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Intravascular microstructures in trabecular bone tissues of *Tyrannosaurus rex*

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Abstract – Histological analyses of trabecular tissue from the limb bones of a *Tyrannosaurus rex* revealed the presence of small (average 25 µm) round microstructures in the vascular channels of the bone. These bony tissues otherwise evidenced minimal diagenetic change, and no secondary mineral deposition was observed in the vessel channels. While we have published analyses of the bony tissues of this specimen, we have not published data obtained on these small intravascular microstructures. Several characteristics link these microstructures to endogenous biological components, although their origin is not confirmed, and several hypotheses are considered. A discussion of the meaning of the term 'organic preservation' and a suggestion of criteria that should be met to be described as such is included. © Elsevier, Paris.

dinosaur / *Tyrannosaurus* / intravascular structures / organic reservation

Résumé – Microstructures intravasculaires dans l'os trabéculaire du *Tyrannosaurus rex*. L'examen histologique d'os trabéculaire provenant d'os longs de *Tyrannosaurus rex* a révélé la présence de petites microstructures arrondies (de 25 µm en moyenne) dans la lumière des canaux vasculaires. Ces tissus osseux ne présentent par ailleurs qu'un minimum de transformations diagénétiques, et l'on n'a pas observé de dépôts secondaires de minéraux dans la lumière des canaux vasculaires. Nous avons déjà publié des analyses concernant ce tissu osseux mais nous présentons ici les premières données concernant les microstructures globulaires observées dans la lumière des canaux vasculaires. Plusieurs caractéristiques les rapprochent de composés biologiques d'origine endogène et bien que leur origine et signification ne puissent encore être démontrées avec certitude, nous passons en revue plusieurs hypothèses les concernant. Ceci nous conduit à discuter ce que l'on entend par « conservation organique » et à proposer des critères à remplir pour que ce type de conservation soit acceptable en tant que tel en paléontologie. © Elsevier, Paris.

dinosaure / Tyrannosaurus / microstructures intravasculaires / conservation organique

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INTRODUCTION

In the spring of 1990, a specimen of *Tyrannosaurus rex* was recovered from the Hell Creek Formation in eastern Montana, and brought to the Museum of the Rockies for preparation. At the time of its discovery, this specimen (MOR 555) was buried under approximately 1 to 1.5 m of stream channel and point bar deposits, and was surrounded by a medium-grained white to light gray sandstone that was well consolidated in the region immediately surrounding the elements under study. The sediments were less consolidated in other regions. Limited coalified plant materials [33] were also present. MOR 555 was approximately 90 % complete, and was articulated except for minimal displacement of the skull, tail vertebrae, and some limb elements, indicating rapid burial post mortem. Multiple analyses at the gross and microscopic levels indicated that diagenetic alteration of the internal trabecular (or cancellous) bony tissues of the femora and tibiae of this specimen [33] was minimal. Vascular channels and osteocyte lacunae were free of secondary crystalline deposits and density measurements were consistent with comparable regions of desiccated modern, unreplaced bone. Electron diffraction pattern analyses (EDPA) showed a high degree of orientation of mineral crystals. This is inconsistent with patterns observed in non-biological systems, but very similar to that seen in extant bone (ibid.).

Amino acid analyses, high performance liquid chromatography (HPLC) and confocal microscopy studies indicated that there were a significant organic components within these bone tissues [33]. However, these components were greatly diminished over that of modern bone, particularly with respect to the more labile amino acids, indicating significant diagenetic alteration of the organic components. Additionally, transmission electron microscopy (TEM) revealed the presence of fibers in ultrathin (~4 Nm) sections of decalcified trabecular bone consistent with degraded collagen fibers (ibid), which showed loss of integrity in the presence of the enzyme, collagenase. The presence of collagen in these tissues was further supported by electrophoretic studies and Western blots which demonstrated positive staining with antibodies raised against avian collagen I [32].

Occurrence of microstructures in trabecular vascular channels

During microscopic analyses, small microstructures were noted in the vascular channels of the unpermineralized trabecular bone of the femora and tibiae of MOR 555. Subsequent microscopic analyses revealed them to be present in vascular channels of the trabecular bone of some other skeletal elements as well. These microstructures were localized within the lumen of the vascular canals that were clearly visible in the relatively unaltered bone. They were present in the vessel chan-

Table I. Elemental analysis of various bone tissues, sandstone matrix, and *T. rex* vascular microstructures.
(Elements listed as Atomic % (Weight %) rounded to nearest tenth). Figures are calculated after excluding oxygen and carbon from the data, as these lighter elements are ubiquitous. In addition, this method does not differentiate carbon or oxygen endogenous to the sample from environmental contaminants. Since oxygen contributed a significant amount to the total elements detected (~ 70 % of ostrich bone [33], excluding these elements exaggerates the proportions of the other elements, in terms of relative percentages.

Tableau I. Analyse élémentaire de divers tissus osseux, de la gangue gréseuse et des microstructures globulaires observées dans les canaux vasculaires de *T. rex* (les éléments sont exprimés en pourcentages pondéraux arrondis à la plus proche dizaine). Les valeurs sont calculées après élimination des données pour l'oxygène et le carbone car ces éléments plus légers sont ubiquistes. De plus, la méthode utilisée ne distingue pas entre carbone et oxygène provenant de l'échantillon ou de l'environnement. Comme l'oxygène représente un pourcentage considérable du total de l'analyse élémentaire (jusqu'à 70 % dans l'os d'autruche [33]), l'élimination de ces éléments entraîne une exagération corrélative, en pourcentage, des autres éléments détectés.

Sample	Na	Mg	Al	Si	P	Cl	Ca	S	Fe
Alligator Bone	8.4 (5.5)	0.9 (0.6)	0.6 (0.5)	0.5 (0.4)	31.7 (27.9)	5.1 (5.2)	52.3 (59.5)	0.6 (0.5)	---
Ostrich Bone	2.5 (1.6)	1.2 (0.8)	---	---	34.7 (29.6)	---	61.5 (68.0)	---	---
*T. rex Bone**	1.0 (0.7)	0.2 (0.15)	0.3 (0.2)	---	27.9 (24.9)	---	51.3 (50.36)	---	---
T. rex Microstructure	2.3 (1.1)	1.0 (0.5)	5.4 (3.0)	2.7 (1.5)	9.2 (5.9)	---	3.4 (2.8)	5.6 (3.7)	70.5 (81.5)
Sandstone 1 **	---	0.2 (0.3)	2.4 (3.5)	18.4 (27.9)	---	---	---	---	---
Sandstone 2 ***	1.68 (.98)	2.19 (1.37)	7.23 (4.99)	41.6 (29.79)	---	0.5 (0.4)	8.5 (8.7)	---	35.7 (50.8)

* Elemental analyses of *T. rex* bone were slightly variable. Above measurements are representative.
** Sandstone type which predominated in fossil setting, including sediments immediately adjacent to the bones under study.
*** Sandstone type found in isolated regions, such as adjacent to ilium or disarticulated metatarsals. Potassium and Manganese were found in trace amounts in this sandstone sample, but were not found in any other samples.

* Les analyses élémentaires des os de *T. rex* se sont révélées assez variables, les valeurs ci-dessus sont représentatives.
** Concerne le type de grès prédominant dans l'environnement fossilifère, en particulier celui au contact des os étudiés.
*** Type de grès observé en isolats locaux, tel qu'adjacent à l'ilion ou à des métatarsiens désarticulés. On a trouvé des traces de potassium et de manganèse dans ce type de grès, mais pas dans les autres échantillons.

nels of all bones examined in this manner, but were primarily restricted to the trabecular bone of the marrow cavities and surrounding endosteal bone. Elemental analyses performed with EDX (energy dispersive X-ray), which we first reported in 1993, demonstrated that the structures were high in iron content [31, 33] although only trace iron, or none at all, was noted in the surrounding bone, micrometers from the microstructures (*table I*), a pattern also noted by Pawlicki and Noworgrodzka-Zagorska [25]. Methodologies are described in Schweitzer et al. [33].

These microstructures varied in diameter from approximately 10 μm to 40 μm, averaging approximately 25 μm (averages calculated on measured diameters of 100 microstructures in thin sections of the trabecular tissues of tibia and fibula). Light microscopy demonstrated that these structures were abundant in the vessel channels of some regions of the bone (*figure 1A*). They exhibited a central core region that appeared opaque in light microscopy (*figure 1B*), and had a central bulge (*figure 1C*). The central region was different in both elemental distribution and morphology, with a network-like appearance visible in scanning electron microscopy (SEM, *figure 1D*). The region surrounding the core was translucent in light microscopy, and was amorphic in SEM (*figure 1B, D, E*). These characteristics, combined with the relatively unaltered state and organic content of the bone, suggested that the microstructures might have had an organic origin. Therefore, we hypothesized that these microstructures could represent a geological process, or alternatively, they could represent diagenetic alteration of organic structures present in the vessel channels of this specimen post mortem.

Pyrite formation and framboidal morphologies

A strictly geological origin was first considered as a source for these vascular microstructures. Pyrite framboids, which adopt a spherical habit, were the most obvious consideration. However, the data we gathered were not consistent with that presented in the literature for pyrite formation in general or framboids in particular.

Figure 1. A. Light micrograph. Microstructures in vascular channels of trabecular tissues of *Tyrannosaurus rex* (MOR 555) tibia. Magnification × 100, scale bar = 50 μm. **B.** Magnification of microstructures from a different bone regions, showing the translucent outer region, and the opaque central core. Magnification × 400, scale bar = 20 μm. **C.** Scanning electron micrograph (SEM) of microstructures in vessel channel, showing the biconvex properties of the microstructures. **D.** Microstructure cut in cross section, verifying morphological differences between the central core and the outer part of the structures, corresponding to the translucent region seen in LM. A geometric or network like appearance is clearly visible in the central region. No microcrystals are visible, but a regular structure can be seen. **E.** Single microstructure at higher magnification, showing the variation in the microstructure from internal to outer regions. **F.** SEM image of a diagnostic pyrite framboid. Microcrystalline structures are clearly evident, and the overall morphology is very different from that seen in the specimen in the current study. This micrograph (F) was generously provided by Dr. Y. Dauphin.

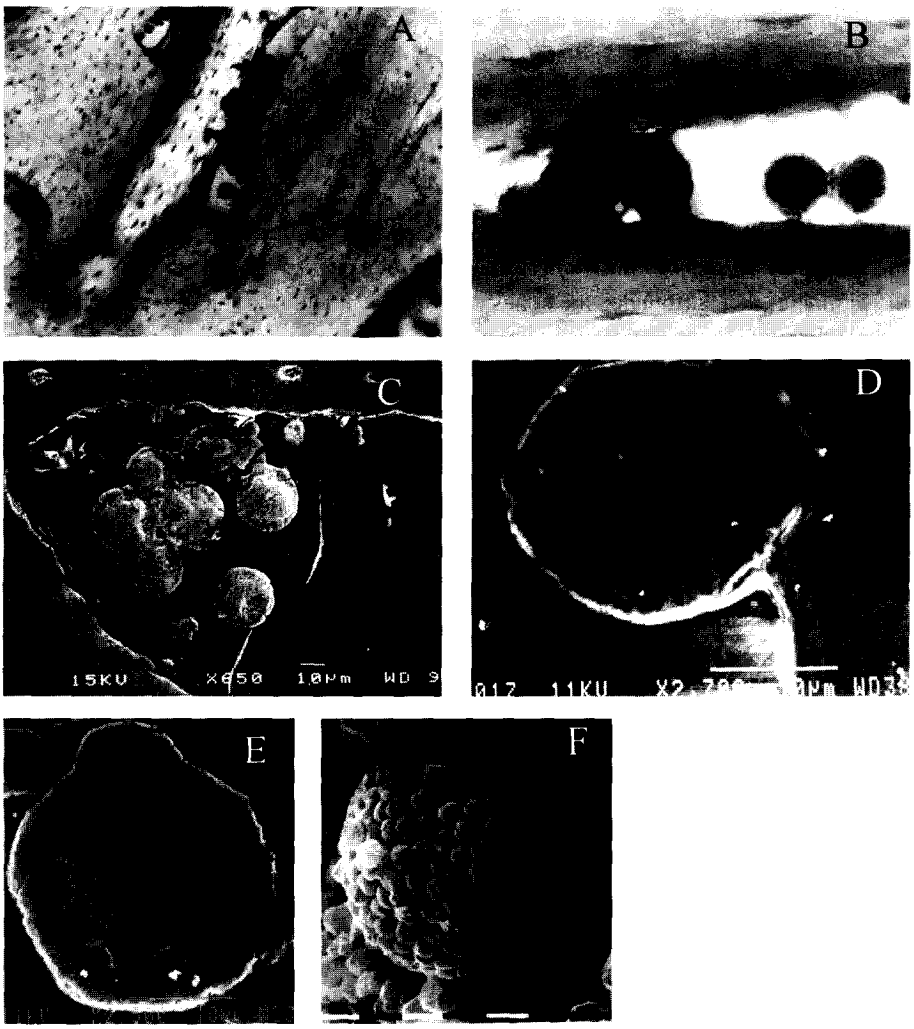

Figure 1. Microstructures globulaires dans un canal vasculaire du tissu osseux trabéculaire du tibia de *Tyrannosaurus rex* (specimen MOR 555). **A.** Microscopie optique en transmission, lumière ordinaire, grandissement × 100, échelle = 50 µm. **B.** Agrandissement d'une microstructure globulaire provenant d'une autre région montrant la portion externe translucide et la portion interne opaque d'un globule, grandissement × 400, échelle = 20 µm. **C.** Même matériel au microscope électronique à balayage (MEB) montrant la disposition biconvexe, globulaire de la microstructure dans la lumière d'un canal vasculaire. **D.** Section diamétrale de la microstructure montrant la différence morphologique entre ses parties centrales et périphériques, cette dernière étant transparente en lumière transmise. Une disposition en réseau géométrique apparaît clairement dans la région centrale. On n'y observe pas de microcristaux mais une structuration régulière. **E.** Une microstructure globulaire isolée à plus fort grandissement montrant la variation de structure de la périphérie vers le centre. **F.** Image d'un framboïde de pyrite caractéristique obtenue au microscope électronique à balayage (MEB). Des structures microcrystallines apparaissent clairement et la morphologie générale diffère nettement de celle des spécimens observés dans la présente étude. Document (F) aimablement communiqué par le Dr Y. Dauphin.

Elemental analyses of these microstructures were not consistent with pyrite. Atomic percent values (Fe/S: 70.5/5.6, or 12.6 iron atoms for every sulfur present in the microstructures) obtained by elemental analyses are not consistent with a chemical formula for pyrite (FeS_2), nor is the distribution of sulfur consistent with pyrite when visualized in element maps (*figure 2*). Elemental analyses of samples of sandstone sediments associated with various regions of the specimen were completely devoid of measurable sulfur, and iron was present only in limited regions of the sediment directly adjacent to the ilium of this specimen (*table I*). No iron was detected in the sediments that surrounded the bones under study. Finally, as can be seen in *figure 1*, crystal faces were not readily visualized on these structures, even at very high magnifications, in contrast to the known morphologies of pyrite framboids (*figure 1F*).

The formation of pyrite involves a series of geochemical reactions, each of which is dependent on the preceding step. For pyrite to form, three things must be available for reaction; reactive iron species, soluble sulfides, and organic matter available for bacterial degradation [1, 2, 4, 39]. The chemical reactions involved in the formation of pyrite are outlined in Canfield and Raiswell [7]. In freshwater and terrestrial systems, the formation of pyrite is severely limited, because sulfate is consumed too rapidly for bacterial reduction to occur [4, 27]. Therefore, pyrite formation is greatly favored in anoxic marine sediments just below the oxic/anoxic interface.

However, pyrite can form in terrestrial environments under certain restricted conditions. Pedogenesis (soil formation) which favors the formation of pyrite is associated with both very acidic conditions (pH 2.8–4.5 [26]) to increase the reactivity of iron species, and reducing environments such as those associated with stagnant waters with low levels of oxygen, which are needed to accomplish the reduction of sulfate to sulfide (H_2S). The reduction of sulfate is usually, although not always, bacterially mediated, but always requires anoxic conditions [4].

Pyrite (FeS_2) is characterized by two-fold symmetry, and the crystal structure of pyrite can take on many forms on the gross level, such as cuboid or octahedron, but is always geometric [7, 39]. This constraint extends to the microscopic level, as can be seen in *figure 1F*.

While several mineral species (e.g. mackinwaite) form from the combination of iron and sulfur, framboidal morphology is virtually exclusive to pyrite [28]; therefore objects identified as framboids should demonstrate iron and sulfur in ratios which reflect the chemical formula of pyrite – FeS_2. Framboid textures are highly ordered, early diagenetic products of increasingly sulfur-rich phases, and the conditions that are limiting for pyrite formation will, of course, also apply to the formation of framboids.

The early diagenetic framboidal pyrite form consists of microcrystals of uniform size and shape in an overall spheroidal habit, with the ratio of crystal diameter to framboid diameter of approximately 1:10 ([7]; *figure 1F*). Framboids will only form in restricted regions immediately subjacent to oxic/anoxic interfaces. Curiously, while bacterial degradation of organic matter is an important factor in the production

of pyrite, the framboidal morphology is generally not demonstrated in pyrite produced under bacterial influence [28].

The average diameter of framboids reported in the literature is approximately 5 μm [39], although in some cases average diameters can be larger. This is less than

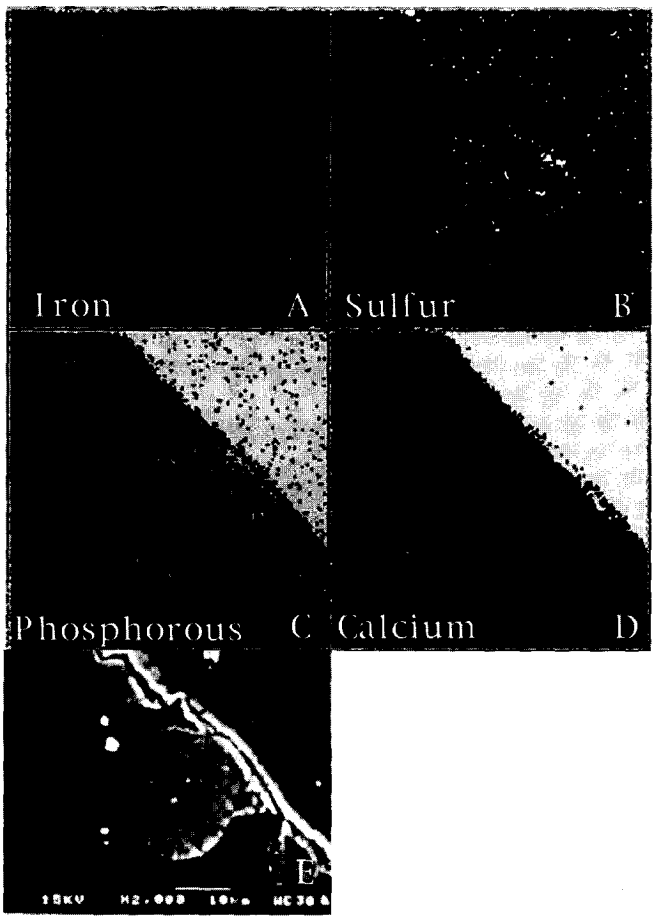

Figure 2. Map of microstructures within vessel channel. **A.** Iron distribution, **B.** Sulfur distribution, **C.** Phosphorous distribution **D.** Calcium distribution, and **E.** Gray image of section used to gather elemental data, slightly reduced. Here, it can be seen that calcium and phosphorous localize to the bone tissue forming the vessel wall, although some phosphorous is found in the microstructures as well. The microstructures consist almost totally of iron, and only minute amounts of sulfur can be seen on the surface of the structures.

Figure 2. Carte de l'analyse élémentaire d'une microstructure en place dans un canal vasculaire. Microsonde à rayons X. **A.** Répartition du fer. **B.** Répartition du soufre. **C.** Répartition du phosphore. **D.** Répartition du calcium. **E.** Image (légèrement réduite relativement à A–D) de la microstructure globulaire utilisée pour l'analyse élémentaire dans le canal vasculaire. On observe que le calcium et le phosphore sont principalement localisés dans la matière osseuse constituant la paroi du canal vasculaire, bien qu'il y ait aussi un peu de phosphore dans la microstructure globulaire. Celle-ci est pour ainsi dire entièrement formée de fer mais on observe aussi un peu de soufre à sa surface.

the average diameter of the microstructures observed in MOR 555 (average of 25 μm). Within a single environment, environmental conditions are essentially homogeneous, thus the crystallites will be affected equally and will reach a similar size. Therefore, variability is usually limited (ibid.), with framboidal diameters increasing with depth of burial [28].

In addition to the microcrystalline texture, framboids are recognized by their spheroidal morphology. However, it has been shown that spherulization is not caused by some physical property resulting from the reaction of iron and sulfur laden water, but is imposed on the system from the outside, by an associated or pre-existing body. Two systems will satisfy the requirements for spheroid formation-organic compounds in the sediments which form globules, or gases released into sediments, forming spherical vacuoles as they become entrapped [28]. During the formation of framboids, organic matter may become mineralized; alternatively, simple organic sacs may form around the framboids [17]. However, this only happens in when the solvents are viscous and non-ionic, conditions not generally met in terrestrial sandstone depositional settings [28].

In some cases, if appropriate solutes are continually supplied, infilling of the original framboid texture can occur. This process is also a function of depth of burial, with greater infilling occurring at greater depths [39]. This infilling process also seems to be dependent on bioturbation, which favors remixing of porewaters [12, 39].

The processes involved in the formation of pyrite in general and framboidal morphologies of pyrite in particular are thus seen to be highly constrained, and vastly favored to occur in marine anoxic environments, because of the availability of dissolved sulfides [17]. Reducing environments, porewaters rich in dissolved sulfides, reactive iron species, and adequate organic sources for bacterial decay are all necessary ingredients in the formation of pyrite.

The depositional environment of MOR 555 is a relatively coarse-grained, well-drained material, which is generally equated with an oxidizing environment [26]. Additionally, the highly acidic environment required for terrestrial formation of pyrite is generally not conducive to the preservation of bone, and therefore was probably not a condition of the depositional setting. Continual supply of the appropriate solutes needed for infilling does not seem to have occurred, or presumably there would be evidence for this in secondary mineral deposition throughout the bone tissues. Finally, the bioturbation which seems to be an important factor in framboidal infilling is not demonstrated in this articulated specimen. Therefore, conditions for the formation of pyrite, and in particular the framboidal morphology of this mineral, are not met by the conditions of burial for MOR 555.

Cellular morphologies

Red blood cells of living organisms are extremely variable in size, shape, and cytoskeletal features. Diameters of circulating vertebrate cells can range from 65 μm (20 000 μm^3 volume) in some amphibians to 4–5 μm (25 μm^3) in some mammals [24]. The erythrocytes of birds and reptiles are consistently larger than mature circulating red blood cells of mammals, and are much more resistant to shear stresses, due to unique cytoskeletal adaptations [9, 24]. Non-mammalian erythrocytes are all nucleated, while the mature cells in mammals (with one exception, the camel) are anucleate. However, a small percentage of circulating red cells in mammals do contain very small, nonfunctional pyknotic nuclei. By contrast, in birds and reptiles the nucleus is large, and remains capable of cellular function until late in the life of the cell. In addition, the nucleus of red blood cells in birds contains nuclear hemoglobin, which has the effect of pushing the DNA into a regular mesh-like or geometric pattern as the cells age [6].

In addition to size variability of red blood cells among taxa, there is a wide range of red blood cell diameters during the ontogeny of the red cell lineage within a single individual. In the blood forming compartments, which include the trabeculae of long bones in reptiles and birds [30], diameters can vary two- to five-fold during maturation of the circulating cell from the precursor stem cell. In avian erythropoetic compartments, variation is also observed in cell morphologies, with cells not obtaining their definitive, slightly ovate shape until directly before maturation, in what is known as the orthochromatic stage [16]. Therefore, in living vertebrates, the variation in both size and morphology of red blood cells is greatest in the erythropoietic compartments.

DISCUSSION

The preservation of soft tissues has long been noted in the fossil record; however these descriptions are based upon morphological similarity, and not upon rigorous molecular or chemical analyses. Therefore, a clarification of terms is indicated. Morphological preservation of soft tissue is not organic preservation, in the sense that regardless of the detail and level of structural appearance, preservation of the original molecular components of the tissue is not guaranteed. Exquisite morphological preservation may simply reflect exact geochemical replication of originally organic material with mineral species. This occurs most often with phosphate compounds (proposed by Martill in 1992 to explain preservation of biconcave structures identified as blood cells in Paleozoic fossil fish), silicification which preserves plant morphologies, or pyritization (described as a means of soft tissue preservation by Allison in 1988). Such subcellular detail has been described in fossils dating to the Ordovi-

cian, yet without evidence of any endogenous molecular preservation [36, 37]. However, other work shows a high degree of correlation between morphological preservation and organic (molecular) preservation [15]. Thus it can be seen that while detailed morphological preservation does not guarantee molecular or organic preservation, it is more likely to occur in tissues that demonstrate reduced diagenetic alteration on the morphological level.

When claiming that labile structures such as cells, tissues or molecules remain over the course of geological time, multiple lines of evidence must be presented to support such hypotheses, even for specimens which are fairly recent, such as those identified by Maat [18, 19]. However, Maat did not claim, nor did he offer any evidence that these structures are preserved as organic material, as no analyses, such as amino acid analyses, antibody work, or spectroscopy, were done which would support such a claim. Until such studies are performed, the organic nature of these cells as noted by Martill and Unwin [23], though certainly possible, remains unproven.

Several criteria have been proposed for consideration in the analyses of fossil bone for structures believed to be cellular in nature, including 1) strong morphological similarities; 2) similar size values to known components of extant relatives; 3) high abundance or occurrence, and 4) presence of characteristic biomarkers localized to the structures in question [23]. By these criteria, then, mere morphological similarity should never be regarded as sole evidence for organic preservation. However, the fourth criteria has not been met by other descriptions of 'organic preservation' [20, 23].

While we concur with these proposed criteria, we would add further restrictions, such as evidence for truly "organic" preservation on other levels. Identification of cellular or molecular features such as collagen fibers under electron microscopy, in addition to chemical analyses (DNA or amino acids sequences) or in situ antibody work could be attempted to detect epitope preservation [8].

Another consideration in proposing preservation of truly organic structures is examination of the depositional setting for a logical mechanism for such preservation, whereby the natural degradation processes are slowed or arrested. For example, concretionary barriers are known to form around organic structures very early in the diagenetic process [5]. Once formed, this barrier constitutes an essentially closed system, preventing further degradation. Additionally, biomolecules are known to be stabilized by conditions that allow minimal exposure to water and UV radiation, and reduced exposure to lytic enzymes secreted by microbes of decay [10], conditions enhanced by rapid burial.

Alternatively, characteristics of the molecules under study may enhance its preservation potential. For example, the formation of vertebrate bone [11, 13, 14] or teeth [14] involves the deposition of apatite crystals on previously secreted collagen fibrils. Incorporation of the fibrils within the core of the mineral crystals acts as a closed system, stabilizing those parts of the protein molecules within [11, 13].

In our studies of MOR 555, we observed microstructures within the trabecular vessel channels that demonstrated strong, though certainly not identical, morphological similarities to red blood cells of living taxa; indeed, identical conservation would not be expected after 65 Ma, and some diagenetic alteration most certainly would have occurred. The size range for these microstructures falls well within those reported in the literature for both reptilian and avian circulating cells. The average size range is slightly larger than those observed in modern birds; however, if dinosaur cells, like bird cell sizes could be correlated to overall body size [16], this would be expected. Clearly, these structures are not functional cells. However, one possibility is that they represent diagenetic alteration of original blood remnants, such as complexes of hemoglobin breakdown products, a possibility supported by other data that demonstrate that organic components remain in these dinosaur tissues.

Finally, multiple lines of evidence supported the preservation of heme-derived compounds in extracts of dinosaur bone [34]. These experiments, however, did not directly address the origin or state of preservation of the small vascular microstructures, as we were not able to perform the conclusive experiments of localizing heme signals to the small microstructures, rather than whole bone extracts. This is the reason we stated "... we have not identified the origin of the small microstructures, and have not linked the heme signals directly to these structures" [35]. Although they are not consistent with pyrite framboids, they may indeed be geological in origin, derived from some process as yet undefined; they may have their origin as colonies of iron-concentrating bacteria or fungal spores, or they may be the result of cellular debris, which clumped upon death, became desiccated, and then, through diagenetic processes such as anion exchange or others not yet elucidated, become complexed with other, secondary degradation products.

CONCLUSION

The fossil record is capable of phenomenal preservation, and the limits of this preservation have yet to be determined. However, it must be recognized, as we have proposed, that morphological preservation is not the equivalent of organic preservation at the cellular and/or molecular level. Reports of muscle fibers, hair, blood vessels and other originally organic structures [18–20, 22, 29, 38], or the microstructures reported in this paper, cannot be accepted as 'organic' remains unless subsequent tests prove that exquisite morphological preservation extends to the molecular level. If, however, further tests on structures similar to those observed in MOR 555 show that these microstructures do reflect original blood components, hypotheses regarding blood morphologies, oxygen carrying capacities, and other physiological characteristics may be proposed. Additionally, if similar microstructures can be found in dinosaurs from many different depositional settings, geochemi-

cal interactions that may result in their formation may be studied, and insights into the fossilization process may be gained.

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