Bone 57 (2013) 300–310

Contents lists available at ScienceDirect

Bone

journal homepage: www.elsevier.com/locate/bone

Original Full Length Article

Measurement, variation, and scaling of osteocyte lacunae: a case study in birds

Michael D. D'Emic [a,*], Roger B.J. Benson [b]

[a] Anatomical Sciences Department, Stony Brook University, Stony Brook, NY 11794, USA
[b] Department of Earth Sciences, University of Oxford, South Parks Road, Oxford OX1 3AN, UK

ARTICLE INFO

Article history:
Received 3 April 2013
Revised 16 July 2013
Accepted 11 August 2013
Available online 15 August 2013

Edited by: David Burr

Keywords:
Osteocyte
Physiology
Histology
Bird
Metabolism
Genome size

ABSTRACT

Basic issues surrounding osteocyte biology are still poorly understood, including the variability of osteocyte morphology within and among bones, individuals, and species. Several studies have suggested that the volume or shape of osteocytes (or their lacunae) is related to bone and/or organismal growth rate or metabolism, but the nature of this relationship, if any, is unclear. Furthermore, several studies have linked osteocyte lacuna volume with genome size or growth rate and suggested that osteocyte lacuna volume is unrelated to body size. Herein the scaling of osteocyte lacuna volume with body mass, growth and basal metabolic rates, genome size, and red blood cell size is examined using a broad sample of extant birds within a phylogenetic framework. Over 12,000 osteocyte lacuna axes were measured in a variety of bones from 34 avian and four non-avian dinosaur species. Osteocyte lacunae in parallel-fibered bone are scalene ellipsoids; their morphology and volume cannot be reliably estimated from any single thin section, and using a prolate ellipsoid model to estimate osteocyte lacuna volume results in a substantial (ca. 2–7 times) underestimate relative to true lacunar volume. Orthogonal thin sections reveal that in birds, even when only observing parallel-fibered, primary, cortical bone, intra-skeletal variation in osteocyte lacuna volume and shape is very high (volumes vary by a factor of 5.4 among different bones), whereas variation among homologous bones of the same species is low (1.2–44%; mean = 12%). Ordinary and phylogenetically informed bivariate and multiple regressions demonstrate that in birds, osteocyte volume scales significantly but weakly with body mass and mass-specific basal metabolic rate and moderately with genome size, but not with erythrocyte size. Avian whole-body growth rate and osteocyte lacuna volume are weakly and inversely related. Finally, we present the first three-dimensionally calculated osteocyte volumes for several non-avian dinosaurs, which are much larger than previously reported values and smaller than those of large extant avians. Osteocyte volumes estimated from a single transverse section and assuming prolate morphology, as done in previous studies, are relative underestimates in theropod dinosaurs compared to sauropod dinosaurs, raising the possibility that no major change in osteocyte volumes (and genome size) occurred within Theropoda on the lineage leading to birds. Osteocyte volume is intertwined with several organismal attributes whose relative importance varies at a number of hierarchical levels.

© 2013 Elsevier Inc. All rights reserved.

Introduction

Reconstructing the physiology of extinct tetrapods is a branch of paleontology with a rich history, commonly focused on histological study (e.g., [1–4]). When they occur, lines of arrested growth in long bones such as the humerus and femur can be used to construct growth curves depicting mass (or size) versus age. These show the overall pattern and quantitative growth rates for a given species [5]. However, for some extinct animals such as sauropod dinosaurs, growth lines are rarely present [6], rendering this type of skeletochronology often inapplicable. Alternative approaches include classification into histological ontogenetic growth stages (e.g. [3,7]) and correlations between bone vascularity patterns and growth rates [8]. However, these proxies are either qualitative or yield inconsistent or imprecise results [9]. Aside from lines of arrested growth, no bone histological proxy has been developed to reliably and precisely reconstruct an extinct animal's growth rate, though models that produce a range of results are beginning to be developed [10].

The morphology of bone-forming cells is a logical candidate proxy for bone growth rates, because their size and shape vary within and among bones of animals that grow at different rates [11–14]. Bone-forming cells (osteoblasts) are embedded within bone via the differential secretion of osteoid by neighboring cells [15]. Once mature (i.e., stellate, fully embedded in osteoid as mineralization progresses), osteoblasts are referred to as osteocytes. Osteocytes have a variety of functions, including ion regulation, mechano-sensation, and a role in bone repair [16,17]. Osteocytes reside in small spaces within bones called lacunae, and are connected to one another via networks of cellular projections located inside tubes

* Corresponding author.
E-mail addresses: michael.demic@stonybrook.edu (M.D. D'Emic), roger.benson@earth.ox.ac.uk (R.B.J. Benson).

8756-3282/$ – see front matter © 2013 Elsevier Inc. All rights reserved.
http://dx.doi.org/10.1016/j.bone.2013.08.010

within bone called canaliculi [18]. Because lacunae and canaliculi correspond well with osteocyte shape and volume as bone is forming [19,20] and are generally well preserved in fossils [2,21], they provide a window into one aspect of cellular biology in deep time.

Osteocyte lacunae vary in volume, shape, and density depending on the sample. Both neontological (e.g., [20,22–26]) and paleontological (e.g., [21,27–29]) studies have investigated osteocyte morphology, with the latter category often incorporating data from both extant and extinct animals. Modern anatomical studies have largely focused on a few model organisms (e.g., chicken, human, dog) and on intra-bone variation in osteocyte lacuna morphology (e.g., [12,22]). These studies measured or estimated osteocyte (or osteocyte lacuna) volume using axis measurements from one thin section, two orthogonal thin sections, or several serial thin sections observed under light microscopy or scanning electron microscopy. These studies found that osteocyte volume varies depending on bone identity (e.g., femur versus scapula; [22]), bone tissue organization (e.g., woven versus lamellar; [20]), location within a bone (e.g., midshaft versus metaphysis; [25]), and distance from a vascular canal [26]. This variation has been tied to aspects of physiology in some cases. For example, Zallone [23] and Volpi et al. [24] studied the relationship between bone growth rate and osteocyte lacuna volume in trabecular bone of the tibia of the dog and the chick, respectively. Both studies reported a strong positive correlation between osteoblast 'secretory territory' (equivalent to the volume of the osteoblast divided by the area touching the growth surface, i.e., the axis of the cell perpendicular to the surface of apposition) and the thickness of osteoid deposited. Marotti [11] found a positive relationship between osteoblast volume and bone growth rate, and further suggested that total osteocyte volume is proportional to bone growth rate.

In contrast to these taxonomically focused neontological studies (including studies of intraspecific varitation), paleontological studies have largely investigated osteocyte lacuna variation using broad taxonomic samples but ignored lower-level sources of variation (intraspecific, intra-individual, intra-bone). To date, three studies have measured osteocyte lacuna volume in a wide variety and large number of amniotes [21,28,29], and these reported a large (nearly ten-fold) degree of variation among taxa. Substantial intra-skeletal variation in osteocyte volume was later reported in several species [30]. Using these taxonomically broad samples, Organ et al. [21] reported a relationship between osteocyte lacuna volume and genome size in amniotes ($R^2 = 0.56$; $R^2 = 0.32$ under a generalized least-squares regression accounting for phylogeny) and applied that relationship to calculate genome size in several non-avian dinosaurs. They reported that non-avian theropod dinosaurs had small osteocyte lacunae (and thus small genomes), and tentatively suggested that theropods may have had bird-like metabolic rates and small red blood cell (erythrocyte) sizes [21]. Organ et al. [21] argued that organisms with high metabolic rates should have smaller red-blood cell sizes, because smaller cells have a higher surface area to volume ratio, allowing more efficient gas transfer (see also [31–35], but see [36] for a differing viewpoint). However, the mechanism behind the Organ et al. hypothesis includes an assumption that osteocyte volume is somehow linked to erythrocyte size. Specifically, this hypothesis predicts that small osteocyte lacuna volumes correlate with small red blood cell sizes, a conjecture that has not yet been demonstrated. Intermediate osteocyte lacuna volumes were later reported for several sauropodomorph dinosaurs [29], and it was found that osteocyte volume was not correlated with body size in dinosaurs.

In summary, studies by neontologists and paleontologists seem to suggest opposing hypotheses for the relationship between osteocyte volume and bone growth rates or metabolic rates. The results of Organ et al. [21] suggest that animals with higher basal metabolic rates have smaller osteocytes (e.g., birds and bats). Because amniote growth and metabolic rates are proportional (Fig. 5 in [37]), this implies that osteocyte volume should correlate negatively with growth rate. In contrast, Marotti [11] suggested that larger osteocytes descend from larger osteoblasts, which deposit bone faster, implying that osteocyte volume should correlate positively with growth rate.

The study of osteocyte lacunae has implications beyond reconstructing the physiology of extinct vertebrates. Recently, several studies have integrated data from cellular biology, ecology, and physiology to investigate the evolution of metabolism across large clades such as mammals or birds (e.g., [34,38]). Models have been developed to study interactions among the number and volume of cells and cellular metabolic rates, which combine to produce organismal attributes such as basal metabolic rate and body mass [38]. Savage et al. [38] identified two types of cells: those with relatively constant cellular mass per species and varying cellular metabolic rates ('type I' cells; e.g., erythrocytes, fibrocytes, hepatocytes, most cells of the lung), and those with cellular masses proportional to body mass with invariant metabolic rates ('type ii' cells; e.g., adiposites, neurons). Whether osteocytes represent type i or ii cells remains to be determined. However, first the basic relationships among osteocyte volume, body mass, and physiology must be understood. Herein, we explore the relationships between osteocyte volume and several species-specific characteristics such as growth and metabolic rates, body mass, and genome size using a broad sample of modern birds.

Materials and methods

Data

Species-specific body mass [39], growth rate [40], dry erythrocyte area (www.genomesize.com/cellsize), genome size (www.genomesize.com), and basal metabolic rate [41,42] were gathered for the avian species for which histological data on lacuna dimensions were obtained (see below). Mass-specific basal metabolic rates, used in our analyses, were calculated as (basal metabolic rate) / (body mass)$^{0.66}$, using the 0.66 coefficient for birds derived previously [43] and supported by our smaller dataset. Because several of the species in the dataset were sexually dimorphic in body mass, average body mass for each sex was selected for the appropriate sex of the specimen (if known). The most widely available data on growth rate are in the form of the growth parameter K (day^{-1}), which is proportional to overall growth rate in models fitted to plots of age versus mass [40]. The K calculated from a logistic growth model was selected because it is the value most often provided [40]. For three species studied for which K was unavailable (*Dendroica pensylvanica*, *Quiscalus quiscula*, *Spizella arborea*), its value was estimated as the average generic value for K [40]. This is justifiable in those cases because K did not vary substantially (less than 10%) among species in the same genus. Species for which data on genome size, growth rate (K), or basal metabolic rate could not be found were parsed prior to regressions including these variables (see Supplemental information Appendix A). Thus, of 34 species for which histological sections of the femur were made (see below), analyses involving genome size included only 19, analyses involving basal metabolic rate included only 21, analyses involving growth rate K included only 15, and analyses involving erythrocyte area included only 10.

Sixty-nine bird bones were thin-sectioned twice each (at orthogonal angles: i.e. sagittally and transversely; Fig. 1) to produce 138 thin sections in which osteocyte lacunae were observed. All birds were wild-caught except for the free-range, farm-raised *Dromaius* (from Great Lakes Emu Products, Midland, Michigan) and *Meleagris* (from Adams Fairacre Farms, Newburgh, New York). The sample originally included a cage-raised domestic chicken (*Gallus gallus domesticus*), but its osteocytes (and bone histology in general) were very different from those of the non-domesticated, wild birds, so it was excluded from the dataset. The sample was broad in terms of phylogeny (Fig. 2) and body mass (approximately 10–120,000 g). Bird bones and their thin sections are reposited in the University of Michigan Museum of Zoology (UMMZ) and the University of Michigan Museum of Paleontology

Download English Version:

https://daneshyari.com/en/article/5890907

Download Persian Version:

https://daneshyari.com/article/5890907

Daneshyari.com