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Thyreophoran vertebrae from the Callovian (Middle Jurassic) of the Vaches Noires cliffs (Normandy, France), with remarks on the dinosaur assemblage from the Vaches Noires

Vertèbres de thyréophore du Callovien (Jurassique moyen) des falaises des Vaches Noires (Normandie, France) ; remarques sur l'assemblage de dinosaures des Vaches Noires

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ABSTRACT

Two associated incomplete thyreophoran dorsal vertebrae from the Callovian Marnes de Dives Formation of the Vaches Noires cliffs, on the Normandy coast, are referred to an indeterminate stegosaur that appears to be different from *Lexovisaurus*, previously reported from the Callovian of western France. These vertebrae are the first evidence of thyreophorans from the Vaches Noires and complement the dinosaur assemblage from this locality, which hitherto consisted of several theropod taxa and an indeterminate sauropod. The dinosaur record from the Vaches Noires is heavily dominated by theropods and this imbalance is difficult to explain. A possible explanation may be that the dinosaur sample from the Vaches Noires is too small to be statistically significant and representative of the original faunal assemblage from which it is derived.

Mots clés :
Dinosauria
Thyreophora
Stegosauria
Vertèbres

RÉSUMÉ

Deux vertèbres dorsales de thyréophore associées provenant de la formation des Marnes de Dives (Callovien) des falaises des Vaches Noires, sur la côte normande, sont rapportées à un stégosaure indéterminé qui paraît être différent de *Lexovisaurus*, déjà signalé dans le Callovien de l'Ouest de la France. Ces vertèbres sont le premier indice de la présence de

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Normandie

thyréophores aux Vaches Noires et complètent l'assemblage de dinosaures de ce site, qui jusqu'ici se composait de plusieurs taxons de théropodes et d'un sauropode indéterminé. La liste des dinosaures des Vaches Noires est fortement dominée par les théropodes, et ce déséquilibre est difficile à expliquer. Une explication possible pourrait être que l'échantillon de dinosaures des Vaches Noires est trop réduit pour être statistiquement significatif et représentatif de l'assemblage faunique initial dont il est issu.

1. Introduction

The Vaches Noires cliffs, on the Normandy coast, between the towns of Villers-sur-Mer and Houlgate (Calvados), are one of the main sources of Jurassic dinosaurs in France, theropod vertebrae having been described and illustrated (as belonging to crocodiles) from there by Cuvier as early as 1808 (Buffetaut, 2011, 2013a; Cuvier, 1808). Since then, a number of additional specimens have been discovered in the Callovian, and to a lesser extent in the Oxfordian, beds of the Vaches Noires, and are kept in both public and private collections. The vast majority of these fossils belong to theropods (Buffetaut, 2013b), the only exception apparently being a sauropod vertebra briefly mentioned by Bigot (1895) and destroyed by Allied bombings in 1944 (Bigot, 1945). In the present paper, we describe two stegosaur vertebrae from the Vaches Noires, which are an addition to the dinosaur diversity from this important locality, and we discuss the unusual and strongly unbalanced composition of the dinosaur assemblage from the Vaches Noires.

2. Geographical and geological setting

The specimen (a limestone block containing two vertebrae) belongs to the collection of the late Jean-Claude Gaillard, now kept at the Museum of the Fabrique des savoirs (Réunion des musées métropolitains) in Elbeuf-sur-Seine (Seine-Maritime, Normandy, France), under collection number 2012.4.100. The only indication about its provenance is that it comes from the Vaches Noires, a stretch of cliffs about 5 km long between Villers-sur-Mer to the east and Houlgate to the west. The stratigraphic provenance of the fossils can only be surmised from the lithology of the matrix still surrounding them: the bones are enclosed in a boulder of very hard grey limestone. In all likelihood, this block originated from one of the limestone layers interbedded in the Marnes de Dives Formation at the base of the cliffs (Lebrun and Courville, 2013; Rioult, 1980). Most of the vertebrate fossils from the Vaches Noires come from this formation, which is Late Callovian in age (Rioult, 1980). A few have been found in the Marnes de Villers and in the Oolithe ferrugineuse de Villers, of Oxfordian age, which crops out higher up in the cliffs, but there is absolutely no evidence of oolites in the fossil-bearing block and the specimen certainly does not come from the latter formation. A Late Callovian age can therefore be accepted for the thyreophoran vertebrae described below.

The Marnes de Dives were deposited in a marine environment but contain elements derived from a nearby continental area (Rioult, 1980), including dinosaur remains (such an occurrence is by no means unusual: Buffetaut, 1994b).

3. Description

As mentioned above, the specimens described here (Fig. 1) are enclosed in a block of very hard limestone and it has not been possible to free them completely from this matrix. To judge from the water-worn appearance of the bones, the block probably was collected as a boulder lying on the beach at the base of the cliffs. Three bones are visible: an incomplete vertebra consisting of the centrum and part of the neural arch, an isolated neural arch and a small bone fragment, 50 mm in length, that may have been part of a rib. The occurrence of several bones together is worth noting, as most of the dinosaur specimens from the Vaches Noires are isolated bones, with the notable exception of some of the *Streptospondylus* vertebrae originally described by Cuvier (1808) and the distal end of a tibia and a fibula with the accompanying astragalus and calcaneum (Buffetaut, 2013a, b). Although the stegosaur vertebrae in question are associated, they are not articulated: the isolated neural arch has rotated 180° in a horizontal plane so that its caudal end faces the caudal end of the more complete vertebra; moreover, it has also rotated nearly 90° in a vertical plane, so that its cranial margin now faces ventrally relative to the other vertebra. It should be noted that the isolated neural arch has a neural canal and neural arch pedicels that are not as dorsoventrally elongate as those of the more complete vertebra, which suggests that the neural arch is from a more cranial part of the vertebral column. The specimens were certainly part of a single skeleton, which was disarticulated before fossilization, at least some of its elements nevertheless remaining in close contact. The possible rib fragment shows no significant features and the description will therefore concentrate on the vertebral elements.

Vertebra: the specimen consists of the centrum, which is largely incomplete ventrally, and part of the neural arch, missing several of its apophyses. The centrum is massive, showing no evidence of pleurocoels or apophyses. The fact that the parapophyses are not located on the centrum shows that the vertebra belongs to the dorsal section of the vertebral column. The cranial face of the centrum, which is free of matrix, is very slightly concave, with a slight

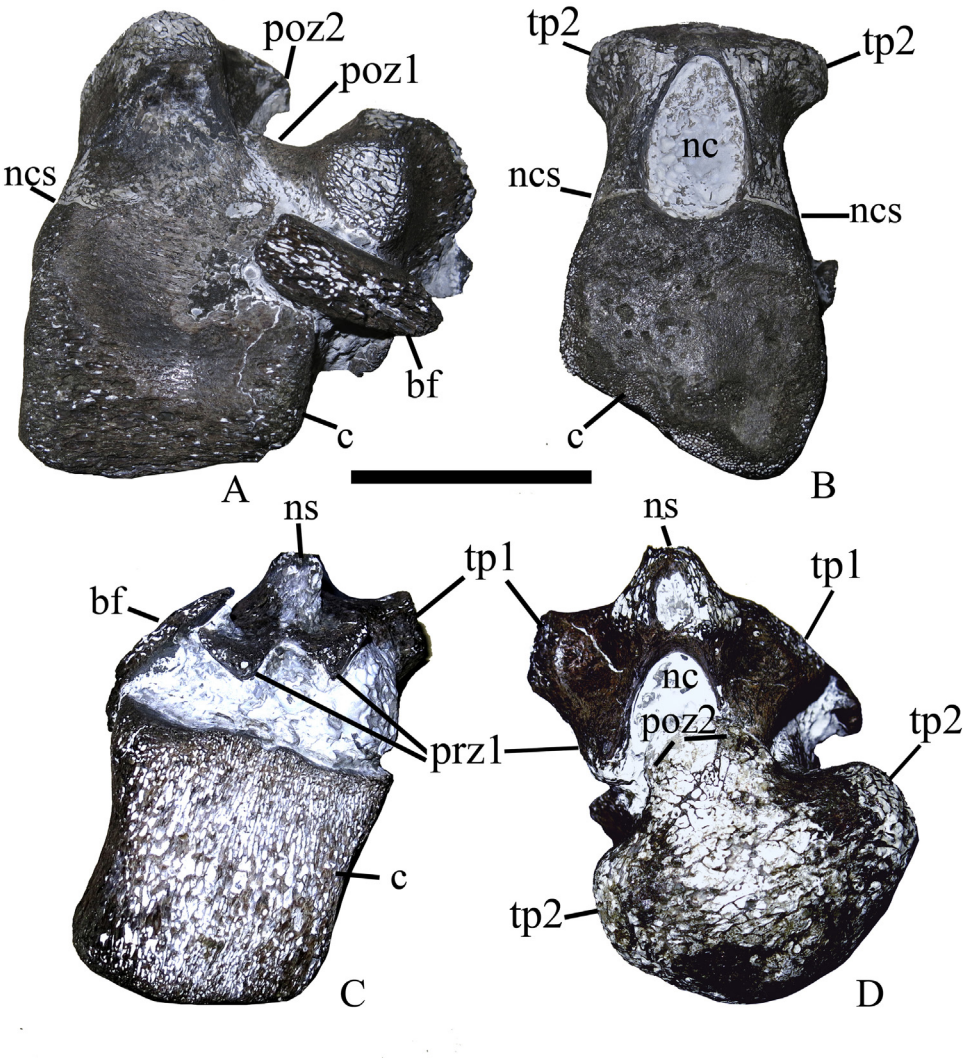

Fig. 1. Associated thyreophoran vertebra and neural arch in a limestone block from the Callovian of the Vaches Noires cliffs (Fabrique des savoirs, Elbeuf, France, No. 2012.4.100). A. Vertebra in left lateral view, isolated neural arch in right lateral view. B. Vertebra in cranial view. C. Isolated neural arch in cranial view, vertebra in ventral view. D. Isolated neural arch in caudal view, vertebra in dorsal view. bf: bone fragment; c: centrum; nc: neural canal; ncs: neurocentral suture; ns: neural spine; poz1: postzygapophysis of isolated neural arch; poz 2: postzygapophysis of vertebra; prz1: prezygapophysis of isolated neural spine; tp1: transverse process of isolated neural arch; tp2: transverse process of vertebra. Scale bar: 50 mm.

Fig. 1. Vertèbre et arc neural de thyréophore associés dans un bloc de calcaire callovien des falaises des Vaches Noires (Fabrique des savoirs, Elbeuf, n° 2012.4.100). A. Vertèbre en vue latérale gauche. Vertèbre en vue craniale, arc neural isolé en vue latérale droite. B. Vertèbre en vue craniale. C. Arc neural isolé en vue craniale, vertèbre en vue ventrale. D. Arc neural isolé en vue caudale, vertèbre en vue dorsale. bf : Fragment osseux ; c : centre ; nc : canal neural ; ncs : suture neurocentrale ; ns : épine neurale ; poz1 ; postzygapohyse de l'arc neural isolé ; poz2 : postzygapophyse de la vertèbre ; prz1 : prézygapophyse de l'épine neurale isolée ; tp1 : processus transverse de l'arc neural isolé ; tp2 : processus transverse de la vertèbre. Barre d'échelle : 50 mm.

protrusion in the center. As preserved, it is as tall as wide (60 mm), but as a part is missing ventrally it was certainly taller than wide and oval in outline. The centrum is somewhat constricted in its middle part, which makes it slightly hourglass-shaped in ventral view. The caudal face is largely obscured by the matrix and by the isolated neural arch, but it can be seen that it was slightly concave. The centrum is slightly longer ventrally (63 mm) than dorsally (55 mm at the base of the neural arch), which makes it somewhat wedge-shaped in lateral view. In ventral view, the internal bony tissue is clearly visible at the level of the oblique break.

The limit between the centrum and the neural arch is clearly visible in cranial view because the neurocentral suture, at the base of the neural pedicels, is not fully fused (the suture becomes less clearly visible caudally). This shows that the vertebra belonged to a not fully grown individual – in agreement with its relatively small size. The neural arch is not complete dorsally, having suffered intense abrasion (probably after the block became detached and was subjected to the action of the waves at the base of the cliff). The prezygapophyses and the neural spine are missing, only the base of the transverse processes and the inception of the postzygapophyses are preserved.

The neural canal is clearly visible in cranial view; it is mostly enclosed by the neural arch, only its ventral part being bordered by the centrum. It is much higher (40 mm) than wide (24 mm) and teardrop-shaped. It is bordered laterally by tall, relatively thin neural pedicels. The transverse processes arise from the dorsal parts of the pedicels and diverge from the horizontal at an angle of about 45°. They are much worn and show few details; in particular, the position of the parapophyses cannot be ascertained. On the lateral faces of the neural arch, a ridge arises obliquely from the caudal margin and reaches the transverse process. The postzygapophyses are very incompletely preserved. What is left appears as two small hook-like caudally facing processes separated by a matrix-filled triangular space that directly overhang the caudal exit of the neural canal.

Isolated neural arch: this element appears to have separated from the missing centrum at the level of the neurocentral suture, which confirms that the animal was not fully grown. It seems to have undergone some distortion during fossilization. The presygapophyses are fairly well preserved and diverge from each other at an angle of about 90°. They are separated by a deep triangular embayment. Their articular surfaces are nearly flat and limited caudally by a pair of rounded depressions adjoining the base of the neural spine. The neural spine is largely missing and rather thin (10 mm at its widest). The robust transverse processes are very incompletely preserved, especially on the right side. The left one diverges from the neural spine at an angle of about 90°. Their cross-section is subquadrangular. As on the more complete vertebra, a well-marked blunt ridge issues from the caudo-lateral corner of the neural arch and rises along the side of the transverse process. No evidence of the parapophyses can be seen. The postzygapophyses are almost completely destroyed. They are separated at their inception by a deep oval matrix-filled pit. Below the postzygapophyses, the dorsal part of the neural canal can be seen. It is narrower than high and, as on the better-preserved vertebra, it must have been teardrop-shaped.

4. Identification

The position of the more complete vertebra in the vertebral column can be determined based on the absence of any trace of parapophyses on the centrum. The parapophyses must have been placed on the neural arch (although their position cannot be determined because of the incompleteness of the neural arches). This clearly shows that the vertebra belongs to the dorsal series and in view of the similarities between the two available neural arches, it can be assumed that this applies to both specimens. The fact that the parapophysis is not positioned on the lateral surface of the neural arch below the transverse process implies that it was somewhere on the lateral side of the process, close to its base, and this in turn suggests that the vertebrae are not from the anteriormost part of the dorsal series.

The massiveness of the centrum, without any indication of lateral depressions or pleurocoels, distinguishes it from the vertebral centra of the dinosaur groups previously reported from the Vaches Noires, viz. the Theropoda and the Sauropoda. Several characters support an attribution to a stegosaur, in particular the high and narrow pedicels of the neural arch enclosing an equally high and narrow neural canal. This combination of features is present to a greater or lesser degree in all stegosaurs, reaching an extreme in forms with an extremely tall and narrow neural arch such as *Stegosaurus* or *Kentrosaurus*. Ankylosaur vertebrae are similar in some respects to those of relatively basal stegosaurs, so that the possibility that the specimen may belong to an ankylosaur should be considered, all the more so that this group of thyreophorans is known from the Lower Oxford Clay, with the genus *Sarcolestes*. Unfortunately, the vertebrae of *Sarcolestes* are unknown. Some Late Cretaceous ankylosaurs (e.g., *Edmontonia*) do show a high and narrow neural canal and pedicels (Russell, 1940). However, known vertebrae of Jurassic ankylosaurs, such as *Myrmoorapelta maysi*, from the Morrison Formation of the United States (Kirkland and Carpenter, 1994), have neural canals and pedicels that are not as dorsoventrally elongate as neural canals and pedicels in the Vaches Noires specimens. Even in Early Cretaceous ankylosaurs, such as polacanthids, this elongation remains moderate (Blows, 2015). It therefore seems more likely that the specimen belongs to a stegosaur.

An identification beyond Stegosauria indet. does not seem to be possible on the basis of this material. However, some comparisons with other Jurassic stegosaurs can be made. Carpenter et al. (2001) distinguished three "styles" of stegosaur dorsal vertebrae on the basis of the tallness of the neural arch. The "low neural arch style" is represented by the genera *Huayangosaurus*, *Dacentrurus*, and *Hesperosaurus*. The "medium neural arch style" corresponds to the condition seen in *Chialingosaurus*, *Chunkingosaurus*, and *Tuojiangosaurus*. *Stegosaurus*, *Kentrosaurus*, and *Wuerhosaurus* exemplify the "tall neural arch style". Although these differences in neural arch height do not seem to clearly reflect phylogenetic positions (see Maidment et al., 2008), it is worth noting that the vertebrae from the Vaches Noires belong to the "low neural arch style", with the transverse processes arising at the level of the upper part of the neural canal, whereas in the other "styles" they arise at a higher level on the dorsally elongate neural arch. Interestingly, the condition in the Vaches Noires vertebrae closely resembles that in *Huayangosaurus taibaii* (Carpenter et al., 2001; Maidment et al., 2006; Zhou, 1984), a stegosaur from the Late Jurassic (Wang et al., 2018) Xiashaximiao Formation of Sichuan (China), which is recovered in a rather basal position in recent stegosaur phylogenetic analyses (Maidment et al., 2008; Raven and Maidment, 2017). By contrast, *Lexovisaurus*, as exemplified by the partial skeleton (Galton, 1990; Galton et al., 1980; Hoffstetter and Brun, 1956, 1958 – see Buffetaut and Morel, 2009, about why we think the genus name *Lexovisaurus* should be retained) from the Callovian of Argences, 25 km southwest of the Vaches Noires, has much taller neural arches, corresponding to the "medium neural arch style" of Carpenter et al. (2001). This also applies to the isolated vertebra from the Callovian of Sarthe referred to cf. *Lexovisaurus* by Buffetaut and Morel (2009). The co-occurrence of these two distinct vertebral morphotypes in the Callovian of western France apparently indicates the presence of two distinct stegosaur taxa, with *Lexovisaurus* and a possibly more basal taxon – a previously unsuspected diversity.

5. Remarks on the composition of the dinosaur assemblage from the Vaches Noires

The dinosaur assemblage from the Vaches Noires (and their western continuation at Dives, which is no longer accessible) is very heavily dominated by theropods (e.g., Allain, 2001; Buffetaut, 1994a; Buffetaut and Enos, 1992; Buffetaut et al., 1991a, b, 2010; Cuvier, 1808; Douvillé, 1885; Knoll et al., 1999; Morière, 1853; Piveteau, 1923; Plasse and Buffetaut, 2016; Taquet and Welles, 1977). Besides the stegosaur vertebrae described in the present paper, an exception is the sauropod vertebra reported by Bigot (1895, 1945) as having been found in the Oxfordian of Dives (it may actually have come from Callovian beds: Bigot placed the vertebrate-bearing beds at the base of the Vaches Noires cliffs in the Oxfordian rather than the Callovian – see, for instance, Bigot, 1939). Although Bigot referred it to the genus *Cetiosaurus*, it is preferable to consider it as Sauropoda indet. The dinosaur assemblage from the Vaches Noires therefore mainly consists of theropods, certainly belonging to several taxa (Buffetaut, 2013a, b). This very heavy dominance of carnivorous forms obviously cannot reflect exactly the composition of the dinosaur fauna on the land areas (in all likelihood the Armorican Massif) adjacent to the marine basin in which the fossil-bearing sediments were deposited. Interestingly, other Callovian localities close to the Vaches Noires have yielded other types of dinosaurs and theropods are not especially frequent there. Notably, the clay pit at Argences, about 25 km southwest of the Vaches Noires, has yielded a partial stegosaur skeleton (Galton, 1990; Galton et al., 1980; Hoffstetter and Brun, 1956, 1958) and a sauropod scapula (Buffetaut, 1995), whereas theropods have not been reported from that site. The Lower Oxford Clay (Peterborough Member) of England, which is an equivalent of the Marnes de Dives, has yielded a dinosaur assemblage that is much more complete and balanced than that from the Vaches Noires, comprising theropods, sauropods, ornithopods, stegosaurs, and ankylosaurs (Martill, 1988). Despite the fact that the Oxford Clay dinosaurs were probably derived from a different land mass (? the Anglo-Brabant Massif), the comparison emphasizes the unusual composition of the Vaches Noires assemblage. Interestingly, the dinosaur assemblage from the Kimmeridgian of Normandy (mainly from the cliffs close to Le Havre), which comes from a depositional environment not very different from that of the Marnes de Dives, is not dominated by theropods; it includes stegosaurs, ornithopods, sauropods, and theropods (Buffetaut and Cacheleux, 1997; Buffetaut et al., 1991a, b).

Selective collecting cannot explain the predominance of theropods at the Vaches Noires. Vertebrate remains are relatively rare there and collectors, whether professional or private, simply collect all the specimens they find. Moreover, on-the-spot identification is usually difficult and there is no reason why theropods should be preferentially collected.

It could be argued that theropod carcasses had a better buoyancy and may have been carried farther offshore than those of other dinosaurs. The hollow bones of theropods may seem to support that hypothesis, but it is not especially convincing in view of what is known of the drifting times and distances of vertebrate carcasses as studied by Schäfer (1962). Moreover, such an explanation would imply that the depositional area corresponding to the Vaches Noires cliffs was farther away from the coast than, for instance, the Argences area where stegosaur and sauropod remains occur, a supposition that cannot really be substantiated by paleogeographical reconstructions.

It could also be argued that theropods had a lifestyle that made it more likely for them to be carried into the marine environment, but the above-mentioned instances of the Oxford Clay and the Kimmeridgian deposits of Normandy are not in agreement with such an inference.

To sum up, as already mentioned by Buffetaut (1994b), there is no clear explanation for the dominance of theropod remains in the Callovian deposits of the Vaches Noires. It should be remembered, however, that the total number of dinosaur specimens reported from the Vaches Noires remains small. In addition to the sauropod specimen recorded by Bigot (1895), the stegosaur vertebrae described in the present paper demonstrate that dinosaurs are not represented exclusively by theropods at the Vaches Noires. Because of the low total number of dinosaur specimens, it cannot be excluded that the apparent dominance of theropods may simply express the fact that the sample is too small to yield statistically significant results. Statistical tests could be used to test this hypothesis, but a thorough review of all the available dinosaur material from the Vaches Noires and its precise stratigraphic provenance is needed before this can be attempted.

6. Conclusions

The associated dorsal vertebrae described in the present paper are the first record of a thyreophoran from the Vaches Noires cliffs, issuing in all likelihood from the Callovian Marnes de Dives Formation at the base of the cliffs. Although the incompleteness of the material precludes any precise identification, these vertebrae can clearly be referred to a thyreophoran and very probably to a stegosaur; their low neural arches are different from the tall neural arches of *Lexovisaurus*, the only stegosaur hitherto described from the Callovian of Normandy, thus indicating the occurrence of more than one taxon. These thyreophoran vertebrae increase the diversity of the dinosaur assemblage from the Vaches Noires, which had hitherto yielded a number of theropod specimens and a single sauropod vertebra. The marked predominance of theropod remains at the Vaches Noires remains difficult to explain; it may simply show that the sample of dinosaur fossils from that locality is too small to be statistically significant.

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