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Phornphen Chanthasit

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**The ornithopod dinosaur *Rhabdodon* from the Late Cretaceous of France:
anatomy, systematics and paleobiology.**

**Le dinosaure ornithopode *Rhabdodon* dans le Crétacé supérieur de France:
anatomie, systématique et paléobiologie.**

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Chapter 1:

Introduction

Ornithomimidae was a very diverse herbivorous dinosaur group which was widespread on various continents through the Early Jurassic - Late Cretaceous time span (Norman et al. 2004). *Rhabdodon* is a medium-sized ornithomimid dinosaur from the Late Cretaceous of Europe.

Rhabdodon was first known from dentary fragments with teeth and some postcranial elements discovered in the mid-nineteenth century at la Nerthe, in the Bouches-du-Rhône region of southern France. Because of the characteristic fluted teeth, Matheron erected a generic name for this new *Iguanodon*-like dinosaur and described it as a new species, *Rhabdodon priscum* (later amended to *Rhabdodon priscus*) on the basis of the remains from la Nerthe (Matheron, 1869a, 1869b).

Since that time, abundant additional remains attributed to *Rhabdodon* have been regularly reported not only from France but also from other European countries (Spain, Romania, Austria and Hungary) (Bunzel, 1871; Seeley, 1881; Nopcsa, 1900 and 1902; Pereda-Suberbiola and Sanz, 1999; Weishampel et al., 2003; Sachs and Hornung, 2006; Godefroit et al., 2009; Ösi, 2004). It cannot be denied that *Rhabdodon* was one of the dinosaur taxa that dominated terrestrial faunas during Late Cretaceous times in Europe.

In particular in France, several Late Cretaceous continental deposits have yielded numerous dinosaur remains including *Rhabdodon*. *Rhabdodon* localities are distributed in different regions in southern France, Var, Bouches-du-Rhône, Gard, Hérault, Aude and Ariège (Gervais, 1877; Lapparent, 1947; Buffetaut and Le Lœuff, 1991; Le Lœuff, 1991; Buffetaut et al., 1996 and 1999; Pincemaille, 1997; Sigé et al., 1997; Garcia et al., 1999; Pincemaille-Quillévéré 2002; Allain and Pereda-Suberbiola, 2003). Besides *Rhabdodon priscus* which represents most of French remains, another species, *Rhabdodon septimanicus*, was subsequently erected by Buffetaut and Le Lœuff (1991) on the basis of a characteristic dentary from a Late Cretaceous locality at Montouliers (Hérault). As *R. priscus* and *R. septimanicus* were found in the same formation of Grés à Reptiles, the validity of the latter species was doubted and considered as a junior synonym of *R. priscus* by some authors. In

addition, the morphological variation of *Rhabdodon* from Saint-Chinian was also mentioned by Buffetaut (2005). These issues have been in debate and raise the question:

How many species of *Rhabdodon* existed in Southern France?

The question of the variability of *Rhabdodon* has remained unanswered for a long time because of the lack of well-preserved material to affirm the validity of *R. septimanicus* and because a great number of *Rhabdodon* specimens discovered in France have never been studied in detail.

In the late twentieth century, systematic excavations have been conducted in many Late Cretaceous localities in southern France, such as Cruzy, Campagne-sur-Aude, Vitrolles, Aix-en-Provence and Fox-Amphoux. The recent discoveries provide very abundant vertebrate remains which allow a better understanding of the diversity of Late Cretaceous faunas in southern France. *Rhabdodon* is one of the most found taxa in the course of those excavations. A great number of *Rhabdodon* specimens are housed in many institutes and private collections in France, however the majority of them have never been studied. Therefore, the primary objectives of this study are as follows:

- to accomplish the osteological description of undescribed material and observe the morphological variation among this material,
- to answer the question: How many species of *Rhabdodon* existed in Southern France based on the new material and
- to better understand the palaeobiology of *Rhabdodon* and achieve a reconstruction of this animal.

The debate about the morphological variability of *Rhabdodon* is not restricted only to France but the diversity of *Rhabdodon* has been also suggested from different localities in other countries in Europe. Many species were proposed for this European taxon and were diversely allied to hypsilophodontids, camptosaurids, and iguanodontids. An overview of the taxonomic history of this taxon will be provided further in this work. Recently, Weishampel et al. (2003) erected *Zalmoxes* as a new genus on the basis of cranial and postcranial material from Transylvania in Romania and they suggested two species, *Zalmoxes robustus* and *Zalmoxes shqiperorum* as members of this genus. In addition, Weishampel et al. (2003) have placed *Zalmoxes* in a new family, Rhabdodontidae, which includes *Rhabdodon* as sister-taxon. It therefore seems that now there are two genera representing non-hadrosaurid

ornithopods in the Late Cretaceous of Europe. On the basis of this previous work on this dinosaur group, the supplementary objectives of this thesis are the following:

- to anatomically compare *Rhabdodon* with other related taxa, especially *Zalmoxes*, in order to reevaluate the diversity of this dinosaur group and
- to understand the systematics and the phylogenetic relationships of *Rhabdodon* with other taxa.

Following the objectives of this study, the principal parts of this thesis will consist of:

- An overview of the taxonomic history of *Rhabdodon*,
- Recent discoveries and the geographical and geological setting of main localities in southern France,
- The osteological description of *Rhabdodon* material from those localities,
- The systematics and the phylogenetic relationships of *Rhabdodon* and related taxa and
- A discussion about the distribution, paleobiogeographical implications and palaeobiology of *Rhabdodon*.

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Chapter 2:

Overview of the taxonomic history of *Rhabdodon*

The discovery of the first late Cretaceous dinosaur of Europe was an unexpected consequence of the work of tunneling the railway (Paris-Lyon-Marseille) at la Nerthe in the Bouches-du-Rhône region in France, for which Philippe Matheron, a geologist, was responsible in 1844. Matheron (1846) described some remains of a reptile which included some teeth. These teeth reminded him of a tooth, figured by Cuvier (1824), which was a tooth of the *Iguanodon* found by Gideon Mantell in Great Britain. Matheron perceptively observed the resemblance and differences between the teeth. Finally in 1869, on the basis of the unique characteristics of the fluted teeth, Matheron proposed a generic name for this dinosaur, *Rhabdodon*.

« ...les restes d'un grand reptile terrestre nouveau qui avait les plus grands rapports avec l'*iguanodon* et auquel, à raison de ses dents cannelées, je propose de donner le nom générique de *Rabdodon*¹. »

(Matheron, 1869a: p.32)

The new gigantic reptile remains had been recovered from lacustrine marls in the upper part of the Rognacian stage (an equivalent of the Maastrichtian). These remains included fragments of vertebrae, humerus, femur, tibia and dentary fragments with teeth. He described these elements and assigned them to a new species, *Rhabdodon priscum* (amended to *Rhabdodon priscus*) which was the first dinosaur from Provence. He also regarded this dinosaur as a close relative of *Iguanodon*.

¹ According to Brinkmann (1986), when *Rhabdodon* Matheron, 1869 was established two different spellings were used by the author: *Rabdodon* in the text of Matheron (1869a), *Rhabdodon* in the text of Matheron (1869b) and at the top of the tables in Matheron (1869a). Gervais (1877), Gaudry (1890, p. 222) and Zittel (1890, p. 763) were the first authors to quote this genus, and they adopted *Rhabdodon* as the correct original spelling. All later workers, including Matheron (1892) have adhered to this.

Almost 80 years after the first description of *Rhabdodon*, additional French material was reported again by a French paleontologist, l'abbé Albert-François de Lapparent in his memoir about the dinosaurs from the Upper Cretaceous of southern France (Lapparent, 1947). Lapparent described various dinosaur remains including an ornithopod referred to *Rhabdodon priscus*, Matheron 1869 and he also considered *Rhabdodon* as related to *Iguanodon* but notably smaller in size. These *Rhabdodon* specimens consist not only of cranial elements which include a quadrate, fragments of dentary and maxilla and some teeth but also a great number of postcranial elements. Because of his work, *Rhabdodon* from several Campanian-Maastrichtian localities in Provence and Languedoc became much better known.

As early as the discovery of *Rhabdodon* in southern France, Bunzel (1871) described a new vertebrate fauna from a coal mine at Muthmannsdorf in Niederösterreich (Eastern Austria) and erected some new taxa including an ornithopod dinosaur, *Iguanodon suessi*. Later, Seeley (1881) noticed that *Iguanodon suessi* had significantly diagnostic differences to *Iguanodon* Mantell, 1825 so that he erected the new genus *Mochlodon* for this species. This genus *Mochlodon* was also considered as including ornithopod material from the Hațeg basin of Transylvania. Some of this material from Romania was referred to *Mochlodon suessi* and some referred to a new species *M. robustus* (Nopsca 1900, 1902). Firstly, Nopsca (1901) regarded *Mochlodon* as a hypsilophodontid but later (Nopsca 1902, 1904) he suggested it was closely related to *Camptosaurus* from the Late Jurassic of America. In 1915, Nopsca considered the similarities between *Mochlodon* and *Rhabdodon* as sexual dimorphism and he referred *Rhabdodon* to Camptosauridae.

Until later researches on European dinosaurs in the 1980s, *Mochlodon* had been used for all material referred to *Rhabdodon* and *Mochlodon* by Weishampel and Weishampel (1983), Weishampel (1984), Norman (1984a, b), Milner and Norman (1984) for the reason that *Rhabdodon* Matheron, 1869 was in conflict with an earlier named living snake, *Rhabdodon* Fleischmann, 1831. *Mochlodon* was regarded as a hypsilophodontid or dryosaurid ornithopods in these works; however, it was suggested as a member of Iguanodontia by Sereno (1986) and Carroll (1988). The conflict of the generic name was solved when the conservation of *Rhabdodon* Matheron, 1869 was accepted by the International Commission on Zoological Nomenclature which suppressed the senior homonym *Rhabdodon* Fleischmann, 1831 (Brinkmann, 1986; ICZN 1988) and Brinkmann (1986) determined the synonymy of *Rhabdodon* and *Mochlodon* as in the favor of *Rhabdodon*. The later work of Brinkmann (1988) suggested *Rhabdodon* as a

hypsilophodontid ornithopod, nevertheless in more recent studies by Norman and Weishampel (1990) and Weishampel (1990) *Rhabdodon* was regarded as an euornithopod (*sensu* Weishampel, 1990).

In the last two decades, paleontological excavations in southern France have been carried out systematically and have resulted in many great fossil vertebrate discoveries. A new species, *Rhabdodon septimanicus*, was suggested on the basis of the dentary of a juvenile individual discovered in a late Cretaceous locality at Montouliers (Hérault, France) (Buffetaut and Le Lœuff, 1991). The validity of *R. septimanicus* was questioned differences with *R. priscus* being ascribed to individual differences and/or sexual dimorphism (Allain and Pereda Suberbiola, 2003). Later, this species was accepted as a result of the systematic reassessment of Rhabdodontidae by Weishampel et al. (2003).

Besides Montouliers, in the Saint-Chinain region, there are a number of Late Cretaceous vertebrate sites, for instance at Combebelle, Plo-Saint-Pons and Cruzy, which have provided significant *Rhabdodon* remains (Buffetaut et al., 1999; Buffetaut, 2005a, b). Furthermore, *Rhabdodon* material was also discovered at an Early Campanian locality in the Villeveyrac basin. The Late Cretaceous vertebrate fauna of Villeveyrac has actually been known since 1872 by Bleicher's work. Some of the vertebrae mentioned by Bleicher (1872) were revised by Gervais (1877) and interpreted as belonging to *Rhabdodon*. According to a systematic revision of old collections and recent excavations, Buffetaut et al. (1996) described the *Rhabdodon* of Villeveyrac and suggested that this material could be referred to *cf. Rhabdodon priscus*.

Rhabdodon was mostly based on isolated material, so that this dinosaur remained poorly understood for more than a century, until in 1995, the first partial articulated skeleton of an ornithopod dinosaur finally was found in the lower Maastrichtian of Couperigne near Vitrolles. It was identified and described as *Rhabdodon priscus* (Garcia et al., 1999; Pincemaille-Quillevéré, 2002). Although some of these remains are not quite well preserved and most of them are deformed, Pincemaille-Quillevéré (2002) suggested that *Rhabdodon* is a member of Iguanodontia and closely related to *Tenontosaurus* from the Early Cretaceous of North America (see also Pincemaille-Quillevéré et al. 2006).

Besides the remains of *Rhabdodon* from France, Austria and Romania, Ösi (2004) reported some teeth of a herbivorous dinosaur recovered from an Upper Cretaceous (Santonian) locality at Iharkút in Hungary. These remains are referred to Rhabdodontidae indet. In addition, *Rhabdodon sp.* is present in many localities in Spain, primarily from the Upper Cretaceous of Laño quarry (Pereda-Suberbiola and Sanz, 1999).

In the most recent taxonomic reevaluation of *Rhabdodon*, Weishampel et al. (2003) carried out a cladistic analysis as part of the revision of the material from the Hațeg basin, Transylvania. They defined the Romanian material as a new genus, *Zalmoxes* (sister-group of *Rhabdodon*), including *Z. robustus* (Nopcsa, 1900, 1902) (type species) and *Z. shqiperorum* Weishampel, Jianu, Csiki and Norman, 2003, within a new family, Rhabdodontidae.

These non-hadrosaurid ornithopods are among the most common dinosaurs known from the Late Cretaceous of Europe (in France, Spain, Austria, Romania and Hungary). As mentioned above, *Rhabdodon* has a long and complicated taxonomy history. Because of its morphological variability between different localities, many species have been proposed for this European taxon and it was diversely allied to hypsilophodontids, camptosaurids, iguanodontids and to the recently erected group of rhabdodontids. Solving the problem of the taxonomic diversity of the Rhabdodontidae therefore is one of the objectives of my work, and the phylogenetic relationships of *Rhabdodon* will be reevaluated in a following chapter of this dissertation.

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Chapter 3:

The discovery and geological setting of the main

Rhabdodon localities in France

Rhabdodon is represented in most of the Late Cretaceous (Campanian-Maastrichtian) vertebrate localities in southern France. These non-marine deposits are widely distributed in the Var region of Provence in south-eastern France, through the Aix-en-Provence basin in Bouches-du-Rhône, in the Gard region, then westward to Saint-Chinian south of the Montagne Noire in Hérault, and to the Aude valley near the foothills of the Pyrenees, with the westernmost occurrence in Ariège (Figure 3.1)(see also Appendix I: Rhabdodontid locality list).

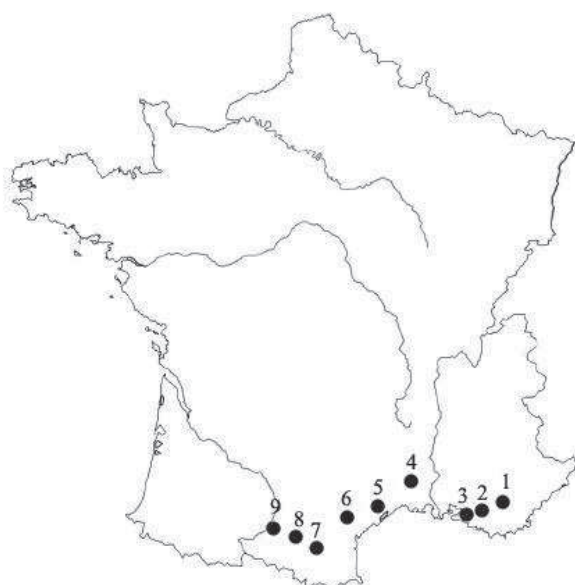


Figure 3.1 The distribution of *Rhabdodon* localities in different departments of France: Var(1), Bouches-du-Rhône (2-3), Gard (4), Hérault (5-6), Aude (7) and Ariège (8-9) respectively from East to West. **1** : Fox-Amphoux; **2** : Trets-La Boucharde, Roques-Hautes, Rousset; **3** : Vitrolles-Courperigne, La Nerthe; **4** : Champ-Garimond; **5** : Villeveyrac; **6** : Cruzy, Montouliers, Quarante; **7** : Campagne-sur-Aude, Rennes-le-Château; **8** : Dreuilhe; **9** : Le Mas d'Azil

In this chapter, I shall focus only on the discovery and the geological setting of the main localities which yield abundant *Rhabdodon* remains and where excavations are still being undertaken. In addition, the unpublished material which is described in this thesis was recovered from these main localities in different departments of France as follows:

3.1 Department of Var

Main Locality: Fox-Amphoux

3.1.1 The discovery

Fox-Amphoux basin is located in the northern part of Var (Provence) in south-eastern France. Fox-Amphoux is one of the Upper Cretaceous localities which are rich in dinosaur remains. The vertebrate localities of Fox-Amphoux were firstly excavated by Lapparent in 1939 at Métiesson (Lapparent, 1947) (Figure 3.2). Paleontological excavations at Fox-Amphoux were carried out again in 1979 by Broin et al. (1980) through a program of research on the continental Mesozoic ecosystems. Afterward, many vertebrate discoveries were made at sites near Fox-Amphoux by both professionals and amateurs. Despite the fact that a majority of vertebrate remains, including dinosaurs, from this region are in private collections (notably the Méchin collection), studies of the specimens have been allowed and proved the biodiversity of the Late Cretaceous fauna from Fox-Amphoux in several scientific works (Buffetaut et al. 1988, 1995, 2000 and 2006; Tong et al. 1998; Chanthasit and Buffetaut 2009). Moreover, because of the kindness of Patrick and Annie Méchin, I had the opportunity to study their collection and many complete *Rhabdodon* specimens from that collection are consequently described in this work.

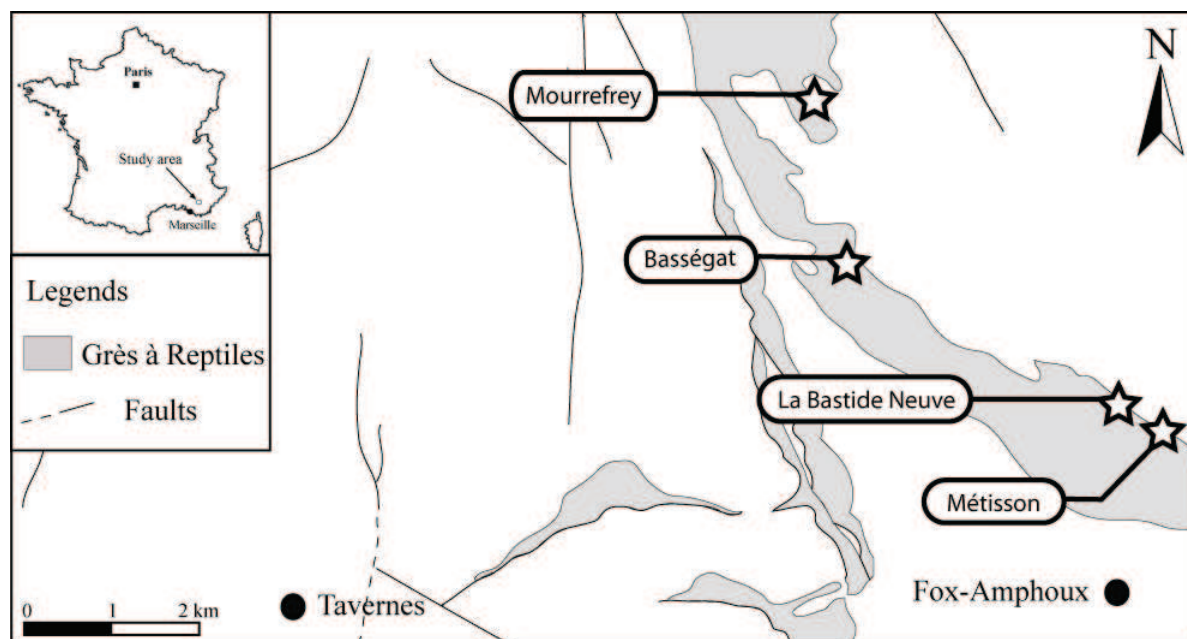


Figure 3.2 Geographical locations of different localities that yielded *Rhabdodon* remains and geological boundary of the Grès à Reptiles Formation near Fox-Amphoux. (Modified from BRGM, geologic map Notice Tavernes 1:50,000)

3.1.2 Geological setting

Rhabdodon has been found at many sites in the vicinity of Fox Amphoux village such as la Bastide Neuve, Métiſson, Basségat and Mourrefrey (Figure 3.2). At Bastide Neuve, the fossiliferous beds are composed of yellowish sandy clays corresponding to fluvial deposits. At other localities, such as Métiſson, the bones are found in sandstones. This non-marine formation is situated in the southern part of the Montmeyan syncline and belongs to the Grès à Reptile Formation which is considered as the lower part of the Rognacian, or equivalent in age to the early Maastrichtian based on magnetostratigraphy (Westphal and Durand, 1990). Furthermore, the association of herbivorous dinosaurs represented mostly by titanosaurs and *Rhabdodon* characterizes the late Campanian to early Maastrichtian in southern France (Le Lœuff et al., 1994), whereas late Maastrichtian assemblages are dominated by hadrosaurid dinosaurs, which have not been reported from Fox Amphoux. Besides *Rhabdodon*, it has yielded an abundant and diverse vertebrate assemblage (Buffetaut et al., 2006), including turtles, crocodylians, pterosaurs, dinosaurs (ankylosaurs, titanosaurs, dromaeosaurs), and flightless birds.

3.2 Department of Bouches-du-Rhône

Main localities: Vitrolles-Couperigne and along the A8 highway.

3.2.1 The discovery

- Vitrolles-Couperigne

Dinosaur remains from Bouches-du-Rhône have been reported since the nineteenth century (Matheron, 1869). A systematic revision was done by Lapparent (1947) and his work indicated that vertebrate fossils, including dinosaurs, are widely distributed in this part of Provence. Since then, the Late Cretaceous vertebrate sites of this region attracted the interest of many paleontologists; however, in most instances only fragmentary or unarticulated *Rhabdodon* remains were found. Then, in 1993, the first almost complete *Rhabdodon* skeleton was found at the Vitrolles-Couperigne locality which is situated south of Vitrolles near the locality of Couperigne, a few kilometers from Marseille Provence Airport (Figure 3.3). The systematical excavations were carried out in 1994 by a team from the Muséum d'Histoire Naturelle d'Aix-en-Provence and the Institut des Sciences de

l'Evolution de Montpellier (Garcia et al., 1999; Pincemaille-Quilleveré, 2002). Then in 2007, following a project of SNCF to fill the whole area to meet the same level as the railway and create a settling basin, the Muséum d'Histoire Naturelle d'Aix-en-Provence contacted and asked permission from the town of Vitrolles, SNCF and the region to organize an excavation before this area became inaccessible. The museum finally reached its objective in September 2007. Although this new attempt yielded nothing interesting at the first site, surprisingly fifty meters from where the first skeleton was found a second partial articulated skeleton referred to *Rhabdodon* was exposed. The elements of the latter skeleton are less scattered and more articulated and they were preserved in better condition (Chanthasit et al., in review).

- A8 Highway

Following the campaigns of exploration that took place in late 2004 and early 2005, about 10 potential sites were identified throughout the area affected by the enlargement of A8 highway (Figure 3.3). The recently excavated vertebrate fossils sites are located along the A8 highway about 15 kilometers east from Aix-en-Provence between Châteauneuf-le-Rouge and Saint Maximin-la-Sainte-Baume. These paleontological excavations were finally started in 2006 as a project of the partnership between the ESCOTA (réseau autoroutes Estérel, Côte d'Azur, Provence et Alpes), the Community of the Pays d'Aix (CPA) and the Muséum d'histoire naturelle d'Aix-en-Provence. Systematic excavations are financed by ESCOTA and CPA organized the excavations with the scientific monitoring of Muséum d'histoire naturelle d'Aix-en-Provence. At the end of 2006 some of those sites proved exceptional both in quantity and quality of specimens. After an interruption due to lack of funding, this project was renewed again in January 2010 and vertebrate remains are continually unearthed from these remarkable localities.

3.2.2 Geological setting

- Vitrolles-Couperigne

Vitrolles is situated in a syncline of the Aix-en-Provence basin which yielded numerous dinosaur bones and eggshell sites. The Vitrolles-Couperigne site consists of a succession of marls and limestones which are situated fifty meters below the Rognacian limestone (see Garcia et al., 1999, Fig.1). The *Rhabdodon* skeleton was found in a grey

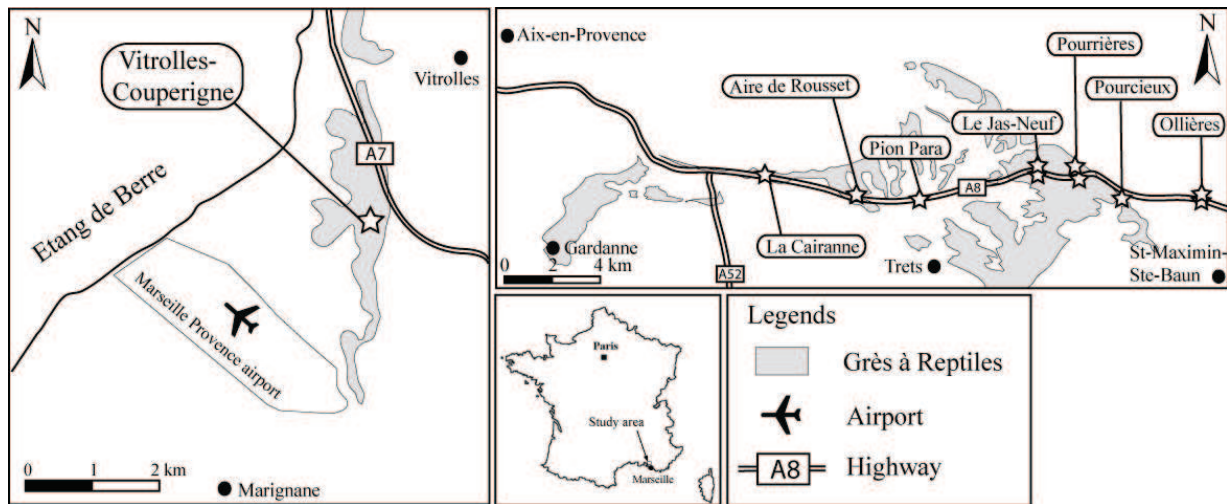


Figure 3.3 The geographical and geological location of Vitrolles-Couperigne locality (on the left) and A8 sites (on the top right). (Modified from BRGM, geologic map Notice Martigues 1:50,000)

sandy marl bed with carbonate cementation, the lithology of which indicates a floodplain environment. There are also some theropod and crocodile teeth and a few indeterminate large bones which probably belong to a sauropod from the same level as *Rhabdodon*. Above this facies there is an alternation of limestones, from which dinosaur eggshell fragments, gastropods and charophytes have been also recovered by screen washing. A few meters below the *Rhabdodon* level, microfossils and a crocodile tooth were recovered from grey marly limestone and some crocodile vertebrae and other reptiles remains were found in yellowish marl situated in the lower bed. On the basis of the presence of typical plants and malacofauna, Garcia et al. (1999) suggested an Early Rognacian (Early Maastrichtian) age for the site, which is also supported by stratigraphic correlation.

- A8 Highway

The excavated sites along the A8 highway which have yielded *Rhabdodon* remains include Pourrières, Le Jas neuf, and La Cairanne (Figure 3.3). The lithology of these sites is various as reported by Dutour and Berton (2007). Pourrières and Le Jas-Neuf sites are composed of red clay superimposed with sandstone. The majority of bones were discovered from the well cemented fine to medium grained sandstone. Although the rock is very hard, the fossils are very well preserved. The sandstone beds correspond to former meandering stream deposits during successive floods with more or less violent current. The vertebrate assemblage includes teeth of dinosaurs, crocodiles and a shark, and titanosaur remains

which probably belong to a single individual. At La Cairanne site, the fossils were recovered from the red sandy clays interbedded between sandstone beds. Some particular areas showed exceptional concentrations of fossils. 25 theropod teeth, numerous tendon fragments and an incomplete sacrum of *Rhabdodon* were found in an area of 2 m² with a depth of 40 cm. This fossiliferous pocket could be interpreted as a depression in which the elements were deposited and were covered immediately by the sediments. The age of this site has not yet been confirmed but the faunal assemblage suggests a Campano-Maastrichtian ecosystem as present in other localities in southern France.

3.3 Department of Hérault

Main Locality: Cruzy (Massecaps)

3.3.1 The discovery

The village of Cruzy is situated a few kilometers south of Saint-Chinian (Hérault), 30 kilometers west of Béziers. The Late Cretaceous vertebrate remains of Saint-Chinian were first mentioned by Paul Gervais in 1877. Almost twenty years later, abundant fossil bones were eventually discovered near Saint-Chinian by Miquel (1897). These remains were subsequently described by Depéret (1899, 1900a, b), Nopcsa (1929) and Lapparent (1947). *Rhabdodon* was initially reported from Quarante and Montouliers by Lapparent (1947, 1954). Later the discovery of a dentary at Montouliers indicated a greater faunal diversity since this lower jaw belonged to a new species of *Rhabdodon*, *Rhabdodon septimanicus* (Buffetaut and Le Lœuff, 1991). The Late Cretaceous vertebrates of Saint-Chinian attracted attention again mainly because of members the Association Culturelle, Archéologique et Paléontologique de l'Ouest Biterrois (ACAP) who actively explored the Late Cretaceous continental deposits of this region. Consequently a significant vertebrate fossil site was discovered at Massecaps near Cruzy in 1996. Since then systematic palaeontological excavations have been carried out at several localities near Cruzy and Villespassans, by the collaboration of ACAP and the Centre National de la Recherche Scientifique (CNRS). The *Rhabdodon* material described in this work was found in the course of these excavations at Massecaps, Montplo, Combebelle, Plo Saint Pons and Sainte-Foy (Figure 3.4). Massecaps seems to be the most productive site for vertebrate fossils and it has been excavated until today.

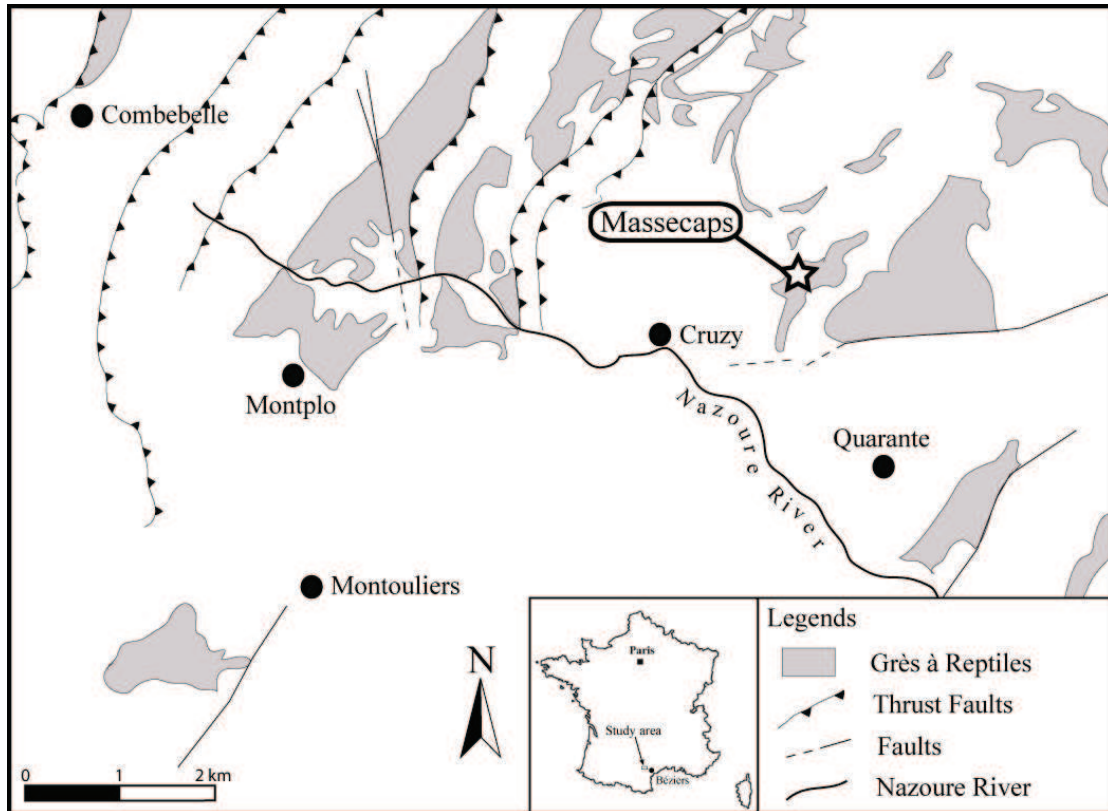


Figure 3.4 The geographical and geological location of Marsecaps and sites around Cruzy which have yielded *Rhabdodon* remains. (Modified from BRGM, geologic map Notice Béziers 1:50,000)

3.3.2 Geological setting

At Marsecaps, the vertebrate remains are mostly scattered through varicolored clays which sometimes contain iron oxide nodules, and are cut by unfossiliferous sandy channels. Vertebrate remains were occasionally found in oxidized coarse-grained deposits as shown by black gravel accumulations. It would appear to be a floodplain deposit, containing bones in various states of preservation (Buffetaut et al., 1999). The fossil vertebrate assemblage of the Marsecaps locality includes fishes, amphibians, turtles, crocodylians, pterosaurs, dinosaurs (ankylosaurs, sauropods and theropods), birds and mammals (Buffetaut, 2005). The dominant terrestrial faunal elements in this locality are the herbivorous dinosaurs (Saltasauridae and *Rhabdodon*) that are also found in many other Late Campanian and Early Maastrichtian localities in southern France. Besides the macrofauna, the Marsecaps site also contains microvertebrate remains.

3.4 Department of Aude

Main locality: Campagne-sur-Aude (Bellevue)

3.4.1 The discovery

The presence of dinosaur bones was mentioned in the upper Aude valley as early as the late nineteenth century, notably by paleontologist Paul Gervais in 1877. In spite of discoveries of dinosaur remains in the late 19th to early 20th century, it seems that the upper Aude Valley localities were disregarded by the paleontologists for a while, until in 1982, a bone fragment was found by a hunter near Campagne-sur-Aude village. This discovery resulted finally in the first scientific excavations at Bellevue locality in 1989, conducted by a CNRS team led by Eric Buffetaut and Jean Le Lœuff (Buffetaut et al., 1989). Afterwards, the excavations at Campagne-sur-Aude have been organized annually by the “Musée des dinosaures d’Espéraza” and the “Dinosauria” association. Consequently, in the last two decades Bellevue has become the largest French dinosaur site with more than 4000 specimens unearthed. Moreover it cannot be denied that the discovery of ‘Eva’, a nearly complete and partially articulated skeleton of the saltasaurid sauropod *Ampelosaurus atacis* Le Lœuff, 1995 makes Bellevue an exceptional locality (Le Lœuff, 1995 and 2005).

3.4.2 Geological setting

The Bellevue locality is situated in Campagne-sur-Aude village which lies in the upper Aude valley, 50 km south of Carcassonne. The geology of the upper Aude valley has been studied since the late nineteenth century and a stratigraphic succession was proposed by Bilotte (1985). The vertebrate remains of Bellevue are recovered from the lower part of the “Marnes Rouges Inférieures Formation”, probably the transition zone between the Marls of Maurine and the underlying Estous sandstone (Figure 3.5). A palynological study suggests that the Marls of Maurine belong to the Early Maastrichtian (Bilotte, 1985).

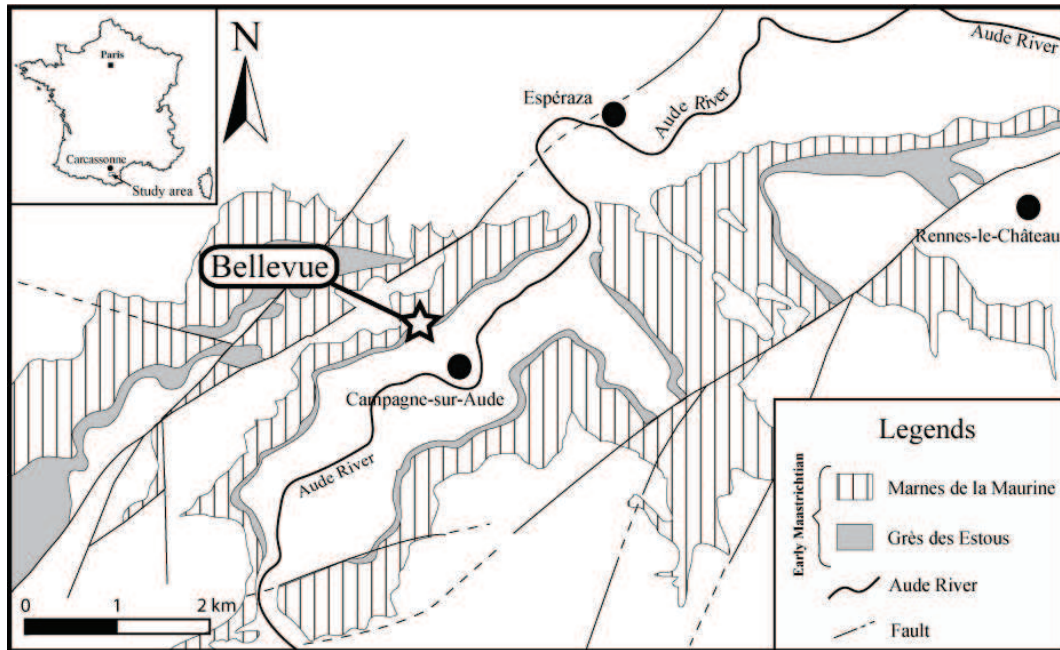


Figure 3.5 The geographical and geological location of Bellevue locality and geological boundary of Early Maastrichtian in the Aude Valley. (Modified from BRGM, geologic map Notice Quillan 1:50,000)

The sedimentary strata of this site are composed of purplish red sandy clay irregularly interbedded with sandstone lenses. The rust-colored sediments are related to oxidation and indicate an ancient floodplain. The presence of interbedded coarse-grained deposits and fresh water faunal remains suggest a fluvial environment. According to the facies assemblage, the site is interpreted as presumably the overbank deposits of a meandering stream (Leclerc, 2007). As in other continental Late Cretaceous localities in southern France, the vertebrate assemblage of Bellevue includes bony fish, turtles, crocodiles, pterosaurs and dinosaurs, among which *Rhabdodon* is one of the most common taxa in this site.

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Chapter 4:

Osteology of *Rhabdodon* from the Late Cretaceous of southern France

4.1 Material and Methods

The material described in this work consists of both cranial and postcranial elements from the main localities in southern France mentioned in the previous chapter. The majority of specimens has been found in the course of the systematic excavations organized by different institutions; Association culturelle archéologique et paléontologique de l'Ouest Biterrois (ACAP) and Musée de Cruzy, Dinosauria and Musée des Dinosauriens d'Espéraza, Muséum d'Histoire Naturelle Aix-en-Provence, Centre National de la Recherche Scientifique; and collected for several years in various French collections. Some of the specimens were found in the course of my thesis, during which I have had the opportunity to participate in excavations (in 2005-2009) with ACAP at Cruzy and the Dinosauria association at Espéraza. Some of those recent specimens were prepared by me in the laboratories of Musée de Cruzy, Musée des Dinosauriens, Espéraza and University Claude Bernard Lyon 1. Most of specimens referred to *Rhabdodon* are isolated except two partial articulated skeletons from Vitrolles which are housed in the Muséum d'Histoire Naturelle d'Aix-en-Provence and were described by Pincemaille-Quillévéré (2002) and Chanthasit et al. (in review). The osteological description of undescribed material has been done and the anatomical measurements of specimens are shown in Appendix II.

Institutional abbreviations:

CM – Collection Méchin, Vitrolles, France

FSL – Université Claude Bernard Lyon1, Villeurbanne, France

MC – Musée de Cruzy, France

MDE – Musée des Dinosauriens, Espéraza, France

MHN_AIX_PV – Muséum d'Histoire Naturelle Aix-en-Provence, France

MNHN – Muséum National d'Histoire Naturelle, Paris, France

SYSTEMATIC PALEONTOLOGY

Order ORNITHISCHIA Seeley, 1887

Suborder ORNITHOPODA Marsh, 1881

EUORNITHOPODA (sensu Weishampel 1990)

Infraorder IGUANODONTIA Sereno, 1986

Family RHABDODONTIDAE Weishampel, Jianu, Cziki & Norman, 2003

Rhabdodon Matheron, 1869

4.2 Description

4.2.1 Skull and mandible

The cranial material of *Rhabdodon* is poorly known. Some elements including the maxilla, quadrate, braincase, dentary, surangular and teeth have been found isolated and described from various localities in southern France (Matheron, 1869; Lapparent 1947; Buffetaut and Le Lœuff 1991; Pincemaille-Quillévéré, 2002; Pincemaille-Quillévéré et al. 2006). In this work, I will describe some additional cranial elements, most of them having been discovered at a locality near the village of Quarante (Hérault). These remains from Quarante were found in the same area of a few square meters. It can be assumed that these elements belong to a single individual. The description includes also some cranial material from Cruzy, Montouliers, Bellevue (Campagne-sur-Aude) and Fox-Amphoux.

I. *Premaxilla* (MC- QR 1, QR 2, QR 3, QR 4, QR 6, CR.QR 3,)

A bone fragment MC-QR.02 (Figure 4.1D) is the dorsal process of a left premaxilla. MC-QR 1, 3, 4, and 6 are compounded and form the maxillary process (Figure 4.1E) which hypothetically belongs to the same left premaxilla as MC-QR.2. The right premaxilla MC-CR.QR.03 (Figure 4.1A-C) is more complete but it is partly crushed on the lateral surface and its anterior tip is missing.

Dorsally, the nasal process of the premaxilla forms a posterior tapering process. This process is triangular in cross section and has a sharp ridge on the lateral surface; this ridge is

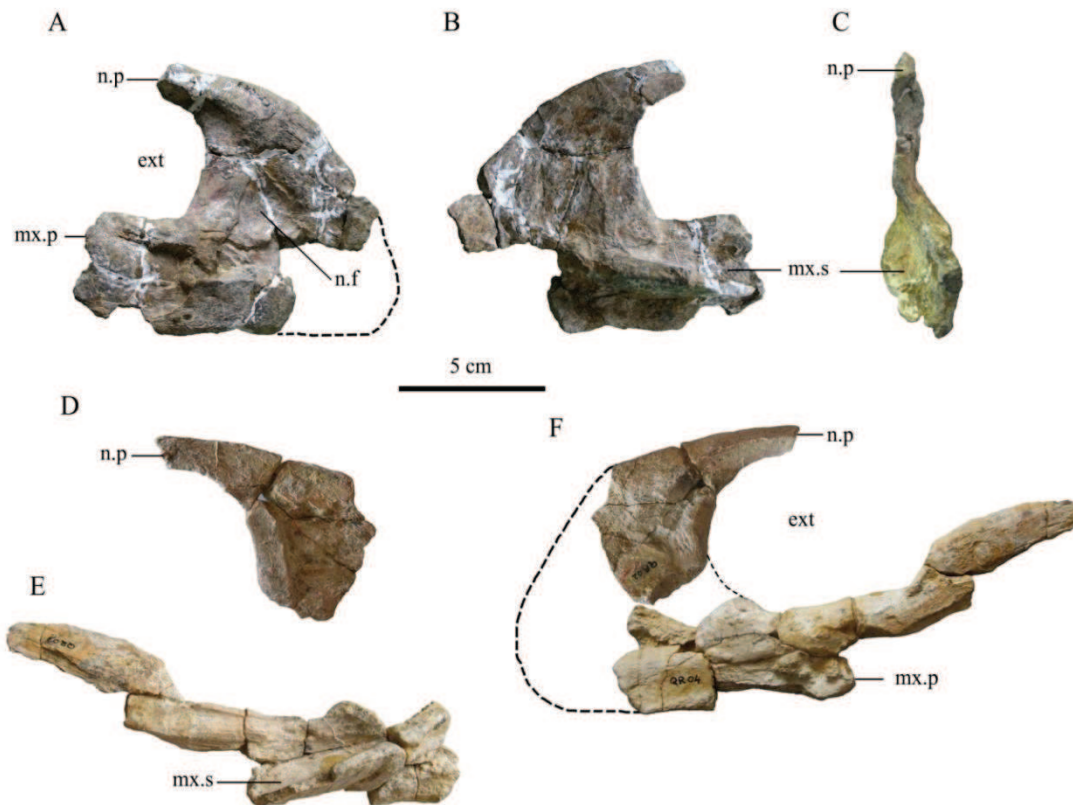


Figure 4.1. Right premaxilla MC-CY.QR.3 in lateral (A), medial (B) and caudal (C) views. A fragment of left premaxilla MC-QR.2 (D), MC-QR 1, 3, 4 and 6 (E) in medial view. A reconstruction of left premaxilla in lateral view. Abbreviations : ext = external naris, mx.p = maxillary process, mx.s = maxillary suture, n.f = narial fossa, n.p = nasal process.

expanded anteriorly into a convex dorsal and anterior surface on the main body of the premaxilla. Ventral to this convex surface, the moderately large narial fossa is expanded anteroventrally and has a thin posterior edge which forms the anterior rim of the external naris. The narial fossa is limited posteroventrally by the posterior process (maxillary process) of the premaxilla. The posterior process is elongate, extends lateroposteriorly and is directed slightly upward at the posterior end, forming the ventral rim of the external naris. The external naris is consequently relatively longer than tall.

The medial surface of the premaxilla is flat and scarred by the ligaments for the attachment with the other premaxilla. There is a longitudinal groove to receive the anteromedial process of the maxilla. The sutured groove with the maxilla is significantly longer than in *Zalmoxes*, and this corresponds to the fact that the maxilla of *Rhabodon* has a longer premaxillary process than that of *Zalmoxes*. The maxillary suture is delimited ventrally by a scarred bony plate which also forms the roof of the buccal cavity. This plate is

enlarged but thinned posteriorly. Above the maxillary suture, there is a thin ridge which extends posteriorly on the posterior process of the premaxilla. The ventral border of the premaxilla is narrow and rugose and there is no evidence of premaxillary teeth.

II. *Maxilla* (MC-QR 9; MDE-C3.111; MHN_AIX_PV.2008.1.42; FSL 530513)

The maxilla of *Rhabdodon* is one of the rarely found cranial elements, although maxillary teeth are found at most localities in southern France. From previous works, the maxilla of a juvenile or young adult *Rhabdodon* from a Late Campanian locality at Velaux described by Thouand (2004) seems to be the most complete specimen, however its anterior part is missing.

The new maxilla from Quarante (MC-QR 9) (Figure 4.2 A, B) appears to be more complete in the anterior part and the dorsal processes. It is characterized by a very prominent, long premaxillary process that fits into the recess of the posterior process of the premaxilla. Contrary to MDE-C3.111 (Figure 4.2 E), the premaxillary process of the maxilla is relatively short. The premaxillary process is triangular in cross-section, offset medially and it bears a step-like ridge on the medial surface. The anterior end of the maxilla is grooved and scarred. Dorsally, the premaxillary process forms a sharp, slightly dorsal curved ridge extending to the most rostral end and this ridge is limited at the anterior end of the tooth row. A deep oval depression is present laterally anterodorsal to the tooth row. This depression is also present in MDE-C3.111 and it is presumably the attachment area for the conjoined anterior tip of the vomers (Weishampel et al. 2003).

Posterior to the premaxillary process, the medial surface of the maxilla is convex transversely and forms a rounded dorsal bar above the tooth row. Dorsally, the maxilla forms a thin, flat sheet-like process. This process is anteriorly curved upward and may contact the nasal. The posterior edge of this process forms the anterior margin of the antorbital fenestra. Posteriorly, another process projects vertically. The latter process is smaller, stouter than the more anterior one and it has a slightly twisted thickened distal end. This process was presumably overlapped by the lacrimal.

The lateral wall of the tooth-bearing region of the maxilla MC-QR 9 is compressed and fractured. The lateral foramina cannot be observed in this specimen. Numerous foramina are visible on the lateral aspect of the maxilla MDE-C3.111. In a juvenile specimen MHN_AIX_PV.2008.1.42 (Figure 4.2 F, G), the jugal suture of the maxilla forms

a wedge-shaped overhang on the posterior part of the lateral wall. The posterior end of the maxilla is blunt, ridged and grooved and this is the sutural area for the ectopterygoid.

The medial wall of the tooth-bearing portion is marked by the alveolar foramina (Figure 4.2 C, D). The alveolar foramina are connected to each other by a neurovascular groove. The maxilla MC-QR 9 contains ventrally eleven tooth positions while MHN_AIX_PV.2008.1.42 has nine and the incomplete maxilla MDE-C3.111 has eight tooth positions.

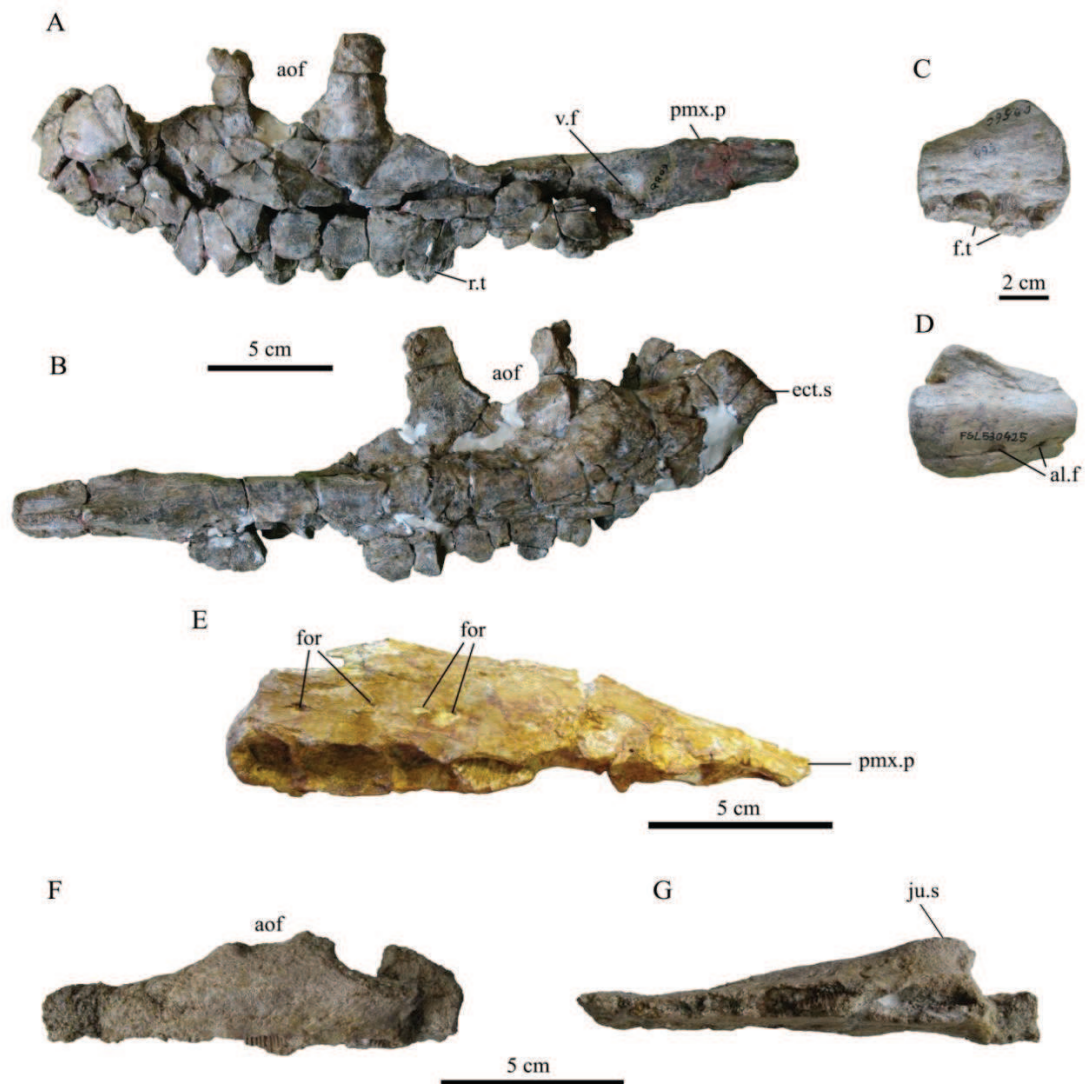


Figure 4.2 Right maxilla MC-QR 9 in lateral (A) and medial (B) views. A fragment of left maxilla FSL 530513 in lateral (C) and medial (D) views. Right maxilla MDE-C3.111 (E) in lateral view. Left maxilla MHN_AIX_PV.2008.1.42 in lateral (F) and ventral (G) views. Abbreviations: al.f = alveolar foramen, aof = antorbital fenestra, ect.s = ectopterygoid suture, f.t = functional tooth, ju.s = jugal suture, pmx.p premaxillary process, r.t = replacement tooth, v.f = fossa for the attachment with the vomer.

III. *Quadrate* (CM-397, 501, 653, 718; MC-CY.QR 5, CY.QR 6)

Two forms of quadrate can be distinguished; the quadrate MC-CY.QR.5 (Figure 4.3 A-C) is more robust than others (CM-397, 501, 653, 718). The upper end of the quadrate has a relatively small, convex, oval articular head which fits to the squamosal. This head slightly projects posteriorly from the main shaft of the quadrate. Caudal to and beneath the dorsal head, there is a thin buttress which extends vertically downward then curves medially to the main body of the quadrate. Below this buttress, the quadrate shaft is slightly bowed anteroposteriorly and meets the mandibular articulation at the distal end.

Rostrally, on the quadrate shaft two wings are developed. The first wing is a lateroanteriorly expanded thin sheet of the jugal ala which runs along most of the quadrate length. The anterior margin of the jugal ala is dominated by a scarred depression for the quadratojugal suture, the limit of the suture being marked by a rough edge. The jugal ala is incomplete in all known specimens so that the paraquadratic foramen cannot be observed. On the medial side of the bone, another wing arises ventrally above the ventral limit of the lateral wing (jugal ala) and extends dorsomedially to form the pterygoid ala. In MC-CY.QR 5 the pterygoid ala is developed distinctively far from the distal articulation and strongly curved ventrally by comparison with other specimens. The pterygoid ala is thick in the ventral part, thinning dorsally and eventually joins the quadrate head. Between these two alae, the quadrate forms a concave heavily scarred surface along its length.

The distal articular condyles are ventrally convex, asymmetrically developed. The lateral condyle is rounded, slightly larger and extends distally, it articulated with the surangular, while the medial condyle is rather narrow and directed dorsomedially away from the lateral one. The mandibular articulation of the robust specimen (MC-CY.QR 5) is significantly broader than the main body of the quadrate.

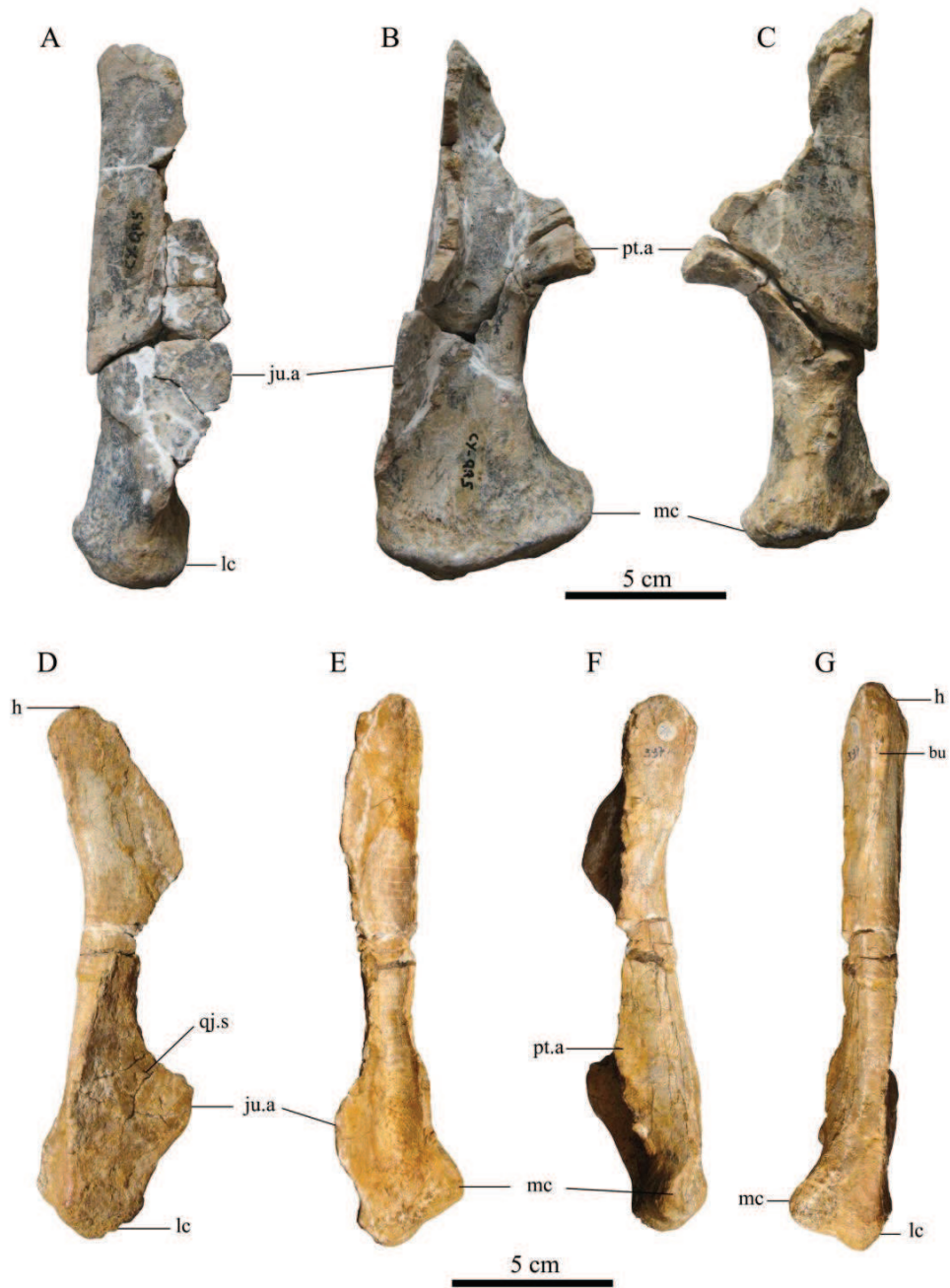


Figure 4.3 Right quadrate MC-CY.QR 5 in lateral (A), anterior (B) and medial (C) views. Right quadrate CM-397 in lateral (D), anterior (E), medial (F) and posterior (G) views. Abbreviations: bu = buttress, h = quadrate head, ju.a = jugal ala, lc = lateral condyle, mc = medial condyle, pt.a = pterygoid ala, qj.s = quadratojugal suture.

IV. *Frontal* (MC-QR 8)

Only the right frontal MC-QR8 can be identified (Figure 4.4). The posterior end is not completely preserved, however the frontal is longer than wide. Dorsally, the frontal is quite flat except at the suture with the postorbital where the frontal is slightly flared upward. The lateral rim bears well developed insertion markings and curves rostocaudally. In the anterior part, the frontal edge for the nasal and for the adjacent frontal is thin. The interfrontal suture is thickened in its more posterior part and it is straight. Ventrally, the frontal shows a complex concave surface representing the impression of the roof of the endocranial cavity. A strongly curved ridge delimits the orbital roof of the frontal from the other concave surfaces.

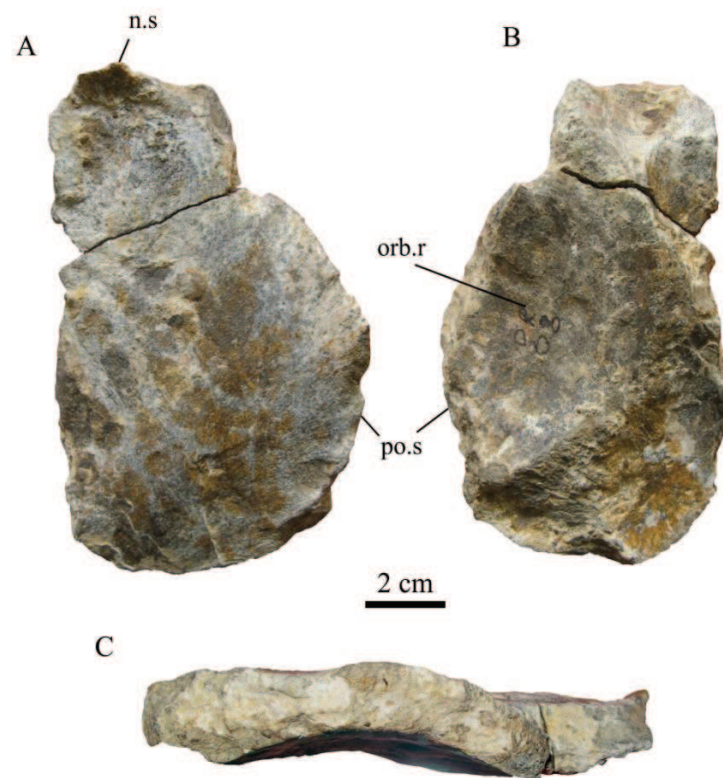


Figure 4.4 Right frontal MC-QR8 in dorsal (A), ventral (B) and lateral (C) views. Abbreviations: n.s = nasal suture, orb.r = orbital roof, po.s = postorbital suture.

V. *Braincase*

The braincase of *Rhabdodon* is known from several localities in southern France and some specimens have been described by Pincemaille-Quillévére et al. (2006). More recently I have described two new specimens identified as braincases of *Rhabdodon* from localities at Fox-Amphoux and Cruzy and presented them in a poster communication. All braincases from southern France are compared between them and with other ornithopods in that work which I attach here as the following note:

BRAINCASE OF *RHABDODON* (DINOSAURIA: ORNITHOPODA)
: NEW SPECIMENS FROM THE LATE CRETACEOUS OF SOUTHERN FRANCE.

Phornphen CHANTHASIT

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Introduction

Since the first description in 1869 of *Rhabdodon priscus* from the early Maastrichtian of La Nerthe (Bouches-du-Rhône) by Matheron, *Rhabdodon* remains have been found continually in several Campanian-Maastrichtian localities in Europe, especially in southern France. However, the majority of specimens of *Rhabdodon* are postcranial elements while cranial remains have rarely been found, and they are not well preserved, particularly the braincase. A detailed description of the *Rhabdodon* braincase was given by Pincemaille-Quillévére et al. (2006) even though it was based on incomplete specimens.

Recently, two braincases of ornithopod dinosaurs have been found at the Masecaps locality near the village of Cruzy (Hérault) and at the Bastide-Neuve locality at Fox-Amphoux (Var) (Figure 1). Both localities are considered to be Late Campanian- Early Maastrichtian in age (Buffetaut et al., 1999; Westphal et Durand, 1990) and they have yielded abundant remains of *Rhabdodon* and other vertebrates.

Description

The braincases MC-M1575 and CM-699 (Figure 2 and 3), belong to juvenile individuals. They are more complete than those of Rhabdodontidae including *Zalmoxes* described in previous works (Weishampel et al., 2003; Pincemaille-Quillévére et al., 2006).

The occipital condyle comprises the kidney-shaped basioccipital and the condylids of the exoccipitals. The basioccipital forms the ventral margin of the foramen magnum while the exoccipitals form the lateral and partial dorsal walls of the foramen magnum. Relative to the size of the occipital condyle, the lateral walls of the foramen magnum of *Rhabdodon* are shorter than those of *Zalmoxes*.

As in *Camptosaurus*, *Hypsilophodon*, *Dryosaurus*, and *Zalmoxes*, the supraoccipital is not excluded from the dorsal margin of the foramen magnum whereas it is in *Iguanodon*,

Ouranosaurus, *Tenontosaurus* and hadrosaurids. The supraoccipital is inclined with a tapered ascending process contacting the parietals dorsally, and it also extends laterally with a small hump to overlap the dorsal border of the paroccipital process.

The paroccipital processes of *Rhabdodon* are long, slightly curved and oriented posterolaterally. The distal ends are slightly expanded and point ventrally. To the contrary, the paroccipital processes of *Tenontosaurus* are short and oriented more mediodorsally. In *Zalmoxes*, the paroccipital processes are more curved and oriented more dorsally than in *Rhabdodon*.

The basioccipital is longer than the basisphenoid as in *Tenontosaurus* and *Zalmoxes*, while it is the reverse in *Thescelosaurus* and *Zephyrosaurus*, and they are subequal in *Hypsilophodon*. The basipterygoid processes of the braincase of *Rhabdodon* are relatively longer and directed more laterally than those of *Zalmoxes*.

Although the major cranial nerve foramina are hardly visible in both specimens, the braincase of *Rhabdodon* MC-M4 (Pincemaille-Quillévéré et al., 2006) shows that the distribution of cranial nerves along the lateral surface of the braincase is homologous to that of *Tenontosaurus*.

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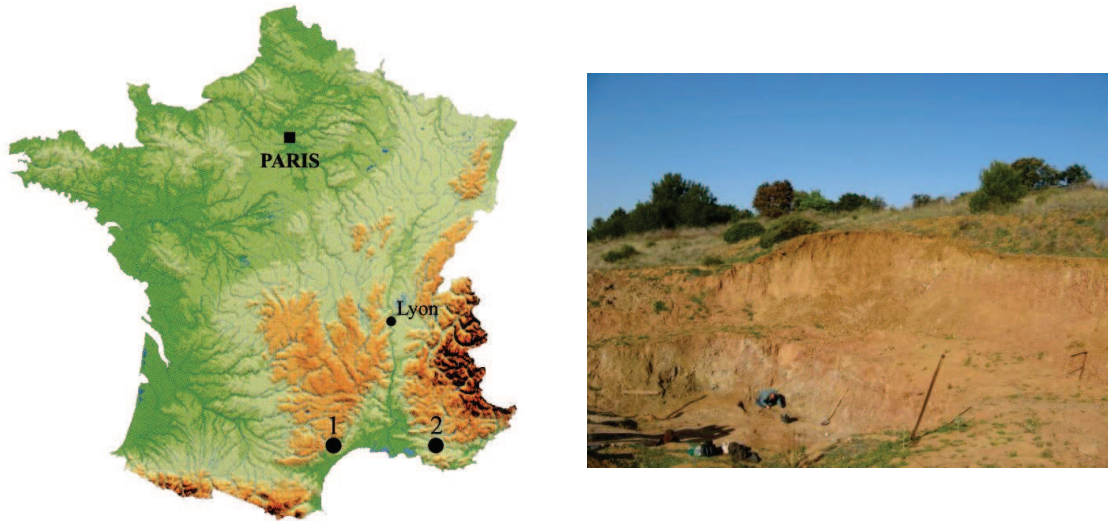


Figure 1. A map showing the localities, 1 - Cruzy (Hérault) and 2 - Fox-Amphoux (Var) in southern France and (on the right) Masecaps site near Cruzy.

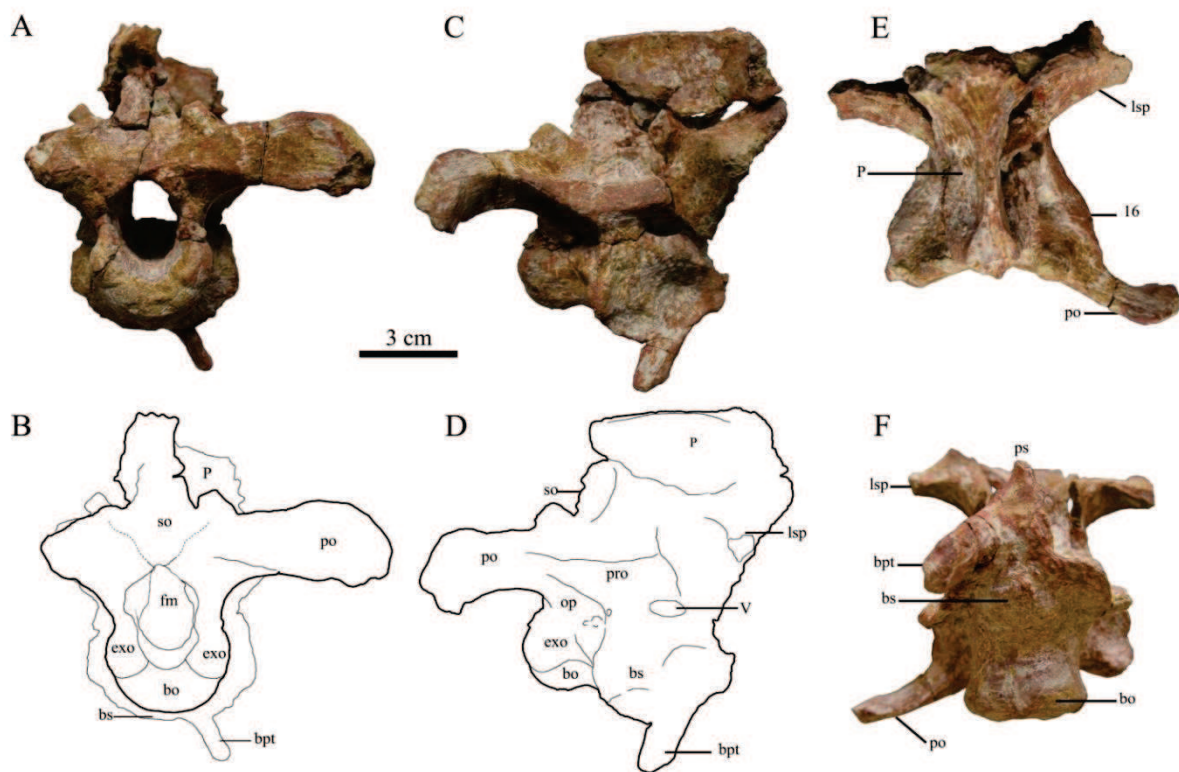


Figure 2. Braincase MC-M1575 from Masecaps, Cruzy in occipital (A-B), right lateral (C-D), dorsal (E) and ventral (F) views. Abbreviations : bo – basioccipital, bs – basisphenoid, exo – exoccipital, fm – foramen magnum, fo – foramen ovale lsp – laterosphenoid, op - opisthotic, P – parietal, po – paroccipital process, pro – prootic, ps – parasphenoid, so – suparoccipital.

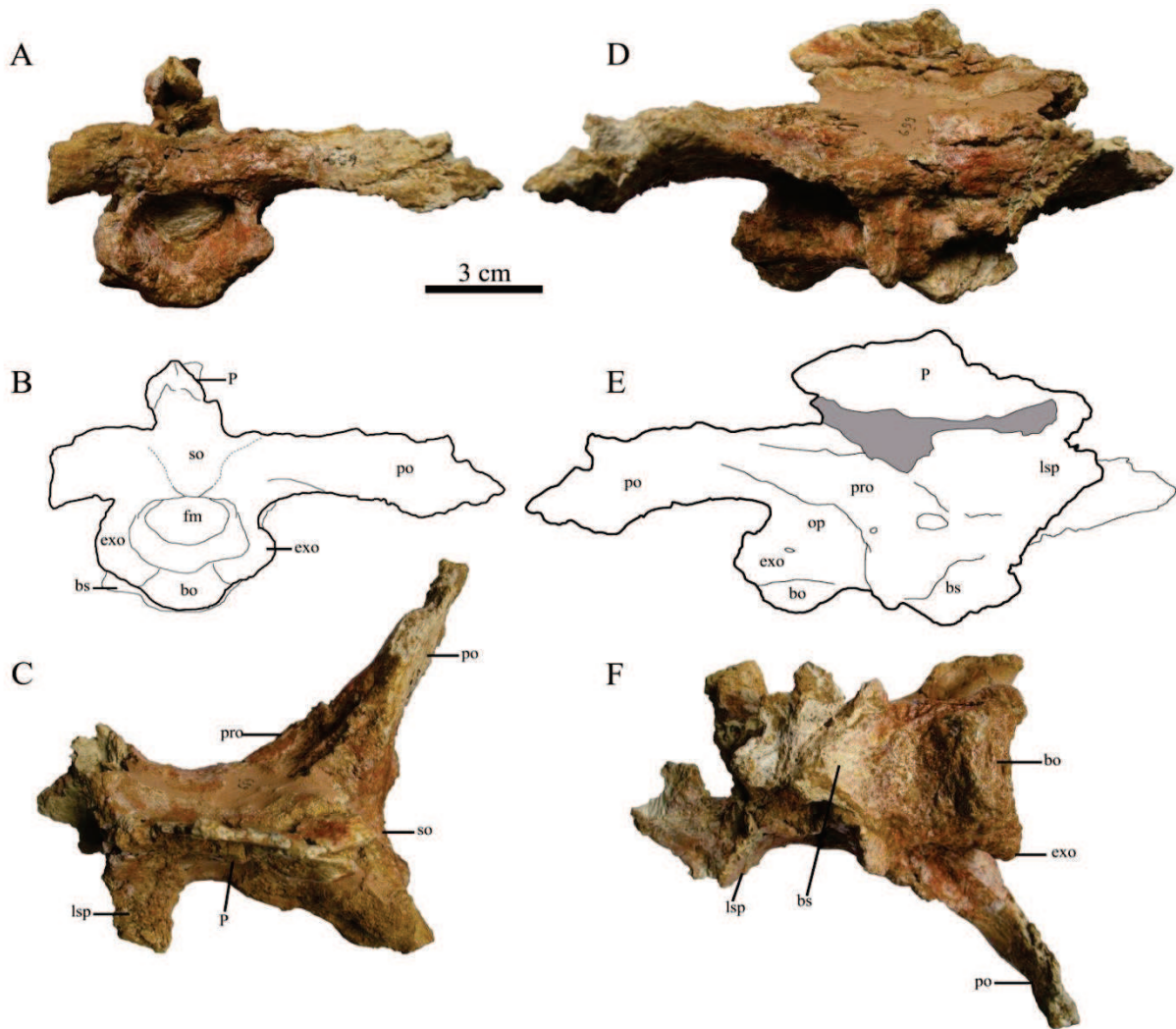


Figure 3. Braincase CM-699 from La Bastide Neuve, Fox-Amphoux in occipital (A-B), dorsal (C), right lateral (D-E) and ventral (F) views. See abbreviations in Figure 2.

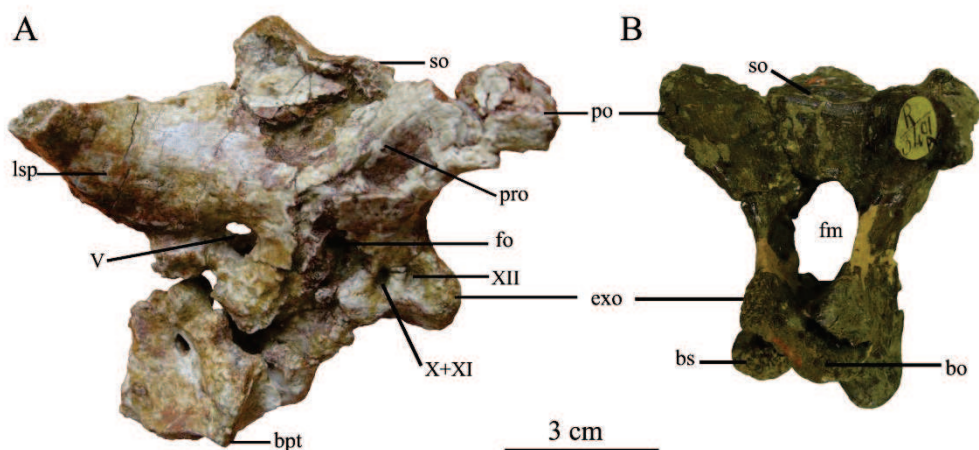


Figure 4. A : *Rhabdodon*. Braincase MC-M4 in left lateral view. B : *Zalmoxes robustus*. Braincase BMNH R.3401 in occipital view. See abbreviations in Figure 2.

VI. *Dentary* (CM-443, 587, 709, MC-M 23, M 27, CY_QR 1, CY_QR 2; MDE-C3.1280, MDE-C3.1407)

The dentary of *Rhabdodon* shows variability both in size and in shape. The dentary of *Rhabdodon* bears from nine to eleven alveoli. The dentary length ranges from 126 to 368 mm. (See Table of dentary measurements in Appendix II).

Dorsally, the dimensions of the anteriormost and posteriormost alveoli are relatively smaller than those from the middle portion of the alveolar row. The tooth row of the dentary is more or less straight or slightly concave on the lateral edge (Figure 4.5). The concavity of the tooth-bearing portion is well marked in the dentary of *Rhabdodon septimanicus* (Buffetaut and Le Lœuff, 1991). This diagnostic character of *R. septimanicus* is present in the remarkably large dentaries from Quarante (MC-CY_QR 1 and MC-CY_QR 2) (Figure 4.6). In dorsal view, the alveolar row of MC-CY_QR 1 and MC-CY_QR 2 is remarkably concave outward while the mandibular symphyseal region is curved inward.

Immediately anterior to the front end of the tooth row, the dorsal dentary margin is steeply inclined and converges with the upward sloping ventral margin to form the symphyseal rim. The symphyseal region is rough and bears ridges and grooves on the medial surface. On the anterolateral surface, prominent depressions are developed with large and numerous small foramina which are associated with the attachment of the prementary. In MC-CY_QR 1 and MC-CY_QR 2, the symphyseal region is slightly bent downward and displaced more anteriorly compared with other specimens, as the dorsal and ventral margins are farther prolonged anteriorly to form the dentary symphysis.

Laterally, in most specimens the dorsal and ventral margins are mainly straight and parallel while some specimens have a curved ventral edge (MC-CY_QR 1, MC-CY_QR 2). The lateral surface of the dentary is convex dorsoventrally. The buccal platform with a laterally rounded edge along the tooth row is prominent in CM-443, CM-587, CM-709, MC-M 23 and MDE-C3.1407 (Figure 4.5). This platform is sloped down and forms only a convexity along the lateral wall of the dentary MC-CY_QR 1, MC-CY_QR 2 and MDE-C3.1280. Two large foramina are visible laterally on the oblique platform or in the upper half of the lateral surface somewhat just posterior to the dentary mid-length. Numerous small foramina are also present on the lateral wall in the lower part of the dentary.

The coronoid process ranges in shape from a robust to a thinner and elongate projection. It rises and projects dorsoposteriorly at various angles to the dentary body, ranging from 90° to 125° in lateral view. In MDE-C3.1280 the distal end of the coronoid process is slightly curved and directed anteriorly at the dorsal end. The coronoid process lies

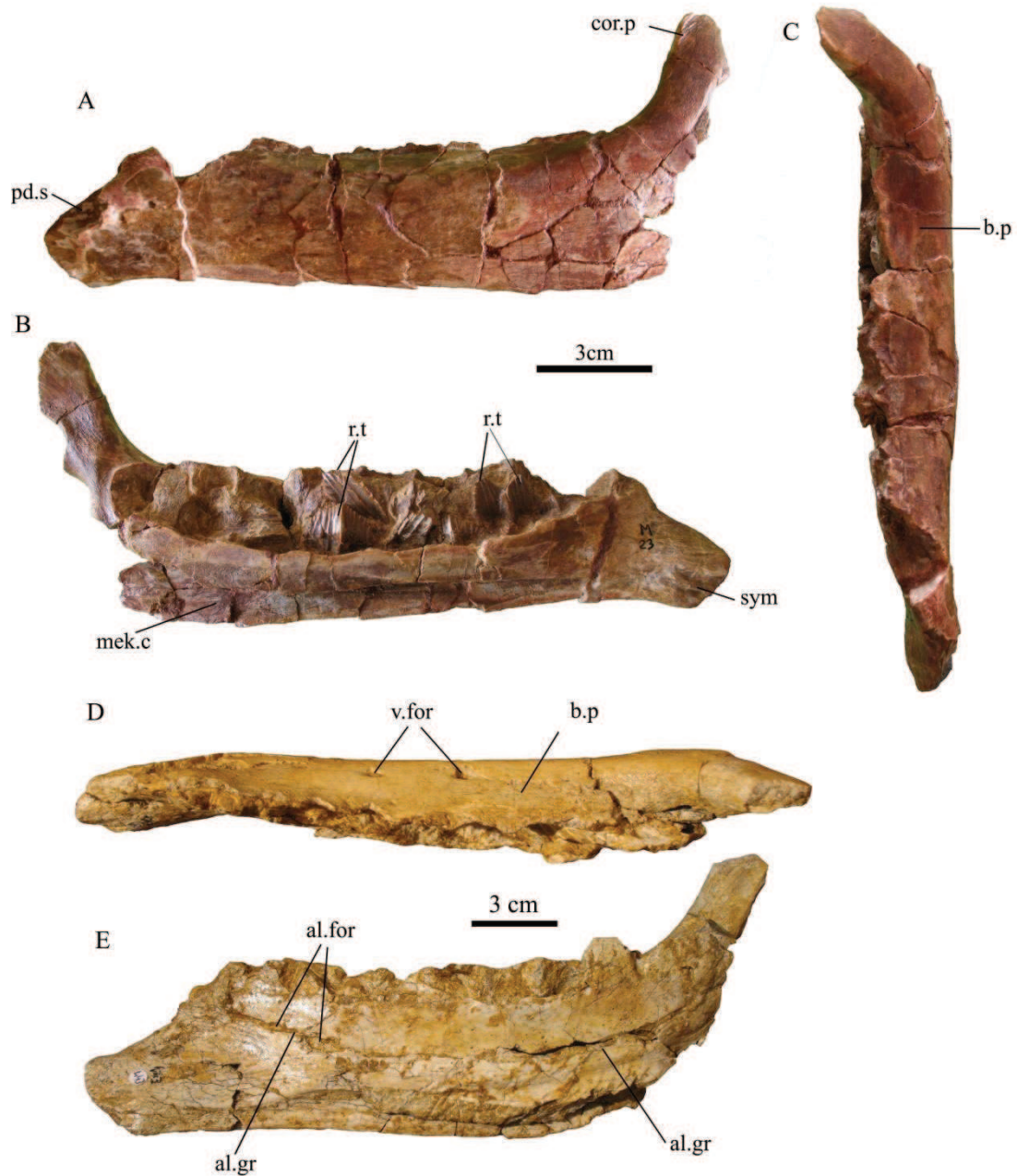


Figure 4.5 Left dentary MC-M 23 in lateral (A), medial (B) and dorsal (C) views. Right dentary CM-443 in dorsal (D) and medial (E) views. Abbreviations: al.for = alveolar foramen, al.gr = alveolar interconnection groove, b.p = buccal platform, cor.p = coronoid process, mek.c = Meckelian canal, pd.s = prementary suture, r.t = replacement tooth, sym = dentary symphysis, v.for = neurovascular foramen.

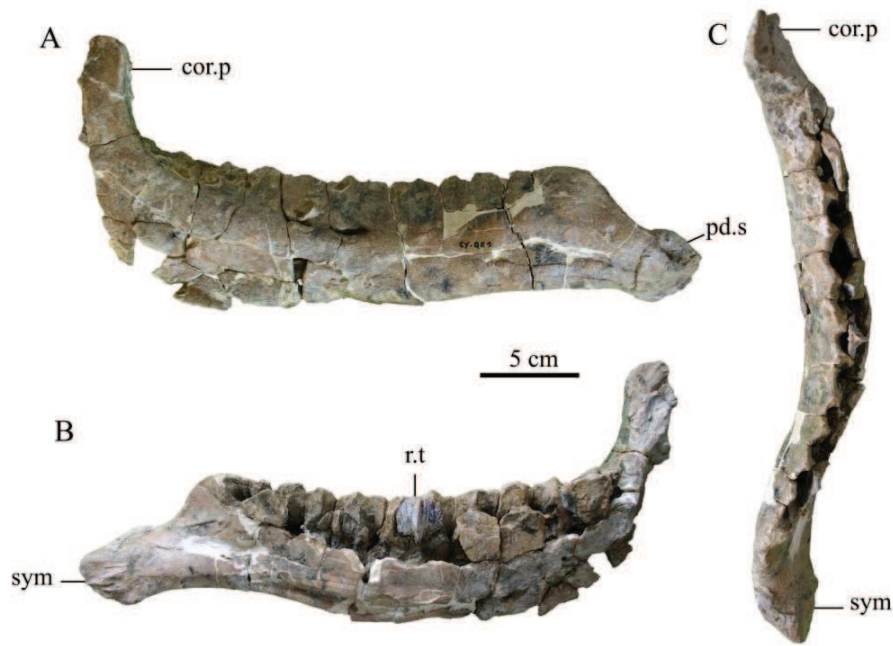


Figure 4.6 Right dentary MC-CY.QR 1 in lateral (A), medial (B) and dorsal (C) views. See abbreviations in figure 5.

laterally to the most posterior teeth. Laterally, the coronoid process is striated at the distal end. The medial surface of the coronoid process has an oblique striated facet and a large depression with minor ridges distally. Posteriorly, the coronoid process is irregular and has a deep dominant groove associated with the protruding bone for the attachment to the surangular.

Medially, the dentary is gently convex dorsoventrally and marked by the alveolar foramina and the alveolar interconnection groove. The Meckelian canal ventrally extends almost the total dentary length. The canal is deep, wide open posteriorly and then it becomes gradually narrower and shallower anteriorly to form only a shallow groove before the symphyseal region.

VII. *Angular* (MC-QR 22)

The left angular MC-QR 22 (Figure 4.7) is a thin long bone and has an elongate triangular shape in lateral view. The anterior and posterior extremities of the bone are tapering. The anterior end is narrow, triangular in cross section while the posterior one is more prominent, oval in cross section and bears clear ridges and grooves. Laterally, the anterior part shows a gently concave and scarred surface, which was overlapped by the posterior part of the dentary. The upper edge of the bone is thin while the ventral border is

thickened to form the lower edge of the jaw. Medially, the bone is concave ventrally and strongly ridged. On the dorsomedial surface, a small shallowly depressed area extends along the posterodorsal part of the angular to fit to the ventral part of the surangular.

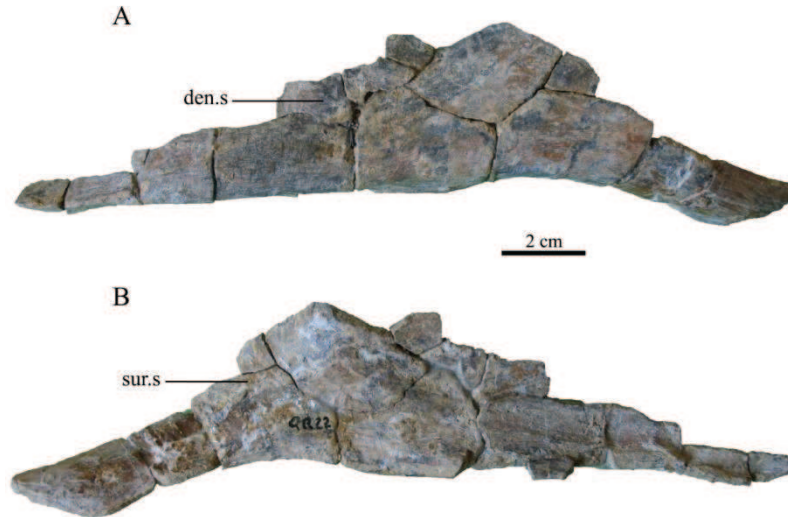


Figure 4.7 Left angular MC-QR 22 in lateral (A) and medial (B) views. Abbreviations: den.s = dentary suture surface, sur.s = surangular suture surface.

VIII. Surangular (MHN_AIX_PV.1999.10)

The right surangular MHN_AIX_PV.1999.10 is well preserved, crescent-shaped in lateral view, convex laterally and concave medially (Figure 4.8). It consists of two anterior and posterior processes which are both directed dorsally. The anterior process is transversely thick with rounded lateral and medial borders. The anterodorsal end of this process is thickened, however the anteriormost part of the surangular, where it is strengthened with the posterior edge if the coronoid process of the dentary is not preserved. Beneath this process, the bone forms a curved thin wall which slots inside the posterior part of the dentary and there is probably an anterior surangular foramen but it is not completely preserved in this specimen. More posteriorly the dorsal margin is extended outward and forms a lip-like projection with a rough lateral apex. This lip forms the lateral margin of the glenoid for the quadrate lateral condyle and the attachment area for the jaw joint ligaments. On the medial side, anteroventrally to the prominent lip, there are two foramina, the anterior foramen being slightly bigger than the posterior one. These foramina are variously present in iguanodontian ornithopods but absent in hadrosaurids (Norman, 1998).

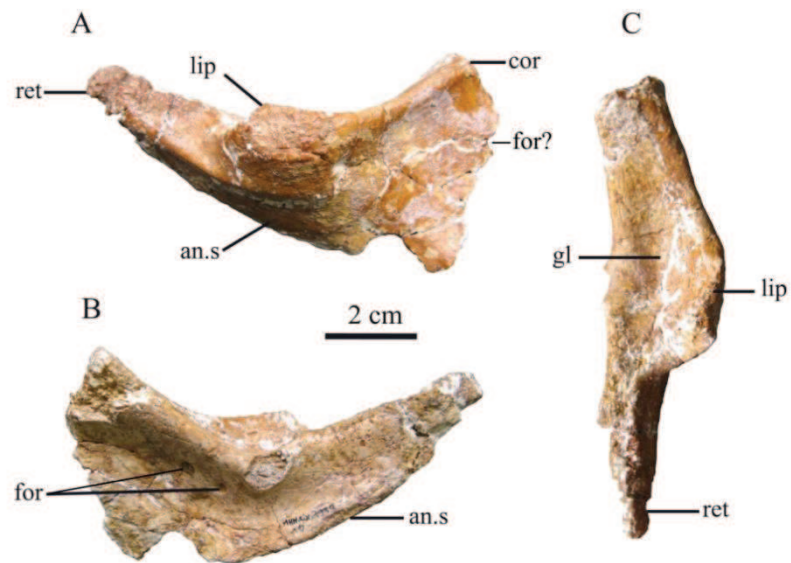


Figure 4.8 Right surangular MHN_AIX_PV.1999.10 in lateral (A), medial (B), dorsal (C) views. Abbreviations: an.s = angular suture, cor = coronoid portion of the surangular, for = surangular foramen, gl = glenoid articulation with the quadrate, lip = lateral lip-like margin, ret = retroarticular process.

Posterior to the quadrate cotylus, the surangular is tapered and directed upward, forming the lateral portion of the retroarticular process. Ventrally, the suture with the angular runs along most of the surangular length and there is also a narrow groove seen on the medial side to fit firmly to the angular bone.

4.2.2 Dentition

Teeth of *Rhabdodon* are known from all localities, although they are mostly found isolated. *Rhabdodon* is characterized by its distinctive fluted maxillary and dentary teeth.

I. Maxillary teeth (CM-297, 326, 554, 657, MC-M 4190, M 4196, M 4260; MDE-C3.897, C3.1412; MHN_AIX_PV_Fox)

The maxillary teeth (Figure 4.9) are subrectangular in outline, slightly taller than wide. They are lens-shaped in cross-section. The buccal surface of the maxillary crown is covered by a thick layer of enamel and bears several subequal, sharp ridges. These vertical ridges are more or less parallel and there are smooth, longitudinal grooves lying between the

ridges. Marginal denticles are present along the mesial and distal margins of the crown and also on the dorsal margin in the unworn crowns (Figure 4.9C). The density of ridges on the buccal side of teeth does not appear to have increased during the ontogeny as shown by a scatter plot of the relationship between the maxillary tooth width and the number of ridges on the teeth in figure 4.10A. A well-defined cingulum forms the border of the crown and separates it from the root. The tooth crown is wider than its root and the roots of fully erupted and functional teeth are very long and taller than the crown.

Medially, the tooth is thinly enamelled and bears shallow longitudinal ridges. In more mature teeth, the medial shallow ridges disappear and two asymmetrical oblique wear facets are developed on the occlusal surface. These facets merge as a single sloping wear facet with a sharp margin on the heavily worn teeth.

The teeth are closely packed together as shown by the groove on the mesial and distal edges of the teeth and as seen in the maxilla FSL530513 (Figure 4.2C). From an observation of the alveoli of the maxilla, the most anterior tooth seems to be the smallest and the tooth size gradually increases and reaches its maximum about just distal to the middle of the tooth row. The emplacement of the maxillary teeth cannot be precisely determined as a complete maxillary dentition has not yet been found. There are two teeth per tooth family, as reported by Weishampel et al. (2003). As seen in figure 4.9D, the erupting replacement tooth is closely applied to the medial surface of the functional tooth. The adjacent teeth appear to be at different stages of eruption but the replacement sequence is still poorly understood.

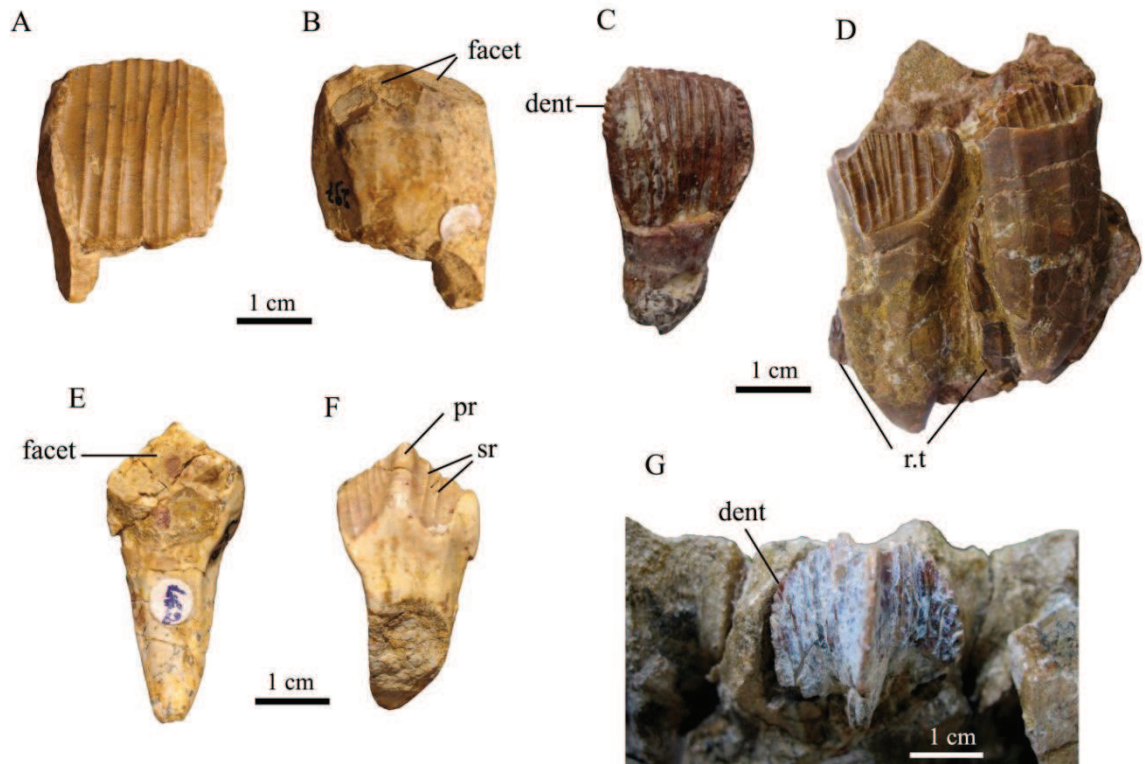


Figure 4.9 Maxillary teeth, CM-297 in labial (A), in lingual (B) views, MHN_AIX_PV_Fox (C) in labial view, MC-4190 (D). Abbreviations: dent = denticle, facet = wear facet, pr = primary ridge, r.t = replacement tooth, sr = subsidiary ridge.

II. Dentary teeth (CM-462, 475, 502-508, 655, MDE-C3.809, C3.1413, D37, D27, MC-M 47, M 1329, M 3583, M 3837).

The dentary teeth are different from the maxillary teeth in having a broader, diamond-shaped crown. In the opposite way to the maxillary teeth, the dentary teeth are thickly enameled in the lingual surface and the wear facets are present on the buccal side. A sharp to rounded prominent primary ridge is present slightly distal to the midline of the crown on the lingual surface. On each side of the primary ridge, there are several, sharp lower-relief subsidiary ridges diverging vertically to the dorsal margin of the crown. Marginal denticles are also present on the dentary crown. The cingulum of the dentary teeth is not as prominent as in that of the maxillary teeth.

The scatter plots between the number of the subsidiary ridges and the tooth width (Figure 4.10B and C) do not show an obvious relationship that could indicate that the number of the ridges is increases or decreases during the ontogeny.

The root of the dentary teeth is labially curved, tapering and slightly narrower than the crown width and it is longer than the crown. The mesial and distal sides of the root are grooved, indicating a closely packed dentition. As in the case of the maxillary teeth, the replacement sequence of dentary teeth cannot be determined.

Medially, the wear facet is shallowly concave, inclined buccally. The major facet is formed on the distal portion of the occlusal surface and obliquely inclined toward the mesial wear facet. The occlusal surface bears a single facet in the heavily worn teeth. The occlusal facet bears microstriae oriented more or less perpendicularly to the transverse axis of the tooth, as seen in dentary tooth MDE-D 37.

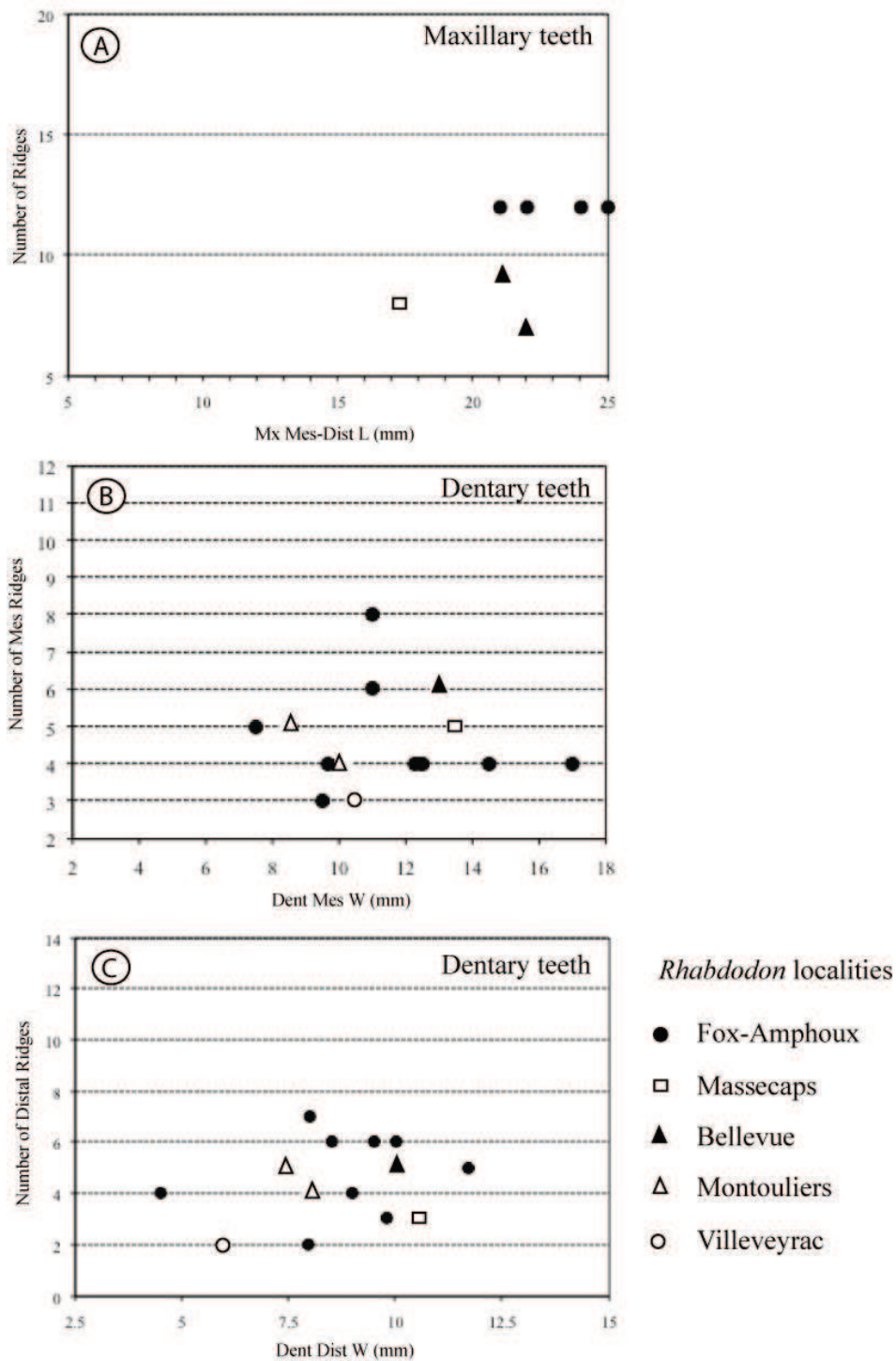


Figure 4.10 Scatter plots, (A) between the number of the ridges on the buccal surface of the maxillary crown and the tooth width (Mx Mes-Dist L), (B) between the number of secondary ridges mesial to the primary ridge on the lingual surface of the dentary crown and the mesial width (Dent Mes W), (C) between the number of secondary ridges distal to the primary ridge on the lingual surface of the dentary crown and the distal width (Dent Dist W). (see Table of measurement in Appendix II)

4.2.3 Postcranial Skeleton

I. Axial skeleton

A complete articulated axial skeleton of *Rhabdodon* has never been found, nevertheless partially articulated vertebrae have been reported from some localities, especially from the late Campanian of the Vitrolles-Couperigne localities (Pincemaille-Quillévéré, 2002; Chanthasit et al., in review). The vertebral column has been consequently described on the basis of various isolated specimens from different localities. The total number elements in the vertebral column cannot be determined.

I.1 Cervical vertebrae and ribs (CM-86, 405, 441, 679; MC-M 30, M-4058)

Cervical vertebrae are rarely found. The total number of the cervical series cannot be estimated. Some cervical remains have been recovered and are described here.

Only a single isolated atlas (CM – 86) (Figure 4.11) from Brégoux (Fox-Amphoux) is known. The atlas consists of the intercentrum and two neural arches. The odontoid is presumably unified as a part of the axis. In the atlas CM-86, the neural arch is fused to the intercentrum as in the atlas of *Ouranosaurus nigeriensis*. The intercentrum is narrow and subcrescentic. The anterior surface bears a large shallow depression for the occipital condyle articulation. This depression is inclined obliquely to the long axis of the skull and expanded dorsomedially toward the neural arches. The ventral edge of the intercentrum is sharp while the dorsal surface is rounded and strongly curved, resulting in a very narrow neural canal compared with other ornithopods. Posteriorly, the intercentrum is convex because of a ridge in the middle but concave dorsomedially for receiving the odontoid process (Figure 4.11C). The neural arch is attached on the lateral side of the intercentrum. The neural arch continues the depression formed by the intercentrum. Dorsally, the two neural arches are not fused to each other even though they are also expanded medially (Figure 4.11B). An irregular tapering horn-like process is developed dorsoposteriorly on the neural arch and curved medially. The postzygapophysis is not well defined. The lateral and ventral surfaces are rounded and show no evidence of diapophysis. This suggests that the cervical ribs are not present yet on the atlas as in *I. bernissartensis* (Dollo, 1883) and *Ouranosaurus* (Taquet, 1976) whereas in *I. atherfieldensis*, *Hypsilophodon*, and maybe *Tenontosaurus*, the first pair of cervical ribs is situated on the atlas (Hooley, 1925; Galton, 1974; Forster, 1990).



Figure 4.11. Atlas CM – 86 in anterior (A), dorsal (B) and posterior (C) views. Abbreviations: ic = intercentrum, na = neural arch, oc.c. = surface for occipital condyle, od.p = surface for odontoid process.

The axis is also rarely found. A single axis MC-M4058 (Figure 4.12) from the Masecaps locality is not well-preserved. The odontoid process of the atlas is sutured in the middle of the anterior facet of the axis centrum. The odontoid process is wedge-shaped, triangular in lateral view and flattened dorsally. The odontoid process is tapering and horizontally projects forward.

As preserved, the axis centrum is longer than wide and high and constricted laterodorsally. It is difficult to distinguish the intercentrum of the axis from the centrum. The neural spine arises between the prezygapophyses. The dorsal end of the neural spine is broken, however it extends notably anteroposteriorly over the neural arch. The neural canal is high and wide.

The prezygapophyses project anteriorly and face ventrolaterally as in *Iguanodon bernissartensis*. The postzygapophyses are not preserved but seem to be situated lower than the prezygapophyses. Although the lateral and posterior parts are damaged, on the left lateral wall, a diapophysis is present on the lateral surface of the neural arch. Generally, the axis of *Rhabdodon* is similar to that of *Zalmoxes* (Weishampel et al. 2003).

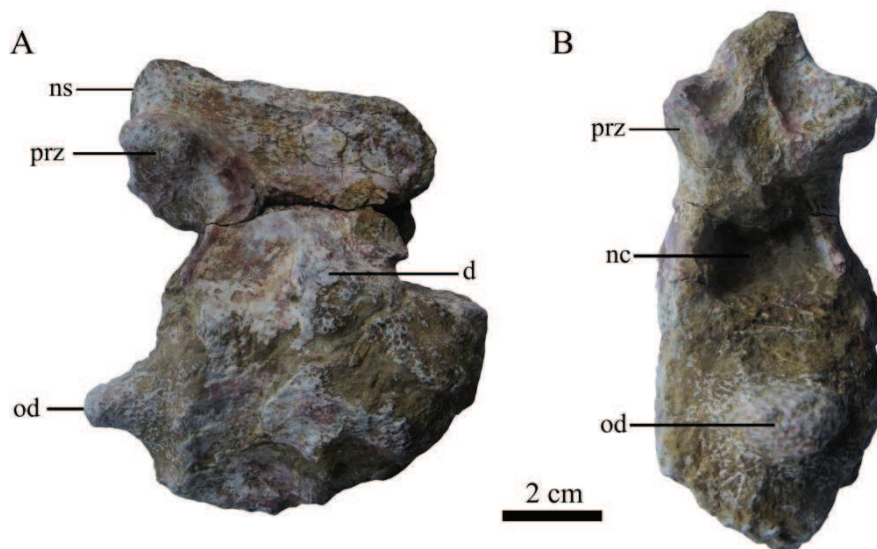


Figure 4.12 Axis MC-M4058 in left lateral (A) and anterior (B) views. Abbreviations: d = diapophysis, na = neural arch, nc = neural canal, od = odontoid process, prz = prezygopophysis.

Concerning the subsequent cervical vertebrae, four articulated anterior cervical vertebrae have been discovered as part of the partial articulated skeleton of *Rhabdodon priscus* from Vitrolles-Couperigne found in 1995. Pincemaille-Quillévére (2002) described the diagnostic features of these vertebrae which belong to the anterior part of the cervical series. The centra are opisthocoelous, bearing well-developed neural spines with a cranial orientation and the transverse processes extend anteroposteriorly. However, the interpretation of the cervical vertebrae from Vitrolles is still uncertain because the specimens are deformed.

Some other anterior cervical vertebrae are known from Masecaps (MC-M 30) (Figure 4.13 A, B, C) and Bastide Neuve (CM-679) (Figure 4.13 D, E). Despite the fact that MC- M 30 lacks the ventral part of the centrum, the neural arch and the zygapophyses are quite well-preserved. It is the reverse in specimen CM-679, in which the centrum is complete but the neural arch is incomplete.

The centrum of the anterior cervical vertebrae is as long as high and it is slightly opisthocoelous to platycoelous. The anterior facet is broad, wider than high. The centrum is transversely compressed, with concave lateral walls and a rounded ventral keel. The parapophysis is situated just behind the lateral margin of the anterior articular facet, below the neurocentral suture. This angular parapophysis is continued by a horizontal ridge at the middle of the centrum. The neural arch is wide and robust, enclosing the sub-circular neural canal. Anteriorly, the transverse processes project laterodorsally from the laterodorsal

surface of the neural arch. The transverse process supports the prezygapophysis dorsally as well as the diapophysis laterally. The large curved postzygapophyses arise just after and above the transverse processes. The postzygapophyses are widely divergent and prolonged backward. They bear the large oval zygapophyseal facets which face ventrolaterally. The neural spine is incompletely preserved, however it shows an oval, laterally compressed neural spine base arising from the middle of the anterodorsal rim of the neural arch. Although the size of the neural spine cannot be exactly estimated, it tends to be more prominent than those of *Zalmoxes* which apparently are only a small conical spine.

Cervical CM-441 (Figure 4.13 F, G, H) is from the middle part of the cervical series. The centrum is as long as wide and higher proportionally compared with the anterior cervical vertebrae. The centrum is also compressed laterally and keeled ventrally. Compared to the anterior cervicals, the neural arch of CM-441 is taller and supports more robust transverse processes which are inclined more dorsally. The transverse processes still bear both the prezygapophyses and the diapophyses. The articular facet of the prezygapophyses is larger, erected upward and faces dorsomedially. The diapophysis is larger and developed more posteroventrally on the transverse process. The parapophysis is situated more dorsally, closer to the neurocentral suture. The postzygapophyses are less opened but project more upward. The articular surface is also prominent and faces ventrolaterally as in the anterior cervicals. The neural spine is displaced more posteriorly. As the main part of the spine is broken, the orientation of the neural spine cannot be confirmed. However, I think the neural spine of *Rhabdodon* seems not to be strongly oriented cranially, probably it is curved initially anteriorly and subsequently turns backward. The cranial orientation of the spines of the cervical vertebrae of *Rhabdodon priscus* from the Vitrolles-Couperigne locality is presumably a result of deformation. Nevertheless, the neural spines of the cervical vertebrae of *Rhabdodon* from Vitrolles-Couperigne are remarkable for their size which distinguishes it from other ornithopod dinosaurs.

The cervical ribs are hardly known. The first pair of cervical ribs must have started at the axis as mentioned above. According to the size and the position of the parapophysis and the diapophysis, it is suggested that the cervical ribs of the anterior to mid cervical vertebrae had well-separated double heads and that the capitulum was slightly larger than the tuberculum.

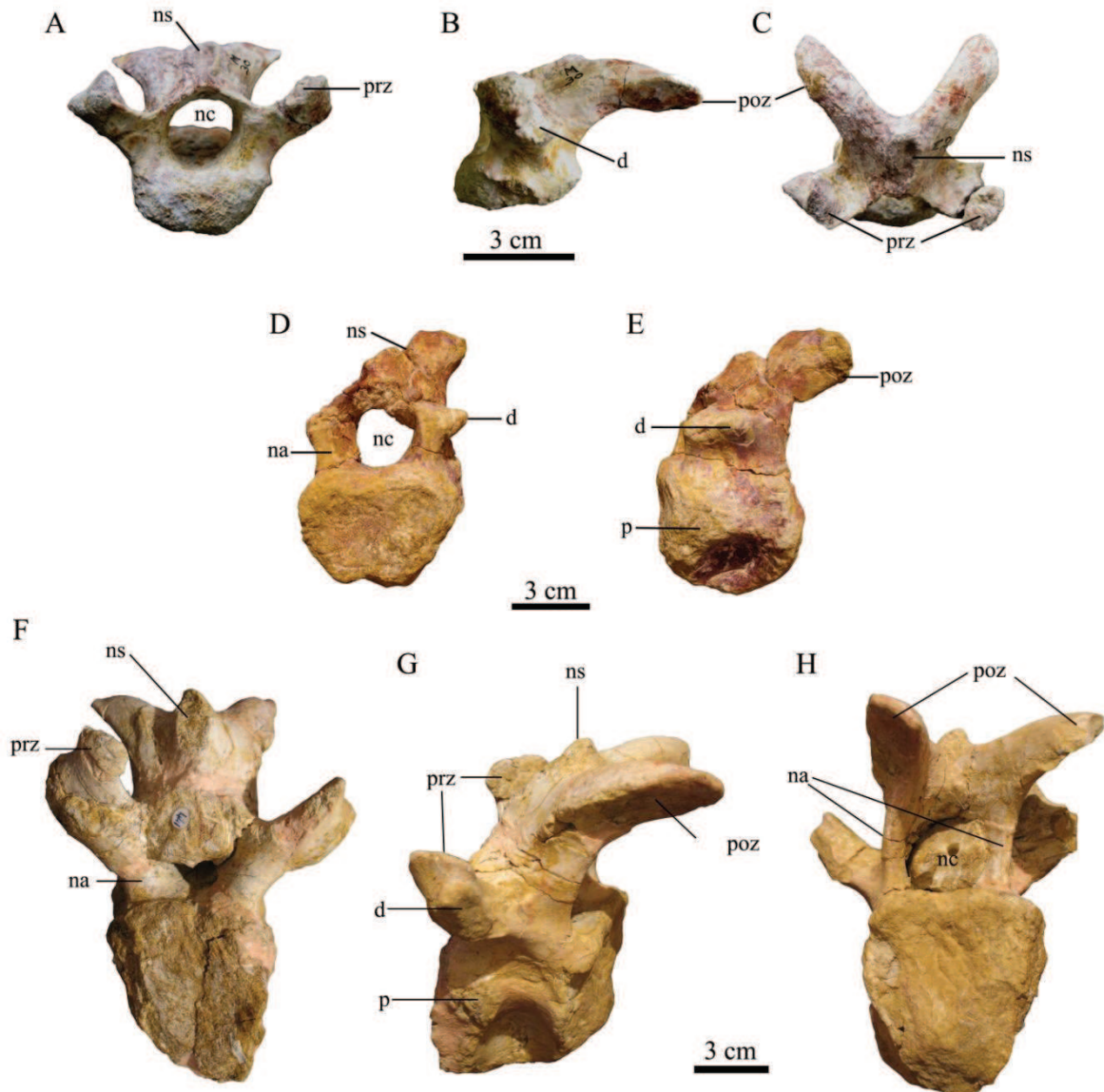


Figure 4.13 Anterior cervical vertebrae, MC-M30 in anterior (A), left lateral (B) and dorsal (C) views, CM-679 in anterior (D) and left lateral (E) views. Mid-cervical vertebra CM- 441 in anterior (F), left lateral (G) and posterior (H) views. Abbreviations: d = diapophysis, na = neural arch, nc = neural canal, ns = neural spine, p = parapophysis, prz = prezygapophysis, poz = postzygapophysis.

1.2 Dorsal vertebrae and ribs (CM-3, 142, 379, 380, 400, 416, 445, 446, 496, 498, 499, 564, 581, 527, 647, 710; MC- M 38, M 220, M 261, M 537, M 626, M 948, M 1080, M 1116, M 1131, M 1149, M 1699, M 2333, M 2828, M2705, M 3179, M 3395, M 3896, M 4012, M 4395, M 4532, MOB 56; MDE-C3 413, C3 973, C3 1400, C3 1556, C3 02.102, C3 02.137, C3 03.50; MNHN 8)

The most complete dorsal series was described by Pincemaille-Quillévére (2002). Sixteen dorsal vertebrae were found from a partial articulated skeleton of *Rhabdodon*

priscus from Vitrolles-Couperigne in 1995. This possibly indicates that *Rhabdodon* had at least 16 dorsal vertebrae as in *Iguanodon bernissartensis* (Norman, 1980) and *Ouranosaurus nigeriensis* (Taquet, 1976). The sixteen dorsal vertebrae described in that previous work are not well preserved. Most of them were found as isolated centra or neural arches so that some characters of dorsal vertebrae remain uncertain.

Additional isolated dorsal vertebrae described herein are more complete and well-preserved though they are from different localities.

Anterior dorsal vertebrae (Figure 4.14) have a very short, higher than wide centrum. The centrum of anterior dorsals is gently opisthocoeleous. The lateral wall is axially concave and the ventral surface forms a thin keel in the middle. The centra from the middle dorsal series (Figure 4.15) become longer and as wide as high while they are shortened and higher than wide in posterior dorsal vertebrae (Figure 4.16). The articular facet is more circular with a rounded edge through the anterior to middle series and the centrum becomes platycoelous and amphicoelous in the posterior dorsal vertebrae. Laterally, the dorsal and ventral margins of the centrum are parallel. The anterior and posterior articular facets of the posterior dorsals are slightly convergent ventrally.

The neural arch of the anterior dorsal vertebrae is tall and wide then it becomes shorter and narrower in more posterior elements. The neural arch extends from the anterior surface to the posterior one along the centrum length in the anterior dorsals, then it is slightly shortened through the subsequent dorsal vertebrae. The neural canal which is large in the anterior dorsal vertebrae is reduced and rounder in cross-section in posterior vertebrae.

The transverse processes are directed dorsolaterally (about 45 degree from the vertical), curved and pointed slightly caudally in anterior dorsals. These processes become shorter and reoriented more horizontally through the series. The parapophysis is positioned on the lateral surface of the neural arch at the base of the transverse process in anterior dorsals. Through the dorsal series, the parapophysis forms a vertically elongated concavity and it gradually moves dorsally along the transverse process, closer to the diapophysis. The parapophysis and the diapophysis are eventually merged into a large tubercle at the distal end of the transverse process of the posterior dorsals (Figure 4.16). The prezygapophyses are developed cranially on the proximal part of the transverse process of the anterior dorsal vertebrae. They migrate medially closer to each other than on the cervical vertebrae and are separately erected from the transverse process on the dorsal margin of the neural canal in

posterior dorsal vertebrae. The articular surfaces are slightly concave and they face dorsomedially. The prezygapophyses are more prominent in more posterior dorsals.

The postzygapophyses of the anterior dorsal vertebrae are well separated and face ventrolaterally but they do not extend as strongly backward as in the cervical vertebrae. The postzygapophyses extend farther beyond the centrum in more posterior dorsals and the oval articular surface becomes gradually larger in more posterior dorsals.

The neural spines in the proximal dorsal series are tall, forming more than a half of the total height of the vertebra (See also fig.4 Chanthasit et al., in review). They are compressed laterally, narrow, tapered upward and slightly curved posteriorly. The neural spines are inclined more posteriorly in the mid-posterior series. The neural spines are expanded anteroposteriorly as a large, long rectangular blade and gradually become longer, being more than four times taller than the centrum in the most complete specimens (CM-142, CM-44, CM-581 and MC-MN 32). The neural spines are axially longitudinal oval in cross-section with sharp anterior and posterior ridges in the middle along the proximal portion of the spines. The neural spine ends with a thick rugose dorsal tip. The neural spine of some specimens (CM-142 and MC-MN 32) shows a slightly sigmoidal curvature in anterior view (Figure 4.15 D, E). This may be a taphonomic effect.

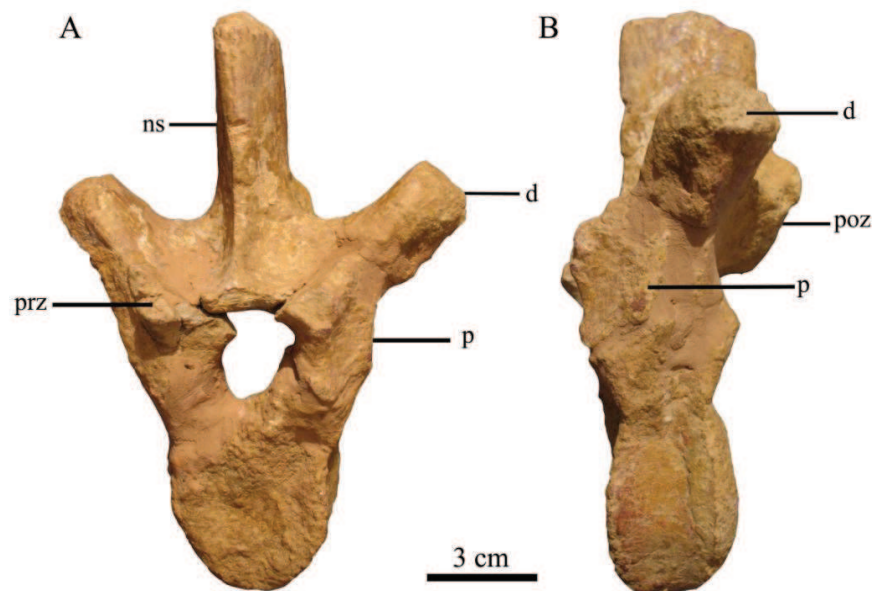


Figure 4.14 Anterior dorsal vertebra CM-379 in anterior (A) and left lateral (B) views. Abbreviations: d = diapophysis, ns = neural spine, p = parapophysis, prz = prezygapophysis, poz = postzygapophysis.

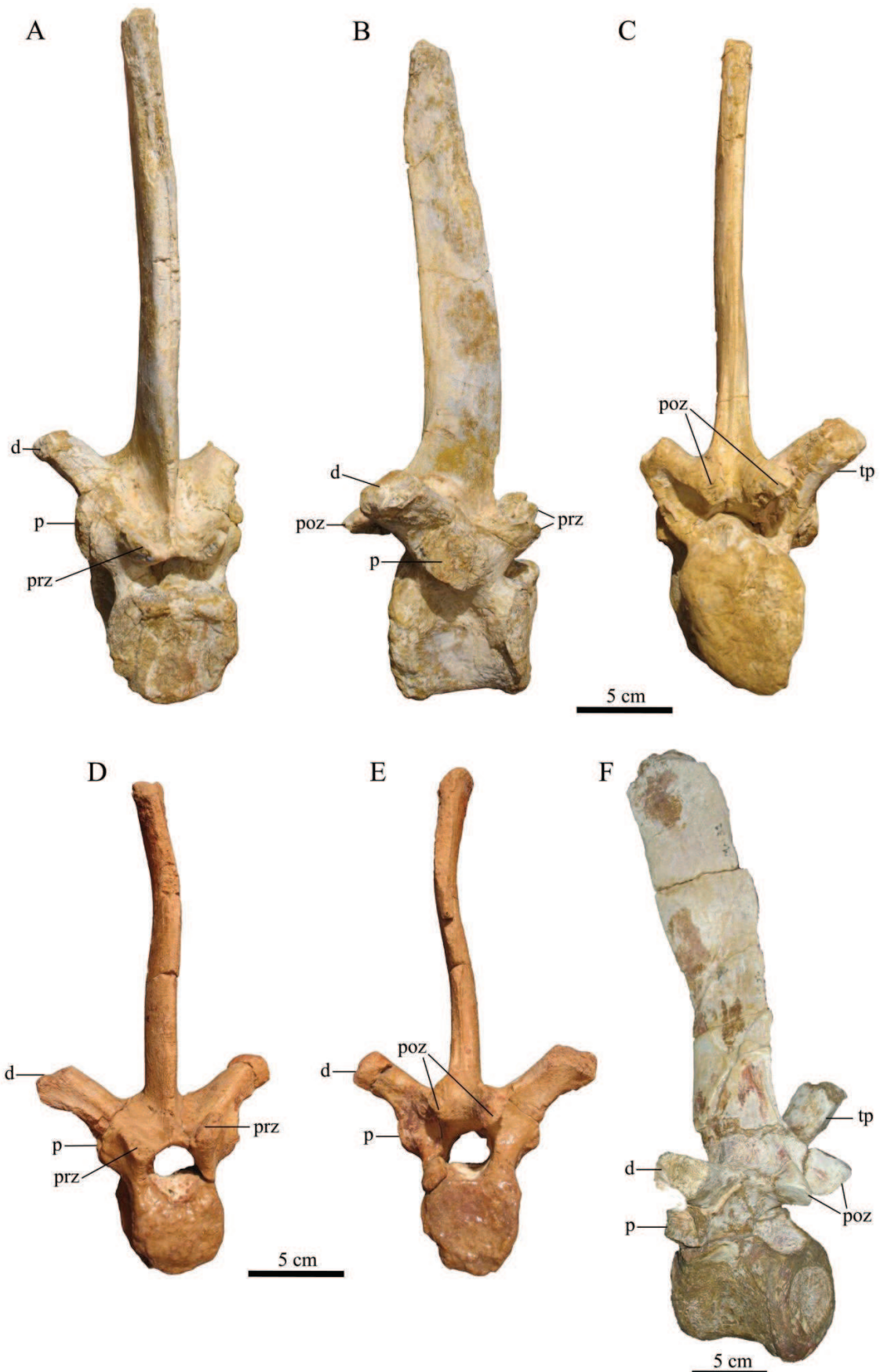


Figure 4.15 Mid dorsal vertebrae, CM-581 in anterior (A), right lateral (B), posterior (C) views, CM-142 in anterior (D) and posterior (E) views and MC-MN32 in posterior-lateral view. Abbreviations: d = diapophysis, p = parapophysis, prz = prezygapophysis, poz = postzygapophysis, tp = transverse process.

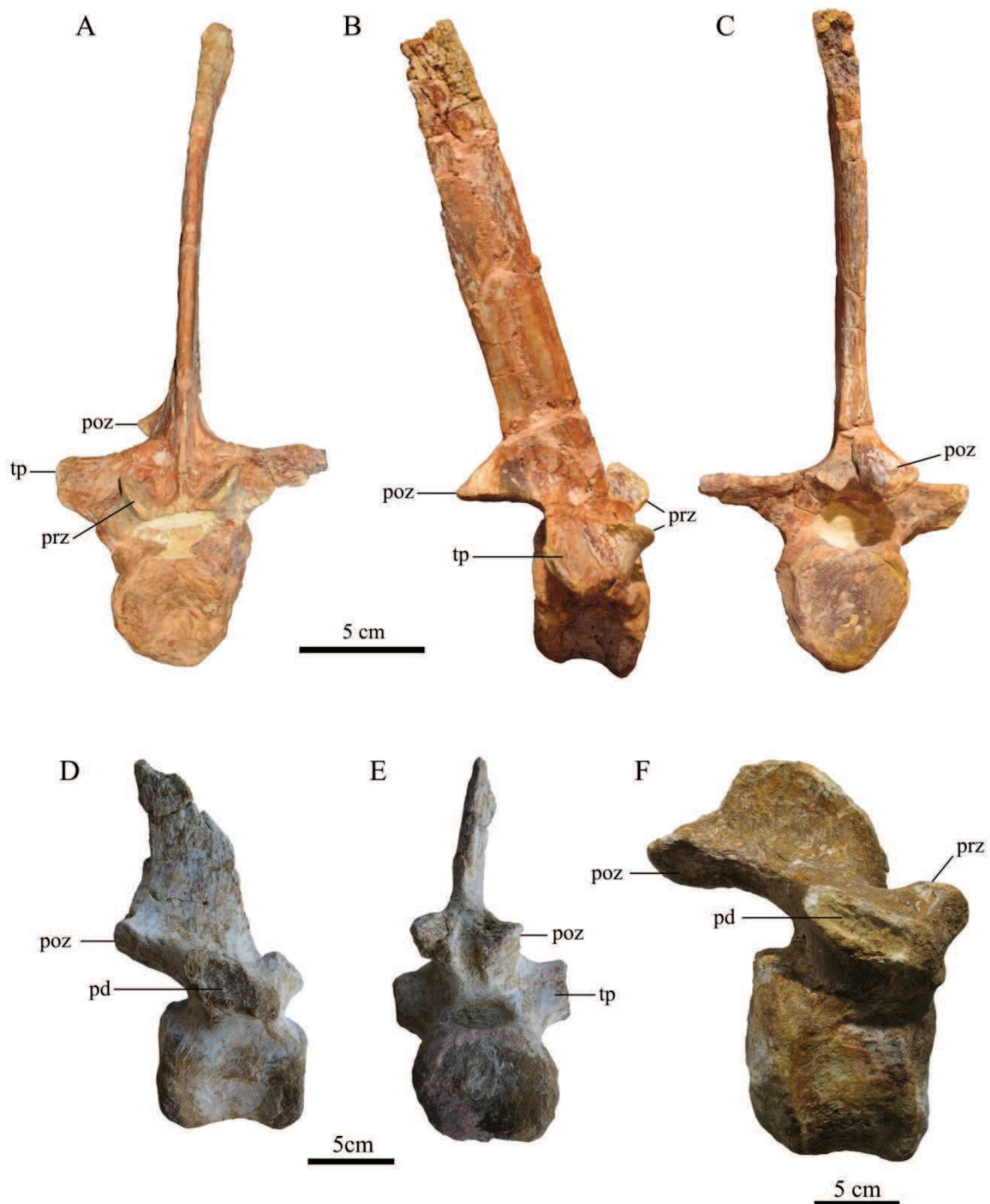


Figure 4.16 Posterior dorsal vertebrae, CM-496 in anterior (A), right lateral (B) and posterior (C) views, MDE-C3.03.50 in right lateral (D) and posterior (E) views and MDE-C3.1400 in right lateral view. Abbreviations: pd = paradiapophysis, prz = prezygapophysis, poz = postzygapophysis, tp = transverse process.

Dorsal ribs are usually found fragmentary. They are of various sizes and shapes, corresponding to their position along the dorsal series (Figure 4.17). Most of the dorsal ribs are doubled-headed except for those articulating with the posterior dorsal vertebrae which

are single-headed. In anterior thoracic ribs, the capitulum and the tuberculum are widely separated. The capitulum is supported by a long, slender capitular process with a slightly expanded round articular surface. The tuberculum is at first sub-equal in size to the capitulum then in more posterior ribs, the tuberculum is shortened, dorsoventrally expanded and becomes more prominent than the capitulum. The articular surface of the tuberculum is concave and oval in shape. Subsequently, the capitulum and the tuberculum move closer to each other and the tubercular process disappears. The dorsal ribs are curved around the thorax. On the proximal portion, the costal surface is anterodorsally convex and forms a ridge continually from the tuberculum whereas it is concave posteriorly with a shallow groove. The dorsal margin is proximally sharp while the ventral one is rounded along the costal length. The dorsal ribs are anteroposteriorly compressed in the proximal part of the shaft. The shaft is tapered at the distal tip in the anterior series but it gradually becomes laterally compressed in its distal part in the more posterior ribs. In the posterior series, the capitulum and the tuberculum are merged as a single articulation with the paradiapophysis and costal shafts are short and tapered distally.

I.3 Sacrum (**CM**-621; **MC**-M 1233, M 1739, M 1882, PSP 1; **MDE**-C3 134, C3 135, C3.04.72)

On the basis of the most complete sacral series of *Rhabdodon* from Vitrolles-Couperigne (Pincemaille-Quillévéré, 2002; Chanthasit et al. (in review), the sacrum of *Rhabdodon* is composed of six true co-ossified sacrals, which are possibly fused with the sacrodorsal and the last dorsal vertebrae as in *Iguanodon*, *Hypsilophodon* and *Zalmoxes* (Norman, 1980, 1986; Galton 1974; Weishampel et al. 2003; Godefroit et al. 2009). The sacrum of *Tenontosaurus* consists of five fused true sacrals and a sacrodorsal. Besides the sacrum from Vitrolles, the sacrum MC-PSP 1 (Figure 4.18) from Plo-Saint-Pons seems to be the best preserved with six co-ossified vertebrae. The sacrum is arched anteroposteriorly. The first vertebra of MC-PSP 1 is interpreted as a sacrodorsal. The centrum has a rounded anterior articular surface and it is laterally compressed with a rounded keel on the ventral surface as in the posterior dorsal vertebra. The transverse process is partly broken, situated on the dorsal part of the neural arch. The centrum is posteriorly expanded and bears laterally the first pair of sacral ribs. The first sacral ribs are developed at the joint between the sacrodorsal and sacral one. The sacral ribs of sacral two to sacral five are also located at the joint with the preceding sacral. The first sacral ribs are oriented caudally while the others are

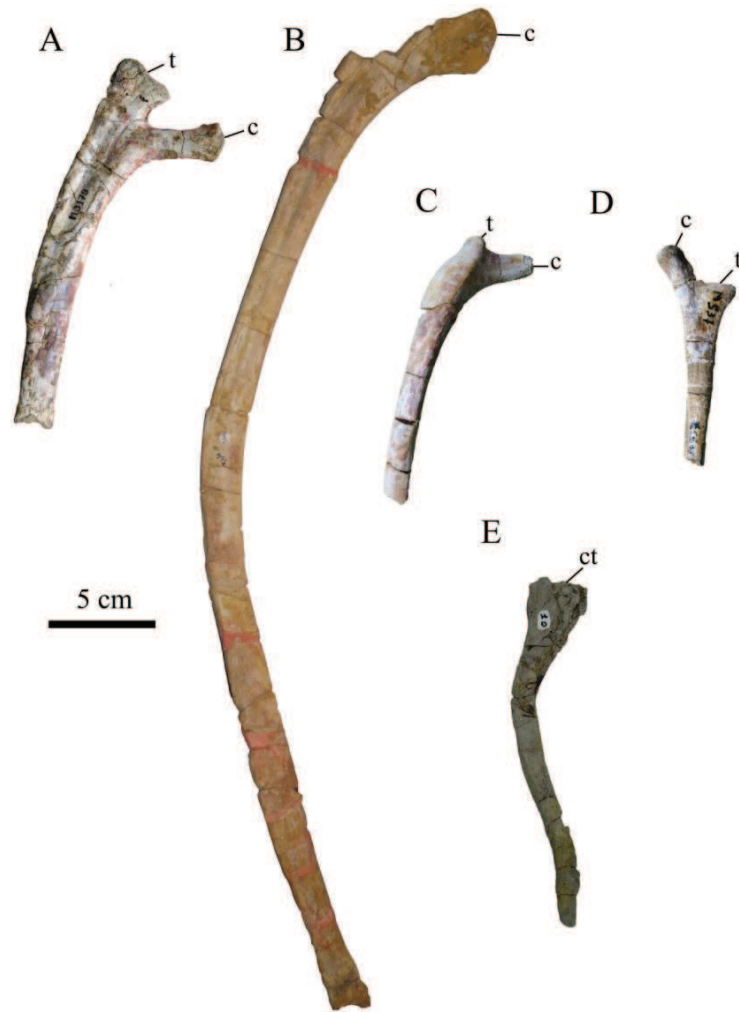


Figure 4.17 Anterior-mid dorsal ribs, MC-M 3179 (A) and CM-564 (B) in posterior view; middle dorsal rib, MC-M 1699(C) in anterior view; middle-posterior dorsal rib, MC-M 537 (D) in posterior view; posterior rib, MHN-AIX-PV 2007.B8.10 (E) in posterior view. Abbreviation: c = capitulum, ct = merged capitulum and tuberculum, t = tuberculum.

directed laterally. The second pair of sacral ribs is obviously prominent, massive and extends to the ventral limit of the centra. The third, fourth and fifth sacral ribs are situated dorsally on the centrum and the neural arch. The sacral ribs are expanded distally and coalesced at their distal end and form a thick rugose sacral yoke for attachment to the ilium.

The sacral centra are laterally compressed and ventrally rounded. The centra become more constricted through the series. The neural arch of true sacrals migrates anteriorly beyond the posterior margin of the preceding vertebra. The neural spines are partly preserved in MC-PSP 1, however it shows a rectangular spine with a sharp anterior and rounded posterior margins. The neural spines of the sacrum are slightly inclined posteriorly.

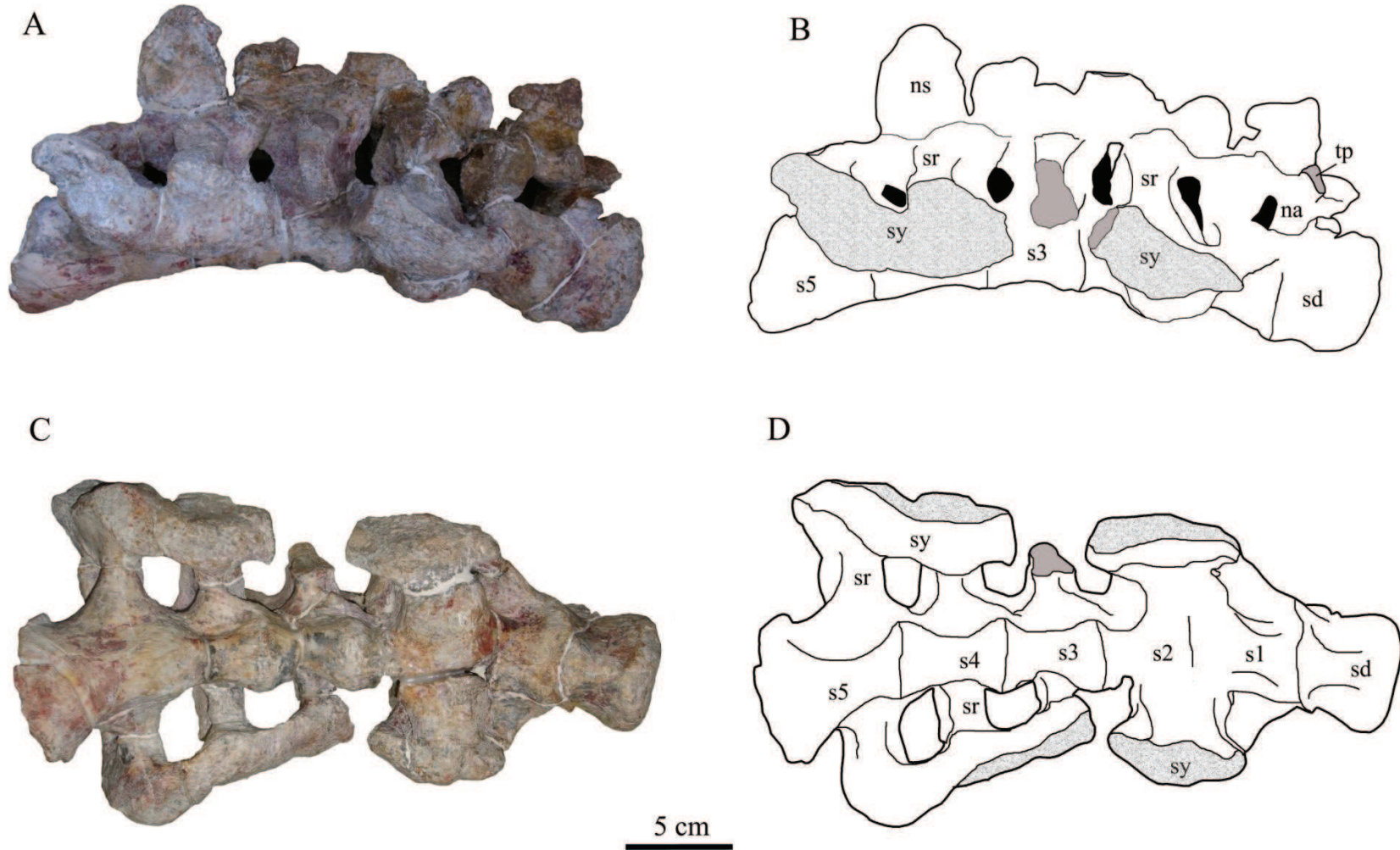


Figure 4.18 Sacrum MC-PSP 1 in right lateral (A, B) and ventral (C, D) views. Abbreviations: na = neural arch, ns = neural spine, s = sacral, sd = sacrodorsal, sy = sacral yoke, tp = transverse process.

I.4 Caudal vertebrae (CM- 2, 4, 8, 176, 378, 386- 389, 401- 404, 420- 422, 439, 447, 448, 454, 469, 491, 518, 525, 569, 575, 583, 585, 596, 601, 613, 614, 627, 646, 653, 688, A1, A3; MC-M 950, M 1403, M 1414, M 1800, M 2483, M 3589, M 4028, M 4119, MN 30, MN 36, PSP 5; MDE-C2.82.8, C3 28, C3 35, C3 36, C3 106-C3 110, C3 249, C3 257, C3 337, C3 343, C3 344, C3 416, C3 504, C3 507, C3 611, C3 655, C3 775, C3 823, C3 881, C3 967, C3 980, C3 990, C3 995, C3 996, C3 1128 , C3 1136, C3 1145, C3 1152, C3 1152, C3 1156, C3 1176, C3 1177, C3 1183, C3 1191, C3 1197, C3 1282, C3 1300, C3 1414, C3 1421, C3 1551, C3 02.102, C3 02.137, C3 05.58, C3 08.55, C3 08.59, RC 10-9, Vil 39; FSL 530515; MHN.AIX.PV.1999.76, 77, MHN_AIX_PV.2000.7, MHN.AIX.PV.2001.12, 13, 16, 20, 112)

In the first caudal vertebrae, the centra are platycoelous, short and as wide as high, with heart-shaped articular surfaces and a rounded ventral keel (Figure 4.19). The centra retain the same shape but they are amphicoelous, increased in length and become gradually higher than wide through the proximal to middle caudal series. Subsequently, the centra become smaller in diameter but still proportionally lengthen along the tail. The lateral wall of the caudals is compressed, concave anteroposteriorly, and then becomes flatter in succeeding caudal vertebrae. Ventrally, the ventral keel is expanded anteriorly and posteriorly and inclined upward to form the haemapophyseal facets for the chevrons. The anterior haemapophyseal facet for the haemal arch is less prominent than the posterior one. The haemapophyseal facets become insignificant in posterior caudal series. A ventral groove is present in the middle caudal series and becomes less prominent in distal caudals.

The anterior caudal vertebrae bear transverse processes on the lateral wall of the centrum below the neurocentral suture. The transverse processes are laterally projected more or less horizontally and slightly curved cranially. The transverse processes decrease gradually in size down the series and eventually disappear in more posterior caudals where they become only an axial ridge on the dorsal half of the centra.

The neural arch of caudal vertebrae is low and narrow. The neural canal is small, rounded in cross-section. In proximal caudals, the prezygapophyses are prominent and extended anterodorsally and the articular facets are steeply inclined and face medially. The articular facets become vertical, narrower and elongate cranially down the caudal series. The postzygapophyses of the caudal vertebrae are less prominent than those of the preceding vertebral series. Through the caudal series, the articular facets become smaller, narrowly spaced and eventually merged as a single protuberance on the posterior margin of

the neural spine. The neural spine is still large, thick, straight and extended dorsally in anterior to middle caudal vertebrae. The neural spine becomes shorter and narrower and inclined caudally in successive caudals and the spine tends to disappear in most distal ones.

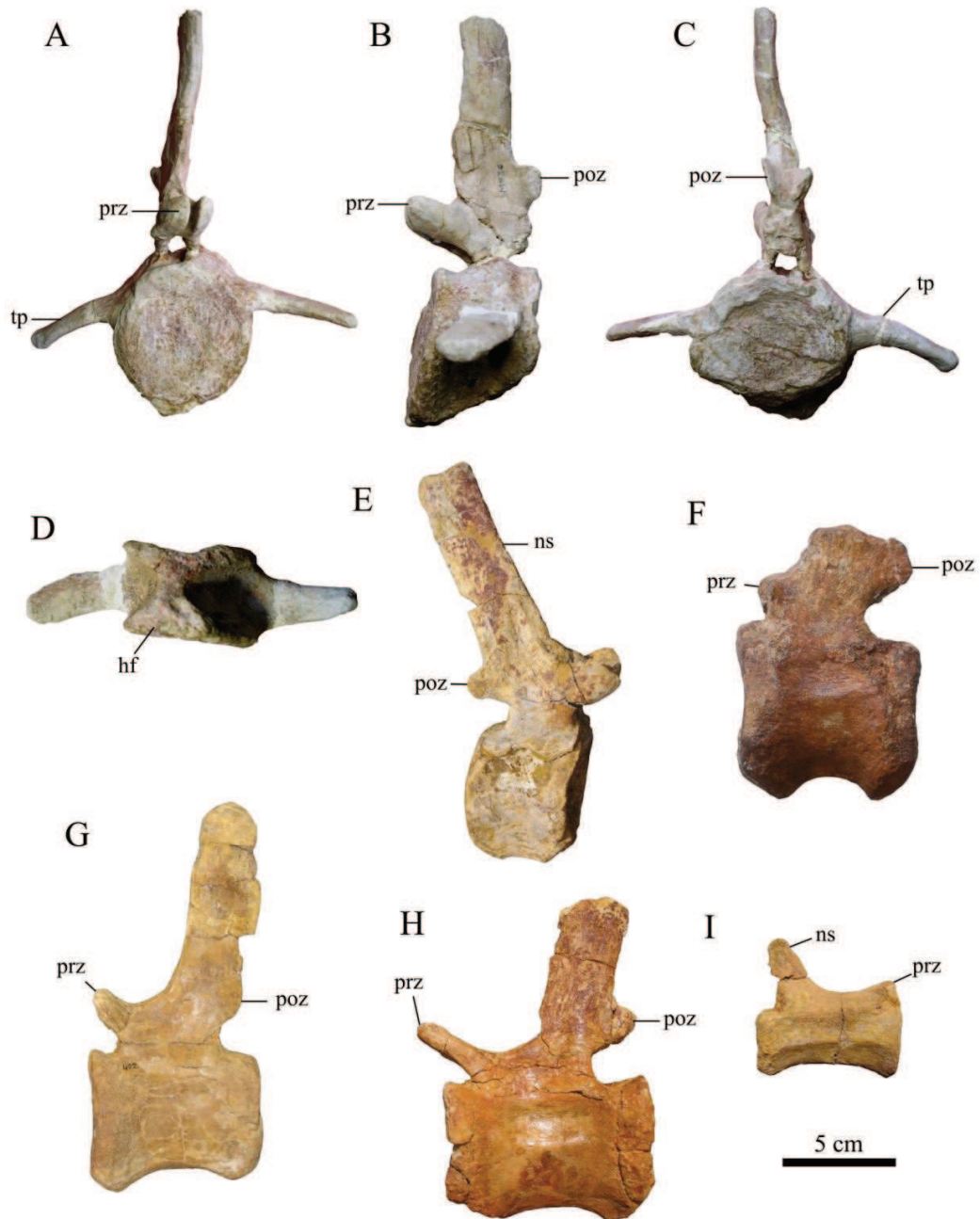


Figure 4.19 Anterior caudal vertebrae, MC-MN36 in anterior (A), left lateral (B), posterior (C), ventral (D) views and CM-469 (E) in right lateral view. Middle caudal vertebra MDE-C3 108 (F) in left lateral view. Mid-posterior caudal vertebrae CM-402 (G) and CM-646 (H) in left lateral view. Posterior vertebra CM-601 (I) in right lateral view Abbreviations: hf = haemapophyseal facet, prz = prezygapophysis, poz = postzygapophysis, tp = transverse process.

The chevrons of *Rhabdodon* (CM 355, 408, 409, 487, 555; FSL 300.005; MC-M 2, 3,543, 845, 2378) (Figure 4.20) were mostly found isolated from different localities. Thus, the total number of chevrons in a series of caudal vertebrae cannot be determined. The first chevron probably begins between the first and the second caudal vertebrae but its size should be insignificant because of the diminished haemapophyseal facets on the ventral surface of the most anterior caudal vertebrae. The chevrons are of various lengths. The chevron length presumably increased from anterior to mid-caudal vertebrae then decreased and the chevrons finally disappeared down the tail. However the transition in size along the series cannot be exactly defined and hypotheses can be made on the basis of shape and the haemapophyseal facets of the caudal vertebrae. In spite of the size, there are only few differences between the chevrons along the caudal series.

The proximal end of the chevrons is expanded transversely. The articular facet is unequally bisected, the anterior surface for the preceding caudal centrum being smaller than the posterior surface for the following one. A shallow axial groove separates two lateral bosses on the dorsal surface (Figure 4.20 B), these bosses go beyond the lateral walls of the chevrons in some specimens (MC-M2378, CM-409, CM-487). The haemal canal is oval and not very high compared with the chevron length. The haemal canal is completely enclosed by the laterally compressed haemal arches which are reunited to form the chevron spine below the canal. Posteriorly, below the haemal canal the chevron is concave and the haemal arches continue as two ridges to the middle of the chevron spine. The haemal spine is compressed transversely. The distal end is flat, slightly expanded and curved caudally. In some specimens (CM-487 and FSL 300.005) the chevrons are compressed axially, straight and the lateral surfaces are rounded. This variation of the chevrons could be related to the different positions in the caudal series.

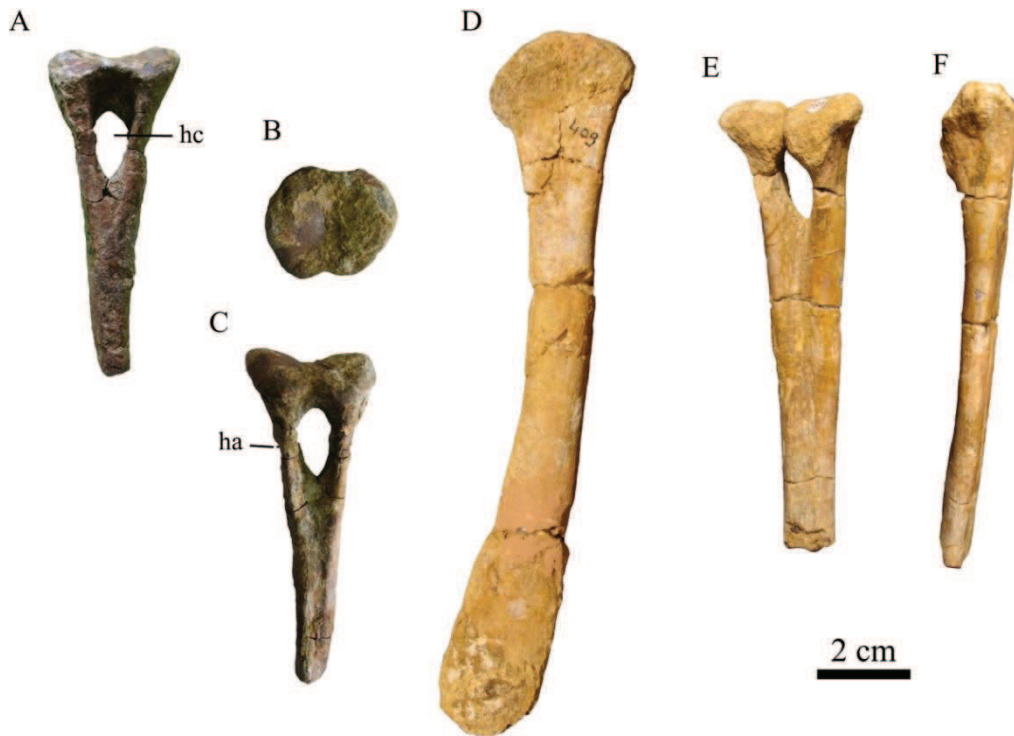


Figure 4.20 Chevrons, MC-M 543 in anterior (A), dorsal (B), posterior (C) views, CM-409 in right lateral view and CM-487 in posterior (E) and right lateral (F) views. Abbreviations: ha = haemal arch, hc = haemal canal.

1.5 Ossified tendons

The ossified tendons are usually found fragmentary and it can hardly be recognized whether they belong to *Rhabdodon*. The best occurrence of ossified tendons in *Rhabdodon* has been described by Chanthasit et al. (in review) on the basis of the ossified tendons found associated with the new partial skeleton of *Rhabdodon priscus* from the Vitrolles-Couperigne locality. The ossified tendons are angular to rounded rods with striations along the length. They are distributed along the vertebral column, particularly concentrated on the posterior dorsal vertebrae and sacrum. Both epaxial and hypaxial ossified tendons are present in the caudal series where we can see them on neural spines (Figure 4.21) and chevrons (See fig.8G Chanthasit et al., in review) respectively. Moreover, as in figure 4.21, the presence of the ossified tendons on the mid-posterior caudal vertebrae indicates that the ossified tendons of *Rhabdodon* probably were present up to the posterior part of the vertebral column. The arrangements of ossified tendons are difficile to discern. They seem to be divided in two groups of tendons. The first group is represented by longitudinal

tendons running down the vertebrae with a small degree of inclination and the second group represented by relatively short tendons crossing obliquely as present on the neural spine.

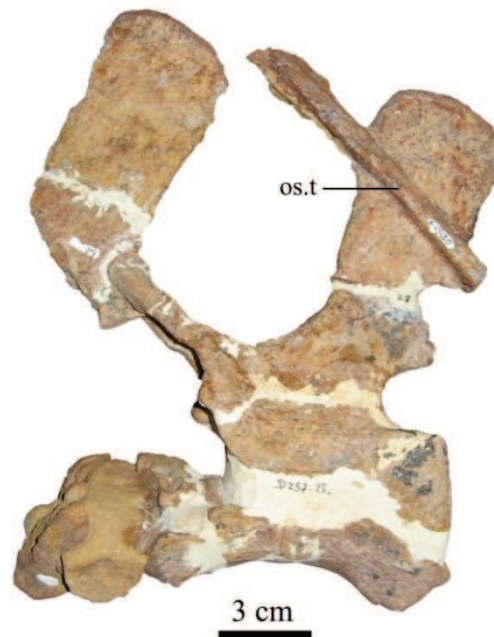


Figure 4.21 The ossified tendon is oriented obliquely on the neural spine of the mid-posterior caudal vertebra. Abbreviation: os.t = ossified tendon.

II. Appendicular skeleton

II.1 Pectoral Girdle

II.1.1 Scapula (CM-611, MC-M 3036, MDE- C3 105, C3 116, C3 321, C3 412, C3 700, C3 713, C3 1013, C3 1295, C3 1559, C4 115, D 200)

The scapula of *Rhabdodon* is characterized by its remarkable posterodorsal expansion (Figure 4.22), however it is less marked in a juvenile individual (MC-3036). The posterodorsal border is arched. At the constricted neck, above the ventral articulation, the anterior and posterior rims remain more or less parallel up to the mid-length of the scapula before the posterior border gradually curves downward and diverges from the anterior one. The anterior rim is nearly straight along all its length but it also slightly curves upward at the distal end forming a rounded angle with the dorsal border.

The scapula is slightly bowed anteroposteriorly as it follows the outer contour of the rib cage. The anterior and posterior edges are thin and rounded while the dorsal edge is slightly thickened and rugose. From the neck, the scapula is thickened and flared to form the articulation with the coracoid. The lateral surface of the scapular blade is continually convex up to the neck then it is concave as a diagonal depression between the glenoid region and

the acromial process to form the deltoid fossa. The glenoid forms an acute angle with a sharp caudally curved posteroventral margin from the neck and it is ventrally thickened and concave to form a part of the glenoid cavity. The coracoid articular surface is convex anteroposteriorly and particularly extended anteriorly where the acromial process is formed. The coracoid articular surface covers more than 70% of the ventral border of the scapula.

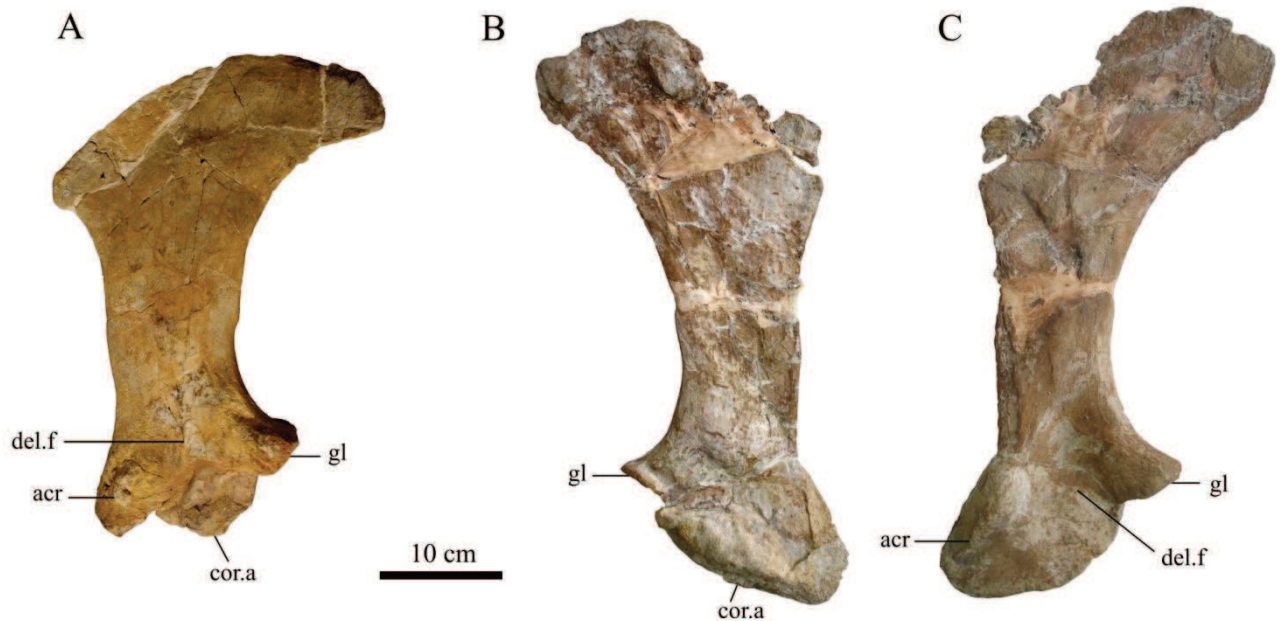


Figure 4.22 Left scapulae, CM-611 (A) lateral view and MDE-C3 1013 in medial (B) and lateral (C) views. Abbreviations: acr = acromial process, cor.a = coracoids articulation, del.f = deltoid fossa, gl = glenoid.

II.1.2 Coracoid (CM-534, 612; MC-2567, MDE-C3 394, C3 457, C3 735, C3 994, C3 1549)

The coracoids of *Rhabdodon* are mostly not well preserved except for a nearly complete left coracoid CM 612 (Figure 4.23). The coracoid forms a thin body with a transversely thickened rugose scapular articulation and a well developed sternal process.

The swollen and rugose articular surface for the scapula is expanded on the dorsomedial side of the coracoid. Next to the scapular articulation, the thickened glenoid region is tilted laterally to continue the arc of the glenoid of the scapula. Just below the glenoid, the smooth posterior rim of the coracoid is abruptly curved and joins the ventral edge to form a hook-like sternal process. The ventral and anterior rims are rugose, slightly thickened and give a rounded outline to the coracoid. The medial surface is concave. The

lateral surface shows distinctively a thick rugose muscle scar on the anterior border. The round coracoid foramen is located beneath the articular surface for the scapula and approximately centered between the anterior and posterior borders. Medially, the coracoid foramen runs posterodorsally, passes through the coracoid and appears to be more open in lateral view.

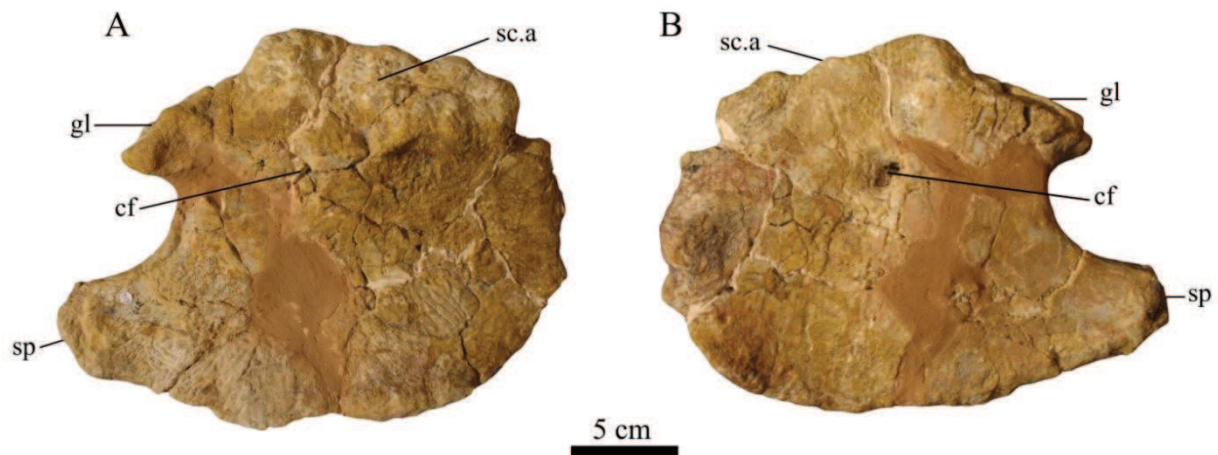


Figure 4.23 Left coracoid CM-612 in medial (A) and lateral (B) views. Abbreviations: cf = coracoid foramen, gl = glenoid, sc.a = scapula articulation, sp = sternal process.

II.2 Forelimb

II.2.1 Humerus (CM-451, 472, 597; MC-M 29, M 3925, M 4765; MDE-C3.993, C4.9; MNHN-34, MNHN-035)

The humerus of *Rhabdodon* is robust with a well-developed deltopectoral crest. The deltopectoral crest runs along the proximal half on the lateral rim of the humerus. The deltopectoral crest is expanded and more rugose distally while it decreases in width and becomes smoother toward the head. The deltopectoral crest turns anteromedially, forming the lateral limit of an anterior concave surface (bicipital sulcus) on the proximal part of the humerus. Immediately below this crest, the humeral shaft is constricted, narrower than the proximal part. However, in the left humerus CM-597 (Figure 4.24 F), the humeral shaft is not very slender proportionally compared to the width of the proximal and distal parts as in a humerus of *Rhabdodon* from Vitrolles-Couperigne (Chanhasit et al., in review).

The humerus is curved medially and the proximal end of the humerus is transversely expanded. The proximal end is also anteroposteriorly thickened particularly at the mid-width to form a prominent boss of the humeral condyle on the posterior surface. The humeral condyle is rounded and protrudes posteriorly.

The distal part of the humeral shaft is extended mediolaterally, slightly bowed and twisted anteriorly relative to the upper part. The rounded, unequal articular condyles are developed on the distal articular surface. The ulnar and radial condyles are separated anteriorly by a narrow moderately developed coronoid fossa (flexor groove) and posteriorly by a broad shallow olecranon fossa (extensor groove). The ulnar condyle is slightly larger and extends below the radial condyle.

II.2.2 Ulna (CM-481, MDE-C3 1171, C3 1196, RC 4.01)

The ulna of *Rhabdodon* is proximally dominated by a triangular extended head with a prominent olecranon process (Figure 4.25). The blunt, rugose olecranon process projects dorsally above the ulna and the dorsal surface articulates with the humerus. Cranially to the olecranon process, the rugose surface is extended, flattened and inclined forward to form the narrow cranial coronoid process. This cranial process continues as a round, narrow, dorsoventrally curved ridge down to the ulnar shaft. The lateral coronoid process projects laterally to the olecranon process. The lateral coronoid process is larger than the cranial coronoid process and forms a round ridge which is more posteriorly curved distally. Laterocranially, between the cranial and lateral coronoid process, the proximal shaft form a concave surface to receive the proximal head of the radius. This proximal concave surface of the radii of both *Rhabdodon* and *Zalmoxes* is shallower and less prominent than that of *Tenontosaurus* as the cranial coronoid process of the latter is prolonged more cranially from the olecranon process.

The ulnar shaft is narrow and transversely compressed. Distally, the ulnar shaft is slightly expanded and mildly bent mediocaudally. At the distal end, a shallow depression is present craniomedially for the distal end of the radius.



Figure 4.24 Left humerus MC-4765 in anterior (A), lateral (B), dorsal (C), posterior (D) views. Left humerus CM-451(E) and CM-597 (F) in anterior view. Abbreviations: dpc = deltopectoral crest, hc = humeral condyle, ra.c = radial condyle, ul.c = ulnar condyle.

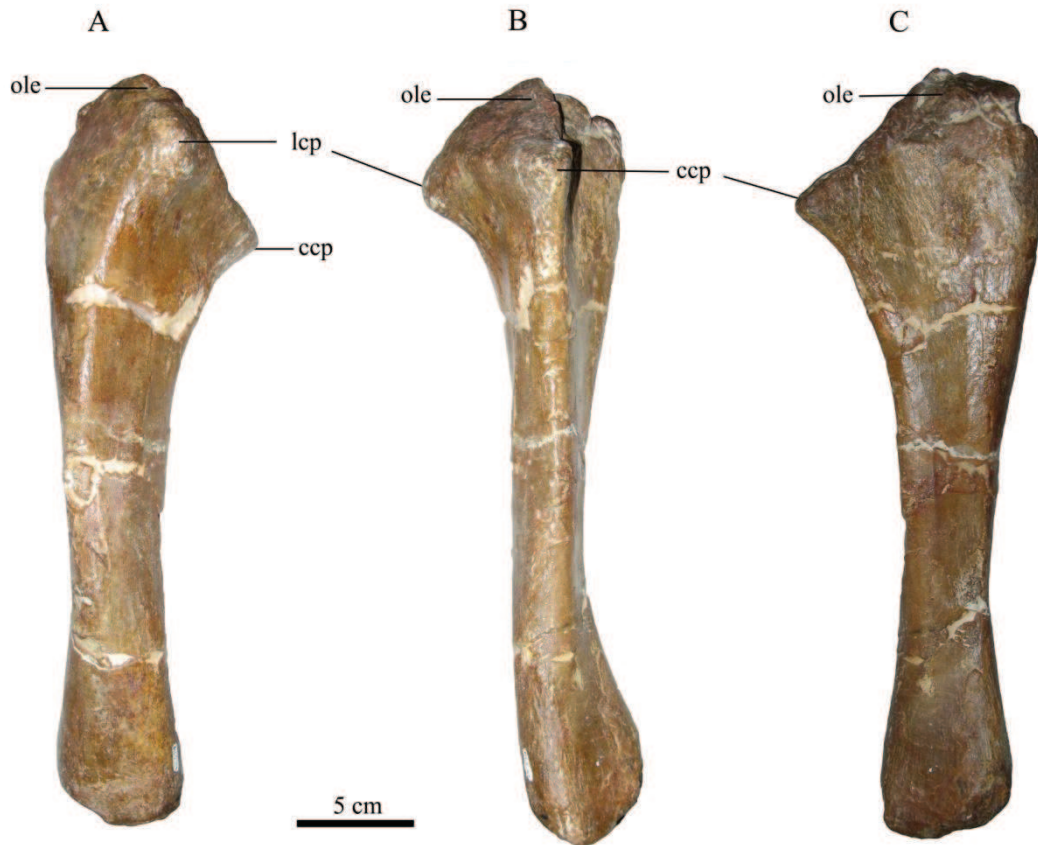


Figure 4.25 Right ulna MDE-RC 4.01 in posterolateral (A) anterior (B) and medial (C) views. Abbreviations: ccp = cranial coronoid process, lateral coronoid process, ole = olecranon process.

II.2.3 Radius (CM-610, 629; MDE-C3.118, C3.1003)

The radius is a straight, long bone with expanded extremities (Figure 4.26). The shape of the head of the radius varies from round to oval as in *Tenontosaurus* (Foster, 1990). The radial head is rounded in MDE-C3.1003 while in CM-610, 629 and MDE-C3.118, the head is laterally compressed with the tapered end pointing cranially. The proximal articular surface is slightly concave and rugose. Only a short distance below the compressed proximal articulation, the radial shaft bulges medially, becomes round and forms a sub-triangular cross section. On the other hand, the radial shaft of MDE-C3.1003 is rounded and slender almost along the whole radius length.

A shallow ridge is present on the medial surface and ends posteriorly as a small rugose boss at the distal end. The distal part of the shaft is flattened and largely flared so that it is broader than the proximal head in lateral view as shown in CM-629 and C3-118, whereas this distal expansion is less marked in CM-610 and MDE-C3 1003. The distal end

is slightly twisted laterally relative to the proximal end. The distal articular surface is gently convex. The anterior border of the distal articulation is narrower and extended more distally than the posterior one.

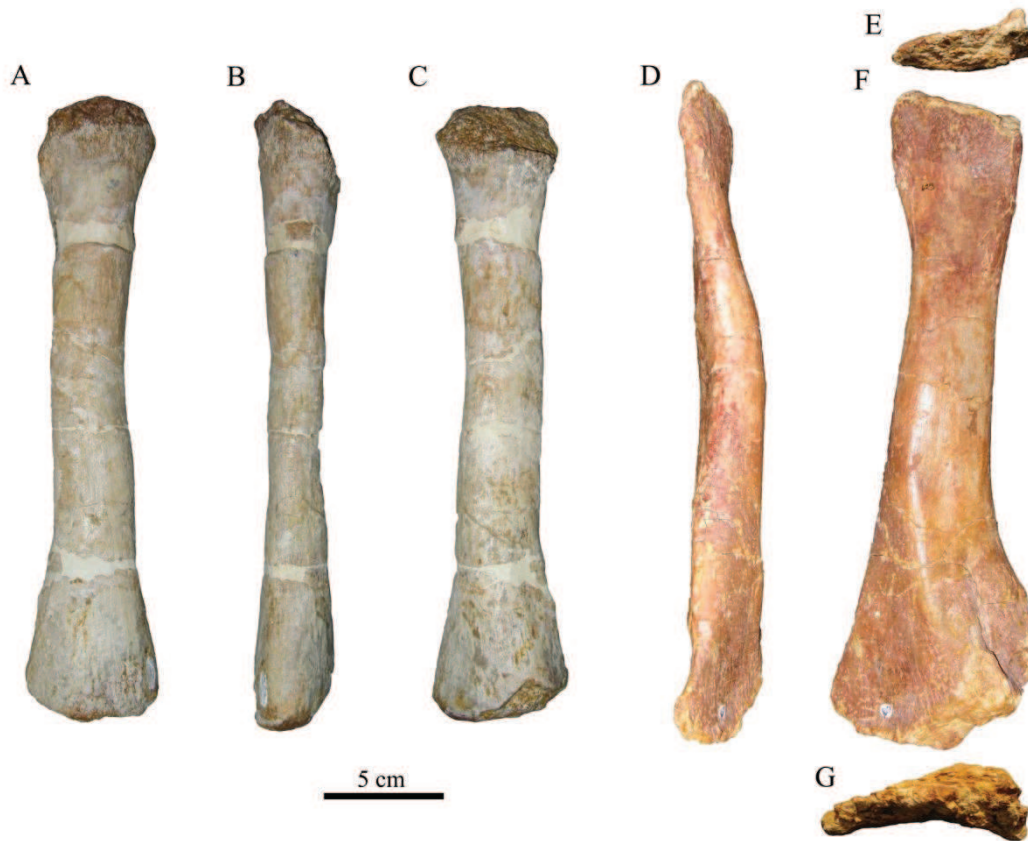


Figure 4.26 Right radius CM-C3.1003 in lateral (A), anterior (B) and medial(C) views. Right radius CM-629 in anterior (D), dorsal (E) medial (F) and ventral (G) views.

II.2.4 Metacarpals and digits (CM 399, 663, 702; MC-M 4232, MDE-C3 597)

The manus of *Rhabdodon* is hardly known. A phalangeal formula cannot be provided because only a few hand elements are found (Figure 4.27).

Metacarpals MDE-C3.597 and CM-702 (Figure 4.27 A, B) are elongate and dorsoventrally flattened. The proximal end is expanded more significantly than the distal one. The shaft is contracted with curved lateral margins. The metacarpal CM-702 is more or less symmetrical in shape. The distal end has a symmetrical articular surface which extends dorsoventrally. The proximal end is not strongly curved as in MDE-C3.597. It could be interpreted that the metacarpals CM-702 and MDE-C3.597 belong to digits III and II respectively.

Metacarpal CM-399 (Figure 4.27 D) is short, robust and dorsoventrally compressed. The proximal and distal ends are slightly expanded. The proximal articular facet is sub-circular in outline. The surface is slightly concave and inclined laterally. The distal end has a rounded articular surface which extends dorsoventrally. The ventral surface of the shaft is flat. From comparison with the metacarpals of other ornithopods, this specimen is metacarpal V.

Metacarpal CM- 663 is proportionally longer than CM-399. The proximal and distal ends are expanded while the shaft is very constricted in the middle. The proximal articular surface is large, rounded dorsoventrally and inclined inward. The shaft is dorsoventrally compressed. The distal end is incomplete. Metacarpal CM-663 probably belongs to digit IV.

The morphological features of the metacarpals suggest that the manus of *Rhabdodon* did not form a compact unit or was packed together only with a small contact area on the proximal end.

An ungual phalanx MC-M 4232 is short, broad and dorsally convex. The proximal surface is concave. The proximal articulation is extended distally for a short distance, then the medial and lateral edges are expanded as a ledge on each side to support the nail groove. The nail groove is not well defined in this specimen. The lateral and medial ledges are shortly convergent at the distal tip. The ventral surface is concave and asymmetrically divided by a prominent ridge which lies obliquely to the long axis of the ungual.

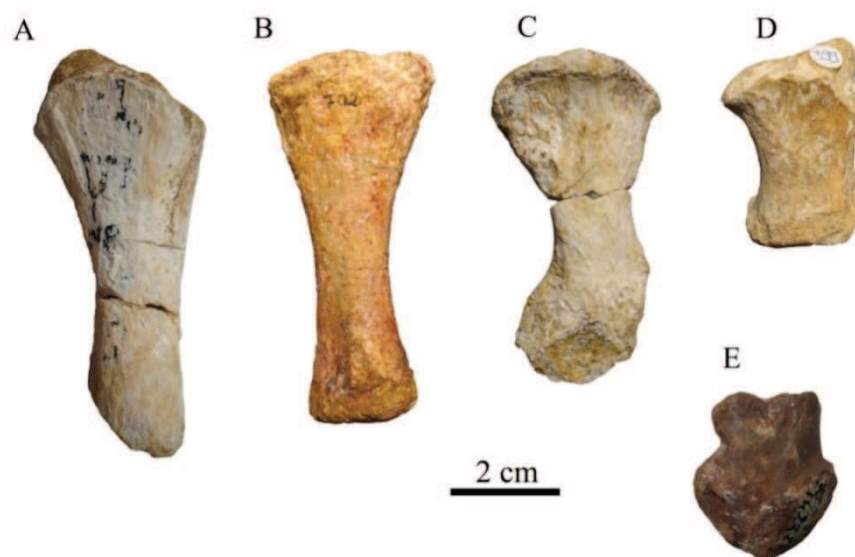


Figure 4.27 Metacarpals, MDE-C3.597 (A), CM-702 (B), CM-663(C), and CM-399 (D) in dorsal view. Ungual phalanx MC-M 4232 (E) in dorsal view.

II.3 Pelvic Girdle

II.3.1 Ilium (CM-377, 397, 531, 567, 635, 686; MC-MOB 3, MOB 59, PSP 3; MDE-C3.1050, D157.28)

The ilium has a long ventrally curved anterior process (maximum 38 % of the total length of the ilium). The anterior process is strongly arched in CM-531, CM-635, MC-MOB 59 while those of CM-377, 397, 567, 686 and MDE-D157.28 are less arched (Figure 4.28), however the tip of the anterior process does reach the same level as the pubic peduncle in lateral view as it does in *Tenontosaurus* (Forster, 1990). This anterior process is slightly twisted laterally and the anterior end is expanded ventrally in some specimens (CM-397, MDE-D157.28). Medially, the main blade of the ilium is slightly concave. This concave surface is narrowed anteriorly and eventually becomes a ridge with a sub-triangular cross section on the anterior process.

The striated, raised dorsal margin of the ilium is narrowed on the anterior process but it is thickened toward the iliac blade. The dorsal edge is sub-equally thick and it is neither flared nor significantly everted as in the ilium of *Zalmoxes*. The dorsoposterior margin of the ilium is laterally thickened and rugose. The posterior margin curves downward to join the ventral border where the brevis shelf is very poorly developed. In lateral view, the dorsal border of the ilium is approximately straight above the acetabulum and it is slightly convex on the postacetabular blade. In dorsal view, the ilium is slightly sinuous.

The pubic peduncle extends anteroventrally, forming the anterior rim of the acetabulum, and the pubic peduncle is triangular in cross section. The acetabulum forms a round, quite deep embayment without a supraacetabular rim. The acetabulum is limited posteriorly by a well developed ischial peduncle. The ischial peduncle is laterally expanded as a thick, rounded boss with a rugose ventral surface to attach with the ischium. The ischial peduncle is ventrally rounded and curved upward to meet the ventral margin of the postacetabular blade.

Medially, the ilium bears a rugose depression covering all the ventral portion of the iliac blade which indicates the attachment scars of the sacral ribs. This rough depression extends initially from near the anterior tip of the pubic peduncle to the posterior rim of the postacetabular blade. The attachment scar is limited by an irregular curved thin ridge approximately at the mid height of the iliac blade.

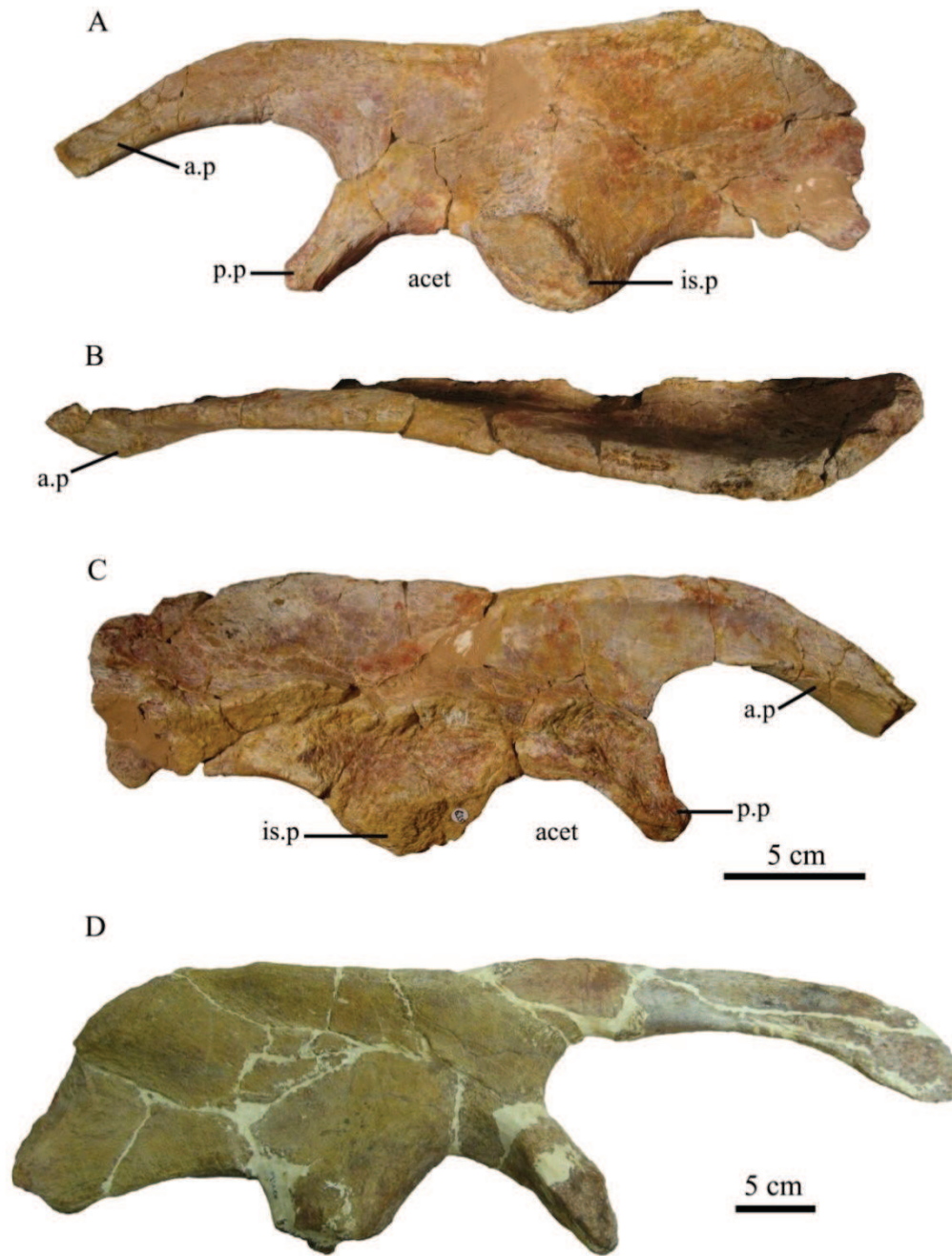


Figure 4.28 Left ilium CM-635 in lateral (A), dorsal (B) and medial (C) views. Right ilium MDE-D157.28 (D) in lateral view. Abbreviations: acet = acetabulum, a.p = anterior process, is.p = ischial peduncle, p.p = pubic peduncle.

II.3.2 Pubis (CM-630; MDE-C3.02.104, C3.04.95)

The pubis of *Rhabdodon* consists of a pre-pubic process with a large pubic foramen and a post-pubic rod although the latter is broken and incompletely preserved in all specimens.

The pre-pubis (Figure 4.29) forms the anteroventral rim of the acetabulum. The proximal articulation of the pubis is transversely expanded particularly at the rugose surface for the acetabular margin. Dorsocranially to the acetabular margin, there is a rugose, rounded puboiliac articular surface to which the pubic peduncle of the ilium is attached. Ventral to the acetabular margin, a small rounded area for the ischium is present above the proximal post-pubic rod. The post pubic rod is broken, only the proximal part is preserved in CM-630. This rod seems to be thin and tapered, however its length could not be estimated.

From the articular area, the pre-pubic process extends cranially and is slightly bent medially at the distal end. The pre-pubic process of CM-630 is laterally compressed and becomes thinner distally, while in MDE-C3.02.104 and MDE-C3.04.95, the pre-pubic process is less compressed, narrower and oval in cross-section at the distal end (Figure 4.29 C, D). The pre-pubic process is dorsally curved. Although the pre-pubic process of the *Rhabdodon* skeleton from Vitrolles (Chanthasit et al., in review) shows a ventrally expanded border at the distal end, in lateral view the dorsal and ventral borders are more or less parallel all along the pubic length in three pubes described here.

A deep oval pubic foramen is situated below the articular surface for the ischium. The pubic foramen is completely enclosed and canted lateroventrally.

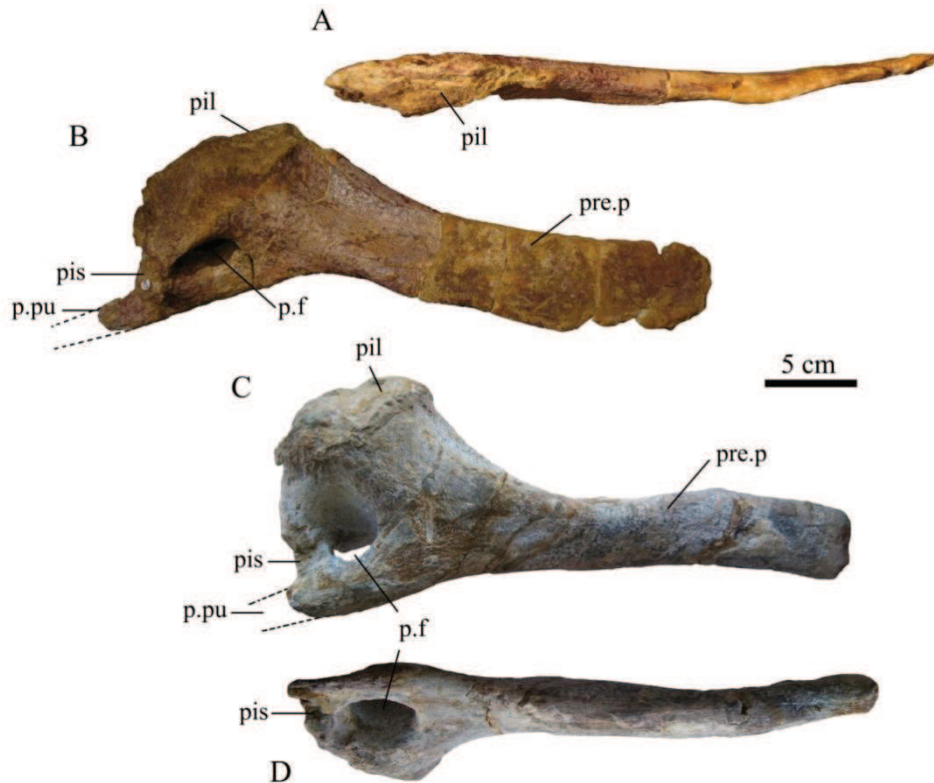


Figure 4.29 Right pubis CM-630 in dorsal (A) and lateral (B) views. Left pubis MDE-C3.04.95 in medial (C) and ventral (D) views. Abbreviations: p.f = pubic foramen, pil = puboiliac articular surface, pis = puboischial articular surface, p.pu = post-pubic rod, pre.p = pre-pubic process.

II.3.3 Ischium (CM-398, 433, 565, 566; MC- M 24, M 1252, M 1960, M 2111, M 3180, M 4821, MOB-sn, PSP 2; MDE- C3.115, C3.167, C3.439, C3.722, C3.991, C3.02.152, C3.08.63)

The ischium is a long shaft of bone with Y-like separated proximal articular ends for the ilium and the pubis (Figure 4.30). Two articular peduncles are separated by a thin-edged, embayment with a concave lateral surface which forms the posteroventral rim of the acetabulum. The iliac peduncle is distinctly larger than the pubic peduncle. The iliac peduncle of the ischium is laterally compressed, directed dorsally and ends with a slightly concave oval articular surface. The pubic peduncle is more slender, elongate, directed ventroanteriorly and terminated by a sub-circular articular facet.

Distally to these two peduncles, the ischial shaft is gradually tapered for a distance and then the ventral margin forms a flared tab-like obturator process. The obturator process projects ventromedially and is situated in the proximal half of the ischium. The ischial shaft

is laterally compressed and thickened posteriorly to the obturator process and then flattened at the distal shaft. It is broad in its proximal part and approximately parallel-sided in the middle then the ventral margin gradually expands up to the thickened rugose distal end. The dorsal margin of the ischial shaft is rounded but it is sharpened at its distal end, conversely to the ventral margin which is narrow, sharp on the proximal half and thickened on the distal portion. The lateral surface of the shaft is convex while the medial surface is slightly concave. Some ischia (CM-398, 433, 566) are bowed anteroposteriorly in the distal half and some (CM-565, MC-1960, MC-MOB-sn, MDE-C3.02.152 (Figure 4.30D) have an approximately straight ischial shaft. Both straight and bowed shafts are possibly found in the same individual in some cases, for example the ischia from the *Rhabdodon priscus* skeleton of Vitrolles-Couperigne (Pincemaille-Quillévére, 2002) and those of *Tenontosaurus* (Forster, 1990).



Figure 4.30 Right ischium CM-398 in lateral (A), ventral (B) and medial (C) views. Left ischium MDE-C3.02.152 (D) in medial view. Abbreviations: il.p = iliac peduncle, ob.p = obturator process, p.p = pubic peduncle.

II.4 Hindlimb

II.4.1 Femur (CM-287, 519, 543, 608; MC-M 1955, M 3088, MN41, VC8, VC9; MDE-C3.114, C3.146, C3.267, C3.338, C3.349, C3.514, C3.546, C3.739, C3.972, C3.974, C3.978, C3.992, C3.1118, C3.1168, C3.1270, C4.1, D204; MHN.AIX.PV.2008.1.11)

The femur of *Rhabdodon* is robust and bowed anteroposteriorly (Figure 4.31). The medial margin of the femur is concave whereas the lateral one is almost straight. The femoral shaft is anteroposteriorly compressed, however, it is more rounded and curved dorsoventrally in juvenile specimens (CM-287, MC-M 1955, MC-M 3088, MDE-C3.546, MHN.AIX.PV.2008.1.11). The lateral and medial margins of the shaft are rounded. The proximal part of the femur is concave on the anterior surface. Its mid shaft is convex anteriorly, making it subtriangular in cross section.

The hemispheric femoral head is rugose and directed anteromedially. The head is connected to the anteroposteriorly compressed proximal end which expands laterally into large trochanters. The lesser trochanter is oriented anterolaterally and separated from the greater trochanter by a shallow depression on the posterolateral side. The greater trochanter is dominant as a large boss protruding posteriorly. The greater trochanter occupies approximate 70% of the trochanteric area. Laterally the trochanters form a flat to slightly concave surface and are narrowed distally to the femoral shaft.

The pendant fourth trochanter is positioned medioposteriorly on the posterior surface and distally extended slightly beyond the mid length of the femur. The fourth trochanter ends with a rounded hook pointing posteroventrally. A rugose, large, oval depression extends dorsoventrally anterior to the fourth trochanter and this depression is limited by a sharp border on the medial margin of the femur (Figure 4.31C).

The femur is largely expanded distally forming two well-developed distal condyles. These two distal condyles extend posteriorly, showing a boot-like shape in medial view (Figure 4.31C) and they are separated from each other anteriorly by a broad shallow intercondylar or extensor groove and posteriorly by a deeper intercondylar (flexor) groove. The medial condyle is transversely larger but the lateral condyle extends more distally. The lateral condyle includes a condylid which is a long narrow posterior projection and situated medially to the groove for *m. iliofibularis*.

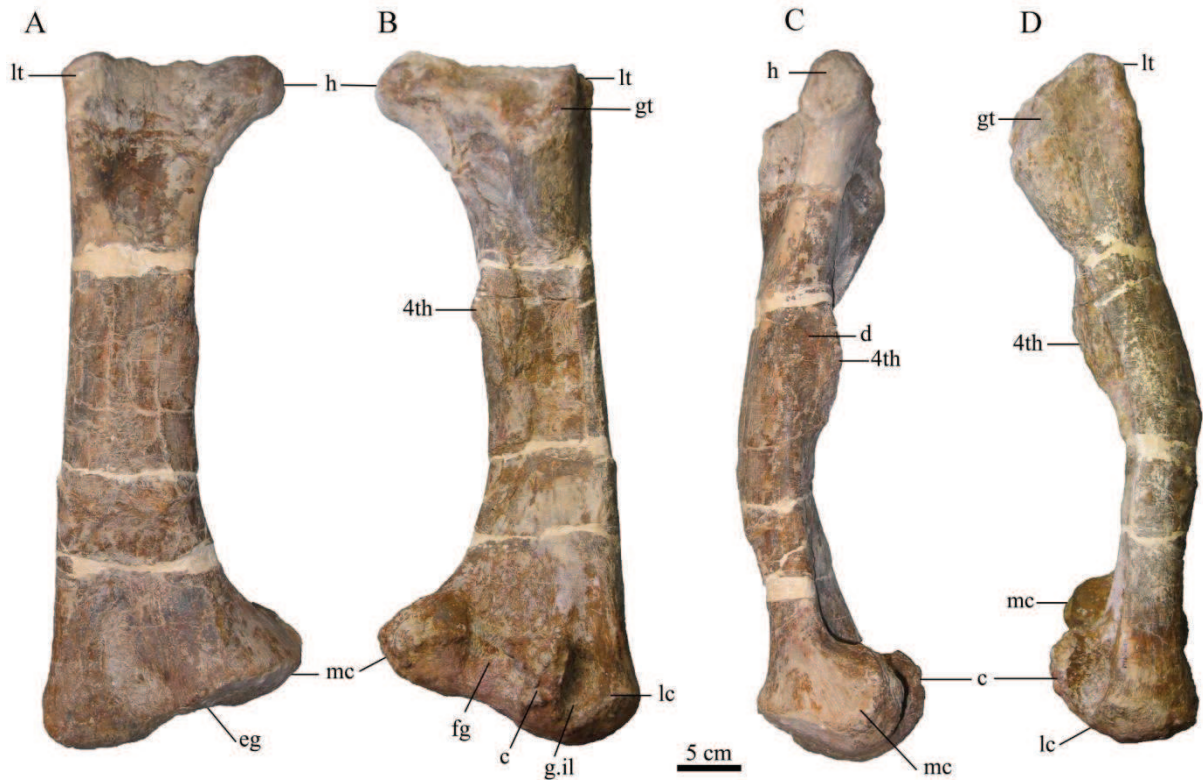


Figure 4.31 Right femur MC-MN 41 in anterior (A), posterior (B), medial (C) and lateral (D) views. Abbreviations: 4th – fourth trochanter, c = condylid, d = depression, eg = extensor groove, fg = flexor groove, g.il = groove for *m. iliofibularis*, gt = greater trochanter, h = femoral head, lc = lateral condyle, lt = lesser trochanter, mc = medial condyle.

II.4.2 Tibia (CM-139, 364, 500, 631; MC-M3115; MDE-C3.112, C3.195, C3.300, C3.305, C3.310, C3.975, C3.983, C3.1129, C3.1189, C3.1194, C3.08.49, C4.06)

The tibia of *Rhabdodon* is a moderately robust long bone with an anteroposteriorly expanded proximal end and transversely expanded distal end (Figure 4.32). It is relatively straight, more slender and shorter than the femur.

The proximal end of the tibia is narrowed anteriorly to form a round-edged cnemial crest which continues distally over only one fifth of the tibial length. Posteriorly to the cnemial crest, the proximal end is widened and forms a lateral condyle which projects laterally and is separated from the posterior end of the proximal articulation by a deep narrow groove. This lateral condyle fits the caudal proximal articulation of the fibula.

Distally from the proximal end, the tibia is tapered and sub-rounded in cross section. The rounded cnemial crest is transformed into a small sharp ridge and extends distally to become the lateral edge of the distal end. The tibial shaft is twisted and lateromedially re-expanded into a broad malleolus and the articulation with the tarsus. The distal end is somewhat separated anteriorly by an open shallow flexor groove. The lateral malleolus of the distal end extends more distally than the medial one and bears a flattened anterior surface for articulation with the distal end of the fibula.



Figure 4.32 Right tibia MDE-C3.1189 in lateral (A), anterior (B) and posterior (C) views. Abbreviations: ast.f = astragalar facet, cn.c = cnemial crest, lc = lateral condyle.

II.4.3 Fibula (CM-667, 677, MC-M 30MOB 62, MOB 85)

The fibula (Figure 4.33) is a long, thin bone with an expanded and laterally compressed proximal end. The proximal end extends anteroposteriorly and the anterior end is thickened. The proximal head is concave medially and convex laterally and shows densely rugose and striated marks. Distal to the proximal end, the fibula tapers to a narrow shaft. The proximal two thirds of two the shaft are convex laterally and slightly concave medially with thin rounded anterior and posterior borders. Distally, the fibula is twisted,

forming a sharp ridge which gradually turns posteriorly from the medial surface. The posteromedial surface is flattened and anterolaterally it is rough and slightly convex where it contacts the tibia. The distal end is slightly expanded transversely, extended posteriorly and slightly thickened to attach to the calcaneum.



Figure 4.33 Left fibula MC-MOB 85 in lateral (A), medial (B), anterior (C) and posterior (D) views. Abbreviation: tib.f = tibial facet.

The tarsus of *Rhabdodon* is poorly known, probably because these small bones are difficult to identify in the field so that it is possible that the tarsus is missed during the excavations. Nevertheless, a calcaneum was found fused to a fibula of *Rhabdodon* (MHN_AIX_PV.2008.1.18) discovered at the Jas-Neuf Sud site. The calcaneum is a small nearly square bone with a posterior concave surface and it is thinner at the proximal articulation with the fibula than at the distal end.

II.4.4 Metatarsals and digits (CM-116, 449, 590, 600, 632, 634; MC-M 36, M 37, M 221, M 541, M 570, M 814, M 874, M 1222, M 2812, M 4232, M 4729, MOB 9, MOB sn; MDE-C3.374, C3.510)

The pes of *Rhabdodon* consists of a compact unit of tightly fitting metatarsals and the digits terminate with large hoof-like, pointed unguals.

Four different forms of metatarsals can be distinguished among all specimens. This indicates that the pes of *Rhabdodon* consists of at least four packed metatarsals or four digits. In CM-632 and MDE-C3.510, the metatarsal is short and compressed laterally and expanded dorsoventrally at both proximal and distal ends (Figure 4.34 A). The shaft is strongly constricted. The distal end is rounded. The lateral surface is flat. The medial surface has a muscle scar on the proximal part of the shaft to attach to the adjacent metatarsal. Both these specimens are interpreted as metatarsal I.

Metatarsals CM-116, CM-590, CM-634 are considered as metatarsals II. The proximal end of metatarsal II is laterally compressed and markedly expanded dorsoventrally beyond its shaft (Figure 4.34C). The proximal end is thickened in the dorsal part and thin in the ventral part. The proximal surface is convex dorsoventrally. The shaft is strongly curved dorsally and contracted from the proximal end then it is re-expanded up to the distal articular condyle. The shaft is slightly divergent from metatarsal III in its distal portion (Figure 4.34D).

MDE-C3.374 and MC-M 874 can presumably be identified as metatarsals III. Metatarsal III is elongate, straight and proportionally the longest metatarsal. The proximal end is dorsally expanded, more so on the lateral border than on the medial one, and the lateral surface is proximally concave to fit metatarsal II. Ligament scars are markedly present on both sides of the shaft. The distal articulation is rounded in lateral view and the two distal condyles are more or less symmetrically divided and sub-equal in size.

Metatarsal CM-449 has an irregularly twisted shaft. It is scarred and concave on the medial surface while it is rather smooth and rounded on the lateral side. The shaft is slightly bowed laterally away from the neighboring metatarsal at the distal end. Metatarsal CM-449 ends with an oblique, rounded distal articular condyle. This specimen could be interpreted as metatarsal IV.



Figure 4.34 Right metatarsal I MDE-C3.510 (A) in medial view. Right metatarsal II CM-634 in medial (B) and dorsal (C) views. Right metatarsal III MC-M 874 in dorsal (D) and lateral (E) views. Left metatarsal IV CM-449 in lateral (F), dorsal (G) and medial (H) views.

A phalangeal formula for the pes of *Rhabdodon* cannot be suggested since all phalanges were found isolated. The phalangeal count of *Tenontosaurus* is 2-3-4-5-0 as in *Hypsilophodon*, while the pes of *Iguanodon* and *Ouranosaurus* has a 0-3-4-5-0 phalangeal formula. The morphological features of the digits as well as the number of the metatarsals of *Rhabdodon* are comparable to those of *Tenontosaurus*. It could be suggested that *Rhabdodon* has the same phalangeal count as *Tenontosaurus*, which is 2-3-4-5-0.

The proximal ends of all phalanges are concave and divided by a median ridge into two depressions. The phalanges are slightly compressed dorsoventrally and end with an expanded saddle-shaped distal surface. The ventral surface is slightly arched and wider than the dorsal one. The proximal part of the ventral surface carries a scarred area for the insertion of the flexor tendon. The first phalanx is massive and does not bear a dorsal process on the proximal end as in other phalanges (Figure 4.35 A, B). The following

phalanges are shorter and smaller distally (Figure 4.35 D-F). The proximal articulation is well-developed and deeply concave as compared with the first phalanx. The proximal and distal articular surfaces are limited, with everted margins. The depression on the distal articulation is continued dorsally to receive the dorsal process of the next phalange

The ungual phalanges of *Rhabdodon* are arched proximodistally, broad, dorsally convex and distally pointed (Figure 4.35 G-I). The proximal surface is concave and widened ventrally. The proximal articulation is slightly contracted and extends distally for a short distance, then the nail grooves are developed along the ungual sides. The nail grooves are supported by the medial and lateral ledges which converge at the distal tip. The medial and lateral edges are also prolonged and pointed proximally so the unguals are arrow-like in outline. The ventral surface is concave and densely scarred on the proximal half.

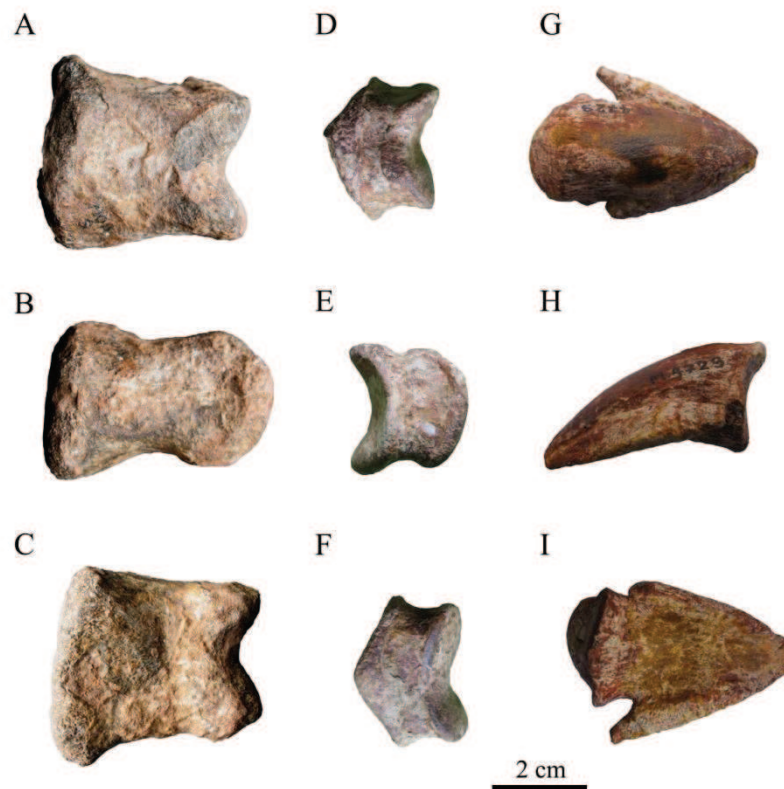


Figure 4.35 Proximal phalanx MC-MOB-sn (A-C), distal phalanx MC-1222 (D-F) and ungual phalanx MC-4729 (G-I) in dorsal (top), lateral (middle) and ventral (bottom) views.

Most of the postcranial material referred to *Rhabdodon* described above was found isolated and originated from various localities. This poses a problem for the reconstruction of this animal. Fortunately, among the recently discovered vertebrate remains at the Vitrolles-Couperigne locality, there is a new partial skeleton of *Rhabdodon priscus*, which is the second individual of *Rhabdodon* from this site. The description of this new skeleton and the faunal diversity at the Vitrolles-Couperigne locality are described in the following paper.

4.3 New partial articulated skeleton of *Rhabdodon priscus* (Dinosauria: Ornithopoda) from the Late Cretaceous of Vitrolles-Couperigne, Bouches-du-Rhône, southern France.

(in review, Bulletin de la Société géologique de France)

New partial articulated skeleton of *Rhabdodon priscus* (Dinosauria: Ornithopoda) from the Late Cretaceous of Vitrolles-Couperigne, Bouches-du-Rhône, southern France.

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Keywords – Dinosauria, Ornithopoda, Rhabdodontidae, Late Cretaceous, southern France

Abstract. - A new partial articulated skeleton of an ornithopod dinosaur, *Rhabdodon priscus* has been discovered at the Vitrolles-Couperigne locality (Bouches-du-Rhône, France), not far from the first partial articulated skeleton of *R. priscus* found in 1995. The new remains include only elements of the postcranial skeleton. Many vertebrae and ribs are preserved. The posterior dorsal vertebrae were found articulated and placed next to the fused sacrum. The pelvic girdle was partially articulated. Numerous ossified tendons are well preserved. This new material is comparable in size to the first one and there are many skeletal elements in common. This new find provides some additional data on *Rhabdodon* which help to distinguish from its sister-taxon, *Zalmoxes*. New studies on the stratigraphy and floral and faunal assemblages of the site indicate that this locality is late Campanian in age.

Un nouveau squelette partiel de *Rhabdodon priscus* (Dinosauria : Ornithopoda) du Crétacé supérieur de Vitrolles-Couperigne, Bouches-du-Rhône, Sud de la France.

Mots-clés. – Dinosauria, Ornithopoda, Rhabdodontidae, Crétacé supérieur, Sud de la France

Résumé. – Un nouveau squelette partiellement articulé du dinosaure ornithopode *Rhabdodon priscus*, a été découvert dans le gisement de Vitrolles-Couperignes (Bouches-du-Rhône, France), non loin du premier squelette partiellement articulé de *R. priscus* mis au jour en 1995. Les nouveaux restes ne contiennent que du matériel post-crânien, avec de nombreuses vertèbres et côtes en bon état de conservation. Les vertèbres dorsales postérieures ont été découvertes articulées et proches des

vertèbres sacrées fusionnées entre elles. La ceinture pelvienne est également partiellement articulée. De nombreux tendons ossifiés sont bien préservés. Ce nouveau matériel est comparable en taille au premier spécimen mis au jour et les deux squelettes partagent les mêmes caractéristiques ostéologiques. Cette découverte fournit de nouvelles données plus précises sur *Rhabdodon*, qui aident à le distinguer de son taxon-frère, *Zalmoxes*. De nouvelles études sur la stratigraphie et les assemblages floristiques et fauniques du site indiquent un âge Campanien supérieur.

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Introduction

Rhabdodon is one of the most common dinosaurs from the Late Cretaceous of southern France. *Rhabdodon* has been known since the 19th century when the first specimens were discovered at la Nerthe locality (Bouches-du-Rhône, France) [Matheron, 1869]. Afterwards, many excavations in Campanian-Maastrichtian continental deposits, especially in southern France (Aude, Hérault, Gard, Var, Bouches-du-Rhône), have revealed abundant dinosaurian remains referred to Rhabdodontidae Weishampel *et al.*, 2003 [Buffetaut & Le Lœuff, 1991; Buffetaut *et al.*, 1996, 1999; Garcia *et al.*, 1999; Pincemaille-Quillévéré, 2002; Pincemaille-Quillévéré *et al.*, 2006; Sigé *et al.*, 1997].

Vitrolles-Couperigne is a remarkable locality in Bouches-du-Rhône that yielded the first partial articulated skeleton of *Rhabdodon priscus* in 1995. These remains are considered as the most complete skeleton of a single individual of *Rhabdodon* discovered so far in Europe. Unfortunately, the preservation of the material is not good. Most of bones are fractured and deformed. In 2007, the Muséum d'Histoire Naturelle d'Aix-en-Provence started new excavations at the Vitrolles-Couperigne site. In the course of these excavations, a second partial articulated skeleton referred to *Rhabdodon* was recovered and a reassessment of the stratigraphy was done. The elements of the new skeleton are in better condition and less scattered than those of the first find. This new material is described in the present paper, together with a review of the stratigraphy and floral and faunal content of the site.

Geological setting and stratigraphy

The Vitrolles-Couperigne site is located in the city of Vitrolles, in the Couperigne industrial area, where a new train station was built between 2007 and 2008 (fig. 1). The site was already excavated in 1994-1995, which led to the discovery of an almost complete skeleton of *Rhabdodon priscus* [Garcia *et al.*, 1999; Pincemaille-Quillévéré, 2002]. Surface collection on a hillock located thirty metres away from the skeleton had yielded isolated bones of *Rhabdodon priscus* and *Ischyrochampsia meridionalis*. The material described in this study comes from this hillock which

was completely excavated layer by layer before the beginning of the construction of the station. This hillock consisted of a succession of more or less calcareous marls and limestone layers. The observed stratigraphic sequence belongs to the lower part of the Rognacian (or Lower Argiles Rutilante Formation, Cojan and Moreau, 2006), a local stage corresponding to the top of the non-marine Late Cretaceous, thirty metres below the Rognac Limestone (or Calcaire de Rognac Formation, Cojan and Moreau, 2006) (fig. 2). It rests on an important red and yellow clay layer, also known as “argiles bariolées” (variegated clays, B1). Above this level, the first four marly limestone layers, passing from yellow-grey (B2) to grey colour (B3, B4) and the marly limestones (B5, B6) are fossiliferous. The first compact limestone layer (B7), one metre thick, has yielded no macrofossils and no organic microremains were found using chemical operations. It is followed by a last fossiliferous grey marly level (B8). The studied sequence ends with another similar compact limestone (B9), three metres thick, which was removed before the beginning of the fieldwork. The two *Rhabdodon* sites at Vitrolles-Couperigne do not show the same stratigraphic sequences. However, the top of the red and yellow clay level (B1) and the first limestone layer, under the *Rhabdodon* skeleton (B7), can be used for a precise correlation. Thus, the first *Rhabdodon* discovered in 1994 should be of the same age as the new material from level B8 described in this study.

A considerable diversity of plant and animal fossils was recovered in the course of the excavations (Appendix I). Macrofossils were discovered at three levels (B2, B4 and B8) and show the presence of *Rhabdodon priscus*, dromaeosaurids, ankylosaurs, turtles and crocodiles. In addition, large scale screen-washing operations have revealed remains of lissamphibians, squamates, fishes?, various types of isolated eggshell fragments, invertebrates (gastropods, ostracodes) and green algae (charophytes, dasycladales?), particularly in levels B4 and B6. The study of all these fossils (macro and microremains) is still in progress. The fossil assemblages from the 1994-1995 excavations and these presented here show a close resemblance at high taxonomic levels, with charophytes, gastropods, turtles, dromaeosaurids and crocodiles. But precise comparisons are difficult because the previous discoveries have not been described in detail. In addition, Garcia *et al.* [1999] did not specify the exact origin of the *Rhabdodon* and *Ischyrochampsia* remains discovered from the hillock.

The preliminary list presented here (Appendix I) complements the general biotic assemblage from Vitrolles-Couperigne with the addition of new taxa, especially among charophytes, (*Microchara sp.*), gastropods, ostracodes, lissamphibians and turtles (*Solemys* aff. *vermiculata*).

The associated fossils provide precise stratigraphic indications, particularly on the basis of charophytes and invertebrates. The best stratigraphic biomarkers are charophytes. Among them, *Peckichara cancellata* Grambast indicates the Lower Rognacian [Feist and Freytet, 1983; Riveline *et al.*, 1996; Nieves Lopez-Martinez *et al.*, 2001] whereas other taxa, some ostracodes and gastropods, span the whole Rognacian [Babinot *et al.*, 1983]. A recent magnetostratigraphic study of the Aix Bassin places the Rognac Limestone at the level of the Campanian-Maastrichtian boundary [Cojan and Moreau, 2006] and, consequently, the Vitrolles-Couperigne stratigraphic sequence in the Upper Campanian (Chron 33N) and not in the Lower Maastrichtian [*contra* Garcia *et al.*, 1999; Pincemaille-Quillévéré, 2002].

Description of the *Rhabdodon* material

The material described in this work includes only postcranial elements, some of which found in articulation and some isolated (fig. 3). This new partial articulated skeleton has several elements in common with the partial skeleton referred to *Rhabdodon priscus* [Pincemaille-Quillévéré, 2002], previously discovered from a nearby site. Moreover, these elements shared by the two skeletons provide comparable diagnostic features. It thus appears that the Vitrolles-Couperigne locality has yielded remains of two distinct partially articulated *Rhabdodon* skeletons. All specimens are presently housed in the Muséum d'Histoire Naturelle d'Aix-en-Provence (Appendix II). The measurements of complete and nearly complete elements are shown in Table 1.

Institutional Abbreviations

MHN-AIX-PV, Muséum d'Histoire Naturelle d'Aix-en-Provence

Systematics

Order ORNITHISCHIA Seeley, 1887

Suborder ORNITHOPODA Marsh, 1881

EUORNITHOPODA (sensu Weishampel 1990)

Infraorder IGUANODONTIA Sereno, 1986

Family RHABDODONTIDAE

Weishampel, Jianu, Cziki & Norman, 2003

Genus *Rhabdodon* Matheron 1869

Species *Rhabdodon priscus*, Matheron 1869

Material – a partial skeleton MHN-AIX-PV 2007.B8. 1-5, 7-51, 53-54, 56-67, 69, 72-73, 75-81, 83-87 and 89-99.

Description

Axial skeleton

No cervical vertebra has been preserved and some vertebrae (MHN-AIX-PV 2007. B8.11, 65, 77) could not be identified precisely. The anterior dorsal vertebra (MHN-AIX-PV 2007.B8.34) (fig. 4) is short and the centrum is approximately as wide as high. The anterior articular facet is concave whereas the posterior facet is slightly convex. The lateral walls are concave and the centrum is keeled ventrally forming a heart-like shape in anterior view. The transverse processes are elongate and oriented dorsolaterally. The parapophysis and diapophysis are separated, on the proximal and distal part of the transverse process respectively. The prezygapophyses face dorsomedially. The postzygapophyses are well separated and face ventrolaterally. The neural spine is tall, forming more than half the total height of the vertebra. It is narrow, tapered upward and curved posteriorly at the extremity.

The dorsal vertebra MHN-AIX-PV 2007.B8.1 which probably belongs to the middle to posterior dorsal series is incomplete and deformed. Its centrum is more rounded, as wide as high and it is amphicoelous. The posterior dorsal vertebrae (MHN-AIX-PV 2007.B8. 47, 56, 64, 66, 67) were

found partially articulated (fig. 5A, B). These vertebrae are amphicoelous. The transverse processes become shorter and oriented more horizontally in the posterior dorsal series. The parapophysis shifts progressively upward and finally merges with the diapophysis on the transverse process of the last posterior dorsal vertebra (fig. 5E; pd). The neural spine of the posterior dorsal vertebrae is large, rectangular in shape. It is at least two times higher than the centrum height. The posterior margin is slightly curved and the upper part of the spine is extended anteroposteriorly. The prezygapophyses are inclined dorsomedially. The postzygapophyses are less opened and their prominent oval facets face ventrolaterally. The postzygapophyses are prolonged more posteriorly behind the centrum and they are also situated more dorsally in more posterior vertebrae.

Dorsal ribs are preserved near the vertebrae. Their different forms and sizes indicate different types of articulation with dorsal vertebrae. In anterior thoracic ribs, the capitulum and the tuberculum are widely separated into two branches (fig. 6). The articular surfaces of anterior ribs are sub-equal in size and subcircular. The shafts of these ribs are proximally concave in posterior view and become rounded in the middle and mediolaterally compressed at the distal end. More posteriorly the tuberculum is shortened but its articular surface is oval and more prominent than the capitulum. The costal shaft is curved and more compressed anteroposteriorly and it is narrower distally. In the most posterior ribs, the capitulum and the tuberculum are merged as a single articulation with the para-diapophysis. These ribs are arched and tapered distally.

The sacrum of this *Rhabdodon* skeleton was found in two pieces separated by a minor fault (fig. 7). They are deformed and compressed laterally. This fused sacrum comprises the last dorsal vertebra, the sacrodorsal vertebra and sacrals one to five. Sacral six is not completely preserved. The last dorsal vertebra which fused to the sacrum shows the same characters as the previous dorsal vertebra (MHN-AIX-PV 2007.B8.47). The right lateral side of the centra of the sacrodorsal and the first true sacral are covered by the ossified tendons but not the left lateral side. This suggests that the ossified tendons should not be present on the centrum and must have been displaced from elsewhere during fossilisation. Sacral two was cut by the fault; its central part is MHN-AIX-PV 2007.B8.14 and its neural spine MHN-AIX-PV 2007.B8.15. The sacral ribs of sacral two to four project laterally while the ribs of sacral five are oriented more anteriorly. These sacral ribs arise at the co-

ossified junction between the centra and are linked to each other by a massive lateral bar which contacts the medial surface of the ilium. The neural spines of the sacrum look like those of posterior dorsal vertebrae, however they are higher and expanded dorsally and become very close to the adjacent spines, and were possibly fused together.

Caudal vertebrae were found near the pelvic girdle, some of them are articulated. The caudal vertebrae are not well preserved and deformed (fig. 8). The centrum is wide but short in the anterior members of the caudal series whereas it is longer than wide and compressed laterally in the posterior ones. The lateral wall of the caudals is concave anteroposteriorly, becoming flatter in succeeding caudals. Ventrally, the centra bear the haemapophyseal facets on the ventral margin of two articular facets which the posterior haemapophyseal facet is more prominent than the anterior one. The transverse process is situated on the lateral wall of the centrum (fig. 6 A, B) and projects more or less horizontally. The transverse process diminishes gradually and disappears in the posterior caudals. The prezygapophyses of the anterior caudals cannot be observed, however, in a mid-posterior caudal (MHN-AIX-PV 2007.B8. 19) the prezygapophysis is extended anterodorsally. It is narrow and faces medially and tapers in the posterior series. The postzygapophyses are much less prominent than those of the dorsal vertebrae. They are short and eventually merged as a single bulge on the posterior margin of the neural spine. The neural spine is still large in anterior to middle caudal vertebrae and then it becomes shorter and narrower in more posterior ones.

Some chevrons were recovered around the caudal vertebrae. Their proximal end is expanded. Dorsally, the articular facet is unequally bisected by a transverse ridge into a larger anterior and a smaller posterior facet for articulation with the haemapophyseal facets of the centrum. Beneath this articular head, there is an oval haemal canal which is completely enclosed. The haemal arches continue as two ridges on the posterior surface down to the middle of the chevron spine. The distal margin is curved backward and flat at the distal end.

Ossified tendons are quite well preserved, some of them having been found in situ with the vertebrae. The ossified tendons are distributed all along the dorsal, sacral and caudal vertebrae, however they were found more densely packed over the posterior dorsal vertebrae and the sacrum. Moreover, the tendons could be also arranged on the chevrons as shown in figure 8G. These ossified

rods tend to have mainly two shapes (angular and rounded) and to be oriented in two directions (longitudinal and oblique). The longitudinal tendons lie side by side whereas the oblique ones lie apart from each other (fig. 9). Long striations are present on the tendon surface. The displacement of tendons, for example on the sacral centra (fig. 7), and scattered well-preserved tendons suggest that ossified tendons were not fused to bones.

Forelimb

The right humerus (MHN-AIX-PV 2007.B8. 2) is incomplete, lacking the proximal articulation, and it is compressed anteroposteriorly. The humeral condyle is not preserved. The deltopectoral crest (fig. 10) is limited to the proximal half of the humerus. The crest is expanded and more rugose distally while it decreases in width and becomes smoother toward the head. The deltopectoral crest is bent anteromedially, forming a concave surface (bicipital sulcus) on the proximal part of the humerus. At mid-length, the shaft is narrowed; however, it is not very slender relative to the width of the proximal and distal parts. Distally, the humerus is also expanded to form the distal articulation. Although the ulnar and radial condyles are incomplete, the coronoid and olecranon fossae are visible between the distal condyles as broad triangular grooves in anterior and posterior views respectively.

The right radius (MHN-AIX-PV 2007.B8.54) (fig. 10C) is not well preserved. It is compressed lateromedially and bowed dorsoventrally. It is slender at mid-shaft and expanded at each end. Because of poor preservation, the proximal and distal ends cannot be observed.

Pelvic girdle

The right ilium ((MHN-AIX-PV 2007.B8. 93) and ischium (MHN-AIX-PV 2007.B8. 17) were found articulated (fig. 11). The ilium is not complete and compressed lateromedially. Only the iliac blade posterior to the acetabulum is preserved. The dorsal margin is posteriorly convex. The ischial peduncle of the ilium meets the iliac peduncle of the ischium by its ventral edge, forming the posterior rim of the acetabulum. Above this process, a rugose depression is present on the medial face and limited by an irregular curved thin ridge. This depression for the attachment of a sacral rib

extends to the posterior margin of the ilium. The posterior ventral margin of the ilium is slightly inclined upward.

Both ischia were recovered but the left one (MHN -AIX-PV 2007.B8. 9) (fig. 12A) is incomplete, lacking the proximal articulations. The iliac peduncle of the ischium is larger than the pubic peduncle. These two peduncles are separated by an embayment which forms the posteroventral rim of the acetabulum. The obturator process is situated on the proximal half of the ischium and is projected medially. The ischial shaft is laterally flattened in cross-section and it is broad in its proximal part and approximately parallel-sided in its middle part. The distal half of the ischium is bowed and its distal end is slightly expanded ventrally.

Both the left and right pubes were recovered but only the pre-pubes are preserved (fig. 12). The pre-pubis forms the anteroventral rim of the acetabulum. It is laterally compressed. The pre-pubic process is extended forward and its distal end is expanded dorsoventrally and curves downward. The proximal articulations are divided into the facet for the ilium projecting dorsally and the facet for the ischium projecting ventrally. The former facet is larger than the latter one. A deep oval pubic foramen with an anterior shallow depression is present just below the articulation for the ischium.

Hindlimb

Few hindlimb bones have been found. There are only a fragment of femur and an unguis phalanx which were recovered from the same bed as the other *Rhabdodon* remains. Nevertheless, a left femur (MHN-AIX-PV 2008.B2.11) was found in a lower bed from which some other reptile remains were recovered. The left femur is incomplete, lacking the proximal and distal ends. The fourth trochanter is long (13 cm) and has a shallow depression anteriorly. The femoral shaft is large, straight and transversely expanded at the proximal and distal ends.

The unguis phalanx (MHN-AIX-PV 2007.B8. 81) (fig. 13) is broad. It is sheared and compressed dorsoventrally. The unguis is flattened and slightly arched ventrally. Its proximal end is concave dorsoventrally and divided by a vertical ridge into sub-equal adjacent depressions. The dorsal margin of this articular facet is prolonged more proximally than the ventral one. From the

articular margin, both sides of the ungual are slightly tapering in the proximal part where the ligament scar is clearly visible in dorsal view. Then, the lateral and medial sides are expanded as a long round ridge supporting well developed claw grooves extending to the distal tip of the ungual.

Discussion and conclusion

This new partial articulated skeleton of *Rhabdodon priscus* is comparable in size to the first one. The new material described above provides information about some osteological features which are missing in the first found skeleton, as listed below:

1) The neural spines of the dorsal vertebrae and the sacrum are two to three times higher than the centra. They are still prominent in anterior caudal vertebrae, but less prominent in the more posterior ones. *Ouranosaurus* and *Iguanodon* possess more developed neural spines whereas the neural spines of *Zalmoxes* are short, as high as the centra of the dorsal vertebrae.

2) The sacrum consists of eight fused vertebrae; the last dorsal, the sacrodorsal and six true sacral vertebrae. This character is shared with *Iguanodon* and *Zalmoxes*.

3) A great number of ossified tendons over the sacrum and the neighboring area around the posterior dorsal and anterior caudal vertebrae suggest that the vertebral column was probably held more or less horizontally. The ossified tendons were probably arranged in a double layer as in *Iguanodon*. Both epaxial and hypaxial ossified tendons are present in the caudal skeleton, as in *Tenontosaurus*. These characters are unknown in *Zalmoxes*.

4) The humerus is not very constricted at mid-shaft while it is narrowed in *Zalmoxes*. The deltopectoral crest of the humerus is prominent and forms an angle with the humeral shaft. This character is shown more distinctively in *Zalmoxes shqiperorum*.

5) An obturator process is present in the proximal half of the ischium. This process cannot be observed on the right ischium of the first skeleton found in 1995, but it is present on the left one. This may be a taphonomic effect. On the other hand this character is absent in *Zalmoxes*.

6) The ischial shaft is compressed laterally and slightly curved anteroposteriorly whereas that of *Zalmoxes* is ovoid in cross-section and distinctively curved downward and forms a boot-like distal end in *Zalmoxes shqiperorum*.

7) The iliac blade is deep and straight and it is sub-equally thick along the dorsal margin. In contrast to *Zalmoxes*, the iliac blade faces ventrolaterally and the posterior dorsal margin is expanded and everted.

The recent systematic analyses of *Rhabdodon* principally based on the first partial articulated skeleton of *Rhabdodon priscus* [Pincemaille-Quillévéré, 1997, 2002] suggest that *Rhabdodon priscus* has the closest relationship with *Zalmoxes robustus* and *Z. shqiperorum* from the Late Maastrichtian of Romania [Weishampel *et al.*, 2003]. All these taxa are placed in the same family Rhabdodontidae of Iguanodontia, by Weishampel *et al.*, [2003]. The anatomical information provided by the new skeleton from Vitrolles-Couperigne discussed above confirms that *Rhabdodon priscus* differs notably from *Zalmoxes* in having very tall neural spines on the vertebrae, possessing an obturator process on the ischium, a flat ischiac shaft and a non-everted dorsal margin of the ilium. These diagnostic postcranial characters were already included in the recent systematic analysis of Weishampel *et al.* [2003]. No new cranial material is known from Vitrolles-Couperigne. The identical fluted teeth and probably other cranial characters mentioned by Godefroit *et al.* [2009] represent the best synapomorphies for Rhabdodontidae so far. While *Zalmoxes* and *Rhabdodon* are closer to *Tenontosaurus*, from the Aptian of the United States, than to other iguanodontians, *Rhabdodon priscus* from Vitrolles-Couperigne is closer to *Tenontosaurus* than *Zalmoxes* on the basis of postcranial characters. This could suggest that the common ancestor of the rhabdodontid dinosaurs evolved in North America, and then dispersed to Europe and eventually evolved in geographical isolation on the various European landmasses during the Late Cretaceous.

Although the identification of floral and faunal elements is still in progress, the complete exploitation of the Vitrolles-Couperigne site (layer by layer with screen-washing operations) suggests that the local biodiversity was richer than previously described [Garcia *et al.*, 1999], especially at the level of the micro-flora and fauna. Nevertheless, the preliminary picture of the biotic composition depicts a precise life environment. The alternating thick compact limestone layers and marls are very rich in charoptytes typical of fresh water. The most represented gastropods (*Cyclophorus*, *Melanania*, *Physa*, *Pyrugulifera* and *Viviparus*) are also characteristic of this environment often charged in mud such as lakes, ponds and swamps in a warm and wet climatic

context [Fabre-Taxy, 1951, 1959]. This observation is in agreement with the presence of lissamphibians which are essentially bound to this type of aquatic environment. The other present vertebrates such as squamates, turtles (*Solemys*) and dinosaurs such as *Rhabdodon* and ankylosaurs, which were not confined to the lakeside, may have come to the peri-lacustrine zone to find food or nesting sites. From this zone, small bones and eggshell fragments were carried by streams and accumulated in the lake or in the pond. The occurrence of small theropods such as dromaeosaurs was probably linked to the presence of easily accessible animal carcasses in shallow water, a rather opportunistic behaviour. The limited dislocation of the skeletons of *Rhabdodon* and the lack of some anatomical parts (head, members and tail) could be explained by a combination of a slow current and scavenger activity, the predators taking the extremities of the skeleton.

The stratigraphic distribution of the flora and fauna presented in this study can yet suffer from a bias linked to the quantity of studied sediments. New studies will enable to confirm or enrich the taxonomic lists for each layer and then to compare this biodiversity with those known from other sites such as Champs-Garimond [Sigé *et al.*, 1997], Cruzy [Buffetaut *et al.*, 1999], La Neuve [Garcia *et al.*, 2000], La Rouquette [Massieux *et al.*, 1987], Laño [Astibia *et al.*, 1999] and Villeveyrac [Buffetaut *et al.*, 1996]. These comparisons are necessary in order to understand the palaeobiogeographical relationships of some taxa (lissamphibians, squamates, turtles) in southern France during the Late Cretaceous (Campanian and Maastrichtian).

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FIG. 1 - Location map of Vitrolles-Couperigne localiy. 1: Vitrolles Limestone, 2 : Argiles Upper Argiles Rutilantes, 3 : Calcaire de Rognac, 4 : Lower Argiles Rutilantes.

FIG. 1 – Carte localisant le gisement de Vitrolles-Couperigne. 1:Calcaire de Vitrolles, 2 : Argiles Rutilantes supérieures, 3 : Calcaire de Rognac, 4 : Argiles Rutilantes inférieures

FIG. 2 - Log of Vitrolle-Couperigne site and positioning in chronotratigraphic and general lithostratigraphic context (*not at scale). 1 : red and variegated (B1) clays, 2 : sandstone, 3 : clays with gypsum, 4 : limestone (B7, B9), 5 : Alternation of marls and limestones, 6 : grey and yellow marls (B2), or grey marls (B4, B8) or grey marls with black joint (B3), 7 : grey marl with limestone nodules (B5), 8 : thin marly limestone lens (B6), 9 : Layers yielding *Rhabdodon* remains (B2, B8).

FIG. 2 - Log du site de Vitrolles-Couperigne et repositionnement dans les contextes chronostratigraphiques et lithostratigraphiques généraux (*coupe non à l'échelle). 1 : argiles rouges et bariolées (B1), 2 : grès, 3 : argiles à gypse, 4 : calcaire (B7, B9), 5 : alternance de marnes et calcaires, 6 : marnes jaunes et grises (B2), ou seulement grises (B4, B8) ou grises avec jointures noires (B3), 7 : marne grise avec nodules calcaires (B5), 8 : lentilles de calcaires fins et marneux (B6), 9 : couches contenant les restes de *Rhabdodon* (B2, B8).

FIG. 3 - Map of the bones as they were found in the course of the excavations. The numbers are those used in the present description (see Appendix: List of skeletal elements). Reconstruction of partial skeleton showing positions of the bones discovered at the site in grey.

FIG. 3 – Plan des os, tels qu' ils ont été trouvés au cours des fouilles. Les chiffres sont ceux utilisés dans la description (voir Annexe: Liste des éléments du squelette). Reconstruction du squelette partiel, montrant les positions des os découverts sur le site en gris.

FIG. 4 - Anterior dorsal vertebra (MHN-AIX-PV 2007.B8.34) in anterior (A), left lateral (B) and posterior(C) views. Abbreviations: d = diapophysis, ns = neural spine, p = parapophysis, poz = postzygapophysis, prz = prezygapophysis.

FIG. 4 - Vertèbre dorsale antérieure (MHN-AIX-PV 2007.B8.34) en vues antérieure (A), latérale gauche (B) et postérieure(C). Abréviations: d = diapophyse, ns = épine neurale, p = parapophyse, poz = postzygapophyse, prz = prézygapophyse.

FIG. 5 - Associated posterior dorsal vertebrae (MHN-AIX-PV 2007.B8.47, 67, 56) in right lateral view (A). Dorsal vertebra MHN-AIX-PV 2007.B8. 66 found next to MHN-AIX-PV 2007.B8.56 in posterolateral view. The second dorsal vertebra from the last (MHN-AIX-PV 2007.B8. 47) in anterior (C), posterior (D) and left lateral (E) views. Abbreviations: d = diapophysis, ns = neural spine, p = parapophysis, pd = paradiapophysis, poz = postzygapophysis, prz = prezygapophysis, tp = transverse process.

FIG. 5 - Vertèbres dorsales postérieures associées (MHN-AIX-PV 2007.B8.47, 67, 56) vue latérale droite (A). Vertèbre dorsale MHN-AIX-PV 2007.B8. 66 trouvé à côté de MHN-AIX-PV 2007.B8.56 en vue postérolatérale. La deuxième vertèbre dorsale à partir de l'arrière (MHN-AIX-PV 2007.B8. 47) en vues antérieure (C), postérieure (D) et latérale gauche (E). Abréviations: d = diapophyse, ns = épine neurale, p = parapophyse, pd = paradiapophyse, poz = postzygapophyse, prz = prézygapophyse, tp = processus transverse.

FIG. 6 - Anterior dorsal rib (MHN-AIX-PV 2007.B8. 3) in posterior view (A), mid-posterior dorsal rib (MHN-AIX-PV 2007.B8. 41) in anterior view (B), posterior dorsal rib (MHN-AIX-PV 2007.B8. 10) in lateral view. Abbreviations: c = capitulum, ct = merged capitulum and tuberculum, t = tuberculum.

FIG. 6 - Côte dorsale antérieure (MHN-AIX-PV 2007.B8. 3) en vue postérieure (A), côte dorsale mi-postérieure (MHN-AIX-PV 2007.B8. 41) en vue antérieure (B), côte dorsale postérieure (MHN-AIX-PV 2007.B8. 10) en vue laterale. Abréviations : c = capitulum, ct = capitulum et tuberculum, fusionné, t = tuberculum.

FIG. 7- Sacrum MHN-AIX-PV 2007.B8. 14 (on the right) and 15(on the left) in right lateral view.

Abbreviations: ld = last dorsal vertebra, os.t = ossified tendons, s = sacral, sd = sacrodorsal vertebra, sr = sacral rib.

FIG. 7- Sacrum MHN-AIX-PV 2007.B8. 14 (à droite) et 15(à gauche) en vue latérale droite.

Abréviations: ld = dernière vertèbre dorsale, os.t = tendons ossifiés, s = vertèbre sacrée, sd = vertèbre sacrodorsale, sr = côte sacrée.

FIG. 8 - Anterior caudal vertebrae, MHN-AIX-PV 2007.B8.43 in anterior view (A), MHN-AIX-PV 2007.B8. 21 in left anterolateral view (B), MHN-AIX-PV 2007.B8. 4 in right anterolateral view (C) and mid to posterior caudal vertebra MHN-AIX-PV 2007.B8. 19 in right lateral view (D). Chevrons, MHN-AIX-PV 2007.B8.73 in anterolateral (E) and posterolateral (F) views, MHN-AIX-PV 2007.B8.90 in right lateral view (G). Abbreviation: hc = haemal canal, os.t = ossified tendon, poz = postzygapophysis, prz = prezygapophysis, tp = transverse process. 5 cm and 3 cm scale bars are for caudal vertebrae and chevrons respectively.

FIG. 8 - vertèbre caudale antérieure MHN-AIX-PV 2007.B8.43 en vue antérieure (A), MHN-AIX-PV 2007.B8. 21 en vue antérolatérale gauche (B), MHN-AIX-PV 2007.B8. 4 en vue antérolatérale droite (C) et vertèbre caudale moyenne à postérieure MHN-AIX-PV 2007.B8. 19 en vue latérale droite (D). Chevrons, MHN-AIX-PV 2007.B8.73 en vues antérolatérale (E) et postérolatérale (F), MHN-AIX-PV 2007.B8.90 en vue latérale droite (G). Abréviations: hc = canal hémal, os.t = tendon ossifié, poz = postzygapophyse, prz = prézygapophyse, tp = processus transverse. 5 cm et 3 cm sont des barres d'échelle pour les vertèbres caudales et les chevrons, respectivement.

FIG. 9 - Ossified tendons. Abbreviations: ns = neural spine, os.t = ossified tendons.

FIG. 9 - Tendons ossifiés. Abréviations: ns = neural spine, os.t = ossified tendons.

os.t = tendons ossifiés

FIG. 10 - Right humerus MHN-AIX-PV 2007.B8. 2 in anterior (A) and posterior (B) views. Right radius MHN-AIX-PV 2007.B8. 54 in medial view(C). Abbreviations: dpc=deltpectoral crest, rac=radial condyle, ulc=ulnar condyle.

FIG. 10 - Humérus droit MHN-AIX-PV 2007.B8. 2 en vues antérieure (A) et postérieure (B). Radius droit MHN-AIX-PV 2007.B8. 54 en vue mediale (C). Abréviations: dpc= crête deltopectorale, rac= condyle radiale, ulc= condyle ulnaire.

FIG. 11 - Articulated right ilium MHN-AIX-PV 2007.B8. 93 and ischium MHN-AIX-PV 2007.B8. 17 in medial view. Abbreviations: acet = acetabulum, il = ilium, il.p = iliac peduncle, is = ischium, is.p = ischial peduncle, ob.p = obturator process, p.p = pubic peduncle.

FIG. 11 - Ilion droit MHN-AIX-PV 2007.B8. 93 et ischion droit MHN-AIX-PV 2007.B8. 17 en connexion en vue médiale. Abréviations: acet = acétabulum, il = ilion, il.p = pédoncule iliaque, is = ischion , is.p = pédoncule ischiatique, ob.p = processus obturé, p.p = pédoncule pubien.

FIG. 12 - Left ischium MHN-AIX-PV 2007.B8. 9 in medial view (A). Pre-pubis, MHN-AIX-PV 2007.B8.7 (B) and MHN-AIX-PV 2007.B8. 12 (B) in lateral view. Abbreviations: ob.p = obturator process, p.f = pubic foramen, pre.p = pre-pubic process.

FIG. 12 – Ischion gauche MHN-AIX-PV 2007.B8. 9 en vue médiale (A). Pré-pubis, MHN-AIX-PV 2007.B8.7 (B) et MHN-AIX-PV 2007.B8. 12 (B) en vue laterale. Abréviations: ob.p = processus obturé, p.f = foramen pubien, pre.p = processus pré-pubien.

FIG. 13 - An ungual phalanx ((MHN-AIX-PV 2007.B8. 81) in dorsal (A) and lateral (B) views.

FIG. 13 - Une phalange unguéale ((MHN-AIX-PV 2007.B8. 81) en vues dorsale (A) et laterale (B).

Appendix I: Floral and faunal assemblage found in the different layers of Vitrolles-Couperigne stratigraphic sequence.

Taxa	Layer								
	B1	B2	B3	B4	B5	B6	B7	B8	B9
Charophyta									
<i>Heptorella brachyceras</i>		+							
<i>Microchara cristata</i>		+							
<i>Microchara sp.</i>		+							
<i>Peckichara cancellata</i>			+	+	+				
<i>Peckichara sertulata</i>			+	+	+	+			
Charophyta?									
<i>Dasykladaceae indet.?</i>				+		+			
Gastropoda									
<i>Bauxia disjuncta</i>								+	
<i>Clausilia patula</i>		+		+					
<i>Cyclophorus luneli</i>								+	
<i>Cyclophorus solarium</i>				+					
<i>Melania gourreti</i>		+							
<i>Palaeostoa cureti</i>								+	
<i>Palaeostoa meridionalis</i>				+					
<i>Physa pygmæa</i>		+							
<i>Pyrgulifera armata</i>		+		+					
<i>Viviparus beaumonti</i>								+	
taxa indet.		+	+	+	+	+	+	+	
Ostracoda									
aff. <i>Cypridopsis</i> sp.				+					
<i>Frambocythere tumiensis ferrerii</i>				+	+				
<i>Paracandona occitanica</i>				+				+	
taxa indet.		+							
Pisces?									
taxa indet.				+		+			
Lissamphibia									
Anura indet.				+					
Palaeobatrachidae indet.?				+					
Scapherpetontidae indet.?				+					
Sirenidae or Proteidae indet.?				+					
Chelonia									
<i>Solemys cf. vermiculata</i>		+							
taxa indet.						+			
Squamata									
Lacertilia indet.						+			
taxa indet.						+			
Crocodylia									
taxa indet.		+		+		+		+	
Dinosauria									
Ankylosauria indet.				+					
Dromaeosauridae indet.				+				+	
<i>Rhabdodon priscus</i>		+						+	
Isolated Eggshells									
types indet.	+	+	+	+	+	+		+	

Appendix II: List of skeletal elements.

Number	Nature
MHN-AIX-PV 2007.B8.1	dorsal vertebra
MHN-AIX-PV 2007.B8.2	right humerus
MHN-AIX-PV 2007.B8.3	rib
MHN-AIX-PV 2007.B8.4	caudal vertebra
MHN-AIX-PV 2007.B8.5	tendon
MHN-AIX-PV 2007.B8.7	left pre-pubis
MHN-AIX-PV 2007.B8.8	rib
MHN-AIX-PV 2007.B8.9	left ischium
MHN-AIX-PV 2007.B8.10	rib
MHN-AIX-PV 2007.B8.11	vertebra
MHN-AIX-PV 2007.B8.12	right pre-pubis
MHN-AIX-PV 2007.B8.13	tendon
MHN-AIX-PV 2007.B8.14	sacrum(1)
MHN-AIX-PV 2007.B8.15	sacrum(2)
MHN-AIX-PV 2007.B8.16	tendon
MHN-AIX-PV 2007.B8.17	right ischium
MHN-AIX-PV 2007.B8.18	caudal vertebra
MHN-AIX-PV 2007.B8.19	caudal vertebra
MHN-AIX-PV 2007.B8.20	chevron
MHN-AIX-PV 2007.B8.21	caudal vertebra
MHN-AIX-PV 2007.B8.22	caudal vertebra
MHN-AIX-PV 2007.B8.23	caudal vertebra
MHN-AIX-PV 2007.B8.24	caudal vertebra
MHN-AIX-PV 2007.B8.25	tendon
MHN-AIX-PV 2007.B8.26	tendon
MHN-AIX-PV 2007.B8.27	tendon
MHN-AIX-PV 2007.B8.28	undetermined bone
MHN-AIX-PV 2007.B8.29	vertebra
MHN-AIX-PV 2007.B8.30	tendons
MHN-AIX-PV 2007.B8.31	rib
MHN-AIX-PV 2007.B8.32	rib
MHN-AIX-PV 2007.B8.33	rib

Number	Nature
MHN-AIX-PV 2007.B8.34	dorsal vertebra
MHN-AIX-PV 2007.B8.35	rib
MHN-AIX-PV 2007.B8.36	rib
MHN-AIX-PV 2007.B8.37	rib
MHN-AIX-PV 2007.B8.38	rib
MHN-AIX-PV 2007.B8.39	rib
MHN-AIX-PV 2007.B8.40	rib
MHN-AIX-PV 2007.B8.41	rib
MHN-AIX-PV 2007.B8.42	neural spine
MHN-AIX-PV 2007.B8.43	caudal vertebra
MHN-AIX-PV 2007.B8.44	tendon
MHN-AIX-PV 2007.B8.45	tendon
MHN-AIX-PV 2007.B8.46	tendon
MHN-AIX-PV 2007.B8.47	dorsal vertebra
MHN-AIX-PV 2007.B8.48	rib
MHN-AIX-PV 2007.B8.49	tendon
MHN-AIX-PV 2007.B8.50	rib
MHN-AIX-PV 2007.B8.51	tendon
MHN-AIX-PV 2007.B8.53	rib
MHN-AIX-PV 2007.B8.54	right radius
MHN-AIX-PV 2007.B8.56	dorsal vertebra
MHN-AIX-PV 2007.B8.57	caudal vertebra
MHN-AIX-PV 2007.B8.58	rib
MHN-AIX-PV 2007.B8.59	rib
MHN-AIX-PV 2007.B8.60	rib
MHN-AIX-PV 2007.B8.61	rib
MHN-AIX-PV 2007.B8.62	rib
MHN-AIX-PV 2007.B8.63	rib
MHN-AIX-PV 2007.B8.64	dorsal vertebra
MHN-AIX-PV 2007.B8.65	vertebra
MHN-AIX-PV 2007.B8.66	dorsal vertebra
MHN-AIX-PV 2007.B8.67	dorsal vertebra

Number	Nature
MHN-AIX-PV 2007.B8.69	fragment of femur
MHN-AIX-PV 2007.B8.72	caudal vertebra
MHN-AIX-PV 2007.B8.73	chevron
MHN-AIX-PV 2007.B8.75	tendons
MHN-AIX-PV 2007.B8.76	undetermined bone
MHN-AIX-PV 2007.B8.77	neural spine
MHN-AIX-PV 2007.B8.78	rib
MHN-AIX-PV 2007.B8.79	tendon
MHN-AIX-PV 2007.B8.80	fragment of rib
MHN-AIX-PV 2007.B8.81	ungual phalanx
MHN-AIX-PV 2007.B8.83	rib
MHN-AIX-PV 2007.B8.84	rib
MHN-AIX-PV 2007.B8.85	rib
MHN-AIX-PV 2007.B8.86	chevron
MHN-AIX-PV 2007.B8.89	tendon
MHN-AIX-PV 2007.B8.90	chevron
MHN-AIX-PV 2007.B8.91	tendon
MHN-AIX-PV 2007.B8.92	chevron
MHN-AIX-PV 2007.B8.93	right ilium
MHN-AIX-PV 2007.B8.94	rib
MHN-AIX-PV 2007.B8.95	rib
MHN-AIX-PV 2007.B8.96	rib
MHN-AIX-PV 2007.B8.97	rib
MHN-AIX-PV 2007.B8.98	undetermined bone
MHN-AIX-PV 2007.B8.99	Tendons
MHN-AIX-PV 2008.B2.11	femur

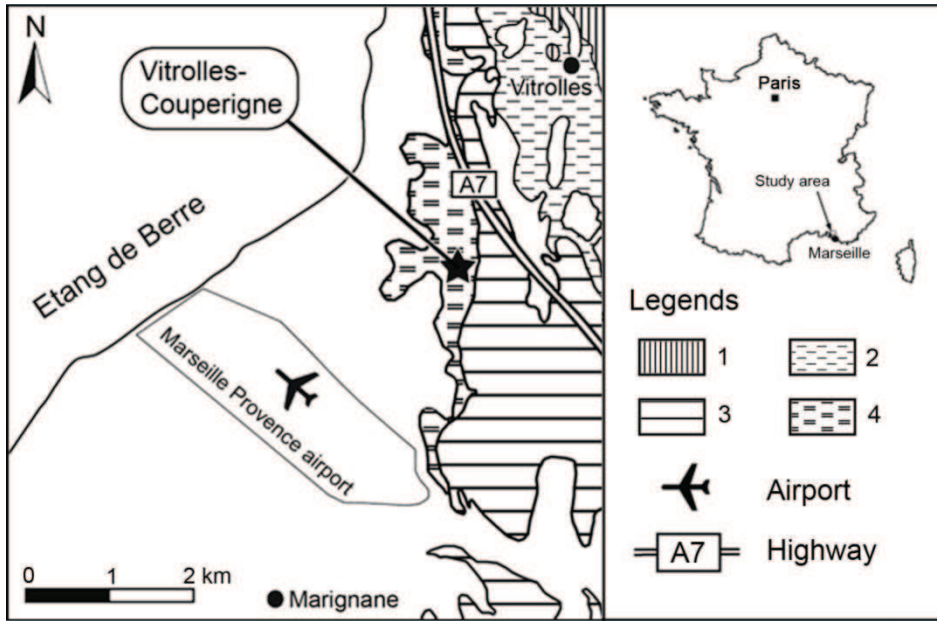


Figure 1

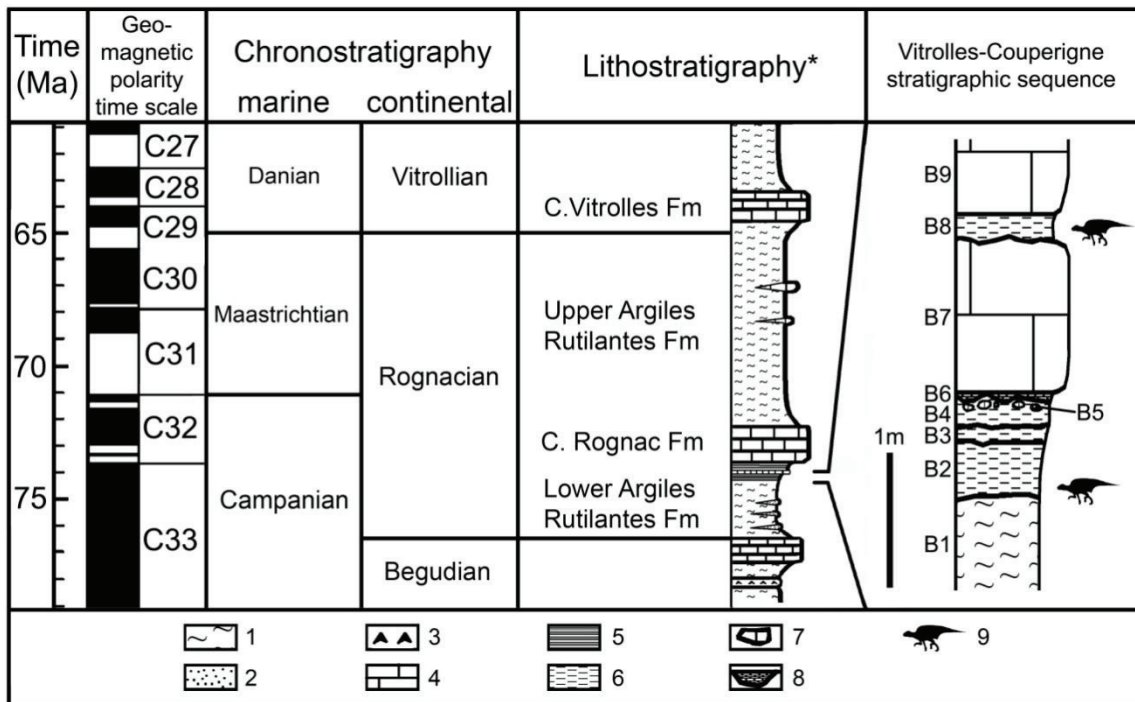


Figure 2



Figure 3

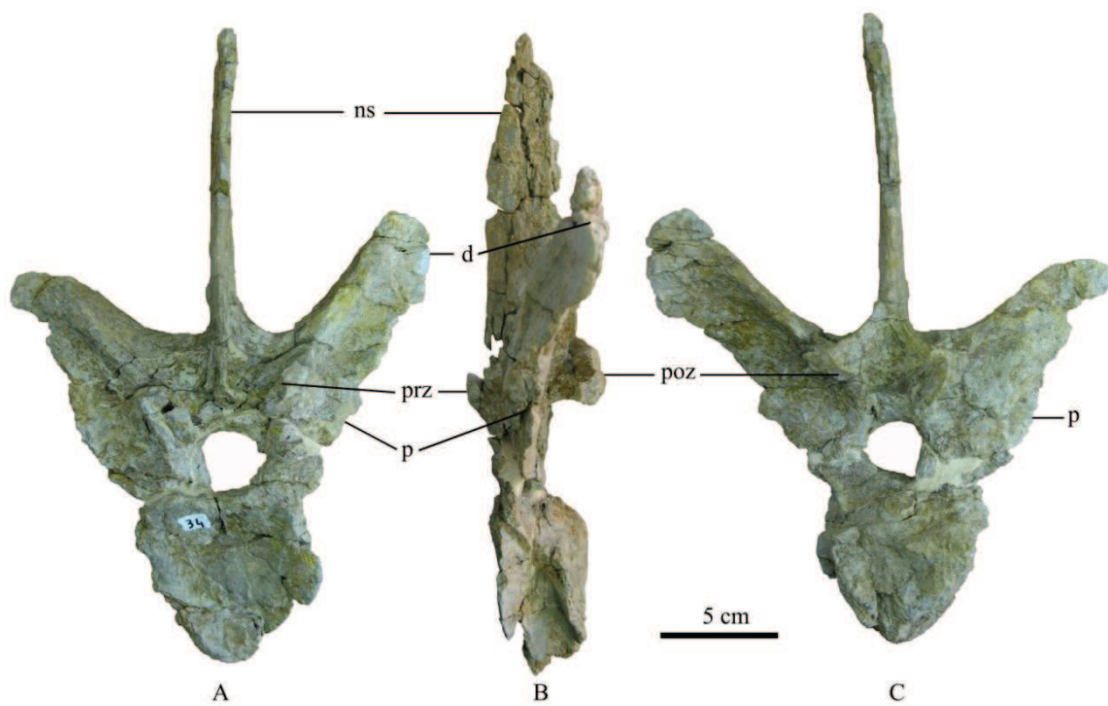


Figure 4

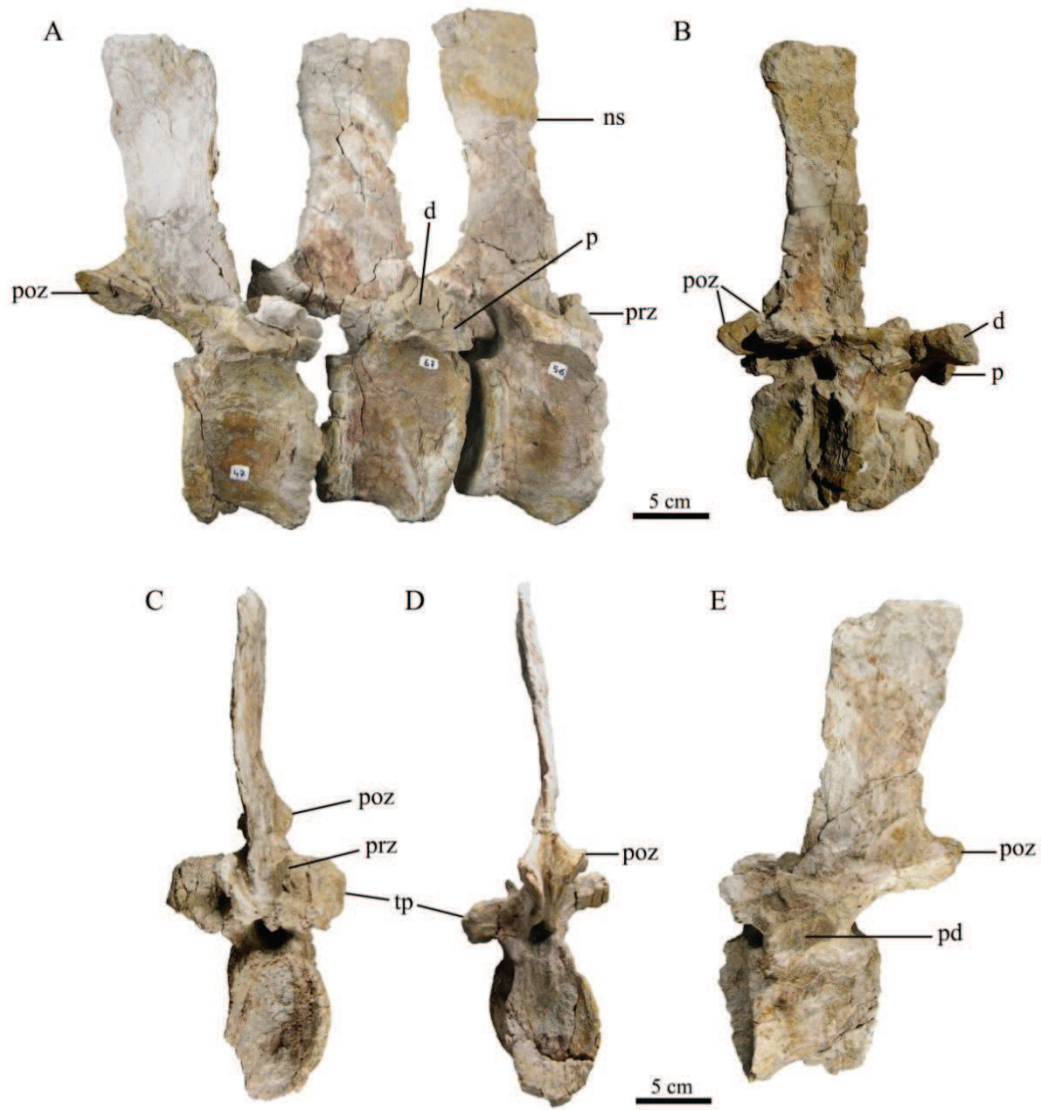


Figure 5



Figure 6

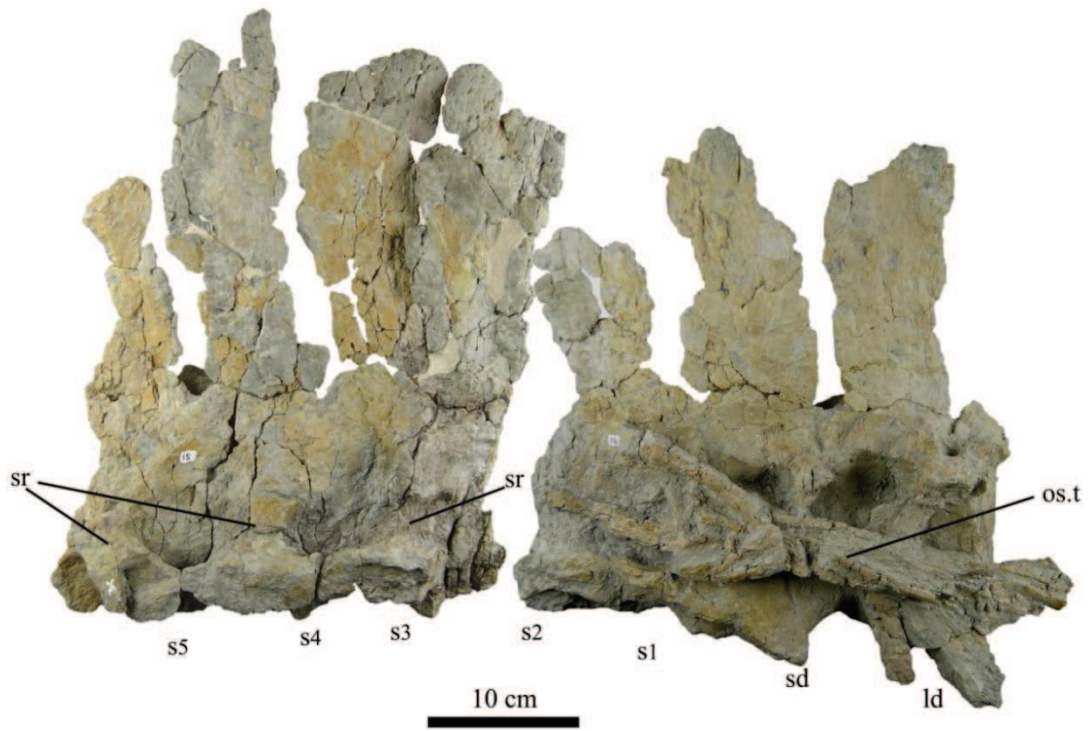


Figure 7

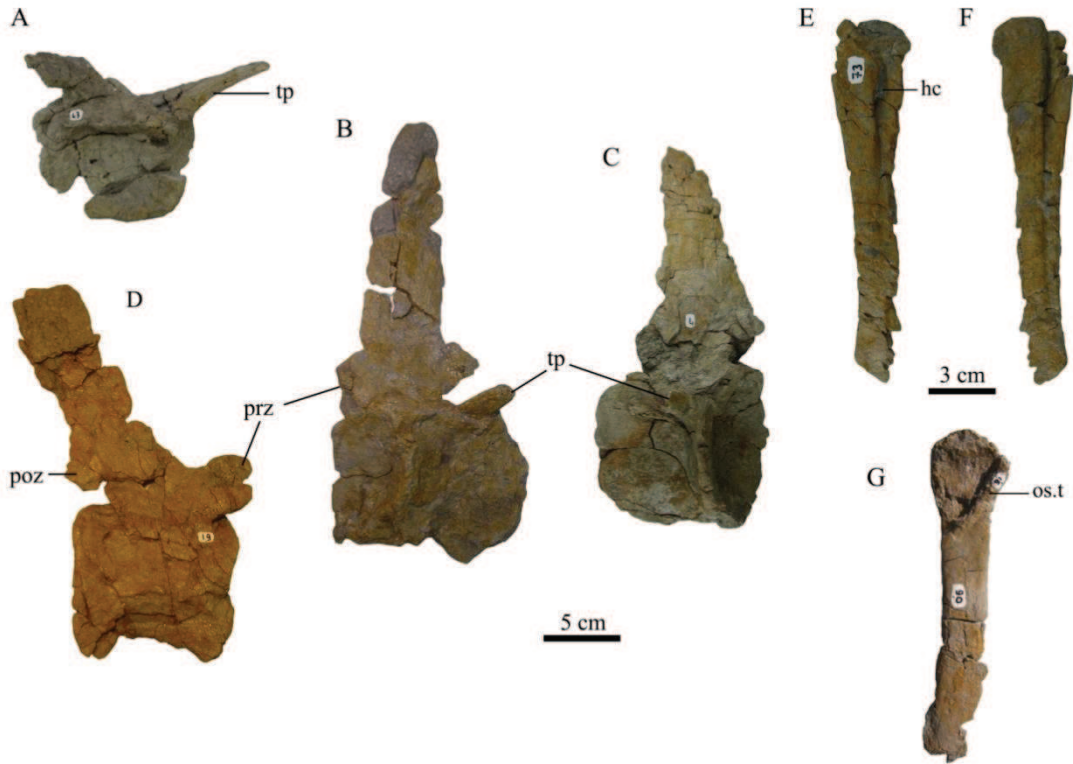


Figure 8



Figure 9

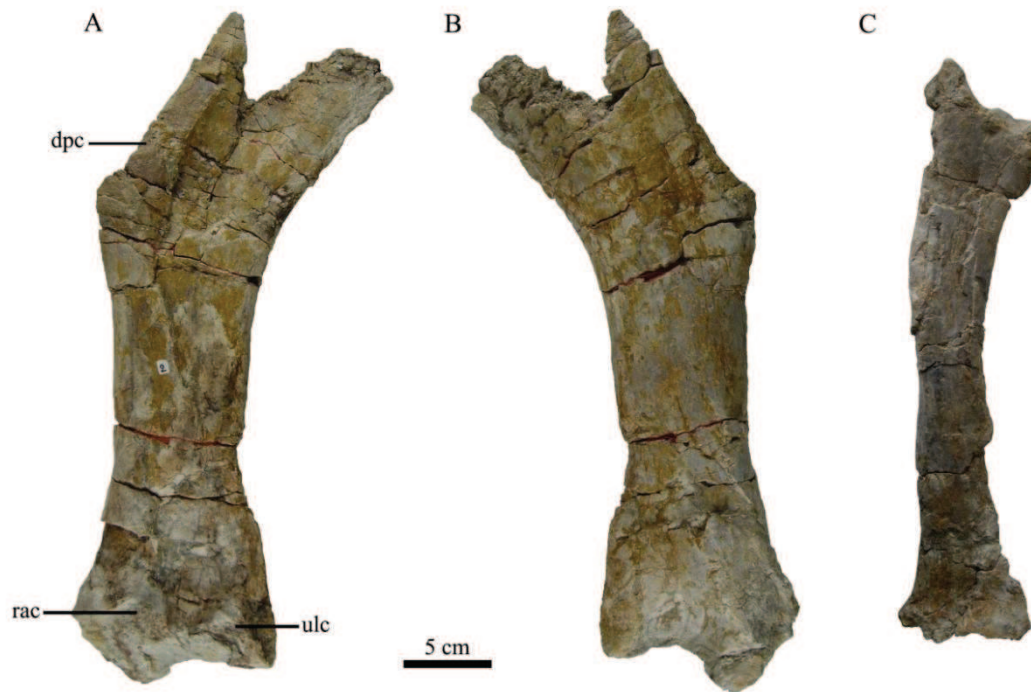


Figure 10

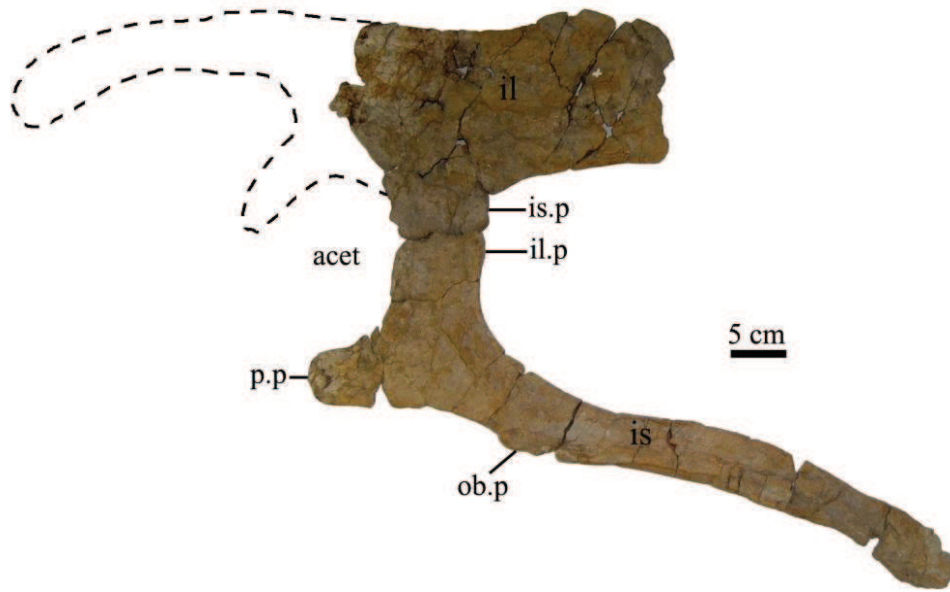


Figure 11

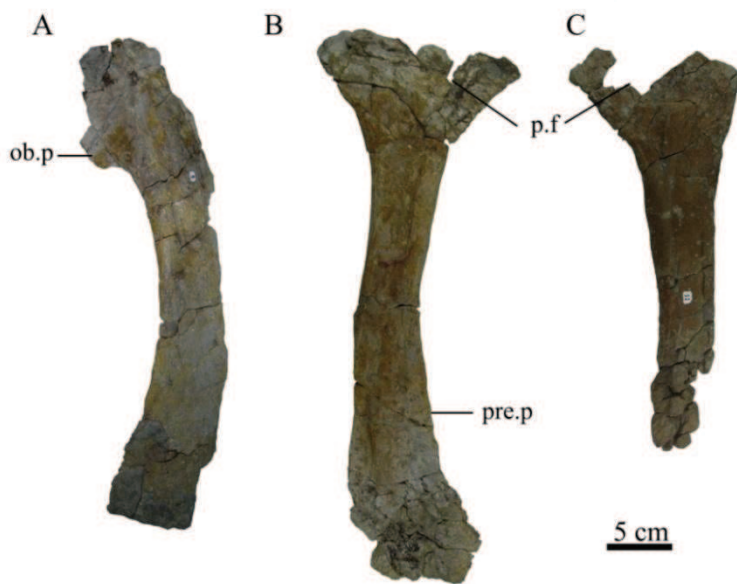


Figure 12

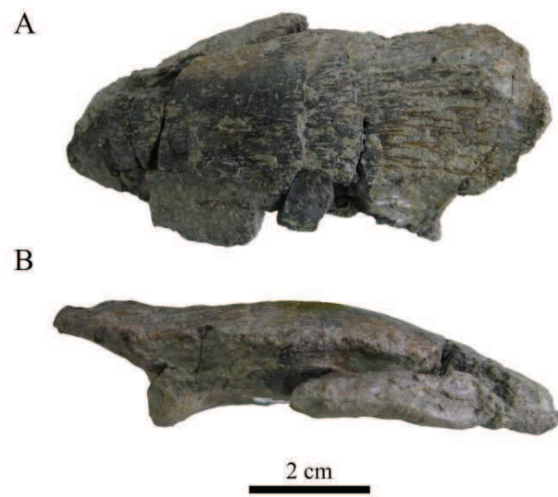


Figure 13

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Chapter 5:

Systematics

5.1 Discussion of the morphological variation in *Rhabdodon* and in Rhabdodontidae.

Rhabdodon remains from different localities in France described in the previous part reveal some morphological differences. The comparison between these new French specimens and with the taxa in Rhabdodontidae including *Rhabdodon priscus*, *Rhabdodon septimanicus*, *Zalmoxes robustus*, *Zalmoxes shqiperorum* (Matheron, 1869; Lapparent, 1947; Buffetaut and Le Lœuff, 1991; Buffetaut et al. 1996; Pereda-Suberbiola and Sanz, 1999; Pincemaille-Quillévéré, 2002; Pincemaille-Quillévéré, 2006; Weishampel et al., 2003; Godefroit et al., 2009) suggest the following aspects of the morphological variability.

5.1.1 Cranial aspects

I. *Premaxilla*

- The maxillary (posterolateral) process of the premaxilla is relatively short in *Zalmoxes robustus* while in the maxilla from Quarante, this process is prolonged with a more prominent recess on the medial surface to receive the premaxillary process of the maxilla.

- The external naris is more widely open in the specimen from Quarante.

These could suggest that at least two forms of snout are present among the rhabdodontids. The skull of *Rhabdodon* from Quarante has a distinctive long and widely open external naris with an arched nasal region whereas that of *Zalmoxes* has a short and relatively less prominent nasal region. However, both premaxillae do not show a flared beak as in hadrosaurine ornithopods.

II. Maxilla

- The premaxillary process of the maxilla is variable in *Rhabdodon* from different localities in France. The maxilla from Quarante has a longer premaxillary process than those of *Rhabdodon* from the Bellevue site and Highway A8 (Aix-en-Provence) and those of *Zalmoxes*.

The lengthened premaxillary process of the maxilla from Quarante corresponds to a posteriorly prolonged maxillary (posterolateral) process of the premaxilla from the same locality. The specimens from the Bellevue site and the Highway A8 (Aix-en-Provence) also suggest a short anterior region of the skull as in *Zalmoxes*.

III. Quadrate

- The asymmetrically developed articular condyles for the mandible of the quadrate are present in French specimens, as in the quadrates of *Zalmoxes*. Weishampel et al. (2003) mentioned that the asymmetry of the distal condyles associated with the orientation of the squamosal cotylus implies an oblique orientation of the quadrate relative to the sagittal plane of the skull. Consequently, this character is diagnostic not only for *Zalmoxes*, as reported by Godefroit et al. (2009), but for Rhabdodontidae as a whole. However, Godefroit et al. (2009) mentioned that the asymmetry of the distal condyles also characterizes the more derived hadrosaurid clade (Weishampel et al. 1993; Godefroit et al. 1998)

- The robustness of the quadrate shows some variability in French specimens although it is present in both Romanian species. The quadrate from Quarante is significantly more robust, especially for the mandibular articular condyles, as compared with the quadrates from Fox-Amphoux. This may reflect a difference in the mandibular joint and in the resistance against the masticatory force.

-The caudal protuberance beneath the quadrate head which is bounded by a postquadratic process of the squamosal is present as a narrow vertical buttress in French quadrates. This buttress is slightly shorter and rounded in *Zalmoxes robustus* while it is absent in *Zalmoxes shqiperorum*. The development of the caudal buttress appears to be also variable in *Tenontosaurus tilletti* and *Camptosaurus dispar* (Weishampel, 1984).

IV. Braincase

Two juvenile braincases referred to *Rhabdodon* from Cruzy and Fox-Amphoux do not show any significant differences between them but they can be distinguished from the braincase of *Zalmoxes*.

- The lateral walls of the foramen magnum of *Rhabdodon* are shorter than those of *Zalmoxes*.

- The paroccipital processes of *Rhabdodon* are directed more or less horizontally in occipital view while those of *Zalmoxes* are more curved and oriented more dorsally.

- The basiptyergoid processes of the braincase of *Rhabdodon* are relatively longer and directed more laterally than those of *Zalmoxes*.

V. Dentary

The morphological features of the dentary are clearly variable among the rhabdodontid dinosaurs. Buffetaut and Le Lœuff (1991) erected *Rhabdodon septimanicus* and distinguished this species from *R. priscus* on the basis of the diagnostic characters of the dentary from Montouliers. The new dentaries described in this thesis show a variability similar to that present in *R. septimanicus* in the following characters.

- The strong curvature of the alveolar row is regarded as one of diagnostic features of *Rhabdodon septimanicus* while most dentaries of *R. priscus* and *Zalmoxes* are relatively straight or slightly concave. However, a dentary discovered in the Late Campanian La Boucharde locality (Allain and Suberbiola, 2003) and the newly found dentaries from Quarante have a tooth row that is remarkably curved outward, as in *R. septimanicus*.

- The shelf lateral to the tooth row is usually present in *Rhabdodon* and *Zalmoxes* dentaries. This well-marked angled shelf is not obvious in a dentary from Bellevue and it is absent in the dentaries from Quarante and La Boucharde, as in *R. septimanicus*. However, the dentary of *R. septimanicus* shows a more smoothly rounded lateral surface.

- The coronoid process of the *R. septimanicus* dentary is in prolongation of the alveolar row. This character is also present in the dentaries from Quarante and La Boucharde while in other dentaries the distal part of the dentition is laterally shrouded by the anterior region of the coronoid process.

On the basis of the dentary characters, the dentary from La Boucharde is possibly referred to *Rhabdodon septimanicus*. Regarding the dentary from Quarante, besides the shared characters with *R. septimanicus*, it has a distinctively anteriorly displaced dentary symphysis and the anterior end is obviously curved downward. Moreover, its size is significantly larger than that of other dentaries. The dentary from Quarante may belong to an adult *R. septimanicus* in which the symphyseal region is well-developed and the general size is large, or it may belong to another species of the genus *Rhabdodon*.

Besides the variability of the dentary mentioned above, the coronoid process has two different forms, robust and gracile, in both *R. priscus* and *R. septimanicus*. Moreover, the inclination of the coronoid process is also shown in various degrees ranging from nearly 90° to 125°. These features may reflect sexual dimorphism and/or individual variation.

VI. Dentition

The most obvious type of variation in the teeth in Rhabdodontidae is the density of ridges on the tooth surface.

- The number of ridges on the buccal surface of maxillary teeth and the number of secondary ridges on the labial surface of dentary teeth of Rhabdodontidae can be divided generally into two groups. As shown in the scatter plot below (Figure 5.1), the number of ridges on the buccal surface of maxillary teeth of *Rhabdodon* is generally lower than that of *Zalmoxes*, however some maxillary teeth of *Rhabdodon* have a greater width. This happens to be the same in dentary teeth. The wider *Rhabdodon* dentary teeth do not bear more secondary ridges on the labial surface. When they are of the same size, teeth of *Zalmoxes* bear a greater number of ridges than those of *Rhabdodon*.

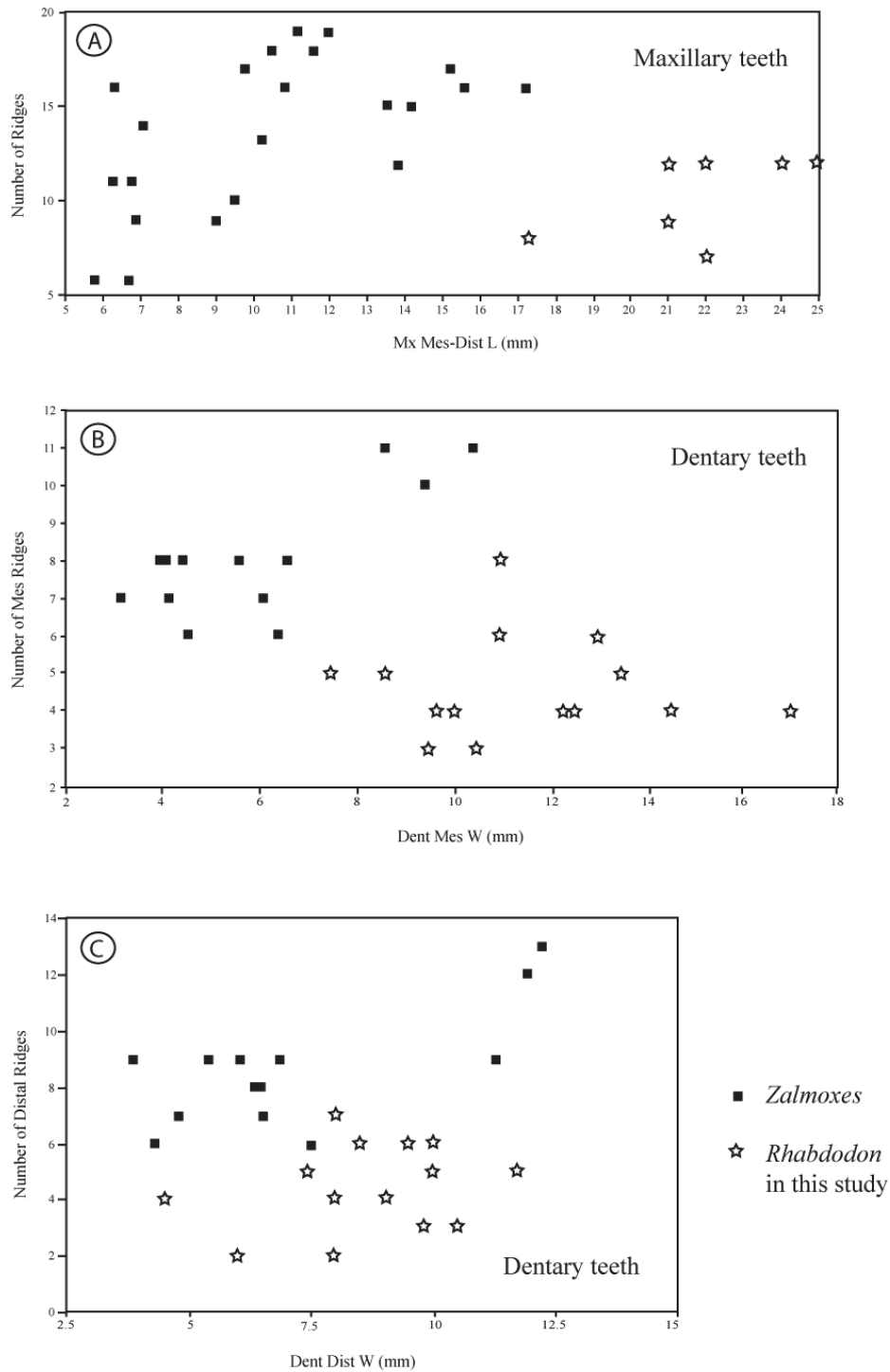


Figure 5.1 Scatter plots modified from Weishampel et al. (2003) and including the plots in figure 8; A) between the number of the ridges on the buccal surface of the maxillary crown and the tooth width (Mx Mes-Dist L), B) between the number of secondary ridges mesial to the primary ridge on the lingual surface of the dentary crown and the mesial width (Dent Mes W), C) between the number of secondary ridges distal to the primary ridge on the lingual surface of the dentary crown and the distal width (Dent Dist W).

5.1.2 Postcranial aspects

I. *Vertebrae*

- The neural spine of the dorsal vertebrae of *Rhabdodon* from southern France is much more prominent than in *Zalmoxes* (at least twice and a half higher than the height of the centrum). Among French specimens, the neural spine of adult individuals shows some differences. The dorsal vertebrae of the partial articulated skeletons of *Rhabdodon* from Vitrolles-Couperigne bear comparatively broader, but shorter neural spines (two-three times the height of the centrum) while in the dorsal vertebrae from Saint-Chinian, Fox-Amphoux and Villeveyrac (Buffetaut et al. 1996) the neural spines are four times taller than the centrum. This variation in French specimens may suggest sexual dimorphism.

II. *Scapula*

- Two distinct forms, robust and slender, are present in both *Zalmoxes* and *Rhabdodon*. The scapular neck of the robust scapula is not very constricted compared with the proximal articulation with the coracoid.

- The anterior rim of the scapula of *Zalmoxes* is nearly straight throughout its entire length while the anterior rim of the *Rhabdodon* scapula is slightly curved upward and diverges from the main shaft.

- The strong expansion of the posterodorsal border of the scapula is common in *Rhabdodon* as the anterior and posterior rims are widely divergent at the distal end. The dorsal expansion varies in *Zalmoxes robustus* (less expanded in the slender form and more so in the robust form)

Zalmoxes shqiperorum seems to have a distinctive scapula compared with other rhabdodontids. According to Weishampel et al. (2003) and Godefroit et al. (2009), the scapula of *Zalmoxes shqiperorum* possesses some autapomorphic characters in having a narrow, strap-like scapular blade with a sharply expanded posterodistal end and a prominent flared acromial process.

III. *Humerus*

- The robustness of the humeral shaft varies from robust to slender. Pereda-Suberbiola and Sanz (1999) remarked that the ratio of the humeral length to the minimal transversal diameter of the shaft ranges from 6 to 7 in a large humerus from Provence to 9-

10 in a small Transylvanian specimen. The robustness ratio of the humeri described in this work ranges widely from 5 to 9. It appears that the humeri of Rhabdodontidae are greatly variable in size, however this is probably related to the ontogenic changes as mentioned in Pereda-Suberbiola and Sanz's work.

- The deltopectosal crest is more distinctively projected anterolaterally in the the humeri of *Zalmoxes* than in those of *Rhabdodon*. Moreover, the deltopectoral crest of the humerus of *Zalmoxes shqiperorum* is particularly prominent, extending beyond the proximal half of the humerus while in other rhabdodontids this crest is limited to the proximal half of the humerus.

IV. Ilium

- The acetabulum of the ilium of *Zalmoxes robustus* is of limited extent, consisting of a narrow, shallow breach between the rugose pubic peduncle and the enormous, lenticular ischial peduncle while the acetabulum of *Rhabdodon* and *Z. shqiperorum* is well-developed and forms a concave rounded embayment on the ventral part of the ilium. This narrow acetabulum is an autapomorphic character for *Zalmoxes robustus*

- A supra-acetabular shelf is present on the dorsal margin of the ilium of *Zalmoxes* but it is absent in *Rhabdodon*.

- The preacetabular process of the ilium of *Zalmoxes* is remarkably twisted and faces ventrolaterally while that of *Rhabdodon* is more or less in the same plane as the iliac blade. The preacetabular process of ilia of *Rhabdodon* is strongly arched in some specimens and less so in others. The latter character may indicate individual variation/sexual dimorphism. This variation is also reported in *Hypsilophodon* (Galton, 1974 and 2009).

V. Ischium

- The obturator process is located on the proximal half of the ischial shaft in *Rhabdodon* while this process is absent in the ischium of *Zalmoxes*.

- The ischial shaft is notably curved ventrally in the ischium of *Zalmoxes*. This character was regarded as synapomorphic for *Zalmoxes*. According to new material of *Rhabdodon* from Vitrolles-Couperigne, the ventrally curved ischial shaft is present in *Rhabdodon* as well. This variability is also present in *Tenontosaurus tilletti* (Forster 1990). Consequently, this character is excluded from the diagnosis of the genus *Zalmoxes*.

- The distal end of the ischium is not significantly expanded in *Rhabdodon* and *Zalmoxes robustus* while the ischium of *Z. shqiperorum* ends with a boot-like expanded distal end.

VI. Pubis

- Two forms of the prepubic process are found among French specimens. The prepubic processes from Fox-Amphoux and Vitrolles form a flattened blade while the prepubic process from the Bellevue site is less compressed and has a rather rounded shaft. The prepubic process of *Zalmoxes* is very slender and forms a rod-like process.

- An enclosed oval prepubic foramen is present in all French specimens but it seems to be absent in *Zalmoxes shqiperorum*.

VII. Femur

- The robustness is also variable among adult specimens from France. The femoral shaft is significantly narrower than the proximal and distal ends in the gracile form while the femoral shaft is broad and not significantly different in width from the proximal end in the robust form. In *Zalmoxes*, the femur has a rather rounded and slender shaft compared with its extremities and its length.

- The femur of *Z. shqiperorum* bears a better developed lesser trochanter compared with other rhabdodontids.

- The study of new French specimens reveals that the fourth trochanter of some *Rhabdodon* femora is located beyond the midshaft of the femur, as in *Zalmoxes*. Therefore this character cannot not be regarded as synapomorphic for *Zalmoxe* contrary to the opinion of Weishampel et al. (2003).

5.1.3 Conclusion

1. According to morphological observations on new *Rhabdodon* remains from southern France, at least two species were represented, *Rhabdodon priscus* and *Rhabdodon septimanicus*. *Rhabdodon priscus* includes all specimens except the type specimen of *R. septimanicus*, a dentary from La Boucharde and the cranial material from Quarante. The dentary from the Late Campanian of La Boucharde is referred to *Rhabdodon septimanicus*. The cranial elements from Quarante provide sufficiently diagnostic characters to suggest another variety of *Rhabdodon* in France, however the dentary from Quarante shares three diagnostic characters with *R. septimanicus*. I therefore consider that the Quarante material can be referred to as *cf. Rhabdodon septimanicus*.

2. Besides the dentary that distinguishes *R. septimanicus* from *R. priscus*, there are no other sufficiently distinctive postcranial characters to describe French specimens as another different taxon. The variation within *Rhabdodon priscus* could be interpreted as the intraspecific variability. The differences in robustness as well as the differences in the neural spine probably suggest sexual dimorphism. However the extent of sexual dimorphism in the postcranial skeleton is poorly known. The different morphological features are possibly due to the individual or ontogenic variability as reported in other groups of Ornithopoda (Forster, 1990; Galton, 2009).

3. New data from French material confirm some diagnostic characters of *Rhabdodon* and suggest the exclusion of some synapomorphic characters of Rhabdodontidae and of *Zalmoxes* defined by Weishampel et al. (2003). The systematic and phylogenetic analysis will be reevaluated and discussed in the following part.

5.2 Phylogenetic relationships of *Rhabdodon*

As briefly mentioned in Chapter 2, since the first description of *Rhabdodon* this European taxon was diversely allied to hypsilophodontids, camptosaurids, iguanodontids and to the recently erected group of rhabdodontids. The study of Weishampel et al. (2003) apparently represents the most recent phylogenetic analysis which includes *Rhabdodon* in the cladogram. However in their work a great number of data about *Rhabdodon priscus* are missing. This study will follow mainly the cladistic analysis of non-hadrosaurid Euornithopoda of Weishampel et al. (2003) and also includes new data about *Rhabdodon priscus* in the dataset to reevaluate the relationships of Rhabdodontidae and the phylogenetic position of *Rhabdodon*.

The analyses were based on 15 terminal species following Weishampel et al. (2003). 75 characters (23 cranial, 12 dental and 40 postcranial) from Weishampel et al. (2003) matrix were polarized by successive out-group comparisons with *Heterodontosaurus tucki* and Marginocephalia. The description of new remains referred to *Rhabdodon priscus* from southern France provides some additional characters missing in previous works. Although the validity of *Rhabdodon septimanicus* is accepted in this work and new material referred to cf. *Rhabdodon septimanicus* is reported, most of its skeleton is still poorly known. I therefore do not include this species in this analysis.

Rhabdodon priscus has been recoded in the matrix of Weishampel et al. (2003) (See the matrix in Appendix III.2). Some differences in coding are noted in Appendix III.1. As coded in the dataset, *Rhabdodon priscus* is 60% complete instead of 40% in previous works.

The analysis was run under PAUP* (version 4.0b10 for 32-bit Microsoft Window, Swofford 2001) under a branch-and-bound search with both accelerated transformation (ACCTRAN) and delayed transformation (DELTRAN) options. All characters were run unordered without weighting.

5.2.1 Results

The analyses result in three most parsimonious trees of 151 steps with a consistency index (CI) of 0.530, a retention index (RI) of 0.770 and rescaled consistency index (RCI) of 0.408. The strict consensus tree which is given by this analysis is identical to that of Weishampel et al. 2003) in Figure X.

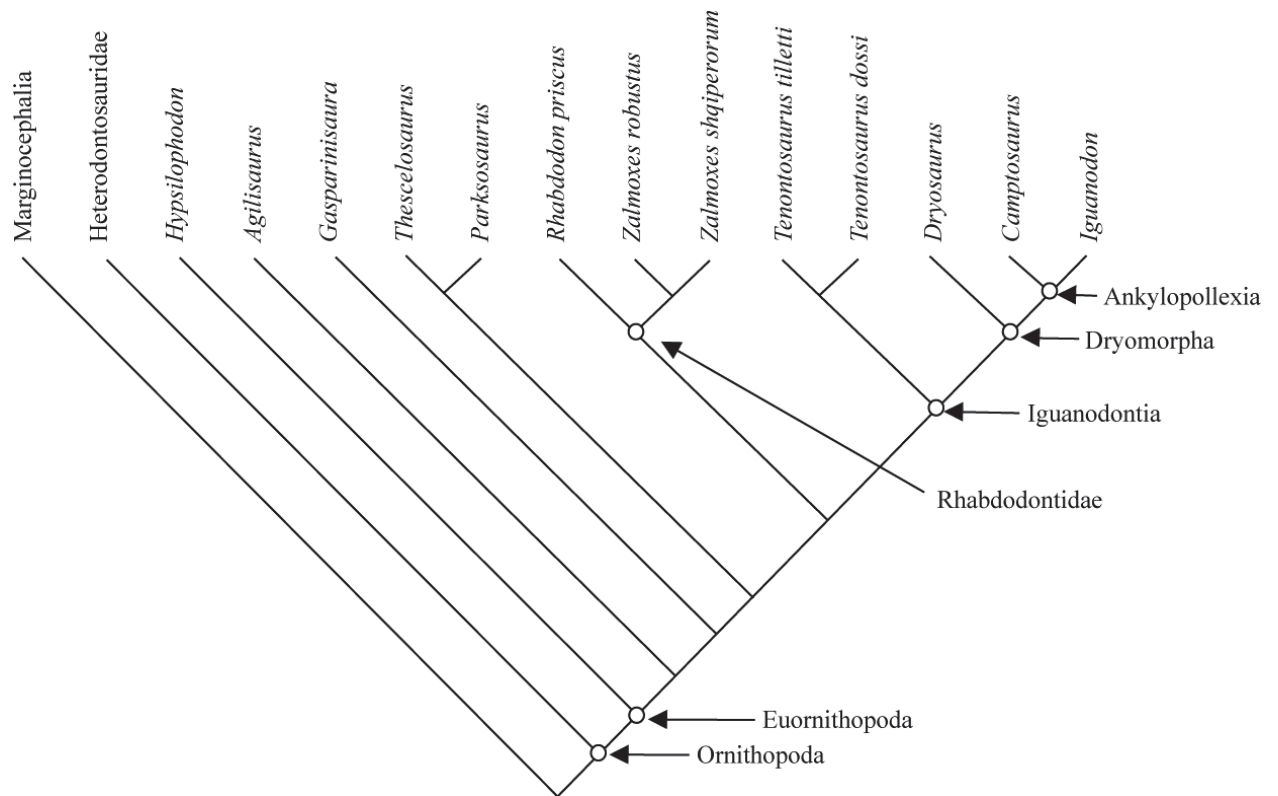


Figure 5.2 Consensus tree of the three most parsimonious trees from this study.

This study focused on the systematic revision of *Rhabdodon priscus*, together with *Zalmoxes* and Rhabdodontidae. Only the characters attributed to *Rhabdodon priscus* and *Zalmoxes* will be discussed in detail and associated with the morphological variation mentioned above to suggest the amended diagnoses of these taxa.

From the present cladistic analysis, *Rhabdodon* is distinguished from its sister group by the following characters:

1. Ossified epaxial tendons arranged in double-layered lattice. (character 42, identified with both ACCTRAN and DELTRAN; convergent in Ankylopollexia)
2. A wide scapular neck (character 43, identified with both ACCTRAN and DELTRAN; convergent in *Iguanodon*, *Hypsilophodon*, and the clade consisting of the common ancestor of *Parksosaurus* and *Thescelosaurus*)
3. Robust radius (minimum radial width is equal or more than 10% of radial length) (character 47, identified with DELTRAN, with ACCTRAN; it is a synapomorphy for Rhabdodontidae; convergent in Ankylopollexia and it is identified as an apomorphy of *Thescelosaurus*).

4. Hoof-shaped ungual of manual digits II-IV (character 54, identified with DELTRAN; with ACCTAN; it is a synapomorphy for Rhabdodontidae; convergent in *Iguanodon*).

5. An elongate flattened prepubic process (character 63, with both ACCTAN and DELTRAN; convergent in Iguanodontia). However, this feature shows a variability in the prepubis from Bellevue in which the rounded prepubic process is rather rounded than laterally flattened.

6. Hoof-shaped ungual of pedal digit II-IV (character 75, identified with DELTRAN; with ACCTAN; it is a synapomorphy for Rhabdodontidae; convergent in *Iguanodon*)

Zalmoxes robustus and *Zalmoxes shqiperorum* are united as sister-species on the basis of the following characters:

1. Long, narrow sternal process of the coracoid (character 44, identified with ACCTAN; with DELTRAN), this character is autapomorphic for *Z. shqiperorum*.

2. Deltopectoral crest emerges much more abruptly from the humeral shaft. (character 46, identified with both ACCTAN and DELTRAN; this character is convergent in *Tenontosaurus* and *Hypsilophodon*)

3. Strongly twisted preacetabular process of the ilium (character 56, identified in both ACCTAN and DELTRAN).

4. Absence of the obturator process (character 58 identified in both ACCTAN and DELTRAN; reversal of the condition at Euornithopoda)

5. Distinctly downwardly curved ischial shaft (character 60, identified in both ACCTAN and DELTRAN; convergent in Dryomorpha)

6. Ovoid to subcylindrical cross-section of the ischial shaft (character 61, identified in both ACCTAN and DELTRAN; convergent in Dryomorpha)

7. Distinctively bowed femur in anterior view (character 65, identified in both ACCTAN and DELTRAN; convergent in *Dryosaurus* and *Parksosaurus*)

In the present study, *Rhabdodon* and *Zalmoxes* form a node-based clade of Rhabdodontidae as in the analysis of Weishampel et al. (2003). According to this study, Rhabdodontidae is diagnosed by the following 3 features:

1. Expansion of the posterior process of the jugal to form the ventral margin of the infratemporal fenestra (character 11, identified with ACCTAN; with DELTRAN it is

apomorphic for *Z. robustus*, this feature is also apomorphic for *Agilisaurus* and convergently apomorphic for Dryomorpha)

2. More than 10 ridges on the lingual side of the dentary tooth crowns. (character 32, identified with both ACCTAN and DELTRAN)

3. A straight to slightly convex dorsal margin of the ilium in lateral view (reversal of character 55, identified with both ACCTAN and DELTRAN; this feature, a sinuous dorsal iliac margin, is apomorphic at the level of the clade consisting of the common ancestor of *Gasparinisaura* and Iguanodontia, it is also reversed in *Camptosaurus*).

3. Absence of metatarsal V (character 74, identified with ACCTAN; with DELTRAN it is restricted to be apomorphic to *Z. robustus*; it is also convergently apomorphic for Ankylopollexia).

5.3 Conclusion

1. *Rhabdodon* differs from *Zalmoxes* in having horizontally directed paroccipital processes, long and laterally directed basiptyergoid processes, a lower ridge density on the maxillary and dentary tooth crowns, prominently high neural spines on dorsal vertebrae (at least twice and a half higher than the height of the centrum), ossified epaxial tendons arranged in double-layered lattice, a wide scapular neck, an elongated flattened prepubic process, a straight to slightly bowed femur in anterior view, hoof-shaped unguals of manual and pedal digits II-IV.

2. Rhabdodontidae is considered as a sister group of Iguanodontia. It is diagnosed by the following features: more than 10 sharp ridges on the lingual side of the crowns of the dentary teeth, a straight to slightly convex dorsal margin of the ilium. Potential apomorphies of Rhabdodontidae include an expansion of the posterior process of the jugal to form the ventral margin of the infratemporal fenestra, a robust radius, hoof-shaped unguals of manual and pedal digits II-IV, the absence of metatarsal V.

3. An amended diagnosis of *Zalmoxes* may include the following features: deltopectoral crest emerging much more abruptly from the humeral shaft, strongly twisted preacetabular process of the ilium, absence of the obturator process, distinctly downwardly curved ischial shaft, ovoid to subcylindrical cross-section of the ischial shaft, distinctively bowed femur in anterior view.

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Chapter 6:

Discussion

6.1 Geographical and temporal distribution of *Rhabdodon*

Rhabdodon was initially erected on the basis of a dentary with its characteristic fluted teeth from La Nerthe (Bouches-du-Rhône, France) (Matheron, 1869). Medium-sized ornithopods, distinguished from other groups by this distinctive type of dentition have been recovered from several Late Cretaceous terrestrial localities and appear to be endemic to Europe (France, Spain, Romania, Austria and Hungary).

According to the previous works and this present study, a certain amount of diversity within this dinosaur group has been suggested. *Rhabdodon* and its sister taxon, *Zalmoxes* form a recently defined family, Rhabdodontidae Weishampel, Jianu, Cziki and Norman, 2003. At the moment, the non-hadrosaurid ornithopod remains discovered in France and Spain are referred to genus *Rhabdodon* and the remains from the Early Campanian of Austria and the Maastrichtian of Romania are referred to *Zalmoxes* (Weishampel et al., 2003; Sachs and Hornung, 2006, Godefroit et al., 2009). The material from Hungary does not provide sufficiently diagnostic features to define it at the generic level, it is consequently considered as Rhabdodontidae indet. on the basis of the teeth (Osi, 2004). The remains from the Santonian Iharkut locality of Hungary seem to be the oldest among the rhabdodontid dinosaurs.

Rhabdodon is widely distributed in Campanian-Maastrichtian continental localities of southern France as mentioned in Chapter 3. The earliest appearance of *Rhabdodon* in France is represented by *Rhabdodon priscus* remains from the Early Campanian of Villeveyrac basin (Buffetaut et al., 1996). The age of Villeveyrac basin has been confirmed recently by the magnetostratigraphic study of Benammi et al. (2006). The most recent remains of *Rhabdodon* seem to be from the Vitrolles-La-Plaine locality which is dated as Maastrichtian (Valentin et al. 2009).

Both *Rhabdodon priscus* and *R. septimanicus* (including cf. *R. septimanicus* described in this study) from the Saint-Chinian area were discovered in the Grès à Reptiles

Formation (Late Campanian - Early Maastrichtian). The type of *Rhabdodon septimanicus* was found at a locality near Montouliers while a productive site, Masecaps, yielding *Rhabdodon priscus* is located at the neighbouring village, Cruzy. Despite the fact that the precise dating of most of the French localities is usually difficult and is still uncertain, it cannot be excluded that these two species coexisted during the same time interval as in the case of *Zalmoxes robustus* and *Z. shqiperorum* which are regarded as sympatric (Godefroit et al., 2009).

The Late Campanian to Maastrichtian dinosaur fauna of southern France is dominated by *Rhabdodon* and titanosaurs. This faunal assemblage seems to be replaced during the late Maastrichtian by a different assemblage, from which *Rhabdodon* is absent and in which hadrosaurs play an important part (Le Lœuff et al., 1994). The co-occurrence of *Rhabdodon* and a basal hadrosaurid in southern France is reported from a Maastrichtian locality in Provence (Valentin et al., 2009). *Rhabdodon* and the hadrosaurids apparently occupied a similar ecological niche in the Maastrichtian. They most probably competed for food resources. With the evolutionary success of their jaw mechanism and dentition, the hadrosaurs may have started to occupy that niche in southern France prior to the Late Maastrichtian and finally replaced *Rhabdodon* in the Late Maastrichtian.

6.2 Paleobiogeographical implications

The fossil record shows that *Rhabdodon* is distributed in southern France over a long period ranging from Campanian to Maastrichtian. As revealed in the phylogenetic study, the European family, Rhabdodontidae, is a close relative to Iguanodontia. As described in Chapter 4 and according to previous studies (Pincemaille-Quillévéré, 2002; Chanthasit et al. in review), *Rhabdodon* shares several osteological characters in particular the postcranial elements with *Tenontosaurus tilletti*. This could suggest that the common ancestor of the rhabdodontid dinosaurs evolved in North America, and then dispersed to Europe. For much of the Jurassic and Cretaceous, Europe was composed of several major islands and some of which had occasional contact with North America or Asia. The split-up of the Euroamerican palaeogeographical province during the Aptian caused the European taxa to evolve separately from North American taxa (Upchurch et al., 2002).

As discussed in the preceding chapter, *Zalmoxes* can be clearly distinguished from *Rhabdodon*, it indicates that these two rhabdodontids evolved separately in geographical

isolation. The geographical and temporal distribution of *Rhabdodon* and *Zalmoxes* suggest that these two taxa diverged as early as the Early Campanian.

In the Late Cretaceous, Europe was indeed a vast archipelago; the southern, western, central and eastern domains of Europe consisted of a string of medium to small-sized islands separated from each other by shallow epicontinental seas (Pereda-Suberbiola, 2009) (Figure 6.1). The taxonomic variability among Rhabdodontidae would be the result of geographical, ecological (island) and temporal (localities with various stratigraphic positions) variability.

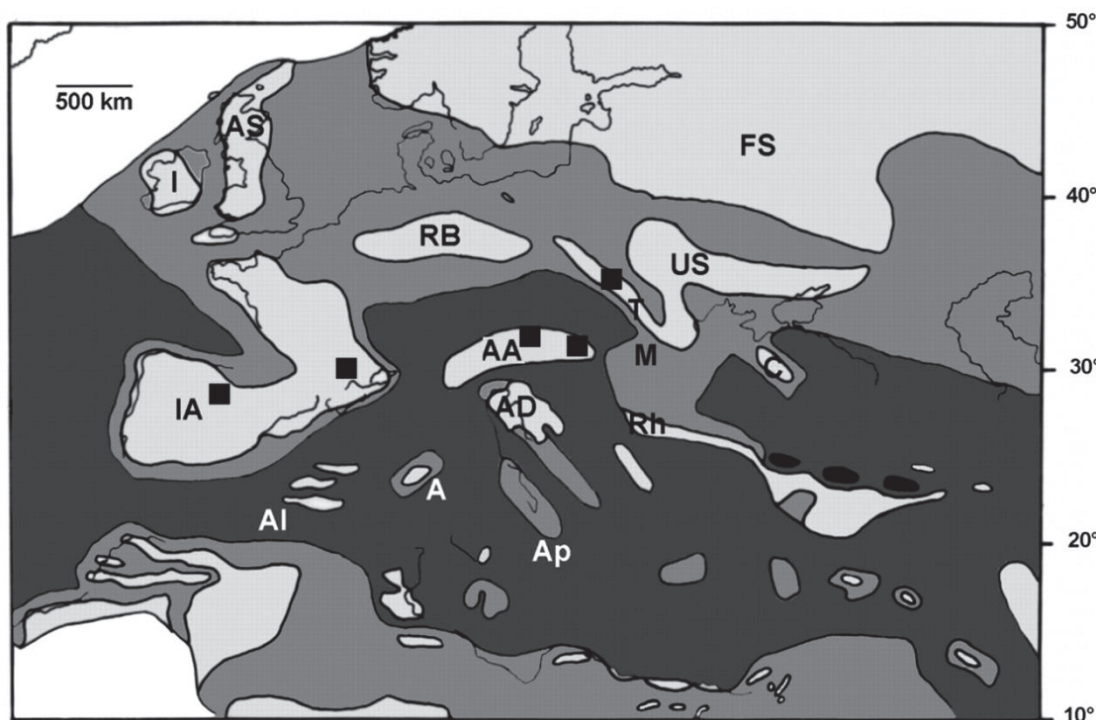


Figure 6.1 Simplified palaeogeographical map of Europe and Peri-Tethyan area between latitudes 10° and 50° N for the Late Cretaceous (Maastrichtian), the black squares indicate the distribution of Rhabdodontidae. Key: A, Apennine platform; AI, Alboran islands; Ap, Apulian platform; AA, Austroalpine island; AD, Adriatic-Dinaric island; AS, Anglo-Scottish island; C, Crimean island; FS, Fennoscandian shield; I, Irish island; IA, Ibero-Armorican island; M, Moesian platform; RB, Rhenish-Bohemian island; Rh, Rhodope; T, Transylvanian basin; US, Ukrainian shield. Colour marks: light, exposed land; light grey, epicontinental seas; dark grey, oceanic basins; white, unknown; black, volcanics. (Modified from Pereda-Suberbiola, 2009)

However, the palaeobiogeographical affinities of the Late Cretaceous continental fauna of Europe are complex. The faunas are commonly considered to show a mixed pattern resulting from the addition of "Asiamerican" and Gondwanan forms to European taxa. An example from southern France is provided by the dromaeosaurid, *Variraptor mechinorum* which shows the closest affinities with the Asian taxa (Chanthasit and Buffetaut, 2009) (APPENDIX IV) while in this study *Rhabdodon* is considered as relatively close to North American taxa.

6.3 Feeding

The information concerning the jaw function is quite poor as the cranial elements related to the jaw mechanism are rarely found. A pleurokinetic jaw mechanism could be suggested for *Rhabdodon*. The posterior broadening of the maxillary process of the premaxilla provides a loosened maxilla-premaxilla joint and allows the lateral motion of the maxilla. The dentition of *Rhabdodon* shows an elaborate pattern. The maxillary and dentary teeth are covered with a thicker layer of enamel on one side than on the other. The thickly enameled surface is more durable to wear so that a sharp edge is formed while the thinly enameled surface is less resistant and forms an obliquely inclined occlusal surface. The sharp edge would provide the cutting action. The wear of the longitudinal ridges on the thickly enameled surface provides the serrations which enhance the sharpness of the cutting edge. The surangular bears a well developed lateral lip shrouding the lateroventral portion of the quadrate. This structure indicates a strong attachment for the ligaments and thus stability at the quadrate-mandible joint. The robust dentary and a well-developed coronoid process indicate a powerful jaw closure. This could be related to a resistant type of food. The narrow premaxillae influence the shape of the beak that is also narrow. As suggested by Weishampel et al. (2003), *Zalmoxes* had the potential to be a selective feeder by using its narrow beak to select preferred food items. *Rhabdodon* could also have same feeding habits.

6.4 Posture and locomotion

A great number of ossified tendons over the sacrum and the neighbouring area around the posterior dorsal and anterior caudal vertebrae suggest that the vertebral column was probably held more or less in horizontal position. *Rhabdodon* may have been primarily quadrupedal. It has a robust forelimb. The humerus possesses a well-developed deltopectoral crest. The ulna bears a prominent olecranon. The manus is short and robust. It is likely that the forelimb supported the body weight and was adapted for standing or walking as a quadruped. However, the metacarpals were not firmly packed together and with a short manus and forearm, *Rhabdodon* was probably incapable of rapid quadrupedal locomotion but probably stood bipedally for rapid locomotion. The tibia is shorter than the femur and the position of the fourth trochanter is relatively low compared with the condition in a cursorial animal (Gregory, 1912). These characters limited the capacity of *Rhabdodon* for fast running. On the basis of the osteological description, a reconstruction of *Rhabdodon* can be proposed as shown on the following figure.

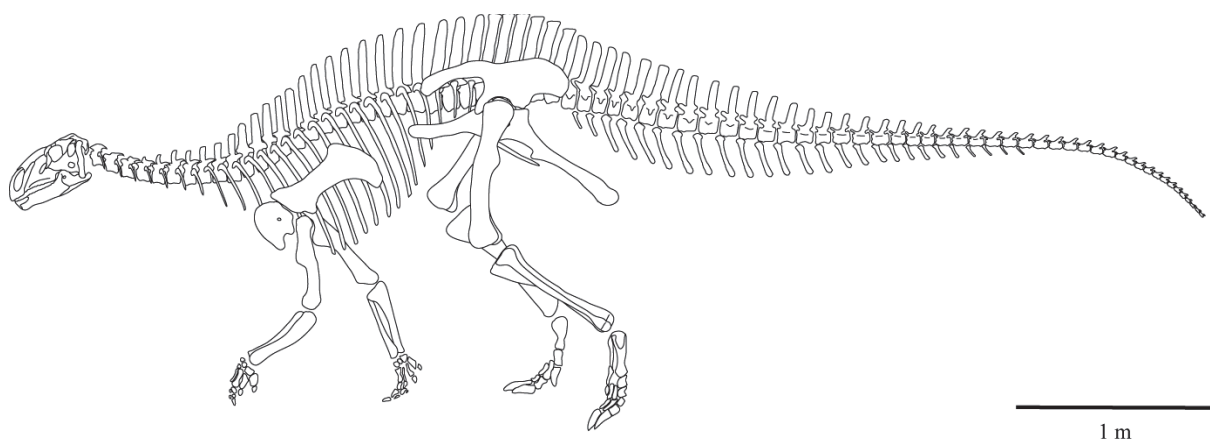


Figure 6.2 A skeletal reconstruction of *Rhabdodon* based on composite elements from southern France.

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Chapter 7:

Conclusions

The study of the ornithopod dinosaur *Rhabdodon* from the Late Cretaceous of France can be concluded as follows:

7.1 The validity of *Rhabdodon septimanicus*

The study of undescribed material of *Rhabdodon* having been discovered in various localities in southern France provides more information on the osteology of *Rhabdodon*. New cranial elements have been described. Most of them have been discovered at a locality near the village of Quarante (Hérault) and it can be assumed that these elements belong to a single individual. The material from Quarante, particularly the premaxilla, maxilla and dentary, shows several distinctive characters and can be distinguished from the material from other localities. The premaxilla bears an elongated posterolateral (maxillary) process and a large opening of the external naris. The premaxillary process of the maxilla from Quarante is relatively long compared with those of other localities. Nevertheless, the dentary from Quarante shares diagnostic characters with that of *Rhabdodon septimanicus* Buffetaut & Le Lœuff, 1991. Consequently, on the basis of the dentary the Quarante material can be referred to as cf. *Rhabdodon septimanicus*. Furthermore, the *Rhabdodon* remains from Quarante provide additional elements and diagnostic characters for *R. septimanicus*. The morphological diagnosis of *R. septimanicus* including the Quarante material supports the validity of this species. However, besides the skull, no postcranial elements referred to *R. septimanicus* can be distinguished from other taxa.

7.2 The variation of the genus *Rhabdodon*

There is some morphological variation in the cranial and postcranial skeleton between *Rhabdodon* specimens from different localities and between specimens coming from the same locality. Concerning the cranial skeleton, excluding the diagnosis of the dentary of *R. septimanicus* and of the maxilla from Quarante mentioned above, the dentaries of *Rhabdodon* show robust and gracile coronoid processes and various degrees of coronoid

process inclination. In the postcranial skeleton, there are some differences in the development of neural spines, in the robustness of the pectoral girdle and limb bones and in various features of the pelvic bones. These morphological differences are not distinct and are insufficient to define French specimens as another separate taxon. Consequently, the variation within *Rhabdodon priscus* could be interpreted as an intraspecific variability which is possibly due to individual or ontogenic variability or sexual dimorphism. However the associated cranial and postcranial material of *R. septimanicus* is still unknown, it cannot be excluded that some postcranial bones which show the morphological differences could belong to *R. septimanicus*. In the present state of our knowledge, it can be concluded that two species, *Rhabdodon priscus* and *Rhabdodon septimanicus*, were represented in the Late Cretaceous of France. *R. septimanicus* can be distinguished from *R. priscus* by the dentary diagnosis defined by Buffetaut and Le Lœuff (1991) and the diagnostic characters of referred material from Quarante mentioned above.

7.3 Anatomical comparison and systematics

Rhabdodon is placed in Rhabdodontidae with its sister taxon, *Zalmoxes*. The new specimens described in this work suggest several distinctive morphological features between *Rhabdodon* and *Zalmoxes* especially the postcranial elements. The osteological description of new specimens from southern France allows the reassessment of the phylogenetic relationships of *Rhabdodon* among Rhabdodontidae and with other Euornithopoda. This study follows the most recent cladistic analysis by Weishampel et al. (2003). New data from French material of *Rhabdodon priscus* have been recoded in the matrix of Weishampel et al. 2003 with 18 additional characters which were missing in previous work (APPENDIX III).

In spite of the fact that the phylogenetic position of *Rhabdodon* given by the present study is in agreement with previous work, French material suggests the exclusion of some synapomorphic characters of Rhabdodontidae and of *Zalmoxes* defined by Weishampel et al. (2003). The anatomical comparison and the phylogenetic analysis suggest an amended diagnosis of *Rhabdodon*, of *Zalmoxes* and of Rhabdodontidae.

7.4 Paleobiology

Rhabdodon was most likely a facultatively bipedal ornithomimid with at least occasional quadrupedal locomotion. It is characterized primarily by its elaborate dentition and probably had a sophisticated mastication. *Rhabdodon* appears to be exclusively distributed in Europe ranging from the Early Campanian to the Early Maastrichtian. It is probably represented only in France and Spain as the remains from Romania and Austria are referred to its sister taxon *Zalmoxes* (Pereda-Suberbiola and Sanz, 1999; Weishampel et al., 2003; Sachs and Hornung, 2006, Godefroit et al., 2009) and the Hungarian material has not yet been verified at the generic level (Ôsi, 2004) nevertheless the teeth are clearly different from those of *Rhabdodon*.(Buffetaut, pers.comm. 2010)

The phylogenetic study suggests that the European family, Rhabdodontidae, is a close relative to Iguanodontia. Among the iguanodontids, *Rhabdodon* is particularly close to *Tenontosaurus tilletti* as they share several postcranial features. This could suggest that the common ancestor of the rhabdodontid dinosaurs evolved in North America, and then dispersed to Europe. *Rhabdodon* and *Zalmoxes* eventually evolved separately on the European archipelago. The geographical and temporal distribution of *Rhabdodon* and *Zalmoxes* suggest that these two taxa diverged as early as the Early Campanian.

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APPENDIX I

Rhabdodontid Locality List

APPENDIX I : Rhabdodontid Locality List

Country	Region	Department	Locality	Stratigraphic Horizon	Age	Faunal List	Rhabdodontid Material
France	Midi-Pyrénées	Ariège	Le Mas d'Azil	Grès de Labarre	Late Campanian- Early Maastrichtian	Chelonia, Crocodylia, Saltasauridae, Nodosauridae, <i>Rhabdodon</i>	incomplete humerus, caudal vertebra, phalanges
			Anticlinal de Dreuilhe	Grès de Labarre	Late Campanian- Early Maastrichtian		caudal vertebra, a fragment of femur, metatarsus
	Languedoc- Roussillon	Aude	Bellevue	Lower Marnes de la Maurine	Early Maastrichtian		dentary, teeth, postcranial material
			Campagne- les-Bains	Grès des Estous	Early Maastrichtian	Lepisosteidae, Chelonia, Eusuchia, Saltasauridae, Nodosauridae, Dromaeosauridae, <i>Rhabdodon</i>	postcranial material
			Rennes-le- Château	Marnes de la Maurine	Early Maastrichtian		dentary, ulna, caudal vertebra
	Hérault	Villevyrac		dark sandy clay of Fuvelian	Early Campanian	Sparidae, Lepisosteidae, Anura, Chelonia, Eusuchia, Nodosauridae, Dromaeosauridae, <i>Rhabdodon</i>	teeth and postcranial elements (Buffetaut et al. 1996)
			Saint Chinian	Grès à Reptiles	Late Campanian- Early Maastrichtian	<i>Rhabdodon sp.</i>	vertebrae
			Quarante	Grès à Reptiles	Late Campanian- Early Maastrichtian	Chelonia, Crocodylia, Saltasauridae, Nodosauridae, <i>Rhabdodon</i>	cranial elements, a pair of dentary, caudal vertebra

Country	Region	Department	Locality	Stratigraphic Horizon	Age	Faunal List	Rhabdodontid Material
France	Languedoc-Roussillon	Hérault	Montouliers	Grès à Reptiles	Late Campanian- Early Maastrichtian	Chelonia, Theropoda, Maniraptora, Saltasauridae, Nodosauridae, <i>cf Rhabdodon</i> , <i>Rhabdodon septimanicus</i>	dentary (type) (Buffetaut and Le Lœuff, 1991), braincase (Pincemaille-Quillévéré et al. 2006), maxillary fragment, long bone fragment, phalanges, unguals
			Massecaps	Grès à Reptiles	Late Campanian- Early Maastrichtian		some cranial elements and postcranial material
			Combebelle	Grès à Reptiles	Late Campanian- Early Maastrichtian		2 femora
			Sainte-Foy	Grès à Reptiles	Late Campanian- Early Maastrichtian	Lepisosteidae, coelacanth, Chelonia, Amphibia, Squamata, Crocodilia, Pterosauria, Dromaeosauridae, Enantiornithes, Saltasauria, Nodosauridae, <i>Rhabdodon</i> , Mammalia	femoral fragment
			Plo Saint Pons	Grès à Reptiles	Late Campanian- Early Maastrichtian		vertebra, sacrum, ilia
			Mont Plo Nord	Grès à Reptiles	Late Campanian- Early Maastrichtian		vertebrae, femur,
			Quarante	Grès à Reptiles	Late Campanian- Early Maastrichtian		cranial elements, vertebra, fibula fragment
	Gard	Champ-Garimond	red clays of Begudo-Rognacien	Maastrichtian	Lepisosteidae, coelacanth, Chelonia, Amphibia, Squamata, Crocodilia, Pterosauria, Dromaeosauridae, Saltasauria, Nodosauridae, <i>Rhabdodon</i>	teeth, vertebra, fragment of humerus	

Country	Region	Department	Locality	Stratigraphic Horizon	Age	Faunal List	Rhabdodontid Material
France	Provence-Alpes-Côte d'Azur	Bouches-du-Rhône	Vitrolles-Couperigne	sandy marl of Lower Rognacian	Early Maastrichtian	Crocodylia, another reptile, <i>Rhabdodon priscus</i>	cranial elements, 2 partial articulated skeletons (Pincemaille-Quillévére, 2002)
			La Boucharde	Fluvio-lacustrine sandstone of Begudian	Late Campanian-Early Maastrichtian	Chelonia, Crocodylia, Dromaeosauridae, Saltasauria, Nodosauridae, Ceratosauria, <i>Rhabdodon</i>	cranial and post cranial material
			La Nerthe	lacustrine marl of upper Rognacian	Maastrichtian	Chelonia, Crocodylia, Saltasauria, <i>Rhabdodon priscus</i>	dentary (Type), teeth, postcranial material (Matheron, 1869)
			Roques-Hautes	Red marl with lenticular sandstone of Lower Rognacian	Early Maastrichtian	Crocodylia, Dromaeosauridae, <i>Rhabdodon</i>	femur
			Rousset	Clay and sandstone of Lower Rognacian	Early Maastrichtian	<i>Rhabdodon</i>	femur
	Var	Métisson	Grès à Reptiles	Late Campanian-Early Maastrichtian	Chelonia, Crocodylia, Abelisauridae, Dromaeosauridae, Saltasauria, Nodosauridae, <i>Rhabdodon</i>	teeth, vertebrae, femora, tibiae, metatarsi, phalange	

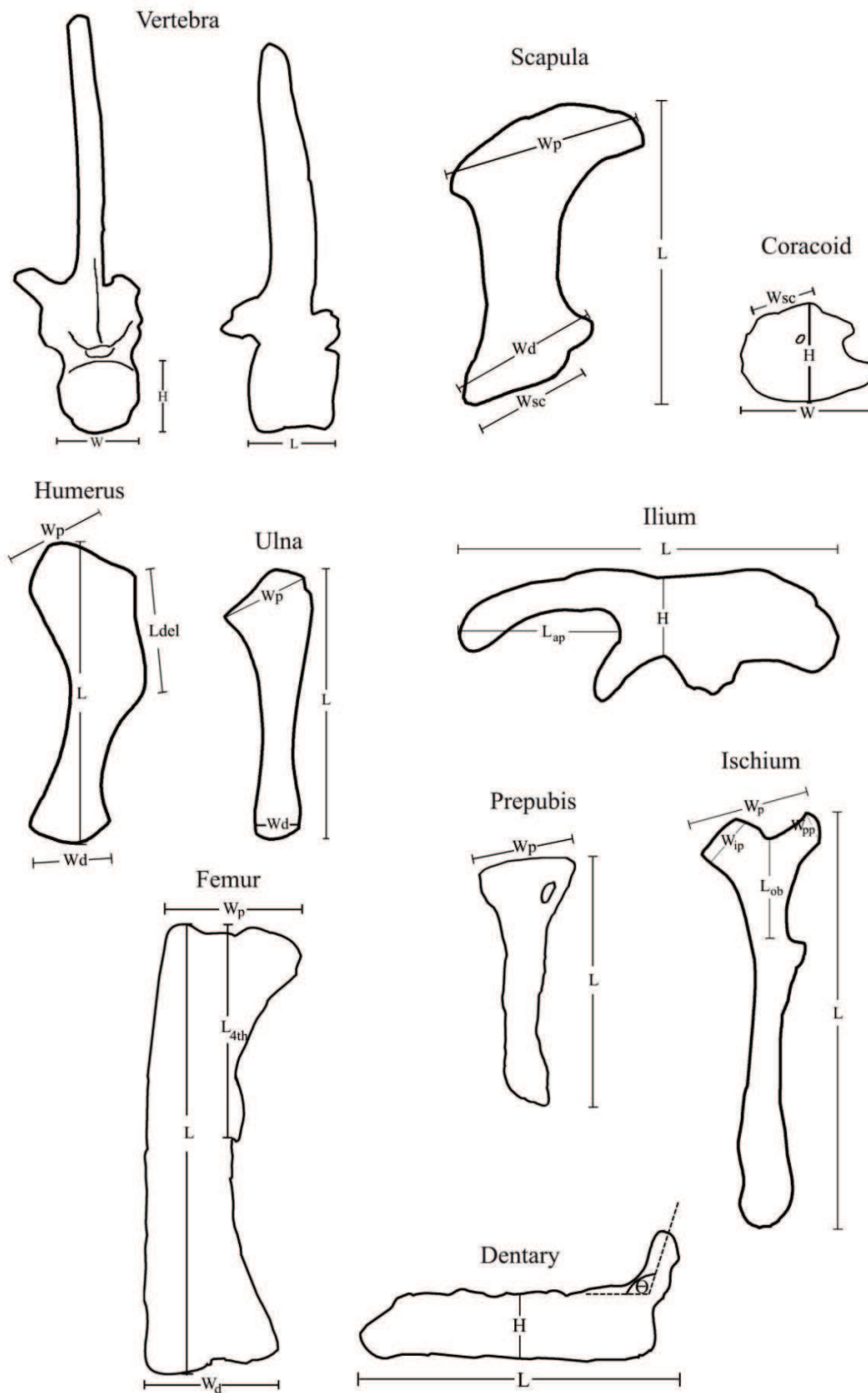
Country	Region	Department	Locality	Stratigraphic Horizon	Age	Faunal List	Rhabdodontid Material
France	Provence-Alpes-Côte d'Azur	Var	La Bastide Neuve	Grès à Reptiles	Late Campanian-Early Maastrichtian	Chelonia, Crocodylia, Pterosauria, Abelisauridae, Dromaeosauridae, Enantiornithes, <i>Gargantuavis</i> , Saltasauria, Nodosauridae, <i>Rhabdodon</i>	cranial and postcranial material
			Basségat	Grès à Reptiles	Late Campanian-Early Maastrichtian		vertebrae, fragment of femur, tibia, metatarsus, phalanges
			Mourfrey champ	Grès à Reptiles	Late Campanian-Early Maastrichtian		vertebrae, femur, tibia, metatarsus
Spain	Castilla y León	Burgos	Laño	L1A, L1B, L2 of Laño quarry	Late Campanian	Chondrichthyes, Osteichthyes, Chelonia, Amphibia, Squamata, Crocodylia, Pterosauria, Dromaeosauridae, Saltasauria, Nodosauridae, <i>Rhabdodon</i> , mammalia	teeth, vertebrae, humerus, femora (Pereda-Suberbiola and Sanz, 1999)
Austria	Niederösterreich	Wiener Neustadt	Muthmannsdorf	Grünbach Formation, Gosau Group	Early Campanian	Chelonia, Crocodylia, Pterosauria, Nodosauridae, <i>Zalmoxes</i>	Dentary, teeth, fragment of parietal, fragment of scapula, radius?, femur, tibia, manual ungual (Sachs and Hornung, 2006)
Hungary	Central Transdanubia	Veszprém	Iharkút	Csehbánya Formation	Santonian	fish, frog, turtle, crocodile, Theropoda, Nodosauridae, Rhabdodontidae	Teeth, dentaries (Osi, 2004)

Country	Region	Department	Locality	Stratigraphic Horizon	Age	Faunal List	Rhabdodontid Material
Romania	Transylvania	Hunedoara	Sânpetru	Sânpetru Formation	Maastrichtian	Chelonia, Amphibia, Squamata, Crocrodilia, mammalia, Theropoda, Sauropoda, Ankylosauria, <i>Zalmoxes robustus</i> and <i>Z. shqiperorum</i>	cranial and postcranial material (Weishampel et al., 2003)
			Nălaț-Vad	Sânpetru Formation	Maastrichtian	birds, mammalia, Theropoda, Sauropoda, <i>Zalmoxes shqiperorum</i>	cranial and postcranial material (Godefroit et al. 2009)
		Sălaj	Someș Odorhei	Jibou Formation	Maastrichtian	Chelonia, Crocrodilia, <i>Zalmoxes</i>	vertebrae, scapula (Codrea and Godefroit, 2008)

APPENDIX II

**The anatomical measurements of the *Rhabdodon*
elements described in this work**

Appendix II.1: Diagram showing the basis of the measurements of the specimens.



The measurements of other long bones use the same basis as for the femur

L = Total length, Wp = Width of the proximal end and Wd = Width of the distal end

Appendix II.2 Origin of the specimens:

CM = Fox-Amphoux localities

MC-CY.QR/MC-QR = Quarante locality

MC-M = Masecaps locality, Cruzy

MC-MN = Mont-plo locality

MC-MOB = Montouliers locality

MC-PSP = Plo-Saint-Pons locality

MC-VC = Combebelle locality

MDE-C2 = Le Pylône locality, Campagne-sur-Aude

MDE-C3 = Bellevue locality, Campagne-sur-Aude

MDE-C4 = Campagne-les-Bains locality, Campagne-sur-Aude

MDE-D = Montouliers locality

MDE-RC = Rennes-le-Château locality

MDE-Vil = Villeveyrac locality

Appendix II.3 Table of measurements of dentaries.

No.	L/R	L	H	θ	No. of alvioli
CM-587	L	>186	54	-	9
CM-443	R	236	52	125	9
CM-709	L	152	38	115	9
MC-CY.QR 1	R	330	6.3	104	11
MC-CY.QR 2	L	368	6.3	110	11
MC-M23	L	177	3.7	114	10
MDE-C3 1280	L	126	30.0	91	9
MDE-C3 1407	L	>180	53	120	10

Appendix II.4 Measurements of maxillary teeth.

No.	Mesial-distal length (Tooth Width)(mm)	Number of ridges
CM-297	24	12
CM-326	25	12
CM-554	22	12
MC-M 4190	17	8
MDE-C3 892	21	12
MDE-C3 1412	22	7
MNH_AIX_PV_Fox	21	9

Appendix II.5 Measurements of dentary teeth.

No.	Mesial width (mm)	No.of mesial ridges	Distal width (mm)	No.of distal ridges
CM-462	9.5	3	8.5	6
CM-475	9.7	4	7.97	2
CM-502	12.3	4	11.7	5
CM-503	17	4	9.8	3
CM-504	14.5	4	9.5	6
CM-505	11	6	8	7
CM-506	7.5	5	4.5	4
CM-507	11	8	10	6
CM-508	12.5	4	9	4
CM-655	10.5	3	6	2
MC-M 3583	13.5	5	10.5	3
MDE-C3 809	13	6	10	5
MDE-D27	10	4	8	4
MDE-D37	8.6	5	7.4	5

Appendix II.6 Measurements of vertebrae (mm).

Nature	No.	L	W	H
Atlas	CM-86	21	38	33
Axis	MC-4058	58	29	32
Anterior cervical	CM-679	39	47	38
	MC-M 30	28	29	>12
	MDE-C3.1417	35	27	32
Posterior cervical	CM-441	49	47	60
Anterior dorsal	CM-379	28	38	48
Middle dorsal	CM-142	43	38	39
	CM-445	63	58	59
	CM-446	37	47	55
	CM-581	75	48	60
	CM-527	40	47	50
	CM-710	60	57	63
	MC-MN 32	77	59	53
	MDE-C3 1556	72	55	56
Posterior dorsal	CM-3	59	56	81
	CM-416	57	82	77
	CM-496	39	45	43
	MC-M 948	58	54	55
	MC-M 1149	53	57	46
	MC-M 2705	37	34	39
	MC-M 3395	50	47	55
	MC-M 3896	50	46	46
	MC-M 4012	52	60	46
	MDE-C3 413	50	63	56
	MDE-C3 973	65	57	60
	MDE-C3 1400	65	56	65
	MDE-C3 03.50	65	64	51
	MNHN 8	64	43	62

Nature	No.	L	W	H
Dorsal?	MC-M 626	34	38	38
	MC-M 1116	34	35	31
	MC-M 1080	36	41	36
	MC-M 220	55	72	59
	MC-M 261	58	49	54
	MC-M 38	56	68	57
	MDE-C3 02.102	68	79	85
	MDE-C3 02.137	62	64	61
Anterior caudal	CM-403	59	55	85
	CM-404	42	69	74
	CM-569	49	61	64
	CM-585	43	50	50
	CM-688	79	57.5	98
	MC-M 0950	55	60	49
	MC-M 2483	59	72	76
	MC-M 4028	35	36	39
	MC-MN 30	62	53	51
	MC-MN 36	42	63	68
	MDE-C3 35	65	60	70
	MDE-C3 110	62	65	72
	MDE-C3 257	61	65	61
	MDE-C3 337	67	86	91
	MDE-C3 343	31	40	43
	MDE-C3 344	68	85	88
	MDE-C3 507	70	67	56
	MDE-C3 611	72	70	73
	MDE-C3 655	64	85	62
	MDE-C3 775	64	60	70
	MDE-C3 881	50	60	65
	MDE-C3 1136	68	60	60
	MDE-C3 1145	58	90	80
	MDE-C3 1177	30	14	20
	MDE-C3 1183	79	38	47
	MDE-C3 1197	75	59	70
	MDE-C3 1421	62	52	65

Nature	No.	L	W	H	
Proximal-Mid caudal	CM-2	75	60	60	
	CM-389	50	55	70	
	CM-469	42	34	59	
	CM-525	43	59	73	
	CM-653	43	38	48	
	MC-M 3589	36	38	41	
	MC-PSP 5	46	51	48	
	MDE-C3 109	67	62	76	
	MDE-C3 416	74	80	83	
	MDE-C3 980	68	48	68	
	MDE-C3 1191	47	35	44	
	MDE-C3 1414	65	54	68	
	MDE-Vil 39	48	23	42	
	MHN.AIX.PV.2001.12	61	67	71	
	MHN.AIX.PV.2001.16	74	69	66	
	MHN.AIX.PV.2001.20	69	63	63	
	MHN.AIX.PV.2001.112	73	47	77	
	Mid-caudal	CM-4	76	49	55
		CM-378	59	33	50
		CM-386	67	47	70
CM-387		70	40	60	
CM-388		57	40	75	
CM-401		71	34	57	
CM-402		71	42	64	
CM-447		86	63	64	
CM-448		83	33	61.5	
CM-575		80	45	68	
CM-583		77	43	88	
CM-596		81	40	59	
CM-613		56	39	48	
CM-646		80	44	58	
CM-A1		81	36	62	
CM-A3		61	46	60	
MC-M 4119		54	45	43	
MDE-C3 28		81	50	65	

Nature	No.	L	W	H
Mid-caudal	MDE-C3 106	82	63	78
	MDE-C3 107	92	49	63
	MDE-C3 249	72	53	56
	MDE-C3 823	77	55	53
	MDE-C3 990	75	40	50
	MDE-C3 995	63	50	55
	MDE-C3 996	65	43	55
	MDE-C3 1152	82	42	45
	MDE-C3 1152	70	58	58
	MDE-C3 1156	78	45	57
	MDE-C3 1176	66	42	67
	MDE-RC 10-9	85	50	58
	MDE-C2.82.8	78	38	45
	Posterior caudal	CM-8	72	37
CM-176		63	31	38
CM-420		56	17	30
CM-421		51	23	28
CM-422		42	21	25
CM-439		79	37	54
CM-454		52	28	39
CM-491		56	23	29
CM-518		53.5	25	36
CM-601		55.5	22	28
CM-614		56	27.5	37
CM-627		71	30	37
MC-M 1414		69	50	47
MDE-C3 36		82	46	68
MDE-C3 108		73	47	73
MDE-C3 504		86	40	53
MDE-C3 967		49	25	29
MDE-C3 1128		-	35	35
MDE-C3 1282		77	38	53
MDE-C3 1300		74	38	38
MDE-C3 03.45		53	36	47
MDE-C3 08.55		79	37	47

Nature	No.	L	W	H
Posterior caudal	MDE-C3 08.59	76	38	52
	MHN.AIX.PV.1999.76	65	54	41
	MHN.AIX.PV.1999.77	85	50	-
	MHN.AIX.PV.2000.7	54	35	29.3
	MHN.AIX.PV.2001.13	61	25	46

Sacrum	MC-PSP 1	sc	s1	s1	s3	s4	s5	
		L	40	45	42	36	38	56
		W	36	35	34	24	21	20

Appendix II.7 Measurements of appendicular skeleton (mm).

Nature	No.	L/R	L	Wp	Wd	Wm	Wsc
Scapula	CM-611	R	400	185	275	98	130
	MDE-C3.321	L	423	-	-	85	133
	MDE-C3.1013	L	470	200	-	95	150
	MDE-C3.1559	R	> 220	63	-	-	-
			H	W	Wsc		
Coracoid	CM-534	L	145	177	100		
	CM-612	L	171	225	120		
	MC-M 2567	R	-	167	93		
	MDE-C3.994	L	92	82	62		
	MDE-C3.735	R	115	120	80		
	MDE-C3.457	R	145	153	83		
			L	Wp	Wd	Ldel	Wm
Humerus	CM-451	L	359	122	98	120	51
	CM-472	L	310	107	87.7	102	54
	CM-597	L	>285	102	80	110	60
	MC-M 0029	L	325	-	-	185	37
	MC-M 3925	L	260	73	69	124	44
	MC-M 4765	L	280	96	79	154	50
	MDE-C3.993	R	233	61	52	120	51
	MDE-C4.9	L	260	68	62	130	-
	MNHN-034	L	380	107	90	190	60
	MNHN-035	R	>330	112	107	160	57
Ulna	CM-481	L	>245	-	63		
	MDE-C3.1171	R	276	86	46		
	MDE-C3.1196	R	163	48	28		
	MDE-RC.4.01	R	322	105	56		
Radius	CM-610	R	225	46.5	55		
	CM-629	R	273	±54	83		
	MDE-C3.118	R	350	-	115		
	MDE-C3.1003	R	250	50	56		

			L	Wp	Wd		
Metacarpal	CM-399		37	25	20		
	CM-663		60	31	22		
	CM-702		69	31	22		
	MDE-C3.597		78	33	-		
Ilium	CM-377	R	L 345	Lap 92	H 92		
	CM-397	L	345	97	112		
	CM-531	R	323	122	85		
	CM-567	R	425	147	110		
	CM-635	L	285	98	67		
	CM-686	L	119	-	44		
	MC-PSP3	L	>222	-	81		
	MDE-C3.1050	R	-	162	-		
	MDE-D 157.28	R	535	228	106		
Pre-pubis	CM-630	R	L 317	Wp 150	Wd 47		
	MDE-C3.04.95	L	309	131	37		
Ischium	CM-398	L	L 490	Wp 160	Hob 111	Wip 55	Wpp 29
	CM-433	R	490	150	112	63	43
	CM-565	L	540	±170	140	59	40
	CM-566	L	367	122	113	45	32
	MC-M 1252	L	-	70	87	-	-
	MC-M 1960	L	±227	75	60	-	22
	MC-M 2111	L	-	>65	75	27	-
	MC-M 3180	R	-	-	95	31	-
	MC-M 4821	R	-	105	104	41	29
	MC-MOB sn	R	420	190	113	75	40
	MDE-C3.115	R	-	163	111	60	43
	MDE-C3.439	L	-	128	119	-	-
	MDE-C3.722	L	-	150	120	66	45
	MDE-C3.991	L	-	146	110	±47	31
MDE-C3.02.152	R	320	94	97	35	18	

			L	Wp	Wd	L4th	4th	
Femur	CM-287	R	±375	90	110	188	80	
	CM-519*	L	>350	90	90	-	58	
	CM-543	L	530	150	162	300	82	
	CM-608	L	535	160	>130	310	85	
	MC-M1955	R	>260	75	70	130	60	
	MC-M3088	R	340	105	120	180	80	
	MC-MN41	R	500	168	200	245	85	
	MC-VC8	L	±570	±152	±190	±280	100	
	MC-VC9*	R	>580	-	±180	±290	96	
	MDE-C3.146*	L	-	170	-	280	100	
	MDE-C3.114	L	405	110	120	190	70	
	MDE-C3.267	R	530	170	190	295	9.5	
	MDE-C3.338	R	540	170	180	280	95	
	MDE-C3.349	L	±385	97	107	190	75	
	MDE-C3.546	R	199	34	50	-	-	
	MDE-C3.739*	L	±360	80	110	180	56	
	MDE-C3.972*	L	±410	95	120	190	67	
	MDE-C3.974	L	610	170	175	290	90	
	MDE-C3.978	L	540	165	>160	310	110	
	MDE-C3.992	R	>305	-	-	152	60	
	MDE-C3.1118	L	570	150	190	280	100	
	MDE-C3.1168	L	560	±140	170	±270	90	
	MDE-C3.1270	L	360	90	±90	-	-	
	MHN_AIX_PV_ 2008.1.11	R	258	64	72	134	54	
				L	Wp	Wd		
	Tibia	CM-139	R	420	105	145		
CM-364		R	380	100	150			
CM-631		R	455	91	145			
MC-M3115		R	>163	-	48			
MDE-C3.112		L	275	84	93			
MDE-C3.195		L	-	92	-			
MDE-C3.300		?	>470	235	-			
MDE-C3.310		L	485	144	150			
MDE-C3.975		R	485	105	151			

			L	Wp	Wd
Tibia	MDE-C3.1129	R	435	125	145
	MDE-C3.1189	R	335	90	102
	MDE-C3.1194	R	490	62	114
	MDE-C4.06	L	>275	80	±70
Fibula	CM-677	L	>290	75	27
	CM-667	L	390	68.5	31
	MC-MOB 62	L	±410	72	32
	MC-MOB 85	L	±400	89	36
	MC-3072	R	284	45	23
		I-IV	L	Wp	Wd
Metatarsus	CM-116	II	144	84	46
	CM-449	IV	121	44	34
	CM-590	II	130	61	38
	CM-632	I	117	71.5	55.3
	CM-634	II	132	80	38
	MC-874	III	115	45	30
	MDE-C3.374	III	127	47	28
	MDE-C3.510	I	68	47	31
			L		
Phalange	MC-M 36		19		
	MC-M 37		21		
	MC-M 1222		22		
	MC-MOB 9		50		
	MC-MOBsn		32		
Ungual	CM-600		65		
	MC-M 221		37		
	MC-M 541		40		
	MC-M 570		53		
	MC-M 814		40		
	MC-M 2812		38		
	MC-M 4232		30		
	MC-M 4729		48		
	MC-MOBsn1		22		
	MC-MOBsn2		70		

APPENDIX III

APPENDIX III.1

Based on the new French remains described in this thesis, *Rhabdodon priscus* has been recoded in the matrix of Weishampel et al. (2003). Some additional characters of *Z. shqiperorum* from Godefroit et al. (2009) missing in previous analysis have been also coded. Some differences in coding are following:

13. *Paroccipital process, horizontal and slightly widened distally (0), distinctly pendant distal end (1)*. The paroccipital processes of the braincase from France laterally direct more or less horizontally and its distal ends are not distinctively expanded. It is therefore coded as (0).

14. *Supraoccipital. Supraoccipital forms the dorsal margin of the foramen magnum (0), supraoccipital is excluded from participating in the dorsal margin of the foramen magnum by the paired exoccipitals (1)*. The supraoccipital forms partly the dorsal margin of the foramen magnum in *R. priscus*; it is coded as (0)

22. *Coronoid process shape, oblique and short (0), distinctly elevated (1)*. The coronoid process of *Rhabdodon dentary* is elongated dorsally; it is coded as (1).

23. *Shrouding of the distal dentition by the coronoid process, the dentary dentition ends immediately prior to the elevation of the coronoid process (0), the distal extent of the dentary dentition is laterally shrouded by the anterior region of the coronoid process (1)*. The distal dentition is shrouded by the anterior region of the coronoid process of the dentary in *R. priscus*. It is coded as (1)

25. *Number of maxillary teeth 12 or fewer tooth positions (0), between 13 and 15 (1), more than 15 positions (2)*. All maxillae of *R. priscus* bear less than 12 tooth position. This character is coded as (0)

30. *Number of dentary tooth positions. 13 or fewer tooth positions (0), between 14 and 17 positions (1), 18 or more positions (2)*. Most of *Rhabdodon dentary* has less than 13 tooth positions, it is coded as (0)

37. *Number of dorsal vertebrae, 15 or fewer (0), 16 or more dorsals (1)*. At least 16 dorsal vertebrae were found with the partial articulated skeleton of *R. priscus* (Pincemaille-Quillévéré, 2002). It is consequently coded as (1)
41. *Hypaxial tendons within the tail. absent (0), present (1)*. Ossified tendons are found also on the tendon of *R. priscus*. It is coded as (1)
42. *Ossified epaxial tendons longitudinally arranged along the epaxial region of the dorsal, sacral and caudal vertebrae (0), epaxial tendons arranged in a double-layered lattice (1)*. The ossified tendons associated with the partial articulated skeleton of *R. priscus* from Vitrolles were found in two forms on the dorsal and sacral vertebrae. The first form is long and somehow longitudinal arranged and the second one is relatively short and obliquely oriented. It could be therefore coded as (1).
46. *Deltopectoral crest of the humerus rounded in lateral view (0), emerges much more abruptly from the humeral shaft and angular profile to the crest*. The humerus of *R. priscus* bear a prominent deltopectoral crest but this crest do not emerge much more abruptly from the humeral shaft. This character is coded as (0)
47. *Robust radius. gracile (minimal radial width is lesser than 10%) (0), robust (minimal radial width is equal to or greater than 10% radial length) (1)*. The radii of *R. priscus* has minimal width equal or greater than 10%. It is therefore coded as (1)
54. *Hoof-shaped ungula of manual digits II and III. claw-like (0), hoof-shaped (1)*. The ungual of pedal digits in *R. priscus* is hoof-shaped. It is coded as (0).
56. *Precetabular process of the ilium same plane as the iliac body (0), distinctly twisted (1)*. The precetabular process of *R. priscus* is in the same plane as the iliac body, coded as (0).
57. *Acetabulum and supra-acetabular rim. Relatively large and concave with a dorsal supra-cetabular rim (0), narrow and reduced no supra-acetabular rim (1). Relatively large and no supra-acetabular rim (2)*. In this study, another condition is added. The

ilium of *R. priscus* and *Z. shqiperorum* has a large and concave but the supra-acetabulum rim is absent.

61. *Cross-section of the ischial shaft laterally flattened in cross-section (0), ovoid to subcylindrical (1)*. The ischial shaft of *Rhabdodon* is transversely compressed thus it is coded as (0).

69. *Position of the fourth trochanter entirely on the proximal half of the femur (0), at midshaft or on the distal half of the femur (1)*. The fourth trochanter of several femora from southern France is located at the midshaft of the femur, this character is therefore coded as (1) (contra Weishampel, 2003)

74. *Metatarsal V. present (0), absent (1)*. This character was coded as (1). It is coded as unknown (?) in this work. Although, the metatarsal has never been found, it is still uncertain whether the Metatarsal V is present in *R. priscus*.

75. *Hoof-shaped unguals in pedal digits II-IV. claw-shaped (0), hoof-shaped (1)*. The ungual in pedal digits of *R. priscus* is in hoof-shaped however it is pointed at the distal end.(1)

APPENDIX III.2 Taxon-Matrix (modified from Weishampel et al. 2003)

	10		20		30		40		50		60		70			
Ancestor	0000	0	00000	0	0	00000000	0000000000	000	0	000000	0000000000	0000000000	0000000000	000	0	0
Marginocephalia	0000	0	00000	0	0	00000000	0000000000	000	0	000000	0000000000	0000100000	0000000000	000	0	0
Heterodontosauridae	0000	0	00100	0	0	10000000	0010000010	000	0	000000	0000010000	0000000000	0000000001	000	0	0
<i>A.multidens</i>	0?00	1	0?000	1	1	00000???	010?201002	001	0	000000	???0000000	?000000100	0020000000	000	0	0
<i>Th.neglectus</i>	1??0	?	?????	?	1	11???????	010??01002	001	0	101011	1010001000	0000100100	0021010010	?00	0	0
<i>P.warreni</i>	1?10	1	??0??	?	1	????0???	0??22110?2	001	?	??1011	1010000???	????10?100	0021101000	?00	0	0
<i>H.foxii</i>	0000	0	00000	0	1	00001000	0000001011	101	1	100001	1010100000	0000000100	0020000000	001	0	0
<i>G.cincosaltensis</i>	0?10	1	????0	0	?	0001????	01??001110	00?	?	1??1??	100001????	????1001??	??20001000	0??	?	0
<i>T.tilletti</i>	1111	1	10011	0	0	10011110	1112010010	100	1	111110	1000110000	0110100100	0011010011	100	0	0
<i>T.dossi</i>	1111	?	10011	0	0	10?1??10	1?11010010	100	1	1?0110	10000?0?0?	01?0100100	0011010011	100	0	0
<i>D.altus</i>	0110	0	10110	1	0	100????1	0112211111	100	1	1?0110	000?010000	?1?0100111	1110110001	111	0	0
<i>D.lettowvorbeckii</i>	0110	0	10110	1	0	100??011	0112111110	100	1	1?0110	0000010???	?1?0100111	1110110001	111	0	0
<i>C.dispar</i>	1110	0	11110	1	0	10110111	1112210111	100	0	101110	0100011111	1110000111	1111010011	101	1	0
<i>I.atherfieldensis</i>	1110	1	11110	1	0	11110111	1112210112	100	0	111110	0110011111	1111100111	1111011111	111	1	1
<i>I.bernissartensis</i>	1110	1	11110	1	0	11110111	1112210112	100	0	111110	0110011111	1111100111	1111011111	111	1	1
<i>R.priscus</i>	????	?	?????	?	?	00??????	111?011010	111	1	1?111?	1110011???	???1002100	0011010011	1??	?	1
<i>Z.robustus</i>	1011	?	00001	1	0	10010101	1112022010	111	1	1??11?	??0?1?????	????011001	10?1110011	1??	1	?
<i>Z.shqiperorum</i>	????	?	?????	?	1	?????????	111??????0	111	1	1??1??	1001???????	????012001	1121110?11	1??	?	?

A, “*Agilisaurus*”; *Th*, *Thescelosaurus*; *P*, *Parksosaurus*; *H*, *Hypsilophodon*; *G*, *Gasparinisaura*; *T*, *Tenontosaurus*; *D*, *Dryosaurus*; *C*, *Camptosaurus*; *I*, *Iguanodon*; *R*, *Rhabdodon*; *Z*, *Zalmoxes*

APPENDIX IV

New data on the Dromaeosauridae (Dinosauria: Theropoda) from the Late Cretaceous of southern France

PHORNPHEN CHANTHASIT¹ and ERIC BUFFETAUT²

Key-words – Dinosauria, Dromaeosauridae, Late Cretaceous, France

Abstract. – Since the first discovery of dromaeosaurid remains from the Late Cretaceous of southern France, two genera and species, *Variraptor mechinorum* LE LOEUFF & BUFFETAUT, 1998, and *Pyroraptor olympius* ALLAIN & TAQUET, 2000, have been erected. Their validity and possible synonymy have been debated. New remains of Dromaeosauridae from Late Campanian – Early Maastrichtian localities near Cruzy (Hérault) and Fox-Amphoux (Var) are described. A sacrum from Hérault is remarkably comparable to that of *Variraptor*. An ilium from Fox-Amphoux and the holotype sacrum of *Variraptor mechinorum* probably belong to the same individual. Shared elements between *Variraptor* and *Pyroraptor* do not show any diagnostic characters. The question of the synonymy between *Variraptor* and *Pyroraptor* is still unresolved on the basis of these new specimens. Nevertheless, the available evidence suggests that these two species may be valid. The specimens from Cruzy suggest that faunal interchange between Europe and Asia lasted longer than that between Europe and North America, and that European dromaeosaurids evolved on their own during the Late Cretaceous isolation of Europe.

Données nouvelles sur les Dromaeosauridae (Dinosauria: Theropoda) du Crétacé supérieur du Sud de la France

Mots-clés. – Dinosauria, Dromaeosauridae, Crétacé supérieur, France.

Résumé. – Depuis la première découverte de restes de Dromaeosauridae dans le Crétacé supérieur du Sud de la France, deux genres et espèces, *Variraptor mechinorum* LE LOEUFF & BUFFETAUT, 1998, et *Pyroraptor olympius*, ALLAIN & TAQUET, 2000, ont été créés. Leur validité et leur possible synonymie ont fait l'objet de discussions. De nouveaux restes de Dromaeosauridae provenant de gisements d'âge campanien supérieur – maastrichtien inférieur près de Cruzy (Hérault) et de Fox-Amphoux (Var) sont décrits. Un sacrum venant de l'Hérault est remarquablement comparable à celui de *Variraptor*. Un ilion de Fox-Amphoux et le sacrum (holotype) de *Variraptor mechinorum* appartiennent probablement au même individu. Les éléments en commun à *Variraptor* et *Pyroraptor* ne montrent pas de caractères diagnostiques. La question de la synonymie entre *Variraptor* et *Pyroraptor* demeure non résolue d'après ces nouveaux spécimens. Toutefois, les données disponibles suggèrent que ces deux espèces peuvent être valides. Les spécimens de Cruzy suggèrent que les échanges fauniques entre l'Europe et l'Asie persistent plus longtemps que ceux entre l'Europe et l'Amérique du Nord, et que les Dromaeosauridae européens évoluèrent indépendamment pendant l'isolement de l'Europe au Crétacé supérieur.

INTRODUCTION

Dromaeosaurids were first reported from France by Buffetaut *et al.* [1986] on the basis of some teeth from Late Cretaceous sediments of Provence and Languedoc. A few years later, dromaeosaurid postcranial remains were found at the Maastrichtian locality of Roques-Hautes, Bouches-du-Rhône [Le Lœuff *et al.*, 1992]. Later, a dromaeosaurid humerus and vertebrae were discovered at the Bastide Neuve locality (Fox-Amphoux, Var) in the "Grès à Reptiles" Formation (Late Campanian to Early Maastrichtian). Le Lœuff and Buffetaut [1998] erected the first French dromaeosaurid taxon, *Variraptor mechinorum*, on the basis of this material. Subsequently, a new dromaeosaurid of Late Campanian to Early Maastrichtian age from La Boucharde (Bouches-du-

Rhône) was named *Pyroraptor olympius* by Allain and Taquet [2000] on the basis of some disarticulated postcranial elements possibly from a single individual.

Allain and Taquet [2000] suggested that *Variraptor mechinorum* is a *nomen dubium* because they assumed that its distinguishing features were insufficient and that part of the diagnosis was based on specimens found in a different locality from that of the holotype. However, it has been questioned whether the holotypic and referred material from La Boucharde is relevant enough to define *Pyroraptor* and reject *Variraptor* (Le Lœuff, pers. com.).

The purpose of the present paper is to describe new dromaeosaurid material from several sites in southern France (fig. 1), including the Bastide-Neuve locality of Fox-Amphoux (Var), where the holotype of *Variraptor* was found, and

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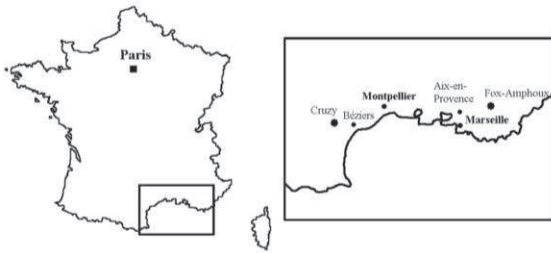


FIG. 1 – A map showing dromaeosaurid localities in the regions of Fox-Amphoux (Var) and Cruzy (Hérault), in southern France.
 FIG. 1 – Carte montrant les gisements à dromaeosauridés dans les régions de Fox-Amphoux (Var) et Cruzy (Hérault) dans le sud de la France.

some localities near the village of Cruzy (Hérault). On the basis of these new specimens, we also examine how many dromaeosaurid taxa can be recognized on the basis of the material, from the same time interval (Late Campanian to Early Maastrichtian [Buffetaut and Le Loeuff, 1991]), collected in southern France.

LOCALITIES AND GEOLOGICAL SETTING

Fox-Amphoux

The Bastide-Neuve locality, which has yielded the dromaeosaurid material described here, is in yellowish sandy clays. It has yielded an abundant and diverse vertebrate assemblage [Buffetaut *et al.*, 2006], comprising turtles, crocodylians, pterosaurs, ornithischians (with an ankylosaur and the ornithomimid *Rhabdodon*), sauropods (represented by Saltasauridae), theropods (including the type of the dromaeosaurid *Variraptor mechinorum*), and birds.

Massecaps (Cruzy)

Since 1996, systematic palaeontological excavations have been carried out at several localities near the villages of Cruzy and Villespassans (fig. 1) a few kilometres south of Saint-Chinian (Hérault), by the Association Culturelle, Archéologique et Paléontologique (ACAP) de l'Ouest Biterrois and the Centre National de la Recherche Scientifique. The material described in this paper was found in the course of these excavations at Massecaps, Combebelle and Plo Saint Pons.

At Massecaps, the vertebrate remains are scattered through a thickness of about 1 m of variegated clays, which sometimes contain iron oxide nodules, and are cut by unfossiliferous sandy channels. It would appear to be a floodplain deposit, containing bones in various states of preservation [Buffetaut *et al.*, 1999]. Burrows belonging to a “scaly” type already described by Plaziat [1971] from the Upper Cretaceous and early Tertiary of southern France are common. The fossil vertebrate assemblage from the Massecaps locality includes fishes, amphibians, turtles, crocodylians, pterosaurs, dinosaurs (ankylosaurs, ornithomimids, sauropods and theropods), birds and mammals [Buffetaut, 2005]. The dominant terrestrial faunal elements in this locality are the herbivorous dinosaurs (Saltasauridae, *Rhabdodon*) that are also found in many other Late Campanian and Early

Maastrichtian localities in southern France. The Saltasauridae – *Rhabdodon* association does seem to be characteristic of this age, in contrast to late Maastrichtian faunas where hadrosaurids are dominant [Le Loeuff *et al.*, 1994; Buffetaut *et al.*, 1997]. Besides the macrofauna, the Massecaps site also contains microvertebrate remains. The Plo Saint-Pons locality, between the villages of Cruzy and Bize, and the Combebelle localities, near the village of Villespassans, have been less thoroughly excavated than Massecaps but appear to contain a similar vertebrate assemblage.

MATERIAL

The new material consists of some teeth and post-cranial elements from the localities described above. An ilium, an ulna and some teeth, were found at Bastide Neuve; they are currently in the private collection of Patrick and Annie Méchin in Vitrolles. Most of the specimens described in the present paper were found at Massecaps, including teeth (MC-M 324, MC-M 561 and MC-M 938), a femur (MC-M187) and an ungual phalanx (MC-M228), while some teeth were found at Combebelle (Villespassans) and a sacrum (MC-PSP6) was found at Plo Saint Pons between Cruzy and Bize. They are kept in the Museum of the Association Culturelle, Archéologique et Paléontologique de l'Ouest Biterrois at Cruzy.

Furthermore, previously reported specimens of *Variraptor mechinorum*, including the sacrum (MDE-D169) from Bastide Neuve and the femur (cast MDE-D49) from Fox-Amphoux were also considered. Anatomical measurements of all specimens are shown in table I.

Institutional abbreviations:

AMNH – American Museum of Natural History, New York.
 BMNH – Department of Palaeontology, The Natural History Museum, London.
 CM – Collection Méchin, Vitrolles, France.
 IGM – Mongolian Institute of Geology, Ulan Baatar, Mongolia.
 MC – Musée de Cruzy, France.
 MCZ – Museum of Comparative Zoology, Harvard University.
 MDE – Musée des Dinosaures, Espéraza, France.
 OMNH – Oklahoma Museum of Natural History, Norman, Oklahoma.

DESCRIPTIONS AND COMPARISONS

Fox-Amphoux locality

Teeth

Like the teeth from Massecaps and Combebelle described below, the teeth from Fox-Amphoux (CM-186, CM-218, CM-537 and CM-684) are laterally compressed and recurved backward. Tooth CM-537 is serrated on both anterior and posterior carinae, whereas the others bear denticles only on the posterior carina. Basally, there is an elongate depression on each lateral surface of the crown (fig. 4C, H). The denticles show the same characteristics as those of the teeth from Massecaps and Combebelle (see below).

TABLE I. – Table of measurements (mm).
 TABL. I. – Tableau de mesures (mm).

Teeth	Anterior denticles/ mm	Posterior denticles/ mm	DSDI	FABW (mm)	
MC-M324	7	6	1.17	5.0	
MC-M561	7	6	1.17	4.3	
MC-M938	6	5	1.20	–	
MC-VC1	–	4	–	–	
MC-VC2	–	3	–	6.0	
CM-186	–	3	–	4.6	
CM-218	–	4	–	7.1	
CM-537	6	5	1.20	5.9	
CM-684	–	8	–	6.7	
Ilium (CM-645) length	230				
Ulna (CM-307) length	145				
Sacrum(MC-PSP6) length	134				
	S1	S2	S3	S4	S5
ventral midline length	20.4	26	28.4	28.6	22.6
centra transverse width	24.4	15.6	16.4	16.9	20.9
Femur (MC-M187) length	214				
Ungual (MC-M228) length (along outer curve)	46.6				

Ilium

The dorsal margin of the ilium (CM-645) is apparently more curved than those of *Bambiraptor*, *Deinonychus* and *Velociraptor*, which are relatively straight. The iliac blade (fig. 2) is tall but thin. The distal extremity of the blade is transversely expanded and more tapered than the proximal end. The anterior rim is not well preserved, it bends sharply downward from the anterodorsal angle before it curves posteriorly. From the anterior ventral corner, the iliac blade margin is inclined inward and extends to the pubic peduncle. The pubic peduncle is slightly longer and markedly larger than the ischiadic peduncle. It has a subrectangular section while that of the ischiadic process is sub-triangular. The pubic peduncle is directed posteroventrally. The acetabulum is horseshoe-shaped with the sus-acetabular rim forming a sharp ridge around it on the lateral face. The preacetabular region of the ilium (anterior end to mid acetabulum) is longer than the postacetabular one (mid-acetabulum to posterior end) whereas it is the reverse on the ilium of *Velociraptor* [Norell and Makovicky, 1997].

In dorsal view, the ilium is not straight but slightly curved in the anterior region, as a result this part is concave laterally (fig. 2D). Medially, on the upper region of the iliac blade near the mid dorsal rim, there is a rugose groove-ridge feature (fig. 2C). Moreover, rough depressions and striations are remarkably visible above the ischiadic peduncle, acetabulum and pubic peduncle and are presumably related to the insertion of the transverse processes of the sacrum. When the sacrum MDE-D169, the type of *Variraptor mechinorum*, and this ilium, which both come from the same locality, are matched, it appears that these striated depressions on the ilium correspond to the transverse

processes of the sacrum. This strongly suggests that these two elements belong to the same individual.

Ulna

This specimen is a left ulna (CM-307) (fig. 3). The ulna is quite slender and curved, being convex posterolaterally. Its cross-section is proximally sub-triangular, becoming sub-oval at midlength and a flattened oval in the distal part. Both proximal and distal ends are not well preserved. The olecranon process, which normally is erected proximally between two lateral condyles is incomplete although the pits on the posterior face of the process are shown (fig. 3D). The rough proximal articular surface was possibly sub-triangular and inclined from the olecranon process toward the radius, as in the ulnae of *Velociraptor* [Norell and Makovicky, 1999] and *Deinonychus* [Ostrom, 1969]. The two condyles do not seem to open out as much as in *Deinonychus*. On the anterior surface of the ulna just between these two condyles, a gentle longitudinal concavity lies distally to the ulnar midshaft, and becomes a convexity forming a rounded ridge, while a sharp margin is present on the posterior face. There is no deep depression on the lateral face of the ulna as reported in *Pyroraptor* [Allain and Taquet, 2000]. The distal extremity is flattened lateromedially. No remarkable features are preserved on it.

Localities in Hérault

Isolated teeth

All specimens are lateral teeth; maxillary and dentary teeth cannot be distinguished. The teeth from Masecaps (MC-M324, MC-M561, MC-M938) and Combeville (MC-VC1, MC-VC2) are laterally compressed and recurved posteriorly. Their apex lies behind the level of the posterior end of the base of the tooth. A plane passing through the carinae divides the tooth into sub-equal halves, the lingual portion being thicker and more convex. The anterior carina slightly twists toward the lingual surface. Both carinae of most specimens are denticulated, except on teeth MC-VC1 and MC-VC 2 (fig. 4C), which lack denticles on the anterior margin. Posterior denticles appear all along the tooth length while the anterior ones gradually diminish, being replaced by a smooth ridge toward the base of the tooth. The denticles are smaller on the anterior carina than on the posterior one (DSDI is 1.18 on average). Denticles are rectangular in shape and usually erected perpendicularly; however they are occasionally oblique to the posterior tooth margin by pointing toward the tooth apex (fig. 4D).

The teeth from the above-mentioned localities in Var and Hérault share some characters with velociraptorine (*Saurornitholestes*, *Deinonychus*, *Velociraptor*) teeth [Currie *et al.*, 1990], which are diagnosed by the apex extending behind the base of the crown and elongate pointed denticles.

Sacrum

The sacrum from Plo Saint-Pons (MC-PSP6) (fig. 5) consists of five fused vertebrae with co-ossified neural spines as in other Dromaeosauridae. The first centrum is shorter but transversely wider than the others. The midsacrales are transversely compressed; the last sacral is comparable in width with the first sacral. Sacral centra show the same

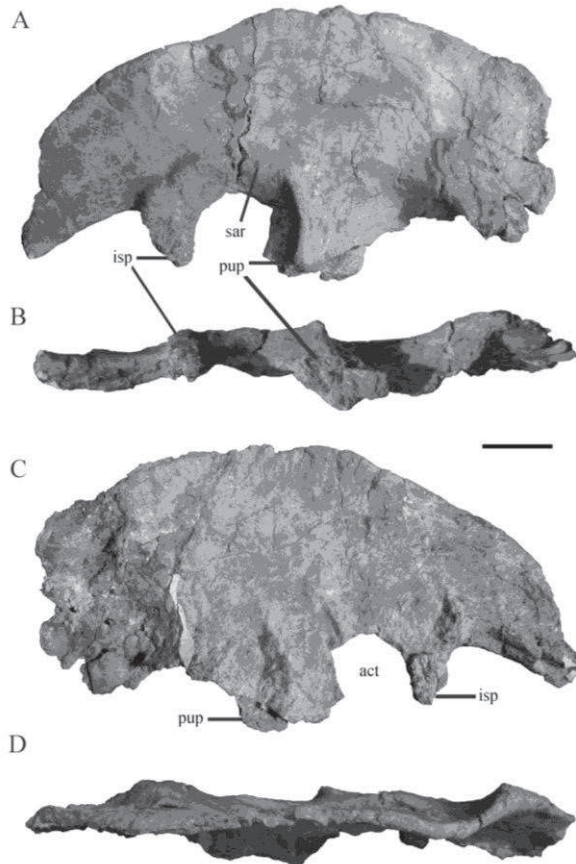


FIG. 2 – Dromaeosaurid right ilium from Bastide-Neuve (CM-645) in lateral (A), ventral (B), medial (C) and dorsal (D) views. Abbreviations: act = acetabulum, isp = ischiadic peduncle, pup = pubic peduncle, sar = sus-acetabular rim. Scale equals 3 cm.

FIG. 2 – Ilium droit de dromaeosauridé de Bastide-Neuve (CM-645) en vues latérale (A), ventrale (B), médiale (C) et dorsale (D). Abréviations : act = acetabulum, isp = pédoncule ischiatique, pup = pédoncule pubien, sar = bord sus-acétabulaire. Échelle : 3 cm.

width and length proportions as those of sacrum MDE-D169, the type of *Variraptor mechinorum*, while in *Microraptor zhaoianus* XU *et al.*, 2000, the anterior three sacral centra are enlarged posteriorly and in *Ornithodesmus cluniculus* [Howse and Milner, 1993] all sacral centra have sub-equal widths. The ventral surfaces of the centra are slightly concave anteroposteriorly and transversely rounded. A shallow longitudinal ventral groove is present across the suture between sacral three and sacral four and expands posteriorly on the fifth centrum as in *Velociraptor mongoliensis* and other maniraptorans [Norell and Makovicky, 1997, 1999]. This sulcus is deeper and more obvious in the type of *Variraptor mechinorum*, which presumably indicates that it belongs to an older individual, as a similar condition is seen in old individuals of *Saurornitholestes langstoni* [Norell and Makovicky, 1997].

In lateral view (fig. 5A), the centrum of sacral one possesses a deep oval pneumatic foramen in each lateral

concave wall, whereas the sides of centrum two show only a concavity and no pneumatic foramen is visible on the more posterior centra. These fossae in the lateral wall of the first centrum are also well-developed in the sacrum (BMNH R4463) of an undescribed small theropod from the Late Cretaceous of Mexico Ranch, Alberta [Howse and Milner, 1993] and in the first two sacral vertebrae (BMNH R187) of *Ornithodesmus cluniculus*. However deep oval pneumatic foramina are not present in the sacrum of *Variraptor mechinorum*, but there are two deep and narrow fossae on the ventral face of its first centrum instead. Darren Naish (pers. com.) notes that the pneumatisation of centra is polymorphic in dromaeosaurids. For example, concerning the sacrum of *Bambiraptor feinbergi*, Burnham [2004] briefly noted that there are foramina on the lateral surfaces of the centra just under the transverse sacral ribs as reported for *Saurornitholestes*. Two specimens of *Velociraptor mongoliensis* also show the variability of this pneumatic feature: sacral vertebrae of IGM 100/985 do not possess pneumatic foramina, whereas those of IGM 100/986 have a pneumatic foramen on the second sacral.

The first and the second sacral vertebrae each have a small intervertebral foramen opening into the neural canal anterior to the transverse processes. Only a deep fossa is visible on the third sacral vertebra in the same position as the foramina on preceding vertebrae.

The transverse processes of sacral one presumably originated from the neural arch, while the transverse processes



FIG. 3 – Dromaeosaurid ulna from Bastide-Neuve (CM-307) in lateral (A), anterior (B), medial (C), and posterior (D) views. Scale equals 2 cm.

FIG. 3 – Ulna de dromaeosauridé de Bastide-Neuve (CM-307) en vues latérale (A), antérieure (B), médiale (C) et postérieure (D). Échelle : 2 cm.

of sacral two, four and five arise from the centrum. The bases of the transverse processes of sacral two and four overlap the junction with sacral three and sacral five respectively. The transverse processes of sacral two are oriented anterolaterally; conversely, sacral four has posterolaterally and dorsally directed transverse processes. The transverse processes of the third sacral vertebra are laterally directed and situated just posterior to the junction with sacral two. Sacral five has posterolaterally directed transverse processes originating from the middle of its centrum. Small deep foramina are visible in the anterodorsal bases of the transverse processes of sacral two to four while there are shallower but wider depressions in sacral five. The transverse processes of sacral four also bear distinct thin laminae and thin fossae posteriorly.

In cranial view (fig. 5D), the anterior articular surface of the centrum of sacral one is slightly concave and has a dorsoventrally compressed oval shape. Caudally (fig. 5E), the fifth sacral vertebra resembles the proximal caudal

vertebrae of *Deinonychus* [Ostrom, 1969, Fig. 38]. It has a roughly rectangular articular surface, which is concave and slightly dorsomedially tilted. The edge of the articular face is quite rounded and bears a pair of oval facets in its ventrolateral corner, which probably represents a secondary surface of articulation with the first caudal vertebra [Howse and Milner, 1993]. Sacral five has well-developed postzygapophyses with inclined oval facets.

In dorsal view (fig. 5B), there is a deep anteriorly tapered depression along the axis of the sacrum across the fusion between sacral four and five. A neural platform is visible only on sacral four where the diapophyses fuse with the laminae extending from the base of the neural spine. This character is also present in *Variraptor*. Conversely, in *Velociraptor* and *Ornithodesmus* the neural platforms extend all along both sides of the fused neural spines [Norell and Makovicky, 1997; Howse and Milner, 1993]. Besides, *Saurornitholestes* and *Ornithodesmus* differ from this sacrum and from *Variraptor* in having dorsally arched sacra.

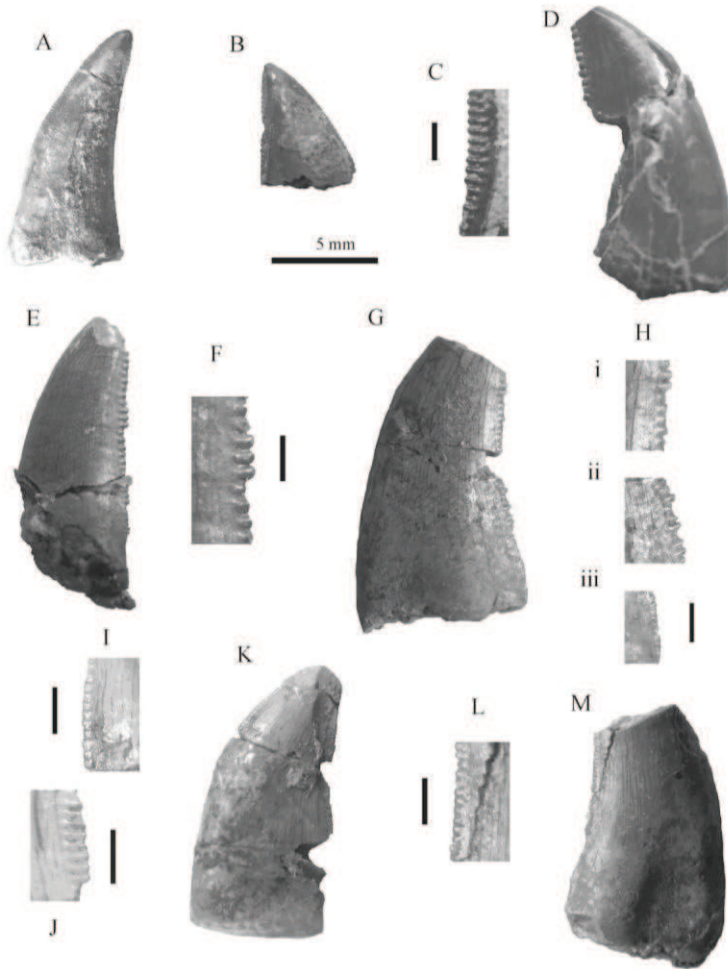


FIG. 4 – Dromaeosaurid isolated teeth from Massecaps, Combeville and Bastide-Neuve. A, MC-M561. B, MC-M938. C, agrandissement des denticules postérieures de MC-VC1. D, MC-VC2. E, dent CM-186. F, agrandissement des denticules postérieurs CM-186. G, dent CM-218. H, agrandissement des denticules postérieurs distaux (i.) médiaux (ii.) et proximaux (iii.) de CM-218. I, agrandissement des denticules antérieurs de CM-537. J, agrandissement des denticules postérieurs CM-537. K, dent CM-537. L, agrandissement des denticules postérieurs CM-684. M, dent CM-684. L'échelle est 5 mm pour les dents complètes et 1 mm pour le reste.

Femur

This right femur (MC-M187) (fig. 6) is bowed and anteriorly convex. The anterior face of the proximal part of the shaft is depressed. The femoral head is roughly oval and has a ligament scar posteriorly as in *Deinonychus* [Brinkman *et al.*, 1998] and *Velociraptor* [Norell and Makovicky, 1999]. The head is directed anteromedially and is oblique at approximately 110° to the shaft. The neck is not constricted, making the femoral head confluent with the greater trochanter. The lesser trochanter is anterolateral to and nearly level with the greater trochanter. Both of them are completely fused together, unless they are separated by a very shallow groove that is preserved posterolaterally as a shallow

longitudinal depression below the lesser trochanter as described in *Deinonychus* [Ostrom, 1976] and in *Velociraptor* [Norell and Makovicky, 1999]. The posterior trochanter is probably present on the proximal posterior surface of the femur just below the greater trochanter. The fourth trochanter is reduced. It is present posteromedially only as a narrow lip bordering a posterior longitudinal groove with a linear muscle scar. A shallow depression is also visible lateral to this groove. The reduced fourth trochanter and the presence of the lip-groove are distinctly shown in *Velociraptor* [Norell and Makovicky, 1999]. However these features are absent in *Deinonychus* [Ostrom, 1976]. The reduction or absence of the fourth trochanter is also shared by troodontids (*Sinornithoides*, *Saurornithoides*) but this femur can be

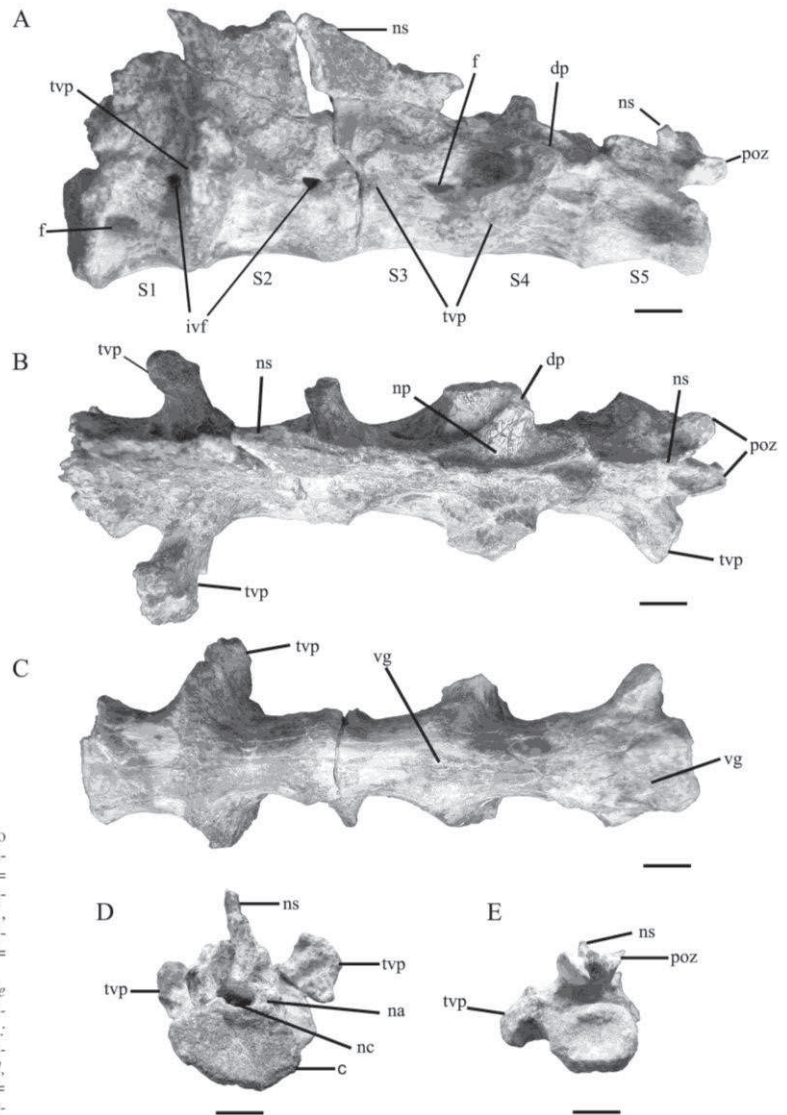


FIG. 5 – Dromaeosaurid sacrum (MC-PSP6) from Plo Saint Pons in lateral (A), dorsal (B), ventral (C), cranial (D) and caudal (E) views. Abbreviations: c = centrum, dp = diapophysis, f = fossa, ivf = intervertebral foramen, na = neural arch, nc = neural canal, np = neural platform, ns = neural spine, poz = postzygapophysis, s = sacral, tvp = transverse process, vg = ventral groove. Scale equals 1 cm.

FIG. 5 – Sacrum de dromaeosauridé (MC-PSP6) de Plo Saint Pons en vues latérale (A), dorsale (B), ventrale (C), craniale (D) et caudale (E). Abréviations : c = centrum, dp = diapophyse, f = fossa, ivf = foramen intervertébral, na = arc neural, nc = canal neural, np = plate-forme neurale, ns = épine neurale, poz = postzygapophyse, s = sacrée, tvp = processus transverse, vg = sillon ventral. Échelle : 1 cm.

distinguished by the angle between the mediolateral plane of the shaft and the long axis of the femoral head. This angle is oblique in dromaeosaurids and on the studied femur, but it is perpendicular in troodontids [Currie and Peng, 1993].

A small vascular foramen appears below the posterior trochanter and level with the fourth trochanter. Also in posterior view, there is a remarkably sharp ridge below the midpoint of the shaft, which then runs down to the distal part (fig. 6B); as a result the femoral shaft is sub-angular in cross section. This character has not been mentioned in other dromaeosaurids, except, perhaps, in *Velociraptor* [Norell and Makovicky, 1999]. The ridge on this femur probably represents the caudal (or posterior) intermuscular line (Hutchinson, pers. com.)

The midshaft is stout compared with the distal and proximal ends. Distally, the anterior intercondylar groove is not present; instead, coarse linear muscle scars are visible. Conversely, the posterior intercondylar groove distinctly divides the distal shaft into two ridges (the lateral one being wider) and then expands to form the well-developed open popliteal fossa by which the distal articulation is divided into a medial and a lateral condyle (fig. 6B).

Ungual phalanges

The unguinal phalanx MC-M228 (fig. 7A) belongs to digit III or IV of the left pes. It is strongly curved and robust. In proximal view, the oval articular facet is symmetrically bisected by a vertical ridge. The dorsal ridge is slightly prolonged proximally. A flexor tubercle is present ventrally on the proximal end and limited by the lower tip of the articular facet.

The grooves on the sides of this claw are not at the same level, being slightly lower on the lateral side than on the medial side; however, both of them converge into one at the dorsal end of the claw tip. This character is shared with other dromaeosaurs [Kirkland *et al.*, 1993]. However this claw is not as strongly curved as the unguis of digit II, which must be also have been larger and more trenchant. In addition, the cross section of this specimen is triangular, having a flat ventral surface like the unguis of pedal digits III and IV of *Deinonychus antirrhopus* (OSTROM, 1969), unlike the second claw which has a tapering oval cross-section. The unguis of digit III and IV have never been clearly differentiated in dromaeosaurids.

Besides the pedal claw, an incomplete manual claw (no numbered) (fig. 7B) was also found at Masecaps. It is strongly curved and compressed laterally, however the dorsal and ventral margins are rounded. The articular facet is oval and ridged asymmetrically. A large flexor tubercle projects ventrally below the lower margin of the articular facet. A distinct groove extending from the base of the flexor tubercle to the extremity is present on each lateral side of the claw.

DISCUSSION AND CONCLUSION

New dromaeosaurid remains from southern France

As shown by the morphological features described above, the new dinosaur remains from southern France belong to the Dromaeosauridae. The sacrum from Plo Saint Pons closely resembles the sacrum of *Variraptor mechinorum*, and we therefore consider that it belongs to *Variraptor*. Both these two sacra can be distinguished from the sacra of other dromaeosaurid

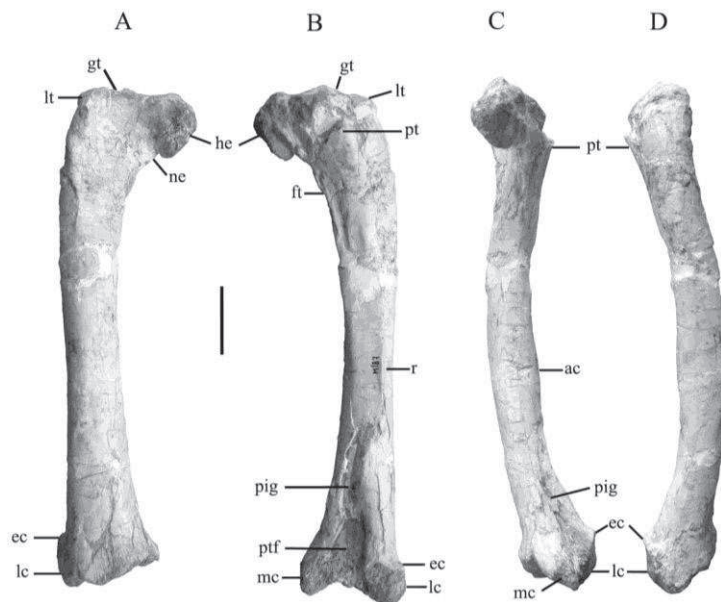


FIG. 6 – Dromaeosaurid right femur from Masecaps (MC-M187) in anterior (A), posterior (B), medial (C), lateral (D) views. Abbreviations: d = depression, ec = ectocondylar tuber, ft = fourth trochanter, gt = greater trochanter, he = head, lc = lateral condyle, ls = ligament scar, lt = lateral trochanter, mc = medial condyle, pig = posterior intercondylar groove, pt = posterior trochanter, ptf = popliteal fossa, r = ridge and vf = vascular foramen. Scale equals 3 cm.

FIG. 6 – Fémur droit de dromaeosauridé de Masecaps (MC-M187) en vues antérieure (A), postérieure (B), médiale (C) et latérale (D). Abréviations : d = dépression, ec = tubérosité ectocondylaire, ft = quatrième trochanter, gt = grand trochanter, he = tête, lc = condyle latéral, ls = attache ligamentaire, lt = trochanter latéral, mc = condyle médial, pig = sillon intercondylaire postérieur, pt = trochanter postérieur, ptf = fosse poplitée, r = crête et vf = foramen vasculaire. Échelle : 3 cm.

dinosaurs. The ilium from Fox-Amphoux, which presumably belongs to the same individual as the sacrum of *Variraptor mechinorum*, also shows some diagnostic features separating it from other dromaeosaurids. The femur from Masecaps shares more characteristics with the femora of Asian taxa than with those of North American taxa.

Although the remains from Cruzy and Fox-Amphoux share synapomorphic characters with North American and Asian dromaeosaurids (relationships with South American and African forms are more difficult to assess, because of the paucity of relevant elements in common), they also exhibit features that are developed differently and distinguish them. In the late Cretaceous, the European continental faunas seem to have been largely isolated from both North American and Asian assemblages, and the differences observed between the French remains and Late Cretaceous dromaeosaurid dinosaurs from other continents can probably be explained by divergent evolution from a common ancestor.

The problem of the French dromaeosaurid species

Variraptor mechinorum LE LÆUFF & BUFFETAUT, 1998 and *Pyroraptor olympius* ALLAIN & TAQUET, 2000 have been erected on the basis of material from the same region (southern France) and from the same time interval (Late Campanian to Early Maastrichtian). It is open to debate whether these two species may correspond to the same taxon. On the basis of our study of new specimens, and of the original material of *Variraptor* and *Pyroraptor*, there are two aspects that are worth discussing:

The nature of the type material

In contrast to *Pyroraptor olympius*, all the material of which was discovered at La Boucharde (Bouches-du-Rhône), the material originally referred to *Variraptor* was derived from 3 localities, as follows:

- a humerus, an ilium and the holotypic specimen including the articulated last dorsal vertebra and sacrum were discovered at the Bastide Neuve locality (Fox-Amphoux, Var)
- a femur was found at the Métiesson locality (Fox-Amphoux, Var)
- a cervico-dorsal vertebra and a sacro-caudal vertebra were found at Roques-Hautes (Bouches-du-Rhône)

This is one of the reasons why Allain and Taquet [2000] have regarded *Variraptor mechinorum* as a *nomen dubium* (ALLAIN & TAQUET, 2000). However, Le Læuff and Buffetaut [1998] clearly distinguished the holotype from the referred material. The humerus and ilium from Bastide Neuve were referred to *Variraptor mechinorum* because they are from the same locality as the holotype, and may be from the same individual (similarly, the reason why the type material of *Pyroraptor olympius* was considered as being from a single individual by Allain and Taquet is that it was all collected from a single locality). The material from Roques-Hautes was referred to *Variraptor mechinorum* because the sacro-caudal has exactly the same shape as sacral five from Bastide Neuve.

The preservation of the two French dromaeosaurid type series is in fact quite similar. *Pyroraptor* remains are quite well-preserved but disarticulated, it is therefore uncertain whether they belong to a single individual although they are from the same locality. Remains of *Variraptor* are also quite

well-preserved and the last dorsal vertebra and sacrum, which constitute the holotype, were articulated when they were found; it is unquestionable that they belong to the same individual. Moreover, as mentioned above, the ilium from Bastide-Neuve matches the type sacrum remarkably well and is in all likelihood from the same individual.

Validity of the diagnoses

Allain and Taquet [2000] claimed that the holotype of *Variraptor mechinorum* has no distinguishing features and most of the diagnostic characters are based on the referred material, and that Le Læuff and Buffetaut [1998] did not list valid apomorphies of the holotype of *Variraptor mechinorum*. However, if we consider the holotypic posterior dorsal vertebra of *Variraptor mechinorum* in detail, it is distinguishable from the dorsal vertebrae of other dromaeosaurids. *Deinonychus* has a longer centrum and larger dorsal pleurocoels. *Velociraptor* has no posterior dorsal pleurocoels. *Microraptor* lacks dorsal pleurocoels and the last dorsal vertebra is more elongate. The last dorsal of *Sinornithosaurus* is less compressed anteroposteriorly than in *Variraptor*. In addition, our comparison with the sacra of other dromaeosaurids shows that the sacrum of *Variraptor* exhibits diagnostic characters, as noted above.

Similarly, in the case of *Pyroraptor*, several supposedly diagnostic characters were also not clearly defined. Although the ventrally concave metatarsal II and the deep depression on the proximolateral part of the ulna (one of paratypes of *Pyroraptor*) are unknown in other Dromaeosauridae, some of the characters considered as diagnostic, for example, the strongly curved ungual claw and the distally grooved and asymmetrical metatarsal, are also present in



FIG. 7 – Dromaeosaurid ungual phalanges from Masecaps. A, a pedal claw (MC-M228) in medial view. B, a manual claw. Abbreviations: af = articular facet, ft = flexor tubercle, gr = groove, r = ridge. Scale equals 1 cm.
FIG. 7 – Phalanges unguéales de dromaeosauridés de Masecaps. A, griffe du pied (MC-M228) en vue médiale. B, griffe de la main. Abréviations : af = facette articulaire, ft = tubercule flexeur, gr = sillon, r = crête. Echelle : 1 cm.

other dromaeosaurid theropods. No diagnostic features were provided for the holotype of *Pyroraptor olympius*, which is a second claw of the left pes. Allain and Taquet [2000] only noted that the claw of *Pyroraptor* is strongly curved and could be compared to *Saurornitholestes* material [Sues, 1978; Currie, 1995].

Including the new material described in the present paper, the ulna is the only element in common to the two species *Variraptor mechinorum* and *Pyroraptor olympius*. It is also difficult to provide a solution to this dilemma, because, while the sacrum from Plo Saint Pons and the femur from Masecaps can be compared with those of *Variraptor*, there is no material from the Cruzy area that is in common with what is known of *Pyroraptor*. The problem of the lack of common elements between *Variraptor* and *Pyroraptor* also affects the coding of characters. If the characters chosen are from the cranial and axial skeleton, more codable material is known for *Variraptor* than for *Pyroraptor*. If the characters are taken from the appendicular skeleton, on the other hand, the *Pyroraptor* material is more codable.

Consequently, on the basis of the available material, it is impossible to decide whether *Variraptor mechinorum* and *Pyroraptor olympius* are synonymous. As both the type material of *Variraptor mechinorum* and that of *Pyroraptor*

olympius show distinctive characters, both taxa may be valid. However, despite a slight apparent difference in the ulna, it cannot be excluded that all the dromaeosaurid material currently known from the Late Cretaceous from southern France belongs to a single species. If future discoveries were to confirm this, then *Pyroraptor olympius* would have to be considered as a junior synonym of *Variraptor mechinorum*. Pending the discovery of more complete, articulated material, however, the question of the number of dromaeosaurid taxa in the Late Cretaceous of southern France cannot be answered with complete certainty.

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Title: The ornithopod dinosaur *Rhabdodon* from the Late Cretaceous of southern France: anatomy, systematics and paleobiology.

Abstract: The ornithopod dinosaur *Rhabdodon* was named by Matheron in 1869 and a first species, *Rhabdodon priscus*, was proposed on the basis of a dentary fragment with its diagnostic teeth from the Late Cretaceous of Bouches-du-Rhône in southern France. A new species, *R. septimanicus*, was subsequently erected by Buffetaut and Le Loeuff (1991) based on a characteristic dentary from a Late Cretaceous locality at Montouliers (Hérault). The validity of the latter species was in debate, the question being how many species of *Rhabdodon* existed in Southern France. Abundant unpublished material (both cranial and postcranial) of *Rhabdodon* discovered in recent excavations at various localities in southern France is described, as a result of which the anatomy of this animal is now better known. A reconstruction of *Rhabdodon* is proposed. *R. septimanicus* is considered as valid by including new cranial elements from Quarante (Hérault). Two species of *Rhabdodon* undoubtedly coexisted in the same time interval (Late Campanian – Early Maastrichtian) in southern France. The phylogenetic analysis confirms that *Rhabdodon* can be placed in a distinct family, Rhabdodontidae, which also includes its sister taxon, *Zalmoxes*, from which it is distinguished by numerous postcranial characters. Rhabdodontidae has a close relation with Iguanodontia. It is suggested that the common ancestor of the rhabdodontid dinosaurs evolved in North America, and then dispersed to Europe and eventually evolved in geographical isolation on the various European landmasses during the Late Cretaceous.

Key-words: Ornithopoda, Rhabdodontidae, *Rhabdodon*, anatomy, Late Cretaceous, Southern France

Titre : Le dinosaure ornithopode *Rhabdodon* dans le Crétacé supérieur de sud de la France: anatomie, systématique et paléobiologie.

Resumé : Le dinosaure ornithopode *Rhabdodon* a été nommé par Matheron en 1869 et la première espèce, *Rhabdodon priscus*, a été proposée sur la base d'un fragment dentaire avec ses dents très caractéristiques découvert dans le Crétacé supérieur des Bouches-du-Rhône dans le Sud de la France. Une nouvelle espèce, *R. septimanicus*, a ensuite été proposée par Buffetaut et Le Loeuff en 1991 sur la base d'un dentaire trouvé dans une localité du Crétacé supérieur à Montouliers (Hérault). La validité de cette nouvelle espèce était en débat, la question étant de savoir combien d'espèces de *Rhabdodon* existaient dans le Sud de la France. Un abondant matériel inédit (crânien et postcrânien) de *Rhabdodon*, découvert récemment au cours de fouilles sur divers sites du Sud de la France, est décrit, de sorte que l'anatomie de cet animal est désormais mieux connue. Une reconstitution de *Rhabdodon* est proposée. *R. septimanicus* est considéré comme valide à la suite de l'inclusion de nouveaux éléments crâniens de Quarante (Hérault). Deux espèces de *Rhabdodon* ont certainement coexisté durant le même période (Campanien supérieur – Maastrichtien inférieur) dans le Sud de la France. L'analyse phylogénétique confirme que *Rhabdodon* peut être placé dans une famille des Rhabdodontidae avec son taxon-frère, *Zalmoxes*, dont il se distingue par de nombreux caractères postcrâniens. Les Rhabdodontidae sont proches des Iguanodontia. Il est suggéré que l'ancêtre commun des rhabdodontidés a évolué en Amérique du Nord, puis s'est dispersé en Europe et a finalement évolué dans l'isolement géographique de l'archipel européen au cours de du Crétacé supérieur.

Mots-clés : Ornithopoda, Rhabdodontidae, *Rhabdodon*, anatomie, Crétacé supérieur, Sud de la France