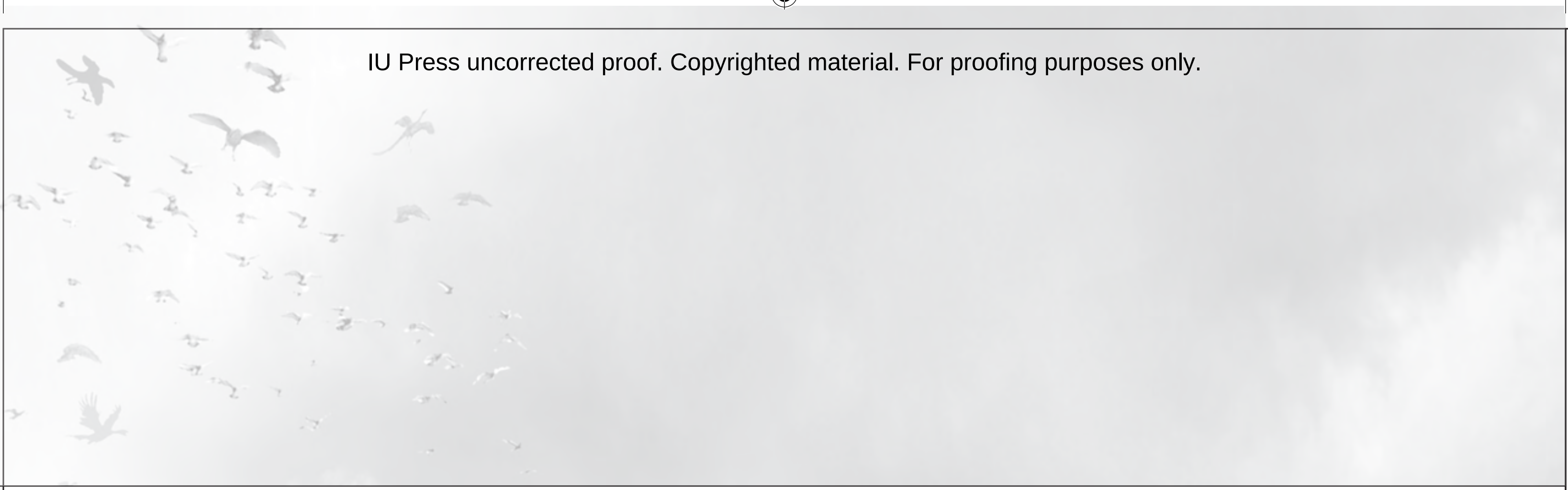
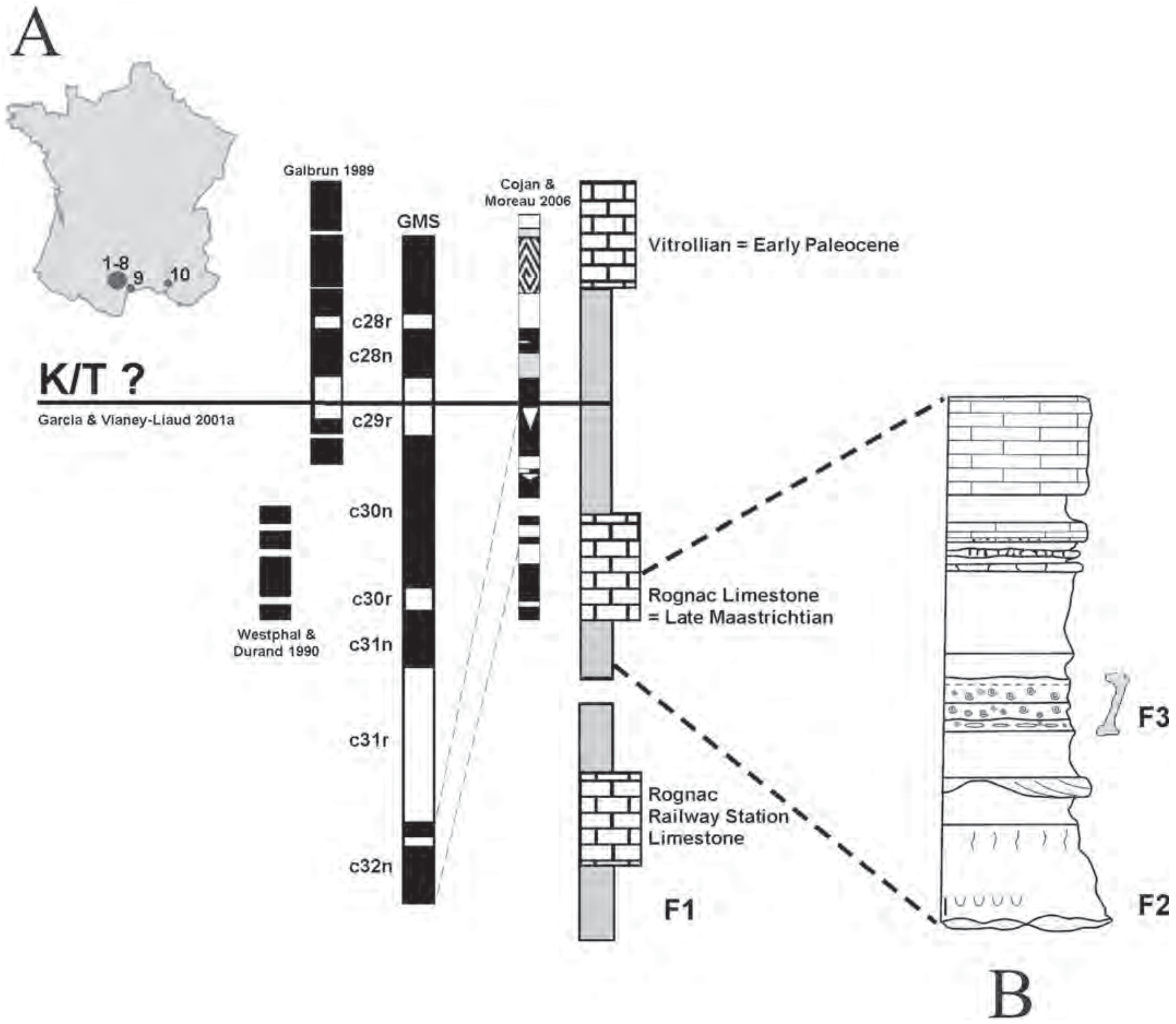



A
1-8
9
10
Galbrun 1989
GMS
Cojan & Moreau 2006
Vitrollian = Early Paleocene
c28r
c28n
K/T ?
Garcia & Vianey-Liaud 2001a
c29r
c30n
Westphal & Durand 1990
c30r
c31n
c31r
c32n
Rognac Limestone = Late Maastrichtian
Rognac Railway Station Limestone
F1
F2
F3
B

# First Late Maastrichtian (Latest Cretaceous) Vertebrate Assemblage from Provence (Vitrolles-la-Plaine, Southern France)

## 32

**Xavier Valentin, Pascal Godefroit, Rodolphe Tabuce, Monique Vianey-Liaud, Wu Wenhao, and Géraldine Garcia***

A Late Maastrichtian locality from Provence (southwestern France) has yielded a diversified vertebrate fauna, including a "zhelestid" mammal, *Valentinella vitrollense*, in association with lacertilians, cryptodiran chelonians, alligatoroid crocodilians, and a varied dinosaur fauna including Neoceratosauria, Coelurosauria, Titanosauria, basal Iguanodontian, and Hadrosauridae. It is the first noticeable report of the occurrence of hadrosaurids in Provence. The morphology of the dentary and dentary teeth suggests that the hadrosaurid material belongs to a noneuhadrosaurian hadrosaurid, close to *Telmatosaurus transsylvanicus* and *Tethyshadros insularis*, also known from the Late Cretaceous of Europe. It is clearly different from hadrosaurid material previously described in Europe. However, the material discovered so far is still inadequate to erect a new taxon. This new site offers new perspectives on the diversity and evolution of the European vertebrate ecosystems during the Maastrichtian. Indeed, the association of hadrosaurids with titanosaurids and *Rhabdodon* is unusual in the latest Cretaceous of southern France. It questions the hypothesis of the replacement in Western Europe of an Early Maastrichtian fauna dominated by titanosaurid sauropods and *Rhabdodon* by a Late Maastrichtian assemblage dominated by hadrosaurids.

**32.1.** A, Map showing the location of the main French sites with hadrosaurid remains dated from the Late Maastrichtian. 1, Ausseing. 2, Auzas. 3, Cassagnau. 4, Le Jadet. 5, Lestaillats. 6, Mérignon. 7, Peyrecave. 8, Tricouté. 9, Le Bexen, 10, the locality of Vitrolles-La-Plaine. B, Schematic stratigraphic column of Vitrolles section with paleomagnetic data and global magnetostratigraphic scale (GMS). Log of Vitrolles-la-Plaine with fossiliferous levels: F1, Vitrolles-Couperigne locality, where one skeleton of *Rhabdodon priscus* was collected (Garcia et al., 1999); F2, dinosaur eggs organized in clutches; F3, location of the studied assemblage. No precise correlation have been proposed by Galbrun (1989) and Westphal and Durand (1990) for the Rognac Limestone in this part of Basin. The results (dotted lines on B) suggested by Cojan and Moreau (2006) are inexact because they did not take into account the diachronism and the large thickness variation of this formation across the Basin, as already demonstrated by Garcia and Vianey-Liaud (2001a).

## Introduction

Late Cretaceous continental deposits are widely exposed in southern France. Nevertheless, in spite of intensive field investigations during the last 20 years, the main localities that have yielded a diverse Late Maastrichtian continental fauna were restricted so far to the western part of southern France. All of them (Fig. 32.1) are located in the foothills of the Pyrenees, from the eastern Corbières in the east to both sides of the Garonne Valley in the west, via the Plantaurel in Ariège (see, e.g., Paris and Taquet, 1973; Le Lœuff et al., 1994; Laurent et al., 1999, 2002).

Vitrolles-La-Plaine is the first Late Maastrichtian site from Provence that contains diverse articulated and scattered reptile bones associated with mammal remains. This chapter is a preliminary description of the fauna collected during different fieldwork sessions in 1998–1999 and two main excavation campaigns in spring 2007 and 2008.

*Institutional abbreviations.* ISEM, Institut des Sciences de l'Évolution, Université Montpellier II, Montpellier, France; UP, Université de Poitiers, Poitiers, France.

## Geological Setting

The Vitrolles-La-Plaine site is located in the eastern part of the Aix Basin, close to Lake Berre. It was discovered during a geological survey by one of us (X.V.) in 1997, in Upper Cretaceous deposits near the town of Vitrolles (Garcia, 1998; Garcia and Vianey-Liaud, 2001a). It corresponds to a succession of clays and mottled marls with some interbedded sandstone lenses, topped by the thick lacustrine Limestone of Rognac. By using the stratigraphic distribution of the egg species, Garcia and Vianey-Liaud (2001a) have demonstrated that the Limestone of Rognac, present in the western and eastern areas of the Aix Basin, is clearly diachronous throughout the basin and corresponds to a Late Maastrichtian age in its western part.

The vertebrate remains are scattered through a 1.5-m-thick lignite marl layer containing freshwater and terrestrial gastropods (*Pyrgulifera armata*, *Pupilla* sp., *Lychnus bourguignati*, *L. matheroni*, and *Cyclophorus heliciformis*) and a single bivalve (*Unio cuvieri*).

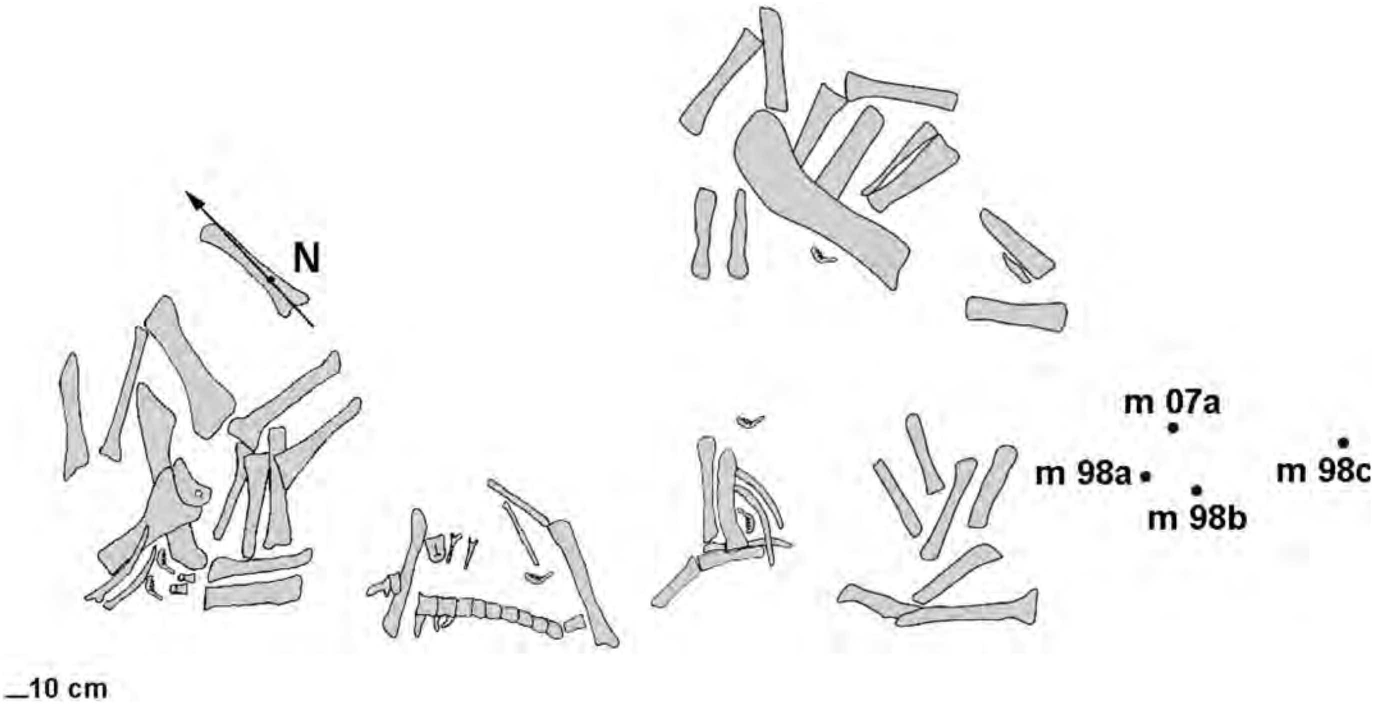
The co-occurrence of typical "Rognacian" gastropods (*Lychnus matheroni* and *Pyrgulifera armata*), charophytes (*Peckichara sertulata*, M. Feist, pers. comm.) and dinosaur eggs belonging to the Maastrichtian oospecies *Megaloolithus mamillare* (Fig. 32.3), as well as the position of the site just below the Rognac Limestone (Fig. 32.1), clearly indicate that the Vitrolles-La-Plaine locality is Late Maastrichtian in age (Garcia and Vianey-Liaud, 2001a).

The Vitrolles-La-Plaine fossil locality is clearly an allochtonous assemblage of elements belonging to numerous animals of different sizes. The rare associated skeletal elements indicate that the vertebrate carcasses were disarticulated before reworking (Fig. 32.2). Dense elements, such as limb bones, appear overrepresented at Vitrolles-La-Plaine, although lighter elements (vertebrae, skull bones), are proportionally rarer. This suggests hydraulic sorting during transportation (Voorhies, 1969). Moreover, most of the long bones are broken off at both ends, and the fractured edge is always quite rounded (abrasion levels 2–3; Fiorillo, 1988). This feature indicates that the bones were significantly reworked after being broken (Fiorillo, 1988). Behrensmeyer (1988) observed that fresh limb bones from large mammals often showed no evidence of breakage during vigorous hydraulic reworking. According to Ryan et al. (2001) and Eberth and Getty (2005), large numbers of broken limb bones indicate a destructive history before or during final reworking. Thus, it is more likely that many limb elements discovered at Vitrolles-La-Plaine experienced an earlier taphonomic episode, such as the breakdown of trabecular bone and collagen (Eberth and Getty, 2005), that weakened the specimens and increased their susceptibility to hydraulically induced breakage.

## Biodiversity of Vitrolles-la-Plaine Locality

### Eggs

Eggshells were collected in three levels of the section (Fig. 32.1, F1 [see also Garcia et al., 1999]; F2 and F3) and include prismatic (Fig. 33.3 D), ratite (Fig. 33.3E), and geckonoid (Fig. 33.3F) morphotypes. Complete spherical eggs organized in small clutches containing five to eight eggs (a total of 30 eggs were found in the same nesting layer; Fig. 33.3A) were unearthed in level F2, 4 m under the vertebrate level F3. This egg spatial



**32.2.** Map indicating the repartition of vertebrate specimens collected during three field missions since 1998. The mammal remains (labeled "m") are concentrated in the same area of the excavation.

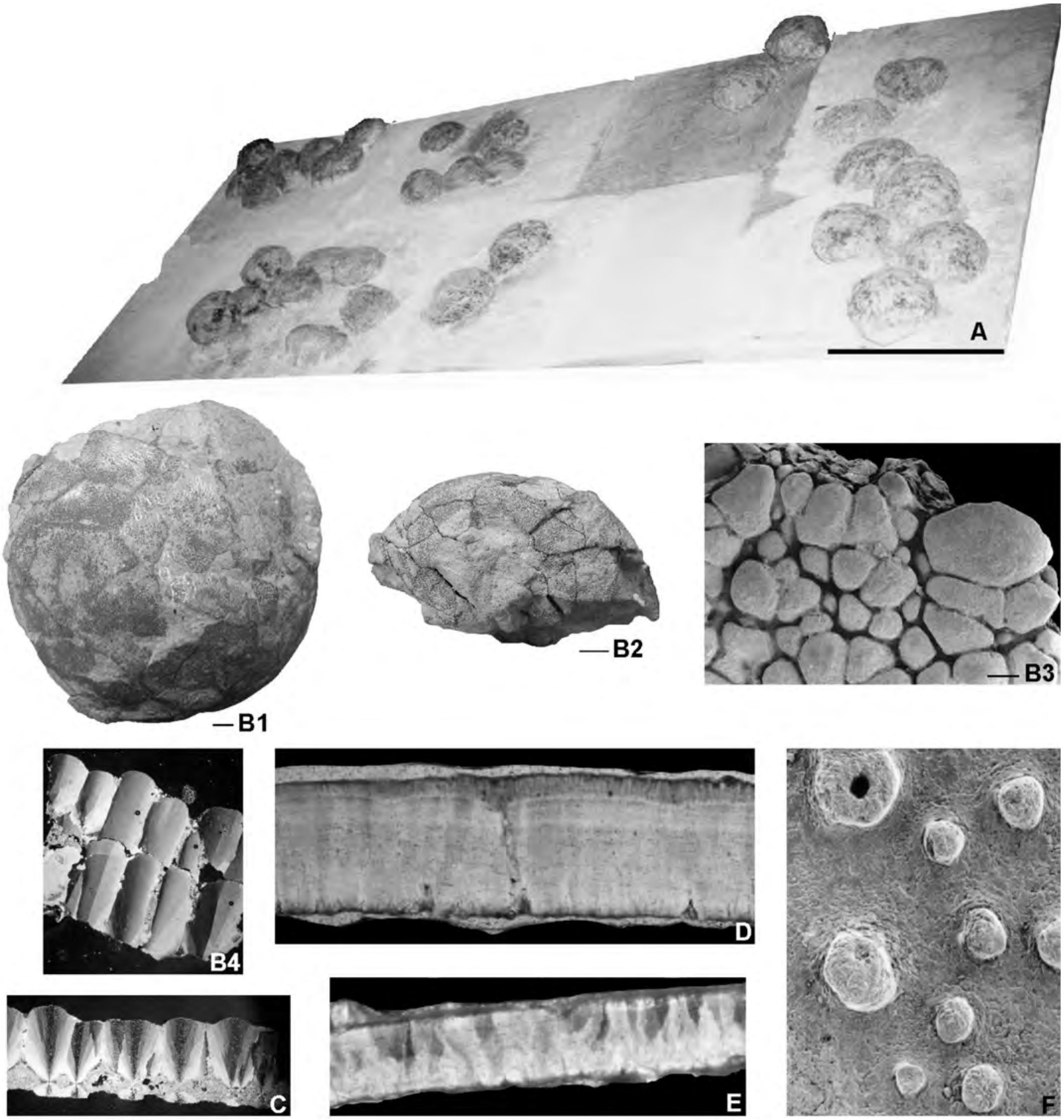
arrangement with randomly structures has already been described for this ootaxa (Garcia, 1998; Vianey-Liaud and Garcia, 2000; Cousin, 2002). One pathological egg with two superimposed eggshell layers (Fig 33.3, B1–B4) was discovered with the normal eggs, suggesting a reproduction system closer to modern avians that laid their eggs, one ovum per oviduct, over a long period of time (Varicchio et al., 1997). All belong to the megaloolithid oospecies *Megaloolithus mamillare* (Vianey-Liaud et al., 1994, Garcia and Vianey-Liaud, 2001a, 2001b), present in several sites of southern Europe (Vianey-Liaud and Lopez-Martinez, 1997; Garcia, 1998) and typically representing an ootaxa of the Maastrichtian continental deposits (Garcia and Vianey-Liaud, 2001a). Classically, the megaloolithid eggs are assigned to titanosaurian sauropods (Grellet-Tinner et al., 2006; Sander et al., 2008); the most convincing evidence for this assignment is the discovery in Argentina of embryonic remains inside eggs (Chiappe et al., 1998). However, this attribution was recently questioned by Grigorescu et al. (2010).

## Fishes

Rare fish remains are exclusively represented by isolated lepisosteid scales; all these scales are particularly thick, rhomboidal in shape, and covered by ganoine. Lepisoteid scales compose the majority of fish remains discovered in Late Cretaceous continental deposits from southern France (Laurent et al., 1999).

## Squamates

Only one fragmentary dentary containing some incomplete straight teeth (Fig. 32.4A) indicates the presence of an indeterminate lacertilian at Vitrolles-La-Plaine (J.-C. Rage, pers. comm.). Squamates are also rare in other Maastrichtian assemblages from Europe (Tremp Basin from Spain:



Lopez-Martinez et al., 2001; localities from of the Garonne Valley in France: Laurent et al., 2002; Hateg and Transylvanian basins from Romania: Folie and Codrea, 2005; Codrea et al., 2010), with the occurrence of Iguanidae, Scincomorpha, and Anguimorpha (Pereda-Suberbiola, 2009).

## Chelonia

Turtle remains are not abundant, and they are mostly represented by isolated carapace plates with a typical reticulate ornamentation. They are tentatively referable to the cryptodiran turtle *Solemys*, originally described from the Campanian of Laňo in Spain (Lapparent de Broin and Murelaga, 1996) and also recorded in several localities of the southern France (Lapparent de Broin and Murelaga, 1999; Pereda-Suberbiola, 2009).

**32.3.** A–C, *Megaloolithus mamillare*. A, Eggs exposed in the level F2 of Vitrolles-La-Plaine. Scale = 1 m. Pathological egg in dorsal (B1) and lateral (B2) views. Scale = 1 cm. B3, Outer ornamentation with abnormal nodes. Scale = 1 mm. B4, Radial view showing the two pathological layers (original magnification, ×40). C, Radial view of normal eggshell *M. mamillare* (original magnification, ×40). D, Prismatic morphotype in radial view with pore canal (original magnification, ×40). E, Ratite morphotype in thin section (original magnification, ×100). F, Outer surface with a dispersituberculate ornamentation with pore opening in node (scanning electron micrograph, original magnification ×35).

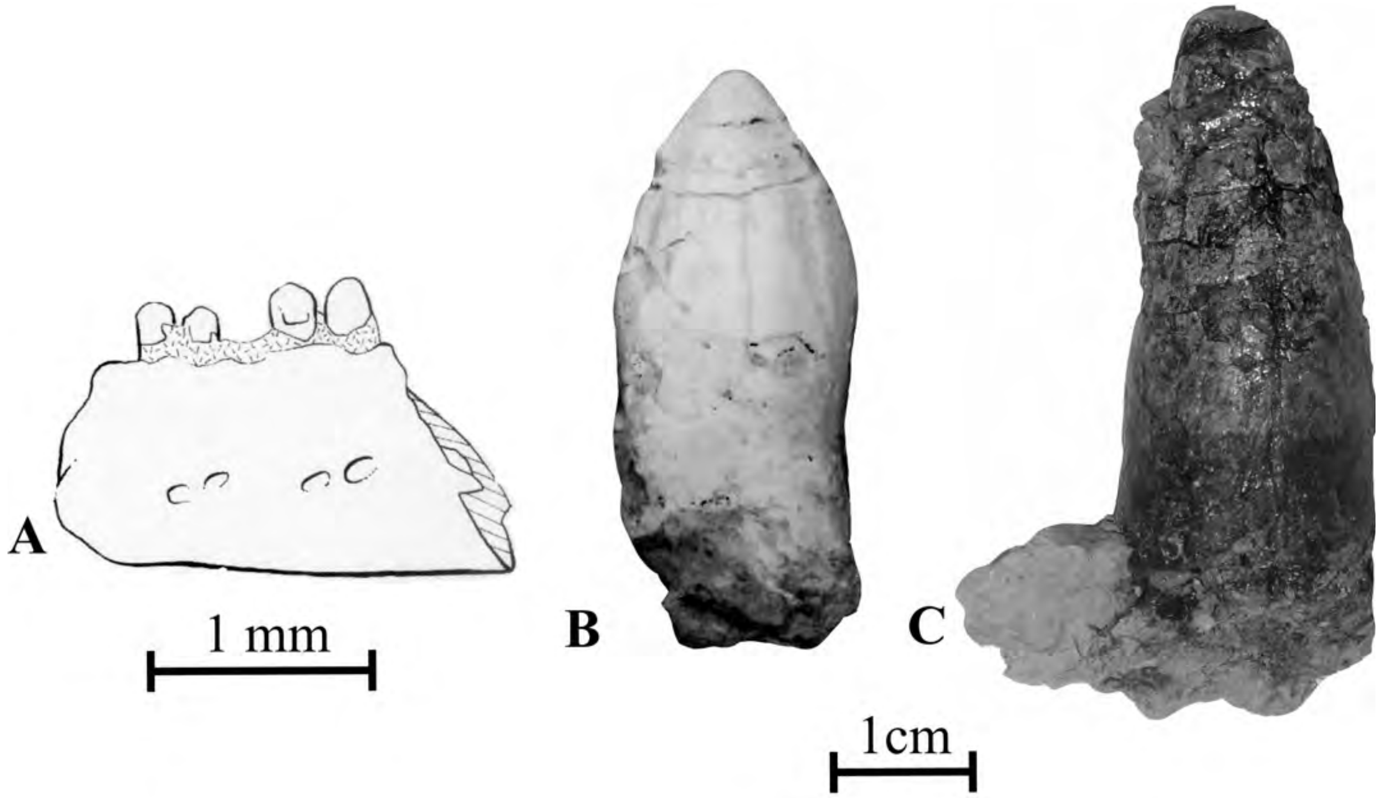
## Crocodylia

Isolated crocodilian teeth are rather abundant at Vitrolles-La-Plaine. They have lanceolate and robust crowns, with a circular base, two prominent carinae, and a blunt apex. Variations in their morphology clearly depend on their position in the jaws and on the size of the animal (Fig. 33.4B,C). They closely resemble the teeth of the alligatoroids *Musturzabalsuchus buffetauti*, from the Campanian of Laño in Spain (Buscalioni et al., 1997), and those of *Massaliasuchus affuveliensis*, from the Santonian–Campanian of Bouches-du-Rhône (Martin and Buffetaut, 2008). Nevertheless, the enamel of the teeth from Vitrolles-La-Plaine appears smooth, although it is profusely ridged with the margins crenulated in *Musturzabalsucuhus* (Buscalioni et al., 1999); the ornamentation is more discrete in *Massaliasuchus*, consisting of small wrinkles on the surface of the enamel (Martin and Buffetaut, 2008). Of course, precise identification of crocodilian taxa on the basis of isolated teeth remains conjectural. However, the presence of alligatoroids at Vitrolles-La-Plaine is likely because these crocodilians were common components of Late Cretaceous deposits in North America and Europe (Martin and Buffetaut, 2008).

## Neoceratosauria

Several limb bones belonging to medium-sized theropods have been unearthed from Vitrolles-la-Plaine locatilty. Because of the poor preservation of this material, most diagnostic characters are unfortunately not preserved.

A right femur from Vitrolles-la-Plaine (Fig. 32.5A,B) resembles the holotype of *Tarascosaurus salluviscus* Le Lœuff and Buffetaut, 1991. Originally described as belonging to the family Abelisauridae (Le Lœuff and Buffetaut, 1991), *Tarascosaurus* was subsequently regarded as a nomen dubium (Rauhut, 2003) or a potential Abelisauroidea incertae sedis (Tykosky and Rowe, 2004). Like in *Tarascosaurus*, the cranial side of the proximal portion of UP-VLP-98C-001 is narrow, virtually reduced to a prominent ridge starting for the lesser trochanter and extending along the proximal third of the bone (Fig. 32.5A). The lesser trochanter is positioned low on the femur, probably well below the level of the femoral head. Like in *Tarascosaurus*, it is mediolaterally wide but not prominently developed, and in cranial view, it occupies a median position above the proximocranial ridge. The presence of a nutritive foramen, characteristic for *Tarascosaurus* (Le Lœuff and Buffetaut, 1991), cannot be ascertained in UP-VLP-98C-001. The femoral head is not preserved in UP-VLP-98C-001. In cranial view, the femoral shaft is convex externally, but it may also be a consequence of postmortem deformation. The fourth trochanter forms a large, bladelike structure on the caudomedial shaft of the femur (Fig. 32.5B); its apex is located at the level of the proximal third of the bone. The distal end of the femur is incompletely preserved. The medial epicondyle is exceptionally developed (Fig.



**32.4.** A, Lacertilian left dentary in labial view. B, UP-VLP-07-00, alligatoroid tooth in lingual view. C, UP-VLP-07-002, alligatoroid tooth in labial view.

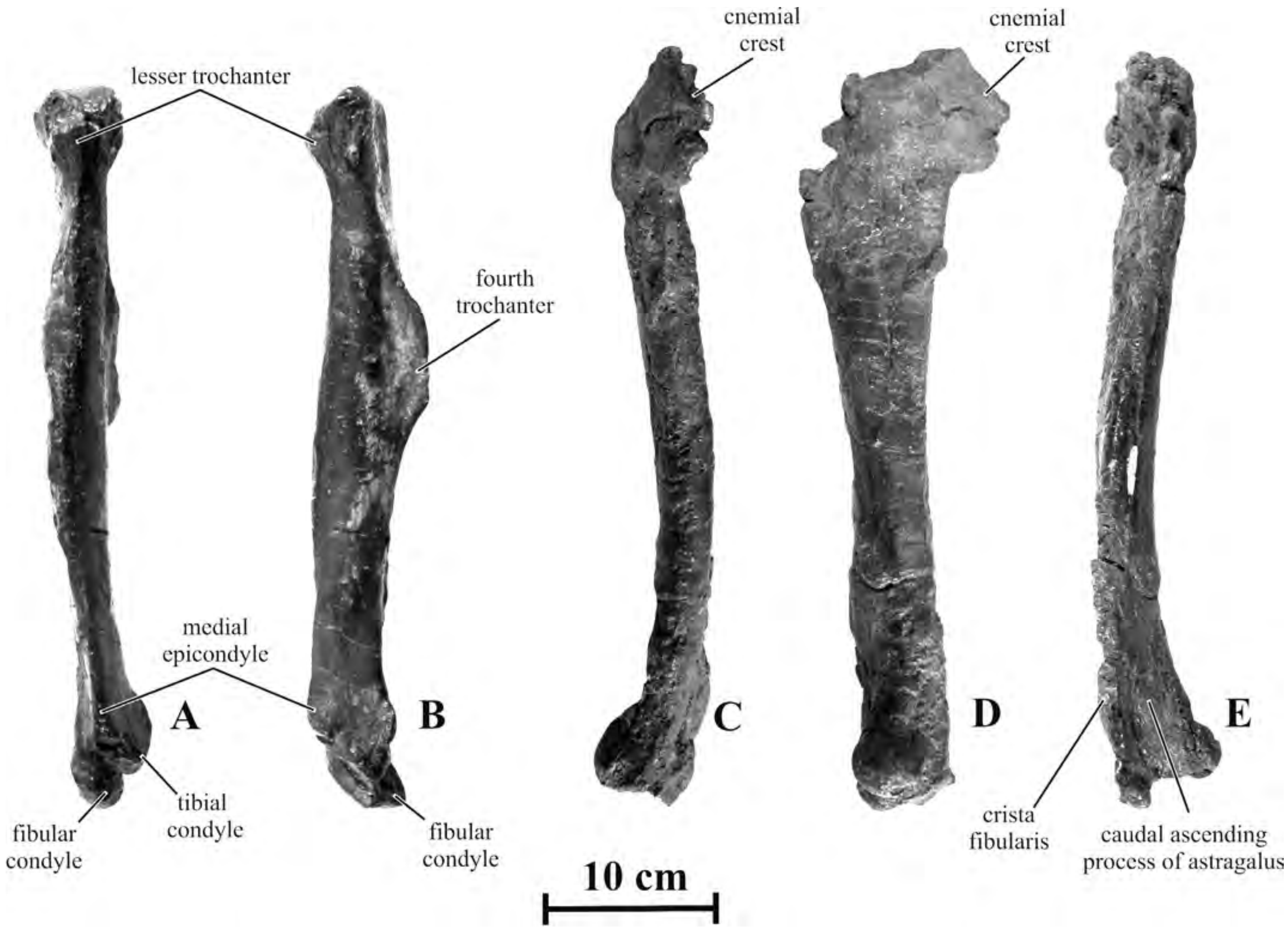
32.5A,B), as it is usually observed in abelisauroids (Sampson et al., 2001; Tykosky and Rowe, 2004). In UP-VLP-98C-001, it is oriented quite cranially above the tibial condyle, although it is usually oriented medially in typical abelisauroids (see, e.g., Carrano et al., 2002, fig. 14a).

UP-VLP-98A-002 is a left tibiotarsus (Fig. 32.5C–E) that closely resembles another specimen previously described from the Late Campanian of La Boucharde (Allain and Pereda-Suberbiola, 2003). Although it is incompletely preserved and deformed, its cnemial crest is clearly craniocaudally longer than its articular condyles (Fig. 32.5C,D), which is regarded as a synapomorphy for Neoceratosauria (Tykosky and Rowe, 2004). The tibial shaft is transversely compressed and convex laterally. The distal end of the tibiotarsus is better preserved in UP-VLP-98A-002. It is triangular in distal view and slightly enlarged transversely. The cranial side of the tibia is reduced to a rounded ridge on the distal quarter of the bone. As it is usual in Neoceratosauria (Tykosky and Rowe, 2004), there is a well-developed crista fibularis on the lateral side of the distal tibia (Fig. 32.5E). The astragalus is fused to the distal end of the tibia. It forms a high caudal ascending process along the distal quarter of the tibia (Fig. 32.5E).

Even if they are poorly preserved, these limb bones can be confidently referred to as neoceratosaurian theropods. Tortosa et al. (2010) also recently reported the presence of abelisaurid neoceratosaurians in latest Cretaceous deposits from Provence.

### Coelurosauria

Isolated theropod teeth have also been discovered at Vitrolles-La-Plaine. The *Richardoestesia* morphotype, known from latest Cretaceous localities

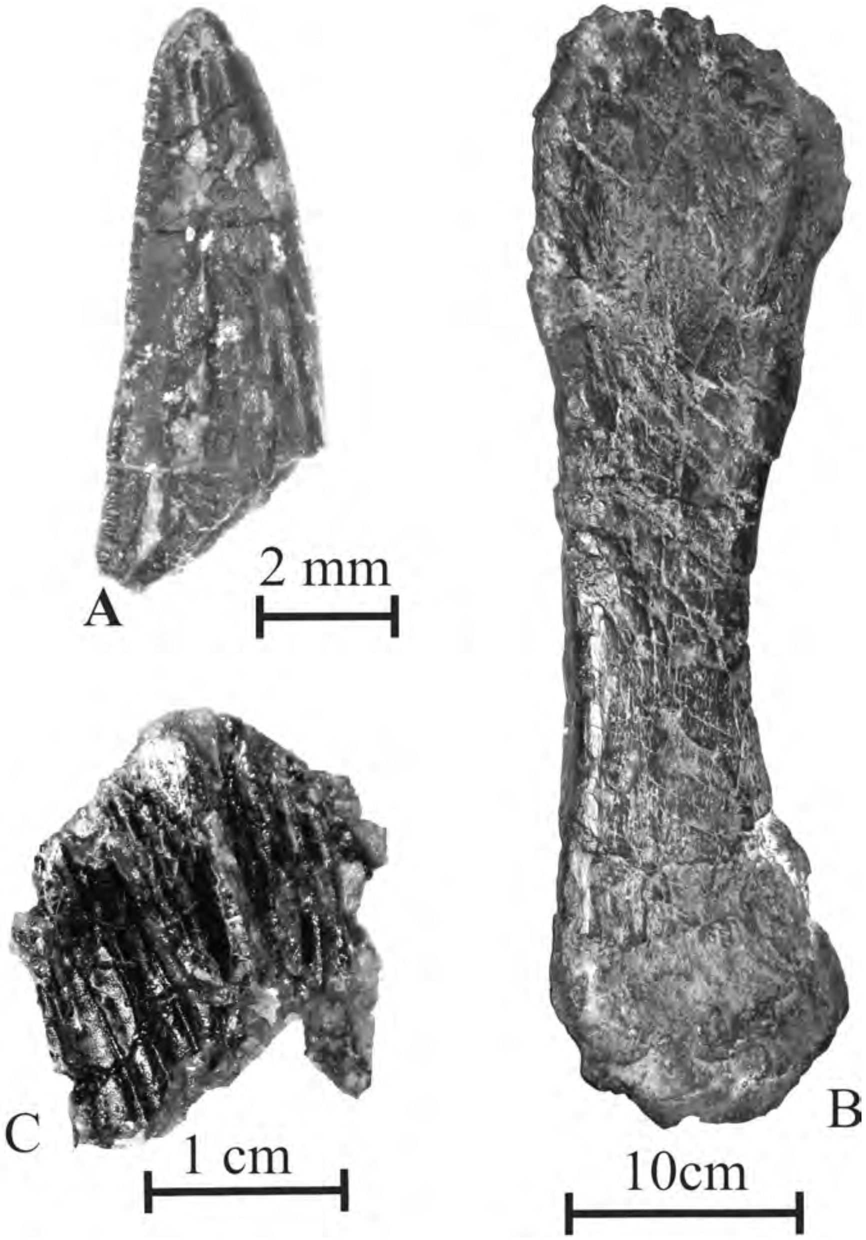


**32.5.** A, B, UP-VLP-98C-001, right femur of a Neoceratosauria indet. in cranial (A) and medial (B) views. C–E, UP-VLP-98A-002, left tibiotarsus of a Neoceratosauria indet. in cranial (C), medial (D), and caudal (E) views.

in western North America (e.g., Currie et al., 1990; Sankey, 2001) and Romania (Codrea et al., 2002), is represented by several laterally compressed teeth, characterized by their slight curvature and by the presence of minute serrations along the distal carina only (Fig. 32.6A). Similar isolated teeth were also collected in the lower part in the section (Fig. 32.1, Level 1). Maastrichtian representatives of the *Richardoestesia* morphotype, as discovered at Vitrolles-La-Plaine, are usually less recurved distally than the Campanian ones (Currie et al., 1990; Codrea et al., 2002).

### Titanosauria

Some compressed limb bones (humerus [Fig. 32.6B], femur, and tibia) were found during the third field campaigns. Their proximal and distal ends are not well preserved, but their size and robustness indicate that they belonged to fairly large animals. Unfortunately, any diagnostic characters allowing it to be referred to one of the three valid titanosaur species currently recognized on the Iberian–Armorican island—*Ampelosaurus atacis* (Le Lœuff, 1995, 2005), *Lirainosaurus astibiae* (Sanz et al., 1999), and *Atsinganosaurus velauciensis* (Garcia et al., 2010)—have not been preserved on this material. The material collected in 2007 and 2008 needs to be prepared in laboratory before being studied in detail for accurate identification.



**32.6.** A, UP-VLP-08-001, Coelurosauria tooth (*Richarddoestesia* morphotype) in lateral view. B, UP-VLP-98B-001, left humerus of a Titanosauria indet. in cranial view. C, UP-VLP-08-002, basal Iguanodontia (*"Rhabdodon"*) dentary tooth in labial view.

## Basal Iguanodontia

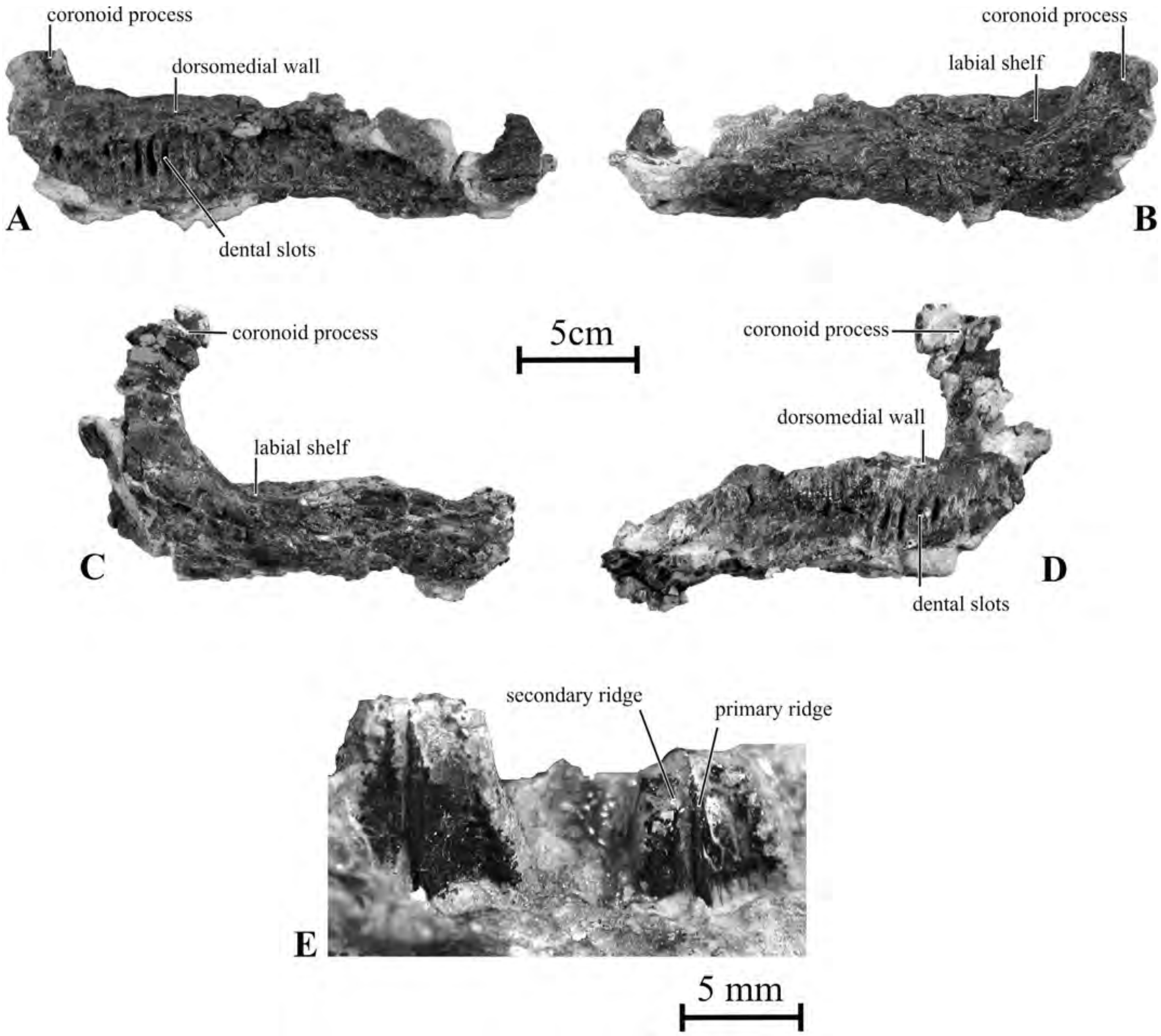
Massive isolated teeth (Fig. 32.6C) closely resemble those of the basal Iguanodontia *Rhabdodon*, the most common dinosaur of Late Cretaceous vertebrate assemblages from southern France (Allain and Pereda-Suberbiola, 2003). The enamel is distributed on both sides of the crowns. The lingual side of the dentary teeth is characterized by a strong median primary ridge and by more than eight slightly divergent on either sides of the primary ridge. There is no real cingulum, but a thin enameled lip marks the base of the distal part of the crown. The labial side is heavily worn. The crown of the maxillary teeth is devoid of a primary ridge, but numerous subequal, slightly vertically divergent ridges cover the buccal surface of the crown. The lingual side is heavily worn.

Systematic revisions of the *Rhabdodon* material from southern France are currently in progress in order to clarify the intrageneric variability (how many species?) and the individual differences linked to sexual dimorphism (Chanthasit and Buffetaut, 2007; Goussard, 2009).

### Hadrosauridae

Five dentaries were collected in the Vitrolles-La-Plaine locality (Fig. 32.7). All are crushed and incomplete. Because of their small size, they probably belong to juvenile specimens. The dentary ramus appears long and only slightly recurved ventrally. The dental battery is formed by narrow parallel-sided grooves (Fig. 32.7A,D); this character is synapomorphic for advanced Hadrosauroidea, including *Batyrosaurus*, *Probactrosaurus*, *Eolambia*, *Protohadros*, and Hadrosauridae (see Appendix 19.2 in Chapter 19 in this book, character 53). Even in juveniles, the dental battery is formed by more than 25 tooth families and is proportionally higher than in *Batyrosaurus*, *Probactrosaurus*, *Eolambia*, and *Protohadros*, suggesting that the hadrosauroid from Vitrolles-La-Plaine was more derived than these taxa and was probably a Hadrosauridae (the most recent common ancestor of *Bactrosaurus* and *Parasaurolphus*, plus all the descendants of this common ancestor; see Chapter 20 in this book). Moreover, the dental battery extends far caudally to the level of the apex of the coronoid process (Fig. 32.7A,D), a character found in Euhadosauria (sensu Weishampel et al., 2003: Hadrosaurinae + Lambeosaurinae) and *Telmatosaurus transylvanicus*. The coronoid process of the dentary is narrow and much higher than the dentary ramus (Fig. 32.7C,D). Although this character is unusual among hadrosaurids, it may be partially explained by ontogeny: juveniles are usually characterized by a proportionally higher coronoid process than older specimens (P.G., pers. obs.). The coronoid process is laterally offset and separated from dentition by a wide shelf (Fig. 32.7B), as is usual in hadrosauroids except *Bolong* and *Jinzhousaurus* (Appendix 19.2, character 48). It is distinctly curved rostrally (Fig.32.7C,D), like in Euhadrosauria and *Tethyshadros insularis* (Dalla Vecchia, 2009). Like in basal hadrosauroids, the apex of the coronoid process is only slightly expanded rostrally, and the surangular apparently formed much of the caudal margin of the coronoid process. In Euhadrosauria, on the contrary , the dentary forms nearly all of the rostrocaudally greatly expanded apex, and the surangular is reduced to a thin sliver along caudal margin and does not reach the dorsal end of the coronoid process (Appendix 19.2, character 49).

The dentary teeth are lanceolate and narrow (Fig. 33.7E). Their lingual side bears a strong primary ridge that divides the crown into two subequal halves. This character is shared by Euhadrosauria and *Telmatosaurus transsylvanicus*. A secondary ridge is developed on the mesial half of the crown and reaches the apex of the tooth, like in basal hadrosauroids, but also in *Tethysahdros insularis* (Dalla Vecchia, 2009). In Euhadrosauria and *Telmatosaurus transsylvanicus*, on the other hand, the secondary ridge is usually absent or faintly developed (Weishampel et al., 1993). The margins of the crown are denticulate; denticulations are usually less developed in Euhadrosauria.

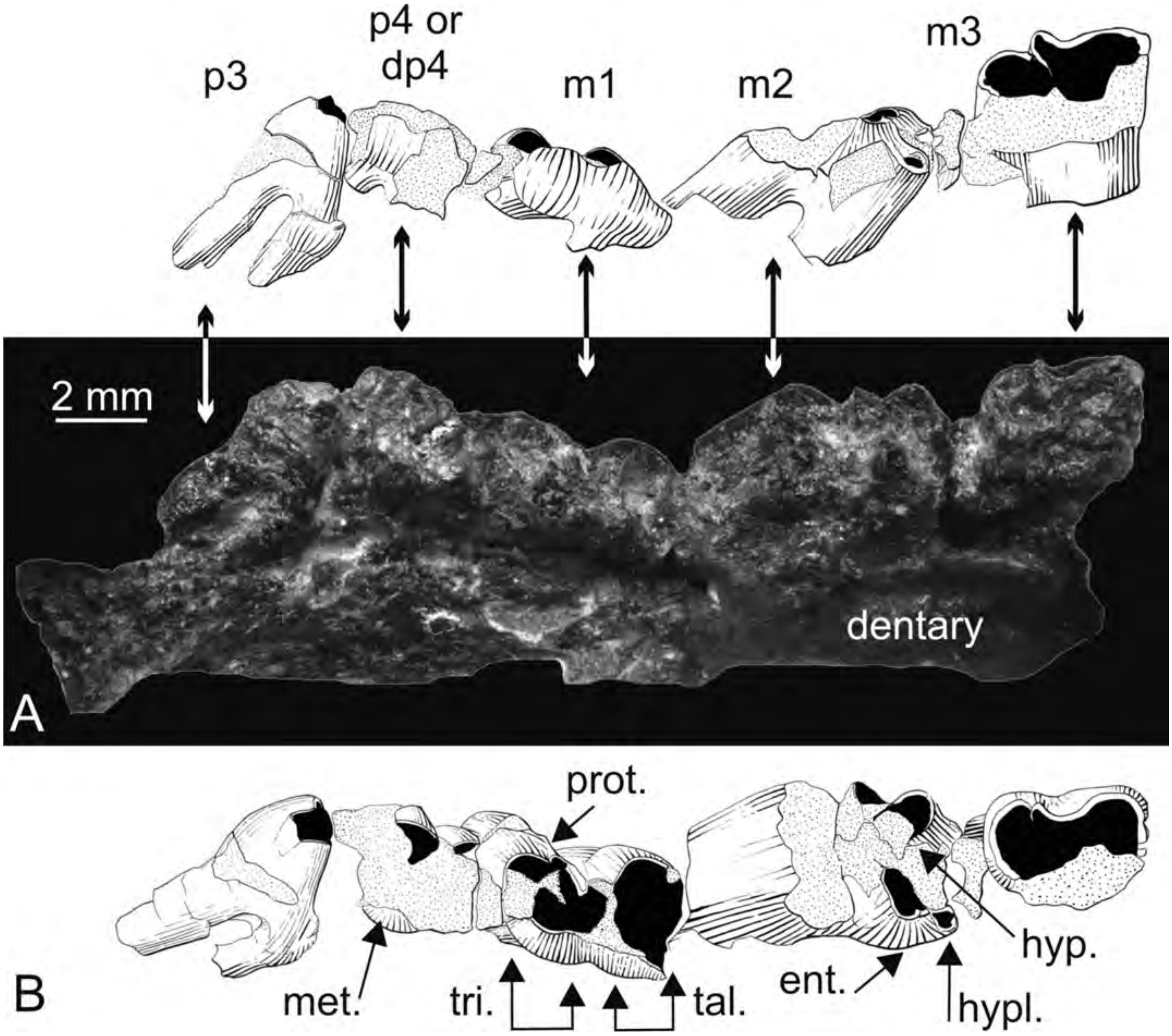


**32.7.** Hadrosaurid dentaries. A, B, UP-VLP-07 P15-001, left dentary in lingual (A) and labial (B) views. C, D, UP-VLP-07 P03-001, right dentary in labial (C) and lingual (D) views. E, UP-VLP-08E-001, detail of dentary teeth.

Therefore, the mosaic of characters observed on the dentaries and dentary teeth from Vitrolles-La-Plaine suggests that these fossils belong to a noneuhadrosaurian Hadrosauridae, close to *Telmatosaurus transsylvanicus* and *Tethyshadros insularis*, also from uppermost Cretaceous deposits of Europe. Moreover, these dentaries display a potential autapomorphy that we did not observe in any other hadrosauroid: along at least the caudal third of the dentary, the dental slots do not reach the dorsal border of the dentary ramus but are bordered dorsally by a medial wall that raises medially from the shelf at the base of the coronoid process (Fig. 32.7A,C). The biomechanical significance of this character remains enigmatic.

## Mammalia

In 1998–1999, and more recently in 2007, the excavations at Vitrolles-La-Plaine yielded some fragmentary remains of a eutherian mammal,



**32.8** *Valentinella vitrollense,* ISEM/VLP-2 (holotype) in lingual (A) and occlusal (B) views. *Abbreviations:* met, metaconid; pro, protoconid; tri, trigonid; tal, talonid; ent, entoconid; hyp, hypoconid; hypl, hypoconulid.

*Valentinella vitrollense* (Tabuce et al., 2004). The specimen discovered in 2007, still undescribed, corresponds to a lingual part of an upper molar retaining a prominent protocone and a distinct low cingular hypocone.

The Upper Cretaceous fossil record of eutherians is scanty in Europe: only two genera, *Labes* and *Lainodon*, were known in France and Spain before the discovery of *Valentinella* (Pol et al., 1992; Sigé et al., 1997; Gheerbrant and Astibia, 1999). On the basis of several dental traits, such as the hypoconulid–entoconid twinning and the anteroposteriorly short trigonid on m1–3, *Labes*, *Lainodon*, and *Valentinella* are ascribed to the "zhelestids."

The "zhelestids" are a paraphyletic unit well documented from the Cenomanian through Turonian of Uzbekistan and Kazakhstan. Other species from the Coniacian through Paleocene are also known in North America and Japan (Archibald, 2007). Most "zhelestids" are known only from fragmentary dental remains, but several taxa from Uzbekistan are now documented by associated cranial and dental remains in addition to ear regions (Ekdale et al., 2004) and referred postcranial elements (Chester et al., 2007, 2008, 2010). The "zhelestids" were initially regarded as being at the origin of both "condylarths" and Cenozoic ungulates within the Ungulatomorpha clade (Archibald et al., 2001). A recent broader-scale phylogenetic analysis argues, however, that the morphological similarities observed in "zhelestids" and ungulate placentals are only due to convergences. "Zhelestids" are now positioned near the base of the Eutheria clade in the mammalian tree (Wible et al., 2007).

## Conclusions

Vitrolles–La-Plaine is currently among the most diversified Late Maastrichtian sites in southern France. The vertebrate fauna, composed of at least 11 taxa, includes a "zhelestid" mammal, *Valentinella vitrollense*, in association with lacertilians, cryptodyran chelonians, alligatoroid crocodilians, and a diversified dinosaur fauna including Neoceratosauria, Coelurosauria, Titanosauria, basal Iguanodontia, and Hadrosauridae.

For the first time, hadrosaurid dinosaurs are formally recognized in Provence. The morphology of the dentary and dentary teeth suggests that this hadrosaurid material belongs to a basal form, close to *Telmatosaurus transsylvanicus* and *Tethyshadros insularis*, also from the Late Cretaceous of Europe. It apparently differs from the hadrosaurid material hitherto described, but the material at hand is too fragmentary and too poorly preserved to justify the erection of a new taxon.

The association of hadrosaurids with titanosaurids and *Rhabdodon* is unusual in the latest Cretaceous of southern France. Previous works based on sites in southern France have concluded that an important faunal replacement related to environmental changes occurred in southern Europe during the Late Cretaceous: a Late Campanian–Early Maastrichtian fauna dominated by titanosaurid sauropods and *Rhabdodon* was replaced by a Late Maastrichtian assemblage dominated by hadrosaurids (e.g., Le Lœuff et al., 1994). This hypothesis has already been challenged by recent discoveries in northern Spain (Lopez-Martinez et al., 2001): the hadrosaurid *Pararhabdodon isonensis* (including *Koutalisaurus kohlerorum*) from the Tremp Basin is considered as Early Maastrichtian to early Late Maastrichtian in age (Pereda-Suberbiola et al., 2009). The presence of hadrosaurids, titanosaurs, and *Rhabdodon* in the allochtonous assemblage from Vitrolles-La-Plaine suggests that these animals lived together in southern France during the latest Cretaceous. However, it is highly probable that they lived in different environments. Their co-occurrence in the allochtonous assemblage from Vitrolles-La-Plaine can easily be explained by taphonomical processes (hydraulic transport) that concentrated, in the same level, bones of animals living in various environments. However, it cannot be excluded that older Late Campanian–Early Maastrichtian sediments, containing dinosaur fossils (titanosaurs, basal Iguanodontia), were reworked and that the Vitrolles-la-Plaine assemblage is consequently a mixing of faunas of different ages.

It may be concluded Vitrolles-La-Plaine potentially offers new perspectives on the diversity and evolution of vertebrate ecosystems in southern Europe during the Maastrichtian. However, further research is needed in this site in order to clarify its taphonomy.

## Acknowledgments

We gratefully acknowledge the Vitrolles Municipality, particularly the mayor, G. Obino, for permission to conduct our research in this part of the Aix Basin. Logistical and field assistance were provided by L. Blein, R. Dumont, S. Jiquel, R. Licand, B. Marandat, F. Mebrouk, D. Roggero, S. Rafa, J. Sudre, and E. Turini.

## References

Allain, R., and X. Pereda-Suberbiola. 2003. Dinosaurs of France. Comptes Rendus Palevol 2: 27–44.

Archibald, D. J. 2007. Zhelestids: stem eutherians or basal laurasiatherians, but no evidence for placental orders in the cretaceous. Journal of Vertebrate Paleontology 27: 41A.

Archibald, J. D., A. O. Averianov, and E. G. Ekdale. 2001. Late Cretaceous relatives of rabbits, rodents, and other extant eutherian mammals. Nature 414: 62–65.

Behrensmeyer, A. K. 1988. Vertebrate preservation in fluvial channels. Palaeogeography, Palaeoclimatology, Palaeoecology 63: 183–199.

Buscalioni, A. D., F. Ortega, and D. Vasse. 1997. New crocodiles (Eusuchia: Alligatoroidea) from the Upper Cretaceous of southern Europe. Comptes rendus de l'Académie des Sciences de Paris (ser. 2) 325: 525–530.

———. 1999. The upper Cretaceous crocodilian assemblage from Laño (northcentral Spain): implications in the knowledge of the finicretaceous European faunas. Estudios Museo de Ciencia Naturales de Alava 14: 213–233.

Carrano, M. T., S. D. Sampson, and C. A. Foster. 2002. The osteology of *Masiakasaurus knopfleri*, a small abelisauroid (Dinosauria: Theropoda) from the Late Cretaceous of Madagascar. Journal of Vertebrate Paleontology 22: 510–534.

Chanthasit, P., and Buffetaut E. 2007. The distribution and new localities of the Late Cretaceous ornithopod dinosaur *Rhabdodon* in southern France. 12th European Workshop of Vertebrate Palaeontology, 12

Chester, S., E. Sargis, F. Szalay, J. D. Archibald, and A. O. Averianov. 2007. A functional analysis of mammalian humeri from the Late Cretaceous of Uzbekistan. Journal of Vertebrate Paleontology 27 (supplement to 3): 58A.

Chester, S., E. Sargis, F. Szalay, J. D. Archibald, and A. O. Averianov. 2008. Therian femora from the Late Cretaceous of Uzbekistan. Journal of Vertebrate Paleontology 28 (supplement to 3): 63A.

Chester, S. G. B., Sargis, E. J., Szalay, F. S., J. D. Archibald, and A.O. Averianov. 2010. Mammalian distal humeri from the Late Cretaceous of Uzbekistan. Acta Palaeontologica Polonica 55: 199–211.

Chiappe, L. M., L. M. Coria, L. Dingus, F. Jackson, A.Chinsamy, and M. Fox. 1998. Sauropod embryos from the Late Cretaceous of Patagonia. Nature 396: 258–261.

Codrea, V., T. Smith, P. Dica, A. Folie, G. Garcia, P. Godefroit, and J. Van Itterbeeck. 2002. Dinosaur egg nests, mammals and other vertebrates from a new Maastrichtian site of the Haţeg Basin (Romania). Comptes rendus Palevol 1: 173–180.

Codrea, V., O. Barbu, and C. Jipa-Murzea. 2010. Upper Cretaceous (Maastrichtian) land vertebrate diversity in Alba District (Romania). Bulletin of the Geological Society of Greece 43: 594–601.

Cojan, I., and M. G. Moreau. 2006. Correlation of terrestrial climatic fluctuations with global signals during the Upper Cretaceous–Danian in a compressive setting (Provence, France). Journal of Sedimentary Research 76: 589–604.

Cousin, R. 2002. Organisation des pontes des Megaloolithidae Zhao, 1979. Bulletin trimestriel de la Société géologique de Normandie et des Amis du Muséum du Havre, Éditions du Muséum d'Histoire Naturelle du Havre 89: 1–176.

Currie, P. J., J. K. Rigby Jr., and R. E. Sloan. 1990. Theropod teeth from the Judith River Formation of southern Alberta, Canada; pp. 107–125 in: K. Carpenter and P. J. Currie (eds.), Dinosaur systematics: approaches and perspectives. Cambridge University Press, Cambridge.

Dalla Vecchia, F. M. 2009. *Tethyshadros insularis*, a new hadrosauroid dinosaur (Ornithischia) from the Upper Cretaceous of Italy. Journal of Vertebrate Paleontology 29 (4): 1100–1116.

Eberth, D. A., and M. A. Getty. 2005. Ceratopsian bonebeds: occurrence, origins, and significance; pp. 501–506 in P. J. Currie and E. B. Koppelhus (eds.), Dinosaur Provincial Park, a spectacular ancient ecosystem revealed. Indiana University Press, Bloomington.

Ekdale, E. G., D. J. Archibald, and A. O. Averianov. 2004. Petrosal bones of placental mammals from the Late Cretaceous of Uzbekistan. Acta Palaeontologica Polonica 49: 161–176.

Fiorillo, A. R. 1988. Taphonomy of the Hazard Homestead Quarry (Ogallala Group), Hitchcock County, Nebraska. University of Wyoming Contributions to Geology 26: 57–98.

Folie, A., and V. Codrea. 2005. New lissamphibians and squamates from the Maastrichtian of Hateg Basin, Romania. Acta Palaeontologica Polonica 50: 57–71.

Galbrun, B., 1989. Résultats magnétostratigraphiques à la limite Rognacien-Vitrollien: précisions sur la limite Crétacé-Tertiaire dans le Bassin d'Aix-en-Provence. Cahiers de la Réserve géologique de Haute-Provence, Digne 1: 34–37.

Garcia, G. 1998. Les coquilles d'œufs de dinosaures du Crétacé supérieur du sud de la France: Diversité, paléobiologie, biochronologie et paléoenvironnements. Ph.D. thesis, University of Montpellier II, Montpellier, 313 pp.

Garcia, G., and M. Vianey-Liaud. 2001a. Dinosaur eggshells as new biochronological markers in Late Cretaceous continental deposits. Palaeogeography, Palaeoclimatology, Palaeoecology 169: 153–164.

———. 2001b. Nouvelles données sur les coquilles d'œufs de dinosaures de Megaloolithidae du sud de la France: systématique et variabilité intraspécifique. Comptes Rendus de l'Académie des Sciences de Paris 332: 185–191.

Garcia, G., M. Pincemaille, B. Marandat, M. Vianey-Liaud, E. Lorenz, H. Cappetta, G. Cheylan, J. Michaux, and J. Sudre. 1999. Découverte du premier squelette presque complet *de Rhabdodon priscus* (Dinosauria, Ornithopoda) dans le Maastrichtien inférieur de Provence. Comptes Rendus de l'Académie des Sciences de Paris 328: 415–421.

Garcia, G., S. Amico, F. Fournier, E. Thouand, and X. Valentin. 2010. A new titanosaur genus (Dinosauria, Sauropoda) from the Late Cretaceous of southern France and its paleobiogeographic implications. Bulletin de la Société Géologique de France 181: 269–277.

Gheerbrant, E., and H. Astibia. 1999. The Upper Cretaceous mammals from Lano (Spanish Basque Country). Estudios del Museo de Ciencias naturales de Alava 14: 295–323.

Grellet-Tinner, G., L. Chiappe, M. Norell, and D. Bottjer. 2006. Dinosaur eggs and nesting behaviors: a paleobiological investigation. Palaeogeography, Palaeoclimatology, Palaeoecology 232: 294–321.

Goussard, F. 2009. *Zalmoxes*, *Rhabdodon* and Rhabdodontidae: how many genera and how many species?; p. 51 in P. Godefroit and O. Lambert (eds.), Tribute to Charles Darwin and Bernissart iguanodons: new perspectives on vertebrate evolution and early cretaceous ecosystems. Royal Belgian Institute of Natural Sciences, Brussels.

Grigorescu, D., G. Garcia, Z. Csiki, V. Codrea, and A.-V. Bojar. 2010. Uppermost Cretaceous megaloolithid eggs from the Haţeg Basin, Romania, associated with hadrosaur hatchlings: search for explanation. Palaeogeography, Palaeoclimatology, Palaeoecology 293: 360–374.

Lapparent de Broin, F. de, and X. Murelaga. 1996. Une nouvelle faune de chéloniens dans le Crétacé supérieur européen. Comptes Rendus de l'Académie des Sciences de Paris 323: 729–735.

———. 1999. Turtles from the Upper Cretaceous of Laňo (Iberian Peninsula). Estudios del Museo de Ciencias Naturales de Alava 14: 135–211.

Laurent, Y., L. Cavin, and M. Bilotte. 1999. Découverte d'un gisement à vertébrés dans le Maastrichtien supérieur des Petites-Pyrénées. Comptes Rendus de l'Académie des Sciences de Paris 328: 781–787.

Laurent, Y., M. Bilotte, and J. Le Loeuff. 2002. Late Maastrichtian continental vertebrates from southwestern France: correlation with marine faunas. Palaeogeography, Palaeoclimatology, Palaeoecology 187: 121–135.

Le Lœuff, J. 1995. *Ampelosaurus atacis* (nov. gen., nov. sp.), un nouveau Titanosauridae (Dinosauria, Sauropoda) du Crétacé supérieur de la Haute Vallée de l'Aude (France). Comptes Rendus de l'Académie des Sciences de Paris 321: 693–699.

———. 2005. Osteology of *Ampelosaurus atacis* (Titanosauridae) from southern France; pp. 115–137 in V. Tidwell and K. Carpenter (eds.), Thunder-lizards: the sauropodomorph dinosaurs. Indiana University Press, Bloomington.

Le Lœuff, J., and E. Buffetaut. 1991. *Tarascosaurus salluvicus* nov. gen., nov. sp., un nouveau dinosaure théropode (Abélisauridé) du Crétacé supérieur (Campanien inférieur) du synclinal du Beausset (Bouches-du-Rhône, France). Geobios 25: 585–594.

Le Lœuff, J., E. Buffetaut, and M. Martin. 1994. The last stages of dinosaur faunal history in Europe: a succession of Maastrichtian dinosaur assemblages from the Corbières (southern France). Geological Magazine 131: 625–630.

Lopez-Martinez, N., J. I. Canudo, L. Ardevol, X. Pereda-Suberbiola, X. Orue-Extbarria, G. Cuenca-Bescos, J. I. Ruiz-Omenaca, X. Murelaga, and M. Feist. 2001. New dinosaur sites correlated with Upper Maastrichtian pelagic deposits in the Spanish Pyrenees: implications for the dinosaur extinction in Europe. Cretaceous Research 22: 41–61.

Martin, J. E., and E. Buffetaut. 2008. *Crocodilus affuvelensis* Matheron, 1869 from the Late Cretaceous of southern France: a reassessment. Zoological Journal of the Linnean Society 152: 567–580.

Paris, J. P., and P. Taquet. 1973. Découverte d'un fragment de dentaire d'hadrosaurien (reptile dinosaurien) dans le Crétacé supérieur des Petites Pyrénées (Haute Garonne). Bulletin du Muséum d'Histoire Naturelle de Paris 130: 17–27.

Pereda-Suberbiola, X. 2009. Biogeographical affinities of Late Cretaceous continental tetrapods of Europe: a review. Bulletin de la Société Géologique de France 180: 57–71.

Pereda-Suberbiola, X., J. I. Canudo, J. Company, P. Cruzado-Caballero, and J. I. Ruiz-Omeñaca. 2009. Hadrosauroid dinosaurs from the Latest Cretaceous of the Iberian Peninsula. Journal of Vertebrate Paleontology 29: 946–951.

Pol, C., A. D. Buscalioni, J. Carballeira, V. Francés, N. Lopez-Martinez, B. Marandat, J. J. Moratalla, J. L. Sanz, B. Sigé, and J. Villatte. 1992. Reptiles and mammals from the Late Cretaceous new locality Quintanilla del Coco (Burgos province, Spain). Neues Jahrbuch für Geologie und Paläontologie 184: 279–314.

Rauhut, O. W. M. 2003. The interrelationships and evolution of basal theropod dinosaurs. Special Papers in Palaeontology 69: 1–213.

Ryan, M. J., A. P. Russell, D. A. Eberth, and P. J. Currie. 2001. The taphonomy of a *Centrosaurus* (Ornithischia: Ceratopsidae) bone bed from the Dinosaur Park Formation (Upper Campanian), Alberta, Canada, with comments on cranial ontogeny. Palaios 16: 482–506.

Sampson, S. D., M. T. Carrano, and C. A. Forster. 2001. A bizarre predatory dinosaur from the Late Cretaceous of Madagascar. Nature 409: 504–506.

Sander, P. M., C. Peitz, F. Jackson, and L. M. Chiappe. 2008. Upper Cretaceous titanosaur nesting sites and their implication for sauropod dinosaur reproductive biology. Palaeontographica A 284: 69–107.

Sanz, J. L., J. E. Powell, J. Le Lœuff, R. Martínez, and J. Pereda Suberbiola. 1999. Sauropod remains from the Upper Cretaceous of Laño (northcentral Spain). Titanosaur phylogenetic relationships. Estudios del Museo de Ciencias Naturales de Alava 14 (Num. Esp. 1): 235–255.

Sankey, J. T. 2001. Late Campanian southern dinosaurs, Aguja Formation, Big Bend, Texas. Journal of Paleontology 75: 208–215.

Sigé, B., A. D. Buscalioni, S. Duffaud, M. Gayet, B. Orth, J.-C. Rage, and J. L. Sanz. 1997. Etat des données sur le gisement crétacé supérieur continental de Champ-Garimond (Gard, Sud de la France). Münchner Geowissenschaftliche Abhandlungen 34: 111–130.

Tabuce, R., M. Vianey-Liaud, and G. Garcia. 2004. A eutherian mammal in the latest Cretaceous of Vitrolles, southern France. Acta Paleontologica Polonica 49: 347–356.

Tortosa, T., E. Buffetaut, Y. Dutour, and G. Cheylan. 2010. Abelisaurid remains from Provence (Southeastern France): phylogenetic and paleobiogeographic implications; p. 82 in 8th meeting of the European Association of Vertebrate Palaeontologists, Aix-en-Provence, June 7–12, 2010.

Tykosky, R. S., and T. Rowe. 2004. Ceratosauria; pp. 47–70 in D. B. Weishampel, P. Dodson, and H. Osmólska (eds.), The Dinosauria. 2nd ed. University of California Press, Berkeley.

Varicchio, D. J., F. Jackson, J. J. Borkowski, and J. H. Horner. 1997. Nest and clutches of the dinosaur *Troodon formosus* and the evolution of avian reproductive traits. Nature 385: 247–250.

Vianey-Liaud, M., and G. Garcia. 2000. The interest of french Late Cretaceous dinosaur eggs and eggshells; pp. 165–176 (extended abstracts) in A. M. Bravo and T. Reyes (eds), 1st International symposium on dinosaurs eggs and babies. Isona i Conca Della, Catalonia, Spain.

Vianey-Liaud, M., and N. Lopez-Martinez. 1997. Late Cretaceous dinosaur eggshells from the Tremp Basin, southern Pyrenees, Lleida, Spain. Journal of Paleontology 71: 1157–1171.

Vianey-Liaud, M., Mallan, P. O. Buscail, and C. Montgelard. 1994. Review of French dinosaur eggshells: morphology, structure, mineral, and organic composition; pp. 151–183 in K. Carpenter, K. F. Hirsch and J. R. Horner (eds.), Dinosaur eggs and babies. Cambridge University Press, New-York.

Voorhies, M. R. 1969. Taphonomy and population dynamics of an Early Pliocene vertebrate fauna, Knox County, Nebraska. Contributions to Geology, University of Wyoming Special Paper 1.

Weishampel, D. B., D. B. Norman, and D. Grigorescu. 1993. *Telmatosaurus transsylvanicus* from the Late Cretaceous of Romania: the most basal hadrosaurid dinosaur. Palaeontology 36: 361–385.

Weishampel, D. B., C.-M. Jianu, Z. Csiki, and D. B. Norman. 2003. Osteology and phylogeny of *Zalmoxes* (n. g.), an unusual euornithopod dinosaur from the latest Cretaceous of Romania. Journal of Systematic Palaeontology 1: 65–123.

Westphal, M., and J. P. Durand. 1990. Magnétostratigraphie des séries continentales fluvio-lacustres du Crétacé supérieur dans le synclinal de l'Arc (Région d'Aix-en-Provence, France). Bulletin de la Société Géologique de France 8: 609–620.

Wible, J. R., G. W. Rougier, M. J. Novacek, and R. J. Asher. 2007. Cretaceous eutherians and Laurasian origin for placental mammals near the K/T boundary. Nature 447: 1003–1006.