

**GÉOLOGIE ET PALÉONTOLOGIE DU GISEMENT DE GADOUFAOUA**

(APTIEN DU NIGER)

CHAPITRE III

OSTÉOLOGIE D'*OURANOSAURUS NIGERIENSIS*,  
IGUANODONTIDÉ DU CRÉTACÉ INFÉRIEUR DU NIGER

Philippe TAQUET 1976 Cahiers de Paléontologie, CNRS, Paris

**GEOLOGY AND PALEONTOLOGY OF THE GADOUFAOUA DEPOSIT**  
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CHAPTER III

**OSTEOLOGY OF *OURANOSAURUS NIGERIENSIS*, IGUANODONTID FROM  
THE LOWER CRETACEOUS OF NIGER**

pp. 57 – 63, 102, 106 – 113, 118 – 120, 155 – 168      translated by Philip J Addis 2002

A. INTRODUCTION

During the mission to reconnoitre the locality of Gadoufaoua, in January 1965, I had the opportunity to prospect a good part of the central region of this palaeontological site. It was in the course of one of these searches, that I discovered the skeleton described below.

It was located in a region situated 7 km to the south-east of the wells of Elrhaz, 400 m from the camp of the Two Trees, geographic coordinates = 16° 42' lat., 9° 20' long.

The collection of the skeleton took place the following year, during the first important expedition organised on the deposit by the Centre National de la Recherche Scientifique and the Muséum National d'Histoire Naturelle (see historic account of the expeditions). It was well managed with the assistance of A. F. LAPPARENT, L. GINSBURG, B. LOIRET and lasted ten days.

CONDITIONS OF DEPOSIT

The animal was lying on its left flank, relatively little disturbed. The bones of the pelvis, the majority of the dorsal vertebrae, and a good part of the caudal vertebrae were in articulation; the other vertebrae were found several centimetres from the others, but in order. The neck was folded back on itself, above the back. The forelimbs, the hindlimbs, the bones of the anterior part of the skull and the mandible were disarticulated and a little more dispersed.

The enclosed plan of the excavation (fig. 9) gives the orientation and the position of the different bones of the skeleton. The whole assembly was spread over an area of 15 m<sup>2</sup>.

Several bones of the skeleton, which were reduced in number, were eroded by the wind and sand and were in a poor state of conservation, several pieces moreover were not retrieved. It is a matter of the following bones:

- the two femurs, of which remain only two distal articular condyles. The left tibia, and left metatarsals, astragalus and calcaneus, the phalanges of the left hindfoot, the last caudal vertebrae, several chevrons from the extremity of the tail.
- On the skull: only the left lacrimal, the right quadratojugal, the articular, the stapes, the left maxilla were all absent.

All the other bones were in a perfect state of preservation and had not suffered from deformation with the exception of several vertebrae and several ribs.

The level at which the skeleton was discovered constituted the superior part of the GAD 5, partly situated above a sandstone and conglomerate layer well readily identifiable, forming a cliff (cliff of Elrhaz, fig. 3 ).

#### OTHER FRAGMENTS ATTRIBUTED TO *OURANOSAURUS NIGERIENSIS*

The bones attributable to *O. nigeriensis* are fairly numerous in the Gadoufaoua deposits. To this species belonged notably a vertebral column very eroded by sandstorms of the level of the Innocents. Although damaged, this skeleton remains notwithstanding very spectacular as is witnessed in the photograph 1, Pl VI.

Of numerous isolated fragments, teeth, limb girdle bones, vertebrae etc....have equally been gathered during the course of different expeditions.

We have discovered at last in 1970, 4 km south of the "level of the innocents", a second skeleton nearly complete of *Ouranosaurus nigeriensis*, on the edge of a small landing strip laid out by the CEA in 1964. This skeleton (Pl. IX – fig. 2) is slightly less well conserved than the skeleton recovered in 1966; the skull in particular was not recovered, but the bones of the rest of the body were less displaced than on the specimen of 1966.

B – SYSTEMATICS  
Class REPTILIA  
Order ORNITHISCHIA  
Sub-order ORNITHOPODA  
Family IGUANODONTIDAE MARSH 1895

*Ouranosaurus*, gen. nov.

Etymology:

*Ourane*: Arabic name signifying, valour, courage, recklessness. This name is given by the Touareg of Niger and by the Berbers of Algeria for the sand monitor.

*Sauros*: (masculine name, from the Greek: *Sauros*) = lizard

Type species: *Ouranosaurus nigeriensis*, gen. nov.

Diagnosis: the same as that of the type species.

***Ouranosaurus nigeriensis*, sp. nov.**

Fig. 9 – 74, Pl. VII – XXIV

Etymology: *O. nigeriensis*, by allusion to its country of origin, Niger.

Type specimen: GDF 300 – a practically complete skeleton displayed in the National Museum of Niger. Niamey<sup>1</sup>.

Paratype: GDF 381 – MNHN – a nearly complete skeleton which lacks the skull.

Locality of type: Camp of the two trees, 7 km S.E. of Elrhaz, 16°42' lat. 9°20' long. Deposit of Gadoufaoua, GAD 5 formation (upper part of the formation of Elrhaz), Tégama series, Aptian.

Locality of the paratype: 4 km south of the formation of the Innocents, east border of airfield, lat. 16°26', long. 9°8', Gadoufaoua deposit, GAD 5 (upper part of the formation of Elrhaz), Tégama series, Aptian.

Reference specimens: GDF 301, coracoid of large dimensions. GDF 302, femur.

Distribution: Deposit of Gadoufaoua GAD 5, Elrhaz formation, Tégama series, Aptian, north-east Niger.

Comment: the name *Ouranosaurus nigeriensis* was employed for the first time by myself in July 1972, at the time of the public presentation of the skeleton GDF no. 300 in the context of an exhibition organised by the *Centre National de la Recherche Scientifique* and the *Muséum National d'Histoire Naturelle au Parc Floral de Vincennes*. This name was taken up again in an article appearing in the journal "Sciences et Avenir" in September 1972, but accompanied neither by diagnosis or photograph, then in the book "I Dinosauri del Teneré" published in December 1972: a photograph of the skeleton of *Ouranosaurus nigeriensis* was given there, without diagnosis.

DIAGNOSIS – Iguanodontid of medium dimensions (7 m in length), bipedal. Skull very long, not very broad and relatively little height, of which the greatest height is at the level of the nasal protuberances. Snout long and fine, ending in a duck-bill. Premaxillaries extremely elongated, straight, widened anteriorly separating posteriorly the nasals from the maxillae. External nares easily seen in dorsal view. Orifice of convergence between the nasal canals situated very far back. Short prementary, wider than long. Maxilla little elevated. Nasal short carrying a rounded dorsal protuberance. Small preorbital fenestra.

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<sup>1</sup> A complete cast of the type specimen is in the collection of the MNHN

Orbit circular, at the same height as the inferior temporal fossa. The postero-external process of the squamosal is straight and horizontal covering very little the paroccipital process. The paroccipital process raised, wide, oblique towards the front. Occipital condyle wide, flattened. Basipterygoid process directed especially laterally. Superior temporal fossae wide, very divergent towards the anterior. Dentary raised anteriorly, little raised posteriorly, at the dorsal border carrying anteriorly a long diastema. Retro-articular process pronounced. Teeth of the *Iguanodon* type, covered on one side by enamel, crown crenellated.

Vertebral formula: 11 – 17 – 6 – 40 – Tail relatively short. Neural spines of dorsal vertebrae extremely long. Ischium long, straight, enlarged distal foot, obturator process very proximal, obturator canal very narrow. Pubis very narrow, prepubic process very elevated and well developed, pubic rod straight, much shorter than the ischium, enlarged at the distal extremity. Ilium slender, with pre-acetabular process equal to half the overall length, dorsal border convex, with outline of anti-trochanter, acetabulum shallow, post acetabular indentation little marked. Upward process on posterior but not anterior of astragalus. Tridactyl foot. Phalangeal formula 0 – 3 – 4 – 5 – 0. Humerus long and practically straight. Manus very fine with fifth metacarpal in the form of bony spur of small dimensions, not directed laterally. Phalangeal formula 1 – 3 – 3 – 3 – 3 or 4.

### C. DESCRIPTION

The description of the bones of the skeleton of *Ouranosaurus nigeriensis* is nine tenths based on the skeleton GDF no. 300 gathered in 1966. However we have used in order to complete this, a few of the bones from the skeleton gathered in 1972 (GDF no. 381). These bones are the homologues of those which are absent or poorly preserved in the type. This is the case with the femur, the coracoid, the metacarpals, and the metatarsals and phalanges, the latter permitted us to complete the phalangeal formula of the fore- and hind-feet. All the pieces described hereafter, save where otherwise indicated, belong however to the skeleton of the type *Ouranosaurus nigeriensis*.

While comparing the different bones from the skeleton of *Ouranosaurus nigeriensis* with their homologues in the Iguanodontidae and the Hadrosauridae, I made reference to works and to descriptions of the classical specimens; but with regard to these specimens it appears to me to be necessary to make a number of observations:

- My comparisons were made from classic specimens of *Iguanodon* found in the Wealden of Great Britain, in particular with the bones preserved on the famous block from Maidstone, and belonging to *I. mantelli* (OWEN 1851, Pl. XXXIII and XXXIV). They also referred to equally to the isolated specimens attributed to *I. mantelli*, pieces described in a very detailed manner and admirably figured by OWEN.

- Despite these descriptions, the numerous bones of the skeletons of *I. mantelli* of Great Britain remain insufficiently known. For the skull, few of the elements feature in these

descriptions. Only some fragments of the maxilla (HULKE 1886, OWEN 1851) a fragment of the surangular (HULKE 1878) and the dentary are known.

- A poorly preserved fragment of the rear-skull of *Iguanodon* has been described by HULKE (1871, Pl. XI). This piece, damaged and very incomplete, is the only one which, with several further details given by DOLLO with regard to the study of the skull of *Iguanodon bernissartensis*. BOULENGER 1881, gives the elements of the neurocranium of *Iguanodon*.

-The description of the skeleton of *Iguanodon atherfieldensis*. HOOLEY 1925, given by HOOLEY is certainly the most complete and the most precise which one has of an *Iguanodon*. Unfortunately, the skull of *Iguanodon atherfieldensis* is incomplete: lacking the roof of the skull, the neurocranium, the nasals and the prementary.

- DOLLO has described in a particularly remarkable series of notes (1882 to 1906) the abundant material found at Bernissart (Belgium). This material comprises a complete skeleton of *I. Mantelli* and 20 skeletons of *I. Bernissartensis*. The notes of DOLLO, in general, have permitted the correction of several errors and give a precise picture of that which were the *Iguanodons*. DOLLO had planned to give later a detailed description, unfortunately he was not able to follow up his project so that 95 years after the discovery of the *Iguanodons* of Bernissart, one does not possess a detailed work on the anatomy of the skull and on the individual variations of the 20 specimens of Brussels. Added to that the study of these specimens is rendered difficult owing to the more or less pronounced crushing of the skulls, by the obliteration of the cranial sutures, and by pyritisation. Lastly problems of systematics arrived to complicate the problem further. It is necessary to stress, after OSTROM (1970), that we do not know today if the different species created are valid, if there are 1, 2 or 3 different species of *Iguanodon*.

I have compared on the other hand the bones of the skeleton of *Ouranosaurus nigeriensis* with those of *Camptosaurus medius* MARSH 1894, *C. dispar* MARSH 1879 and *C. browni* GILMORE 1909 of North America, all three described by GILMORE, with those of *Tenontosaurus tilletti* OSTROM 1970 of North America and described by OSTROM, those of *Dysalotosaurus lettow-vorbecki* POMPECKJ 1920 from Eastern Africa described by JANENSCH.

My comparisons were carried out equally on the admirably preserved skeletons of the hadrosaurids of North America described notably by LULL, LAMBE, OSTROM, etc...or from Asia described by ROZHDESTVENSKIY and GILMORE.

I have been able as well to see the material constituting the principal genera and species of the Iguanodontidae and Hadrosauridae in different museums: the *Iguanodons* of Bernissart in the Musée Royal des Science Naturelles de Belgique, the skeleton of *Dysalotosaurus* exhibited at the Museum of Berlin, the skeletons of *Camptosaurus* at Yale and Salt Lake City, and of *Tenontosaurus* at Yale, the principal hadrosaurids in different museums in the United States and Canada, also using the cast of the skeleton of *Iguanodon bernissartensis* exhibited at the Muséum National d'Histoire Naturelle and the

complete skeleton of *Anatosaurus* sp. purchased from Barnum BROWN in 1911 and also present in the collection of the Muséum National d'Histoire Naturelle.

## CRANIAL SKELETON

The skull of *Ouranosaurus nigeriensis* is of a considerable length (670 mm). In lateral view, the rear-cranium is raised from the posterior edge of the squamosal up to the level of a protuberance present on the nasal (fig. 10 and Pl. XIII). After this the height diminishes progressively towards the anterior until the anterior extremity of the premaxillaries. The dorsal surface of the skull thus makes a marked angle at the level of the nasal protuberance. The height of the skull is maximal at the level of this protuberance.

The muzzle is long with a straight dorsal border, the nostrils are very well developed, very elongated and visible in dorsal view.

The maximum width of the skull (244 mm) is relatively small and is situated at the level of the orbits. The length of the skull is equal to just under 3 times the maximum width<sup>2</sup>.

The skull is relatively low in height (260 mm). In occipital view, the skull thus appears nearly as wide as high.

The profile of the skull of *Ouranosaurus nigeriensis* can call to mind that of the skull of certain hadrosaurids such as *Anatosaurus annectens* or *A. saskatchewanensis* (cf. LULL and WRIGHT 1942, Pl. 16 and 17). These ones also possess an elevated rear-skull, but mainly at the level of the frontals, with a straight, duck-billed muzzle. With the Iguanodontidae, in contrast, as for example in *Iguanodon*, the height of the skull diminishes progressively from the rear of the squamosal up to the anterior extremity of the premaxillary, and the muzzle curves ventrally as in the beak of a parrot.

If the length of the skull of *Ouranosaurus nigeriensis* reaches that of the skull of *Iguanodon bernissartensis* (680 mm), the dimensions of the bones of the postcranial skeleton are nearer to those of the smaller and more slender species, *Iguanodon mantelli*. Even if the skulls of *Ouranosaurus nigeriensis* and *Iguanodon bernissartensis* are the same length, the skull of the former is very little elevated (260 mm) in comparison with that of the latter (470 mm).

The part of the mandible anterior to the coronoid process of the dentary bears teeth along 2/3 of its length as in the Hadrosauridae, and not on 3/4 as in the Iguanodontidae.

To aid in the understanding of the text, we have used the method adopted by OSTROM in his osteological description of the skulls of the Hadrosauridae (1961), and divided the description of the skull of *Ouranosaurus* into three sections:

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<sup>2</sup> We shall see at the end of the description the differences in proportion of the skull of *Ouranosaurus nigeriensis* in comparison with that of *Iguanodon*

- 1) the neurocranium
- 2) the maxillary region
- 3) the mandible.

## 1. THE NEUROCRANIUM

The neurocranium of *Ouranosaurus nigeriensis* just like the that of the iguanodontids and the hadrosaurids forms a relatively massive braincase, of which the individual elements are closely fused together. The neurocranium is made up of both dermal and endochondral bones.

The neurocranium of the iguanodontids is much less well known than that of the hadrosaurids, and the skull of *Ouranosaurus nigeriensis* offers the opportunity to describe for the first time and in detail the complete assemblage of the neurocranium of an iguanodontid.

As with the skull of the hadrosaurids, numerous problems concerning the relationships between the different bones could not be resolved here in the description of the skull of *Ouranosaurus nigeriensis* as a result of the obliteration of most of the cranial sutures.

The neurocranium of *Ouranosaurus nigeriensis* comprises as in the hadrosaurs the exoccipitals and the supraoccipital posteriorly, the opisthotic and the prootic laterally, the parietals and the frontals dorsally, the basioccipital and the basisphenoid ventrally, the laterosphenoid, orbitosphenoid, parasphenoid and the presphenoid anteriorly.

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## AXIAL SKELETON

### VERTEBRAL COLUMN

The vertebral column of *Ouranosaurus nigeriensis* comprises:

- 11 cervical vertebrae
- 17 dorsal vertebrae
- 6 sacral vertebrae
- 40 caudal vertebrae

being in total 74 vertebrae.

The vertebral column of *Iguanodon bernissartensis* possesses 85 vertebrae; that of *Iguanodon mantelli* 81 vertebrae (QUINET 1969); that of *Iguanodon atherfieldensis* probably had fewer vertebrae than *Iguanodon bernissartensis*, but the total number is not known; the number of vertebrae of *Camptosaurus* is 77; the total number of vertebrae in *Ouranosaurus nigeriensis* is then relatively low. Among the Hadrosauridae the number of



vertebrae is much more extensive: for example in *Anatosaurus*, one counts 12 cervical vertebrae, 20 dorsal vertebrae, 9 sacral vertebrae, 37 to 38 caudal vertebrae (there being a total variation of between 78 and 119 according to species).

Cervical vertebrae  
Fig. 35, 36, 37 and 38

All the cervical vertebrae of the skeleton which we describe are conserved. They are opisthocoelous with the exception of the atlas whose shape is distinctive and adapted for the articulation of the neck with the skull.

*Iguanodon* equally possesses opisthocoelous cervical vertebrae, atlas excepted, while in *Camptosaurus*, the 2<sup>nd</sup> and 3<sup>rd</sup> vertebrae are platycoelous. There are 11 cervical vertebrae in *O. nigeriensis* (10 in *I. mantelli* and *I. bernissartensis* and 11 in *I. atherfieldensis*).

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3<sup>rd</sup> to 11<sup>th</sup> Cervical vertebrae  
Fig. 38 and 39

The cervical vertebrae of *O. nigeriensis* are relatively small and narrow and grow in dimension from the third vertebrae up to the eleventh vertebra.

Centrum  
Fig. 38.4, ce

The anterior articular face of the centrum is very convex, slightly higher than wide, of oval shape. It is separated dorsally from the rest of the body of the centrum by a very marked transverse canal, especially at the level of the neural canal. The posterior articular face of the centrum is deeply concave, wider than high, oval, with a slight dorsal indentation at the level of the neural canal. The centrum is wider posteriorly than anteriorly, with a slight transverse constriction in the middle part. Anterior and posterior articular faces are reunited ventrally by a strong keel, longitudinal and rounded. The width of this keel increases from the anterior up to the posterior cervical vertebrae.

The *parapophyses* (p) are pre-eminent on the lateral faces of the centrum; they are found just behind of the anterior articular face and in a dorsal position. Between each parapophysis and the ventral keel a deep depression is excavated. The anterior side of this depression is steep, the posterior side is slightly inclined in level (this depression seems to be the homologue of the pleurocoelous cavity of the vertebrae of the theropods). The extent of this depression increases from the anterior cervical vertebrae to the posterior cervicals. A nutrient foramen pierces the bottom of each depression just below the parapophysis.

The articular facet of the parapophysis destined for the capitulum of the cervical rib is oval in shape; its long axis is horizontal from the third to the seventh vertebra; it is inclined towards the front from the eighth to the eleventh. Each facet is slightly concave and turned weakly towards the rear. Some cervical ribs are still attached to the cervical vertebrae by the parapophysis (as for example on the sixth vertebra – fig. 38.6).

Fig. 39. – *Ouranosaurus nigeriensis* gen. et sp. nov. GDF 300. Sixth cervical vertebra, posterior view; c.cer, cervical rib; ce, centrum; c.n, neural canal; d, diapophysis; post.zyg, postzygapophysis; pr.zyg, prezygapophysis.

### Neural arch

The zygapophyses of the cervical vertebrae of *O. nigeriensis* are powerful processes equipped with wide articular facets; they are found at the level of the neural canal. The prezygapophyses (pr.zyg) are carried by a short process. Their articular facets in the shape of wings border on the lateral side of the neural canal. They are oval, flat, parallel with the longitudinal axis of the vertebra and face medially, dorsally and slightly posteriorly.

Ventral to the articular facet of the prezygapophysis and almost at a right angle to the process which carries it, develops a second process whose extent increases from the third to the eleventh vertebra. This process constitutes the diapophysis. The axis of alignment of the diapophysis is vertical on the anterior cervicals, then inclines towards the exterior to become horizontal on the posterior cervical vertebrae. The extremity of the diapophysis is slightly bulbous and bears an articular facet at first flattened dorso-ventrally, then more oval, facing ventrally and laterally. On this facet the tuberculum of the rib will come to articulate; this is fused to the diapophysis on the fourth cervical vertebra (fig. 38.4).

The posterior part of the neural arch is made up the two symmetrical branches, directed dorso-posteriorly, of the postzygapophyses (post.zyg). The axis of alignment of these postzygapophyses is horizontal on the anterior cervical vertebrae then becomes more oblique with a posterior border situated more dorsally at the level of the posterior cervicals. At the same time the length of the postzygapophyses increases from the front towards the back of the neck, on the last cervical vertebrae, the postzygapophyses extend very greatly beyond the posterior face of the centrum and overhang half of the centrum of the vertebra following. The dorsal border of the postzygapophyses is curved with a dorsal convexity.

The distal extremity of the postzygapophyses widens notably, the ventral borders are thickened into folds. The articular facets are orientated ventrally and laterally; they are flat or very slightly concave. The two postzygapophyses unite in the median plane to form the roof of the neural canal, but only on the posterior half of the vertebra. The neural canal remains visible dorsally on all the anterior half of the vertebra. At the point of convergence the two superior borders of the postzygapophyses is found a dorsal spur, slightly curved towards the rear, with the anterior border rounded and thickened. This

spur increases in size from the anterior cervical vertebrae up to the posterior cervicals. It constitutes the outline of the neural spine which one finds to be so developed at the level of the dorsal vertebrae.

Immediately behind this spur and between the two diverging borders of the postzygapophyses is found a V-shaped depression. The branches of the V are directed towards the back; the floor of the depression is a horizontal osseous blade which forms the roof of the neural canal. This depression, narrow and elongated at the level of the anterior cervical vertebrae, becomes enlarged then diminishes in length on the posterior cervical vertebrae and no longer exists after the tenth cervical vertebra.

The neural canal is circular in the first cervicals; it becomes wider than high after the sixth cervical vertebra.

The space between the articular facet of the diapophysis and the facet of the parapophysis increases in length from the anterior to the posterior cervical vertebrae.

There do not appear to be any perceptible differences between the cervical vertebrae of *Iguanodon atherfieldensis* and those of *Ouranosaurus nigeriensis* (from the third to the eleventh vertebra).

The outline of the neural spine is absent on the last cervical vertebrae of *Camptosaurus browni* (cf. GILMORE 1909, fig. 14, 1 and 2).

In placing the cervical vertebrae in articulation (the postzygapophyses of one vertebra lying on the prezygapophysis of the vertebra following) one can observe the existence at the level of the neck of *O. nigeriensis* of a sigmoidal curvature, a curve which appears to be much less accentuated than that of the neck of the specimens of *Iguanodon mantelli* or *I. bernissartensis* such as have been restored by DOLLO.

In *O. nigeriensis*, the skull forms an angle of  $120^{\circ}$  with the atlas and axis. The third cervical vertebra is oblique with respect to the axis of alignment of the axis, then the neck is oblique from the front towards the back and from top to bottom from the third cervical vertebra to the fifth cervical vertebra. The obliquity diminishes after the sixth vertebra and the neck becomes horizontal at the level of the ninth vertebra to straighten slightly in a dorsal direction at the level of the tenth and eleventh cervical vertebrae. From this middle position, the radius of curvature of the neck can certainly increase or decrease. In figure 73, the neck is placed in the high position.

#### Dorsal vertebrae

Fig. 38, 40, 41 and Pl. 21, fig. 4, Pl. 22, fig. 1 to 3

Thirteen dorsal vertebrae are preserved in the skeleton described here. According to the survey at the time of the excavation it is easy to state that between the last cervical and

the first dorsal vertebra conserved *in situ*, there is a zone eroded by sandstorms where the vertebrae have been either displaced or destroyed. Probably missing in the vertebral series are the first 4 dorsals. The dorsal vertebrae following are well in place as far as the level of the sacrum, and were hardly displaced at all.

The number of dorsal vertebrae which *Ouranosaurus nigeriensis* possessed then was 17, as in *Iguanodon atherfieldensis* (18 in *I. bernissartensis* and *I. mantelli*).

### Centrum

The centrum of the dorsal vertebrae of *Ouranosaurus nigeriensis* is platycoelous (on the posterior dorsal vertebrae, the posterior face of the centrum is slightly concave). The length of the centrum varies little along the series of the vertebrae (from 110 to 115 mm); the height is equally relatively stable and increases slightly on the 3 last dorsals. The width which is slight on the first dorsal vertebrae (60 to 65 mm) increases at the level of the 5 last dorsals to reach 80 mm.

The anterior and posterior face of the centrum of the dorsal vertebrae are in the form of a trapezoid. The dorsal border of these faces is wide, lightly curved at the level of the neural canal, and the ventral border is very straight at the level of the anterior dorsals, wider and more rounded at the level of the posterior dorsals, but never reaching the dimensions of the dorsal border. The lateral borders and the anterior and posterior faces are elevated, slightly convex, their convexity becoming more and more pronounced on the posterior dorsals.

The body of the centrum widens transversely at the level of the anterior and posterior faces; the lateral faces of the centra are then concave antero-posteriorly, separated from the anterior and posterior borders by the strong rounded rim. The lateral faces on the other hand are near to plane dorso-ventrally. The ventral border of the centrum is long, thin and sharp-edged on the first dorsal vertebrae, then it shortens and becomes more rounded on the posterior dorsals; the ventral border is concave, the radius of curvature of that concavity increases from front to back in the vertebral series.

Unlike the cervical vertebrae, the centrum no longer bears parapophyses. These have migrated dorsally and are found on the neural arch.

### The Neural Arch

It is more elevated and more pronounced than on the cervical vertebrae. Anteriorly, the process of the prezygapophysis is separate and distinct from the process of the diapophysis. The prezygapophyses have become important. They are in the form of wings with the long axis horizontal. They are nearly plane, and oval in form. The

prezygapophyses, as a result of their greater development at the level of the dorsal vertebrae, slightly exceed the level of the anterior face of the centrum.

On the lateral side of each prezygapophysis is located the articular facet of the parapophysis, this facet which receives the capitulum of the rib is particularly wide on the 7<sup>th</sup>, 8<sup>th</sup>, and 9<sup>th</sup> dorsals (which carry the largest ribs). Its size increases from the 1<sup>st</sup> to the 9<sup>th</sup> dorsal vertebra only to diminish after, and become limited, at the level of the 11<sup>th</sup>, 12<sup>th</sup>, and 13<sup>th</sup> vertebrae, to an oval surface situated between the prezygapophysis and the transverse process (diapophysis). This surface overhangs above the body of the wing of the prezygapophysis. The parapophysis, at the level of the posterior dorsals, subsequently migrates progressively towards the exterior, along the anterior border of the diapophysis to form a cylindrical process alongside the diapophysis, but separated from it by a fissure (15<sup>th</sup> vertebra). Finally, on the 16<sup>th</sup> and 17<sup>th</sup> dorsal vertebrae, the parapophysis becomes merged with the diapophysis and fused completely with it.

The diapophyses are very powerful; the strongest and the longest are found on the 5<sup>th</sup>, 6<sup>th</sup>, 7<sup>th</sup>, and 8<sup>th</sup> vertebrae; then their importance diminishes on the middle dorsal vertebrae, and increases again very slightly on the posterior dorsal vertebrae.

These diapophyses spread out laterally from the base of the neural spine and just behind the prezygapophyses, with a maximum inclination towards the top and a slight post-axial tilt on the 5<sup>th</sup>, 6<sup>th</sup>, 7<sup>th</sup> and 8<sup>th</sup> dorsal vertebrae, then they become horizontal and even curve very slightly in a ventral direction with a weak posterior orientation at the level of the middle dorsal vertebrae (10<sup>th</sup>, 11<sup>th</sup>, 12<sup>th</sup>, 13<sup>th</sup>). Finally, at the level of the last dorsals (15<sup>th</sup>, 16<sup>th</sup>, 17<sup>th</sup>) they are slightly dorsally oblique, and especially turned towards the front.

The different orientations of the diapophyses of the dorsal vertebrae of *Ouranosaurus nigeriensis* are similar to those which HOOLEY has observed on the vertebral column of *Iguanodon atherfieldensis* (1925, p. 25). The preaxial inclination of the diapophyses of the last dorsal vertebrae is normal and is not due to post-mortem modification, as already emphasized by HOOLEY for *Iguanodon atherfieldensis*.

In section the diapophyses are triangular at the level of the anterior dorsal vertebrae, each diapophysis having a flat posterior face. After the 8<sup>th</sup> dorsal vertebra, the section is also still triangular, but with a ventral border, a posterior border, and an antero-dorsal border. On the 12<sup>th</sup>, 13<sup>th</sup>, and 14<sup>th</sup> vertebrae, the section becomes oval with the long axis orientated antero-posteriorly. This oval is more flattened on the 15<sup>th</sup>, 16<sup>th</sup> and 17<sup>th</sup> vertebrae as a result of the addition of the parapophysis alongside the diapophysis. The facets intended for the tuberculum are placed on the anterior half of the distal extremity of the diapophyses and are turned towards the front and bottom.

The diapophyses are separated from the articular facets of the prezygapophyses by a deep depression with an anterior opening. This depression is particularly deep on the anterior dorsal vertebrae and progressively loses its importance in the middle and posterior dorsals.

The postzygapophyses extend greatly towards the rear beyond the posterior face of the centrum. They present in the form of two symmetrical blades orientated longitudinally and converging anteriorly with each other. The articular facets of the postzygapophyses face ventral and laterally. They are oval with the long axis aligned slightly oblique from top to bottom and from back to front.

Each facet is linked by a sharp border to the neural spine. The two borders unite towards the top in the sagittal plane; the two articular facets leave in between them a fissure open towards the rear, a fissure which is extended dorsally to the base of the neural spine.

### Neural spines Fig. 41

These are characteristic of *Ouranosaurus nigeriensis* as a result of their extreme elongation and can attain 3.9 times the height of the centrum (being 630 mm for a centrum height of 160 mm).

Their length increases progressively along the dorsal series and reaches its maximum at the level of the 10<sup>th</sup>, 11<sup>th</sup>, and 12<sup>th</sup> vertebrae, and decreases progressively after that.

The neural spine, which was rudimentary on the posterior cervical vertebrae becomes very significant from the 5<sup>th</sup> dorsal vertebra (where its height reaches 320 mm). The lateral faces of each neural spine are lightly convex on the anterior dorsal vertebrae, then flattened transversely from the 7<sup>th</sup> dorsal; the spine is then an elongated plate, wider distally than proximally, with a rounded anterior and posterior border, these borders are parallel for all the length of the spine at the level of the first dorsals, they move away from each other towards the top from the 8<sup>th</sup> dorsal and become parallel again at the 15<sup>th</sup> dorsal.

The neural spines are vertical up to the 11<sup>th</sup> dorsal, then curve lightly towards the anterior from the 11<sup>th</sup> to the last dorsal vertebra.

“One can wonder if such anterior inclination did not exist originally on the dorsal vertebrae of the skeleton of *Iguanodon mantelli* exhibited in Brussels (CASIER, 1960, Pl. XIX); as a result of deformations at the time of fossilisation, the neural spines of these vertebrae were perhaps after all slightly inclined towards the rear.”

The neural spine of the 5<sup>th</sup> dorsal terminates in a beak turned towards the rear, which perhaps served as an attachment for tendons.

The thickness of the neural spines stays noticeably constant (10 mm) save at the level of their superior edge which is slightly thickened and rounded; the base of the neural spine thickens evenly progressively on joining up with the rest of the neural arch.

The posterior edge of the neural spine of the last dorsal vertebra is hollowed out in to a canal as in *Camptosaurus* (cf. GILMORE 1909, p.234); the anterior border of the neural spine of the first sacral vertebra becomes lodged in this canal.

The neural spines are moderately well developed in *Camptosaurus browni*, *Tenontosaurus tilletti*, *Dysalotosaurus lettow-vorbecki*; they are longer in *Iguanodon bernissartensis* and *Iguanodon mantelli*, but they do not reach the length of those of *Ouranosaurus nigeriensis* (in the region of 2.7 times the height of the centrum in *Iguanodon mantelli*, around 3.9 times in *Ouranosaurus nigeriensis*. On the skeleton of *Iguanodon atherfieldensis*, exhibited in London (SWINTON 1965, Pl. 16), the neural spines are incomplete and it is not possible to make comparisons.

The great elongation of the neural spines of the vertebrae of *Ouranosaurus nigeriensis* is thus characteristic, it is the greatest elongation so far seen among the different species of the ornithopods.

A network of intertwined ossified tendons would have been applied to the neural spines as in *Iguanodon*. But in the case of the skeleton of *Ouranosaurus nigeriensis* described here, the pieces were slightly disarticulated and the excavation only yielded several fragments of ossified tendons. The lateral surfaces of the neural spines, smooth up to the 10<sup>th</sup> dorsal vertebra become afterwards rugose, marked by raised osseous ridges which are the remains of the ossified tendons or their attachments.

Regarding the arrangement of all the neural spines of the dorsal, sacral and caudal vertebrae, it is interesting to note the following points:

- the neural spines of the dorsal vertebrae are vertical, then inclined towards the front.
- The neural spines on the sacrum are vertical.
- The neural spines on the caudal vertebrae are inclined towards the rear.

These different inclinations must have had as their aim to respond to the forces exerted along the body of the animal at the level of the vertebral column. There is a symmetrical arrangement of the neural spines on either side of the sacrum (cf. paragraph on the reconstruction of the skeleton of *Ouranosaurus nigeriensis*).

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Caudal vertebrae  
Fig. 40, 43, 44 and Pl. XXI, fig. 3 and 5

There are 33 caudal vertebrae preserved on the skeleton of *Ouranosaurus nigeriensis* which I describe here. The centrum of the 1<sup>st</sup> vertebra is absent, but the neural spine is

preserved. 2 vertebrae must be missing together between the 24<sup>th</sup> and 27<sup>th</sup> caudals, and two others between the 29<sup>th</sup> and 32<sup>nd</sup> vertebrae; finally, the last caudal vertebra has not been found. The total number of caudal vertebrae in *Ouranosaurus nigeriensis* then must have been 40.

This number is relatively low. There are 44 caudals in *Camptosaurus* (cf. GILMORE 1909, p. 239), 51 in *Iguanodon bernissartensis*. The number of caudal vertebrae in *Iguanodon atherfieldensis* and *mantelli* is not known. *Iguanodon mantelli* must have possessed an number of caudal vertebrae close to that of *Iguanodon bernissartensis*.

Neural spines are present from the first to the 36<sup>th</sup> caudal vertebra whereas they have completely disappeared beyond the 27<sup>th</sup> caudal in *Iguanodon bernissartensis*.

#### Anterior caudal vertebrae

#### Centrum

The centrum is massive; its articular faces are platycoelous, slightly concave (without which one could describe them as amphicoelous) and of a form nearly square. The anterior articular surface is a little larger than the posterior.

The antero-ventral angle of the centrum is truncated by a concave articular facet, in the form of a flattened crescent; a second facet in the form of a crescent slightly more elevated truncates equally the postero-ventral angle of the centrum. These articular facets are intended for the chevrons (ch, fig. 43). The articulation with the chevrons is inter-vertebral: the antero-dorsal articular facet of a chevron becomes applied against the postero-ventral articular facet of a vertebra, while the postero-dorsal facet of the same chevron is applied to the antero-ventral articular facet of the vertebra immediately behind.

The articular surfaces destined for the chevrons are convergent ventrally and only allow between them, at the level of anterior caudal vertebrae, a space of little length and very concave constituting the ventral border of the centrum, the extent of this space will increase progressively after the anterior caudal vertebrae until the posterior caudals.

There are no chevrons at the base of the two first caudal vertebrae. The 3<sup>rd</sup> caudal vertebra bears an articular facet solely on its postero-ventral angle.

The lateral faces of the centra are concave antero-posteriorly, plane dorso-ventrally, slightly higher than long. The dorsal border of the centrum is equipped with a strong transverse process (considered as a rib fused to the vertebra), directed towards the exterior, horizontal and slightly inclined towards the rear (cos, fig. 43). This process is present on the first 15 caudal vertebrae.



It is present on the first 13 caudals in *Camptosaurus* and *Iguanodon bernissartensis* (the process is called *costoïde* by DOLLO (1883, p. 245); in the Ornithopoda from 10 to 18 anterior caudal vertebrae bear this process (ROMER 1956, p. 273).

These processes are flattened dorso-ventrally with an anterior and posterior border approximately parallel, except at the level of their distal extremity where the posterior border is curved towards the rear. The length of the process decreases along the caudal series, from the front towards the rear.

### Neural arch

The prezygapophyses, winglike in form, possess oval articular facets which face medially and a little dorsally. They advance little beyond the level of the anterior surface of the centrum and are less developed than on the dorsal vertebrae.

Likewise the postzygapophyses are less developed and only slightly overhang the posterior face of the centrum. Their articular facets are orientated ventrally and laterally.

Prezygapophyses and postzygapophyses are situated on the same horizontal plane on the anterior caudal vertebrae and are progressively shifted in relation to the others in a caudal direction. The prezygapophyses are more ventral than the postzygapophyses.

The neural canal is oval, and slightly higher than it is wide.

The neural spine is long, inclined towards the rear, flattened transversely, with a thin anterior and posterior edge. The spine is slightly enlarged towards the distal extremity. The extremity possesses a thickened border, wider anteriorly than posteriorly.

### Posterior caudal vertebrae

The centrum becomes more long than high; so the lateral faces are rectangular, almost flat antero-posteriorly, slightly convex dorso-ventrally.

The anterior and posterior articular surfaces are weakly concave and as high as wide. The facet is split into two apophyses separated by a notch. The neural arch becomes more elevated and narrow.

The prezygapophyses do not go past the level of the anterior face of the centrum. The postzygapophyses, shifted dorsally with respect to the prezygapophyses, are no more than two small separate articular facets, overhanging the base of the neural spine.

The neural spine which is attached more or less in the middle of the dorsal border of the centrum of the anterior caudal vertebrae is situated here at the postero-dorsal angle of the vertebrae, and is inclined markedly to the rear.

The anterior articular facets for the chevrons have disappeared and the articulation of the chevron is made solely with the rear of each vertebra. The posterior articular facets also disappear on all the last caudal vertebrae.

There are few anatomical differences between the caudal vertebrae of *Ouranosaurus nigeriensis* and those of *Iguanodon mantelli* figured by OWEN (1851, Pl. VIII and IX). There exists between them a slight difference of proportion: the caudal vertebrae of *Iguanodon mantelli* have a centrum proportionally less high than in *Ouranosaurus*.

### Chevrons

25 chevrons were retrieved during the excavation of the skeleton of the type *Ouranosaurus nigeriensis*; 19 of these chevrons are in a good state of preservation and 6 are fragmentary. The chevrons of the terminal part of the tail broke through on the Reg and are in a poorer state than the chevrons of the proximal part of the tail. There are probably 3 chevrons missing and the total number of chevrons in *O. nigeriensis* can be estimated at 28. So in *O. nigeriensis*, out of a total of 36 caudal vertebrae, 28 carried ventrally a chevron. There are 34 chevrons out of a total of 51 caudal vertebrae in *Iguanodon bernissartensis*.

The two first caudal vertebrae, situated immediately behind the sacrum do not carry chevrons, as is proved by the absence of an articular facet at the antero-ventral and postero-ventral borders of the second caudal vertebra (the first caudal vertebra was not recovered during the excavation).

The third caudal vertebra only possesses a single articular facet situated postero-ventrally, so it does not carry a chevron cranially, but carries one caudally; in *Iguanodon bernissartensis* (cf. DOLLO, 1883, p. 245), it is equally the 3<sup>rd</sup> caudal vertebra which carries the first chevron.

The chevrons of *O. nigeriensis*, then, are placed from the rear of the third caudal vertebra up to the rear of the 31<sup>st</sup> caudal vertebra. Their form is very similar to that of their homologues in the other Iguanodontidae, in anterior view, they have the form of a Y of which the two superior branches are reunited by an osseous bridge; these two branches remain distinct in the Hadrosauridae. The bony bridge of the proximal extremity of the chevrons carries an articular facet slightly concave and directed dorso-anteriorly, and a concave articular facet directed dorso-posteriorly; the articulation of the chevrons with the vertebrae has been studied previously (cf. anterior caudal vertebrae).

The chevrons diminish in length from front to rear. Their length is less pronounced than that of the neural spine.

The opening situated between the two branches of the Y is relatively wider than that of the chevrons of *Camptosaurus dispar* (cf. GILMORE 1909, fig. 20, p. 244), but are still of little height.

The body of the chevron thins progressively towards its distal extremity; this latter is flattened transversely. The anterior chevrons are slightly recurved towards the rear, the median chevrons are practically straight and the posterior chevrons are inclined slightly towards the rear (they are all straight in the Hadrosauridae).

There is little difference besides the height, between the anterior and posterior chevrons; the posterior chevrons possess a proximal extremity proportionally wider antero-posteriorly; they only articulate with the vertebrae with anterior facet, so only with the posterior articular facet of the caudal vertebrae. A little before the extremity of the tail, the chevrons have a tendency to fuse with the vertebra which precedes them (for example vertebra no. 67).

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#### D – DIMENSIONS OF *OURANOSAURUS NIGERIENSIS*. INDICES

*Ouranosaurus nigeriensis* has a length (7 m) included between that of *Iguanodon bernissartensis* (9 m 50) and that of *Iguanodon mantelli* (6 m). The skeleton presents the same general aspect as that of the skeleton of *Iguanodon mantelli* (specimen from Brussels), but its skull is proportionally longer and wider and the neural spines of the dorsal vertebrae are proportionally much longer (fig. 73).

SKULL (dimensions and indices):

The length of the skull of *O. nigeriensis* (670 mm) reaches that of the skull of *I. bernissartensis* (680 mm), while the postcranial skeleton is closer in its dimensions and its gracility to the postcranial skeleton of *Iguanodon mantelli*. However the skull of the latter species nevertheless only measures 515 mm.

Furthermore, if the lengths of the skulls of *O. nigeriensis* and *I. bernissartensis* are identical, the skull of the first is very little elevated (260 mm) in comparison with that of the second (470 mm).

The height/length ratio of the skull of *O. nigeriensis* is rather different from those of the different species of *Iguanodon*:

	height/length
<i>O. nigeriensis</i>	0.38
<i>Anatosaurus annectens</i>	0.43
<i>I. mantelli</i>	0.53

<i>I. atherfieldensis</i>	0.55
<i>I. bernissartensis</i>	0.67

One can state then that at an equal height, the skull of *O. nigeriensis* or a hadrosaur such as *Anatosaurus annectens* is much more elongated than that of species of *Iguanodon*.

The width/height ratio of the skull is 0.93 in *O. nigeriensis* (the skull is nearly as wide as high). This ratio is 0.71 in *I. bernissartensis*. But the value of this index is approximate as a result of the probable lateral flattening of the skull of the individual from measurements were obtained (cast from the gallery of the *Museum National d'Histoire Naturelle*, donated by the *Institut Royal des Science Naturelles de Belgique*).

A diagram (fig. 72 a-f) shows the differences in proportion which exist in the skull for the following species: *Anatosaurus copei*, *Ouranosaurus nigeriensis*, *Iguanodon bernissartensis*, *I. atherfieldensis*, *Camptosaurus* sp., *Edmontosaurus regalis*.

It can be stated that according to the diagram the part taken by the premaxillaries in making up the skull is proportionally greater in *Ouranosaurus nigeriensis* and *Anatosaurus copei* than in *Iguanodon*.

Fig 72. – Comparison of the profile of the skulls of several Iguanodontids and several Hadrosaurids (scaled to the same length). a, *Camptosaurus* sp. (after ROMER 1956, fig. 32A, p. 148). b, *Anatosaurus copei* (after LULL & WRIGHT 1942, fig. 54, p. 158). c, *Edmontosaurus regalis* (after LULL & WRIGHT 1942, fig. 52, p. 152). d, *Ouranosaurus nigeriensis*, gen et sp nov. e, *Iguanodon bernissartensis* (after DOLLO, 1882, Pl. IX, fig. 1). f, *Iguanodon atherfieldensis* (after ROMER 1956, fig 32B, p.148).

#### LIMBS (dimensions and indices)

It is interesting to compare the lengths of the anterior and posterior limbs with those of other Ornithopods, as well as the relationship of the lengths of the radius to the humerus, the tibia to the femur, as these relationships can bring some indications on the possible posture of *O. nigeriensis*.

GALTON (1970 and 1971) in two recent works has compared different indices established from measurements of the anterior and posterior limbs, and measurements of the trunk of dinosaurs both bipedal and quadrupedal, and quadrupedal mammals in order to attempt to clarify what was the bearing, or the posture of the Hadrosauridae.

We have used the indices defined by GALTON, while adding to them those that we have established from measurements of the limbs and the trunk of *O. nigeriensis*, *I. mantelli* and *I. bernissartensis* (specimens from IRSNB and MNHN).

#### a) Table E: Measurements of the bones of the limbs in the Iguanodontidae

From these figures, GALTON (1970) defined the length of the anterior limb as being the length: humerus + radius + 3<sup>rd</sup> metacarpal, and the length of the posterior limb as being:

femur + tibia + 3<sup>rd</sup> metatarsal (the phalanges are not utilised as they are less frequently conserved).

Table F: by way of comparison, we add the indices of a theropod (bipedal): *Struthiomimus altus* and a sauropod (quadrupedal): *Apatosaurus* (after GALTON 1970)

b) Measurements of the anterior and posterior limbs of the iguanodonts:

	Length ant. limb	Length post. limb
<i>O. nigeriensis</i>	1100	1925
<i>I. bernissartensis</i>	1610	2300
<i>I. mantelli</i>	875	1640
<i>I. atherfieldensis</i>	762	1510

To these measurements, GALTON adds the length of the trunk, which is the distance derived between the glenoid cavity and the acetabular cavity. This length is 1425 mm in *O. nigeriensis*.

The indices defined by GALTON are the following:

hindlimb/forelimb, hindlimb/trunk, radius/humerus, metacarpal III/humerus, tibia/femur, metatarsal III/femur.

The indices calculated by GALTON (1970) for a certain number of hadrosaurs and the indices which we have calculated for the iguanodontids are below (see table F).

It is possible, from the this table and according to the work of GALTON, to make the following remarks for *O. nigeriensis*.

- 1) The index hindlimb/forelimb = 1.74. It is equal to that of *Procheneosaurus praeceps* and greater than all the other hadrosaurs analysed by GALTON. It is less than that of *Iguanodon mantelli* and *I. atherfieldensis*. This index is contained between that of the hadrosaurs and that of the “gracile” iguanodonts.
- 1) The index hindlimb/trunk = 1.35. This is equal to that of *Iguanodon atherfieldensis*. For GALTON, the quadrupedal dinosaurs had an index between 0.69 and 1.08; the hadrosaurs (bipeds according to GALTON) had an index between 1.22 and 1.44 (GALTON 1970, p. 466). *Ouranosaurus nigeriensis* then is placed in the second category.
- 2) The index radius/humerus = 0.75. This index is close to that of *Iguanodon mantelli* or *Struthiomimus*. It is below that of the hadrosaurs analysed by GALTON. This index in the quadrupedal dinosaurs is contained between 0.49 and 0.72 (GALTON, p.466).

- 3) The index metacarpal III/humerus = 0.23. It is close to that of *I. mantelli* and *I. bernissartensis*. In the quadrupeds, this index is found between 0.17 and 0.26, but in this case the forelimb is graviportal, the metacarpals and phalanges are short and wide.
- 4) The index tibia/femur = 0.92. It is close to that of *Procheneosaurus praeceps* but also to that of *I. mantelli*. It does not exceed 0.75 in the quadrupedal dinosaurs.
- 5) The index metatarsal III/femur = 0.34, as in the hadrosaurs and iguanodontids. It does not exceed 0.26 in the quadrupedal dinosaurs.

These indices, which must be used with care, seem nonetheless to indicate that *Ouranosaurus nigeriensis* is a bipedal dinosaur (according to index 2, 5, and 6), of which the forelimb is however shorter in comparison with the hindlimb than in the hadrosaurs, but proportionally longer than in the other iguanodonts, such as *I. mantelli* and *I. atherfieldensis* (index 1).

The radius and the metacarpals are proportionally shorter in relation to the humerus, than in the hadrosaurs.

#### POSTURE OF *OURANOSAURUS NIGERIENSIS*

The arguments developed by GALTON (1970) on the subject of the posture of the Hadrosauridae seems in part valid for *Ouranosaurus nigeriensis*: it appears in particular difficult to place the ilium in a position as oblique as is generally represented in the Iguanodontidae such as *Iguanodon mantelli* and *Iguanodon bernissartensis*: the lack of depth of the acetabular cavity of the ilium, the delicacy of the pubic peduncle of the ilium do not indeed appear to be compatible with a very oblique position of the ilium.

On the other hand the lack of length of the tail (which plays an important role in balancing in the hadrosaurs, according to GALTON), the absence of an antitrochanter as powerful as in the hadrosaurs, the great development of the neural spines of the dorsal vertebrae give reason to suppose that *Ouranosaurus nigeriensis* was an animal less agile, less cursorial and less fast than were the Hadrosauridae.

Our reconstruction (fig. 73) takes account of these elements and we have shown *O. nigeriensis* in a position less vertical than *Iguanodon* and less horizontal than *Anatosaurus annectens* such as is figured by GALTON in his recent study (1970, fig. 5).

#### E – COMPARISONS AND DISCUSSION

## INTRODUCTION

Before comparing the different characters of the skeleton of *Ouranosaurus nigeriensis* to those of the Iguanodontidae and Hadrosauridae, it is necessary to make the following remarks:

The systematic status of the different genera and species of hadrosaurids is in its totality relatively clear, following numerous detailed studies by American and Canadian authors, on material of an exceptional quality. Similarly the iguanodontids *Camptosaurus* from the Upper Jurassic of North America, *Dysalotosaurus* from the Upper Jurassic of Eastern Africa, *Tenontosaurus* from the Lower Cretaceous of North America (Aptian-Albian of Wyoming and Montana) are well characterised and known. It is not the same with the Ornithopods of Europe (Great Britain and Belgium) and more particularly the Iguanodontids which are known even since 1822 and which are represented by an abundance of material, although sometimes very fragmentary. A great confusion exists indeed on the subject of the definition of the different species of Iguanodontidae. I shall go so far as to write that the Wealdian swamps in which the European iguanodonts wallowed was but a puddle of water in comparison to the taxonomic mire in which they wallow today. Into this swamp, only OSTROM has recently dared to venture. After having studied the material in the Museums of Brussels and London, he has, in a work dating from 1970 (p. 131-134) given a clarification regarding that which he called the chaotic state of the nomenclature of the species of the ornithopods from the Wealden. It seems to me then essential before any comparison to give a brief summary of OSTROM'S conclusions.

- 17 species of ornithopods coming from the Wealdian beds of Great Britain and Belgium have been described since MANTELL'S discovery in 1822.
- Of these 17 species, 4 according to OSTROM can be detached easily enough from the batch. One of these 4 species falls into synonymy and only the following three species remain valid:
  - *Hypsilophodon foxii* HUXLEY 1870, hypsilophodont recently redescribed by GALTON.
  - *Vectisaurus valdensis* HULKE 1879, ornithopod clearly distinct from *Iguanodon* and *Hypsilophodon*.
  - *Stenopelix valdensis* MEYER 1859, an animal which is possibly a psittacosaurid.

The 13 remaining species all belong to the family of the iguanodonts. OSTROM has attempted to sort them out and to regroup these species created on sometimes very fragmentary remains.

- The example of *Streptospondylus major* OWEN 1842 and of *Streptospondylus recentior* OWEN 1851 created on the same cervical vertebra shows how far the confusion had gone (OSTROM 1970).

While admitting his difficulties and to underline that the problem of classification may perhaps be resolved by modern methods of multifactorial analysis, OSTROM provisionally regrouped these 3 species. Only three species will be valid, and they all three belong to a single and unique genus, *Iguanodon* (in place of the 4 genera previously defined).

These species become the following:

- A robust iguanodon (= *Iguanodon bernissartensis* ? BOULENGER 1881).
- A gracile iguanodon (= *Iguanodon mantelli* ? MEYER 1832).
- A completely inferior iguanodon from the Wealden (Wadhurst Clay) (= *Iguanodon dawsoni* ? LYDEKKER 1888).

In this classification, *Iguanodon atherfieldensis* HOOLEY 1925 is considered to be a juvenile of *Iguanodon bernissartensis*.

But this division into 3 species is presented with the title of hypothesis and OSTROM recognises that there may exist in fact only two species of *Iguanodon* or even perhaps only one. He does not omit to indicate that *Iguanodon mantelli* (the Brussels specimen) and *Iguanodon atherfieldensis* are perhaps female *Iguanodon*, while the male is represented in this case by *Iguanodon bernissartensis* (idea expressed by NOPSCA in 1929). There must be, according to OSTROM a biometric analysis of the collection of skeletons discovered at Bernissart to resolve this question.

On the plan of the systematics, OSTROM notes lastly, as well as SWINTON (1970) that the first description of the tooth type of *Iguanodon* found by MANTELL in 1822 is due to HOLL in 1829, before the description of MYER (1832) creating the species *mantelli*. HOLL created on this tooth the species; *Iguanodon anglicum*; *Iguanodon mantelli* should then be named *Iguanodon anglicum* and in the case where there is a single species of *Iguanodon* in place of the three species defined by OSTROM, it must obviously be named *Iguanodon anglicum* HOLL 1829.

But when OSTROM regroupes the 13 species of Iguanodontidae of the Wealden of Europe, he places the type tooth of *Iguanodon anglicum* with the fragments attributed to *Iguanodon bernissartensis* (moreover he does not give the reason). If one follows then the reasoning of OSTROM, the robust iguanodon (= *Iguanodon bernissartensis*) must be named in fact *Iguanodon anglicum*, that is to say a name of a species which has up to now represented the "gracile iguanodons". One can conceive that before such chaos, the comparison of *Ouranosaurus nigeriensis* with the species of *Iguanodon* is not going to be any easier.

I shall leave for the time being the systematic aspect of the problem and I shall compare *O. nigeriensis* to the specimens of *Iguanodon bernissartensis* (robust form from the Museum of Brussels), *Iguanodon atherfieldensis* (the sole specimen in the British Museum), and *Iguanodon mantelli* (the sole specimen in the Museum of Brussels).



*O. nigeriensis* is an Iguanodontid

The structure of the pelvis and the hindlimb of *Ouranosaurus nigeriensis* permit me to place this dinosaur easily among the Ornithischia, and in particular among the Ornithopoda.

*O. nigeriensis* is further an iguanodontid as is shown by comparison of its characteristics with those which define this family. The characteristics of the iguanodontids set out by ROMER (1956, p. 628-629) are the following:

- head a little larger than that of the hypsilophodonts. One or two supraorbitals, external nares large. Premaxillary without teeth. Teeth in a single row with enamel present on one side of the tooth only. 26 to 28 presacral vertebrae, comprising 9 or 10 cervicals (it would be preferable to describe 9 to 11 cervicals since *Iguanodon atherfieldensis* possesses 11 cervical vertebrae) 17 to 18 dorsals, 4 to 6 sacrals, cervicals and anterior dorsals opisthocoelous. Scapula long, straight and slender. Anterior process of ilium elevated. Posterior process curved; antitrochanter lacking, but superior border of ilium a little curved towards the exterior. Anterior process of the pubis moderately large, pubis in general a little shortened. Pubis and ischium curved. Ischium slender distally, obturator process well developed, placed proximally. Humerus equal to 55% of the length of the femur. Radius equal to two thirds of the length of the humerus. Tibia equal to 90% of the length of the femur. Carpals developed to a varying degree. No ascending process on astragalus. Ungual phalanges of the manus in the form of a blunt claw or hoof. Thumb present, variable development. Digit III and IV of the manus with 3 phalanges. Digit V reduced. On the pes, digit I shortened or reduced to a metatarsal, digit V absent or represented by a metatarsal spur. Ungual phalanges in the form of claws. Metatarsal III equal to around 40 to 50% of the length of the tibia.

The great majority of these characters are present on the skeleton of *Ouranosaurus nigeriensis*.

Only the following characters are different in *O. nigeriensis*:

- 11 cervical vertebrae and not 10 (but it is known that *Iguanodon atherfieldensis* which is an iguanodontid typically also possesses 11 cervical vertebrae).
- Scapula curved and not straight.
- Ischium wide and not narrow distally.
- Posterior branches of pubis and ischium straight and not curved.

Fig. 74 – Map of the distribution of iguanodontids in the world (after CASIER 1960, modified).

COMPARISON OF *O. NIGERIENSIS* WITH DIFFERENT SPECIES OF IGUANODONTIDS

a) *Dysalotosaurus lettow-vorbecki* POMPECKJ 1920.

*D. lettow-vorbecki* of the Upper Jurassic of Eastern Africa has been placed according to the authors either in the Hypsilophodontidae or in the Iguanodontidae. The absence of premaxillary teeth seems however to be a decisive element in making this species an Iguanodontid. *D. lettow-vorbecki* can be distinguished from *O. nigeriensis* by its very small dimensions, by its skull which is short and elevated, by its 9 cervical vertebrae, its 16 dorsal vertebrae and its 4 sacral vertebrae, by its curved femur and its tibia which is longer than the femur.

b) *Camptosaurus dispar* MARSH 1897.

The different species of camptosaurs, in particular *Camptosaurus dispar* are distinguished with ease from *Ouranosaurus nigeriensis*. In the camptosaurs, the skull is little elevated, the form of the muzzle is different, the placement of the communicating orifice between the external nares is very anterior, the adornments of the crown of the teeth is more simple, and the enamelled face of the tooth is equipped with numerous secondary crests. The neural spines of the vertebrae are short, the vertebral formula is different (9 – 16 – 5 – 38), digit I of the manus is well developed with a free 1<sup>st</sup> metacarpal, the prepubic blade of the pubis is little elevated, the pubic rod is very long and curved, and digit I of the pes is well developed.

However several cranial characters existing in *O. nigeriensis* are found again in *Camptosaurus dispar*: the premaxillaries are very developed towards the rear and the nasals are separated from the premaxillaries; the dorsal and ventral borders of each premaxillary are parallel, the nasals are short, the parietals are wide. The posterior process of each squamosal is horizontal and extended towards the rear, the quadrate is curved towards the front and the basiptyergoidal processes are directed ventro-laterally and not ventrally as in all the other ornithopods.

Regarding *Camptosaurus*, OSTROM (1970, p. 103) argues that the long and low shape of the skull, the width of the skull, the short quadrate curved towards the front and the basiptyergoidal processes directed ventro-laterally suggest that *Camptosaurus* is perhaps on an aberrant line and that it could not have been ancestral to the Cretaceous ornithopods. Without wishing to establish any affiliation between *Camptosaurus* and *Ouranosaurus*, we remark that there is no fundamental gap between these two genera.

c) *Anoplosaurus curtonotus* SEELEY 1879.

This species has been described according to fragmentary and scanty material found in the Cambridge Greensand (Cenomanian) of Great Britain. This species is represented by material too incomplete to be able to compare with *Ouranosaurus nigeriensis*.

d) *Craspedodon lonzeensis* DOLLO 1883.

This species was created according to 3 teeth found in the Santonian of Belgium. The crenellations of the border of the crown, just as the presence of a cingulum at the base of the crown permit these teeth to be distinguished from those of *O. nigeriensis*, as well as those of *Iguanodon*.

e) *Kangnasaurus coetzei* HAUGHTON 1915.

This dinosaur of the Cretaceous of Bushmanland (South Africa) is known by a maxillary tooth, a straight femur and by several fragments of tibia, fibula and femur. The crown of the tooth of *Kangnasaurus*, wider than it is high, equipped with a prominent median keel and numerous secondary ridges is much closer to that of the teeth of *Rhabdodon* than those of the teeth of *Iguanodon* and *Ouranosaurus*.

f) *Rhabdodon priscum* MATHERON 1869.

This iguanodontid from the Upper Cretaceous of Europe (Transylvania = Hungary, and Provence) is better known than *Kangnasaurus coetzei*. It is quite different from *Ouranosaurus nigeriensis* both by the morphology of its teeth, by the smallness and the shape of the different bones of the skull, in particular the maxilla, as well as by the shape and dimensions of the bones of the limbs.

g) *Iguanodon* MANTELL 1825

The genus *Iguanodon* was created by MANTELL in 1825. The subsequent discovery of the specimens of Bernissart (21 skeletons) enabled DOLLO (1882, p. 175) to give a more complete diagnosis of *Iguanodon*; here it is:

“Edentulous premaxilla. A single row of teeth in the maxilla and mandible. Cervical vertebrae opisthocoelous, dorsal biplanar, caudals amphicoelous. Sternal bones paired. Forelimbs reduced. Five functional digits on the manus, the first transformed into a spur. Pre-pubic blade projecting freely forward. Pubic rod shorter than ischium. Femur longer than the tibia. 3 functional digits in the pes with rudimentary styloid on first toe.”

This diagnosis makes little call on cranial characters. It permitted DOLLO to include in the genus *Iguanodon* 3 species: *Iguanodon prestwittchii* HULKE 1880, *Iguanodon mantelli* MEYER 1832 and *Iguanodon bernissartensis* BOULENGER 1881. Now the material attributed to the species *prestwittchii* was placed in the genus *Cumnoria* by SEELEY in 1888 then in the genus *Camptosaurus* by WOODWARD and SHERBON in 1890 and the diagnosis of DOLLO came to be made obsolete. The most recent diagnosis of *Iguanodon* and which summarises best the characters of this genus was given by STEEL (1969, p. 17). I have taken from it some different elements while adding several important characters in

comparing them with the characters of *Ouranosaurus*; the characters distinguishing *Ouranosaurus* from *Iguanodon* are the following:

<i>Ouranosaurus</i>	<i>Iguanodon</i>
Skull as high as wide.	Skull higher than wide, transversely compressed.
Maximum height of the skull between the nasals and squamosals.	Maximum height at the level of squamosals.
Duck-billed muzzle.	Parrot-beaked muzzle.
Predentary flattened wider than long with median and ventral protuberance.	Predentary elevated longer than wide lacking median protuberance.
Premaxillaries very long with parallel dorsal and ventral borders.	Premaxillaries quite long, curved ventrally.
External nares largely visible in dorsal view.	External nares little visible in dorsal view.
Orifice of convergence of external nares very posterior.	Orifice of convergence of external nares very anterior.
Nasals short with paired protuberance.	Nasals long and flat.
Posterior process of squamosals horizontal directed towards the rear.	Posterior process of squamosals directed ventrally.
Quadrate slightly oblique towards the front.	Quadrate almost vertical.
Paroccipital process very oblique towards the front.	Paroccipital process vertical.
Occipital condyle wide, little elevated.	Occipital condyle protruding as high as wide.
Superior temporal fossa wide, very divergent towards the front.	Superior temporal fossa relatively narrow, little divergent towards the front.
Retro-articular process developed towards the rear and top.	Retro-articular process short.
Dentary with diastema in front of tooth row.	Dentary without diastema.
Anterior extremity of dentary more	Dentary with parallel borders.

elevated than posterior extremity.

Neural spines of dorsal vertebrae very long. Neural spines of dorsal vertebrae moderately long.

Tail short.

Tail relatively long.

Ischium with very narrow obturator canal. Ischium with wide obturator canal.

Ilium with well marked outline of antitrochanter.

Ilium with faint outline of antitrochanter.

1<sup>st</sup> and 5<sup>th</sup> digits of manus not separated from axis of alignment of arm.

1<sup>st</sup> and 5<sup>th</sup> digits of manus separated from axis of alignment of arm.

No 1<sup>st</sup> metatarsal.

Rudimentary 1<sup>st</sup> metatarsal.

#### 1 – Comparison of *Ouranosaurus nigeriensis* with *Iguanodon bernissartensis*

*O. nigeriensis* can be distinguished from the specimens of *I. bernissartensis* of Brussels by the characters set out in the preceding list to which it is necessary to add the following differences: its dimensions more reduced, its limbs less robust and more slender, its short spur on digit I, the number of cervical and dorsal vertebrae (11 and 17 in place of 10 and 18),

it is possible that *I. bernissartensis* had 11 cervical vertebrae and 17 dorsals. There is a controversy on this subject between DOLLO and BOULENGER (DOLLO 1883). DOLLO thought that the last vertebra considered as cervical by BOULENGER is in fact the 1<sup>st</sup> dorsal.

the much longer neural spines, the slender scapula, with a curved and not straight border, the minimum width of the scapula being 8 times the length instead of 6, the absence of an open canal extending the coracoid foramen at the proximal border of the coracoid, the shape of the raised anterior blade of the pubis, the pubic rod straight and not curved. The ischium straight and not curved, the preacetabular process of the ilium equal to one half of the length of the ilium (and not equal to a third), the length of the forelimb equal to around half of the length of the hind limb and not to two thirds, the 4<sup>th</sup> trochanter situated one third down the femur (and not in the middle).

#### 2 – *Ouranosaurus nigeriensis* and *Iguanodon mantelli*

*O. nigeriensis* is distinguished from the specimen of *Iguanodon mantelli* of Brussels by the characters defined in paragraph g and by the supplementary differences following: its dimensions are greater, the skull is proportionally larger in comparison with the rest of the skeleton, the orbit is circular and not wider than it is high (but the skull of *I. mantelli* in Brussels is perhaps slightly flattened), the superior temporal fossae are wider, there are

11 cervical vertebrae in place of 10, 6 sacral vertebrae in place of 5, the external blade of the 2<sup>nd</sup> metatarsal is situated in the distal third of the bone and not in the middle of its length.

The characters shared by *O. nigeriensis* and *I. mantelli* are equally numerous:

The minimum width of the scapula is contained more than 8 times in its maximum length, the coracoid foramen is closed by a suture, the sternal plates are narrow and only slightly indented medially, the forelimbs are about half the length of the hindlimbs, the spike on the digit of the manus is reduced, the preacetabular projection of the ilium is equal to half the total length of this bone, the prepubic blade is thin and raised, the 4<sup>th</sup> trochanter is situated in the middle of the length of the femur.

### 3- *Ouranosaurus nigeriensis* and *Iguanodon atherfieldensis*

The comparison of *Ouranosaurus nigeriensis* and *I. atherfieldensis* is more limited as the skull of the latter species is not complete. The prementary, the nasals, the roof of the skull, the neurocranium are not conserved.

*O. nigeriensis* can be distinguished from *I. atherfieldensis* by its much greater dimensions, by its much longer premaxillaries and lacking a transverse canal on the dorsal border; the nares are confluent more posteriorly, the maxilla is more elevated, the postero-external process of the squamosal is horizontal and not vertical, the quadrate is more oblique towards the front, a diastema is present in front of the tooth row of the mandible. The anterior extremity of the dentary is more raised, the anterior border of the scapula is curved, the humerus is more straight, the outline of the antitrochanter is more developed, the 1<sup>st</sup> and 5<sup>th</sup> digit of the manus are not separated from the alignment of the long axis of the arm.

On the other hand, *O. nigeriensis* and *I. atherfieldensis* possess numerous characters in common: these characters are those defined above in the comparison of *O. nigeriensis* with *I. mantelli* with besides the fact that the premaxillaries of *Iguanodon atherfieldensis* are equally little curved ventrally with a dorsal border and a ventral border which are parallel.

### 4 – *Ouranosaurus nigeriensis* and *Iguanodon orientalis*

ROZHDESTVENSKIY (1952) has described under the name of *Iguanodon orientalis* a maxilla and a scapula found in the east of the Gobi Desert at Kamarin-Khural. The maxilla of *I. orientalis* is considerably longer and the length of the scapula is equal to 6 times the minimum width of the body of the bone and not 8 times as in *O. nigeriensis*.

h) *O. nigeriensis* compared to *Probactrosaurus gobiensis* and *Probactrosaurus alashanicus*

The Sino-Soviet expeditions have collected in Mongolia (ROZHDESTVENSKIY 1966) on the site of Iren Nor near to Maortu, an abundance of material comprising iguanodontids and Hadrosaurids, material distributed in three successive levels: Aptian, Albian and Cenomanian. The iguanodontids belonged to two species: *Probactrosaurus gobiensis* and *P. alashanicus*. For ROZHDESTVENSKIY (1966) the characters of these Iguanodontids herald those of the hadrosaur *Bactrosaurus johnsoni* found in the Cenomanian of the same region and the succession *P. gobiensis*, *P. alashanicus*, *B. johnsoni* will be an example of the rapid transition which must have taken place between the Iguanodontids and the hadrosaurs.

*O. nigeriensis* possesses in common with *P. gobiensis* and *P. alashanicus* the following characters: its fronto-temporal region is relatively elevated, the extremity of the scapula is wide, the preacetabular part of the ilium has a sub-triangular shape, the ischium is straight, the 4<sup>th</sup> trochanter is situated in the middle of the length of the femur.

But apart from the elevation of the fronto-temporal region and the absence of the curvature of the ilium, the characters are those characters which are common to the iguanodontids and it is normal to find them in *Probactrosaurus* and *Ouranosaurus*.

*O. nigeriensis* is distinguished from *P. gobiensis* and *P. alashanicus* by its greater dimensions, by the length to height ratio of the skull of 2.8 and not 2, by the contact between frontal and parietal being tortuous and not straight, by the separation one from the other in the sagittal plane of the squamosals, by the quadrate slightly oblique towards the front and not straight, the confluence of the external nares is very posterior and not anterior, the skull is wider at the level of the orbits, there is no rudimentary 3<sup>rd</sup> row of teeth.

#### *O. NIGERIENSIS* AND THE HADROSAURS

*O. nigeriensis* calls to mind the hadrosaurs in a certain number of its characters: the skull is elevated in the fronto-temporal region. The occipital region is wide, the nasals are rounded (which is the case in some, but not all the hadrosaurs), the muzzle is elongated and includes the premaxillaries widened into a duck-bill, the nasals are large and wide, very visible in dorsal view, the orifice of convergence between the external nares is situated well to the rear, there is a diastema in front of the tooth row (between the prementary and the 1<sup>st</sup> tooth of the dentary) the retro-articular process is well developed, the neural spines are long, the tail is laterally compressed with elevated neural spines, the prepubic process is elevated and very well developed, the ischium is straight and widened distally into a foot (as in some hadrosaurs), the obturator process is narrow, the forelimb is relatively less long, in comparison with the hindlimb, than in the iguanodontids, the lip on the external border of the 2<sup>nd</sup> metatarsal is in a very distal position.

The form of the muzzle, the length and the anterior width of the premaxillaries call to mind that which can be seen in *Anatosaurus annectens* or *Edmontosaurus regalis*; the canal present on the anterior border of the external wing of the quadrate exists equally in *Edmontosaurus* sp. The prementary is quite close to that of *Mandschurosaurus mongoliensis* and *Bactrosaurus johnsoni*, the nasals make one think, by the presence of their protuberances, of those of *Aralosaurus tubeiferus*. The ischium is relatively close to that of *Bactrosaurus johnsoni*.

## DISCUSSION

According to the various preceding comparisons, we can deduce that *O. nigeriensis* is an iguanodontid close to *Iguanodon* and which presents the most characters in common with *I. mantelli* and *I. atherfieldensis*.

If we uniquely base our arguments, in these comparisons of *O. nigeriensis* with the different species of *Iguanodon*, on the characters of the post-cranial skeleton, we must place this iguanodontid from Niger in the genus *Iguanodon*; the weak differences revealed at the level of the post-cranial skeleton justify the creation of a species different from *Iguanodon mantelli* or *I. atherfieldensis*, which one could call *Iguanodon nigeriensis*, just like there exists an *Iguanodon orientalis* distinct from *I. mantelli* and *I. atherfieldensis*.

But it appears to me on the contrary that to these weak differences must be added the much more important differences at the level of the morphology of the skull. The form of the muzzle and the profile of the skull, among other elements, are quite distinct from those which one can see in *Iguanodon*.

What importance can be accorded to these cranial characters peculiar to *Ouranosaurus nigeriensis*?

A series of examples chosen from among the ornithopods near to the iguanodontids, which the hadrosaurs are, gives, it would seem, good elements of appreciation of this question.

The hadrosaurs of North America are known principally from three successive formations: the Belly River Formation, then that of Edmonton, then that of Lance, which corresponds approximately to a period extending from the Santonian up to the Upper Maastrichtian. It is known that the hadrosaurs experienced a remarkable expansion and diversified into numerous genera and species: 12 genera and 29 species (OSTROM 1961). The systematics of these genera and species is based essentially on cranial morphology.

- *Edmontosaurus regalis* can only be distinguished from *Anatosaurus saskatchewanensis* by the form and the development of the premaxillaries (LULL and WRIGHT 1942, p. 155).



- *Procheneosaurus praeceps* is distinguished from *Cheneosaurus tolmanensis* essentially by the greater development of the nasals at the summit of the skull (OSTROM 1961, fig. 14A and B, p. 67).
- *Prosaurolophus maximus* is distinguished from *Saurolophus osborni* or from *Brachylophosaurus canadensis* (OSTROM 1961, p. 85, fig. A to C) above all by the lesser development and the different form of the nasals.
- *Corythosaurus casuaris* is distinguished from *Hypacosaurus altispinus* by the greater development of the nasals participating in the cap which surmounts the cranial roof of these two genera of hadrosaurs.
- Finally, in their work on the hadrosaurs of North America, LULL & WRIGHT (1942, p. 180) giving the diagnosis of *Procheneosaurus* and comparing this genus to *Corythosaurus* write: “the hind limbs, in their proportions, the ratio of the segments of the limbs, the form of each of the bones, etc.....compare closely with *Corythosaurus*. In fact save perhaps for the skull and the pubis, there are few distinctions between the skeletons of these genera save in those which concern the height”.

Let us add that in the diagnoses of these numerous genera of hadrosaurs, the morphology of the teeth practically does not come into it.

To take an example, no longer among the reptiles, but among the mammals, the diversity of the cranial outgrowths of the hadrosaurs brings to mind those which exist in the Antelopidae and Cervidae: their horns (or horn cores) or their antlers constitute good indicators of generic or specific variations, although differences may exist furthermore on the post-cranial skeleton.

The characters of the skull of this iguanodontid of Niger, in particular at the level of the nasals and the premaxillaries, seem to me then, in the light of the preceding examples, to take on a real systematic importance and to plead in favour of a generic distinction from *Iguanodon*; they justify in my opinion the creation of a new genus.

The principal evolutionary tendencies of the Ornithopoda (Psittacosauridae and Pachycephalosauridae excepted) have been summarised by STEEL (1969, p. 5). One can distinguish in the Ornithopoda a hypsilophontid stage, then an iguanodontid stage, finally a hadrosaurid stage. What is the position of *Ouranosaurus nigeriensis* in relation to these 3 stages?

Transformations in the Ornithopoda

*Ouranosaurus nigeriensis*

General increase in all the dimensions of the skeleton.

Height midway between that of Hypsilophodontidae and that of Hadrosauridae.

Skull becoming proportionally wider.

Skull a little wider than that of Iguanodontidae, near to that of hadrosaurs.

Loss of canine teeth and premaxillary teeth.

No canine and premaxillary teeth, as in iguanodonts and hadrosaurids.

Multiplication of number of dental rows.	Iguanodontid stage.
Increasing number of presacral vertebrae, cervical vertebrae going from 9 (Hypsiloph.) to 15 (Hadrosauridae), sacral vertebrae going from 4 to 8.	Iguanodontid stage 11 cervical, 6 sacral vertebrae.
Centra of cervical vertebrae at first little opisthocoelous, becoming strongly opisthocoelous, the first dorsals becoming equally opisthocoelous.	Iguanodontid stage.
Neural spines increasing in length.	Length of neural spines greater than in the iguanodontids and the hadrosaurs.
Ilium with development of an antitrochanter.	Outline of an antitrochanter (between iguanodontids and hadrosaurs).
Anterior process of pubis becoming elevated.	Anterior process of pubis elevated (between iguanodontids and hadrosaurs).
Pubic bar becoming progressively reduced.	Iguanodontid stage.
Obturator process of ischium becoming more proximal.	Obturator process proximal (between iguanodontids and hadrosaurs).
Humerus becoming shorter with respect to the length of the femur.	Iguanodontid stage.
Radius tending to increase in length with respect to the length of the humerus.	Iguanodontid stage.
Digits I and V of the manus reduced and then eliminated.	Iguanodontid stage.
Tibia longer than the femur then decreasing in length.	Iguanodontid stage.
Digits I and V of the pes reduced then eliminated.	Between iguanodontids and hadrosaurs.
Metatarsals becoming shorter in relation to the tibia.	Iguanodontid stage.

*Ouranosaurus nigeriensis* is an iguanodontid close to *Iguanodon* but by some of its characters, a little more evolved than the classic iguanodontids of the Lower Cretaceous (Wealdian). It is the only iguanodontid to possess a domed cranial roof at the level of the nasals. *Ouranosaurus nigeriensis*, on the stratigraphic plan is a little more recent (Aptian) than the majority of the representatives of the genus *Iguanodon* (Wealdian) with the exception of the specimen of *Iguanodon mantelli* from Maidstone which is Lower Aptian.

*Ouranosaurus nigeriensis*, with some of its characters more evolved than those of the Iguanodontidae, is found rather at the same stage as *Probactrosaurus gobiensis* and

*Probactrosaurus alashanicus*; but while with the former, the cranial modifications of the hadrosaur type consist above all of a modification of the profile of the skull, of the form of the nasals, the premaxillaries, the prementary and in front of the dentaries; in the latter the modifications concern essentially the development of a rudimentary 3<sup>rd</sup> row in the dentition. On the other hand all three have been found in the level of the end of the Lower Cretaceous (Aptian or Albian), all three are clearly different from the iguanodontids from the start of the Lower Cretaceous, all three are placed just before the appearance of the first hadrosaurs of the Cenomanian.