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 radia-
le 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

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 bernissart-
tensis 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 bipe-
dal 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 orienta-
tion.
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: Cl+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 weight-bearing structure and it seems unlikely that locomotion was the primary function of this limb.
ACKNOWLEDGEMENTS

I am very grateful to Dr. Philippe Taquet and the staff at Museum National d’Histoire Naturelle in Paris for help and guidance I received during my stay there. I would like to thank Phil Currie and David Norman for helpful comments and corrections, and Fedor A. Steeman for comments and most of the illustrations. I am also thankful for the help I received from the people connected with the Erasmus network, and from my supervisor Niels Bonde. Furthermore I would like to thank Pierre Bultynck and Dirk Nolf at the Royal Institute of Natural Sciences of Belgium in Brussels for help and assistance at my visit there. Den Ingwersenske Fond supported me financially, as did the Erasmus program.

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Note reçue le 15-09-1997 acceptée après révision le 28-02-1998