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Cavities in the compact bone in tetrapods and fish and their effect on mechanical properties

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ABSTRACT

Bone includes cavities in various length scales, from nanoporosities occurring between the collagen fibrils and the mineral crystals all the way to macrocavities like the medullary cavity. In particular, bone is permeated by a vast number of channels (the lacunar–canalicular system), that reduce the stiffness and, more importantly, the strength of the bone that they permeate. These consequences are presumably a price worth paying for the ability of the lacunar–canalicular system to detect changes in the strain environment within the bone material and, when deleterious, to trigger processes like modeling or remodeling which 'rectify' it. Here we review the size and density of the various types of cavities in bone, and discuss their effect on the mechanical properties of cortical bone.

In this respect the bones of advanced teleost fish species (probably the majority of all vertebrate species) are an unsolved conundrum because they lack bone cells (and therefore lacunae and canaliculi) in their skeleton. Yet, despite being acellular, some of these fish can undergo considerable remodeling in at least some parts of their skeleton. We address, but do not solve this mystery.

1. Introduction

The compact bone of most extant vertebrates contains cavities: the marrow cavity, nutrient vascular channels, primary vascular channels and Haversian canals, osteocyte lacunae and canaliculi and nanoporosities. We describe all cavities in bone of the type described below, whether or not they contain or are filled with fluid or fat and other soft tissues. There are, of course, many questions that can be asked about these cavities, and this review will deal with some of them, namely:

What are the cavities in bone, how big are they, and what shape do they have?
Do they act as stress concentrators? What effect do they have on Young's modulus and strength characteristics of the material bone? (We use the phrase 'stress concentrators' interchangeably with 'strain concentrators' from now on.)
Does the lacunar–canalicular system in bone, with its contents (osteocytes and osteocytic processes) act as a signaling system?
What is the physiological and mechanical significance of the tubules in dentin?
How does the absence of the lacunar–canalicular system in the advanced teleosts affect their bone's mechanical and physiological properties?

Compact bone has cavities at five levels; the marrow cavity or similar large cavities, easily visible to the naked eye; the large channels for the nutrient arteries entering the bone from the periosteal and endosteal surfaces; the vascular channels and other large cavities visible on sections (the VP system, vascular porosity); the osteocyte lacunae, with their associated canalicular processes (see Fig. 1). If they are considered as unified they are called the 'lacunar–canalicular system' and this porosity is called the 'lacunar–canalicular porosity' (LCP). While it is very often helpful to think of the LCP system as unified, the lacunar and the canalicular porosity are usually considered separately, because though they presumably act together in bone remodeling, they will have different effects on mechanical properties. Furthermore the imaging required for the canalicular system usually requires a greater resolution than that required for the lacunar system, and so different imaging devices are often used. Finally, there is what may be called the nanoporosity, which is the space occupied by water in bone at the lowest level, some of which can be removed only by drying, heating above 100 °C or other relatively drastic measures. There are some other cavities that may be present, such as microcracks, or canals of Williamson and small elongated cavities in some teleost acellular bone that we shall consider later.

We shall deal first with the shape and density of the cavities in compact bone, and see what effect the presence of voids, and the strain concentrations they produce may have on the material properties of the bone. (The stress concentration is usually abbreviated to *Kt*. That is, when the global stress = σ, the actual local stress near

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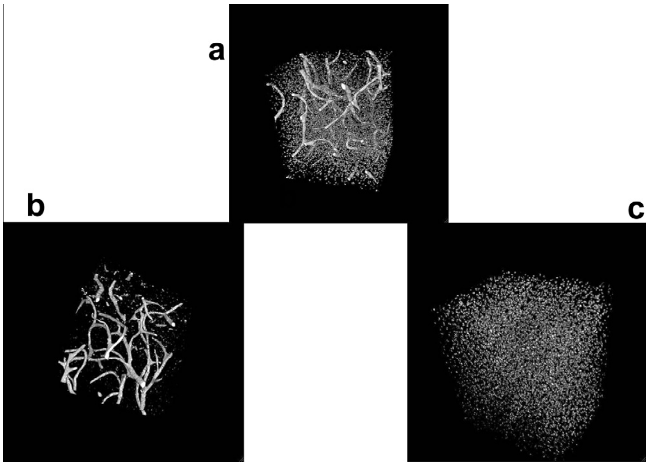

Fig.1. Synchrotron based microtomography of a volume of interest (VOI) of rat cortical bone. (a) All voids within the VOI, showing lacunae and blood vessels. (b) Same VOI, showing only the blood vessels (voids of >650 μm^3). (c) Same VOI, showing only the lacunae (voids of 100–650 μm^3).

a stress concentrator = $Kt \cdot \sigma$; similarly, if the global strain = ε, the actual local strain = $Kt \cdot \varepsilon$. These relationships hold in the elastic region: if post-yield events are being considered, these relationships get more complicated.)

The general kinds of cavities in vertebrate mineralized structures are shown in Table 1.

2. Size, shape and porosity of cavities in tetrapods and their effect on mechanical properties

2.1. Central cavity of long bones

The analysis of this has been fairly well worked out. See for instance (Currey and Alexander, 1985) or, if the reader wishes for discussion of various types of bone including flat bones and cancellous bones as well as tubular long bones (Currey, 2002). The analysis of flat bones and other bones containing much cancellous bone is very complicated and beyond the scope of this paper. Here we shall deal only with the cortical part of tubular bones.

It is often said that tubular bones have a central cavity in order to make the bone as light as possible. This, though true, is not very helpful, because the next question that must be asked is 'How big should the cavity be and how thin-walled should the bones be, and what will the saving in mass be in their being hollow with their lumen either empty except for air or filled with yellow, fatty marrow rather than being solid bone?' Among bones of different species there is a huge variation in the value of R/t, the ratio of the external radius to the thickness of the wall (Fig. 2).

At a ratio of 1 there is no marrow cavity, and this is found essentially only in a few water-living amniotes such as some crocodil-

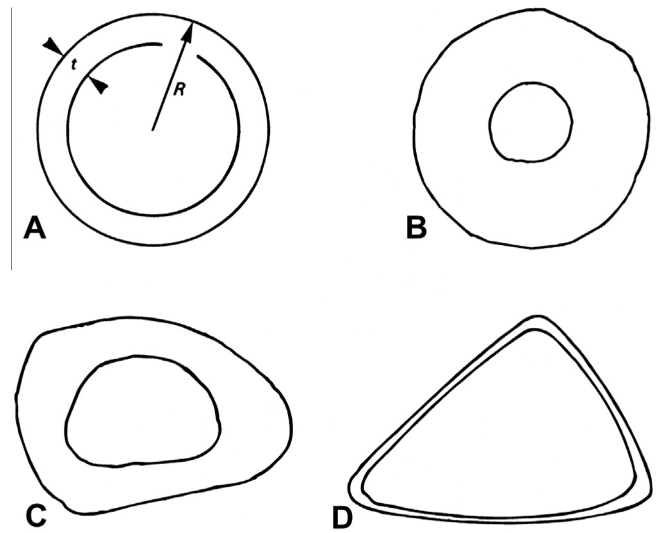

Fig.2. (a) Conventions used for *R*, *t* in the text. (b, c, d) Sketches of bones with different values of R/t; (b) Alligator femur. R/t 1.5; (c) Camel tibia $R/t = 2.4$; (d) Pteranodon (a pterodactyl) first phalanx. $R/t = 11$. From Currey and Alexander (1985) by permission of the Zoological Society of London.

Table 1
The occurrence of cavities in vertebrate mineralized structures.

Group	Tissue	Vascular cavities lacunae canaliculi	Odontoblast processes	Comments All mineralized tissue has some nanoporosity. All enamel has only this nanoporosity
Cartilaginous fish	Bone	No	No	Little bone in cartilaginous fish, except in very limited places, though there is very stiff calcified cartilage
	Dentin	Vascular cavities	Yes	Many different kinds of dentin, particularly in scales in extinct groups
Underived bony fish	Bone	Yes	No	There are very few extant underived bony fish species compared with those of neoteleosts
	Dentin	Vascular cavities	Yes	Many different kinds of dentin, particularly in scales in extinct groups
'Advanced' fish the neoteleosts. Ca. half of all vertebrate species	Bone	Some have vascular cavities	No	A variety of tubular structures have occasionally been reported to exist within acellular bone, including the so-called canals of Williamson which contain processes of surface osteoblasts
	Dentin	Vascular cavities	Yes	Various types of dentin, particularly in scales
Amphibians	Bone	Yes	No	Very few vascular channels in extant forms. Because of low metabolic rate?
	Dentin	Vascular cavities inextinct groups	Yes	Different kinds of dentin, particularly in scales, in extinct groups
Reptiles	Disorganized bone	Yes	No	
	Lamellar Bone	Yes	No	
	Dentin	No	Yes	
Birds	Bone	Yes	No	Canaliculi very tortuous No teeth and no scales, and therefore no dentin in extant birds
Mammals	Disorganized bone	Yes	No	Lacunae more subspherical than in lamellar bone, whose lacunae are like oblate ellipsoids, sometimes prolate ellipsoids
	Lamellar bone	Yes	No	See above re disorganized bone. A long axis of lacunae lies parallel to the collagen orientation
	Dentin	No	Yes	Odontoblast tubules, may have peritubular dentin