이학석사 학위논문

Bone histological study on *Koreaceratops hwaseongensis* and two other dinosaurs in Korea

한국의 코리아케라톱스 화성엔시스와 두 종류 공룡에 대한 뼈조직학 연구

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이 논문을 이학석사 학위논문으로 제출함

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박성준의 석사 학위논문을 인준함

2021년 8월

위 원 장____________________

부 위원장____________________

위 원____________________

ABSTRACT

The surge of dinosaur findings in the Republic of Korea during the last three decades has boosted Korean dinosaurs' public interest. However, the fragmentary and incomplete nature of the Korean dinosaur fossils prevents us from obtaining many academic data from such discoveries. We tried to remedy this problem by observing not the outer morphology but the inner microstructures of the Cretaceous dinosaur fossils via thin section histology. We sampled the tibia and fibula of *Koreaceratops hwaseongensis* with two unidentified theropod and sauropod dorsal ribs in hopes of uncovering their phylogeny, environment, and mechanics. Our research showed that all of the bones exhibit poor histological preservation due to microbial degradation. The microscopical tunnels made by invading microorganisms had rendered the bones into an amalgam of globules and foci. Consequently, almost all of the histologic features like lacunae, canaliculi, and lamellar in the bone cortex had been erased. However, a few remaining traces of histological features like the vasculature and growth marks enabled us to determine that the growth pattern of *Koreaceratops hwaseongensis* is very similar to that of *Protoceratops andrewsi*. Both species exhibit zonation with a bit of bone remodeling in their tibiae and lines of arrested growth with an extensive bone remodeling in their fibulae. We also noticed that the only histological similarity between *Koreaceratops hwaseongensis* and the more basal ceratopsians *Psittacosaurus mongoliensis* and *P. lujiatunensis* is the longitudinal and reticular vasculature in their fibulae. These suggest that *Koreaceratops* is much closer to *Protoceratops* than *Psittacosaurus* in terms of phylogeny. The fibula of *Koreaceratops hwaseongensis* showed a constant osseous drift that initially drifted toward the medial axis but abruptly changed to the anterior axis in the final growth interval. The right tibia's final growth exhibiting an anteromedial osseous drift also suggests that the *Koreaceratops hwaseongensis* experienced a change in its right hind-limb's biomechanics before death. The number of growth zone transitions in its tibia suggests that the *Koreaceratops* individual was approximately eight years old at its death. The absence of an external fundamental system or decreasing vascularity in the outer cortex indicates the individual was not close to physical or sexual maturity. The predominatly longitudinal vasculature of *Koreaceratops hwaseongensis* long bones suggests it experienced a moderate growth tempo like other primitive ceratopsians. The two other dinosaur ribs did not reveal much histological information due to intense bone remodeling and heavy microbial erosion. It implies that these bones were buried in a semi-arid climate regime favorable for microbial bone decomposition, thus suggesting that the Korean peninsula during the Cretaceous had this semi-arid climate. The heavily remodeled cortex of a sauropod dorsal rib suggests that, at least for sauropods, the proximal section of an anterior dorsal rib may not always be a reliable alternative to long bone histology.

Keywords: *Koreaceratops*, Ceratopsia, Histology, Bone histology, Early Cretaceous, Korea
Student Number: 2018-20080

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CHAPTER 1

INTRODUCTION

1.1. Study Background

For the last 100 years, many fossilized vertebrate bones that originate from the Cretaceous period to the middle Miocene epoch have been unearthed in South Korea (Choi and Lee, 2017). The rate of discovery of these fossils has drastically increased relatively recently, for most of their discoveries have been reported during the last three decades. The notable vertebrate species found in South Korea are predominantly from the Cretaceous period, which include a couple of endemic species like a freshwater fish *Jinjuichthys cheongi* (Kim et al., 2014), an anguimorph lizard *Asprosaurus bibongriensis* (Park et al., 2015), a crocodyliform *Hadongsuchus acerdentis* (Lee, 2005), a basal ornithopod *Koreanosaurus boseongensis* (Huh et al., 2011), and a basal neoceratopsian *Koreaceratops hwaseongensis* (Lee et al., 2011).

Despite the recent explosive increase of the discoveries and interests in vertebrate fossils of Korea, the overall quantity and quality of information extracted from the excavated specimens are severely limited. It is because most of the vertebrate bones that have been found are incomplete and fragmentary except for some fish fossils (Choi and Lee, 2017). Although *Koreaceratops hwaseongensis* was preserved only with the lower body, it is worth noting that it is the first articulated dinosaur skeleton ever found in Korea (Lee et al., 2011). *Koreanosaurus boseongensis* is missing its head, three limbs, tail, and pubic bones, not to mention that its surviving bones are only partially preserved (Huh et al., 2011). The crocodyliform *Hadongsuchus acerdentis* only has its skull preserved (Lee, 2005). The anguimorph lizard

Asprosaurus bibongriensis only has one-third of its skull along with a partial upper limb preserved (Park et al., 2015). It becomes impossible to approximate their lifestyle, locomotion, age, and growth pattern in such situations.

In many cases, the only information that can be obtained from such paltry sum of bones is often limited to what clade the specimen belongs to (e.g., theropod, sauropod, ornithopod, etc.), and, in lucky cases, a new species name can be christened if the bones do not match any known vertebrates of the same clade. In a nutshell, the traditional paleontological study of simply observing the external morphology on such poorly preserved vertebrate fossils hardly yields much information. That is the current situation of Korean vertebrate paleontology; although the vertebrate fossil discoveries are rising rapidly, it is not easy to get significant research results beyond the taxonomy.

This problem becomes apparent with discovering a basal neoceratopsian dinosaur, *Koreaceratops hwaseongensis,* in 2008 (Lee et al., 2011). The specimen was collected from the Tando Beds (Albian) of the Cretaceous Tando Basin, Hwaseong City, Gyeonggi Province, South Korea. It is of particular importance to Asian basal ceratopsians of the Albian age due to its limited basal ceratopsian fossil record. However, it was rather disappointing that the specimen was discovered only with the lower body, such as a series of caudal vertebrae, ischia, tibiae, fibulae, and feet. Therefore, the amount of information acquired from the *Koreaceratops hwaseongensis* was quite limited without the upper body and skull. The somewhat well-preserved tail provided some ideas on its potential lifestyle: its unusually long neural spines in the caudal vertebrae were suggested for the ability of swimming, which was advocated by Brown et al. (1940) but rejected by Bailey (1997). The absence of forelimbs and the partial preservation of the hind limbs in the *Koreaceratops* make it challenging to determine whether it was a bipedal or quadrupedal animal. It is best predicted to be a bipedal animal considering its phylogenic position (Lee et al., 2011). Apart from these speculations, we do not have much clue on *Koreaceratops*' lifestyle and growth pattern.

If the external morphology cannot provide much information, the alternative is to see what is inside, specifically, the internal microstructures. That is where the study of bone histology comes to play. The study of bone microstructures can reveal four primary types of information about a specimen: ontogeny, phylogeny, mechanics, and environment (Horner et al., 1999, 2000; de Ricqlès et al., 2001; Padian et al., 2001). A growing bone can keep a record of this information in its microstructures and textural patterns, ready to be studied by the field of bone histology.

In fact, there have been histological studies in Korean vertebrate fossils before, such as the transmission electron microscope study in the correlation between the preserved microstructure and nanostructure of the *Koreanosaurus boseongensis* femur bone (Kim et al., 2017). Another one is the taphonomic and paleoenvironmental study based on thin sectioned dinosaur bone fragments found in the Lower Cretaceous Hasandong Formation of the Gyeongsang Supergroup, South Korea (Paik et al., 2001). However, neither of these papers technically deal with the 'four signals' (ontogeny, phylogeny, mechanics, and environment) of bone histology.

1.2. Purpose of Research

In this project, the paleo-histology was used on some dinosaur bone fossils found in Korea to expand the academic database in Korean vertebrate paleontology. Unlike the previous thin section histology studies on Korean fossils, the histology technique was applied to uncover and interpret the fossil's phylogeny, mechanics, and environment by examining its microstructures.

In addition to *Koreaceratops*, the histological thin section studies were conducted upon other dinosaur bones found in South Korea and compare them to *Koreaceratops*. Doing so might allow us to gain more insight into the life histories of the Korean dinosaurs and observe the pattern of diagenesis in Korean fossils. For this purpose, two isolated and fragmented dorsal ribs of an unidentified theropod and a sauropod found in South Korea were used.

CHAPTER 2

MATERIALS AND METHOD

2.1. Specimen Acquisition

The specimen of the *Koreaceratops hwaseongensis* (Fig. 1) and the dorsal rib of an unidentified theropod (Fig. 2) were provided by Prof. Young-Nam Lee of the Paleontological Lab, Seoul National University. *Koreaceratops* was found in 2008 at Tando beds (Albian) of the Tando Basin, Hwaseong City, Gyeonggi Province, South Korea (Lee et al., 2011). The bone samples were acquired from the fractured ends of its right tibial and fibular shafts (Fig. 1). The unidentified theropod dorsal rib was excavated from the Lower Cretaceous Sihwa Formation (Albian) in 2002 at Gojeong-ri dinosaur egg site (National Monument 414), Hwaseong City (Lee, 2008). The sampling for the thin section was made in its proximal part (Fig. 2). The sauropod dorsal rib (Fig. 3) was collected from the Lower Cretaceous Hasandong Formation (Aptian) of Yuljin-ri, Yulgok-myeon, Hapcheon County, Gyeongsangnam-do, South Korea, by the honorary professor Haang-Mook Kim of Pusan National University (Kim, 1983). Its proximal part was cut for the thin section.

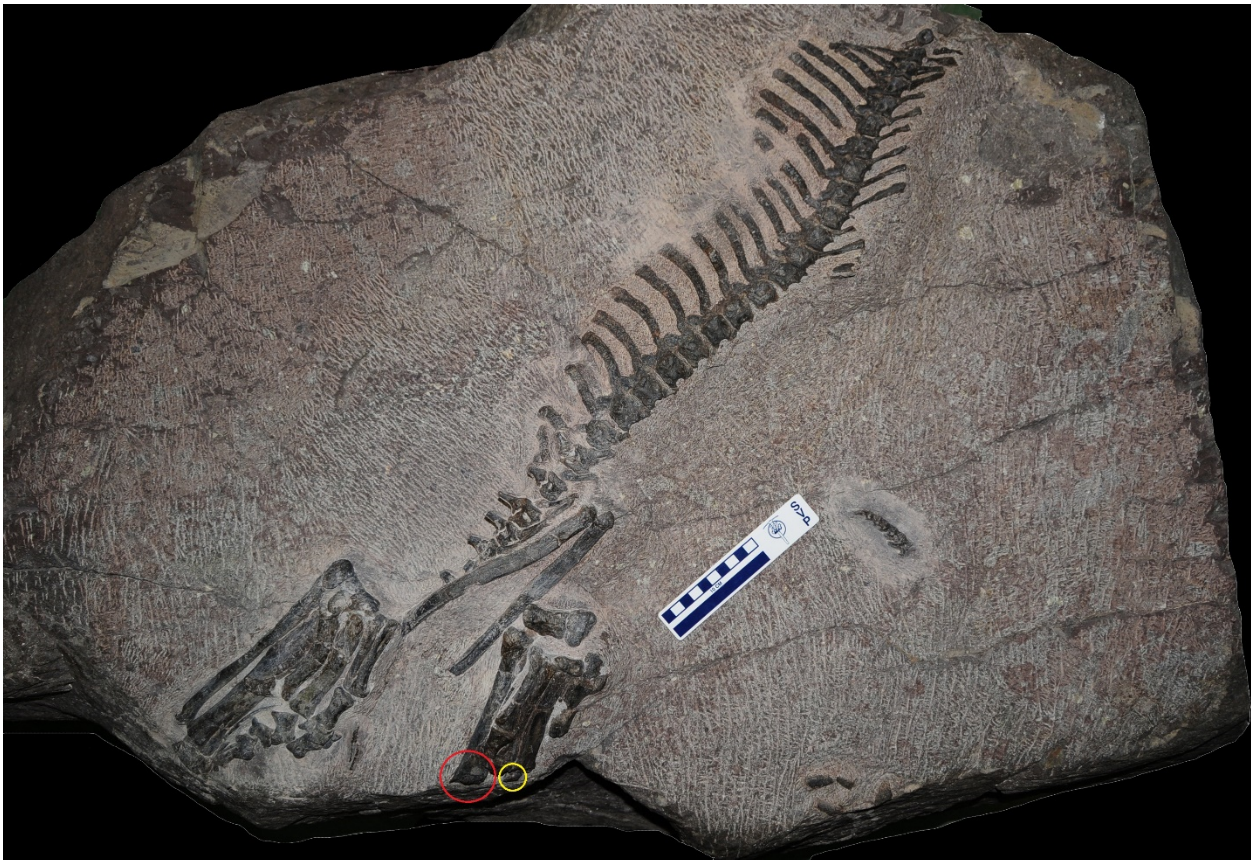

Figure 1.

The holotype of the *Koreaceratops hwaseongensis* found from the Cretaceous Tando Beds, Republic of Korea. The circles mark the portion of the bones cut out by using a portable automatic saw and processed into thin histological sections. The red circle marks the right tibia, while the yellow circle highlights the right fibula.

Figure 2.

An unidentified theropod dorsal rib found in the Cretaceous Gojeong-ri dinosaur egg site, Republic of Korea. The proximal portion of the rib was so poorly preserved that the mid-shaft had to be sampled instead. The red circle marks the portion of the bone that was cut and made into thin section slides.

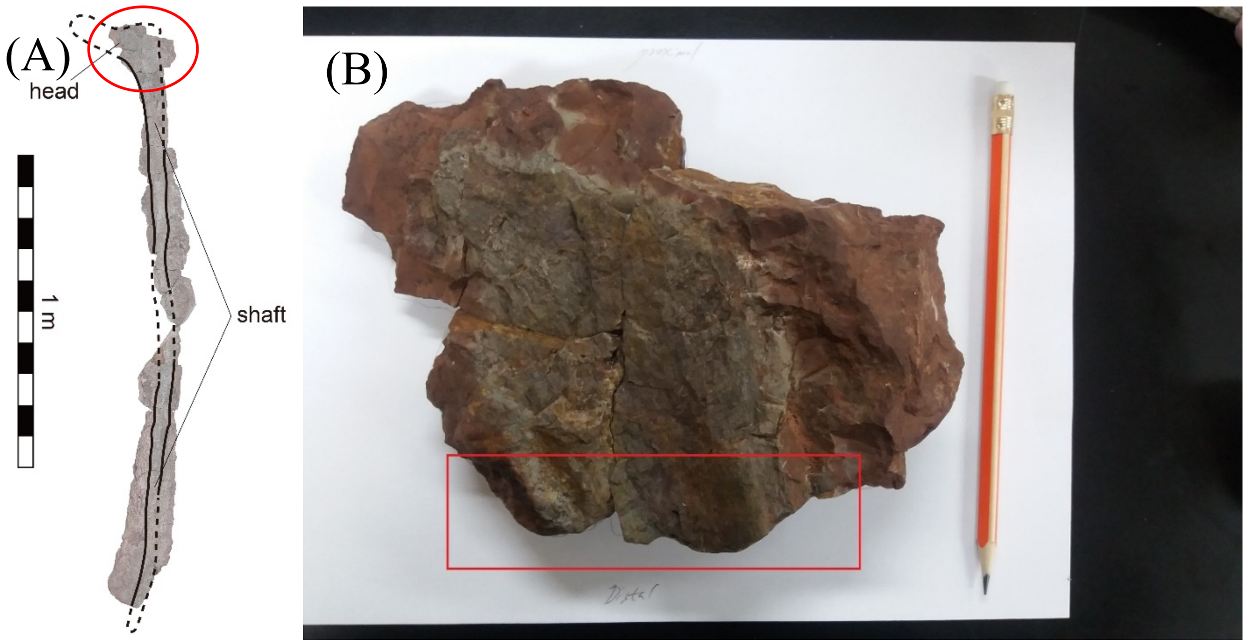

Figure 3.

(A) The whole dorsal rib of the unidentified sauropod discovered in the Hasandong Formation, Republic of Korea. The red circle marks the proximal portion, which was used for this study. (B) The most proximal portion of the unidentified sauropod dorsal rib was used for this study. The red box marks the portion of the bone that was cut.

2.2. Thin Sectioning

The thin sectioning procedures for this study were based on instructions written on the book "Bone Histology of Fossil Tetrapods" edited by Kevin Padian and Ellen-Thérèse Lamm (2013). Thin sections were produced using supplies and tools in the Sedimentary Geology Lab and Paleontological Lab in the School of Earth and Environmental Sciences, Seoul National University. However, just in case of a catastrophic production failure of thin sections, some bone samples were sent to GemTec (a commercial company, Korea) and thin sectioned there.

First, the bones of interest were photographed, and their dimensions were measured before sectioning. Then, small portions marked on the *Koreaceratops* right tibia and fibula were cut out using an automatic saw (Fig. 1). The same cutting procedures were applied to the marked areas of the two ribs (Figs. 2, 3).

Next, each sliced bone section was separately placed inside an empty container and filled with a mixture of liquid epoxy resin and its hardener solution. Then, the containers were placed inside a vacuum chamber and thoroughly vacuumed until all air bubbles are extracted. Once the resins had been fully hardened with fossil samples firmly entombed inside, the resin blocks were removed from their respective containers and sliced by an automatic saw. The resin blocks were cut along their longitudinal and transverse axis in a thickness of 1 cm. These were then individually glued onto a glass slide via a clear epoxy glue. Once the epoxy glue had fully hardened, the bone specimens on the glass slides were ground and polished until they were about tens of micrometers thick. The finished slides were observed, photographed, and interpreted via microscopes.

2.3. Method of Analysis

2.3.1. Analysis of the specimen's age and maturity

The vertebrate animal's age at death can be recorded in its bones in the form of growth marks. These marks can either be cyclical or non-cyclical. Cyclical growth marks represent annual growth, and studies have shown that all vertebrates exhibit this annual growth marking in their bones in one way or another (Castanet et al., 1993). The cyclic growth marks are easily distinguished from non-cyclical growth marks because the former exhibit regular patterns and encircle the entire bone cortex (Padian et al., 2013). Non-cyclical growth marks are typically formed as a response to a specific event experienced by vertebrate animals. They do not show regular patterns and are confined to a portion of the cortex.

The easiest recognizable form of cyclical growth is the lines of arrested growth (aka. LAGs), which record a complete halting of bone growth in the form of a thin, dark line in the bone cortex (Padian et al., 2013). Another form of cyclical growth is called the annulus, a thin layer of bone growth comprised of slowly grown bone texture. The third form of cyclical growth mark is called the zonation, which are zones of the cortex that experienced accelerated or decelerated growth.

The spacing of these growth marks can potentially tell if the specimen had reached a somatic or sexual maturity before death. It is known that the spacing between the growth marks changes from wide to narrow as the specimen approaches maturity (Padian et al., 2013). Some vertebrates who reach their maximum size may display what is called the external fundamental system (Cormack, 1987), which are closely packed annuli that are devoid of vasculature and bone cells in the outermost bone cortex.

2.3.2 Analysis of bone cortical texture and vasculature

Apart from growth rings, the texture and vasculature of a bone can tell us about the animal's growth pattern. Bone textures can come in patterns like lamellar, woven, parallel, fibro-lamellar, and Haversian systems (Padian et al., 2013). Bone vasculature can be found in the laminar, plexiform, longitudinal, reticular, and radial forms when the bone is cut transversely.

Lamellar bone textures are characterized by a plywood-like structure and are the slowest growing pattern. In contrast, the woven bone is noted by its disorganized structure that reflects its most rapid growth among bone types. Parallel bones are similar to lamellar bones in that both exhibit closely packed bone fibers and grow slowly. However, unlike lamellar, parallel bones do not form plywood-like structures. The fibro-lamellar bone is "broadly defined here as a bone complex composed of a woven-fibered scaffolding and intervening primary osteons of varying orientations" (Padian and Lamm, 2013, p. 520). Fibro-lamellar bone is known as a bone type that grows fast and yet remains structurally strong. The Haversian system results from bone remodeling that forms as bones adjacent to a vascular canal are removed and replaced by numerous layers of lamellae deposited concentrically around the vascular canal. These newly made circular lamellar bones are called secondary osteons and are easily distinguished by the cement lines that delineate and highlight their existence. A bone texture pattern composed of these secondary osteons is called the Haversian system.

Longitudinal vasculature is seen as little circles in a transverse cut of a bone since it is basically a straight tube running in a longitudinal direction (Padian et al., 2013). Laminar vasculature is seen as canals orientated parallel to the bone's circumference and, if those canals are connected radially, can be called plexiform. If the connecting canals are oriented in a slanted fashion and not radially, it is called a reticular vasculature. If the entire vasculatures are oriented radially like a fan, it is called radial vasculature.

CHAPTER 3

RESULTS

3.1. *Koreaceratops* right fibula

The finished slide of the sectioned *Koreaceratops* fibula produced a bone cortex that is roughly elliptical in shape (Fig. 4). The bone had been fractured during its excavation and experienced seawater erosion in the Tando embankment before its discovery (Lee et al., 2011). As a result, only two-thirds of the cortex is structurally well preserved for observation. The cortical dimensions are 1.5 centimeters for its major axis and approximately 1 centimeter for its minor axis.

The section slide showed a highly vascularized bone cortex with light brown coloration. Some red, rootlet-like structures can be observed permeating from the posterior portion of the cortex and into the medullary cavity. The cortex also contains clumps of black minerals that reside in some of the vascular cavities or bleed into the cortex itself (Fig. 4A).

The preservation of the bone's histological features is poor; for almost all of the lacunae, concentric lamellae and canaliculi were not observable in the cortex. Only the erosion rooms and vasculature patterns remain fully preserved (Fig. 4A). Consequently, it is difficult to discern any osteons or determine the bone texture of the cortex. When viewing the bone cortex under the microscope at higher magnification, the bone cortex can be seen as preserved as an amalgam of foci and globules (Fig. 5).

The medullary cavity is relatively small, its dimensions measuring 1.2 mm on its major axis and 1 mm on its minor axis and partially encircled by a lamellar bone. The lamellar bone is thickest in the lateral region and is absent in the medial region of the medullary cavity (Fig. 6). Immediately adjacent to the surrounding lamellar bone is a hoard of erosion rooms that populate the peri-medullary cortex. The erosion rooms even stretch into the posterior and lateral part of the mid-cortex, with the erosion rooms located in the medial part of the peri-medullary area being relatively more extensive than the others (Fig. 4B).

The *Koreaceratops* fibula seems to be heavily remodeled histologically, suggested by the near absence of growth marks in its cortex. However, a portion of the primary bone was preserved in the anteromedial region of the cortex (Figs. 4A, 7). Here possibly three lines of arrested growth (LAGs) were observed: growth marks that record an annual halt of bone growth (Chinsamy 1994). If true, then the bone located between the lines would represent an unaltered record of the specimen's annual growths (Francillon-Vieillot et al. 1990; Ricqlès et al. 1991; Castanet et al. 1993; Sander and Klein 2005; Köhler et al. 2012).

From the preserved primary bones in the anteromedial part of the fibula, we can deduce the growth patterns of *Koreaceratops* fibula during the last three years of its life.

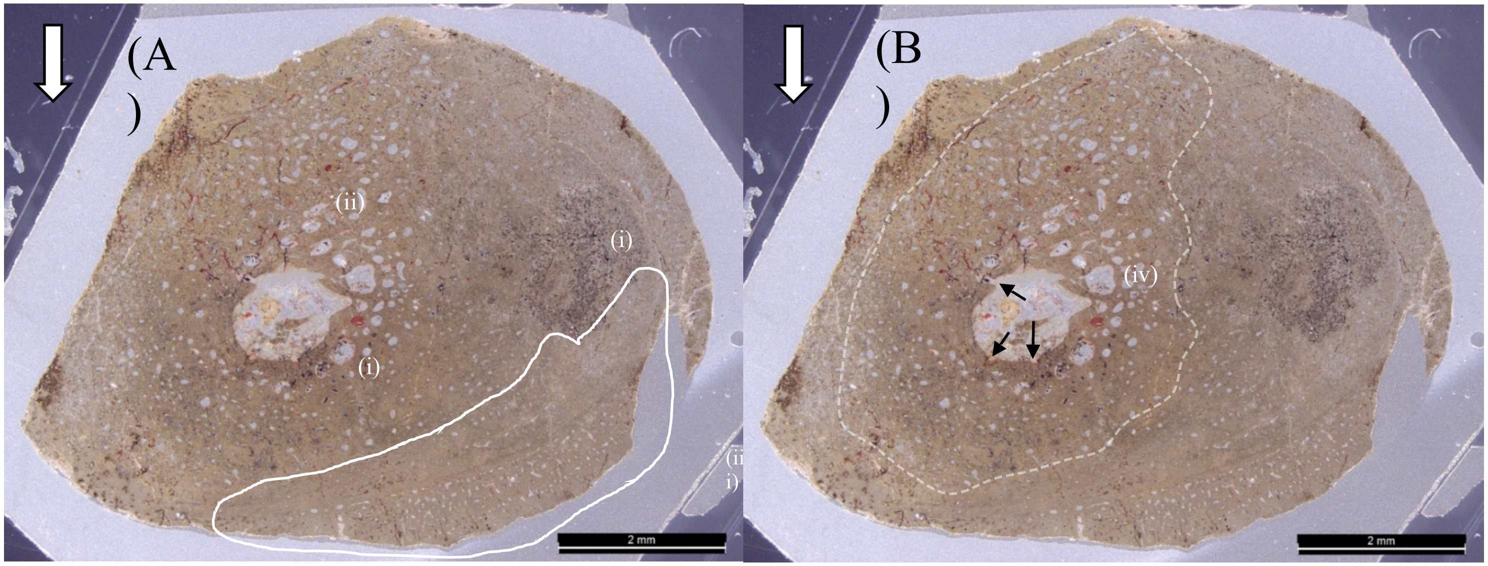

Figure 4.

(A) The overall view of the finished thin section of *Koreaceratops hwaseongensis* right fibula. Note the poor preservation state of the histological features, though the erosion rooms and vasculature remain preserved. (i) Black materials, which probably are remnants of fungal hyphae fossilized into ferromanganese minerals, can be seen populating some of the erosion rooms and the cortex itself. (ii) Red string-like structures can be seen permeating the cortex from the posterior portion and into the medullary cavity. (White solid circle) The anteromedial portion of the cortex still retains some primary bone. The rest of the cortex has been remodeled and pockmarked with erosion rooms. The white arrow on the upper left points to the anterior direction. Section thickness is 20 micrometers and observed under a normal light.

(B) The same section slide but with white dashed lines to mark the full extent of erosion rooms. Note that they are not limited near the medullary cavity and stretch deep into the posterior and lateral parts of the cortex. (iv) The cortical bone medial to the medullary cavity can be seen being eroded as well as being holed by erosion rooms of considerable size, suggesting a trabecularization of the region. Black arrows mark the primary Volkmann canals. Scale bar is 2 mm.

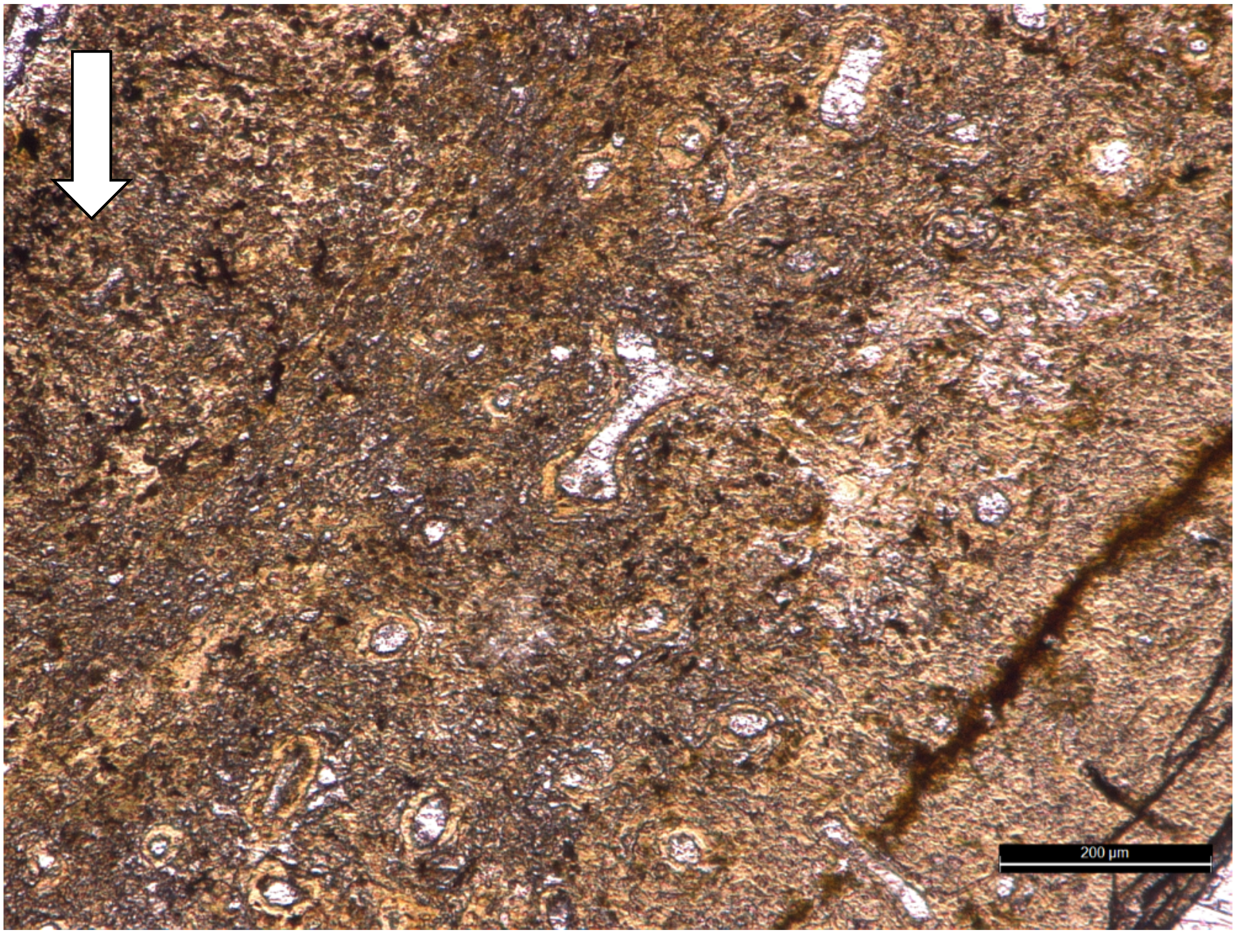

Figure 5.

A close-up view of the bone cortex of *Koreaceratops hwaseongensis* right fibula. Note how the bone is composed as an amalgam of foci and globules. Only the vascular canals and erosion rooms are preserved, though the preservation state is so poor that it is sometimes difficult to differentiate the two. Section slide is 20 micrometers thick and observed under a normal light. The white arrow on the upper left points to the anterior direction. Scale bar is 200 micrometers.

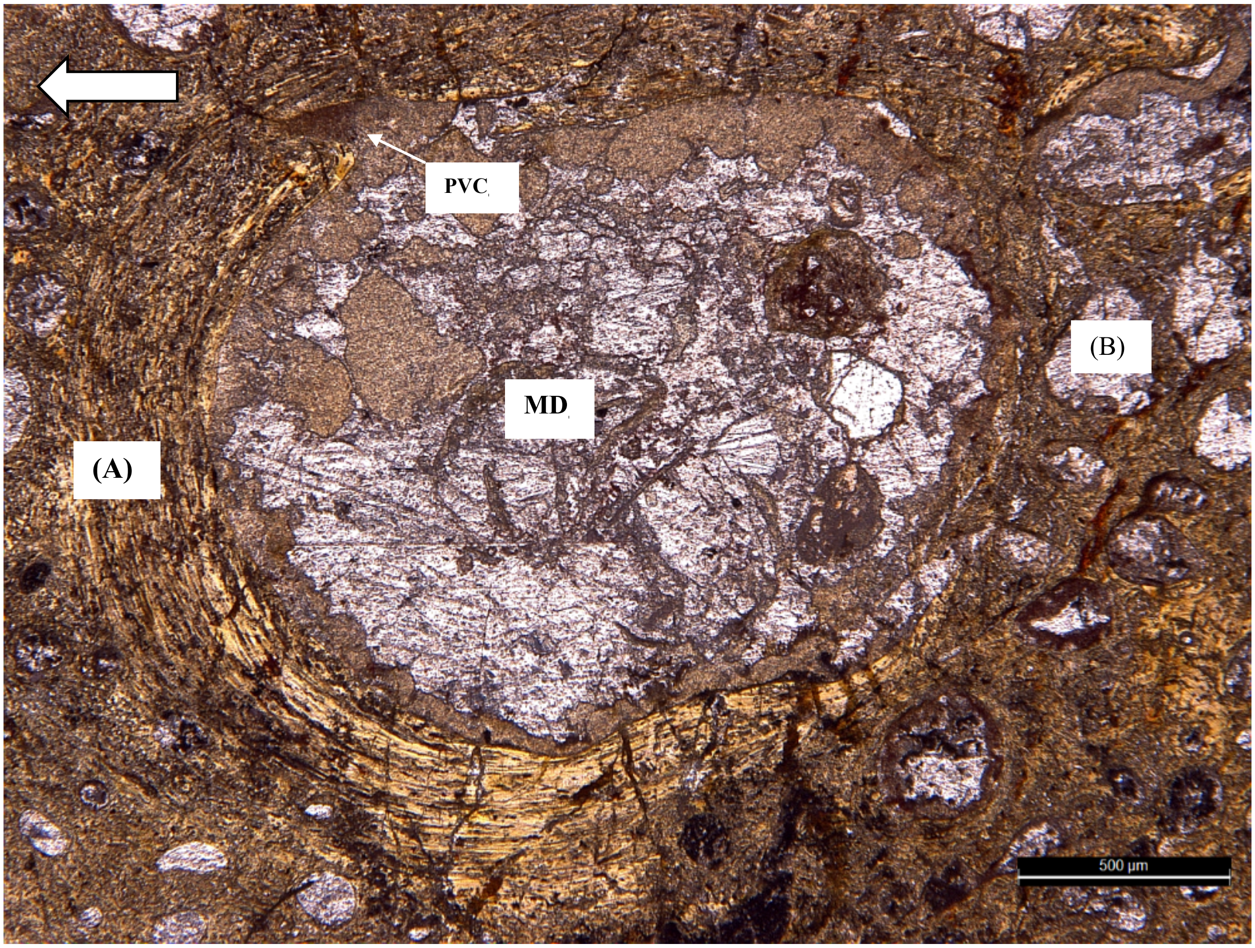

Figure 6.

A close-up view of the *Koreaceratops hwaseongensis* right fibula medullary cavity from a different slide. The cavity is partially surrounded by lamellar bone, which is (A) quite thick in the lateral portion and (B) non-existent on the medial side. This kind of structure pertains to an endosteal lamellar pocket seen in osseous drift. Section slide observed under a normal light.

The white arrow on the upper left points to the lateral direction. The scale bar is 500 micrometers.

3.1.1. The fibular growth two years before death

The innermost preserved growth ring (Fig. 7a), the growth record two years before death, shows the thickest growth ring at the medial region that progressively becomes thinner toward the anterior region. The vasculature of this growth ring is predominantly longitudinal, with a tiny amount of reticular canals present in the medial region. The longitudinal canals are very small and relatively sparsely populated.

3.1.2. The fibular growth a year before death

The second innermost growth ring preserved (Fig. 7b) records the growth a year before the specimen's death. This growth interval shows the same growth pattern as the year before it. The growth ring shows the same width transition from being thick in the medial region to thinner in the anterior region. The vasculature pattern is also the same as the year before it: predominantly longitudinal vasculature with a few reticular canals at the medial side.

3.1.3. The fibular growth on the year of its death

The final year for the *Koreaceratops* fibular growth was interesting because it significantly differed from the previous two years. In terms of regional variation in growth thickness, it was the anterior, not medial, ring that experienced more growth. As a result, the final growth ring thickness narrows medially instead. In addition, the overall volume of growth experienced in this growth ring was enormous, for its thickness is as big as two previous worth of growth put together. The pattern of vasculature in the outermost growth ring is also different from the previous growths, for its displays a much higher vascular density and predominantly reticular vasculature. The outermost fringe of the cortex even shows radially elongated osteon canals (Fig. 7c).

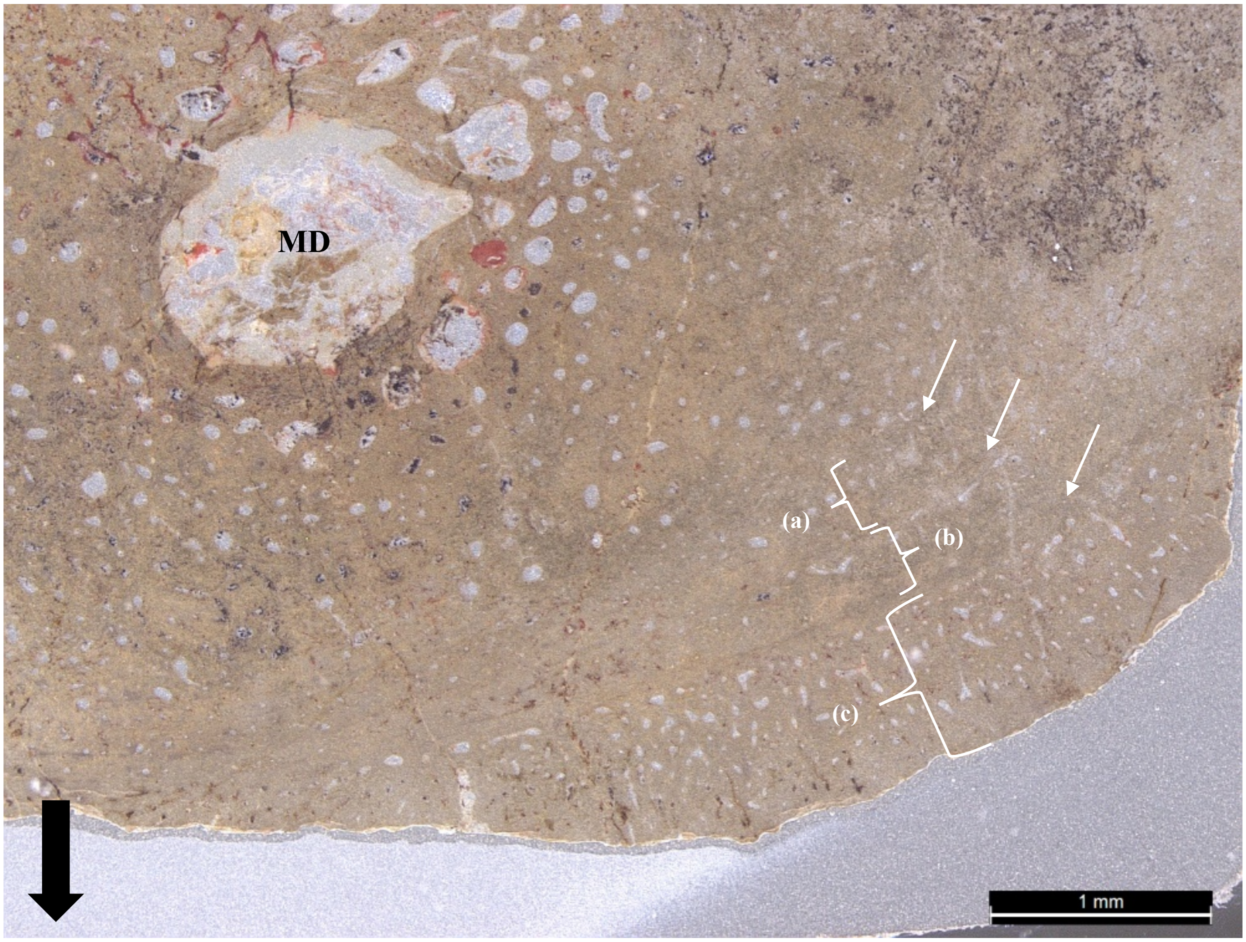

Figure 7.

A magnified view of the anteromedial region of the *Koreaceratops hwaseongensis* right fibula cortex, which preserves some primary bone. The white arrows mark the location of the three surviving lines of arrested growth. (a) The growth interval two years before death. Exhibits primary longitudinal vasculature with a few reticular canals medially. Growth thickness tapers anteriorly. (b) The growth interval a year before death, not much different from the prior growth interval. (c) The growth interval on the year of the specimen’s death. Showing an unusually thick growth as significant as two previous years' worth combined, as well as the growth tapering medially. Vasculature in the final year is mostly reticular with longitudinal canals and even has radially elongated osteon canals on the outside. The scale bar is 1 mm. Section slide observed under a normal light.

The black arrow located on the bottom left points to the anterior direction.

MD: Medullary cavity.

3.2. *Koreaceratops* right tibia

The overall shape of the transversely sectioned *Koreaceratops* right tibia resembles that of a fat chicken egg, with the posterior portion having a more elliptical shape (Fig. 8A) while the anterior portion is somewhat rounded (Fig. 8B). The total diameter of the sectioned tibia is about 2.5 cm, while the diameter of the medullary cavity is about 1.15 cm. The bone cortex of the *Koreaceratops'* right tibia is, as the right fibula, poorly preserved histologically. All signs of lacunae, concentric lamellae, and canaliculi have been replaced by globules and foci. Only the vasculature and erosion rooms are preserved, while neither lines of arrested growth nor annuli were visible (Figs. 9, 10).

The bone cortex did show signs of what seems to be a zonation. The zonation seen in *Koreaceratops hwaseongensis* tibia is very similar to that observed in *Protoceratops andrewsi* long bones (Fostowicz-Frelik and Slowiak, 2018). In the *Koreaceratops* right tibia, the zonation is visible as circumferentially alternating bands of dark and light brown colors throughout the entire cortex. The zonation was very clear when the slide thickness was about 200 micrometers thick (Fig. 11A) but became less pronounced as the slide became thinner (Fig. 11B). Due to the poor preservation of histological features, it is difficult to deduce the exact bone textures of each zone.

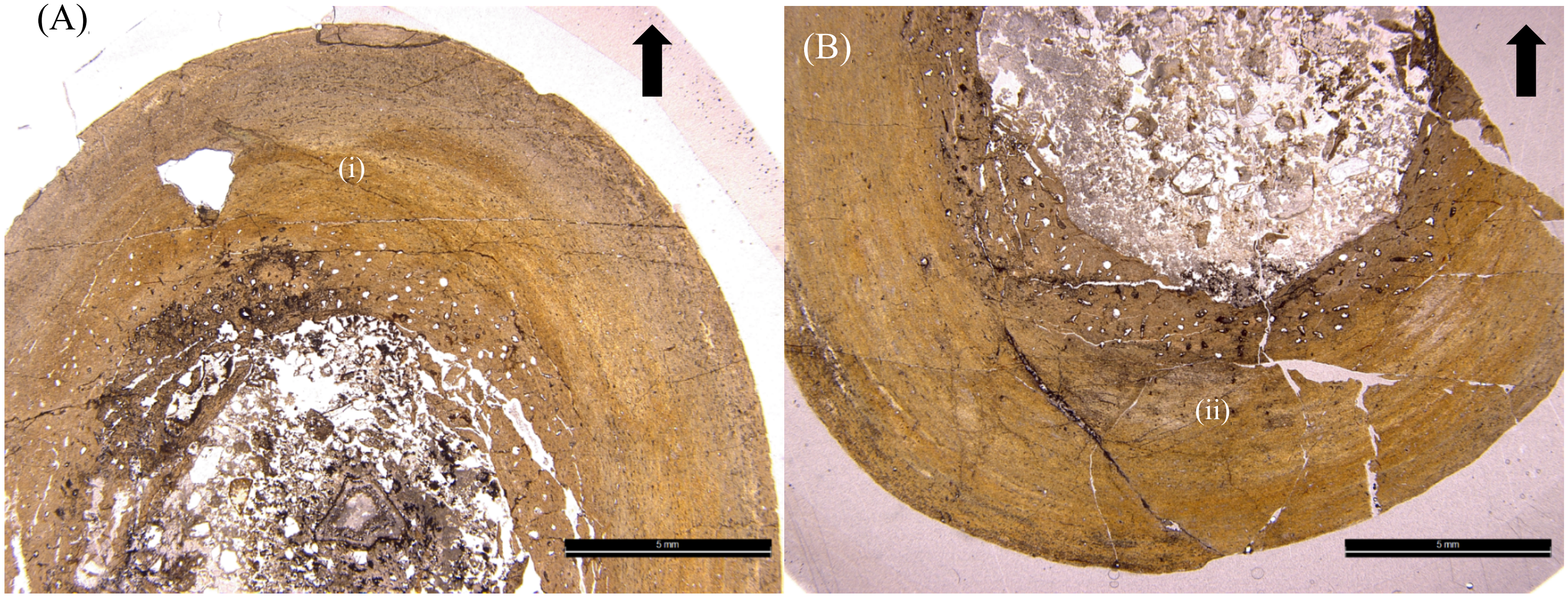

Figure 8.

An overview of the finished thin section slides showing (A) the posterior half and (B) anterior half. The peri-medullary cortex is in a very poor preservation state and is in a fragmented state. Notice that the (i) posterior portion of the mid-cortex is much narrower and possesses thicker zones than the (ii) anterior mid-cortex. The black arrows point to the posterior direction. Both section slides are 20 micrometers thick. The scale bar is 5 mm. Section slides observed under a normal light.

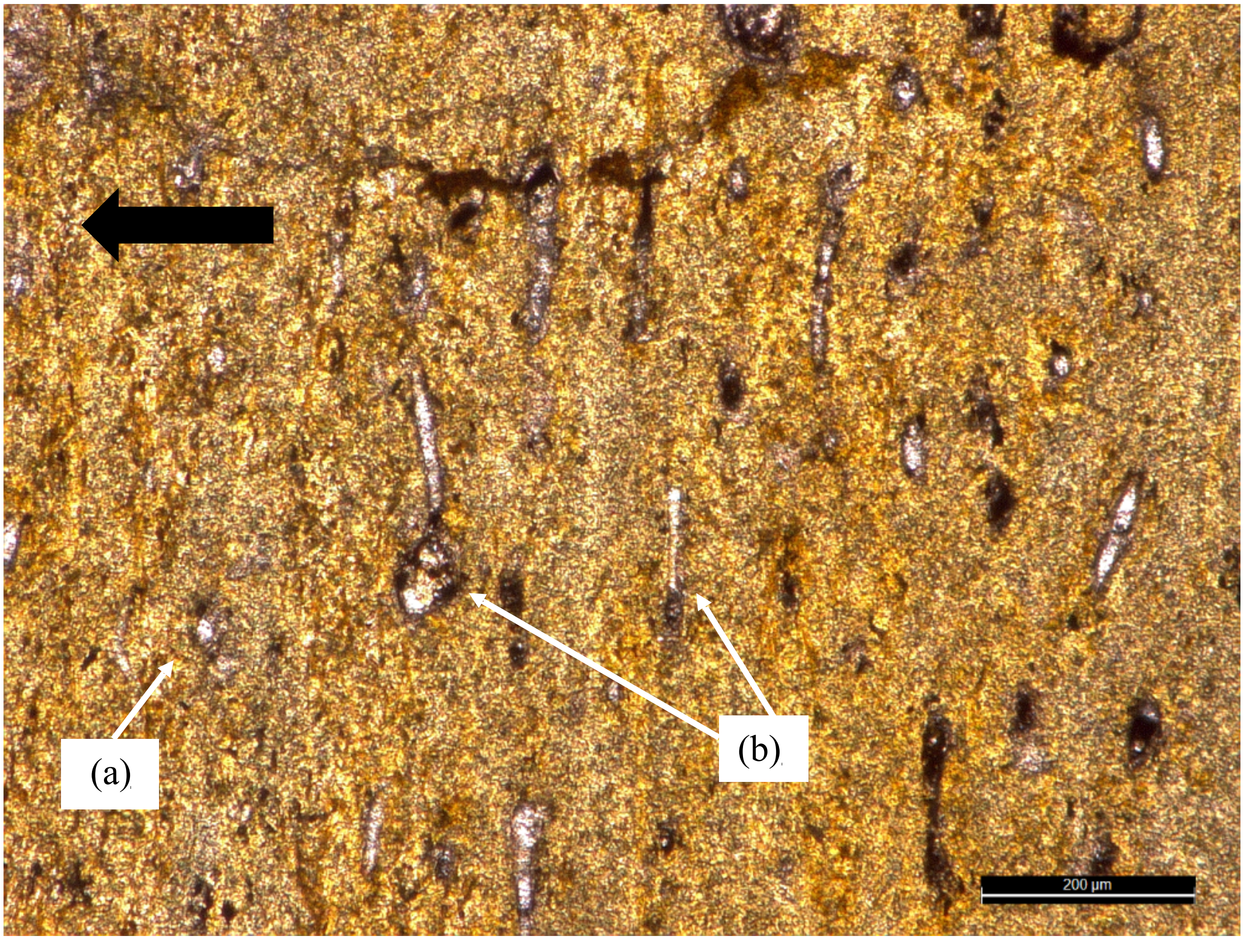

Figure 9.

A close-up of the *Koreaceratops hwaseongensis* right tibia cortex. Notice the very poor preservation of the histological features. Only the vasculature, such as (a) longitudinal with (b) circumferentially elongated osteon canals, are preserved. The black arrow points toward the outer cortex. The section slide thickness is 20 micrometers. The scale bar is 200 micrometers. Section slide observed under a normal light.

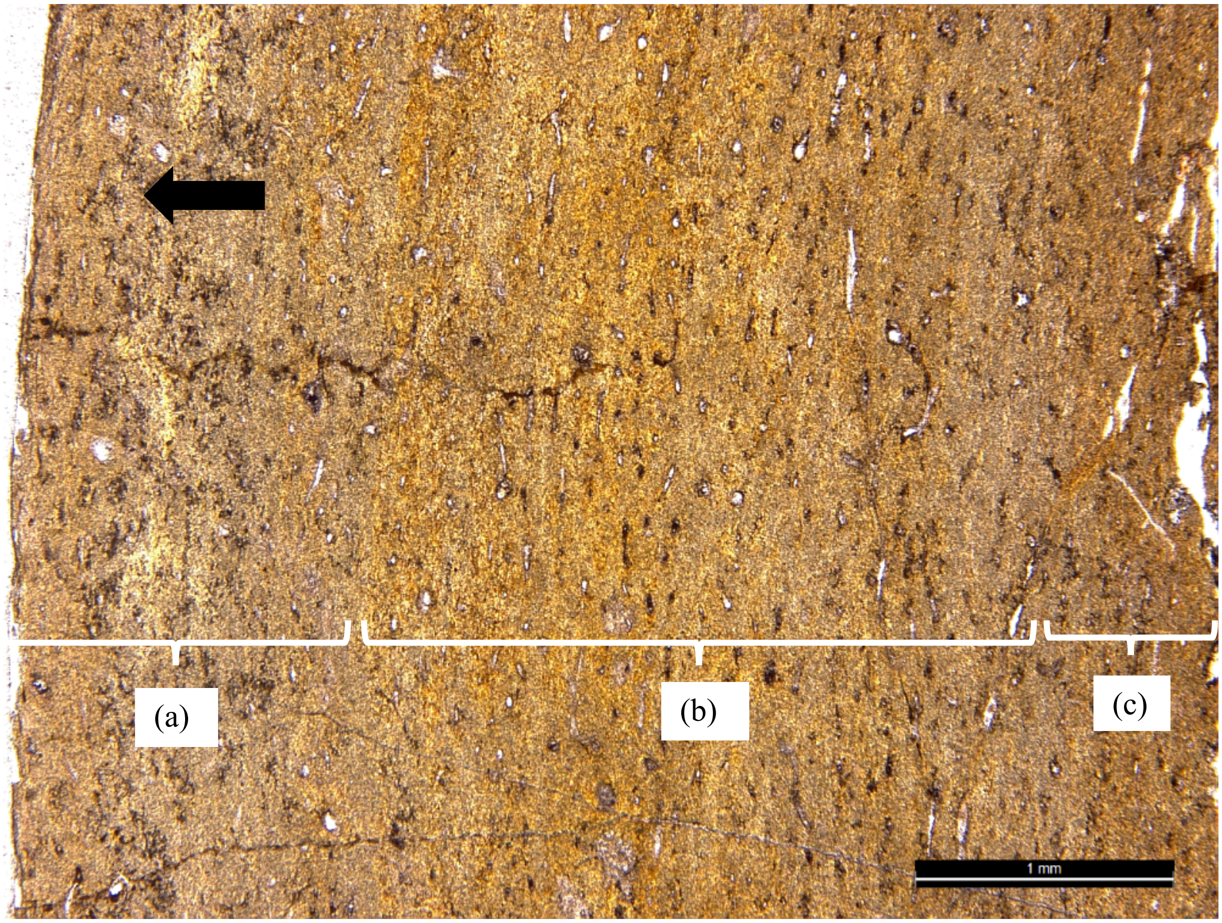

Figure 10.

A magnified view of the lateral cortex of *Koreaceratops hwaseongensis* right tiba. Notice the uniform vasculature of longitudinal and circumferentially elongated osteon canals throughout the (a) Peri-cortical, (b) mid-cortical, and (c) remnants of the peri-medullary cortex. Growth marks can be faintly seen as zonation. The section slide is 20 micrometers thick and the black arrow points to the lateral direction. The scale bar is 1 mm. Section light observed under a normal light.

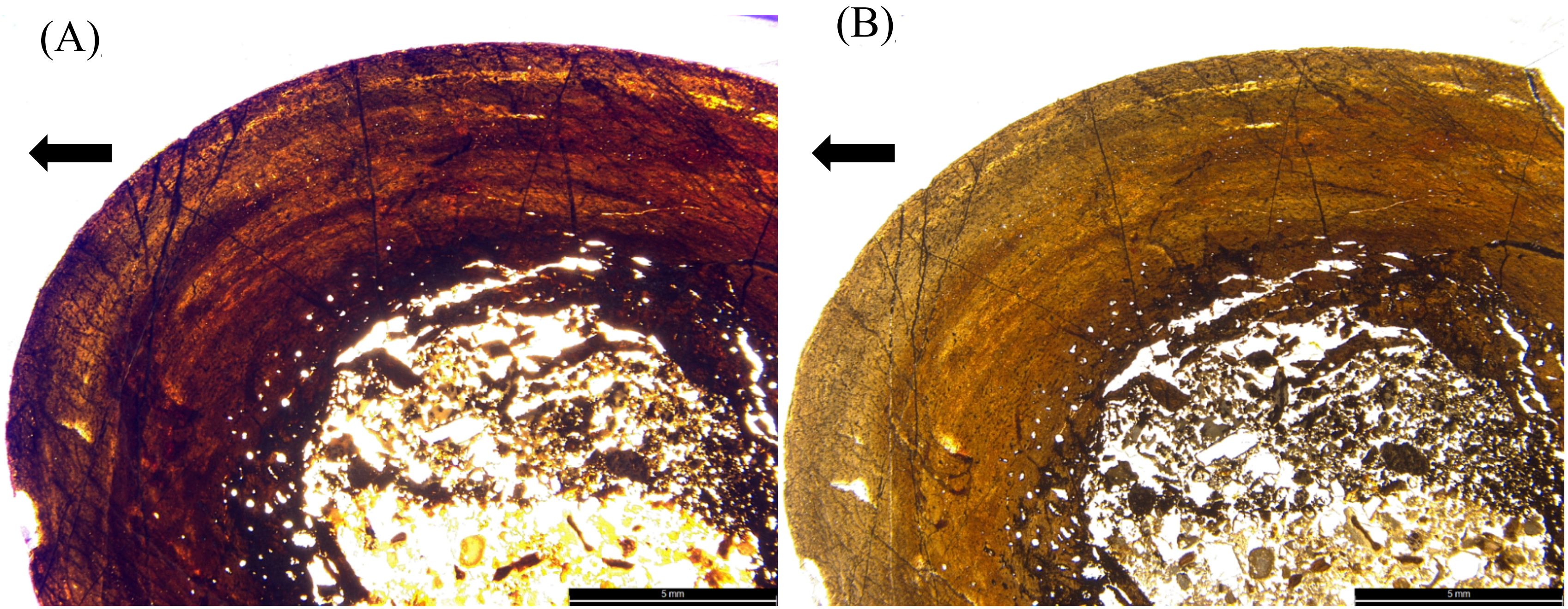

Figure 11.

Comparison of the zonation visibility in the posteromedial cortex of *Koreaceratops hwaseongensis* right tibia. The visibility was evident when the slide was about (A) 200 micrometers thick but significantly faded when the slide was ground to less than (B) 90 micrometers thick. The zones become less pronounced as the slide becomes even thinner. The black arrows point to the posterior. The scale bar is 5 mm.

Slide (A) is observed under polarized light, while (B) is under normal light.

3.2.1. Peri-medullary cortex

The medullary cavity is filled with a matrix composed of two different types of sediment, with the medial half composed of dark sands and lighter sands in the lateral half. The peri-medullary region of the cortex is structurally poorly preserved, as most of the area has pretty much disintegrated. Still, multiple small erosion rooms can be seen that evenly populate the peri-medullary cortex, and these do not venture deep into the mid-cortical region. There are no signs of inner circumferential lamellar. The vasculature pattern in the peri-medullary cortex is challenging to determine due to the very poor structural and histological preservation (Fig. 12).

3.2.2. Mid-cortex

The mid-cortical region of the cortex exhibits longitudinal vasculature with circumferentially elongated osteon canals, and they may or may not be filled with black materials (Figs. 10, 14).

The bone zonation is most clearly seen in this mid-cortical region. The zonation of the bone is exhibited as circumferentially alternating bands of light and dark brown colors (Figs. 13, 14, 15). The color of the zone does not necessarily correlate to the vascular type, but they somewhat correspond to the degree of the vasculature. The light brown zones typically possess less vasculature than the dark brown zones (Figs. 14, 15). The number of zone transitions is difficult to count in the posterior part of the mid-cortex, while in the anterior region, about seven transitions were counted (Fig. 15a).

The thickness of the zones differed according to the sagittal plane. The zones in the posterior part of the cortex (Fig. 13) are somewhat thicker than the zones in the anterior region

(Fig. 15). It may explain why the posterior part of the cortex has an elliptical shape while the anterior portion is more rounded, giving the entire bone cortex a shape of a chicken egg. In the anterior portion of the cortex, the zones become slowly thicker in each growth cycle (Fig. 15a), while the zones in the posterior one seem to maintain the same thickness throughout the entire growth (Fig. 13).

3.2.3. Peri-cortex

The vasculature of the peri-cortical region of the cortex is the same as the longitudinal with circumferentially elongated primary osteon canals seen in the mid-cortex (Figs. 10a, 15b).

The overall color of the peri-cortex is less pronounced than the mid-cortical and peri-medullary regions, and the reduced opaqueness makes the zones less discernable (Fig. 10a). However, two dark brown zones with a single light brown zone in between are discernable in the posterior part of the peri-cortex (Fig. 13b). Its anterior portion, however, shows a single thick growth zone (Fig. 15b).

The outermost anteromedial portion of the cortex was intriguing because it has a single growth zone with high vascular density and is unusually thick (Fig. 15b). The thickness of this final growth zone is a thick as the two previous zones put together.

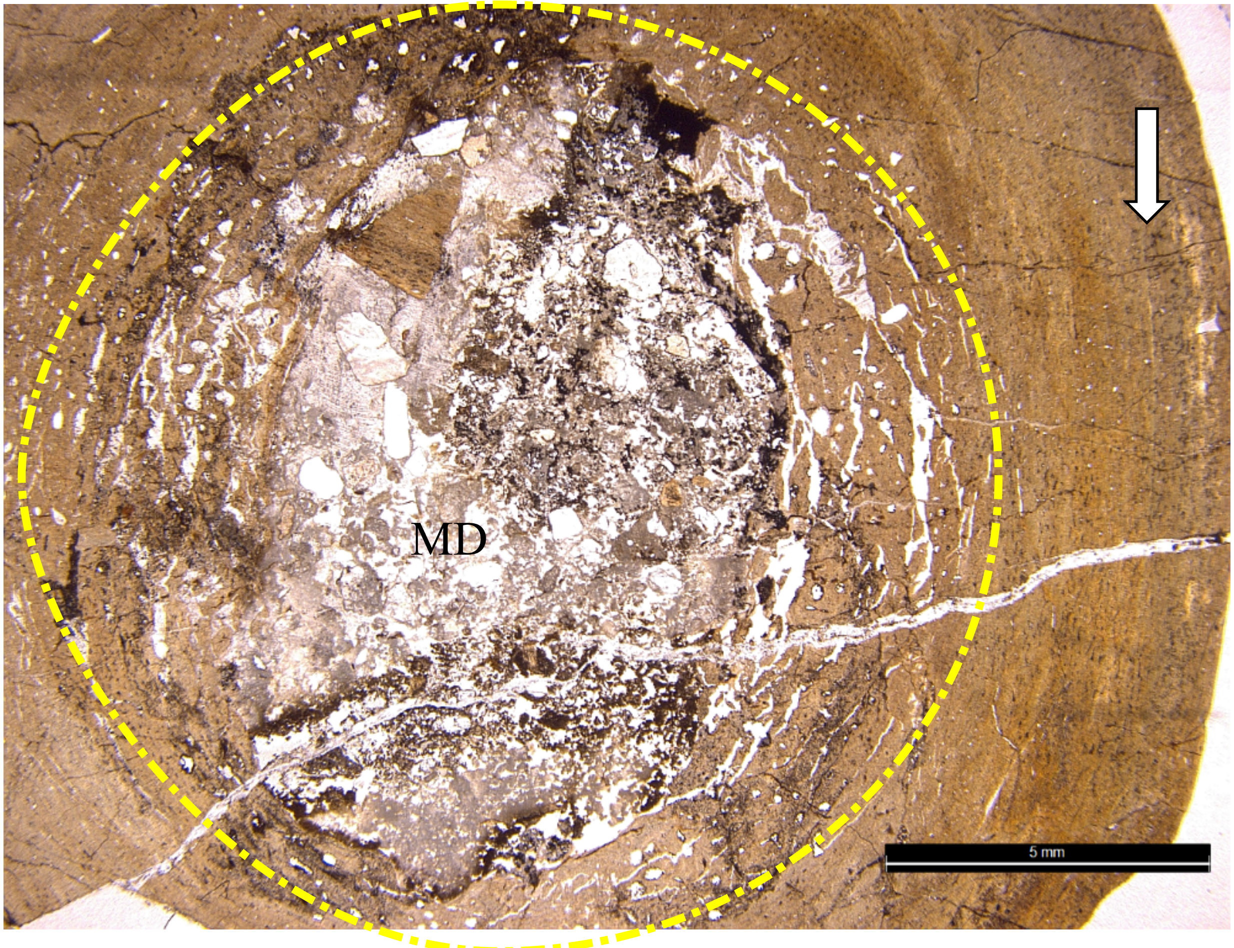

Figure 12.

The medullary cavity and its surrounding cortex of *Koreaceratops hwaseongensis* right tibia. The peri-medullary region of the cortex (Within the dashed yellow circle) is poorly preserved structurally and histologically. The preserved erosion rooms in the tibia are small and mostly confined within the peri-medullary cortex. There are no signs of inner circumferential lamellar. The white arrow points to the anterior direction. The section slide is 20 micrometers thick. The scale bar is 5 mm.

MD: Medullary cavity. Section slide observed under normal light.

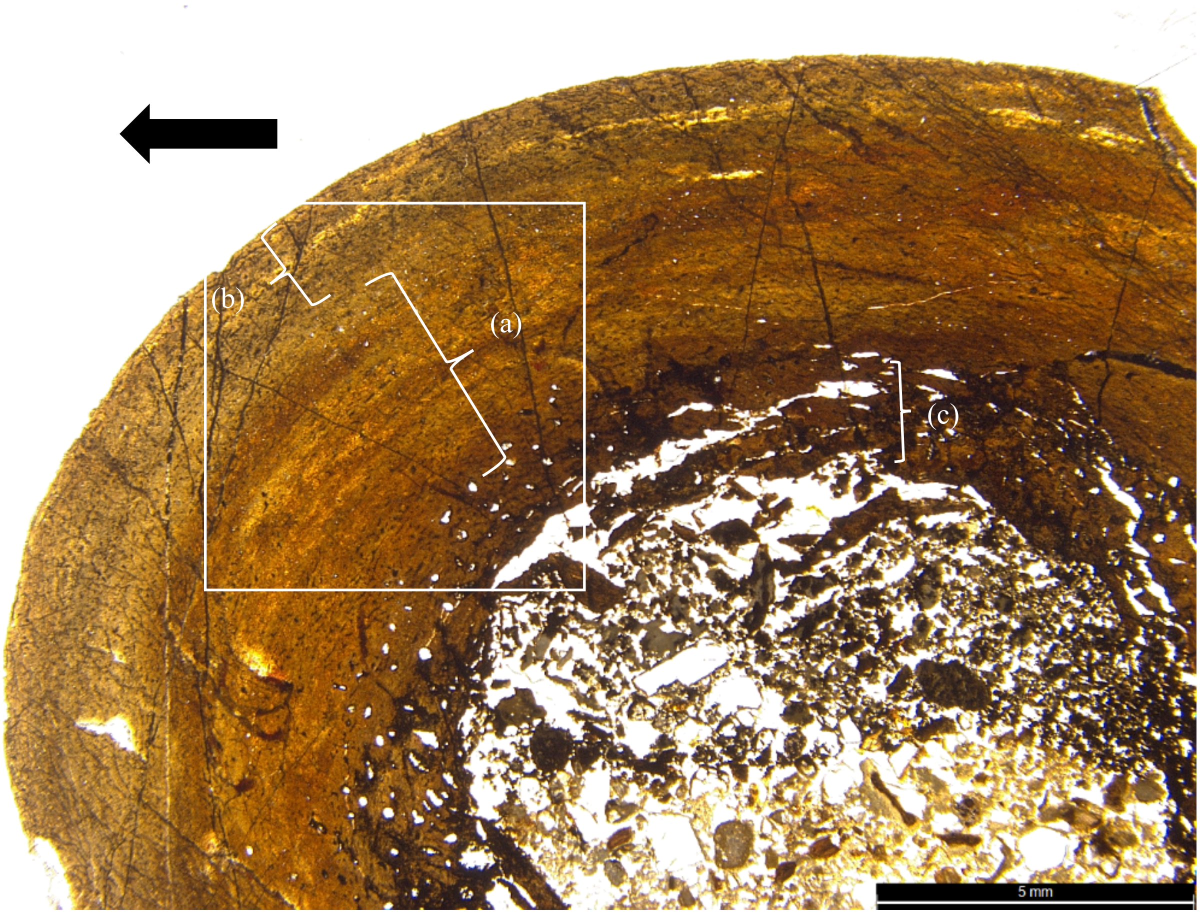

Figure 13.

The posterior medial view of *Koreaceratops* right tibia, showing an overview of the zonation in the mid-cortical and peri-cortical regions of the cortex. The zones manifest as dark brown and light brown bands. Note the similar thickness of the zones from the inner to outer cortex. (a) Zonation in the mid-cortex shows much darker coloring compared to (b) the zonation in the peri-cortex. (c) The peri-medullary region is in a disintegrated state. The black arrow points to the posterior direction. The slide thickness is 90 micrometers. The scale bar is 5 mm. Section slide observed under normal light.

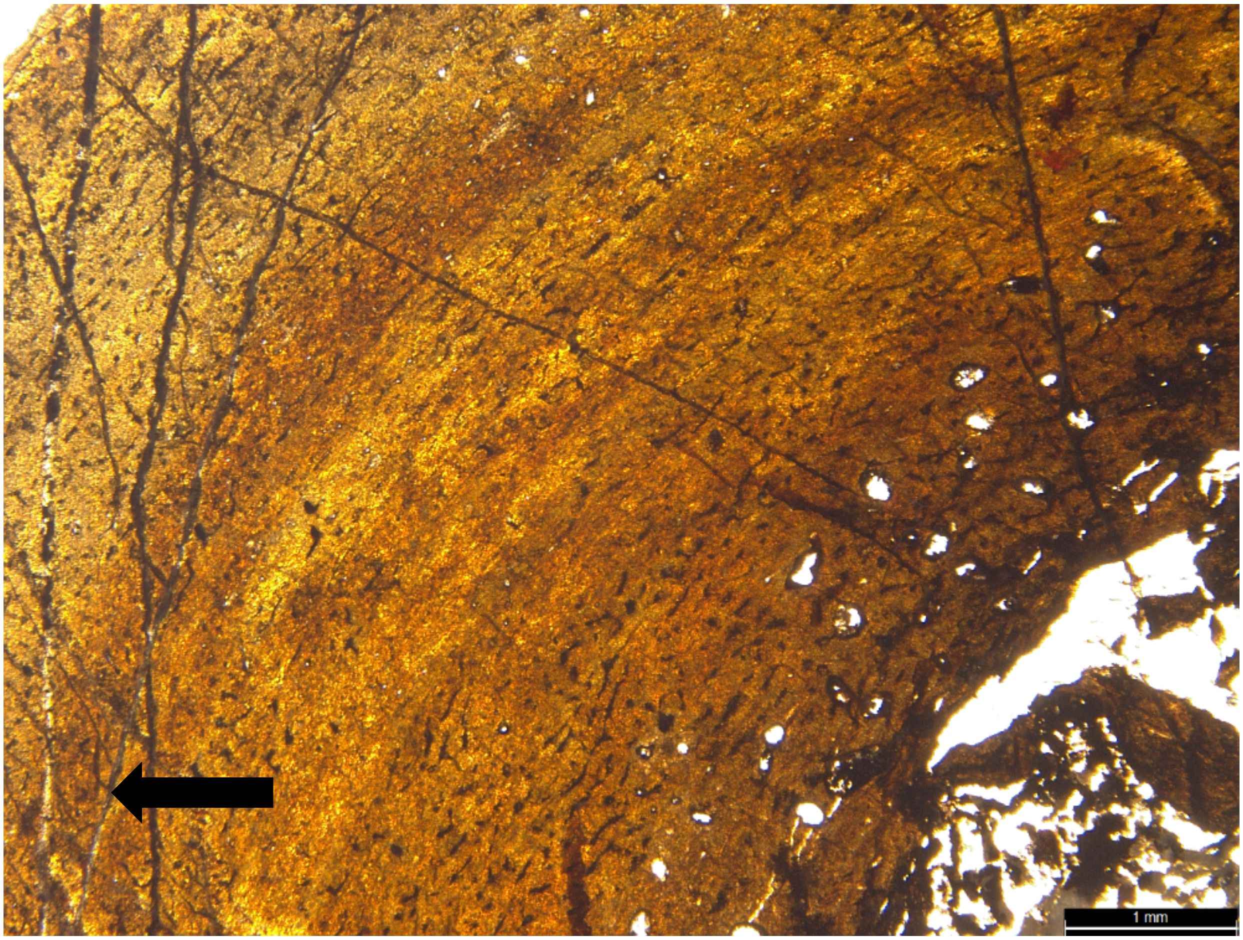

Figure 14.

A magnified view of the squared area in Figure 13. We can see here that the entire cortex possesses longitudinal and circumferentially elongated osteon canals for vasculature, with the peri-medullary region having a slightly longer circumferential elongation of the canals. The dark brown zones are typically well-vascularized, while the light brown zones have sparse vascularization, suggesting that the darker zones are the faster-growing bone type compared to light brown zones. The poor histological preservations prevent us from knowing the exact bone texture. The vascular canals may or may not have black material infillings. The black arrow points to the posterior direction. The slide thickness is 90 micrometers. The scale bar is 1 mm. Section slide observed under normal light.

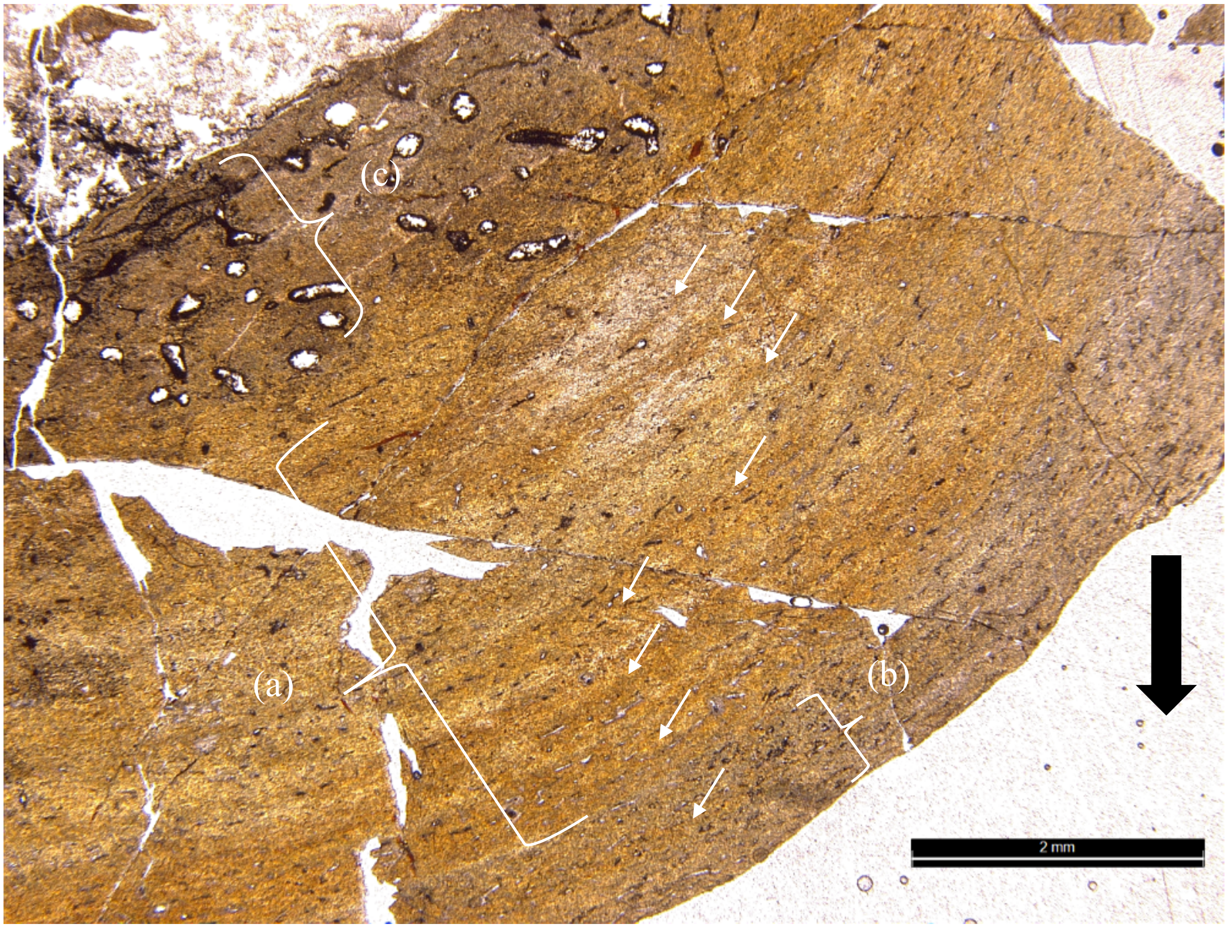

Figure 15.

A close-up of the anteromedial part of the *Koreaceratops* right tibia. The thickness of each zone is much narrower than the posterior region shown in Figure 10. (a) The mid-cortical region of the cortex, with seven white arrows marking the dark brown zones. We can see the dark brown zones steadily becoming thicker toward the outer part of the cortex, while the light brown zones steadily become thinner. (b) The final growth here shows an unusually thick growth for a single growth interval, comparable to the final growth seen in the anteromedial portion of the right fibula. (c) Peri-medullary cortex with small circular erosion rooms. The black arrow points to the anterior direction. The slide thickness is 20 micrometers. The scale bar is 2mm. Section slide observed under normal light.

3.3. Theropod Dorsal Rib

The section slide of the theropod dorsal rib showed a greyish white cortex that has been severely cracked and torn (Figs. 16A, 16B). Cracks large and small permeate throughout the bone, with many fissures occurring along the cement lines of secondary osteons (Fig. 17). The medullary cavity is devoid of cancellous bone and is filled with purple sandstone matrix and bone fragments (Fig. 16). Overall, it looks as if the bone had expanded and exploded, then all glued back together with the matrix.

The specimen has lost all traces of lacunae, lamellae, and canaliculi. Magnification of the cortex shows the bone being extensively pockmarked by foci (Fig. 17). However, cement lines survive in the form of fissures, which pertain to secondary osteons. The secondary osteons delineated by the cracks are devoid of any microstructures associated with osteons, save for the longitudinal canals located in the middle. Consequently, the Haversian system in this specimen looks like flat, glassy doughnuts (Fig. 17). Such Haversian bones cover the entire rib (Fig. 16), suggesting that the bone was completely remodeled.

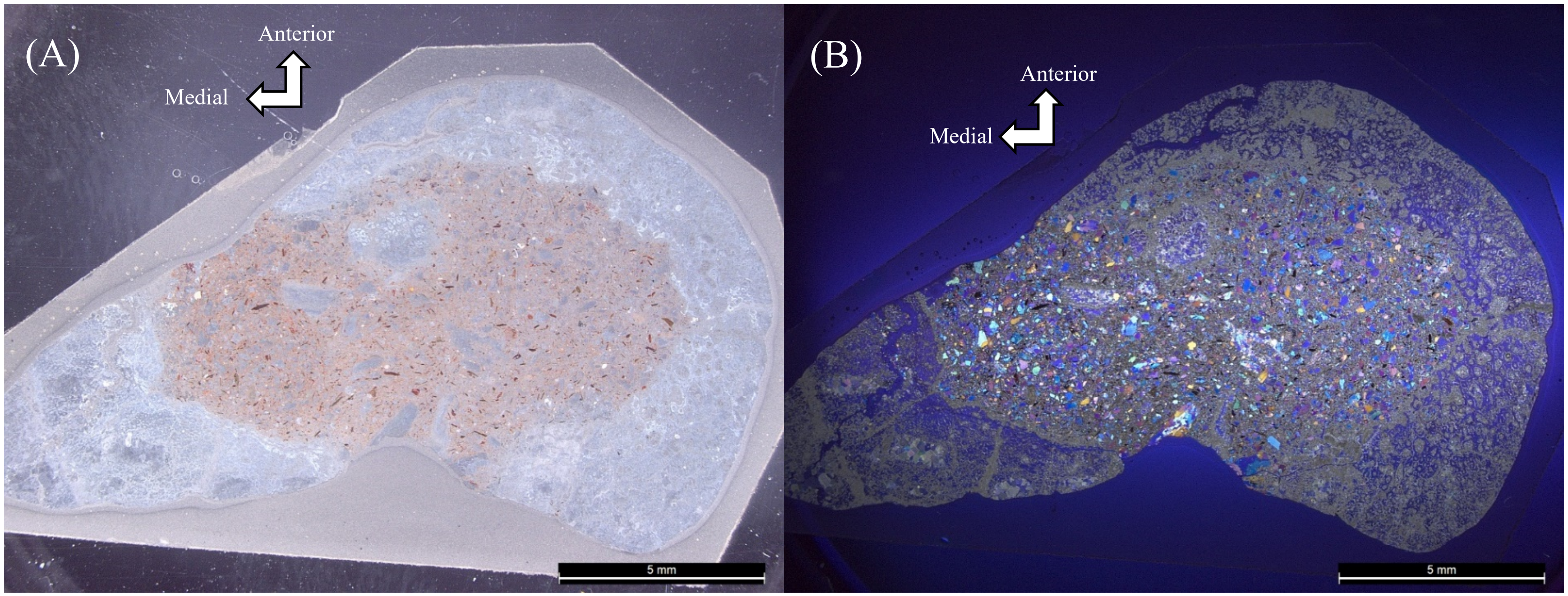

Figure 16.

An overall view of the unidentified Korean theropod dorsal rib cortex under (A) normal light and (B) polarized light. The bone is in a very poor preservation state, both histologically and structurally. The cortex contains many large and miniscule fractures, with large chunks of the bone missing. The bone remodeling is 100 percent throughout the cortex, as seen by the secondary osteons blanketing the entire cortex. The section slide is 20 micrometers thick. The medullary cavity is devoid of cancellous bone and is filled with sandy matrix and bone fragments. The scale bar is 5 mm. Slide (A) is observed under normal light, while (B) is observed under polarized light.

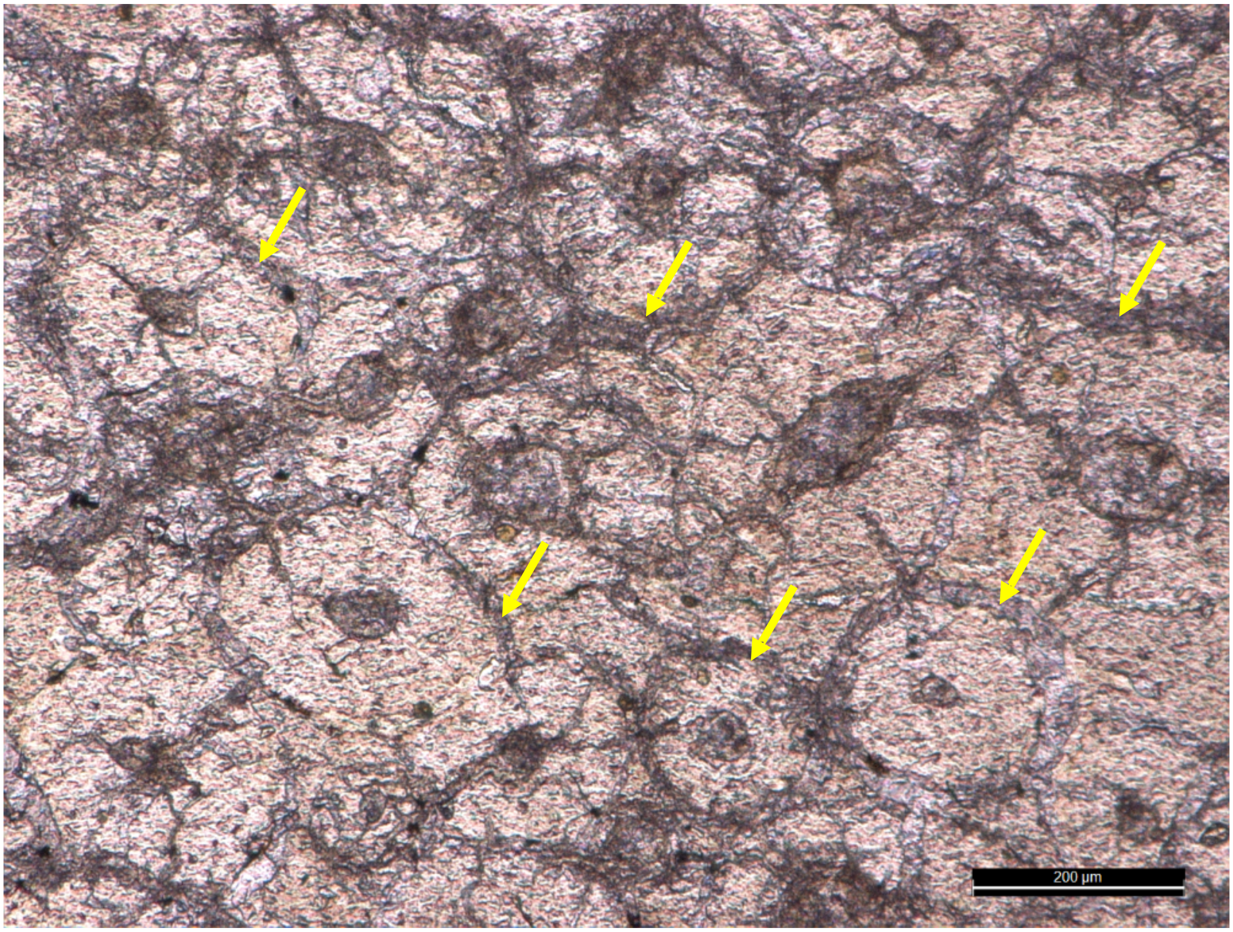

Figure 17.

A close-up view of the unidentified theropod dorsal rib cortical surface. Note that foci and globules have erased nearly all histological features. Osteon canals and cement lines of the secondary osteons are relatively well preserved. The micro-fractures occurred mainly along the cement lines (Yellow arrows) of the secondary osteons. The scale bar is 200 micrometers. Section slide observed under normal light.

3.4. Sauropod Dorsal Rib

Most histological features have been erased: no signs of lacunae, lamellae, or canaliculi. The cortex is instead heavily pockmarked by foci (Fig. 19B). The bone is highly vascularized, with an extensive network of cancellous bones in the medullary cavity and erosion cavities around it (Fig. 18). The cortex shows tightly packed vasculatures that are in primarily longitudinal form and filled with some black material. Most of these longitudinal vasculatures are not from the primary bones because almost all of them are surrounded by cement lines and thus are part of the secondary osteons (Fig. 19A). It means that the majority of the bone cortex was remodeled into the Haversian system. Nevertheless, there are slivers of primary bone preserved: the outermost anterior portion of the rib contains a band of primary bone that sports a longitudinal-laminar vasculature (Fig. 20).

The outermost medial portion of the rib also did manage to preserve a small amount of primary bone and growth marks (Fig. 21A). It contains approximately four lines of arrested growth, with longitudinal canals deployed in a parallel fashion between the growth marks. There are no signs of cement lines in these longitudinal canals, suggesting that they are primary osteons. The presence of vasculature between the lines of arrested growth implies that the growth lines are not an external fundamental system. However, the very thin thickness of the growth intervals suggests that the specimen was almost within maturity (Fig. 21B).

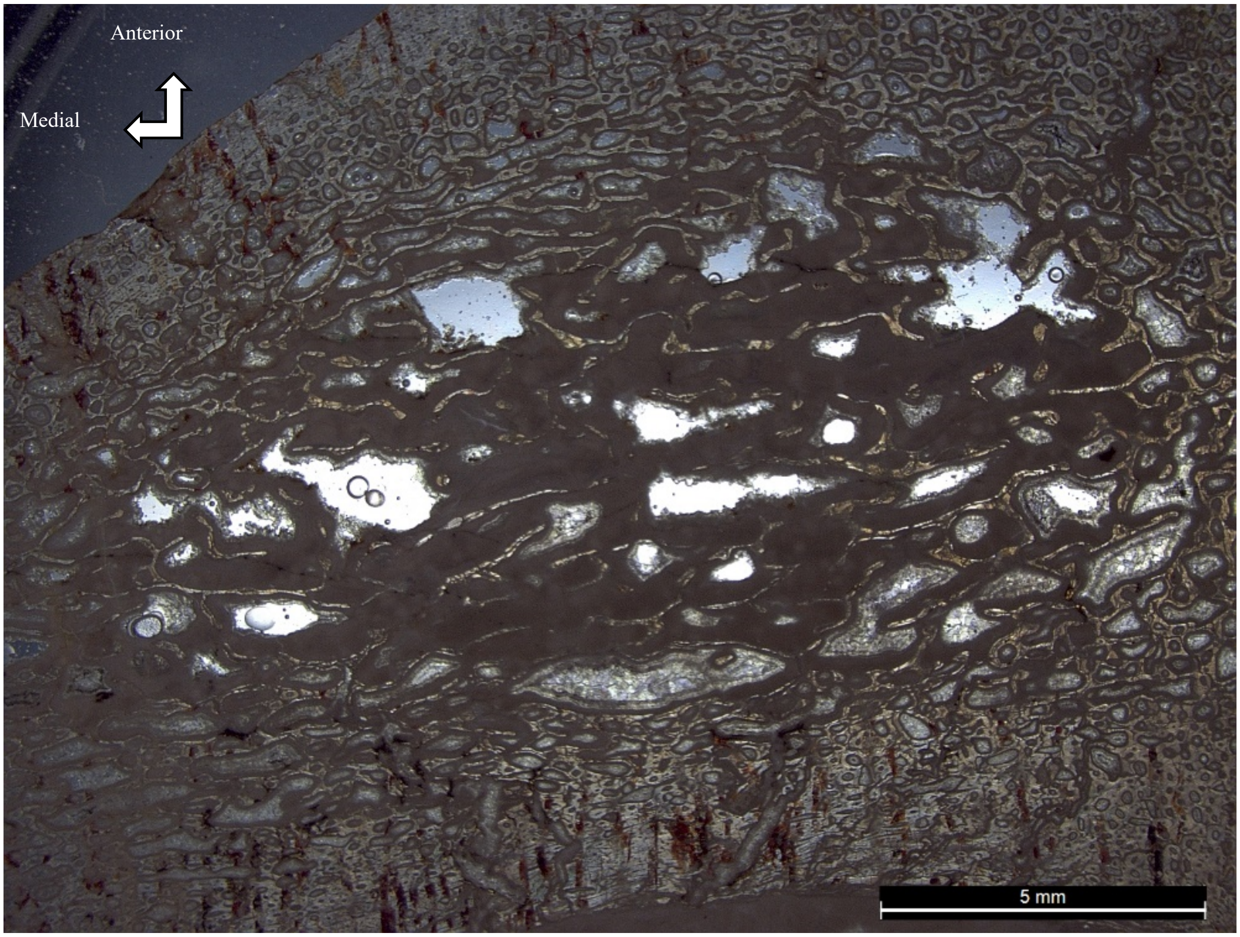

Figure 18.

Overview of the medullary cavity and its surrounding cortex of the unidentified Korean sauropod dorsal rib. The medullary cavity is filled with cancellous bone and some matrix. Numerous erosion rooms densely populate both the peri-medullary and mid-cortex. The scale bar is 5 mm. Section slide observed under normal light.

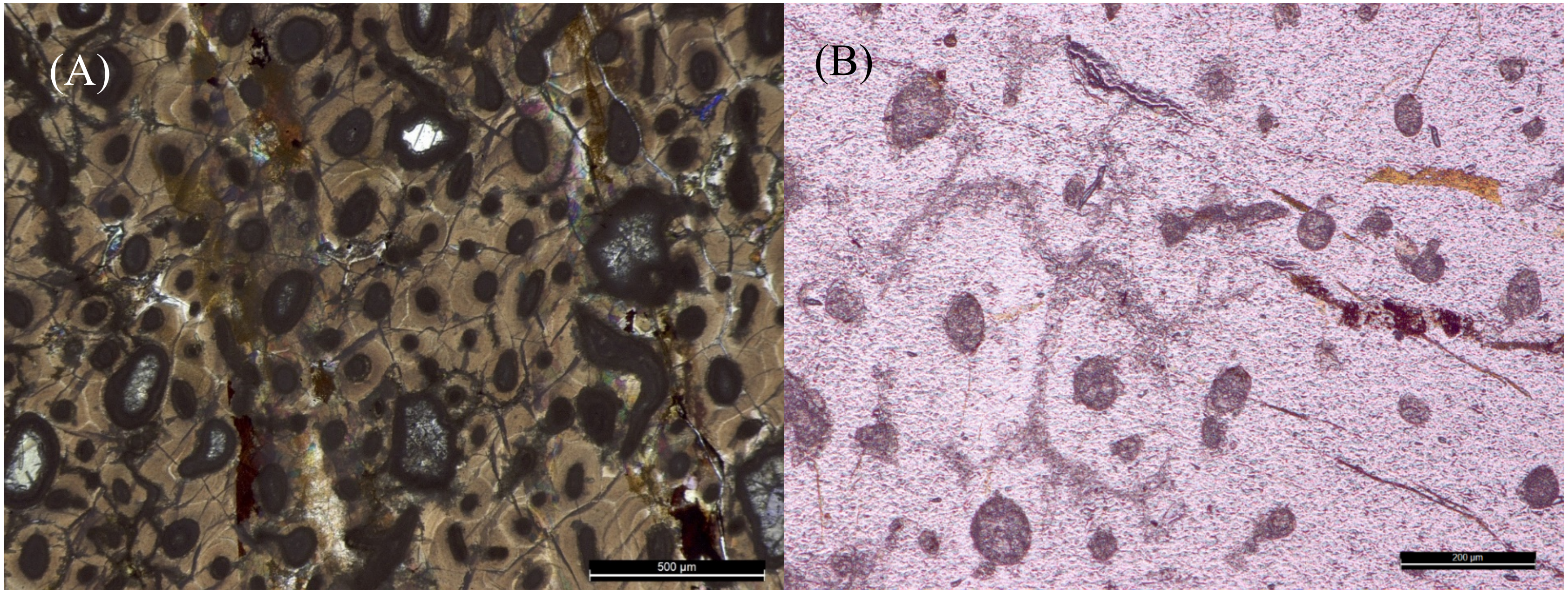

Figure 19.

(A) A close-up view of the unidentified Korean sauropod dorsal rib cortex at section thickness of 150 micrometers. Most of the longitudinal canals are filled with black material and are surrounded by cement lines. The micro-fractures occur in a tile pattern and do not necessarily occur along the cement lines. The scale bar is 500 micrometers.

(B) The same cortex when ground to a thickness of 30 micrometers. The cement lines are mostly erased but clearly show the foci and globules making up the cortical structure. The scale bar is 200 micrometers. Both slides observed under normal light.

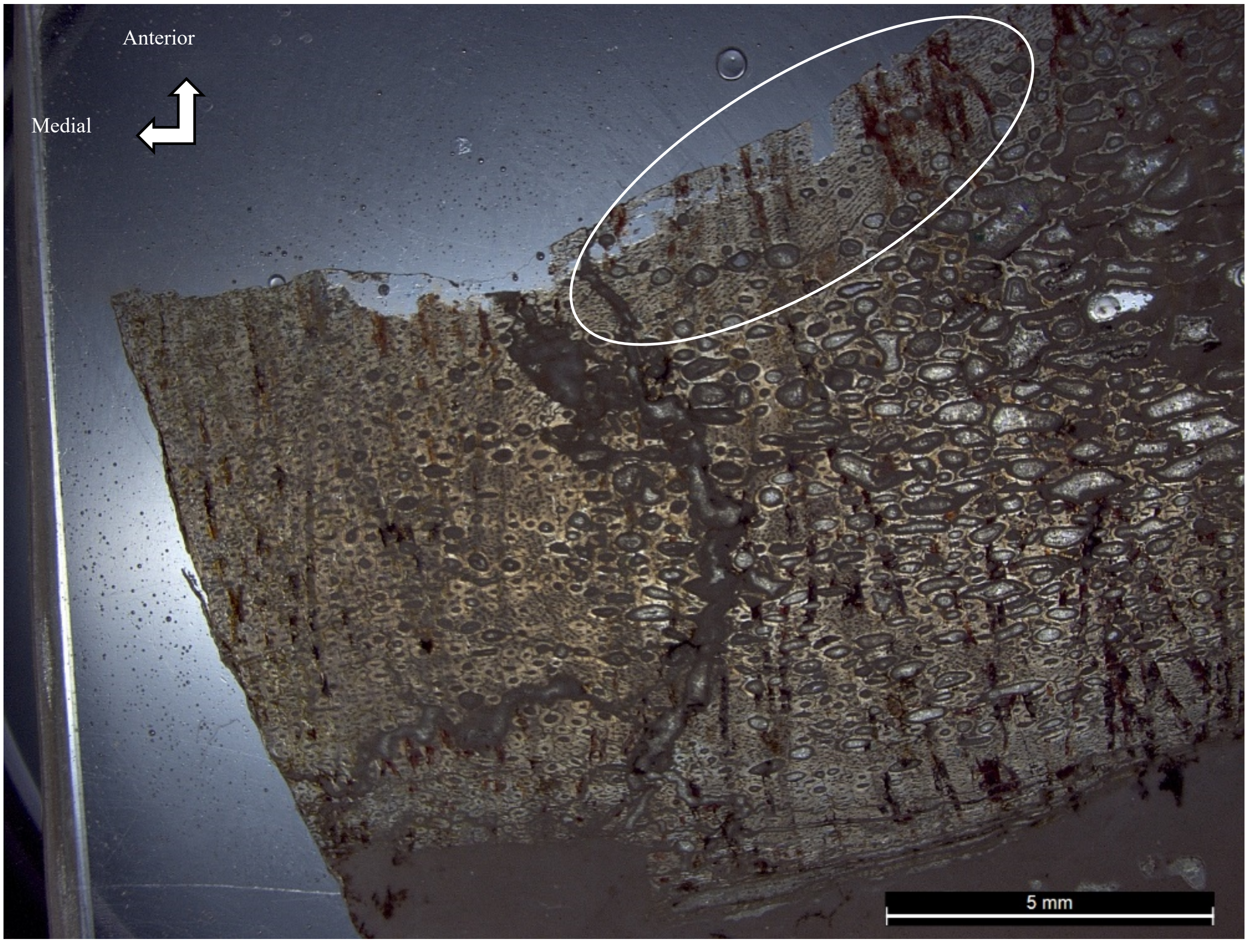

Figure 20.

A portion of the unidentified Korean sauropod dorsal rib cortex with a small primary bone (within the white circle). The vasculature here is longitudinal-laminar. The scale bar is 5 mm. Section slide observed under normal light.

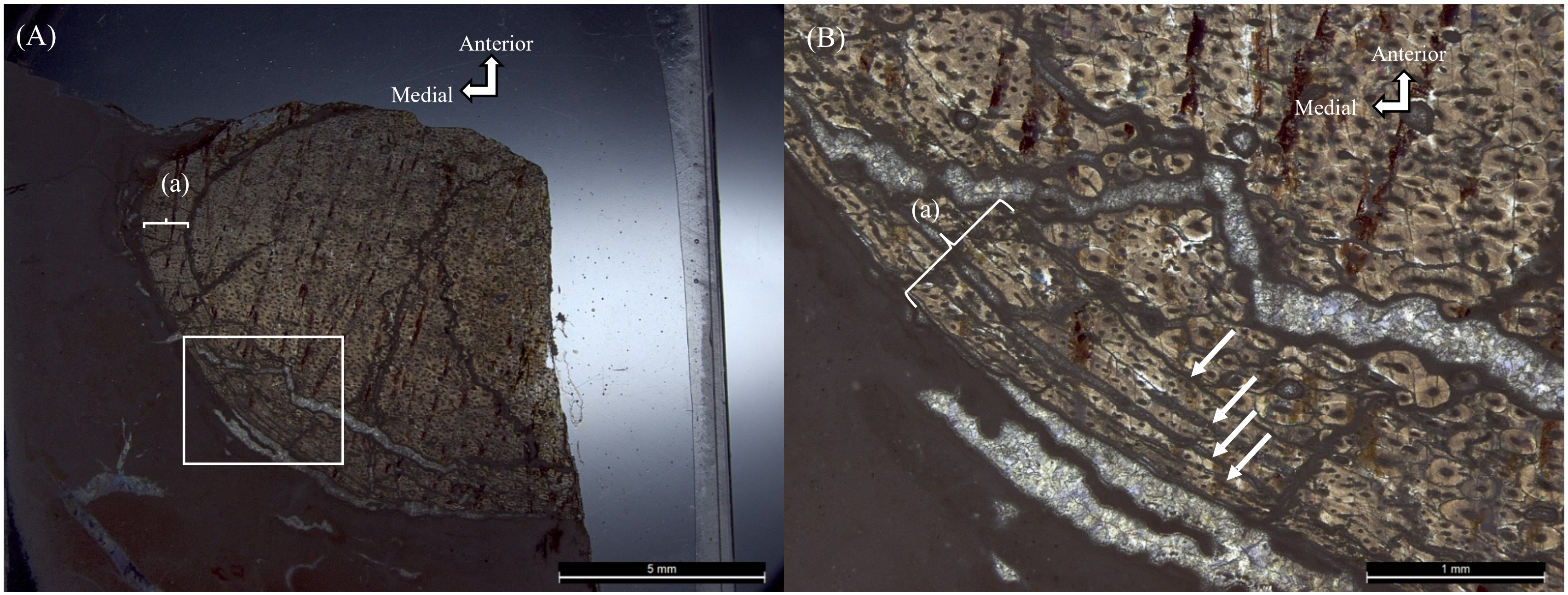

Figure 21.

(A) The most medial portion of the unidentified Korean sauropod dorsal rib. It was this region where the primary bone (a) was most well preserved. Scale bar is 5mm.

(B) The magnified version of the squared area in (A), showing a total of four lines of arrested growth (white arrows) in the primary bone (a). The vasculature between the lines suggests that these are not an external fundamental system, but the very narrow width between the lines pertains to the near maturity of the specimen at death. Scale bar is 1mm. Both slides observed under normal light.

CHAPTER 4

INTERPRETATIONS

4.1. The preservation state of the histological features

One of the most striking aspects of all the Korean dinosaur fossils used in this study is that most of their histological features are not well preserved. Bone textures had been smudged beyond recognition, the lacunae and canaliculi are almost absent, and growth marks are preserved in faint traces. The only well-preserved histological feature is the bone's vasculature. A similar preservation state was reported in the left femur of the *Koreanosaurus*, and the phenomenon was attributed to intense pressure and calcite intrusion during its diagenesis (Kim et al., 2017). However, upon closer inspection, it turned out that the microstructures of the *Koreaceratops* bones are composed of what seems to be tunnels and foci (Figs. 9, 17, 19B). Further research showed that the histological microstructures of the Korean fossil samples, especially those of *Koreaceratops*, closely resembled the bio-eroded human bones described by Hackett (1981).

He attributes bacteria and fungi to the destruction of a bone's histological features. The organisms demineralize the bone to gain access and consume the collagen, and this loss of collagen degrades the histological preservation of a bone (Hedges, 2002). The organisms then redeposit the bone minerals as waste, an act called 'cuffing,' which creates hyper-mineralized rims surrounding the tunnels and foci. It results in preserving the bone's outer morphology because the hyper mineralized rims in the bone act as support beams, while the innards are ravaged beyond recognition (Hackett, 1981). The ultimate result of such bioerosion is an obliteration of all histological features in a structurally sound bone except for its vasculature.

Hackett (1981) details that the tunnels and foci excavated by the microbes may or may not be devoid of contents. Empty tunnels are the norm because the redeposited minerals need to be flushed out with water to expose the fresh bone beneath in order for the tunneling to continue. In other cases, and especially in the mid-cortical bone regions, the tunnels may be filled with clearly biogenic fibrils in origin. Fibrils from freshly exhumed bones are typically black, while those from older bones appear as streaming bundles of refractile fibers. The reason why they are abundant in mid-cortical regions of a bone is thought to be because of the abundance of fresh bones for sustenance. Hackett (1981) also noted that osteon canals of a bone might be filled with plant rootlets and tubules of fungal origin. Whether the fibrils are bacterial or fungal in origin is not yet certain (Hackett, 1981). However, studies done by Owocki et al. (2016) and Suarez et al. (2018) reported black fibrous materials in their dinosaur bone histology, which they argued to be fungal mycelia that fossilized into ferromanganese crusts.

The description of bio-eroded bone by Hackett (1981) closely matches the state of preservation in the Korean dinosaur fossils used in this study. The entire bone cortex is riddled with tunnels and foci in all section slides (Figs. 5, 17, 19B). The bio-degradation experienced by the bones was so great to the point where most signs of lacunae, lamellae, cement lines, and canaliculi have been erased. Only their vasculature is preserved intact.

Many vascular canals and bone cortex in the Korean dinosaur bone samples are filled with black materials (Figs. 4, 19, 22). Judging by their location and appearance, they resemble the fibrils left by invading microorganisms (Hackett, 1981) and the remains of fungal mycelia fossilized as ferromanganese crusts (Owocki et al., 2016; Suarez et al., 2018). In the *Koreaceratops* fibula, these black clumps exist in high concentrations around the medullary cavity and medial part of the cortex, but not so much around the peri-cortical region (Fig. 4A). It is in line with the description made by Hackett (1981): the organisms start from the bone surface and dig their way into the cortex.

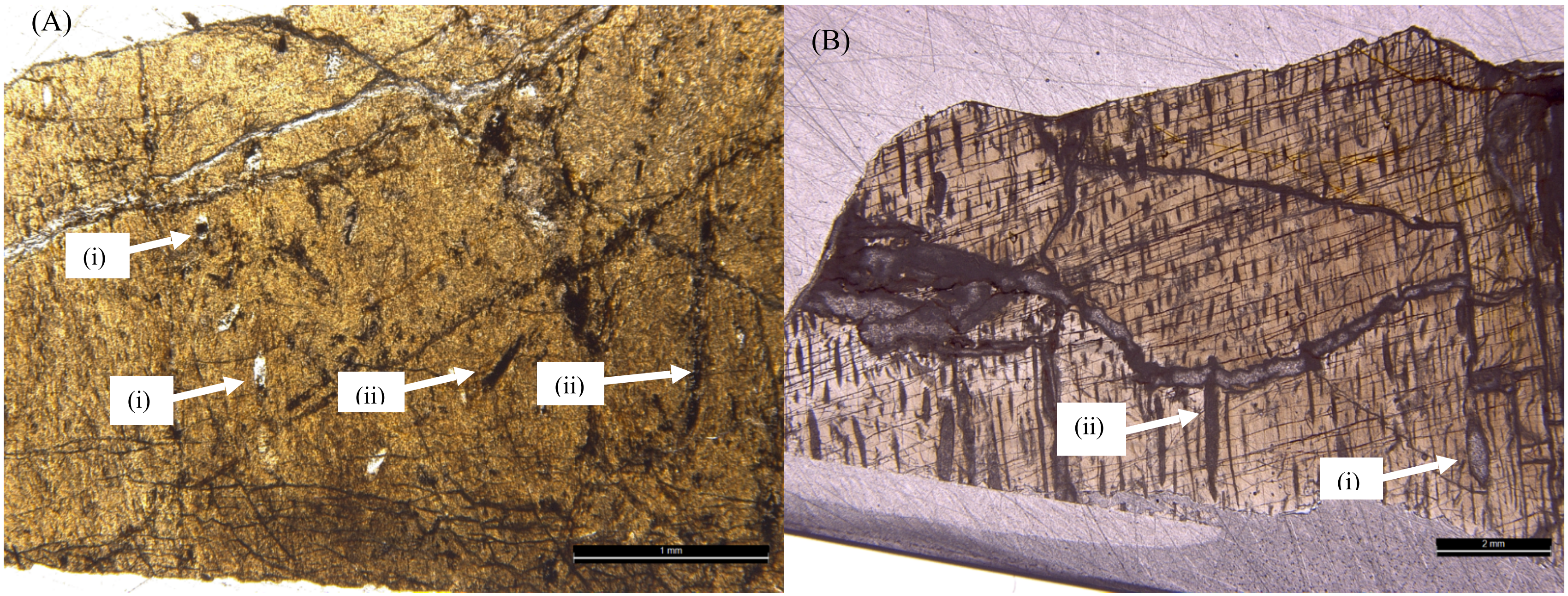

Figure 22.

Longitudinal section slides of (A) *Koreaceratops* right tibia and (B) unidentified Korean sauropod dorsal rib. Both slides show vasculature canals being (i) partially and (ii) fully filled with black materials. The black materials greatly resemble the hyphae and fibrils produced by fungi and bacteria in bio-degrading bones. The very poor preservation of histological features in the bones used in this study is most likely due to such bio-erosion before fossilization. Scale bar for (A) is 1mm and (B) 2mm. Both slides observed under normal light.

4.2. *Koreaceratops* right fibula

The preserved histological features of the *Koreaceratops* right fibula all point to a rapid osseous drift during the last three years of its life. The asymmetric growth of the growth intervals suggests the bone initially drifted toward the medial axis, then abruptly changed to the anterior axis during the final year (Fig. 7). Further evidence of an osseous drift is the bone resorption and deposition in the peri-medullary area, the hallmark of osseous drift (Enlow, 1962). The medullary cavity of *Koreaceratops* fibula is partially encircled with what initially seemed to be an endosteal bone, much like the one seen in a sub-adult *Psittacosaurus lujiatunensis*. However this is not so because the partially completed endosteal bone in a sub-adult *Psittacosaurus* is noted to be thin (Zhao et al., 2019). In contrast, the supposed endosteal bone in *Koreaceratops* fibula is very thick on the lateral side that sharply narrows to non-existence toward the medial side (Fig. 6). A similar phenomenon has been reported as a histological indicator for modeling drift, and it is called endosteal lamellar pocket (Maggiano et al., 2011). Endosteal lamellar pocket, or ELP, can be described as a semi-circular lamellar bone sequentially deposited on the medullary cavity surface opposite of drift direction. The ELP is also distinguished from other primary bones in that it possesses not longitudinal vasculature but primary Volkmann's canals. Primary Volkmann's canals are radial canals that penetrate from the medullary cavity and into the ELP, basically providing vascular supply to the ELP (Maggiano et al., 2016). The lamellar bone partially surrounding the medullary cavity of *Koreaceratops* fibula fits the description of ELP; it is formed on the opposite side of the drift direction, is a semi-circle, and possesses primary Volkmann's canals (Figs. 4, 6). On the side of the medullary cavity opposite the ELP, there are large resorptions of the bone cortex in the direction of the bone drift. These large erosion cavities observed in the medial parts are trabecularization of the cortex due to resorption (Fig. 4B).

A noteworthy aspect of the *Koreaceratops* fibula is the hoard of smaller erosion rooms that extend deep into the posterior and lateral mid-cortical zone (Fig. 4B). These could be previously deposited endosteal lamellar pockets in the process of being remodeled. It is because the hoard of erosion rooms is mainly located opposite to the osseous drift directions and their relatively small cavity size compared to the cavities in the trabecularized medial peri-medullary cortex.

As mentioned above, the *Koreaceratops* right fibula showed an exciting burst of growth in the final year of its life. The final growth interval in the anterior region of the cortex was thickest of all time, thicker than its two previous worth of growth put together. The final growth switched from low vascular density to high and possessed mostly reticular canals instead of longitudinal (Fig. 7c). It has been documented that bone growth rate increases with increased vascular canal density and bones with reticular canals grow faster than bones with longitudinal canals (Amprino, 1947; Ricqles et al., 1983, Castanet et al., 1996). All this points to a significantly increased growth speed in the final growing season. A similar phenomenon was reported in the fibula, femur, and tibia of four to six-year-old *Psittacosaurus lujiatunensis* and is interpreted as potential evidence of the postural shift from quadrupedality to bipedalism during its ontogeny (Zhao et al., 2013).

It is known that a bone cortex becomes thicker in the direction of increased mechanical stress it receives (Minns et al., 1975). Judging from the right fibula's long history of osseous drift and accelerated final growth, the *Koreaceratops* individual experienced constant biomechanical stress in its right hind limb. The sudden change in drift direction from medial to anterior axis may suggest a change in postural gait. Whether the acceleration of growth and change in drift direction in the *Koreaceratops* right fibula alone supports postural change is inconclusive. The absence of forelimbs and femur in the *Koreaceratops* individual prevents us from determining its method of locomotion before death, and the sudden accelerated growth in the right hind limb alone does not necessarily mean a change in postural gait.

4.3. *Koreaceratops* right tibia

The tibia of *Koreaceratops* showed a very different growth pattern from the fibula in terms of vasculature and growth marks.

The tibia maintains the vasculature pattern of longitudinal and circumferentially elongated primary osteons throughout the cortex. It suggests that the growth speed of the tibia was relatively constant. The vasculature may show changes in canal density according to the zone's color. The light brown zones possess less dense vasculature than the dark brown zones, but they do not exhibit changes in actual canal type (Figs. 10, 14). Consequently, the light brown zones are considered as a more slowly growing bone, probably lamellar of parallel-fibered, while the dark brown zones could be fibro-lamellar. The relatively good preservation of longitudinal and circumferentially elongated osteon canals throughout much of the cortex suggests a lack of secondary osteons. Also, the preserved zonations and the even distribution of small erosion rooms around the peri-medullary region only suggest that the tibia did not experience much bone remodeling or drift.

The spacing of growth zones in each cycle is roughly similar to the thickness of the cycle before it. The only exception to this is the final growth zone in the anteromedial region, for it shows a growth interval that is relatively thicker than its previous zones (Fig. 15b). Although this zone's vasculature type and density is pretty much the same as the fast-growing dark brown zones elsewhere in the cortex, the fact that the growth bulge is limited to the anteromedial side of the cortex suggests a change in biomechanical stress direction. It is somewhat similar to the shift of cortical growth direction seen in the outermost growth in *Koreaceratops* right fibula, but not as drastic since the vasculature type remains unchanged.

Judging from the total maximum number of eight zone alterations (Fig. 15), the minimum age of *Koreaceratops* before death can be estimated to be eight or nine years old. The absence of external fundamental systems and no signs of decreasing vascular density suggests that this individual was not physically or sexually mature.

4.4. Sauropod Dorsal Rib

The histological result of the unidentified Korean sauropod's dorsal rib was rather disappointing. It has been documented that sauropods do not keep well-preserved histological features in their long bones (Klein and Sander, 2008; Sander et al., 2011a). Later, Waskow and Sander (2014) proposed using the dorsal ribs as an alternative to long bones in sauropod bone histology. This idea was applied on *Camarasaurus* sp. (Sauropoda) dorsal ribs, and the research showed that the *Camarasaurus* dorsal ribs showed minimum bone remodeling in their most proximal regions, just after the capitulum. Of the dorsal ribs sampled, the third most anterior dorsal rib of *Camarasaurus* showed a maximum preservation of 87 percent of the growth record, counting at least 38 lines of arrested growth on its medial side of the cortex (Waskow and Sander, 2014).

The fact that the Korean sauropod dorsal rib used in this study had its proximal region preserved, and judged to be anterior rib due to its straight shape, made us have high hopes for its results. However, the produced histological slide of the specimen showed a bone cortex that was not only poorly preserved histologically but also heavily remodeled by secondary osteons (Figs. 20, 21).

A tiny band of primary bone exists in the outermost region of the anterior part of the cortex, and this place exhibits longitudinal-laminar vasculature and is devoid of any growth marks (Fig. 20). However, the amount preserved here was too small to deduce the sauropod's growth pattern. Another sliver of primary bone is shown in the medial portion of the rib section, and it preserved approximately five lines of arrested growth in the outermost part of the cortex (Fig. 21). The vasculature of the growth intervals between the lines of arrested growth is all longitudinal. We know that these are lines of arrested growth and not external fundamental systems due to the presence of vasculature between the lines (Cormack, 1987).

Despite sampling the optimal region of the most desirable dorsal rib, the results were simply not worth the effort. The cortex is so heavily remodeled that it would contain very little information to deduce its growth pattern even if it was spared from bioerosion. This disappointing result suggests that rib section histology may not always be a suitable alternative to long bone histology in sauropods.

The histology of our Korean sauropod dorsal rib differs from that of *Koreaceratops* fibula for the sauropod rib managed to preserve the cement lines of secondary osteons (Fig. 19A). This discrepancy can be explained by different types of tunnels/foci that organisms deploy as they bio-erode a bone's microstructure. Hackett (1981) documented the types of such bone eroding procedures: Wedl tunnels, longitudinal tunnels, budded tunnels, and lamellate foci. Wedl tunnels and lamellate foci are known to cross the cement lines of osteons, while longitudinal and budded tunnels are confined mainly within the cement lines (Hackett, 1981). The reason why only the cement lines are well preserved in the Korean sauropod rib section is probably due to the destruction procedures being limited to longitudinal and/or budded tunnels. Although it is assumed that fungi and bacteria make the tunnels and foci, their exact species are not known yet (Hackett, 1981).

4.5. Theropod Dorsal Rib

The poor quality of the theropod dorsal rib histology was predicted from the get-go. The bone's outer morphology was severely weathered before burial and fossilization (Lee, 2008). The proximal region of the rib was so poorly preserved that its mid-shaft was used instead (Fig. 2). The produced histology slide of the rib section showed a cortex that was 100 percent remodeled by secondary osteons, with chunks of missing bones and large crevices filled with matrix (Fig. 16).

One small interesting aspect of this theropod rib was that the histological features are preserved in a way very similar to the Korean sauropod rib used in this study. Both dorsal rib bones have the vasculature and cement lines preserved, while the rest of the histological features are nowhere to be seen (Fig. 17). It could mean the two rib bones were bio-eroded by similar organisms that created only longitudinal and budded tunnels. However, since we do not know the exact organisms and species responsible for such tunneling, we cannot deduce much further.

CHAPTER 5

DISCUSSION

5.1. Comparisons to *Psittacosaurus mongoliensis* and *P. lujiatunensis*

Dinosaurs like *Psittacosaurus mongolienses* and *P. lujiatunensis* are among the most basal members of the suborder Ceratopsia, much more primitive than the neoceratopsian *Koreaceratops hwaseongensis* (Lee et al., 2011). True to their phylogenic differences, *Koreaceratops* and *Psittacosaurus* bone histology do not show many similarities.

Both *Psittacosaurus mongoliensis* and *P. lujiatunensis* are known to exhibit well-preserved lines of arrested growth in all of their long bones (Erickson and Tumanova, 2000, Zhao et al., 2013, Zhao et al., 2019). *Koreaceratops,* on the other hand, only shows a paltry amount of lines of arrested growth in the outermost part of its right fibula, with the rest of its growth marks obliterated by bone remodeling. The right tibia of *Koreaceratops* did not show any signs of lines of arrested growth and showed exhibited zonation instead.

Koreaceratops and *Psittacosaurus* shared some similarities in the fibula vasculature. Both *Psittacosaurus mongoliensis* and *P. lujiatunensis* show alternating longitudinal and reticular vasculature in all of their long bones (Erickson and Tumanova, 2000; Zhao et al., 2013; Zhao et al., 2019). While radial canals have been reported in the femur and tibia of an eight-year-old *Psittacoaurus mongoliensis* (Erickson and Tumanova, 2000), the phenomenon was later attributed as a response to a pathology (Zhao et al., 2019). In the *Koreaceratops* right fibula, the surviving primary bones display the similar longitudinal and reticular vasculature pattern seen in *Psittacosaurus*. The same cannot be said for the *Koreaceratops* right tibia, for it displays longitudinal vasculature with circumferentially elongated osteon canals uniformly throughout its cortex.

It is known that bones of basal ceratopsians are primarily devoid of secondary osteons (Chinnery and Horner, 2007; Erickson et al., 2009). *Psittacosaurus* follows this pattern and retains most of its long bones' growth marks, with bone remodeling limited to the inner cortex (Erickson and Tumanova, 2000; Zhao et al., 2013; Zhao et al., 2019). The right tibia of *Koreaceratops* follows the same pattern but not in its right fibula. The *Koreaceratops* right fibula displays massive remodeling that spared only the outer anteromedial portion of the primary bone.

The lamellar bone partially surrounding the medullary cavity of *Koreaceratops* fibula may be mistaken as an incomplete endosteal bone is also shown in a sub-adult *Psittacosaurus lujiatunensis*. However, the lamellar bone in *Koreaceratops* fibula seems more likely to be an endosteal lamellar pocket that forms during an endocortical drift. It is further supported by the presence of bone trabecularization on the opposite side of its lamellar pocket. The very poor histological and structural preservation of the *Koreaceratops* tibia's peri-medullary region makes us unable to confirm the presence of endosteal lamellar in that area. However, the even distribution of small erosion rooms around the medullary cavity suggests that there was no drift.

Osseous drift has been reported in *Psittacosaurus mongoliensis* and *P. lujiatunensis* in the form of changing circumferential vascular patterns (Erickson and Tumanova, 2000; Erickson et al., 2009; Zhao et al., 2019), which is also the case for the *Koreaceratops* fibula. However, unlike *Psittacosaurus*, the *Koreaceratops* fibula possesses endosteal lamellar pockets with trabecularization in the peri-medullary cortex. The presence of erosion rooms deep into the mid-cortex suggests that the bone drift in *Koreaceratops* fibula was heavy and life-long.

5.2. Comparison to *Protoceratops andrewsi*

The *Koreaceratops* long bone histology showed remarkable similarities to that of sub-adult *Protoceratops andrewsi*. In 2018, Fostowicz-Frelik and Slowiak documented that the tibia, femur, and humerus of *Protoceratops andrewsi* do not show lines of arrested growth in their bone cortex. Instead, intercalating zones of different bone textures, also known as zonation, occur as substitutes (Fostowicz-Frelik and Slowiak, 2018). *Koreaceratops* follows this pattern by exhibiting zonation in its tibia cortex. In *Protoceratops andrewsi*, the zonation is formed by alternating zones of parallel-fibered and woven fibered bones. The exact bone texture of each zone in *Koreaceratops* is challenging to find out due to poor histological preservation. Instead, the existence of zones in the *Koreaceratops* tibia is discerned by its color and its degree of vascularization. In *Protoceratops andrewsi*, the darker zones are made of woven bones, while lighter zones are composed of parallel fibered bones (Fostowicz-Frelik and Slowiak, 2018). The zonation is the same in the *Koreaceratops* tibia since the light brown zones are typically less vascularized and thinner than the dark brown bands, suggesting that the light brown zones grew much slowly.

Comparisons of the femoral, humeral, and tibial bone cortex of *Protoceratops andrewsi* showed that the tibia preserved the maximum number of zones (Fostowicz-Frelik and Slowiak, 2018). If the same pattern can be applied to *Koreaceratops*, the eight dark brown zones in the tibia represent the maximum recorded age of the specimen.

The tibiae of both *Koreaceratops* and sub-adult *Protoceratops andrewsi* exhibit predominantly longitudinal vasculature. The difference is that the *Protoceratops andrewsi* tibia showed predominantly longitudinal canals in the peri-cortical region, longitudinal-reticular canals in the mid-cortex, and somewhat laminar canals in the peri-medullary region (Fostowicz-Frelik and Slowiak, 2018), while *Koreaceratops* tibia, on the other hand, maintains longitudinal with some circumferentially elongated osteon canals throughout the whole cortex. The only change in the vasculature is the more pronounced circumferential elongation of the osteon canals in the peri-medullary cortex (Fig. 14).

The limited scope of bone remodeling in the tibia is seen in both *Koreaceratops* and *Protoceratops andrewsi*. Both species have limited traces of remodeling in their tibia via the presence of small erosion cavities stationed evenly around the medullary cavity. In *Protoceratops andrewsi,* these erosion cavities are either filled or lined with lamellar bone (Fostowicz-Frelik and Slowiak, 2018); the same cannot be said in *Koreaceratops* tibia due to its very poor histological preservation.

The histology of fibula showed limited similarities between *Koreaceratops* and *Protoceratops andrewsi*. In *Protoceratops andrewsi*, the fibula is the only long bone that exhibits lines of arrested growth and annulus instead of zonation (Fostowicz-Frelik and Slowiak, 2018). *Koreaceratops* follows this pattern via the presence of lines of arrested growth and no zonation in its fibula. The main difference between the two is that in *Protoceratops andrewsi*, the fibula maintains longitudinal vasculature throughout the entire bone cortex (Fostowicz-Frelik and Slowiak, 2018). It contrasts to *Koreaceratops*, for its fibula exhibits either longitudinal or reticular canals and change vasculature patterns circumferentially.

The fibula was shown to have the highest level of bone remodeling among the long bones of *Protoceratops andrewsi* (Fostowicz-Frelik and Slowiak, 2018; Horner et al., 2000; Chinsamy-Turan, 2005). Similarly, the *Koreaceratops* fibula is more remodeled than its tibia. The degree of bone remodeling in the fibula is also similar between *Protoceratops andrewsi* and *Koreaceratops*. An adult *Protoceratops andrewsi* fibula preserved four to five lines of arrested growth in its primary bone, with the rest being destroyed by secondary bones and osseous drift (Fostowicz-Frelik and Slowiak, 2018). It is somewhat similar to the fibula of *Koreaceratops*, which managed to preserve just three lines of arrested growth amid all the remodeling and bone drift.

5.3. Relationships of *Koreaceratops* with *Psittacosaurus* and *Protoceratops*

The histological results of *Koreaceratops* right tibia and fibula support the proposed phylogenic tree: the neoceratopsian *Koreaceratops* is located between the more primitive *Psittacosaurus* and the more derived *Protoceratops*, though with much closer similarity toward the *Protoceratops andrewsi*.

The histological features observed in *Koreaceratops* right fibula and tibia are very much similar to those of *Protoceratops andrewsi*, though a hint of basal Ceratopsian features is still present. Both *Koreaceratops* and *Protoceratops andrewsi* exhibit zonation as growth marks, have predominantly longitudinal vasculature in their tibia, show more bone remodeling in their fibula than the tibia, and the presence of lines of arrested growth in their fibula only. *Koreaceratops* still possesses the basal ceratopsian *Psittacosaurus* feature of circumferentially alternating longitudinal and reticular vasculature patterns, although this too is limited to its fibula only.

A histological feature unique to *Koreaceratops hwaseongensis* is that, unlike *Protoceratops andrewsi* and *Psittacosaurus*, its tibia did not show circumferentially alternating vascular patterns. Instead, the right tibia of *Koreaceratops* showed longitudinal and circumferentially elongated osteon canals throughout the whole cortex. It suggests that the tibia of *Koreaceratops* did not experience significant growth spurts and its cortical growth thickness depended primarily on seasonal conditions as in *Protoceratops andrewsi* (Fostowicz-Frelik and Slowiak, 2018). The primarily longitudinal canals in *Psittacosaurus* and *Protoceratops andrewsi* long bones meant that the two species probably grew in a moderate tempo (Fostowicz-Frelik and Slowiak, 2018), implying that the same may be the case for longitudinal canal dominated *Koreaceratops hwaseongensis*.

5.4. Paleoclimate of Cretaceous Korea

Hackett (1981) noted that the microbial tunneling of buried bones occurs best in an environment with moderate soil moisture and seasonal fluctuation in temperature and water table. Congruently, microbial histological degradation enhanced by seasonally wet-dry climate has been reported in an *Auroraceratops rugosus* skeleton from the Albian Zhonggou Formation of Gansu Province, China (Suarez et al., 2018). It has been argued that the paleoclimate of the southern parts of the Korean peninsula, like Early Cretaceous Hasandong time, was semi-arid with seasonal wet-dry cycles (Paik, 2000; Paik et al., 2001). The poor preservation of histological features in the *Koreanosaurus* left femur (Kim et al., 2017) and all of our Korean dinosaur fossil samples supports the seasonal semi-arid paleoclimate of Cretaceous Korea.

CHAPTER 6

CONCLUSIONS

Our research showed that the very poor histological preservations in all of our Korean dinosaur fossils used in this study are not due to pressure or calcite intrusion but via microscopic tunnels made by fungi and bacteria. All of the bones sampled for histology are riddled with globules and foci made by microbes, along with the presence of their fibrils fossilized into black ferromanganese crusts.

The observation of *Koreaceratops hwaseongensis* (KIGAM VP 200801) long bone histology revealed that its right hind limb experienced an osseous drift and growth spurt toward the anteromedial direction. The specimen was apparently experiencing a change in its biomechanics that was intense and life-long. The absence of forelimbs and limited sampling on the right hind limb only prevents us from concluding that such drift is a sign of the shift in postural gait. The lack of the external fundamental system or decreased vascularity in the outer part of the cortex suggests that *Koreaceratops hwaseongensis* was not yet mature physically or sexually.

The comparisons of histological results of *Koreaceratops* to those of other ceratopsians like *Psittacosaurus* and *Protoceratops andrewsi* showed that *Koreaceratops* shared more similarities with *Protoceratops andrewsi* than *Psittacosaurus*. Both *Koreaceratops* and *Protoceratops andrewsi* display zonation of their tibiae and lines of arrested growth in their fibulae, as well as more bone remodeling in their fibulae than their tibiae. Both *Koreaceratops* and *Psittacosaurus* share the presence of reticular canals and circumferential changes in the vascular patterns in their fibulae. Such observation conforms to the phylogenic placement of *Koreaceratops*, which places it between the more primitive *Psittacosarurus* and more derived *Protoceratops andrewsi*. The exact placement of *Koreaceratops hwaseongensis* in the Ceratopsian family tree would be enhanced by the discoveries of more basal ceratopsians and more extensive histological studies of them in the future.

The intensive bio-degradation of histological features in all sampled Korean dinosaur fossils offers support to semi-arid with seasonally wet-dry paleoclimate in the Cretaceous Korean peninsula.

The heavily remodeled proximal dorsal rib of a Korean sauropod suggests that rib bones may not always be reliable for histological studies. Instead, the rib bone histology may be more species-specific than previously thought.

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국문초록

지난 30 년 동안 대한민국에서 공룡 발견이 급증하면서 한국 공룡에 대한 대중의 관심이 높아졌습니다. 그러나 발견된 한국 공룡 골격화석들은 전부 파편적이고 불완전하여 많은 학문적 데이터를 얻지 못했습니다. 이를 해결하기 위하여 얇은 뼈단면 조직학 연구를 통해 백악기 공룡 화석들의 외부가 아닌 내부 미세 구조를 관찰하였습니다. 공룡들의 계통 발생, 고환경 및 역학을 뼈 조직학으로 밝히기 위해 수각류와 용각류의 갈비뼈, 그리고 *Koreaceratops hwaseongensis* 의 경골과 비골을 샘플링했습니다. 연구결과 채취된 모든 공룡뼈들은 미생물 분해로 인해 조직학적 보존이 불량한 것으로 나타났습니다. 침입한 미생물에 의해 만들어진 미세한 터널들은 공룡뼈를 소구체와 병소의 덩어리로 만들었습니다. 결과적으로 뼈 피질의 lacunae, canaliculi 및 lamellar 와 같은 거의 모든 조직학적 특징들이 지워져 있었습니다. 그러나 혈관 구조와 성장 표시와 같은 조직학적 특징의 몇 가지 남은 흔적들을 통해 코리아케라톱스 화성엔시스의 성장 패턴이 프로토케라톱스 앤드류아이의 성장 패턴과 매우 유사하다는 것을 확인할 수 있었습니다. 두 종 모두 경골에 약간의 뼈가

재형성되고, 비골에는 광범위한 뼈가 재형성되는 동시에 성장이 멈추는 선 (Lines of arrested growth)을 가지고 있습니다. 또한 코리아케라톱스 화성엔시스와 원시 각룡류 *Psittacosaurus mongoliensis* 와 *P. lujiatunensis* 사이의 유일한 조직학적 유사성은 비골의 세로 및 망사 혈관 구조라는 것을 발견했습니다. 이는 코리아케라톱스가 계통발생 측면에서 프시타코사우루스보다 프로토케라톱스에 훨씬 더 가깝다는 것을 의미합니다. 코리아케라톱스 화성엔시스의 비골은 처음에는 내측 축으로 이동하였으나 최종 성장 구간에서 앞축으로 급격히 변하는 일정한 골 유동을 보였습니다. 오른쪽 경골의 최종 성장이 앞쪽 내측 골 편류를 보이는 것은 코리아케라톱스 화성엔시스가 죽기 전에 오른쪽 뒷다리의 생체 역학에 변화를 경험했음을 시사합니다. 경골의 성장 영역 전환 횟수는 코리아케라톱스 개체가 사망 당시 약 8 세 였음을 시사합니다. External fundamental system 이 없고 외피 질의 혈관이 감소하지 않는 것은 코리아케라톱스가 신체적 또는 성적으로 성숙하지 않았음을 나타냅니다. 코리아케라톱스 화성엔시스 장골의 세로형 혈관이 다수인 혈관 구조는 다른 원시 각룡류와 마찬가지로 온건한 성장 속도를 경험했음을 시사합니다. 수각류와 용각류 공룡의 갈비뼈들은 심한 뼈 재형성과 심한 미생물 침식으로 인해 조직학적 정보를 별로 얻을 수 없었습니다. 이는 뼈가

미생물에 의한 뼈 분해에 유리한 반 건조 기후 체제에 묻혔음을 의미하며, 이는 백악기 동안 한반도가 미생물 뼈 분해에 유리한 반건조기후를 가졌음을 시사합니다. 심하게 재형성 된 용각류 갈비뼈의 피질은 갈비뼈의 근위 부분이 항상 장골 조직학을 대신할 신뢰할 수있는 대안이 아닐 수 있음을 시사합니다.

주요어: 코리아케라톱스, 각룡류, 조직학, 뼈조직학, 전기 백악기, 대한민국

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