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Systematic palaeontology (Vertebrate palaeontology)

Additional dinosaur teeth from the Cenomanian (Late Cretaceous) of Charentes, southwestern France

Nouvelles dents de dinosaures du Cénomanien (Crétacé supérieur) des Charentes, Sud-Ouest de la France

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ABSTRACT

Some isolated teeth of theropod and sauropod dinosaurs from the Cenomanian (Late Cretaceous) of Charentes are described. Two new teeth of Troodontidae confirm the presence of this theropod family, previously based on a single specimen. New dental morphotypes are recognized within Dromaeosauridae and Brachiosauridae in comparison with those already known from Charentes. Lastly, a very small tooth is tentatively assigned to an embryonic or neonatal sauropod. The palaeobiogeographical history of European hadrosauroids is briefly discussed. This history was probably more complex than it appears, involving exchanges with both North America and Asia as early as the mid-Cretaceous (Albian–Cenomanian).

Mots clés :
Dinosauria
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Crétacé
Cénomanien
Charentes
France

RÉSUMÉ

Quelques dents isolées de dinosaures théropodes et sauropodes du Cénomanien (Crétacé supérieur) des Charentes sont décrites. La présence de la famille des Troodontidae, auparavant basée sur une unique dent, est confirmée par deux nouveaux spécimens. De nouveaux morphotypes dentaires sont reconnus au sein des Dromaeosauridae et des Brachiosauridae, par rapport aux spécimens précédemment décrits. Enfin, une dent de très petite taille pourrait provenir d'un sauropode nouveau-né ou au stade de l'embryon. La paléobiogéographie des hadrosauroides européens est brièvement discutée. Celle-ci était probablement plus complexe qu'il n'y paraît, impliquant à la fois des échanges avec l'Amérique du Nord et l'Asie dès la partie moyenne du Crétacé (Albien–Cénomanien).

1. Introduction

The French record of dinosaurs is scarce for the early Late Cretaceous, as underlined by Buffetaut et al. (1991), Buffetaut and Pouit (1994), and Allain and Pereda-Suberbiola (2003). Recently, Vullo et al. (2007)

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identified six dinosaur taxa (i.e., Carcharodontosauridae, Dromaeosauridae, Troodontidae, Brachiosauridae, *Probactrosaurus*-grade Iguanodontoidea, Nodosauridae) on the basis of isolated teeth present in the Cenomanian vertebrate assemblages of Charentes (Aquitaine Basin, southwestern France). A few additional dinosaur specimens have been found since this publication, and are described in the present article. Although no further dinosaur taxa have been recognized, these remains represent new dental morphotypes or allow a better description of some taxa that were known in Charentes by only one specimen (e.g., Troodontidae). In addition, the dinosaurian (sauropodan?) origin of a very small fragmentary tooth, characterized by a peculiar ornamentation of the enamel, is discussed. As underlined by Vullo and Néraudeau (2008), the dinosaurs and several other vertebrate groups (e.g., crocodyliforms, mammals) from the Cenomanian of Charentes provide key information on the palaeobiogeographical history of the Late Cretaceous fauna of the European archipelago. Further comments, especially about derived iguanodontian dinosaurs, can be made with regard to some recently published works.

2. Geological setting

Cenomanian deposits outcrop widely in the northern part of the Aquitaine Basin (southwestern France), especially in the Charentes region. The material described in this work comes from two Charentes localities: Font-de-Benon (sand quarry) at Archingeay-Les-Nouillers between Rochefort and Saint-Jean-d'Angely (Charente-Maritime department), and La Buzinie (road section) at Champniers near Angoulême (Charente department). Both localities are Early Cenomanian in age, but the former is slightly older than the latter (included into the B1 and B2 subunit, respectively) (Vullo, 2007; Vullo and Néraudeau, 2008; Vullo et al., 2003, 2007). Detrital deposits that have yielded the dinosaurs specimens indicate a shallow marine, near-shore environment (Vullo, 2007). Besides the dinosaur remains, these coastal assemblages have yielded abundant selachian teeth and other continental elements, such as teeth and bones of frogs, lizards and mammals at Font-de-Benon and amber and wood at La Buzinie (Vullo, 2007; Vullo and Néraudeau, 2008).

3. Systematic palaeontology

The abbreviations used to describe the theropod teeth are: BW: Basal Width; DSDI: Denticle Size Difference Index (mesial denticle density/distal denticle density: Rauhut and Werner, 1995); FABL: Fore-Aft Basal Length (mesiodistal length of the base of the crown: Currie et al., 1990). All the specimens are stored in the palaeontological collections of the Musée d'Angoulême (MA), Angoulême, Charente department, France.

3.1. Theropoda

3.1.1. Dromaeosauridae

Material: one nearly complete tooth from La Buzinie (MA BZN 8).

Description: this tooth (Fig. 1A–D) is unworn and nearly complete (height = 16.8 mm), missing only the distal part of its base. The crown is slender and weakly recurved distally. The labiolingual compression of the crown is not well marked (FABL estimated between 4.5 and 5 mm; BW estimated to ~3 mm; BW/FABL = 0.6–0.67). The mesial and distal carinae are serrated and bear 6.1 and 4.5 denticles per mm, respectively. This gives a DSDI value of 1.36. The mesial carina, not reaching the base of the crown, is regularly convex whereas the distal one is almost rectilinear. These carinae are placed in the midline of the crown, and the lingual and labial faces are equally developed. The lingual and labial faces are smooth, except a few slight transverse bands.

Remarks: since the work published by Vullo et al. (2007), a few additional dromaeosaurid teeth have been recovered from several Charentes localities. Among these specimens, the tooth described here displays an interesting morphology, characterized by a very slender crown. The very weak curvature of the crown, as defined by Sankey et al. (2002), is another distinctive feature of this specimen. The DSDI value matches the range of published dromaeosaurid values. This new specimen represents an additional morphotype, distinct from those previously described by Vullo et al. (2007), and probably corresponds to an anterior tooth. It is very similar morphologically to an anterior tooth from the Early Cretaceous (Barremian–Aptian) of eastern Russia (Averianov et al., 2003, fig. 4a, b). The teeth from Charentes can be compared to the few dromaeosaurid teeth that have been described from the Late Cretaceous (Campanian–Maastrichtian) of southern France. *Pyroraptor* from La Boucharde (Bouches-du-Rhône department) has teeth that are similar in general morphology, size, and DSDI (Allain and Taquet, 2000). Some isolated teeth from various localities of the departments of Hérault and Var, referred to an indeterminate dromaeosaurid by Chanthasit and Buffetaut (2009), are also similar but have a lower DSDI (values $\leq$ 1.20).

3.1.2. Troodontidae

Material: two complete teeth from Font-de-Benon (MA FDB 8, MA FDB 9).

Description: both specimens are similar and correspond to small, well preserved teeth (Fig. 1E–J). The labiolingual compression of the crown is relatively weak (measurements of MA FDB 8 and MA FDB 9 are, respectively: FABL = 0.98 and 1.16 mm; BW = 0.32 and 0.38 mm; BW/FABL = 0.58 for both specimens). The crown is slightly recurved distally. The mesial carina, not serrated, is strongly convex. The distal carina bears two or three strong denticles, plus another minute one placed basally. The lingual face is rather flattened and shows two longitudinal broad and shallow grooves, placed medially and along the mesial carina. The labial face is more convex.

Remarks: the new specimens described here confirm the presence of an unambiguous troodontid theropod in the Cretaceous of Europe. These two teeth are identical in size and morphology to the tooth previously described by Vullo et al. (2007), suggesting that this troodontid taxon might have been characterized by a weak heterodonty. The Charentes troodontid is clearly distinct from taxa (e.g.,

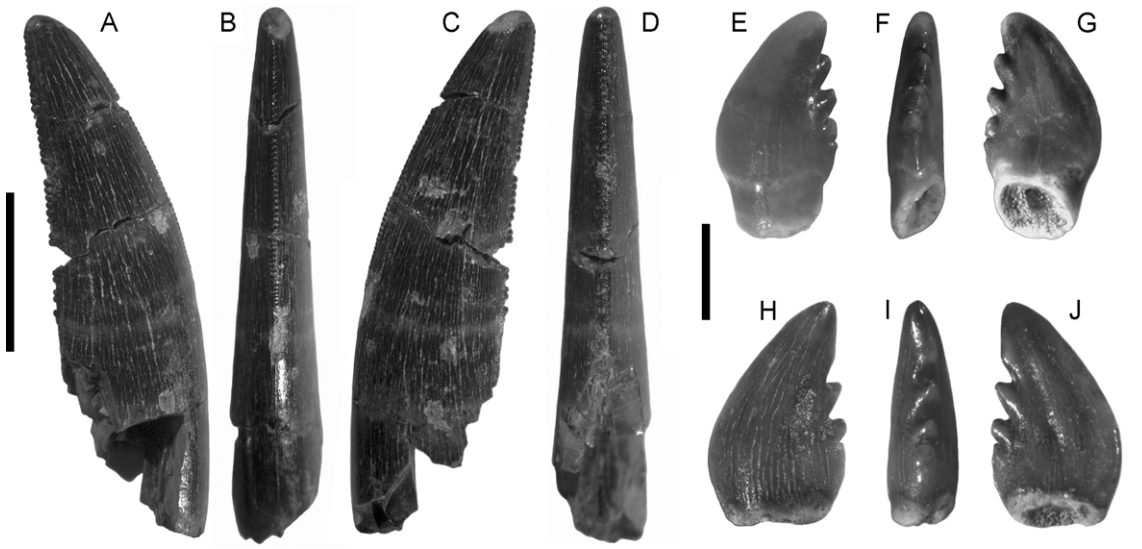

Fig. 1. Theropoda from the Cenomanian of Charentes. **A–D**. Dromaeosaurid tooth (MA BZN 8) in **A**, **C**, lateral, **B**, mesial, and **D**, distal views. **E–G**. Troodontid tooth (MA FDB 8) in **E**, labial, **F**, distal, and **G**, lingual views. **H–J**. Troodontid tooth (MA FDB 9) in **H**, labial, **I**, distal, and **J**, lingual views. Scale bars: 5 mm (**A–D**) and 1 mm (**E–J**).
Fig. 1. Theropoda du Cénomanien des Charentes. **A–D**. Dent de dromaeosauridé (MA BZN 8) en vues **A**, **C**, latérale, **B**, mésiale, et **D**, distale. **E–G**. Dent de troodontidé (MA FDB 8) en vues **E**, labiale, **F**, distale, et **G**, linguale. **H–J**. Dent de troodontidé (MA FDB 9) en vues **H**, labiale, **I**, distale, et **J**, linguale. Barres d'échelle : 5 mm (**A–D**) et 1 mm (**E–J**).

Byronosaurus, *Mei*, *Urbacodon*) that are characterized by the complete absence of denticles on both tooth carinae (Averianov and Sues, 2007; Norell et al., 2000; Xu and Norell, 2004). Among troodontids with serrated teeth (Averianov and Sues, 2007; Currie et al., 1990; Sankey et al., 2002), the most striking feature of the Charentes form is its strongly reduced number of distal denticles. The teeth of *Troodon* and *Pectinodon* generally have more than seven distal denticles, and their mesial carina can also be serrated. It is worth to note that the teeth which are most similar to our specimens correspond to an unnamed form from the Cenomanian of Uzbekistan (Averianov and Sues, 2007, fig. 5d–h). All specimens come from the same basal Cenomanian sandy layer of Font-de-Benon, and this troodontid seems to be absent in younger Charentes localities.

3.2. Sauropoda

3.2.1. Brachiosauridae

Material: one incomplete tooth from La Buzinie (MA BZN 9).

Description: this specimen (Fig. 2) corresponds to an incomplete tooth, of which only the apical part of the crown is preserved. In labial view, the crown is symmetrical and shows a relatively pointed apex. In basal view, the convex labial face is more developed than the lingual face, which is more flattened. On the lingual face, some very slight oblique, arcuate wrinkles are present along the carinae. In lateral view, the apex is slightly bent lingually. The two carinae are well marked, and do not bear any denticles. The apex do not show any wear facet.

Remarks: only two unambiguous sauropod teeth, recurved distally, were previously reported from the Cenomanian of Charentes and assigned to Brachiosauridae (even if the assignment to a non-brachiosaurid basal titanosauriform cannot be totally excluded) (Vullo et al., 2007). The third specimen described here is also referred to Brachiosauridae but corresponds to another dental morphotype, with a crown mesiodistally symmetrical. It is very similar to a ?brachiosaurid tooth from the Late Jurassic (Kimmeridgian) of Portugal (Rauhut, 2000, 2001). Semi-spatulate, symmetrical (anterior?) teeth are also known in the Early Cretaceous brachiosaurid *Astrodon* (Carpenter and Tidwell, 2005, fig. 3.2h). Although represented by two dental morphotypes, all brachiosaurid material from Charentes may belong to the same taxon, as suggested by the heterodonty observed in *Astrodon* (Carpenter and Tidwell, 2005, fig. 3.2g–j) and possibly *Paluxisaurus* (Rose, 2007, fig. 6). Similar heterodonty, wear pattern, and tooth morphology are also present in *Abydosaurus*, a brachiosaurid recently described on the basis of a complete skull from the Albian of Utah (Chure et al., 2010, fig. 4d–e). Among basal Titanosauriformes, the three teeth from Charentes can be distinguished in particular from those of euhelopodids by their narrower crown, a labiolingual compression less marked, and a different wear pattern (Barrett and Wang, 2007; Buffetaut and Suteethorn, 2004; Canudo et al., 2002). In addition, it is worth noting that no sauropod specimens corresponding to chisel-like teeth, typical of derived titanosaurs, have been identified within the new dinosaur material. The presence of derived titanosaurs in the Cenomanian of Charentes, suggested by Buffetaut and Pouit (1994) on the basis of a single doubtful tooth, cannot therefore be confirmed.

3.2.2. ?Sauropoda indet.

Material: one incomplete tooth from Font-de-Benon (MA FDB 10).

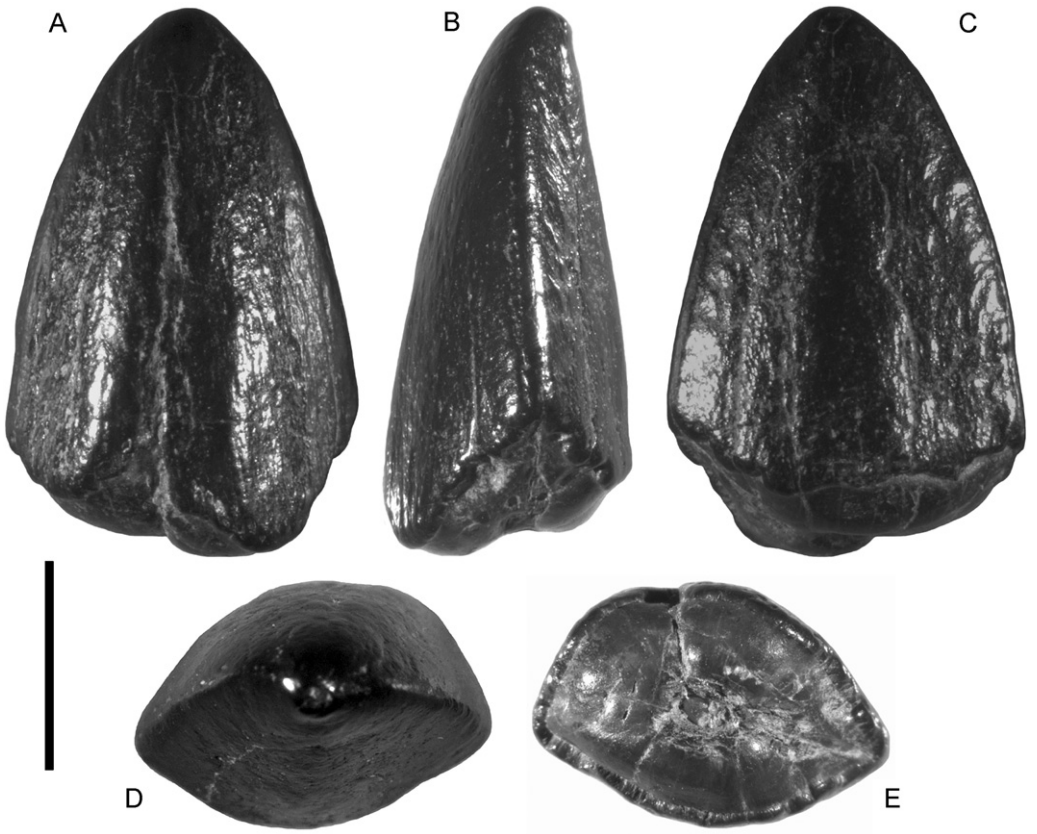

Fig. 2. Sauropoda from the Cenomanian of Charentes. **A–E**. Brachiosaurid tooth (MA BZN 9) in **A**, labial, **B**, mesial or distal, **C**, lingual, **D**, apical, and **E**, basal views. Scale bar: 5 mm.
Fig. 2. Sauropoda du Cénomanien des Charentes. **A–E**. Dent de brachiosauridé (MA BZN 9) en vues **A**, labiale, **B**, mésiale ou distale, **C**, linguale, **D**, apicale, et **E**, basale. Barre d'échelle : 5 mm.

Description: this incomplete tooth (Fig. 3) is very small (original length probably less than 3 mm) and the apical part is missing. The crown is labiolingually compressed. The only preserved carina is strongly rounded and devoid of denticles. The cross-section shows an enamel layer which is rather thick, indicating a high enamel/dentine ratio (i.e., total enamel area/total tooth area: García and Cerda, 2010). The enamel surface is marked by numerous small pits, more developed on one side of the crown.

Remarks: dental features of embryonic sauropod dinosaurs are poorly known. Chiappe et al. (1998, 2001) briefly described the teeth of some titanosaur embryos from the Late Cretaceous of Argentina. Their size, about 2 mm in length, is similar to our specimen. However, these teeth have a smooth enamel surface and are cylindrical in shape. The enamel pattern observed on the specimen from Font-de-Benon, characterized by the presence of small pits, is known in some sauropod teeth. It is worth noting that the brachiosaurid teeth previously reported from the Cenomanian of Charentes display an irregular, rugose enamel surface marked by similar pits (Vullo et al., 2007). The same ornamentation can also be present in the brachiosaurid *Astrodon* (Carpenter and Tidwell, 2005, fig. 3.4e, f) and other basal titanosauriforms (Barrett and Wang, 2007). Recently, the teeth previously reported by Chiappe et al. (1998, 2001) have been redescribed in detail by García and Cerda (2010). These authors have observed that the enamel/dentine ratio decreases through ontogeny. Similarly, we can note that the enamel layer is proportionally thicker in MA FDB 10 than in MA BZN 9 and the other two sauropod teeth from Charentes. Because of its peculiar features (i.e., spatulate crown, high enamel/dentine ratio, pit ornamentation), MA FDB 10 is therefore tentatively assigned to a sauropod. The presence of remains of neonatal or juvenile sauropods in coastal sediments would not be surprising since evidence of dinosaur nests at the sea shore was already reported (López-Martínez et al., 2000; Sanz et al., 1995).

4. Comments on European hadrosauroid palaeobiogeography

Recently, Sues and Averianov (2009) have regarded the iguanodontian teeth from Charentes as one of the earliest hadrosauroids (without excluding the hypothesis they belong to a derived non-hadrosauroid iguanodontian like *Protohadros*). These authors claim that this material (together with some other isolated teeth from England, western Russia, and Uzbekistan) witnesses the first radiation of non-hadrosaurid hadrosauroids, which occurred during the Late Abian–Turonian. The most

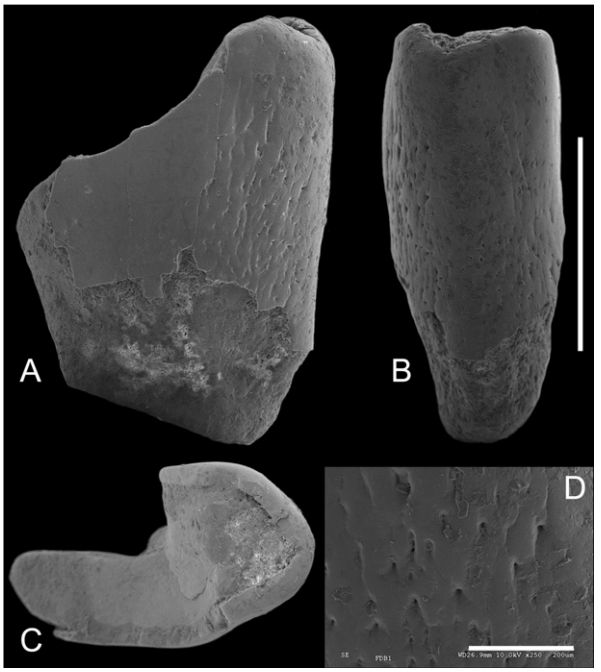

Fig. 3. A–D. ?Sauropoda from the Cenomanian of Charentes. Incomplete tooth tentatively assigned to an embryonic or neonatal sauropod (MA FDB 10) in **A**, ?labial, **B**, mesial or distal, and **C**, occlusal views. **D**, detail of the enamel surface showing the pattern of small pits. Scale bars: 1 mm (**A–C**) and 200 μm (**D**).
Fig. 3. A–D. ?Sauropoda du Cénomanien des Charentes. Dent incomplète, attribuée avec doute à un sauropode embryonnaire ou nouveau-né (MA FDB 10) en vues **A**, ?labiale, **B**, mésiale ou distale, et **C**, occlusale. **D**, détail de la surface de l'émail montrant les petites perforations. Barres d'échelle : 1 mm (**A–C**) et 200 μm (**D**).

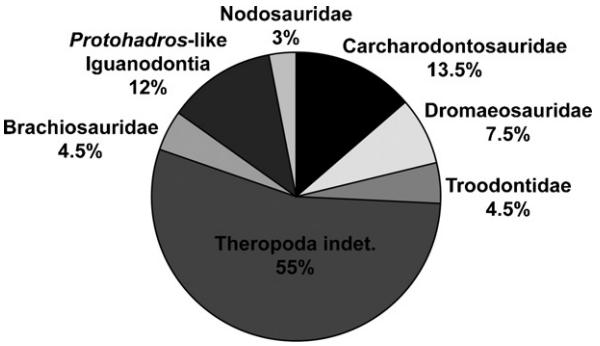

Fig. 4. Relative abundances of the dinosaur taxa from the Early Cenomanian of Charentes, in terms of teeth recovered (percent of total specimens; $n = 66$). Theropod teeth are greatly dominant, although most of these specimens correspond to indeterminable fragments at the family level. It is worth noting that herbivorous forms are represented by less than one quarter of the specimens.
Fig. 4. Abondances relatives des taxons de dinosaures du Cénomanien inférieur des Charentes, en termes de dents récoltées (pourcentage du nombre total de spécimens ; $n = 66$). Les dents de théropodes sont largement dominantes, même si la majorité de ces spécimens correspond à des fragments indéterminables au niveau familial. Il est intéressant de noter que les formes herbivores sont représentées par moins d'un quart des spécimens.

derived non-hadrosauroid iguanodontian (*Protohadros*, from the Cenomanian of Texas) would suggest a North American origin for this hadrosauroid radiation. This implies that a faunal dispersal event may have occurred from eastern North America to Europe in the early Late Cretaceous (Head, 1998). However, some recent works dealing with the palaeobiogeography of Late Cretaceous hadrosauroid dinosaurs (Dalla Vecchia, 2009) or continental tetrapods (Pereda-Suberbiola, 2009) from Europe have not taken into account the Cenomanian material from Charentes in their scenarios. Pereda-Suberbiola (2009, fig. 3) favours the hypothesis that the main faunal dispersal event which occurred in the early Late Cretaceous was from Asia to Europe and did not involve North America (a dispersal route from Africa to Europe may also have existed). Similarly, Dalla Vecchia (2009) proposes that hadrosauroids colonized the European archipelago from Asia during a series of dispersal events started during the Late Campanian. The palaeobiogeography history of European hadrosauroids is likely more complex but remains unfortunately poorly documented for the early Late Cretaceous (Cenomanian) and devoid of data for the Turonian–Santonian interval (Sues and Averianov, 2009). Indeed, faunal dispersal events between North America and Europe may have occurred during the entire Late Cretaceous in addition to the migrations from Asia. Among European hadrosauroids, some forms might also have evolved by vicariance. A re-appraisal of the post-cranial bones found in association with the hadrosauroid teeth from Charentes, previously assigned tentatively to ?*Iguanodon* sp. (Néraudeau et al., 2003), is needed in order to clarify the taxonomic affinities of this form and thus provide new information on the early history of duck-billed dinosaurs in Europe.

5. Conclusions

The new specimens described here complete our knowledge of the dinosaur fauna from the Cenomanian of Charentes. With several dozens of dinosaur teeth recovered to date, the vertebrate microfossil localities of Charentes are the richest ones for the European early Late Cretaceous. The locality of Font-de-Benon, characterized by an assemblage composed of minute remains, proves to be especially important regarding the search for small forms (e.g., troodontids, juveniles). The theropod teeth, representing almost 80% of the dinosaur specimens, are significantly dominant in the Charentes assemblages (Fig. 4). Both palaeoecological and taphonomical explanations are probably involved for such an overrepresentation of predatory dinosaurs. The same observation can be made for the Cenomanian Kem Kem beds (Morocco), in which theropod fossils represent 89% of the dinosaur material (field data from the Gara Sba locality: McGowan and Dyke, 2009). Future research and prospecting in the Cenomanian of Charentes will probably provide further specimens and new information (systematics, palaeobiogeography) on the dinosaur taxa present in the mid-Cretaceous paralic environments of the western part of the European archipelago.

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