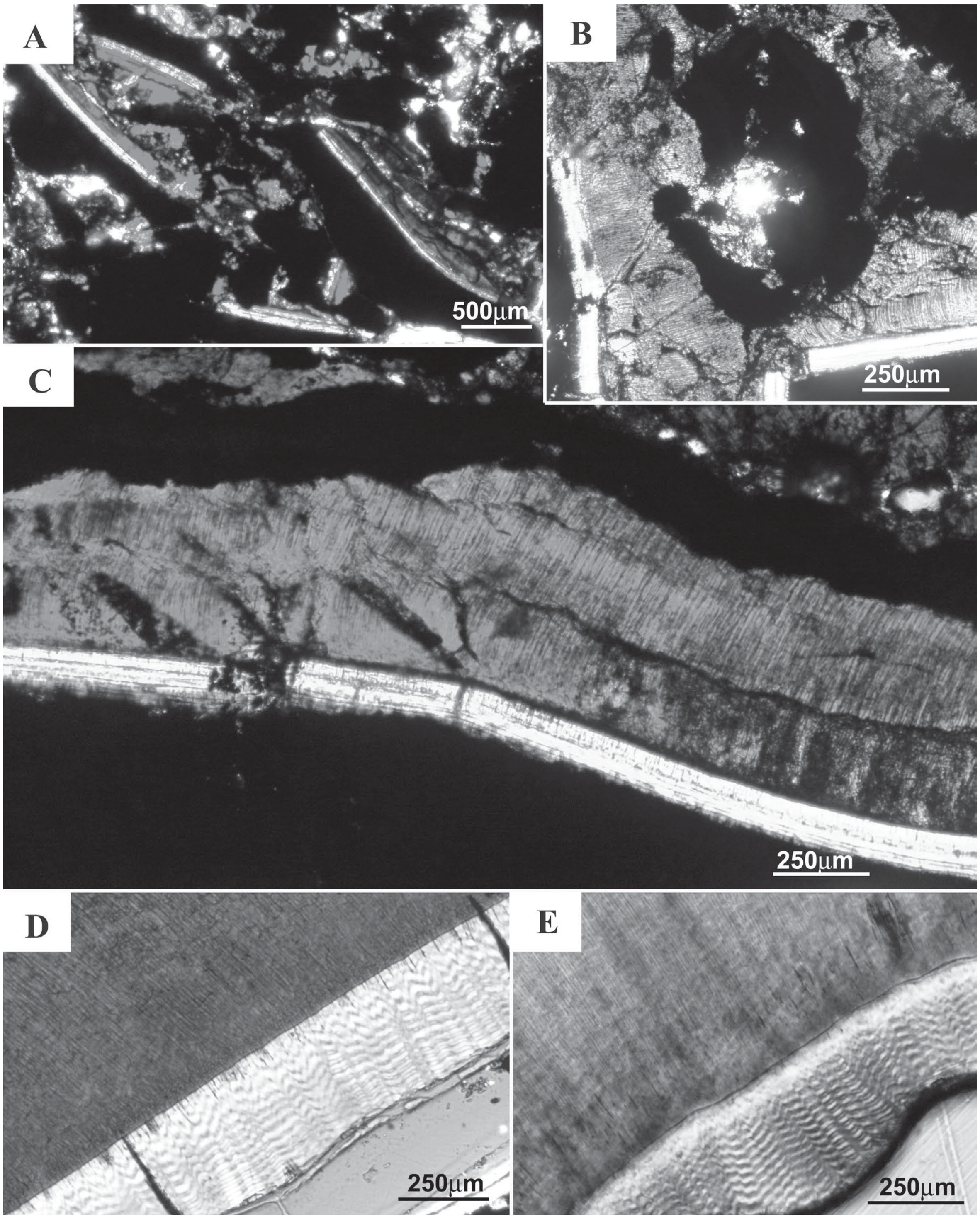
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Histological Assessment of Vertebrate Remains in the 2003 Bernissart Drill

12

Armand de Ricqlès*, Pascal Godefroit, and Johan Yans

After the 2003 drilling in the Iguanodon Sinkhole at Bernissart (BER 3 borehole), examination of the column revealed stony dark grayish remains at levels −296.5 m and −309 m, and hence within the Wealden clays levels. Microscopic examinations of the remains (paleohistology) conclusively demonstrate the occurrence of bone and tooth tissues. Whether the histological characteristics of the tissues allow a precise identification, especially whether the remains belong to *Iguanodon*, is quite another matter. The small teeth material clearly does not belong to ornithopod dinosaurs; however, their precise taxonomic origin cannot be assessed. However, the bony material shows structures compatible with a dinosaurian origin. A survey of the literature devoted to *Iguanodon* bone and tooth histology, as well as comparisons with *Iguanodon bernissartensis* bone and tooth material and with *Bactrosaurus johnsoni* teeth, do not demonstrate that the material definitely belongs to *Iguanodon*, although the possibility is likely for several reasons, detailed herewith. Comparison between "fresh" (from the borehole) and "old" (kept in the RBINS for more than 130 years under ordinary conditions) *Iguanodon* bones also allows checking the degradation process experienced by pyritized bones at the tissue level.

12.1. A, BER 296.5, section 1, general view of the apical region (tip) of two small teeth, plus tooth fragment. B, BER 296.5, section 3, detail of possibly the proximal region of a small tooth crown (broken). Irregular large, rounded bays in the dentine may be evidence of biological dentinoclasy linked to tooth replacement. C, BER 296.5, section 3, detail of dentine and enamel along a tooth crown. The thin, highly birefringent enamel is nonprismatic and appears to be divided in four to five superimposed sheets; the numerous dentine canaliculi are obvious. D, *Iguanodon bernissartensis* from Bernissart (RBINS unregistered specimen "H"), detail of the enamel–dentine junction (EDJ) in a maxillary tooth. The thick enamel shows extensive superimposed zigzagging bright and dark bands, typical of advanced ornithopod enamel; the thickness of the dentine toward the pulp cavity would extend upward over the full height of the plate. E, *Bactrosaurus johnsoni* maxillary tooth; detail of the EDJ for comparison. Superposition of the bandings in the enamel suggests the fake occurrence of juxtaposed vertical pillars forming the tissue.

Introduction

In 2002–2003, three new boreholes were drilled within and around the Iguanodon Sinkhole at Bernissart. They provided exceptional material used for a multidisciplinary research to improve our knowledge of the *Iguanodon*-bearing Wealden facies (see Chapter 1 in this book). Detailed examination of the BER 3 column revealed stony dark grayish remains at levels −296.5 m and −309 m, and hence within the Wealden clays levels. The likeliness that those remains could be vertebrate skeletal fragments was high because of their phosphatic nature and because the borehole was drilled at the presumed site where the Bernissart iguanodons were discovered in 1878. Microscopic examinations of these fragments (paleohistology) conclusively demonstrate that these fragments are actually bone and tooth remains. Here, we describe the histology of the skeletal fragments discovered in the BER 3 borehole. Histological comparisons are attempted with data compiled from the literature and also with bone and teeth fragments taken from *Iguanodon bernissartensis* and *Bactrosaurus johnsoni* specimens. The "fresh" material from the borehole is also compared with "old" bones discovered at Bernissart between 1878 and 1881 in order to check at the tissue level the degradation process experienced by pyritized bone.

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

Material and Methods

Four fragments of a few cubic centimeters each were carefully extracted from the BER 3 column for examination by histological technics. The fragments, numbered Bernissart 3 296.5, Bernissart 3 309 A, Bernissart 3 309 B, and Bernissart 3 309 C, were dried and embedded in resin under gentle vacuum, with the resin temperature monitored to secure a slow polymerization. The resulting blocks were trimmed and sawed with a thin diamond/copper circular blade and further processed to obtain thin sections following routine paleohistological techniques (e.g., Wilson, 1994).

For comparative purposes, a fragment of rib and one maxillary tooth from *Iguanodon bernissartensis* (RBINS unregistered specimen "H"; see Norman, 1986, appendix 1), and maxillary and dentary teeth from *Bactrosaurus johnsoni*, a basal hadrosaurid from the Iren Dabasu Formation in Inner Mongolia (P.R. China), were also histologically processed. The resulting thin sections were examined under dissecting and compound microscopes, in ordinary and polarized lights. Some preliminary analyses by x-ray diffraction and scanning electron microscopy were also conducted to check differences between fresh material from the borehole and the old bones discovered at Bernissart between 1878 and 1881.

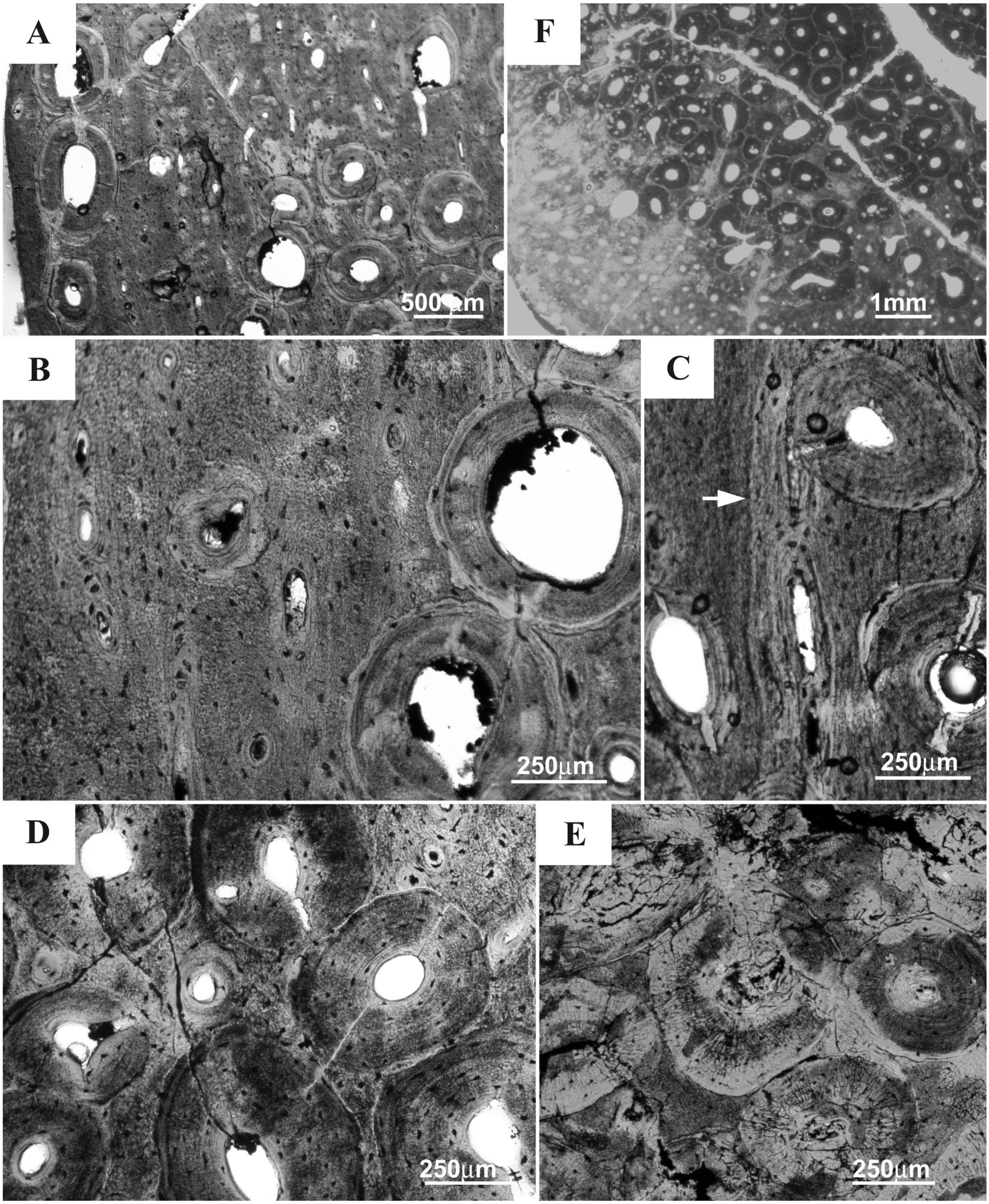
Histological Description

The Bernissart 3 296.5 specimen. All the sections show compact bone fragments around a small cavity filled with a black material containing some tooth remains. The bone fragments have a complex structure of compacted secondary endosteal trabeculae and Haversian systems. The absence of Sharpey fibers indicates that the observed bone tissues are not of periosteal or dermal origin. The bone tissue is entirely secondary (reconstructed in vivo) and varies from region to region. Typical mature secondary osteons (Haversian systems) are locally superimposed on each other (Fig. 12.2E). Other structures suggest large secondary endosteal trabeculae collapsed on each other.

The tooth remains (Fig. 12.1A–C) suggest numerous thin elongate small teeth. The crown may have been cylindrical with a pointed arch-shaped apex ending in a rather acute tip (Fig. 12.1A). The enamel is thin, highly anisotropic under crossed Nicols, and nonprismatic. It is divided into four to five superimposed sheets (Fig. 12.1C). The dentine shows the traditional radially oriented canaliculi and some evidence of a clastic activity locally, perhaps linked to tooth replacement (Fig. 12.1B). No root system or ankylosis on dentigerous bone could be observed.

The Bernissart 3 309A, B, C specimens. These specimens show a more or less dense Haversian bone tissue intimately associated with massive pyrite deposition. Some regions apparently preserve the natural free surface of the bone (Fig. 12.2A), and it is possible to observe there some primary (periosteal) bone tissue, more or less invaded by secondary osteons (Haversian systems) (Fig. 12.2B). The secondary osteons are numerous, forming a dense Haversian bone with superposition of osteon generations. It is nevertheless still possible to observe remains of primary (periosteal) bone tissues forming some of the interstitial systems between the secondary osteons (Fig. 12.2D). The primary bone tissue appears to be a poorly defined modulation of the fibrolamellar complex, where small longitudinal primary osteons are the prevailing vascular component (Fig. 12.2A–D). The circular and especially

12.2. A, BER 309 C, section 3, low-power view of a subperiosteal surface in cross section; scattered Haversian reconstruction into the primary cortex; some large, unfinished secondary osteons almost reach the bone surface, which does not show an external fundamental system (EFS). B, BER 309 C, section 3, detail of the primary bone tissue forming the superficial cortex. A few poorly developed small primary osteons oriented longitudinally permeate the tissue. C, BER 309 B, section 1, detail of the primary cortex with a LAG (=line of arrested growth; arrow) parallel to the bone-free surface. D, BER 309 C, section 1. The deep cortex is formed by large secondary osteons (=Haversian systems) with extensive evidence of periosteal bone tissue still forming the interstitial systems between them. E, BER 296.5, section 3; detail of dense Haversian bone in superimposed generations. F, Rib of IRSNB unregistered specimen "H," section 4; general view of the cortex at low magnification. After more than a century of pyrite degradation, the whole structure is fragmented by multiple larger, smaller, and minute cracks. The numerous whitish spots (in the secondary osteons) are artifacts caused by the resin monomer having differentially permeated the tissue along the minute cracks before polymerization.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radial vascular canals are almost lacking. There is some evidence of lines of arrested growth (LAGs) parallel to the free surface of the bone (Fig. 12.2C).

Iguanodon Bone and Tooth Histology: A Bibliographical Survey

Iguanodon Mantell, 1825, appears to be one of the first dinosaurs submitted to histological analyses. In Queckett's catalog (1855), one can easily recognize dense Haversian tissue as depicting *Iguanodon's* compact bone structure. The rediscovery of old thin sections of fossil bone created in the 1870s at the request of Professor Paul Gervais at the Paris Museum was recently published (Ricqlès et al., 2009b). It unveils previously unknown early thin sections from *Iguanodon.* Some of the thin sections were made in England, while others appear to have been processed in Paris. The material predates (1875–1876) the Bernissart discovery (1878) and would thus come from England, although its precise origin is unknown. One section (made in England) depicts coarse cancellous bone of secondary origin, and the two others show primary bone of the laminar type, with little Haversian reconstruction. The structures of the latter sections (Ricqlès et al., 2009b, fig. 2C) of compact bone suggest an immature, actively growing individual.

Most later histological descriptions of *Iguanodon* are based on the Bernissart material. Seitz (1907) meticulously described (1907, 325–330) and figured (1907, pl. 10, fig 58; pl. 11, figs. 59–61) the bone structures of *Iguanodon* from a left femur. To summarize his findings in modern terms, he observed (1907, fig. 58) a primary bone cortex formed by a fibrolamellar complex dominated by longitudinal primary osteons, with evidence of growth cycles and of rather discrete, scattered reconstruction by secondary osteons of larger diameters than the primary osteons. At higher magnification (1907, fig. 59) the bone tissue shows a good structural preservation, with a precise morphology of the bone cells lacunae and of their canaliculi. The primary bone tissue is permeated by numerous longitudinal primary osteons and shows evidence of lines of arrested growth, and perhaps also of Sharpey fibers locally. The larger, well-finished secondary osteons interrupt the primary structures and clearly show the reversion line at their periphery. Another region (1907, fig. 60) experienced a more intensive process of bone substitution, as evidenced by the higher density of secondary osteons and their partial superposition. A very peculiar image at high magnification (1907, fig. 61) is provided by Seitz, showing a vascular canal cut longitudinally and filled up by what is tentatively interpreted as mass of blood cells (*blutkörperchen*). His discussion of this observation (1907, 329–330) interestingly predates the current findings and discussions (e.g., Martill and Unwin, 1997; Schweitzer and Horner, 1999; Schweitzer et al., 2005) on pyrite framboids versus original organic remains in fossil bones.

Nopcsa and Heidsieck (1933) and Gross (1934) both used *Iguanodon* in their paleohistological studies. The first one mostly dealt with the histological differences likely to be observed following the ontogeny of ornithopods, suggesting that several recognized ornithopod taxa were merely ontogenetic growth stages, a situation further analyzed by more recent researches (Chinsamy, 1995; Horner et al., 2000, 2009; Knoll et al., 2010). Gross (1934) described dinosaur bone tissues following the then-recent understanding of bone fibrillar organization brought by, for example, Weidenreich (1930), noting important distinctions among types of primary bone tissues and dense Haversian bone among dinosaurs. Regarding *Iguanodon*, Gross referred to Seitz's material and described (1934, 759, fig. 21) dense Haversian tissue in polarized light, noticing that the lamellar organization of the secondary osteons is identical to the situation observed in mammals and that the two groups cannot be distinguished on this basis. Enlow and Brown's (1957, 203) descriptions of ornithischian dinosaur bone derived in part from Seitz (1907) and Gross (1934). Indeed, *Iguanodon* tissues in Seitz (1907, pl. 10, fig. 58, and pl. 11, fig. 60) appear in Enlow and Brown (1957, respectively pl. 23, fig. 4, and pl. 22, fig. 9). Among his important studies of dinosaur bone tissues, Reid (1985) described primary bone in an *Iguanodon* femur (1985, plate 1, figs. 5 and 6). The tissue appears as the familiar modulation of the fibrolamellar complex described as laminar, with the characteristic development of superimposed rows of circular vascular canals uniting the longitudinal primary osteons. However, as noted by Reid, the structural differences between the fibrous (woven) and lamellar (osteonal) components of the complex are almost indistinguishable under ordinary light (1985, fig. 5), but become obvious only under crossed Nicols (1985, fig. 6). Interestingly, this tissue closely resembles the one forming the thin sections of *Iguanodon* processed at the request of Professor Paul Gervais in about 1875 (see above). From another point of view, Reid (1984, 1997) also used *Iguanodon* to analyze and illustrate the growth dynamics in the length of the long bones in the epiphyses of dinosaurs.

More recently, focus has turned toward the detection of proteins and other organic components in *Iguanodon* bones. Embery et al. (2000) reported extraction of noncollagenous proteins from a rib cortex with a dense Haversian structure. The bone comes from the collections of the British Natural History Museum in London, and hence its origin is presumably from the United Kingdom and not from Bernissart. Later works on the same material (Embery et al., 2003) provided evidence for the partial preservation of biomolecules from both the compact and the cancellous bone tissues. A glycoprotein akin to osteocalcin, phosphoproteins, and mucopolysaccharides was recovered, all fractions of the extracellular bone matrices whose high interactions with the phosphatic mineral phases may be linked to their amazing preservation potential.

The tooth histology of *Iguanodon* and other advanced ornithopods is peculiar and diagnostic. As observed in thin sections in *Iguanodon*, *Rhabdodon*, and various more advanced ornithopods including *Bactrosaurus* and neonate, juvenile, and adult *Maiasaura* (pers. obs.), the enamel has a characteristic structure, autapomorphic for the group. The highly anisotropic enamel shows zigzag structures, from the enamel–dentine junction to almost its outer free surface (Fig. 12.1D,E). The zigzags are superposed in an ordered way, causing the subjective appearance of vertical pillars set side by side. Analysis by scanning electron microscopy allows us to interpret this enamel as a "coarse wavy enamel" for most of the enamel thickness and as a "fine wavy enamel" forming a very thin layer at the surface (Sander, 1999, pl. 15, figs. 1–3), according to this Sander's terminology. The appearance under crossed Nicols probably derives from what Sander describes as the "staggered" or "whorled" arrangement of the enamel crystallites.

The dentine is a thick, regular orthodentine, showing very numerous faint growth cycles parallel to the enamel–dentine junction. The dentine canaliculi are long and gently curling toward the pulp cavity (Fig. 12.1D,E). Irregularities in the shape of the enamel–dentine junction and/or local differences in dentine centripetal growth create a complex situation at the level of the front where the dentine reaches the pulp cavity. There, the dentine does not completely fill up various extensions of the pulp cavity. In this way, many elongate canals are formed, and the dentine can be described as a vasodentine in the circumpulpar region.

Discussion

The bone tissues observed at level −309 m in the Bernissart borehole closely resemble previous descriptions of adult dinosaurian bone tissues (dense Haversian bone) in general, and particularly of *Iguanodon.* Direct comparison with a small Bernissart *Iguanodon* rib (RBINS, unregistered specimen “H,” diameter 12×20 mm; Fig. 2F) even suggests that the material collected at −309 m might pertain to an early adult animal because of the low number of superposed generations of secondary osteons, leaving some primary tissues between them; and the incomplete Haversian replacement in the superficial region, leaving a region of primary bone of periosteal origin (Fig. 12.2A–D). The occurrence of LAGs in this primary bone (Fig. 12.2C) and its poor vascularity suggest that this individual was close to the adult condition, although a clear external fundamental system was not observed. What can be observed in bone fragments from level −296.5 m concurs with the ones from −309 m. In both cases, dense Haversian tissues are observed, with a moderate amount of substitution cycles among the secondary osteons (Fig. 12.2E). Lack of radial cracks at the periphery of the secondary osteons is not characteristic for an early aquatic taphonomic episode (Pfretzschner, 2000).

The primary periosteal bone does not show all the tissue variability already observed in *Iguanodon.* The primary bone tissue appears moderately vascularized by longitudinally oriented primary osteons, with a grossly pseudolamellar organization and some evidence of LAGs (Fig. 12.2C). There is no evidence of the laminar pattern of the fibrolamellar complex, as described by, for example, Reid (1985), suggesting active growth (perhaps among grossly immature individuals), nor of an external fundamental system suggesting a mature adult condition with almost no further growth (e.g., Horner et al., 2009). Instead, a moderately active radial growth with some cyclicity seems indicated, again suggesting an almost mature or subadult condition.

The teeth observed at level −296.5 m (Fig. 12.1A–C) clearly differ in size and structure from the ones of *Iguanodon* and other Iguanodontia (e.g., *Bactrosaurus johnsoni*, Fig. 12.1D,E). Their small size, slenderness, and thin enamel do not fit with crushing functions. Histological comparisons with teeth of the Bernissart actinopterygians (15 species), urodeles (*Hylaeobatrachus*), and crocodiles (*Goniopholis*, *Bernissartia*) have not been attempted. The very small size probably exclude a crocodilian origin (apart from tiny neonates or juveniles); the lack of a bicuspidate apex and a pedicellate structure does not support a lissamphibian origin, and both size and statistics would favor an actinopterygian origin, although no teeth structures peculiar to them (acrodine, etc.) could be observed. Unfortunately, the lack of information on the mode of ankylosis of the teeth and on the occurrence of a root precludes further diagnosis. There is also no clear evidence of actual (anatomical) relationships with the surrounding bone fragments.

The tooth structure of *Iguanodon* does not show significant histological differences with those of *Bactrosaurus* (Fig. 12.1D,E). In both cases, the thick enamel is highly structured, and as explained by Sander (1999, 74), this enamel structure may indeed be regarded as a diagnostic feature or autapomorphy for advanced ornithopods (iguanodontids and hadrosaurids).

Comparisons between fresh (from the borehole) and old (from the RBINS) bony material are interesting because they clearly reflect at the histological level the physicochemical changes induced in the fossils by the oxidation of pyrite under standard museum conditions (Ricqlès and Yans, 2003; see also Chapter 11 in this book). RBINS unregistered specimen "H" (rib) was extracted during the 1878–1881 period and probably received preparation standard at that time (Godefroit, 2009) before thereafter being kept in a wood drawer under standard museum conditions of temperature and humidity. Histological observations compared to the fresh specimen show an advanced process of fragmentation of the museum material at both organ and tissue levels (Fig. 12.2E). The intimate tissue structure is hardly changed, if at all, but the ground color of the tissue has changed (with localized whitish spots), perhaps indicting chemical changes (see Chapter 11 in this book), and above all, the tissue shows multiple cracks that weaken its structure. They are well underlined by the embedding plastic medium; under gentle vacuum, the fluid plastic monomer percolated into the bone, following the multiple cracks, and ultimately permeated the bone before hardening by polymerization. Without this process, it would have been impossible to obtain thin sections from the material.

Preliminary chemical analyzes by x-ray diffraction show a spectacular decrease of the pyrite spikes in the museum-kept specimen, compared to the fresh specimens taken from the borehole. This is in agreement with the more detailed analytical results of Leduc (Chapter 11 in this book).

Concluding Remarks

This histological description of the fragments from BER 3 borehole definitely brings evidence of the occurrence of bone and tooth materials at the −296.5 m and −309 m levels. The tooth material definitely does not belong to *Iguanodon;* its most likely origin is from one of the 15 species from seven actinopterygian (bony fishes) orders described from Bernissart (Godefroit, 2009, 131). It is likely that histological comparisons with the teeth of the actinopterygian taxa known from Bernissart will allow precise determination.

What agrees with a dinosaurian origin for the bone fragments at the −309 m level are the general structure suggesting an origin from large- to very large-size bones; the prevalence of dense Haversian bone tissue, known to be common among large mature dinosaurs; and the occurrence of primary bone tissues with primary osteons also known from the external cortex of submature dinosaurian bones.

The bone tissue structures observed from the borehole match reasonably well with the ones already described for *Iguanodon*, but for all that, no diagnostic structures (as would have been the case for teeth) remain to compel us to ascribe the finds to this taxon. We are left only with the statistical likelihood argument to consider that we are dealing with *Iguanodon*—a tentative conclusion that is neither disproved or enforced by any available data.

Whatever it may be, the lucky occurrence of bone and tooth material at two superposed levels in a small-diameter drill again emphasize the fossil abundance and value of the Wealden sediments within the Iguanodon Sinkhole.

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