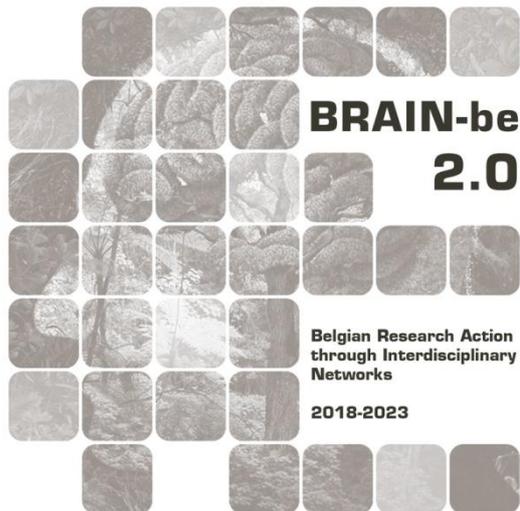


Iguanodon 2.0

**Shepherding the 'Belle-Epoque' Bernissart Iguanodon collection
into the 21st Century**

PASCAL GODEFROIT (IRSNB) – CHRISTOPHE MALLET (ULiège) – PIM KASKES (VUB)

Pillar 2: Heritage science



NETWORK PROJECT

IGUANODON 2.0

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into the 21st Century

Contract - B2/202/P2/Iguanodon 2.0

FINAL REPORT

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Published in 2025 by the Belgian Science Policy Office
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Pascal GODEFROIT (IRSNB); Christophe MALLET (ULiège); Pim KASKES (VUB). *Shepherding the “Belle Epoque” Bernissart Iguanodon collection into the 21st century* - Final Report. Brussels: Belgian Science Policy Office 2025 – 30 p. (BRAIN-be 2.0 - (Belgian Research Action through Interdisciplinary Networks))

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ABSTRACT

Context

Discovered in 1878 in a Belgian coal mine, the Bernissart Iguanodons, represent one of the most iconic palaeontological finds in history. Over 25 complete and articulated skeletons of *Iguanodon* were unearthed, offering the first full view of dinosaur anatomy. These fossils, housed at the Royal Belgian Institute of Natural Sciences (RBINS), are central to both scientific research and public exhibition. However, due to their fragile condition—mainly caused by pyrite degradation—there is an urgent need for advanced conservation and documentation techniques.

Objectives

The Iguanodon 2.0 project aimed to:

1. Digitally document the entire Bernissart collection using high-resolution 3D scanning.
2. Analyze past restoration techniques and their impact.
3. Assess the current physical and chemical integrity of the fossils.
4. Develop a preventive and curative conservation protocol.
5. Enhance scientific and public access to the collection through digital platforms.

Results

1. Digitization and 3D Modeling

- Over 2,000 bones were scanned, resulting in 4 TB of data.
- A complete digital atlas of *Iguanodon bernissartensis* is being created.
- The data enabled studies on intraspecific variation, pathologies, and skin impressions.

2. Paleohistology and Geochemistry

Non-invasive techniques (CT, μ CT, μ XRF, LIBS, FTIR, AFM-IR) revealed:

- The presence and localisation of 30 mineral phases, including pyrite.
- Insights into diagenetic processes and restoration materials.
- Isotopic data suggesting *Iguanodon bernissartensis* was non-migratory, living in a restricted area with well-marked seasonality.

3. Mechanical Integrity

- Finite Element Analysis (FEA) showed the iconic thumb spike could withstand up to 5000 N, supporting its use as a defensive or social tool.

Conclusions

The Iguanodon 2.0 project:

- Set a new benchmark for fossil conservation.
- Digitally preserved a national scientific treasure.
- Enabled new research avenues in palaeobiology and taphonomy.
- Provided interactive public access to the collection via web platforms and museum installations.

It aligns with RBINS’s strategic goals for 2020–2025, enhancing the heritage value, conservation, and accessibility of its collections.

Keywords

Bernissart Iguanodons, conservation, scientific heritage, 3D digitization, geochemical analyses, valorisation.

1. INTRODUCTION

In 1878, the Bernissart coalmine produced one of the greatest palaeontological discoveries ever: more than 25 complete articulated skeletons of the dinosaur Iguanodon. As the first complete skeletons ever discovered, they gave scientists and the public an impressive demonstration of what dinosaurs really looked like. As early as 1878, the Bernissart treasure became one of the major assets of the Belgian scientific patrimony and was entrusted to the care of the Belgian State and deposited at the Musée royal d’Histoire naturelle in Brussels (now, RBINS). The astonishing array of Iguanodon skeletons remains one of the most impressive displays of dinosaurs worldwide and the main attractor for visitors in the RBINS Museum.

Despite their huge size and massive morphology, the Bernissart Iguanodons are extremely fragile. After their death around a swamp 125 million years ago, their carcasses were rapidly covered by clay sediments and their decomposition occurred in an oxygen-free environment. In such conditions, sulphate-reducing bacteria produced hydrogen sulphide by hydrolysis of the organic matter present in this environment and its combination with detritic and biogenic iron led to the crystallization of abundant pyrite in bone pores. In contact with damp air, the pyrite oxidises to form limonite and iron sulphate, inevitably leading to the disintegration of the bone containing them (Leduc, 2012). As soon as they were extracted from the Bernissart pit, this process led to the embrittlement of Iguanodon bones. Once they arrived in Brussels, the bones were impregnated with a carpenter’s glue-based gelatine and the pyrite was systematically curretted from the bones. Some vertebrae contained more than 1 kg of pyrite, and some long bones, up to 3 kg! Despite their fragility, the best-preserved Iguanodon specimens were mounted in a lifelike gait and exhibited to the public as soon as 1883. Between 1933 and 1937, all the skeletons were dismantled to treat important damages resulting from 30 years of exposure to varying temperatures and humidity sustained as museum exhibit. A mixture of alcohol and a coccid insect-based lacquer (shellac) was used to soak the bones in the hope of stopping the degradation of pyrite. However, at the time, the Janlet Wing was in utter disrepair after WWII; in the 1970’s, the mounted Iguanodon skeletons were even covered by plastic sheeting as it was regularly raining inside their cage! Consequently, from 2004 until 2007, a full preservation treatment was needed: the Iguanodon skeletons were again completely restored at the occasion of the renovation of the Janlet Wing. All the bones were reinforced by a solution of acetone and synthetic polyvinyl acetate alcohol and new glass cages were constructed to protect the skeletons. On that occasion, the RBINS realized that previous restoration campaigns, at the end of the 19th century and in the 1930’s had not been documented, which led to an uncomfortable feeling of working in the dark.

The 19th Century decision to display the complete Bernissart Iguanodon collection in the permanent galleries of the Museum evidently had important long-term implications on the preservation of this inestimable treasure. Limiting further pyrite degradation and hampering its growth requires controlled temperatures and hygrometry, as it is the case today. Regular thorough inspection of the bones to detect fragilized areas is complicated by the iron structure enchasing the specimens and by the fact that their skulls stand over 4 meters. Moreover, the Bernissart Iguanodons constitute one of the key reference collections for dinosaur scientists, who regularly request access the original specimens for their studies. Each visit inside the Iguanodons cages poses a risk to security of the visitors and of the precious fossils. Therefore, a full scale, state of the art preservation and conservation project is imperative.

2. STATE OF THE ART AND OBJECTIVES

In 1878, the now world-famous Bernissart mine produced one of the greatest palaeontological discoveries ever: more than 20 complete articulated skeletons of the dinosaur *Iguanodon*. As the first complete skeletons ever discovered, they gave scientists and the public an impressive demonstration of what dinosaurs really looked like. As early as 1878, the Bernissart treasure became a major asset of the Belgian scientific patrimony and was entrusted to the care of the Belgian State and deposited at the Musée royal d’Histoire naturelle (now, Royal Belgian Institute of Natural Sciences, RBINS) in Brussels. The astonishing array of *Iguanodon* skeletons remains one of the most impressive displays of dinosaurs worldwide, and the main attractor for visitors in the RBINS Museum.

The study of the Bernissart Iguanodons was entrusted to a young naturalist, Louis Dollo, who completely revolutionized the scientific approach to fossil material. While studying in detail several parts of the *Iguanodon* skeletons, Dollo was adopting a forensic approach to understanding these fossils. He developed a new style of palaeontology that became known as palaeobiology: palaeontology can be expanded to investigate the biology, and by implication the ecology and the behaviour of extinct creatures. Dollo first examined the basis for the creation of a new species, *Iguanodon bernissartensis*, as distinct from *I. mantelli*, originally described from the Lower Cretaceous of England. Dollo established an overall similarity in anatomy between the smaller and more gracile species from Bernissart (RBINS R57) and the remains of the ‘Mantel-piece’ collected in Maidstone, Kent (England) and therefore by convention identified RBINS R57 as *Iguanodon mantelli* (now, *Mantellisaurus atherfieldensis*). With respect to the larger species, Dollo circumvented the problems of sexual dimorphism by demonstrating a wide range of anatomical differences: skull proportions, size of narial openings, shape of the orbit, size and shape of the infratemporal openings, shape of scapular blade, completeness of external coracoid foramen and overall shape of the coracoid, size of the humerus, proportions of the manus and pollex, shape of anterior pubic blade. Dollo finally concluded that the larger specimens merited being considered as separate species, *I. bernissartensis*. Dollo’s final contribution to the *Iguanodon* story was published in 1923 as a synthetic study, to honour the centenary of Mantell’s original paper. He identified *Iguanodon* as an ecological equivalent of the giraffe. Its inferred “kangaroo-like” posture enabled it to reach high into the trees to gather its fodder, which it was able to draw into its mouth by using a long, muscular tongue. The image of Iguanodon as a gigantic kangaroo-shaped creature, as depicted by Dollo, became iconic for more than 60 years, and was reinforced by the distribution of full-sized replicas of mounted skeletons of Iguanodon from Brussels to many of the great museums around the world.

Despite their huge size and robust morphology, the Bernissart Iguanodons are extremely fragile. After their death around a swamp 125 million years ago, their carcasses were rapidly covered by clay sediments and their decomposition occurred in an oxygen-free environment. In such conditions, sulphate-reducing bacteria produced hydrogen sulphide by hydrolysis of the organic matter present in this environment, and its combination with detritic and biogenic iron led to the crystallization of abundant pyrite in bone pores. In contact with damp air, the pyrite oxidises to form limonite and iron sulphate, which inevitably led to the disintegration of the surrounding bone. As soon as the bones were extracted from the Bernissart pit, this process led to their embrittlement. Once they arrived in Brussels, the bones were impregnated with a carpenter’s glue-based gelatine and the pyrite was systematically curretted from the bones. Some vertebrae contained more than 1 kg of pyrite, and some long bones up to 3 kg! The remaining cavities were filled with ‘carton-pierre’, a stable mixture of paper, glue and talc.

It was rapidly decided to mount the best-preserved *Iguanodon* specimens in a lifelike gait. In 1882, the first complete specimen (individual ‘Q’, IRSNB R51, the holotype of *Iguanodon bernissartensis*) was assembled and mounted by L. De Pauw and his team in the St. George Chapel of the Nassau Palace. The bones were suspended from scaffolding by ropes that could be adjusted so as to obtain the most lifelike position for the complete skeleton, which was then supported by an iron framework. This first mounted specimen was publicly exhibited in 1883 in a glass cage constructed in the interior court of the Nassau Palace. In 1884, the cage was lengthened to accommodate a second specimen (individual ‘T’, IRSNB R57, the only complete specimen of *Mantellisaurus atherfieldensis*) and a selection of fossils of the Bernissart flora and fauna. However, the Nassau Palace Chapel quickly became too small for the storage, preparation, mounting and

exhibition of numerous bulky skeletons. In 1891, the Iguanodons were transported to the new location of the Musée royal d'Histoire naturelle in the Leopold Park. In 1899, five specimens were mounted in a glass cage close to the entrance of the museum. From 1902 onwards, the whole Bernissart exhibition was permanently installed in the newly constructed Janlet Wing of the MRHNB. Eleven complete specimens were exhibited in a lifelike gait, while twelve more-or-less complete and eight fragmentary individuals were displayed in situ within the rock matrix.

Between 1933 and 1937, all the skeletons were dismantled to treat important damages resulting from 30 years of exposure to varying temperatures and humidity sustained as museum exhibits. A mixture of alcohol and a coccid insect-based lacquer ('shellac') was used to soak the bones in the hope of stopping the degradation of pyrite. However, the Janlet Wing was in utter disrepair after WWII; in the 1970's, the mounted *Iguanodon* skeletons were even covered by plastic sheeting as it was regularly raining inside their cage! Consequently, from 2004 until 2007, a full preservation treatment was needed: the *Iguanodon* skeletons were again completely restored at the occasion of the renovation of the Janlet Wing. All the bones were reinforced by a solution of acetone and synthetic polyvinyl acetate alcohol and new glass cages were constructed to protect the skeletons. On that occasion, the RBINS realized that previous restoration campaigns, at the end of the 19th century and in the 1930's had not been documented, which led to an uncomfortable feeling of working in the dark.

Based on more than 300 bone fragments sampled on the 'en gisement' specimens at the occasion of this last restoration campaign, the bone diagenesis of the Iguanodon skeletons was investigated. Using x-ray diffraction and EDS analysis, about 30 mineral phases in the fossil *bones* of the Bernissart Iguanodons were identified. During burial, recrystallisation took place: the slightly crystallized carbonated apatite-(CaOH) (the mineral phase of fresh-bone tissue) was replaced by well crystallized carbonated apatite-(CaF) currently present in the *Iguanodon* bones. Whereas some minerals infiltrated the bones during cavity filling by the sediment (detrital quartz, “argillaceous” phyllosilicates, anatase and rutile), others are authigenic and precipitated in the cavities during burial (pyrite, barite, sphalerite, celestine and to a lesser extent quartz) or after the exhumation (other sulphates, oxides and/or hydroxides). Pyrite is the most abundant authigenic mineral in the Iguanodon fossil bones, making them very brittle.

At the occasion of his first visit, on April 13, 1878, the MRHNB head preparator Louis De Pauw promised the Bernissart coalmine director Gustave Fagès that the skeletons collected in the Sainte-Barbe mine will be safely consolidated, restored and mounted should those fossils be donated to the Belgian state (and the MNHNB, of course !). The present project aims at respecting De Pauw's initial promise, which mark the starting point of the scientific research around the Bernissart collection, and at ensuring the long-term preservation and storage of this unique and fantastic collection, while augmenting its scientific value, and rejuvenating its potential for science communication. We will use a battery of cutting-edge methods to understand the nature and extent of past restorations, evaluate the current physical integrity of the specimens, propose a new and consistent protocol to monitor, and carry out the first digital restoration of the Bernissart Iguanodons. We propose:

- (1) Detailed, macro and micro-scale 3D cartographies of selected specimens to identify the restored zones, the preferential accumulation areas of pyrite inside the bones, and the restoration techniques used at the end of the 19th Century and during the 1930's; for this we will use X-ray imaging, CT and μ CT scans.
- (2) Palaeohistological analyses of the fossilized bone tissue using non-destructive methods (micro- and nano-CT scans) for assessing nano-scale damage caused by pyrite and its derivative minerals to the bone microstructure. To document restoration techniques used at various times in history, and catalogue the damage done by pyrite decay, high resolution (25 μ m) major and trace element geochemical maps will be produced with non-invasive and non-destructive techniques such as micro-X-ray fluorescence (μ XRF), Laser induced breakdown spectroscopy (LIBS) and Infrared spectroscopy coupled atomic force microscopy (AFM-IR).
- (3) In parallel with (2), full quantitative geochemical characterization of the 'fresh' and treated bones, using XRD and infrared spectroscopy (FTIR, AFM-IR) will be carried out, using XRD and FTIR spectroscopy. Also coupled with virtual histological analyses, an investigation into whether the different treatments really stabilized the bone microstructure and the damages done by pyrite will be conducted.

(4) A bone prosthesis protocol, where large and heavy bones will be surface scanned, retrodeformed where necessary and 3D printed in their accurate in-vivo shape. Prostheses and retrodeformed bones will be 3D printed and added to exhibit specimens to ensure optimal conservation of bones at risk and maintain like-like public displays

(5) Identification of the preferential fragility zones in the fossilized *Iguanodon* bones. The data from the CT, μ CT scans, and surface scans will be subjected to mechanical numerical modelling. These analyses will be used to identify preferential fragility zones in the Bernissart Iguanodon skeletons, to be treated in priority by further restoration programs. This approach will lead in the future to more targeted and focused conservation measures.

(6) Those analyses will serve to establish a preventive and curative conservation protocol to ensure the long-term preservation of the entire Bernissart collection, which also contains dozens of turtles, crocodiles, fish, and plants. In the same time, fragilized Iguanodon bones will be moved to safer repositories and replaced by printed 3D models. This project will establish a benchmark for curative conservation of dinosaur skeletons across the globe.

This project is fully in line with RBINS 2020-2025 Strategic Option for Collections: “By 2025, we will have improved the Heritage Value of our collections and databases in the national and international contexts: higher quality, better conservation and easier access”. The Bernissart collection is also the core of Research Theme 3.1. “Meso-Cenozoic biostratigraphy and ecosystem evolution” of RBINS Research Strategy 2018-2022.

3. METHODOLOGY

Since their discovery, the fossil bones of the Bernissart Iguanodons were treated for conservation in several empirical ways. Those successive treatments considerably slowed down but did not stop the alteration of pyrite; as a result, the *Iguanodon* skeletons must be regularly inspected for degradation by the RBINS technical team. During the last restoration campaign, the bone diagenesis of the Bernissart Iguanodon skeletons was investigated. Based on this study, we now have a clearer view about the diagenetic processes leading to the current mineral composition of the *Iguanodon* bones, which constitutes a solid base in the perspective to develop better conservation techniques for the fossils.

To achieve this objective, we need further quantitative information about the extent and precise protocol of past restorations and about the distribution of the different mineralogical phases leading to the fragility of the fossil bones. Different methods of geochemical analyses potentially complement each other in understanding the chemical composition and structure of the examined materials. Some techniques, such as Infrared spectroscopy, are more suited to document organic chemical bonds, whereas others (μ RF, LIBS), are more suited for detecting specific elemental compositions. Our approach is aimed at being inclusive and complementary towards these different geochemical aspects.

To understand the chemistry of the *Iguanodon* bones, we need to carry out analyses on treated bone samples, previously taken at the occasion of the last restoration campaign of the collection, and also on samples of ‘fresh’ *Iguanodon* bones, which were never treated, discovered at the occasion of the 2002-2003 drilling campaign in the Iguanodon Sinkhole at Bernissart. The reason for this is that we are interested in the composition of the entire bone, inside and out, and also because unfortunately none of the devices can hold entire bones in their measuring stations. This approach increases the scientific value of the samples, and the non-invasive geochemical methods we apply also preserve them for future analyses.

In this project, we will also repurpose 3D scanning and modelling approaches used in research in morphology and applied physiotherapy for the conservation of fossil heritage to take fossil digitization a giant leap further. Our approach is twofold:

- (i) Obtain (ultra) high-quality 3D data for Bernissart Iguanodons using a combination of high-resolution laser surface scanning, computed tomography (CT), and micro-CT (μ CT).
- (ii) Use 3D modelling software and 3D printers to generate and print prostheses and replacement bones. These replacement bones can be retrodeformed versions of the original fossils, where cracks, compression, shear, etc. have been removed.

To document restoration techniques used at various times in history, and catalogue the damage done by pyrite decay, it is therefore necessary for RBINS to collaborate with high-ranked laboratories that possess the necessary equipment and capacities for carrying out those important non-destructive and non-invasive analyses: CT, μ CT and surface scans, non-destructive palaeohistology, micro-X-ray fluorescence (μ XRF), laser induced breakdown spectroscopy (LIBS) and infrared spectroscopy (FTIR and AFM-IR, see Methodology). It is of course impossible to investigate in detail all the Bernissart Iguanodon skeletons within the limited time of this project. We shall therefore concentrate our efforts on two important specimens: the holotype of *Iguanodon bernissartensis* (RBINS R51) and the referred specimen of *Mantellisaurus atherfieldensis* (RBINS R57). All those macro- and microscopic information will be further integrated to produce 3D virtual models that will be analysed by engineers to identify preferential fragility zones in the Bernissart Iguanodon skeletons to be treated in priority by further restoration programs. This approach will lead in the future to more targeted and focused conservation measures. Integrating all those cutting-edge methodologies for establishing a preventive and curative protocol to ensure the long-term preservation of fossil material is a pioneering approach that has never been explored or tested.

Gender will, of course, be seriously considered as a transversal dimension throughout the project. It is unfortunate that the promoters of the projects are all males – this partly results from decades-old biases in academia – but any sex will have equal opportunities to be recruited as contractual researchers in the scope of this project. Special attention will also be given to gender sensitive points. It is indeed established that gender problems often originate in such in private-time vs. work-time inadequacies in the work sphere. We

will ensure that all daily activities (flexible working hours, teleworking availability, meetings during working hours, etc.) and exceptional activities (workshops and other meetings in Belgium and abroad, etc.) maintain an ideal work-life balance for all members of this project. The team leaders are well aware about the issues and behaviours involved in harassment and abuse (see for example the recent #Respect campaign at ULiège uliege.be/cms/c_11108564/fr/campagne-respect); they are therefore responsible for any problems or issues that could possibly arise within their respective teams, and will enforce a strict compliance of rules and regulations regarding this pressing issue. BeWiSe, the Association of Belgian Woman in Science (<https://www.bewise.be>), has its headquarters at the RBINS, and this project will support BeWiSe and will act according to its recommendations. A better gender balance is present in the follow-up committee of the present project. This project does not involve humans as research objects, so gender is not relevant to the research topic, methodology, and outcomes.

1. Surface scanning and 3D bone modelling:

We aim to digitize the external surface of all individual bones of two important specimens: the holotype of *Iguanodon bernissartensis* (RBINS R51) and the referred specimen of *Mantellisaurus atherfieldensis* (RBINS R57), as well as all damaged/at risk bones in all other specimens. We will use a Creafom HandySCAN 300, a portable laser scanner that can generate precise models (0.2mm resolution) of bones within 10-30 min (including post-processing). This scanner is available from ULiège; the ULiège team has already generated several hundred surface scans over the last three years, ranging from miniscule teeth to giant sea reptile skulls.

Following the scanning procedure, we will use 3D modelling softwares (Creafom VXmodel™; 3D Systems Geomagic DesignX™) to fill cracks and missing parts in original bone models. Subtracting the original model from the new cleaned model will then yield a digital “prosthesis” that will be 3D printed and placed into the original bone. 3D scanning has been widely used in the physiotherapeutic industry, rising in popularity and application for orthosis and prosthesis manufacture for human rehabilitation. For this project, bones that are crushed and deformed will be retrodeformed using 3D CAD software, using pristine specimens as a morphological guide, and then eventually 3D printed at life size. Printing fees will not be covered by the present project, but by other RBINS cost centres managed by OD Public. Thus, biologically realistic displays (e.g. opened/closed mouths, flexed necks, gripping hand claws, etc.) will be made possible with minimal risk to the most fragile boney elements.

2. CT scanning and virtual paleohistology:

Paleohistology is the study of fossilized tissues, usually biomineralized such as bone, teeth and eggshell, and in rare cases also preserved soft tissues. A previous investigation with invasive paleohistological techniques yielded valuable information on the iguanodon growth and species diversity. With this technique, we also obtained a localized glimpse on the complex preservation history of these bones. Cross sections immediately revealed the use of plaster to stabilize the bones, and unsettling large amounts of pyrite infill. However, these snapshots are only informative for a very small area within a bone, and it remains unclear how the pyrite is distributed throughout the entire bones, which complicates conservation efforts. Currently, blooms of pyrite decay are treated and removed whenever they are noticed on the bone specimens by staff members. This is only to prevent further damage to the specimen, which by this stage has already been affected to some degree. To document the extent of pyrite and other potentially hazardous metal sulfide infill as well as the nature of the plaster and ‘carton pierre’ stabilizing residues within the bones, we need to perform non-invasive Computed Tomographical scans at ULiège, and μ -CT scans at RBINS on selected bones. The CT and micro CT scanners are timeintensive, and will be used on bones that are either very small s (see above).

CT scanning will be operated at ULiège, using a Siemens Somatom Confidence Sliding Gantry, while μ CT scanning will be processed at RBINS using the RX EasyTom (RX Solutions, Chavanod, France; <http://www.rxsolutions.fr>) and the XRE UniTom (XRE, Ghent, Belgium, <https://xre.be/>). The RX Easytom machine has a maximum resolution voxel size of 4 μ m, the XRE one of 500 nm. Scanning can be completed with different beam voltages up to 150 (RX) and 120 (XRE) kV and with a range of different filters (e.g. copper, aluminum, stainless steel, et cetera ...) at different thicknesses. EasyTom Micro CT Scanner allows to scan fossil material both in Laminography and Tomography (usual CT scan technique). Laminography is an X-ray technique based on the relative motion of an X-ray source, a detector, and an object where the X-ray source and the detector are moved synchronously in opposite directions. This non-destructive technique is generally used for inspection of large flat electronic components. The application of this technique in the

field of palaeontology was pioneered at RBINS, to study the fine anatomy of the skull of a basal paravian dinosaur. This technique permits to scan eccentric regions of a fossil trapped in a slab of rock with a very high resolution (up to 16 μm) and is useful for accessing fine anatomical structures, including the tiny cavities. Coupling the laminography and the tomography techniques allows particularly detailed and fine bone reconstructions.

The following licenses (and freewares) are currently available at RBINS for segmentation, volume rendering, and 3D modelling: AmiraTM 5.3.3. (ThermoFisher ScientificTM), Dragonfly ORS, Avizo, GeoMagic (©09.2019), Blender, Gom Inspect, MeshLab, MeshMixer, LHPFusionbox and Agisoft Metashape. CT-scan data analysis and segmentation will be performed at a calculation station (CS) adequately set to process and store the volume of scan data, and exclusively devoted to this project. The CS will be located at the office space supplied by the RBINS, with no risk of external interference that may slow down its development.

3. Geochemistry:

Since their discovery at the start of the Belle Epoque era, the *Iguanodon* specimens have been treated with various consolidants, including “Shellac” and “Colle de Lyon”. Colle de Lyon, or animal glue, is a gelatinous protein colloid glue made of animal connective tissues, through hydrolysis of collagen. It is therefore striking that collagen signal was not detected in a Bernissart Iguanodon sample studied with Raman spectroscopy. However, the study was performed without control techniques to verify obtained results, and exemplifies the need for an in-depth analysis with different methods. Our approach is aimed at being inclusive towards different chemical aspects of the materials. Therefore, a quantitative geochemical mapping of the Bernissart Iguanodon bones will be conducted using complementary approaches: micro X-Ray Fluorescence spectroscopy, Fourier Transformed Infrared spectroscopy (FTIR) and atomic force microscope infrared spectroscopy (AFM-IR) available at VUB, and Laser induced breakdown spectroscopy (LIBS) at UMONS. μXRF uses an X-ray source to induce a fluorescence effect in the sample, whereas infrared spectroscopy and LIBS use a laser to induce a signal. μXRF generates spectrograms with peaks characteristic for each chemical element, whereas IR and LIBS generate spectra, as well as high resolution ($\sim 25 \mu\text{m}$) elemental maps, with peaks typical of molecular vibrational energies.

Micro-XRF is a totally non-destructive technique to carry out elemental mapping of major and trace elements down to a resolution of 25 μm . The approach proposed here uses the new generation Bruker M4 Tornado table-top energy-dispersive scanner (Bruker Nano GmbH, Berlin, Germany). X-ray fluorescence (XRF) allows the characterization of the elemental abundances in a sample from the fluorescence spectrum emitted after the sample is excited by an X-ray source. The micro-XRF technique combines the advantages of an automated microscope-guided high-precision movable stage system with the spectral resolution of a high-energy X-ray source to allow fast, nondestructive and high-resolution (25 μm) elemental analysis. To achieve the small spot size needed for high-resolution measurements, X-rays from either the rhodium or tungsten source are focused using a polycapillary lens. This focuses the X-ray beams with minimized energy loss, enabling the instrument to yield well-resolved XRF spectra of small surfaces on the sample without the use of a synchrotron radiation source. The polycapillary focusing and XYZ moving stage of the table-top IXRF device enable the formation of line scans and two-dimensional maps on the sample surface. The dimensions of the vacuum chamber of the micro-XRF device make it possible to measure sample surfaces of up to 200 mm \times 160 mm. No sample coating is necessary, and the method is fully nondestructive allowing, the measurement of rare and unique samples from museum collections, such as fragment of Iguanodons bones of max. 20 cm long.

An excitation energy (30 W) and a vacuum chamber enable the generation of better-resolved point spectra and results in more accurate measurements in the lower energy part of the spectrum ($< 5 \text{ keV}$). Different source filters are included in the system to increase the spectral resolution for elements in the central energy range (5 to 15 keV) of the XRF spectrum. Source filters are thin (1m scale) films of metal placed in front of the X-ray source to block X-rays of certain energy ranges in order to reduce noise (and increase signal to noise ratio) in other regions of the spectrum (for example, 5 to 15 keV) where fluorescence peaks of elements of interest appear. These improvements allow quantitative trace elemental analysis to be carried out rapidly in a nondestructive manner for all elements heavier than sodium.

FTIR, AFM-IR. Recently acquired Fourier Transformed Infrared (FTIR) micro-spectroscope (Hyperion 4000, Bruker Nano Systems, Hercules Foundation 2016), and atomic force microscopy infra-red spectroscopy (AFM-IR) (NanoIR2, Anasys Instruments, <http://www.anasysinstruments.com/products/nanoir2/>, Hercules

2016) make it possible to apply a wide range of infrared spectroscopic resolutions. The FTIR at the AMGC lab works with attenuated total reflection and provides a spatial resolution at micrometer scale. It will serve as initial probe level for finding organic residues in our samples, and select samples for higher resolution investigation with AFM-IR. AFM-IR, also available at VUB, is a recent technique allowing in situ determination of macromolecules at very high sub-micrometer spatial resolution. It also works by irradiating a region of a sample with light from a tunable infrared laser but instead measures the resulting photothermal expansion of the sample with the cantilever tip of an atomic force microscope (AFM). Thermal expansion of the sample occurs only when molecular vibrations excited by absorbed IR photons from the tunable laser source return to their ground vibrational state through the transfer of energy in the form of heat to the lattice. Because the signal detected in AFM-IR is in proportion to the sample absorption, absorption spectra obtained by the AFM-IR technique correlate very well to conventional IR absorption spectra collected in transmission. Using an AFM tip to detect the thermal expansion pulse is the key to measuring IR absorption below the conventional diffraction limit. The AFM tip can sense and map variations in thermal expansion from IR absorption to better than 100 nm spatial resolution. Further, the AFM detection sensitivity is sufficient to enable chemical identification of samples at a scale of tens of nanometers. The machine thus makes it possible to characterize nanometer scale differences in functional groups (e.g. carboxylic acid, amine, amide groups) present at the surface of materials, thereby allowing deeper investigation of organic residues such as collagen. Collagen may be present from two potential sources: preserved collagen of the dinosaur, collagen derived from the preservatives used in historic times, or both. If present, we can characterize the molecular configuration of the collagen and distinguish the two with the IR method, as fossil collagen usually undergoes Maillard reactions during deep time. We do not expect to see this kind of browning reaction in the historical animal glue collagens.

LIBS. Laser-Induced Breakdown Spectroscopy uses a high-power pulsed laser for in-situ chemical analysis with spot sizes ranging from 10 to 500 μm . When exposed to a high laser power density, typically $> 1 \text{ GW/cm}^2$, a very small portion of the irradiated material surface (of the order of ng) is vaporized and forms a luminous plasma that can be analysed with a fast optical spectrometer. LIBS spectra are rich, carrying both elemental and molecular but also (plasma-induced) luminescence information about the sample. In particular, impregnation resins can be detected in parallel with elemental analysis based on the emission of molecular CN, even if carbon-bearing minerals such as calcite are present. The intensity of atomic and molecular emissions in laser-induced plasmas usually covers several orders of magnitude, which yields highly-contrasted chemical maps in which the distribution of both major and trace-elements can be simultaneously observed. The main advantages of LIBS are its high-speed measurement capability (a few seconds or less for spot analysis); its relative simplicity, which allows its easy integration in portable instruments; and its quasi-non-destructive nature, as photo-ablation craters are barely or not visible to the naked eye. In addition, there are virtually no requirements for sample size and preparation. Because of these advantages, among others, LIBS was implemented in the analytical system (ChemCam) of the Curiosity rover, which is currently investigating the surface of planet Mars. The next rover, ready to be launched in July 2020 is also equipped with a LIBS hyphenated with a Raman detector (SuperCam). UMONS has developed an in-house LIBS system 4 years ago based on a Nd:YAG laser at 266, 532 and 1064 nm wavelength. The system is successfully operating for spot analysis and geochemical profiling or mapping, including on large samples (up to 500 x 150 mm). This year, a small-footprint, fast DPSS laser will be implemented, which will add portability to the system along with other improvements (faster analysis and double-pulse LIBS capability). LIBS is very complementary to μXRF , as it is more sensitive to light elements, but may suffer from spectral interferences when many heavy elements are present. Several manufacturers of portable instruments now propose both XRF and LIBS bundled in one carrying case to ensure the best of both worlds. Arsenic (see 2.2, position regarding impact) is easily detected by LIBS, which will be useful for visualizing the dispersion of the mixture used for the first arsenic-loaded treatment. Current research in the frame of the Brain-be Screen-LIBS project shows that in Pb-Zn ores, arsenic (and thallium, which is even more toxic) can be detected below detection limit of a typical EDS (Energy Dispersive Spectroscopy) system (about 0.1%).

4. Mechanical Integrity of the Bernissart Iguanodon Bones (incl. Finite Element and/or Finite Difference Analysis):

In the past, *Iguanodon* bones were treated against pyrite disease by applying up to three different impregnating materials (to prevent oxidation of microscopic pyrite scattered into the bone material), and by picking macroscopic pyrite nodules. To date, it is not known how these treatments have affected the

mechanical integrity of the bones. In particular, pyrite picking resulted in the removal of substantial amount of original bone material, as part of the pyrite replaced original bone; this most likely introduced mechanical weaknesses in some specimens. In addition, it is currently unknown as to what extent the chemical treatments have improved the mechanical properties of the bones, and to what depth the treatments have penetrated.

In order to understand the mechanical behavior of an isolated bone in the skeleton, numerical modelling can be used by applying either finite element (FEA) or finite difference methods (FDA). Both approaches need a good 3D description of the object and the physical and mechanical properties of its components. Based on the position of the bone in the skeleton, one can assess the weight transmission in the structure, and then the forces to be applied at the boundaries of the object. Different combinations of solicitations will be simulated in order to assess the stresses and strains fields and the possible failure or damaging mechanisms. The object will be meshed in a way such that the composing elements can reproduce as close as possible the varying composition. Scanning techniques like CT-scan can help in building the geometry and determining the materials composing the object.

4. SCIENTIFIC RESULTS AND RECOMMENDATIONS

WP1: 3D Modelling the individual bones (Surface scans; ULiège and RBINS):

This Work Package forms the base of the Iguanodon 2.0 project and its output far exceeded its initial objectives and our expectations. From September 2021 to the end of August 2022, we proceeded to the complete surface 3D digitization of **all the specimens** of *Iguanodon bernissartensis*, although it was initially intended to digitize only the holotype of *Iguanodon bernissartensis* (specimen R51) and the mounted specimen of *Mantellisaurus atherfieldensis* (specimen R57). We spent the first 6 months of the project elaborating a reliable and replicable digitization method, with acquisition tests using various 3D scanning methodologies (photogrammetry, laser scanner, turntable scanner, handled structured-light surface scanner, with multiple resolutions). After this initial phase mainly led on the holotype of *I. bernissartensis*, we developed a protocol based on the use of portable structured-light surface scanners (Artec Eva and Artec Spider). These scanners are easy to handle, able to work at high speed and to capture texture information, while proving to be poorly sensible to the brightness of the bones from the Bernissart site. After the completion of the digitization of the two specimens R51 and R57, we decided to continue the digitization campaign on all the other specimens. By the end of August 2022, all specimens exhibited at the Institute of Natural Sciences (both those mounted in bipedal position and those exhibited “en gisement”) were disassembled, digitized bone by bone, and reassembled in their glass cages. The specimen exhibited at the “Musée de l’Iguanodon” in Bernissart, also belonging to the RBINS collections, was also digitized in early 2022. During the second half of 2022, after the completion of the digitization of the exhibited specimens, we decided to complete the data acquisition by scanning the specimens stored in the collections of the RBINS. This phase, focusing only on well-preserved bones, was completed by early 2023. We estimate that between 90 and 95% of the dinosaur remains from the Bernissart sinkhole have been digitized in high-precision 3D. This data acquisition represents more than **2,000 3D models** weighing more than **4 TB of raw data**. Both the raw 3D data and the reconstructed 3D models are stored in the long-time storage service hosted at the Institute of Natural Sciences, ensuring their preservation for the next decades.

Now that most of the Belgian remains of *Iguanodon* have been digitized, new scientific questions are being explored, and opens up decades of future research. Results of WP1 were already exploited in the scope of the following scientific researches:

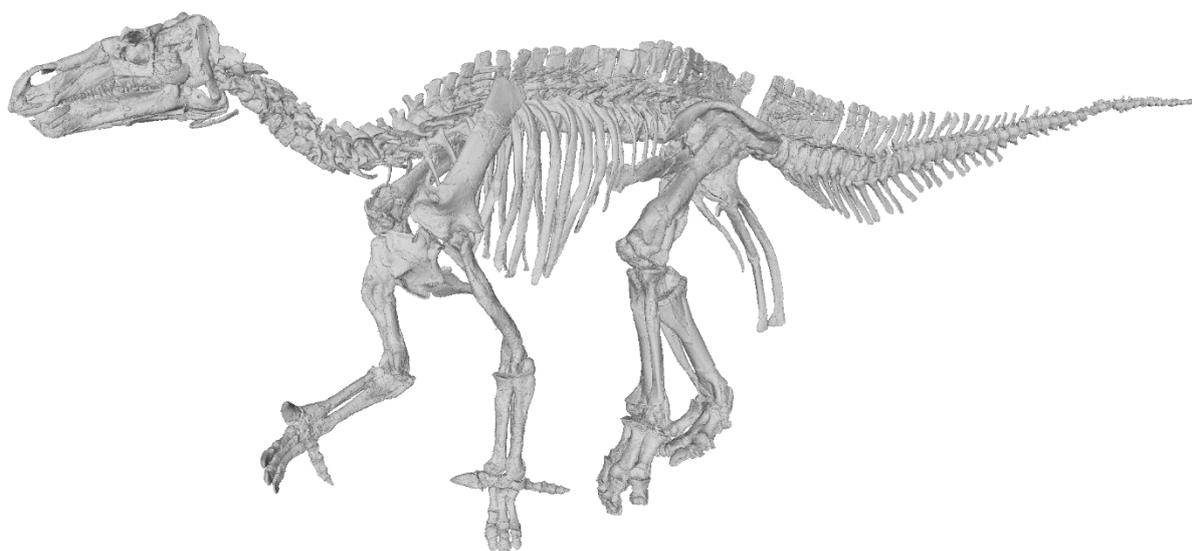


Figure 1: complete 3D reconstitution of the holotype of *Iguanodon bernissartensis* (specimen R51) in quadrupedal stance.

1. **Comprehensive digital 3D atlas of *Iguanodon bernissartensis***, using the Orthanc platform currently being implemented at RBINS for the gestion of virtual collections (Fig. 1). This 3D atlas of the morphology of *Iguanodon* will be published together with an explanation of the detailed digitization protocol, summarizing the aims, the difficulties and the solutions encountered during the 3D digitization campaign. This publication will settle a common basis for all following scientific works on the palaeobiology of *Iguanodon* (Fig. 2), and, more generally, the digitization of populations of large fossil vertebrates.

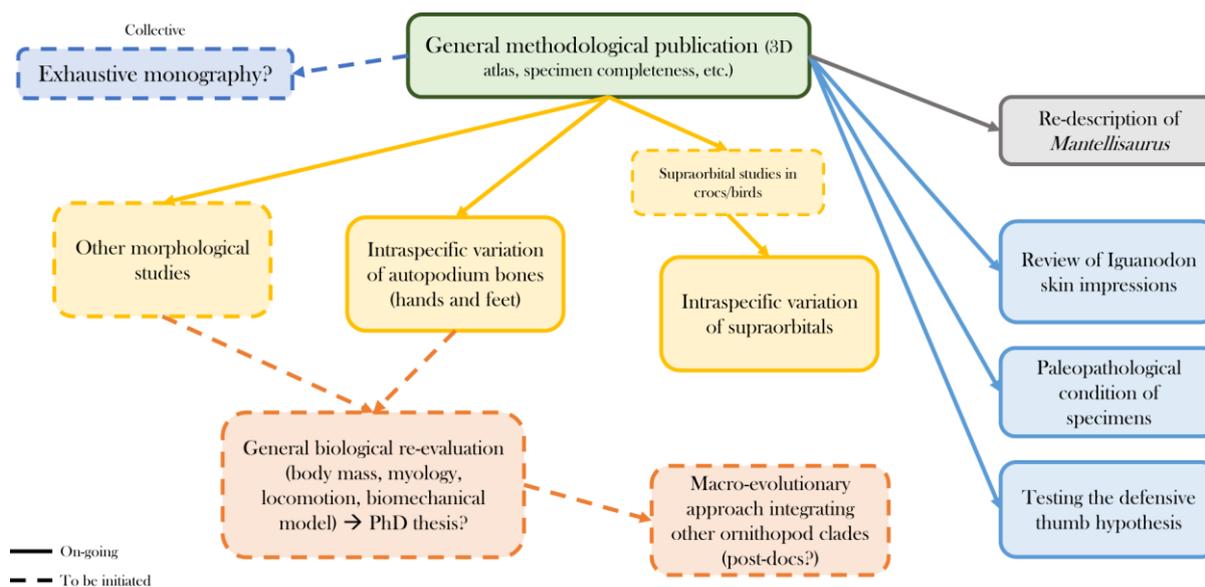


Figure 2: provisional workflow for the next years regarding the 3D acquisition and data analysis.

2. **Intraspecific variation within *Iguanodon bernissartensis***. The 3D dataset gathered during the project allowed us to develop an innovative approach of 3D geometric morphometrics to explore the shape variation of isolated bones in *Iguanodon bernissartensis*, to quantify and qualify this intraspecific variation and to understand its origin. This exploration focused first on autopodium parts (Fig. 3), notably through the Master’s thesis of Loralie André (supervision V. Fischer and C. Mallet), and on supraorbital bones (Fig. 4). Our first results tend to indicate that, beyond taphonomic deformations, an underestimated intraspecific variation of bone shape does exist within the species *I. bernissartensis*, likely associated with phenotypic variation between adults and subadults and/or between males and females. These preliminary results plead for more awareness of intraspecific variability when dealing with dinosaur bones in general, and ornithopod bones in particular, to better inform on the populational versus systematic signal on bone shape variation. This exploratory work led to communications and posters in international congresses (see paragraph 6.) and will soon lead to publications in international peer-reviewed journals. In parallel, the exhibited specimen of *Mantellisaurus atherfieldensis* is redescribed with a complete segmentation of its skull and its postcranial remains. The 3D data will also nourish a PhD project on the locomotion of *Iguanodon*, which we will submit for funding next academic year (Fig. 2).

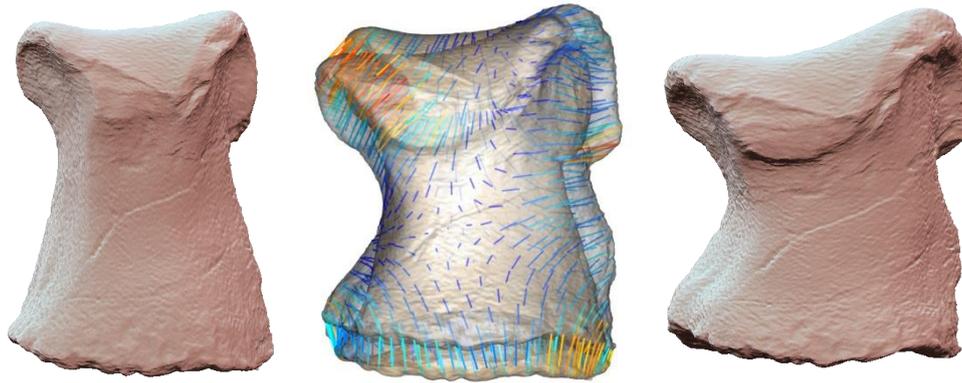


Figure 3: shape variation observed in the first phalanx of the digit 2 of the pes in *Iguanodon bernissartensis* using 3D geometric morphometrics. After placing landmarks on the 3D volumes, a Generalized Procrustes Analysis allows the creation of a morphospace and the visualization of the shape variation along different axes of variation. Visible differences of shape (torsion and symmetry) are observable between the theoretical shapes of the minimum (left) and maximum (right) axis of variation. Central figure shows the superposition of the two shapes associated with the relative displacement and intensify of displacement of the landmarks (vectors) between these minimum and maximum.

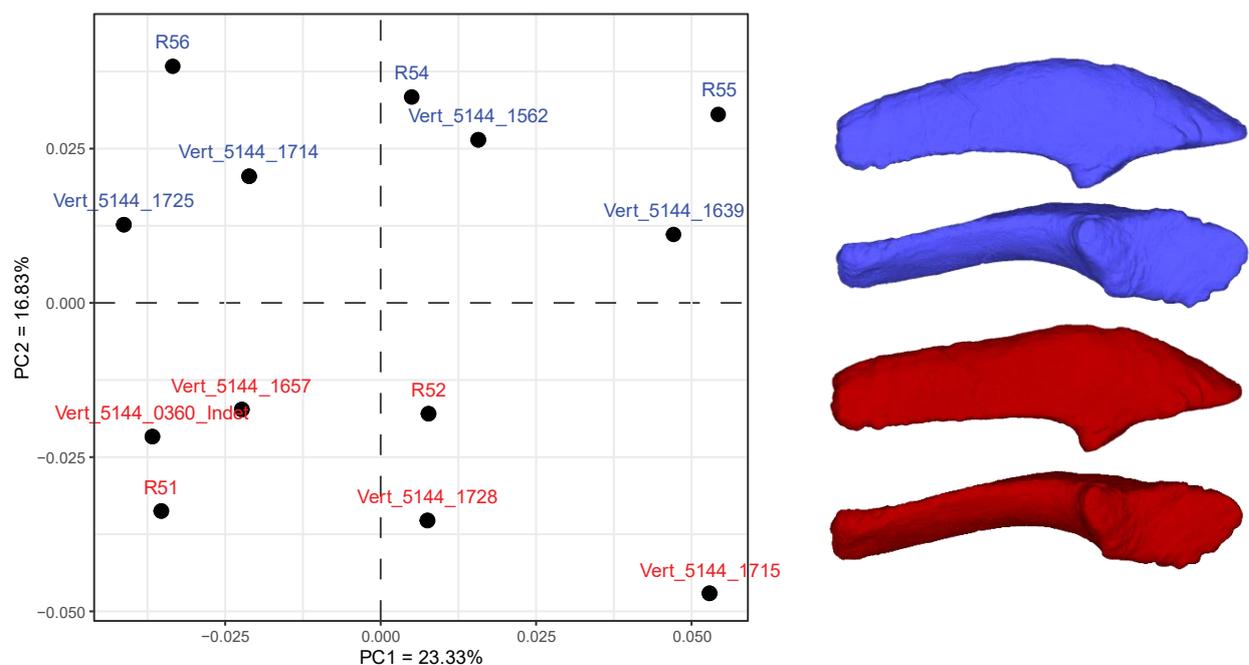


Figure 4: shape variation of the supraorbitals of *Iguanodon bernissartensis* using a 3D geometric morphometrics approach. Left: morphospace of the 13 specimens included in the analysis, showing a marked separation between two groups along the second axis of variation (PC2). Right: meanshape of the supraorbital in each of the two groups (red and blue) highlighted by the morphospace.

3. **Palaeopathological condition of the Bernissart Iguanodons.** This project was also a unique opportunity for Filippo Bertozzo to investigate in detail the health of the Bernissart *Iguanodon* individuals and of the population as a whole. Surprisingly, although most of the individuals discovered are fully mature individuals, few pathologies (mainly healed fractures) could be identified. It means that the populations was obviously quite healthy. These observations contrast sharply with what can be observed among more advanced Late Cretaceous iguanodontian populations the duck-billed dinosaurs (Hadrosauridae). Concretely, the palaeopathological

observations collected in the scope of the Iguanodon 2.0 project have already been exploited as comparative material in a paper investigating frequent injuries observed in the proximal portion of the hadrosaurid tail, and that were tentatively interpreted as fractures caused by the male crushing the backbones of the female during mating (Bertozzo et al., 2025).

4. **Review of skin impressions.** Besides their skeletons, patches of skins are also preserved around some of the Bernissart Iguanodon specimens. They have been analysed using both photogrammetry and multispectral imaging at RBINS. Preserved skin patches are mainly concentrated on the proximal portion of the tails. They show small tubercles (between 1 and 3 mm in diameter, with slight variation in shape), with irregularly positioned flower-like feature-scales. The same patterns are also represented by isolated, fragmentary skin material. Whilst small and nearly homogeneous tubercles are shared with hadrosaurids and other iguanodontian taxa (*Mantellisaurus*, *Tenontosaurus*), the flower-like feature-scales are less common, found only in the hadrosaurid *Lambeosaurus*. A shared feature between non-hadrosaurid ankylopollexians and hadrosaurids comprises the proportions between body size and tubercles, with small scales in a large body. We hypothesize that the smaller tubercles allowed more flexibility in the body of these iguanodontians. Small tubercles are also present in non-ornithomimid ornithischians, such as in *Psittacosaurus*. Nonetheless, tubercles increase in size with body volume along ceratopsian evolution, in contrast with the skin homogeneity in the large, derived ornithomimids. Concretely, those skin observations collected in the scope of the Iguanodon 2.0 project have already been exploited in a paper describing the exceptionally-preserved integument in a new ‘spiked’ iguanodontian from the Lower Cretaceous of China (Huang et al., in press).

WP 2. CT scanning and virtual palaeohistology (IRSNB):

In the course of the Iguanodon 2.0 project, the RBINS microCT scanner was used to study the thumbs of RBINS R51 and of Vert-5144-1657, the pathological chevron in RBINS R56, as well to investigate the intracranial structures of a new iguanodontian from the Lower Cretaceous of Portugal and the tiny skull of a *Jeholosaurus* specimen from the Lower Cretaceous of China. We also established a collaboration with John van Gulik from Canon Facility in Zoetermeer (Netherlands) for CT scanning the pathological dorsal vertebrae in R51 and the skull of R57. Those data were already exploited in the scope of the following scientific researches:

1. **A gracile Bernissart Iguanodon desperately looking for an identity.** Since its discovery in 1879, the ‘gracile’ Bernissart Iguanodon RBINS R57 has been referred to different species: *Iguanodon mantelli* (Dollo, 1882), *Iguanodon atherfieldensis* (Norman, 1986), *Dollodon bampingi* (Paul, 2008), *Iguanodon seeleyi* (Carpenter & Ishida, 2010), and *Mantellisaurus atherfieldensis* (Norman, 2012). With the exception of Dollo and Norman, they author never had access to the skull of this specimen, mounted on the specimen in exhibition, so part of their arguments were based on characters that couldn’t be easily checked. Combined surface and Ct scanning of the skull of R57 (Fig. 5) is therefore a unique opportunity to propose an in-depth and richly illustrated revision of

this skeleton and firmly identify this specimen. A large monograph is currently prepared by F. Bertozzo and P. Godefroit, to be published in 2026.

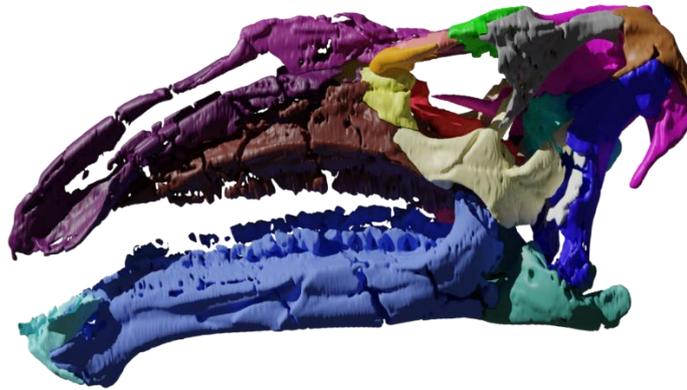


Figure 5: Digital reconstruction of the skull of RBINS R57, in left lateral view.

2. **Reconstruction of the intracranial structures of *Cariocecus bocagei*, a new iguanodontian dinosaur from the Lower Cretaceous of Portugal.** In the scope of the Iguanodon 2.0 project, we reconstructed the endocast, cranial nerves and inner ear of *Cariocecus bocagei* via segmentation of micro-computed tomography scanning, showing similarities with other iguanodontian dinosaurs, including the Bernissart specimens (*Iguanodon bernissartensis* and “*Mantellisaurus atherfieldensis*”). We propose the most detailed inner ear soft-tissue reconstruction for a dinosaur so far, including the macula and sub-branches of the vestibulocochlear nerve, supported by the extant phylogenetic bracket (Fig.6; Bertozzo et al., 2025).

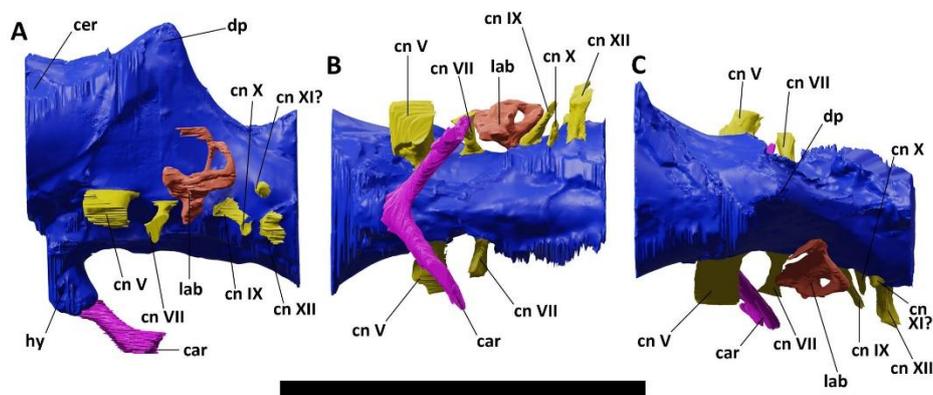


Figure 6: Digital reconstruction of the endocast of *Cariocecus bocagei*, a new iguanodontian from the Lower Cretaceous of Portugal in left lateral (A), ventral (B) and dorsal (C) views. Scale bar = 10 cm (From Bertozzo et al., 2025).

3. **Digital reconstruction of the skull of *Jeholosaurus shangyuanensis*, a small basal ornithopod from the Lower Cretaceous of China.** Using the RBINS microCT scanner, we studied a well-preserved skull of a juvenile ornithopod from the Liaoning Province of China. This skull reveals interesting details about the skull anatomy of basal ornithopods and, therefore the ancestral condition for iguanodontians. All the skull elements were segmented and extrapolated for description (Fig. 7). The endosseous labyrinth is tentatively reconstructed, although the disarticulation of the neurocranial bones hampers its complete reconstruction. Thanks to the analysis of previously undescribed inner neurocranial bones (such as the prootics, the exoccipital/ophistotic, basioccipital, and basisphenoid), we improve the previous phylogenetical scoring for *J.*

shangyuanensis, and propose an updated perform a phylogenetical analysis of ornithopods, including iguanodontians.

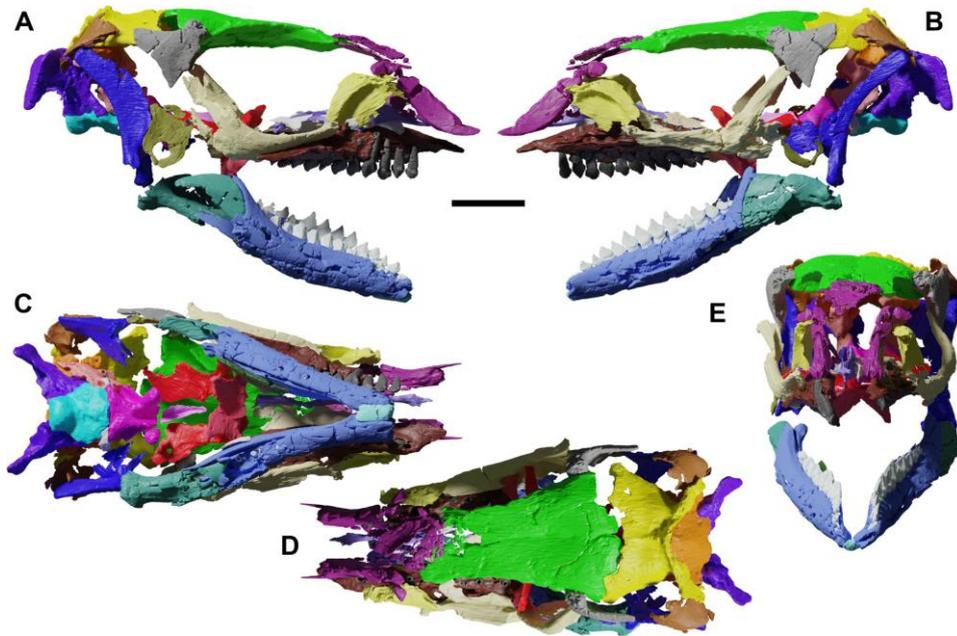


Figure 7: Digital reconstruction of the skull of Jeholosaurus shangyuanensis from the Lower Cretaceous of China in right lateral (A), left lateral (B), ventral (C), dorsal (D), and rostral (E) views. Scale bar = 1 cm (From Bertozzo et al., 2025).

WP3: Geochemical analyses (VUB, UMons, IRSNB):

During this project, the major and trace element geochemistry of *Iguanodon* bones and teeth was analysed at the VUB and UMons in order to get a better idea of the palaeoenvironment, taphonomy and diagenetic history of the *Iguanodon* bonebed at Bernissart. In conjunction, the geochemistry (carbon isotopes and major/trace element composition) of *Iguanodon*-bearing sediments from the Ber-3 drill core were analysed for additional details on the sedimentary environment, and the geological age of the fossil-rich deposit.

Details are listed below:

1. Detailed micro-X-ray fluorescence (μ XRF) and Laser Ablation Inductively Coupled Plasma Mass Spectrometry (LA-ICP-MS) has been carried out on *Iguanodon* bone and teeth samples to infer the taphonomic history of the Bernissart bonebed. In total 18 bones, 2 teeth and 3 coprolites have been analysed by Pim Kaskes (VUB-AMGC) in 2023 with non-destructive μ XRF analysis (Bruker M4 Tornado), focussing on high-resolution (25 μ m) semi-quantitative element mappings and quantitative linescans. A subselection of this (8 bone fragments and 1 tooth) were analysed using LA-ICP-MS (Teledyne Iridia laser ablation system equipped with an Agilent 8900 ICP-QQQ-MS Advanced Applications) in February and December 2024. Point linescans at 25 μ m were performed for quantitative analysis of Ca, Sc, Mn, Zn, Sr, Y, Ba, REEs, Hf, Pb, Th, and U, and complemented with a series of bone apatite standards. The μ XRF trace element mappings and linescans of 18 bone and tooth fragments, belonging to eight specimens distributed throughout two bone-bearing zones, revealed similar intra-bone trends with steep declines in light rare earth elements, such as cerium, with increasing cortical depth. Such a homogeneous geochemical pattern throughout different regions within the Bernissart bonebed (at -322 m depth) suggests that the individuals shared a similar taphonomic and diagenetic history, strengthening a scenario of rapid burial of the skeletons over a depositional scheme involving longer-term attritional processes. LA-ICP-MS transects revealed rapidly

declining REE profiles although relatively low in absolute concentrations and with relatively low REE ratios such as for La/Yb. This likely hints to a rapid burial in a lacustrine environment (see Fig.8-10).

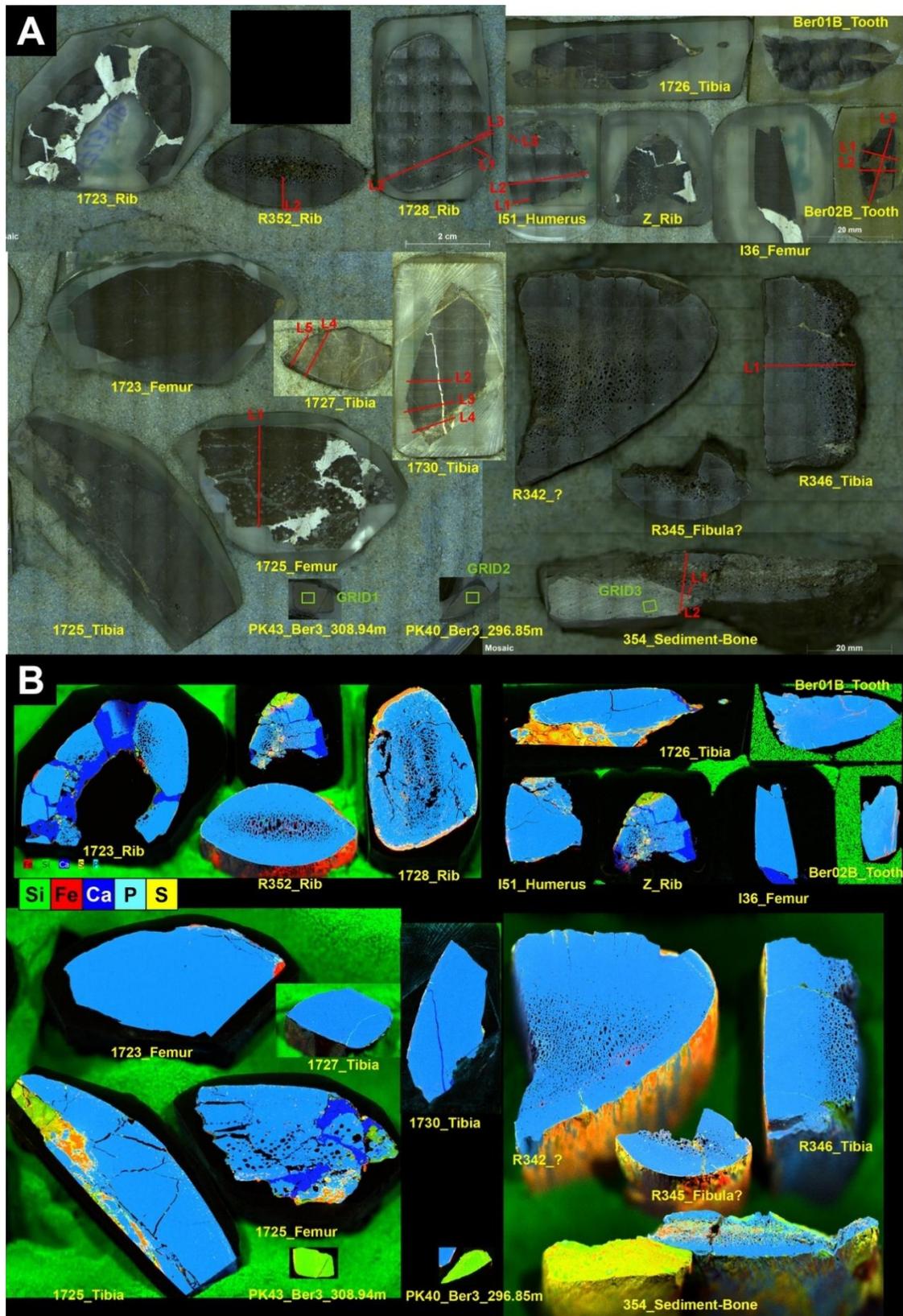


Figure 8. A) Overview of Iguanodon bone and tooth samples analysed with μ XRF during this project, B) these are visualized as multi-element maps (FeSiCaPS) (Kaskes et al., in prep.).

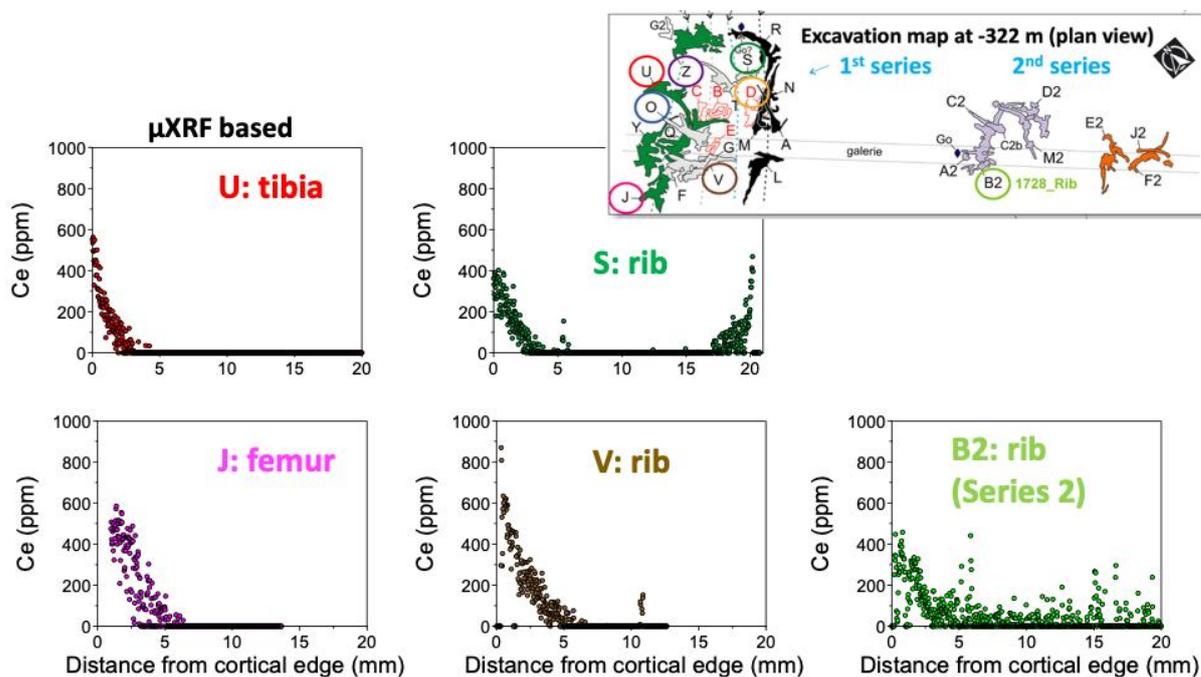


Figure 9. Overview of Iguanodon bones analysed with μ XRF linescans to obtain concentration profiles of REEs such as cerium, showing in general steep intrabone concentration profiles (Kaskes et al. 2024 – NHM conference).

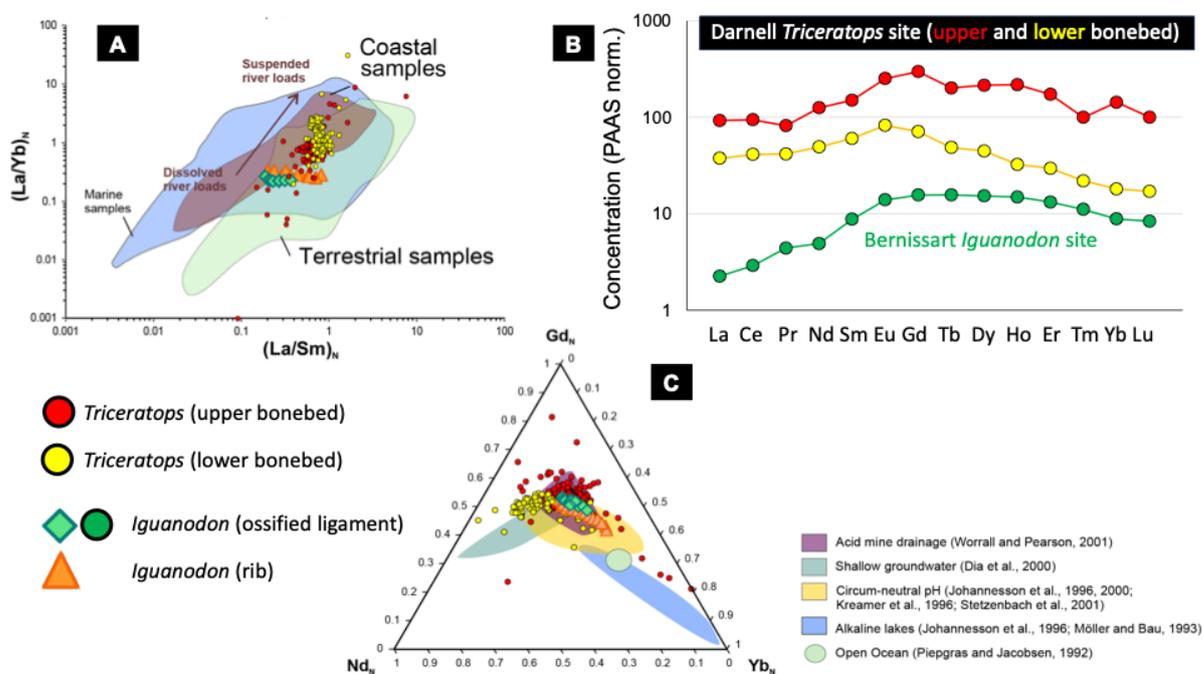


Figure 10. Discrimination diagrams (from Decrée et al., 2025; Kaskes et al. 2024 - EWLA) based on LA-ICP-MS analyses on Iguanodon bones, compared also to a comparative bonebed study of Triceratops. (A) $(La/Yb)_N$ vs. $(La/Sm)_N$ diagrams [normalization values from Taylor and McLennan (1985)]; fields are taken from Herwartz et al. (2013b); (B) Spider diagram showing REE patterns of the Bernissart site compared to two Triceratops bonebed values. (C) Nd_N – Gd_N – Yb_N ternary diagram of REE signatures (normalised to the North American shale composite; Gromet et al., 1984).

2. The Ber-3 drill core – penetrating the Bernissart *Iguanodon* sinkhole, has been sampled and high-resolution organic carbon isotope ($\delta^{13}\text{C}$) analysis has been performed on clay-rich sediments to finetune the chronology of the bonebed. In total, 152 sediment samples of the Ber-3 drill core were powdered by Pim Kaskes and his bachelor student Kasper Sleypen (VUB), and analyzed for major and minor element concentrations using μXRF spotanalysis, followed by organic carbon isotope ($\delta^{13}\text{C}$) and total organic carbon analysis (using a Euro EA Elemental Analyzer (CHNS) - Euro Vector HT-PyrOH combustion system coupled to a Nu-Instruments Horizon 2 isotope ratio mass spectrometer). Chemostratigraphy of the Ber-3 drill core showed a slight negative $\delta^{13}\text{C}$ anomaly at ~ 24 m above the bone-bearing layer, which can be used as a crucial tie-point in constraining the age of the Bernissart bonebed (see Figs. 11-12).

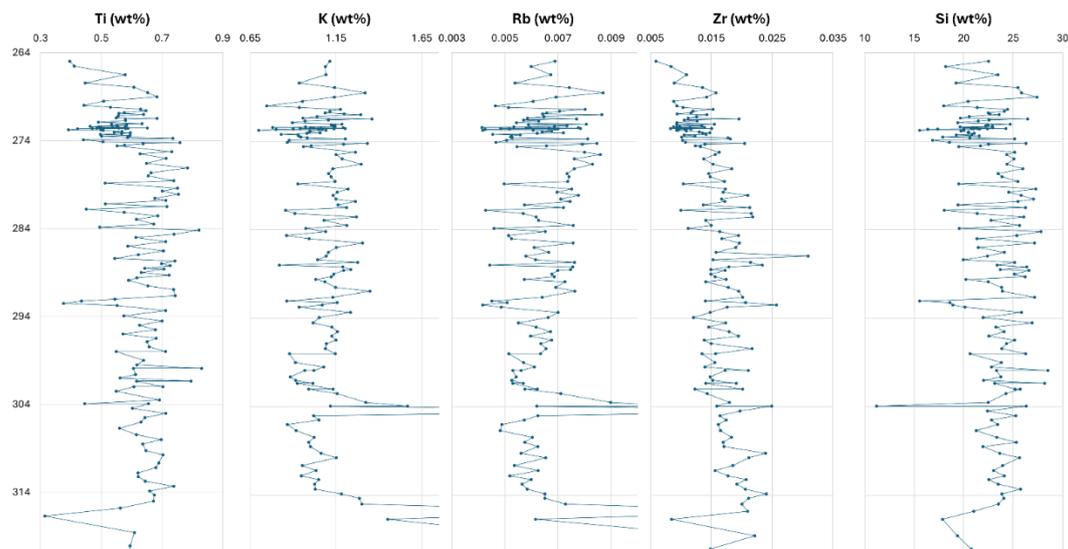


Figure 11. Plot of Ti, K, Rb, Zr, and Si (in wt%) along the Ber3 core section between 264 m and 321 m, based on bulk powder μXRF analysis (from Sleypen, 2024). The colour coding of the units refers to subdivisions made in the Ber 3 drill core stratigraphy by Baele (see above). Red= unit 1, orange= unit 2a, yellow= unit 2b, purple= unit 3, green= unit 4.

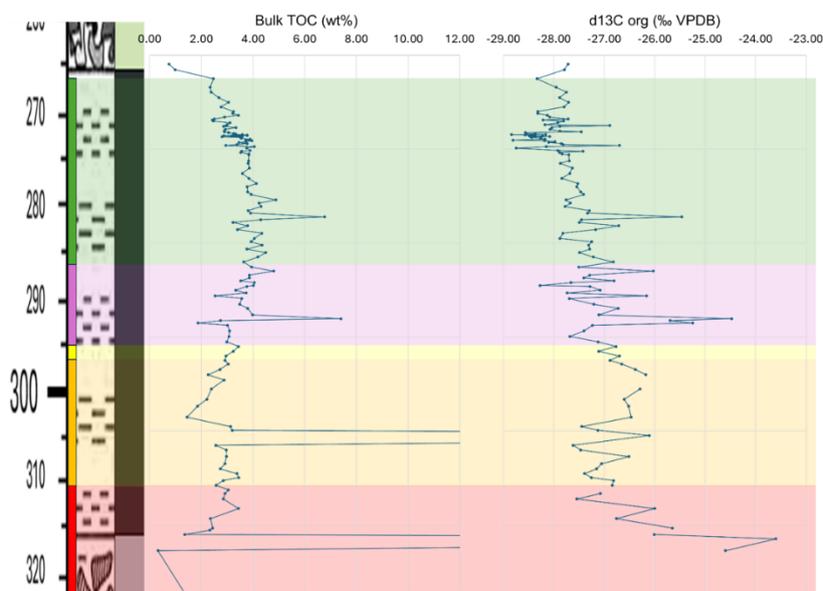


Figure 12. Plot of the Bulk TOC (wt%) and $\delta^{13}\text{C}$ (‰VPDB) next to the stratigraphic column of the Ber3 core section between 264 m and 321 m (from Sleypen, 2024). The colour coding of the units refers to subdivisions made in the Ber 3 drill core stratigraphy by Baele (see above). Red= unit 1, orange= unit 2a, yellow= unit 2b, purple= unit 3, green= unit 4.

3. The rare earth elements (REE) contents and the Sr and O isotope compositions of fossil bones and teeth have been widely used as proxies to study vertebrate palaeoecology, palaeoenvironments and taphonomy. However, the interpretation of these data is often hindered by the complexity of diagenetic processes and history. The present study uses in-situ analyses (trace elements and Sr isotopes using laser ablation inductively coupled plasma mass spectrometry, LA-ICPMS, and secondary ion mass spectrometry, SIMS) to investigate with unmatched precision the diagenetic processes that affected the bones and teeth of *Iguanodon bernissartensis* over geological time, but also to provide clues about the paleoenvironment during the late Barremian-early Aptian period and the migratory behaviour of the Bernissart Iguanodons. More precisely, combined REE and isotope geochemistry highlights the importance of Fe-Mn oxyhydroxides in the uptake and release of REE by bones, and the change of diagenetic fluids over time. They also emphasize the crucial role played by the brines issued from the dissolution of deep-seated Viséan evaporites in the system, which brought considerable amount of S into the sinkhole lake where iguanodons massively and suddenly died. The in-vivo Sr and O isotope signatures obtained on the teeth suggest that *Iguanodon bernissartensis* was a non-migratory species, living and grazing in a quite restricted area corresponding to a limited region during the Wealden. The O isotope data further indicate that the seasonality was well marked at the time, with cold(er)/wet winter and hot(ter)/dry summer (Fig. 13; Decrée *et al.*, in press).

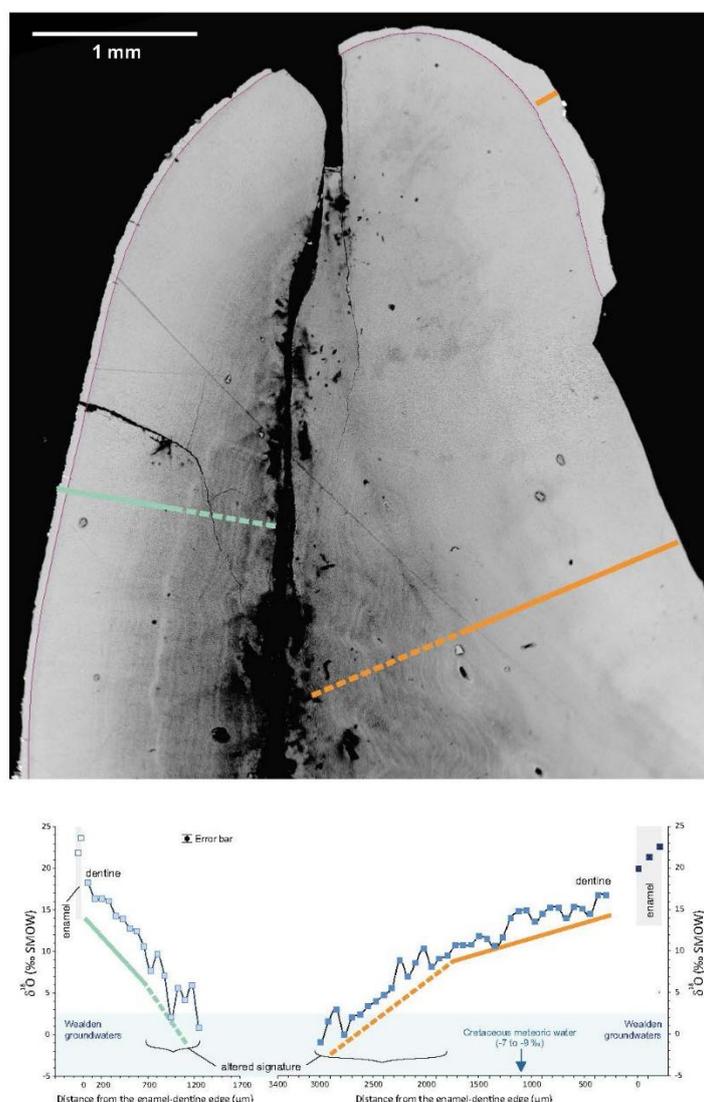


Figure 13. O isotope profile (in-situ $d^{18}O$ obtained using SIMS) throughout the tooth of an iguanodon (sample Igd2) from Bernissart. The $d^{18}O$ values of potential fluid sources are presented for comparison purposes: reconstructed Wealden groundwaters and Cretaceous surface/meteoric waters.

WP 4. Assessing the mechanical behaviour of the Bernissart Iguanodon bones (IRSNB and ULiège):

Since the earliest reconstruction of *Iguanodon* by Gideon Mantell and Benjamin Waterhouse Hawkins during the 19th century, one of the most intriguing osteological features was its putative “nasal horn”. The bone was placed on the snout of the skull after the bone was presumably collected by Gideon’s wife, Mary Mantell, in 1824, one year prior to the famous publication of Mantell baptizing *Iguanodon* at the Royal Society of London. The “horn” was later identified to be the ungual of the first manual digit (“thumb”) by Louis Dollo thanks to the several complete *Iguanodon* skeletons from the Bernissart Sinkhole in Belgium. Included in the large monograph by Norman in 1980, the spike-like thumb was speculated to be a defensive weapon or an intraspecific display apparatus intraspecific weapon. However, this hypothesis, which led to many speculations about *Iguanodon*’s behavior, was never quantitatively tested biomechanically. Here, we applied Finite Element Analysis and Range of Motion tests to identify the mechanical resistance of the thumb and the movement of the arm to measure force and speed during a strike. The right thumb of RBINS R51 was scanned using a microtomographic scanner (microCT; Fig. 14), segmented in the software Avizo and meshed for FEA in Hypermesh and Abaqus using standard bone properties. The pectoral girdle and the forelimb elements were digitized from the holotype RBINS R51, imported in Blender and muscles were reconstructed as bars following published muscular reconstructions. Results of the analyses tested with and without a keratinous sheath (estimated to overlap the bone by ca. 20%) show that the thumb could resist an impact force of up to 5000 N, with peak stresses restricted to a small apical region (Fig. 15). The conical shape helps to dissipate the forces along the longitudinal axis. The results were further validated against the talon of a rooster (*Gallus lafayetii*) due to the similar functional structure of the claw and the analogous swinging movement of the limb. Our results suggest that the spike-like thumb of *Iguanodon* could be used as a weapon, either for intraspecific sparring or defense against a predator, or both. However, this assumption needs to take account of the disparity of thumb dimensions across the other iguanodontian taxa (e.g. *Ouranosaurus*, *Mantellisaurus*, *Bolong*), implying that the structure might have had different uses across the taxa, hence under different ecological pressures.

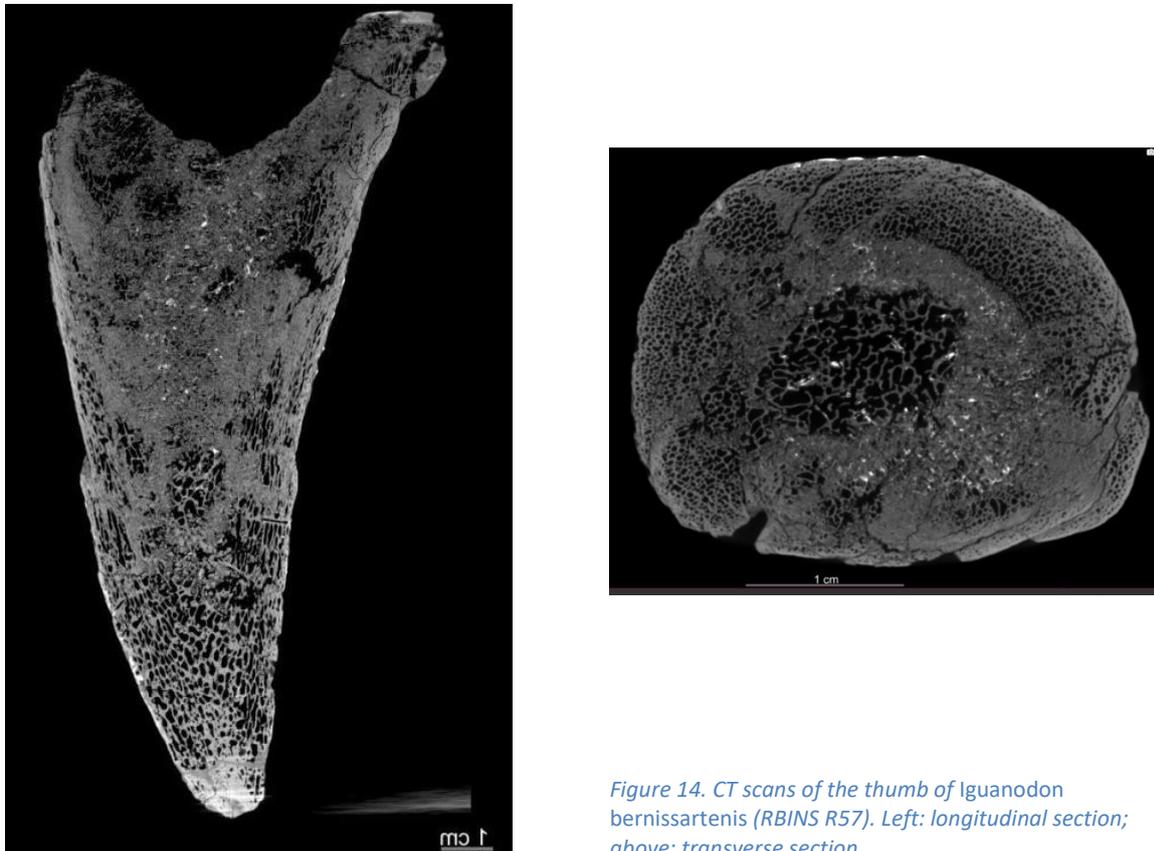


Figure 14. CT scans of the thumb of *Iguanodon bernissartensis* (RBINS R57). Left: longitudinal section; above: transverse section.

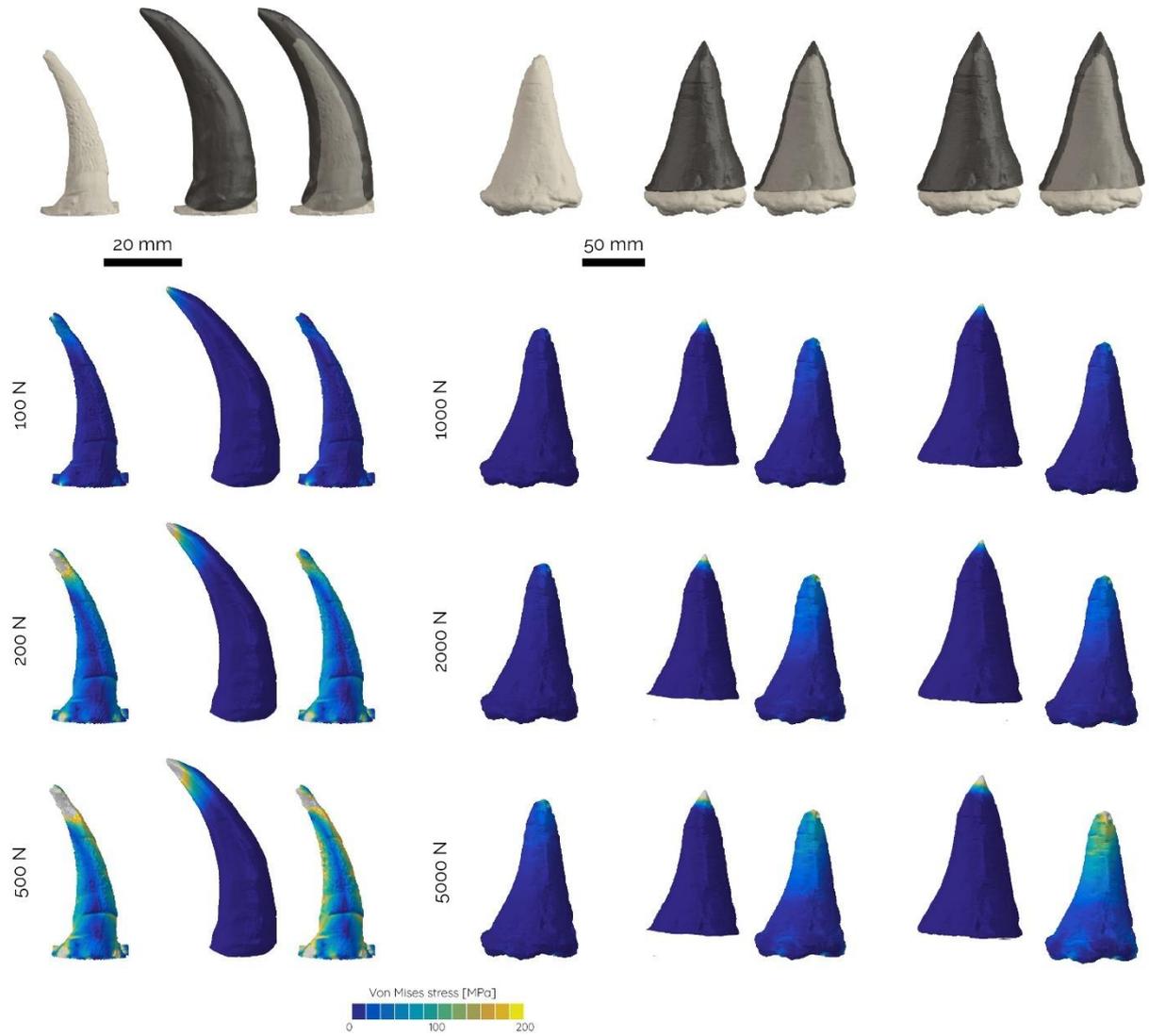


Figure 15. von Mises stress values in the Iguanodon thumb (right) and in the talon of a rooster at applied forces of 500, 200, and 100 N.

5. DISSEMINATION AND VALORISATION

Valorization of the 3D data

One of our central goals for this project is to ensure a decent dissemination of our data to all audiences while protecting them against unauthorized use. That is why we are settling an internal solution using the Orthanc platform, developed by the UCL. This platform is dedicated to the management of all kinds of imagery data, notably 3D data. We are currently preparing all the data related to the holotype of *Iguanodon bernissartensis* to create a comprehensive 3D atlas bone by bone, allowing both general audience and scientific researchers to have access to 3D models directly using their Internet browser, while preventing any unauthorized download of these data. This access will take the form of a dedicated page on the internet website of the Institute, currently in construction: <https://collections.naturalsciences.be/ssh-paleontology/masterpieces/bernissart>.

In 2023, we worked together with the company Laetoli Productions to propose a complete reconstructed and animated skeleton of *Iguanodon bernissartensis* to the general audience, using the data of the project. This animated and detailed skeleton can be accessed in the “Vertébrés.fr” application on the website of Laetoli Productions: <https://www.laetoli-production.fr/webgl/vertebres/?ar=public&specimen=Iguanodon%20bernissartensis%20RBINS-R51>

In 2023, the “Musée de l’Iguanodon”, located in the town of Bernissart and exhibiting a skeleton of *I. bernissartensis* belonging to the collections of the Institute of Natural Sciences, was closed during several months for renovation. In collaboration with L. Savignat, director of the “Musée de l’Iguanodon”, the 3D models of the exhibited specimen have been used to create an interactive support in the permanent exhibition, allowing the public to virtually reconstruct the skeleton on tactile panels.

All along the project, we received several journalists from Belgium and foreign countries to cover the digitization campaign in different TV broadcasts:

2024: “*Iguanodons: Spektakulärer Dinosaurier-Fund im belgischen Bernissart*”, ARD1, September 9th. <https://www.ardmediathek.de/video/wir-im-saarland-grenzenlos/iguanodons-spektakulaerer-dinosaurier-fund-im-belgischen-bernissart/sr/Y3JpZDovL3NyLW9ubGluZS5kZS9HTC1XSU1TXzE0NDI3OC9zZWNoaW9uLzE>

2022: « *Les dinosaures de Jurassic World sont au cinéma mais leurs squelettes sont en Belgique et ils se font scanner* », RTBF, June 22th. <https://www.rtf.be/article/les-dinosaures-de-jurassic-world-sont-au-cinema-mais-leurs-squelettes-sont-en-belgique-et-ils-se-font-scanner-11010118>

2022: « *Pour leur sauvegarde dans le temps, les iguanodons de Bernissart sont scannés par les paléontologues* », NoTélé, May 28th. <https://www.notele.be/it61-media115684-pour-leur-sauvegarde-dans-le-temps-les-iguanodons-de-bernissart-sont-scannes-par-les-paleontologues.html>

6. PUBLICATIONS

Master theses

André, L., 2024. Variation morphologique des éléments de la main chez *Iguanodon bernissartensis*. Master thesis in Geology, Université de Liège (supervised by Valentin Fischer and Christophe Mallet).

Sleypen, K. – 2024 - High-Resolution geochemistry of the Ber3 drill core to unravel the paleoenvironment and age of the Bernissart *Iguanodons*. Masterr thesis in Chemistry, Vrije Universiteit Brussel (supervised by Steven Goderis and Pim Kaskes).

Papers in IF journals

Bertozzo, F., Camilo, B., Araújo, R., Manucci, F., Kullberg, J.C., Cerio, D.G., Feijó de Carvalho, V., Marrecas, P., Figueiredo, S.D. & Godefroit, P., 2025. *Cariocecus bocagei*, a new basal hadrosauroid from the Lower Cretaceous of Portugal. *Journal of Systematic Palaeontology*, **23(1)**, 2536347. <https://doi.org/10.1080/14772019.2025.2536347>

Bertozzo, F., Kecheng, N., Vallée-Gillette, N. & Godefroit, P., 2025. Anatomical description and digital reconstruction of the skull of *Jeholosaurus shangyuanensis* (Dinosauria, Ornithopoda) from China. *PLoS ONE*, **20(1)**: e0312519. <https://doi.org/10.1371/journal.pone.0312519>.

Decrée, S., Leduc, T., Godefroit, P., Deloule, E., Coint, N., Huyskens, M.H., Mansur, E.T., Debaille, V. & Baele, J.-M., 2025. Tracing in-vivo and post-mortem processes in *Iguanodon bernissartensis* teeth and bones using in-situ trace element, oxygen and Sr analyses: implication for paleoecology, paleoenvironment and diagenesis. *Palaeogeography, Palaeoclimatology, Palaeoecology*, in press.

Huang, J., Wu, W., Mao, L., Bertozzo, F., Dhouailly, D., Robin, N., Pittman, M., Kaye, T.G., Manucci, F., He, X., Wang, X. & Godefroit, P., 2025. An Early Cretaceous iguanodontian dinosaur with histologically-preserved spike-like cutaneous appendages. *Nature Evolution & Ecology*, in press.

Abstracts of communications in international symposia

Bertozzo, F., Lautenschlager, S. & Mallet, C., 2025. “You get the thumb”: The role and function of the spike-like pollex in *Iguanodon bernissartensis* (Dinosauria, Ornithopoda) via biomechanics approaches. 85th edition of the Society of Vertebrate Paleontology (SVP2025), Birmingham, UK, November 12-15 2025 (POSTER) <https://vertpaleo.org/svp-annual-meeting-2/>.

Bertozzo, F., Mallet, C., During, M.A.D., Fischer, V. & Godefroit, P., 2023. Morphology of the skull of *Mantellisaurus atherfieldensis* (Dinosauria, Ornithopoda) from the Bernissart sinkhole, Belgium. In: Alba, D.M., Marigó, J., Nacarino-Meneses, C., Villa, A. (Eds.), Abstract book of the 20th Annual Conference of the European Association of Vertebrate Palaeontologists, Sabadell, Spain, June 26 – July 1 2023. *Palaeovertebrata*, Special Volume 1-23. DOI:10.18563/pv.eavp2023 (ORAL COMMUNICATION).

Bertozzo, F., Mallet, C., Rocchi, R., Fischer, V. & Godefroit P., 2023. “House of the *Iguanodon*” – New Palaeobiological perspectives on *Iguanodon* from the digitization of the historical collection in Belgium. 6th International Meeting of Early stage career Researchers in Palaeontology, 2023, Lourinhã, Portugal, April 11– 15 2023 (ORAL COMMUNICATION).

Godefroit, P., 2023. Iguanodon 2.0: Shepherding the "Belle Epoque" Bernissart Iguanodon collection into the 21st century. Abstract book of the International Symposium on lithosphere evolution and environmental changes in Northeast Asia, Changchun, China, August 22-24 2023 (INVITED LECTURE).

Kaskes, P., Borremans, W., Goderis, S., & Claeys, P., 2024. Blasting dinosaurs in Brussels: new μ XRF and LA-ICP-MS setup to unravel the origin of fossil bonebeds. 16th edition of the European Workshop on Laser Ablation (EWLA2024), Ghent, Belgium, July 2-5 2024 (ORAL PRESENTATION). <https://ewla2024.ugent.be/>

Kaskes, P., Goderis, S., Schulp, A.S., Godefroit, P. & Claeys P. 2025. Blasting dinosaurs in Brussels: tracing the taphonomic history of Cretaceous bonebeds using μ XRF and LA-ICP-MS. 85th edition of the Society of Vertebrate Paleontology (SVP2025), Birmingham, UK, November 12-15 2025 (POSTER) <https://vertpaleo.org/svp-annual-meeting-2/>

Kaskes, P., Rey, K., Robin, N., Baele, J-M., Godefroit, P. & Claeys, P., 2024. Revisiting the Bernissart *Iguanodon* Bonebed in Belgium: new taphonomic and stratigraphic insights based on trace element geochemistry and carbon isotopes. International Symposium: 200 Years of the Dinosaurs: New Perspectives on an Ancient World, 2024 Natural History Museum, London, UK, January 11-12 2024 (ORAL PRESENTATION). <https://www.nhm.ac.uk/our-science/study/events/dinosaur-conference-2024.html>

Mallet, C., Baele, J.-M., Bertozzo, F., Claeys, P, Fischer, V. & Godefroit, P., 2022. Iguanodon 2.0 - Faire entrer la collection « Belle Epoque » des Iguanodon de Bernissart dans le 21^{ème} siècle. Congress of the "Association Paléontologique Française" (APF), Montpellier, France, May 30 – June 3 2022. DOI: 10.13140/RG.2.2.19444.22406 (ORAL COMMUNICATION).

Mallet, C., Godefroit, P. & Fischer, V., 2024. Dimorphic eyebrows? Intraspecific shape variation of palpebral bones in *Iguanodon bernissartensis* (Ornithischia, Dinosauria). 8th International Geologica Belgica Luxemburga International Meeting, Liège, Belgium, September 11–13 2024. DOI:10.13140/RG.2.2.28783.24480 (ORAL COMMUNICATION).

Mallet, C., Rocchi, R., Bertozzo, F., Godefroit, P. & Fischer, V., 2023. Drivers of intraspecific variation in *Iguanodon bernissartensis* (Ornithischia, Dinosauria): a preliminary 3D investigation of foot bones. In: Alba, D.M., Marigó, J., Nacarino-Meneses, C., Villa, A. (Eds.), Book of Abstracts of the 20th Annual Conference of the European Association of Vertebrate Palaeontologists, Sabadell, Spain, June 26 – July 1 2023. *Palaeovertebrata*, Special Volume 1-23. DOI: 10.18563/pv.eavp2023 (POSTER).

Mallet, C., Rocchi, R., Bertozzo, F., Godefroit, P. & Fischer, V., 2023. Variation de la forme des autopodes chez *Iguanodon bernissartensis* (Dinosauria, Ornithischia) : résultats préliminaires issus du projet Iguanodon 2.0. Congress of the "Association Paléontologique Française" (APF), Villers-sur-Mer, France, June 5– 9. DOI: 10.13140/RG.2.2.20316.60800 (ORAL COMMUNICATION).

7. ACKNOWLEDGEMENTS

We are particularly grateful to the Belspo staff, and particularly to Georges Jamart and Maaïke Vancauwenberghe for their enthusiastic help in the course of the Belspo project. We also want to take this opportunity to thank all the members of our follow-up Committee, for their informed and benevolent advices throughout this project: Eileen Murphy, David B. Norman, Heinrich Mallison, and Lucile Savignat.

We sincerely thank the people that have been involved in the digitization process at some parts of the project: Aurore Mathys and Riccardo Rocchi. We also thank all the people that contributed, even for a few hours, to the disassembly and the reassembly of all the specimens of Iguanodons in the glass cages of the Institute of Natural Sciences: Soraya Bengattat, Léa De Brito, Thierry Hubin, Elodie-Laure Jimenez, Raphus team members, Mathys Rotonda, Nathan Vallée-Gillette.