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NOTES ON THE MORPHOLOGY AND THE ORIENTATION OF THE FORELIMB OF *OURANOSAURUS NIGERIENSIS*

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Abstract : The forelimb of *O. nigeriensis* was closely examined. In the wrist, the intermedium is fused to the radiale and not, as previously thought, to the ulnare. The morphology of the forelimb, and particularly that of the radius and ulna, has implications regarding the orientation of the manus. In the articulated forelimb, the palm of the manus would have faced nearly medially, not posteriorly, as it has often been portrayed. The medial orientation is even more pronounced in the forelimb of other iguanodontids.

Key words: Dinosauria, Ouranosaurus, carpus, manus

Notes sur la morphologie et l'orientation de la patte antérieure d'*Ouranosaurus nigeriensis*

Résumé : La patte antérieure d'*O. nigeriensis* a été examinée. Dans le poignet, l'intermédiaire est soudé au radial et non, comme on le pensait, à l'ulnaire. La morphologie de la patte antérieure (en particulier du radius et de l'ulna) a des implications sur l'orientation de la main. La paume de la main était orientée médialement, et pas postérieurement. Cette orientation médiale est encore plus prononcée chez les autres iguanodontidés. (traduit par la rédaction).

Mots clés : Dinosauria, Ouranosaurus, carpe, main.

INTRODUCTION

The almost complete skeleton of *Ouranosaurus nigeriensis* from the Lower Cretaceous was found in 1965 in the Gadoufaoua locality in Niger. It was recovered in 1966, and thoroughly described by Taquet in 1976 as a gracile iguanodontid, closely related to the hadrosaurs.

The carpus of *O. nigeriensis* is similar to that of other members of the family Iguanodontidae. The main differences are the degree of fusion among the individual carpal bones, and to some extend the robustness of the carpus.

The ornithopods related to *O. nigeriensis* are generally considered to be predominantly bipedal (Gilmore, 1909; Galton 1974; Forster, 1990, 1997a,b; Norman & Weishampel 1990; Fastovsky & Weishampel, 1996; Sues, 1997). However, on the basis of the hind- and forelimb ratio, a heavily fused carpus and the relatively robust morphology of the manus, Norman concluded that *Iguanodon bernissartensis* spent most of its time in a quadrupedal posture (Norman, 1980).

The posture of *O. nigeriensis* was described by Taquet as being less vertical than the classical bipedal reconstruction of *Iguanodon* by Dollo (Dollo, 1883), but less horizontal than the *Edmontosaurus (=Anatosaurus) annectens* reconstruction made by Galton (1970). The reconstruction Taquet made was thus bipedal, as was the reconstruction in Fastovsky and Weishampel (Taquet, 1976; Fastovsky & Weishampel, 1996). Other reconstructions show *O. nigeriensis* in a quadrupedal posture. The orientation of the limb of these reconstructions has been with the palm of the manus facing posteriorly (Lambert, 1993; Glut, 1997). However, closer examination of the morphology of the forelimb suggests a different orientation.

THE CARPUS

The carpus of an iguanodontid has a distinct structure that differs from other ornithopods, and is often used to support the monophyly of the family Iguanodontidae (Dodson, 1980; Sereno, 1997). The iguanodontid carpus usually consists of three proximal, and four to five distal carpals (carpal II was probably cartilaginous, and thus not preserved in some iguanodontids, including *O. nigeriensis*).

Furthermore metacarpal I is believed to fuse with the radiale in all iguanodontids. The carpals are heavily ossified, and individual bones can be fused together (Norman & Weishampel, 1990).

The carpus of *O. nigeriensis* consists of two elements of fused carpals (fig. 1). The larger one of the two elements articulates proximally mainly with the radius, and the smaller element articulates only with the ulna. The large element was originally described as fused radiale, carpals I, III and IV as well as metacarpal I. The small element was assumed to be composed of intermedium, ulnare and carpal V (Taquet, 1976). Dodson also found the fusion of the proximal carpals to be between ulnare and intermedium (Dodson, 1980). However, among iguanodontids fusion between intermedium and ulnare is unusual. It is seen only in *I. bernissartensis*, where all the carpals are fused to form one solid carpus block. A carpus where the intermedium is fused to ulnare but not to radiale is therefore unknown in other iguanodontids. However, carpuses in which the intermedium is fused to radiale but not to ulnare are known in *I. atherfieldensis* (Hooley, 1925) and in *Camptosaurus* (Norman, pers. com.). Closer inspection of the carpus of *O. nigeriensis* reveals that the intermedium is actually part of the large carpal element (fig. 2), and therefore is fused to the radiale, and not to the ulnare.

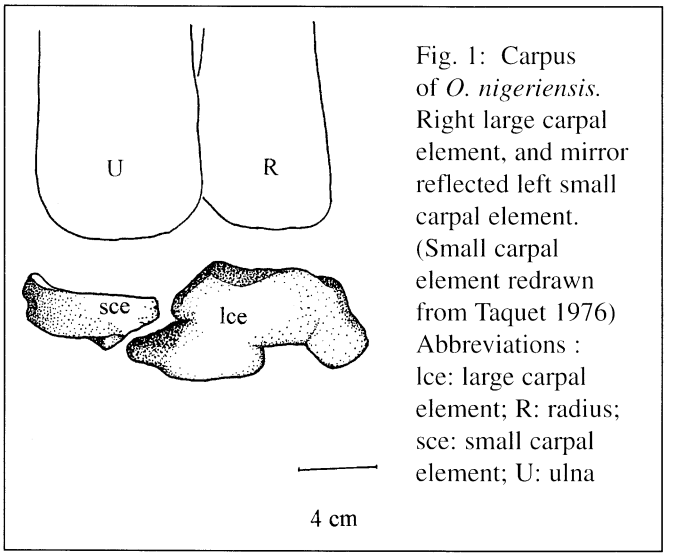

Fig. 1: Carpus of *O. nigeriensis*. Right large carpal element, and mirror reflected left small carpal element. (Small carpal element redrawn from Taquet 1976) Abbreviations : lce: large carpal element; R: radius; sce: small carpal element; U: ulna

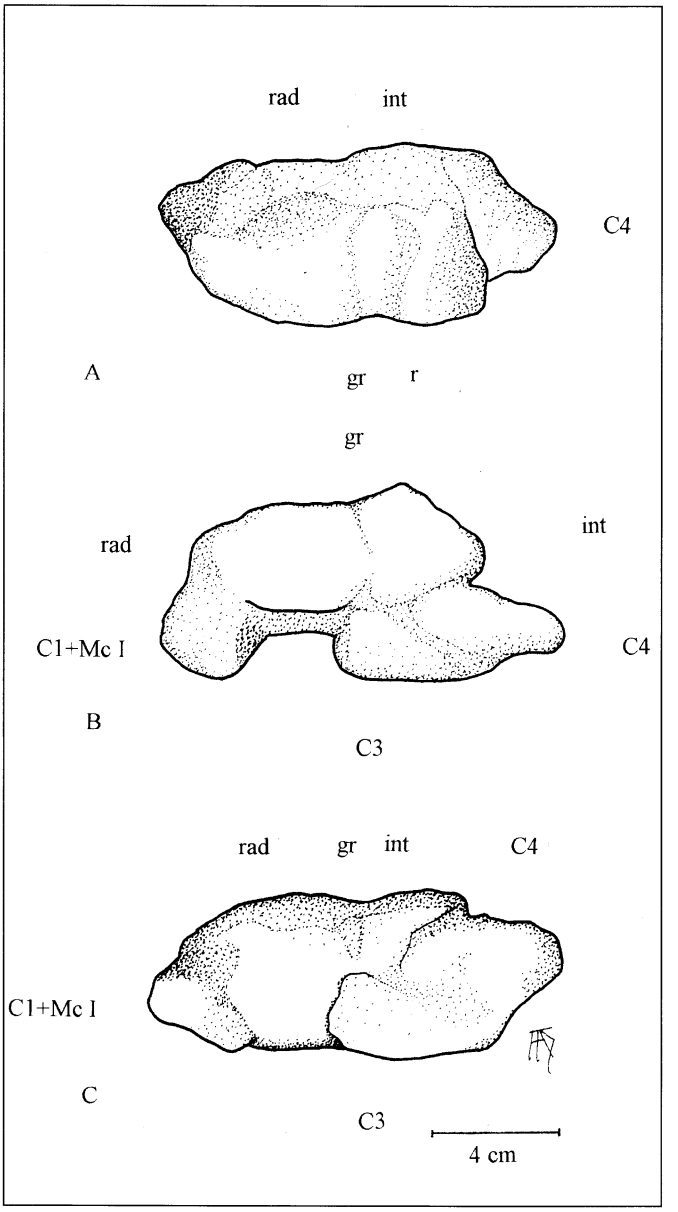

Fig. 2: Carpus of *O. nigeriensis* Large carpal element in A palmar view; B proximal view; C distal view. Abbreviations: C1+Mc I; carpal 1 and metacarpal I; C3: carpal 3; C4: carpal 4; gr: groove marking the border between intermedium and radiale; int: intermedium; r: ridge marking the border between the radius articulation and part of the ulna articulation; rad: radiale.

Both of the large carpal elements are preserved in the holotype of *O. nigeriensis* (GDF 300), although the right element is somewhat better preserved. The large element from the left forelimb lacks some details otherwise indicating the presence of the individual bones integrated in the block. However, on the proximal end of the right large carpal element, a shallow, slightly sigmoid groove is visible, where fusion between radiale and intermedium would be expected. Similar grooves can be found on the distal side, and the surface facing the palm of the manus (fig. 2). Furthermore, the large carpal element articulates with the radius, as well as part of the ulna. In most "reptiles" and in other dinosaurs the intermedium articulates with both the ulna and the radius (Romer, 1956). This is indeed the case in other iguanodontids. It is therefore more logical that in *O. nigeriensis* the intermedium is part of the larger carpal element, and fusion is between radiale and intermedium.

ORIENTATION OF MANUS

The distal articulation of the radius with the ulna partly determines the orientation of the manus in an articulated forelimb. The distal end of the radius is always in articulation with the carpals related to digit I (Paul, 1986). In quadrupeds, the radius is most often found articulating on the medial side of the ulna (Carroll, 1988). By having the articulation in this position, digit I will also be oriented medially when the forelimb is on the ground, and the palm of the manus therefore faces posteriorly. This orientation with the palm facing posteriorly has often been used in quadrupedal reconstructions of iguanodontids, including *I. bernissartensis, I. atherfieldensis* and *O. nigeriensis* (Norman, 1980; Hallett, 1986; Harris, 1986; Lessem, 1992; Glut, 1997). However, the distal radial articulation is not positioned medially in these iguanodontids. In *O. nigeriensis* the radial articulation is on the antero-medial side of the ulna, and in *I. bernissartensis* and *I. atherfieldensis* it is on the anterior side.

The humeri of these animals have well defined ranges of movement when articulated in the glenoid, but movements involving twisting around its long axis are not possible. The two condyles of the distal end of the humerus direct the movements of the lower arm, and no movements around the long axis of the arm are allowed by the elbow. Mainly anteroposterior movement is possible for the forelimb, but a limited range of lateral movement is allowed by the glenoid. The carpus of iguanodontids is heavily ossified and does not allow much, if any, axial rotation of the limb. Therefore, as the distal radial articulation on the ulna is not situated medially in iguanodontids, turning the palm of the manus posteriorly would not have been possible for *O. nigeriensis*, and certainly not for *I. bernissartensis* (Rasmussen, in prep.). When the forelimb touched the ground, the manus of *O. nigeriensis* would have been oriented with the palm facing posteromedially, whereas the palm of the two other iguanodontids would have faced medially. A cast of *I. bernissartensis* has been mounted in a quadrupedal posture, with the palm of the manus facing posteriorly in the Musée Royal d'Histoire Naturelle in Brussels. The shoulder and the elbow are disarticulated, which is the only way that the forelimb can get in this position (Rasmussen, in prep.).

CONCLUSIONS

The carpus of *O. nigeriensis* has its own unique morphology, but is not as different from the carpuses of other iguanodontids as previously thought.

In *O. nigeriensis* the fusion of the proximal carpals is between intermedium and radiale, as it tends to be in all iguanodontids. Only in *I. bernissartensis,* where all carpals are fused, is there fusion between intermedium and ulnare. The orientation of the distal articulation for the radius on the ulna is anteromedial in *O. nigeriensis*; implying that in a quadrupedal stance, the palm of the manus would face posteromedially. In most quadrupeds, the palm of the manus faces posteriorly. The orientation of the manus of *O. nigeriensis* appears less adapted for locomotion than in animals with a posteriorly facing palm.

The morphology of the manus of *O. nigeriensis* is much like that of *Camptosaurus*, in which there was an obvious weightbearing function of the forelimb, unlike in the iguanodonts. On the other hand, the forelimb is lightly built and short relative to the hindlimb. It does not appear to be a robust weightbearing structure and it seems unlikely that locomotion was the primary function of this limb.

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