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New data on the theropod diversity from the Middle to Late Jurassic of the Vaches Noires cliffs (Normandy, France)

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ABSTRACT

Dinosaur remains found at the Vaches Noires cliffs (Calvados, Normandy) have usually been discovered by amateur palaeontologists. The bones come from carcasses which drifted away from a nearby land (Armorican Massif) during the upper Callovian and lower Oxfordian. Most of these bones belong to private collections and are hardly accessible. Consequently, many of these bones were never described. Thus, and for the first time, private and public collections are gathered to obtain a global vision of theropod remains from the Vaches Noires cliffs. Most of the dinosaur remains from this locality belong to theropods. Some bones are from the same individual but have been isolated as a result of cliff erosion and tidal action which also mixed specimens from different stratigraphic levels. This over-representation of theropod remains is enigmatic because it is not found in other similar deposits. A specific way of life is likely to explain that fact, but it could also be a simple statistical effect due to a limited sample. At least 3 taxa are tentatively identified: *Streptospondylus altdorfensis* Meyer, 1832, another megalosauroid and an allosauroid.

KEY WORDS
Dinosaurs,
Theropods,
Streptospondylus,
Diversity,
Callovian,
Oxfordian,
Vaches Noires cliffs.

RÉSUMÉ

Nouvelles données sur la diversité des théropodes du Jurassique moyen à supérieur des falaises de Vaches Noires (Normandie, France).

Les restes de dinosaures trouvés aux Falaises des Vaches Noires (Calvados, Normandie) ont principalement été découverts par des paléontologues amateurs. Ces os proviennent vraisemblablement de cadavres ayant flottés depuis les terres les plus proches (Massif armoricain) pendant le Callovien supérieur et l'Oxfordien inférieur. La plupart de ces ossements appartiennent à des collections privées et sont difficilement accessibles. En conséquence, beaucoup de spécimens n'ont jamais été décrits. Ainsi et pour la première fois, différentes collections – notamment privées – sont réunies afin d'obtenir une vision d'ensemble sur les restes de théropodes des Vaches Noires. La majorité des restes de dinosaures appartiennent à des théropodes. Quelques os appartiennent à un même individu mais ont été isolés suite à l'érosion de la falaise et à l'action des vagues qui ont aussi mélangés les spécimens provenant de niveaux stratigraphiques différents. Cette surreprésentation des restes de théropodes est énigmatique, car elle ne correspond pas à ce qui est trouvé dans d'autres gisements analogues. Elle pourrait être expliquée par un mode de vie particulier, mais aussi par un simple effet statistique dû à un échantillonnage limité. Au moins trois taxons sont provisoirement identifiés : *Streptospondylus altdorfensis* Meyer, 1832, un autre Megalosauroidea et un Allosauroidea.

MOTS CLÉS
Dinosaures,
Théropodes,
Streptospondylus,
Diversité,
Callovien,
Oxfordien,
Falaises des Vaches Noires.

INTRODUCTION

The Vaches Noires cliffs in Calvados, Normandy have been the site of two and a half centuries of French geological and paleontological research (Dicquemare 1776; Cuvier 1800, 1808; Morière 1878; Douvillé 1912; Piveteau 1923; Wenz 1970; Taquet & Welles 1977; Buffetaut 1994a, b; Buffetaut *et al.* 1991; Buffetaut & Enos 1992; Bardet *et al.* 1993; Taquet 1994; Knoll *et al.* 1999; Brignon 2016a). For a long time, this coastal site between Villers-sur-Mer and Houlgate has attracted curious laymen as well as professionals and still yields new fossils every year; hence, new studies are frequently published as well (Allain 2001; Liston 2008; Buffetaut *et al.* 2010; Buffetaut 2013; Charbonnier & Gendry 2013; Courville 2013; Gendry 2013; Plasse & Buffetaut 2016; Buffetaut & Tabouelle 2019). The Vaches Noires cliffs, as many other Normandy deposits or those of the Oxford Clay Formation in England, are representative of Middle to Late Jurassic marine environments (Buffetaut 1994a; Martill 1988; Dugué *et al.* 1998). At that time, Europe was an archipelago in the Tethys Sea (Bradshaw *et al.* 1992). Consequently, numerous fossils of marine animals have been collected, including ammonites, bivalves and marine reptiles. Sometimes, remains of dinosaurs have also been found. These remains are from floating carcasses that came from the nearest land areas (Buffetaut 1994a). During the Callovian and Oxfordian, the location of the current Vaches Noires cliffs was at most a few dozen kilometres away from the coast of the Armorican Massif (Bradshaw *et al.* 1992), where the dinosaurs probably lived. Most of the dinosaur remains from the Vaches Noire cliffs are isolated and fragmentary. Some bones apparently spent a long time on the sea floor before being buried in sediment, as shown by the growth of marine organisms (oysters and serpulids) on their surface.

Streptospondylus altdorfensis Meyer, 1832 is the most complete dinosaur of the Vaches Noires locality found by a local collector abbé Bacheley around 1770. Initially figured and described as parts of a marine crocodilian by Cuvier (1800, 1808), the history of its interpretation is long and complicated (Allain 2001), mostly because of the incomplete nature of the remains. Even the provenance of the bones from the Vaches Noires cliffs (near Honfleur following Cuvier) was subject doubt (Allain 2001). However, a study of Bacheley's note and history (Brignon 2016b) confirmed the Vaches Noires Cliffs origin of the type specimen. *Streptospondylus* Meyer, 1830 is only known from postcranial elements housed at the Muséum national d'Histoire naturelle, Paris (MNHN). It has been referred to Megalosauroidea (Allain 2001). *Piveteausaurus divesensis* (Walker, 1964) – also housed at the MNHN – represented by a braincase, is the second named dinosaur from the locality (Piveteau 1923; Taquet & Welles 1977). The systematic position of the latter is disputed between Megalosauroidea (Taquet & Welles 1977) and Allosauroidea (Allain 2001). Allosauroids are also assumed to be present at the Vaches Noires cliffs according to isolated elements (Knoll *et al.* 1999; Buffetaut *et al.* 2010).

Quite a few of the dinosaur remains from the Vaches Noires were found by amateur paleontologists and are housed in private collections. Some of them were already studied and it appears that most of these bones belong to theropods (Buffetaut 2013; Plasse & Buffetaut 2016). Many bones from private collections and recently discovered bones are still unstudied. Nevertheless, they are essential for the study of theropod diversity from the Vaches Noires Cliffs, even if they are isolated and their precise stratigraphic origin is often unknown.

The aim of this study is to gather and describe bones from 6 different collections, most of which are private, and to provide new insights on known specimens. Systematic assignments and associations to the same taxon or even the same individual were made. The minimum number of taxa and individuals is also discussed in order to propose hypotheses about the overrepresentation of theropods at the Vaches Noires.

TABLE 1. — Specimen inventory from the Vaches Noires cliffs housed in private collections. Studied specimens are in bold.

Source Collection	Specimen number	Clearing methods (if known)	(re)evaluated stratigraphic origin	Bone type	Taxonomic assignment
Anicolas	**A1**	–	Oxfordian marls (lower Oxfordian)	Left maxilla and dentary in occlusion	Allosauroidea indet.
Association Paléontologique de Villers-sur-Mer, Col. Enos	**APVSM1**	–	Callovian or Oxfordian marls	Fused frontals	Allosauroidea indet.
Association Paléontologique de Villers-sur-Mer, Col. Drijard	**APVSM2**	–	Callovian or Oxfordian marls	Caudal vertebra	Tetanurae indet.
Bülow	**B1**	acid	Oolithes Ferrugineuses de Villers	Right premaxilla	Megalosauridae indet.
	B2	acid	Callovian or Oxfordian marls	Indeterminate fragment	Indeterminate
	B25192	acid	Callovian or Oxfordian marls	Braincase	Allosauroidea indet.
	B3	acid	Callovian or Oxfordian marls	Cervical vertebra	Allosauroidea indet.
	B4	–	Callovian or Oxfordian marls	Dorsal vertebra	Tetanurae indet.
	B5	acid	Oolithes Ferrugineuses de Villers, lower Oxfordian	Dorsal vertebra	?Streptospondylus altdorfensis
	B6	–	Oolithes Ferrugineuses de Villers, lower Oxfordian	Dorsal vertebra	Indeterminate
	B7	–	Callovian or Oxfordian marls	Caudal vertebra	Tetanurae indet.
	B8	–	Oolithes Ferrugineuses de Villers, lower Oxfordian	Caudal vertebra	Indeterminate
	B9	–	Callovian or Oxfordian marls	Indeterminate ingual	Tetanurae indet.

ABBREVIATIONS

MNHN.F	Muséum national d'Histoire naturelle, Paris, collection de Paléontologie;
MPV	Musée Paléospace l'Odyssée, Villers-sur-Mer;
OUM	Oxford University Museum, Oxford.

MATERIAL AND METHODS

MATERIAL

Thirty-four specimens were examined. Most of them are isolated remains. They come from upper Callovian to lower Oxfordian beds of the Vaches Noires cliffs. These bones were gathered from 6 different collections (Tables 1; 2). Four of them are private and are listed below. Specimens from these collections (or without number) were numbered following their collections and previous articles.

The Anicolas collection is here represented by a single specimen, a maxilla and a dentary in occlusion. It was found at the bottom of the cliffs in 2002. No cleaning was made on this specimen, as required by the owners.

The Bülow family provide one of the main private collection of the study. The specimens were discovered in the second half of the XXth century by the late Max Bülow. The collection is represented by 10 specimens of various nature (cranial and axial), most of which were acid-prepared. One of them, a braincase, has already been studied (Knoll *et al.* 1999).

The Enos and Drijard collections belong to the Villers-sur-Mer Paleontological Association (APVSM). The association provides one specimen of each collection: two fused frontals found in 1989 by Jérôme Enos and a caudal vertebra (Drijard). The first specimen was found at the bottom of the cliffs and did not require preparation. Origin and preparation methods are unknown for the second specimen. The fused frontals have already been studied (Buffetaut & Enos 1992).

The three other collections are public ones. The first is the municipal collection of Houlgate. It includes two specimens found by the late Frédéric Nicolet: a distal part of femur and a caudal vertebra. The date of discovery as well as the method of preparation is unknown. Both of these bones were studied and figured in Buffetaut (1994b).

The second is the Paléospace collection and the main public source of specimens of this study. The Pennetier collection was private when the study began but has now been donated to the Paléospace. The Pennetier collection is one of the most important of the study. It comprises 12 specimens, discovered at the bottom of the cliffs during the 70s-80s. The remains include various elements (cranial, appendicular and axial), which were mainly mechanically prepared. One of them has already been described: the fragment of a maxilla of the Pennetier collection (Buffetaut *et al.* 1991). There are few other theropod bones housed in the Paléospace collection. A hand-prepared dorsal vertebra already described by Plasse & Buffetaut (2016) is the most noticeable specimen. According to these authors, the vertebra is the same as the one mentioned in Bigot (1938).

The last is the MNHN collection of palaeontology. Thanks to a donation in 2019 by Nathalie Poussy two new specimens were added to the study. They consist of a femur and a vertebra found between 1989 and 1991. The femur was acid and hand-prepared by the preparation team of the MNHN. The MNHN also allowed access to the types specimens of *Streptospondylus altdorfensis* and *Piveteausaurus divesensis.*

TABLE 2. — Specimen inventory from the Vaches Noires cliffs housed in public collection. Studied specimens are in bold.

Source Collection	Specimen number	Clearing methods (if known)	(Re)evaluated stratigraphic origin	Bone type	Taxonomic assignment
Mairie d'Houlgate. Col. Nicolet	**NMH1**	-	Marnes de Dives, upper Callovian	Left femur (distal end)	Megalosauridae indet.
Mairie d'Houlgate. Col. Nicolet	**NMH2**	-	Marnes de Dives, upper Callovian	Caudal vertebra	Tetanurae indet.
Paléospace l'Odyssée	**MPV V795**	-	Callovian or Oxfordian marls	Caudal vertebra	Tetanurae indet.
Paléospace l'Odyssée	**MPV V869**	manual	Oxfordian marls (lower Oxfordian)	Dorsal vertebra	Tetanurae indet.
Paléospace l'Odyssée	MPV V878	acid	Callovian or Oxfordian marls	Indeterminate vertebra	Indeterminate
Paléospace l'Odyssée	MPV V885	-	Callovian or Oxfordian marls	Indeterminate long bone (femur fragment?)	Indeterminate
Paléospace l'Odyssée	MPV V886	-	Oolithes ferrugineuses de Villers; lower Oxfordian	Indeterminate long bone (femur fragment?)	Indeterminate
Paléospace l'Odyssée (formerly Pennetier)	**MPV 2020.1.1**	manual	Callovian or Oxfordian marls	Left maxilla	Allosauroidea indet.
Paléospace l'Odyssée (formerly Pennetier)	**MPV 2020.1.2**	-	Callovian or Oxfordian marls	Proximal end of left tibia	Tetanurae indet.
Paléospace l'Odyssée (formerly Pennetier)	MPV 2020.1.3	-	Oolithes ferrugineuses de Villers; lower Oxfordian	Indeterminate long bone	Indeterminate
Paléospace l'Odyssée (formerly Pennetier)	**MPV 2020.1.4**	manual	Callovian or Oxfordian marls	Caudal vertebra	Tetanurae indet.
Paléospace l'Odyssée (formerly Pennetier)	**MPV 2020.1.5**	manual	Callovian or Oxfordian marls	Caudal vertebra	Tetanurae indet.
Paléospace l'Odyssée (formerly Pennetier)	**MPV 2020.1.6**	-	Callovian or Oxfordian marls	Caudal vertebra	Tetanurae indet.
Paléospace l'Odyssée (formerly Pennetier)	**MPV 2020.1.7**	-	Callovian or Oxfordian marls	Dorsal vertebra	Tetanurae indet.
Paléospace l'Odyssée (formerly Pennetier)	**MPV 2020.1.8**	manual	Callovian or Oxfordian marls	Caudal vertebra	Tetanurae indet.
Paléospace l'Odyssée (formerly Pennetier)	**MPV 2020.1.9**	acid	Oxfordian marls (lower Oxfordian)	Dorsal vertebra	Allosauroidea indet.
Paléospace l'Odyssée (formerly Pennetier)	**MPV 2020.1.10**	-	Callovian or Oxfordian marls	Dorsal vertebra	?*Streptospondylus altdorfensis*
Paléospace l'Odyssée (formerly Pennetier)	**MPV 2020.1.11**	acid/manual	Oxfordian marls (lower Oxfordian)	Cervical vertebra	?*Streptospondylus altdorfensis*
Paléospace l'Odyssée (formerly Pennetier)	**MPV 2020.1.12**	-	Oolithes Ferrugineuses de Villers; lower Oxfordian	Caudal vertebra	Tetanurae indet.
MNHN (formerly Poussy)	**MNHN.F.RJN471**	acid/manual	Marnes de Villers (H14); lower Oxfordian	Right femur (proximal and distal end)	Megalosauridae indet.
MNHN (formerly Poussy)	**MNHN.F.RJN472**	–	Oolithes Ferrugineuses de Villers; lower Oxfordian	Dorsal vertebra	?*Streptospondylus altdorfensis*

Other more recently discovered specimens (2012-2017) from the collection of Jean-Philippe Pezy were examined and present, as usual, remains of theropods but also a sauropod caudal vertebra (EM pers. obs). Unfortunately, we were not allowed to figure these specimens.

Some of the theropod remains (as the type of *Streptospondylus*) were found more than two centuries ago and have since had a long history in private and public collections. Others were found only a few years ago. As a result, many dates of discovery are unclear, and origins are often unknown, even if the study of the matrix usually allows to confirm that a bone is from the Vaches Noires.

Because they come from different collections, fossil preservation and cleaning methods are not the same. Furthermore, most of the remains were found at the bottom of the continually eroding cliffs. The bones are then hardly ever found *in situ* so that their preservation is directly conditioned by the time they spend on the beach, where they are subjected to the tides. Thus, they are more or less abraded and water-worn.

Finally, the preservation of the fossils from the Vaches Noires complicates their interpretation (taxonomic and stratigraphic). Therefore, out of the 34 available specimens, only 26 have actually been studied, because they contain anatomical and taxonomic information. The others were too damaged, indistinctive and/or uninformative. The studied remains consist of five cranial, three appendicular, and 20 axial elements (two cervical, seven dorsal, nine caudal vertebrae).

Stratigraphy

Because bones were not found *in situ* in the cliffs, stratigraphic assignment was not always possible. Thus, specimen origin is often reduced to "Callovian or Oxfordian marls". In some cases, more precision is possible from matrix study. For example, ochre marls with ferruginous ooliths are characteristic of the formation called Oolithe Ferrugineuse de Villers (H15 level as defined by Hébert 1860 maintened by Dugué *et al.* 1998). Fossil content may also be useful. The shells of the oyster *Actinostreon gregareum* Sowerby, 1816 are Oxfordian marls indicator. All the studied bones come from marly levels, dating from either the upper Callovian or lower Oxfordian (Dugué *et al.* 1998). The lower part of the Vaches Noires cliffs corresponds to the Marnes de Dives (upper Callovian). Many vertebrates remains – such as those of marine reptiles – are found there (Buffetaut *et al.* 1991; Bardet 2013; Hua 2013). Those bones were mainly found *in situ* in the marls so that their source is clear. This is not the case with the theropod remains studied here. Because of the abundance of vertebrates found in these Callovian marls, many theropod remains found at the bottom of the cliffs were previously assigned to the Marnes de Dives (Taquet & Welles 1977; Buffetaut *et al.* 1991, 2010; Knoll *et al.* 1999). This attribution is not justified by any stratigraphic markers. Drawing a distinction between Marnes de Villers, Marnes de Dives and Argile à *Lopha gregarea* Sowerby, 1816 (the main marl levels in the cliffs) is not possible without stratigraphic markers. Consequently, all the bones without a precise stratigraphic origin were defined as being from Callovian or Oxfordian marls. The stratigraphic origin is also unclear for *Streptospondylus* (Allain 2001) and *Piveteausaurus* Taquet & Welles, 1977. Indeed, the origin of *Piveteausaurus* was Oxfordian according to Piveteau (1923) and Callovian in Taquet & Welles (1977). To sum up, stratigraphic placement is variably precise and is summarised in Fig. 1.

Methods

Taxonomy and comparative anatomy

The studied remains were compared with other Vaches Noires theropods but also with English species of similar Middle to Late Jurassic age, which are also preserved in marine sediments. These are the Callovian *Eustreptospondylus oxoniensis* (Walker, 1964), the Bathonian *Megalosaurus bucklandi* Mantell, 1827, and the Oxfordian *Metriacanthosaurus parkeri* Huene, 1923. All of them belong to Tetanurae. Other members of the clade served for comparisons. For example, well-known theropods such as the Kimmeridgian/Tithonian Megalosauroidea *Torvosaurus* Galton & Jensen, 1979, and the Oxfordian Allosauroidea *Sinraptor dongi* Currie & Zhao, 1994, were used as a benchmark for anatomic and taxonomic identification of the bones. Because of its well-known osteology (Madsen 1976), the most useful Tetanurae was undoubtedly *Allosaurus fragilis* Marsh, 1877. Taxonomic assignments were realised using discriminant or synapomorphic characters from phylogenetic studies on Tetanurae (Rauhut 2003; Brusatte & Sereno 2008; Benson 2010; Carrano *et al.* 2012). Because most of the bones have been found isolated and lack diagnostic features, their taxonomic identification is often limited to superfamily level. The nomenclature follows Wilson (1999) and Wilson *et al.* (2011) for vertebral structures, and Witmer (1997) and Hendrickx & Mateus (2014) for cranial structures. Referring specimens to the same individual is easy when there is a direct anatomical connection, but this is hardly ever the case. That is why the minimum number of individuals (MNI) was estimated using taxonomy, stratigraphic position and bone dimensions.

SYSTEMATIC PALEONTOLOGY

THEROPODA Marsh, 1881
TETANURAE Gauthier, 1986
Super family Megalosauroidea Fitzinger, 1843
Family Megalosauridae Fitzinger, 1843

Megalosauridae indet.

Cranial skeleton

Premaxilla

Material. B1, a right premaxilla (Fig. 2).

Stratigraphy. Oolithe Ferrugineuse de Villers (H15) as defined by Hébert (1860) maintained in Dugué *et al.* (1998), according to the ferruginous ooliths of the matrix. Lower Oxfordian.

The posterodorsal part of the premaxilla is fractured and the nasal process is missing, clearly cut at its base. The maxillary process is also absent. The medial side is eroded, revealing dental alveoli and replacement teeth (Fig. 2B). The bone is massive. It is 170 mm high under the ventral margin of the nostril and 160 mm long. By comparison with theropods skulls, notably *Allosaurus fragilis* (Madsen 1976), the entire skull length must have exceeded one meter. Similarly to *Torvosaurus tanneri* Galton & Jensen, 1979, the premaxillary body is as long as it is wide (Britt 1991). The lateral side is pierced by more than 15 foramina. Most of them are wider than 5 mm and concentrated in the anteroventral corner of the bone. They are interpreted as perforations for trigeminal nerve branches of the neurovascular system (Barker *et al.* 2017). As in *Torvosaurus tanneri* (Britt 1991) the anterior part of the bone slopes rearward (Fig. 2A). The medial surface is flat to form the symphysis with the left premaxilla. The width of the bone at this level is 80 mm so that the entire snout width was about 160 mm. A depression linked to the external nares is visible in the posterodorsal corner. Thus, the premaxillary body is quite anteriorly placed relative to the nostril. The angle between the basis of the nasal process and the alveolar margin is about 60°. This is more similar to *Eustreptospondylus* Walker, 1964, *Dubreuillosaurus valesdunensis* (Allain, 2002) and *Torvosaurus* than to *Sinraptor* Currie & Zhao, 1993 or *Allosaurus* Marsh, 1877. Posteriorly, the contact facet with the maxilla is visible. It is flat and medially oriented, with three foramina. The subnarial foramen is placed dorsally on the facet (Fig. 2C). On the medial face, the interdental plates are broken so that replacement teeth are visible. However, they do not seem to be fused in their ventral margin. The para-

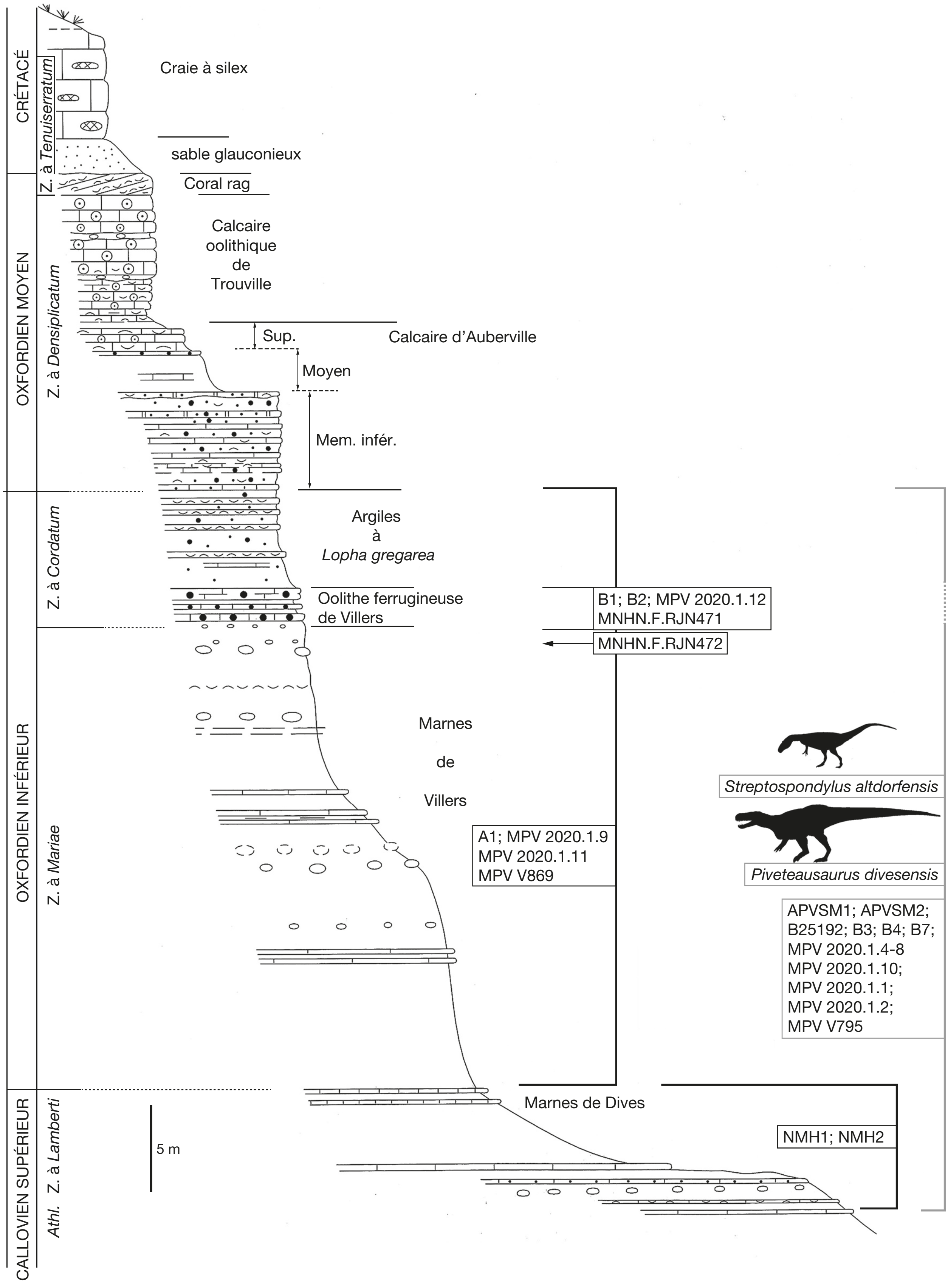

FIG. 1. — Vaches Noires cliffs synthetic log with studied specimen position. **Grey interval** indicates unclear provenance; **dotted line** is for easily recognizable Oolithes Ferrugineuse de Villers (modified from Dugué *et al.* 1998).

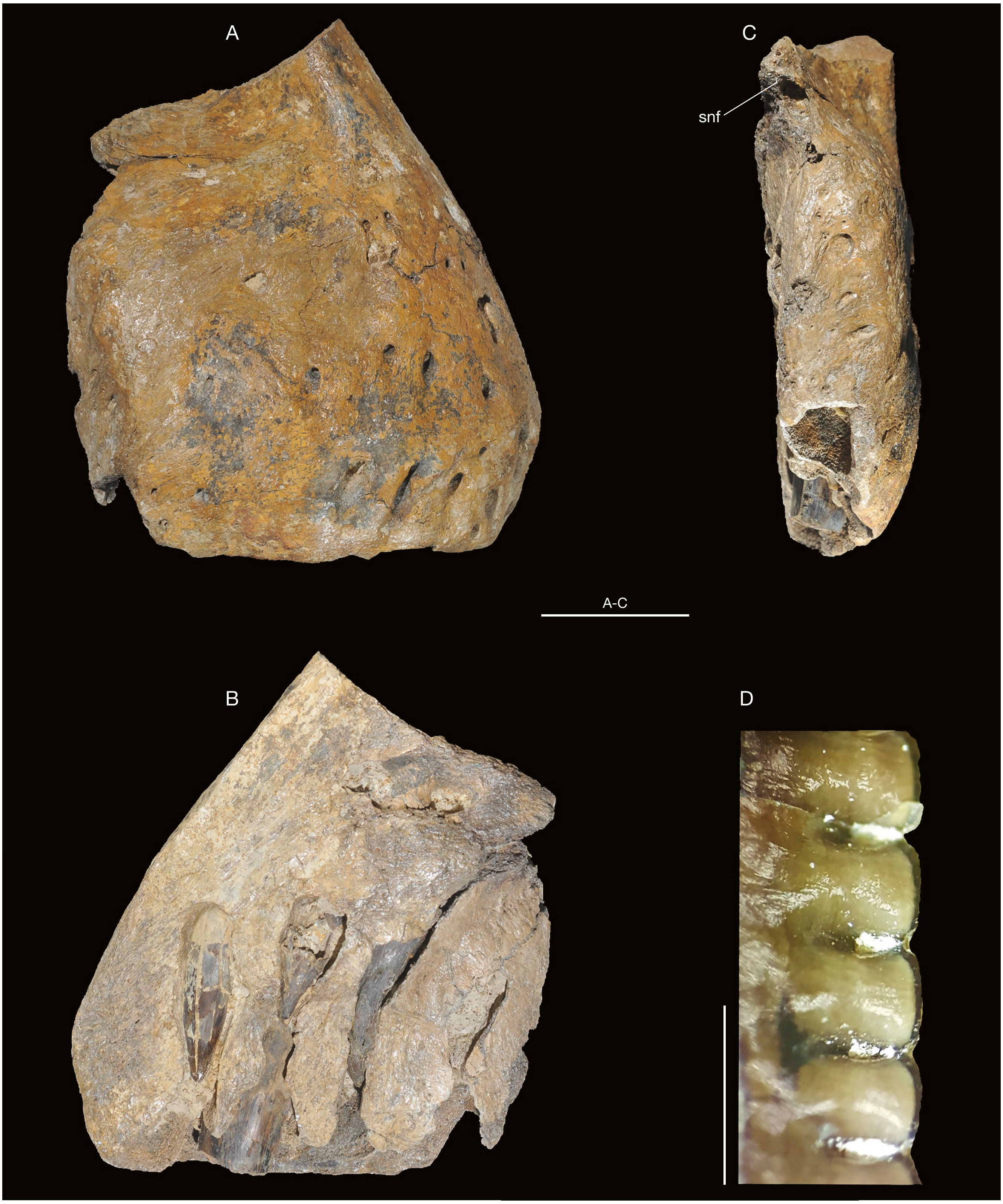

Fig. 2. — Megalosauroidea indet., left premaxilla (**B1**), Oolithes Ferrugineuses de Villers, in lateral (**A**), medial (**B**) and posterior (**C**) views. Distal denticles of a replacement tooth of the first alveoli in lingual view (**D**). Abbreviations: **snf**, subnarial foramen. Scale bars: A-C, 5 cm; D, 1 mm.

dental lamina separates the interdental plates from the body of the premaxilla body. In ventral view, 4 ellipsoidal alveoli are visible. They are mediolaterally oriented, with an erupted tooth in the second one. This tooth is transversally broken at the level of the ventral margin of the premaxilla (Fig. 2C, D). Above this tooth, the apex of a replacement tooth is visible.

The first and third alveoli bear only one replacement tooth each. Denticles are mainly visible on the teeth of the first and second alveoli (Fig. 2D). There are seven mesial denticles per five millimetres; they are subrectangular and perpendicular to the crown. However, these dental characteristics are very similar to those of both allosauroids and megalosauroids (except spinosaurids) so that they do not help to differentiate these groups (Hendrickx *et al.* 2014).

APPENDICULAR SKELETON

Femora

Material. right femur MNHN.F.RJN471(Fig. 3); NMH1, a distal end of a left femur.

Stratigraphy. Found *in situ* in the Marnes de Villers (H14 level according to Hébert [1860] maintained by Dugué *et al.* [1998]). Lower Oxfordian (MNHN.F.RJN471). Marnes de Dives Callovian marls according to the Nicolet collection catalogue made by Max Bülow and Michel Rioult (NMH1).

The diaphysis is missing so that the femur MNHN.F.RJN471 is in two parts (Fig. 3A, B). Both extremities are quite fractured and eroded, especially the proximal one. Only the base of the articular head is preserved. The proximal part of the greater trochanter is broken, as well as the lesser trochanter. The fourth trochanter is missing because this part of the diaphysis is not preserved. The distal part is broken anteromedially. The crista tibiofibularis is missing, leaving a subrectangular base. The femur is massive and belongs to a very large theropod. The complete bone may have been up to one metre in length.

In posterior view, a ligament groove is visible just lateral to what could be the emplacement of the base of the articular head. Below that structure, in the long axis of the bone a 10 mm long oval foramen is visible. Because the middle part of the diaphysis is missing as well as the head, the orientation of the latter cannot be reconstructed. The greater trochanter is a 55 mm large bony plate on the lateral side of the bone. Its anterior middle margin is slightly convex proximodistally. The lesser trochanter is a thick blade of bone detached from the diaphysis and anteriorly oriented (Fig. 3C). Even though it is damaged, it probably did not reach the proximal margin of the femur, as is the case in basal tetanuran and non-tetanuran theropods (Carrano *et al.* 2012). A protuberance distally positioned on the trochanter could be a remain of the accessory trochanter, but abrasion makes the observation unclear. A bulge is visible medially to the most distal point of the lesser trochanter, which is interpreted as an attachment for the iliofemoralis muscle (Hutchinson 2001)

The distal extremity of the femur is 229 mm wide mediolaterally so that it is larger than the other femur (NHM1) described by Buffetaut (1994b). In distal view, both condyles remain visible. The lateral one is rounded and the medial one is narrower and elongate (Fig. 3F). The medial condyle bears deep and wide striations (one posterior and one anterior) but they may have been exaggerated by erosion. The medial condyle is anteroposteriorly oriented, but the articular facet seems more posterior. As a result, in medial view, the bone takes the shape of a reversed J (Fig. 3E). The medial condyle bears a striking feature above the broken area: a very thick and high mesiodistal crest extending on the midline of the distal diaphysis. The crest peaks at about 40 mm relative to the lateral side. This structure makes the cross section of the diaphysis triangular (Fig. 3D). This is very different from the condition in *Streptospondylus,* in which this area is flat. There is no depression for the femorotibialis externus (Hutchinson 2001; Carrano *et al.* 2012) on that crest in contrast to what is seen in allosauroids (Benson 2010; Carrano *et al.* 2012; Hendrickx & Mateus 2014). Moreover, the crest is rounded and thick in contrast with some allosauroids such as *Allosaurus* and *Sinraptor* (Currie & Zhao 1994). A similar morphology of the structure is mentioned by Hendrickx & Mateus (2014) on a distal fragment of a femur referred to *Torvosaurus*. This hypertrophied mesiodistal crest is present in the two species of the genus, but it is reduced as compared with MNHN.F.RJN471 (Hendrickx & Mateus 2014) insofar as it does not make the cross section triangular (Siegwarth *et al.* 1997). In *Megalosaurus* Buckland, 1822 the mesiodistal crest is poorly developed (Benson 2010; Hendrickx & Mateus 2014). The extensor groove is only visible in its most proximal part. The flexor groove is convex and 30 mm wide.

Genus *Streptospondylus* Meyer, 1830

?***Streptospondylus altdorfensis*** Meyer, 1832

AXIAL SKELETON

Cervical vertebra

Material. MPV 2020.1.11, an anterior cervical vertebra (Fig. 4).

Stratigraphy. Lower Oxfordian marls according to the *A. gregareum* shells in the matrix.

The specimen is quite damaged, especially on the left lateral side, so that the prezygapophyses, the diapophyses and a part of the articular facet are missing. Only the base of the postyzagophyses and the neural spine are preserved. The latter is slightly deformed. The margins of the posterior articular facet are fractured.

The ophistocoelous centrum is laterally invaded by deep pleurocoels, as in *Sinraptor* and *Eustreptospondylus* (Fig. 4C). These are much less open in *Allosaurus* (Madsen 1976). The parapophyses are reduced and placed posteroventral to the anterior articular facet (Fig. 4A). In ventral view, the centrum is considerably compressed laterally. As in *Eustreptospondylus,* it is very short (Sadleir *et al.* 2008). The dorsal margin of the anterior articular facet is offset from the neural canal. The neural arch represents more than half of the vertebra. The prezygapophyse extends beyond the centrum with a mediodorsally oriented facet. Posterior to the prezygapophyse and lateral to the neural canal there is a deep and oval centroprezygapohyseal fossa (Wilson *et al.* 2011). Above the neural canal the spinoprezygapohyseal fossa is visible. In right lateral view, the ventrally oriented diapophysis and the prezygapophysis merge together anteriorly. Posterior to this, between the postzygo-

Fig. 3. — Specimen MNHN.F.RJN471, right femur of an indeterminate Megalosauridae from H14 level of Marnes de Villers, in anterior (**A**) and lateral (**B**) views; proximal end in proximal view (**C**); distal end in proximal (**D**), medial (**E**) and distal (**F**) views. Abbreviations: **eg**, extensor groove; **gt**, great trochanter; **lc**, lateral condyle; **lt**, lesser trochanter; **mc**, medial condyle; **mdc**, mesiodistal crest. Scale bar: 10 cm.

diapophyseal and centropostzygapohyseal laminae, a deep depression is present (Fig. 4C). This structure is similar to that in *Eustreptospondylus* but different from the deeply excavate postzygapophyseal centrodiapophyseal fossa of *Sinraptor*. A strong ridge is present extending from the lateral side of the prezygapophysis to the postzygapophysis. The extension of this ridge, as well as the centropostzygapophyseal lamina are not visible due to the break of the postzygapophysis. Yet it is

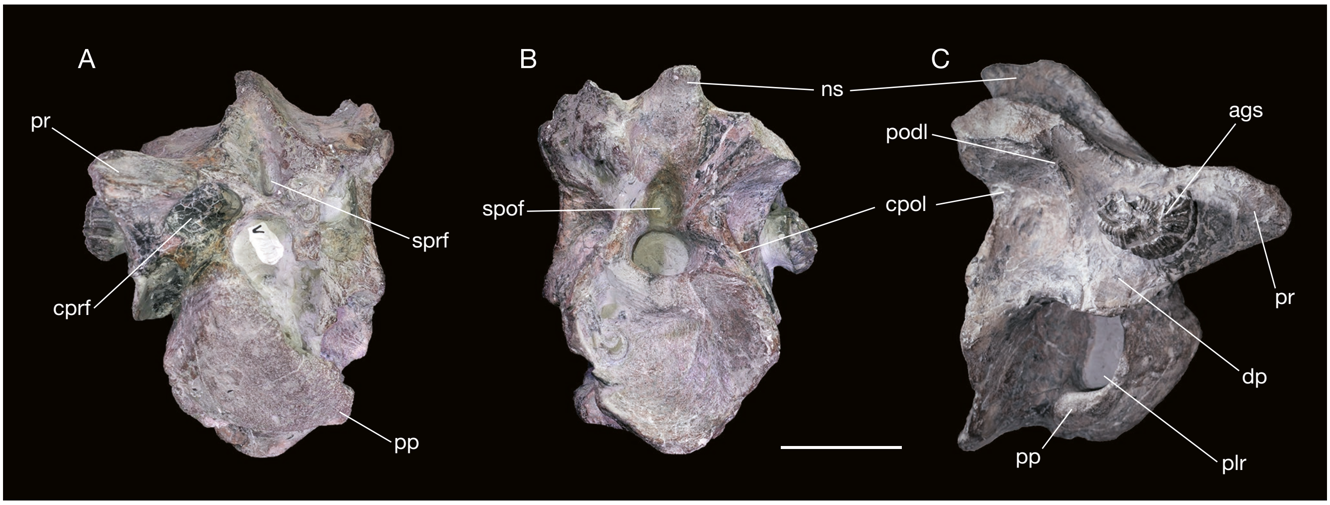

Fig. 4. — ?*Streptospondylus altdorfensis*, anterior cervical vertebra (MPV 2020.1.11), Oxfordian marls, in anterior (**A**), posterior (**B**) and right lateral (**C**) views. Abbreviations: **ags**, *Actinostreon gregareum* shell; **cpol**, centropostzygapophyseal lamina; **cprf**, centroprezygapophyseal fossa; **dp**, diapophysis; **ns**, neural spine; **plr**, pleurocoele; **podl**, postzygodiapophyseal lamina; **pp**, parapophysis; **pr**, prezygapophysis; **spof**, spinopostzygodiapophyseal fossa; **sprf**, spinoprezygapohyseal fossa. Scale bar: 5 cm.

Fig. 5. — Specimen MNHN.F.RJN472, anterior dorsal vertebra of *Streptospondylus altdorfensis* from Oolithes Ferrugineuse de Villers, in left lateral (**A**), posterior (**B**), dorsal (**C**) and ventral (**D**) views. Abbreviations: **pcd**, pleurocentral depression; **pp**, parapophysis; **vp**, ventral plateau. Scale bar: 5 cm.

possible that this ridge represents the epipostzygapophyseal lamina. In posterior view, the spinopostzygapohyseal fossa opens ventrally into the neural canal (Fig. 4B). However, this could be artificial and due to erosion. Based on the position of its base, it seems that the neural spine was limited to a posterior position in contrast with *Allosaurus* (Madsen 1976). The short nature of the centrum, the position of the parapophyses as well as the ventral orientation of the diapophyses indicate an anterior cervical vertebra, likely the third or fourth.

Dorsal vertebrae

Material. MNHN.F.RJN472, an anterior dorsal vertebra (Fig. 5). Dorsal vertebrae MPV 2020.1.10 and B5. (Fig. 6A, B)

Stratigraphy. Oolithe Ferrugineuse de Villers according to the ferruginous ooliths of the matrix. Lower Oxfordian (MNHN.F.RJN472 and B5). Oxfordian or Callovian marls (Pen5).

MNHN.F.RJN472. Only the centrum of the vertebra is present. It is anteriorly eroded as well as on the posterodorsal left side. A large opening is present on the left side of the anterior face but this seems artificial. The dorsal fracture is below most of the neural canal (except for anterior remains) as well as below the neurocentral suture, which is not visible.

The specimen is quite long (134 mm long and 126 mm wide) and ophisthocoelous (Fig. 5A, B). The centrum has concave ventral and lateral faces, so that it bears large pleurocentral depressions. In ventral view, the ventral face of the centrum presents a 35 mm wide plateau (Fig. 5D) very similar to that seen on the dorsal vertebrae of *Streptospondylus* (Allain 2001). Parapophyses are poorly preserved but discernible on each side. They are anterodorsally placed, just below the neurocentral suture (Fig. 5C). Based on the osteology of *Allosaurus* and *Torvosaurus* (Madsen 1976; Britt 1991) the position of the parapophyses, below the neurocentral suture, suggests an anterior dorsal

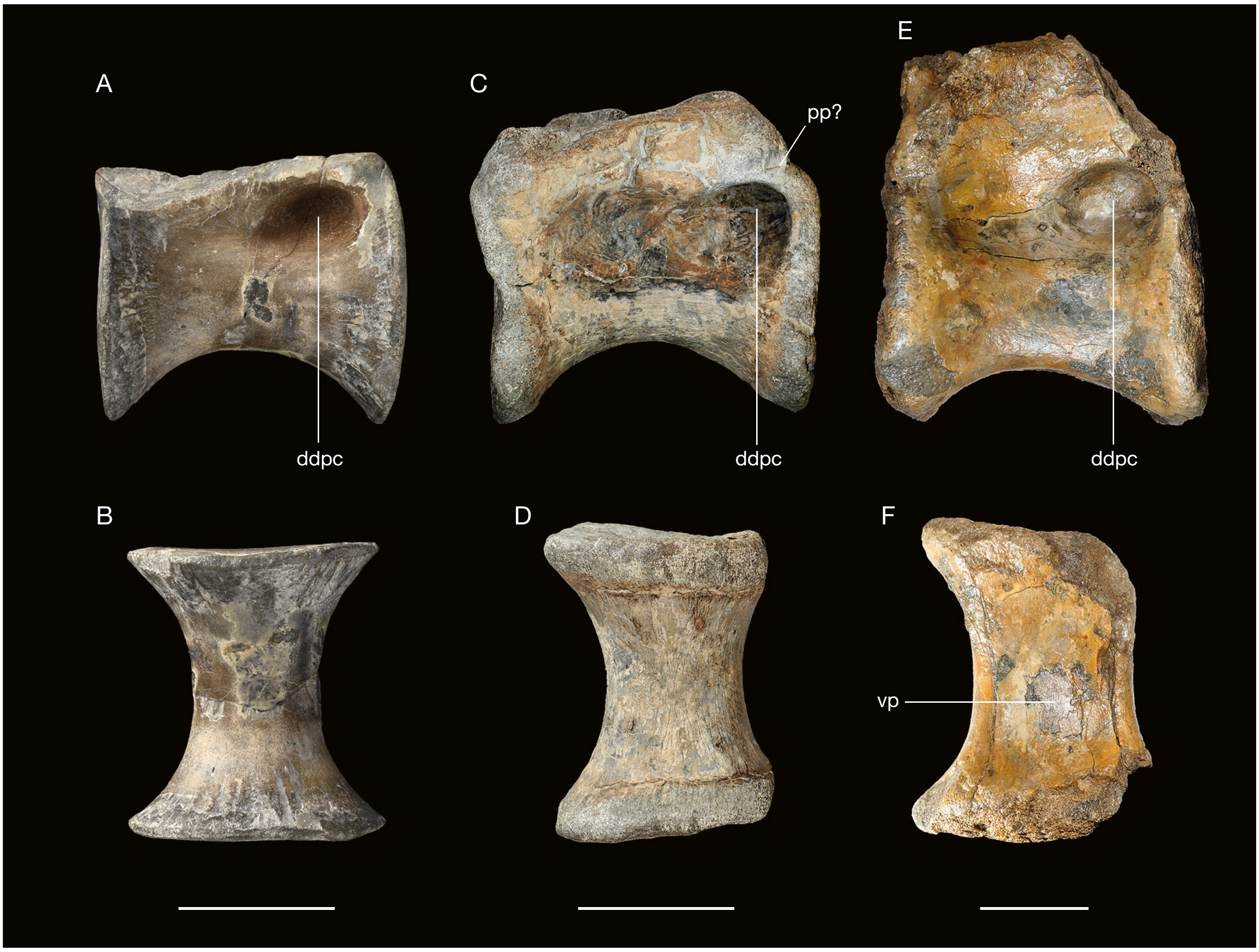

Fig. 6. — Dorsal vertebrae of *Streptospondylus altdorfensis* from Vaches Noires cliffs. Specimen MNHN.F.RJN82 of the type specimen of *Streptospondylus altdorfensis* in right lateral (**A**) and ventral (**B**) views. Specimen MPV 2020.1.10 (Callovian or Oxfordian marls) in right lateral (**C**) and ventral (**D**) views. Specimen B5 (Oolithes Ferrugineuse de Villers), in right lateral (**E**) and ventral (**F**) views. Abbreviations: **ddpc**, double pleurocentral depression; **vp**, ventral plateau. Scale bars: 5 cm.

vertebra, the fourth or fifth. However, the centrum is much elongated and opisthocoelous for an anterior dorsal vertebra. This is not seen in *Allosaurus* or *Torvosaurus* but is similar to *Streptospondylus* and *Eustreptospondylus* (Sadleir *et al.* 2008).

MPV 2020.1.10. Only the centrum, and the right neural arch margin are preserved (Fig. 6C). The right side of the centrum is also better preserved than the left one. The neural canal is visible as a concave trough filled with matrix. The base of what is interpreted as the right parapophysis is badly preserved but allows an orientation of the specimen.

The overall size of the vertebra is equivalent to those of the lectotype of *Streptospondylus* like MNHN.F.RJN82 (MNHN 8789 in Allain 2001). Longer than high, the centrum is platycoelous to slightly amphicoelous. It is laterally and ventrally concave. There is no flat area on the centrum ventrally. On each side and below the parapophyses, pleurocentral depressions are much deeper anteriorly. This results in a second rounded depression distinct from the rest of the concavity. This feature is called here a double pleurocentral depression. This feature is similar to the condition in the dorsal vertebrae of *Streptospondylus* (see Fig. 6A) and *Eustreptospondylus* (Allain 2001; Sadleir *et al.* 2008) and considered as an autapomorphy of the former. The neurocentral suture is still visible above the pleurocentral depression. Eroded but visible anteriorly, the right parapophysis is astride slightly above the neurocentral suture. This character is found on most dorsal vertebrae; therefore, a more precise positioning is not possible. Based on the position of the parapophysis, this vertebra is interpreted as a sixth or more posterior dorsal vertebra.

B5. The specimen is rather damaged, only the central part of the centrum as well as the neural arch, around the neural canal, are visible (Fig. 6D). The anterior, posterior and dorsal parts of the bone are highly eroded. Thus, the articular facets are poorly preserved.

Despite the erosion, some anatomical features are observable. The centrum is massive: 140 mm long and 100 mm high. This vertebra is larger than MPV V869 and should belong to a very large theropod. As in MPV 2020.1.10, and *Streptospondylus* and *Eustreptospondylus* dorsal vertebrae, it

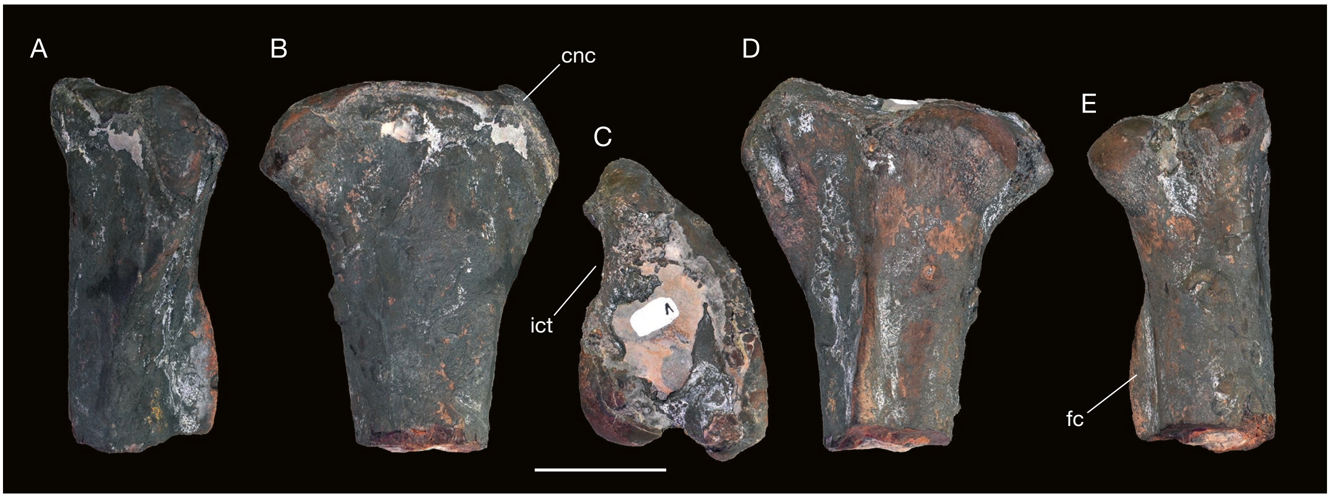

FIG. 7. — Specimen MPV 2020.1.2, proximal end of left tibia of ?*Streptospondylus altdorfensis* from Callovian or Oxfordian marls, in anterior (**A**), medial (**B**), proximal (**C**), lateral (**D**), posterior (**E**) views. Abbreviations: **cnc**, cnemial crest; **fc**, fibular crest; **ict**, incisura tibialis. Scale bar: 5 cm.

is laterally excavated by an anteriorly double pleurocentral depression. Foramina 3 mm in diameter are visible in the middle of the depressions. There are three on the right side and one on the left side. The ventral part of the centrum is flat so that it forms a 70 mm wide plateau. This feature is visible in MPV V869, MNHN.F.RJN472 and the dorsal vertebrae of other Megalosauroidea, such as *Streptospondylus* (Allain 2001). In right lateral view, two eroded areas anterior and posterior to the neural canal are likely remains of the anterior and posterior centrodiapophyseal laminae.

APPENDICULAR SKELETON

Tibia

Material. MPV 2020.1.2, a proximal end of a left tibia (Fig. 7).

Stratigraphy. Callovian or Oxfordian marls.

The specimen is quite well preserved. The proximal articular surface is slightly fractured and eroded. The proximal side is 110 mm long and 65 mm wide. In posterior view, the lateral condyle is more distal than the medial one. Thus, the articular face is laterodistally oriented, as in *Eustreptospondylus* (Sadleir *et al.* 2008) (Fig. 7E). Both condyles are equivalent in size, and a groove separates them posteriorly. Their shape is also reminiscent of *Eustreptospondylus,* especially the lateral one that is flat to slightly concave in proximal view. In dorsal view, the cnemial crest is anterolaterally placed (Fig. 7C). Its anterolateral end is proximally directed in lateral view. A crest is present along its lateral side. This structure forms the anterior margin of the incisura tibialis which separates the cnemial crest from the lateral condyle. This anterior depression allows the proximal contact with the fibula. In contrast with *Allosaurus,* in which the incisura tibialis is rectangular and deep, that of MPV 2020.1.2 is shallow, as in *Megalosaurus* and *Eustreptospondylus* (Sadleir *et al.* 2008; Benson 2010). There is a bony blade extending along the distal half of the specimen corresponding to the crista fibularis (Fig. 7A, D). This crest is in a central position on the diaphysis. The structure does not extend to the proximal surface of the tibia. The size of the specimen is small and equivalent to that of OUMNH J.13558, the juvenile type of *Eustreptospondylus* that is smaller than *Streptospondylus* (Allain 2001; Sadleir *et al.* 2008).

Suborder TETANURAE Gauthier, 1986
Super family ALLOSAUROIDEA Currie & Zhao, 1994

Allosauroidea indet.

CRANIAL SKELETON

Maxilla and dentary

Material. A1 a left maxilla with dentary, MPV 2020.1.1, a left maxilla (Fig. 8).

Stratigraphy. A1: lower Oxfordian marls according to the *A.gregareum* shells of the matrix. MPV 2020.1.1: indeterminate between Oxfordian and Callovian marls.

Discovered in 2002 at the bottom of the cliffs by the Anicolas family, the specimen A1 is a fragment of maxilla and dentary in occlusion, held together by matrix.

A1 Maxilla. The bone is 220 mm long and 115 mm high as preserved. Matrix is still present on the medioventral side between the teeth and on the anterior margin (further preparation was not allowed by the owners). As a result, the medioventral part of the specimen is not visible. The bone is obliquely fractured posteriorly and dorsoventrally so that two alveoli are visible in dorsal view. Only the basis of the ascending process is preserved. Fractures are – as often with Vaches Noires cliffs fossils – eroded and water-worn. The teeth are poorly preserved and shattered. As in *Sinraptor*, the anterior ramus of the maxilla is very short, with a rounded shape (Fig. 8A). In anterior view, the

Fig. 8. — Allosauroidea indet., left maxilla and dentary in occlusion (**A1**), lower Oxfordian Marnes de Villers, in lateral (**A**) and medial (**B**) views; mesial denticles of the fourth maxillary tooth in lateral view (**C**); mesial denticles of the second dentary tooth in lingual view (**D**); apex of the third dentary replacement tooth in lingual view (**E**). Abbreviations: **aof**, antorbital fossa; **aor**, antorbital ridge; **amp**, anteromedial process; **dt**, dentary tooth; **mg**, Meckelian groove; **mt**, maxillary tooth. Scale bars: A, B, 5 cm; C-E, 1 mm.

eroded anteromedial process protrudes from the ramus. In medial view, the articular crest and groove of this structure are visible but eroded. A sagittally fractured medial shelf is placed posterior to the anteromedial process. This shelf medially delimits the maxillary antrum located above it. This structure is a cavity at the base of the ascending process delimited anteriorly and posteriorly by preantral and postantral struts respectively. Among Avetheropoda the antrum is laterally and medially open so that it forms a maxillary fenestra (Fig. 9) (Carrano *et al.* 2012; Witmer 1997; Hendrickx & Mateus 2014). Thus, in megalosauroids like *Torvosaurus*, *Eustreptospondylus* or *Dubreuillosaurus*

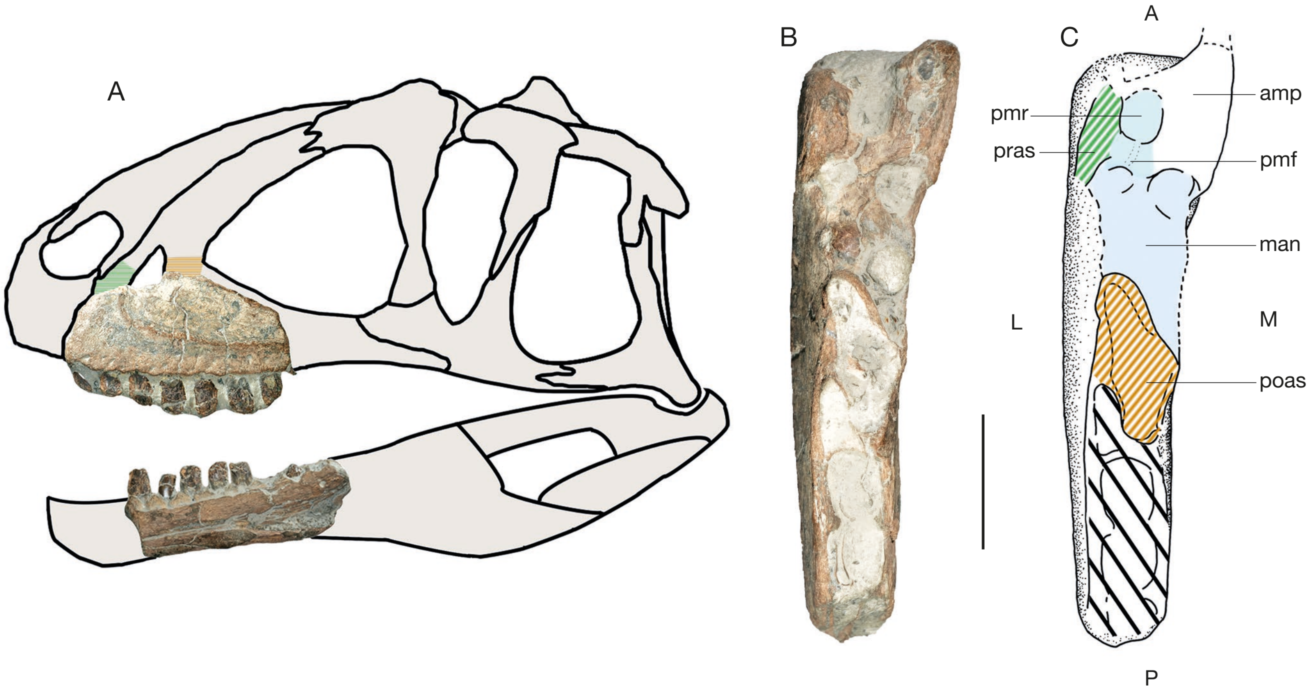

Fig. 9. — Allosauroidea indet., left maxilla and dentary (**A1**). Tentative positioning of A1 specimen in an "allosauroid like" skull (**A**); maxillary in dorsal view (**A**) and interpretative drawing (**C**). Abbreviations: **amp**, anteromedial process; **man**, maxillary antrum; **pmf**, promaxillary fossa; **pmr**, promaxillary recess; **poas**, postantral strut; **pras**, preantral strut. Scale bar: 5 cm.

Allain, 2005, the antrum is medially closed so that they bore a maxillary fossa (Britt 1991; Allain 2002; Sadleir *et al.* 2008; Hendrickx & Mateus 2014) in contrast with allosauroids like *Allosaurus*, *Acrocanthosaurus* or *Sinraptor* (Madsen 1976; Currie & Zhao 1994; Eddy & Clarke 2011; Chure & Loewen 2020). In our specimen the preantral and postantral struts are not preserved but their bases are visible dorsally by differentiating bony surfaces from fractures (Fig. 9B). The basal surface of the promaxillary fenestra is perceptible ahead of the antrum with the promaxillary recess diving into the matrix (Fig. 9B; C). In dorsal view, there are no fractures laterally to the antrum and its surface seems natural. Thus, the structure opens mediolaterally between the antorbital fossa and medial shelf. As a result, it is possible to determine that the specimen bore a maxillary fenestra (Fig. 9). In lateral view, the antorbital fossa is clearly delimited by a polished rim, the remains of an antorbital crest (Fig. 8A). This fossa strongly invades the maxilla. Below, foramina 5 mm in diameter pierce the ventral margin over its whole length. Seven much fractured teeth are visible, missing their apical parts. On some of them, denticles can be observed (Fig. 8C) but no carina is fully preserved.

Dentary A1. This fragment of dentary (Fig. 8B) is 220 mm long and 70 mm high as preserved. It is broken anteriorly and posteriorly. The main surface of the bone has flaked off so that some parts of the cortical bone are missing. Almost all the lateral surface is covered by the matrix. A longitudinal concavity, posteriorly wide and decreasing to a thin groove (about 2 mm wide) anteriorly is visible on the medial surface. This structure is filled by matrix. It corresponds to the contact area with the splenial bone posteriorly and the Meckelian groove anteriorly. Because of the matrix, it is not possible to see foramina near the groove opening. Interdental plates are unfused. They are rectangular at their base, with a triangular top. This shape is similar to the condition in *Sinraptor* and specimen MPV 2020.1.1., in which, moreover, the interdental plates are unfused, in contrast with *Allosaurus* (Madsen 1976). To judge from the reduced size of the posterior alveoli and the dorsoventral widening of the bone, the fragment is supposed to be the posterior part of a dentary (Fig. 9). As for the maxilla, teeth are poorly preserved. Six are erupted in the first five and the eighth alveoli. In the fourth alveolus, the apex of a replacement tooth is visible (Fig. 8E). Because the teeth are splattered, no carina is fully preserved on the dentary teeth, a dental morphology and comparison with other Vaches Noires remains is then not very reliable. Only part of the mesial carina of the second dentary tooth is preserved. It bears sixteen roundedmesial denticles per five millimetres (Fig. 8D). Their shape seems different from those on the maxilla as they are more bulbous and well distinct from the crown (Fig. 8C, D).

Maxilla MPV 2020.1.1. Already described by Buffetaut *et al.* (1991), this fragment of a left maxilla from the Pennetier collection was attributed to *Megalosaurus* sp. The stratigraphic position of this specimen is unclear. Buffetaut *et al.* (1991) referred it to the Upper Callovian, supposedly

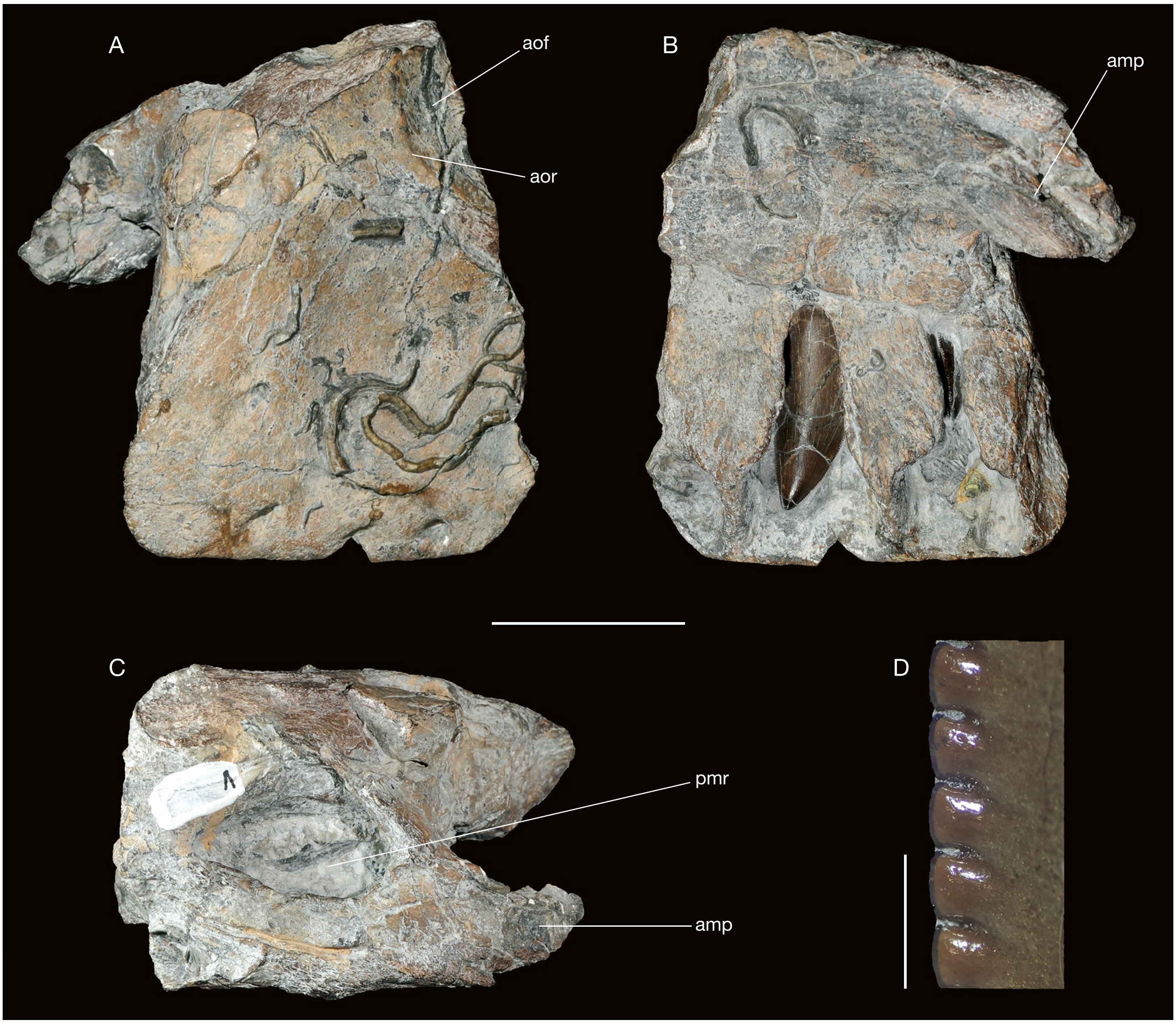

FIG. 10. — Allosauroidea indet., right maxilla (MPV 2020.1.1), in lateral (**A**), medial (**B**) and dorsal (**C**) views. Details of mesial denticles from a replacement tooth of the second alveoli in lingual view (**D**). Abbreviations: **aof**, antorbital fossa; **aor**, antorbital ridge; **amp**, anteromedial process; **pmr**, promaxillary recess. Scale bar: A-C, 5 cm; D, 1 mm.

torn from the Marnes de Dives by a storm. All the other bones from the Pennetier collection are supposed to come from Oxfordian marls (Pennetier: pers.com). However, because there is no stratigraphic marker on the specimen, the origin of MPV 2020.1.1 must be given as Callovian or Oxfordian marls.

The specimen corresponds to the anterior part of a left maxilla (Fig. 10) which was originally in contact with the premaxilla. This fragment is characterised by its massive appearance, a deep dorsal depression near the anteromedial process, as well as a large depression underneath it (Buffetaut *et al.* 1991). The first corresponds to the promaxillary recess of the promaxillary fenestra, diving into the anterior ramus (Witmer 1997; Hendrickx & Mateus 2014) (Fig. 10C). This structure is in the anterior part of the ascending process directed towards the nasal. As a result, it had to be placed more anteriorly than in *Megalosaurus*, *Dubreuillosaurus* or even *Allosaurus* (Madsen 1976; Allain 2002; Benson 2010). Such a configuration, with a remarkably short anterior ramus, is visible in *Sinraptor* as well as in some carcharodontosaurids such as *Acrocanthosaurus* (Eddy & Clarke 2011) and *Carcharodontosaurus* Stromer, 1931 (Brusatte & Sereno 2007) but also in specimen A1. The relative proportions of the anterior ramus and the anteromedial process are also similar to the latter specimen, as well as the position of the antorbital fossa. The anteromedial process is not directly dorsal to the interdental plates as in *Sinraptor*, but rather raised and ventral to the dorsal margin of the anterior ramus as in *Allosaurus*. Although only the anteroventral corner is preserved, the antorbital fossa is similar to specimen A1 so that the rim is clearly visible, unlike in *Megalosaurus*. However, MPV 2020.1.1 is much more massive than A1. This

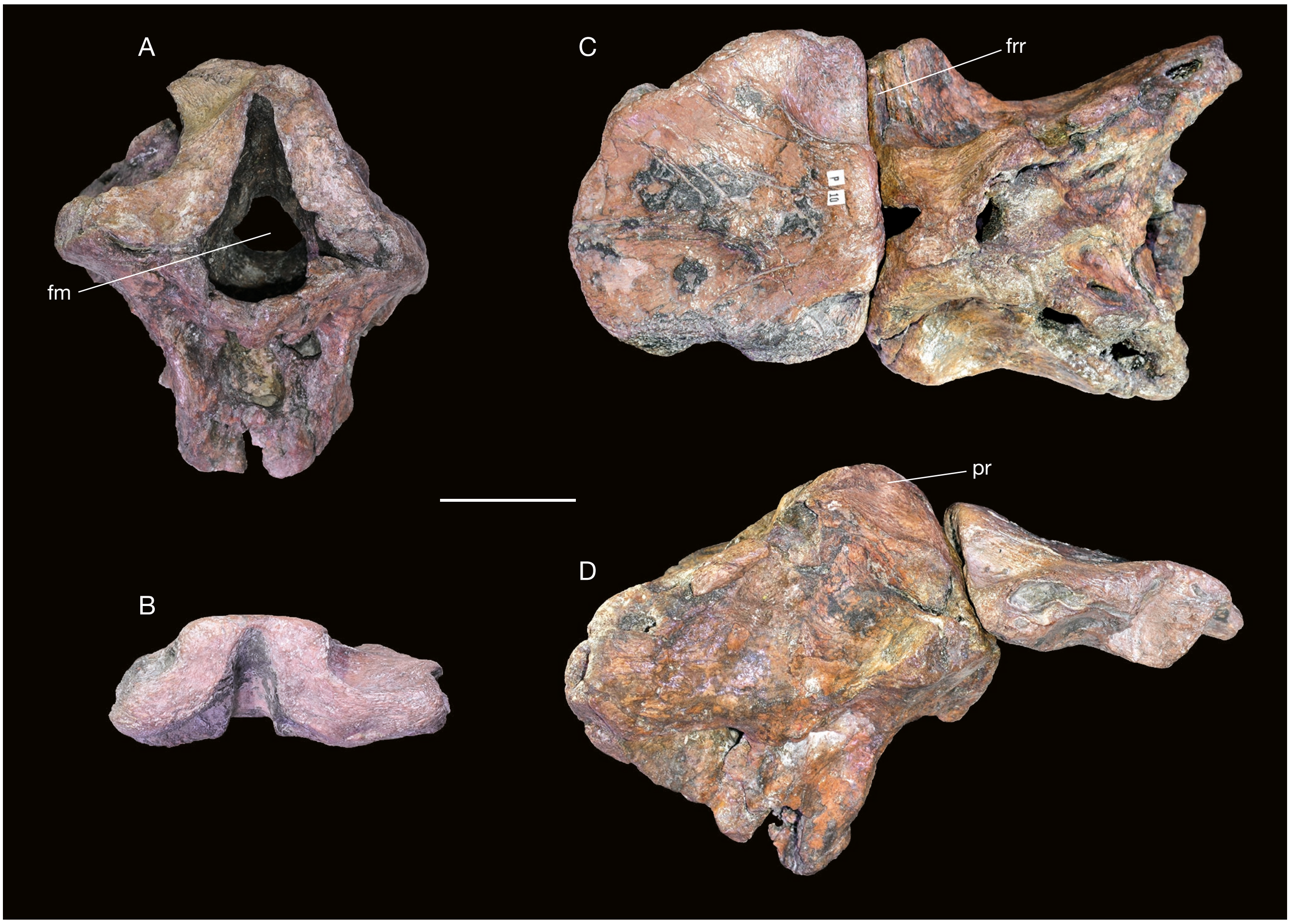

FIG. 11. — Allosauroidea indet., braincase (B25392) and frontals (APVM1). Braincase in anterior view (**A**); frontals in posterior view (**B**); associated specimens B25392 and APVM1 in dorsal (**C**) and right lateral (**D**) views. Abbreviations: **fm**, foramen magnum; **pr**, parietal; **frr**, frontal remains on B25392. Scale bar: 5 cm.

may indicate two related taxa or different stages or sexual dimorphism in the same species. These assumptions could be verified if, after cleaning, the large depression under the anteromedial process is also found in A1. As in Sinraptor (Currie & Zhao 1994), the interdental plates are nor fused or ornamented, but much more spaced although this may have been emphasized by erosion. The denticles on the teeth of MPV 2020.1.1 are subrectangular and there are about nine per five millimetres (Fig. 10D).

Braincase and frontals

Material. APVSM1 associated frontals, B25392 braincase (Fig. 11).

Stratigraphy. Callovian or Oxfordian marls.

Both specimens were already described by Buffetaut & Enos 1992 (frontals, Fig. 11B) and Knoll *et al.* 1999 (braincase, Fig. 11A). After combining the specimens from the Enos (APVSM1) and Bülow (B25392) collection, it is now clear that these bones belong to the same individual. This was already proposed (Knoll *et al.* 1999) and is now confirmed. The bone determined as the sphenethmoid in Knoll *et al.* (1999) on the braincase coincides with the attachment area on the specimen APVSM1. The supposed sphenethmoid is then here identified as remains of the frontals still fused with the parietal. (Fig. 11B). Therefore, the specimens were separated by a fracture, not by separation along a sutural surface. Differences between these specimens and *Piveteausaurus* and *Eustreptospondylus* were already noticed (Buffetaut & Enos 1992; Knoll *et al.* 1999). One is the flatness of of the dorsal surface of the frontals, which is not seen in APVSM1. Indeed, in APVSM1, the frontoparietal suture is raised, as in *Allosaurus* (Madsen 1976; McClelland 1990). In contrast, a flat dorsal surface of the frontals is visible in megalosauroids such as *Eustreptospondylus* and *Dubreuillosaurus*. Moreover, unlike the latter two theropods, but as in *Allosaurus*, the frontals are short and wide (Allain 2002). Another distinctive feature is the reduced participation of the supraoccipital to the dorsal margin of the foramen magnum (Knoll *et al.* 1999). This character is typical of most Allosauroidea (Allain 2001, 2002). Because of these previous similarities with *Allosaurus* and members of the superfamily, braincase B25392 + frontals APVSM1 are interpreted as belonging to an indeterminate allosauroid. This assignment is supported by the similarities with *Allosaurus* found by the neuroanatomical study of the braincase (Knoll *et al.* 1999).

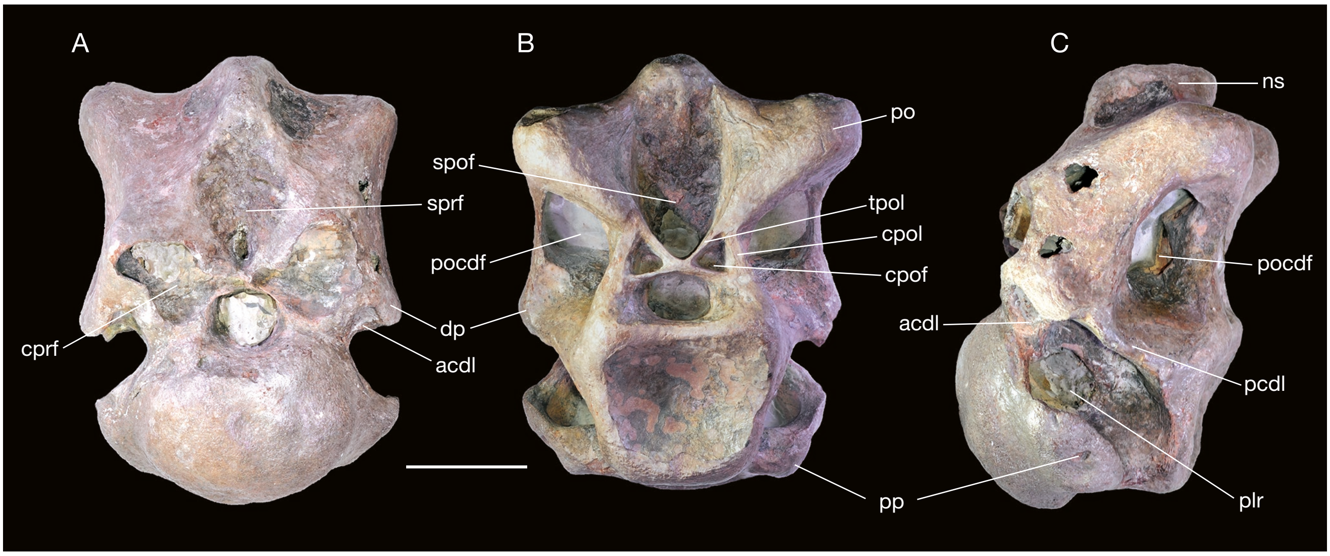

Fig. 12. — Specimen B3, anterior cervical vertebra of an indeterminate Allosauroidea from Callovian or Oxfordian marls, in anterior (**A**), posterior (**B**) and left lateral (**C**) views. Abbreviations: **acdl**, anterior centrodiapophyseal lamina; **cpol**, centrodiapophyseal lamina; **cpof**, centropostzygapophyseal fossa; **cprf**, centroprezygapohyseal lamina; **dp**, diapophysis; **ns**, neural spine; **pcdl**, posterior centrodiapophyseal lamina; **plr**, pleurocoel; **po**, postzygapophysis; **pocdf**, postzygapophyseal centrodiapophyseal fossa; **pp**, parapophysis; **spof**, spinopostzygodiapophyseal fossa; **sprf**, spinoprezygapohyseal fossa. Scale bar: 5 cm.

Axial skeleton

Cervical vertebra

Material. B3, an anterior cervical vertebra (Fig. 12).

Stratigraphy. Callovian or Oxfordian marls.

B3 is rather well-preserved but water-worn (Fig. 12A). The prezygapophyses and neural spine are broken so that only their bases are visible. The diapophyses are not complete and epipophyses are missing. The posterior articular facet is probably reduced in size because of abrasion of its borders. The deepest parts of the fossae are often hidden by matrix.

The centrum is short and opisthocoelous. The articular facets are wider than high. The vertebra is stocky, as in the Cretaceous theropod *Megaraptor namunhuaiquii* Novas, 1998 (Calvo *et al.* 2004). This contrasts with the strongly opisthocoelous and elongate vertebrae of *Eustreptospondylus* (Sadleir *et al.* 2008). The specimen has strongly pneumatized centrum and neural arch, much more than in *Allosaurus*. Pleurocoels expand over the major part of the centrum (Fig. 12C). As in many theropods, they are medially divided into two deep fossae by a bone lamina (Currie & Zhao 1994). The anterodorsally oriented parapophyses are in the anteroventral corner of the centrum. Their base merges with the ventral margin of the centrum so that they form the anterior half of it. As seen in the fifth cervical of *Sinraptor*, a depression is present on the ventral face of the centrum. The oval and convex anterior facet is wider than high. The posterior facet is concave and subquadrangular (Fig. 12B). Its peculiar shape is likely accentuated by erosion. This facet is ventrally offset by 40° relative to the anterior one so that the centrum has a flexed appearance (Fig. 12C). Half of the vertebra consists of a stocky neural arch. A rugose spinoprezygapohyseal fossa is present above the neural canal. It is the scar of the interspinous ligament (Currie & Zhao 1994). In anterior view, fractures on the prezygapophyses make their hollow nature visible. Lateroventral to them there is a triangular fossa formed by the centroprezygapohyseal laminae and anterior centrodiapophyseal laminae. The slightly concave diapophyses are ventrally oriented and laterally triangular. They are supported by the anterior centrodiapophyseal laminae and a strong, nearly horizontal, posterior centrodiapophyseal lamina. Both struts frame the centrodiapophyseal fossa medially and ventrally. As seen in *Sinraptor*, the posterior centrodiapophyseal laminae also form the ventral margin of a large and deep postzygapophyseal centrodiapophyseal fossa. The postzygapophyses are thick but eroded and water-worn. However, their articular facet is visible and ventrolaterally oriented. The postzygapophyses laterally frame a deep spinopostzygapophyseal fossa. Below the latter, two small symmetrical fossae are present (Fig. 12C). They are surrounded dorsally by the interpostzygapophyseal lamina, laterally by the centropostzygapophyseal lamina and ventrally by the neural canal. They match the centropostzygapophyseal fossae (Wilson *et al.* 2011). As in *Megaraptor*, they are particularly well-defined. The neural spine is worn by erosion and very reduced anteroposteriorly. The bent look of the centrum indicates an “S-shaped” neck of which *Allosaurus* is a classic example. According to the diapophyses vertical orientation and following Madsen (1976), the specimen is likely a fifth cervical vertebra.

Cervical/Dorsal vertebra

Material. MPV 2020.1.9, last cervical or first dorsal vertebra (Fig. 13).

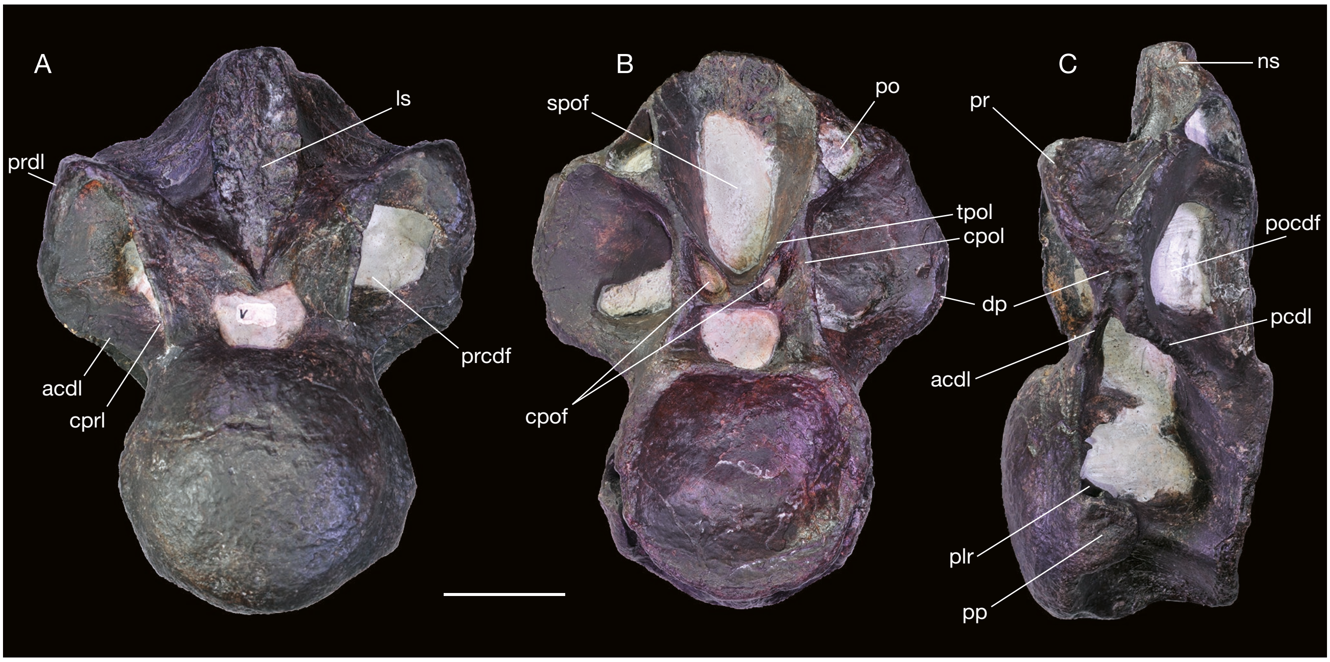

FIG. 13. — Specimen MPV 2020.1.9, first or second dorsal vertebra of an indeterminate Allosauroidea from Oxfordian marls, in anterior (**A**), posterior (**B**) and left lateral (**C**) views. Abbreviations: **cpof**, centropostzygapophyseal fossa; **acdl**, anterior centrodiapophyseal lamina; **cpol**, centrodiapophyseal lamina; **cpof**, centropostzygapophyseal fossa; **cprl**, centroprezygapophyseal lamina; **dp**, diapophysis; **ls**, ligament scar; **ns**, neural spine; **pcdl**, posterior centrodiapophyseal lamina; **plr**, pleurocoel; **po**, postzygapophysis; **pocdf**, postzygapophyseal centrodiapophyseal fossa; **pp**, parapophysis; **pr**, prezygapophysis; **prcdf**, prezygapophyseal centrodiapophyseal fossa; **prdl**, prezygodiapophyseal lamina; **spof**, spinopostzygodiapophyseal fossa. Scale bar: 5 cm.

Stratigraphy. Lower Oxfordian marls according to the *A.gregareum* shells in the matrix.

The vertebra is well preserved but the diapophyses and postzygapophyses are fractured. The distal part of the neural spine is missing. The specimen is highly pneumatized, but fossae are filled by the matrix.

The centrum is opisthocoelous and laterally pneumatized with a large pleurocoel on each side, as in B3. These pleurocoels are horizontally divided by a bony lamina. The suboval parapophyses are just below the pleurocoels, at half the height of the centrum. The ventral face of the centrum bears a pronounced ventral keel interpreted as an hypapophysis. The anterior articular facet is rounded and convex. As in vertebra B3, the facet extends laterally to merge with the parapophyses. The posterior articular facet is concave and slightly ventrally inclined. MPV 2020.1.9 is particularly pneumatized and bears the same laminae and fossae as B3. The prezygapophyses have subtriangular, dorsomedially oriented facets. In lateral view, they connect with the anterodorsal part of the diapophyses via a strong prezygodiapophyseal lamina. The spinoprezygapophyseal fossa is only visible just above the neural arch. A wide and high scar is present all over the anterior side of the neural spine. Large triangular fossae are present below the prezygapophyses on the lateral side. They are framed anteriorly by the centroprezygapophyseal laminae, dorsally by the prezygodiapophyseal laminae and ventrally by the anterior centrodiapophyseal laminae. These cavities correspond to the prezygapophyseal centrodiapophyseal fossae (Wilson *et al.* 2011) (Fig. 13A). The anterior centrodiapophyseal laminae and posterior centrodiapophyseal laminae merge laterally to support the diapophysis above the centrodiapophyseal fossa (Fig. 13C). The position of the laminae and the fossae indicates that the diapophyses were horizontally oriented. In lateral view the diapophyses are triangular. There is a large postzygapophyseal centrodiapophyseal fossa posteriorly to the diapophysis. This structure is framed ventrally by the posterior centrodiapophyseal lamina, dorsally and posteriorly respectively by the postzygodiapophyseal and centropostzygapophyseal laminae. Only the triangular bases of the postzygapophyses remain. They are higher than the diapophyses, hollow and matrix-filled. This shows once again the highly pneumatized condition of the vertebra. A large postspinal fossa is present medially to the postzygapophyses. Above it, as in B3, two small symmetrical fossae are visible (Fig. 13B); they are framed in the same way as in the other specimen (B3), but more elongated. Between these two centropostzygapophyseal fossae, a quadrangular vertical strut is visible. This structure is to be replaced by the hyposphene, to articulate with the hypantrum, in more posterior vertebrae. The vertical strut seems quite developed and it could indicate an early development the hyposphene/hypantrum complex, in contrast with *Allosaurus* and *Torvosaurus,* in which it appears from the fifth to the sixth dorsal (Madsen 1976; Britt 1991). *Sinraptor* possesses this articulation as early as the first dorsal (Currie & Zhao 1994). The preserved part of the neural spine is thin and is limited to a bony link between the spinoprezygapophyseal and spinopostzygapophyseal fossae. The bottoms of both these fossae bear an interspinous ligament scar. By comparison with *Allosaurus*, the low position of the parapophyses and the presence of a hypapophysis indicate a last cervical or first or dorsal vertebra.

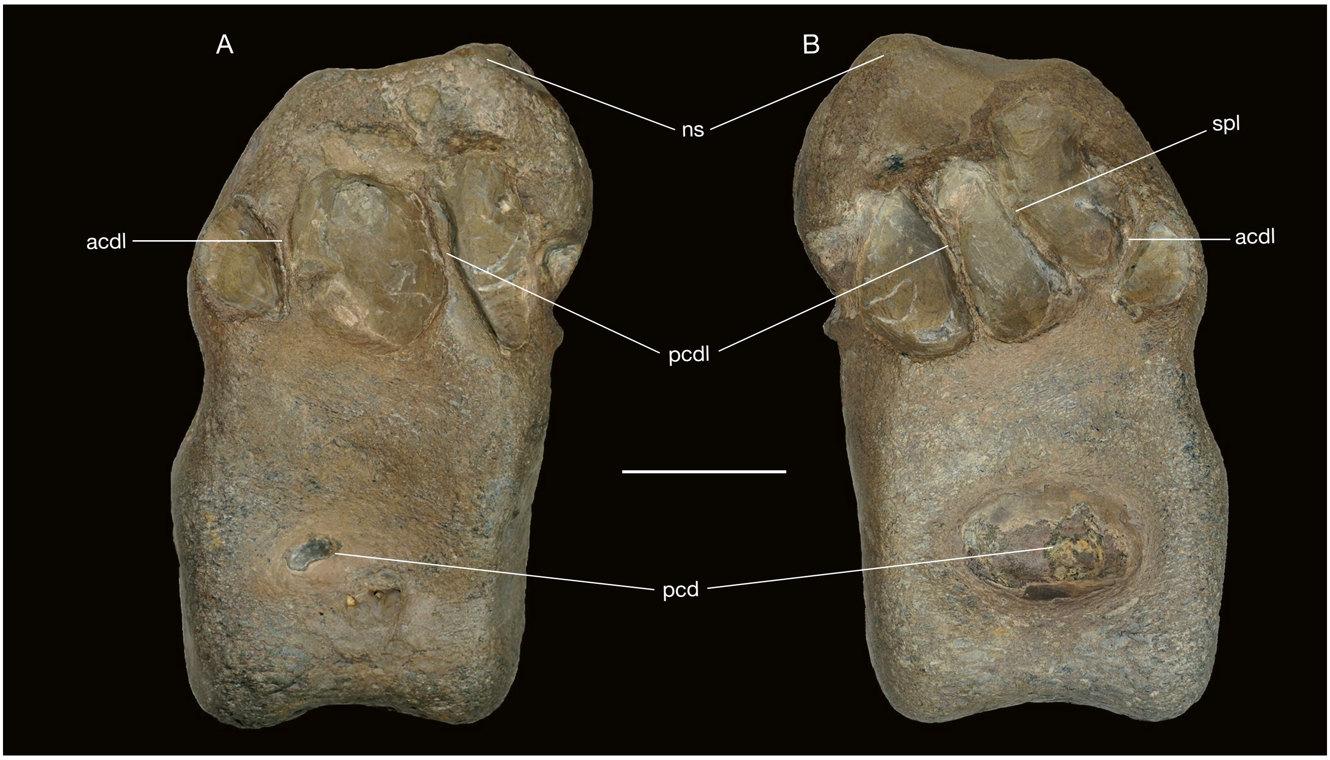

Fig. 14. — Specimen B4, dorsal vertebra of an indeterminate tetanuran from Callovian or Oxfordian marls, in left lateral (**A**) and right lateral (**B**) views. Abbreviations: **acdl**, anterior centrodiapophyseal lamina; **ns**, neural spine; **pcd**, pleurocentral depression; **pcdl**, posterior centrodiapophyseal lamina; **spl**, supplementary lamina. Scale bar: 5 cm.

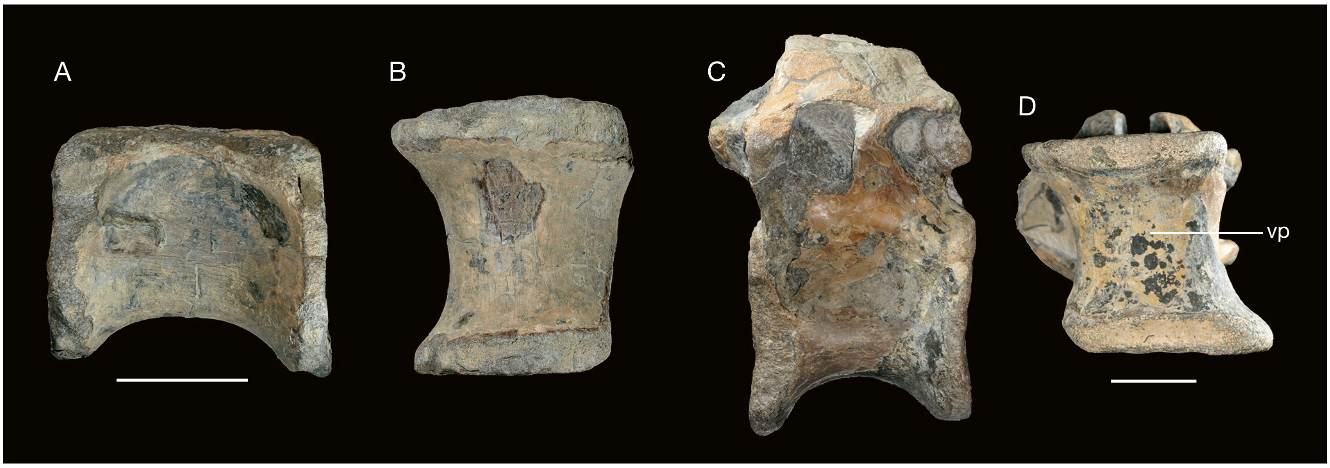

Fig. 15. — Dorsal vertebrae of an indeterminate tetanuran from Callovian or Oxfordian marls. Specimen MPV 2020.1.7 (Callovian or Oxfordian marls) in left lateral (**A**) and ventral (**B**) views. Specimen MPV V869 (Oxfordian marls), in left lateral? (**C**) and ventral (**D**) views. Abbreviations: **vp**, ventral plateau. Scale bars: 5 cm.

Tetanurae indet.

Axial skeleton

Dorsal vertebrae

Material. dorsal vertebrae B4 (Fig. 14) and MPV 2020.1.7 (Fig. 15A, B) and posterior dorsal vertebra MPV V869 (Fig. 15C, D).

Stratigraphy. Oxfordian or Callovian marls (MPV 2020.1.7 and B4). Lower Oxfordian marls according to the *A. gregareum* shells in the matrix (MPV V869).

B4. The vertebra is so eroded and water-worn that it does not appear to be a bone at first sight. Despite the strong erosion, the neural arch is still preserved and attached to the centrum. All of the apophyses are missing and only the base of the neural spine is visible. Articular facets are not preserved. This preservation state is remarkable and differs from other Vaches Noires remains studied here. It is the result of a long time period on the foreshore.

The bottom of a pleurocentral depression is still visible on each lateral side. According to the strong erosion, these should have been quite deep. The neural canal is anteriorly and posteriorly visible as a rounded depression. Remains of the hyposphene are present, above a triangular depression and allow the orientation of the specimen. Oddly enough, the bone laminae of the neural arch are clearly visible (Fig. 14). Despite the absence of the apophyses, anterior and posterior centrodiapophyseal as well as centropostzygapophyseal laminae are observable and frame their corresponding fossae (Wilson *et al.* 2011) Another peculiarity of the specimen is the asymmetry of these laminae. Indeed, in right lateral view, an additional lamina is visible in the centre of what should be the centrodiapophyseal fossa (Fig. 14B). The lamina issues from the same base as the anterior centrodiapophyseal lamina but its end is posteriorly oriented. This additional structure comes with a different orientation of the dorsal end of the posterior centrodiapophyseal lamina on each side of the vertebra. Indeed, the latter is anteriorly oriented on the right side and posteriorly oriented on the left side. The dorsal margin of the spinopostzygapophyseal fossa is anteriorly oriented and is elliptical, as well as the spinoprezygapophyseal fossa.

Because parapophyses are absent and the specimen is very eroded, a clear positioning of the vertebra is impossible. According to the phylogeny of Carrano *et al.* (2012), the anterior orientation of the neural spine on dorsal vertebrae is a synapomorphy of Allosauroidea. However, considering the poorly preservation of the specimen a taxonomic assignment above Tetanurae will not be attempted. Moreover, the preserved part of the neural spine is too incomplete to discern a real character state and this orientation could be artificial.

MPV 2020.1.7. Only the centrum of the vertebra is preserved (Fig. 15A). The left laterodorsal margin and the borders of the articular facets are eroded. The parapophyses are not visible. Thus, the preservation state prevents a clear orientation of the bone. The slightly greater depth of one side of the pleurocentral depression could indicate the front.

The centrum is platycoelous to slightly amphicoelous and is 110 mm long. It is much less concave laterally and ventrally than MPV 2020.1.7 and B5. This condition may be emphasised by erosion. Nevertheless, pleurocentral depressions are still much shallower. The right neurocentral suture is flat and clearly visible so that the individual may have been a juvenile. The neural canal is visible only medially. A 4 mm wide oval foramen pierces its centre.

The centrum shape seems to indicate a middle to posterior dorsal vertebra, but the absence of the parapophyses prevents a more precise positioning. Moreover, the state of preservation is too poor for a taxonomic assignment. And yet, this clade is use here more as a baseline, taking into account that the group is far more represented than others during Middle to Late Jurassic, especially in Europe (Rauhut *et al.* 2016). MPV 2020.1.7 is different in shape with a transversally wider centrum bearing shallower lateral depression than MPV 2020.1.10 and B5 so that it may indicates a different taxon, tentatively referred to Tetanurae

MPV V869. The vertebra was already described by Plasse & Buffetaut (2016) and defined as a thirteenth and last dorsal vertebra belonging to an allosauroid (Fig. 15C, D).

According to Madsen (1976), the last presacral vertebra of Allosaurus is the fourteenth. The number of cervical and dorsal vertebrae of the theropod have been discussed in Evers *et al.* (2015) so that it is assumed that *Allosaurus* had, as many other basal tetanuran rather 10 cervicals and 13 dorsals instead of 9 and 14. Then, Plasse & Buffetaut (2016) made a positioning correction with the *Allosaurus fragilis* vertebra used as comparison and figured (Plasse & Buffetaut 2016: Fig. 2) that represents the fourteenth of Madsen (1976) but numbered as the thirteenth which indicate the last presacral vertebra. Parapophyses are potentially visible in the shape of an eroded area lateral to the centroprezygapophyseal fossae. If that is correct, they were located at the anterior base of the diapophyses and at the same level as the prezygapophyses, which supports the already established positioning. The specimen is therefore a last dorsal/thirteenth vertebra. Despite the previous detailed description, the specimen was not compared with *Megalosaurus bucklandii*, particularly with a posterior dorsal vertebra of the paralectotype (OUMNH J.13577), which has important similarities with MPV V869. Among them is the flat area on the ventral side of the centrum, also present in *Torvosaurus* (Britt 1991). This feature is also present in *Streptospondylus* (Allain 2001). The quite deep pleurocentral depression on each side of the vertebra is similar to *Megalosaurus* as well as to other megalosauroids such as *Torvosaurus* (e.g. Britt 1991). In the posterior dorsals of *Allosaurus* and *Sinraptor*, this structure is absent or less deep (Madsen 1976; Currie & Zhao 1994). Regarding the neural arch, the "ridge" present in *Megalosaurus bucklandi* (OUMNH J.13577), which splits the "infrapostzygapophyseal" fossa (Benson 2010), is also present and very similarly placed in MPV V869. This structure is the centropostzygapophyseal lamina anteriorly framing the centropostzygapophyseal fossa (Wilson 1999; Wilson *et al.* 2011).

On the basis of these new observations, the assignment to Allosauroidea is less certain. The vertebra also bears similarities with *Megalosaurus bucklandi* and other megalosauroids. Thus, MPV V869 may also belong to the latter group. As a result, the specimen is referred to an indeterminate Tetanurae.

Caudal vertebrae

Material. Anterior caudal vertebrae NMH2, anterior to middle caudal vertebra B7 (Fig. 16). Successive middle caudal vertebrae MPV 2020.1.4, MPV 2020.1.8 and MPV 2020.1.5 (Fig. 17). Middle to posterior caudal vertebrae APVSM2 (Fig. 18), MPV V795 and MPV 2020.1.6 (Fig. 17); terminal caudal vertebra MPV 2020.1.12.

Stratigraphy. Marnes de Dives, Callovian marls according to the Nicolet collection catalogue made by Max Bülow and Michel Rioult (NMH2). Oxfordian or Callovian marls (B7, APVSM2, MPV 2020.1.4, MPV 2020.1.5, MPV 2020.1.6, MPV 2020.1.8 and MPV V795). Oolithe Ferrugineuse de Villers according to the ferruginous ooliths of the matrix. Lower Oxfordian (MPV 2020.1.12).

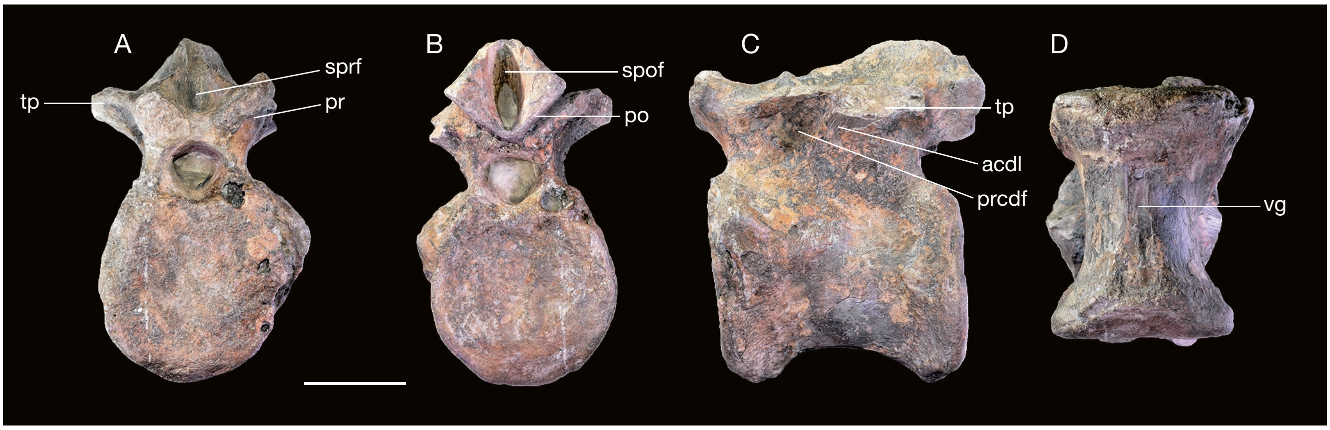

Fig. 16. — Specimen B7, anterior caudal vertebra of an indeterminate tetanuran from Callovian or Oxfordian marls, in anterior (**A**), posterior (**B**), left lateral (**C**) and ventral (**D**) views. Abbreviations: **acdl**, anterior centrodiapophyseal lamina; **po**, postzygapophysis; **pr**, prezygapophysis; **prcdf**, prezygapophyseal centrodiapophyseal fossa; **spof**, spinopostzygapophyseal fossa; **sprf**, spinoprezygapophyseal fossa; **tp**, transverse process; **vg**, ventral groove. Scale bar: 5 cm.

NMH2. This vertebra from the Nicolet collection was already described by Buffetaut in 1994. It was interpreted as an anterior caudal vertebra belonging to an indeterminate theropod. One of the remarkable features of the specimen is the "triangular depression" posterior to the prezygapophyses (Buffetaut 1994b). This structure is laterally framed by a thick anterior centrodiapophyseal lamina and dorsally by the prezygodiapophyseal lamina and could be identified as the prezygapophyseal centrodiapophyseal fossa (Wilson *et al.* 2011). Its position, like that of the transverse process; is quite posterior. The anterior centrodiapophyseal lamina is reduced and the fossa absent in *Eustreptospondylus* (Sadleir *et al.* 2008). These structures are not visible in *Allosaurus* but very similar to the condition in *Metriacanthosaurus parkeri* (OUM.J.12144/11).

B7. The vertebra is quite well preserved (Fig. 16). The transverse process and the right prezygapophysis are broken, but their bases are still visible, as is the neural spine. The left anterior part of the centrum seems inflated and is shattered so that it forms a protuberance (Fig. 16A). The centrum is 105 mm long and 75 mm wide. Following Madsen (1976), these proportions match the caudal vertebra of *Allosaurus fragilis* anterior to the thirtieth. Indeed, posterior to this position the centra become significantly more elongated so that they become twice as long as wide. Moreover, the neural arch is quite high and not flattened, supporting an anterior positioning of the specimen. The centrum is still longer than high (Fig. 16C) in contrast with the anterior caudal vertebrae (until about the seventh). Although incomplete, the neural spine seems quite thick Therefore, B7 should be located between the seventh and sixteenth vertebrae, more posteriorly than NMH2. The centrum is platycoelous and ventrally concave. The ventral face bears a groove limited laterally by two thin ridges of bone, as well as chevron facets anteriorly and posteriorly (Fig. 16D). The neural canal is subtriangular, laterally compressed in its ventral part by an enlargement of the pedicels of the neural arch. This is similar to *Dubreuillosaurus* and *Eustreptospondylus* (Sadleir *et al.* 2008). A thick anterior centrodiapophyseal lamina as well as a fossa reminiscent of NMH2, are visible. The transverse processes seem quite posteriorly and horizontally oriented. The left prezygapophysis bears a mediodorsally inclined facet. The spinoprezygapophyseal laminae are well defined and nearly horizontal. They are posteriorly oriented and merge with the base of the neural spine, forming a deep horizontal spinoprezygapophyseal fossa. The postzygapophyses are well preserved and bear lateroventrallymediolaterally inclined subrectangular facets (Fig. 16B). The postzygapophyses frame the spinopostzygapophyseal fossa anteriorly. The latter is vertical, in contrast with the spinoprezygapophyseal fossa. The neural spine, of which only the base is preserved, is quite posteriorly located on the neural arch.

Both specimens bear similar features such as the "triangular depression" already noticed by Buffetaut (1994b). Therefore, these two vertebrae should belong to closely allied taxa. It is also possible that they belong to the same individual. A precise positioning of these specimens is not possible considering the number of caudal vertebrae of a theropod. *Allosaurus fragilis,* like many other theropods such as basal Tetanurae, has about fifty (Allain & Chure 2002). Regarding the significant morphological variation within a theropod tail (Madsen 1976), a taxonomic assignment for an isolated specimen cannot be precise beyond Tetanurae.

MPV 2020.1.4, 2020.1.8, 2020.1.5. These three vertebrae are anatomically successive and thus they are interpreted as belonging to the same individual (Fig. 17D, E). However, they were not found at the same time and place at the bottom of the cliffs by the Pennetier family. The matrix, the shape and the size as well as apposition of postzygapophyses to prezygapophyses and articular facets clearly indicate their connection. Their right side is covered with serpulids. MPV 2020.1.4 is the better preserved, its neural arch being clearly observable (Fig. 17A, B). Only the base of the right transverse process, the neural spine and right prezygapophysis remain. The neural arches of MPV 2020.1.8 and MPV

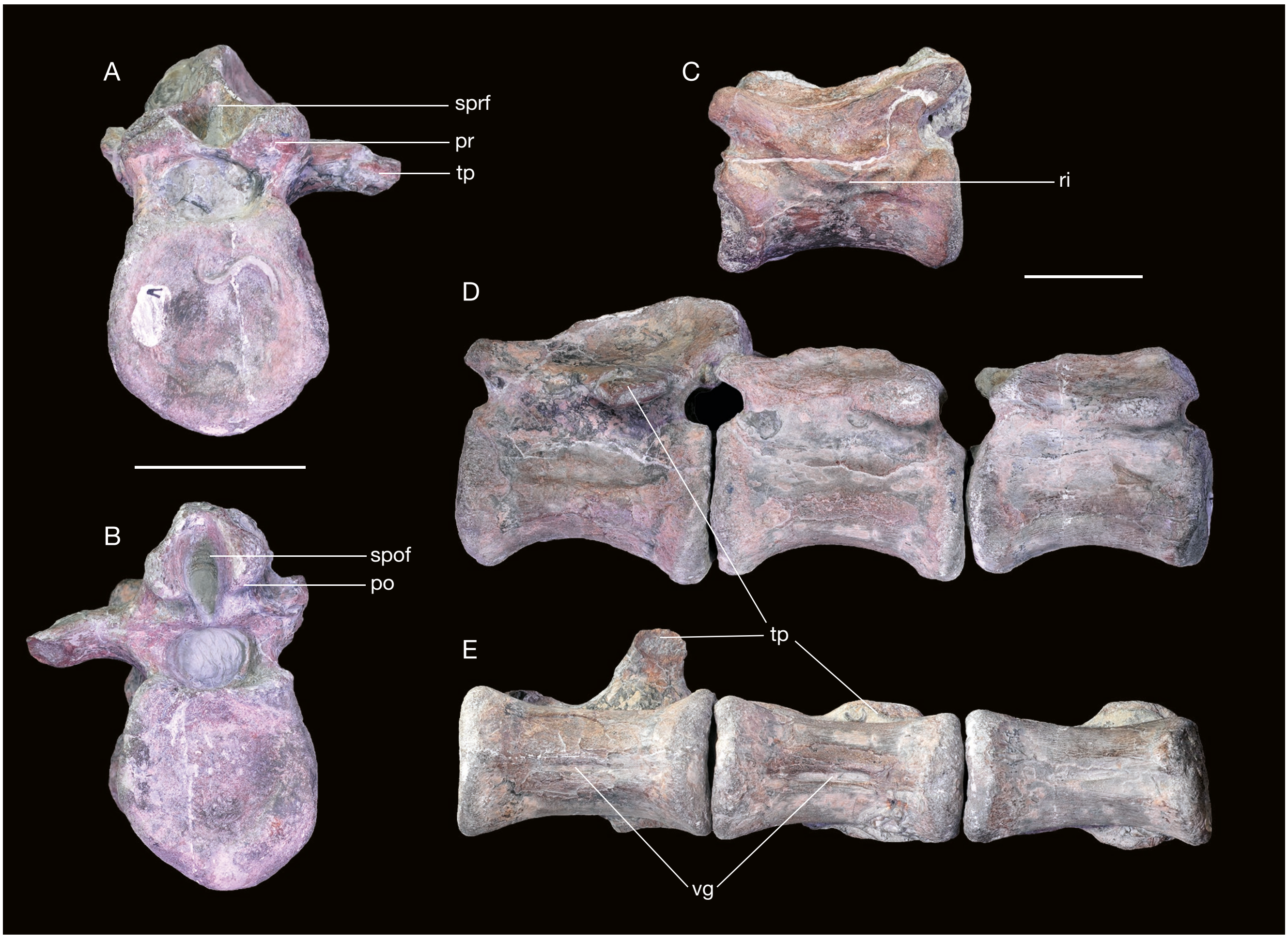

Fig. 17. — Indeterminates tetanuran caudal vertebrae of the former Pennetier collection from Callovian or Oxfordian marls. Specimen MPV 2020.1.4 in anterior (**A**), posterior (**B**) views. MPV 2020.1.6 specimen in left lateral (**C**) view. Successive caudal vertebrae MPV 2020.1.4, 8 and 5 in left lateral (**D**) and ventral (**E**) views. Abbreviations: **po**, postzygapophysis; **pr**, prezygapophyse; **ri**, ridges; **spof**, spinopostzygapophyseal fossa; **sprf**, spinoprezygapophyseal fossa; **tp**, transverse process; **vg**, ventral groove. Scale bars: 5 cm.

2020.1.5 are quite eroded. Both have quite well preserved prezygapophyses but not postzygapophyses, the common base of which is not visible. These 3 vertebrae have slightly amphicoelous centra which are almost twice longer than wide. The size of the centrum gradually decreases slightly along the series. Their ventral face bears a 20 mm to 30 mm longitudinal groove (Fig. 17E). The neural arch is flattened as compared to B7, but still well developed. As in *Poekilopleuron bucklandi* Eudes-Deslongchamp, 1837, the transverse processes are in the posterior half of the vertebrae (Allain & Chure 2002). The spinoprezygapophyseal and spinopostzygapophyseal fossae (the latter is only visible on MPV 2020.1.4) have a similar shape as in B7 which suggests a posterior development of the neural spine. The presence of transverse processes indicates that these vertebrae are anterior to the “transition point” as defined by Russell (1972). These structures are absent posterior to this point. In *Allosaurus fragilis*, it corresponds to the twenty-seventh vertebra (Madsen 1976; Allain & Chure 2002). Based on the quite elongated centra as well as the rather low neural arches, these bones should be placed between the sixteenth and twenty-seventh vertebrae. The quite high position of the diapophyses could restrict the interval to the first twenty vertebrae. However, this positioning is questionable because of the isolated nature of the bones as well as the morphological variation within theropods.

APVSM2. the vertebra is quite eroded, especially on its right lateral side. Thus, most of the preserved structures are worn (Fig. 18). The bases of the pre- and postzygapophyses as well as the left transverse process are visible (Fig. 18A, B). Only an abraded ridge -different from a natural bone surface- allows to discern the placement of the neural spine. The specimen has the same dimensions as MPV 2020.1.8 but is larger than MPV 2020.1.5, which indicates a different individual. The centrum is highly concave posteriorly and does not bear a ventral groove (Fig. 18D), as in *Eustreptospondylus* (Sadleir *et al.* 2008). This structure is, however, present in many theropods on their caudal vertebrae (Madsen 1976). The neural arch is also different from that of the previous specimens. What remains of the base of the transverse process indicates a low position, below the neural canal (Fig. 18C).

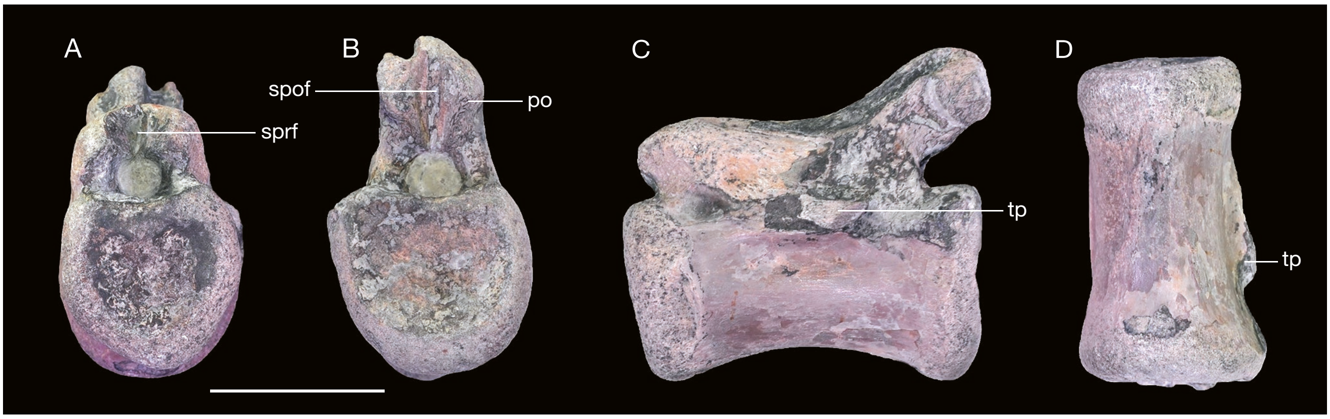

Fig. 18. — Specimen APVM2, caudal vertebrae of an indeterminate tetanuran from Callovian or Oxfordian marls, in anterior (**A**), posterior (**B**), left lateral (**C**) and ventral (**D**) views. Abbreviations: **po**, postzygapophyse; **spof**, spinopostzygapophyseal fossa; **sprf**, spinoprezygapophyseal fossa; **tp**, transverse process. Scale bar: 5 cm.

This is similar to caudal vertebrae just before the "transition point" (22 to 26 in *Allosaurus fragilis* Allain & Chure 2002). In contrast with the posterior position of the neural spine in MPV 2020.1.4, 8, 5, here it seems to expand all along the vertebra.

MPV V795 and MPV 2020.1.6. these vertebrae are quite damaged and cracked on the neural arch. Thus, a detailed description is not possible, and they are not figured. MPV 2020.1.6 is the better preserved. Like APVSM2, there is no ventral groove on the centrum. They present ridges or crests more or less notable instead of true transverse processes (Fig. 17C). These are eroded but allow to position the vertebrae after the "transition point". However, MPV 2020.1.6 is larger than MPV 2020.1.5 and APVSM2, and thus it indicates a third individual.

Finally, the analysis of all these specimens suggests that there are at least 3 individuals. The variable morphology of vertebrae along a caudal series does not allow to determine whether they belong to different taxa. However, some specific features on some of the vertebrae, such as the ventral groove of MPV 2020.1.4, 8, 5, support that hypothesis. At least, MPV 2020.1.12 from the Oolithe Ferrugineuse de Villers, the stratigraphic origin of which is different from that of the other caudal vertebrae, indicates a fourth individual.

DISCUSSION

THE THEROPOD DIVERSITY OF THE VACHES NOIRES CLIFFS

During the Middle and Late Jurassic, Tetanurae represented the majority of large theropods, with the two clades Megalosauroidea and Allosauroidea (Allain *et al.* 2012; Rauhut 2003; Benson *et al.* 2010; Carrano *et al.* 2012; Rauhut *et al.* 2016; Rauhut & Pol 2019). Both groups were apex predators in their environments (Benson 2010; Brusatte 2012). The specimens of the present study show that these two clades are present in the Vaches Noires cliffs. The assignments for each group are often imprecise above the rank of the superfamily Allosauroidea or Megalosauroidea.

?Streptospondylus altdorfensis

MNHN.F.RJN472, MPV 2020.1.2, MPV 2020.1.10, MPV 2020.1.11 and B5 are the only specimens tentatively referred to the species level. Their assignment to *Streptospondylus altdorfensis* is discussed here.

The anterior dorsal vertebra MNHN.F.RJN472 is similar to that of *Streptospondylus* with a longer than high and strongly opisthocoelous centrum (Allain 2001). It is noteworthy that these characteristics are also present in *Eustreptospondylus* (Sadleir *et al.* 2008). The ventral plateau of the vertebra, also seen in the B5 specimen is also known in *Streptospondylus* (Allain 2001). The dorsal vertebrae MPV 2020.1.10 and B5 are very similar and likely represent two different ontogenic stages of the same species or two closely related taxa. Both possess, as does *Streptospondylus,* a double pleurocentral depression. These features as well as the provenance from the same deposit led us to assign these three vertebrae to *Streptospondylus altdorfensis*. Moreover, MPV 2020.1.10 is very similar in size to the type specimen. Thus, it is even possible that it belongs to the same individual. It is noteworthy that the remaining base of the neural arch is fused in this specimen, in contrast with other known dorsal vertebrae of *Streptospondylus altdorfensis*. The autapomorphic double pleurocentral depression observed in *Streptospondylus* is also present in *Eustreptospondylus* and bring additional support to the close phylogenetic link between these two genera (Walker 1964, Allain 2001). The cervical vertebra MPV 2020.1.11 and the tibia MPV 2020.1.2 bear striking similarities with *Eustreptospondylus*: short centrum, same fossae and laminae on the cervical vertebra, same articular surface orientation and alike shape incisura tibialis and condyle on the tibia. This suggests a closely related form. Using these similarities, the more complete English theropod is used to refer specimens to its less complete French equivalent.

A proximal part of left femur from the Pezy collection resemble that of *Eustreptospondylus* in some aspects (EM pers.obs). In terms of size and preservation, it is reminiscent of the distal part of the femur of *Streptospondylus*. The angle of the articular head, the position of the fourth trochanter (not visible in anterior view), as well as the thick and large lesser trochanter, are the same in *Eustreptospondylus*. Thus, it is possible that this specimen is the proximal end of MNHN.F.RJN93 (MNHN 9645 in Allain 2001).

Indeterminate Megalosauridae

B1, MNHN.F.RJN471, NMH1 are referred to an indeterminate Megalosauridae.

Although it is incomplete, the premaxilla B1 shows important similarities with the megalosaurid *Torvosaurus*. It is indeed higher than long below the external naris and possess as described by Britt (1991) a snout that slops rearward. Moreover, according to Carrano *et al.* 2012, an acute snout (inferior to 70°) with an anterior rather than ventral development of the premaxilla relative to the external nares is synapomorphic of Megalosauridae. Thus, the assignment of B1 to this clade seems appropriate. Noteworthy that it differs from *Torvosaurus* by having four premaxillary teeth instead of three (Britt 1991). The presence of a close relative of *Torvosaurus* is supported by the German Callovian megalosaurid *Wiehenvenator albati* Rauhut, Hübner & Lanser, 2016 which appears to be the sister-taxon of *Torvosaurus* (Rauhut *et al.* 2016). *Torvosaurus* is one of the largest Jurassic theropod known. During the Late Jurassic, it is present in North America with *Torvosaurus tanneri* (Britt 1991) but also in Europe (Portugal) with *T. gurneyi* Hendrickx & Mateus, 2014. As a result, the palaeobiogeographical and palaeoecological context supports the hypothesis of a torvosaurid relative in the Vaches Noires.

On the distal end of the two femora MNHN.F.RJN471 and NMH1, the absence of a large depression on the anterior surface of the medial condyle is a characteristic of megalosauroids (Benson 2010; Carrano *et al.* 2012; Hendrickx & Mateus 2014). Moreover, the remarkable mesiodistal crest in MNHN.F.RJN471 running from the medial condyle to the midline of the distal shaft is similar (although more pronounced here) to *Torvosaurus*. Thus, it seems appropriate to assign this femur to a Megalosauridae close to *Torvosaurus*. This femur is a massive bone, indicating a very large theropod. It is probably the largest theropod femur hitherto found in France, as compared with other femoral remains (Buffetaut 1994b; Buffetaut *et al.* 1995; Allain 2001, 2005). It is clearly different from the anterior surface of the femur of *Streptospondylus,* in which a such developed mesiodistal crest is absent, and thus belongs to another taxon. The NMH1 femur described by Buffetaut (1994b) presents a similar thick mesiodistal crest (although it is weaker) and based on this shared feature both specimens are interpreted as belonging to the same taxon. However, MNHN.F.RJN471 is larger so that they indicate two different individuals.

Indeterminate Allosauroidea

A1, MPV 2020.1.1, B3, MPV 2020.1.9, are interpreted as belonging to indeterminate Allosauroidea. This assignment is discussed here.

Regarding morphological similarities between the two maxillae A1 and MPV 2020.1.1, it is likely that they belong to closely related taxa. The presence of a maxillary fenestra (see Fig. 9) is informative to differentiate megalosauroids from allosauroids. Indeed megalosauroid like *Eustreptospondylus* or *Dubreuillosaurus* possess a maxillary fossa (medially closed maxillary fenestra *sensu* Allain (2002) and Rauhut & Pol (2019) here considered as maxillary fossa) in contrast to more derived Tetanurae (Allosauroidea and Coelurosauria) (Allain 2002; Carrano *et al.* 2012 ; Hendrickx & Mateus 2014; Rauhut & Pol 2019). A1, with a maxillary fenestra and hence MPV 2020.1.1, appear closer to allosauroids like *Allosaurus* or *Sinraptor* (Madsen 1976; Currie & Zhao 1994; Chure & Loewen 2020). It is then relevant to assign the specimens to an indeterminate Allosauroidea. In addition to this, following Carrano *et al.* (2012), the peculiar short anterior ramus similar to *Sinraptor* would allow to assign the maxillae to a metriacanthosaurid.

The description and placement of the cervical B3 and the cervical/dorsal MPV 2020.1.9 was especially helped and supported by comparisons with *Allosaurus* and *Sinraptor* (Madsen 1976; Currie & Zhao 1994). The two vertebrae are highly pneumatized and present an organization of laminae similar to that of the two above-mentioned allosauroids. In contrast to megalosauroid, the centra are rather short. Yet, *Torvosaurus* is an exception with short and well pneumatized vertebrae. However, the rim around the anterior articular facet is absent in these specimens although clearly marked in *Torvosaurus* and megalosauroids (Britt 1991; Carrano *et al.* 2012) Furthermore, the highly pneumatized nature of these two vertebrae is more closely comparable to *Sinraptor.* Indeed, in *Allosaurus*, pleurocoels are relatively smaller than in Sinraptor and the specimens described here. (Madsen 1976). This seems appropriate considering the Oxfordian age of *Sinraptor* (Currie & Zhao 1994) and *Metriacanthosaurus* Walker, 1964, another metriacanthosaurid, which is stratigraphically and geographically close from above specimens. Finally, considering their dimensions and similarities, it is possible that these two bones belong to the same taxon or even the same individual.

MINIMAL NUMBER OF TAXA AND INDIVIDUALS

The study of 26 specimens allows to determine that, at least, three different taxa were found in the Vaches Noires cliffs. The first is an indeterminate Allosauroidea (Fig. 19A) with a minimum of two individuals: one being represented by the A1 specimen and the other by the maxillary fragment MPV 2020.1.1. To these allosauroids can be added the vertebrae B3 and MPV 2020.1.9 and the reconstructed braincase APVSM1+B25392 (Fig. 5). The second taxon is *Streptospondylus*, represented by potentially 4 individuals: one is the type specimen to which the vertebra MPV 2020.1.10 and the femur of the Pezy collection (EM pers. obs) may be associated. The second is represented by the

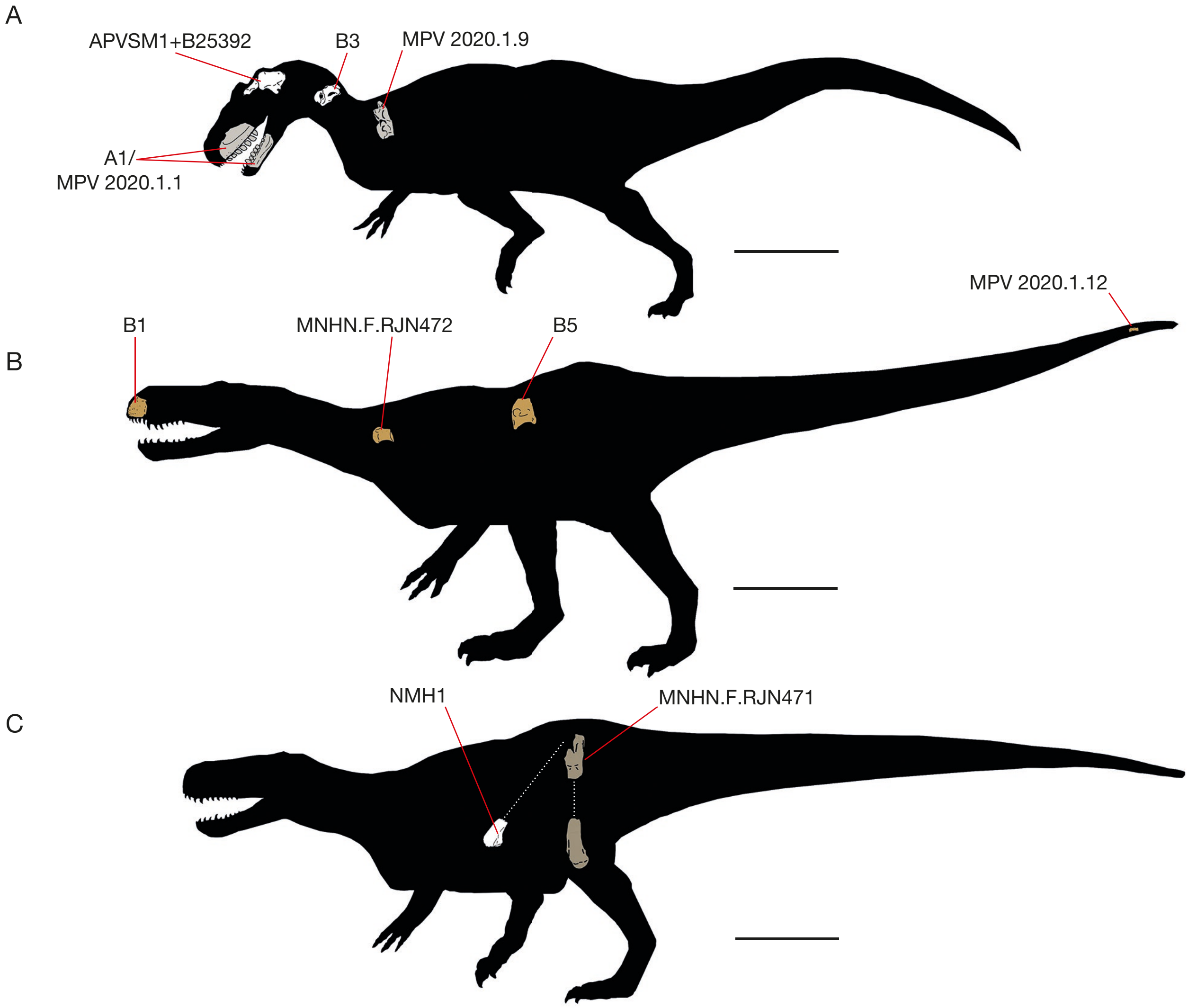

FIG. 19. — Representation of the supposed three theropods taxon of the Vaches Noires cliffs with anatomic referred specimen positioning. Indeterminate Allosauroidea (**A**). *Streptospondylus altdorfensis* with the probable individual from Oolithes Ferrugineuse de Villers (**B**). Indeterminate Megalosauroidea distinct from *Streptospondylus altdorfensis* (**C**). Scale bars: 1 m.

cervical vertebra MPV 2020.1.11. Then, the tibia MPV 2020.1.2 referred to *Streptospondylus* is smaller than the type specimen and indicates a third individual, the size of *Eustreptospondylus oxoniensis* OUM J.13558. The last is a large adult from the Oolithe Ferrugineuse de Villers (Fig. 19B). This one is based on specimens B1, B5, MPV 2020.1.12 and MNHN.F.RJN472 and could be the single theropod known from this formation. The last taxon is an indeterminate Megalosauridae with two large individuals represented by femora (Fig. 19C): one is NMH1 and the other is MNHN.F.RJN471 from H14 level of the Marnes de Villers. However, the distinction between this taxon and *Streptospondylus* is subject to caution because it is based on the femur MNHN.F.RJN93, which is a referred specimen of *Streptospondylus* (Allain 2001). Nevertheless, these two types of femur still indicate two different megalosauroids. The rest of the bones from the Callovian and Oxfordian marls without more detailed taxonomic assignments are mostly vertebrae. None of their stratigraphic origin and size seem to increase the MNI. Thus, it has to be noticed that these specimens of indeterminate Tetanurae as well as other bones that were not considered in this study (i.e the allosaurid metatarsal described by Buffetaut *et al.* [2010]) might be parts of the above-mentioned individuals. Likewise, *Piveteausaurus*, represented by a unique braincase is problematic. First, it has received various taxonomic assignments: Allosauroidea following Allain (2001) or Megalosauroidea in Carrano *et al.* (2012). Moreover, a braincase does not increase the MNI in terms of anatomical concordance with the whole studied specimens which are mainly axial elements. It is the same for its stratigraphic origin, which is unknown. Thus, it is also possible that it belongs to one of the above individuals or might even be a braincase of *Streptospondylus,* as already thought by Piveteau (1923) and Walker (1964), and although this braincase is certainly of a much bigger animal than the type of *Streptospondylus*. A new study of *Piveteausaurus* in order to clarify its taxonomic affinities is thus essential and in progress (Monvoisin *et al.* pers comm.).

TABLE 3. — Summary table of minimal individuals and taxa from Vaches Noires cliffs. *Piveteausaurus divesensis* (Walker, 1964) is with dotted frame because it represents a taxon and specimen that could possibly merge with above taxa and specimens. *Piveteausaurus divesensis* is then not used as a unit of the minimal number of individual (MNI)/Minimal number of taxa (MNT). Reportable specimens are specific to an individual or taxon. Distributable specimen belongs to Tetanurae and could, with MNI and MNT hypothesis be part of mentioned taxon and individuals without increasing their numbers. Bold "distributable" specimens are incompatible (dimension and anatomy) with each other.

Taxon	Representant specimen/ minimum individual	Reportable specimen	"Distributable" specimen
Streptospondylus altdorfensis Callovian or Oxfordian marls	Type specimen (lectotype) MNHN.F.RJN78 à RJN92 + rapported material MNHN.F.RJN93	MPV 2020.1.10	Dorsal vertebrae: B4, MPV 2020.1.7, MPV V869
?*Streptospondylus altdorfensis* Oxfordian marls	MPV 2020.1.11	–	
?*Streptospondylus altdorfensis* Callovian or Oxfordian marls	MPV 2020.1.2	–	Caudal vertebrae: **APVSM2**, B7, NMH2, **MPV 2020.1.4**, MPV 2020.1.5, MPV 2020.1.8, **MPV2020.1.6**, MPV V795
?*Streptospondylus altdorfensis* (Megalosauroidea from Oolithes ferrugineuses de Villers)	B1, B5, MNHN.F.RJN472	MPV 2020.1.12	
Megalosauridae indet. (distinct from *Streptospondylus altdorfensis*), Oxfordian marls	MNHN.F.RJN471	–	
Megalosauridae indet. (distinct from *Streptospondylus altdorfensis*), Callovian or Oxfordian marls	NMH1	–	
Allosauroidea indet., Oxfordian marls	A1	APVSM1+ B25192, B3, MPV 2020.1.9	
Allosauroidea indet., Callovian or Oxfordian marls	MPV 2020.1.1		
Piveteausaurus divesensis, Callovian or Oxfordian marls	Type specimen (MNHN.F.1920-7)	–	–

With a minimum number approach, there are three theropod taxa at the Vaches Noires cliffs and eight individuals (Table 3). Many of them come from the lower Oxfordian (Marnes de Villers, Oolithe Ferrugineuse de Villers and Argiles à *Lopha gregarea*) instead of the traditionally envisioned upper Callovian (Marnes de Dives). Moreover, they are based on several observations that are subject to bias especially for taxonomic assignments. Nevertheless, the information gathered from these bones indicates an overestimation of the number of theropod individuals, leading to an over-representation that does not reflect the real composition of an ecosystem.

NEW INSIGHTS ABOUT THE THEROPOD OVER-REPRESENTATION OF THE DEPOSIT

As mentioned before, most of the dinosaur remains from the Vaches Noires cliffs belong to theropods. Only very scarce remains of other groups have been found. A caudal vertebra from the Pezy collection (EM pers.obs) represents the second bone referred to a sauropod but also the only one that is left because the first, a vertebra mentioned by Bigot in 1895, was destroyed during World War II (Bigot 1945; Buffetaut 2013; Plasse & Buffetaut 2016). The recently described thyreophoran vertebrae (probably from a stegosaur) add another clade to the Vaches Noires Cliffs dinosaurs (Buffetaut & Tabouelle 2019). However, theropod remains are still over-represented. Most of these remains belong to large carnivorous dinosaurs that represent obvious apex predators. It is difficult to imagine an ecosystem mainly composed of predators. Indeed, it is usually accepted that predators are less abundant than their prey (Farlow 1993; Naish *et al.* 2004; Läng *et al.* 2013). Overabundance of theropods found in other deposits is often explained by an environment that is not suitable to the development of a sufficient flora to feed herbivores (Naish *et al.* 2004; Läng *et al.* 2013). However, studies of the palaeoflora of the Armorican massif during the Bathonian to Oxfordian show that coastal forests were present and thus allowed the development of a herbivorous population (Le Couls *et al.* 2016; Le Couls 2017). Therefore, the Vaches Noires Cliffs assemblage obviously does not faithfully reflect the ecosystem from which the animals are derived. Noteworthy the marine taphocoenosis bring a consequent bias to reconstruct a terrestrial ecosystem. However, in other similar marine deposits, like the Callovian clay pit at Argences (Calvados, Normandy), no theropod remains were found, but a sauropod (Buffetaut *et al.* 1995) and stegosaurs (Hoffstetter & Brun 1956; Galton *et al.* 1980; Galton 1990; Allain & Suberbiola 2003) (Buffetaut & Tabouelle 2019) have been reported. Still in Normandy, but from the Kimmeridgian, similar marine deposits, have yielded a more balanced fauna with theropods, sauropods, stegosaurs and ornithopods. (Buffetaut 1994a; Buffetaut & Cacheleux 1997; Allain & Suberbiola 2003). As in the Vaches Noires cliffs, the Oxford Clay Formation of England includes both Callovian and Oxfordian marls. However, the preserved fauna is more diverse, with many dinosaur groups (Martill 1988; Lomax & Tamura 2014; Buffetaut & Tabouelle 2019). Thus, the over-representation of theropods at the Vaches Noires is enigmatic and many hypotheses have been put forward to explain it. It is possible that theropods frequented coastlines to feed on beached carcasses, which made them more likely to end up in the sea. Piscivorous tendencies among theropods have been demonstrated by geochemical studies, notably in spinosaurid megalosauroids (Amiot *et al.* 2010; Brusatte 2012; Allain *et al.* 2012). Other megalosauroids were likely to feed on fish, as shown by the gastric remains of *Poekilopleuron* Eudes-Deslongchamps, 1838 (Allain 2005). This hypothesis is also supported by the fact that megalosauroids may have preferred nearshore environments as suggested by the study of theropod paleogeographic distribution of Rauhut *et al.* (2016). Moreover, theropod swimming tracks have been found, supporting occasionally aquatic behaviour (Milner *et al.* 2006; Ezquerra *et al.* 2007). However, these tracks are from freshwater environments. Nevertheless, a possible nearshore palaeobehaviour is not sufficient to explain the over-representation, because, as explained before, other marine deposits and especially the Oxford Clay present a more balanced fauna. Finally, a statistical effect is more likely (Buffetaut & Tabouelle 2019). Indeed, the Vaches Noires cliffs are a 5 km long costal outcrop which has yielded only a few dinosaurs remains so that it is difficult to compare it with a much more extensive geological formation such as the Oxford Clay. The over-representation may be due mainly to the small sample available from the Vaches Noires and may not represent the real ecosystem of nearby islands (i.e Armorican massif).

Another peculiar aspect of the Vaches Noires cliffs is the way fossils are found, especially concerning dinosaur bones from marls situated above the Marnes de Dives, which crop out at the bottom of the cliffs. These remains, usually collected on the beach at the bottom of the cliffs, come from marl flows, the result of which is a huge mixing of the different fossil-bearing layers. Only index fossils or a peculiar matrix can help to identify the exact origin of specimens. It was traditionally argued that dinosaur remains from the Vaches Noires cliffs are scattered because of the long time they have spent floating in the sea, during which they decomposed before dropping to the bottom (Buffetaut 1994a, 2013). However, partial to quite complete skeletons have been found in other similar deposits. It is the case with *Eustreptospondylus* or other Oxford Clay dinosaurs (Martill 1988; Lomax & Tamura 2014) or even the *Lexovisaurus* from the clay pit of Argences (Hoffstetter & Brun 1956; Galton *et al.* 1980; Galton 1990). As a matter of fact, it is likely that specimens from fossiliferous layers in cliffs that flow to the foreshore are originally more complete but dissociated by natural erosion. Then those bones are collected at various times by various people so that they are kept apart. This contributes to the over-representation of theropods, insofar as it inflates the sample size. This effect is demonstrated here with the MNI of 8 individuals. Although not absolute, it demonstrates the probable inflation of the number of theropods yielded by the Vaches Noires cliffs. An explicit example are the bones from the same individual found in different collections (i.e APVSM1 frontals with B25392 braincase). Another is the history of the type specimen of *Streptospondylus altdorfensis*. The bones of that theropod were gathered at different times and not mentioned in the same article although they came from the same skeleton (Allain 2001). Moreover, a new succession of vertebrae, in direct connection with previously known ones has been recovered (RA, unpublished data).

THE CONTRIBUTION OF THE FOSSILS FROM THE VACHES NOIRES TO OUR KNOWLEDGE OF THEROPODS

The study of unpublished specimens has provided new insights about theropod diversity at the Vaches Noires. For example, *Streptospondylus*, an iconic dinosaur from that locality is now better known, since it is now known from the Oxfordian. The highly pyritised type specimen rather indicates more Callovian provenance, but as mentioned before, an unambiguous dating is not possible. Thus, with newly referred specimens of this study, *Streptospondylus* is known from the Oxfordian and possibly the Callovian. Based on our observations, it seems that this theropod, hitherto know from a juvenile (Allain 2001) could reach a very large size, when adult, in the size range of *Torvosaurus*. The probably close relationships between *Streptospondylus* and *Eustreptospondylus* are once again highlighted. A comparative study of these two taxa is highly needed and could provide new insights about the validity of their division into two genera, especially if this distinction is in fact based on different ontogenic stages. Moreover, there are similarities between Jurassic faunas from Normandy and England, leading to taxonomic revision. This is for example the case with the stegosaur genus *Lexovisaurus* Hoffstetter, 1957, present in the English and French Callovian. It is currently considered to be a *nomen dubium* and replaced by *Loricatosaurus* Maidment, Norman, Barrett & Upchurch, 2008 (Maidment *et al.* 2008), but this suggestion is debated (Buffetaut & Morel 2009). The supposed «source» of dinosaurs from these two marine deposits are considered as distinct: London-Brabant Massif for the Oxford Clay and Armorican Massif for the Vaches Noires cliffs and other localities in Normandy (Buffetaut 2013), both representing Jurassic insular ecosystems from the European Archipelago (Bradshaw *et al.* 1992).

Despite the limited number of remains and their fragmentary nature, the specimens from the Vaches Noires cliffs have scientific value. They represent remains from a peculiar evolutionary context for theropods. During the Middle to Late Jurassic a faunal transition is observed with a faunal turnover from megalosauroids dominated faunas to allosauroids ones (avetheropods in a broad sense) (Benson 2010; Rauhut *et al.* 2016). Although it may provide from an artifact of preservation according to the same authors (Rauhut *et al.* 2016, 2018), this effect is also visible in time calibrated trees of recent theropod phylogenies (Carrano *et al.* 2012; Hendrickx *et al.* 2015; Rauhut *et al.* 2016). The presence of both groups in the Vaches Noires cliffs is therefore informative. Megalosaurids are represented by large size predators and some appear to be close relative to megalosaurines. It is noteworthy that after the Callovian, megalosaurids yet quite common in Europe (Rauhut *et al.* 2016, 2018) were hitherto represented by the single genus *Torvosaurus,* known in North America and Portugal during the Kimmeridgian and Tithonian (Britt 1991;

Hendrickx & Mateus 2014; Rauhut *et al.* 2016). The studied remains found as close relative to *Torvosaurus*, as well as the Callovian megalosaurid *Wiehenvenator albati* Rauhut, Hübner & Lanser, 2016, also close to the genus according to Rauhut *et al.* (2016), suggest the establishment and wide distribution of megalosaurines theropod, surviving through the late Jurassic (Rauhut *et al.* 2016; Malafaia *et al.* 2017). However, during this transition period, allosauroids are rather rare, especially in European deposits, the Oxfordian *Metriacanthosaurus* being the only member known (see Rauhut *et al.* 2016: table 3). The description of allosauroid remains in the present study provide thus new insights about their presence in the European Archipelago. This is all the more important considering the fragmentary nature of *Metriacanthosaurus*. Indeed, this theropod is problematic because it has not been fully described. It is clear that the entire material lacks a complete review. Despite this, *Metriacanthosaurus* is the type genus of the Metriacanthosauridae, a subclade of allosauroids (Benson 2010; Carrano *et al.* 2012). Therefore, the status of the family is likely not definitive. In addition to this, the A1 specimen has similarities with metriacanthosaurids also know in China, with the contemporaneous genus *Sinraptor* (Currie & Zhao 1994). Finally, Allain (2005) and Rauhut *et al.* (2016) suggest that megalosauroids might have preferred nearshore environments (the origin of the studied bones), whereas allosauroids tend to occur in inland environments. Thus, the rarity of allosauroids in the European Archipelago could be explained by a preferential ecological niche. Finally, finding remains of allosauroids despite the environment supposedly not being their preferred option might reinforce the idea of a faunal transition between megalosauroids and allosauroids.

CONCLUSIONS

Dinosaur remains from the Vaches Noires cliffs are mostly isolated and disseminated among several collections. Bringing together dinosaur specimens from this locality provided unprecedented insight into dinosaur diversity. Moreover, it appears that some bones from different collections may be part of the same individual. The isolated nature as well as the supposed dispersion of the specimens led us to try to determine a MNI. Thus, a minimum of 8 individuals could be established, representing at least three taxa. Two of the three taxa are megalosauroids: one is the already known *Streptospondylus* with more individuals larger than the type specimen. The other one is a large megalosaurid. The third taxon is an allosauroid. This study provides evidence of large theropods, closely related to *Torvosaurus,* during the Callovian/Oxfordian interval, which may represents a time of faunal turnover so that *Torvosaurus* is the only megalosaurid genus known during the Late Jurassic. The period is therefore important for theropod evolution.

Unfortunately, dating bones from the Vaches Noires cliffs is, as well as their finding, hazardous. However, it seems that the traditional Callovian origin of many dinosaur bones is unconfirmed, and that a large part of the specimens studied here comes from the Oxfordian layers. In order to have a better understanding of the Vaches Noires cliffs, a palynological study might be of great help. Finally, dinosaur remains represent a tiny proportion of what we can learn from the Vaches Noires cliffs. However, specimens from private collections undoubtedly present a certain scientific interest so that it is important – as was the case in the present study – to have access to them.

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