

Coldcase

Re-opening of the Bernissart Iguanodon Crime Scene

Pascal GODEFROIT (Royal Belgian Institute of Natural Sciences) – Jean-Marc BAELE (UMons) –
Philippe Claey's (VUB) – Koen Stein (VUB) – Cyrille Prestianni (RBINS) – Sébastien Olive (RBINS)

Axis 3: Cultural, historical and scientific heritage



COLDCASE

Re-opening of the Bernissart Iguanodon Crime Scene

Contract - BR/143/A3/COLDCASE

FINAL REPORT

PROMOTORS: Pascal Godefroit¹, Jean-Marc Baele², Philippe Claey³

AUTHORS: Pascal Godefroit¹, Jean-Marc Baele², Philippe Claey³, Cyrille Prestianni¹, Sébastien Olive¹, Koen Stein³

¹Royal Belgian Institute of Natural Sciences, OD Earth & History of Life', Rue Vautier 29, B-1000 Brussels

²Umons, Department of Geology and Applied Geology, Place du Parc 20, B-7000 Mons

³ VUB, Analytical, Environmental & Geochemistry Laboratory, Pleinlaan 2, B-1050 Brussels



Published in 2020 by the Belgian Science Policy Office
WTCIII
Simon Bolivarlaan 30 Boulevard Simon Bolivar
B-1000 Brussels
Belgium
Tel: +32 (0)2 238 34 11 - Fax: +32 (0)2 230 59 12
<http://www.belspo.be>
<http://www.belspo.be/brain-be>

Contact person: CALVO DEL CASTILLO Helena
Tel: +32 (0)2 238 36 15

Neither the Belgian Science Policy Office nor any person acting on behalf of the Belgian Science Policy Office is responsible for the use which might be made of the following information. The authors are responsible for the content.

No part of this publication may be reproduced, stored in a retrieval system, or transmitted in any form or by any means, electronic, mechanical, photocopying, recording, or otherwise, without indicating the reference :

Godefroit, P., Baele, J.-M. , Claeys, Ph., Prestianni, C., Olive, S. & Stein, K. Final Report. Re-opening of the Bernissart Iguanodon Crime Scene. Brussels: Belgian Science Policy Office 2020 – 64 p. (BRAIN-be - Belgian Research Action through Interdisciplinary Networks)

TABLE OF CONTENTS

ABSTRACT	5
1. INTRODUCTION	6
2. STATE OF THE ART AND OBJECTIVES	8
3. METHODOLOGY	10
4. SCIENTIFIC RESULTS AND RECOMMENDATIONS	20
5. DISSEMINATION AND VALORISATION	53
6. PUBLICATIONS	59
7. ACKNOWLEDGEMENTS	61
ANNEXES	62

ABSTRACT

From 1878 until 1881, an exceptional series (37-38 specimens) of sub-complete and articulated skeletons of *Iguanodon* were unearthed from a single Lower Cretaceous locality at Bernissart (Belgium), revealing for the first time the anatomy of dinosaurs; following this discovery, considerable advances were made possible about the biology of these fantastic animals. However, the causes of the mass-accumulation of fully-articulated iguanodon skeletons and other vertebrates in the Iguanodon Sinkhole remain obscure: most of the hypotheses proposed so far consider the karstic collapse structure (sinkhole) from which the fossils have been unearthed as a simple receptacle for the carcasses.

However, our study in the frame of the Coldcase Project shows that sinkhole formation processes may have played an active role in the trapping of iguanodon herds along with other taxa. We have now solid evidences that the Iguanodon Sinkhole records a depositional sequence evolving upwards from proximal debris flows to distal “turbidites”. Sediment input in the Bernissart Lake thus originated from the sinkhole margins, which repeatedly failed and slid. The fossiliferous layers would then coincide with maximum deepening of the sinkhole, when sliding hazard was greatest. The Iguanodons may have triggered slidings due to their weight, which would explain the monospecificity of the assemblage of, large vertebrates. This scenario also provides a mechanism for the liberation of H₂S initially stored in the lake bottom, increasing the number of *Iguanodon* deaths by drowning and possibly affecting aquatic animals.

Keywords: Bernissart Iguanodons, dinosaurs, Lower Cretaceous, taphonomy, mass-deaths.

1. INTRODUCTION

Bernissart is a former coal-mining village in southwestern Belgium, situated 21 km south of Mons and less than 1 km from the Franco-Belgian frontier. In the 19th century, the Bernissart Coal Board limited Company dug three coal extraction pits on the Bernissart territory. With a depth of 422, the Sainte-Barbe pit was the deepest. In spite of a rather archaic technology, the daily production for the three extraction pits was about 800 tons during the 1870's.

On February 28, 1878, miners digging a horizontal exploration gallery from the Sainte-Barbe Pit, 322 m below ground level suddenly encountered disturbed rocks indicating that they were penetrating inside a vertical 'cran', a local term meaning a pit formed by natural collapse through the coal seams that was filled especially with clayey deposits normally located above the coal measures. One month later, on April 5, while they were inspecting the deposits, the mine director Gustave Fagès and the Engineer Léon Latinis found strange objects, with an oval cross-section and a fibrous texture, which were rapidly identified as fossils bones. On the 7th of May 1878, P-J Van Beneden announced to the Belgian Academy of Science that a major new discovery of fossils had been made at a colliery in Bernissart. Among the fossils were teeth that could be identified as belonging to the dinosaur named *Iguanodon*. What was to emerge from Bernissart over the next three years of intensive excavation (supervised by the staff of the Royal Museum of Natural History, Brussels) was genuinely spectacular: a large number of virtually complete skeletons of dinosaurs, crocodiles, rare amphibians and insects, thousands of fossil fish, an abundance of coprolites and a diverse flora (Norman, 2012).

The discovery of the Bernissart *Iguanodons* quickly became a corner stone in the history of geology and palaeontology. From 1878 until 1881, about 30 complete and articulated skeletons of *Iguanodon* were unearthed from Lower Cretaceous ('Wealden') deposits at Bernissart (Belgium), revealing for the first time the anatomy of dinosaurs; following this discovery, considerable advances were made possible about the biology of these fantastic animals. These extraordinary discoveries, not surprisingly, attracted the attention of some of the great palaeontologists of the time: Albert Seward FRS (Cambridge) described the flora from Bernissart, Charles Eugène Bertrand (Lille) described the coprolites and Ramsay Traquair FRS (Edinburgh) described the fish. Following the departure of George Albert Boulenger in 1881, a young engineer, Louis Dollo, was appointed 'Aide Naturaliste' at the Royal Belgian Museum of Natural History and was offered the opportunity to describe the dinosaurs collected from Bernissart. (Norman, 2012)

The Bernissart discovery also led to the first large-scaled palaeontological excavation worldwide. Ingenious excavation techniques, still used by palaeontologists in the field today, had to be invented to bring back to the surface heavy and fragile fossil blocks that were unearthed at a depth of 322 m. The success of these pioneering excavations is undoubtedly the result of the fruitful collaboration between the technical staff from the 'Musée Royal d'Histoires Naturelles' and the miners and mining engineers from the 'Charbonnages de Bernissart'. Besides the fossils, many manuscripts and plans are preserved in the palaeontological collections of the RBINS relating to the original excavations at Bernissart. They allow the precise reconstruction of the circumstances of the discovery of these fantastic dinosaurs.

However, the processes leading to the local accumulation of so many complete skeletons remain unexplained. In the Coldcase project, we planned to use non-invasive advanced technologies to produce an integrated formation-model for the world-class iguanodon deposit of Bernissart:

- **Computed 3D mapping** of the 1878-1881 excavation plans and drawings will replace each individual skeleton in its precise environmental and stratigraphic framework, in order to check whether the skeleton concentration results from cyclic catastrophic events, as suggested by previous studies (Baele et al., 2012), or from attrition processes.
- **Core logger** at large scale and **microXRF** at higher resolution for key intervals on the core drilled through the Bernissart Wealden deposits, for assessing palaeoenvironmental changes through sedimentology, composition of the sediment and evolution of the type and concentrations in organic matter.
- **Palaeohistological, molecular palaeontology, and biogeochemical studies** of the *Iguanodon* bones and teeth will be important for reconstructing the age structure, palaeoenvironments, dietary adaptations, and interactions with the environment of the *Iguanodon* population at Bernissart.
- **Analyses of multiple tracers (isotopes, trace elements, molecular biomarkers, etc.)** will clarify the role of site-specific geological factors, such as possible upwellings of sulfate-rich brines boosting cyanobacterial development and/or H₂S production by sulphate-reducing bacteria, which could explain inferred cyclic mass-death scenarios.

The Bernissart Iguanodons constitute a unique fossil assemblage of worldwide reputation that represents an integral part of the Belgian cultural and scientific heritage. This study will shed light on the processes that led to this unique accumulation of dinosaur bones some 125 million years ago.

2. STATE OF THE ART AND OBJECTIVES

Since 1878, geologists and palaeontologists have tried to explain the processes leading to the formation of the unique accumulation of more than 30 sub-complete and articulated dinosaur skeletons within the Early Cretaceous Iguanodon Sinkhole at Bernissart. 117 similar sinkholes are known within the Carboniferous basement of the Mons Basin, but only one has yielded dinosaur remains (Godefroit et al., 2012). On the basis of geological sections of the site, Dupont (1878, 1897) hypothesized that the Bernissart locality represented a narrow gorge ('crevasse') in which iguanodontids lived, died, and were periodically buried during flooding episodes.

Soon, Cornet and Schmitz (1898) assessed that the accumulation of numerous iguanodontids skeleton at Bernissart was clearly a slow attritional process, resulting from sliding / stacking of carcasses of dead animals in a subsiding lake.

Dollo (1923) also proposed several possible scenarios for the Iguanodon accumulation at Bernissart: Bernissart was some kind of dinosaur graveyard by Early Cretaceous time, or flashfloods selectively killed the older and less agile animals. He also suggested that some iguanodontids specimens from Bernissart showed evidence of a violent death, maybe through combats.

Casier (1960) provided two further explanations for mass-burial at Bernissart. Based on the supposition that iguanodontids usually retreated into water to escape from predators or other startling events, he first supposed that some dinosaurs might have inadvertently slipped into the steep-sided marshy depression at Bernissart. In a second hypothesis ('Hippopotamus' hypothesis), Casier assumed that iguanodontids were amphibious and therefore dependant on a permanent body of water; a period of low rainfall may have led to these animals becoming mired in the muddy ooze around shrinking water-holes.

Norman (1987) more recently compared Bernissart with another Early Cretaceous iguanodontid bonebed in Nehden, Germany, and refuted mass-kill scenarios based on a more detailed taphonomical analysis. Bultynck (1989) also spoke for an attritional scenario, agreeing with the sinkhole environment hypothesis previously developed by Cornet and Schmitz (1898).

Baele et al. (2012) proposed and discussed several taphonomic scenarios within the specific geological and environmental specificities of the so-called Lower Cretaceous Bernissart paleolake. Based on sedimentological and taphonomic evidences, attrition and obrution processes appear less likely than mass-death by drowning and/or intoxication,. Contamination of the aquatic environment by sulfate-rich brines related to deep solution-collapse processes could support the hypothesis of intoxication by H₂S or biological toxins as direct or indirect lethal agent in a context of seasonally shrinking water.

Nevertheless, all these hypotheses have never been tested so far and therefore remain 'nice stories'. The aim of the present project is to produce an integrated formation-model for the iguanodon-rich deposit of Bernissart. A series of taphonomic elements ('indices'), collected from different sources (fossils, iconographic documents, drilling and core data), will be investigated to reconstruct the circumstances of the iguanodon demise:

- **The analysis of the 'crime scene'.** The distribution of the skeletons within the sinkhole is particularly important. Are the skeletons randomly distributed and oriented within the sinkhole or are they organized into discrete bonebeds with or without preferential orientations?
- **Forensic analyses of the victims.** Structure of the Bernissart Iguanodon population through palaeohistological studies; traces of predation, scavenging, trampling; analyses of multiple tracers (stable isotopes, trace elements, etc.) for reconstructing their diet...
- **Looking for collateral victims.** The Iguanodons were not the only fossils found at Bernissart. The proposed taphonomic scenario explaining the local accumulation of iguanodontid skeletons must also take those collateral victims into consideration. Particularly interesting is the abundant fish fauna, which will potentially provide key information about the evolution of the ecological conditions reigning in the Bernissart lake/swamp. So far no or little attention has been devoted to the other fossil present in the deposit. Investigating the cause of massive fish die-off could help understanding why many iguanodons accumulated at Bernissart.
- **Cross-checking the witness testimonies.** The relationships between the Bernissart Iguanodons and their environment must also be clarified. Large-scale paleoecological reconstructions exist for whole Mons Basin (e.g. Spagna et al., 2012). We shall focus more on the local circumstances based on drilling and core data: isotopic work ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) on organic matter and palaeobotanical changes across the bone layers; core logger at large scale & microXRF at higher resolution for key intervals, ...

Based on these taphonomic elements, three possible taphonomic models, which can explain such a local concentration of skeletons in a limited area, will be evaluated:

- **Passive attrition scenario** ("*natural death*" scenario), resulting from normal biological activity under normal circumstances, but requiring efficient and exceptional processes of concentration and conservation. In this case, it will be necessary to understand the mechanisms leading to the local concentration of the skeletons, and consequently reconstruct the paleoenvironments at very high-resolution.
- **Obrution scenario** ("*accidental*" scenario): quick burying of a population of iguanodon resulting from catastrophic sedimentary events. The latter remain to be identified through further sedimentological investigations.
- **Catastrophic scenario** ("*murder*" scenario): mass death caused either by herding or abnormal behaviour under perilous situation. In this case, the collected taphonomic elements will be used to reconstruct the causes of death (or recovering the "murder weapons": exhaustion/starvation, miring, drowning, poisoning/suffocation, mass predation,...) and then to propose a profile of the mass or serial killer (predators, wildfires, floods, droughts, H_2S from deep brines, cyanobacteria,...).

3. METHODOLOGY

3.1. DATA

The Bernissart collection at the RBINS – The recovered fossil assemblage from the Iguanodon Sinkhole includes fresh-water animals, which lived in the lake, and terrestrial animals that lived around the lake. The fresh-water component mainly consists of more than 3 000 fishes belonging to at least 15 different taxa. One amphibian, six turtle, and four crocodilian specimens complete the fresh-water fauna. Terrestrial vertebrates are mainly represented by the iguanodontids. The Bernissart Iguanodons consist of at least 43 specimens, including 25 complete to moderately complete (> 60% of the skeletal elements) individuals (see Norman, 1986 for a detailed catalogue of the iguanodontid specimens in the collections of the RBINS) and 18 partial skeletons or fragmentary material. At least 33 specimens are referred to as *Iguanodon bernissartensis*; six other incomplete individuals also probably belong to this taxon (Norman, 1986). On the other hand, the smaller iguanodontid *Mantellisaurus atherfieldensis* is only represented by one complete specimen and likely by one incomplete skeleton. A small tooth, caudal vertebrae, and ossified tendons collected from the coal tips possibly represent a third *M. atherfieldensis* specimen (Norman, 1986). Non-iguanodontid dinosaurs are represented by only one theropod phalanx. One hemipteran wing completes the terrestrial fauna from Bernissart. Numerous coproliths belonging to Danish-dog sized carnivorous reptiles were discovered in Bernissart pit (Bertrand, 1903), but their producer (crocodile, theropod, other?) remains unknown. Numerous fossil plants were also collected, with abundant remains of the fern *Weichselia* (Seward, 1900), which also thrive in swamps.

Original drawings and maps – Many documents (maps, drawings, sections, reports and others) from both public and private sources were searched and inventoried (Fig.1). Public sources include archives at RBINS, UMons, and Walloon Region (Mining Administration). We also had the opportunity to access the unique private collection of Houzeau de Lehay family, with among others a series of cross-sections of the Iguanodon sinkhole. More than 60 documents from RBINS were inventoried and more than 50 from other sources.

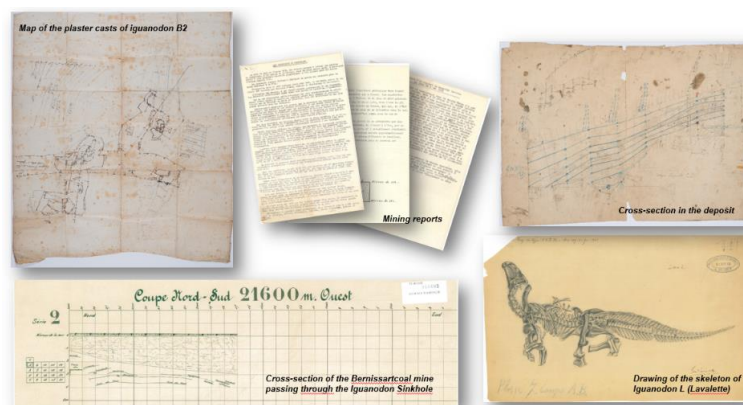


Fig. 1 – Example documents that were inventoried and processed for task 1.1.

Drilling and core data - In 2002-2003, three new boreholes were drilled within and around the Iguanodon Sinkhole at Bernissart. Initially, the aim of this drilling program was to evaluate the chances of finding more fossils and to understand the genesis of the Iguanodon

Sinkhole. In October 2002 the drilling program started with a completely cored well (named BER 3) using the PQ wireline technique. BER 3 reached 349.95 meters of Thanetian, Late Cretaceous, Early Cretaceous and Westphalian sediments (Yans et al., 2005; Yans, 2007). During the operations, different parameters were recorded: rate of penetration, core recovery and a brief core description (Tshibangu et al., 2004). BER 3 provided exceptional material to improve our knowledge of the Iguanodons-bearing Wealden facies. Another borehole (BER 2) also cut Wealden facies (Spagna and Van Isterbeeck, 2006). The formation processes of the Iguanodon Sinkhole were documented by sedimentological studies of the lacustrine Wealden facies (including clay mineralogy, granulometry and magnetic susceptibility; Spagna et al., 2008; Spagna et al., 2012), and by characterization of the organic matter with Rock-eval, palynofacies, soluble alkane content, carbon isotope and structural analyses (Schnyder et al., 2009). Interestingly, bone fragments were recovered in at least 4 levels within the Wealden facies of BER3. These fragments were studied using paleohistology (de Ricqlès et al., 2012) and diagenesis of the bone fragments (Leduc, 2012). Further studies on drilling and core data from BER 3 will therefore complement the analyses from the material collected at the occasion of the 1878-1881 excavations.

3.2. METHODS

Palaeohistology

Palaeohistology is the study of fossilized tissues, usually biomineralized such as bone, teeth and eggshell, and in rare cases also preserved soft tissues. It is a relatively new approach in vertebrate palaeontology and an inherently invasive technique. Loss of morphological information may be prevented with special casting techniques. Wherever complete sectioning is not possible, histological core drilling (Stein and Sander, 2009), a technique to take small histological samples from designated areas in large bones, can be applied. This method has many other advantages, including that samples can be taken directly from specimens in the collection, without the need for loan and transportation of heavy or fragile fossils. Such “fossilopsies” provide the bulk samples for polish sections, thin sections, and histochemical and stable isotope analyses. Femoral samples are preferred for histological studies, because the femur is an element that is commonly well preserved, and readily identified. However, samples of other bones can be taken to assess the preservation of the growth record, and quality of growth marks throughout the skeleton. This provides a more robust sample frame for skeletochronological analysis.

Skeletochronological methods can be applied to estimate ages, reconstruct growth curves, life tables and survivorship curves for the Bernissart Iguanodon population. Vertebrate bones and teeth follow circadian rhythms and growth rate analysis by quantifying growth marks in fossil bone has become a widely adapted method. Growth marks in bone and teeth are identified, counted and fitted on known growth models. Depending on which model provides a better fit, conclusions about the growth and development of taxa may also document their ecology. For example, animals in stressed environments with confined resources tend to have a skewed population structure with a higher number of adult individuals and a high juvenile mortality rate. Analyses of osteocyte lacuna density will be performed in parallel with growth rate analyses.

Stable isotope analyses of phosphatic material

Stable isotopes are alternative forms of elements with different molecular weights that are found naturally and do not decay radioactively. Stable isotope analysis of elements such as carbon, nitrogen and sulphur is used in ecology to trace the flow of nutrients through food webs and assess trophic levels. Over the last 10 years, oxygen and carbon isotopes measured in phosphatic fossil fragments (bones, tooth-enamel...) and/or the limited carbonate fraction associated with bioapatite (or hydroxylapatite= $\text{Ca}_{10}[\text{PO}_4]_6[\text{OH}]_2$) were used to diagnose palaeoenvironmental conditions (see Amiot et al., 2010 for example). Their use in a larger palaeoecological framework is just starting.

Phosphate fossil preserved in sediments are much less subject to post-depositional alteration and diagenesis due to extremely slow isotope exchange between apatite oxygen and water oxygen than their carbonate counterparts, providing a more reliable record of paleoenvironmental parameters; this is especially true when considering enamel, which is one of the most resistant biological material (Zazzo et al. 2004). However, few laboratories in the world master the complex technique of $\delta^{18}\text{O}$ analyses in phosphates. The classic conversion of apatite O_2 to CO_2 gas measured in the mass spectrometer represents a long, tedious and meticulous, procedure strongly limiting sample throughput (Longinello and Nuti, 1973). Recently, Lécuyer et al., (2007) pioneered a new faster and cheaper technique by dissolving apatite from bones or teeth and forming a silver-phosphate precipitate that is then reduced to CO using high-temperature Elemental Analyser (EA)-pyrolysis before direct injection in continuous flow mode into the mass spectrometer. Through the EA-pyrolysis the analyses can be automated for the high sample volume necessary for paleoenvironmental studies. In 2013, a new state of the art *Nu Perspective* mass spectrometer has installed at the VUB (Hercules project) with as peripheral a high-temperature EA – Pyrolysis system (EuroVector HT-PyrOH High Temperature Carbon Reduction Furnace). The goal is to use this instrumentation to develop the AgPO_4 extraction technique at the VUB and expand the existing isotopic arsenal by acquiring the capability to measure stable isotope ratios in phosphatic materials. Testing of the methodology has already started through a couple of master theses in biology (ex. Lars Christiaens, 2014, Paleocology of Mesozoic Marine Reptiles Using Stable Isotope Composition of Bones and Teeth). Collaborations exist with Dr. Romain Amiot UMR-CNRS 5125, “Paléoenvironnements et Paléobiosphère”, at the University of Lyon I, and Prof. Michael Joachimsky at the University of Erlangen, Germany who master the technique and have already measured apatite material from pliosaur teeth and dinosaurs bones extracted at the VUB.

Within the framework of the project the $\delta^{18}\text{O}$ analyses in phosphates ($\delta^{18}\text{O}_{\text{PO}_4}$) was developed at the VUB using the Nu-Perspective IRMS (FWO Hercules funding). The selected method is based on that of Lécuyer et al. (2007). The extraction method was refined and modified to attain the size of < 1 mg material, which is ideal to work on precious museum collections both in paleontology and archeology. The AMGC $\delta^{18}\text{O}_{\text{PO}_4}$ approach was tested and optimized using standards, a selection of bones and teeth of modern and fossil organisms as well as inter-laboratory sample comparison procedures in order to obtain a robust and reliable analytical methodology, which delivers reproducible results.

About ~ 100 analyses (including duplicates and triplicates) were carried out on the RBINS iguanodon materials in the framework of the Msc thesis of Jeroen Van Woensel (KULeuven 2018). The data is currently being reviewed and re-interpreted for publication.

Sedimentological analyses

Sedimentological analyses of key-intervals in the Ber3 borehole provide the environmental setting and its variation with time. Most of the fossiliferous deposit is composed of varve-like, laminated clayey sediments, which are not observed in any other Wealden deposit in the Mons Basin. However, the factors controlling cyclic sedimentation in the so-called Bernissart lake are yet unidentified. In addition, a series of sedimentological features such as microfaults, color banding, coal clasts, etc. have been recognized but not examined in detail (Spagna & Van Itterbeeck, 2006). Their study provides a framework, which is necessary for interpreting geochemical data, and second clarify the role of site-specific factors, in particular the relation between the environment at the surface and deep-seated geological processes in the sinkhole beneath. Sedimentological analysis of undisturbed clayey sediments requires specific treatment before thin-sectioning, such as vacuum-impregnation with a low-viscosity and extra-long curing time resin as used in soil sciences. The sedimentological content of the Ber3 section was analyzed using X-Ray Diffraction (XRD), Laser-Induced Breakdown Spectroscopy (LIBS), and micro-X-ray fluorescence spectrometry (μ XRF).

XRD is a non-destructive test method used to analyse the structure of crystalline materials. It is used to identify the crystalline phases present in a material and thereby reveal chemical composition information. Identification of phases is achieved by comparison of the acquired data to that in reference databases. X-ray diffraction is useful for evaluating minerals, polymers, corrosion products, and unknown materials. In most cases, the samples analyzed at Element are analyzed by powder diffraction using samples prepared as finely ground powders.

LIBS uses a high-power pulsed laser for in-situ chemical analysis with spot sizes ranging from 10 to 500 μ m. When exposed to a high laser power density, typically > 1 GW/cm², a very small portion of the irradiated material surface (of the order of ng) is vaporized and forms a luminous plasma that is analysed with a fast optical spectrometer. LIBS spectra are rich, carrying both elemental and molecular, but also plasma-induced luminescence information about the sample. 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 photoablation 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, 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). LIBS is very complementary to μ XRF, 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. LIBS is used in this project in parallel with μ XRF to map the distribution of elements across entire coprolite sections in order to assess if/how the

diagenetic history has affected phosphate chemistry. The measurements, conducted on an approximate basis of 100 samples, serve for screening and selecting the best (i.e. the least diagenetically altered) specimens for further observation and analysis.

μXRF is a totally non-destructive technique that produces high resolution (< 25 μm) elemental mapping of major and trace elements. This project uses the new generation Bruker M4 Tornado table-top energy-dispersive scanner (Bruker Nano GmbH, Berlin, Germany). A sample is excited using a X-ray source and the elemental abundances is determined based on the emission of a fluorescence spectrum. The μXRF technique combines the advantages of an automated microscope-guided high-precision movable stage system with the spectral resolution of a highenergy X-ray source to produce fast, non-destructive and high-resolution (<25 μm) elemental analysis. A small spot size needed for high-resolution measurements is produced by focusing using X-rays from either the rhodium or tungsten source using a polycapillary lens. This precisely aims the X-ray beams with minimized energy loss, enabling the instrument to yield well-resolved XRF spectra of small surfaces. The polycapillary focusing and XYZ moving stage of the table-top μXRF device enable the analyses of specific point-locations as well as the formation of line scans and two-dimensional maps on the sample surface. The result is a detailed characterisation of elemental changes across the sample as well as local compositions, leading to mineralogical determination. The dimensions of the vacuum chamber of the micro-XRF device make it possible to measure sample surfaces of up to 200 mm x 160 mm; this implies that whole coprolites can be analysed. No sample coating is necessary, and the method is fully non-destructive allowing the measurement of rare and unique samples from museum collections. Quantitative major and trace elemental analysis are carried out rapidly for all elements heavier than sodium.

Rock-Eval analysis

Pyrolysis is the decomposition of organic matter by heating in the absence of oxygen. Organic geochemists use pyrolysis to measure richness and maturity of potential source rocks. In a pyrolysis analysis, the organic content is pyrolyzed in the absence of oxygen, then combusted. The amount of hydrocarbons and carbon dioxide released is measured. The most widely used pyrolysis technique is named 'Rock-Eval'. This is a widely used petroleum screening technique developed primarily for ancient sedimentary rocks and kerogens, which is now routinely for the characterization of ancient and recent lacustrine or marine sediments.

In Rock-Eval pyrolysis, a sample is placed in a vessel and is progressively heated to 550°C under an inert atmosphere. During the analysis, the hydrocarbons already present in the sample are volatilized at a moderate temperature. The amount of hydrocarbons are measured and recorded as a peak known as S1. Next pyrolyzed is the kerogen present in the sample, which generates hydrocarbons and hydrocarbon-like compounds (recorded as the S2 peak), CO₂, and water. The CO₂ generated is recorded as the S3 peak. Residual carbon is also measured and is recorded as S4.

The percent total organic carbon (TOC) is actually a value that is calculated, not measured directly, using the following formula: %TOC = [0.082(S1+S2) + S4]/10 (Tissot & Welte, 1984).

Units are usually given as wt % organic carbon per weight of dry rock (milligrams hydrocarbon per gram of rock).

3D computed mapping

3D computed mapping of the deposit based on original documents provides an unprecedented integrated view of the scene. This technique has been applied to the region from which the fossils were unearthed. The skeletons have been replaced as close as possible to their original position along with all documented stratigraphic and mining data. Then extracting views in any desired section helps understanding the geometrical relationships between the fossils and their sedimentological environment, which is crucial for testing the various taphonomical scenarios available so far. Rendering realistic views of the scene will then be easy and potentially provide us with a very attractive mean of disseminating the research to the public.

Data processing. The documents were first digitized (rasterized) either with a digital scanner or by taking pictures under standardized conditions (light and geometry, Fig.2). A special attention was given to minimizing distortion by flattening the documents between a hard board and a glass plate.



Fig. 2 – A large drawing from the RBINS archives is being digitized.

Scaling and vectorization. Most of the original documents have been drawn at a 1:20 scale. Once digitized, they were scaled in order to have real scale in the GIS (Geographical Information System)(Fig.3). Contours, lines, drawings, grids, areas, etc. were then vectorized either automatically, semi-automatically (user-assisted) or manually depending on the quality of the document. Only semi-automatic and manual vectorization methods were possible due to the poor quality of the documents.

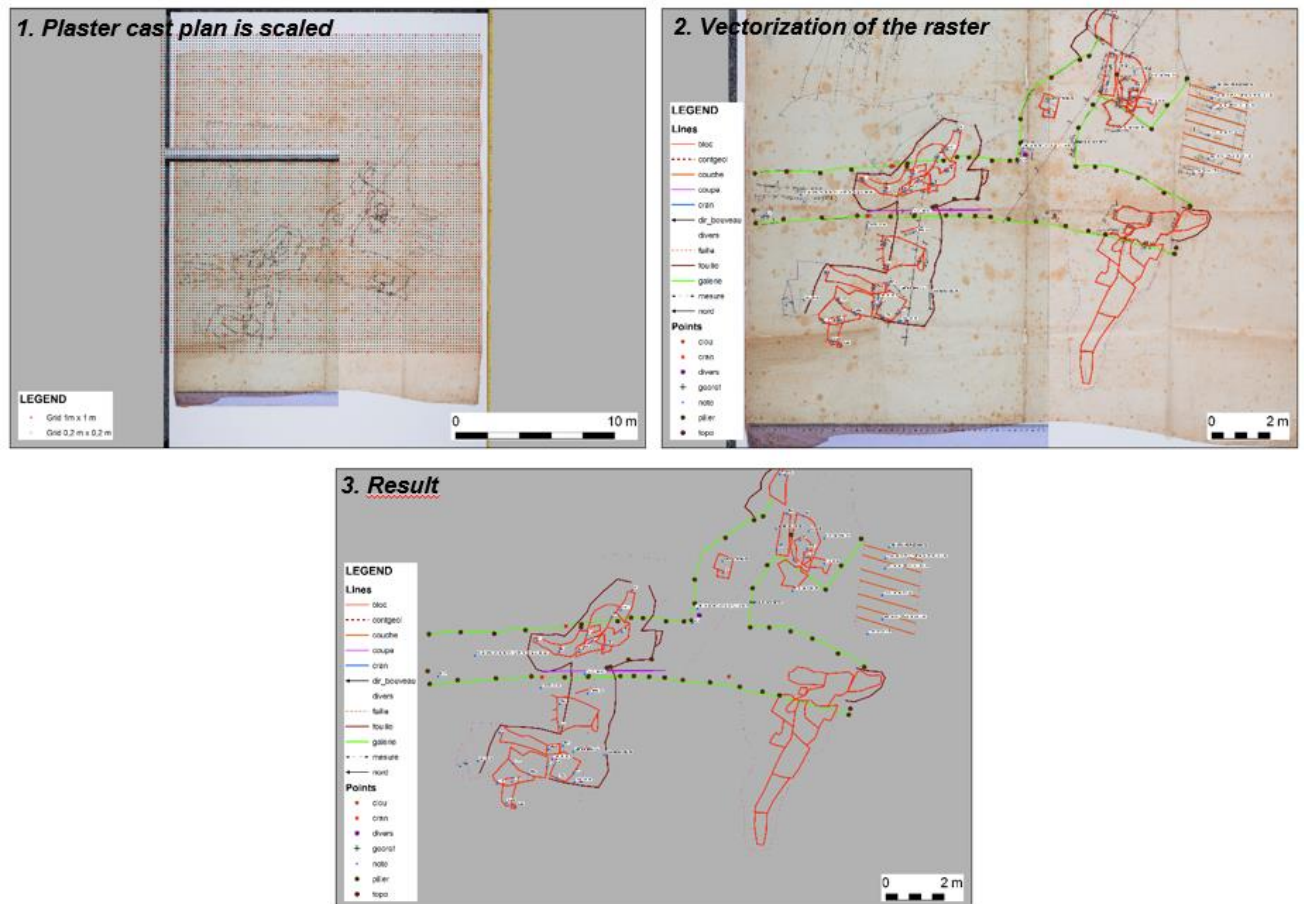


Fig. 3 – A plan for iguanodon plaster casts after scaling (1) and vectorization (2). (3) shows the resulting vectors without raster background.

All information in the documents was categorized, digitized and recorded in tables for further database search (Fig.4). Example features are plaster cast, excavation contour line, gallery wall, wood pillar, fault, reference nail, comment, etc. Example usage of this database: a user simply enter “lignite” to select the documents in which this keyword appears, allowing for fast and extensive search in the data collection.

This step necessitated a thorough examination and comparison of all the documents with many containing raw inscriptions from different authors, which make it difficult to decipher. In addition, bleaching due to aging of these documents have faded, sometimes effaced the information. A particular attention was put on finding reference elements (wood pillars, reference nails, shape of the galleries and all particular detail of the scene) in order to establish geometrical connections between the different sources of information.

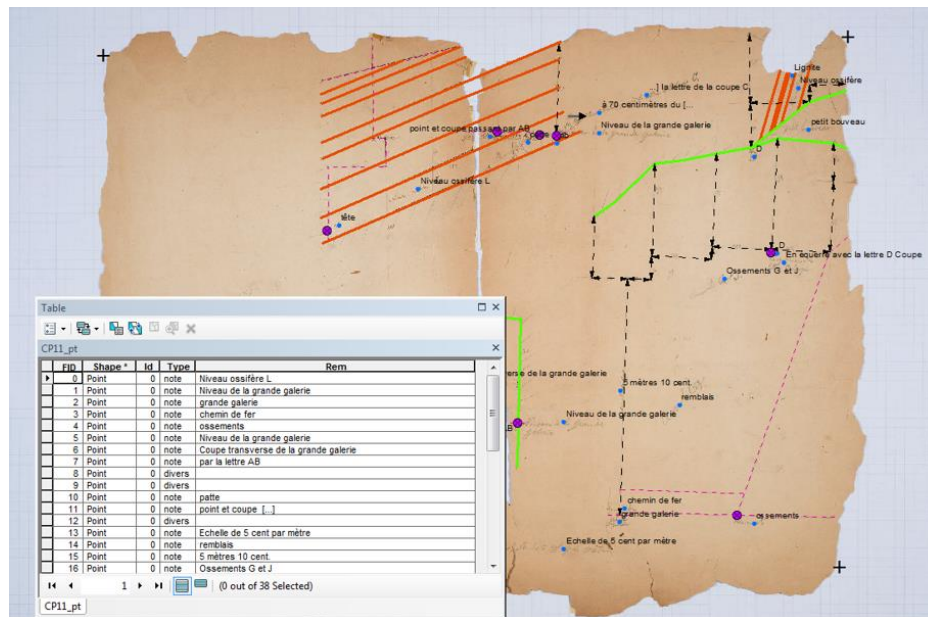


Fig. 4 – A vectorized document (geological cross-sections) with its data table.

The database was expanded to features outside the Iguanodon sinkhole for providing a well-documented geological context but also a complete 3D scene at large scale, which could be used for dissemination purposes (Fig.5). The geological data includes the coal seams, major boundaries such as top Paleozoic basement and the sinkhole walls. Mining and exploration data were added, such as galleries, shafts and boreholes (2002 drilling survey).

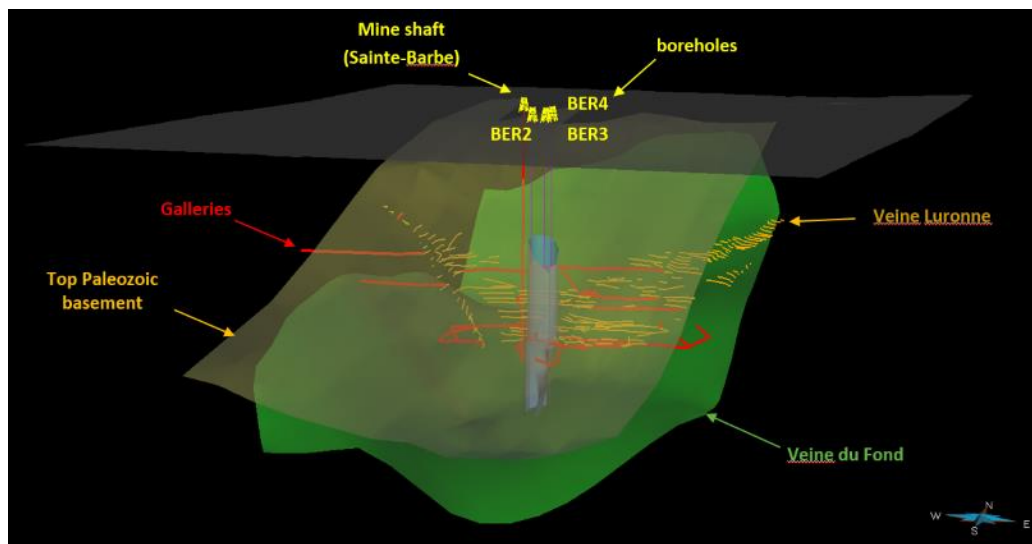


Fig. 5 – Example view of the 3D model depicting the geological and mining context of the Iguanodon sinkhole. The Luronne coal seam is displayed a series of traces, which is closer to the original data in the mining plans, while the Veine du Fond seam was interpolated as a full surface. The iguanodon sinkhole is the blue-grey cylinder-like object in the middle. The modeled area is ca. 1 x 1 km.

In total, 28 skeletons were digitized and geo-located, which is equivalent to ca. 500 plaster casts. Other vectors includes > 1000 lines and > 1000 points for the different features in the documents.

Special attention was given to the plaster casts, which are the main features for locating and orienting the Iguanodons in the scene. The task was quite tricky as while the method used for locating in XY coordinates (“wooden board method”) is fairly well explained, no information exists on the way the dip of the skeletons was taken into account. Therefore, we have hypothesized that the plaster casts were not levelled but projected on the bedding plane (Fig. 6). It thus assumed that the reference nail used for measuring distance was lying in the same plane as the skeleton. Then the dip of the skeletons were inferred from the dip of the corresponding layer in the cross-section.

The approximate location of the Iguanodons was firstly based on the excavation map redrawn by Baele et al. (2012) from Norman (1986). Then, the relative position was checked against reference elements such as gallery walls, excavation boundaries, orientation, distance to diverse known features, etc. Finally, the dip was applied in order to give each Iguanodon his proper orientation in the deposit. This part of the work, together with the vectorization itself, was very time-consuming as the preservation quality of most documents is poor. In addition, many documents appear to be working documents that were not all updated (for certain documents there are several versions with no date). Through this exercise, a few inconsistencies were found such as Iguanodons A3 and B3, which do not belong to group 3 (-356 m) as previously thought, but to group 2 (-322 m).

From the 3D model and its database it is possible to produce 3D views including all the desired features but also plans (Fig. 7), which will help us in deciphering the crime scene through the rest of the project.

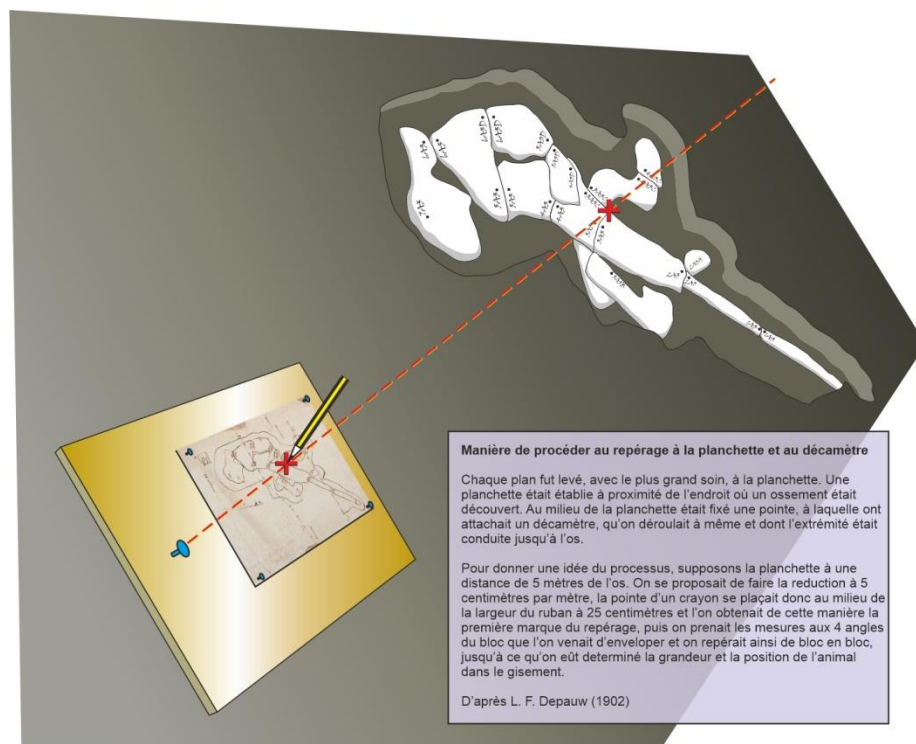


Fig. 6 – Methodology for orientating the Iguanodon skeletons (their plaster casts). Originally, the location of the individuals was carried out with the “wooden board method”, which was applied in the bedding (flattening) plane. Then the dip was inferred from retrieving each individual in the cross-sections.

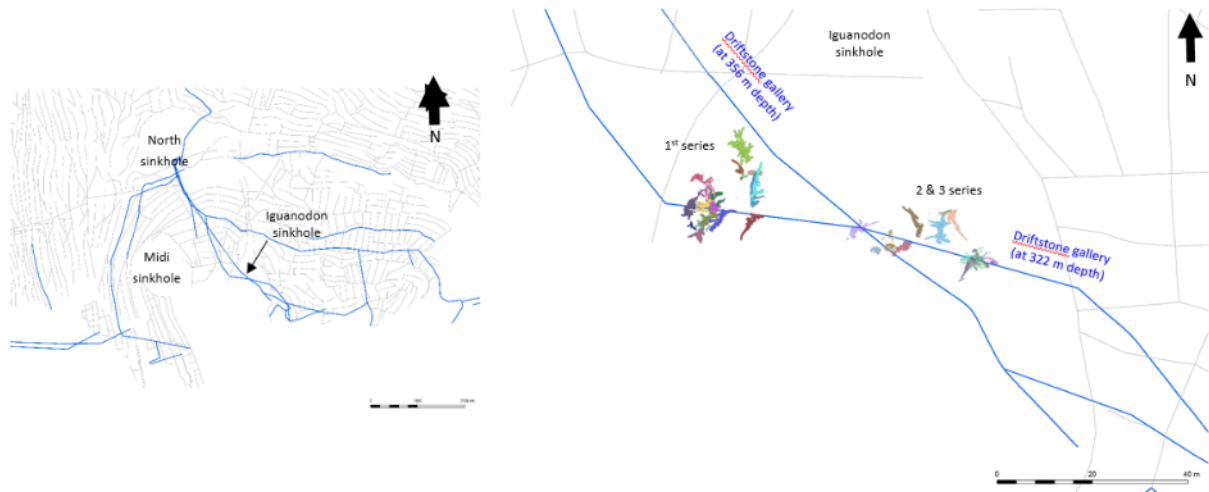


Fig. 7 – Example output from the 3D modelling of the Iguanodon sinkhole. Left : projection of the coal seam Luronne and the galleries around the three sinkholes of Bernissart. Right: detail of the iguanodon sinkhole with projected iguanodons.

4. SCIENTIFIC RESULTS AND RECOMMENDATIONS

WORK PACKAGE 1 – ANALYSIS OF THE ‘CRIME SCENE’

Reconstructing the processes that lead to the local accumulation of the *Iguanodon* skeletons at Bernissart first requires a precise understanding of the distribution and orientation of the skeletons within the sinkhole (Task 1.1): a random distribution of the skeletons within the sinkhole would speak for attrition processes, whether the presence of discrete, bone-beds with or without preferential orientations would rather support catastrophic events. The original maps and drawing realized at the occasion of the excavations were never studied in detail, although they appear particularly precise and accurate, thanks to the fruitful collaboration between mining engineers and excavation technicians.

Reconstructing the living environment of the Bernissart Iguanodon is also fundamental for understanding the conditions of their death. The reconstruction of the Bernissart palaeoflora around the Bernissart Lake is a key element that was still missing, as it remained unstudied since the pioneering works of Seward in 1900 (Task 1.2).

Task 1.1 - 3D view of the crime scene (UMons)

The geological and taphonomical models are a great source of inspiration for the main purpose of the project: unravelling the cause of animal mass-death at Bernissart at Lower Cretaceous times. During task 1.1, we have designed a workflow to process the available data and build 3D models allowing the reconstruction of the geometry of the Iguanodon sinkhole (i.e. « le Cran aux Iguanodons »), its neighboring environment and the excavation works. This 3D model (1) allows to investigate spatial and chronological relationships in the crime scene and (2) provides an unprecedented, modern view of the deposit, which will provide us with a good starting point for dissemination to the public.

All the gathered clues will not be detailed here since they are being validated. However, our results provide us with an updated morphology of the Iguanodon sinkhole (Fig. 8), which is not purely cylindrical but button-hole shaped. This is an important finding, which possibly explains why Edouard Dupont interpreted the iguanodon deposit as related to a valley (the so-called “Iguanodon Valley”). Moreover, the Iguanodon sinkhole is clearly widening upward, i.e. it is funnel-shaped. This, together with the button-hole morphology in plan view, already looked unusual to 19th century miners and mining engineers, who were used to encounter sinkholes with their typical cylindrical and narrowing-upward morphology (reversed funnel). The geological sections we have examined also show that the host rock on the western side of the sinkhole has collapsed ca. 100 m relative to the eastern side. All these observations point to the presence of an open crack or a fault at the location of the Iguanodon sinkhole. Intense deformation of the geological strata kilometers around the sinkhole shows that in fact all the area was subjected to intense collapse. In other words, the Iguanodon Sinkhole is probably unique on a geological point of view as it is unique on a paleontological of view as well (the two nearby sinkholes have no fossil dinosaurs yet they contain Wealden formations of similar age and composition). The existence of open fractures and faults that may have created a communication between the surface and the deep geothermal, sulphate-rich reservoir is of crucial importance for our project as H₂S intoxication and/or poisoning by cyanotoxins liberated by vigorous cyanobacteria blooms are regarded as possible causes of mass-death in the Bernissart swamp environment at Lower Cretaceous times.

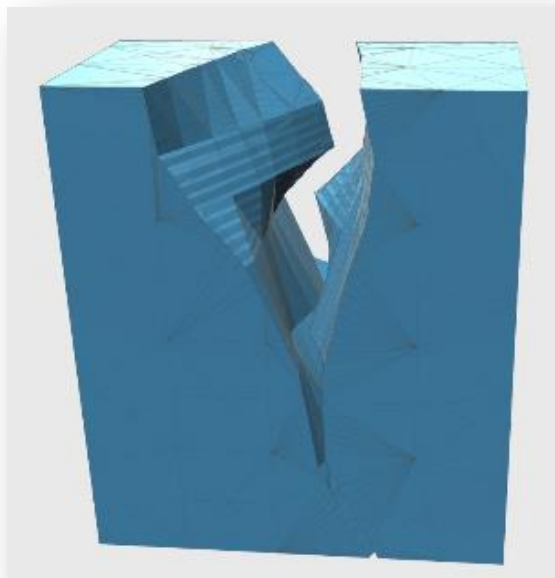


Fig. 8 – Simplified 3D model of the Iguanodon sinkhole after a series of unpublished cross-sections from a private collection. The side length of the block is ca. 100 m and its top is at ~300 m depth below the surface.

Task 1.2. – Reconstructing the palaeoenvironment of the Bernissart Lake (RBINS)

In the framework of the Coldcase project, paleobotanical investigation has been centered on three main topics that are (1) the redescription and taxonomic update of the Bernissart flora, (2) a restudy of the fern species *Weichselia reticulata* and (3) the restudy of the pinaceous cone content in Bernissart and coeval wealden deposits.

The Bernissart Wealden flora

The Bernissart flora is well known worldwide as characteristic of the Barremian deposits of northern Europe. Despite its interest and the abundance of available fossils in the RBINS collections, it remained unstudied since the pioneering works of Seward in 1900. In the course of the Coldcase project, a systemic and exhaustive reinvestigation of the fossil plant content has been performed. This reinvestigation led to a publication presently under revision and entitled “Taxonomic revision and palaeoecological interpretation of the plant assemblage of Bernissart (Barremian, Belgium)”. The main results can be summarized as follow:

The Lower Cretaceous plant assemblage of Bernissart (Fig. 9) includes one undetermined “aquatic plant” taxon, nine fern taxa (*Cladophlebis* sp., *Hausmannia dichotoma*, *Phlebopteris dunkeri*, *Matoniaceae indet.*, *Ruffordia goeppertii*, *Onychiopsis psilotoides*, *Coniopteris* sp., *Korallipteris* sp., and *Weichselia reticulata*), aff. genus *Taeniopteris* (of unknown affinity), and five undetermined conifer organs (one stem, two types of seed, one cone, and a dispersed bract). Two lithologies are identified, both consisting of grey clays, one with a smooth surface while the other is more irregular. A large number of available specimens has permitted the study of the species richness and relative abundance of the locality and both

lithologies. The taphonomical analysis of the specimens, including the preservation of the remains, fragment size, and associations between taxa, together with the diversity analyses, results in four assemblages: “algae” in the water column of the lake; a vegetation composed of *Weichselia* and *Phlebopteris* closest to the lake margin; *Hausmannia*, *Onychiopsis* and the other ferns further away from the margin; and Matoniaceae indet., conifers and aff. *Taeniopteris* even further away from the depositional site. In general, the plant assemblage at Bernissart consists of an open vegetation, which probably belonged to an early successional stage that was burnt frequently by wildfires.

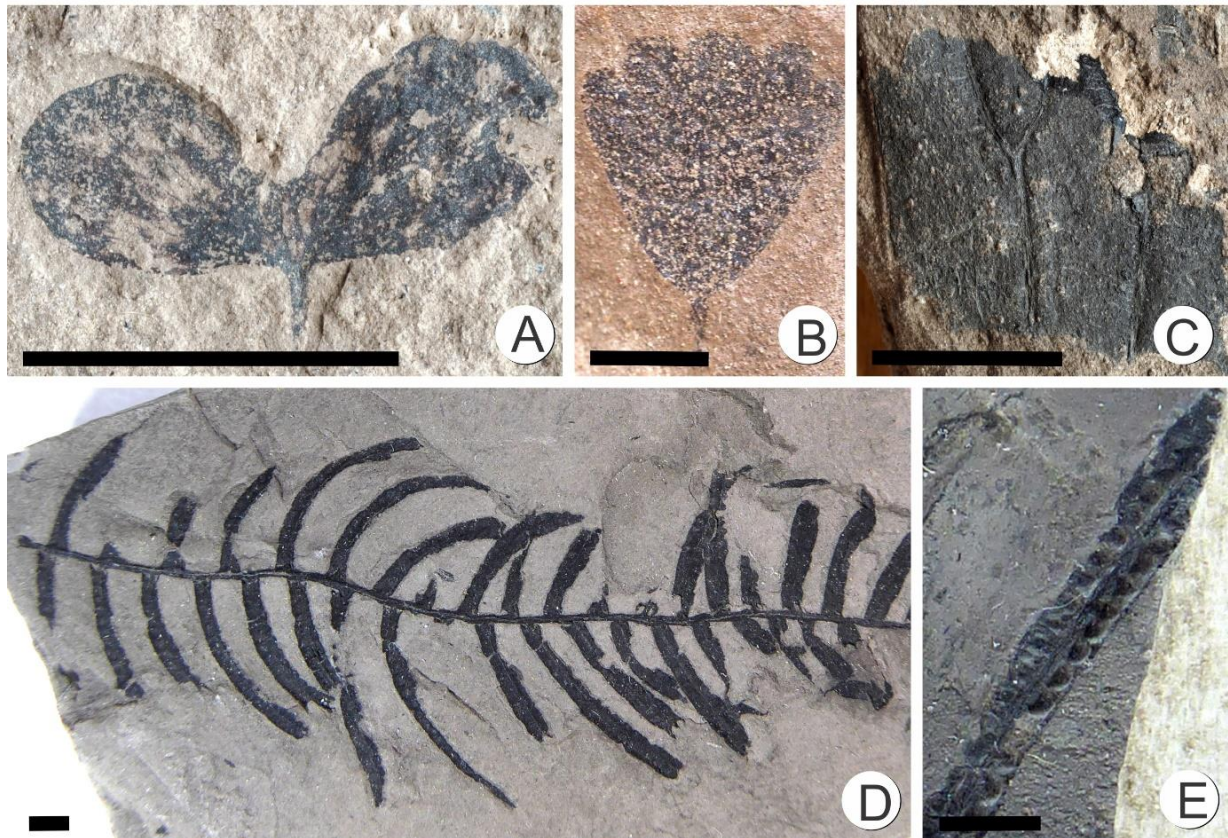


Fig. 9 - Example of fossil plants encountered in the Wealden of Bernissart. A – C *Hausmannia dichotoma*. D – E, *Phlebopteris dunkeri*. Scale = 0.5 cm.

Weichselia a common, but difficult to classify fern

The most abundant plant in the Bernissart wealden deposits is the fern *Weichselia reticulata*. It represents up to 98 % of the assemblage. However, despite this abundance, this fern remains relatively poorly understood and still fails to be classified properly. The Bernissart deposits present some of the best-preserved remains of this fern including exceptional anatomically preserved stem material. This represented an invaluable opportunity to understand the architecture and affinities of the plant. The stem material was studied using a non-destructive CT-scan approach. It allowed for the anatomy to be understood and for several hypotheses to be proposed concerning either the organization of the plant, its habit and ecology as well as biological affinities. This work led to two publications among which one is already accepted and the other is in preparation. The main results can be summarized as follow.

The Mesozoic is a key period in fern evolution, with the rise of most modern families. *Weichselia reticulata* is a widely distributed Jurassic-Cretaceous fern that has been suggested to belong to the Matoniaceae or possibly the Marattiaceae. The most accepted

classic whole-plant reconstruction for this species is based on stem and foliage material from the Barremian/Aptian locality of Négresse (Bernissart, Mons Basin, Belgium). In this work, two of these stems are revised and analysed by CT-scan imaging, providing new information on their internal anatomy and external morphology. The results show that *Weichselia reticulata* has a unique anatomy, distinct from all other extant or fossil ferns (Fig.10). Stem external morphology suggests adaptations to stressful environments, as it presents scale insertions, and a thick cortex. Especially noteworthy is the presence of structures interpreted as aerophores or nectaries at the base of putative roots and petioles that could suggest a need for extra ventilation of the frond or interactions with animals. While these new results do not settle the question of the systematic affinities of *Weischelia*, they provide new information about its autoecology and allow us to test the validity of previous whole-plant reconstructions.

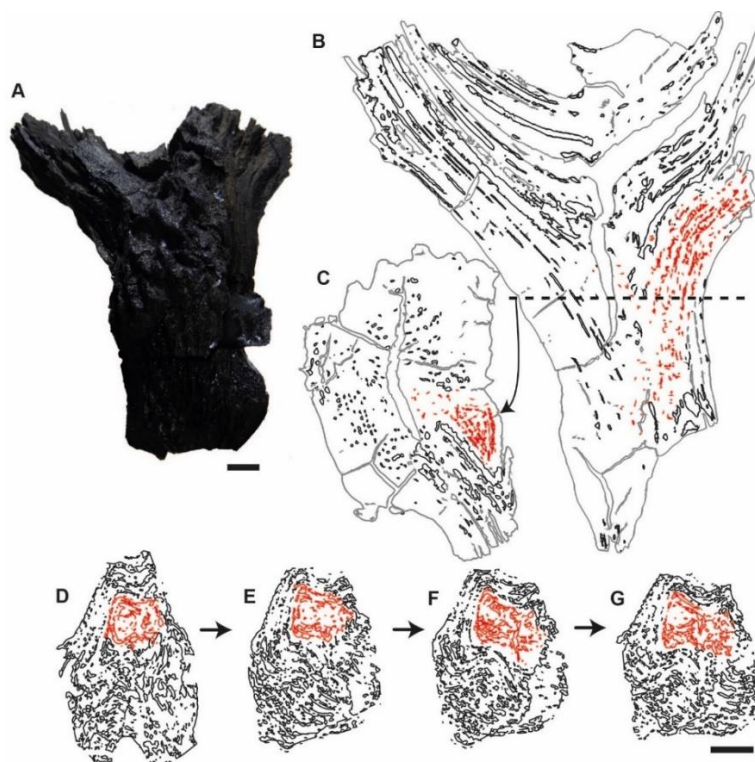


Fig. 10 - A. morphology of the stem of *Weichselia reticulata*. B-G. Identification of the vascular system. Scale bars = 1 cm.

Diversity dynamics of the Pindominated by the ferns aceae in the Lower Cretaceous of Belgium

The above-mentioned systematic revision of the Bernissart Wealden material led the rediscovery of an exceptionally abundant, diversified and well-preserved collection of fossil pinaceous cones in the collections of the RBINS. This collection represents undoubtedly the largest collection worldwide of Lower Cretaceous cones. It allows for detailed taxonomic studies to be made. For the first time, a statistically-sound quantitative approach could be undertaken in order to quantify the phenotypic variability of fossil material. A PhD student was hired in order to restudy this collection. A first paper by Léa de Brito and Cyrille Prestianni and entitled "*Pityostrobus andraei* from the Barremian (Cretaceous) of Belgium: revision" has been accepted in the "International Journal of Plant Sciences". It can be summarized as follow:

In the Lower Cretaceous (145.0-100.5 Ma), important floristic changes took place. They were notably marked by a peak of diversity in conifers and more precisely in the Pinaceae family. This expansion is particularly clear among the numerous female cone taxa found mainly in Western Europe and North America. Exceptional deposits in the Belgian Wealden facies (Barremian-Albian, 125.0 – 100.5 My, La Louvière, Houdeng-Aimeries), have delivered hundreds of exceptionally well-preserved pinaceous cones. This material is presently revised in the scope of the Coldcase project. The most abundant species, *Pityostrobus andraei* (COEMANS) SEWARD, 1919 has been restudied following traditional morphometric methods to test intra- and interspecific variations (Fig. 11). The descriptions and measurements show that two clearly distinct morphotypes have been included in the species concept of *P. andraei*. 50% and 25% of the specimens belong to two morphotypes named A (n=66) and B (n=30), respectively. Accordingly, a new species is described (*Pityostrobus gerriennei* sp. nov.). This increases the species diversity of Pinaceae known for the Lower Cretaceous of Belgium. This work allows for the first time the application of statistical tests on a large pinaceous fossil sample.

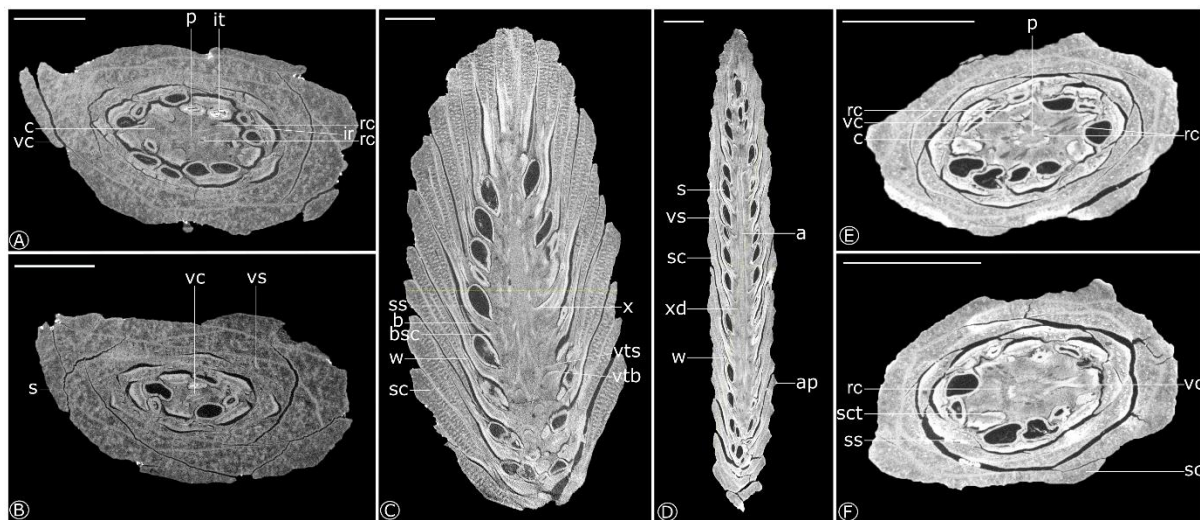


Fig. 11 - μ -CT scan images showing the anatomy of *Pityostrobus andraei*.

In addition to the results gathered in order to answer the specific questions of the Coldcase project, the latter has led to a renewed interest in the diversity dynamics of plants at the base of the Cretaceous. It led to the establishment of new fruitful collaborations with investigators of coeval deposits in Europe, especially the Las Hoyas Barremian (Spain) and the Wealden of the United Kingdom. It has opened the gate for a completely new field of investigation at the RBINS and allows for the Belgian collections and scientific results to be included in a much larger context.

WORK PACKAGE 2 – FORENSIC ANALYSES OF THE VICTIMS

In any criminal investigation, investigators first focus on the victims themselves: who are they, what relationship do they have with their families and neighbors, what is their health record? And, in the case of serial or mass crimes, how many victims can we identify and what are the links between them?

Task 2.1. The Iguanodontia: a family snapshot (RBINS)

It is well known that the vast majority of criminals are close relatives of their victims. The Bernissart Iguanodons are the most famous representatives of a large 'family' (or clade, according to the jargon of biologists): the Iguanodontia. However, the links between the different members of this 'family' are particularly complex and still poorly understood. So let's dive back into the Iguanodontia family saga, in order to better understand who our Bernissart Iguanodons really are.

A new phylogeny of Iguanodontia

The first *Iguanodon* fossils (isolated teeth) were discovered in 1825 in England and the genus *Iguanodon* became, in 1841, one of the four founding member of the Dinosauria. Since the mid-1800s *Iguanodon* has become a taxonomic grab-bag containing species spanning most of the Early Cretaceous of the northern hemisphere. And the Iguanodontia clade is now regarded as one of the largest and most diversified dinosaur group, being represented on all the continents, from Middle Jurassic up to latest Cretaceous deposits.

In 1994, Weishampel et al. published the first edition of *The Dinosauria* book, which quickly became the ultimate reference for dinosaur specialists, but also for a larger public, with complete and up-to-date information about each dinosaur group. The third edition will be published in 2021 and Pascal Godefroit (RBINS) is in charge, together with his Canadian colleague David Evans, to write the chapter about Iguanodontia. It is therefore a unique opportunity to publish an updated synthesis on the osteology, systematics, phylogeny, palaeogeography, and palaeontology of iguanodontian dinosaurs and, therefore, to better understand the 'familial' environment of Bernissart Iguanodons, in the scope of the Brain-be Coldcase project.

So far, 132 iguanodontian genera are found valid (>50 nomina dubia). Fig. 12 is the result of our new phylogenetic analysis and illustrates the calibrated (temporal and geographical) relationships between iguanodontians. South America is regarded as the ancestral geographical area of the common ancestor for Iguanodontia. During the Upper Jurassic, iguanodontians were already well diversified and had an African-European-North American distribution. The clade Iguanodontidae only includes, in the present study, *Iguanodon bernissartensis* and *Mantellisaurus atherfieldensis*, both from Late Barremian – Early Aptian deposits of England and Bernissart. This clade is, in our phylogeny, weakly supported by two synapomorphies: the dorsal margin of the rostral edentulous region of the dentary forms a well-pronounced concavity in lateral view at the level of the articulation of the dentary and the presence of epaxial tendons extending onto the cervical vertebrae. By the late Barremian-early Aptian, Neoiguanodontia were in fact already widely distributed across Laurasia, with the earliest records of Asian Iguanodontia in China. During the Aptian-Albian ('mid-Cretaceous'), Iguanodontia had achieved a virtually cosmopolitan distribution,

expanding to Gondwana. Our parsimony-based analysis reconstructs North America as the most likely ancestral geographical area for Hadrosauridae.

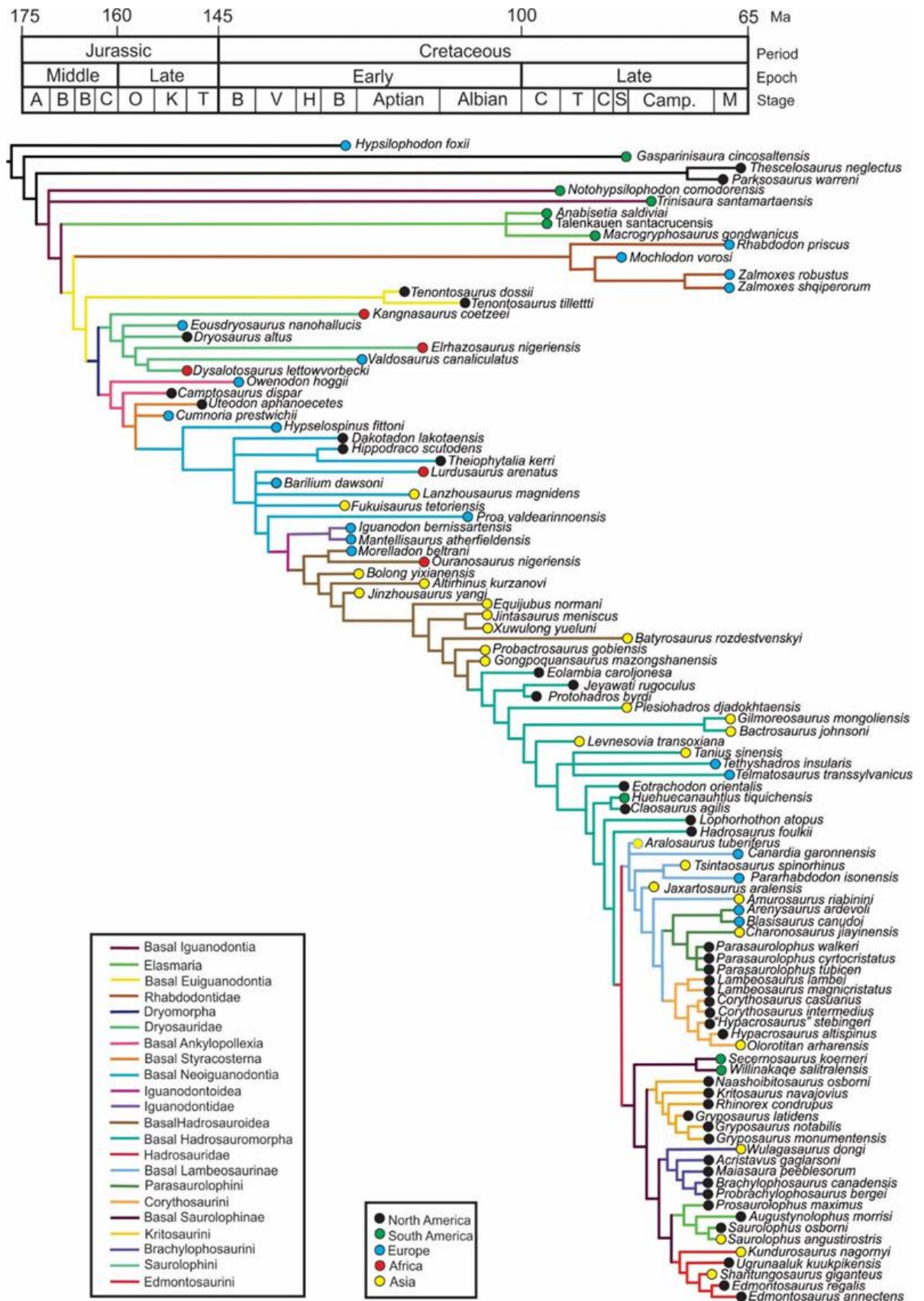


Fig. 12 – Calibrated phylogenetic analysis of Iguanodontia

A new phylogeny of Ornithischian dinosaurs

If the phylogeny of the clade Iguanodontia, and the position of the Bernissart Iguanodons within this clade, have now been clarified, the position of Iguanodontia within Ornithischians remains poorly constrained. In a recent paper (Dieudonné et al., 2020), we attempted at providing a revised framework for ornithischian phylogeny, based on an exhaustive data compilation of already published analyses, a critical re-evaluation of osteological characters and an in-depth checking of characters scoring to fix mistakes that have accumulated in previous analyses; we have also included recently described basal ornithischians, marginocephalians and ornithopods. 'Heterodontosaurids' are recovered as a paraphyletic group of basal Marginocephalia that progressively lead to the dome-headed 'true' pachycephalosaurs. 'Heterodontosaurids' consequently fall within Pachycephalosauria *sensu* Sereno, 1998 (Fig. 13). The reconfiguration of basal cerapodan relationships pulls the origins of ornithopods to the earliest stages of the Jurassic. Based on the present analysis, we also discussed ornithopod relationships, with a particular focus on basal Iguanodontia. *Tenontosaurus* is found as the basalmost iguanodontian. The monophyly of Rhabdodontomorpha in a position more derived than *Tenontosaurus* is supported by the present analysis (Fig.14).

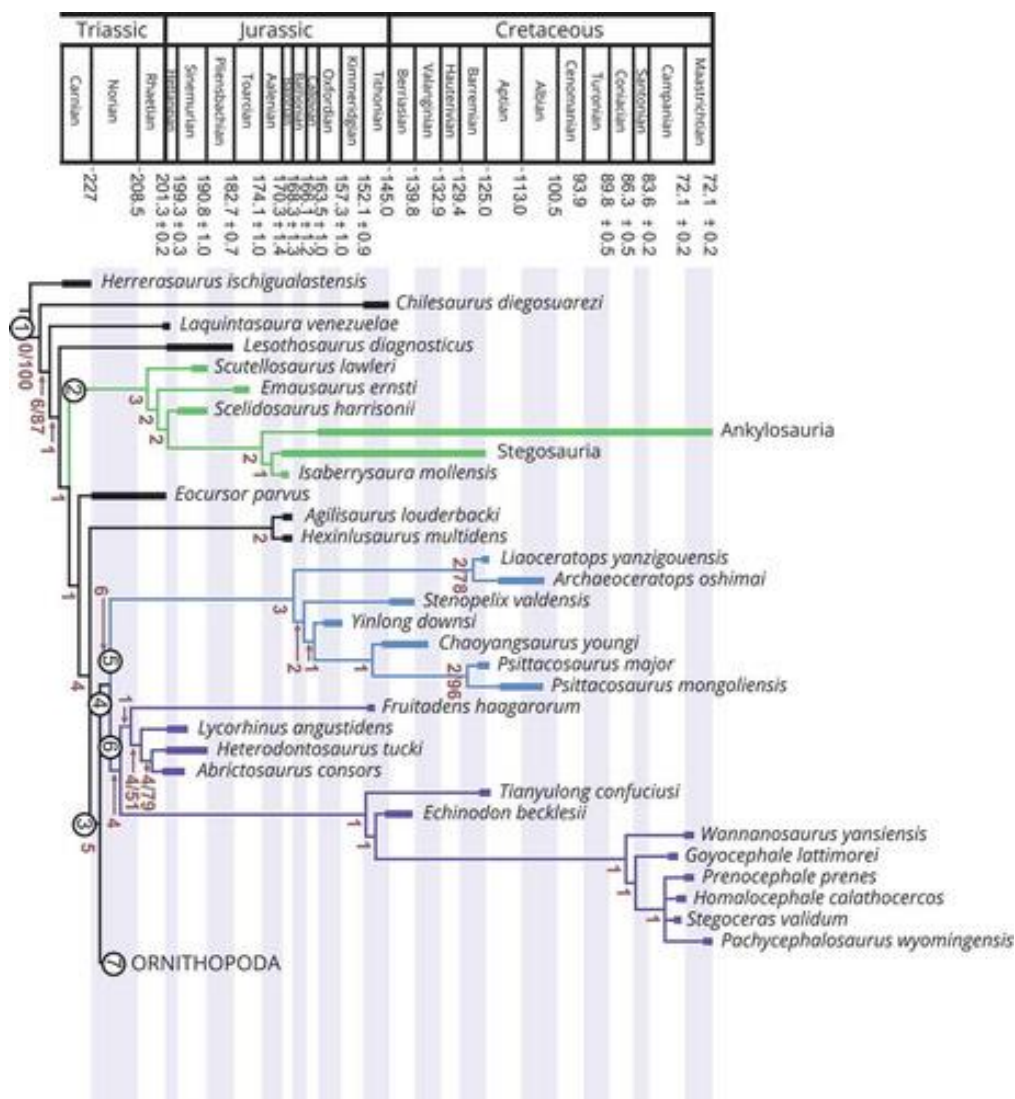


Fig. 13 – New phylogenetic analysis of basal ornithischian dinosaurs (Dieudonné et al., 2020)

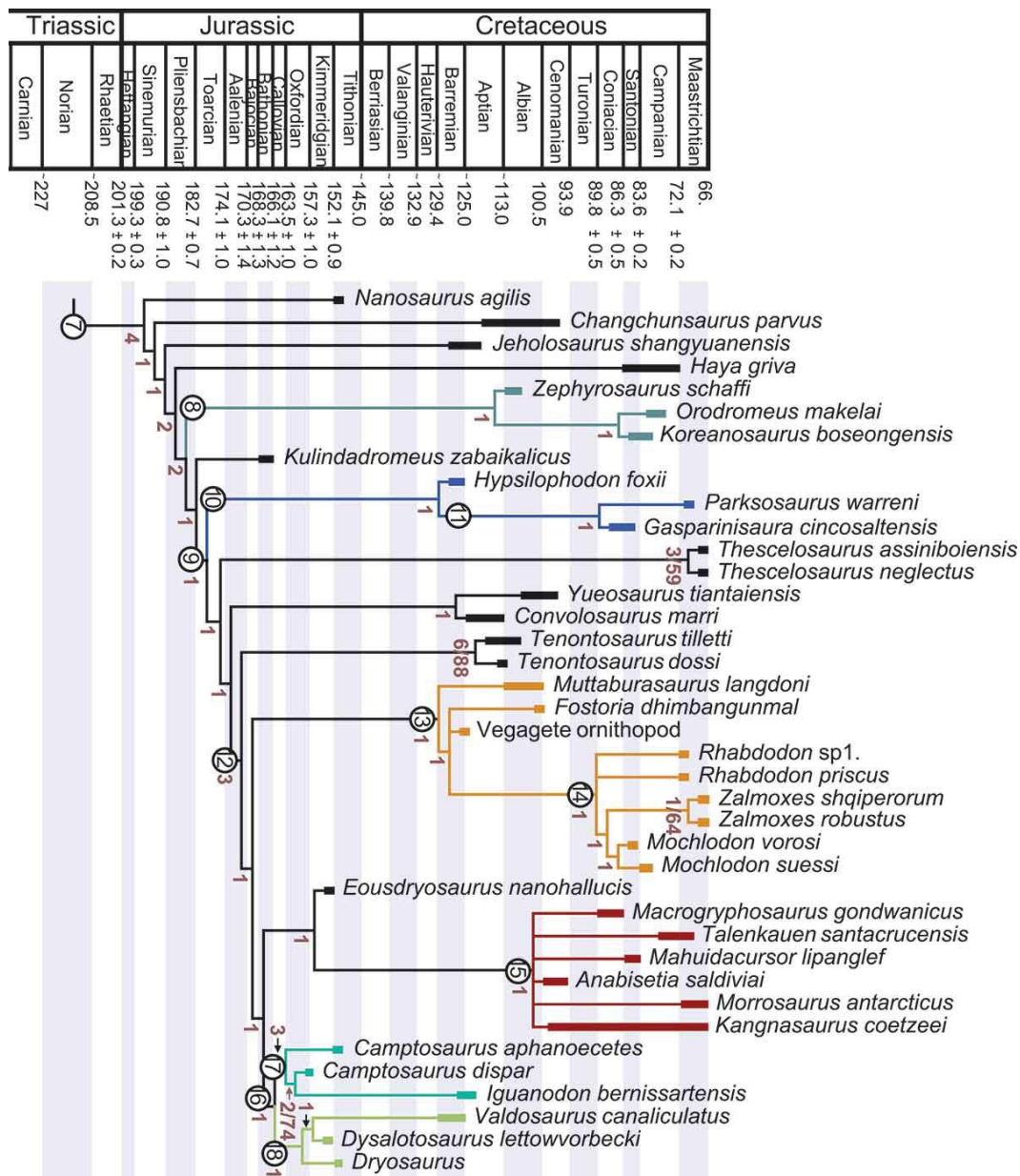


Fig. 14 – New phylogenetic analysis of basal Ornithomimidae (Dieudonné et al., 2020)

Enlarging the Iguanodontia family: a new basal Iguanodontia with enlarged teeth from Provence

Godefroit et al. (2017) described a new rhabdodontid Iguanodontia, *Matheronodon provincialis*, from the Upper Cretaceous of Provence (France). Rhabdodontids are basal iguanodontian dinosaurs and characteristic elements of Late Cretaceous dinosaur faunas in Europe. Disarticulated elements of a of *Matheronodon* have been discovered in 2009 in the late Campanian (Late Cretaceous) of Velaux-La Bastide Neuve, Bouches-du-Rhône Department, southern France. *Matheronodon* is characterized by the extreme enlargement of both its maxillary and dentary teeth, correlated to a drastic reduction in the number of maxillary teeth (4 per generation in MMS/VBN-02-102, Fig. 15). The intervalveolar septa on the maxilla are alternately present or resorbed ventrally so as to be able to lodge such enlarged teeth. The rhabdodontid dentition and masticatory apparatus were adapted for producing a strict and powerful shearing action, resembling a pair of scissors. With their

relatively simple dentition, contrasting with the sophisticated dental batteries in contemporary hadrosaurids, *Matheronodon* and other rhabdodontids are tentatively interpreted as specialized consumers of tough plant parts rich in sclerenchyma fibers, such as *Sabalites* and *Pandanites*.

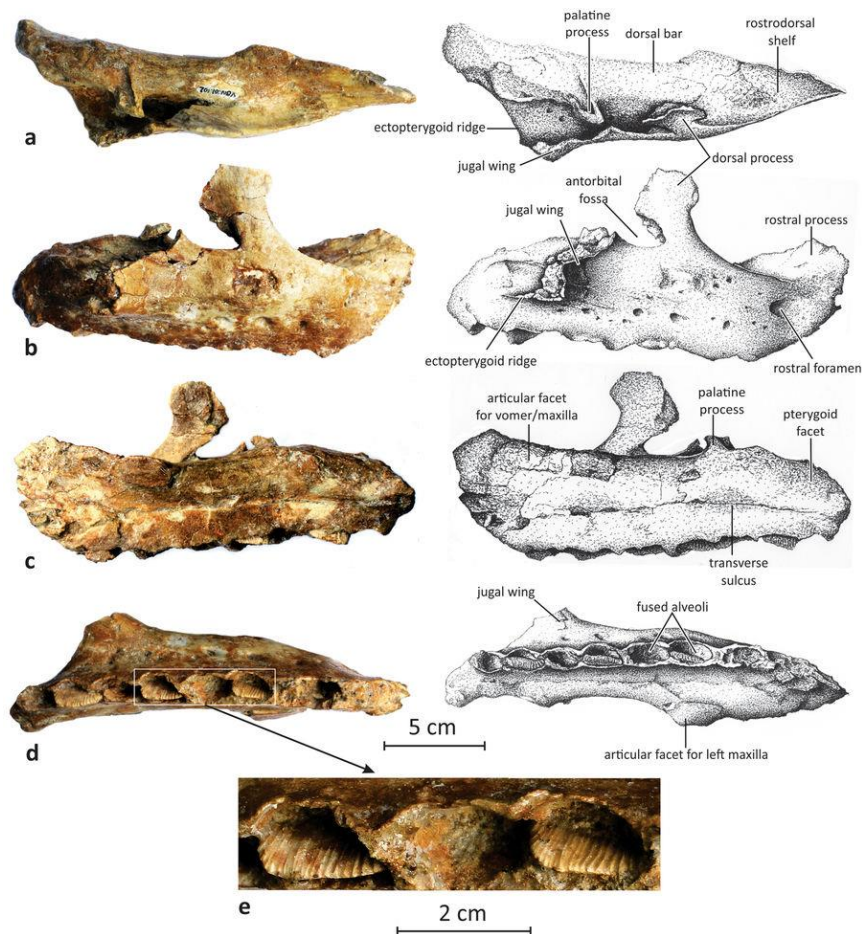


Fig. 15 - Holotype maxilla of *Matheronodon provincialis*, showing the enlarged maxillary teeth (Godefroit et al., 2017)

Task 2.2. Intraspecific variability of the Bernissart Iguanodon population (RBINS)

Intraspecific variability can be defined as those differences occurring among individuals of the same species regardless of type (morphological, behavioural, ecological, genetic, etc.). Two sources of intraspecific variations can be distinguished: ontogenetic variability (age-dependent) and individual variability (age-independent). Individuals of different ages are subject to both ontogenetic and individual variation; thus, individual variation can only be studied in individuals of approximately the same age and development stage. In ornithopods, studies of morphological ontogenetic variation are rare but usually rather detailed. In contrast, studies of individual variation are even scarcer and less detailed, including some attempts to identify sexual dimorphism, despite the importance of individual variation in systematic, phylogenetic and ontogenetic studies in dinosaurs. The main problem in studies of individual variation in dinosaurs is the usually low number of comparable individuals

discovered of a single species; thus, the results cannot be considered statistically significant. *Iguanodon bernissartensis* is represented by an exceptional series (37-38 specimens) of subcomplete specimens from a single locality. Most of them are approximately the same size and can be considered 'adults', while three smaller specimens may represent 'subadults'. As part of his extensive and detailed monograph about *I. bernissartensis*, Norman (1980) briefly described some variations in its cranial and postcranial skeleton. Here, we report the results of a more detailed study of the individual variation in the postcranial skeleton of the larger, similarly sized *I. bernissartensis* specimens from Bernissart. However, the smaller 'sub-adult' specimens were also examined, and any ontogenetic variation is discussed. These observations are evaluated against those of other specimens of this taxon from other regions of Europe. Moreover, the implications of this work for systematic, phylogenetic, and ontogenetic studies in Iguanodontia are explored. Finally, we discuss the importance of individual variation in *I. bernissartensis* for evaluating the validity of the early Barremian basal styracosternan '*Delapparentia turolensis*'.

Verdù et al. (2017) showed that individual variation in the postcranial skeleton of *I. bernissartensis* is more important than previously stated and includes the following characters: significant variation in the height and (occasionally) shape of the axial neural spine; the number of co-ossified sacral vertebrae (unfused posterior sacral or first caudal incorporated as sacro-caudal); the development of a hemal groove along the ventral surface of the middle caudal vertebrae; different degrees of curvature (including the dorsal and ventral margins) and distal flaring of the scapular blade; the relative breadth of the deltopectoral crest, the curvature of the shaft, the width of the distal end and the relative ventral projection of the ulnar condyle in the humerus (Fig. 16); the length and expression of the nail grooves in the pollex (even in the same individual); the orientation of the preacetabular process, the contour and lateral flaring of the dorsal margin, and the height of the postacetabular process of the ilium; minimal differences in the relative length and height of the prepubic blade; the curvature of the ischiatic shaft and the morphology and size of the booted distal end; the morphology of the fourth trochanter (from triangular to trapezoid) and the curvature of the femoral shaft; and finally, the proximal length of the tibia. Moreover, the height of the neural spine of the axis and the breadth of the deltopectoral crest of the humerus are suspected to be ontogenetically dependent, although more data are necessary to confirm this hypothesis. In some cases, the individual variation reported in *I. bernissartensis* is congruent with that found in other ornithopods (e.g., variation in the distal flaring of the scapular blade in the rhabdodontid *Zalmoxes robustus* and in the basal hadrosauroid *Mantellisaurus atherfieldensis*), but this is not always the case (e.g., apparently invariable contour of the dorsal margin of the ilium in the basal ankylopollexian *Camptosaurus dispar* and in the basal hadrosauroid *M. atherfieldensis*). Regardless, the use of these characters in systematic and phylogenetic studies of styracosternan iguanodontians should be avoided, or variation should at least be considered. Especially when very different states of the same character can be observed in *I. bernissartensis* (e.g., ventrally deflected vs. anteriorly directed preacetabular process; triangular vs. trapezoidal fourth trochanter), such characters could be regarded as potentially diagnostic in isolated or fragmentary material or would introduce phylogenetic noise that would interfere with properly resolving evolutionary relationships between taxa. When such variable characters cannot be avoided in systematics and phylogenetics, we therefore advise (1) to use the most frequent morphotype in the sample (e.g., dorsoventrally expanded axial neural spine, curved preacetabular process in the ilium, and curved ischiatic shaft in the ischium) so that the less frequent morphotypes are treated as aberrant forms; (2) to define the character in other ways (e.g., both the triangular and trapezoid fourth trochanter can be recognized as a tab-shaped fourth), or (3) to indicate the total range in variation for the taxon in question.

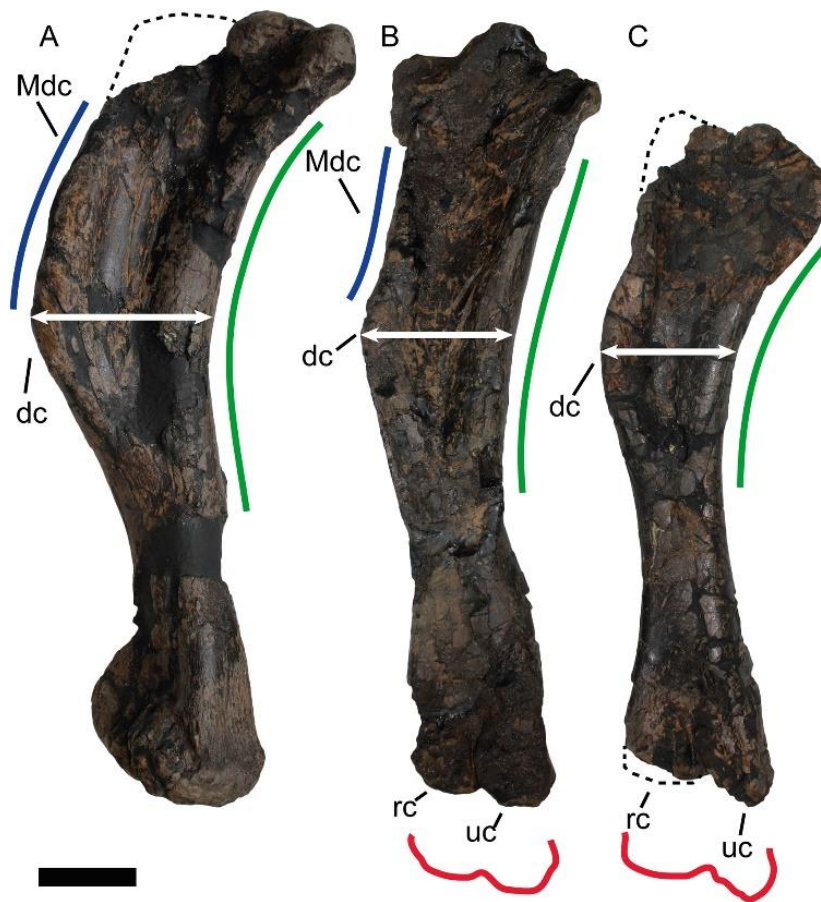


Fig. 16 – Intraspecific variation of the humerus in *Iguanodon bernissartensis* (Verdù et al., 2017)

Illustrating the importance of individual variation in *I. bernissartensis* in systematic studies, the validity of the basal styracosternan '*Delapparentia turolensis*' from the lower Barremian of Spain (Fig. 17) was evaluated. All the characters regarded as diagnostic for this taxon actually fall within the range of intraspecific variation found in *I. bernissartensis*, including the high neural spine of the axis regarded as autapomorphic for '*D. turolensis*'. For these reasons, we consider the holotype of '*D. turolensis*' as belonging to an indeterminate species of *Iguanodon*. In addition, new measurements suggest that the forelimb/hindlimb and humerus/femur ratios in 'sub-adult' specimens (~68% and ~79%, respectively) are consistent with those in 'adults'. Thus, a shift in gait during ontogeny cannot be detected based on these ratios alone. Future studies of juvenile and adult specimens of *I. galvensis* will hopefully shed light on this controversial biological aspect of *Iguanodon*. The present study also suggests that individual variation should be considered an important source of variation in ontogenetic studies of Iguanodontia, and comparisons among the different ontogenetic stages should be attempted using a large number of specimens (when available). Finally, no direct evidence of sexual dimorphism has been found in the postcranial skeleton of *I. bernissartensis*, even though some characters have a bimodal distribution (e.g., absence or presence of a ventral furrow in the middle caudal vertebrae, large and short pollexes, etc.).

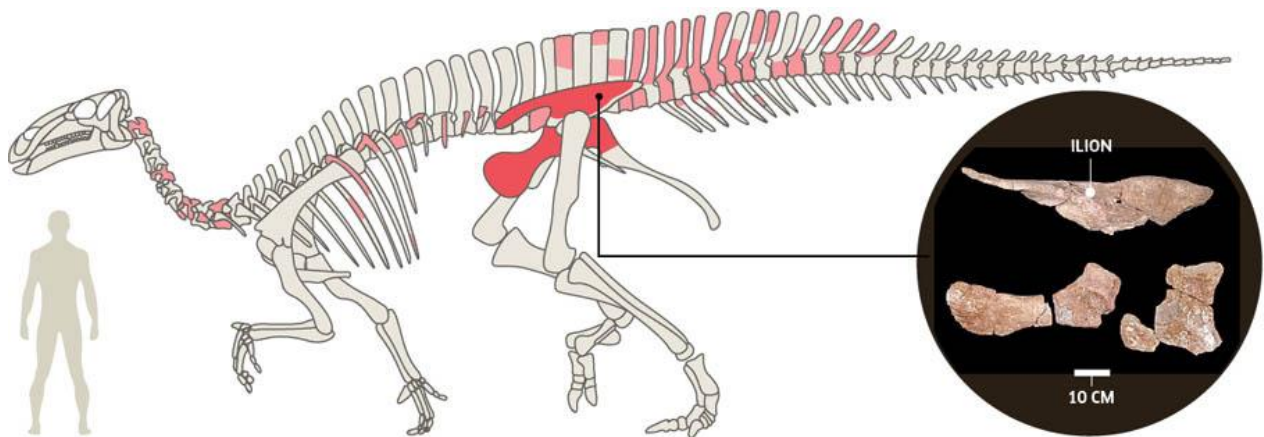


Fig. 17 – Holotype of *Delapparentia turolensis*, an Early Cretaceous iguanodontid from Spain. The preserved parts of the skeleton are in red (Verdù et al., 2017)

Task 2.3. Reconstructing the age profile of the Bernissart Iguanodon population (VUB)

Evaluating the age of the victims when they died is particularly interesting to understand the cause of their death. Therefore, in taphonomical studies, age-frequency distributions are useful for interpreting the origins of vertebrate assemblages. The observed profile at Bernissart can be compared with two theoretical endpoints representing catastrophic and attritional distributions (Lyman, 1994). In a catastrophic profile (resulting from a nonselective mass mortality), the relative size of age-classes matches those of the living population, with the difference between adjacent classes being equivalent to attritional mortality during the transition from one class to the next. In an ideal attritional profile (resulting from the slow accumulation of vertebrate carcasses selectively killed or dead during a relatively long period), the relative size of the age-classes reflects the attritional mortality during the transition from one class to the next (Lyman, 1994). The profile shows peaks that correspond to ages in which mortality rates are the highest, usually among the very young and, to a lesser extent, the very old. In this case, the age profile of the fossil assemblage is distinctly different from the age profile of the living population, and younger and older individuals are overrepresented.

To evaluate the age of the Bernissart Iguanodons at their death, we sampled successfully all but one of the requested individuals of *Iguanodon bernissartensis* with minimally invasive techniques. The paleohistological samples e.g. reveal the original features of the vascular network and the lacunocanalicular system of the bone cells (osteocytes) (Fig. 18). Moreover, the unique broad sample of bone tissues of different *Iguanodon* individuals already allows us to assess development and growth of the taxon. Most individuals were still actively growing upon their death. They show mature tissues, indicating most had reached several years of age. Two of the individuals in the collection are rather small and look more gracile than the other iguanodons. These were previously described as *Mantellisaurus atherfieldensis*, but others have hypothesized “*Mantellisaurus*” individuals were merely juveniles. Our bone histological analysis shows that the “*Mantellisaurus*” individuals were of similar

developmental age as the much larger *Iguanodon bernissartensis*. Their considerable size differences, but same ontogenetic age supports that the *Mantellisaurus atherfieldensis* and *Iguanodon bernissartensis* individuals indeed belonged to different taxa. This means at least two taxa are present among the Bernissart iguanodontids. Our bone histological results also indicate that both *Iguanodon bernissartensis* and *Mantellisaurus atherfieldensis* generally grew fast, likely reaching adult size within a decade. However, a clear difference in growth trajectory can be seen between *I. bernissartensis* and *M. atherfieldensis*, justifying their taxonomic distinction.

Finally, it should be noted that though some variation in histological maturity exists, no juveniles are known in the Bernissart iguanodont fossil population. Both *Iguanodon bernissartensis* and *Mantellisaurus atherfieldensis* are also present in the contemporary bonebed locality of Nehden (Germany), from which hundreds of mostly disarticulated bones with similar preservation were uncovered. Younger individuals (<50% max size) are well represented in the Nehden assemblage, contrasting with the situation observed at Bernissart.

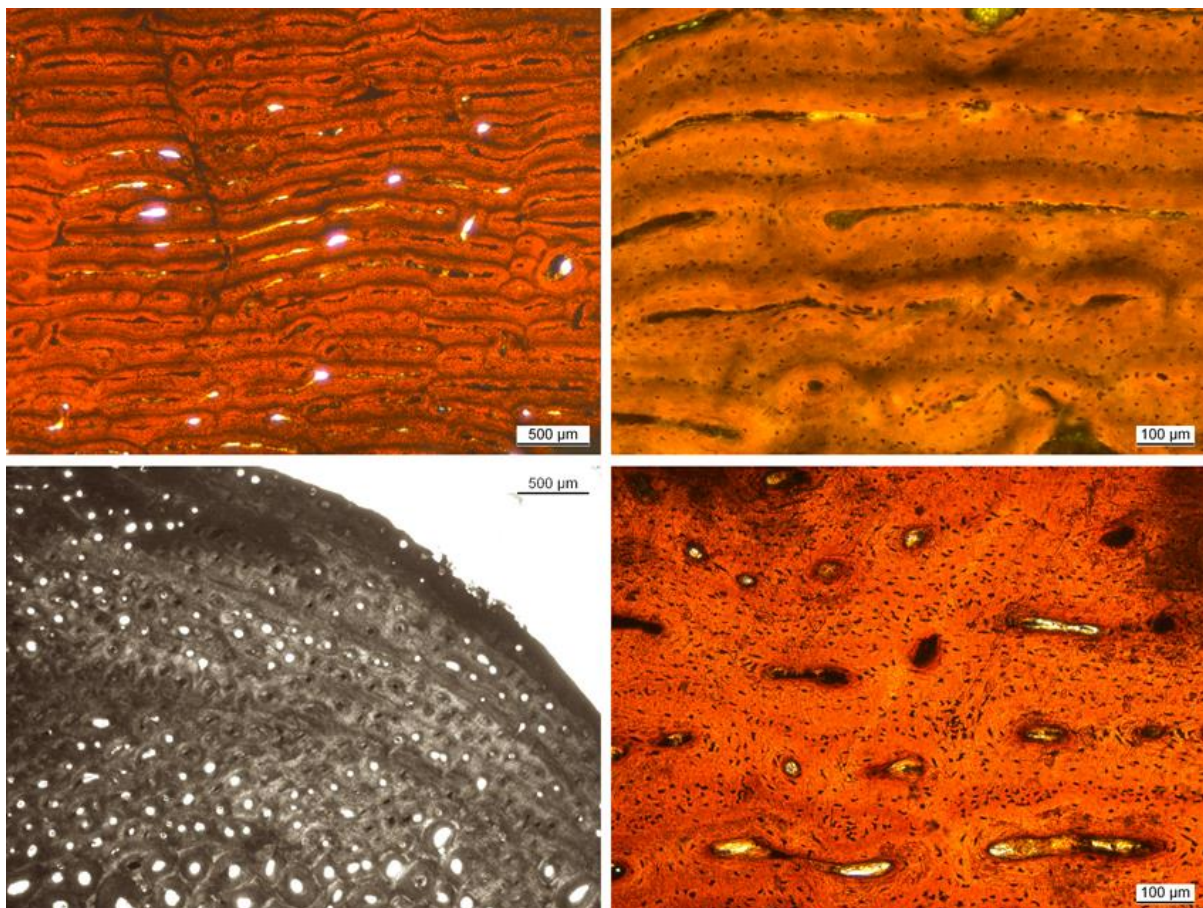


Fig. 18 – Palaeohistological samples in *Iguanodon* bones.

The age profile of the *Iguanodon bernissartensis* population from the Iguanodon Sinkhole at Bernissart is not compatible with an attritional mortality scenario. In attritional dinosaur assemblages, late juveniles and small subadult individuals usually represent over 90% of the recovered fossils (Lauters et al., 2008). This is not the case for the *I. bernissartensis* assemblage discovered at Bernissart, largely dominated by adult specimens. This age profile is more consistent with one or several catastrophic, non-selective, scenario(s): in a

catastrophic profile, the age-class abundance of the assemblage corresponds to the age profile of the living population when the catastrophic event happened (Lyman, 1994). In any case, the Iguanodon Sinkhole does not represent an equivalent of the 'Elephant's Graveyard' for those dinosaurs.

Task 2.4. Palaeopathology of the Bernissart Iguanodons (Queen's University Belfast / RBINS)

The health record of the Bernissart Iguanodon population is evidently an important element to understand the cause of the death of so many individuals during one or several apparent catastrophic event(s). Were those individuals already weakened by illnesses or wounds inflicted by predators? To tackle this question, a PhD thesis entitled 'Disease in the Early Cretaceous – A comparative study of Iguanodon and hadrosaur palaeopathology' started in September 2017, in collaboration with Eileen Murphy, Queen's University Belfast. Prof. Murphy is one of the members of the Coldcase project. This project is supported by EU COFUND (SPaRK) doctoral training programme. Filippo Bertozzo (formerly with AMGC-VUB) was selected as the PhD candidate in August 2017 and Pascal Godefroit is his co-supervisor. This PhD project is evidently partly based on a detailed study of the Bernissart Iguanodon collection.

Fossilized maladies recognized in the Bernissart specimens comprise traumas, infections, spondyloarthropathies and developmental anomalies. The pathologies have been subdivided by body region, with particular occurrences in dorsal vertebrae, the distal region of the tail, ribs, and pes. Some of these "lesions" are considered pseudopathologies because Bernissart Iguanodon specimens suffer from pyrite oxidation, which results in deformation and/or cavities resembling pathological conditions. The total number of palaeopathologies in Bernissart Iguanodons is lower than in other ornithopods, but this apparent "good health" of the population should be examined under the lens of the osteological paradox. It is possible that these dinosaur populations were comprised of healthy individuals and others suffering from severe diseases, which gave no time for their bodies to react and start the healing process. In the future, the data collected from the Bernissart specimens will be included in a complete list of ornithopod palaeopathologies to analyze any phylogenetic and/or ecological influences on the occurrence of traumas and diseases in the clade.

Task 2.5. Looking for collateral victims (RBINS)

The Bernissart Iguanodons are not the only victims buried in the Iguanodon Sinkhole at Bernissart. Fresh-water animals, which lived in the Bernissart Palaeolake, are also represented by abundant fossils, including one amphibian, six turtles, four crocodilian, and more than 3 000 fishes. The distribution of fish fossils within the Iguanodon Sinkhole is not clear, so first-hand examination of the original iconographic material is necessary. De Pauw (1898) reports an accessory fish bone-bed ("bed II") at the footwall of the cavity created for excavating an iguanodon from bed IV. However he claimed that the main fish bone-bed was lying 4 m below and also contained chelonians and crocodiles. This bone-bed is not indicated in the original figure and the comment on its location is puzzling because '4 m below' would stratigraphically correspond to bed I or II. Perhaps De Pauw did not use stratigraphical but local references as the excavation chamber had a complex geometry and the ground was irregularly dipping. It is therefore impossible to locate this main fish bonebed without further precision.. It is particularly important to find a solution to this problem, because one of these fish-rich beds was used as stratigraphical marker for drawing the

geological section (Cornet and Schmitz, 1889). It will be also interesting to know whether the fish fauna suffered from catastrophic death events.

An in-depth revision fishes from the Bernissart Sinkhole will also be necessary to assess the biodiversity of the fresh-water fauna and therefore to provide precious information about the physic-chemical conditions within the Bernissart Palaeolake. The English palaeontologist Traquair (1911), who studied the Bernissart ichthyofauna, identified 16 different taxa. Unfortunately, his descriptions were quite superficial and the proposed systematic, mainly based on morphometric analyses, must be completely reconsidered in the light of modern anatomical and phylogenetic standards. Taverne (1981, 1982, 1999) started the revision of the Bernissart actinopterygians, but from the 16 taxa described by Traquair, at least 10 still require a complete revision. The Bernissart crocodile fauna was also revised in the scope of the Coldcase project.

Revision of the actinopterygian fish fauna

If the Cretaceous locality of Bernissart, is well known for the Iguanodons, it has also yielded about 3,000 fossil fishes. In the frame of the Coldcase project, which aims to understand the ecological and geological conditions in the Bernissart lake/swamp during the Barremian, a revision of the actinopterygian fauna from Bernissart has been launched. The revision of the ichthyofauna has started with taxa, unstudied since 1911: *Coccolepis macroptera*, *Lepidotus bernissartensis*, *L. brevifulcratus* and *L. arcuatus*. The study shows that the material attributed to both genera could likely be attributed to other genera and that the reduced actinopterygian taxic diversity found at Bernissart confirms the lacustrine to swampy environment (Olive et al., 2017)

The coccolepidid *Coccolepis macroptera*, was named by Traquair at the beginning of the 20th century. The systematic revision of several taxa of the family Coccolepididae during the last two decades, not only led to changes in the taxonomic status of these taxa, but also to a much better knowledge of these fishes in general. In the light of this achievements, *C. macroptera* was revised and, as a result, placed in its own new genus *Barbalepis*. *Barbalepis* is a coccolepidid fish with the following combination of characters: lower jaw long and robust; pectoral fins proportionally much smaller than the pelvic fins; some dermal bones covered with a fingerprint-like thin striation and some others smooth; free area of scales covered with tubercles and overlapped area with a thin striation; fin rays smooth; anal fin inserted at the first modified haemal spine (Fig. 19). Olive et al. (2019) described this fish with taxonomic conclusions regarding the family Coccolepididae, and discussed the paleogeographic and paleoenvironmental history of the group, which indicates that the origin of the family predates its first occurrence in the known fossil record and that coccolepidids became restricted to freshwater environments during the Jurassic.



Fig. 19 – *Barbalepis* specimen from Bernissart (scale bar = 1 cm; Olive et al., 2019).

Lepidotes bernissartensis is a species of holostean ray-finned fish from the Barremian–Aptian of Bernissart, Belgium, described by Traquair in 1911. In the scope of the Coldcase project, Cavin et al. (2019) revised its anatomy, which led them to include this species in the genus *Scheenstia*, and to consider *L. brevifurcratus* and *L. arcuatus*, both from Bernissart, synonymous with *S. bernissartensis* (Fig. 20). They also performed a cladistic analysis in order to assess the phylogenetic position of *S. bernissartensis* and to do an updated appraisal of the evolutionary history of the ginglymodians (Fig. 21). *Scheenstia* is included in the Lepidotidae and placed in a pectinated position between the basal genus *Lepidotes* and the more derived members of the family (other species of *Scheenstia*, *Isanichthys* and *Camerichthys*). The nodes within the lepidotids are weakly supported. Although *S. bernissartensis* is not directly related to *S. mantelli* from the Wealden of Europe, the two species have similar palaeoenvironments and stratigraphical ranges. Taken as a whole, the ginglymodians experienced several episodes of diversification that are spatially and temporally restricted. The oldest episode involved basal ginglymodians and occurred in the Middle Triassic, in marine environments along the northern margin of the Tethys. A second episode affected the Semionotidae and occurred in freshwater environments of North America and Europe in the Late Triassic and Early Jurassic. The remaining Semionotiformes, Macrosemiidae and Callipurbeckidae, ranged from the Triassic to the Early Cretaceous and were mostly marine. Among the Lepisosteiformes, two clades, the Lepidotidae and the Lepisosteoidi, show episodes of diversification, first in marine and then in freshwater environments.

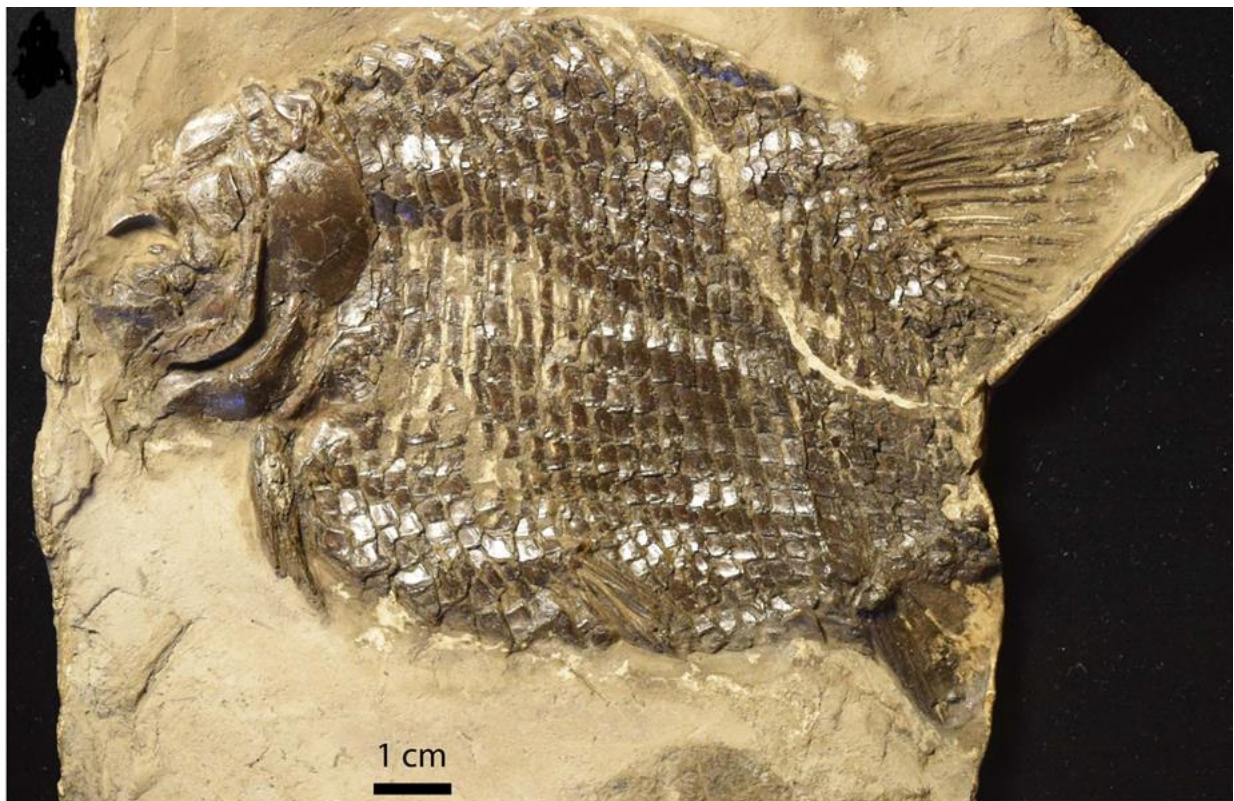


Fig. 20 – *Scheenstia bernissartensis* specimen from Bernissart (Cavin et al., 2019).

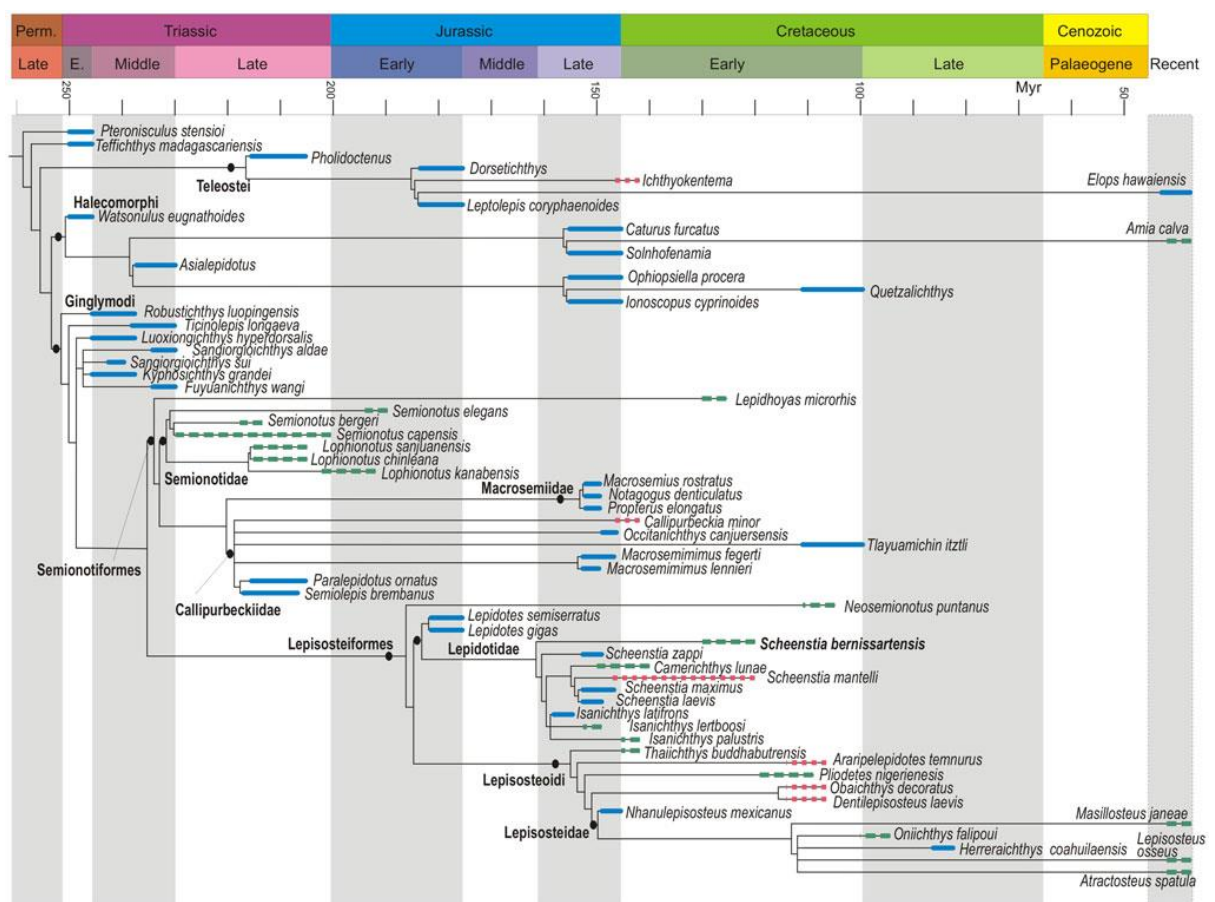


Fig. 21 - Time-scaled tree of the neopterygian crown-group, showing the phylogenetic relationships of *Scheenstia bernissartensis* (Cavin et al., 2019)

Finally, Olive et al. (2020) revised the pleuropholid specimens from Bernissart, initially described as *Pleuropholis* sp. by Traquair, and named a new species, *Pleuropholis germinalis*. This new species is supported by a novel combination of characters, i.e. preopercular canal in the middle of the preopercle ventral branch, leptolepid notch in the median-dorsal part of the dentary, smooth posterior edges of preopercle and flank scales, and maxilla short and upturned (Fig. 22).

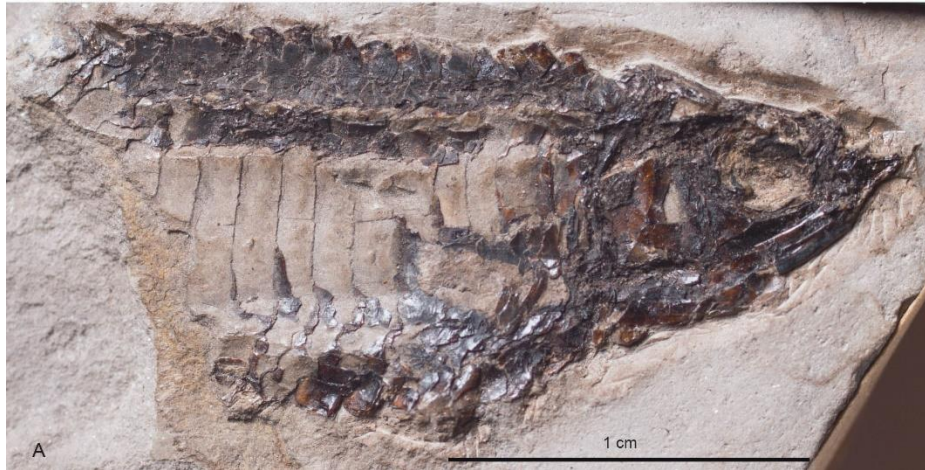


Fig. 22 – *Pleuropholis germinalis* specimen from Bernissart (Olive et al., 2020)

Revision of the fresh-water crocodiles from Bernissart

Martin et al. (2017) revised two crocodile specimens from the Lower Cretaceous of Bernissart, originally referred by Louis Dollo to *Goniopholis simus*, and consisting of fully articulated skeletons, one missing the skull and mandible (Fig. 23). Comparison of these specimens with recently revised specimens from the Wealden of England indicate that the Belgian specimens are in fact referable to the goniopholidid *Anteophthalmosuchus hooleyi*. The Belgian specimens are the most completely known representatives not only of this species but also of any Goniopholididae. Study of the postcranial skeletons from Bernissart reveals that the appendicular skeleton closely resembles that of derived neosuchians. The dorsal and ventral shields present a morphology directly comparable to other goniopholidids and pholidosaurids. Such observations stress the necessity to gather an osteological database of postcranial elements to test relationships of the various neosuchian lineages. Goniopholididae were relatively diverse during the Early Cretaceous of Europe, and depending on taxonomic opinion, three to five genera are recognized: *Anteophthalmosuchus*, *Goniopholis*, *Hulkepholis*, and possibly *Vectisuchus* and *Nannosuchus*.

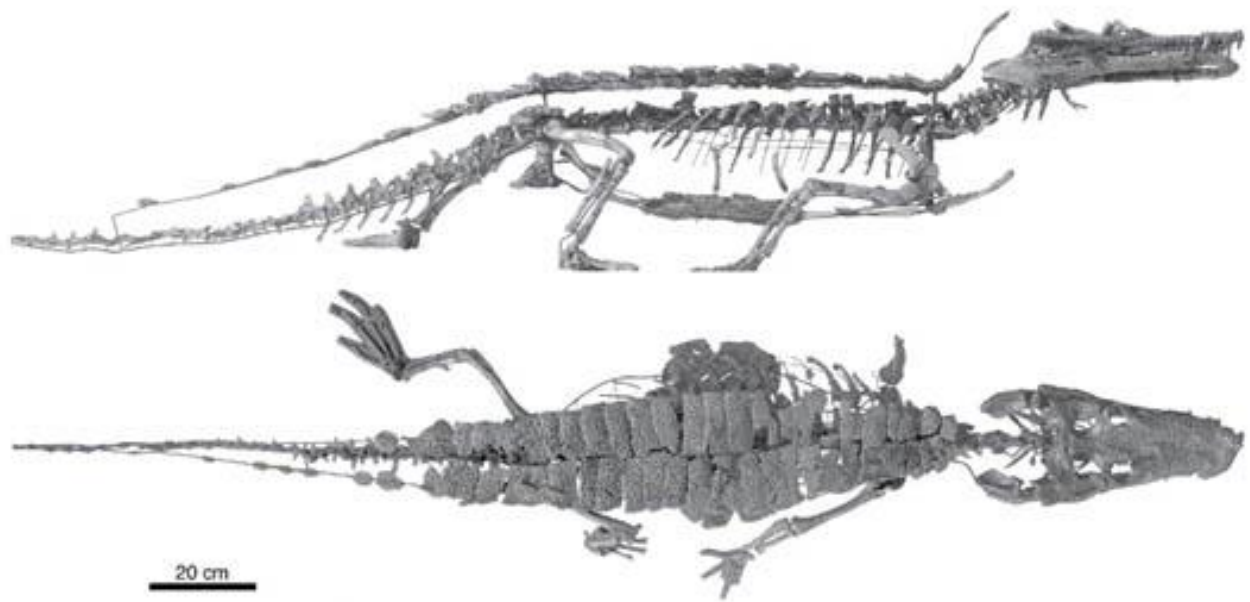


Fig. 23 – Complete skeleton of *Anteophthalmosuchus hooleyi* from Bernissart

Bernissartia fagesii, the smaller crocodylian from Bernissart (Fig. 24), has long been considered a key taxon for understanding the origin of Eusuchia, but more recent hypotheses found support for a more basal position, as an ally to goniopholidids, paralligatorids or atoposaurids. Because many details of the anatomy of the type specimen are hidden by glue and the sediment adhering to the fossils, a number of characters are pending confirmation. Based on computed tomography data, Martin et al. (2020) extracted bones of the cranium and mandibles, described new characters and re-evaluated anatomical details in the lectotype specimen. Their phylogenetic analysis confirms that *B. fagesii* is a derived neosuchian, unrelated to atoposaurids, goniopholidids and paralligatorids. They recover *B. fagesii* and *Koumpiodontosuchus aprosdokiti* in a basal position within Eusuchia, together with Susisuchidae, a group of gondwanan neosuchians containing *Susisuchus* and *Isisfordia*, which here form a polytomy with Hylaeochampsidae (Fig. 25). The presence/absence of pterygoid-bound internal choanae cannot be used to fully resolve relationships at the neosuchian–eusuchian transition because of the variability of this character even at the familial level, as recently reported within susisuchids and bernissartiids. There is no doubt that true eusuchians were present in Laurasia as early as the Early Cretaceous, the hylaeochampsid *Hylaeochampsia vectiana* being the oldest (Barremian) undoubted representative. But whether the Eusuchia were also present in southern landmasses depends on solving the phylogenetic position of susisuchids and other less known gondwanan forms within or outside Eusuchia.



Fig. 24 – Complete skeleton of *Bernissartia fagesii* from Bernissart

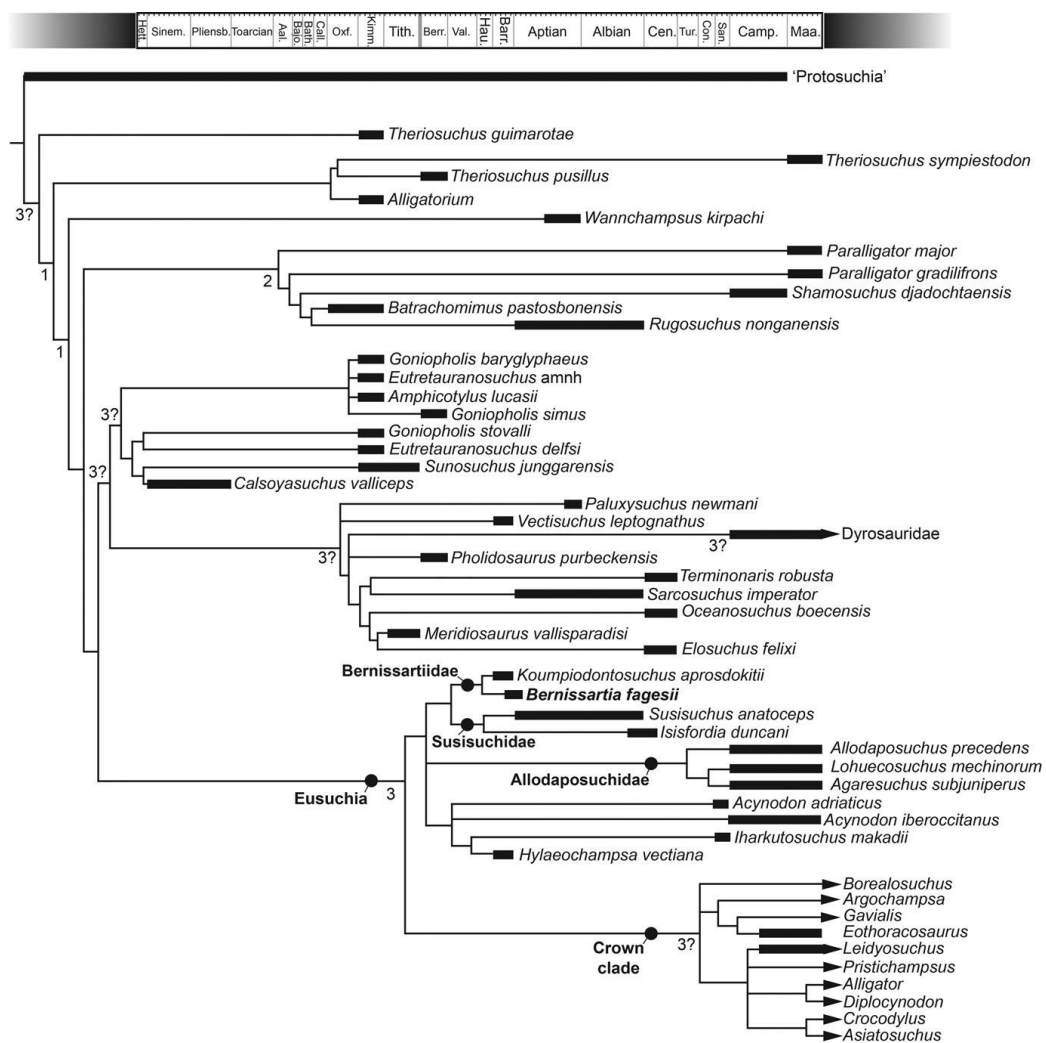


Fig. 25 - Time-scaled tree of derived neosuchian crocodiles, showing the phylogenetic relationships of *Bernissartia fagesii* (Martin et al., 2020)

WORK PACKAGE 3 - CROSS-CHECKING THE WITNESS TESTIMONIES (UMons)

The aim of the Work Package is to detect any changes in the lacustrine palaeoenvironments, input of clastic material by short flood events, presence of soot, redox conditions, etc. that could be related to either proposed death-scenario for the Bernissart palaeofauna (see WP4). It also aims at clarifying a number of palaeoenvironmental aspects, in particular the relationships between the formation of the so-called Bernissart Palaeolake, the accumulation of iguanodontids along with other taxa and the deep sinkhole beneath. By inducing a local high subsidence rate, the Bernissart sinkhole may be envisioned as a “passive” trap for lake sediments and carcasses, preserving them from subsequent alteration and erosion. Detailed structural, sedimentological and geochemical investigations using high-resolution techniques on selected key-intervals in the BER 3 cores provide the necessary information for evaluating the scenarios for the Bernissart Iguanodons mass-death. Taking into account the geological specificities of Bernissart’s area and their potential impact on the palaeoenvironment during Lower Cretaceous times should constrain the possible death-scenario. An exceptional fossil deposit requires exceptional geological processes, not only chance. Indeed, major sinkholes due to deep evaporite dissolution such those occurring in Hainaut are exceptional in density and dimension (>1500 m in length; the Flénu sinkhole is the world’s largest karstic pipe in terms of vertical offset; Quinif and Licour, 2012) and geological longevity.

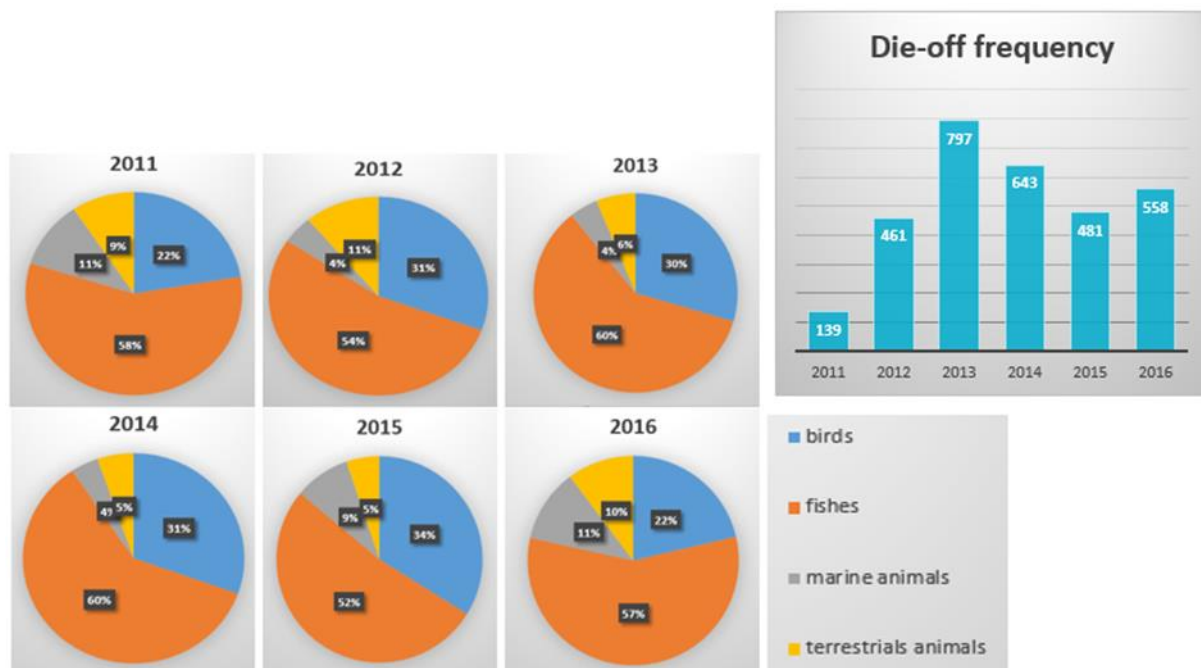


Fig. 26 – Frequency and assemblage of mass-death cases over the last 5 years.

Mass-deaths in Nature

A study of mass-death in current natural environments was first conducted in order to have a comparative basis and collect information on the evidence to be searched such as biomarkers. The present inventory of animal mass-death in nature was performed by compiling reported cases mainly from the 5 last years. All relevant information was recorded into a database: time, location, assemblage, casualties, causes (if known), etc. In total, 3079 cases were recorded. It appears that mass-death is actually common in Nature, with hundreds of cases a year (Fig. 26). Fishes and birds dominate but large animal die-offs are not rare. Meteorological and biological causes are equal in frequency. Droughts, floods and colds are predominant meteorological factors, while for biological factors, most are unknown or uncertain and poisoning/intoxication (mostly by cyanobacteria and H₂S – Tables 1 and 2) is ranked second. Multiple causes are probable in a number of cases but extremely difficult to assess. This study will be useful for evaluating our taphonomical scenarios and searching the right evidence. Among the causes that were not considered previously in our investigation, lightning strikes appear as mass-killers that operate every year (323 reindeers killed by a single lightning strike in Norway in 2016 – 120 sheep in Kirghizstan the same year). However, such cause would be extremely difficult to evidence. As we favor a geological influence on mass-death at Bernissart, the presence of the sinkhole with sulphate-saturated water in the porosity of its filling materials could have acted as a high-conductivity body in the underground and attracted lightning strikes within the area but the literature so far does not support this (the influence of topographical factors would be far greater than geological factors on strike location).

animal	casualties	cause, emanating medium	dead in	date	location	country	reference
horse	1	green alga	1 min	28/7/09	Côtes-d'Armor	France	Sacco, 2009; Ducreux, 2010
human	1	green alga	10 min	22/7/09	Côtes-d'Armor	France	Goudet, 2009
dogs (13 and 25kg)	2	green alga		12/7/08	Côtes-d'Armor	France	Borezée et al., 2011
human		green alga		5/5/99	Côtes-d'Armor	France	Borezée et al., 2011
human	1	green alga		summer 1989	Côtes-d'Armor	France	Ducreux, 2010
human	3	waste water		22/2/96			Ducreux, 2010
human	5	viscera		27/6/05		Germany	Ducreux, 2010
human	2	unrefrigerated meat					Ducreux, 2010
human		sewer	30 min				Ducreux, 2010
human	2	green alga		15/1/15	Manche	France	Ducreux, 2010
human	1	sewer	< 5 min	1/5/00			Querellou et al., 2005
boars	36	green alga		24/7/11	Côtes-d'Armor	France	AFP le monde, 2011
nutria	3	green alga			Côtes-d'Armor	France	AFP le monde, 2011
badger	1	green alga			Côtes-d'Armor	France	Puchaux et al., 2011

Table I – Reported cases of death caused by H₂S in EU

animal	casualties	toxins	date	causes	Country	Reference
calves/heifers	100	MYC	1970 to 1995	livestock watering	Switzerland	Afssa, Afsset, 2006
heifers	4	MYC	1978		Norway	Chorus I. and BartramJ., 1999
cows	3		1979		England	Chorus I. and BartramJ., 1999
cattles	16		1983		Germany	Chorus I. and BartramJ., 1999
lambs	20	MYC-LR	1989		England	Chorus I. and BartramJ., 1999
sheep	20	MYC		watering in a lake	England	Afssa, Afsset, 2006
dogs	20		1975		Denmark	Chorus I. and BartramJ., 1999
	9		1982		Sweden	Chorus I. and BartramJ., 1999
	1/3		1984		Finland	Chorus I. and BartramJ., 1999
	14	MYC-LR	1989		England	Chorus I. and BartramJ., 1999
	3 (1990), 1 (1991)	ANA-A	1990-1991	drinking contaminated water	Scotland	Edwards et al., 1992
	1		1992	bathing	France	Afssa, Afsset, 2006
	2				Germany	Nehring, 1993
	26 (2002) / 6 (2003)	ANA-A	4/8/2002 29/09/2002 24/07/2003 26/08/2003	bathing and watering	France	Bertrand et al., 2004 ; Silvano, 2005
	2/3	ANA-A	11 et 14/09/2003		France	Silvano, 2005
	15	MYC			England	jaeg, 2007
human				soldier during aquatic exercises	England	Metcalf and Codd, 2014 ; Turner et al., 1990; santé Canada, 2002
greater flamingo	579/943	MYC	2001	filter feeders	Spain	
fishes			1988		France	
fishes/mollusc		SAX		filter feeders	Italy	

Table II – Reported cases of death caused by cyanobacteria in EU since 1970

Structural model

A structural model of the clay infilling the Bernissart sinkhole was drawn up based on the detailed analysis of the 19th century excavation sections and measurements of the dip angles of the Ber3 borehole (Fig. 27). This model fits very well with the deformation pattern of the materials that sinkholes literally swallow due to subsidence. This deformation pattern, almost universally observed, consists in a central “plug” of nearly undeformed layered

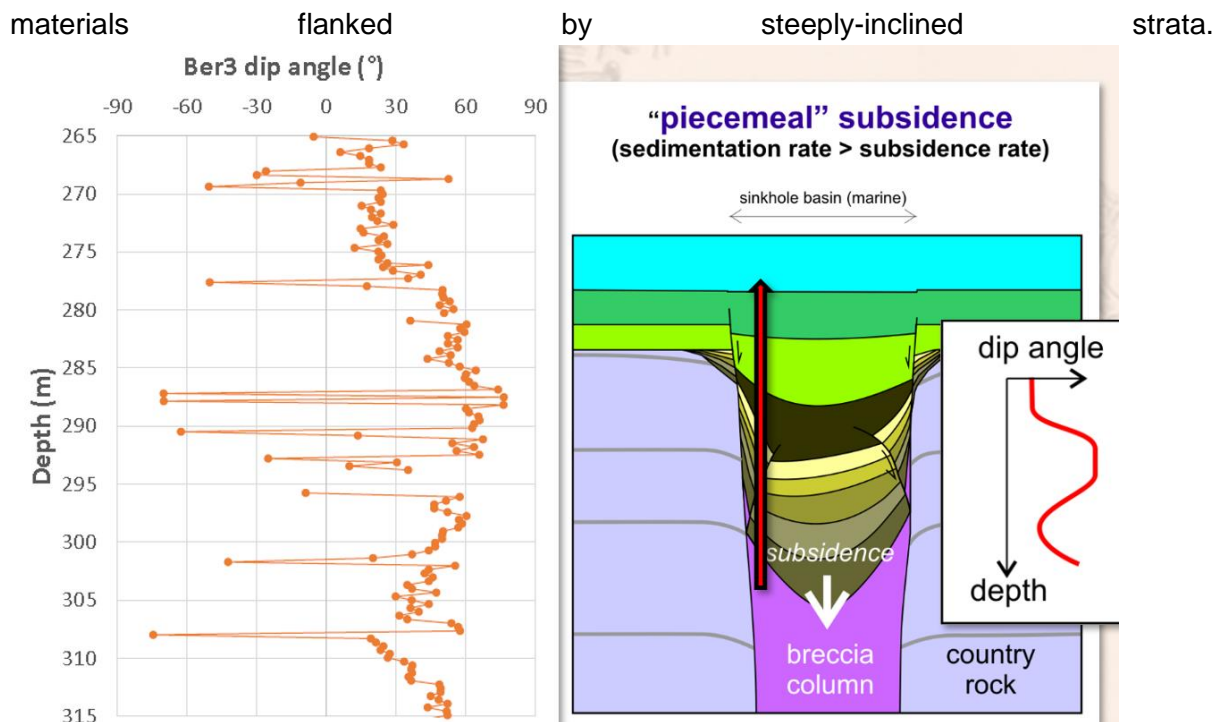


Fig. 27 - Structure of the clay infilling the Bernissart sinkhole. **Left:** log of the dip angle as measured in the Ber3 borehole. Negative values, which represents 10% of the total data number, likely represent disturbed core intervals, not original dip angle. **Right:** structural model of the clay infill and theoretical evolution of the dip angle (inset). Red vertical arrow shows approximate position of the Ber3 borehole.

Sedimentology

Observations of the Ber3 cores at macro- and microscales showed that most of the Bernissart clay consists of graded beds of heterogeneous thickness. Debris flows are occasionally interbedded, especially in the lower part of the borehole. Stratification in the Bernissart clay does not have the regularity nor the seasonal character (e.g., biogenic/minerogenic alternation) of lake varves as previously thought. In contrast, clay strata are strikingly similar to turbidites, i.e. gravity-driven deposits after slumping/sliding of sedimentary masses. The common orientation of many plant debris demonstrates the existence of currents, which could therefore be ascribed to turbidity currents. The mode of deposition of the many recovered coprolites, which was long obscure (Bertrand, 1903), could also be explained by turbiditic sedimentation.

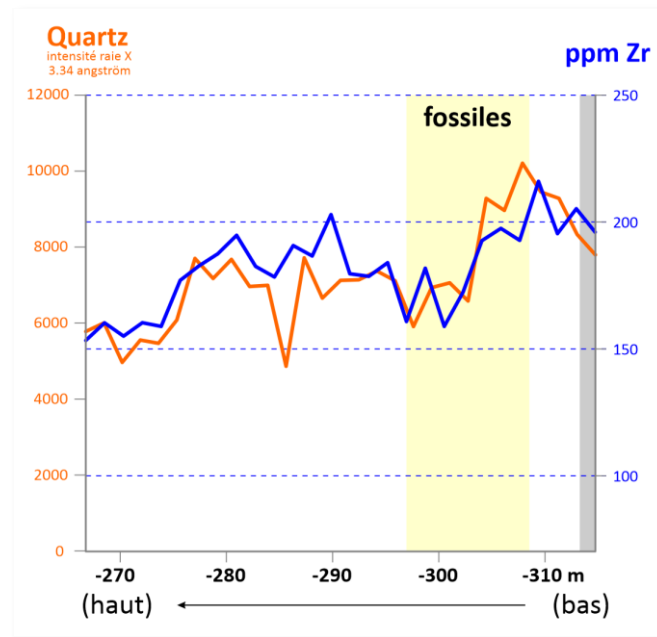


Fig. 28 - Profile for quartz (left) and zirconium (right) concentrations in Ber3 borehole as determined by XRD and XRF, respectively

Laser-Induced Breakdown Spectroscopy (LIBS) analyses, X-ray fluorescence (XRF) and X-ray Diffraction (XRD) of the entire Ber3 section showed a higher abundance of quartz and Zr- and Ti-heavy minerals in the lower part of the borehole (Fig. 28). This would indicate that turbidites were proximal at early stage and more distal in later stages, which is furthermore supported by the observation of finer and more regular turbidite units upwards together with the predominance of debris-flows at the base. As the borehole cores reflects the sedimentary record at a more or less fixed position, which means that the sediment source backed away over time. In addition, while the view of a “flat” environment prevailed up to now, the formation of turbidites and debris-flows required a relief in order to create situations where materials could be destabilized and reworked. The composition of the Bernissart clay, especially with the presence of coal fragments (up to 25 cm in size!), weathered shales and sandstones, and chlorite-rich siderite nodules, demonstrates that the sediments were predominantly, if not exclusively sourced from the nearby Westphalian basement. Putting all this together fits very well within the scenario of sinkhole growth processes, which created a small but steep-walled basin at the beginning and gradually evolved to a wider lake basin by successive sliding and stepping back of the margins. An important implication of this scenario is that the timespan of the formation of the Bernissart deposit may have been much shorter than previously thought. A close analogue in dimension, including the depth of the initial deep-seated collapse that caused subsidence exists in Louisiana (Bayou Corne sinkhole), and it took less than 10 years for the lake basin to reach maturity (Jones and Blom, 2014).

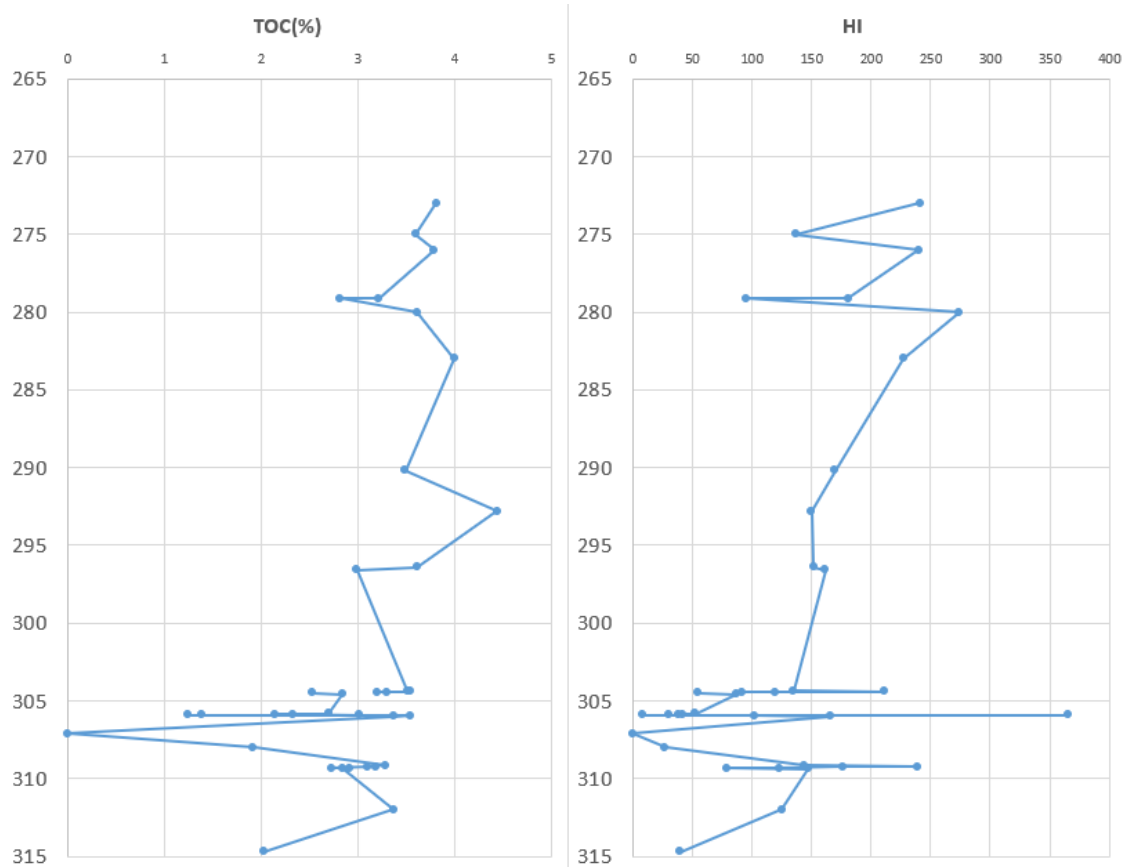


Fig. 29 - Total Organic Carbon (TOC) and Hydrogen Index (HI) of the Bernissart clay from the Ber3 borehole. The fossiliferous interval lies in the lower part of the borehole, ranging from ca. 295 to 310 m.

Organic matter

35 samples from the cores in Ber3 boreholes were analyzed for organic matter (OM) at ISTO-Orléans, France (Prof. J. Jacob). Rock-Eval analyses show that the Total Organic Carbon (TOC) is only a few % and increases slightly upwards (Fig. 29). Hydrogen Index (HI) follows the same trend. The interpretation of these data is complicated by the existence of a dual source of OM in the lake: coal from the Westphalian basement and “fresh” OM from the environment and the lake catchment (mostly microbiota and plant debris, now preserved as lignite). No diatoms were observed (Prestianni, com. or.) The issue of dual OM source was not addressed in previous studies. Coal, as a highly-evolved OM, sourced from continental higher plant, typically has a low HI. Therefore, we could interpret the observed OM trend as reflecting an OM input first dominated by coal and later by an increase of fresh OM, possibly because of an increase in bioproductivity. However, this interpretation would be valid only if the sedimentation rate was constant. Given the results of the sedimentological study, it is likely that the sedimentation rate decreased over time. Therefore, bioproductivity and fresh OM input could have remained constant but were less diluted through the whole record because of the decreasing detrital input.

As a conclusion for WP3, we have now a much clearer view of both the internal structure of the Bernissart clay infilling and the sedimentary dynamics of the Bernissart Lake during the Lower Cretaceous, which, above all, was controlled by the formation and growth of the

sinkhole itself. An evolutionary sequence of the Bernissart sinkhole can now be proposed (Fig. 30).

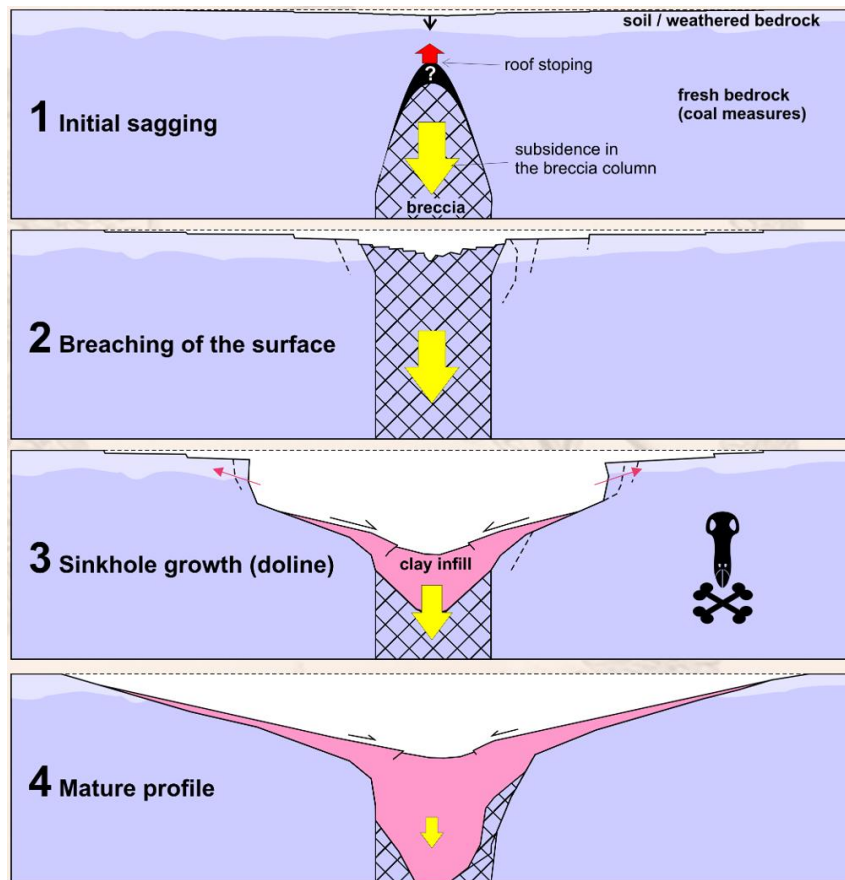


Figure 30. Four-step evolutionary sequence of the Bernissart sinkhole. Note the relief created in stage 3, which caused the sliding and backing away of the margins, and from which the sediments (clay infill) were sourced and deposited as turbidite sequences

WORK PACKAGE 4 – PROFILING THE KILLER

The sinkhole as the prime suspect

The results of WP3 shed new light on the environment of the Lower Cretaceous Bernissart Lake and its dynamics. Before this project, it was acknowledged that the sinkhole activity was only responsible for the “passive” accumulation of the vertebrate carcasses and their fine preservation (see Baele et al., 2012, and references therein). Now, our new findings support strong evidences for an active role of the sinkhole in the death of the Bernissart Iguanodons and other vertebrates.

Wherever they form, sinkholes represent serious collapse and sliding hazards. At Bernissart, there is a cluster of 3 sinkholes of 100 m in diameter within an area of ca. 250 x 250 m (Fig. 32). Two of them were known for a long time (the “Iguanodon” and the “South” sinkhole) but

the third one, which is coalescent to the south with the Iguanodon sinkhole, was only evidenced in the course of the Coldcase project, based on detailed analysis of the mining plans that were drawn up after the excavation of the fossils between 1878 and 1881. Besides extending the area of the Iguanodon sinkhole and thereby multiplying the expected number of fossils that are still buried at Bernissart, the existence of a cluster of closely spaced sinkholes has taphonomic implications. The three sinkholes probably formed simultaneously or close enough in time to add their effects and dramatically increase the instability of the ground around them. Examples of multiple sinkhole formation can be observed today in the Dead Sea, where the dropdown of the sea level due to enhanced human uptake of the Jordan water is responsible for the formation of thousands sinkholes (Fig. 31). It should be noted that the size of the sinkholes as reported in the sections, which is about 100 m, represents the diameter of the breccia pipe at depth, not the size of the subsiding basin at the surface (doline), which was larger, probably 300 m in diameter.

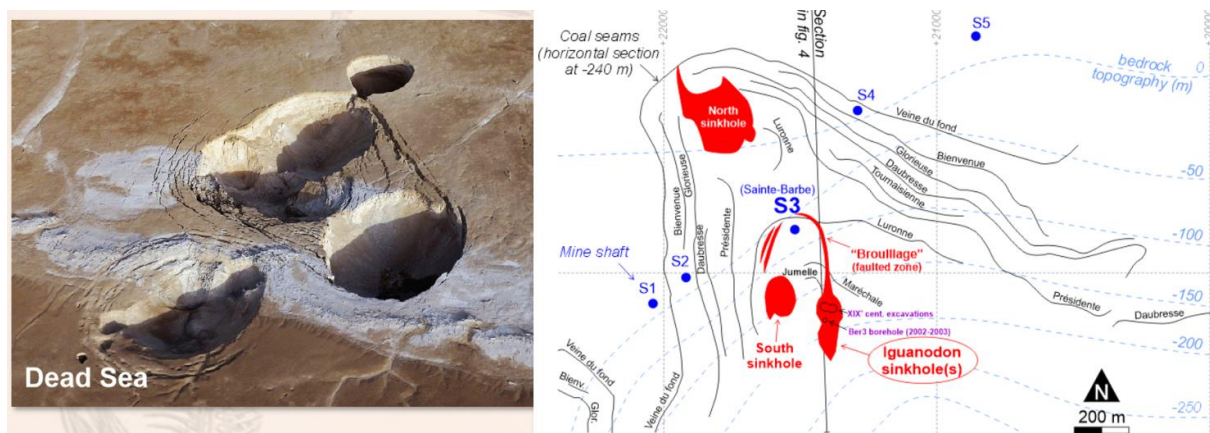


Fig. 31 - Clusters of sinkholes. **Left:** cluster of nearly simultaneous modern sinkhole in the Dead Sea. **Right:** cluster of fossil sinkholes at Bernissart (in red), which formed in the center of an area with high local subsidence, as evidenced by the deformation of the coal seams (dark lines).

Deadly subaqueous slidings

Therefore, it is possible that the Bernissart Iguanodons themselves could have triggered slides and their subsequent submersion in the lake. A potentially similar environment can be found at Lake Sinizzo, Italy, where the banks of this sinkhole-induced lake have been weakened by an earthquake in 2009 (Lanzo et al., 2010; Fig. 32). In this example, it is evident from the heavy fracturing of the banks that a herd of large animals like Iguanodons, weighting each 4 to 5 tons, could have easily triggered sliding by running over the lake shore, especially if the herd was panicking, i.e. when fleeing predators or wildfires, and overcrowded in dangerous areas they would have avoided otherwise. This scenario would for the first time provide us with a plausible explanation for the monospecificity of the large vertebrate fossil assemblage at Bernissart.

However, if landslides are usually envisioned as sudden and brutal events capable of mass-death, sub-aqueous slides could be much slower, as illustrated by the 2013 sliding caught on tape at Bayou Corne, Louisiana (<https://www.youtube.com/watch?v=a7cOSzEKvrQ>). In this example, the destabilized bank mass first sank very slowly and gradually accelerated to reach a high sinking velocity after ca. 10 seconds. While impressive because an entire tree group was swallowed in seconds, the sliding of Bayou Corne was surprisingly not as catastrophic as we would expect by comparison with landslides. The reasons for that are 1)

water slows down gravitational processes because of buoyancy and increased frictional forces and 2) most of the process occurs at depth in the lake with relatively little impact as seen by an observer standing on the surface. If slides at Bernissart followed the same dynamics, which is probable but hard, if not impossible, to demonstrate, and based on the hypothesis that *Iguanodons* could swim, which is also unclear, only the strong down-flow current due to the sinking mass could have drowned those few individuals that could not escape in time out of the slowly crumbling ground. Therefore, it is not clear whether *iguanodon* mass death could be related to a mere submersion alone or if other factors must come into play. However, it is probable that at least a few *iguanodons* could have been drowned in such a situation.



Fig. 32 - Fragilized bank in sinkhole-induced Lake Sinizzo, Italy, after the 6 April 2009 earthquake. The bank is about to slide and sink either spontaneously or after some additional trigger mechanisms.

A message from the collateral victims

This is where the collateral victims must be considered. A rather small number of crocodiles and turtles have been unearthed from the 19th century excavations along with thousands of fishes. There is sufficient evidence in the excavation reports to state that these fossils were concentrated within the *Iguanodon*-rich clay layers except one particular fossiliferous bed that only contains fishes and small reptilians but no *Iguanodons* (a second fish-only fossiliferous bed would exist based on the old documents). Therefore, there is a common cause for the recurring death episodes of both *Iguanodons* and fishes together with the few associated reptilians, and this cause seemingly affected only fishes and small reptilians at least once. This latter observation could be explained by the triggering mechanisms of the slides: *Iguanodon*-rich turbidites would have been triggered by herding dinosaurs while the large but rare spontaneous slides would have killed the local aquatic fauna only. As an alternative for the latter case, the *Iguanodons* could also have triggered the slides but at a longer distance so that their carcasses did not reached the sampling location (or they settled

in another nearby sinkhole basin as 3 coalescent sinkholes are now recognized). The dominant non-fossiliferous turbidite sequences would therefore represent the succession of minor slides, which had no or little ecological impact in the lake.

How could subaqueous slides kill aquatic fauna? Fishes are very sensitive to environmental perturbations and, accordingly, fish mass-deaths are common in nature. Fig. 26 shows that they represent by far the greatest proportion of today vertebrate mass-deaths. Among the consequences of subaqueous slides potentially capable of killing fishes, we have retained turbidity, oxygen depletion and release of toxic gases.

Turbidity may increase dramatically as a consequence of margin slides in sinkhole lakes. However, firstly we are not aware of fish mass-death in such situations and, secondly, brutal turbidity increases may be so common in nature that they pace many aquatic environments (e.g., floods in fluvial settings). Therefore, we can imagine that fishes are adapted to survive turbidity changes.

In lakes, sudden oxygen depletion could arise subsequently to slumping if the sinking sediment mass destabilizes water stratification (Fig. 33), thereby mixing oxygen-depleted or anoxic bottom waters with oxygenated surface waters (lake turnover; Cohen, 2003). The Bernissart Lake, with its steep bottom, closed stagnant water body and abundant organic matter input was certainly stratified. Turnover-driven oxygen depletion is a plausible consequence of major margin slides, which could be supported by the observation of abundant iron oxide-stained laminae in the Ber3 cores. Such red laminae are commonly associated with massive iron oxidation and precipitation in the water column as a consequence of lake turnover (ferrous iron is initially stored in dissolved state in anoxic/dysoxic bottom waters). However, oxygen depletion in lake water cannot kill crocodiles and turtles.

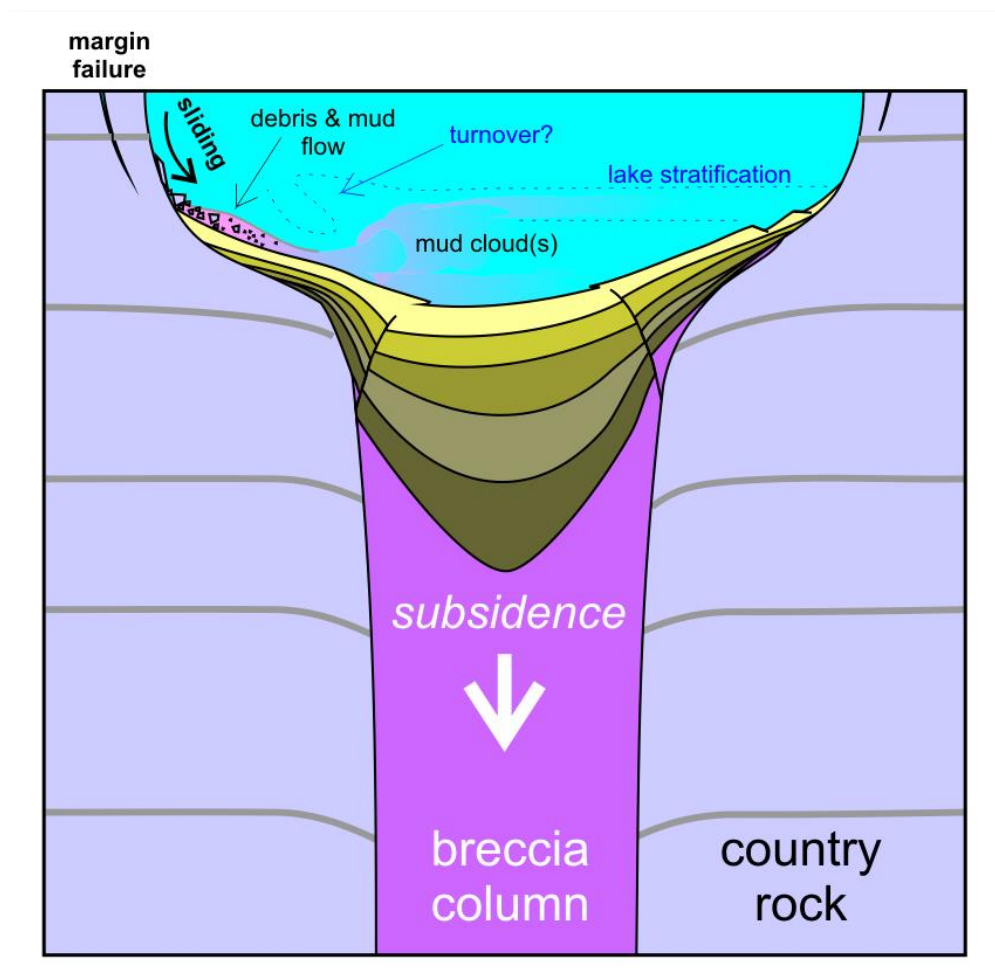


Fig. 33 - Sedimentological model for the sinkhole-induced Bernissart lake at development stage 3 in Fig. 32. Major margin failures and slidings are thought to have been triggered by iguanodon herds.

Return of the hydrogen sulphide?

In a previous study, Baele et al. (2012) hypothesized that H_2S could have been the cause for mass death events at Bernissart. H_2S indeed is an extremely toxic gas (Strickland et al., 2003), which is responsible for dies-offs of many vertebrate taxa, including fishes. The main supporting evidence at Bernissart is the high pyritic sulfur content (0.5 to 2.5%), with a C/S ratio in the range of marine waters, not lacustrine freshwater. Thus, we considered that sulfur is in abnormally high concentration in the Bernissart Lake, where potential sources of sulfur may be found almost everywhere in its environment. Sulfur could be derived from upwelling sulphate-rich geothermal brines from the deep karst responsible for the sinkhole formation (H_2S is effectively present in the sulfate-saturated geothermal brines pumped at Saint-Ghislain in the same geological horizon 10 km from Bernissart) and from the Carboniferous country rock itself, which contains pyrite as demonstrated for example by the rapid formation of sulfuric-rich ponds today in the bottom of the nearby quarry of Hautrage (which is opened in Carboniferous strata).

However, a major flaw of the H₂S hypothesis lies in the lack of viable mechanisms explaining why and how animals were recurrently exposed to high concentrations of the toxic gas. Even if abnormal concentrations of H₂S were likely at Bernissart, the gas is largely disseminated and entrapped in the sediments where it formed and could only diffuse in the water and into the atmosphere at such slow rate that it is not conceivable that lethal concentrations could have been reached, especially for large animals such as Iguanodons. In addition, in many environments where H₂S is produced (mostly by sulfate-reducing bacteria), the gas is partially - if not totally - recycled (oxidized to sulfates) by specialized microbiota that act in consortium with sulfate-reducing bacteria.

Now that we know better the dynamics of the Bernissart Lake, where sinkholes played a major role (starting with the existence of the lake itself), an efficient mechanism for massive degassing can be found. Slides could have caused lake overturn, which stirred up and brought to surface H₂S-rich anoxic bottom waters and/or H₂S-rich sediments, allowing the liberation of the gas in the surface water and atmosphere. The slide of Bayou Corne provided a good illustration of how whirlpools and swirls can turn the water into mud by stirring up unconsolidated bottom sediments. Depending on the geological environment and lake chemistry, turnovers can cause mass-death as for example the massive CO₂ degassing that killed 1746 humans and many more animals around lake Nyos, Cameroon, in 1986. Lake Nyos is a volcanic lake (maar), which accumulated carbon dioxide in bottom waters and the turnover is thought to have been triggered by a landslide. The lake spectacularly turned red after the degassing probably because of iron oxidation and precipitation.

At Bernissart, H₂S could have killed fishes *en masse* together with the few small reptiles around. H₂S could also have killed (additional) Iguanodons, especially those individuals that tried to get out of the water as their head was close to the water surface from which the gas emanated and their struggling and panic would have increased their respiratory rate. In this case, there is no need to reach lethal concentrations, just render the Iguanodons unconscious, which accelerated their drowning. H₂S could also have accumulated around the lake shore as it is heavier than air and the Bernissart Lake was set in low ground. Therefore, additional casualties have possibly been caused on the shore or at a certain (unknown) distance from the lake. The resulting carcasses were not immediately, but later entrained (together with coprolites) to the lake bottom with a lower degree of preservation as a result of scavenging and higher decay rate during their subaerial exposure. Perhaps this process could explain the few isolated bones from carnivorous dinosaurs and crocodiles that were recovered during the excavation.

5. DISSEMINATION AND VALORISATION

PhD and master theses

PhD theses:

De Brito, L. (2018-). *Diversité, évolution et paléobiogéographie des conifères du Crétacé Inférieur de Belgique, application d'approches non destructrices : morphométrie et tomographie à rayon x*. PhD thesis, ULiège/RBINS (promoters, V. Fischer and C. Prestianni).

The following PhD thesis is also partly based on the ColdCase projects, as it includes a revision of the fossil fern from Bernissart, based on data collected in the scope of the ColdCase project, in direct collaboration with Cyrille Prestianni:

Blanco Moreno, C., 2019. *Integrative approach to the Early Cretaceous ferns of Las Hoyas (upper Barremian, Cuenca, Spain) in the light of other European localities*. Unpublished PhD thesis, Universidad Autonoma de Madrid, Spain (promoters: A. Delgado Buscalioni and B. Gomez).

The following PhD thesis is also partly based on the ColdCase projects, as it includes a revision of the pathologies on the Bernissart Iguanodon skeletons. One of the promoter of this thesis is Eileen Murphy, who is a member of the Follow-up Committee of the ColdCase project.

Bertoazzo, F. (2018-): *Suffering leviathans of the past: A comparative study of fossilized pathologies in ornithomimid and ceratopsian dinosaurs*. PhD thesis, Queens College Belfast (promoters: Eileen Murphy, A. Ruffell, and P. Godefroit).

Master theses:

Caux, H., 2017. *Modified laminar bone in sauropod dinosaurs: diagenetic or true biological feature?* Erasmus MSc thesis, Vrije Universiteit Brussel – Université de Lorraine à Nancy (promoters, K. Stein and P. Claes).

De Brito, L., 2018. *Etude de la diversité de *Pityostrobus andraei* (Pinaceae) du Wealdien de Belgique: morphométrie et phylogénie*. MSc thesis, Université de Liège (promoter, C. Prestianni).

Van Woensel, J., 2018. *Trace element and stable isotope composition of dino enamel from SE Morocco & Belgium*, MSc thesis, KULeuven (promoter, Ph. Claes).

Workshop:

In the scope of the 17th Conference of the European Association of Vertebrate Palaeontology, organized by RBINS in Brussels from July 2nd to 6th 2019, a special workshop was organized at Bernissart on July 19 for presenting the results of the Coldcase projects. Sixty-five palaeontologists and geologists, from 27 (mainly European) countries participated in this workshop. The communications presented at the occasion of this workshop were compiled in the following Publication:

Olive, S., Baekle, J.-M., Mortier, T., Stein, K., Lambert, O., Prestianni, C., Smith, T. And Godefroit, P., 2019. 17th conference of the EAVP, 2019, Brussels, *Bernissart workshop and field trip in La Malogne Underground Quarry*, 32 pp.

Presentations during professional meetings:

Baele J., Godefroit P., Spagna P. & Dupuis C., 2019. An introduction to the geology of the Mons Basin and the Bernissart Sinkhole, Belgium. In: 17th conference of the EAVP, 2019, Brussels, Bernissart workshop and field trip, pp. 3-12.

Baele, J.-M., Papier, S., Cobert, C., Dupuis, C., Dupont, N., Kaufmann, O., Martin, T., Spagna, P. & Tshibangu, J.-P., 2019. The Lower Cretaceous Bernissart sinkholes: deadly traps or passive gravediggers? In: 17th conference of the EAVP, 2019, Brussels, Bernissart workshop and field trip: 28.

Baele, J.-M., Papier, S., Spagna, P., Godefroit, P., Tshibangu, K., Martin, T., & Kaufmann, O., 2016. Karst subsidence in the Iguanodon Sinkhole, Bernissart, Belgium. Evidence for active collapse processes during the Lower Cretaceous. In: 5th International Geologica Belgica Meeting, Jan 26-29, University of Mons, Belgium.

Baele, J.-M., Papier, S., & Tshibangu, K., 2019. Insight into the use of LIBS (Laser-Induced Breakdown Spectroscopy) for geochemical core logging. Application to Lower Cretaceous, iguanodon-bearing clay sequence in Ber3 borehole, Bernissart, Belgium. In 26eme Réunion Sciences de la Terre, RST, Lille, France.

Bertoazzo, F., Tanke, D., Murphy, E., Ruffell, A. & Godefroit, P., 2019. A comparison of palaeopathological lesions and diseases between Early and Late Cretaceous ornithomimid dinosaurs. In: Cretaceous & Beyond: paleontology of the Western Interior, abstract volume. Dickinson, North Dakota: 29.

Bertoazzo, F., Murphy, E., Ruffel, A. & Godefroit, P., 2019. Cretaceous diseases: a palaeopathological survey of the Iguanodon specimens from Bernissart (Belgium) In: 17th conference of the EAVP, 2019, Brussels, Bernissart workshop and field trip: 28.

Blanco-Moreno, C., De Brito, L., & Prestianni, C., 2019. A new look at the Bernissart Flora. In: 17th conference of the EAVP, 2019, Brussels, Bernissart workshop and field trip: 29.

Blanco-Moreno, C., Decombeix, A. L. & Prestianni, C., 2019. Use of new technologies in the revision of historical specimens of *Weichselia reticulata* from Bernissart (Barremian-Aptian of Belgium). In: 63rd Annual Meeting of the Palaeontological Association. Valencia, Spain.

Caux, H., Stein, K., Snoeck, C., Klein, N., Sander, M.P. & Claeys, P., 2017. Diagenesis as cause for 'modified laminar bone' in sauropod dinosaurs? 8th Bone Diagenesis meeting Oxford 2107, Program and Abstracts: 39
https://docs.wixstatic.com/ugd/356194_b933f88357584e528d097c7583252933.pdf
(poster prize winner).

Claeys, P., De Winter, N., Stein, K. & Snoeck, C., 2016. Multi-proxy analyses of bioapatites: implications for palaeoecology, palaeoclimatology and bioarchaeology. Poster session presented at Goldschmidt 2016, Yokohama, Japan.

- Garcia, G., Godefroit, P. Gomez, B., Stein, K., Cincotta, A., Lefèvre, U., & Valentin, X. 2017. Extreme tooth enlargement in a new Late Cretaceous rhabdodontid dinosaur from Southern France. Society of Vertebrate Paleontology, 77th Annual Meeting, Meeting program and abstracts: 117.
- Godefroit P., 2019. 140 years ago: the discovery of the Bernissart *Iguanodon*s In: 17th conference of the EAVP, 2019, Brussels, Bernissart workshop and field trip, pp. 13-23.
- Manucci F., Bertozzo F., Maganuco S. & Godefroit P., 2019. Old *Iguanodon* remains shed new light on the evolution of ornithomimid integument. In: 17th conference of the EAVP, 2019, Brussels, Program and abstracts: 66.
- Olive, S., Taverne, L., Cavin, L., Deesri, U. & COLDCASE Team. La bouillabaisse de Bernissart (Belgique, Crétacé inférieur): révision systématique de l'ichtyofaune. Congrès de l'Association Paléontologique française, Meeting program and abstracts: 28.
- Olive, S., Taverne, L., Cavin, L., Deesri, U. & Lopez-Arbadello, A., 2019. The *Bouillabaisse* of Bernissart. In: 17th conference of the EAVP, 2019, Brussels, Bernissart workshop and field trip: 30.
- Olive, S., Taverne, L., Lopez-Arbadello, A., Cavin, L. & Deesri, U. Systematic revision of the Cretaceous actinopterygian fauna from Bernissart, Belgium. Mesozoic Fishes Symposium, Mahasarakham, Thailand, Meeting program and abstracts: 16.
- Prestianni, C. & Blanco-Moreno, C., 2018. La flore de Bernissart revisitée. In : Congrès annuel de l'Association paléontologique Française du 2018. Brussels, Belgium.
- Smith, T., Delfino, M., Folie, A. & Martin, J.E., 2019. Reassessment of Dollo's crocodylomorphs from the Early Cretaceous of Bernissart, Belgium. In: 17th conference of the EAVP, 2019, Brussels, Bernissart workshop and field trip: 31.
- Snoeck, C., De Winter, N., Stein, K. & Claeys, P., 2016. Investigating diagenetic patterns using $\delta^{18}\text{O}_\text{P}$ and $\delta^{18}\text{O}_\text{C}$ in bone and tooth apatite of modern, archaeological and fossil specimens. Abstract from Goldschmidt 2016, Yokohama, Japan.
- Stein, K. 2018. Black beauties: histology and geochemistry of *Iguanodon bernissartensis* from the Early Cretaceous of Bernissart, Belgium. GeoBonn meeting, Bonn 2018, Program and Abstracts, pp. 221-222.
- Stein K., Hübner T., Godefroit P. & Claeys P., 2019. Histology and growth of Wealden *iguanodonts* from Belgium and Germany In: 17th conference of the EAVP, 2019, Brussels, Bernissart workshop and field trip: 32.
- Stein, K., Hübner, T., Hayashi, S., Bolotski, Y. Bolotski, I., Claeys, P., & Godefroit, P., 2018. Osteohistology sheds light on the origin of high growth rates in *Iguanodontia*. 5th International Paleontological Congress, Paris Fossil Week abstract book: 925.
- Stein K., Hübner T., Snoeck C., Bertozzo F., Godefroit P. & Claeys P., 2017. Histology and growth of *Iguanodon bernissartensis*. Annual Meeting of the European Association of Vertebrate Palaeontologists, Munich 2017, Program and Abstracts.

Stein K., Hübner T., Snoeck C., Bertozzo F., Godefroit P. & Claeys P., 2017. Histology and growth of *Iguanodon bernissartensis*. Society of Vertebrate Paleontology, 77th Annual Meeting, Meeting program and abstracts: 198.

Stein K., Snoeck C., Hübner T., Bertozzo F., Godefroit P. & Claeys P., 2017. Preservation and diagenesis of the bones and teeth of *Iguanodon bernissartensis* (Dinosauria: Ornithomimidae) from the Early Cretaceous of Belgium 8th Bone Diagenesis Meeting Oxford 2017, Program and abstracts: 13.

Publications directed to the general public (Fig. 34):

Godefroit, P. (editor), 2017. *Il y a 140 ans, la découverte des Iguanodons de Bernissart. Fossiles, hors-série 8*, 74 pp.

Verbeke, R. & Godefroit, P., 2018 (editors). *Wie vermoorde de iguanodons? Alles over de Belgische dinosauriërs.*



Fig. 34 – Covers of the special issues of *Fossiles* and *Eos* dedicated to the Coldcase project

Conferences for a wider audience:

Baele, J.-M., 2015. *Hécatombes à Bernissart au Crétacé : l'enquête continue*. In : Mons à l'époque des grandes découvertes, Mons, Belgique.

- Baele, J.-M., 2016. *Hécatombes à Bernissart au Crétacé : l'enquête continue*. In : Conférences AILg, Hôtel Dream, Mons, Belgique.
- Baele, J.-M., 2017. *Les iguanodons : caractères exceptionnels du gisement*. In : Colloque du Cercle géologique du Hainaut - Les richesses géologiques de Bernissart, Bernissart, Belgique.
- Baele, J.-M., 2019. *Réouverture d'un dossier vieux de plus de 100 millions d'années : les iguanodons de Bernissart*. In: Congrès des sciences , Mons, Belgique.
- Baele, J.-M., 2020. *Iguanodons de Bernissart, un coldcase de plus de 100 millions d'années*. In : Les Directs du Mumons, Mons, Belgique. <https://www.youtube.com/watch?v=XTobwxBrkM4>
- Godefroit, P., 2020. *La ruée vers l'os : la découverte des Iguanodons de Bernissart il y a 140 ans*. In : Académie royale de Belgique, Classe des Sciences, Bruxelles, Belgique.
- Godefroit, P., 2020. *Qui a vraiment découvert les Iguanodons de Bernissart ?* In : Les Directs du Mumons, Mons, Belgique. <https://www.youtube.com/watch?v=YnfXesKHEGE>
- Papier, S., Baele, J.-M., Martin, T. & Kaufmann, O., 2017. *Cold Case: who's the paleo-killer?* In : Huitième édition montoise du MdC : le Mardi des Chercheurs 2017, UMons, Belgique, 2017", Mons, Belgique.
- Stein, K., 2017. *Esthetica overgewaardeerd: het nut van invasieve en destructieve bemonstering van dinosaurussen en andere vertebratenfossielen*. In: Belgische Vereniging voor Paleontologie at 'Huis Van De Evolutie' in Sint-Gillis-Waas, Belgium.
- Stein, K., 2018. *Evolutie van Iguanodontia in het Krijt van Europa*. In: Paleo Time, Ede, The Netherlands.
- Stein, K., 2018. *Coverage of latest research results on the Belgian iguanodons*. <https://tinyurl.com/y3s4pvll>, <https://tinyurl.com/y4upouly>, <https://tinyurl.com/yy36dlq9>, <https://tinyurl.com/y4yu2qu8>
- Stein, K., 2019. *Wat kan je leren uit de botten van dinosaurussen? Een case studie over de Belgische iguanodons*. In: Stichting GeA Breda, The Netherlands.
- Stein, K., 2019. *Slicing life into dinosaurs: what fossil bone tissues and cells tell us about extinct reptiles*. In: Pint of Science Brussels, Belgium. <https://tinyurl.com/y2b7jrv4>.
- Stein, K. & Godefroit, P., 2018. Duolecture: *Dinosaur bones and feathers*. In: Belgische Vereniging voor Paleontologie at Vrije Universiteit Brussel, Belgium.

Coldcase comes alive: a theatre performance!

To celebrate the end of the Coldcase project, the theatre company 'Passeurs de rêves' has been invited to re-create their promenade spectacle '*Bernissartensis*, a Cold Case', including the results of the present Brain-be project, in the RBINS premises! This spectacle has written and directed by Yves Coumans; this new creation encompasses both the mystery of the discovery of 30 iguanodons in 1878 at Bernissart, its place in the history of paleontology

and finally, the results of the latest investigations into the causes of the death of these dinosaurs.

An actress and two actors play successively a beautiful gallery of endearing characters, including an investigator from the border police, the mother of a minor, a minor, an adult minor who participated in the discovery, an archivist, a stratigrapher, Louis De Pauw, preparator at the Royal Museum of Natural Sciences, two English fossil collector, and Mary Anning, famous fossil collector at Lyme Regis, England (Fig. 35). The actors take the audience from room to room. In each place, a rudimentary scenography is installed. In front of the amused audience, the actors change costumes and characters and approach the scenes in quite different styles of play. Six performances – three in French and three in Dutch – were presented on November 7, 2019, on January 11, 2020, and on February 1, 2020, attracting an enthusiastic audience.



Fig. 35 – Scenes from '*Bernissartensis, a Cold Case*', by the theatre company 'Passeurs de Rêves' (RBINS Museum, February 1, 2020)

6. PUBLICATIONS

Here we list the papers published in scientific journals with IF in the scope of the Coldcase project. To be continued!

Peer-reviewed:

- Blanco-Moreno, C., & Prestianni, C. (under review). Taxonomic revision and palaeoecological interpretation of the plant assemblage of Bernissart (Barremian, Belgium). *Cretaceous Research*.
- Blanco-Moreno, C., Decombeix, A.L., & Prestianni, C. (accepted). New insights on the affinities, autoecology, and habit of the Mesozoic fern *Weichselia reticulata* based on the revision of stems from Bernissart (Mons Basin, Belgium). *Papers in Palaeontology*.
- Cavin, L., Deesri, U., & Olive, S., 2020. *Scheenstia bernissartensis* (Actinopterygii: Ginglymodi) from the Early Cretaceous of Bernissart, Belgium, with an appraisal of the ginglymodians evolutionary history. *Journal of Systematic Palaeontology* **18**(6): 513-527.
- de Winter, N. J., Snoeck, C., & Claeys, P., 2019. High-resolution trace element distributions and models of trace element diffusion in enamel of Late Neolithic/Early Chalcolithic human molars from the Rioja Alavesa region (north-central Spain) help to separate biogenic from diagenetic trends, *Palaeogeography, Palaeoclimatology, Palaeoecology*, 530, <https://doi.org/10.1016/j.palaeo.2019.109260>.BR
- Godefroit, P., Garcia, G., Gomez, B., Stein, K., Cincotta, A., Lefèvre, U., & Valentin, X., 2017. Extreme tooth enlargement in a new Late Cretaceous rhabdodontid dinosaur from Southern France. *Scientific Reports*, **7**: 13098.
- Martin, J. E., Delfino, M., & Smith, T., 2017. Osteology and affinities of Dollo's goniopholid (Mesoeucrocodylia) from the Early Cretaceous of Bernissart, Belgium. *Journal of Vertebrate Paleontology*, **36**: 348-354.
- Martin, J.E., Smith, T., Salaviale, C., Adrien, J., & Delfino, M., 2020. Virtual reconstruction of the skull of *Bernissartia fagesii* and current understanding of the neosuchian–eusuchian transition. *Journal of Systematic Palaeontology*, DOI:10.1080/14772019.2020.1731722.
- McMillan, R., Snoeck, C., de Winter, N. J., Claeys, P., & Weis, D., Evaluating the impact of acetic acid chemical pre-treatment on 'old' and cremated bone with the 'Perio-spot' technique and 'Perios-endos' profiles, *Palaeogeography, Palaeoclimatology, Palaeoecology*, 530, 330-344, 2019, <https://doi.org/10.1016/j.palaeo.2019.05.019>.
- Olive, S., Taverne, L., Brito, P., 2020 (in review). *Pleuropholis germinalis* sp. nov. a new Pleuropholidae (Neopterygii, Teleostei) from the Lower Cretaceous of Bernissart. *Geodiversitas*.
- Olive, S., Taverne, L., & Lopez-Arbarello, A., 2019. A new genus of coccolepidid actinopterygian from the Cretaceous Iguanodon-bearing locality of Bernissart, Belgium. *Cretaceous Research*, **95**: 318-335.

- Olive, S., Taverne, L., Cavin, L., & Deesri, U., 2017. Systematic revision of the Cretaceous actinopterygian fauna from Bernissart, Belgium. *Research & Knowledge*, **3 (1)**: 43-46.
- Verdú, F. J., Godefroit, P., Royo-Torres, R., Cobos, A., & Alcalá, L. 2017. Individual variation in the postcranial skeleton of the Early Cretaceous *Iguanodon bernissartensis* (Dinosauria: Ornithopoda). *Cretaceous Research*, **74**: 65-86.
- Wiemann, J., Fabbri, M., Yang, T.R., Stein, K., Sander, P.M., Norell, M.A., & Briggs, D.E.G., 2018. Fossilization transforms vertebrate hard tissue proteins into N-heterocyclic polymers. *Nature Communications*, **9 (4741)**. doi: 10.1038/s41467-018-07013-3.

7. ACKNOWLEDGEMENTS

We are particularly grateful to the Belspo staff, and particularly to Maaïke Vancauwenberghe and Ria Dhaemers, 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: Eric Domb, Eileen Murphy, David B. Norman, Lucile Savignat, and Johan Yans. And of course to all those scientists who were directly or indirectly involved in the Coldcase project: S. Papier, Th. Martin, N. Dupont, C. Cobert, J.-P. Tshibangu, C. Snoeck, C. Blanco-Moreno, O. Kaufmann, L. Cavin, Th. Smith, A. Folie, L. Taverne, L. de Brito, H. Caux, J. Van Woensel, P. Spagna, F. Bertozzo, F.J. Verdù, T. Hübner, and F. Manucci. The efficient help of Patrice Ferchaud and R. Verbeke, as co-editors respectively for the '*Il y a 140 ans, la découverte des Iguanodons de Bernissart*' and '*Wie vermoordde de Iguanodons?*' special volumes, was particularly precious. The Houzeau de Lehaie family is warmly thanked for the loan of private documents on Bernissart. And we also wish to congratulate the theatre company *Passeurs de Rêves* for their gorgeous performance in '*Bernissartensis*', a coldcase.

ANNEXES

Additional References:

- Amiot, R., Wang, X., Lécuyer, C., Buffetaut, E., Boudad, L., Cavin, L., & Zhang, F., 2010. Oxygen and carbon isotope compositions of middle Cretaceous vertebrates from North Africa and Brazil: ecological and environmental significance. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **297(2)**: 439-451.
- Baele J.M., Godefroit P., Spagna P., & Dupuis C., 2012. Geological model and cyclic mass-mortality scenarios for the Lower Cretaceous Bernissart Iguanodon bonebeds: pp. 155-171 in Godefroit, P. (ed.), *Bernissart Dinosaurs and Early Cretaceous Ecosystems*. Indiana University Press, Bloomington and Indianapolis.
- Bertrand, C. E., 1903. Les coprolithes de Bernissart. 1. Les coprolithes qui ont été attribués aux iguanodons. *Mémoires du Musée Royal d'Histoire naturelle de Belgique*, **4**: 1-154.
- Bultynck, P., 1989. *Bernissart et les Iguanodons*. Institut Royal des Sciences naturelles de Belgique, Bruxelles, 115 pp.
- Casier, E. 1960. *Les Iguanodons de Bernissart*. Institut Royal des Sciences Naturelles de Belgique, Bruxelles, 134 pp.
- Cohen A. S., 2003. *Paleolimnology: The History and Evolution of Lake Systems*. Oxford University Press, Oxford, 500 pp.
- Cornet, J. & Schmitz, G., 1898. Note sur les puits naturels du terrain houiller du Hainaut et le gisement des Iguanodons de Bernissart. *Bulletin de la Société belge de Géologie, Paléontologie et Hydrologie*, **12**: 196-206 and 301-318.
- De Pauw, L., 1898. Observations sur le gisement de Bernissart. *Bulletin de la Société belge de Géologie, Paléontologie et Hydrologie*, **12**: 206-216.
- Dollo, L., 1923. Le centenaire des Iguanodons (1822-1922). *Philosophical Transactions of the Royal Society of London, Series B*, **212**: 67-78.
- Dupont, E., 1878. Sur la découverte d'ossements d'*Iguanodon*, de poissons et de végétaux dans la fosse Sainte-Barbe du Charbonnage de Bernissart. *Bulletin de l'Académie royale de Belgique*, **46**: 387.
- Dupont, E., 1897. *Musée Royal d'Histoire naturelle de Belgique. Guide dans les collections. Bernissart et les Iguanodons*. Brussels, Polleunis and Centerick.
- Godefroit, P., Yans, J., & Bultynck, P., 2012. Bernissart and the Iguanodons: historical perspective and new investigations; pp. 3-22 in: P. Godefroit, P. (ed.), *Bernissart Dinosaurs and Early Cretaceous Ecosystems*. Indiana University Press, Bloomington and Indianapolis.
- Jones, C. E. & Blom, R. G., 2014. Bayou Corne, Louisiana, sinkhole: Precursory deformation measured by radar interferometry. *Geology*, **42(2)**: 111-114.

- Lanzo, G., Di Capua, G., Kayen, R. E., Kieffer, D. S., Button, E., Biscontin, G., Scasserra, G., Tommasi, P., Pagliaroli, A., Silvestri, F., d'Onofrio, A., Violante, C., Simonelli, A. L., Puglia, R., Mylonakis, G., Athanasopoulos, G., Vlahakis, V., & Stewart, J. P., 2010. Seismological and geotechnical aspects of the Mw=6.3 l'Aquila earthquake in central Italy on 6 April 2009. *International Journal of Geoengineering Case Histories*, **1** (4): 206-339.
- Lauters, P., Bolotsky, Y., Van Itterbeeck, J., & Godefroit, P., 2008. Taphonomy and age profile of a latest Cretaceous dinosaur bonebed in Far Eastern Russia. *Palaios*, **23**: 153-162.
- Lécuyer, C., Fourel, F., Martineau, F., Amiot, R., Bernard, A., Daux, V., Escarguel, G., & Morrison, J., 2007. High-precision determination of $^{18}\text{O}/^{16}\text{O}$ ratios of silver phosphate by EA-pyrolysis-IRMS continuous flow technique. *Journal of Mass Spectrometry*, **42**: 36–41.
- Leduc, T., 2012. Diagenesis of the fossil bones of *Iguanodon bernissartensis*, from the Iguanodon Sinkhole at Bernissart (Mons Basin, Belgium); pp.113-136 in: P. Godefroit, P. (ed.), *Bernissart Dinosaurs and Early Cretaceous Ecosystems*. Indiana University Press, Bloomington and Indianapolis.
- Longinello, A. & Nuti, S., 1973. Oxygen isotope measurements of phosphate from fish teeth and bones. *Earth and Planetary Science Letters*, **20**: 337-340.
- Lyman, R. L. 1994. *Vertebrate taphonomy*. Cambridge University Press, Cambridge, 550 pp.
- Norman, D. B., 1980. On the ornithischians dinosaur *Iguanodon bernissartensis* of Bernissart (Belgium). *Mémoires de l'Institut royal des Sciences naturelles de Belgique*, **178**: 1-103.
- Norman, D. B., 1986. On the anatomy of *Iguanodon atherfieldensis* (Ornithischia: Ornithopoda). *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre*, **56**: 281-372.
- Norman, D. B., 1987. A mass-accumulation of vertebrates from the Lower Cretaceous of Nehden (Sauerland), West Germany. *Proceedings of the Royal Society of London, Biological Sciences*, **230**: 215-255.
- Norman, D. B., 2012. Preface; p. xiii in: P. Godefroit, P. (ed.), *Bernissart Dinosaurs and Early Cretaceous Ecosystems*. Indiana University Press, Bloomington and Indianapolis.
- Quinif, Y. & Licour, L. 2012. The karstic phenomenon of the Iguanodon sinkhole and the geomorphological situation of the Mons Bain during the Early Cretaceous; pp. 51-61 in: P. Godefroit, P. (ed.), *Bernissart Dinosaurs and Early Cretaceous Ecosystems*. Indiana University Press, Bloomington and Indianapolis.
- Ricqlès, A. de, P. Godefroit, and J. Yans, 2012. Histological assessment of vertebrate remains in the 2003 Bernissart drill; pp. 149-158 in: P. Godefroit, P. (ed.), *Bernissart Dinosaurs and Early Cretaceous Ecosystems*. Indiana University Press, Bloomington and Indianapolis.

- Schnyder, J., Dejax, J., Keppens, E., Nguyen Tu, T. T., Spagna, P., Boulila, S., Galbrun, B., Riboulleau, A., Tshibangu, J.-P., & Yans, J., 2009. An Early Cretaceous lacustrine record: organic matter and organic carbon isotopes at Bernissart (Mons Basin, Belgium). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **281**: 79-91.
- Seward, A. C., 1900. La flore wealdienne de Bernissart. *Mémoires du Musée Royal d'Histoire naturelle de Belgique*, **1**: 1-39.
- Spagna, P., Dupuis, C., and Yans, J., 2008. Sedimentology of the Wealden clays in the Hautrage quarry. *Memoirs of the Geological Survey of Belgium*, **55**: 35-44.
- Spagna, P. & Van Itterbeeck, J. 2006., Lithological description and granulometric study of the Wealden facies of two borehole core drilled in the 'Cran aux Iguanodons de Bernissart'. *Second Geologica Belgica Meeting*, September 7-8, Liège, Belgium.
- Spagna, P., Yans, J., Schnyder, J., & Dupuis, C., 2012. The palaeoenvironment of the Bernissart Iguanodons: sedimentological analysis of the Lower Cretaceous Wealden facies in the Bernissart area (Belgium); pp.87-96 in: P. Godefroit, P. (ed.), *Bernissart Dinosaurs and Early Cretaceous Ecosystems*. Indiana University Press, Bloomington and Indianapolis.
- Stein, K. & Sander, M., 2009. Histological core drilling: a less destructive method for studying bone histology; pp. 69-80 in M. A. Brown, J. F. Kane, and W. G. Parker (eds.), *Methods In Fossil Preparation: Proceedings of the first Annual Fossil Preparation and Collections Symposium*.
- Strickland, J., Cummings, A., Spinnato, J. A., Liccioe, J. J., & Foureman, G. L., 2003. Toxicological Review of Hydrogen Sulfide. 635/R-03/005 (Washington, DC: US Environmental Protection Agency), 67pp. available at: <http://www.epa.gov/iris/toxreviews/0061tr.pdf>.
- Tissot, B.P. & Welte, D.H., 1984. *Petroleum Formation and Occurrence*, 2 ed. New York, Springer-Verlag, 699 pp.
- Tshibangu, J.-P., Dagrain, F., Deschamps, B., & Legrain, H., 2004. Nouvelles recherches dans le Cran aux Iguanodons de Bernissart. *Bulletin de l'Académie Royale de Belgique, Classe des Sciences*, **7**: 219-236.
- Yans, J., 2007. Lithostratigraphie, minéralogie et diagenèse des sédiments à faciès wealdien du Bassin de Mons (Belgique). *Mémoire de la Classe des Sciences, Académie Royale de Belgique*., 3^{ème} série, **2046**: 1-179.
- Yans, J., Dejax, J., Pons, D., Dupuis, C., & Taquet, P., 2005. Paleontologic and geodynamic implications of the palynological dating of the Bernissart wealden facies sediments (Mons Basin, Belgium). *Comptes rendus Palevol*, **4**: 135-150.
- Zazzo, A., Lécuyer, C., & Mariotti, A., 2004. Experimentally-controlled carbon and oxygen isotope exchange between bioapatites and water under inorganic and microbially-mediated conditions. *Geochimica et Cosmochimica Acta*, **68**: 1-12.