The Venice Specimen of *Ouranosaurus nigeriensis* (Dinosauria, Ornithopoda) (#14454)

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The Venice Specimen of *Ouranosaurus nigeriensis* (Dinosauria, Ornithopoda)

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Ouranosaurus nigeriensis is an iconic African dinosaur recorded by a few specimens including a couple of nearly complete skeletons from the Lower Cretaceous Gadoufaoua locality of the Ténéré desert in Niger. Only the holotype was completely described in the unique paper dedicated to this important dinosaur, although a few bones of the paratype were also included in the description. A mounted skeleton of *Ouranosaurus nigeriensis* is exposed at the Natural History Museum of Venice, Italy since 1975. It was never explicitly established whether it is the paratype and second nearly complete skeleton reported in literature or a third, unreported specimen.

We disentangle herein its complex history (thanks also to an unpublished field map of the paratype) and describe it. It includes the paratype material (found in 1970 and collected in 1972) with the exclusion of the left femur and the right coracoid (which were replaced with plaster copies) and possibly the manual phalanges. Some elements (e.g., the right femur, the right tibia, two dorsal vertebrae and some pelvic bones) were plausibly added from other individual/s. The vertebral column of the paratype is in a fair state of articulation and a better reference for the vertebral count of the taxon respect to the holotype. Some differences are observed between the latter and the Venice specimen. For example, the first dorsals in the Venice specimen are unlike those reported or hypothesized in the holotype, suggesting that the dorsal count could be 15 and the trunk would be consequently shorter; there are five to six more proximal caudals in the Venice specimen than in the holotype; the metacarpus is sensibly different in the two specimens. The linear size of the Venice specimen is about 90% the linear size of the holotype. The osteohistological analysis (the first one for this taxon) of some long bones, a rib and a dorsal neural spine reveals that the specimen is a sub-adult individual; this is supported also by somatic evidence of immaturity. The dorsal 'sail' formed by the elongated neural spines of the dorsal, sacral and proximal caudal vertebrae is unique to this taxon as for

size and shape among ornithopods; a display role is the most probable function for this bizarre structure.

THE VENICE SPECIMEN OF *OURANOSAURUS NIGERIENSIS* (DINOSAURIA, ORNITHOPODA)

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ABSTRACT

Ouranosaurus nigeriensis is an iconic African dinosaur recorded by a few specimens including a couple of nearly complete skeletons from the Lower Cretaceous Gadoufaoua locality of the Ténéré desert in Niger. Only the holotype was completely described in the unique paper dedicated to this important dinosaur, although a few bones of the paratype were also included in the description. A mounted skeleton of *Ouranosaurus nigeriensis* is exposed at the Natural History Museum of Venice, Italy since 1975. It was never explicitly established whether it is the paratype and second nearly complete skeleton reported in literature or a third, unreported specimen.

We disentangle herein its complex history (thanks also to an unpublished field map of the paratype) and describe it. It includes the paratype material (found in 1970 and collected in 1972) with the exclusion of the left femur and the right coracoid (which were replaced with plaster copies) and possibly the manual phalanges. Some elements (e.g., the right femur, the right tibia, two dorsal vertebrae and some pelvic bones) were plausibly added from other individual/s. The vertebral column of the paratype is in a fair state of articulation and a better reference for the vertebral count of the taxon respect to the holotype. Some differences are observed between the latter and the Venice specimen. For example, the first dorsals in the Venice specimen are unlike those reported or hypothesized in the holotype, suggesting that the dorsal count could be 15 and the trunk would be consequently shorter; there are five to six more proximal caudals in the Venice specimen than in the holotype; the metacarpus is sensibly different in the two specimens. The linear size of the Venice specimen is about 90% the linear size of the holotype. The osteohistological analysis (the first one for this taxon) of some long bones, a rib and a dorsal neural spine reveals that the specimen is a sub-adult individual; this is supported also by somatic evidence of immaturity. The dorsal 'sail' formed by the elongated neural spines of the dorsal, sacral and proximal caudal vertebrae is unique to this taxon as for size and shape among ornithopods; a display role is the most probable function for this bizarre structure.

INTRODUCTION

Ouranosaurus nigeriensis and *Spinosaurus aegyptiacus* are the most iconic African dinosaurs because of their outstanding hypertrophic neural spines. *O. nigeriensis* comes from the upper part of the El Rhaz Formation at the Gadoufaoua locality of the Sahara Desert, located 145 km east of Agadez, Niger (Taquet, 1976). The El Rhaz Formation of Niger has yielded a rich dinosaur association including theropods (*Suchomimus, Cristatosaurus*, *Kryptops* and *Eocarcharia*), sauropods (*Nigersaurus*) and the ornithopods *Ouranosaurus* and *Lurdusaurus* (Le Loeuff et al., 2012). Its age was considered to be Aptian by Taquet (1976) and Aptian−Albian by Sereno et al. (1999), but Le Loeuff et al. (2012) have recently proposed a Barremian age.

The detailed anatomical description of *Ouranousaurus nigeriensis* was published by Taquet (1976). Only a few specimens are formally referred to *O. nigeriensis* in that paper: the holotype GDF 300, the paratype GDF 381 and two isolated bones (GDF 301 and 302; Taquet, 1976, p. 58), although the discovery of several in situ specimens is mentioned in that paper (Taquet, 1976, p. 14-15). No other scientific works have been dedicated to this taxon since then, although a few papers dealt with it (Rasmussen, 1998; Dean-Carpentier, 2008; Taquet, 2012). Despite to this and the difficult access to the original holotype material, it is always included in the cladistic analysis of iguanodontian dinosaurs (e.g., Sereno, 1986; Norman, 2004, 2015; Mcdonald et al., 2010a, b, 2012).

Since 1975, a nearly complete and mounted skeleton of *O. nigeriensis* has been exhibited at the Museo di Storia Naturale (Natural History Museum) of Venice, Italy. Apparently, the Venice specimen is not mentioned in Taquet (1976) as well as in any other scientific papers dealing with *Ouranosaurus*. Therefore, it had to be considered as still undescribed.

The aim of our work was: 1) disentangling the complicated history of the *Ouranosaurus* specimens with particular focus on the Venice specimen; 2) to describe the latter and compare its skeletal elements with those published by Taquet (1976) in order to notice differences and get information useful for point 1; 3) to perform the first osteohistological analysis on *O. nigeriensis* sampling some significative bones and get information on the ontogenetic stage of the Venice specimen; 4) to establish whether the bones of the nearly complete mounted skeleton can be reliably referred to a single individual or to more individuals.

Institutional abbreviation: CEA, Commisariat à l'Énergie Atomique et aux énergies alternatives, France; CSRL, Centro Studi e Ricerche Ligabue, Venice, Italy; GDF, Muséum National du Niger, Africa; IRSNB, Institut Royal des Sciences Naturelles de Belgique; MNHM, Muséum National d'Historie Naturelle, Paris, France; MSNVE, Museo di Storia Naturale di Venezia (Natural History Museum of Venice), Venice, Italy; TMP, Royal Tyrrel Museum of Palaeontology, Drumheller, Canada.

MATERIALS AND METHODS

The object of this paper is the Venice specimen of *O. nigeriensis* (Fig. 1), which is catalogued with the number MSNVE 3714. It is apparently a nearly complete skeleton, which is exhibited at the MSNVE mounted in a bipedal posture. It was the object of the bachelor thesis of one of us (FB) under the supervision of FMDV at the University of Bologna in years 2012-2013 (Bertozzo, 2012). The specimen was donated to the MSNVE by the Italian entrepreneur and philanthropist Giancarlo Ligabue (founder of the Centro Studi e Ricerche Ligabue, Venice) in 1975. Since that date, it has been exhibited to the public in the Museum. According to the available information, the specimen underwent two distinct restoration phases. The first preparation of the bones used to assemble the mount was done by French preparators at the Muséum National d'Histoire Naturelle of Paris, France, before 1975 when the skeleton was mounted in Venice. A make-up and remount of the specimen was performed by an Italian private firm in the years 1999-2000. No reports or any kind of available documentation exist about the restoration done on the bones before 1975 and in 1999-2000. A list of the original material is also unavailable.

The history of the *Ouranosaurus* specimens and MSNVE 3714 in particular was traced back based on the papers dealing with the paleontological expeditions to Gadoufaoua (Ligabue et al., 1972; Ligabue & Rossi-Osmida, 1975; Taquet, 1970; 1976; 1998; Boccardi & Boccazzi, 1978), the information supplied by the Centro Studi e Ricerche Ligabue of Venice, and the personal communication from Philippe Taquet. Ronan Allain, MNHN, kindly made available to us a copy of the map of the in situ specimen of *O. nigeriensis* found in 1970 along the landing strip (indicated as GDF 381 in Taquet, 1976), which was drawn by Philip Taquet and is deposited at MNHN.

The specimen is mounted on a metal support. In order to photograph and describe them, all the bones were removed from the support, with the exception of the sacrum, which is fixed to it. In order to have a complete photographic documentation of the specimen, we took pictures of every single bone in its cranial (anterior), caudal (posterior), dorsal, ventral, lateral, and medial views. We used a camera Canon EOS 600D, lens Tamron 17-5 mm F2.8, focal 50 mm and sensitivity 100 ISO. The photographs are stored in the archive of the MSNVE, which is accessible to researches by contacting the responsible for Research and Scientific Divulgation of the Museum. We used a caliper 200 mm long with measurement error of 0.01 mm and a metric string 100 cm long (measurement error of 0.1 cm) to measure the bones. A table with all the measurements is reported in the Supplementary Information. In order to detect the reconstructed parts in each element, we took pictures under UV-light using a Wood Lamp (SKU 51029, emitting ultraviolet light at 4 W).

We consider as proximal caudal vertebrae those with pleurapophyses (often improperly reported as caudal ribs or transverse processes in the literature); middle caudals lack pleurapophyses but have hemapophyses; distal caudals lack pleurapophyses and hemapophyses. The cervical-dorsal transition in the vertebral column was identified following Norman (1986). Centrum height was measured in the caudal (posterior) articular facet; neural spine height was measured as the straight line from the mid-point of the spine in correspondence of the dorsal margin of the postzygapophysis to the apex of the spine. The orientation of the skeletal elements is that hypothesized for the living animal, unless otherwise specified.

Different phylogenetic hypothesis on the iguanodontian ornithopods have been published in the last decade. We choose that by Mcdonald et al. (2012) as a reference, when needed.

Bone surface texture, degree of fusion of the elements and obliteration of the sutures in skulls and vertebrae are the most common approaches to assess the ontogenetic stage of fossil tetrapod individuals (e.g., Brochu, 1996; Werning, 2012). However, histological analysis still remains the most reliable methodology to establish it and to obtain an estimation of the absolute age of the individual (e.g. Chinsamy 2005; Erickson et al. 2004; Erickson 2005). The left humerus, the right femur, the right tibia, the neural spine of the dorsal vertebra 14, and the right dorsal rib 15 were selected for the osteohistological analysis. Core samples were taken from the long bones following the method described in Stein & Sander (2009) and using an electric drill press Timbertech Kebo01 and a cylindrical diamond drill bit (16 mm in diameter, 80 mm in height and with a 2 mm-thick wall). Samples were taken from the diaphysis of the long bones. Only areas lacking evident superficial erosion and surface cracks were selected. The shaft of the rib was transversally cut proximally. This area was selected because it is considered to preserve the most complete growth record (Erickson 2005). The neural spine was cross-sectioned at three different levels: at the base, in the middle, and in the apical part. Samples were then mounted on glass slides, polished up to a thickness of ~70 microns and finally analyzed with Leica DMLP and Nikon Optiphot2-pol microscopes. The type of the microstructure, the density and type of vascular canals, the amount of remodeling, the number of Lines of Arrested Growth (LAGs) and the presence or absence of an External Fundamental System (EFS) are the proxies used in this study to evaluate the ontogenetic stage of the sampled skeletal elements. The definition of the type of arrangement of the vascular canals was based on the orientation of the main axis. LAGs were identified and counted when the arrest in bone deposition was visible at different magnifications and when the interruption was continuous along the slide. When two or more LAGs were tightly spaced in the inner cortex, these were considered as annuli and counted as a single year.

Figure 1: MSNVE 3714, *Ouranosaurus nigeriensis*. The mounted specimen as exhibited today at the Museo di Storia Naturale of Venice. ~~As for~~ scale, the right femur is 920 mm long.

RESULTS

Historical background of the Venice specimen

The historical background of the Venice specimen is quite complicated.

Between 1965 and 1972, five French paleontological expeditions searched for dinosaurs in the Gadoufaoua area of Sahara Desert in Niger (Taquet, 1976). The first one took place in January-February 1965; eight iguanodontian specimens were identified in the site named "niveau des Innocents" and located east of the Emechedoui wells. Two further iguanodontian skeletons, acronymized GDF 300 and GDF 381, were found 7 km south-east of Elrhaz in the Camp des Deux Arbres locality (geographic coordinates 16° 42'/lat., 9° 20'/long).

During the second expedition (February 25th-April 7th, 1966), GDF 300 (a nearly complete but disarticulated and scattered skeleton) and GDF 381 ("un squelette aux deux tiers complet [a skeleton two thirds complete]", p. 54) were collected. The following year, those specimens were carried to Paris for preparation and study. GDF 300 would become later the holotype of *Ouranosaurus nigeriensis* (Taquet, 1976, p. 57). According to Taquet (1976, p. 14), the other specimen (GDF 381) is not described in Taquet (1976), so it cannot be the paratype, although the latter is reported as MNHN-GDF 381 at p. 58. In fact, the skeleton GDF 381 that was found in 1965 100 m from GDF 300 and collected in 1966 is indicated as *"Iguanodontidé trapu* [ponderous Iguanodontid]" at p. 54 and would become later the holotype of *Lurdusaurus arenatus* (see Taquet and Russell 1999). This was confirmed by P. Taquet (pers. comm. to FMDV, 2012). However, Taquet and Russell (1999) contributed to increase the confusion indicating the holotype of *Lurdusaurus arenatus* (which is described as a nearly complete skeleton found in 1965; p. 86) with the acronym MNHN GDF 1700 and referring an isolated right coracoid of *L. arenatus* (probably found in 1970, see Taquet, 1976, p. 54) as GDF 381. According to Taquet and Russell (1999), the material of *Lurdusaurus arenatus* is at the MNHN.

The third expedition in 1969 found some dinosaur material at the In Gall locality (actually outside the Gadoufaoua area), but no *Ouranosaurus* is reported from there.

During the fourth expedition (January 5th-March 23rd, 1970), a skeleton of *Ouranosaurus nigeriensis* without the skull, but in better state of articulation than GDF 300 was discovered 4 km south of the "niveau des Innocents" at the margin of the landing strip built by the CEA, (p. 58); apparently, it also received the field number GDF 381 (see Taquet, 1976, pl. IX, fig. 2). Other vertebrate fossils were collected there, including postcranial elements of the giant crocodile *Sarcosuchus imperator*. Notice that the paratype of *O. nigeriensis* ("un squelette presque complet auquel manque le crane" ["a nearly complete skeleton lacking the skull]) is said to come from "4 km Sud du niveau des Innocents, Bordure Est terrain d'aviation, lat. 16°26', long. 9°8' " ["4 km south of the niveau des Innocents, eastern margin of the airfield, 16°26'/lat., 9°8'/long.] (Taquet, 1976, p. 58) and has the number GDF 381 -MNHN (Taquet, 1976, p. 58). So, the specimen discovered during the fourth French expedition is the paratype. Much confusion is caused by the fact that Taquet (1976, p. 15) does not mention this discovery presenting the results of the 1970 expedition.

During the fifth expedition (January 5th - February 25th, 1972), the *Ouranosaurus* found in 1970 (GDF 381) was excavated and brought to Paris (Taquet, 1976, p. 15 and 60). Apparently, this is the third and last ornithopod skeleton excavated and brought to France by French expeditions, together with GDF 300 and the GDF 381 found in 1965 and collected in 1966.

In 1971, Giancarlo Ligabue and Cino Boccazzi knew about the Gadoufaoua locality during a travel across the Sahara desert (Ligabue et al., 1972). Ligabue led a first Italian expedition (February 3rd-22nd, 1972; at the same time as the fifth French expedition), actually a prospection in order to establish the basis for a future expedition (Ligabue et al., 1972; Boccardi & Boccazzi, 1978). This occurred the following year (November 4th - December 11th, 1973) and was an Italian-French expedition led by Giancarlo Ligabue and Philippe Taquet. A field report and a list of the excavated material was published in Ligabue & Rossi-Osmida (1975); the list included "1 [sic] *Ouranosaurus nigeriensis*" (p. 80). According to Rossi-Osmida (2005), all fossils collected during the Italian expeditions were brought to the MNHM of Paris where they were prepared, restored and casted.

In the formal description of the new species *Ouranosaurus nigeriensis*, Taquet (1976, p. 58) indicated GDF 300 as the holotype, " GDF 381- MNHN " as the paratype, and GDF 301 and GDF 302, a large coracoid and a femur, respectively, as referred material. Despite being reported as a practically complete skeleton missing just the skull (p. 58), only the elements of the paratype that are not preserved in the holotype were described by Taquet (1976); a description or a list of the bones preserved in the paratype was never published. The holotype was brought back to Niger after the study (Taquet, 1976) and it results to be exhibited at the National Museum of Niger in Niamey (Taquet, 1976, pl. IX, fig. 1); the MNHN has only a plaster copy (Currie & Padian, 1997, p. 369; A. Mcdonald, pers. comm. to FB, 2011). No further reference to the paratype is made in the literature, which according to the acronym used by Taquet (1976) should be at the MNHN. Worth of note, no mention to the 1973 Italian-French expedition and the *Ouranosaurus* specimen said to have been collected in that occasion is made in Taquet (1976).

As anticipated above, Giancarlo Ligabue donated a nearly complete skeleton of *O. nigeriensis* (the skull and lower jaw were missing and replaced by copies) to the city of Venice after preparation at MNHN. It was exhibited to the public in 1975 in a room of the MSNVE along with other vertebrate specimens (including a complete skull of the crocodyliform *Sarcosuchus imperator*) supposed to have been collected during the 1973 expedition. Since that date, it has been exhibited to the public in the Museum. At the end of the 90s of the last century, the skeleton was restored and remounted.

The paratype GDF 381- MNHN apparently disappeared, as well as the referred specimens GDF 301 and 302. According to A. Mcdonald (pers. comm., to FB, 2011), and Currie & Padian (1997, p. 369), the MNHM has only a cast of the holotype. According to Currie & Padian (1997, p. 369),

the only original specimen of *O. nigeriensis* other than the holotype is the Venice specimen, indirectly confirming that it is the paratype.
In order to clarify once for ever this issue, we asked P. Taquet whether the specimen exhibited at the MSNVE is the paratype of *O. nigeriensis* (GDF 381 - MNHN in Taquet, 1976) discovered in 1970 and collected in 1972 (as suggested by the above reconstruction, but never expressed explicitly) or another one. He confirmed that it is the paratype and that the missing bones were casted from the holotype (P. Taquet, 2012, pers. comm. to FMDV and FB). He also told us that he mapped the paratype bones in the field and the map is at the MNHN.

The map of the Venice specimen "pro parte"
R. Allain sent us a copy of the field map that P. Taquet told us to refer to the excavation of the paratype in 1972. It is labeled "Ouranosaurus nig - Camp aviation - 1970 - (specimen musée Venice pro parte)" ["Ouranosaurus nig[eriensis] - Airfield - 1970 - (specimen Venice Museum pro parte)"].
Unfortunately, the map that we received is divided into eight sheets distributed in two pdf files, with incomplete information about how to assemble them. Each bone in the sheets is identified by a number, probably to identify the elements to recompose the skeleton once in the laboratory.
One main sheet is the scan of part of the original map made of brownish cardboard with the drawing of an articulated dorsal and sacral segment of a vertebral column adjacent to a slightly displaced proximal part of the caudal segment and some limb and girdles elements. It is evidently the map of the specimen pictured in Taquet, 1976, pl. IX, fig. 2; 1998, fig. 12) and identified as GDF 381, i.e. the paratype of *O. nigeriensis*.
A second sheet, also a scan of the original brownish cardboard, nearly totally overlaps to this one.
A third sheet is the total drawing of the caudal vertebral column segment, overlapping the main sheet; however, it is a poor-quality scan of the photocopy of the original map (the latter is no more available).
A fourth sheet is the map of the cervical segment of the vertebral column and some girdle and limb elements; it does not overlap the main sheet, but comparison with the images in Taquet (1976, pl. IX, fig. 2; 1998, fig. 12) allows to reliably connect the two sheets. We assembled these sheets (Fig. 2); we consider the resulting map as that of the main cluster of bones (that we name cluster 1) of the map of the Venice specimen "pro parte". It includes the bones numbered from 1 to 137, belonging to a semi-articulated skeleton exposing its right side. Numbers 96 (possibly a bone near the ulna) and 97 (fragment of ilium) and relative elements are not in the figure, but they are mentioned in an handwritten note on the map. Also a distal caudal vertebra was not numbered and is not drawn in the map, but it is mentioned in an handwritten note.
Two further sheets are scans of the photocopies of parts of the original map; they represent partly disarticulated elements from the pelvic region with part of the tail and some limb elements of an ornithopod skeleton (Fig. 2). A mark along the margins of the sheets allows joining them, but there is no indication on their spatial relationships with the other sheets. The sheets contain many handwritten notes (in French, of course), but the poor quality of the photocopy/scan does not allow us to understand many of them. Possibly, they give info about the spatial relationships of the sheets, but the fact that also people at the MNHN are unable to assemble the whole map (R. Allain, 2016, pers. comm. to FMDV) suggests that this is not the case. We consider this as the cluster 2 of the map of the Venice specimen "pro parte". As the photos in Taquet (1976, pl. IX, fig. 2) and Taquet (1998, fig. 12) show that other bones occurs "dorsally" respect to the main cluster, we tentatively located there the second cluster, but distance between the two clusters and the orientation of the second could be inaccurate. This cluster includes bones numbered 200, 202-209, 212, 214-231, 233-256 and 258-286. Numbers 210-211, 213 and 257 are in another sheet (see below), while the remaining are apparently missing, supposing a progressive numeration of

the specimens. Also numbers from 138 to 200 are not present in the sheets that we receive from the MNHN, suggesting that one or more sheets are missing or that the two clusters are actually not related.
The seventh sheet is also a poor-quality scan of the photocopy of part of the original map and represents only four bones (numbers 210-11, 213 and 257), including a complete ilium. Also in this case, its spatial relationships with the clusters 1 and 2 are unknown. However, the numeration indicates that this sheet is related to those of the cluster 2 and the location of the numbers in this cluster suggests that its position is possibly that in Fig. 2.
Finally, one sheet reports only the hand writing "Ouranosaurus nig - Camp aviation - 1970 - (specimen musée Venice pro parte)".
We assembled the sheets, excluded the last one, remarking the original drawing line to obtain a line with a consistent and appreciable width (Fig. 2). The poor quality of the scans of the photocopies sometimes prevented the identification of portions of the original lines. We do not know whether they were drawn or not; they simply cannot be seen or they were originally missing in the map. In those cases, we avoided interpretations and left the lines interrupted. We also typewrote the original field identification of the bones by P. Taquet reported in the map, translated into English and sometimes abbreviated; when different from our identification or dubious, we report them in dark gray colour instead of black. Of course, field identification of the skeletal elements could be wrong and the mistake recognized only once the bone is freed from the enclosing rock. Some of the handwritten notes translated into English are also reported typewritten in dark gray. Finally, the sheets of the two clusters and the single sheet with the four bones do not seem to be at the same scale (lengths of some skeletal elements are reported, anyway).
This map confirms once again that the paratype is MSNVE 3714 (although "pro parte") and shows that the generic and specific name was created at least four years before its publication.
The presence of a total of three pubes and possibly three ilia, scapulae and ulnae, as well as a duplication of segments of the caudal vertebral column indicates that at least two individuals are represented in the assembled map and cluster 1 and 2 belong to distinct skeletons.
The correspondence of the bones reported in the map and those occurring in the mounted skeleton is checked below; the implications of the word "pro parte" are discussed in the section Discussion.

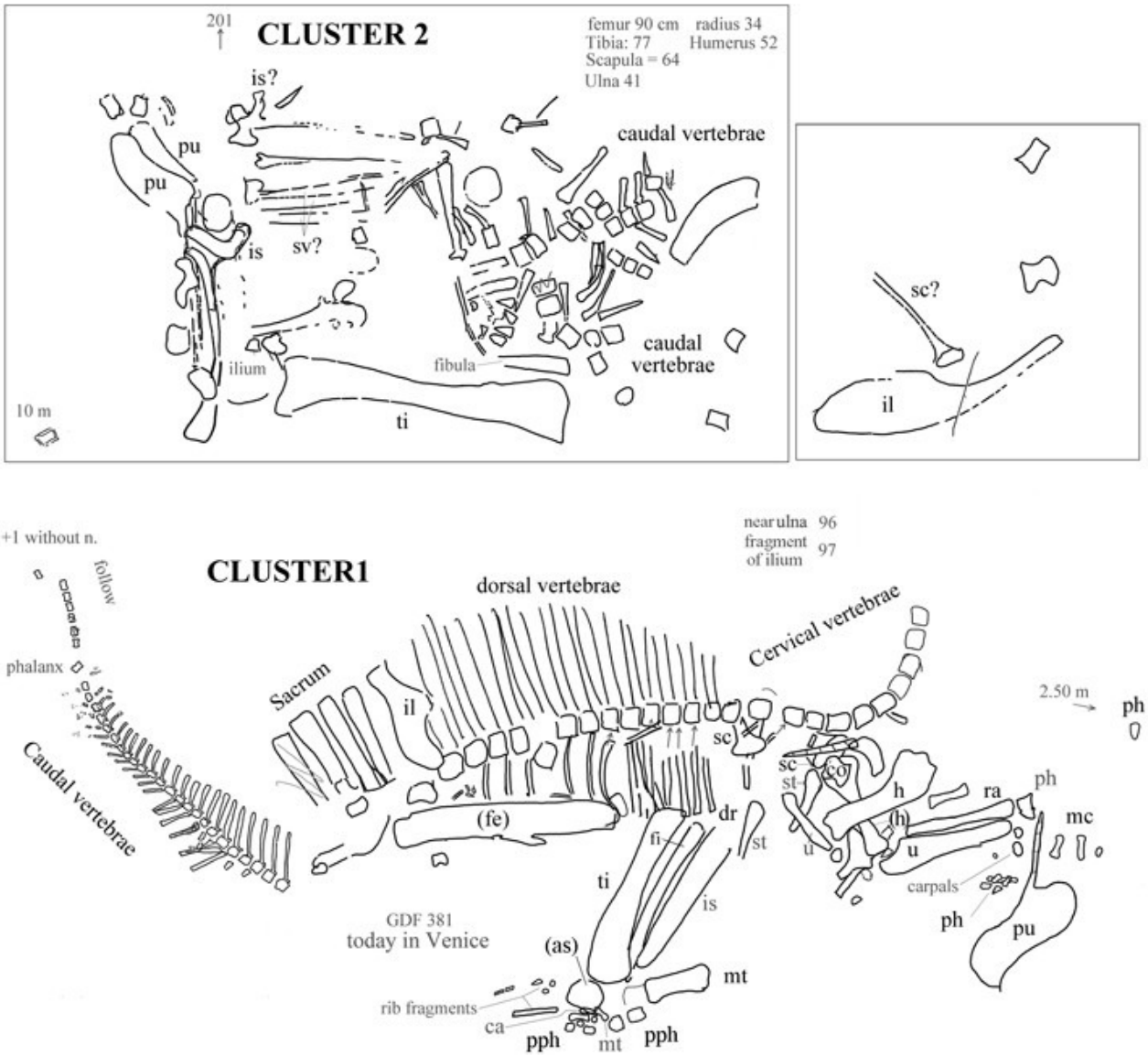


Figure 2: ***Ouranosaurus nigeriensis***, the field map of the remains partly used to mount MSNVE 3714. The map was drawn by P. Taquet and refers to the specimen found in 1970 ("Ouranosaurus nig[eriensis] - Airfield - 1970 - (specimen Venice Museum pro parte)"). The map is made of some assembled sheets (see text for the explanation); the three resulting sheet are not to the same scale, so scale bar is not reported. It was redrawn following the original lines as much as it was possible. Some original handwritten notes have been translated into English and typewritten in dark gray, as well as the lines originally added by Taquet to cancel the wrongly drawn elements. Dark gray names of the bones are the original identifications when their correctness is dubious or not testable; black abbreviations are ours and are partly our bone identification and partly unambiguous original identifications. "Near ulna" and "fragment of ulna" is an handwritten note that refers to collected elements numbered 96 and 97, which were not drawn in the map. Abbreviations: ca, calcaneum; co, coracoid; fe, femur; fi, fibula; h, humerus; il, ilium; mc, metacarpal; mt, metatarsal; ph, manual phalanx; pph, pedal phalanx; pu, pubis; ra, radius; sv, sacral vertebra; sc, scapula; st, sternal plate; ti, tibia; u, ulna . When the elements are reported as left in the original map, they are in brackets.

SYSTEMATIC PALEONTOLOGY

Dinosauria Owen, 1842
Ornithischia Seeley, 1887
Ornithopoda Marsh, 1881
Iguanodontia Dollo, 1888
Ankylopollexia Sereno, 1986
Styracosterna Sereno, 1986
Hadrosauriformes Sereno, 1997 *sensu* McDonald 2010
Hadrosauroidea Cope 1869 *sensu* Sereno, 1986

Ouranosaurus nigeriensis Taquet, 1976

Note: the name *Ouranosaurus nigeriensis* was firstly published by Taquet in Ligabue & Rossi-Osmida (1975, p. 41), without a formal description.

Holotype: GDF 300, a nearly complete skeleton, lacking the left maxilla; the right lacrimal; the right quadratojugal; the stapes; the articulars; the dorsal vertebrae 1 and ?14; the centrum of caudal vertebra 1 and caudals 25-26 and 30-31; most of the distal elements of the tail and some distal chevrons; both femora (only the distal condylar end of one of them was found); the left tibia; the left astragalus and calcaneum; the left metatarsals; and eight pedal phalanges. The skeletal elements in situ were scattered on a 15 m^2 surface. The specimen is exhibited at the Musée National du Niger, Niamey.

Paratype: GDF 381- MNHN (MSNVE 3714, "pro parte", see below), partial skeleton without skull, but preserving the vertebral column in fairly good conditions of articulation and probably missing only the atlas and the distal segment of the tail.

Referred material: GDF 301, large coracoid, and GDF 302, femur (present location unknown; GDF 302 possibly added to MSNVE 3714, see below).

Horizon and Locality: level GAD 5, upper part of the Elrhaz Formation, Tégama Series, Aptian, Aptian-Albian, or possibly Barremian, Early Cretaceous. All specimens are from the Gadoufaoua area of Niger. The holotype comes from the Camp des Deux Arbres locality, 7 km south east of Elrhaz, 16°42' lat. 9°20' long; the paratype was found 4 km south of the Niveau des Innocents locality, along the eastern border of the airfield, 16°26' lat, 09°08' long. The exact locality for GDF 301 and GDF 302 is unknown, but probably it is the same as the holotype.

Emended diagnosis: Basal hadrosauroid dinosaur with the following autapomorphies: thickened, paired domes on nasals, so that nasals extend further dorsally than frontals; dorsal 'sail' made of extremely tall neural spines of the dorsal, sacral and proximal caudal vertebrae (up to 7 times the height of the centrum in the proximal mid-dorsal vertebrae), with a sinusoidal outline (lower peak in the sacral segment); tallest neural spines of dorsal vertebrae flare apically (i.e., the cranial and caudal margins of the spine are not parallel but they diverge regularly basoapically).

Phylogenetic relationships of *Ouranosaurus nigeriensis*

There is no agreement on the phylogenetic relationships of *Ouranosaurus nigeriensis* (e.g., Sereno, 1986; Norman, 2004, 2015; Mcdonald et al., 2010a, b, 2012). On non-cladistic bases,

Taquet (1976) considered *Ouranosaurus* as a derived "iguanodontid" that is closely related to *Probactrosaurus gobiensis*, although he recognized some derived features shared with the hadrosaurids. In his phylogeny of Ornithischia, Sereno (1986) found *Ouranosaurus* to be a member of the Hadrosauroidea and sister taxon of the Hadrosauridae. According to Norman (2004), *Ouranosaurus* is more derived than *Iguanodon bernissartensis* and *Mantellisaurus atherfieldensis,* and basal to non-hadrosaurid iguanodontians (*P. gobiensis*, *Eolambia caroljonesa*, *Protohadros byrdi* and *Altirhinus kurzanovi*). In Mcdonald et al.'s (2012) analysis, *Ouranosaurus* falls within the Hadrosauroidea between a politomy of *Mantellisaurus atherfieldensis* and *Hypselospinus fittoni* (less derived) and *Altirhinus kurzanovi* (more derived) (Fig. 3A). Thus, it is more derived than *Iguanodon bernissartensis*. In the latest published phylogeny by Norman (2015), it occurs in a more basal position (Fig. 3B) as the sister taxon of the clade 'Iguanodontoids' + Hadrosauriformes. The different phylogenetic affinities of the taxon found by the different authors are probably due to the presence of a mix of primitive (e.g., presence of palpebral bone, large and coarsely denticulated dentary teeth with two primary ridges, conical ungual phalanx on manual digit I, and double fibular process of the tibia) and derived (e.g., anterior end of the premaxilla expanded transversely; oral margin of the premaxilla reflected dorsally; long rostral diastema in the dentary; and greatly dorsoventrally expanded distal portion of the prepubic plate) characters.

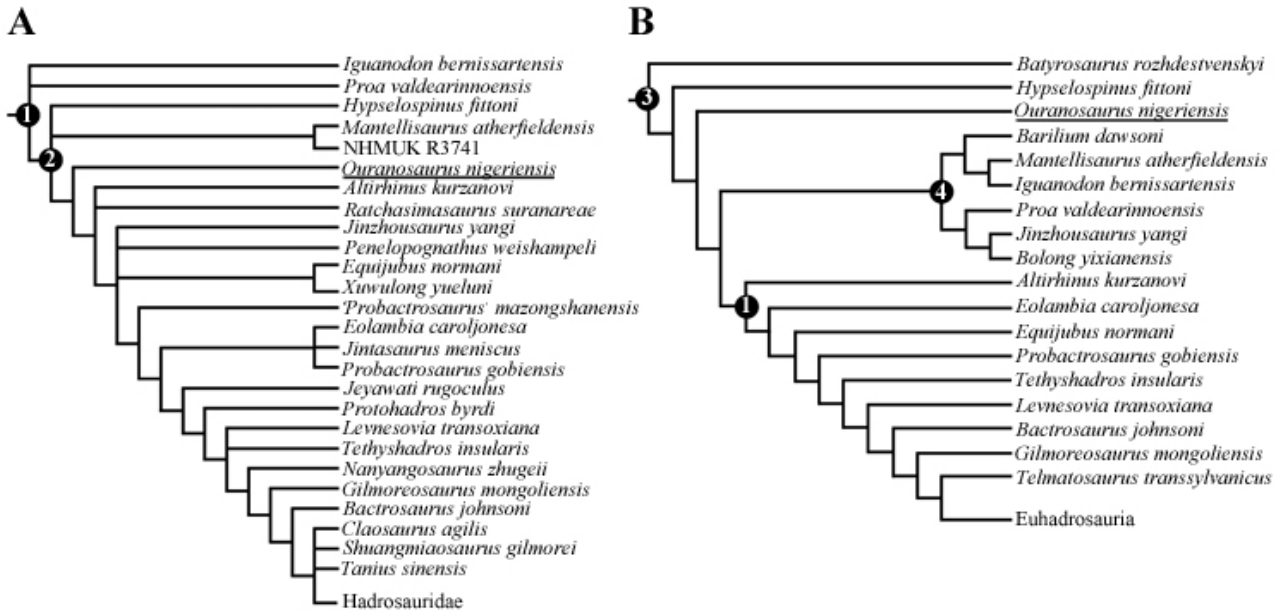


Figure 3: Relationships of *Ouranosaurus nigeriensis*. Cladograms from Mcdonald et al. (2012; Adam consensus tree) (A) and Norman (2015) (B), redrawn. The basal part of the tree is not reported in both cases. Legend: 1 = Hadrosauriformes; 2 = Hadrosauroidea; 3 = Styracosterna; 4 = “Iguanodontoids”.

Description of MSNVE 3714 and comparison with the holotype

MSNVE 3714 is a partial skeleton lacking the whole skull and mandible; the ossified elements of the hyoid apparatus; the atlas; all the cervical ribs; right dorsal ribs 1, 2, 4 - 10, 13 and 15; left dorsal ribs 6, 11, 12 and 14; caudal vertebrae 27 to 31 and those posterior to caudal vertebra 38 (vertebrae 27-31 and 39-43 are plaster copies); the right coracoid; the right carpus; the left metacarpals; the digit I (thumb spike), phalanges II-1 and 2, III-2, IV-1 and V-2 to 4 (ungual) of

the left manus; phalanx II-3 (ungual), III-2 and 3 (ungual), IV-2, and V-3 and 4 (ungual) of right manus; the left femur; and the whole right *pes* (Fig. 4). All these elements, excluded those of the hyoid apparatus, the atlas and the cervical ribs, have been reconstructed. Most of the other bones have also been partly reconstructed and restored (Fig. 4). Elements of the right side are more weathered then those of the left side, because the skeleton lied mostly on the left side (as it is shown by the map).

In this section, the skeletal elements MSNVE 3714 are described and compared with those reported in the map as well as with those preserved in the holotype.

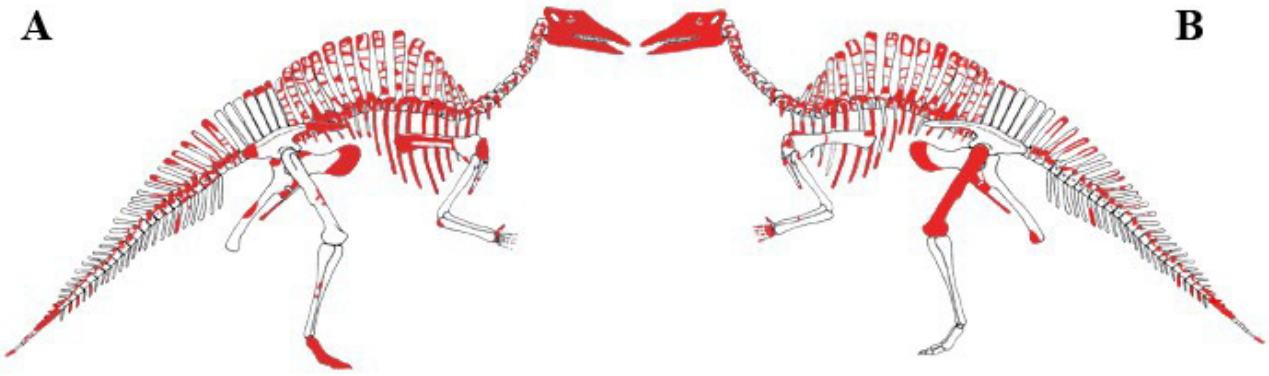


Figure 4: MSNVE 3714, *Ouranosaurus nigeriensis*, original and reconstructed parts in the right (A) and left (B) views. The reconstructed parts are in red.

AXIAL SKELETON

The axial skeleton of MSNVE 3714 is composed of 77 vertebrae, but 10 caudals are totally reconstructed with plaster, so only 66 are actually preserved (Fig. 5A-D). They are all more or less restored; in particular the base of the neural arch, zygapophyses and transverse processes of dorsals and caudals are mostly reconstructed. Curiously, the holotype also preserves remains of 66 vertebrae, but eight elements occurring within those preserved are missing according to Taquet (1976), so the original vertebral column would be at least 74 (but see below). As the axial skeleton of the paratype is in a better state of anatomical articulation respect to the holotype (see Fig. 2), it is a better reference for the vertebral count of *Ouranosaurus nigeriensis*.

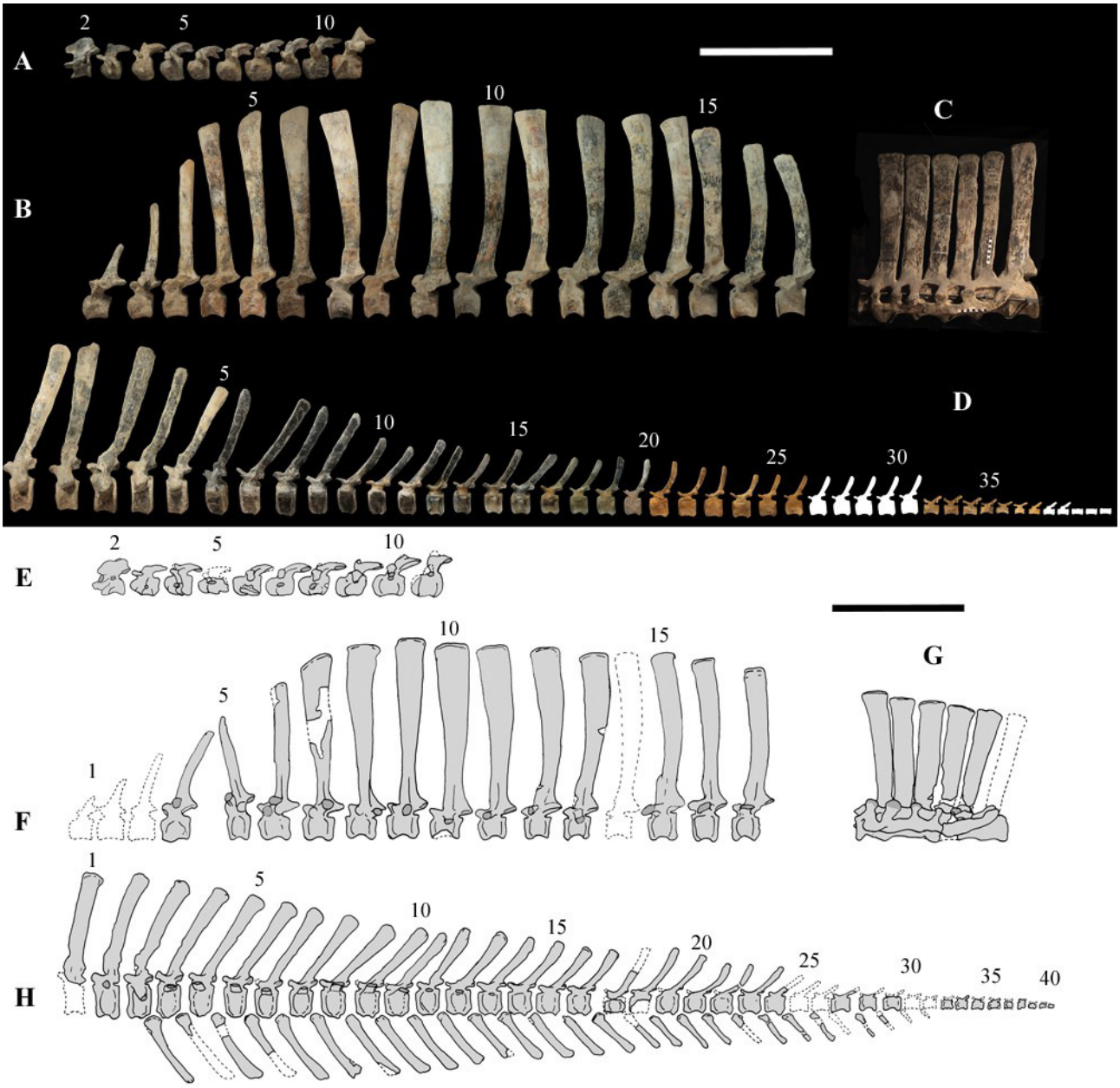


Figure 5: MSNVE 3714 and holotype, vertebrae. MSNVE 3714, the cervical series (A); the dorsal series (B); the sacrum (C); and the caudal series (D). Holotype, the cervical series (E); the dorsal series (F); the sacrum (G); and the caudal series (H). Numbers are progressive within each series. White vertebrae are those of the mount that are totally reconstructed. E-G are redrawn from Taquet (1976). Scale bar equals 50 cm.

Cervical vertebrae. The axis and the following ten presacral vertebrae are preserved, while the atlas is missing (Fig. 5A). The presacral vertebra 11 has the parapophysis that appears to be cut by the neurocentral suture (Fig. 6A), so it is a cervical not the first dorsal according to the definition of first dorsal vertebra by Norman (1986). The presacral vertebra 12 in the mounted skeleton has a relatively tall neural spine and a parapophysis that seems to be at the very base of the neural arch (Fig. 6B), so it is the first dorsal vertebra. The holotype preserves 11 cervical vertebrae (presacrals 1 to 11; Fig. 5E), but the neck was totally disarticulated in situ and presacral

vertebrae 12 to 14 are not preserved according to Taquet (1976). The map of the paratype shows nine articulated cervicals (probably cervicals 2-10), a further centrum that is slightly separated from the adjacent centra (but without the possibility of the presence of another vertebra missing in between) and one that is articulated with a string of 13 dorsal vertebrae with very tall neural spines. The first centrum is probably the cervical 11, while the second is the first dorsal. *Iguanodon bernissartensis*, *Equijubus normani* and *Jinzhousaurus yiangi* have 11 cervicals, *Mantellisaurus atherfieldensis* 10 or 11 (Norman, 2004; Wang et al., 2010; Mcdonald et al., 2014). So, a cervical count of 11 is supported for *Ouranosaurus*.

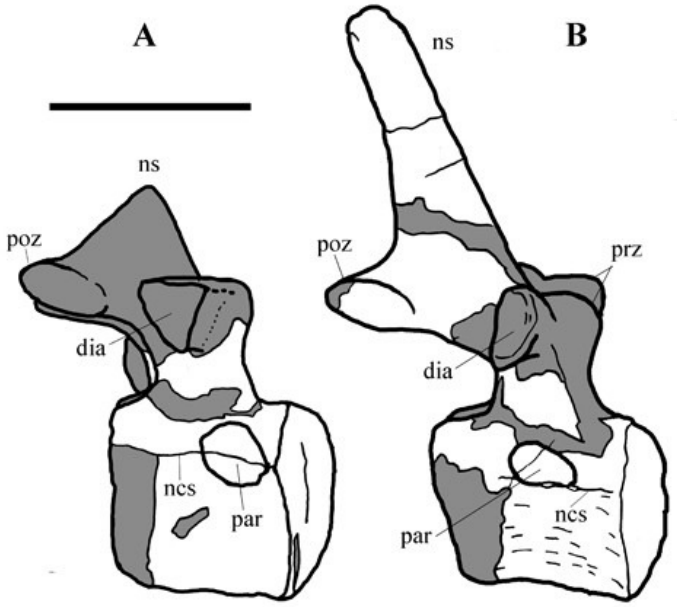


Figure 6: MSNVE 3714, cervical-dorsal transition. The last (11) cervical (A); the first dorsal (B). Both are in left lateral view. Reconstructed parts are in dark gray color. Abbreviations: dia, diapophysis; ncs, neurocentral suture; ns, neural spine; par, parapophysis; poz, postzygapophysis; prz, prezygapophysis. Scale bar equals 10 cm.

In the axis (Fig. 7A1-4), the odontoid process; the prezygapophyses; the cranial portion of the neural arch above the pedicels and parts of the latter; and parts of the centrum were missing and have been reconstructed (prezygapophyses were not reconstructed and lack). The diapophyses are small and knob-like like those of the holotype, but they are mostly reconstructed. The neural spine is low and sub-triangular in lateral outline, with a rounded dorsal margin. A broad circular depression occurs in the middle of both right and left sides of the spine. The neural spine in the axis of the holotype has a different M-like lateral outline (i.e., the dorsal margin is concave in the middle) and seems to lack the lateral depressions (Taquet, 1976, fig. 37B).
Cervicals 3-11 (Figs. 5A, 7B and 7C) do not appear to differ significantly from those of the holotype and those of advanced iguanodontians in general (e.g., Norman, 1980; 1986). However, most of their processes are reconstructed. For example, the long diapophyses and parapophyses are totally reconstructed in cervicals 3 and 4; the long postzygapophyses are both reconstructed in cervical 3, while only the right one is original in cervical 4. In the cervical 5, the long processes bearing the prezygapophyses and diapophyses are made of resin. Small fragments of the neural spine are preserved in the cervicals 8-10. So, the centra are practically all what we have of them for comparison. They are deeply opisthocoelous and bear a median, longitudinal and blunt keel ventrally.

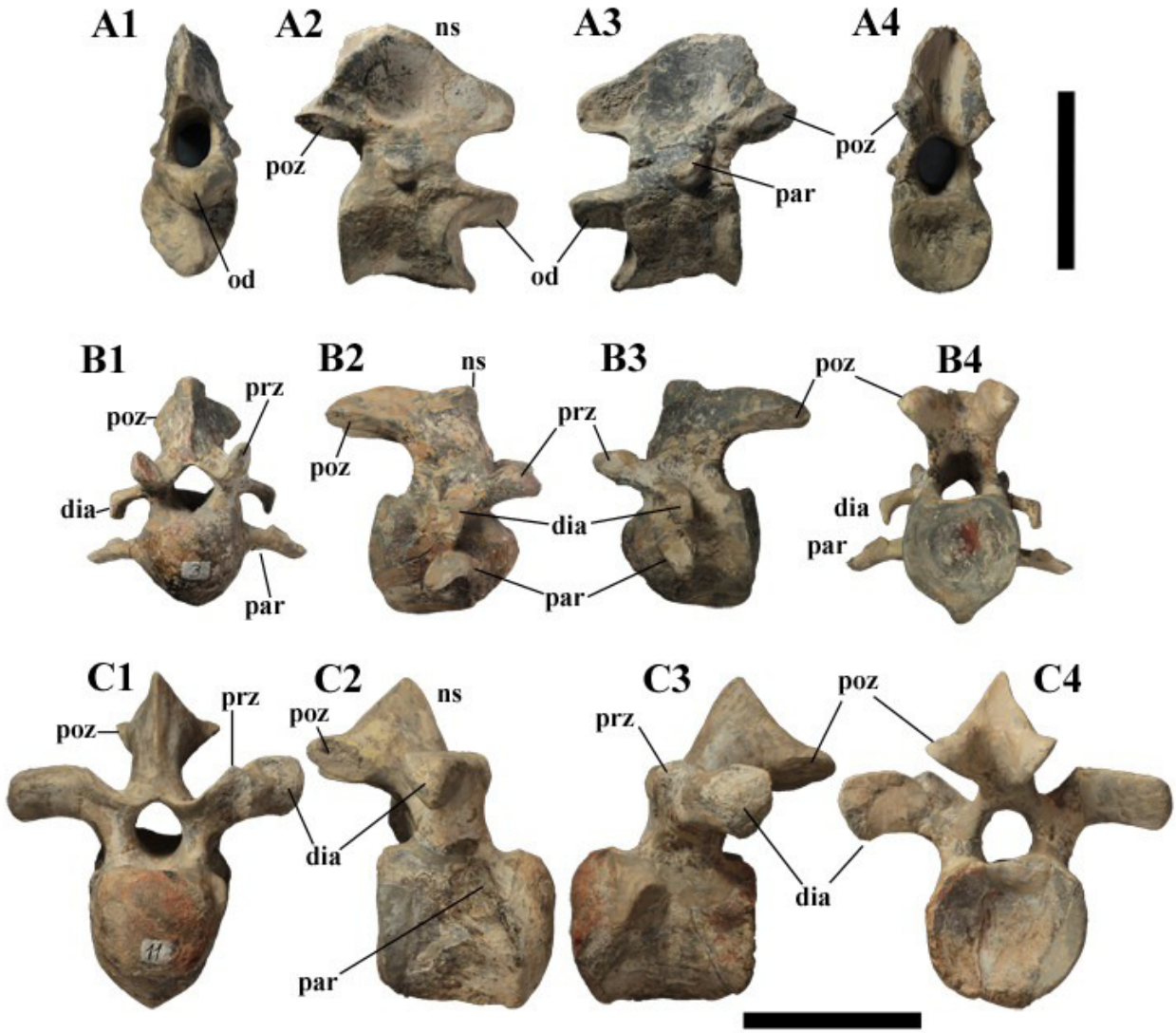


Figure 7: MSNVE 3714, cervical vertebrae. Axis in cranial (A1), right lateral (A2), left lateral (A3), and caudal view (A4); cervical vertebra 3 in cranial (B1), right lateral (B2), left lateral (B3), and caudal (B4) views; cervical vertebra 11 in cranial (C1), right lateral (C2), left lateral (C3), and caudal (C4) views. Abbreviations: dia, diapophysis; od, odontoid process; ns, neural spine; par, parapophysis; poz, postzygapophysis; prz, prezygapophysis. Scale bar equals 10 cm.

Dorsal vertebrae. MSNVE 3714 has 17 dorsals (Fig. 5B). As said above, a string of 14 dorsals in relative anatomical connection is identifiable in the map of the in situ paratype (Fig. 2). A further centrum seems to occur caudal to the last vertebra of the string and displaced ventrally. Thus, MSNVE 3714 has at least two dorsal vertebrae more than the mapped paratype. There are two explanations for this: 1) the two additional vertebrae could have been preserved there, but they were not recognized before preparation or at least one of them could have been covered by a broad element present in that area (plausibly an ilium); 2) two vertebrae from another specimen were added to the paratype material because the holotype was supposed to have 17 dorsals (Fig. 5F). The first explanation seems to be the less probable because that is also the position of the sacrum, which is only partly exposed, as it is composed of six vertebrae but only three are drawn in the map (one is cancelled).

In the dorsals of MSNVE 3714, the peduncles of the neural arches, parapophyses, transverse processes and relative diapophyses are all reconstructed (presumably, taking as reference for proportions and morphology those of the holotype). Also the neural spines, which are the most important feature of those skeletal elements, are heavily restored (Fig. 8).
The centra of the dorsals 1 and 2 are opisthocoelous; from the dorsal vertebra 3 on, the centrum becomes slightly amphicoelous to amphiplatyan. Centra range 87 (vertebra 12) to 112 mm (vertebra 17) in length and are slightly longer than high (elongation is more marked in the dorsal 17; Fig. 9C3). The centrum of dorsal 1 has a ventral longitudinal keel and sub-circular articular surfaces like those of the cervicals (Fig. 9A); the centrum is smaller than that of the last cervical (Fig. 6). The relatively small parapophyses are located just above the neurocentral suture (Fig. 6B). In ventral view, all other dorsal centra are spool-shaped with a keeled ventral margin (Fig. 9A3 and B3); only centrum 17 seems to lack the keel (Fig. 9C3). As the sacral vertebrae have a faint ventral keel or lack it, dorsal 17 could actually be a dorsosacral. The articular facets of the centra 2 to 16 are higher than wide, while it is the reverse in centrum 17.
The morphology of the tall neural spines shows a certain variability (Fig. 8). The spine of dorsal 1 is straight, inclined caudally (60°) and it slightly tapers apically in its basal part, while the apical half has parallel caudocranial margins and does not flare apically (Figs. 6B and 9A1-2); it is only 1.41 times the height of its centrum. The spine of dorsal 2 is incomplete apically. The preserved part is 2.7 times the height of the centrum; as reconstructed, it is about four times the height of the centrum. It is narrow craniocaudally, slightly sloping caudally (about 80°) and slightly recurved; as the cranial and caudal margins are parallel, probably it was not expanded apically (so, the reconstruction is faithful). The spine of dorsal 3 is taller and craniocaudally longer than that of dorsal 2, but it is also incomplete apically. It is straight with nearly parallel craniocaudal margins and it slightly slopes caudally (about 83°). The apex and part of the apical tract of the caudal margin of the spine are reconstructed, but probably the spine was not sensibly expanded craniocaudally. Dorsal 4 has a neural spine that is taller and craniocaudally longer than that of dorsal 3; it is incomplete apically too. It is straight, with its minimum craniocaudal length just below the mid-shaft; cranial and caudal margins diverge above the point of minimum craniocaudal length, so the apex was probably slightly expanded. Unlike the preceding vertebra, the spine slopes cranially (about 85°). Dorsal 5 has a spine that is nearly complete apically and is apparently taller than that of the preceding vertebra. It is straight and only slightly sloping cranially. Its minimum craniocaudal length occurs in the lower third, but it is unclear whether this is a real feature or an artifact of preparation. The cranial and caudal margins diverge above that point, so the spine flares sensibly toward its apex. The latter is not squared. The spine of dorsal 6 is straight vertical. It is incomplete apically, but it is anyway at least as tall as the preceding one. The cranial and caudal margins diverge above the lower third, so the spine flares sensibly toward the apex. Unlike that of the preceding vertebra, the spine of dorsal 7 is recurved cranially. Like spine 6, it flares apically. As the apical portion is partly reconstructed, its squared outline is just hypothetical. The cranial curvature cannot be a real feature, because it would prevent the zygapophyseal and central articulation with the preceding vertebra, unless the spines of the two vertebrae were overlapping laterally. The spine of dorsal 8 is unlike those of the preceding and following vertebrae. It appears to be craniocaudally narrower and is slightly sloping caudally. It also flares above its basal third. The apex is reconstructed, so its squared outline is just hypothetical and its total height is unknown. The spine of dorsal 9 is slightly curved basally, but the rest is straight vertical (Fig. 9B1-2). Flaring starts in the basal part of the spine. If reconstruction is faithful (a part of the apex is preserved but a basal portion is reconstructed), the spine is the tallest (it is seven times the height of its centrum). The apex is partly reconstructed, so its squared outline is just hypothetical. The curvature of the basal part of the spine is more marked in vertebra 10 than in the preceding vertebra. This spine also flares starting from the basal

portion; its apical third is mostly reconstructed, so nothing can be said about its real outline. The whole spine of vertebra 11 seems to be slightly recurved, but its basal part is reconstructed, so this feature could be an artifact. The preserved portion of the apical part shows that this spine was lower than spine 9. Spine 12 seems to be arched basally and straight from mid-shaft on. Its apical portion is mostly reconstructed, so its real height and the shape of its apex are unknown. The following neural spines 13-17 are all arched (less in the spine 15, which is poorly preserved) and flares apically like the preceding ones, although proportionally less than in the mid-dorsals (Fig. 9C1-2). Their craniocaudal length decreases slightly moving caudally. Their height decreases markedly; spine 14 is just slightly lower than spine 11, but the decrease is marked in the following vertebrae 15-17.

The basal part of the spine in vertebrae 5, 7, 8, and 16-17 shows a cranial bump that is made by the cranially expanded prespinal lamina (Figs. 8 and 9C1) and is observed also in the distal dorsals of the holotype (Fig. 5F). All spines are narrow transversely and they do not thicken apically.

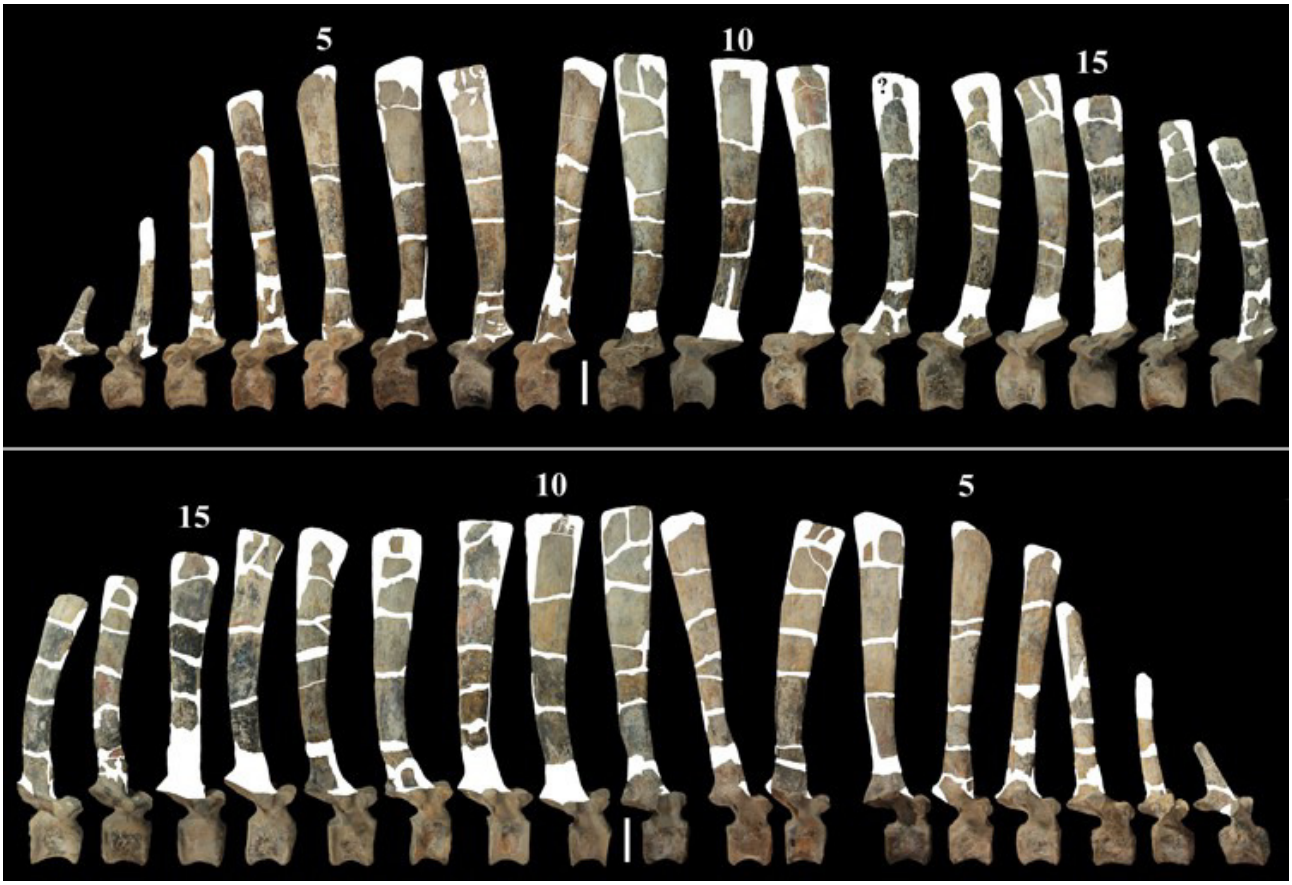


Figure 8: MSNVE 3714, dorsal vertebrae in lateral view. Above, the left side; below, the right side. The parts of the neural spine that have been reconstructed or just covered by resin are highlighted in white. Reconstructed parts of the centrum, transverse processes, zygapophyses and pedicels of the neural arch are not highlighted. Numbers are progressive. Scale bar equals 10 cm.

In the text, Taquet (1976, p. 109) says that 13 dorsals are preserved in the holotype and that the cervical series is separated from the first preserved dorsal by a gap that could be filled by other dorsals or just be caused by displacement. He opts for the first hypothesis, saying that the first four dorsals are probably missing. However, he figures only three dorsal vertebrae as missing (the

presacral vertebrae 12 to 14) in figure 38 (here Fig. 5F). Furthermore, Taquet (1976, p. 109) says that the dorsals following the gap are not displaced (i.e., they are in anatomical connection), but figure 9 of that paper shows this is true only for a segment of just nine mid-dorsal vertebrae. So, it is unclear how he established that four dorsals are missing and the total count of the dorsals is 17 (see Taquet, 1976; figs 38 and 40). The much better articulated vertebral column of the paratype GDF 381 (MSNVE 3714 pro parte) shows that Taquet (1976) is wrong in his reconstruction of the holotype dorsal vertebral string. Only one of the supposedly missing proximal dorsals of the holotype (see Fig. 5F) is present in MSNVE 3714; it corresponds to the first dorsal. The second dorsal of MSNVE 3714 corresponds to the vertebra 4 of the holotype (see Fig. 5F). Dorsal vertebra 5 of the holotype has a cranially sloping neural spine that would cause the crossing with the neural spine of the preceding vertebra when the two vertebrae are in anatomical articulation; furthermore, the spine tapers apically. There is no such a vertebra in MSNVE 3714: dorsal 3 is morphologically like vertebra 6 of the holotype. Dorsal 4 of MSNVE 3714 corresponds to dorsal 7 of the holotype in the relative height and slight cranial slope of the neural spine, but the latter has a paddle-like neural spine. In order to have the same number (17) of dorsal vertebrae as the holotype, MSNVE 3714 must consequently have more mid-posterior elements, as it can be appreciated by comparison of Figures 5B and F. In both cases, the first mid-dorsals tend to have straight vertical neural spines that are craniocaudally expanded apically, while the last mid-dorsals and distal dorsals have arched spines whose craniocaudally expansion decreases moving caudally. However, the number of those elements is different in the two specimens. It is evident that the spines of dorsals 7 and 8 in MSNVE 3714 are different from those of the contiguous vertebrae (Fig. 8); this suggests that those two vertebrae were added to maintain the count of 17 vertebrae reported for the holotype, which is also suggested by the vertebral count in the field map of the paratype. Probably the number of 17 dorsals was originally established because iguanodontians like *Mantellisaurus atherfieldensis* (at that time referred to *Iguanodon*) and *Iguanodon bernissartensis* have 17 or more dorsals (see Taquet, 1976, p. 111). However, the comparison between the holotype, the field map of the paratype and MSNVE 3714 suggests that *Ouranosaurus nigeriensis* had a shorter torso (possibly with 14 dorsals and one dorsosacral) and that the tallest neural spine is that of dorsal vertebra 7.

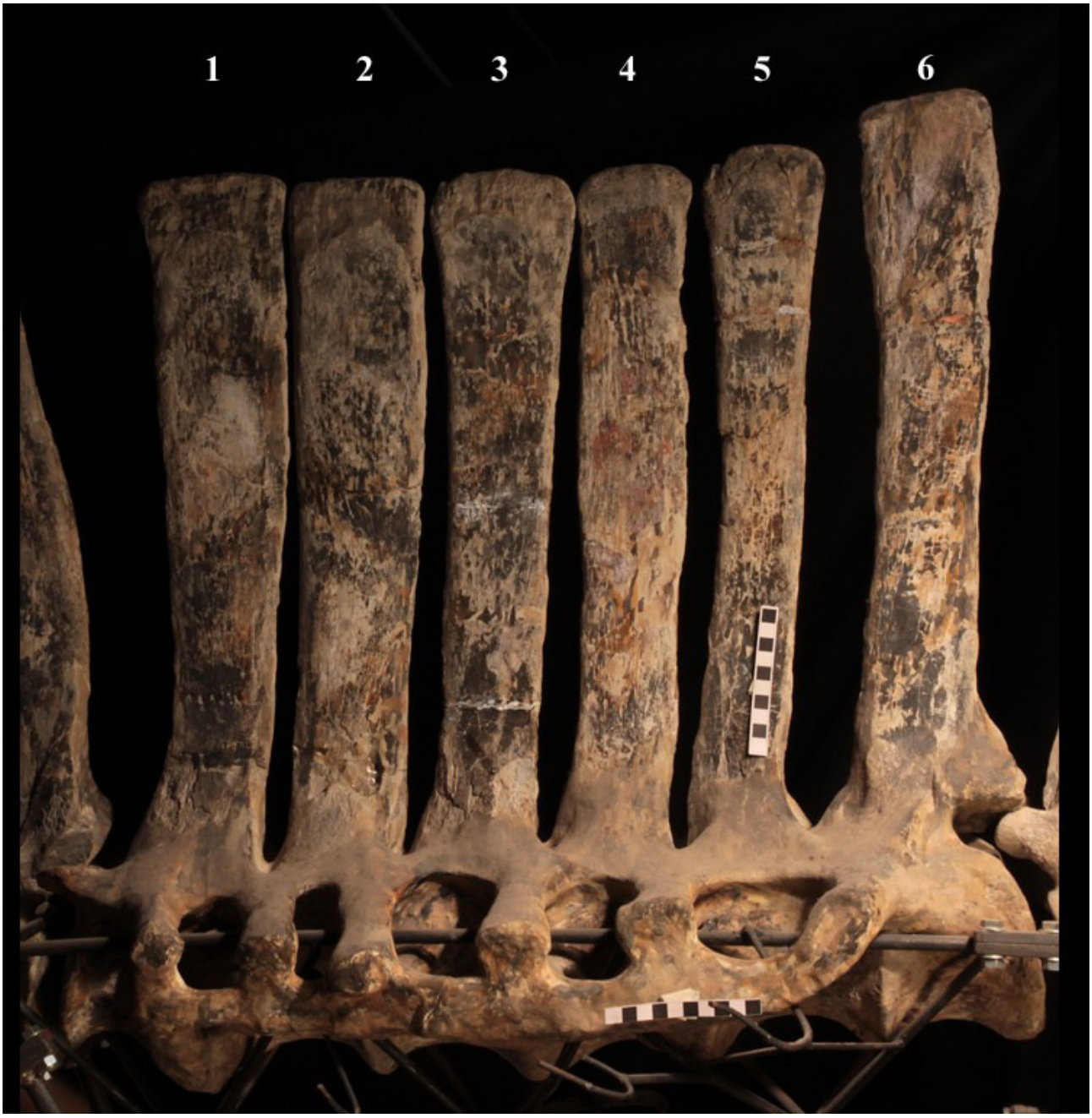
Some inconsistencies regarding the dorsal vertebrae are found in Taquet (1976). The dorsals 10-12 are reported to have the highest neural spines (p. 112), but the tallest is actually the spine of the dorsal 9 (like MSNVE 3714; see Figs. 5F and 8) and height decreases gradually in the following vertebrae, according to the figures 38 and 40 and measurements reported at pages 178-179. Vertebra 9 is the sixth preserved vertebra in the holotype and could be dorsal 7, if only the first dorsal is missing of the preceding dorsals. The highest neural spine is said to be 3.9 times the height of its centrum (p. 112), but it is actually nearly seven times according to figure 38 (7.11 according to measurements at p. 178). The centrum of the dorsal with the highest spine is reported to be 160 mm high, but it is less than 90 mm high in dorsal 8 according to the scale bar in figure 41 and that of dorsal 9 is 90 mm according to measurements at p. 178.

568 **Figure 9: MSNVE 3714, dorsal vertebrae.** Dorsal vertebra 1 in right lateral (A1), caudal (A2),
569 and ventral view (A3); dorsal vertebra 9 in left lateral (B1), cranial (B2), and ventral view (B3)
570 views; dorsal vertebra 17 in left lateral (C1), caudal (C2) and ventral (C3) views. Abbreviations:
571 bpl, 'bump' of the prespinal lamina; kl, keel; par, parapophysis. Scale bars equal 10 cm.

572 **Dorsal ribs**. Only four out of 17 right dorsal ribs are not totally reconstructed and 12 out of 17 on
573 the left side. Their state of preservation is anyway poor and large portions of the shafts are
574 reconstructed in most of them. Practically, they are mostly shaft segments glued together. The
575 *tuberculum* is just a small knob placed dorsolaterally to the *capitulum* forming with it an angle of
576 about 90°. The cross-section of the proximal half of the rib is T-shaped.
577 The map of the in situ paratype shows remains of at least 13-14 dorsal ribs.

578 **Sacral vertebrae.** Like the sacrum of the holotype, that of MSNVE 3714 (Figs. 5C, and 10) is
579 composed of six fused vertebrae. The transverse processes of the vertebrae and the sacral ribs are
580 completely reconstructed. A shallow longitudinal keel occurs in the ventral surface of the sacral
581 centra 1-2, becomes very faint in centra 3-4 and lacks in centra 5-6; centrum 6 has a nearly flat

582 ventral side. The neural spines are straight vertical and only slightly craniocaudally longer at their
583 apex than at their basal part. The spines of sacral vertebrae 1-3 are of similar height; they increase
584 in height from sacral 4 up to 6, which bears the tallest spine. Therefore, the last two sacral spines
585 form the beginning of the caudal hump of the 'sail'. Spines are separated regularly, excluded the
586 last one whose gap from the preceding spine is twice the distance between spine 4 and spine 5.
587 In the map of the in situ paratype (Fig. 2), only three neural spines can be seen in the region of
588 the sacrum; the drawing of a distal fourth one was cancelled as it were erroneously drawn.
589 Possibly, the other three sacrals were covered by rock.
590 Apparently, the trend in neural spine height is the reverse in the holotype: height decreases from
591 sacral 1 to sacral 5 (the spine of sacral 6 is not preserved). Thus, there is an abrupt depression
592 with marginal steps in the 'sail' of the holotype in correspondence of the sacrum (Fig. 5F-H). This
593 condition is probably unnatural and that one in MSNVE 3714, showing a smoother passage from
594 the dorsal to the sacral and from the sacral to the caudal spines (Figs 1 and 5B-D), is perhaps
595 more reliable.



596 **Figure 10: MSNVE 3714, the sacrum**. Left lateral view. Scale bars equal 10 cm.

597 **Caudal vertebrae.** The tail is composed of 43 caudal vertebrae, but five vertebrae (caudals 27 to
598 31) and the terminal string of five vertebrae (caudals 39-43) are made of plaster (Fig. 5D). Thus,
599 the preserved vertebrae are 33. The total caudal count was surely higher (see the caudal count of
600 several dinosaur taxa in Hone, 2012), possibly as high as in the tail of *Iguanodon bernissartensis*,
601 which is composed of 46 caudal vertebrae (Norman, 1980; but it is incomplete) or even much
602 higher (the count is over 75 in TMP 98.58.01, an indeterminate hadrosaurid; FMDV and MF,
603 pers. obs.).
604 There are 20 proximal and 12 (17 including the five that are totally reconstructed) middle caudal
605 vertebrae. The last preserved caudal (caudal 38) seems to be a distal element (see below).

As for the dorsals, 33 caudals are preserved also in the holotype, but two vertebrae between the caudals 24 and 27 are missing as well as two between the caudals 29 and 32 (Taquet, 1976, p. 118; Fig. 5H). However, this reconstruction is hypothetical because the tail was partly disarticulated (Taquet 1976, fig. 9). The holotype has 14-15 proximal caudals (15 according to the text, 14 according to fig. 44) and more than 12 (16 considering the hypothetical ones) mid-caudals. The last nine caudals appear to be distal ones (Taquet 1976, fig. 44); in facts, the facets for the chevron occur up to the posterior of caudal 31 according to the text (p.119), but actually caudal 31 is not preserved in fig. 44!

According to the field map, the first 24 caudals of the paratype are articulated and with the relative chevrons; after a gap containing just an element identified as a phalanx in the handwritten note (but apparently it is a further centrum because of its size and position) and in line with the first segment, another segment of six vertebrae occurs. A further distal centrum is slightly displaced and one labeled as "without number" is not drawn. So, the vertebral count fits with that of MSNVE 3714. The five vertebrae that are totally reconstructed in MSNVE 3714 correspond with those missing in the gap. Therefore, the count obtained from the paratype/MSNVE 3714 seems to be more reliable than that from the holotype.

Iguanodon bernissartensis has 14 proximal, about 22-24 middle and at least 8-10 distal caudal vertebrae (Norman, 1980). *Mantellisaurus atherfieldensis* (IRSNB 1551; Norman, 1986) has 15 proximal and at least 17 middle caudals (the tail is incomplete distally). So, *Ouranosaurus* has four or five more proximal caudals than *Iguanodon bernissartensis* and *Mantellisaurus atherfieldensis* and possibly a more caudally prolonged *M. caudifemoralis* (Persons & Currie 2011).

MSNVE 3714 seems to have a comparatively low mid-caudal count. However, the last and only distal caudal element is probably the one labeled "+1 without n(umber)" in the map, which is not drawn, it was not articulated to the others vertebrae and probably was collected far away from the others. Thus, the actual mid-caudal count of the paratype/MSNVE 3714 "pro parte" could be higher. The mid-caudal counts of the Venice specimen, *Iguanodon bernissartensis* and *Mantellisaurus atherfieldensis* suggest that also the count of the mid-caudals in the holotype is wrong and probably higher than that reported in Taquet (1976).

In MSNVE 3714, centra are slightly amphicoelous in the proximal and first middle caudals to become amphiplatyan caudally. The caudal surface of proximal and middle caudals is more squared than the rounded cranial one because of the presence of the facets for the hemapophysis (Figs. 11A1, B1 and C2). The latter appear in the third caudal, so the first chevron occurs between the caudal 3 and 4. Centra are constricted in the middle and hourglass-like; they are shorter than tall up to vertebra 17 and shorter than broad up to vertebra 19 (Tab. 1). The centrum of the caudals 1 and 2 has a longitudinal ventral keel, which is faintly developed in the caudal vertebra 3; the following centra seem also to be convex ventrally, but they are deformed, poorly preserved or reconstructed. From vertebra 11 up to vertebra 33, the ventral side of the centrum has a broad, median and longitudinal sulcus. This change in convexity seems to occur when the two articular facets for the haemapophysis are placed only caudally in the vertebra; before vertebra 11 the chevrons articulate on facets placed both on the cranial and the caudal ventral extremities of the centrum. This is related also to the relative increase in elongation of the centrum. As anticipated above, the last preserved vertebra (38) seems to lack the articular facets for the hemapophysis. This suggests that it is a distal caudal. A handwritten note in the field map of the paratype informs that the most distal vertebra of the sample is not figured in the map (Fig. 2); probably it was scattered respect to the others and possibly it was the only collected distal element, which was later attached to the last preserved mid-dorsal. Another possibility is that vertebra 38 is just one of the last mid-caudals and the articular facets for the hemapophysis were weathered away.

The lateral surface of the centrum near its articular facets is rough, with longitudinal grooves in some proximal and in all mid-caudal vertebrae (caudals 11-25; Fig. 12A), suggesting the presence of a cap of cartilage. A neurocentral suture is observed in proximal and middle caudal vertebrae (Fig. 12B-D) up to the caudal 25.
The neural arches of vertebrae 32-38 are totally reconstructed.
The pleurapophysis of the proximal caudals is flattened dorsoventrally and scarcely projecting laterally (Fig. 13). It occurs at the base of the neural arch on a ventral expansion of the pedicel overlapping the centrum laterally. It decreases in size along the series becoming knob-like; it disappears totally in the caudal vertebra 21 (Fig. 13C), but in caudals 19 and 20 it is just a small bump (Fig. 13B). It is rarely completely preserved, being often made partly or totally of resin.
The prezygapophyses are reconstructed in all caudals except the right ones in vertebrae 17 and 21. The articular surfaces are oval and face dorsomedially; those of the postzygapophyses are also oval and face lateroventrally.
Neural spines decrease gradually in height moving caudally (Fig. 5D). However, apical portions are reconstructed in spines 1, 3, 5 and 7, as well as segments of the shaft in many others. Spines are mostly spatula-like in lateral view, with a slight craniocaudal apical expansion (Figs. 5D and 11). They are inclined caudally to a different degree. For example, spine of caudal vertebra 2 is only slightly sloping (77.2°), while those of vertebrae 7, 9 and 16 slope 52.7°, 58.4° and 48.6°, respectively (Fig. 5D). Proximal spine are generally straight (Fig. 11A), but spines 6, 10 (Fig. 11B2-3) -12, 14-15 and those posterior to spine 17 (Fig.11C1-2) are arched with concavity facing cranially (Fig. 5D). Non-harmonic variability in sloping may be a restoration bias, because the proximal portion of some neural spine was broken into several pieces that have been glued together and missing portions have been reconstructed. Also the basal arching of spines 3 and 4 (which is not observed in preceding and following spines; Fig. 5D) could be a consequence of restoration.
Neural spine inclination and morphology in the caudals of the holotype are more regular than in MSNVE 3714 (Taquet 1976, figs 40 and 43-44; Fig. 5H); also, the spines of vertebrae 1-4 are slightly arched backward (Fig. 5H), unlike those of the Venice specimen. Proximal caudals 2-7 present a cranially projecting bump of the basal part of the prespinal lamina that occurs only in caudals 1-3 of the holotype.
Hemapophyses (Fig. 11E). There are 26 hemapophyses (chevrons), but seven are totally reconstructed. Hemapophyses 1-18, 20, and 23 are original, although they all present reconstructed parts; chevrons 19, 21-22 and 24 to the last one are totally artificial.
The first hemapophysis is located between caudals 3 and 4, like the holotype, while the last occurs between vertebrae 28 and 29, but it is artificial like the two vertebrae. Hemapophyses are elongated and forked proximally into two pedicels bearing the articular facets. There are two articular facets per pedicel in the chevrons of the first proximal caudal vertebrae, as the pedicel articulates on two centra. The dorsoventral length of the hemapophyses tends to decrease caudally. However, chevron 14 is shorter than chevron 15, both unbroken distally; possibly chevron 14 is in the wrong position and should be placed in a more distal position. The spines are craniocaudally narrow and laterally compressed. They appear to be spatula-like, although many distal portions are damaged. The spine of the hemapophysis 1 is straight, while those of the following elements up to hemapophysis 5 are arched; chevron 6 preserves only its pedicels; chevrons 7 and 8 are only weakly arched; chevron 9 seems to be straight, but the proximal segment of the shaft is reconstructed; chevron 10 is nearly straight; only the distal end is slightly recurved backward in chevron 11; chevron 12 is straight; chevrons 13-17 are slightly recurved; the small last chevrons are poorly preserved and partly reconstructed.
In the field map of the paratype, only the pedicels of the first two chevrons are drawn, between caudals 3 and 4 and 4 and 5, respectively. The following chevrons appear to be entire (with the

exception of chevron 5) up to chevron 17 that is followed by five vertebrae with incomplete or very small chevrons; no chevrons are associated with the last nine vertebrae.
Morphology and sloping of the neural spines and chevrons in the tail of the Venice specimen are less regular and harmonic than in the holotype and, in general, in tetrapod tail skeletons. This is probably a cause of the breakage of the long and thin apophyses and consequent restoration. However, the absence of most of the chevrons 1 and 2 in the paratype map (if not due to their partial concealment into the rock) would suggest that some chevrons were replaced with material from an individual distinct from the paratype, possibly from the cluster 2 occurring near the paratype cluster (Fig. 2).
In both basal and derived iguanodontians, the first chevrons (from just chevron 1 up to chevron 6) taper distally (e.g., *Tenontosaurus tilletti*, Forster 1990, fig. 5A; *Iguanodon bernissartensis*, Norman 1980, fig. 47; *Mantellisaurus atherfieldensis*, Norman 1986, fig. 39; *Xuwulong yueluni*, You et al 2011, fig. 2; *Tethyshadros insularis*, Dalla Vecchia 2009, fig. 1; *Kritosaurus incurvimanus*, Parks, 1920, pl. 1; *Brachylophosaurus canadensis*, Prieto-Marquez, 2001, fig. 52; *Corythosaurus casuarius*, Brown, 1916, fig. 2) and are more inclined caudally than the following chevrons and touch each other (*Iguanodon bernissartensis*, Norman 1980, fig. 47; *Xuwulong yueluni*, You et al 2011, fig. 2; *Tethyshadros insularis*, Dalla Vecchia 2009, fig.1; *Kritosaurus incurvimanus*, Parks, 1920, pl. 1; *Brachylophosaurus canadensis*, Prieto Marquez, 2001, fig. 52). This is not the case of both the holotype and MSNVE 3714 (see Figs 1 and 5H), suggesting that the tails of those skeletons were recomposed and mounted in the wrong way.
Unlike other iguanodontians, no ossified tendons are preserved with MSNVE 3714. According to Taquet (1976, p. 113), they were represented by a few fragmentary remains in the holotype and possibly by their traces on the neural spines of the distal dorsals. Thus, the characteristic lattice occurring laterally on the dorsal to proximal caudal vertebrae of the iguanodontians was at best scarcely developed in this high-spined taxon (contra Organ 2006b).

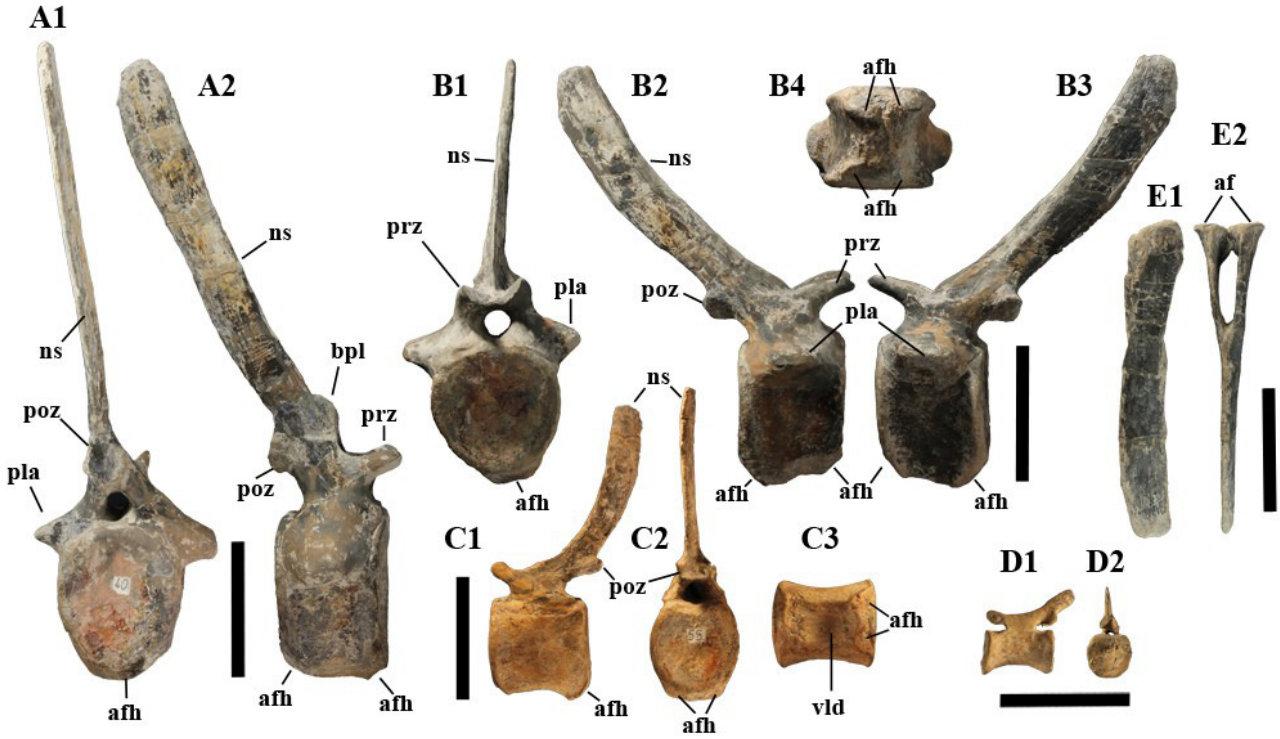


Figure 11: MSNVE 3714, caudal vertebrae. Vertebra 6 in caudal (A1) and right lateral (A2) views; vertebra 10 in cranial (B1), right lateral (B2), left lateral (B3) and ventral (B4) views; vertebra 21 in left lateral (C1), caudal (C2) and ventral (C3) views; vertebra 35 in left lateral (D1) and caudal (D2) views; hemapophysis 8 in left lateral (E1) and cranial (E2) views. Abbreviations: af, articular facets of the hemapophysis, afh, articular facet for the hemapophysis; bpl, bump of the prespinal lamina; ns, neural spine; pla, pleurapophysis; poz, postzygapophysis; prz, prezygapophysis; vld, ventral longitudinal depression of the centrum. Scale bar equals 10 cm.

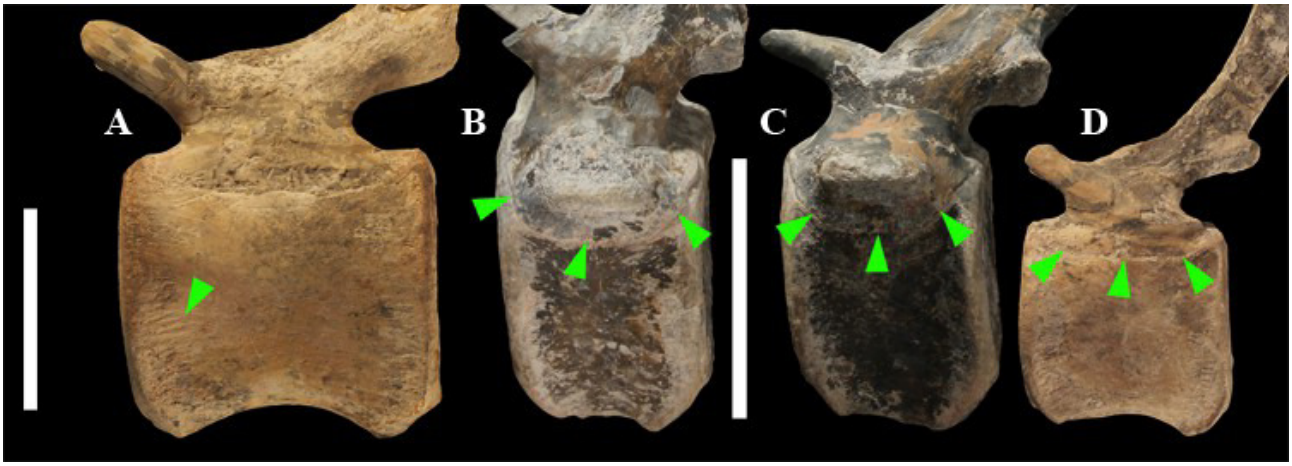
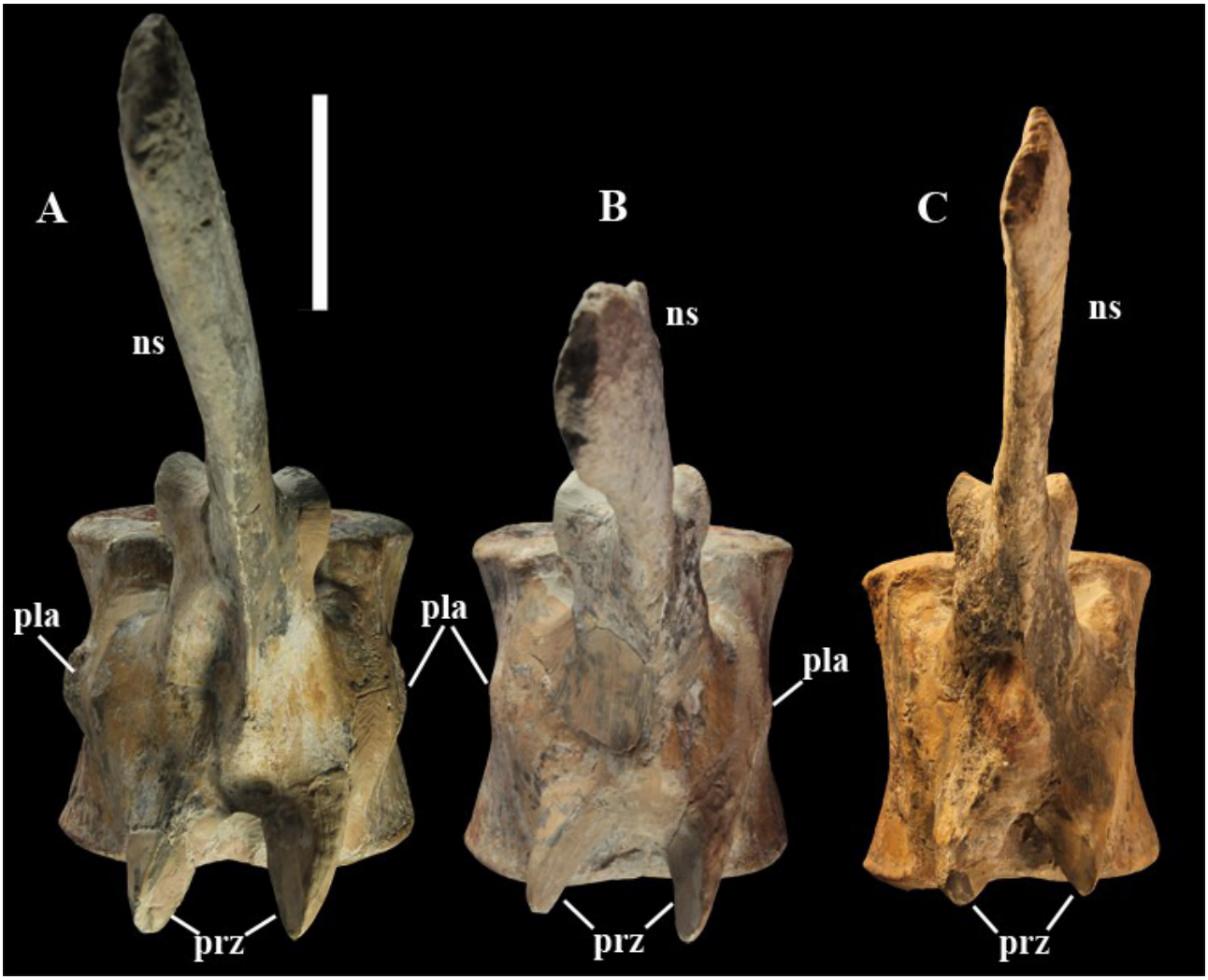


Figure 12: Evidences of osteological immaturity in the caudal vertebrae of MSNVE 3714. Rough surface in vertebral centrum 24 (A); neurocentral suture in vertebra 8 (B); vertebra 10 (C); and vertebra 21 (D). Vertebrae are figured in left lateral view. Arrows point to the grooved surface in A and to the neurocentral suture in B-D. Scale bar equals 5 cm in A and 10 cm in B-D.



740 **Figure 13: Proximal to mid-caudal transition in MSNVE 3714.** Vertebra 18 (A); vertebra 20
741 (B); vertebra 21 (C). They are shown in dorsal view. Abbreviations: ns, neural spine; pla,
742 pleurapophysis; prz, prezygapophysis. Scale bar equals 5 cm.

743 APPENDICULAR SKELETON

744 **Coracoid** (Fig. 14A). The right coracoid is a plaster copy, while the left one is original and
745 smaller than the right one (it is about 8% shorter), its size being only 125 in length and 130 mm
746 in height.
747 The left coracoid is a squared element with a convex, but party damaged, dorsal margin and a
748 concave ventral margin; the cranial margin is shallowly convex, whereas the middle part of the
749 caudal margin between the humeral glenoid facet and the scapular sutural facet is concave
750 (however, this zone is partly reconstructed; Fig. 14A3). The medial surface is shallowly concave,
751 whereas the lateral surface is slightly convex. The caudodorsal part of the element is thickened
752 and bears the rough and nearly triangular sutural surface for the scapula. The coracoid
753 contribution to the humeral glenoid occurs in the caudoventral corner of the bone. The coracoid
754 foramen opens near the caudal margin. The sternal process is damaged and mostly missing.
755 Taquet (1976) described the right coracoid of the paratype (GDF 381) instead of that from the
756 holotype, because of the bad preservation of the latter. The right coracoid of the Venice specimen,

is a plaster replica of the one described and figured by Taquet (1976, p.124, fig. 48). Only one element is identified as a coracoid by the handwritten notes in the field map of the paratype, but it is not specified whether it a left or a right one. The smaller size of the left one respect the right one suggests that it is not the coracoid GDF 301 of the referred material, which is reported by Taquet (1976, p. 58) as "coracoïde de grandes dimensions" (large-sized coracoid).

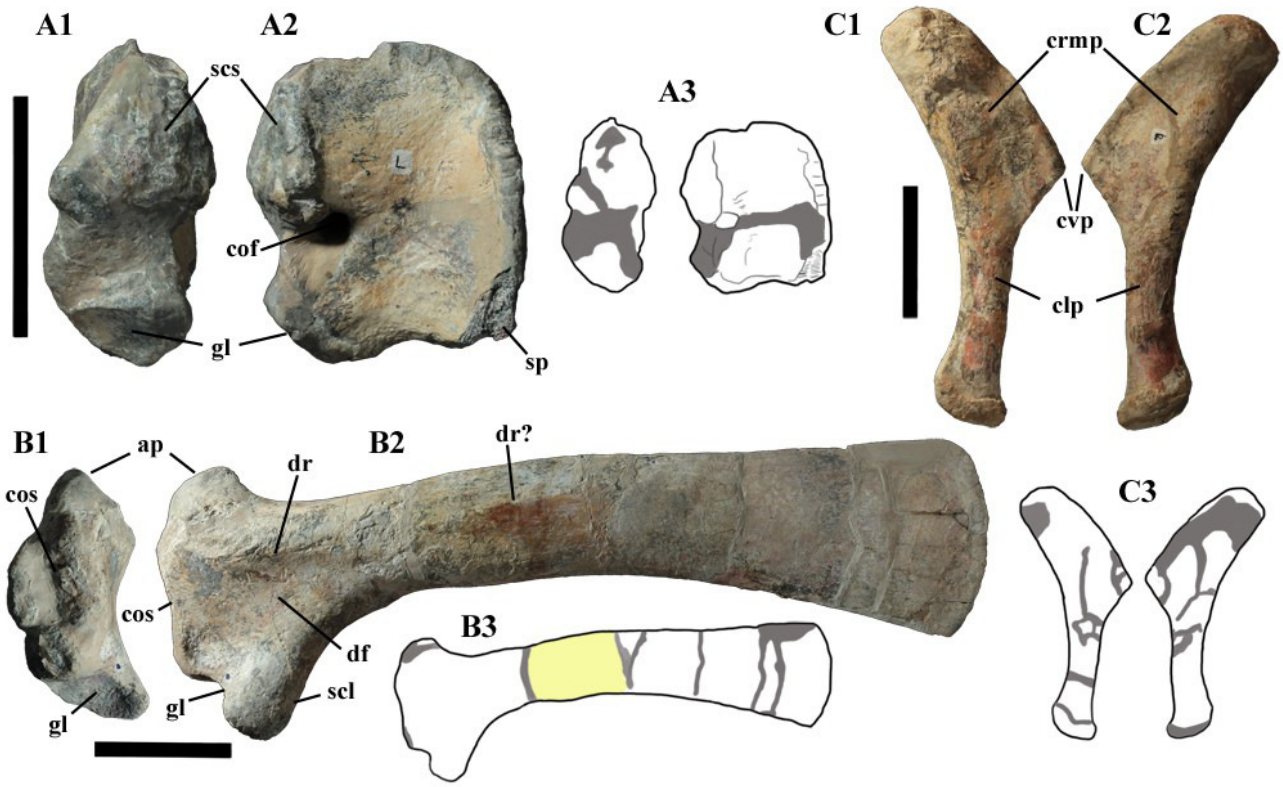
Scapula (Fig. 14B). Both scapulae are preserved, but the blade of the right one is mostly reconstructed. The left scapula is 640 mm long (3% longer than the scapula from the holotype). It is an elongate bone with a thickened and dorsoventrally expanded proximal portion and a strap-like blade. The scapular contribution to the humeral glenoid is an oval and deep depression, which is bordered caudally by a triangular, prominent and ventrocaudally pointing scapular labrum. The sutural surface for the coracoid is located cranially in the middle of the expanded proximal portion.

The prominent acromion process has a rectangular outline (it is longer than high) in lateral and medial views. The scapular blade has a concave ventrocaudal margin and a convex dorsocranial margin; it is slightly arched medially in its proximal part. The latter is relatively thick, whereas the distal portion of the blade is quite thin. The neck is poorly defined. The ventrocaudal and dorsocranial margins are nearly parallel along 2/3 of the blade length and diverges in the last third, so the blade is narrow, expanding into a symmetrical spatula-like shape only distally. The deltoid ridge crosses diagonally the blade in the right scapula; it is barely visible in the left scapula, where its distal portion does not seem to cross diagonally the blade (Fig. 14B2). This suggests that the relative segment of the broken blade (Fig. 14B3) was joined to the others in the wrong way and belongs to a right scapula. The deltoid fossa is evident ventral to the proximal segment of the deltoid ridge.

Two elements (both expanded proximal parts) are identified as scapulae by the handwritten notes in the field map of the paratype (cluster 1); one complete scapula seems to occur also in the cluster 2.

Sternal bones (Fig.14C). Sternal elements are both preserved in MSNVE 3714, although they are partly reconstructed (Fig. 14C3). They hatchet-shaped with an expanded and broad proximomedial portion (the sternal 'paddle') and a rod-like caudolateral process (the sternal 'handle'). Maximum length is 330 mm (6% longer than the holotype sternals). The medial margin of the 'paddle' in both elements is reconstructed, being smooth instead of rough as it should be; many missing fragments, fractures and holes were replaced or filled by resin. The 'paddle' has a triangular caudoventral process. The 'handle' is slightly expanded and thickened to the tip.

Two elements are identified as sternal bones by the handwritten notes in the field map of the paratype.



792 **Figure 14: MSNVE 3714, pectoral girdle elements.** Left coracoid in caudal (A1) and
793 dorsomedial (A2) views; drawings of the left coracoid in caudal and dorsomedial views with the
794 reconstructed parts evidenced in dark gray color. Left scapula in cranial (B1) and lateral (B2)
795 views; drawing of the left scapula in lateral view with the reconstructed parts evidenced in dark
796 gray color. Left sternal plate in dorsomedial (C1) and ventrolateral (C2) views; drawings of the
797 left sternal plate in dorsomedial and ventrolateral views with the reconstructed parts evidenced in
798 dark gray color. The segment of the scapular blade that seems to belong to another individual is
799 marked in yellow. Abbreviations: ap, acromion process; cof, coracoid foramen; clp, caudolateral
800 process ('handle'); crmp, craniomedial plate; cvp, caudoventral process; cos, coracoid sutural
801 surface; df, deltoid fossa; dr, deltoid ridge; gl, glenoid; scl, scapular labrum; scs, scapular sutural
802 surface; sp, broken sternal process. Scale bar equals 10 cm.

803 **Humerus** (Fig. 15A). Both humeri are original in MSNVE 3714. This element (510 mm long;
804 92% the length of the humerus from the holotype) is relatively slender and slightly sigmoid in
805 cranial and caudal views. The caput humeri (humeral head) is a bulge located in the middle of the
806 proximal end of the element and skewed to the caudal surface (Fig. 15A1); it extends along the
807 caudal surface of the proximal portion of the humerus as a distally tapering buttress. Lateral to
808 the caput is a distinct and sub-sphaerical greater (outer) tuberosity; medial to the caput is a
809 scarcely defined medial (inner) tuberosity. The deltopectoral crest is much longer than wide (i.e.,
810 it is scarcely prominent) and symmetric (the apical point is in the middle of the crest and there is
811 no steep distal margin). Its blunt apex is in the proximal half of the humerus. The distal end of the
812 bone bears the radial and ulnar condyles, which are twisted laterally. The first is rounded,
813 pointing more cranioventrally than that of the holotype. The radial condyle is larger than the ulnar
814 one. The condyles are separated by an intercondylar groove.
815 Two elements (both expanded proximal parts) are identified as scapulae by the handwritten notes
816 in field map of the paratype (cluster 1); one complete scapula seems to occur also in the cluster 2.

Two elements are identified as humeri by the handwritten notes in the field map of the paratype and are in their anatomical position (Fig. 2).

Ulna and radius (Fig. 15B). Both radius-ulna pairs are preserved; the elements of each pair are stuck together by glue. The ulna is 415 mm long (88% the length of the holotype ulna) and its shaft is straight in all views. The proximal end is expanded craniocaudally and mediolaterally, and is bears three processes. The well-developed olecranon is the more robust. It is larger and more well-formed than that of the ulna from the holotype (see Taquet, 1976, fig. 51a, c). Two nearly triangular flanges bordering the wide depression for the radius occur distal to the olecranon; the lateral flange is shorter and points craniolaterally, whereas the medial one is longer and points craniomedially. The convex distal articular surface is bean-shaped.
The radius is 350 mm long (84% the length of the radius from the holotype) and its shaft is also straight in all views. Its proximal end is mediolaterally expanded and ovoid in proximal view; its distal end is craniocaudally expanded and is wider than the proximal end. The distal surface is nearly triangular, with a convex lateral margin and a straight medial margin. The proximal and distal portions of the radius lie on cranial depressions of the ulna.
Two elements are identified as ulnae by the handwritten notes in the field map of the paratype; one (probably the left one) is completely exposed, the other apparently fragmentary or just partially cropping out from the rock. Only one radius (probably the left one, which is parallel to the relative ulna) identified as by those notes.

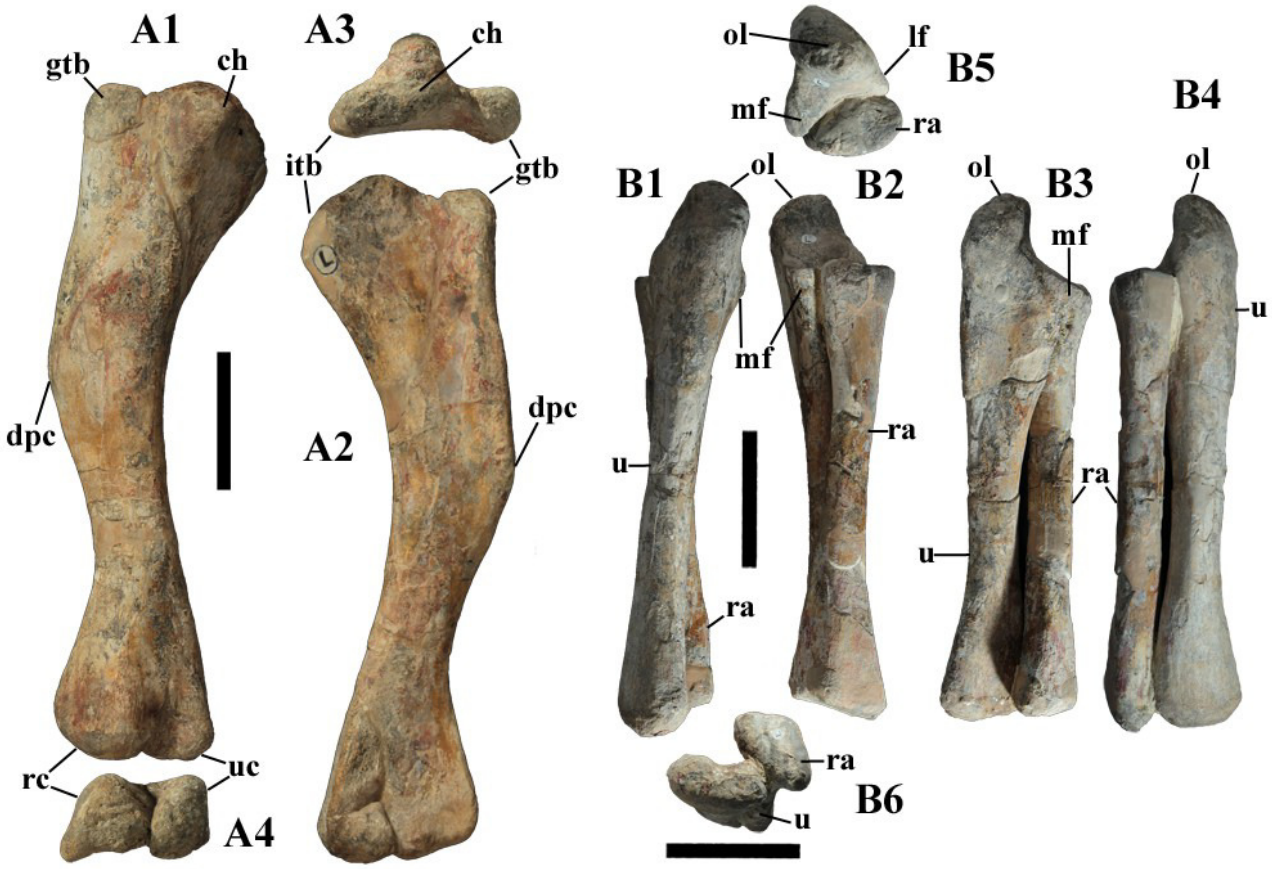


Figure 15: MSNVE 3714, forelimb, long bones. Left humerus in caudal (A1), cranial (A2), proximal (A3) and distal (A4) views; left radius-ulna in caudal (B1), cranial (B2), medial (B3), lateral (B4), proximal (B5) and distal (B6) views. Abbreviations: ch, caput humeri; dpc,

deltopectoral crest; gtb, greater tuberosity; itb, inner tuberosity; lf, lateral flange; mf, medial flange; ol, olecranon; ra, radius; rc, radial condyle; u, ulna; uc, ulnar condyle. Scale bar equals 10 cm.

Carpals (Fig. 16A). Carpals are not preserved in the right forelimb and were not replaced by artificial copies, whereas original elements occur in the left one. There is a proximal row of three carpals, which are stuck by glue to the relative metacarpals (which, however, are artificial); there are no distal carpals. One carpal apparently articulates with phalanx I-1 and metacarpal II, therefore it is in the position of the radiale (which is usually fused with the metacarpal I in basal ankylopollexians); the carpal in the middle articulates with metacarpal III and possibly partly with metacarpal IV and can be identified as the intermedium; the other carpal articulates with the metacarpal IV and should be the ulnar. The 'radiale' has a blocky shape, with a sub-quadrangular outline, an irregular proximal surface and a slightly concave distal surface. The 'intermedium' is the largest of the three and has a quadrangular outline in proximal and lateromedial views (it is dorsoventrally higher than lateromedially wide). A groove divides the medial side of the element into two parts in a way that they appear as two separate elements in that view. The 'ulnare' is a quadrangular blocky element that is proximodistally longer than ventrodorsally high in lateromedial view.

The field map (Fig. 2) shows two rounded elements of the main cluster that are labeled as "carpals" in a handwritten note.

The wrist of the holotype is completely different being formed by two large and proximodistally short proximal elements. The wrist elements of MSNVE 3714 resemble more those of *Iguanodon bernissartensis* (see Norman 1980, fig. 60) and *Mantellisaurus atherfieldensis* (see Norman 1986, fig. 50) in their relatively small size and block-like aspect, but the largest element in both taxa is the radiale, which is fused with metacarpal I. We suspect that those mounted in MSNVE 3714 are not actually carpals or at least they do not preserve their original shape.

Metacarpals (Fig. 16). Metacarpals from the right manus are artificial, whereas those of the left one are original with minor restoration (Fig. 16A2 and B2). Metacarpals III and IV are the longest, metacarpal III being only slightly longer than IV (113 and 108 mm, respectively, in both our and Taquet's measurements). The shortest is metacarpal V (68 mm long; 74 mm according to Taquet's measurements).

Scattered manual remains including two or three metacarpals can be recognized in the region of the forelimb bones in the map of cluster 1 (Fig. 2); because of their position, they plausibly belong to the left forelimb, which is fairly well-articulated.

The orientation of the manus in the following description is the standard one for digitigrade quadrupedal amniotes, although *Ouranosaurus* probably kept the palms facing somewhat medially. Metacarpal II (85 mm long in both our and Taquet's measurements) is straight, relatively slender (it is constricted in the middle) and with expanded extremities. Its proximal end is expanded craniopalmarily and mediolaterally. Its proximal surface has a squared outline and is flat. A longitudinal ridge runs along the medial margin from the proximomedial corner to mid-shaft. The distal end is pointed at its lateropalmar margin; the distal surface has a sub-oval outline and is concave. As underlined by Taquet (1976, p. 131), the metacarpal II from the holotype is more slender and mediolaterally flattened than this metacarpal. Metacarpal III is straight and expanded at both extremities. The proximal end is expanded mediolaterally; the proximal surface has a sub-rectangular outline and is gently convex. The proximal end is more pointed laterally then medially. The craniomedial corner of the proximal surface is craniomedially pointed. The distal end is expanded mediolaterally; a shallow palmodistal groove divides it into two rounded condyles. According to Taquet (1976, p. 131), this metacarpal is unlike that of the holotype, but probably it is a typo: it is written 3 instead of 5. Actually, the metacarpal III of the holotype is

only longer, according to figures 56 and 57a. Metacarpal IV is straight, with proximal and distal ends that are moderately expanded mediolaterally. The proximal surface has an elliptical outline (it is craniopalmarily compressed) and is convex. The lateral surface of the shaft presents a ridge that extends from the proximal to the distal end. The proximal portion of metacarpal IV of the holotype differs in being mediolaterally flattened (Taquet, 1976, fig. 56). Metacarpal V is stout and hourglass-shaped in craniopalmar view, with the distal extremity that is wider than the proximal one. The proximal surface has a rounded outline and is shallowly concave in the middle. The palmar surface is slightly concave, whereas the cranial one is convex. The distal end is expanded palmarily, whereas the proximal one is expanded cranially. A small knob occurs near the distal extremity of the metacarpal at the palmomedial corner. The distal surface has a sub-rectangular outline, with a shallowly concave central part. As underlined by Taquet (1976, p. 131), the metacarpal V of the holotype is completely different, being much slender, nearly as long as metacarpal IV and mediolaterally flattened.

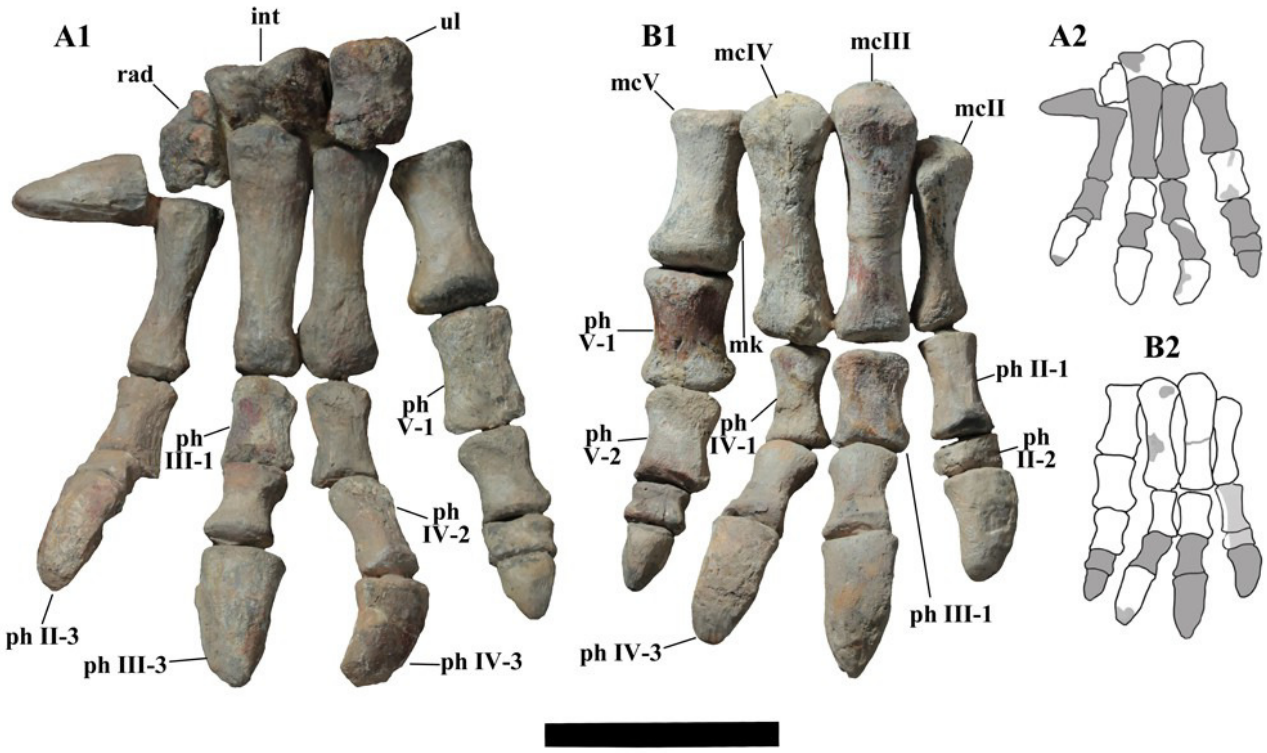
In conclusion, the palm of MSNVE 3714 is sensibly different from that of the holotype, as already noticed by Taquet (1976).

Manual phalanges (Fig. 16). The right manus of MSNVE 3714 preserves seven original phalanges, whereas the left one has six. The field map (Fig. 2) shows two elements of the cluster 1 that are labeled as "phalanx" in handwritten notes, both on the side of the forelimbs. One is an ungual phalanx and occurs 2.5 metres away from the cluster; the other is another, larger and arrow-shaped ungual phalanx. Also a group of four smaller phalanges occurs in the ?left hand region.

Phalanx II-1 (right hand) is hourglass-shaped in palmar and dorsal views, with proximal and distal extremities that are mediolaterally expanded. Its distal end is more dorsopalmarily expanded than the proximal end. The proximal surface has a sub-circular outline and is flat; the distal surface has a sub-triangular outline and is also flat. Its dorsal surface is covered by a film of resin. Phalanx II-2 (right hand) is a small and mediodistally short element, with a slightly concave palmar surface. Its dorsal surface is covered by a film of resin. Its proximal surface has a bean-like outline and is slightly convex; its distal surface has a sub-elliptical outline and is flat. Phalanx II-3 (the ungual; left hand) is hoof-like and elongated; its proximal surface has an elliptical outline and a depression at its center. Phalanx III-1 (preserved in both hands) is a stout and hourglass-shaped element in palmar and dorsal views. Its proximal surface is flat with a sub-elliptical outline. The outline of the distal surface is bean-like with a concave central part. The distal termination bears two rounded condyles that are separated by a broad and shallow depression. The right phalanx III-1 of the paratype figured in Taquet (1976, fig. 57b) is mediolaterally narrower than that in the mounted skeleton (about 28 and 34 mm, respectively); probably Taquet (1976) figures the left phalanx III-1 of the paratype (which is 28 mm wide) instead of the right. Phalanx III-2 is missing in both hands. The ungual phalanx of digit III (phalanx III-3; left hand) is hoof-like and long (it is the longest ungual phalanx). It shows two longitudinal grooves that are parallel to its lateral and medial edges; they start in the upper third of the bone and reach its distal tip. They anchored the keratin sheath of the ungual. The proximal surface has a sub-elliptical outline and a concave center. Phalanx IV-1 (right hand) is hourglass-shaped in palmar and dorsal views, with the distal extremity that is more mediolaterally expanded than the proximal one. The proximal surface has a sub-elliptical outline and is flat. The distal one has a sub-elliptical outline and a slightly convex surface. The sub-triangular distal condyles are separated by a shallow depression that is less broad than that of phalanx III-1. The proximal surface has an elliptical outline and is flat. The distal surface has also an elliptical outline and is slightly convex. This phalanx is more slender than the phalanx IV-1 of the paratype figured by Taquet (1976, fig. 57b). Phalanx IV-2 (left hand) is hourglass-shaped and relatively stout in palmar and dorsal views. As it is partly reconstructed and/or covered by resin, other

morphological details are not reliable. The ungual of digit IV (IV-3; preserved in both hands) is hoof-like and elongated. The proximal articular surface has an elliptical outline and a concave center. Phalanx V-1 (preserved in both hands) is the stoutest manual phalanx and is hourglass-shaped in palmar and dorsal views. The proximal surface has a bean-like outline and a shallowly concave center. The proximal extremity is more dorsopalmarily expanded than the distal one. The palmar surface of the phalanx is slightly concave and presents some thin longitudinal grooves (which are more evident in the right element than in the left one), possibly for muscular insertion or just evidence of a cartilage covering (like in the lateral side of the caudal vertebrae near their articular faces). The distal surface has also a bean-like outline and is slightly convex. Phalanx V-2 (right hand) is also hourglass-shaped in palmar and dorsal views. Its proximal surface has a sub-elliptical outline and a slightly concave center; its distal surface has a bean-like outline and a slightly concave center.

The description of the paratype phalanges by Taquet (1976) is messy. He does not describe or list all the phalanges preserved in that specimen. He just says that seven phalanges from the paratype left hand allowed him to complete his description of the manus (p. 132), but then he refers those phalanges to the right hand in the caption of figure 57. In figure 57c, Taquet (1976) shows the right ungual phalanx V of the paratype, but that phalanx is not preserved in MSNVE 3714. In *Iguanodon* and *Mantellisaurus*, this element is strongly reduced (Norman, 1980, 1986), thus Taquet's assignment is possibly wrong. That phalanx is similar to the left ungual phalanx IV of MSNVE 3714, but with a reversed curvature. The Venice specimen preserves two right phalanges that Taquet (1976) does not utilize in the description of *Ouranosaurus* and does not figure: IV-3 and V-2. Phalanges II-1, III-1, IV-1 in the right manus of MSNVE 3714 are morphologically unlike the corresponding paratype phalanges figured by Taquet (1976). It is unclear whether this is related to the quality of the drawing (which is however unlikely) or they are actually different phalanges. Possibly, the phalanges described by Taquet (1976) were replaced in MSNVE 3714 with other phalanges and the original were sent back with the holotype to Niamey or kept in the MNHN collection as it is the case of other bones from the paratype that were described in 1976 (i.e., the right coracoid and the left femur).

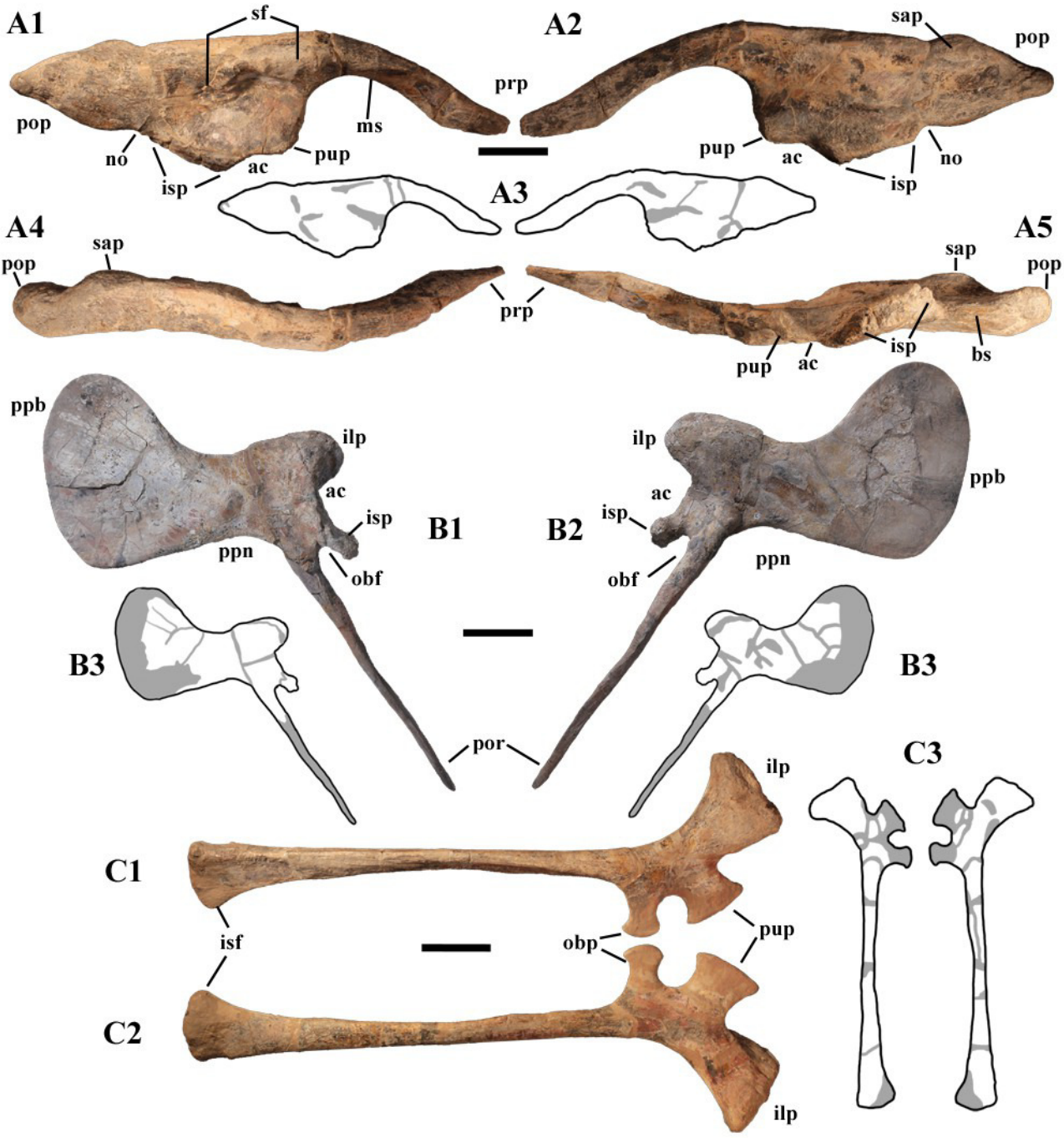


964 **Figure 16: MSNVE 3714, forelimb, *mani* in dorsal (cranial) view**. Left (A1) and right manus
965 (B1). A2 and B2 are the drawings of the left and right manus, respectively, with the totally
966 reconstructed parts evidenced in dark gray color and those just covered by a film of resin
967 coloured in pale gray; also minor reconstructed portions are in pale gray. Abbreviations: int,
968 intermedium; mc II-V, metacarpals II-V; mk, medial distal knob on the metacarpal V; ph II-V,
969 phalanges of manual digits II-V (the last phalanx of each digit is the ungual); rad, radiale; uln,
970 ulnare. Elements without abbreviation are reconstructed. Scale bar equals 10 cm.

971 **Ilium** (Fig. 17A). Both ilia are preserved, but the left is more complete than the right one. The
972 left ilium is 770 mm long (91% the length of the holotype ilium). It is lateromedially compressed
973 and sigmoid in dorsal view. The dorsal margin of the iliac blade between the preacetabular and
974 postacetabular processes is straight in lateral and medial views and thickened. The preacetabular
975 process is long and curved downward; its rostral tip is slightly upturned pointing cranioventrally,
976 like that of the ilium of *Iguanodon bernissartensis* (Norman 1980, figs. 63-64), and tapers
977 rostrally. The preacetabular process is bent laterally in dorsal and ventral views. A prominent
978 ridge crosses diagonally the proximal half of the process in its medial surface, bordering dorsally
979 a broad shelf (medial shelf). The body of the ilium is sub-rectangular and bears facets for the
980 articulation with the sacrum medially. In the left element, the articular ridge is relatively thick and
981 is arched with ventral concavity, apparently not extending caudal to the level of the caudal end of
982 the acetabulum; it is shallower, thinner, straight and extending more caudally in the right ilium.
983 As at least one ilium was detached from the sacrum (as shown in the field map; Fig. 2, see
984 below), probably the pelvis and sacrum were not coossified. The iliac contribution to the
985 acetabulum is a shallow and caudocranially short notch along the ventral margin of the iliac
986 body. The pubic peduncle is broken and mostly missing in both ilia; the ischial peduncle is
987 scarcely projecting, but its articular surface is quite long. The ischial peduncle is separated from
988 the postacetabular process by a notch. The knob-like supracetabular process (antitrocanther) is
989 located just ventral the dorsal beginning of the postacetabular process, skewed caudally with

respect to the acetabulum. The postacetabular process is large, deep and arrowhead-shaped in lateral and medial views. Ventrally, it bears a distinct *brevis* shelf.
Only one element can be referred to an ilium in the cluster 1 of the field map (Fig. 2). It was labeled as "ilium" in a handwritten note that was cancelled as it were wrong. Notwithstanding, that element can plausibly be an ilium because of its outline and position. It seems to lack the long preacetabular process like the right ilium of MSNVE 3714. The left ilium could still be totally inside the rock; this remains speculative in absence of a list of the bones obtained after preparation of the collected blocks in the MNHN laboratories. The word "ilium" is handwritten in a zone of the cluster 2 close to the pubes and at least one ischium, but the outline of the element is not recognizable; another isolated ilium (not labeled as such) is clearly present in this cluster and preserves the long preacetabular process as the left ilium of MSNVE 3714. It could have been used to complete the individual of the cluster 1.
The ilia of MSNVE 3714 are quite similar in lateral and medial views to that of the holotype figured by Taquet (1976). However, the supracetabular process does not correspond with the dorsal hump at the beginning of the postacetabular process, but it occurs in a more cranial position.

Pubis (Fig. 17B). In both pubes, the distal portions of the prepubic blade and the posterior pubic ramus are reconstructed. As reconstructed, they measure 790-810 mm long from the rostral tip of the blade to the tip of the posterior ramus. The neck of the prepubic process is stout, taller than long. The plate-like prepubic blade is much expanded dorsoventrally; it is asymmetrically more expanded dorsally than ventrally. The iliac peduncle is massive and broad in lateromedial view; the ischial peduncle is much smaller and short. Those peduncles form the cranioventral margin of the acetabulum. The preserved proximal portion of the posterior pubic ramus is rod-like and slightly tapers distally; its basal portion is placed medially with respect to the ischial peduncle. The ischial peduncle and the posterior pubic ramus border a notch that should be partially closed caudally by a small process ascending from the pubic ramus to form the obturator foramen, but this is not the case and an obturator foramen is not evident.
Only one element in the cluster 1 of the field map is labeled as "pubis" by a handwritten note (Fig. 2); it is close to the forelimb and apparently is more complete than those of MSNVE 3714. Two apparently complete and parallel ilia (labeled as such by a handwritten note) occur in the cluster 2 close to at least one ischium and a ilium. The considerations made for the ilia are valid also for the pubes.
Differences with the holotype are in the expansion of the prepubic blade, but that part is reconstructed in MSNVE 3714.
Ischium (Fig. 17C). Both ischia are preserved, but some portions are reconstructed, in particular the pubic and obturator processes. They measure 880 mm (105% the length of the ischia from the holotype). The iliac peduncle is large, fan-shaped in lateral and medial views and is directed craniodorsally. Its distal articular surface is oval in outline. The shaft is straight; it tapers up to mid-length then it enlarges gradually up to the distal extremity. The latter has a mediolaterally compressed, dorsoventral expanded and ventrally-pointing 'boot'.
Only one element in the cluster 1 of the field map is labeled as "ischium" by a handwritten note (Fig. 2); it is close and parallel to the ?left fibula and has not the appearance of an ischium. One ischium (labeled as such by a handwritten note) occur in the cluster 2 close to the paired pubes and in its anatomical position respect one of them. The proximal part of another ischium seems to occur in a slightly displaced position, but it is not labeled as such by an handwritten note. The considerations made for the ilia and pubes are valid also for the ischia.
The iliac peduncle of MSNVE 3714 is more robust than that of the ilium from GDF 300 (Taquet, 1976, fig. 60). Furthermore, the shaft is sinuous in the holotype.



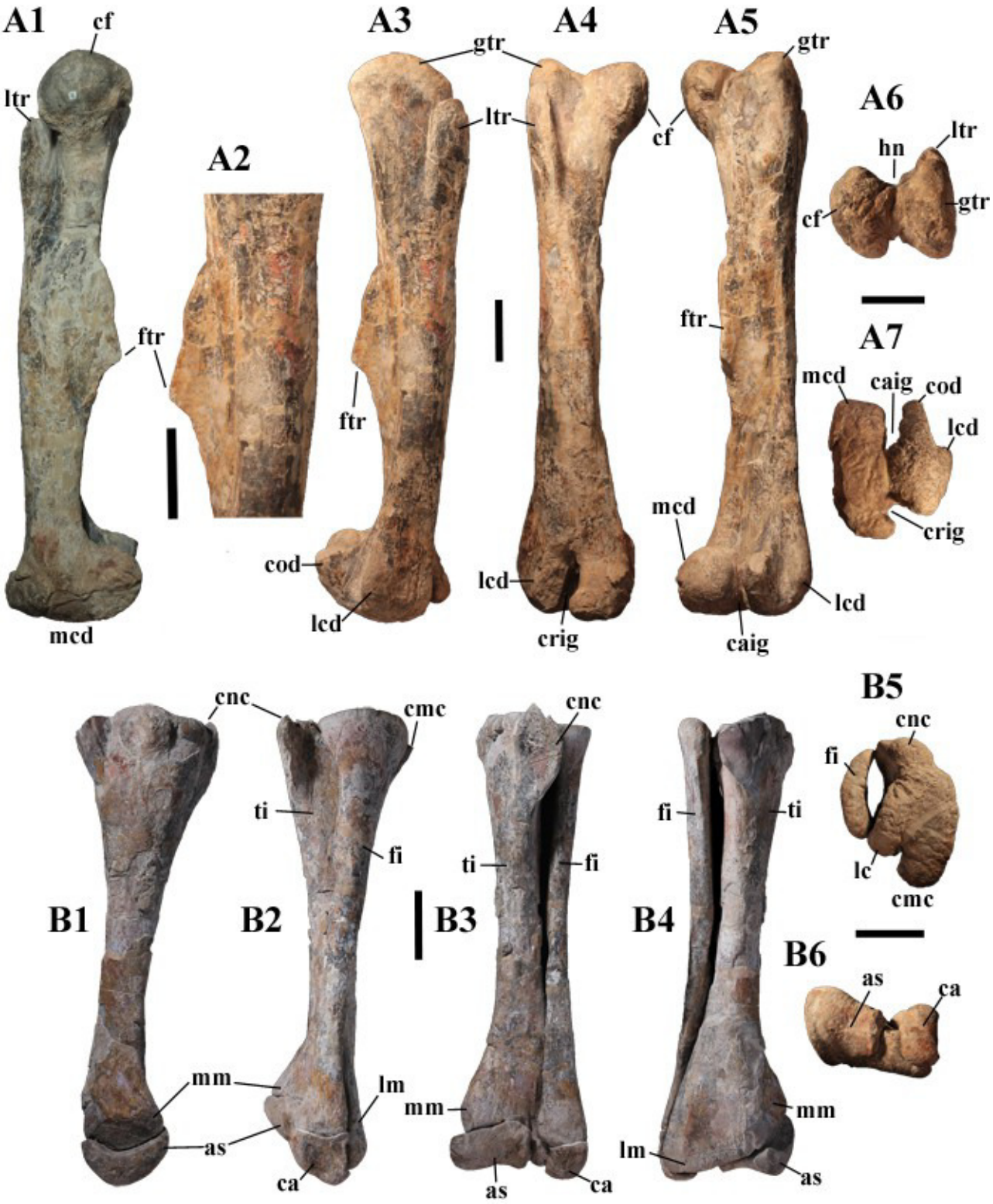
1038 **Figure 17: MSNVE 3714, pelvic girdle elements**. Left ilium in medial (A1); lateral (A2); dorsal
1039 (A4); and ventral (5) views. Left pubis in lateral (B1) and medial (B2) views. Left ischium in
1040 medial (C1) and lateral (C2; upside-down) views. A3, B3 and C3 are the drawings of the
1041 elements of figures A1-B1, B1-B2 and C1-C2, respectively, with the reconstructed parts
1042 evidenced in dark gray color. Abbreviations: ac, acetabulum; bs, *brevis* shelf; ilp, iliac peduncle
1043 of ischium and pubis; isf, distal 'foot' of the ischium; isp, ischial peduncle of ilium and pubis; ms,
1044 medial shelf; no, notch; obf, obturator foramen; obp, obturator process; pop, postacetabular
1045 process; por, posterior pubic ramus (pubis s.s.); ppb, prepubic process; ppn, neck of the prepubic

process; prp, preacetabular process; pup, pubic peduncle of ilium and ischium; sap, supracetabular process; sf, facet for the articulation with sacrum. Scale bar in A1-B1, B1-B2 and C1-C2 equals 10 cm.

Femur (Fig. 18A). The right femur is original, while the left one is a plaster replica. Taquet (1976, pl. 24, figs. 1 and 3) used the left femur of the paratype to describe the femur of *Ouranosaurus* because those of the holotype are partially and poorly preserved. According to the field map, the left femur was the only one preserved in the cluster 1; none occurs in the cluster 2. As the left femur of MSNVE 3714 is just a copy of that figured by Taquet (1976), the original bone was probably sent back to Niger with the holotype or remained in Paris, like the right coracoid and possibly the manual phalanges, although there is no written record about this. The right femur is 920 mm-long, being 8% longer than the left one and much longer than the tibia (129.5%). Its morphology is that common to femora of all advanced iguanodontians. Its shaft is straight in lateral and medial views except for the distal third, which gently curves caudally; it is slender and straight in cranial and caudal views. The caput femoris (head of the femur) is rounded in medial view, nearly triangular in cranial and caudal views, medially directed and set off from the rest of the femur by a distinct neck. The greater trochanter points dorsocaudally in lateral view extending dorsally slightly above the caput, and it is mediolaterally compressed. It forms the whole lateral half of the proximal part of the femur. A shallow depression separates it from the caput. Like in other advanced iguanodontians, the lesser (cranial) trochanter is a mediolaterally flattened, long and tongue-shaped process that is located laterocranially respect to the greater trochanter and separated by a cleft. In the right femur, the lesser trochanter is placed slightly more distally than in the left one. The fourth trochanter is located midway along the mediocaudal margin of the femoral shaft and points caudally. It is not pendent as that in the left femur of the paratype figured by Taquet (1976, fig. 62C): its caudal margin is slightly sigmoid (Fig.18A2) like that of *Hypselosaurus* cf. *fittoni* in Norman (2015, fig. 18). The distal articular end of the femur is craniocaudally expanded and divided into two condyles separated by the cranial intercondylar (for extensor tendons) and the caudal intercondylar (for flexor tendons) grooves (Fig. 18A7). The condyles are more expanded caudally than cranially. The medial condyle is larger than the lateral one and projects distally beyond it. Its cranial extremity is bent laterally partly encircling medially the cranial intercondylar groove. In distal view, this condyle has a roughly rectangular outline. The medial condyle of the left femur (figured by Taquet 1976, p. 142) has a sub-triangular outline, tapers cranially and its cranial extremity is not bent laterally. The lateral condyle expands caudally with a mediolaterally flattened condylid that reaches the level of the caudal end of the medial condyle. The intercondylar grooves are deep; the caudal is slightly deeper and narrower than the cranial one.

Tibia (Fig. 18B). Both tibiae are entirely preserved in MSNVE 3714. In the field map, the cluster 1 preserves only one tibia and fibula, plausibly the left one. A tibia and at least part of a fibula occur in the cluster 2; this might be the right one of MSNVE 3714. The left tibia is 710 mm long, which is 90% the length of the holotype tibia. The tibial morphology is quite consistent within iguanodontians. It is a straight bone that is craniocaudally expanded at its proximal end and mediolaterally expanded at its distal end. A prominent and mediolaterally compressed crest (the cnemial crest) projects cranially from the proximal expansion and curves laterally. The cranial portion of the proximal expansion bears two condyles, a caudomedial condyle (larger) and a lateral one, which are separated each other by a deep and narrow groove. The shaft is straight and ovoid in cross-section, but with a twist of the main axis of the section from craniocaudal proximally to transverse (lateromedial) distally. The distal end is divided into two malleoli, the lateral one extending more distally than the medial one and articulating with the caudoproximal

1093 articular facet of the calcaneum. The medial malleolus is broader than the lateral one in
1094 craniocaudal view, it is slightly bent cranially in lateral view and articulates with the astragalus.
1095 **Fibula** (Fig. 18B). Both fibulae are preserved and are glued to the relative tibiae and cannot be
1096 removed. The left fibula is glued in a slightly wrong position, as it should rest in a shallow lateral
1097 depression of the proximal part of the tibia, bordered by the cnemial crest (Norman 1986, fig.
1098 58F; see also Godefroit et al 1998, p. 44) not on the tibial condyles. The fibula is a straight and
1099 relatively slender bone that is slightly shorter than the tibia. Their extremities are expanded
1100 craniocaudally, the proximal more than the distal one. The proximal expanded portion is
1101 lateromedially flattened and slightly crescentic in proximal view, with a convex lateral margin
1102 and a concave medial margin (Fig. 18B5). The proximal end shows a cranially pointing wing in
1103 lateral and medial views. The distal end is club-shaped, leans against the lateral malleolus of the
1104 tibia and articulates with the calcaneum. In caudal view, a straight longitudinal ridge runs from
1105 near the proximal end to the middle of the shaft. The distal surface is not visible because it is
1106 articulated with the calcaneum.



1107 **Figure 18: MSNVE 3714, hind limb: femur, tibia, fibula and tarsals.** Right femur in medial
1108 (A1), lateral (A3), cranial (A4), caudal (A5), proximal (A6) and distal (A7) views; A2 is a
1109 particular of the fourth trochanter. The left tibia and fibula in medial (B1), lateral (B2), cranial
1110 (B3), caudal (B4), proximal (B5) and distal (B6) views. B5 is the mirrored proximal view of the
1111 right tibia-fibula, because the proximal part of the left tibia-fibula is poorly preserved and badly
1112 mounted. Abbreviations: as, astragalus; ca, calcaneum; caig, caudal intercondylar groove; cf,

caput femoris (femoral head); cmc, proximal caudomedial condyle of tibia; cnc, cnemial crest; cod, condylid; crig, cranial intercondylar groove; ftr, fourth trochanter; gtr, greater trochanter; hn, neck of the femoral head; lc, proximal lateral condyle of tibia; lcd, distal lateral condyle of femur; lm, lateral malleolus; ltr, lesser trochanter; mcd, distal medial condyle of femur; mm, medial malleolus. Scale bar equals 10 cm.

Pes (general). The left pes (Fig. 19) presents original elements, whereas the right one is totally reconstructed. All pedal elements are glued together in the mounted skeleton, so description is limited to the exposed features.
In the field map (Fig. 2), cluster1 shows elements only from the left pes, which are close to the distal end of the paired tibia and fibula. They include bones indicated as astragalus and calcaneum by handwritten notes, and some phalanges; although only one large metatarsal seems to be present in the associated pedal bones, two much smaller elements are identified as metatarsals by handwritten notes. Such a big difference in size must be considered as an 'artistic license'.
Tarsals (Fig. 18B). Astragalus and calcaneum are glued to tibia and fibula, therefore they cannot be observed entirely. The astragalus is quadrangular, but broader medially than laterally, in distal view and cup-shaped in medial view; it is sensibly larger than the calcaneum. Its proximal surface is concave and receives the medial malleolus of tibia. The proximal margin sends two ascending processes: one occurs in the craniolateral corner and the other in the caudomedial corner; both are moderately developed.
The calcaneum is kidney-like in distal view, longer than wide; it is sub-triangular in lateral view, with a convex distal margin. Its proximal articular surface is divided into two deep facets, a cranial one for the fibula and a caudal one for the lateral malleolus of the tibia. It is exactly like the calcaneum of the holotype (Taquet 1976, fig. 67).
Metatarsals (Fig. 19). The morphology of the metatarsus is that common to metatarsi of all advanced large iguanodontians. Metatarsal III is the longest and most robust of the three.
The proximal half of metatarsal II (185 mm long) is mediolaterally flattened; the distal half is slightly bent laterally and the distal end is mediolaterally expanded (the articular surface faces ventromedially). Both the proximal and distal ends are craniocaudally expanded. Most of the lateral face is occupied by the broad and slightly concave articular facet for metatarsal III; this surface is bordered cranioventrally by a crest (the "external blade" of Taquet, 1976, fig. 68B). The proximal articular surface is elliptical, longer than wide, with a convex medial margin and a slightly concave lateral margin. The dorsal craniolateral corner sends a craniolaterally-directed small flange that partially overlaps the corresponding corner of the proximal end of metatarsal III.
Metatarsal III (215 mm long) has a straight and robust shaft that gently curves medially near its proximal end. Its proximal portion is expanded craniocaudally and flattened lateromedially where it bears the convex articular surfaces for the metatarsals IV and II, laterally and medially respectively. The distal end is lateromedially expanded and is divided into lateral and medial condyles by a shallow and wide craniocaudal furrow. Metatarsal IV is slightly longer than II (it is 190 mm long). It is arched laterally and its distal articular surface faces ventrolaterally. Medially, its proximal half presents a deeply concave articular surface for metatarsal III. The cranial half of this surface is on a broad craniomedial flange of the metatarsal that overlaps the metatarsal III. A large knob occurs on the shaft just below the articular surface for metatarsal III. The distal end is transversely expanded and bears two condyles that are separated by a wide and shallow furrow.
Phalanges (Fig. 19). Digits II-IV have three, four and five phalanges, respectively, but II-3 and IV-2 to 4 are totally reconstructed. All terminal phalanges are unguals.
Phalanx II-1 is stout, gently arched laterally and hourglass-shaped in dorsoplantar view. Its distal end is more expanded lateromedially than the proximal end. The proximal surface has a

quadrangular outline and is flat; the distal end is divided into two condyles that are separated by a wide and shallow furrow. Phalanx II-2 is much smaller than phalanx II-1 and has a quadrangular outline in dorsoplantar view. Its proximal surface has a sub-triangular outline; the distal end bears two scarcely developed articular condyles. Phalanx III-1 is large, stout and as long as wide. Its proximal surface has a sub-elliptical outline and is slightly concave. Its distal end bears two scarcely developed articular condyles. Phalanx III-2 is disc-like, much proximodistally shorter than wide lateromedially. Both proximal and distal surfaces have a sub-triangular outline; the proximal one is slightly convex, whereas the distal is concave. Phalanx III-3 has a shape similar to that of phalanx III-2, but it is transversely narrower. The long phalanx III-4 (the ungual phalanx, 70 mm long) is spade-like, dorsoplantarily flattened and slightly arched plantarily; the medial expansion of its distal end is more developed than the lateral one. Phalanx IV-1 is hourglass-shaped in dorsoplantar view and resembles phalanx II-1. Its proximal end is more dorsoplantarily expanded than the distal end. Its proximal surface has a sub-rectangular outline. The distal end is divided into two condyles that are separated by a wide and shallow furrow. The ungual phalanx IV-5 is a tiny element with a squared outline in dorsoplantar view and is gently arched plantarily.

According to Taquet (1976, p. 153), seven pedal phalanges are preserved in the paratype; eight are actually present in the Venice specimen, including unguals III and IV (which should not be present according to Taquet, 1976). Lengths reported by Taquet (1976) correspond with those measured in MSNVE 3714 for the phalanges II-1, II-2, III-1 and III-2. The description of the paratype pedal phalanges by Taquet (1976) contains further mistakes. All those phalanges are considered to be from the right pes in the caption of figure 71; in the text, phalanges II-1, III-1 are reported as left, III-2 as possibly right, while the provenance of phalanges II-2, IV-2 and III-3 is not established. Furthermore, phalanx IV-2 in referred to the holotype in the text, while it reported to belong to the paratype in the caption of the figure. The only ungual phalanx is reported as a right IV-5 in the figure, while the text says only that it is from the right foot; that phalanx does not correspond with the ungual of digit IV of MSNVE 3714 and resembles more the ungual placed at the end of digit III.

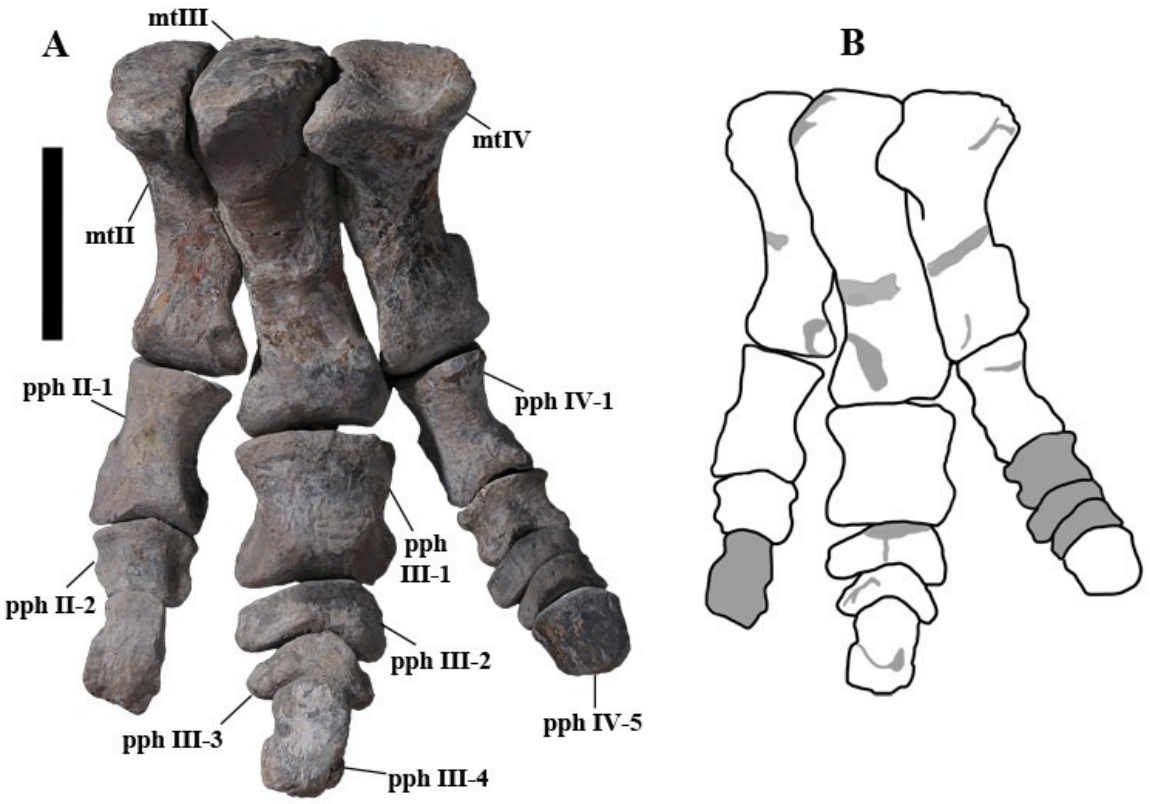


Figure 19: MSNVE 3714, hind limb: pes. Left pes in dorsocranial view. To the right, drawing of the left pes with the totally reconstructed parts evidenced in dark gray colour and minor reconstructed portions in pale gray. Abbreviations: mtII-IV, metatarsals II-IV; pphII-IV, phalanges of pedal digits II-IV (the last phalanx is always the ungual one). Elements without abbreviation are reconstructed. Scale bar equals 10 cm.

Osteohistology of MSNVE 3714

The elements that were sampled for osteohistological analyses are the humerus, the femur, the tibia, the neural spine of a distal dorsal vertebra, and a distal dorsal rib (see Materials and Methods chapter for details).

HUMERUS

The left humerus was sampled on its caudal side at mid-shaft. The cylindrical core sample was 23 mm thick and its diameter was 14 mm (Fig. 20A). The medullary cavity shows relatively few trabeculae, which are generally not connected to each other. Trabecular density is lower in comparison to that present in the femur (see below). The edge of the medullary cavity is neat (Fig. 20B). Erosional cavities are present in the inner compacta; they show a minor density than in the femur (see below). Those cavities have an elliptical or rounded outline and occur in the inner one fifth of the compacta; their density decreases moving toward the outer surface of the cortex. The microstructure of the cortex is fibrolamellar with a matrix composed of woven bone (Fig. 20C-D). Compacted coarse cancellous bone (CCCB; *sensu* Hübner, 2012) occurs in the inner cortex surrounding the erosional cavities (Fig. 20B). Vascularization (*sensu lato*; see Chinsamy, 2005) is mainly composed of well-developed (i.e., large and with many lamellae) primary osteons that become more and more organized (i.e., regularly arranged in the space) towards the outer cortex (Fig. 20C-D). Vascularization has a laminar circumferential arrangement (Fig. 20C-D). The distance between the single vascular canals is relatively high (Fig. 20C-D).

Zonation is present. Four to six LAGs are recognized in the compacta (Fig. 20A); the spacing between successive LAGs decreases moving towards the outer surface of the bone. Secondary osteons and EFS are absent (Fig. 20A-D).

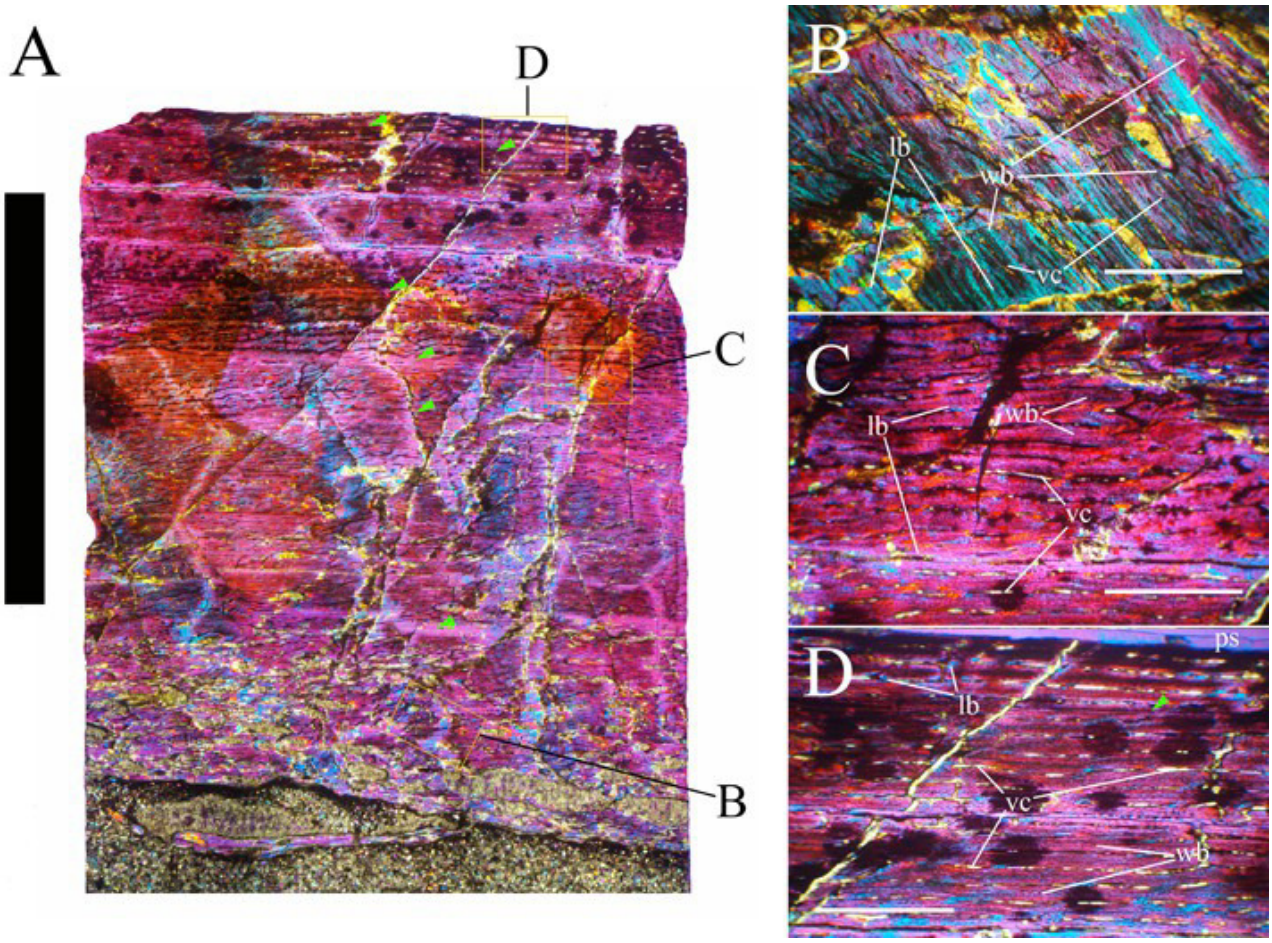


Figure 20: MSNVE 3714, left humerus, thin section. Panoramic view under lambda filter (the outer surface of the bone is at the top of the figure) (A); detail of the progressive transition between the compacta and the medullary cavity, characterized by erosional cavities (B); detail of the fibrolamellar bone and longitudinal vascularization forming the primary bone (C); detail of the microstructure of the outermost cortex showing the absence of an EFS (D); no secondary osteons are observed in the inner cortex. Green arrows point to the LAGs. Abbreviations: lb, lamellar bone; mc, medullary cavity; ps, periosteal surface; vc, vascular canals; wb, woven bone. Scale bars equal 10 mm in A and 1 mm in B-D.

FEMUR

The right femur was sampled on the craniolateral side at mid-diaphysis. The cylindrical core sample was 21 mm thick and its diameter was 14 mm (Fig. 21A). The medullary cavity is characterized by isolated trabeculae. The passage between the medullary cavity and the compact cortex is gradual, because of the presence of many resorption cavities in the inner cortex (Fig. 21B). Resorption cavities tend to decrease in density moving towards the external surface of the cortex, and their outline changes from irregular to rounded or elliptical. The compacta is composed of two different types of bone: the primary and the CCCB. The primary bone is composed of fibrolamellar bone with woven bone forming the matrix (Fig. 21C-D). CCCB bone

is present in the inner most compact bone wall, especially in the areas surrounding the resorption cavities (Fig. 21B). Primary osteons are abundant through all the compact bone. Vascularization is irregularly organized and a clear orientation is not evident. Primary vascular canals are still open, although infilling of lamellar bone is present. Secondary osteons (Haversian systems) cannot be identified in the thin section. No LAGs or annuli can be observed and there is no EFS (Fig. 21A-D).

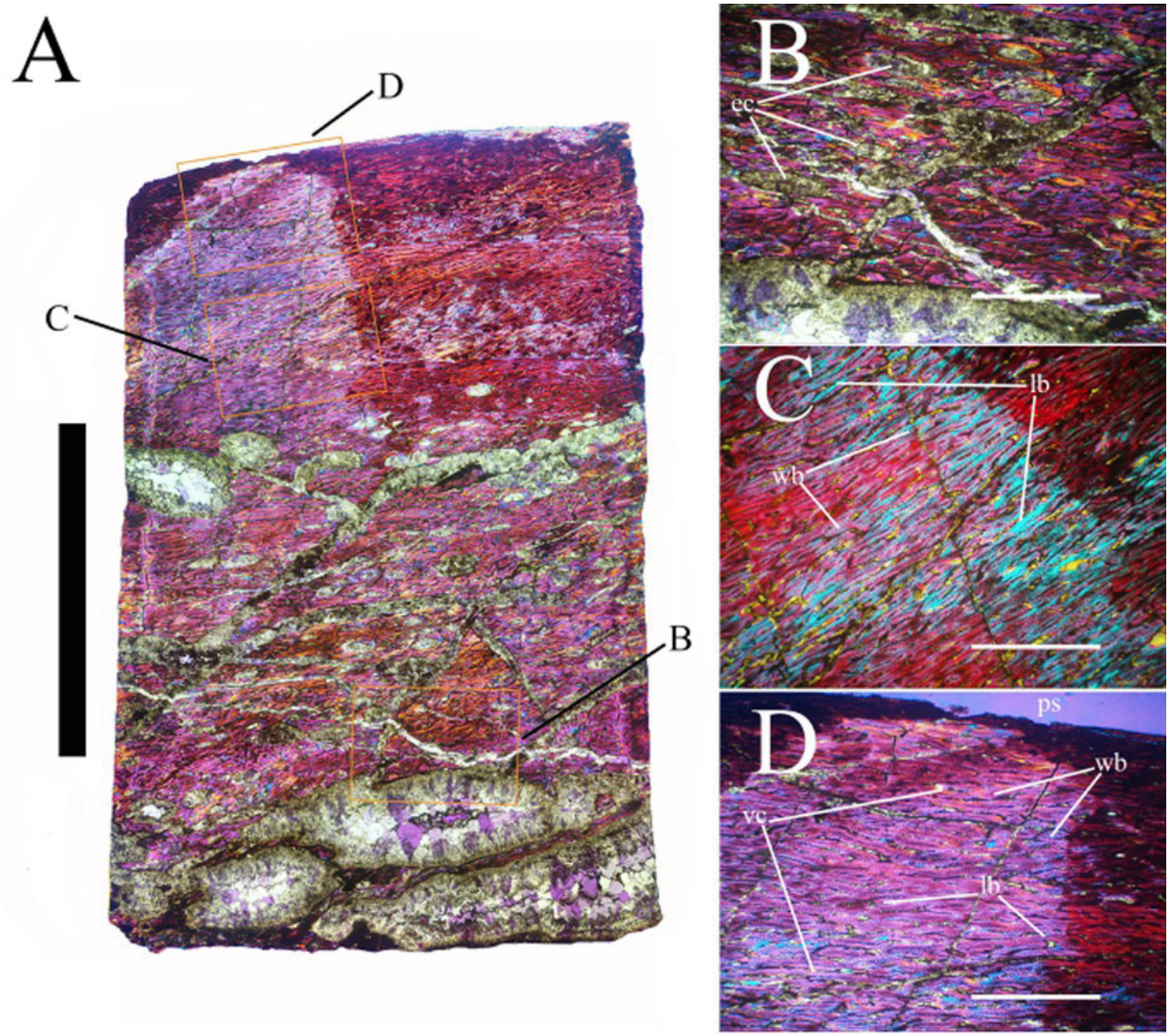


Figure 21: MSNVE 3714, right femur, thin section. Panoramic view under lambda filter (the outer surface of the bone is at the top of the figure) (A); the gradual transition between the compacta and the medullary cavity made of CCB and erosional cavities (B); detail of the plexiform vascularization and fibrolamellar bone forming the primary bone and the absence of zonation and LAGs within the compacta (C); detail of the microstructure of the outermost cortex showing the absence of an EFS (D). Abbreviations: ec, erosional cavities; lb, lamellar bone; ps, periosteal surface; vc, vascular canals; wb, woven bone. Scale bars equal 10 mm in A and 1 mm in B-D.

TIBIA

The right tibia was sampled craniolaterally in the diaphysis, slightly below mid-shaft. The cylindrical core sample was 26 mm thick and its diameter was 14 mm (Fig. 22A). Within the medullary cavity, a typical spongiosa is absent: trabeculae are rarefied (Fig. 22A-B). The boundary between the medullary cavity and the cortex is abrupt and uneven and there is a thin endosteal lamella. The primary bone microstructure is fibrolamellar with woven bone constituting the matrix (Fig. 22C-D). In the inner cortex, vascularization is irregular in its orientation, density and organization. Primary osteons are well developed and generally with a laminar circumferential orientation. Locally, reticular arrangement of the primary vascular canals is observed. Organization of primary vascular canals increases towards the outer surface of the bone. Infilling of lamellar bone is present in those canals, which, however, are not completely filled. Secondary osteons are abundant in the innermost cortex, extending over one fifth to one sixth of the compact bone wall thickness (Fig. 22A). Unlike all other sampled long bones, erosional cavities are absent. Six LAGs occur in the compact bone wall. There is no EFS (Fig. 22D).

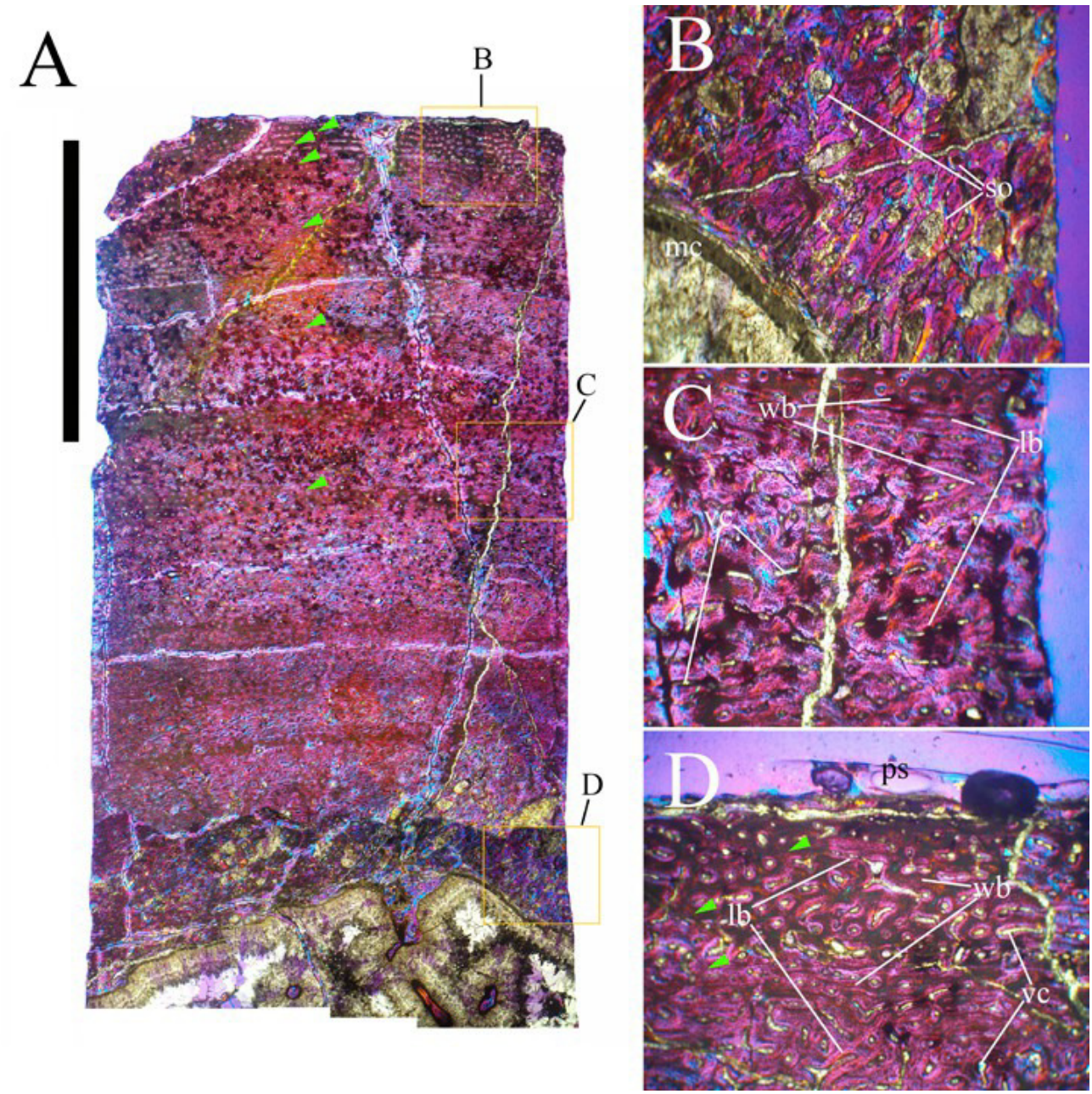


Figure 22: MSNVE 3714, right tibia, thin section. Panoramic view under lambda filter (the outer surface of the bone is at the top of the figure) (A); gradual transition between the compacta and the medullary cavity made of CCB and erosional cavities (B); detail of the deeper cortex, showing zonation of the primary bone, irregular vascularization and fibrolamellar bone (C); detail of the outermost cortex showing the absence of an EFS (D); note the remodeling in the inner compacta). Abbreviations: lb, lamellar bone; mc, medullary cavity; ps, periosteal surface; so, secondary osteons; vc, vascular canals; wb, woven bone. Green arrows point to the LAGS. Scale bars equal 10 mm in A and 1 mm in B-D.

Neural spine

The neural spine of dorsal vertebra 14 was cross-sectioned in the basal third, in the middle, and in the apical third (Figs. 23A, 24A and 25A). The cross-section is oval proximally becoming rectangular in the central and distal segments. The medullary cavity is filled with spongiosa (Fig. 23B, 24B and 25B). The boundary between the medullary cavity and the cortex is not abrupt, as

erosional cavities occur between the trabecular structure of the medullar cavity and the compact cortex (Figs. 23C, 24C and 25C). The compacta becomes thinner and thinner moving from the proximal part of the spine towards its apical part. The microstructure is fibrolamellar and tends to become more organized moving towards the outer surface of the bone. Evidence of the presence of Sharpey's fibers is observed on the lateral surfaces of the spine in the proximal section. No Sharpey's fibers are found in the other two thin sections. Primary vascularization is prevalently longitudinal and becomes more organized and rarified moving through the outer cortex towards the outer surface. Haversian systems are generally present in the inner half of the compacta (Figs. 23B-C, 24 B-C and 25B-C). Six, four, and three LAGs are identified in the proximal, median and distal sections, respectively. We consider six or seven LAGs the most reliable count to establish the age of the individual, because the base of the neural spine is expected to preserve the most complete growth record. The spacing between the zones decreases moving towards the outer surface of the bone. An EFS is absent (Figs. 23D, 24D and 25D).

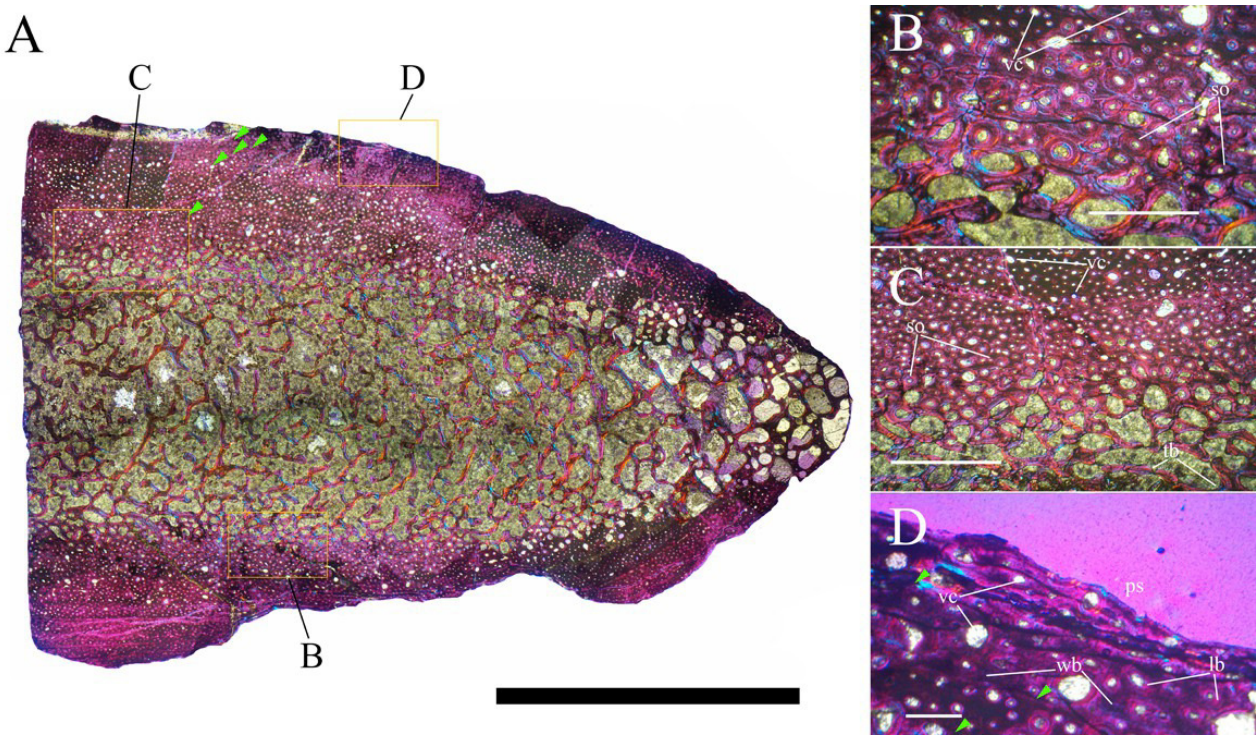


Figure 23: MSNVE 3714, neural spine of dorsal vertebra 14, transverse thin section of the basal third. Panoramic view of the cranial half of the section (A); Haversian systems in the inner most cortex (B); transition between the compacta and the medullary cortex with erosional cavities and remodeling (C); detail of the outer cortex showing absence of an EFS and outermost LAGs (D). Abbreviations: lb, lamellar bone; ps, periosteal surface; so, secondary osteons; tb, trabeculae; vc, vascular canals; wb, woven bone. Green arrows point to the LAGS. Scale bars equal 10 mm in A, 1 mm in B and C, and 500 microns in C.

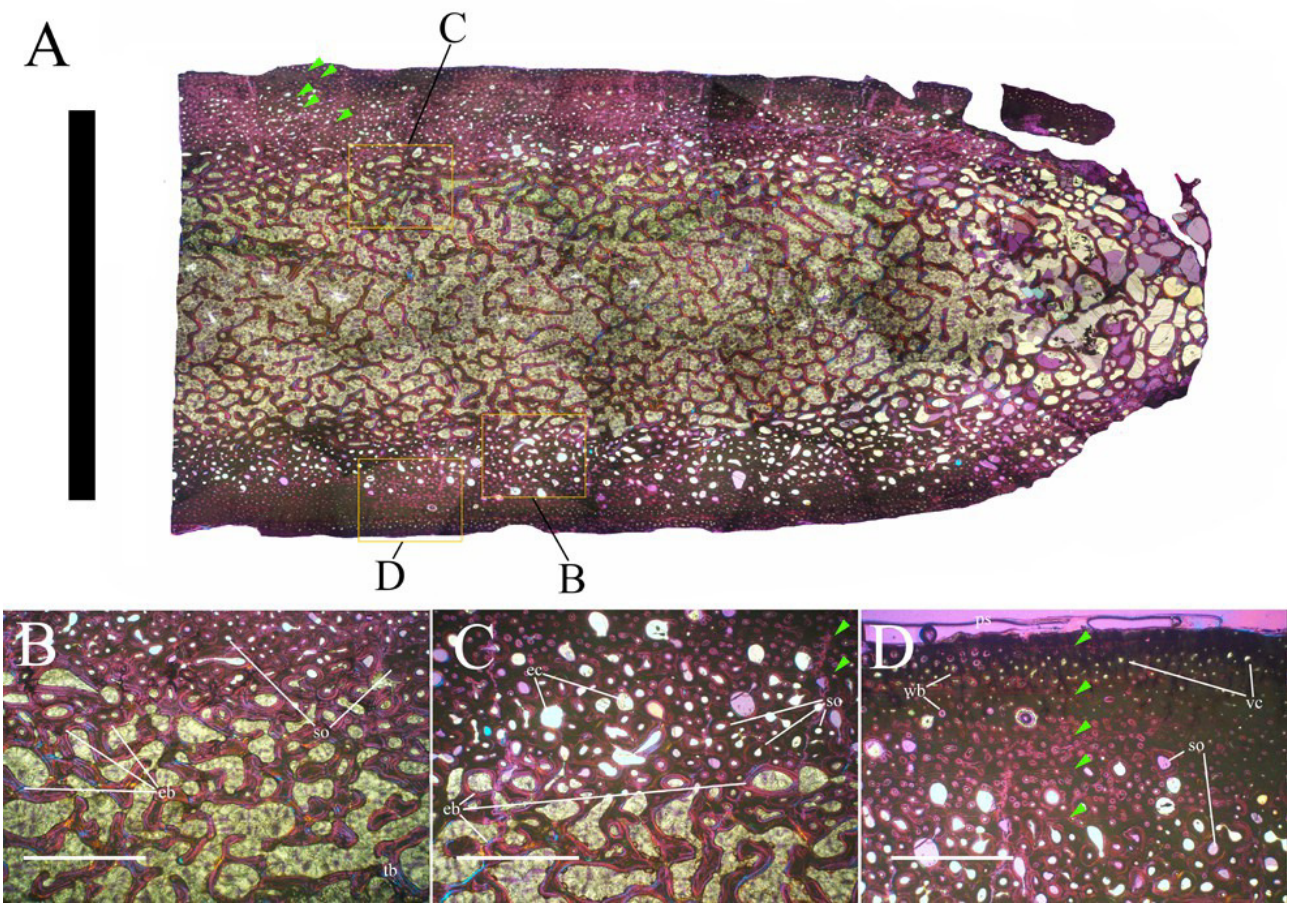


Figure 24: MSNVE 3714, neural spine of dorsal vertebra 14, thin section of the median part. Panoramic view of the cranial half of the section (A); Haversian systems in the inner most cortex and endosteal bone (B); gradual transition between the compacta and the medullary cortex with erosional cavities and marked remodeling of the primary bone (C); detail of the outer cortex showing absence of an EFS and zonation of the primary bone (D). Abbreviations: eb, endosteal bone; ec, erosional cavities; ps, periosteal surface; so, secondary osteons; tb, trabeculae; vc, vascular canals; wb, woven bone. Green arrows point to the LAGS. Scale bars equal 10 mm in A and 1 mm in B-D.

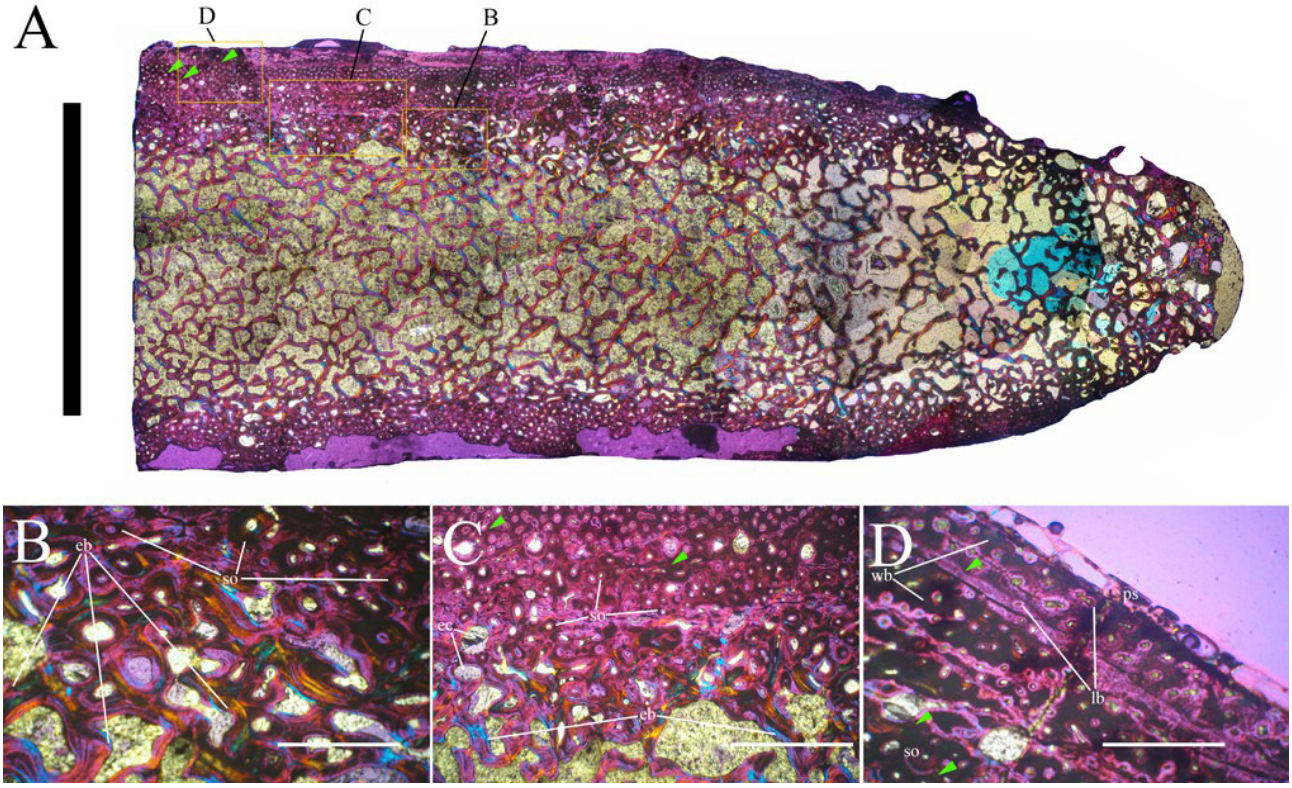


Figure 25: MSNVE 3714, neural spine of dorsal vertebra 14, transversal thin section of the apical third. Panoramic view of the cranial half of the section; notice how the compact cortex becomes thinner trending through the top of the neural spine (A); detail of the Haversian systems in the inner most cortex and endosteal bone (B); gradual transition between the compacta and the medullary cortex (C; notice the erosional cavities and deep remodeling of the primary bone); detail of the outer cortex with outermost LAGs but without an EFS (D). Abbreviations: eb, endosteal bone; ec, erosional cavities; lb, lamellar bone; ps, periosteal surface; so, secondary osteons; wb, woven bone. Green arrows point to the LAGS. Scale bars equal 10 mm in A and 1 mm in B-D.

DORSAL RIB

The transversal cross section of the proximal part of the dorsal rib 15 has an oval outline. The cortex of the lateral side is heavily eroded; its maximum thickness is 17 mm (Fig. 26A). The medullary cavity is filled with spongiosa. The boundary between the spongiosa and the compacta is gradual, the erosional cavities in the inner cortex becoming smaller and fewer moving toward the outer surface of the cortex (Fig. 26B). The microstructure is fibrolamellar with a matrix of woven bone. Primary osteons are well developed and abundant in the outer cortex and have a longitudinal orientation. Vascular canals are partially infilled with lamellar bone, so they are still opened. Primary vascularization is more organized and less dense in the outer cortex. Secondary osteons are present in the innermost cortex (Fig. 26C). Six or seven LAGs can be identified (Fig. 26A); they tend to be more and more closely spaced moving towards the outer surface of the cortex. An EFS is absent (Fig. 26D).

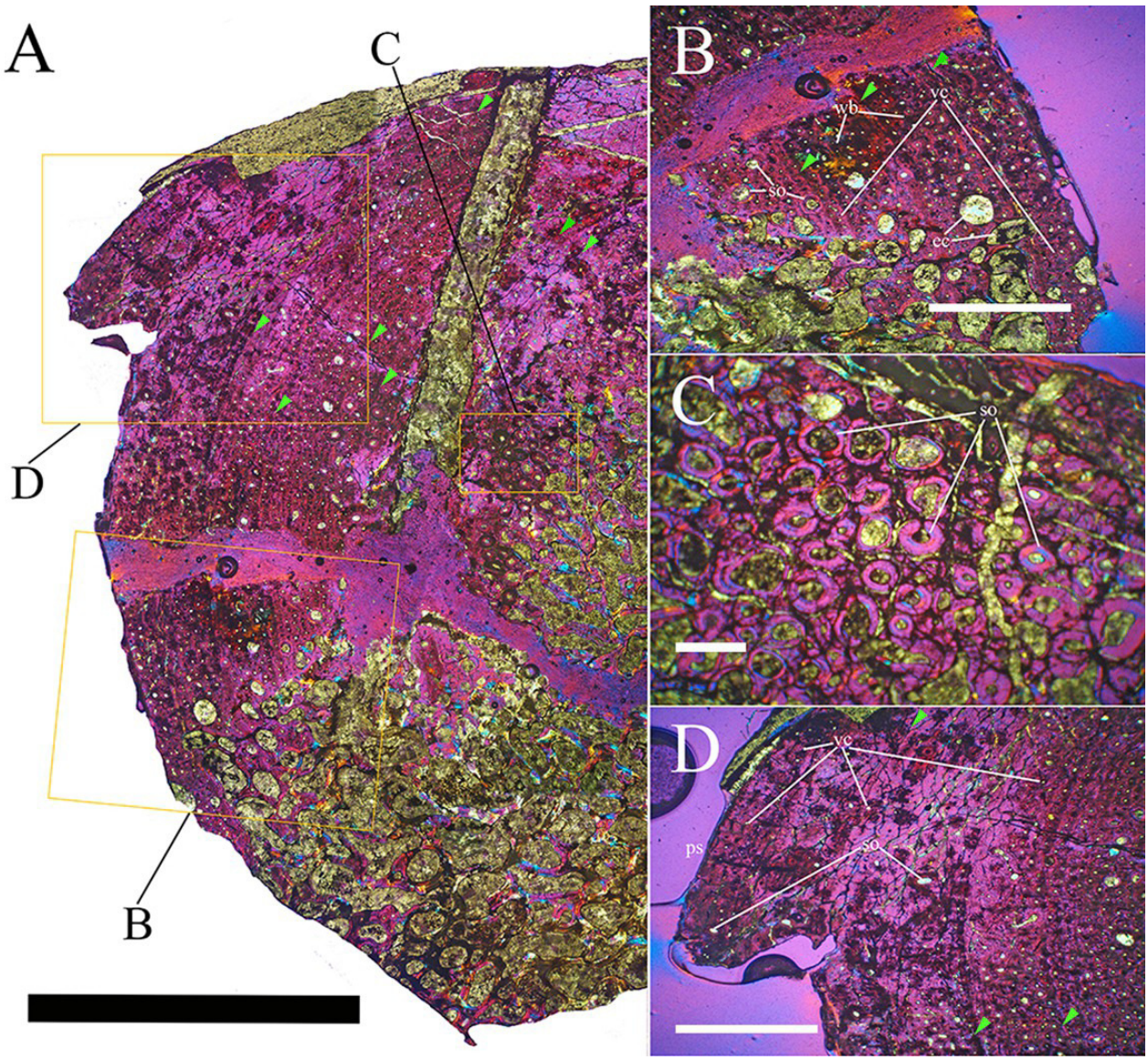


Figure 26: MSNVE 3714, dorsal rib, transverse thin section. Cranio-lateral intersect of the dorsal rib (A); transition between the outer cortex and the medullary cavity (B; note erosional cavities and deep remodeling of the primary bone); Haversian systems in the inner cortex (C); detail of the outer most cortex showing zonation and the absence of an EFS (D). Abbreviations: ec, erosional cavities; ps, periosteal surface; so, secondary osteons; vc, vascular canals; wb, woven bone. Green arrows point to the LAGS. Scale bars equal 10 mm in A, 1 mm in B and D, and 500 microns in C.

DISCUSSION

Is MSNVE 3714 a composite?

The Venice specimen is undoubtedly the paratype GDF 381- MNHN figured in Taquet (1976, pl. 9, fig. 2) and figured in the field map that we received from the MNHN and is labeled "Ouranosaurus nig[eriensis] - Airfield - 1970 - (specimen Venice Museum pro parte)". However, the latter depicts two clusters of bones belonging to two different individuals (Fig. 2). Cluster 1 is most of a quite well articulated skeleton without skull and lower jaw and apparently lacking also

the distal caudals, at least half of the pelvic elements (only an ilium, a pubis and an ischium are present at best), one hind limb, elements of the hands and possibly one coracoid. Cluster 1 is labeled "GDF 381 Today in Venice" in the map. That note was clearly added after the mapping and is a further prove that cluster 1 is the paratype and represents the skeleton exhibited in Venice. Cluster two is a partial skeleton with the pelvic elements, the proximal part of the caudal segment of the vertebral column, part of a hind limb, and possibly the sacrum and a scapula. The words "Pro-parte" used in the caption could mean that only part of the mapped bones was used in the mount of the Venice skeleton and the other elements remained in Paris or were sent back to Niamey with the holotype.

Some of the paratype bones were replaced in MSNVE 3714 with plaster casts, namely the left femur and the right coracoid. Also the original manual phalanges of GDF 381 have apparently been replaced with other phalanges in MSNVE 3714. All those bones were used by Taquet in his 1976 description of *Ouranosaurus*. We hypothesize that they were sent back to Niamey with the holotype in order to keep all the described material in the same place. It is unclear whether this was the fate of the pedal phalanges too, because of their confusing description in Taquet (1976). Of course, this remains speculative in absence of a written documentation attesting it.

Some elements of MSNVE 3714 are not present in the field map of GDF 381: the left coracoid, at least one ilium (probably the left), one pubis, one ischium, the right femur and the right tibia. Furthermore, the distal portions of the first two chevrons lack in the map but are present in the mounted elements and there are two dorsal vertebrae more in the mount than in the mapped skeleton.

The left coracoid could be one of the unidentified or partly emergent from the rock elements of the quite well-articulated shoulder girdle. Other elements were possibly still covered by rock when the map was drawn (e.g., the left ilium and the distal portion of the chevrons). However, it is not plausible that the right femur and tibia were still covered by rock because the skeleton exposed its right side and the exposed hind limb was the left one. We hypothesize that the well-preserved pelvic elements from the cluster 2 were used to integrate the pelvic region of GDF 381 in the mount. Also the right tibia could come from cluster 2, while the right femur could be GDF 302 of the referred material. The two dorsals in excess could come from another specimen or from part of cluster 2 that results to be poorly-traced in the field map and were added to the original vertebral column to maintain the dorsal count of 17 supposed for the holotype. Of course, this remains speculative in absence of a written documentation attesting it.

Therefore, MSNVE 3714 is most probably a composite (as most of the dinosaur mounts in the museums), although it is mostly made of the paratype of *Ouranosaurus nigeriensis*.

Also the osteohistological analysis suggests that the right femur is from an individual that is distinct from the paratype. According to a skeletocronological study on *Hypacrosaurus* (Horner, Ricqlés & Padian, 1999), the best growth record is recorded in the femur, followed by the tibia, dorsal ribs and neural spines. The humerus, the tibia and the dorsal rib growth records in MSNVE 3714 are comparable to each other suggesting that they could belong to the same individual (although the tibia is probably from a different one). The neural spine shows one or two LAGs more than the humerus, the tibia and the dorsal rib. However, this could be due to the lower amount of remodeling and lower density of Haversian systems found in the thin sections of the neural spine. So, also the neural spine could belong to the same individual of humerus, the tibia and the dorsal rib. Following Horner, Ricqlés & Padian (1999), the femur should present a higher number of LAGs, higher density of Haversian systems and a more advanced remodeling respect to humerus, tibia, dorsal rib and dorsal neural spine, if at the same growth stage, but it does not. The lack of outer LAGs and an EFS could be explained with superficial abrasion, but weathering cannot account for their total absence. Of course, we do not think that the cortex of a 920 mm long femur could be produced in a single year. Possibly, LAGs are absent because we sampled a

part of the bone were they are missing. However, the lack of Haversian systems and the higher density of vascularisation still suggest that the femur belong to a more immature individual than that from which the humerus, the tibia, the neural spine and the dorsal rib come from.

Differences with the holotype

Resuming what exposed in the description of MSNVE 3714, this and the holotype differ in some respects. Furthermore, comparison suggests that some mistakes are probably present in the description of the holotype and in the mount of the Venice specimen. MSNVE 3714 and holotype differs in:

1) The outline of the axis neural spine;
2) The morphology of the first dorsal vertebrae, suggesting that of the reconstruction of the proximal tract of the dorsal segment of the vertebral column of the holotype by Taquet (1976) is wrong. Probably, the dorsal count is 15 (14 dorsals and one dorsosacral) instead of 17 in both specimens and the trunk is consequently shorter;
3) The relative height of the spines of the sacral vertebrae;
4) Five or six more proximal caudals in MSNVE 3714 than in the holotype (four to five more than in *Iguanodon* and *Mantellisaurus*);
5) Some minor features of the caudal neural spines;
6) The regularity of the sloping in the neural spines and chevrons in the tail (minor in MSNVE 3714);
7) A more developed ulnar olecranon in MSNVE 3714;
8) The structure of the carpus (that of MSNVE 3714 is probably incomplete or wrongly assembled/reconstructed);
9) The shape of the metacarpals;
10) The position of the supracetabular process of ilium respect to the dorsal hump at the beginning of the postacetabular process (it occurs in a more cranial position in the holotype);
11) The robustness of the iliac peduncle of the ischium (more robust in MSNVE 3714) and the curvature of the shaft (straight in MSNVE 3714).

Most of them are minor differences probably due to intraspecific variability and possibly ontogeneny (however, we do not know the ontogenetic stage of the holotype). Others are caused by mistakes in the preparation or assemblage of the skeletal elements in both specimens. Puzzling is the morphological difference between the elements of the metacarpus. It could be speculatively explained with the intraspecific variability.

Finally, the description of the paratype manual phalanges by Taquet (1976) does not correspond with what observed in the Venice specimen. Possibly, the phalanges described by Taquet (1976) were replaced in MSNVE 3714 with other phalanges and the original were sent back with the holotype to Niamey or kept in the MNHN collection.

Ontogenetic stage of MSNVE 3714

Describing *Ouranosaurus*, Norman (2015, p. 62) writes that "this animal attained a length of 6–7 m when mature." Actually, nobody attempted to establish the ontogenetic stage of the individuals of *Ouranosaurus nigeriensis.* Taquet (1976) does not discuss the ontogenetic stage of GDF 300; he just reports that the elements of the axis of the holotype and the bones of the neurocranium are fused and their boundaries are difficult to recognize. Possibly, these features were considered as an evidence of maturity. However, no information about the obliteration of the neurocentral sutures in the other vertebrae are reported and no osteohistological investigation was attempted. Furthermore, the universal validity of obliteration of cranial sutures as evidence of osteological maturity has been argued by Bailleul et al (2016).

The holotype was estimated to be seven metres long (Taquet 1976, p. 175). The length of the mounted MSNVE 3714 is about 6.5 metres from the tip of the snout to the last preserved caudal vertebra. The total length was probably higher because the total count of the caudal vertebrae in large ornithopods usually ranges between 50 and at least 75 (Hone 2012; FMDV and MF, pers., obs.). The humerus, ulna and tibia of the Venice specimen are 92, 88 and 90% the length of those of the holotype, respectively. This is in agreement with the total length. The linear size of the first is therefore about 10% smaller than that of the holotype. Relative proportions of the two individuals can be seen in Figure 27. Also the size of the other/s individual/s used to complete MSNVE 3714 is approximately the same.

Establishing the ontogenetic stage of MSNVE 3714 was undertaken by the macroscopic observation of the evidence of osteological immaturity of the skeletal elements and by their osteohistological features. The neurocentral sutures in the mid-tail caudals (Fig. 12B-D) and in at least the last cervical vertebra (Fig. 6A) are not obliterated. The rough surface texture of the centrum near its articular facets in mid-caudal vertebrae (Fig. 12A) also indicates a cartilage covering and incomplete ossification. This is suggestive of immaturity (Bennett, 1993; Brochu, 1996; Irmis, 2007). The osteological immaturity of the paratype is supported also by the unfusion of ilia and sacrum, which is the case of the holotype too.

The increasing organization of vascular canals toward the outer surface, the presence of Haversian systems, the decreasing spacing between LAG's and the absence of an EFS observed in the thin sections of tibia, neural spine and dorsal rib suggest that these skeletal elements belonged to a sub-adult individual (sensu Horner et al., 2000). In the humerus, the increasing organization of vascular canals toward the outer surface, the decreasing spacing between LAG's and the absence of EFS, but the absence also of Haversian systems, is also compatible with a sub-adult growth stage sensu Horner et al. (2000).

The conclusions are that a 7 metres-long individual of *Ouranosaurus nigeriensis* (including a minimum of 20 missing distal caudals) was not fully grown, although probably close to adultness.

In crocodiles, the obliteration of the neurocentral suture during ontogeny starts in the tail and ends in the neck (posterior-anterior sequence of neurocentral closure; Brochu, 1996). This is the case of most ornithopods, although not all (e.g., Zheng et al., 2012), while that pattern was not followed in several saurischian dinosaurs (Irmis, 2007). Actually, there is considerable variation of both the sequence and timing of neurocentral suture closure within archosaurs (Irmis, 2007). The condition in *Ouranosaurus* suggests that it did not follow a simple posterior-anterior or anterior-posterior sequence of neurocentral closure and that obliteration occurred relatively late in the ontogeny, when the individual was close to adultness.

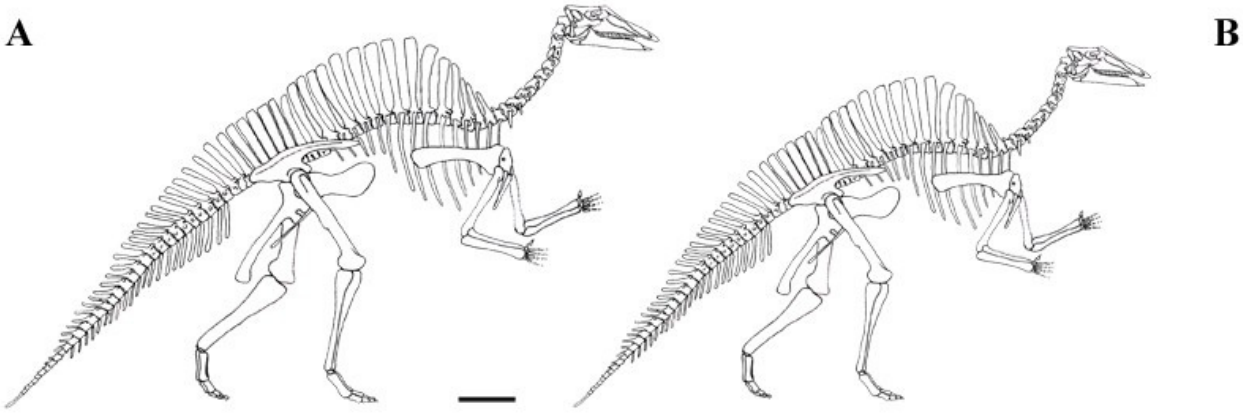


Figure 27: Size of the holotype and MSNVE 3714. Holotype (A) and MSNVE 3714 (B). Redrawn and modified from Taquet (1976). Scale bar equals 50 cm.

Osteohistological comparison with other ornithopods

The osteohistology of many ornithopod taxa has been studied, including *Hypsilophodon* (Reid, 1984; Chinsamy, et al. 1998); the "Proctor Lake ornithopod" (Winkler, 1994); *Orodromeus* (Horner et al., 2001; Horner et al., 2009); a "hypsilophodontid" from Dinosaur Cove/Flat Rocks, Victoria, Australia (Chinsamy et al., 1998; Woodward et al., 2011); *Rhabdodon* (Nopcsa, 1933; Reid, 1984, 1990; Ősi et al., 2012); *Mochlodon* (Ősi et al., 2012); *Zalmoxes* (Benton et al. 2010; Ősi et al., 2012); *Dryosaurus* (Horner et al., 2001; Horner et al., 2009); *Dysalotosaurus* (Chinsamy, 1995; Hübner, 2012); *Valdosaurus* (Reid, 1984); *Camptosaurus* (Horner et al., 2009); *Tenontosaurus* (Werning, 2012); *Iguanodon* (de Ricqlès et al., 2012); '*Telmatosaurus*' (Benton et al., 2010); *Edmontosaurus* (Reid, 1985); *Maiasaura* (Barreto et al., 1993; Barreto, 1997; Horner et al., 2000, 2001; Woodward et al., 2015); and *Hypacrosaurus* (Horner et al., 1999; Cooper et al., 2008).

Orodromeus shows longitudinal arrangement of the vascular canals, far less dense and complex than that present in more derived ornithopods like *Maiasaura* and *Hypacrosaurus* (Werning, 2012). Remodeling is scarce at the adult ontogenetic stage (Horner et al., 2009). LAGs occur in juvenile individuals; the highest LAGs number is two in sections with EFS (Horner et al., 2009; Werning, 2012). *Orodromeus* is therefore considered as characterized by slow growth (Horner et al. 2009; Werning, 2012). Rhabdodontids (*Zalmoxes* and *Rhabdodon*) and *Tenontosaurus* show higher growth rates than *Orodromeus*, as suggested by the woven bone forming the microstructure, more complex orientation of the vascular canals (radial or circumferential) and the absence of LAGs during the young ontogenetic stage (Werning, 2012). Remodeling is generally present only during the late growth (late sub-adult and adult ontogenetic stages) (Werning, 2012). Moreover, vascularization generally tends to decrease through ontogeny, showing a progressive passage between the initial rapid growth characterized by woven bone to the later slow growth indicated by lamellar bone leading to an EFS (Werning, 2012). More derived Iguanodontians (e.g. *Dryosaurus*, *Dysalotosaurus*, *Valdosaurus*, *Camptosaurus*, *Iguanodon*, *Telmatosaurus*, *Edmontosaurus, Maiasaura* and *Hypacrosaurus*) show the presence of fast deposited woven bone and vascular canals with a more complex and dense pattern (reticular or circumferential canals) (Reid, 1984; Horner et al., 1999; Horner et al., 2000, 2009; Benton et al., 2010; Hübner, 2012; Werning, 2012). Remodeling starts earlier during ontogeny in comparison to the other taxa reported above and widely spaced zones are still present during the sub-adult and adult ontogenetic stages (Reid, 1984; Horner et al., 1999, 2000, 2009; Benton et al., 2010; Hübner, 2012; Werning, 2012). Moreover, LAGs count observed in derived iguanodontians is generally lower than that generally found in the more basal taxa reported above, indicating that the somatic maturity was reached earlier (Reid, 1984; Horner et al., 1999, 2000, 2009; Benton et al., 2010; Hübner, 2012; Werning, 2012). The disorganized tissue type is still present during the sub-adult and adult ontogenetic stage and the passage to the EFS is abrupt (Reid, 1984; Horner et al., 1999, 2000, 2009; Benton et al., 2010; Hübner, 2012; Werning, 2012).

As expected, *Ouranosaurus* shares similar microstructural patterns with derived iguanodontians. The woven bone and the high vascular density with an alternated reticular and circumferential arrangement present in the bone microstructure suggest a fast growth. Remodeling is already present in the sub-adult ontogenetic stage. A fast growth is also supported by the widely spaced LAGs with the presence of the same bone structure and type of vascularization within the zones. The faster growth is phylogenetically coincident with the taxonomical diversification of the derived iguanodontians and their increase in body size (Werning, 2012). It is still unclear whether

the higher growth rates are a consequence or a cause of the increase in body size in the clade (Werning, 2012). However, the large body size of *Tenontosaurus,* coupled with slow growth rates in comparison to those of dryomorphs, suggest that faster growth is a consequence of the body size and not the opposite, because *Ouranosaurus* has an estimated length comparable to that of *Tenontosaurus*, but shows faster growth. As an alternative, *Tenontosaurus* may represent the maximum size an ornithopod could grow with the basal slow growth rates (Werning, 2012).

The function of the back 'sail' of *Ouranosaurus*

Among the Dinosauria, hyperelongation of the neural spines reaches its maximum in the dorsal vertebrae of the theropod *Spinosaurus aegyptiacus* (see Stromer, 1915; Ibrahim et al., 2014), which also lived in northern Africa during the Cretaceous, although 15-20 million years later than *Ouranosaurus*. Its neural spines start to elongate from the first dorsal, reaching the maximum height in the last dorsal; spine height decreases from the first sacral on. They formed a sort of a 'sail' on the back of the animal. The basal segment of those dorsal neural spines is greatly expanded craniocaudally (Ibrahim et al., 2014). The middle segment is narrow and the apical one is expanded with the craniocaudal margins diverging apically, but to a lesser extent than in *Ouranosaurus* (Ibrahim et al., 2014). The spine height is up to ten times the centrum height. The apical portion of the spine has sharp cranial and caudal edges; it is marked by thin vertical striae, and is spaced away from adjacent spines (Ibrahim et al, 2014). According to Ibrahim et al. (2014), the 'sail' had probably a social function, given the low density of vascularization of the bone pointing against a thermoregulatory function. Recently, new skeletons of the giant ornithomimosaur *Deinocheirus mirificus* have shown that this, weird-looking theropod has tall neural spines in the middle dorsals (Lee et al, 2014). The neural spines of the proximal dorsals are relatively low, but spine height increases progressively up to the last dorsal, which has a neural spine that is 8.5 times taller than its centrum height. The base of the neural spines is not craniocaudally expanded as in *Spinosaurus.* All six sacral neural spines are tall as well, and, except for the first sacral, the apical parts of the spines are fused into a midline plate of bone with a straight dorsal margin in lateral view (Lee et al, 2014). No hypotheses have been proposed about the function of the 'sail' in this dinosaur.

In *Ouranosaurus nigeriensis*, the elongation of the neural spines is not restricted to the trunk as in *Spinosaurus* and *Deinocheirus*, but extends to the proximal caudal region. Occasionally, the base of the neural spine (actually, the prespinal lamina) is slightly expanded in the mid-posterior dorsals like in *Spinosaurus*, but this expansion occurs only cranially. The apical portions of the neural spines seem to have vertical striations, like in *Spinosaurus* and *Deinocheirus*. The external cortex is relatively thinner than in *Spinosaurus* (Ibrahim et al., 2014), with a thicker spongiosa. Sharpey's fibers (which are related to the attachment of muscles and ligaments) occur only in the proximal (basal) part of the neural spine in MSNVE 3714. Based on comparison with the musculature of crocodiles and birds (Tsuihiji, 2005; Organ, 2006a), this suggests that muscles of the *M. transversospinalis* group attached just above the base of the neural spines, connecting them at their cranial and caudal edges. The absence of Sharpey's fibers in the thin sections from the middle and apical portions of the spine, plus the absence of muscle insertion marks on the bone surface may indicate that muscles of the *M. transversospinalis* group were not attached to the entire surface of the spines. In extant archosaurs, some muscles of the *M. transversospinalis* group insert on the dorsal margin of the spines; insertion is supposed to occur at the base of the spines in the low-spined synapsid *Sphenacodon* (see Huttenlocker et al., 2010). In *O. nigeriensis*, the apparent basal attachment of those muscles may be related to the hyperelongation of the neural spine. However, caution is due because the absences of Sharpey's fibers and superficial insertion marks could be caused by taphonomic factors and preparation and restoration as well. Ossified tendons have not been found along the vertebral column of the paratype and are reported

as scarcely present in the holotype (Taquet 1976). Ossified tendons along the epiaxial skeleton are an ornithischian general feature, are usually abundant in iguanodontians and organized in a rhomboidal lattice structure (see, for example, Forster, 1990; Organ, 2006a, 2006b; Norman, 2011; Wang et al., 2010). They are associated with the subunits of *M. transversospinalis* (Organ, 2006a). Their scarce development in *Ouranosaurus* also supports a peculiar development of the muscles of the *M. transversospinalis* group in this dinosaur.

In iguanodontian ornithopods the dorsal neural spines are usually much shorter than those of the theropods *Spinosaurus* and *Deinocheirus*. In *Iguanodon bernissartensis*, the taller neural spines are 2.43 times their centrum height in mid-dorsals (Prieto-Marquez, 2008). Neural spines are proportionally taller in a few other ornithopod taxa, but never as in *Ouranosaurus*: the ratio spine/centrum height is > 4.3 in *Morelladon beltrani* (see Gasulla et al., 2015), 4.5 in GPIT 1802/1-7 (Iguanodontia indet.; Pereda-Suberbiola et al., 2011) and 4.18 in *Barbsoldia sicinskii* and *Hypacrosaurus altispinus* (see Prieto-Marquez, 2008).

In *Ouranosaurus*, the 'sail' reaches its maximum height in the mid-proximal dorsals, then decreases up to the sacrum to slightly increase again in the last sacral and first caudals, decreasing gradually in the rest of the tail (a sinusoidal outline; Figs 1 and 5). In *Barsboldia sicinskii* holotype, which preserves the dorsal, the sacral and the proximal caudal vertebrae, the outline of the dorsal portion of the 'sail' is nearly semicircular and only slightly asymmetrical; the sacral and caudal spines reduce their height gradually moving caudally. Due to the fragmentary condition of the specimens, the shape of the 'sail' is unknown in the other taxa mentioned above. The vertebral column of *Hypacrosaurus* is still undescribed. The cast of a composite juvenile individual of *H. altispinus* exhibited at the Royal Tyrrell Museum of Drumheller (Canada) shows a 'sail' where the mid-distal dorsal, the sacral and the first caudal spines have the same height (the curvature of the 'sail' is actually that of the vertebral column). If that assemblage is reliable, its 'sail' is unlike that of *Ouranosaurus*. At the present state of knowledge, the combination of size and shape of the 'sail' of *O. nigeriensis*, is therefore unique.

The only work dealing also with the function of iguanodontian 'sails' is that by Bailey (1997), who supported a thermoregulation role.

The tall spines of *Ouranosaurus* were plausibly a support for a structure like a membrane or a hump (Bailey, 1997). Of course, the definition of such a structure is hampered by the lack of preservation of the soft tissues that were covering the spines. However, the presence of a keratinous covering directly on the bone can be excluded, because of the absence of Sharpey's fibers in the middle and apical portions of the neural spine (Huttenlocker et al., 2010). Vascularization is not particularly dense in neural spines; this does not support a relationship between elongation and increase of blood input through the bone for thermoregulatory (contra Bailey, 1997) or display purposes. A thermoregulatory role of the 'sail' to keep high and constant the body temperature as in ectotherm tetrapods would be unnecessary, if the relatively high growth rates observed in *Ouranosaurus* are related with homeothermy. A social (display) role of the structure like that hypothesized for *Spinosaurus* is possible but, obviously, it is speculative and cannot be tested.

CONCLUSIONS

MSNVE 3714, the Venice specimen of *Ouranosaurus nigeriensis* is the paratype of the species GDF 381- MNHN, found in 1970 and collected in 1972 by a French team, although it lacks some of the original bones (i.e., the left femur and the right coracoid), which were replaced by plaster copies. The field map of the bones found in 1970 shows the presence of at least two individuals, the most complete of which was the paratype. Probably, some skeletal elements from the second individual and possibly other sources (i.e., femur GDF 302) were added to the paratype material

to complete the mounted skeleton for exhibit purposes. Portions of most of the original skeletal elements have been reconstructed or covered by resin during the restoration process.
The Venice specimen shows some minor differences with the holotype that probably reflect intraspecific variability. Its carpus appears to be badly reconstructed and the original manual phalanges possibly replaced by other elements. Other differences are caused by mistakes in the reconstruction of the vertebral column. Probably *O. nigeriensis* had 14 dorsal and one dorsosacral vertebrae, 20 proximal caudal vertebrae, more than the supposed 17 mid-caudal vertebrae and a total caudal count much higher than that represented by the preserved caudal vertebrae. Puzzling are the morphological differences in the metacarpus.
Based on histological analysis, (the first performed on *Ouranosaurus*, a fast growth rate is assumed for this taxon. The samples show features suggesting a sub-adult ontogenetic stage for the paratype and the other/s individual/s used to assemble MSNVE 3714. Immaturity is suggested also by unfusion and superficial texture of some skeletal elements.
The study of MSNVE 3714 suggests also some thoughts about the way scientifically important specimens are managed in the process leading from their discovery to their storage or exhibit in a museum. Loss of scientific information should be avoided as much as it is possible. Often preparation for exhibition purposes reduces the scientific value of the specimen, hiddening osteological features. Even worse, the scientific value of the specimen is often dramatically affected by the total absence or availability of documentation about the material prior and during preparation (including detailed information on the field provenance of each skeletal element, photographs, detailed field notes, detailed description of the preparation and restoration works and materials used in them; Dalla Vecchia et al., 2015). That process must be always under scientific control and documented. All necessary information should be attached to the specimen as the pedigree is attached to a purebred dog.

Supporting Information

Tab.1 - Measurements of the skeletal elements of MSNVE 3714, *Ouranosaurus nigeriensis*.

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