

LATE CRETACEOUS NON-MARINE VERTEBRATES FROM SOUTHERN FRANCE: A REVIEW OF RECENT FINDS

ERIC BUFFETAUT, JEAN LE LOEUFF, LIONEL CAVIN, SYLVAIN DUFFAUD,
EMMANUEL GHEERBRANT, YVES LAURENT, MICHEL MARTIN, JEAN-CLAUDE RAGE,
HAIYAN TONG & DENIS VASSE

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ABSTRACT - During the last few years, systematic prospections and excavations in the non-marine Campanian and Maastrichtian of southern France, from Provence in the East to the valley of the Garonne in the West, have considerably increased our knowledge of the continental vertebrates (fishes, amphibians, turtles, squamates, crocodylians, pterosaurs, dinosaurs, birds and mammals) from that time interval. A succession of faunal assemblages, corresponding to the Early Campanian, the Late Campanian / Early Maastrichtian and the Late Maastrichtian, can now be recognised, with a marked change in the dinosaur fauna during the Maastrichtian, but no clear evidence of decline during the last million years of the Cretaceous. The biogeographical complexity of the Late Cretaceous vertebrate assemblages from southwestern Europe is underlined.

KEYWORDS: LATE CRETACEOUS, SOUTHERN FRANCE, NON-MARINE VERTEBRATES, PISCES, AMPHIBIA, REPTILIA, AVES, MAMMALIA.

RÉSUMÉ - Ces dernières années, des prospections et des fouilles systématiques dans le Campanien et le Maastrichtien continentaux du Sud de la France, de la Provence à l'Est à la vallée de la Garonne à l'Ouest, ont considérablement augmenté notre connaissance des vertébrés continentaux (poissons, amphibiens, tortues, squamates, crocodyliens, ptérosaures, dinosaures, oiseaux et mammifères) de cette période. Une succession d'assemblages fauniques, correspondant au Campanien inférieur, au Campanien supérieur / Maastrichtien inférieur et au Maastrichtien supérieur, peut désormais être reconnue, avec un changement marqué dans la faune dinosaurienne au cours du Maastrichtien, mais pas de preuve claire d'un déclin pendant les derniers millions d'années du Crétacé. La complexité biogéographique des assemblages de vertébrés du Crétacé supérieur du Sud-Ouest de l'Europe est soulignée.

MOTS-CLÉS: CRÉTACÉ SUPÉRIEUR, SUD DE LA FRANCE, VERTÉBRÉS CONTINENTAUX, POISSONS, AMPHIBIENS, REPTILES, OISEAUX, MAMMIFÈRES.

INTRODUCTION

Although crocodylian remains from the Upper Cretaceous of the Aix-en-Provence area were described by Cuvier as early as 1824, the Campanian and Maastrichtian non-marine vertebrate faunas of southern France have remained poorly known until recently. Bones and eggshell fragments later identified as belonging to dinosaurs were found by Pouech in the Upper Cretaceous of Ariège in the 1850s (see Buffetaut 1992; Buffetaut *et al.* 1993; Buffetaut & Le Loeuff 1994; Le Loeuff 1991b, 1992), and in 1869 Matheron was the first to identify dinosaur remains from the Aix basin. Despite these early finds, and later work by Depéret (1899, 1900) in the Saint-Chinian region at the turn of century, the Late Cretaceous dinosaurs and asso-

ciated faunas from southern France attracted little attention until the middle of the twentieth century (Buffetaut *et al.* 1993). In 1947, Lapparent published a monograph on the Late Cretaceous dinosaurs of southern France which remained the standard work on the subject for several decades, although it is now much outdated. In the 1950s and 1960s, much attention was devoted to the fossil eggs of Provence and Languedoc. This resulted in an abundant literature, sometimes of disputable scientific value, but strangely enough the fascination exerted by fossil eggs on some palaeontologists did not extend to the bones of the animals which may have laid them, and little progress was achieved in the knowledge of the Late Cretaceous vertebrate faunas of southern France until the end of the 1980s. Since then, extensive field work by our

group, combining prospection and systematic excavations, often with the help of dedicated amateur palaeontologists, has resulted in a better knowledge of these faunas and of their changes through time. The purpose of the present paper is to review the main recent advances in this field and to examine some of their broader implications. We have restricted our review to localities having yielded skeletal remains. The numerous sites containing fossil eggshells pose different problems and their contribution to the knowledge of the actual composition of the faunal assemblages is very limited. A few vertebrate remains from the non-marine Cenomanian deposits in various parts of southern France (Gard, Dordogne, etc.) were described during the 19th century (see Buffetaut *et al.* 1991, for a review), but most of this material is now lost, and we have restricted our review to the later part of the Late Cretaceous (Campanian and Maastrichtian).

GEOGRAPHICAL AND GEOLOGICAL SETTING

Remains of Campanian and Maastrichtian vertebrates are known to occur in non-marine rocks along a discontinuous belt extending from the Upper Var region of Provence in the east, through the Aix-en-Provence basin, the vicinity of Montpellier, the Saint-Chinian area south of the Montagne Noire, the Corbières and the foothills of the Pyrenees in department Ariège, all the way to the Garonne valley in the west, where non-marine deposits are replaced laterally by marine beds deposited in the gulf which occupied the Aquitaine basin in the Late Cretaceous (Fig. 1). In recent years, all these areas have yielded important new vertebrate fossils.

Dating these non-marine formations has proved difficult, because direct correlations with marine deposits are usually not possible (Buffetaut & Le Loeuff

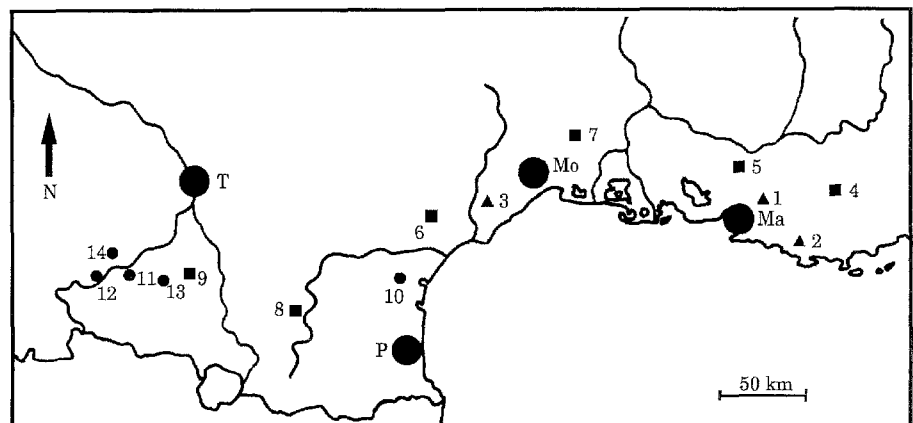
1991a). Palynomorphs, charophytes, freshwater molluscs and ostracodes sometimes occur in those formations, but are not easily used for correlation with the standard stratigraphic scale based on marine organisms. Local stratigraphic names have long been used to subdivide the non-marine Cretaceous of southern France, and the names given to the units originally recognized in Provence (i.e., from oldest to youngest, Valdonnian, Fuvelian, Begudian and Rognacian) have sometimes been applied to more or less similar formations in other regions. Various correlations of these local stages with the standard marine stratigraphic scale have been proposed. In recent years, magnetostratigraphic studies have somewhat clarified the situation. According to Westphal & Durand (1990), the Valdonnian can be correlated with the upper part of the Santonian, and the Fuvelian and most or all of the Begudian correspond to the Campanian. The Rognacian would then be the equivalent of the Maastrichtian.

However, many uncertainties remain about the age of the Late Cretaceous vertebrate-bearing formations of southern France, and the exact placement of the Cretaceous-Tertiary boundary in this area remains a matter of controversy. In the present paper, we present a succession of Late Cretaceous vertebrate faunas which until recently was unrecognised. However, although the order of succession of the various assemblages is well established, doubts remain about the exact age of some of them. For instance, it is still difficult to distinguish late Campanian faunas from early Maastrichtian ones, whereas late Maastrichtian faunas seem to be easily recognisable.

THE GENERAL CHARACTER OF THE FAUNAS

Images of Late Cretaceous non-marine faunas conveyed both by many popular articles and books

FIGURE 1 - Map of southern France showing the main localities mentioned in text. Triangles: Early Campanian. Squares: Late Campanian / Early Maastrichtian. Dots: Late Maastrichtian. 1: Fuveau. 2: Le Beausset. 3: Villeveyrac. 4: Fox-Amphoux. 5: Aix Basin. 6: Cruzy. 7: Champ-Garimond. 8: Upper Aude Valley. 9: Le Mas d'Azil. 10: Montplaisir. 11: Lestaillats. 12: Le Jadet. 13: Mérigon. 14: Tricouté. Carte montrant les principaux sites mentionnés dans le texte. Triangles: Campanien inférieur. Carrés: Campanien supérieur / Maastrichtien inférieur. Ronds: Maastrichtien supérieur.



and by some more specialised ones are largely based on the fossil record from western North America, and to some extent on that from the Gobi Desert. This can be extremely misleading, for the simple reason that by Late Cretaceous times several quite distinct faunal provinces were in existence. The southwest European vertebrate fauna had a peculiar composition of its own, being a mixture of various components, some of them apparently endemic, others showing clear affinities with "Gondwanan" forms (Buffetaut 1989), and yet others being related to "Asiamerican" forms found in western North America and Central Asia (see Le Loeuff, 1991a for a more detailed discussion).

For a long time, our knowledge of the Late Cretaceous vertebrates of southern France was largely limited to large and middle-size forms such as dinosaurs, crocodylians and turtles. Better collecting techniques have resulted in the discovery of much more varied assemblages including fishes, lissamphibians, squamates, turtles, crocodylians, pterosaurs, dinosaurs, birds and mammals. In the following sections, we review what is currently known of the successive faunal assemblages, with special emphasis on new discoveries and reinterpretations.

EARLY CAMPANIAN ASSEMBLAGES

According to the magnetostratigraphic results of Westphal & Durand (1990), the so-called "Fuvelian" beds of the Aix-en-Provence basin can probably be considered as early Campanian in age. "Fuvelian" rocks, both in Provence and in Languedoc, have yielded the oldest non-marine vertebrate assemblage currently known from the Upper Cretaceous of southern France. Some of the main localities are in the type area of the Fuvelian, around Fuveau (Bouches-du-Rhône), where relatively abundant vertebrate remains were found in the course of the exploitation of lignite beds (Matheron 1869); however, modern exploitation techniques now make such discoveries much more difficult. An isolated but important find of theropod bones was made in the lower Campanian of Le Beausset (Var). In Languedoc, the main early Campanian sites are in the Villeveyrac basin (Buffetaut *et al.* 1996), west of Montpellier, where "Fuvelian" beds have been exposed in vast bauxite quarries. Few occurrences of early Campanian vertebrates are currently known farther west. Many of the "Fuvelian" localities apparently correspond to lacustrine deposits, often consisting of greyish marls containing lignite, and the vertebrate fauna they yield often

displays a markedly aquatic character, with a predominance of turtle remains. Crocodylians and fishes are also relatively abundant, but dinosaurs tend to be relatively infrequent.

Various fish remains have been described from the Early Campanian levels of Villeveyrac (Buffetaut *et al.* 1996). They include button-like teeth referred to the Sparidae, and teeth and scales of a lepisosteid. Lepisosteid jaws from the "Fuvelian" of Ventabren (Bouches-du-Rhône) have been referred to *Atractosteus africanus* (Cavin *et al.* 1996). The occurrence of this species also known from the Cretaceous of Africa is biogeographically interesting, and in agreement with the presence in the Upper Cretaceous of southern France of various taxa with Gondwanan affinities.

Anuran remains from Villeveyrac include a frontoparietal belonging to the family Palaeobatrachidae, which appears to be the oldest known representative of the family (Buffetaut *et al.* 1996).

Turtle remains are extremely abundant at some Fuvelian localities, notably Villeveyrac. One of the best specimens from the Villeveyrac basin is an almost complete shell, which has been attributed (Buffetaut *et al.* 1996) to the pelomedusid pleurodiran *Polysternon provinciale* (Matheron 1869). A finely preserved pelomedusid skull from Villeveyrac shows characters of the subfamily Podocnemidinae. It is tentatively identified as the hitherto unknown skull of *Polysternon provinciale* and will be described in detail in a separate paper (Tong, in prep.). A different type of turtle is also known from Villeveyrac, being represented by isolated plates showing a vermiculate ornamentation. They are currently referred to a cryptodiran of uncertain affinities (Buffetaut *et al.* 1996).

Squamates are represented at Villeveyrac by a jaw fragment indicating an indeterminate lacertilian (Buffetaut *et al.* 1996).

Crocodylians are present at most Fuvelian sites, notably in the Fuveau basin, from where Matheron (1869) described "*Crocodylus affuvelensis*", a form which certainly does not belong to the genus *Crocodylus* and is interpreted instead as a mesosuchian of the family Trematochampsidae (Buffetaut 1989). Blunt ornamented teeth belonging to this animal are present at Villeveyrac (Buffetaut *et al.* 1996). A second type of crocodylian, belonging to the Eusuchia, is also present both at Fuveau and at Villeveyrac, but it is represented by very scanty material.

As mentioned above, dinosaur remains are not very abundant in the Fuvelian. In particular, no titanosaurid remains have yet been reported.

Whether this corresponds to a real “titanosaurid hiatus” during part of the Cretaceous in Europe, similar to what has been reported from North America (Lucas & Hunt 1989), or simply to an incomplete fossil record, is still uncertain.

Theropod dinosaurs are represented at Villeveyrac by small laterally compressed and serrated teeth (Buffetaut *et al.* 1986, 1996) which may belong to dromaeosaurids. Larger theropods of the Early Campanian are known only from vertebrae and a partial femur from Le Beausset (Var), described as *Tarascosaurus salluvicus* by Le Loeuff & Buffetaut (1991), and referred to the family Abelisauridae, which is otherwise known from the southern continents.

Ornithopod dinosaurs are represented at Villeveyrac by cranial and post-cranial remains of *Rhabdodon* (Buffetaut *et al.* 1996), an Iguanodontia incertae sedis which seems to have been endemic to Europe. The form from Villeveyrac seems to be similar to *Rhabdodon priscus* MATHERON, 1869, which was originally described from slightly more recent deposits (probably Late Campanian to Early Maastrichtian in age) near Marseille.

A few ankylosaur remains (isolated teeth and scutes) are known from Villeveyrac (Buffetaut *et al.* 1996); tooth morphology suggests that they may belong to the family Nodosauridae.

LATE CAMPANIAN / EARLY MAASTRICHTIAN ASSEMBLAGES

Most of the known Late Cretaceous vertebrate localities of southern France apparently belong to a time interval spanning the Late Campanian and Early Maastrichtian. They include the localities in the Begudo-Rognacian “Grès et argiles à reptiles” of Provence (Var and Bouches-du-Rhône), most of the localities in Gard and Hérault (including the various sites in the Saint-Chinian area originally studied by Depéret, plus a new and promising site at Cruzy), the localities in the Grès des Estous and Marnes de la Maurine in the upper valley of the Aude, and the sites discovered by Pouech in the Grès de Labarre in the vicinity of Le Mas d’Azil (Ariège; our knowledge of the fauna from these sites is mainly based on Pouech’s collection, see Le Loeuff 1991b). Although there are local variations in faunal composition, all these localities yield a relatively homogenous fauna, and at the moment it does not seem possible to distinguish a Late Campanian assemblage from an Early Maastrichtian one (in any case, stratigraphic resolution is rather poor for this interval in the non-marine Upper Cretaceous of southern France).

As compared to the Early Campanian assemblages, which are dominated by freshwater forms, the Late Campanian to Early Maastrichtian ones show a more terrestrial character, with, in particular, a much greater abundance of dinosaurs.

With the exception of lepisosteid scales, fishes are poorly known from these localities. The same applies to amphibians, although a batrachosauroid anuran has been found at Champ-Garimond (Gard; Duffaud *et al.* in prep.).

Turtles are abundant at some localities, with especially well preserved skull and shell material from a new site at Fox-Amphoux. One of the most frequent forms appears to be a large pleurodiran with a shell closely resembling the older *Polysternon provinciale*, but with a more derived skull (Tong in prep.). Another turtle with a reticulate ornamentation on the shell is also present; a recently discovered skull from Fox-Amphoux may soon shed light on its affinities.

Squamates are still poorly known in these assemblages. However, vertebrae of a very large varanoid lizard, perhaps reaching the size of the modern Komodo “dragon”, have recently been found at Cruzy (Hérault) and Montséret (a locality in the eastern Corbières, the age of which is still uncertain: see Tong *et al.* 1993).

Crocodylians are fairly frequent. A large lower jaw from Saint-Estève-Janson (Bouches-du-Rhône) has been described as *Ischyrochampsia meridionalis* by Vasse (1995), and referred to the family Trematochampsidae (Mesosuchia). Large teeth clearly belonging to the same form are known from Le Mas d’Azil (Le Loeuff 1991b). Recently, the Fox-Amphoux area has yielded excellent skulls of a very short-snouted, blunt-toothed alligatorid and of a mesorostral crocodylid.

So far, pterosaurs are represented only by a few poorly preserved hollow bones from the Bellevue locality in the Aude valley.

Dinosaurs are abundant at most localities. In contrast to earlier and later assemblages from southern France, the fauna is clearly dominated by titanosaurid sauropods, which are the most abundant dinosaurs at many localities. The first description was by Matheron (1869), who erected the taxon *Hypselosaurus priscus* on the basis of scanty material from the Aix basin. Since then, most of the sauropod remains from southern France, as well as many of the abundant dinosaur eggs from that area, have been uncritically referred to *Hypselosaurus*. However, as argued by Le Loeuff (1993), *Hypselosaurus priscus* is best considered as a *nomen dubium*. Reports of the occurrence of *Titanosaurus indicus* (also a *nomen dubium*) by Lapparent (1947) are groundless. At

the moment, the only well defined titanosaurid taxon from the Upper Cretaceous of southern France is *Ampelosaurus atacis* described by Le Loeuff (1995) on the basis of abundant material from the Bellevue locality in the Aude valley. Like several other titanosaurids, *Ampelosaurus* possessed a dermal armour of thick bony plates (Le Loeuff, Buffetaut, Cavin, Martin, Martin & Tong 1994).

Theropod dinosaurs are relatively rare. A maxilla from Provence has been identified as belonging to an abelisaurid (Buffetaut *et al.* 1988), and it seems probable that the large predators in the southern French faunas were abelisaurids. Small theropod teeth are found at various localities (Buffetaut *et al.* 1986). Although the affinities of these teeth are not always easily determined, a few bones from Provence clearly indicate the occurrence of a dromaeosaurid theropod (Le Loeuff *et al.* 1992). Newly discovered material (including a sacrum and a humerus) from Fox-Amphoux will soon allow the erection of a new taxon.

Ornithischian dinosaurs are represented mainly by the ornithomimid *Rhabdodon*, which seems to be represented by more than one species (*Rhabdodon priscus* and *R. septimanicus*: see Buffetaut & Le Loeuff 1991b). At some localities *Rhabdodon* is more abundant than titanosaurids, which may reflect ecological differences.

Ankylosaurs are present, but usually not abundant. The material is generally referred to the nodosaurid genus *Struthiosaurus* BUNZEL, but some specimens suggest that ankylosaurids may also be present. Some of the dermal plates from the Aude valley referred to ankylosaurs by Pereda-Suberbiola (1993) have turned out to belong to armoured titanosaurids (Le Loeuff, Buffetaut, Cavin, Martin, Martin & Tong 1994), while a scapula originally referred to a nodosaurid (Pereda-Suberbiola 1993) in fact belongs to *Rhabdodon*.

Remains of large birds have very recently been discovered (Buffetaut *et al.* 1995) at three localities in southern France (Fox-Amphoux, Bellevue and Combeville, Hérault). The material, which is currently under study, includes pelvic elements, a femur and a tibiotarsus. These birds were apparently ground-dwelling forms reaching the size of a cassowary. Their systematic affinities are still uncertain.

Very few mammal remains have so far been found in Late Campanian / Early Maastrichtian beds in southern France. The only certain record is from Champ-Garimond, Gard (Ledoux *et al.* 1966), where two teeth identified as *Labes garimondi*, an insectivore, have been discovered (Pol *et al.* 1992).

A possible incomplete mammal metatarsal has been found in the Grès de Labarre at the Filleit Dam in Ariège (Gheerbrant *et al.* in prep.).

LATE MAASTRICHTIAN ASSEMBLAGES

Few non-marine vertebrate localities of clearly Late Maastrichtian age are currently known in southern France, but they are important because the assemblages they contain reveal a notable faunal change during the Maastrichtian. All of them are located in the foothills of the Pyrenees, from the eastern Corbières (Montplaisir) in the East, through the Plantaurel (Mérigon) in Ariège, to both sides of the Garonne valley (Lestaillats, Tricouté) in the West. The fossil-bearing beds are continental in the East; they become more brackish (Marnes d'Auzas), or even shallow-marine (Calcaire nankin) near the valley of the Garonne. Excavations conducted by our group at several of these sites have revealed a faunal assemblage which seems fairly characteristic of the final part of the Cretaceous in western Europe.

Fishes are very scarce in the strictly non-marine localities. They are much more abundant in the Marnes d'Auzas, with teeth of selachians and osteichthyans (Gheerbrant *et al.*, in prep.). The marine actinopterygian *Enchodus* has recently been described by Buffetaut & Cavin (1995) from the Calcaire nankin at Saint-Martory (Haute-Garonne).

Remains of amphibians, including anurans and possibly urodeles, and lacertilian squamates have been obtained by washing and screening at several sites in the Marnes d'Auzas (Gheerbrant *et al.* in prep.).

Turtle plates are present at several localities, but the material hitherto collected is too fragmentary to warrant precise identifications.

Crocodylians are fairly abundant at several localities (notably Montplaisir), but the available material consists mainly of isolated teeth and procellosous vertebrae. The latter are indicative of eusuchians (see Buffetaut & Cavin 1995).

Dinosaurs are present at most localities. Theropods are represented by small isolated teeth, and two vertebrae from Montplaisir; the latter are indicative of a dromaeosaurid. No titanosaurid remains have so far been found. The dinosaur fauna is largely dominated by hadrosaurid ornithomimids, first reported from the Calcaire nankin of Saint-Martory (Haute-Garonne: Paris & Taquet 1973), and now represented by jaws, teeth and/or postcranial elements at several loca-

lities (Montplaisir, Mérigon, Lestailats, Tricouté: see Le Loeuff, Buffetaut, Cavin, Laurent, Martin, Martin & Tong 1994). This material is currently under study (Laurent, in prep.), and the number of taxa represented is still uncertain. The assemblage at Montplaisir (Le Loeuff *et al.* 1994) is interesting because it includes both juveniles and adults. Ankylosaurs are represented by a scute from Lestailats.

Pterosaurs are known from poorly preserved very thin-walled bones at Montplaisir, and by a very large cervical vertebra at Mérigon. The latter resembles the huge North American *Quetzalcoatlus*, and indicates an animal with a wing span of about 8.5 metres.

Mammals are known from a few incomplete teeth from the Marnes d'Auzas of Peyrecave in Haute-Garonne (Gheerbrant *et al.* in prep.). They are identified as therians, most of them probably tribosphenic.

CONCLUSIONS

This rapid review of our current knowledge of non-marine vertebrates from the Upper Cretaceous of southern France leads to several remarks. Firstly, it should be noted that until recently, the Late Cretaceous faunas from that region were usually considered as forming a homogenous assemblage, within which no subdivisions were attempted. Considering that the Late Cretaceous vertebrate-bearing formations in southern France cover the time-span from the Early Campanian to the Maastrichtian-Danian boundary, which corresponds to some 18 million years, comparison with what is known of faunal evolution at that time in other parts of the world, for instance in North America or Central Asia, clearly showed how unlikely the idea of a single unchanging fauna from the "Fuvelian" to the top of the "Rognacian" was. The very different image we now have (Table 1) is the result of both intensive field work at many localities over a period of several years and of greater attention paid to the age of these localities.

One of the salient points of this image is the notable faunal change which appears to have taken place sometime during the Maastrichtian, and is mainly marked by the replacement of titanosaurid sauropods by hadrosaurid ornithopods as the dominant group of plant-eating dinosaurs (Le Loeuff, Buffetaut & Martin 1994). The possible causes for this replacement are still uncertain, although environmental changes, possibly linked to a marine regression, apparently occurred during the Maastrichtian in Europe (Cojan 1989), and may have had an influence, via a possible change in the vegetation, on the vertebrate fauna. There is no evidence, however, of a major climatic deterioration during the Maastrichtian in southern France, as shown by the presence of crocodylians and other reptiles sensitive to climatic cooling in the Late Maastrichtian localities of that area (Buffetaut & Cavin 1995). Because the exact position of the Cretaceous-Tertiary boundary is still uncertain in the non-marine sections of southern France, and because no Early Palaeocene vertebrate fauna is yet known from that area, it is difficult at the moment to draw definite conclusions about Cretaceous-Tertiary boundary events in that region. However, the Maastrichtian vertebrate record reveals faunal change rather than any marked decline among the groups known at that time (Le Loeuff, Buffetaut & Martin 1994).

Another interesting aspect of the Late Cretaceous vertebrate faunas of southern France is their biogeographical interpretation. As mentioned above, they consist of several components which certainly had different palaeobiogeographical histories. It may be possible to distinguish roughly an old Laurasian component, the origins of which date back to the Early Cretaceous, to which were added Gondwanan and Asiamerican elements. This implies various dispersal events, from different zoogeographical areas, at various times during the Cretaceous. The palaeobiogeographical history of the Late Cretaceous vertebrate faunas of southwestern Europe is currently being investigated in detail, and some of the recent discoveries mentioned above obviously play an important part in these investigations.

TABLEAU 1 - The main features of the succession of vertebrate faunal assemblages in the Campanian and Maastrichtian of Southern France. *Les aspects principaux de la succession des faunes de vertébrés dans le Campanien et le Maastrichtien du Sud de la France.*

Probable age	Important faunal components	Main localities
Late Maastrichtian	Hadrosauridae, Dromaeosauridae, Azhdarchidae	Montplaisir, Mérigon, Lestailats, Tricouté
Late Campanian /Early Maastrichtian	Titanosauridae, <i>Rhabdodon</i> , Abelisauridae, Dromaeosauridae, giant birds, large varanids	Fox-Amphoux, Cruzy, Campagne-sur-Aude, Le Mas d'Azil
Early Campanian	<i>Rhabdodon</i> , Ankylosauria, <i>Tarascosaurus</i> , <i>Polysternon</i>	Le Beausset, Villeveyrac

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**E. BUFFETAUT, S. DUFFAUD, E. GHEERBRANT,
J.-C. RAGE, H. TONG & D. VASSE**

Université Paris 6

CNRS, Laboratoire de Paléontologie des Vertébrés
Case 106, 4 place Jussieu
F-75252 Paris Cedex 05

J. LE LOEUFF, L. CAVIN & Y. LAURENT

Musée des Dinosauriens
F-11260 Espéraza

M. MARTIN

Musée d'Histoire Naturelle de Boulogne-sur-Mer
115 boulevard Eurvin
F-62200 Boulogne-sur-Mer