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Geological Model and Cyclic Mass Mortality Scenarios for the Lower Cretaceous Bernissart *Iguanodon* Bonebeds

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The Iguanodon Sinkhole at Bernissart (Belgium) is an exceptional fossil deposit as a result of the quantity and preservation quality of Cretaceous basal Iguanodontia found by coal mine workers in 1878. Efforts to unravel the processes that caused the accumulation and preservation of many dinosaurs, along with other taxa, are here based on a new geological model that relies on several discrete, continuous bonebeds. Several taphonomic scenarios are proposed and discussed within the specific geological and environmental specificities of the so-called Lower Cretaceous Bernissart paleolake. On the basis of sedimentological and taphonomic evidence, 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 H_2S or biological toxins as a direct or indirect lethal agent in a context of seasonally shrinking water.

Introduction

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The discovery, from 1878 until 1881, of about 40 skeletons of iguanodontid dinosaurs in Lower Cretaceous ("Wealden") deposits at Bernissart (Belgium) is exceptional in the history of paleontology, and immediately it intrigued geologists. Indeed, 117 similar sinkholes are known within Mississippian deposits of the Mons Basin, and only one has yielded dinosaur remains. Outside the Iguanodon Sinkhole, only two dinosaur bones have been identified to date in Wealden outcrops from the Mons Basin (see Chapter 13 in this book). Since 1878, geologists have tried to explain the processes leading to the formation of this unique accumulation. On the basis of geological sections of the site, Dupont (1878, 1897) hypothesized that the Bernissart environment back to Lower Cretaceous times was a narrow gorge (crevasse) in which iguanodontids lived, died, and were periodically buried during flooding episodes. Soon, Cornet and Schmitz (1898) and Cornet (1927) proposed an alternative explanation. They believed that the accumulation of numerous iguanodontids skeleton at Bernissart was clearly a slow, attritional process, resulting from the sliding or stacking of carcasses of dead animals in a subsiding lake. Because the fossiliferous layers were trapped within a sinkhole, they could escape the erosion that removed the coeval surrounding layers in other places in the Mons Basin (Bultynck, 1989).

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Louis Dollo, the original describer of all the terrestrial vertebrates from Bernissart in articles published between 1882 and 1923, proposed several conflicting hypotheses to explain the accumulation of iguanodontid skeletons at Bernissart (see reviews in Casier, 1960, and Bultynck, 1989). After noting that most of the dinosaurs were old-age individuals, Dollo proposed that Bernissart was some kind of dinosaur graveyard by Early Cretaceous times, or that flash floods selectively killed older and less agile animals. He also suggested that some iguanodontid specimens from Bernissart showed evidence of a violent death, maybe through combat.

Casier (1960) provided two further explanations for the mass burial at Bernissart. On the basis of 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 (the *"Hippopotamus"* hypothesis), Casier assumed that iguanodontids were amphibious and therefore dependent 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.

More recently, Norman (1987) compared Bernissart with another Early Cretaceous iguanodontid bonebed in Nehden, Germany, and refuted a mass kill scenarios on the basis of a more detailed taphonomic analysis. Bultynck (1989) also spoke for an attritional scenario, agreeing with the sinkhole environment hypothesis previously developed by Cornet and Schmitz (1898) and Cornet (1927).

Here we present a refined geological model for the Bernissart *Iguanodon* deposit. This model is then used as a framework for evaluating different taphonomic scenarios. We placed emphasis on the role of site-specific geological factors such as subsidence due to solution collapse deep underground and possible upwelling of sulfate-rich brines.

Institutional abbreviation. RBINS, Royal Belgian Institute of Natural Sciences, Brussels, Belgium.

Historical Discovery and Fossil Assemblage

The iguanodon bonebeds were discovered in April 1878 by coal miners excavating a driftstone gallery at level –322 m approximately 250 m south–southeast from the Sainte-Barbe shaft (see Chapter 1 in this book for details on the discovery). Earlier in March, the gallery went through 10 m of faulted and brecciated Pennsylvanian rocks with minor streaks of white sand, pyrite veinlets, and lignite fragments. Then it encountered 60 m of well-stratified Barremian lignitic clay and reentered a zone of heavily fractured rocks (Figs. 14.1 and 14.2). Most fossils were found in the first 14 m of clay, where 14 more or less complete and four partial skeletons were excavated (first series in Fig. 14.2). Eight other iguanodons were found in the second half of the gallery (second series) and three more in a second, deeper gallery (–356 m) that cut through 8 m of Barremian clay (third series). In this latter gallery, a small exploration pit reached the bottom of the clay infill 3–4 m below the ground. A third gallery entered the sinkhole at –242 m and breached a sandy aquifer beyond a 9-m-thick wall of Barremian

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Inside the Iguanodon Grave: Geological Model

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clay. Exploration then continued by a horizontal borehole that showed 5–6 m of this sand and was aborted after having reentered 8 m of clay formation. These are the shallowest Barremian sediments ever recognized in the Iguanodon Sinkhole, and there were no fossils in it (as is seemingly the case for the 26 m of Barremian clay observed in the Sainte-Barbe shaft).

The recovered fossil assemblage includes freshwater animals that lived in the lake, and terrestrial animals that lived around the lake. The freshwater component mainly consists of more than 3,000 fishes belonging to 15 different taxa. Amiiformes are particularly diversified, suggesting swampy and poorly oxygenated waters. One amphibian, six turtles, and four crocodilian specimens complete the freshwater fauna. The terrestrial fauna is largely dominated by iguanodontid dinosaurs: at least 43 specimens were unearthed from 1878 until 1881, including 25 complete to moderately complete (>60% of the skeletal elements) individuals (see Norman, 1986, for a detailed catalog of the iguanodontid specimens in the collections of the Royal Belgian Institute of Natural Sciences) and 18 partial skeletons or fragmentary material. At least 33 specimens are referred to as Iguanodon bernissartensis; six other incomplete individuals probably also belong to this taxon (Norman, 1986). The smaller iguanodontid Mantellisaurus atherfieldensis is only represented by one complete specimen (skeleton labeled "T" in Fig. 14.2) and probably 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). Many aspects of their anatomy indicate that I. bernissartensis and M. atherfieldensis were highly active on land. I. bernissartensis probably spent most of its time in a quadrupedal posture, whereas M. atherfieldensis spent considerable periods of time walking or running bipedally (Norman, 1980, 1986). Noniguanodontid dinosaurs are represented by only one theropod phalanx. One hemipteran wing completes the terrestrial fauna from Bernissart. Numerous coproliths belonging to carnivorous reptiles were discovered in Bernissart pit (Bertrand, 1903), but their producer (perhaps a crocodile or theropod) remains unknown.

Numerous fossil plants were also collected, with abundant remains of the fern *Weichselia* (Seward, 1900), which also thrived in swamps.

Stratigraphy

Cornet and Schmitz (1898) published the only detailed geological section of the Iguanodon Sinkhole, according to the original drawings made by the mining engineer Sohier, who was assisted by De Pauw and Sonnet in his work (Fig. 14.2). Unfortunately, data for the first 14 m, which yielded the greatest number of fossils, were lacking as a result of missing documents. Although Arnould made a general description of this missing zone and collected a few structural measurements, Cornet and Schmitz (1898) preferred not to use this information to fill the gap in their original figure. However, De Pauw (1898) published a geological section from his own observations, which is consistent with the description from Arnould (in Cornet and Schmitz, 1898). De Pauw (1898) wrote that he reported the small-scale details of folds and fractures, but only the general structure was reproduced in his article, and each clay bed was measured (location and thickness).

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The clay sediments in the Iguanodon Sinkhole are well stratified, as was subsequently confirmed by the 2003 coring program (Yans et al., 2005). Both flat and lenticular layerings were identified in the gallery section. Sand and lignite are the major sediments forming lenses, and several lignite beds up to 8 cm thick were observed. This may reflect a more variable (and perhaps shallower) depositional environment than is commonly suggested by varvelike stratification. Hard coal fragments derived from the Pennsylvanian rocks occur along the banks of the lake and are also found concentrated in discrete strata. Continuous millimeter-thick sandy layers clearly separate the clay in decimeter-thick beds (see De Pauw, 1898, fig. 2). Inside each bed, small-scale lamination (a millimeter thick or less) is clearly visible, although the detailed description of the BER 3 and BER 2 cores showed several nonlaminated intervals (Spagna and Van Itterbeek, 2006). Bone fragments were found in these nonlaminated intervals (see Chapter 12 in this book); therefore, they could be significant from a taphonomic point of view, such as homogeneization of the clay material might be due to bioturbation or trampling. However, it is not possible to differentiate between accidental drilling-induced homogenization and the actual absence of original lamination in the clay. These nonlaminated intervals were not described in the nineteenth-century galleries, but whether have they been overlooked or are actually missing remains a pending question.

Sedimentological structures include small-scale faulting, slumping, and erosional surfaces. Small synsedimentary faults are particularly abundant and often show pinching-out structures (*boudinage*) suggestive of soft sediment deformation due to dewatering or degassing.

Structure

The clay beds bounding the sinkhole are steeply (60–70 degrees) inclined (Fig. 14.2). Dip angles rapidly decrease toward the center of the collapse structure, with the strata lying almost horizontally within about 10 m from the walls. This overall flat-bottomed basin structure induced by sinkhole subsidence is slightly more complex as a small anticline appears at approximately 40 m from the western wall. In addition, deformation in the Barremian clay did not proceed merely in folding, but rather by disruption and displacement of a multitude of clay blocks in which parallel stratification is preserved. This is clearly evidenced by plotting the strata dip angle as a function of depth in the BER 3 borehole (Spagna, 2010). The blocky structure of the clay is more pronounced in the eastern part of the sinkhole filling (Fig. 14.2), where subsidence-induced deformation and downdrop amplitude are highest. The structure of the Barremian clay in the iguan-odon sinkhole may therefore be idealized as a north–south elongated, asymmetrical funnel, as suggested by the geological model in Fig. 14.3.

Bonebeds

One critical observation made by De Pauw (1898) is that fossils in the first 14 m of Barremian clay, with the exception of plant remains, were found in discrete 35- to 55-cm-thick layers that are clustered within the first 14 m of Barremian clay (Fig. 14.2). The section of Cornet and Schmitz (1898) is

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unfortunately the only geological record for the second and third series of fossils. Fourteen more or less complete and four partial iguanodon skeletons were excavated from beds I, II, IV, and V, which are stratigraphically distant from each other by approximately 1, 2, and 5 m, respectively. Because there is no obvious change in bed thickness, this could indicate that the cyclic conditions leading to dinosaur accumulation were met at a rate decreasing with time. Skeletons from the excavation plan (adapted from Norman, 1986) are tentatively assigned to fossiliferous beds, although no conclusive attribution was found for the specimens in the central zone (in gray in Fig. 14.2). Another uncertainty arises from De Pauw's comments about the fish bonebeds. In his figure, only bed III is indicated as an accessory fish bonebed observed at the footwall of the cavity created for excavating an iguanodon from bed IV (Bultynck, 1989, fig. 63). However, he claimed that the principal fish bonebed lay 4 m below and also contained chelonians and crocodiles. This bonebed 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 because of the excavation chamber's complex geometry and the ground's irregular surface. It is therefore impossible to locate this bonebed more precisely. Fortunately, on the basis of archive analysis, Gosselin (1997) mentioned a chelonian- and crocodile-bearing bonebed between beds IV and V (bed IVb in fig. 2). Although this point necessitates further verification, we shall consider Gosselin's solution, which we deem consistent with stratigraphic continuity. Indeed, a crocodile seemingly corresponding to bed IVb was found at 38.4 m from the west wall of the sinkhole, and iguanodons from bed IV (second series) were then recovered a little farther eastward. It is worth noting that as a result of its continuity, one of these fish-rich beds was used as a stratigraphical marker for drawing the geological section.

Data for the western region of the iguanodon sinkhole at -322 m thus suggest four dinosaur bonebeds, with one or two additional bonebeds depending on whether bonebeds III and/or IVb are taken into account (De Pauw, 1898, considered five main beds). Although fishes were

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14.2. Detailed geological section and excavation plan of the –322 and –356 m galleries in the Iguanodon Sinkhole at Bernissart (adapted from Cornet and Schmitz, 1898, and Norman, 1986, respectively). The –322 m section, for which a hiatus resulting from missing documents was originally mentioned for the first 14 m, was completed after Van den Broeck (1898). Color correspondence between specimens and bonebeds in the first series of excavation was made only for the lowermost and uppermost beds. The dashed line shows the extension of possible additional bonebed IVb that yielded fossil turtles, crocodiles, and fishes (after Gosselin, 1997).

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14.3. Proposed model section for the Iguanodon Sinkhole based on the continuity of the bonebeds recognized in the -322 m gallery and the BER 3 borehole. Only the lowermost and uppermost bonebeds are indicated (dotted lines). Others lie within the bonebed interval (light gray shading). The findings at -356 m could relate to either the existence of an additional, deeper bonebed (suggested here) or to downwarping of one of the beds above (as depicted in Fig. 3.2).

The Crime Scene: Taphonomy

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found concentrated in bonebeds, isolated fishes apparently also occurred within dinosaur bonebeds. To illustrate this, a fossil fish was observed sandwiched between the left foreleg and the head of an *Iguanodon* (RBINS R51, specimen Q).

Correlation between the western and eastern bonebeds at -322 m is straightforward, although beds III, IV, and IVb were not explicitly reported on the east. This is likely related to the more intense deformation in that region of the sinkhole filling where fewer fossils were recovered. However, it is not clear whether this is due to fossil scarcity or lack of exploration. Indeed, the first western fossil series received more time, attention, and money than limited in-depth exploration in other regions of the deposit.

Correlation with the single (?) bonebed at -356 m is more difficult because of extreme deformation and the lack of stratigraphic markers. As a first explanation, additional, deeper bonebeds would be lying near the bottom of the clay deposit (Fig. 14.3). Excessive subsidence-induced deformation and downdropping of the -322 m bonebeds would provide a second explanation (see Fig. 3.2 in Chapter 3 in this book).

Figure 14.3 shows a nice correspondence between the bonebed occurrences in the nineteenth-century galleries and the 2003 coring program, especially in BER 3, where several bone fragments were found between -396.5 and -309 m in the lower part of the clay formation.

Taphonomic Elements

No detailed taphonomic study is available for the Bernissart bonebeds so far. However, we can summarize the taphonomically relevant elements as follows.

- 1. The terrestrial component (animals that lived around the Bernissart lake) of the vertebrate assemblage is nearly monotaxic (in this case, dominated by multiple individuals of one taxon; Fiorillo and Eberth, 2004; Eberth and Currie, 2005). *Iguanodon bernissartensis* is the dominant species, representing about 90% of the terrestrial specimens discovered at Bernissart.
- 2. Most iguanodontid specimens discovered at Bernissart can be regarded as fully ossified adults. In all specimens, the transverse processes and neural arches are fused to the centra of the vertebrae, and the sacral centra are fused together. Open cranial sutures are absent, even in the smaller *Mantellisaurus atherfieldensis* specimen (Norman, 1986). In some *Iguanodon bernissartensis* specimens (RBINS R55, specimen N, for example), the scapula and coracoid are completely fused together, and the tarsus appears co-ossified to the tibia. Intersternal ossification, which presumably originated within the cartilage of the sternal plate, occurs in most *I. bernissartensis* specimens (Norman, 1980). Norman (1986) recognized three "subadult" specimens of *I. bernissartensis* from smaller individuals, although these are all rather poorly preserved.
- 3. Most iguanodontid skeletons discovered at Bernissart are complete or subcomplete and are articulated. This is also the case for most

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other vertebrates found in this locality, with the notable exception of the theropod isolated phalanx. Some iguanodontid specimens (RBINS R56, specimen L) were found slightly disarticulated. Even incomplete skeletons were found in connection with this locality. The extremely difficult excavation conditions, in dark galleries more than 300 m below ground level, could explain why at least some of the specimens were probably incompletely unearthed and why skeletons might have been partially destroyed by the excavation team. For example, RBINS VERT-5144-1716 (specimen A/B) is a partial skeleton comprising the articulated tail, the posterior portion of the pelvis, and the distal portions of the femur and hind limbs. This was the first skeleton to be systematically excavated and then mounted. The anterior portion of the body was undoubtedly destroyed during initial gallery construction in April 1878 (Norman, 1986).

The presence of subcomplete and articulated skeletons indicates that the iguanodontid carcasses were quickly buried in the sediments of the lake just after the death of the animals. Scavengers (theropods and crocodiles are represented at Bernissart) had limited opportunities for dismembering the carcasses. Moreover, the carcasses were buried in the sediments before they had decayed too much and were kept floating by gases inside the body cavity. Schäfer's (1962) studies on the gradual decay of floating mammal carcasses in the sea (notably those of seals) are especially interesting in this respect because they show that bloated carcasses can drift for more than a month before what is left of them finally settles to the bottom, after having lost a large part of their bony elements. Observations of dead marine mammals cannot be directly extrapolated to carcasses of dinosaurs in a freshwater environment, but they suggest that the gradual decay of floating carcasses certainly leads to the burial in bottom sediments of isolated bones instead of subcomplete skeletons, as observed in Bernissart. In confined lakes, this process is accelerated by the proximity of scavengers.

- 4. The animals are exceptionally preserved. Ossified tendons are not displaced in most cases, and skin impressions can be observed on many specimens. De Pauw (1898) even described the presence of potential flesh relics. Dinosaur skeletons preserved with skin impressions are common in regions of the Western Interior of North America; however, there are only a few detailed taphonomic studies of these occurrences (Anderson et al., 1999). Exceptional soft tissue preservation is evidently the result of critical timing of diagenetic phosphatization due to the rapid postmortem morphological changes that occur in delicate animal tissue. Such mineralization must occur soon after the death of the animal and its burial. Fossilization of soft tissues most usually occurs in anoxic fossilization conditions (Allison and Briggs, 1991).
- 5. Iguanodontid skeletons from Bernissart are usually lying on their side in a rather passive position, and many specimens have their necks bent sharply backward. A notable exception is specimen RBINS VERT-5144-1716 (specimen O), which was discovered lying on its back with its skeleton dorsoventrally flattened. Recurving of the neck over the

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back, or an opisthotonic posture, is observed in many well-preserved amniote skeletons (Faux and Padian, 2007). Numerous postmortem processes have been proposed to account for this posture, including rigor mortis, differential contraction, desiccation, and water currents. However, in their recent experiments and a review that included the clinical literature, Faux and Padian (2007) showed that perimortem processes related to the central nervous system are more likely to produce an opisthotonic posture. The posture is achieved in the final moment of life by muscle spasms and is temporarily fixed by rigor mortis. Preservation in the fossil record of the opisthotonic posture would therefore indicate rapid burial as well as no significant transport or scavenging of the carcasses.

6. Bone modification can be defined as features on bones that were the result of any postmortem, prediagenetic process (e.g., trampling, scavenging, weathering), which alters the morphology of a onceliving bone (Fiorillo, 1991a). At the occasion of the renovation of the Janlet Aisle of the museum of the RBINS, from 2004, the iguanodontid skeletons were entirely dismounted, and all the bones were treated against pyrite. It was a unique opportunity for the technical team to look systematically at bone modification features.

Postmortem fractures other than those resulting from block faulting in the clay mass or excavation incidents could not be observed with certainty. According to Ryan et al. (2001) and Eberth and Getty (2005), the observation of a large number of broken limb bones indicate a destructive history, such as the breakdown of trabecular bone and collagen, before and/or during final transportation. Behrensmeyer (1988, 1991) observed that fresh limb bones from large mammals often show no evidence of breakage during vigorous hydraulic transport. Thus, the absence of broken limb bones in the Bernissart sample suggests that the carcasses were not transported over a long distance and/or they did not experience an earlier taphonomic episode that weakened the specimens and increased their susceptibility to hydraulically induced breakage before final burial.

Perthotaxic features (bone modification processes that are active on the land surface; Clark et al., 1967) could not be positively observed in the iguanodontid bones from Bernissart. Weathering features (flaking and cracking) are apparently absent, indicating that the bones were not exposed subaerially for any significant length of time before or after transportation. Nor have we recognized trample marks, indicative of the trampling activity of another animal whose feet pressed the bone against a sandy surface, which are characterized by shallow, subparallel scratch marks left on the surfaces of bones (see, e.g., Behrensmeyer et al., 1986; Fiorillo, 1984, 1987), in the studied sample. Therefore, the absence of perthotaxic features is additional supporting evidence that the dinosaur bones discovered at Bernissart were quickly buried.

Carnivorous tooth marks on bone surfaces can be identified either as grooves, often several millimeters deep, with a V-shaped cross section or isolated punctures (Fiorillo, 1991b). Tooth marks on

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mammal and dinosaur bones are usually attributed to scavenging and prey carcass utilization, not to the killing process (Fiorillo, 1991a, 1991b). Tooth marks could not be identified with certainty on the bones of the Bernissart iguanodontoids. This observation can be related to the absence of theropod shed teeth at Bernissart and reflects the low incidence of scavenging on the iguanodontid carcasses. Alternatively, it may also be hypothesized that scavengers ate only the fleshy parts of the dead iguanodontid specimens because prey was abundant (Eberth and Getty, 2005). In any case, Fiorillo (1991b) observed that tooth-marked bones are uncommon in dinosaur localities. Theropod dinosaurs did not routinely chew bones during prey carcass utilization. They may have used prey bones more like modern Komodo monitors and crocodiles than mammalian carnivores—that is, by passive consumption rather than by actively seeking out the bones for nutrient intake.

It can therefore be concluded that bone modification is virtually absent for the iguanodontid skeletons from Bernissart. Again, it suggests that the dinosaur carcasses were quickly buried in the sediments after the animals' death.

- 7. Fossil concentration is high, but skeletons are neither systematically piled up nor excessively concentrated in certain regions for a given stratigraphic interval. Rather, they are homogeneously scattered over the strata surface. A simple calculation suggests that each dinosaur bonebed could originate from the burial of a single layer of adjacent, almost side-by-side carcasses: 300 m³ of fossiliferous clay were excavated from the first series from which 17 specimens were collected. Volume by specimen is thus $300/17 = -17 \text{ m}^3$, or $10 \times 3 \times 0.57$ m (length × width × thickness), which is a slight overestimation of the volume that could be filled by a typical iguanodon skeleton in the deposit (bonebed thickness ranges from 0.35 to 0.55 m). Overestimation occurs because some unfossiliferous clay is taken into account. Stretching of strata surface caused by the sinkhole subsidence may also have caused slight dispersion of the skeletons. The stratigraphic correlations established here suggest the presence of a great number of fossil dinosaurs in the Iguanodon Sinkhole, probably exceeding at least 100 specimens. Extrapolation of the first series excavation—that is, 17 iguanodons found within an area of 20×15 m, to the inner 15-m-wide band of a 60×80 m ellipse representing a simplified section of the sinkhole at -322 myields 102 specimens. This estimation assumes no change in fossil concentration, which may be questionable (see below), but it does not consider additional fossils in other areas of the main bonebed group, both in the center and outside, and in possible additional bonebeds in the deepest regions of the sinkhole fill.
- 8. As suggested by Norman (1987), there are three groups of skeletons showing common orientation. However, two of these groups share specimens from different layers (I, II, and IV). Therefore, the common orientation of these skeletons cannot reasonably be explained by hydraulic processes producing exactly the same orientation of the carcasses at different times. Nevertheless, alignment

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is obvious for skeletons in bed V, but they were excavated in a zone that corresponds to a northeast–southwest-oriented syncline hinge showing fractured (and likely displaced) blocks. As an alternative explanation to hydraulic processes (albeit one not completely ruled out here), early subsidence processes in the still-hydroplastic mud could have affected the original orientation of the buried carcasses.

Discussion of elements 7 and 8 stresses the need for better assessment of postdepositional mechanical processes, which could have significantly modified the original orientation and attitude of the original iguanodon carcasses.

9. Although it is not yet firmly established, the absence of lamination in the bonebed sediment could result from bioturbation by burrowing or miring animals when the environment episodically changed to shallower, shrinking water conditions in the lake. However, no observation of contorted bed was made to support the miring hypothesis. No desiccation cracks were described either, and it is unlikely that past researchers could have overlooked these sedimentological structures.

Obrution Scenario

Obrution assemblages are formed by catastrophic sedimentological events. A typical situation is represented by herds buried by bank collapse or landslides triggered by heavy rains or earthquakes (Rogers and Kidwell, 2007). It is worth mentioning this taphonomic category here because sudden ground or bank collapses are valid processes that could have occurred when the sinkhole reached the surface, or later as a consequence of sinkhole margin instability (Fig. 14.4). Although most taphonomic elements do not contradict this hypothesis, sedimentological evidence that could support it, such as medium- to large-scale slumpings, are completely lacking. **14.4.** Synopsis of the taphonomic parameters identified for the Bernissart bonebeds, listed as mortality and preservation parameters from left to right, respectively. Mass death caused either by herding or abnormal behavior under perilous situation is the most likely scenario. Passive attrition, which results from normal biological activity under normal circumstances but requires efficient processes of concentration and conservation, is unlikely. Quick burying resulting from catastrophic sedimentary events (obrution) seems unlikely as well. The possible influence of the specific geological environment of Bernissart by Lower Cretaceous times is shown. See text for details.

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Attrition Scenario

Attritional (or passive attritional) assemblages result from death under normal circumstances but require efficient processes that concentrate as bonebeds the carcasses of animals dead at different times and in different places; hydraulic transportation usually plays an important role in the formation of vertebrate attritional assemblages (Lauters et al., 2008; Behrensmeyer, 2007a; Rogers and Kidwell, 2007). Lignite lenses within the Iguanodon Sinkhole most probably derived from floods that occurred after wildfires. As discussed above (elements 3, 6, and 8), there is no indication that the iguanodontid skeletons were transported over a significant distance, and the carcasses probably did not float for long before being buried. The high skeleton concentration at Bernissart (element 7) could have been achieved by a very low sedimentation rate, such as in some oxbow lakes (hiatal concentration), but this hypothesis is not consistent with sedimentological evidence of cyclic but sustained arenitic sediment influx in likely shallow conditions (see above). Moreover, the exceptional state of preservation of the iguanodontid skeletons (elements 3 and 4) and the absence of bone modification (element 6) indicate that the carcasses were quickly buried just after the death of the animals; these elements also point to high sedimentation rates.

Moreover, the age profile of the Iguanodon bernissartensis population (element 2) is not compatible with an attritional mortality scenario. In an ideal attritional profile, age class abundances reflect the number of animals dying from one class to the next (Lyman, 1994), showing peaks corresponding to ages where mortality rates are the highest: among the very young and, to a lesser extent, the very old. Therefore, in this case, the observed death profile of the fossil assemblage is completely different from the age profile of the living population: younger individuals are overrepresented. In attritional dinosaur assemblages, late juveniles and small subadult individuals represent over 90% of the recovered fossils (Lauters et al., 2008). This is not the case for the I. bernissartensis assemblage discovered at Bernissart, which is largely dominated by adult specimens. This age profile is more consistent with a catastrophic, nonselective scenario: 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).

Mass Mortality Scenario

Mass death assemblages may arise from a variety of causes or combinations of them (Behrensmeyer, 2007a; Rogers and Kidwell, 2007). The living, normal environment can become a lethal trap under certain panic/fleeing or starvation/exhaustion situations caused, for example, by predation or herding (either natural or forced by extreme circumstances). Perilous situations due to environmental or biological hazards, which usually induce abnormal behavior, also increase vulnerability and hence mortality. To date, mass death assemblages of ceratopsid (horned) dinosaurs have been found in Late Cretaceous deposits of western North America (see Dodson et al., 2004 and references therein).

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Wildfires, floods, and drought were likely perilous situations in the Lower Cretaceous environment of Bernissart. Wildfires probably occurred, as shown by lignite beds and typical postfire colluvia in the Lower Cretaceous of Hautrage (Spagna, 2010).

In western North America, large ceratopsid bonebeds in channel deposits indicate that flooding may have been responsible for mass drowning in some cases (Currie and Dodson, 1984). Floods were naturally pacing the sedimentary environment at Bernissart, but there is no sedimentological evidence for extreme or flash floods that could have drowned and buried animals en masse.

Drought is the primary cause of mass death accumulations today (e.g., Corfield, 1973; Haynes, 1988), with carcasses of large herbivores often concentrated around water holes. Evidence of strong seasonality and semiarid conditions in association with ceratopsid bonebeds indicates that drought may also have been a major killing agent for dinosaurs during the Cretaceous (Rogers, 1990). Drought was also probably recurrent in the Bernissart environment, but again, there is no convincing evidence of severe situations, such as mud cracks, evaporitic deposits, or typical paleosols. Nevertheless, drought and concomitant shrinking water could have created circumstances under which the vulnerability of iguanodons was increased—for example, by forcing them to overcrowd around water holes. In this respect, the Iguanodon Sinkhole most probably controlled the location of the residual water body by sustained low ground conditions due to subsidence.

The dominantly clayey composition of sediments in swampy areas such as Bernissart indeed suggests miring as a highly probable cause of death. (Death would actually occur as a result of exhaustion or starvation because of being stuck in the mud.) If sedimentological data could possibly agree with that hypothesis (see discussion of element 9), other observations do not. First, it is surprising that most iguanodons are not lying on their ventral side with their legs fully extended (element 5) if we consider a miring scenario (Rogers and Kidwell, 2007; Weigelt, 1989). The above-mentioned postdepositional processes due to enhanced karstic subsidence are not thought to have changed such a typical miring posture for virtually all the specimens. Second, mired animals cannot sink deep into the mud because of buoyancy (it is far easier to sink into water). Therefore, most mired carcasses have their upper side exposed over a sufficient period of time to permit scavenging (Weigelt, 1989). Contrary to similar trap situations such as tar pits (Behrensmeyer, 2007b), remains of scavengers and/or predators that should have been attracted by mired animals are rare at Bernissart, comprising one theropod phalanx and four crocodile skeletons (with the possible exception of coprolites). Tooth marks cannot be recognized on the iguanodontid bones (element 6), and scavenging damages, if proven, would be obviously be minimal, as indicated by the full articulation and the high degree of preservation of most iguanodontid skeletons (element 4).

Mass drowning remains another possible scenario to explain the high concentration of complete iguanodontid skeletons in lake deposits at Bernissart. However, iguanodontids were probably used to living close to swamp and bog environments, and it is thus difficult to conceive that they could have easily drowned in normal situations. Abnormal, high-vulnerability

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situations such as herding when crossing water bodies or fleeing are therefore possible scenarios to explain mass drowning, but this hypothesis cannot be substantiated by any concrete elements. The opisthotonic posture observed in many skeletons could support the hypothesis of mass drowning because it can be caused by several brain afflictions resulting from drowning but also by asphysiation, lack of nourishment, environmental toxins, or viral infections (Faux and Padian, 2007).

Possible Role of Chemical or Biological Intoxication

Death by gas inhalation is often related to volcanic activity. However, suffocating (CO_2) or poisonous (H_2S) gases are common products of organic matter decay and are frequently released in the sedimentary environment. An example of a recent gas-related fatal accident is provided by the H_2S emanation from a 1-m-thick stand of rotting seaweed that killed a horse and left its rider unconscious on a beach in western France on July 28, 2009. H_2S -based death scenarios at Bernissart may tentatively be hypothesized on the basis of the following observations.

- 1. Pyrite (FeS_2) , a common product of diagenetic H_2S fixation in sediments, is an abundant mineral in the Barremian clays of Bernissart, including the iguanodontid bones (see Chapter 11 in this book).
- H₂S is formed by sulfate-reducing bacteria decomposing organic matter in anaerobic conditions. Barremian clays are indeed rich in organic matter, and there are abundant sedimentological structures possibly attributable to gas escape. Moreover, the preservation of soft tissues also suggests anaerobic conditions for the fossilization of iguanodontids fossils (element 4).
- 3. Artesian, sulfate-rich brines are known in the underlying Mississippian strata. This geothermal (70°C) water is in fact the result of the dissolution of anhydrite layers that induced collapse and subsidence in the Mons Basin, including the Iguanodon Sinkhole. Although most sinkhole fillings, which are composed of predominantly shaley Pennsylvanian rocks, are now rather impervious, uprising flow of deep brines could have existed in the earliest stages of sinkhole formation. Brines could also have arisen from adjacent fractures or faults because the whole Bernissart area was subjected to karstic subsidence processes (Fig. 3.3 in Chapter 3 in this book). Delmer (2000) suggested that sulfate-rich water from underlying Mississippian limestone can locally flow up through Pennsylvanian rocks on the basis of mine records reporting on the technical efforts that were necessary to reduce H₂S concentration in the Bernissart coal mines. Today, deep sulfate-rich geothermal water forms several springs, such as the bubbling spring of Stambruges, the temperature of which is 18°C throughout the year (whereas aquifers are typically 11–12°C). In contrast to other nearby low-temperature conventional springs, life is extremely scarce and monospecific in the warm spring, forming a decametric pool of crystal-clear water in which strange cyanobacterial mats develop.

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Biological intoxication such as cyanobacterial toxicosis (Varrichio, 1995; Koenigswald et al., 2004 and references therein) could also be invoked as a cause of vertebrate death or disease. Increasing temperature caused by sulfate-rich water upwelling along the sinkhole breccia column or some nearby fissure could also have created unusual chemical and biological conditions in the environment, for example by boosting cyanobacterial activity in water and/or sulfate-reducing bacteria in sediments. Of particular significance for both chemical and biological intoxication scenarios, Schnyder et al. (2009) reported a strong positive δ^{13} C anomaly in sedimentary organic matter of the Sainte-Barbe clays excluding fossil wood. They interpreted this anomaly as an enhanced algal-bacterial or macrophytal productivity.

These intoxication scenarios of drinking poisonous water or breathing toxic gas are consistent with the opisthotonic posture and are totally compatible with-and perhaps best explained by-abnormal situations such as droughts, in which iguanodons were forced to seek food or water in biologically hazardous or H₂S-emanating areas. Trampling would have had no other effect but to increase the emanation rate of lethal gas. Animals could have been killed directly or been overcome and then drowned. A context of shrinking water during drought periods is particularly interesting because it could have amplified the effects of springing geothermal brines. It is also consistent with a massive die-off of fishes, which is often reported as anoxia driven but can also be due to H₂S intoxication (Weigelt, 1989). In such situation, mass death accumulation of local freshwater fauna would have logically preceded that of terrestrial animals, and it is therefore normal that fish and iguanodontids bonebeds are separated in the sedimentological record. However, this hypothesis does not explain why the dinosaur bonebeds at Bernissart are near monotypic (element 1); indeed, Iguanodon bernissartensis was not the only large vertebrate to live around the Bernissart lake, and other animal should also have been strongly affected by poisonous waters or toxic gases.

Several discrete and laterally continuous bonebeds occur in the Iguanodon Sinkhole. They are clustered within 8 m of Barremian clay in the lower part of the Sainte-Barbe Clays Formation. Four dinosaur beds plus one or two fish- and freshwater reptile-bearing beds were recognized, although the possible occurrence of earlier-formed beds cannot be ruled out. Cyclic mass death under as yet unresolved conditions should receive more attention than obrution and attrition as formation processes for the Bernissart fossil deposit. Intoxication by H₂S or biological toxins in a context of seasonally shrinking water is an interesting scenario that remains to be assessed; it fits within the specific karstic-induced environment of Bernissart. This includes solution-collapse subsidence processes and possible sulfate-rich brine contamination that could have boosted bacterial/ cyanobacterial activity.

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Geological Model and Cyclic Mass Mortality Scenarios

Conclusions

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References

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- Allison, P. A., and D. E. G. Briggs. 1991. The taphonomy of soft-bodied animals; pp. 120–140 in S. K. Donovan (ed.), The process of fossilization. Belhaven Press, London.
- Anderson, B. G., R. E. Barrick, M. L. Droser, and K. L. Stadtman. 1999. Hadrosaur skin impressions from the Upper Cretaceous Neslen Formation, Book Cliffs, Utah: morphology and paleoenvironmental context. Utah Geological Survey Miscellaneous Publictions 99: 295–301.
- Behrensmeyer, A. K. 1988. Vertebrate preservation in fluvial channels. Palaeogeography, Palaeoclimatology, Palaeoecology 63: 183–199.

. 1991. Terrestrial vertebrate accumulations; pp. 291–335 in P. A. Allison and D. E. G. Briggs (eds.), Taphonomy: releasing the data locked in the fossil record. Plenum, New York.

— . 2007a. Bonebeds through time; pp. 65–97 in R. R. Rogers, D. A. Eberth, and A.R. Fiorillo (eds.), Bonebeds: genesis, analysis and paleobiological significance. University of Chicago Press, Chicago.

- 2007b. Terrestrial vertebrates;
 pp. 318–321 in D. E. G. Briggs and
 P. R. Crowther (eds.), Paleobiology II.
 Blackwell Science, Oxford.
- Behrensmeyer, A. K., K. D. Gordon, and G. T. Yanagi. 1986. Trampling as a cause of bone surface damage and pseudo-cutmarks. Nature 319: 768–771.
- 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.
- Clark, J. R., J. R. Beerbower, and K. K. Kietzke. 1967. Oligocene sedimentation, stratigraphy, paleoecology, and paleoclimatology in the Big Badlands of South Dakota. Fieldiana Geology 5: 1–158.
- Corfield, T. F. 1973. Elephant mortality in Tsavo National Park, Kenya. East Africa Wildlife Journal 11: 339–368.

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- Cornet, J. 1927. L'époque wealdienne dans le Hainaut. Bulletin de la Société géologique de Belgique 50(4): B89–B104.
- Cornet, J., and G. Schmitz. 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.
- Currie, P. J., and P. Dodson. 1984. Mass death of a herd of ceratopsian dinosaurs; pp. 52–60 in W.-E. Reif and F. Westphal, Third Symposium of Mesozoic Terrestrial Ecosystems. Attempto Verlag, Tübingen.
- Delmer, A. 2000. Les gisements houillers du Hainaut. Vol. 1, Le Couchant de Mons. Geological Survey of Belgium, Brussels, 22 pp.
- De Pauw, L. 1898. Observations sur le gisement de Bernissart. Bulletin de la Société belge de Géologie, Paléontologie et Hydrologie 12: 206–216.
- Dodson, P., C. A. Forster, and S. D. Sampson. 2004. Ceratopsidae; pp. 494–513 in D. B. Weishampel, P. Dodson, and H. Osmólska (eds.), The Dinosauria. 2nd ed. University of California Press, Berkeley.
- 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.
- . 1897. Musée Royal d'Histoire naturelle de Belgique. Guide dans les collections. Bernissart et les Iguanodons. Editions Polleunis and Centerick, Brussels.
- Eberth, D. A., and P. J. Currie. 2005. Vertebrate taphonomy and taphonomic modes; pp. 453–477 in P. J. Currie and E. B. Koppelhus (eds.), Dinosaur Provincial Park, a spectacular ancient ecosystem revealed. Indiana University Press, Bloomington.
- Eberth, D. A., and M. A. Getty. 2005. Ceratopsian bonebeds: occurrence, origins, and significance; pp. 501–506 in P. J. Currie and E. B. Koppelhus (eds.), Dinosaur Provincial Park, a spectacular ancient ecosystem revealed. Indiana University Press, Bloomington.
- Faux, C. M., and K. Padian. 2007. The optisthotonic posture of vertebrate

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skeletons: postmortem contraction or death throes? Paleobiology 33: 201–226.

- Fiorillo, A. R. 1984. An introduction to the identification of trample marks. Current Research, University of Maine 1: 47–48.
 —. 1987. Trample marks: caution from the Cretaceous. Current Research in the Pleistocene 4: 73–75.
- . 1991b. Prey bone utilization by predatory dinosaur. Palaeogeography, Palaeoclimatology, Palaeoecology 88: 157–166.
- Fiorillo, A. R., and D. A. Eberth. 2004. Dinosaur taphonomy; pp. 607–613 in D. B. Weishampel, P. Dodson, and H. Osmólska (eds.), The Dinosauria. 2nd ed. University of California Press, Berkeley.
- Gosselin, R. 1997. Summary excavation map of the Bernissart iguanodons (first series) from IRScNB archives. Unpublished files of the 2002–2003 drilling program in the Bernissart sinkhole.
- Haynes, G. 1988. Longitudinal studies of African elephant death and bone deposits. Journal of Archaeological Sciences 15: 131–157.
- Koenigswald, W. V., A. Braun, and T. Pfeiffer. 2004. Cyanobacteria and seasonal death: a new taphonomic model for the Eocene Messel Lake. Paläontologische Zeitschrift 78 (2): 417–424.
- Lauters, P., Y. Bolotsky, J. Van Itterbeeck, and P. Godefroit. 2008. Taphonomy and age profile of a latest Cretaceous dinosaur bonebed in Far Eastern Russia. Palaios 23: 153–162.
- 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.
- . 1986. On the anatomy of *Iguan*odon atherfieldensis (Ornithischia: Ornithopoda). Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre 56: 281–372.
- . 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.
- Rogers, R. R. 1990. Taphonomy of three dinosaur bone beds in the Upper Cretaceous Two Medicine Formation of Northwestern Montana: evidence for droughtrelated mortality. Palaios 5: 394–413.
- Rogers, R. R., and S. M. Kidwell. 2007. A conceptual framework for the genesis and analysis of vertebrate skeletal concentrations; pp. 1–64 in R. R. Rogers, D. A. Eberth, and A. R. Fiorillo (eds.), Bonebeds: genesis, analysis and paleobiological significance. University of Chicago Press, Chicago.
- Ryan, M. J., A. P. Russell, D. A. Eberth, and P. J. Currie. 2001. The taphonomy of a *Centrosaurus* (Ornithischia: Ceratopsidae) bone bed from the Dinosaur Park Formation (Upper Campanian), Alberta, Canada, with comments on cranial ontogeny. Palaios 16: 482–506.
- Schäfer, W. 1962. Aktuo-Palaontologie nach Studien in der Nordsee. Verlag Waldemar Kramer, Frankfurt am Main, 666 pp.
- Schnyder, J., J. Dejax, E. Keppens, T. T. Nguyen Tu, P. Spagna, S. Boulila, B. Galbrun, A. Riboulleau, J.-P. Tshibangu, and J. Yans. 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. 2010. Les faciès wealdiens du Bassin de Mons (Belgique): paléoenvironnements, géodynamique et valorisation industrielle. Ph.D. thesis, Faculté Polytechnique de l'Université de Mons, 138 pp.
- Spagna, P., and J. Van Itterbeeck. 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.
- Van den Broeck, E. 1898. Les coupes du gisement de Bernissart. Caractères et dispositions sédimentaires de l'argile ossifère du Cran aux Iguanodons. Bulletin de la Société belge de Géologie, Paléontologie et Hydrologie 12: 216–243.
- Varrichio, D. J. 1995. Taphonomy of Jack's Birthday Site, a diverse dinosaur bonebed from the Upper Cretaceous Two Medicine Formation of Montana. Palaeogeography, Palaeoclimatology, Palaeoecology 114: 297–323.
- Yans, J. P., Spagna, C. Vanneste, M. Hennebert, S. Vandycke, J. M. Baele, J. P. Tshibangu, P. Bultynck, M. Streel, and C. Dupuis. 2005. Description et implications géologiques préliminaires d'un forage carotté dans le "Cran aux Iguanodons" de Bernissart. Geologica Belgica 8: 43-49.
- Weigelt, J. 1989. Recent vertebrate carcasses and their paleobiological implications. University of Chicago Press, Chicago, 188 pp.

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