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Unusual Endosteally Formed Bone Tissue in a Patagonian Basal Sauropodomorph Dinosaur

IGNACIO A. CERDA,[1,2]* ANUSUYA CHINSAMY,[3]* AND DIEGO POL[1,4]*
[1]Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Av. Rivadavia 1917 (C1033AAJ), Ciudad Autónoma de Buenos Aires, República Argentina
[2]Instituto de Investigación en Paleobiología y Geología, Universidad Nacional de Río Negro, Museo Carlos Ameghino, Belgrano 1700, Paraje Pichi Ruca (predio Marabunta), Cipolletti, Río Negro, Argentina
[3]Department of Biological Sciences, University of Cape Town, Private Bag X3, Rondebosch, Cape Town, South Africa
[4]Museo Paleontológico Egidio Feruglio, Avenida Fontana 140, Trelew, Chubut, Argentina

ABSTRACT

Mussaurus patagonicus (Dinosauria: Sauropodomorpha) is a basal sauropodomorph from the Late Triassic of southern Argentina that is known from a large number of individuals, including juveniles, subadults, and adults. Here, we report on the occurrence of an unusual bone tissue in an individual of *M. patagonicus*. The rather atypical bone tissue is located within the femoral medullary cavity and also occurs within several erosion cavities of the midinner part of the cortex. This tissue is well vascularized and is composed of a matrix that consists of abundant and densely packed osteocyte lacunae. Although some features of this tissue resembles avian medullary bone, the histological features are distinctive and share more features with the pathological, reactive bone produced in extant birds in response to a retrovirus-induced disease (avian osteopetrosis). Here, we also discuss and provide histological features to effectively differentiate endosteally formed medullary bone from pathological avian osteopetrosis. Anat Rec, 297:1385–1391, 2014. © 2014 Wiley Periodicals, Inc.

Key words: bone histology; Dinosauria; Sauropodomorpha; medullary bone; bone pathology; avian osteopetrosis

INTRODUCTION

The presence of “unusual” endosteally deposited bone tissues in non-avian dinosaurs have been previously interpreted as either avian-like medullary bone (Schweitzer et al., 2005; Lee and Werning, 2008; Hübner, 2012) or as pathological tissue (Chinsamy and Tumarkin-Deratzian, 2009). The former is an ephemeral bony tissue that forms before ovulation in the medullary cavities of female bird bones and acts as a calcium source for egg shelling (Taylor and Moore, 1953; Bonucci and Gherardi, 1975; Schraer and Hunter, 1985). Endosteally deposited bone tissues described in the medullary cavities of two non-avian theropods (*Tyrannosaurus rex* and *Allosaurus*) and two ornithopod dinosaurs (*Dysalotosaurus* and *Tenontosaurus*) have been interpreted as

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*Correspondence to: Ignacio Cerda; CONICET, Instituto de Investigación en Paleobiología y Geología, Universidad Nacional de Río Negro, Museo Carlos Ameghino, Belgrano 1700, Paraje Pichi Ruca (predio Marabunta), Cipolletti, Río Negro, Argentina. Fax: +41 02920 428602. E-mail: nachocerda6@yahoo.com.ar

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Fig. 1. Right femur of *Mussaurus patagonicus* MLP 61-III-20-22. Dashed lines show the location and orientation of the thin sections.

homologous to avian medullary bone (Schweitzer et al., 2005; Lee and Werning, 2008; Hübner, 2012). In these dinosaurs, the identification of medullary bone was based on the location of the unusual bone (i.e., within the medullary cavity of long bones), origin (endosteal), and microstructure (spicules of highly vascularized bone tissue). Contrarily, Chinsamy and Tumarkin-Deratzian (2009) reported a distinctive periosteal reactive bone tissue accompanied by endosteal bone deposits in the medullary cavity of an extant turkey vulture (*Cathartes aura*) and a non-avian dinosaur from Transylvania. Given that the endosteal and periosteal reactive bone tissues were pathological in the vulture and that the endosteally formed bone in terms of location and morphology is similar to the medullary bone tissues described in non-avian dinosaurs, Chinsamy and Tumarkin-Deratzian (2009) cautioned that not all endosteally derived bone tissues were homologous to avian medullary bone.

During a recent histological study of limb bones of the basal sauropodomorph dinosaur *Mussaurus patagonicus* from the Late Triassic of Argentina, an unusual endosteally formed bone was observed in a large femur. This tissue was initially interpreted as homologous to that avian medullary bone (Cerda and Pol, 2013), on the basis of its location, origin, and microstructure, and concurred with the reports of medullary bone in non-avian dinosaurs. Here, we provide a detailed histological description of the unusual endosteally deposited bone in *M. patagonicus* and provide evidence for the pathological origin of this tissue.

MATERIALS AND METHODS

The right femur of *M. patagonicus* (collection identification: 61-III-20-22) from the Museo de La Plata (MLP), Argentina was sampled for histological analysis (Fig. 1). The bone measures ~80 cm in length (the distal-most end has been partially eroded), and is part of an incomplete skeleton that includes several appendicular and axial bones, including right ilium, both pubes, both femora, both tibiae, both fibulae, both pes, four dorsal vertebrae, sacrum, and rib fragments (Casamiquela, 1980; Otero and Pol, 2013). The material was collected from the type locality of the Laguna Colorada Formation (El Tranquilo Group; Herbst, 1965; Jalfin and Herbst, 1995), Santa Cruz Province, Argentina. Although this material was originally referred to the genus *Plateosaurus* by Casamiquela (1980), several authors (Galton, 1990; Galton and Upchurch, 2004; Pol and Powell, 2005; Salgado and Bonaparte, 2007) have suggested that these materials belong to *M. patagonicus*, for which several posthatchling individuals were collected at the same locality (Bonaparte and Vince, 1979; Pol and Powell, 2007). The referral of MLP 61-III-20-22 to *M. patagonicus* was recently corroborated by Otero and Pol (2013). For the histological analysis, a complete section of ~3 cm was obtained from the midshaft, below the fourth trochanter. To avoid loss of information about the morphology and size, a cast of the extracted sample was generated and used to reconstruct the sampled bone.

Specimens were prepared for thin sections based on the methodology outlined in Chinsamy and Raath (1992). The preparation of the histological sections was carried out in Museo Paleontológico Egidio Feruglio (Trelew, Argentina). The slices were studied using petrographic polarizing microscope (Nikon E400). Nomenclature and definitions of structures used in this study are derived from Francillon-Vieillot et al. (1990) and Chinsamy-Turan (2005). Although not strictly accurate

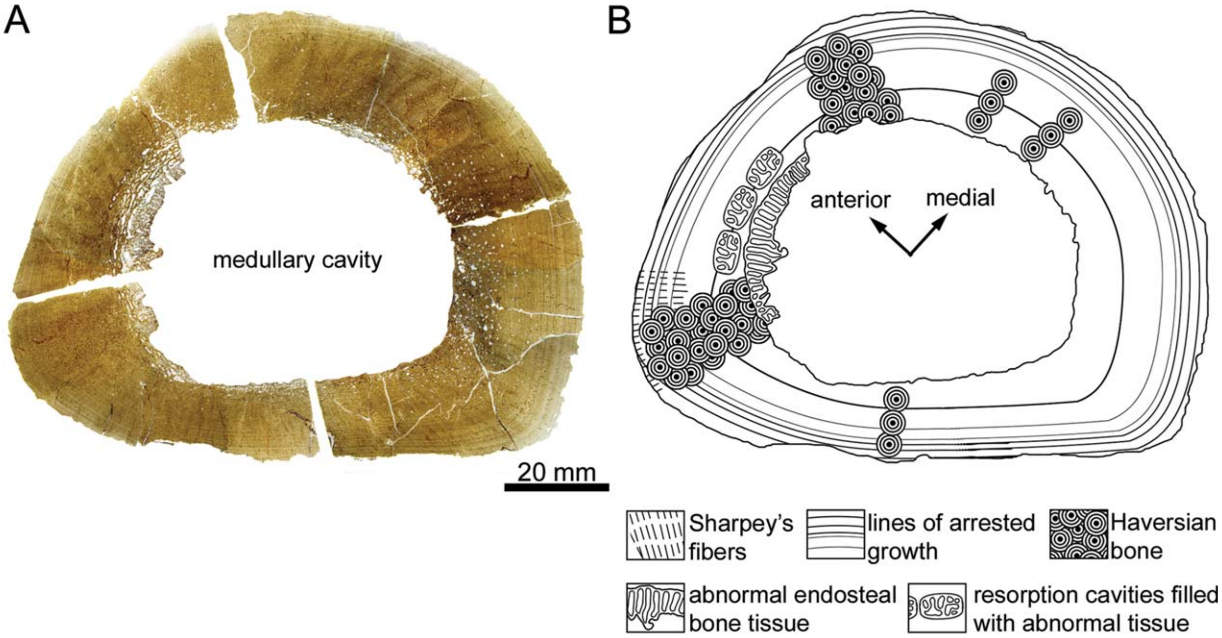

Fig. 2. Complete transverse midshaft section of the right femur of *Mussaurus patagonicus* (MLP 61-III-20-22). **A**: Entire section viewed under normal light. The scheme in **B** indicates the main histological features of the section. High-resolution version of the figure is available from the authors on request.

(Starck and Chinsamy, 2002), we consider the channels within the bone to reflect the extent and organization of vascularization.

DESCRIPTION

The thin section of the femoral midshaft is composed of a thick layer of compact bone, which surrounds a large medullary cavity (Fig. 2). Besides the distinctive microanatomical variation between the inner and the outer cortex, histologically, there is clear variation between the different portions of the cortex (i.e., anterior, posterior, medial, and lateral). The cortical bone tissue consists predominantly of highly vascularized fibrolamellar bone. The fibrous matrix of the fibrolamellar tissue is not regularly woven and, under polarized light, several regions (e.g., anterior region and outer cortex) of the bone appears to be well-organized (showing general anisotropy under crossed nicols). Vascular channels tend to mostly have a plexiform arrangement, although in some regions longitudinally oriented channels predominate. In other areas, instead, a circumferential arrangement of the channels is present. Lines of arrested growth (LAGs) are well developed across the entire compacta, and they tend to be more closely spaced toward the external part of the cortex (Fig. 3A). Closely spaced growth lines indicative of substantial truncation in growth appears to be preserved at the lateral part of the cross section, however, given that the most external part of the cortex has been eroded it is not possible to confirm that this reflects a cessation of growth. Sharpey's fibers, penetrating the cortical bone at straight or slightly oblique angles are especially abundant in the outer cortex at the anterolateral region of the cross section. Secondary osteons are commonly developed in the midmedullary to perimedullary part of the cortex. In the anteromedial and anterolateral regions of the cross section, secondary osteons form two wide "columns" of dense Haversian bone (Fig. 3B). In some areas (e.g., lateral region of the cortex), some LAGs are interrupted by laminae of secondary osteons. Large resorption cavities are present in the perimedullary region (Fig. 3C). The erosion spaces located at the innermost cortex tend to be thin centripetal deposits of secondarily formed lamellar bone. Larger resorption cavities are most commonly developed at the posterior and anterior regions of the cortex.

A distinctive feature of the anterior, lateral half of the section is the presence of a layer of unusual bone that extends centripetally 8 mm from the perimedullary margin (Fig. 3D). The gross microanatomy of this layer is easily observed with the naked eye. The overall structure of this bone tissue is distinctive from that of the compacta. It consists of a finely cancellous structure with bony spicules that project into the medullary cavity (Fig. 3E). A tide line separates it from the internal lamellae of the perimedullary cortex, thereby revealing its endosteal origin. The bone spicules are formed by a matrix that is composed of abundant and densely packed small lacunae (Fig. 3F–H). This osseous matrix is isotropic under polarized light (Fig. 3G). The osteocyte lacunae density is so high that the interosteocyte lacunae space is almost inexistent. Given that the space in which the intrinsic fibers of the bone were deposited is reduced in extreme, the fibrous component of the matrix is poorly developed. The vascular spaces of the spicular network are coated by a thin layer of lamellar bone tissue. Interestingly, this unusual tissue is not restricted to the medullary cavity, and it also occurs within several resorption cavities of the inner compacta (Fig. 3I–K). The unusual bone tissue located inside the resorption cavities tends to be more compact in appearance than the trabecular-like bone in

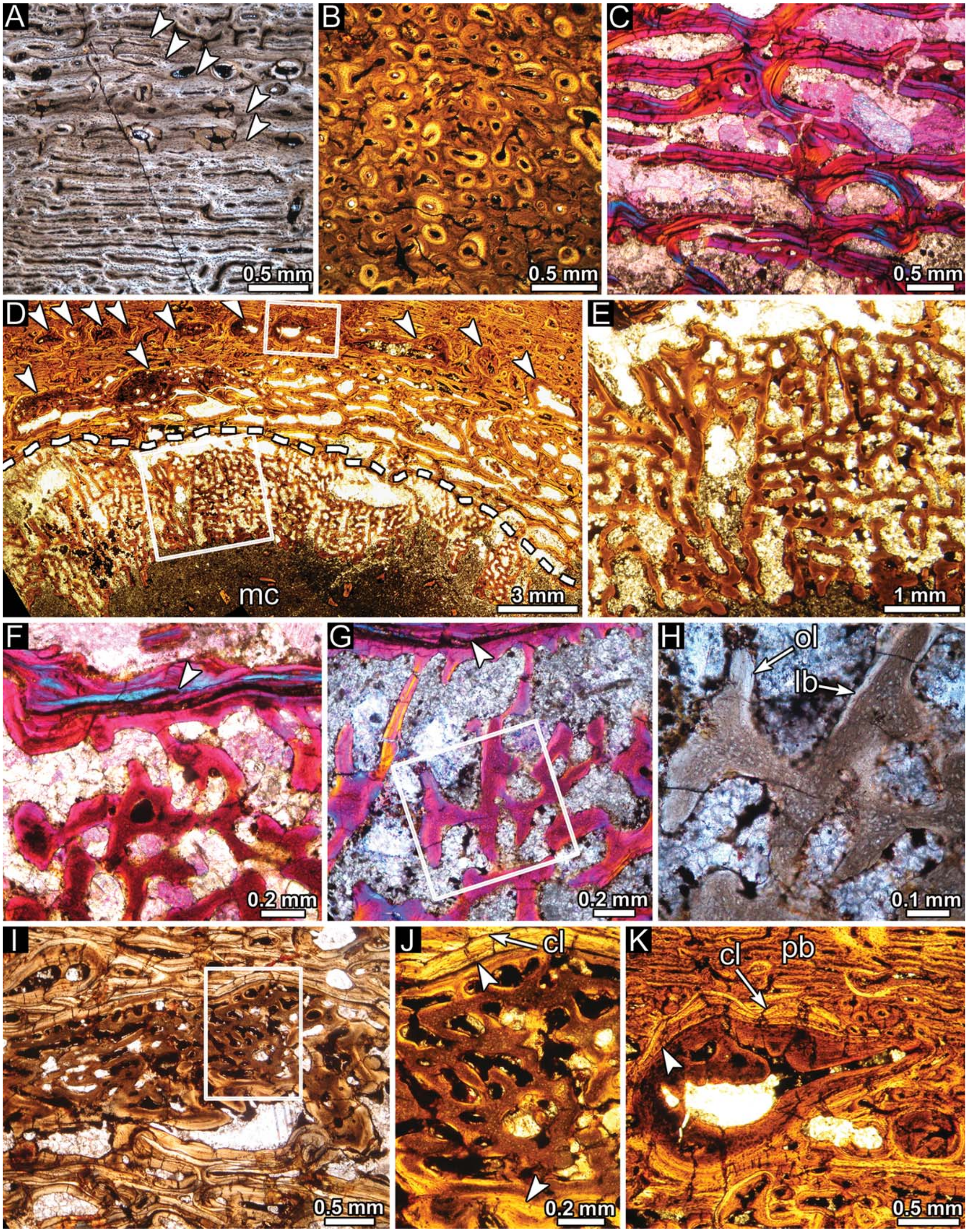

Fig. 3. Histology of *Mussaurus patagonicus* MLP 61-III-20-22. **A**: Compact bone at the mid cortex composed almost entirely of primary bone tissue. Arrowheads indicate LAG. **B**: Dense Haversian bone tissue at the mid cortex. **C**: Large resorption cavities located at the perimedullary region. **D**: General view of the perimedullary region. The dashed line indicates the boundary between the perimedullary cortex and the unusual endosteal bone inside the medullary cavity (mc). Several resorpion cavities filled with abnormal endosteal bone tissue are indicated by arrowheads. **E**: General view of the abnormal endosteally deposited bone tissue (box inset in D). **F, G**: Enlarged view of the abnormal endosteal bone tissue. The arrowhead indicates the boundary between the lamellar bone of the perimedullary cortex and the abnormal tissue. **H**: Detail of the abnormal endosteal bone tissue. (box inset in G). Notice the high density of osteocyte lacunae of the bone matrix. Bony spicules are covered by a thin layer of lamellar bone tissue (lb), which possesses few and elongated osteocyte lacunae. (ol). **I–K**: Resorption cavities of the perimedullary cortex filled with abnormal endosteal bone tissue. (J and K correspond with box inset in I and D respectively). Note that the abnormal endosteal bone was formed inside a resorption cavity partially filled with normal lamellar bone tissue, which is clearly separated from the primary bone (pb) by a cementing line (cl). The arrowheads indicate the boundary between the secondary lamellar bone and the abnormal endosteal tissue. High-resolution version of the figure is available from the authors on request.

the medullary cavity, but both tissues have similar histological characteristics (i.e., a matrix with abundant lacunae-like spaces and vascular channels coated by lamellar deposits of bone). This pattern extends from the inner to mid region of the cortex, where erosion cavities become less abundant and smaller.

DISCUSSION

Besides the presence of unusual bone tissues, the histological analysis of the *M. patagonicus* femur (MLP 61-III-20-22) reveals a large amount of histological variation around the entire cross section. Such histological variation can be attributed to a number of factors. Aside from the more typical development of secondary osteons near the perimedullary cortex, there are also three distinct occurrences of secondary osteons: (1) radiating in small groups from the inner cortex (mostly at the medial region; Fig. 2B); (2) large patches of dense Haversian bone tissue in the anterolateral and anteromedial portions of the cortex and; (3) circumferential laminae of Haversian osteons intersecting some LAGs at the outer cortex. The first two patterns are possibly related with mechanical stress endured by the bone (Currey, 2002). Currey (2002) suggests that during locomotion, stress and strain generate microcracks in particular areas of the bone that induce the differential development of Haversian bone. The presence of massive patches of dense Haversian bone at the anteromedial and anterolateral portions of the cortex is particularly significant, because these regions correspond to the area of insertion of the *femorotibialis internus* and *femorotibialis externus* muscles (Cooper, 1981; Carrano and Hutchinson, 2002; Otero and Vizcaíno, 2008; Otero and Pol, 2013). Given that the forces produced by large muscle mass can generate microcracks in the associated cortical bone (Bennell et al., 1996), the secondary reconstruction recorded at the anteromedial and anterolateral portions of the cortex could be induced by biomechanical forces caused during locomotion.

The distribution of Sharpey's fibers in the compacta is also quite variable. They show a more dense distribution in the outer cortex along the lateral half of the anterior region. As previously mentioned, this region is closely located to the area of insertion of the *femorotibialis* muscles, and the preferential distribution of the Sharpey's fibers is quite likely related to this muscular attachment area.

The reported histological variation across the whole cross section of the femur emphasizes the significance of obtaining complete sections of the bone for histological studies. This is particularly important in this case: if the description was only based on a bone core from the anteromedial or the anterolateral regions, the occurrence of the dense Haversian bone would have led to a very different interpretation of the animal's bone microstructure.

Unusual Endosteal Bone in MLP 61-III-20-22: Pathological or Medullary Bone?

Considering the location of the unusual bone tissue, its microanatomy, and microstructure, we can test whether the unusual tissue is homologous to avian medullary bone or if it is indeed a pathologically formed tissue. In extant birds that produce medullary bone, this tissue is usually formed inside the medullary cavity of long bones (e.g., femur), but can spread to other parts of the skeleton in derived groups (Taylor and Moore, 1953). Schweitzer et al. (2005) noted that the microanatomy of avian medullary bone is variable, and explained this variation in terms of the degree of porosity and orientation of the vascular channels or sinuses. Regardless of the degree of microanatomical variation, the avian medullary bone is characterized by a high degree of vascularization (Bonucci and Gherardi 1975; Schweitzer et al., 2005; Lee and Werning, 2008). Considering the fine microstructure, avian medullary bone is composed of a matrix of fibrous, woven bone tissue, and has randomly oriented fibers (Bonucci and Gherardi, 1975; Scharer and Hunter, 1985; Schweitzer et al., 2005). Given that the interosteocyte lacunae space is almost inexistent in the bone matrix of the abnormal tissue of MLP 61-III-20-22, its fibrous component is poorly developed in comparison with a typical woven tissue. The main feature of the unusual bone of MLP 61-III-20-22 is the extremely high density of osteocyte lacunae. Additionally, the vascular spaces in the abnormal endosteal bone of the sauropodomorph dinosaur are coated by a thin layer of lamellar bone. These features are absent in medullary bone of extant birds (Candlish, 1971; Bonucci and Gherardi, 1975; Schweitzer et al., 2005). Although the position and origin of the unusual endosteal bone in MLP 61-III-20–22 coincides with those inferred as avian-type medullary bone in dinosaurs (Schweitzer et al., 2005; Lee and Werning, 2008; Hübner, 2012), its fine microstructure is quite different from avian medullary bone and supports a pathological origin for this tissue.

Aetiology

Several kinds of osseous pathologies (e.g., Paget disease, osteopetrosis, osteomyelitis) generate reactive endosteal bone tissues in the bones of extant animals and could be related to the formation of abnormal endosteal tissue in MLP 61-III-20-22. The unusual tissue in *M. patagonicus* appears to differ from endosteal reactive bone generated by Paget disease. In this disease, the endosteal reactive bone is mostly composed of lamellar bone (Aoki et al., 1984), which is clearly different from the endosteal tissue formed in MLP 61-III-20-22. Under low magnifications, the microstructure of the abnormal tissue of MLP 61-III-20-22 resembles tissues that form as a product of metastasic cancer, chronic suppurative osteomyelitis, and fracture repairing (e.g., network of spicules arising from the perimedullary surface). However, the reactive bone produced by these diseases is formed by woven bone tissue (Aoki et al., 1984; Rothschild and Martin, 2006). As described above, the extremely high cellularity and poorly developed fibrous component of the mineralized matrix of the abnormal tissue of MLP 61-III-20-22 is atypical of woven bone tissue.

The only disease that produces a reactive endosteal bone tissue similar to that observed in our sample is avian osteopetrosis. This disease is a retrovirus-induced bone disorder characterized by diaphyseal enlargement of the long bones, often associated with other gross histopathological alterations (Holmes, 1961; Bell and Campbell, 1961; Boyde et al., 1978; Frank and Franklin, 1982; Kirev, 1984). The histopathology and aetiology are different from those of mammalian osteopetrosis, which is genetically determined and is related to a failure of resorption of the bone deposited on the calcified cartilage of growth centers, resulting in the failure to produce a normal marrow cavity in the long bones (Tolar et al., 2004; Stark and Savarirayan, 2009). Avian osteopetrosis, instead, produces distinctive periosteal reactive bone deposition accompanied by endosteal bone deposits in the medullary cavity (although in some instances only endosteal reactive bone results) (Holmes, 1961). The microstructure of these reactive bones (periosteal and endosteal) is characterized by the presence of abundant and densely packed osteocyte lacunae, which are embedded in a poorly fibrous matrix (Bell and Campbell, 1961; Boyde et al., 1978; Kirev, 1984). Furthermore, Boyde et al. (1978) noted the presence of coatings of lamellar bone around the vascular spaces. These histological features coincide with our observations in the abnormal endosteally deposited bone tissue in MLP 61-III-20–22. Given that the outermost cortical bone has been eroded in MLP 61-III-20-22, it is not possible to determine if the typical radial bony growths produced commonly in avian osteopetrosis (Boyde et al., 1978; Smith and Morgan, 1984) was present in this specimen.

Implications for the Identification of Avian Medullary Bone in Dinosaurs

The evidence for an avian-like, retroviral induced disease in the Late Triassic basal sauropodomorph dinosaur *M. patagonicus* has several implications: First, as previously pointed out by Chinsamy and Tumarkin-Deratzian (2009), not all endosteally derived tissues in non-avian dinosaurs can be considered homologous to avian medullary bone. Second, if a reactive, well-vascularized endosteal bone is identified within the medullary cavity, it is necessary to determine if other abnormal tissue occurs subperiosteally. If such abnormal periosteal bone is identified, the unusual histology is more likely to be related to a pathological condition. Third, if the abnormal bone is only developed around the perimedullary cavity, the fine microstructure must be thoroughly assessed to discern between the avian medullary bone and the endosteal bone formed as a result of avian osteopetrosis. Thus, it is imperative that future studies reporting endosteal bone tissues in fossil dinosaurs (including birds) must include detailed histological description of such tissues, particularly in terms of the extent of osteocyte lacunae (i.e., cellularity). Also, cellularity needs to be comparatively quantified across multiple pathologies and in medullary tissues.

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