

## A SHORT HISTORY OF DINOSAURIAN OSTEOCYTES.

by

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### ABSTRACT

A recent supposed discovery of dinosaurian osteocytes by Fukuda and Obata (1993) ignored earlier records from more than 20 dinosaurs, dating back 150 years. Some of the bodies they identified as osteocytes are also more likely to represent chondrocytes.

KEYWORDS: Bone histology, osteocytes.

### INTRODUCTION

In a recent paper, Fukuda and Obata (1993) claimed the discovery of dinosaurian osteocytes, in the form of mineral casts of their lacunae and canaliculi seen in hadrosaurid bones, and stated that, despite recent histological studies, "... there is no information on osteocytes in dinosaur bone tissues" (p. 99, para. 1). At that date, however, earlier studies outlined here contained records from more than 20 dinosaurs, dating back 150 years (Quelett 1849), and even electron microscope photographs had been in print since 1966 (Pawlicki, Korbel & Kubiak 1966). This note reviews a range of relevant references, for readers not familiar with them, and also shows that some bodies identified as osteocytes by Fukuda and Obata in the articular surface of a dinosaur limb bone, are more likely to represent chondrocytes.

### Historical outline

First, under the old name "bone cells", the presence of osteocyte lacunae was recorded from bones of the ornithopod *Iguanodon* by Quekett (1849) and of the sauropod *Pelorosaurus* by Mantell (1850). These are the oldest ornithischian and saurischian records respectively. Strictly, Quekett (p. 57) only stated that bones of *Iguanodon* do not differ from those of modern lizards in minute structure; but his numerous figures of lacunae and canaliculi from modern forms (plates 5-8) and from a pterosaur (plate 8, Figure 2) leave no doubt of what he meant. Subsequently Hasse (1878) recorded osteocyte lacunae in a vertebra ascribed to the prosauropod *Thecodontosaurus*, contrasting spindle-shaped examples from periosteal bone with stellate forms seen in a nothosaur (p. 499), and giving a figure which shows their presence in endochondral bone (Figure 24b). Their presence is seen readily in some of Seitz's (1907) photographic figures e.g. Figure 57, *Megalosaurus*; Figures 59-61, *Iguanodon*; Figure 76, "Trachodon" (*Anatosaurus*); and his text, in which he called them "bone corpuscles" (Knochenkörperchen), contains records of their presence and arrangement in bones of *Plateosaurus* (p. 265), *Megalosaurus* (p. 288)

*Brontosaurus* (pp. 302, 303), *Diplodocus* (pp. 304, 306), *Camarasaurus* (p. 311, as "Morosaurus" pp. 322, 324), *Haplocanthosaurus* (pp. 313, 314), *Allosaurus* (pp. 315, 316), *Stegosaurus* (p. 321) *Iguanodon* (pp. 326-328), *Dryptosaurus* (p. 344), *Triceratops* (p. 346), and *Anatosaurus* (pp. 348-350), as "Trachodon". Osteocyte *Stegosaurus* lacunae recorded as from *Zanclodon* (p. 262), which is now considered indeterminate, are probably from a prosauropod (c.f. Benton 1986, pp. 295-297). A preserved canalicular network was noted in *Brontosaurus* (p. 302), though not illustrated, and lacunae affected by fungal enlargement, mineral infilling, loss of canaliculae or complete obliteration were reported from various genera. Records from prosauropods, sauropods, theropods, ornithopods, a stegosaur and a ceratopsian have thus been in print for most of this century; and Seitz's (1970) study contains more such records than any other single paper.

In later work, Moodie (1928) reported the presence of lacunae and canaliculae in Haversian bone from "ossified tendons" of *Anatosaurus* (as "Trachodon") and *Ankylosaurus* (p.2), and that of lacunae is obvious in some of his "Trachodon" figures (Figures 2b, 6a & 6b). Bacterial enlargement of lacunae was also reported (p.2 and Figure 6a). Nopcsa and Heidsieck (1933) found lacunae and canaliculae in periosteal and Haversian bone from a half-grown *Hypacrosaurus*, and in fibro-lamellar tissue from a juvenile *Procheneosaurus* (as "Tetragonosaurus"), reporting round and polygonal lacunae as having diameters between 3-7 $\mu$ , and spindle-shaped examples short diameters between 2-4 $\mu$  (pp. 222, 224, 225). In the juvenile, the presence of lacunae is obvious in their figure (Figure 2); and they reported canaliculae connecting them as forming a network with meshes "about 4 $\mu$ " wide (p. 225). Gross (1934, pp. 755-759) reported the presence and arrangement of lacunae in bone from *Plateosaurus*, *Brachiosaurus* and *Iguanodon*, calling them "bone cells" (Knochenzellen) or simply "cells" (Zellen), and gave figures showing obvious examples in *Brachiosaurus* tissues

(Figures 19 and 20), also noting contrasting arrangements in different parts of secondary osteons (Figure 20). De Lapparent (1947), Figure 6 and Plate 6, figures 1-4, 6) figured bone showing lacunae and canaliculae in *Rhabdodon*, with a drawn figure showing the canalicular network (figure 6c); and Pawlicki, Korbel & Kubiak (1966, Figures 1 and 3) used transmission EM photographs to illustrate these features as seen in an unnamed Gobi dinosaur. Later, Pawlicki (1977) reported concentration of mucopolysaccharide traces around lacunae and canaliculae in *Tarbosaurus*; used optical, transmission EM and SEM photographs (1978, Figures 1-6) to illustrate their form in this genus, also noting two types of fusiform lacunae with differently arranged canaliculae; and discussed (1984) the metabolic significance of dinosaurian lacunae and canaliculae. Reid (1984a, Figure 1) figured mineral filled lacunae and canaliculae from *Iguanodon*, mentioned Mantell's *Pelorosaurus* record (p. 629), and pointed out lacunae shown in Seitz's *Anatosaurus* figure (Reid 1985, p. 141), besides figuring bone with obvious lacunae from *Cetiosaurus*, *Valdosaurus*, *Aristosuchus* (1984a, Figures 2, 3 and 15; 1985, Figures 3, 4 and 8) and *Hypsilophodon* (1984b, Figure 1j). Besides lacunae, canaliculi can be seen in the 1985 *Aristosuchus* Figure; and Chinsamy (1990, p. 78) reported strongly branched examples from *Syntarsus*.

### DISCUSSION

As noted at the start of this study, Fukuda and Oblata's (1993) paper involves two distinct problems. First, it is clear that they were wrong to suppose that nothing was known of dinosaurian osteocytes; and why they should have thought so is puzzling, when so much had been known for so long. Genera cited above, from which preserved lacunae were then known, total two (three?) prosauropods, seven sauropods, six theropods, five ornithomimids, including three hadrosaurs, a stegosaur, an ankylosaur and a ceratopsian. The persistence of lacunae in dinosaurian bones had been known for 144 years (Quekett 1848); many details of their form, arrangement and preservation in over a dozen dinosaurs for 86 years (Seitz 1907); and their dimensions in two hadrosaurs, including a juvenile, for 60 years (Nopcsa & Heidsieck 1933). A transmission EM photograph

had been in print for 27 years (Pawlicki, Korbel & Kubiak 1966), and scanning EM photographs for 15 years (Pawlicki 1978). Some of the relevant publications are probably not widely known (e.g. Hasse 1878); but *Nature*, in which the first EM photograph appeared, is not an obscure journal, and Seitz's classic "Vergleichende Studien" (1907) is required basic reading for anyone working on fossil bone. Perhaps, however, the answer is that osteocytes have not been involved in the controversy over dinosaurian physiology, except indirectly as secondary markers of different types of bone at fibrillar level (e.g. de Ricqlès 1975, p. 59 and Figure 1), and have hence received little or no attention in papers concerned with that topic (e.g. de Ricqlès 1980; Reid 1987). Persons not familiar with studies of bone histology could thus get a false impression that nothing was known about them. Hopefully, this note will make how much we know more widely known.

Second, Fukuda and Obata's sample from a juvenile *Maiasaura* was stated to be compact bone from the upper articular surface of a limb bone (pp. 99-101), and was found to contain casts of lacunae which did not emit canaliculi (p. 101 and Figure 6). This they ascribed to "retardation of bone calcification in the juvenile" and taphonomic damage (pp. 101 and 102). But the articular faces of dinosaurian limb bones are not formed from compact bone, whose presence there would block growth in length, but from calcified cartilage, representing the deep parts of the growth plates under which new endochondral bone was formed (e.g. Reid 1984a, pp. 645 and 646 and Figures 24-27, *Iguanodon*; Reid 1996, Figures 38 and 39, *Allosaurus*; Figures 41 and 81, *Camptosaurus*); and a characteristic of cartilage is that the lacunae occupied by its chondrocytes do not emit canaliculi. Hence it seems likely that the tissue called compact bone was really calcified cartilage; and this would fit the style of calcification which their Figure 6 shows. The preservation of calcified cartilage in dinosaurian bones is again no new discovery, having first been figured by Hasse (1878, Figure 24a) from *Thecodontosaurus*.

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on this continent. Although more have been discovered since (Jacobs *et al.* 1996), our knowledge of Cretaceous African dinosaur faunas is still rather poor. In the African dinosaur assemblages of Cretaceous age sauropods predominate. Thus, the Early Cretaceous sauropods of Africa include diplodocoids, titanosaurids, brachiosaurids and probable camarasaurids (Lavocat 1954; Lapparent 1960; Jacobs *et al.* 1993; Sereno *et al.* 1994; Wilson pers. comm.), although the supposed camarasaurid *Rebbachisaurus* probably belongs rather to the Diplodocoidea (Calvo & Saldado 1995).

The Late Cretaceous sauropod fauna of Africa seems to be less diverse, but is also even less well known than that of the Early Cretaceous. Titanosaurids are present in all African dinosaur-bearing localities of this age, e.g. the Cenomanian of Egypt (Stromer 1932) and Sudan (Werner 1994; Raubut 1995), the Turonian-Santonian of Kenya (Arambourg & Wolff 1969; Jacobs *et al.* 1996; Harris & Russell, unpubl. data), the Coniacian-Santonian of Niger (Bräun *et al.* 1974), the Santonian of South Africa (Kennedy *et al.* 1987; Buffetaut 1988) and the Maastrichtian of Niger (Geigert *et al.* 1954; Taquet 1976). In addition, sauropods are represented by diemosaurids in the Cenomanian of Egypt and Sudan (Stromer 1932; Raubut 1995). For a review of dinosaur occurrences in Africa see also Jacobs *et al.* (1996).

Another titanosaurid is known from the Campanian of Madagascar (Depéret 1896), but as the breakup of Madagascar started in the Callovian (Luger *et al.* 1994), the specimen from Madagascar is not truly African.

Here we report on a sauropod femur from the Maastrichtian part of the Ammonite Hill Member of

## GEOLOGICAL AND STRATIGRAPHICAL SETTING

The Dakhla Formation outcrops not only in the Dakhla Oasis, but in vast areas all over southern Egypt. This Late Cretaceous to Early Tertiary sequence includes transgressive/regressive cycles with distinct regional facies differentiation. The Ammonite Hill Member, introduced by Barthel & Herrmann-Degen (1981: 157), is geographically restricted to the westernmost margin of the Dakhla Basin. It is characterised by the inter-fingering of distal alluvial to deltaic shallow marine sediments (Barthel & Herrmann-Degen 1981). In the westernmost outcrops, the Ammonite Hill Member consists of lightly fossiliferous siltstones, sandstones and limestones (Barthel & Herrmann-Degen 1981). The record of a dinosaur bone in the Ammonite Hill Member reflects terrestrial influence within a shallow marine environment (Figure 1).

In SW Egypt the Dakhla Formation is Middle Campanian to Middle Paleocene in age. The Ammonite Hill Member, representing the westernmost exposures of the Dakhla Formation, is subdivided into a lower Maastrichtian part and an upper Paleocene part (Barthel & Herrmann-Degen 1981). The lower part is dated as Maastrichtian on the basis of the occurrence of the ammonite *Libyceras ismaelii* and shed loads of the oyster *Exogyra overwegi*. Above the last occurrence of *Exogyra overwegi*, the appearance of the very abundant gastropod *Turritello* defines the Cretaceous/Tertiary boundary. Vertebrates, including the sauropod femur, were found in the Maastrichtian part of the Ammonite Hill Member (Barthel & Herrmann-Degen 1981).