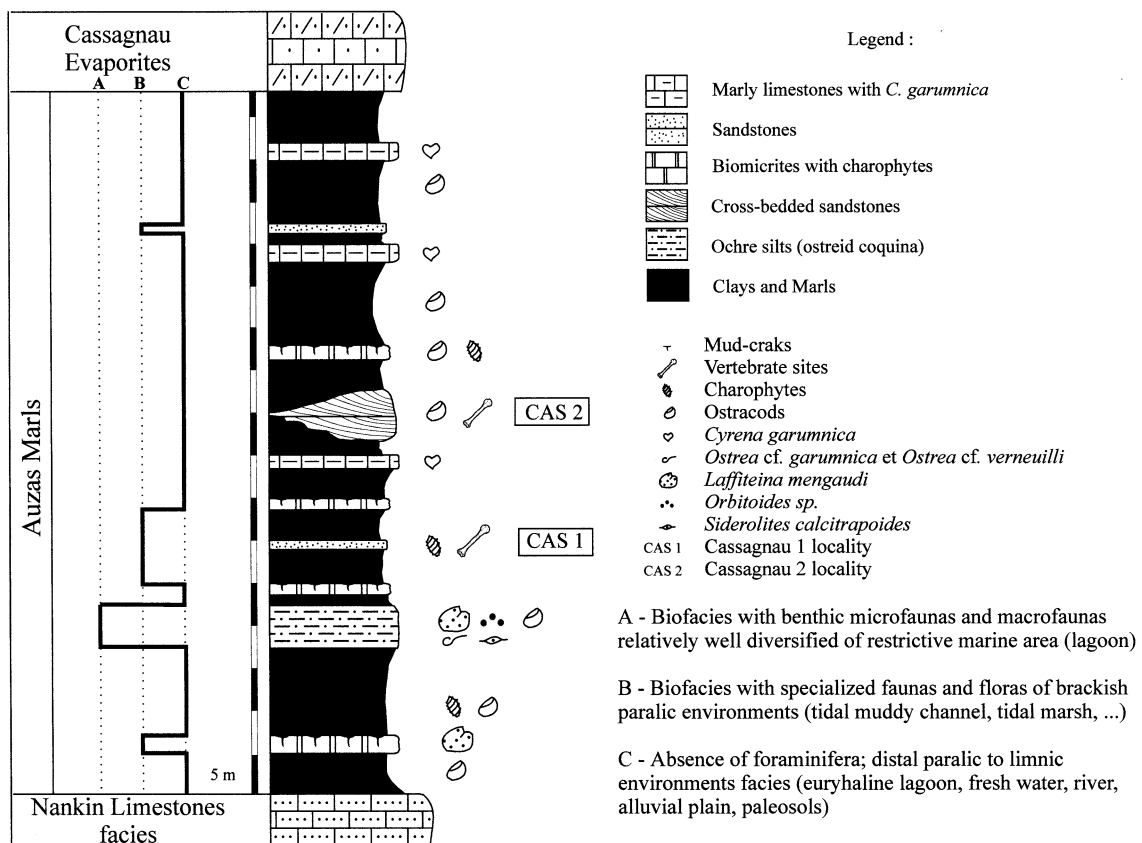


Fig. 3. Ranges show the facies (lithological and biological) in the Auzas Marls Formation at Cassagnau (after Lepicard, 1985).

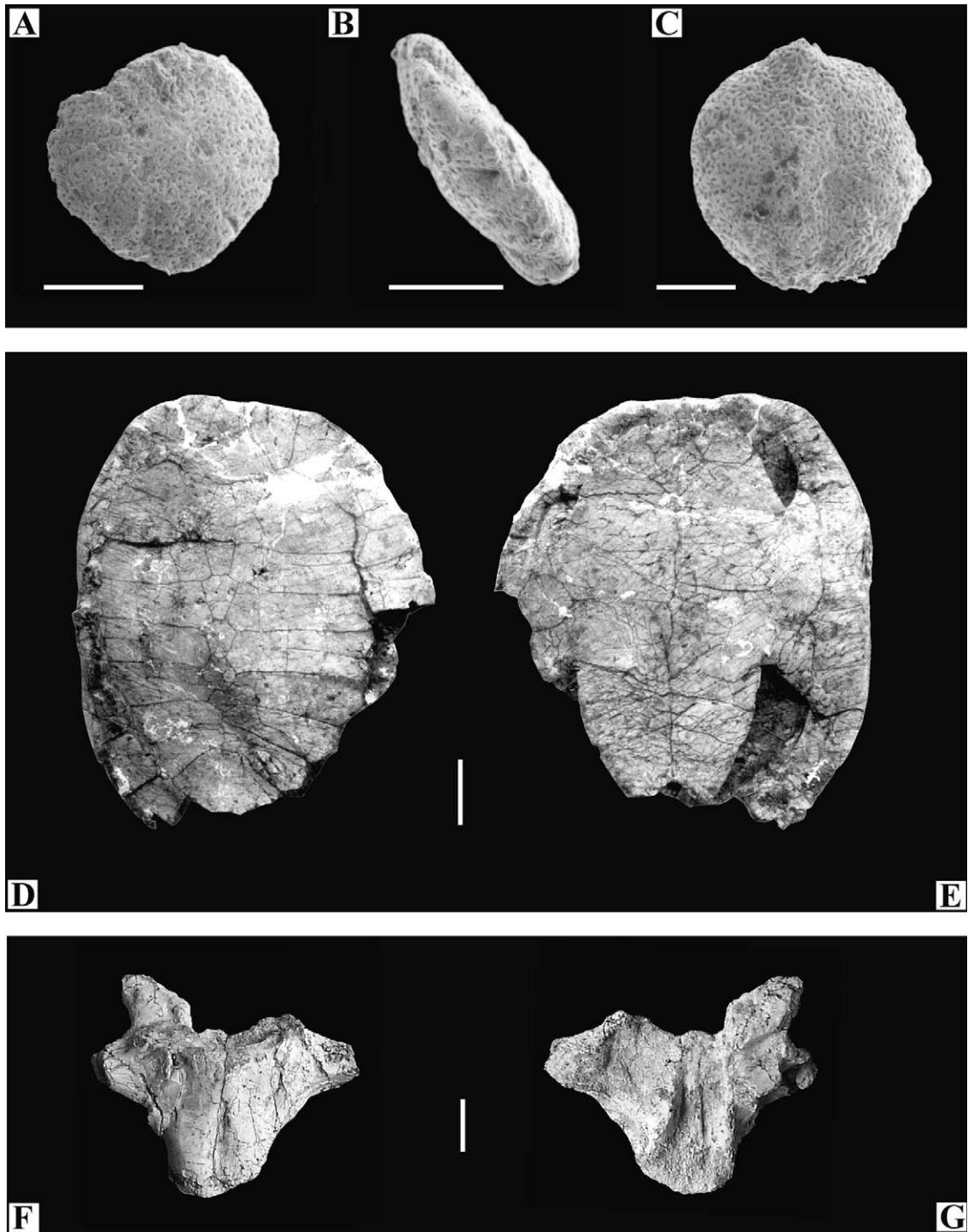


Plate I. *L. mengaudi*: (A) umbilical view; (B) opertural view; (C) spiral view. Scale bars = 500 μ m (photos by D. Grenouillet/SCOM–UPS). Carapace of *Elochelys* nov.sp.: (D) dorsal view; (E) ventral view. Scale bar = 5 cm. Varanoid vertebra: (F) ventral view; (G) dorsal view. Scale bar = 1 cm.

toidid is abundant in the uppermost Maastrichtian of Larcan (25 km from the West of Cassagnau) where the chronological equivalent of the Auzas Marls appears. It seems to be a good marker of the Late Maastrichtian (Mayaroensis Zone) (Bilotte, 1998). *Laffiteina mengaudi* (Plate IA–C) is also present in the confined marine environments (Ségura, 1979; Bilotte, 1980; Tambareau et al., 1997). Finally, many charophytes occur in the Auzas Marls: the last two species of Clavatoracea (*Septorella brachycera*, *Septorella ultima*; Massieux et al., 1979) and 14 species of Characea (Tambareau et al., 1997).

The well-established Late Maastrichtian age of the Cassagnau section is in contradiction with the charophyte scale of Riveline et al. (1996), which suggests an Early Maastrichtian age for *Septorella brachycera* and *Septorella ultima*. A diachronism between the extinction of these charophytes between Northern and Southern Pyrenees could be evoked, but it seems rather unlikely, as the concerned localities are less than 150 km apart. We have already pointed out (Laurent et al., 2001) this contradiction and suggested that it came from the adjustment of this charophyte scale to magnetostratigraphic data obtained from continental deposits. It appears that this scale should rather be adjusted to biochronological evidence obtained from benthic foraminifera and nanoplankton in the marine–continental transitional domain. Work is in progress by our team on this adjustment of the charophyte scale to biochronological evidence.

4. Vertebrates

The remains are kept at the Musée des Dinosaures in Espéraza (MDE). We only give here a preliminary description of the material and more enhanced descriptions will follow once more detailed studies have been undertaken.

4.1. Osteichthyes

Ganoid scales, pointed teeth and one opisthocelous vertebra are referred to the family Lepisosteidae. Two other families were identified: sub-

circular teeth with a finely reticulated, slightly convex crown are referred to the Phyllodontidae. Other circular teeth are more convex with a basal face showing a radiating pattern of thin grooves; they are referred to the family Sparidae. These three taxa were also present at the neighboring locality of Lestailats (Laurent et al., 1999).

4.2. Amphibia

A single fragment of a dentary (MDE-Cas1-156) with several teeth and an interfingering symphysis belongs to an albanerpetontid (S. Duffaud, personal communication).

4.3. Chelonia

A complete carapace (MDE-Cas2-259, Plate ID,E) has been discovered. It belongs to a new species of genus *Elochelys* of the family Bothremydidae. It differs from *E. perfecta* from the Campanian of the Fuveau Basin (Southern France), mainly by its larger size, the presence of a suprapygial, the shape of the vertebrate scutes and the wide posterior part of the intergular scute (Laurent et al., 2002).

4.4. Squamata

A large vertebra (MDE-Cas2-124; length 35 mm; Plate IF,G) belongs to a very large varanoid; this yet undescribed form is known from various Campanian and Early Maastrichtian localities in Southern France. It is its first occurrence in the Late Maastrichtian of Europe.

4.5. Crocodylia

Crocodyles are well represented in Cassagnau; the skull of a longirostrine form (MDE-Cas1-199; Plate IIA) has been referred to *Thoracosaurus neocesariensis* (Laurent et al., 2000). The genus *Thoracosaurus* is known from the Late Cretaceous of North America and the Netherlands and from the Paleocene of Sweden and eastern France (Leidy, 1865; Koken, 1888; Troedsson, 1924; Piveteau, 1927; Carpenter, 1983; Mulder, 1997).

Many cone-shaped to lanceolated teeth with a

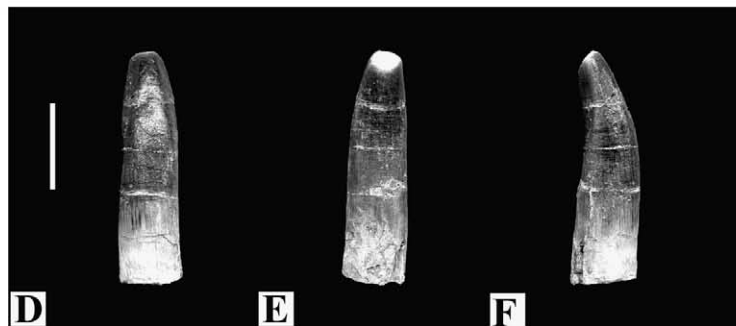
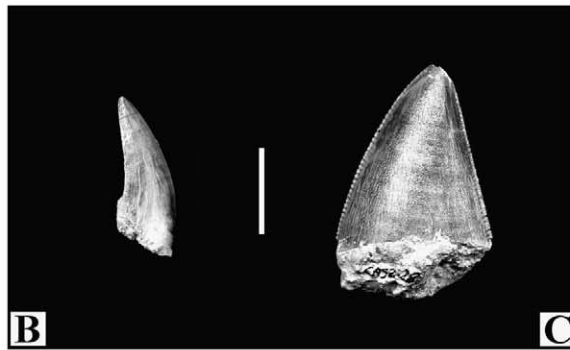


Plate II. Skull of *Thoracosaurus neocesariensis*: (A) dorsal view. Scale bar=5 cm. Undetermined Dromaeosaurid teeth: (B) small form in lingual view; (C) large form in labial view. Scale bar=1 cm. Undetermined titanosaurid tooth: (D) labial view; (E) lingual view; (F) mesial view. Scale bar=1 cm.

slightly convex labial surface are provisionally attributed to *Musturzabalsuchus* sp. (Buscalioni et al., 1997); some teeth (probably more posterior) are thick. Nevertheless, all these teeth are charac-

terized by lingual (and sometimes labial) surfaces longitudinally wrinkled and with ondulated lateral carina. This genus has been created with rostris and mandubilar remains which come from the

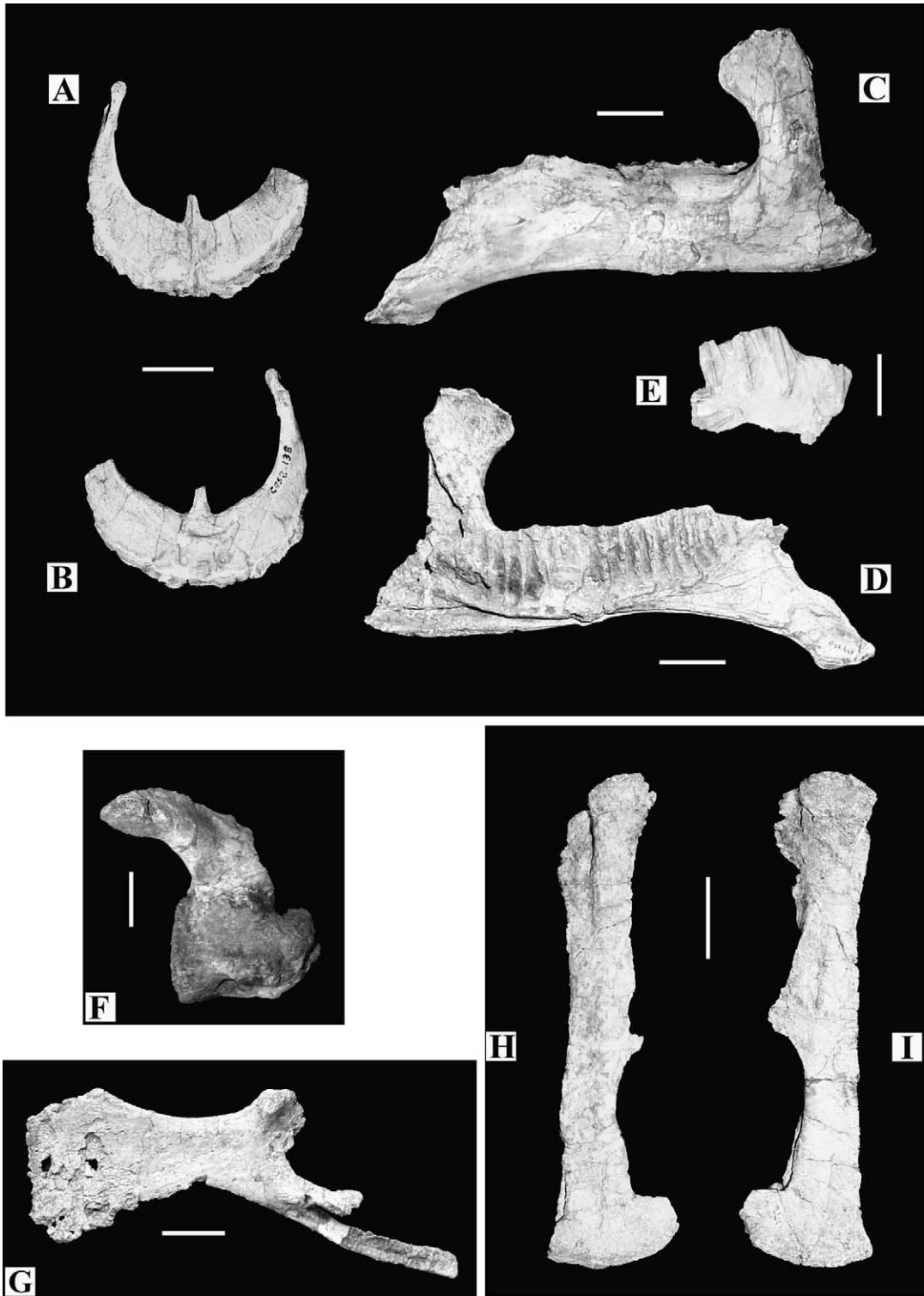


Plate III.

Campano–Maastrichtian site of Laño (Treviño, Spain). *Musturzabalsuchus* is probably present in the Campanian (Fuvelian) of the Fuveau-Valdonne basin (Bouches-du-Rhône, France), and in the Campano–Maastrichtian of Armuña (Segovia Province, Spain) (Buscalioni et al., 1997, 1999). Many other remains are referred to undetermined Crocodylia.

4.6. Dinosauria

4.6.1. Theropoda

Theropod dinosaurs are represented by many serrated teeth. There are denticles on both anterior and posterior carinae. The denticles are straight, not inclined and chisel-like in form, with blood grooves oriented perpendicular to the longitudinal axis of the tooth. All these characteristics suggest affinities to a dromaeosaurid dinosaur (Currie et al., 1990; Plate III). We can observe a small form (MDE-Cas1-92; Plate IIIB) distally curved with a fore–aft basal length (FABL) of about 7 mm and a total length of 18 mm, and a large form (MDE-Cas2-28; Plate IIIC) which shows relatively large serrations on both carinae with 3 denticles/mm.

It should be noted that some of the small teeth might also belong to the giant varanoid; the teeth of the recent *Varanus griseus* are indeed very similar to small theropod teeth.

4.6.2. Sauropoda

Three teeth (MDE-Cas1-10, MDE-Cas2-26, 27) and one metapodial (MDE-Cas2-25) are referred to a titanosaurid sauropod. The crowns are slightly spatulated and the roots are cylindrical (MDE-Cas2-26; Plate IID–F). The buccal face is slightly convex while the lingual face is concave. These teeth are different from the cylindrical teeth of *Lirainasaurus astibiai* from the Late Campanian of Northern Spain (Sanz, 1986; Sanz et al., 1999); they also differ from those of *Ampelosaurus atacis* (Early Maastrichtian of Southern France),

which possess thin rostral and caudal expansions (Le Loeuff, 1995). Titanosaurids were the dominant plant-eating dinosaurs in the Late Campanian and Early Maastrichtian ecosystems in Europe, but are unknown so far in French Late Maastrichtian deposits.

4.6.3. Ornithopoda

Most of the dinosaur bones recovered at Cas-sagnau are hadrosaurid bones, as in other Late Maastrichtian European localities. The most important find is a partial articulated skeleton of a young individual comprising seven cervical vertebrae, two femora, one tibia, two fibulae, three metatarsals and three phalanges. A dentary, a pre-dentary and many other bones were also discovered (Plates III and IV). All this material is provisionally referred to an undetermined Euhadrosauria as a member of the clade Hadrosauridae plus Lambeosaurinae (Weishampel et al., 1993).

The pre-dentary (MDE-Cas2-138; Plate IIIA,B), collected with the dentary MDE-Cas2-248, shows a medio-ventral process pointed posteriorly. The anterior margin is denticulated and not very high. Ventrally there are a series of small aligned nutritive foramina and two others, larger and medially situated. In ventral view, the median parts of the pre-dentary widen for the reception of the dentary rostral extremities.

The dentary (MDE-Cas2-248; Plate IIIC,D) belongs to the same specimen. It is a gracile bone of 160 mm length and 35 mm width (measured in the middle of the bone). The coronoid process is slightly projected rostrally. The lateral side shows a very large nutritional foramina opening anteriorly, near the dorsal margin of the dentary, near the symphyseal region. Six other small foramina open posteriorly.

The dental battery is made up of 21 tooth positions (juvenile specimen) with two preserved replacement teeth. The crowns are diamond-shaped with a single prominent median carina, straight

Plate III. Euhadrosauria indet.: (A) pre-dentary in dorsal view; (B) pre-dentary in ventral view. Scale bar = 2 cm. (C) Dentary in lateral view; (D) dentary in medial view. Scale bars = 2 cm. (E) Teeth in lingual view. Scale bar = 2 cm. (F) Cervical vertebra in lateral view. Scale bar = 1 cm. (G) Pubis in lateral view. Scale bar = 3 cm. (H,I) Femorae in medial view. Scale bar = 3 cm.

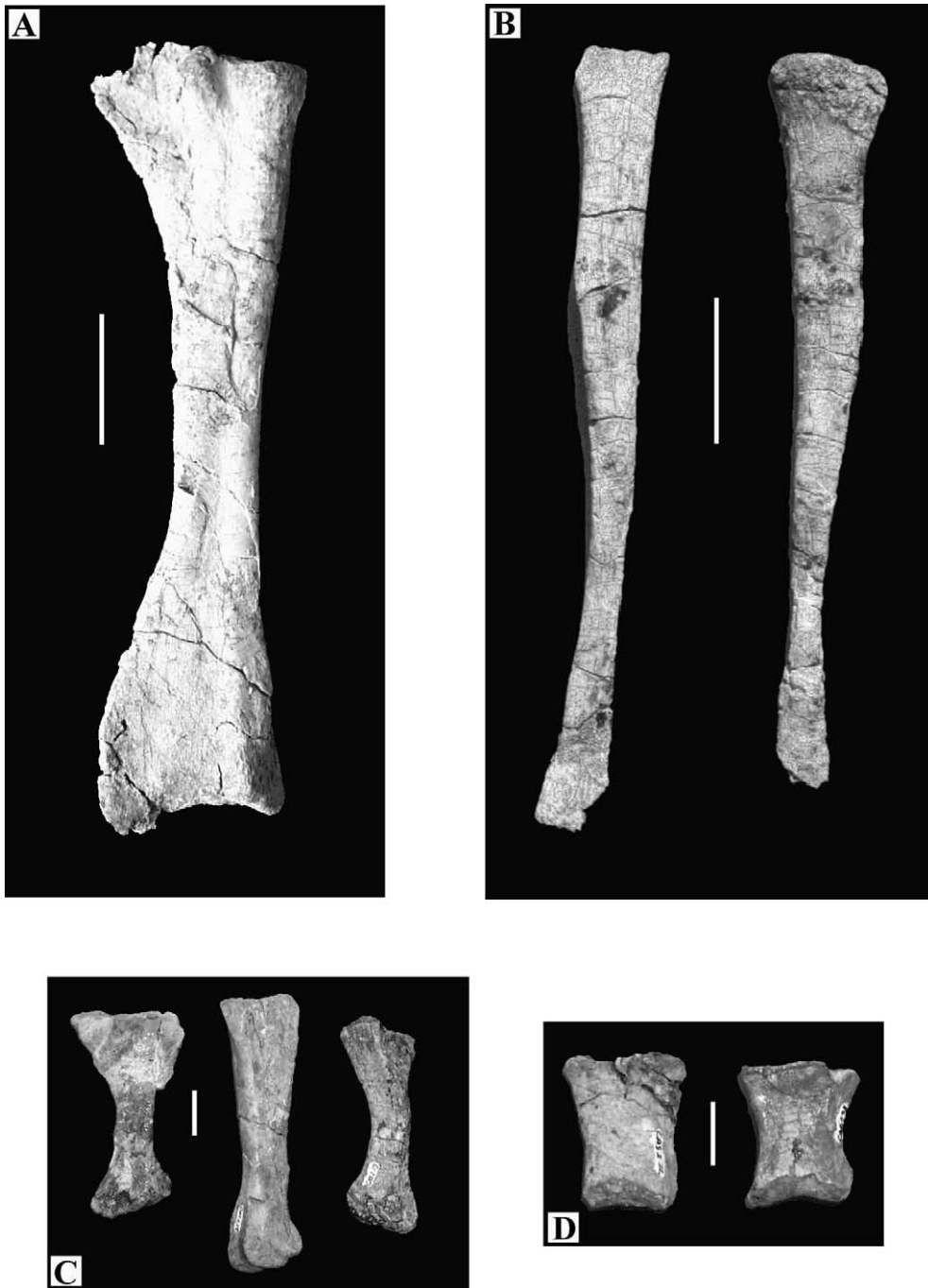


Plate IV. Euhadrosauria indet.: (A) tibia in lateral view. Scale bar=3 cm. (B) Fibulae in lateral view. Scale bar=3 cm. (C) Metatarsals. Scale bar=1 cm. (D) Phalanges. Scale bar=1 cm.

and slightly caudally placed. The crowns are characterized by a complete absence of secondary ridges (MDE-Cas2-11; Plate III E).

A medio-ventral process, more or less developed, characterizes the predentary of *Lambeosaurus lambei* and *Corythosaurus casuarius* (Lambeosaurinae) but this characteristic seems to have little phylogeny value (Brett-Surman, 1989).

The dentary differs from *Telmatosaurus transylvanicus* (Romania) by the absence of distally recurved dentary teeth and mesial denticles not supported by secondary ridges (Weishampel et al., 1993). It also differs from Fontllonga and Valencia undetermined Euhadrosauria (Casanovas et al., 1999a; Company et al., 1998) from Spain, in having a coronoid process inclined rostrally, the absence of secondary ridges on the crowns and a more gracil aspect. Also from Spain, the lambeosaurine *Pararhabdodon isonensis* of Sant-Romà (Casanovas et al., 1999b) differs from our specimen in having a coronoid process inclined caudally and a more prominent mandibular diastema. On the other hand, our specimen is very similar to the dentary described by López-Martínez et al. (2001) from Arèn (Spain) and classified as Euhadrosauria indet.

The cervical vertebrae are typically opisthocoealous (MDE-Cas2-10; Plate III F) with oval articular faces more wide than high.

The pubis (MDE-Cas2-01; Plate III G) is 217 mm long, characterized by a very short neck, a rectangular, relatively short blade with sub-parallel dorsal and ventral borders and an anterior border perpendicular to the dorsal and ventral borders. Brett-Surman (1975, 1989) identifies five different pubic morphologies corresponding to five clades: Edmontosaurini, Hadrosaurini, Saurulophini, Corythosaurini and Parasaurulophini. In these conditions MDE-Cas2-01 is assigned to the Parasaurulophini clade; however, the situation seems more complicated, especially with a juvenile specimen.

The femora (MDE-Cas2-12, 15; Plate III H, I) are 180 mm long, straight but strongly laterally compressed. The femoral head is well individualized, the lesser trochanter is well developed and separated from the greater trochanter by a narrow gutter. The femora show a wing-like prominent

(not pending) fourth trochanter developed on the caudiomedial surface of the shaft.

Our specimens are clearly different from the femur of *Telmatosaurus transylvanicus*, which is slightly bowed laterally and the fourth trochanter has a pending aspect. However, Brett-Surman (1975, 1989) did not find any diagnostical characteristic to characterize any type of femora in hadrosaurids.

A tibia (MDE-Cas2-13; Plate IV A), two fibulae (MDE-Cas2-14, 16; Plate IV B), three metatarsals (MDE-Cas2-17, 18, 19; Plate IV C) and two phalanges (MDE-Cas2-21, 22; Plate IV D) show typical hadrosaur features and any diagnostical characteristics allow us to differentiate between the Lambeosaurinae and the Hadrosaurinae.

4.7. ? Aves

A bird is possibly represented by the proximal part of a scapula (MDE-Cas1-152). It seems to contain the triosseal canal, a characteristic of the enantiornithines (Walker, 1981; Martin, 1995). In Europe, enantiornithines were so far known only from the Late Campanian–Early Maastrichtian localities of Cruzy (Hérault, Southern France; Buffetaut, 1998) and Fox-Amphoux (Buffetaut, 2000). It is their first occurrence in the Late Maastrichtian (work in progress).

5. Comparisons with other localities of the Petites Pyrénées

In recent years our knowledge of Late Maastrichtian European ecosystems has been greatly improved by the discovery of new localities in southwestern France (Fig. 1A). Six sites (Figs. 1A and 4) are presently known in the Petites Pyrénées (department of Haute-Garonne).

The localities of Lestailats (Le Loeuff et al., 1994; Laurent et al., 1999) and Le Jadet (Paris and Taquet, 1973; Buffetaut and Cavin, 1995) belong to the Ausseing Group (Fig. 2); they yielded some taxa unknown at Cassagnau such as neoselachians and enchodontid fishes, and a few osteoderms of a nodosaurid ankylosaur revealing the coexistence of at least two Ornithi-

	Ausseing Group		Auzas Marls Formation			
	JADET Paris et Taquet, 1973 Buffetaut et Cavin, 1995	LESTAILLATS Laurent et al., 1999	PEYRECAVE Gheerbrant et al., 1997	AUZAS Leymerie, 1881 Lepicard, 1985 Le Loeuff et al., 1994	TRICOUTÉ Gheerbrant et al., 1997	CASSAGNAU
Chondrichthyes Selacian Triakidae Rhinobatidae Rhombodontidae Dasyatoidae		neoselacian indet.	<i>Palaeogaleus</i> sp. <i>Rhinobatos</i> sp. <i>Rhombodus blinkhorst</i> <i>Coupatzia</i> cf. <i>fallux</i>			
Osteichthyes Lepisosteidae ? Sparidae Phyllodontidae Enchodontidae	<i>Enchodus</i> cf. <i>faujazi</i>	lepisosteid indet. ?sparid indet. phyllodontine indet.	osteichthyes indet.		osteichthyes indet.	lepisosteid indet. ?sparid indet. phyllodontid indet.
Amphibia Urodela Anura			?urodela indet. ?anoura indet.			albanerpetontid indet.
Reptilia Chelonia Pleurodira		pleurodira indet.				pleurodira indet. <i>Elochelys</i> nov. sp.
Squamata ? Amphisbenian Lacertilian			teiid indet.		?amphisbenian indet.	varanoid indet.
Crocodylia Eusuchia Crocodylidae Alligatoridae	eusuchia indet.	eusuchia indet.	crocodylid indet.	eusuchia indet.	crocodylid indet. alligatorid indet.	eusuchia indet. <i>Thoracosaurus</i> <i>Musturzabalsuchus</i>
Dinosauria Theropoda Sauropoda Ornithopoda Ankylosauria	euhadrosauria indet.	?dromaeosaurid indet. euhadrosauria indet. nodosaurid indet.		euhadrosauria indet.	theropod indet. euhadrosauria indet.	dromaeosaurid indet. titanosaurid indet. euhadrosauria indet.
? Aves						? enantiornithine indet.
Mammalia			therian ? tribosphenic			

Fig. 4. Vertebrate taxa represented in the Late Maastrichtian localities of the Northern Subpyrenean Domain.

schian species during the Late Maastrichtian in Southern France.

All other localities belong to the Auzas Marls Formation (Fig. 4). Gheerbrant et al. (1997) mentioned tribosphenic mammalian teeth at Peyrecave, as well as many chondrichthyans (Triakidae, Rhinobatidae, Rhombodontidae, Dasyatoidae). At Auzas and Tricouté, Le Loeuff et al. (1994) and Gheerbrant et al. (1997) described crocodiles and hadrosaurs.

Cassagnau yielded the richest vertebrate assemblage from this area, with seven different groups (osteichthyans, amphibians, chelonians, squamates, crocodylians, dinosaurs and birds). The absence of chondrichthyans is probably linked to the more brackish environment. The apparent absence of mammals is possibly linked to the small quantity of sediment treated so far at Cassagnau. The sites of the Petites Pyrénées contain one of

the richest Late Maastrichtian continental assemblages of Southern Europe. They are therefore of considerable importance in our understanding of the evolution of the last Cretaceous continental ecosystems in Europe.

6. Conclusions

The Cassagnau locality (Auzas Marls Formation) is referred to the Late Maastrichtian on the basis of micropaleontological evidence obtained in the formation itself (*Hellenocyclina beotica* (Mayaroensis Zone), *Laffiteina mengaudi*) or in the underlying units (*Arkhangelskiella cymbiformis*, *Cribocorona gallica* and *Lithraphidites quadratus*, a typical Tethyan Late Maastrichtian marine nanoflora association (CC 25), and *Orbitoides apiculata*, *Lepidorbitoides socialis*, *Omphalo-*

cyclus macroporus, *Siderolites calcitrapoides*, *Siderolites denticulatus*, a Maastrichtian benthic foraminifera association). The Cassagnau locality (Auzas Marls Formation in general) and the Arén sites (Huesca, Spain) (López-Martínez et al., 2001) are Late Maastrichtian dinosaur localities, stratigraphically well constrained in Europe.

The Late Maastrichtian (i.e. 69–65 Ma) is largely dominated by hadrosaurid dinosaurs, which seem to replace the association *Rhabdodon*–titanosaurids known from earlier strata (Le Loeuff et al., 1994), even though some titanosaurs are still present at Cassagnau. It thus seems that hadrosaurs were present, albeit very rare, in Western Europe before the Late Maastrichtian, when a hadrosaurid radiation occurred in the European archipelago. The reason for this sudden radiation may be linked to the contemporaneous climatic evolution from a sub-tropical to a more temperate climate (Le Loeuff et al., 1994).

However, the Petites Pyrénées assemblage does not support the diminishing of the global dinosaur diversity in Europe during the Late Maastrichtian. The decline of some dinosaur groups is perfectly visible (extinction of the euornithopod *Rhabdodon* and an important decrease of the sauropod forms); however, it would make up for the increase in the ornithopod hadrosaurid group.

The apparent biodiversity is but a part of the real biodiversity (Le Loeuff and Laurent, 2000) and further field work is needed to evaluate the real biodiversity of Late Maastrichtian continental vertebrates in Europe, and their precise extension relative to the KT boundary, but the localities of the Garonne valley now constitute the best place in Europe to test hypotheses of abrupt KTB extinctions drawn from North American studies (Sheehan, 2000).

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