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**A JAW FRAGMENT OF *MEGALOSAURUS* IN THE UPPER CALLOVIAN OF THE VACHES NOIRES
(CALVADOS, FRANCE)***

by

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ABSTRACT

An anterior fragment of left maxilla from a large theropod dinosaur from the upper Callovian of the Vaches Noires cliffs, near Villers-sur-Mer (Calvados), is described and compared to some theropods from the Jurassic of England (*Eustreptospondylus* and *Megalosaurus*) and North America (*Allosaurus*). It is with the representatives of the genus *Megalosaurus*, notably *M. bucklandi* from the Bathonian of Stonesfield, that the resemblances are most significant, and the Villers specimen is designated as *Megalosaurus* sp. The available data suggest an increase in the robustness of the jaws and the size of the teeth in the European Megalosauridae during the Jurassic (perhaps linked to increase in prey size). The possibility of attributing the type of *Piveteausaurus divesensis*, a braincase from the Callovian of Dives (Calvados), to *Megalosaurus* is discussed.

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I. INTRODUCTION

If the remains of marine reptiles (thalattosuchian crocodylians, in particular, but also ichthyosaurs, plesiosaurs, and pliosaurs) are relatively frequent in the upper Callovian beds ("Marnes de Dives") that form the base of the Vaches Noires cliffs, between Villers-sur-Mer and Houlgate, those of dinosaurs are much less so, which is easily explained by the marine setting of sedimentation within which these beds were formed. The dinosaur specimens, incomplete, that are occasionally found there thus deserve to be noted. This is the case with the maxilla fragment from a theropod dinosaur found by two of us (G. and E. PENNETIER) that is the subject of this article, and which brings useful information on the still-unknown theropods of the European Jurassic.

II. PROVENANCE OF THE SPECIMEN

The specimen was discovered on 13 March 1987 on the beach, at the foot of the Vaches Noires cliffs, around 1500 m west of the Villers-sur-Mer parking. It was found at the extreme limit of a mudflow descended from the Oxfordian beds of the cliff, and practically at the contact of the upper Callovian bed (H₁₋₃) that outcrops at low tide (on the stratigraphy of the Vaches Noires cliffs, see RIOULT, 1978a). The associated fossils in the flow come from one of the Oxfordian beds, others from the upper Callovian. Concerning the origin of the jaw fragment, two possibilities can be envisaged: it could have come from the Oxfordian and been entrained up to the point of discovery by the mudflow, or from the upper Callovian and been somewhat displaced upward during a storm (in effect it was found below the level of high tide). This second hypothesis seems the more probably, because most of the remains of fossil reptiles found at the Vaches Noires come from the Callovian beds (Marnes de Dives), even though some were found in the Oxfordian. The state of preservation of the specimen and the few thin remains of matrix (not containing any trace of oolites) that it bears still seem in agreement with this interpretation. Therefore we think that this piece comes from the upper Callovian.

III. DESCRIPTION OF THE SPECIMEN

This specimen (no. 380 in the PENNETIER collection; cast deposited in the Laboratoire de Paléontologie des Vertébrés, Université Paris VI) is the anterior part of a left maxilla (Fig. 1 and Pl. I) showing the three anteriormost alveoli (the posterior edge of the third is broken). The position of the specimen in the skull can thus be reconstructed with a certain precision (Fig. 2). The dorsal part of the bone is incomplete. The medial and lateral surfaces of the specimen bear rather numerous serpulid tubes of fairly large dimensions (diameter reaching 2 to 3 mm). It is thus clear that this bone, once defleshed, remained at the water bottom for a rather long time before its burial, so that these organisms had fixed themselves to its surface and grown there. Moreover, the bones found in the upper Callovian and Oxfordian of the Vaches Noires show fixed organisms very often, which testify to analogous taphonomic phenomena, with burial not immediate.

The lateral surface of the specimen is vertical and more or less flat. In the posterodorsal angle, it bears a fossa at the rounded edge that could be the anterior part of an antorbital fossa, within which would open the antorbital and preantorbital fenestrae. The anterodorsal part also shows a fossa, accentuated by a certain crushing, which could correspond to the border of the subnasal foramen, at the edge of the premaxilla. The lateral surface shows moreover several large nutrient foramina, notably along the alveolar border. This edge is rectilinear and forms an angle of around 80° with the anterior edge, which is slightly anteriorly convex.

The posterior surface of the fragment corresponds to a breakage surface still empty of matrix and showing in cross-section a replacement tooth situated in the third alveolus.

The anterior surface has a complex form because of the anteromedial process. The contact surface with the premaxilla is broad (30 mm) and slightly anteriorly concave in its ventral part. The anteromedial process, very strong, exceeds the level of the anterior edge of the body of the bone anteriorly.

The medial surface shows the alveoli in its ventral part, whose opening is subquadrangular. The interdental plates are well visible. They are not contiguous, but separated by slits open into the interior of the alveoli and showing the replacement teeth that are found there. At the level of the second alveolus, the edges of the plates are damaged, and the slit separating them is this artificially enlarged. A well-marked projection separates the interdental plates from

the more dorsal part of the bone. Above this projection, the anteromedial process strongly covers forward and medially. It bears at its end some deep and complex furrows corresponding to the articulation with the maxillary process of the premaxilla, the anteromedial process of the right maxilla, and also without doubt with the medial contact of the vomer. Below the process, toward the front, is found a deep oval fossa that does not communicate with the sinus visible in dorsal view described below. In the posterior elongation of the process, the dorsal part of the maxilla becomes deep medially.

The dorsal surface of the specimen shows some breakages: the lateral part of the bone and the entire posteromedial region are broken. The preserved surface, very broad posteriorly, is extended anterolaterally by a triangular point inclined ventrally, which constitutes the dorsal surface of the anteromedial process. The most remarkable character is the presence of a vast oval opening (length: 43 mm; width: 28 mm), still partially filled with matrix, that occupies the largest part of the space enclosed between the departure of the anteromedial process and the lateral wall of the bone. There must be the ventral part of a very large maxillary sinus.

Teeth: The replacement tooth present in the first alveolus is slightly visible; it shows a serrated carina perpendicular to the axis of the bone, which does not seem in an entirely normal position, unless there was rotation of the tooth before emplacement in its functional position. The replacement tooth present in the second alveolus, closer to its functional position, is very well preserved and clearly observable (Pl. I, B). Its visible length is 45 mm. It is a blade-shaped tooth of a type typical in large theropods, strongly laterally compressed, weakly recurved, with smooth enamel. The carinae are strongly serrated, with two serrations per millimeter on the anterior carina; these serrations are oblique relative to the edge of the tooth. The replacement tooth present in the third alveolus is only visible in section within the posterior break.

Dimensions

Max length without anteromedial process:	97 mm
Max length with anteromedial process:	105 mm
Maximum width of dorsal part:	67 mm
Maximum height of lateral surface:	115 mm
Length of opening of first alveolus:	30 mm
Length of opening of second alveolus:	33 mm

IV. COMPARISONS

The presence of theropod dinosaur remains in the Jurassic beds of the Vaches Noires has been known for a long time (DOUVILLE, 1885; BIGOT, 1939; RIOULT, 1978a, 1978b). However, among those already described from the Callovian of this locality, and more widely in Normandy, there are hardly any that are directly comparable to our specimen. In effect there are especially postcranial remains (several of which were figured by PIVETEAU, 1923; certain among them are besides of less certain provenance according to TAQUET & WELLES, 1977) and one braincase found at Dives and described by PIVETEAU (1923), then by TAQUET & WELLES (1977). An isolated tooth was figured by PIVETEAU (1923); although a little more robust than those present in our specimen, it is not very different, but one knows that isolated teeth of this type can hardly be used for systematic means, because one finds very similar morphologies among diverse large theropods. A portion of jaw attributed to *Megalosaurus* and from the Marnes de Dives was noted by DOUVILLE (1995), but it was not figured. The diverse remains of theropods noted from other levels of the Jurassic of Normandy (see the list of RIOULT, 1978b) do not include maxillary remains permitting comparisons with the Villers piece.

In these conditions, some comparisons were made especially with theropod maxillae from the Jurassic of England, as well as with *Allosaurus*, from the Morrison Formation (Upper Jurassic) of the United States, described in detail by MADSEN (1976).

The Vaches Noires specimen was notably compared to the maxilla of the type of *Eustreptospondylus oxoniensis* WALKER, 1964, a theropod from the Middle Oxford Clay (upper Callovian) of the environs of Oxford. This specimen, a relatively complete skeleton, was described by PHILLIPS (1871), NOPCSA (1906), HUENE (1926 and 1932), and WALKER (1964). It is a juvenile individual, which obliges a certain prudence in the interpretation of some differences between our specimen and it. These differences are in any event important. Among others, the anteromedial process is not visible in lateral view in *Eustreptospondylus oxoniensis*, because it is entirely hidden in front by the lateral plate of the maxilla. On the other hand, the interdental plates of the Oxford specimen, not joined, are much shorter and straighter than those in the Villers piece, but this could with the rigor be due to a difference of individual age. The most important differences bear on the

morphology of the lateral surface of the maxilla. In effect, in *Eustreptospondylus oxoniensis*, the anterior limit of the antorbital fossa (which contains the antorbital fenestra, as well as a deep preantorbital fossa) is found at the level of the sixth alveolus, that is much farther back than in the Villers specimen (where, it was seen, it is placed at the level of the second alveolus). However, in *Eustreptospondylus oxoniensis*, in front of this fossa the height of the maxilla decreases rapidly and strongly (even if it is considered that the lateral alveolar border of the dentary is very incompletely preserved in this specimen, as shown well in the drawing of HUENE, 1932, pl. 43); one observes a rather abrupt lowering of the dorsal edge of the maxilla at the level of the fourth interdental plate – whereas in *Megalosaurus bucklandi* this lowering is much more gradual. The anterior part of the maxilla of *Eustreptospondylus oxoniensis*, in front of the antorbital fossa, seems this much longer and lower than that of *Megalosaurus bucklandi*. The Villers specimen, in this regard, differs clearly from *Eustreptospondylus oxoniensis*, because this anterior part is short there (because of the anterior position of the edge of the fossa) and high. On the medial surface, the maxilla of *Eustreptospondylus oxoniensis* does not show the oval fossa above the anteromedial process described above on the Villers specimen. These differences seem amply sufficient to not refer the fragment of maxilla from Villers to *Eustreptospondylus oxoniensis*.

Comparison with different specimens from the Jurassic of England referred to *Megalosaurus* reveals on the other hand some resemblances that seem significant. From a systematic point of view, it is necessary however to recall that the remains of *Megalosaurus bucklandi* MEYER, 1832, first described by BUCKLAND in 1824 (it is, as is known, the first scientific description of a dinosaur), do not include a maxilla. The later attributions of maxillae to this species are founded, in most cases, on a common stratigraphic and geographic origin (“Stonesfield Slate”, middle Bathonian of the Oxford region). The Villers piece was notably compared to two specimens in the Oxford University Museum attributed to *Megalosaurus bucklandi*, the left maxillae J 13506 and J 13559, both from Stonesfield. On J 13506, the lateral surface of the bone is not very well preserved; the median surface, better preserved, shows an anteromedian process clearly more slender than that of the Villers specimen, however with a

generally similar form. One sees on J 13506 neither the fossa ventral to the process, nor the large dorsal opening visible on the Villers piece. Another notable difference is the relative breadth of the dorsal part of the maxilla in its anterior region. At the level of the second tooth, both specimens have very similar heights (110 mm for J 13506, 115 mm for the Villers piece). On the other hand, at this level, the dorsal breadth of the Normandy specimen (70 mm) is double that of J 13506 (around 35 mm). The interdental plates of J 13506 are not very well preserved, but they do not seem to have been joined. The general form of the anterior end of the maxilla recalls that of the Villers specimen.

Specimen J 13559, which was mentioned by PHILLIPS (1871), OWEN (1883) and WALKER (1964), is better preserved, notably concerning the lateral surface. This shows above the tooth row a series of vascular foramina larger and more numerous than those on the Villers fossil, and further away (25 to 30 mm) from the alveolar border than on this latter. The region of the antorbital openings is not very well preserved. Nevertheless one sees a large antorbital fenestra advancing up to the level of the fifth alveolus, preceded by a preantorbital fossa. Anteroventral to this, one distinguishes a bony edge limiting the antorbital fossa, and which is found, as on the Villers specimen, at the level of the second interdental plate. The front of the maxilla, in lateral view, presents about the same form as on the Normandy specimen. On the medial surface, the anteromedial process recalls that of the Villers maxilla by the form, but here still it is more slender, although the heights of the two specimens are little different (height of J 13559 at the level of the second alveolus: 105 mm). The noted differences in proportions with J 13506 are thus found here, with a dorsal breadth of 35 mm for J 13559 versus 70 mm for the Villers piece. On the dorsal surface of J 13559, one observes an oval foramen 5 mm in diameter at the site of the large opening of the Villers specimen; on the other hand, J 13559 does not clearly show the fossa ventral to the anteromedial process. The two anteriormost alveoli of J 13559 have about the same dimensions as those of the Villers specimen (30 mm long).

It arises from these comparisons that there exists a general morphological resemblance between the Villers piece and the maxillae coming from the Bathonian of Stonesfield and attributed to *Megalosaurus bucklandi*, but that

the Normandy specimen is clearly more massive and broader in the anterodorsal region. Without doubt there was a little compression during fossilization of the Stonesfield specimens, but it is certainly not sufficient to explain these differences in proportions.

The maxilla fragment from Villers was equally compared to the maxillae of *Megalosaurus* from the Stow-on-the-Wold region (Gloucestershire) and preserved in the Stroud District Museum (Stroud, Gloucestershire) and at the Natural History Museum of London. These specimens come from the Chipping Norton Limestone, attributed to the lower Bathonian. Certain of them have already been described by REYNOLDS, who in 1939 wrongly interpreted a left maxilla (Stow District Museum, 44-1) as a portion of a left mandibular ramus, attributed to *Megalosaurus* without indication of species. This specimen shows a anteromedial process that is rather strong but not extended in front of the lateral part of the bone. Ventral to this process is found a well-marked concavity; on the other hand, dorsally one cannot see the large opening present on the Villers specimen. The interdental plates, not contiguous, are separated by narrow spaces. On the lateral surface, the vascular foramina are further away from the alveolar border, as on the Stonesfield specimens. The contour in front of the maxilla is more rounded than that of the Villers specimen. Specimen R 8303 of the Natural History Museum shows the same characters. The width of the anterodorsal part of the bone is, once again, clearly less than that on the Villers specimen. The anterior alveoli have similar dimensions and form to those of the Villers piece, but the interdental plates, separated from one another by very narrow spaces, are covered by very clear furrows, which are also observed on the Stroud specimen, but not on that from Villers.

Some comparisons were also made with an older *Megalosaurus*, from the "Inferior Oolite" (Bajocian) of the Sherborne region (Dorset). Long attributed to *Megalosaurus bucklandi* (for example, see OWEN, 1883), this material was used as the type of a new species, *M. hesperis*, by WALDMAN (1974). *Megalosaurus hesperis* is distinguished from *M. bucklandi* notably by a higher number of teeth (15 to 18 teeth in the maxilla versus 12 to 13 in the Stonesfield form). The material preserved in London includes a left maxilla (Natural History Museum, R 332) visible in medial view, on a block of matrix. The anterior part is much lower and more gracile

than that of the Villers specimen. The anteromedial process is clearly shorter and weaker, and does not overhand a fossa. The interdental plates are less tall than on the Normandy piece.

There exists in the Upper Jurassic of Europe little material of large theropods that can be compared with the Villers specimen. The presence of these animals is no less attested to by teeth of large size. E. EUDES-DESLONGCHAMPS and G. LENNIER (*in* LENNIER, 1870) founded the species *Megalosaurus insignis* on an isolated tooth of large size (length: 80 mm) from the lower Kimmeridgian of Cap de la Hève (also see LENNIER, 1887). Some other isolated large teeth were subsequently referred to this particularly poorly defined species, coming notably from the Portlandian of the Boulonnais (SAUVAGE, 1874), and from the dinosaur locality of Damparis, in the Jura (LAPPARENT, 1943), which is dated to Oxfordian (BUFFETAUT, 1988) and not Kimmeridgian as LAPPARENT thought. A tooth from the Kimmeridgian of Wiltshire was also attributed to this species by LYDEKKER (1888). These isolated teeth do not lend themselves to significant comparisons with our specimen: as POWELL (1987) remarked, they are not diagnostic, and *Megalosaurus insignis* cannot be considered as a valid species. Some more interesting comparisons are possible with a fragment of left maxilla recently described by POWELL (1987). This fossil, dredged by a trawler off Portland (Dorset), comes from a deep-water region that also bears ammonites indicating a lower Kimmeridgian age. Although this fragment, corresponding to the anterior part of the bone, is strongly eroded, comparison with that from Villers reveals many resemblances, notably with the presence of a strong anteromedial process (of which there remains only the root). The interdental plates, not contiguous, also resembles those of our specimen. The Dorset piece is however larger than that from Normandy, with a height of 164 mm. It was referred to an indeterminate megalosaurid by POWELL (1987).

Some comparisons were also attempted with *Allosaurus*, a well-known theropod from the Morrison Formation (Upper Jurassic, probably Kimmeridgian-Portlandian, from the western United States), in particular using the monograph of MADSEN (1976) on *A. fragilis*. In this animal, the front of the maxilla is clearly more vertical, in lateral view, than in the Villers

specimen. In medial view, the anteromedial process seems more slender, without a ventral fossa. The interdental plates, contrary to that observed in *Megalosaurus* and on our specimen, are contiguous.

From the comparisons above, it arises that it is with the European forms of the genus *Megalosaurus*, rather than with *Allosaurus*, that our specimen shows resemblances. Among the species of *Megalosaurus* in which the maxilla is known, the Villers fragment approaches *M. bucklandi* more than the more gracile *M. hesperis*. Nevertheless, our specimen differs from *Megalosaurus bucklandi* by its clearly stronger thickness in the dorsal region, and by the robustness of its anteromedial process, the height of the bone being in addition little different from that of the Stonesfield specimens. The maxilla fragment from Villers seems thus to have belonged to a animal close to *Megalosaurus bucklandi*, but with a more massive upper jaw. It would be evidently imprudent to found a new taxon on such fragmentary material, and thus we content ourselves with the designation *Megalosaurus* sp. for the Villers specimen. As much as can be judged by such material, it seems intermediate by the robustness between *Megalosaurus bucklandi*, from the Bathonian of Stonesfield, and the very large Kimmeridgian megalosaurid from Dorset described by POWELL (1987). The few available data thus suggest a tendency to increase the robustness of the upper jaw in the European Megalosauridae between the Bajocian and the end of the Jurassic, accompanied, it seems, by an increase in the size of the teeth. Perhaps this must be seen as the expression of a biological "arms race", the increase in strength of the predators corresponding to the increase in size of the prey (sauropods, notably; some fragmentary remains from the Portlandian of the Boulonnais indicate the presence of forms of very large size), and reciprocally.

V. NOTE ON THE THEROPODS OF THE CALLOVIAN OF CALVADOS: THE PROBLEM OF PIVETEAUSAURUS

As was pointed out above, diverse remains of theropod dinosaurs have already been noted in the Callovian of Calvados. Although they do not lend themselves to a direct comparison with the specimen described here, some remarks of a systematic order would seem useful. One of the most interesting specimens is without contest the braincase of large dimensions found in the

upper Callovian of Dives (Couches du Mauvais-Pas) and described for the first time by PIVETEAU (1923) under the name *Streptospondylus cuvieri*. WALKER, in 1964, made it the type of a new species, *Eustreptospondylus divesensis*. In 1977, TAQUET and WELLES underlined the differences between this braincase and that of the type species of the genus *Eustreptospondylus* WALKER, 1964, namely the skeleton of *E. oxoniensis*, from the Callovian of the environs of Oxford; they concluded that it required a new generic name, *Piveteausaurus*, with *P. divesensis* (WALKER, 1964) for the type species. The monospecific genus *Piveteausaurus* is therefore known only by a single specimen, the braincase from Dives, which TAQUET and WELLES showed was as very different from the braincase of *Eustreptospondylus* as from those of *Allosaurus* and *Ceratosaurus*. However, no comparison was possible with the braincase of *Megalosaurus*, because this is not known. In 1906, HUENE certainly described a specimen in the Oxford Museum as being a braincase of *Megalosaurus bucklandi* from Stonesfield, but this identification was contested in 1910 by WOODWARD, who judged it preferable to refer the piece to the sauropod *Cetiosaurus*. In 1926, HUENE aligned with this opinion. It seems well that this is the most probable identification for this specimen, which besides does not come from the Bathonian of Stonesfield (*locus typicus*, as is said, of *Megalosaurus bucklandi*), but from the Bathonian of Kirtlington (Oxfordshire); the locality in question does not seem to have produced other remains attributed to *Megalosaurus*, but is known for having furnished abundant material of sauropods, attributed to *Cetiosaurus* (P. POWELL, personal communication). Examination of a cast of the specimen in question shows that it resembles neither the braincase of *Eustreptospondylus oxoniensis*, not that described by TAQUET and WELLES. In fact, it hardly evokes the braincase of a theropod, but shows some resemblances with the braincases of sauropods, as for example those from the Upper Jurassic of Tendaguru figured by JANENSCH (1935). The attribution to *Cetiosaurus* proposed by WOODWARD and finally accepted by HUENE seems consequently entirely reasonable. It must thus be concluded that the braincase of *Megalosaurus* is unknown. On the other hand, the presence of a theropod of large size in the Callovian of the Vaches Noires attributable to

the genus *Megalosaurus*, judging by the characters of its maxilla, is indicated by the jaw fragment described above. It is consequently legitimate to ask whether the braincase from Dives and the maxilla fragment from Villers do not belong to the same form. Only the discovery of much more complete material, including both the braincase and upper jaw, could confirm or refute this hypothesis. It does not seem impossible, in the current state of our understanding, that the braincase from Dives designated under the name *Piveteausaurus* is in fact that of a *Megalosaurus*.

VI. CONCLUSIONS

The specimen described above apparently indicates the presence of the genus *Megalosaurus* in the Callovian of Normandy. Although the best material currently known of this genus comes from the Bajocian and Bathonian of England, it thus seems well that it persisted for a long time in the Jurassic. Even if numerous more recent remains are too fragmentary to permit an identification to the generic level, the Dorset specimen described by POWELL (1987) shows moreover that the Megalosauridae persisted in Europe at least up to the Kimmeridgian. However, the new material from Normandy does not bring new elements to the subject of the phylogenetic and systematic position of *Megalosaurus*; the point of view of MOLNAR *et al.* (1990), who considered *Megalosaurus* as probably belonging to the carnosaurs, while wishing for supplementary studies to clarify its position, seems at the current time the most reasonable.

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REFERENCES

[Not listed.]

FIGURE and PLATE CAPTIONS

Fig. 1: Fragment of left maxilla of *Megalosaurus* sp. from the upper Callovian of the Vaches Noires (Calvados), PENNETIER collection, no. 380. A: dorsal view; B: posterior view showing the breakage surface and the remains of the third tooth (d) in section; C: lateral view; D: enlargement of part of the edge of the second tooth (see circle in C); about two serrations are counted per millimeter; E: ventral view.

Fig. 2: Reconstruction of a megalosaurid skull (after POWELL, 1987), showing the position (gray) of the maxilla fragment from the Vaches Noires.

Plate I

Anterior part of the left maxilla of *Megalosaurus* sp., from the upper Callovian of the Vaches Noires, near Villers-sur-Mer, Calvados (PENNETIER collection, no. 380). A: medial view; B: replacement tooth situated in the second alveolus, in medial view; C: lateral view. Photos C. ABRIAL. Scale bar: 1 cm.